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Integrating taxon-based, trait-based and trophic-network approaches to study community dynamics in an exploited ecosystem, the Celtic Sea

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Abstract

Marine ecosystems provide many services to humans, with the provision of food being one of the most important in the context of the increasing global population. These ecosystems face many pressures. Among them, fishing has been the main driver of marine ecosystem changes for the last 50 years while the effects of climate change are not yet visible in all ecosystems. It is therefore particularly important to characterize the structure and functioning of the ecosystems that underpin these services as well as the conditions of their stability. For this, the different facets of biodiversity must be considered since these pressures do not have the same consequences on the different facets. Traditionally, biodiversity has been studied from a species-based approaches, but trait-based approaches are increasingly used as they can provide more insights onto the mechanisms driving the structure of the communities. The study of species interactions through networks, and notably through trophic network have also emerged as a useful tool to study ecosystem dynamics. The effective management of fisheries requires more and more information on the whole ecosystem and the different facets of the diversity. To meet this need, this thesis proposes to compare the views of the dynamics of the diversity of a heavily exploited fishing ground, brought by approaches centred on taxon-diversity, trait-based diversity and trophic networks. I used the example of the Celtic Sea which is a very important fishing area for European fisheries. This area is also characterized by a taxonomic richness greater than the adjacent areas due to its localisation at a biogeographical border.

Based on data from the International Bottom Trawl Surveys (IBTS) conduced into the Celtic Sea every year from 2000-2016, video of the seabed I studied the spatio-temporal dynamics of the ecosystem (101 taxa, including fish, elasmobranches, crustacean, bivalves and cephalopods). Assemblages of taxa responding to depth, temperature and chlorophyll a concentration were distinguished and fishing showed a decreased importance as a driver of the structure of the communities after 2009. From a taxon-based view, the Celtic Sea was stable,

but considering trait-based dynamics gave a different message. I characterized the spatial patterns of sensitivity to fishing in the Celtic Sea, using life history traits. The biomass of the sensitive slow life history taxa was highest in the centre of the Celtic Sea and increased over 2000-2016. For 6 of the most sensitive species, this increase could be linked with the local decrease in fishing effort due to the creation of a seasonal closure area. However, since bottom trawl poorly samples the most fragile organisms, non-destructive underwater video samplings were used to provide a more complete description of the sensitivity patterns. Underwater video data revealed slightly different sensitivity patterns, with high values in the west of the Celtic Sea not visible with bottom trawl data only. Finally, based on isotopic data and bibliographical study of feeding interactions, I built the trophic network of the Celtic Sea, resolved at the species' level for 69 species. I related the sensitivity and vulnerability of species to food web topology to evaluate the potentiality for a perturbation to spread from the species to the entire network. The modification of the biomass of sensitive taxa is unlikely to affect the entire network since the most sensitive and vulnerable taxa are not the most central ones. However, further increase in fishing effort on the taxa that are already the most exposed, as well as on forage fish would cause the most detrimental effects on the Celtic Sea ecosystems.

Climate change would lead to an increase of bottom temperature and a decrease of primary productivity in the coming years. Crossing thermic and chlorophyll a concentration *preferenda,* I could warn against the likely change in distribution of several taxa. Cold-water species located in the North of the Celtic Sea will likely move northward in the coming years as this trend would strengthen. The most exposed taxa exhibit traits that respond negatively to temperature and their biomass is thus projected to decrease in the area.

By the time series studied here, this work provides an overview of the trends in biodiversity patterns and its drivers in an exploited fishing ground where fishing has already altered ecosystems, with a now decreasing importance. The different facets of biodiversity considered

here allow to understand the recent evolution of the Celtic Sea but also to put forward the species the most susceptible to be impacted by climate change and to spread its perturbation to the trophic network.

Keywords: Ecosystem approach to fisheries, spatio-temporal dynamics, community ecology, life-history traits, food webs, resource management

Résumé substantiel en français

Les océans fournissent de nombreux services écosystémiques aux populations humaines, allant de la régulation du climat, à la fourniture de protéines animales pour l'alimentation humaine en passant par la provision de services culturels et récréatifs (IPBES, 2019a). De 1961 à 2017, la consommation de poisson a augmenté de 3.1% annuellement et représente 20% des apports en protéines animales de plus de 3.3 milliards de personnes (FAO, 2020). En particulier, les écosystèmes côtiers, bien que ne représentant que 11% de la surface totale des océans assurent 30% de leur productivité primaire et 90% des captures des poissons (Barbier, 2017; Pauly et al., 2002). La conservation de ces services est devenue un sujet de préoccupation majeur et est de plus en plus intégré aux politiques environnementales (IPBES, 2019a; Millennium Ecosystem Assessment, 2005). Il est donc particulièrement important de caractériser la structure et le fonctionnement des écosystèmes qui sous-tendent ces services et les conditions de leur stabilité. Pour cela, différentes facettes de la biodiversité doivent être prises en compte (Craven, Polley, & Wilsey, 2018).

Historiquement la biodiversité a été étudiée au niveau de l'espèce (diversité des taxa) qui est la mesure la plus ancienne et intuitive (Magurran, 2004). Selon la Convention sur la Diversité Biologique de Rio de Janeiro (1992), la définition de la biodiversité reconnaît de façon explicite 3 facettes de la biodiversité : la diversité intra-espèce (diversité génétique), la diversité inter-espèces au sein d'une communauté (diversité des taxons) et la diversité à l'échelle de l'écosystème (diversité des écosystèmes). Depuis les années 1990, les progrès technologiques et l'évolution progressive de l'étude des espèces vers une approche plus écosystémique ont favorisé la prise en compte d'autres facettes de la biodiversité : la diversité phylogénétique ainsi que celle des traits et des fonctions. En particulier, la diversité fonctionnelle concerne l'ensemble des fonctions que les organismes remplissent dans les communautés et les écosystèmes (Díaz & Cabido, 2001) et est souvent utilisée pour lier la diversité au

fonctionnement des écosystèmes. Il est cependant important de distinguer la biodiversité fonctionnelle (relative à une fonction écosystémique) de la diversité des traits. Il est souvent difficile de pouvoir clairement lier une fonction à des traits c'est pourquoi j'utiliserai le terme biodiversité des traits dans cette thèse.

Les activités anthropiques provoquent la diminution de la biodiversité à un rythme sans précédent (IPBES, 2019a; Pimm et al., 2014) et les écosystèmes marins n'échappent pas à cette tendance. Au cours des 60 dernières années, la population humaine est passée de 3 milliards en 1960 à 7,7 milliards en 2019 (United Nations, 2019). Au cours de cette période, la production totale de l'économie mondiale a été multipliée par sept (Roser, 2020) et devrait encore être multipliée par trois à six d'ici 2050. Ces chiffres indiquent une pression continue sur la biodiversité puisque la population humaine et sa croissance économique dépendent de la biodiversité et des services qu'elle soutient. Bien que la biodiversité ait été et soit toujours modifiée par des causes naturelles, les activités humaines sont actuellement les plus puissants moteurs de ces changements. Pour les écosystèmes marins, l'exploitation directe (et principalement par la pêche) est le facteur qui a eu le plus grand impact dans les 50 dernières années, suivie par la perte d'habitat liés au développement des infrastructures côtières et de l'aquaculture (IPBES, 2019b).

De 1974 à 2017, la fraction des stocks de poissons durablement gérés a diminué de 90 à 65,8 % à l'échelle mondiale (FAO, 2020). La pêche non réglementée a provoqué l'épuisement des espèces à l'échelle mondiale et même parfois des extinctions locales (Myers & Worm, 2003; Pauly et al., 2002; Worm et al., 2006). Au-delà de l'effet direct sur les espèces cibles, la pêche affecte de nombreuses autres espèces par le biais des prises accessoires, mais elle a également des effets indirects, entraînant des modifications de la structure et du fonctionnement de l'ensemble des écosystèmes (Jennings & Kaiser, 1998). Pendant de nombreuses années, la pêche a visé en priorité les prédateurs supérieurs et a provoqué la diminution du niveau

trophique moyen au niveau mondial (Pauly et al., 2002) et l'augmentation de la biomasse des espèces de niveau trophique intermédiaire (Pinnegar et al., 2000). Cela a notamment provoqué une modification de la biomasse de traits exprimés avec, par exemple une diminution des espèces d'invertébré fragiles dans les zones chalutées (Tillin, Hiddink, Jennings, & Kaiser, 2006). La pêche peut aussi causer une modification intraspécifique des traits, notamment avec des maturités avancées pour certaines espèces soumises à une forte pression de pêche depuis de nombreuses années (Ernande, Dieckmann, & Heino, 2004; Silva, Faria, & Nunes, 2013). La pêche impacte aussi les habitats des espèces. Le chalutage de fond en particulier est l'une des principales sources de perturbation des fonds marins dans le monde, affectant la structure et le fonctionnement des communautés benthiques (Kaiser et al., 2006). En Atlantique Nord-Est, les débarquements ont atteint un pic à la fin des années 1970 et se sont stabilisés en 1990 à environ 70 % de la valeur maximale. Depuis lors, l'Union européenne a mis en œuvre des politiques de pêche qui ont permis de réduire les pressions exercées par la pêche en diminuant l'effort de pêche et en créant des zones d'interdiction temporaire de la pêche ainsi que des zones marines protégées (Walter, 2010). Les stocks en Atlantique Nord-Est montrent des signes de reconstitution, avec l'augmentation de leur biomasse (FAO, 2020; Fernandes & Cook, 2013b). En parallèle, les effets du changement climatique sont déjà visibles dans certains écosystèmes marins et vont continuer à toucher de nouvelles zones (Henson et al., 2017). Dans ce contexte, il est essentiel de prendre en compte l'effet synergétique du changement climatique et de la pêche sur les communautés.

Face aux conséquences croissantes de la surpêche, les mesures de gestion ont progressivement évolué, passant d'une évaluation stock par stock à une évaluation plus écosystémique (Pauly et al., 2002) dans le cadre de la mise en place de l'approche écosystémique des pêches (Garcia, Zerbi, Aliaume, Do Chi, & Lasserre, 2003). Ce changement de paradigme a conduit à un besoin croissant de données. Les campagnes scientifiques, telles

que les campagnes internationales de chalutage de fond (International Bottom Trawl Surveys IBTS), peuvent fournir de telles données. Toutefois, le but premier de ces campagnes étant de fournir des données pour les évaluations de stock, leurs données ont été relativement peu étudiées sous l'angle des différentes facettes de la biodiversité.

L'étude des dynamiques spatio-temporelles de la diversité est une première étape nécessaire à sa conservation, mais la question de la compréhension des mécanismes à l'origine des patrons de diversité observés peut aussi être posée. La répartition des espèces à l'échelle d'une région résulte à la fois de leur histoire évolutive mais aussi des interactions entre elles et avec l'environnement.

La sensibilité d'une espèce à une perturbation peut être définie comme la possibilité pour cette espèce d'être poussée hors de la gamme des conditions environnementales qu'elle peut supporter. Elle peut être caractérisée sur la base de traits connus pour refléter les capacités de résistance ou de résilience d'une espèce face à une perturbation. En particulier, la pêche impacte les organismes et leur capacité à se rétablir dépend de la dynamique de leur population. Cette dynamique peut être approximée avec des traits liés au cycle de vie (taille maximum, longévité, etc…)(Le Quesne & Jennings, 2012). Selon le compartiment considéré, des traits liés à la résistance physique peuvent être ajoutés (comme pour les invertébrés benthiques par exemple).

L'étude des traits des espèces permet de les regrouper en fonction de leur similarité, mais leurs interactions ont souvent été négligées (Bascompte, 2009). En particulier, la structure du réseau trophique apparaît comme une propriété importante puisqu'elle peut contribuer au maintien de la biodiversité (Bastolla et al., 2009) et a également des conséquences sur la dynamique des communautés et le fonctionnement des écosystèmes (Thompson et al., 2012). La stabilité du réseau trophique peut être étudiée sous l'angle de sa robustesse, i.e. la capacité d'un réseau à résister à la suppression d'espèces, mais aussi à l'aide d'indices prenant en compte la manière dont les espèces sont reliées les unes aux autres. Ces indices, dits de méso-échelle,

permettent d'illustrer le potentiel de propagation à tout le réseau trophique d'une perturbation affectant une espèce. Ces indices peuvent être mis en relation avec les notions de sensibilité des espèces afin d'évaluer la sensibilité du réseau trophique à une perturbation.

La Mer Celtique est située à la limite biogéographique entre la région boréale (qui s'étend jusqu'au Nord de la Norvège) et lusitanienne (qui s'étend au sud jusqu'au Maroc). Cette caractéristique confère à cette zone une richesse supérieure à celle des zones adjacentes et rend potentiellement certaines espèces plus sensibles en raison de leur position en limite de leur aire de distribution (Thomson et al., 2015). Il s'agit d'une zone de pêche particulièrement important pour la France, l'Irlande, le Royaume-Uni, la Belgique et l'Espagne (Mateo, Pawlowski, & Robert, 2017). Au cours de la dernière décennie, plus de 420 000 tonnes ont été débarquées chaque année, provenant principalement de la flotte française (39 % des captures sur la période 2010-2015) (Hernvann & Gascuel, 2020). Similairement à d'autres zones de pêche ayant une longue histoire d'exploitation, les stocks des grands poissons commerciaux, tels que le cabillaud et le merlu, ont été les premiers à atteindre un niveau critique dans les années 1990. L'effort de pêche s'est alors reporté vers les niveaux trophiques inférieurs (Guénette & Gascuel, 2012; Hernvann & Gascuel, 2020). Depuis la mise en place de mesures de gestion plus restrictives dans la cadre de la Politique Commune de la Pêche, les stocks de quelques espèces commerciales (merlan, merlan bleu, sole, flet et, dans une moindre mesure, cabillaud) ont montré des signes d'amélioration.

En me basant sur les données des campagnes EVHOE (Evaluation des ressources Halieutiques de l'Ouest de l'Europe), réalisées chaque année en Mer Celtique, j'ai étudié les dynamiques des différentes facettes de la biodiversité dans cette zone, de 2000 à 2016, et les variables environnementales qui les influencent. Ce travail de thèse permet donc de mettre en regard les informations sur l'état de santé d'un écosystème obtenues à partir de l'étude de

différentes facettes de la biodiversité et d'en tirer les informations nécessaires à son bon management.

Dans le chapitre 1, j'ai réalisé une étude globale des dynamiques de la diversité des taxons en Mer Celtique durant les deux dernières décennies (2000-2016). L'importance conjointe de l'augmentation de la température des fonds marins et de la variation de l'effort de pêche est rarement prise en compte dans l'étude des écosystèmes marins exploités. Basé sur une série chronologique de 17 ans, j'ai étudié les covariations avec l'environnement des différentes composantes d'un écosystème démersal (101 taxons regroupant des poissons, des élasmobranches, des crustacés, des bivalves et des céphalopodes). Mes résultats ont montré que l'augmentation de la température de fond en lien avec le changement climatique en Mer Celtique ne sont pas visibles sur la période considérée (2000-2016). Au cours des deux dernières décennies, les communautés ont été davantage contrôlées par des variables environnementales que par la pêche, probablement en raison de sa longue histoire d'exploitation. À l'échelle de la zone entière, les relations entre les taxons et l'environnement sont restées stables au fil des ans, mais à l'échelle locale, au centre de la mer Celtique, la dynamique des communautés a été dictée par la variation interannuelle de la température. La pêche a été un facteur important de structuration des assemblages d'espèces au début de la série chronologique, mais son importance a diminué après 2009. Cela a très probablement été causé par un changement dans la distribution spatiale de l'effort de pêche, à la suite d'un changement des taxons ciblés, qui sont passés de la langoustine et des poissons blancs (cabillaud, merlan, merlu…) à des poissons d'eau plus profonde telle la baudroie, qui ne covarient pas avec l'effort de pêche. L'augmentation des températures de fond prévues dans les années à venir pourraient entraîner des changements, notamment en ce qui concerne les espèces commerciales d'eaux froides que sont le cabillaud, le merlu, la langoustine et la plie canadienne. Cette étude a permis de montrer que l'analyse de la covariation est un moyen efficace de cibler, parmi un grand nombre de

taxons, ceux qui pourraient être les plus sensibles aux changements du mode d'exploitation par les pêcheries en parallèle de l'augmentation des températures.

Le chapitre 1 a montré la relative stabilité des communautés en Mer Celtique sur la période 2000-2016 en considérant la diversité des taxons. En considérant la diversité des traits obtient-on le même résultat ? La pêche, en raison du prélèvement sélectif des espèces à forte valeur commerciale, a longtemps influencé la dynamique des espèces en fonction de leurs traits d'histoire de vie. La sensibilité à la pêche augmente selon un gradient de stratégies d'histoire de vie qu'on peut qualifier de « rapide » à « lent ». Les espèces à la stratégie d'histoire de vie « lente » (grande taille, longue durée de vie, maturité tardive, donnant naissance à un faible nombre de petits de grande taille) sont celles dont la population demande le plus de temps à retrouver son état initial après une action de pêche. La diminution de la pression de la pêche depuis les années 1980 à l'échelle de l'Atlantique Nord-Est peut avoir eu un effet sur la répartition de ces espèces ainsi que sur une éventuelle augmentation de leur biomasse. En pratique, les stratégies d'histoire de vie sont rarement liées à des mesures de gestion. En outre, l'accent est souvent mis sur les espèces sensibles exploitées ou emblématiques (requins et raies), mais rarement sur les processus d'assemblage à l'échelle de l'écosystème (espèces commerciales et non commerciales). Sur les mêmes données que celles utilisées dans le chapitre 1 (17 années, 101 taxons), j'ai observé une relation négative entre la biomasse des taxons sensibles à la pêche et la pression du chalutage de fond, ainsi qu'une augmentation de leur biomasse en Mer Celtique. A l'échelle de l'ensemble de la Mer Celtique, les taxons ont des traits d'histoire de vie plus similaires qu'attendu au hasard (sous-dispersion). À l'inverse, dans les zones où des taxons sensibles sont présents, j'ai observé une sur-dispersion, qui semble être principalement expliquée par un phénomène de filtre environnemental. À l'échelle locale, nous avons établi un lien entre la diminution de la pression de pêche et l'augmentation de la biomasse de quatre des taxons les plus sensibles, en moins de deux décennies. Cette diminution locale de la pression

de pêche fait suite à la mise en place d'une fermeture saisonnière à la pêche dans le Nord de la Mer Celtique, mettant en évidence l'effet positif de ce type de mesures de gestion en moins de deux décennies.

Cependant, cette étude de la distribution des patrons de sensibilité à la pêche s'est basée sur des données de chalutage, un engin de pêche connu pour mal échantillonner les espèces les plus fragiles. La vidéo sous-marine est une méthode non destructrice en plein développement depuis une dizaine d'années qui permet d'échantillonner la faune benthique fragile. En utilisant des données issues de 54 vidéos sous-marines acquises en 2014, 2016, 2018 et 2019, nous avons cartographié la sensibilité au chalutage des invertébrés épibenthiques et des communautés de poissons en Mer Celtique, et déterminé l'influence relative des variables environnementales et de pêche sur la sensibilité et la distribution des traits. La sensibilité des communautés au chalutage en Mer Celtique est principalement déterminée par un gradient spatial de profondeur et de productivité primaire, qui sépare la zone en deux régions principales : une zone peu profonde et productive, avec une faible sensibilité et une forte proportion d'espèces de poissons, proche de la mer d'Irlande, et une zone plus profonde et moins productive, avec une sensibilité plus élevée et une forte proportion d'organismes fixés et suspensivores. L'intensité de la pêche, bien qu'ayant un effet moindre détermine également la sensibilité des communautés : les zones soumises à une forte pression de pêche sont moins sensibles, ce qui confirme que ces communautés ont déjà été façonnées par une longue histoire de pêche. Ces résultats ont fait l'objet d'un stage de Master 2 que j'ai co-encadré.

Dans les chapitres 1 et 2, je me suis intéressée aux dynamiques de la diversité à l'échelle des espèces. Cependant l'importance de prendre en compte l'échelle de l'écosystème dans les stratégies de conservation est de plus en plus reconnue (Harvey, Gounand, Ward, & Altermatt, 2017). Les dynamiques d'un écosystème peuvent être étudiées grâce aux réseaux d'interactions qu'entretiennent les espèces qui le compose (Tylianakis, Laliberté, Nielsen, & Bascompte,

2010). En particulier, les réseaux d'interactions trophiques sont les plus souvent étudiés. Considérer la sensibilité d'un écosystème à une pression donnée tant au niveau des espèces que de l'ensemble du réseau dans un cadre unifié reste un défi. La réponse des espèces à une perturbation peut être caractérisée grâce à leur sensibilité qui peut être évaluée grâce à des traits biologiques connus pour répondre à cette perturbation. En tenant compte du nombre de lien reliant les espèces, des mesures à méso-échelle, telles que la centralité « *eigenvector centrality* », permettent de savoir si une espèce est fortement reliée à d'autres également fortement reliées. Cela permet de caractériser la capacité de cette espèce à propager une perturbation qui affectera tout le réseau et donc d'évaluer l'influence que cette espèce pourrait avoir sur la robustesse du réseau. La robustesse d'un réseau confronté à la perte de différentes espèces renseigne sur sa sensibilité à certaines perturbations. Cependant, aucun cadre unifié ne permet d'étudier l'influence de la sensibilité des composants d'un réseau sur la sensibilité du réseau lui-même. Dans le 3ème chapitre de ma thèse, j'ai proposé une approche simple basée sur les traits des espèces et la topologie du réseau pour déterminer si la sensibilité d'un réseau à une perturbation dépend de la sensibilité de ses composants ou est déterminée par d'autres paramètres liés à la topologie du réseau. A partir de mesures isotopiques réalisées dans le cadre du projet Ifremer EATME et d'une étude bibliographique réalisée par Pierre-Yves Hernvann au cours de sa thèse, j'ai créé un réseau trophique de Mer Celtique précis à l'espèce, intégrant les 69 taxons les plus communs. J'ai montré que les taxons les plus sensibles à la pression de pêche n'étaient pas les plus prônes à propager une perturbation (i.e. ces taxons ne sont pas les plus centraux), mais que parmi les 10 taxons les plus exposés à la pression de la pêche, 3 faisaient partie des 10 taxons les plus centraux. À l'échelle du réseau, la suppression des taxons les plus exposés à la pêche ainsi que ceux ayant le plus grand nombre de prédateurs menace le plus la robustesse du réseau. Ce cadre simple permettant l'intégration des traits à la topologie du réseau, a montré que la sensibilité au niveau de l'espèce n'implique pas la sensibilité à

l'échelle du réseau et souligne ainsi la nécessité de travailler à l'échelle des réseaux dans les mesures de conservation.

Par ailleurs, les aspects spatiaux des réseaux trophiques sont encore très peu pris en compte dans les mesures de conservation alors qu'ils peuvent renseigner efficacement sur l'échelle spatiale à laquelle peut se propager une perturbation touchant une certaine espèce dans une certaine zone (Gilarranz, 2020; Harvey et al., 2017). En Mer Celtique, malgré une faible modularité du réseau trophique (i.e. pour chaque taxon, le nombre d'interaction avec les taxons de son module par rapport au nombre d'interactions avec ceux hors module n'est pas beaucoup plus grand), le réseau peut être séparé en 3 sous-réseaux (modules). Ces modules ont une structure spatiale marquée : les taxons appartenant à un même module tendant à avoir leur biomasse maximale être dans la même zone de la Mer Celtique.

Les conclusions tirées de l'étude de chacune des facettes de la biodiversité au cours des différents chapitres de ma thèse mettent en avant la plus-value de ces différents aspects dans la compréhension des dynamiques des écosystèmes. En Mer Celtique, ces différentes informations ont permis de révéler l'hétérogénéité de zones auparavant considérées comme homogènes (Ellis, Martinez, Burt, & Scott, 2013). Les conditions environnementales et la topologie du réseau trophique mettent en évidence une nette partition de la mer Celtique entre le nord et le sud d'une diagonale reliant le sud de l'Irlande au sud du Finistère. La zone Sud est caractérisée par des taxons d'eau profonde et chaude qui ont tendance à avoir plus d'interactions trophiques entre eux qu'avec les autres taxons présents en Mer Celtique. Les communautés de cette zone sont homogènes, sauf à l'extrême limite occidentale du talus continental où quelques sites d'échantillonnage regroupent les communautés les plus sensibles, caractérisées par la présence de pennatules *Funiculina quadrangularis*. Inversement, le nord de cette diagonale peut être séparée en 3 sous-zones (1) une au sud de l'Irlande avec des espèces appartenant majoritairement au même module du réseau trophique ; (2) une avec des taxons d'eau froide,

sous forte concentration de chlorophylle a, et historiquement la plus exposée au chalut de fond. Dans cette zone, la diminution de l'effort de chalutage de fond après 2009 et la création d'une fermeture saisonnière de la zone à la pêche ont entraîné l'augmentation de la biomasse des élasmobranches, mais elle accueille également les communautés benthiques les moins sensibles. Cette zone correspond aussi à un module du réseau trophique ; enfin (3) une zone qui possède la plus grande biomasse de taxons sensibles au centre de la Mer Celtique couvrant les 3 modules du réseau trophique. Cette zone est composée de communautés mixtes, avec des taxons ayant un large panel de stratégies d'histoire de vie, de lentes à rapides.

Ces résultats renseignent aussi sur les futures trajectoires possibles de la Mer Celtique face au changement climatique. La zone située au nord-est de la Mer Celtique sera probablement confrontée au plus grand nombre de changements. La longue histoire de chalutage de fond a très probablement conduit à la disparition des taxons benthiques sensibles dans cette zone. Au cours de la période 2000-2016, cette petite zone du nord-est de la Mer Celtique a déjà connu une augmentation significative de la température du fond et devrait donc être confrontée à l'augmentation de température la plus rapide de Mer Celtique dans les années à venir. Cette zone rassemble des taxons commerciaux d'eau froide (i.e. hareng, merlan, églefin et plie). Ces espèces vont probablement se déplacer vers le nord ou vers des zones plus profondes avec l'augmentation des températures en lien avec le changement climatique. Des changements dans les pêcheries de Mer Celtique sont donc à prévoir avec la diminution, voire la disparition de ces espèces. Inversement, en considérant les organismes benthiques et fixes (d'après la vidéo sous-marine), nous n'avons pas montré de relation significative avec la température. Il apparaît donc que les organismes benthiques de Mer Celtique seraient capables de faire face à une certaine augmentation de la température du fond, malgré le fait que la plupart d'entre eux sont fixes ou peu mobiles et ne peuvent pas se déplacer pour éviter l'augmentation des températures. Plus généralement, les taxons (provenant des données de chalutage) qui

gardent leur progéniture et ont une fécondité très élevée ont montré une relation négative de leur biomasse avec la température du fond et sont donc susceptibles d'avoir les plus fortes variations de distribution dans les années à venir. Certaines espèces ayant ces caractéristiques font aussi partie de celles dont la suppression entraînerait la plus faible robustesse du réseau trophique (tourteau, araignée de mer, coquille St Jacques et pétoncle). La production primaire devrait diminuer en Mer Celtique en lien avec le changement climatique et affectera en premier lieu les composantes les plus basales du réseau trophique, qui sont aussi celles dont la perte mène à la plus faible robustesse du réseau trophique. Le réseau trophique de Mer Celtique va donc être confronté à des changements importants dans les années à venir. Il a été établi dans la littérature que la suppression des taxons les plus connectés conduit à la plus faible robustesse du réseau (Curtsdotter et al., 2011; Dunne & Williams, 2009). Nous avons trouvé des résultats contradictoires puisque la suppression des taxons ayant les plus fortes valeurs de centralité (*eigenvector centrality*) entraîne un nombre d'extinctions secondaires similaire à celui attendu au hasard. Certaines spécificités dans la topologie du réseau de la Mer Celtique expliquent ce résultat, notamment par le faible nombre de taxons ayant une très grande valeur de centralité (c'est-à-dire avec un très grand nombre de proies et de prédateurs). La robustesse du réseau lors de la suppression de taxons centraux peut également être liée à l'augmentation de modularité qui en découle puisque la modularité favorise la stabilité du réseau (Stouffer & Bascompte, 2010). La robustesse provient probablement aussi du fait que la suppression des taxons les plus centraux entraîne d'abord la suppression des interactions trophiques redondantes. Les taxons restant après la suppression des taxons les plus centraux ont encore des taxons dont ils peuvent se nourrir.

Cette thèse met en évidence l'importance des données utilisées lors de l'évaluation de la sensibilité d'un écosystème. En effet, les données provenant de chalutage de fond et celles

provenant de vidéos sous-marines mènent à une vision différente de la répartition spatiale de la sensibilité en Mer Celtique. Cela souligne le fait que l'évaluation de la sensibilité à la pêche doit prendre en compte le plus grand nombre possible d'organismes et être basée sur des données provenant de diverses sources afin d'obtenir la vue de l'écosystème la plus complète.

L'intégration de ces différent types de données (chalut, vidéo…) et leur exploitation en utilisant des approches basées sur les taxons, leurs traits et leur interactions au sein de réseaux pourrait permettre de développer des indicateurs pouvant être utilisés dans le cadre de l'Evaluation Intégrée des Ecosystèmes, qui est le cadre méthodologique permettant une mise en œuvre efficace du concept d'approche écosystémique de la pêche en Europe (Levin, Fogarty, Murawski, & Fluharty, 2009). Par exemple, l'utilisation de l'approche STATICO et notamment ses trajectoires temporelles (position annuelle moyenne de l'écosystème dans l'espace des variables environnementales ou dans l'espace des taxons) donneraient des indications sur une augmentation ou une diminution potentielle de la biomasse d'un grand nombre d'espèces en relation avec les modifications environnementales.

A l'issue de ce travail de thèse, de nombreuses perspectives restent encore à explorer. Ces perspectives à l'échelle de la Mer Celtique concernent principalement les effets du changement climatique et leurs impacts en synergie avec la pêche qui reste importante dans cette zone. Il s'agira notamment de caractériser quelles seront les nouvelles espèces arrivant en Mer Celtique, quelles seront celles qui ne seront plus présentes, et quelles seront les conséquences de ces variations sur la distribution des traits, mais aussi sur le réseau trophique. Il serait aussi intéressant de comparer les résultats de cette thèse à l'échelle de l'Atlantique Nord-Est, en se basant sur les données des différentes campagnes de chalutage de fond scientifique disponibles.

Les approches basées sur les traits permettent une compréhension systématique des principales tendances de la biodiversité en réponse aux facteurs environnementaux et

anthropiques et peuvent donc être utilisées pour évaluer l'efficacité des stratégies de gestion. Cependant, il peut être difficile de transcrire les objectifs de gestion en indicateurs de traits (Laughlin, 2014) notamment en raison de l'absence de relation claire entre les traits et leur réponse aux pressions environnementales (Pecuchet, 2017), à l'exception de certaines relations déjà bien établies comme celle entre les traits d'histoire de vie et la pression de pêche (Le Quesne & Jennings, 2012). De nombreuses relations entre les traits et la pression restent à explorer. Par exemple, des traits tels que la sociabilité, la migration, le gonochorisme ou la période de frai pourraient refléter l'adaptabilité des organismes à un environnement en évolution rapide. De plus, les traits peuvent varier d'un endroit à l'autre pour une même espèce, mais les études qui tiennent compte de la variabilité intraspécifique des traits sont encore rares. Le développement de bases de données de traits contribue également à combler cette lacune, notamment celle de Beukhof et al. (2019) qui rassemble différentes valeurs de traits pour une même espèce de poisson, selon le grand écosystème marin (Large Marine Ecosystem LME) dans lequel ils ont été échantillonnés. Les relations trait-pression bien documentées pourraient alors être utilisées pour alimenter des modèles multi-espèces basés sur les traits afin d'appliquer une approche écosystémique des pêches (Barnett, Jacobsen, Thorson, & Cope, 2019). Par ailleurs, dans cette thèse j'ai développé une approche permettant de lier la structure du réseau trophique et la sensibilité des espèces à partir de leur trait d'histoire de vie. Cependant, cette approche manque de développements plus mécanistiques, permettant notamment de prendre en compte les flux entre les espèces. Enfin, ce travail s'est concentré sur le réseau d'interactions trophiques, mais d'autres types d'interactions peuvent être étudiées. Les réseaux peuvent par exemple être utilisés pour une meilleure compréhension des processus d'assemblage, comme l'ont fait Legras et al. (2019) qui ont comparé le réseau de co-occurrence (basé sur les abondances des espèces) et le réseau fonctionnel (basé sur les valeurs des traits des espèces) pour évaluer si les espèces appartenant à un groupe fonctionnel appartiennent au même groupe

de co-occurrence. Plus généralement, l'analyse des réseaux d'interactions dans différents espaces (trophique, taxonomique, fonctionnel, géographique) apparaît comme un domaine de recherche prometteur pour répondre aux questions portant sur l'assemblage des communautés et le fonctionnement des écosystèmes sous un nouvel angle.

Dans le contexte du développement d'une vision holistique de l'écosystème, cette thèse a montré l'avantage de réunir différentes visions de la diversité (basées sur les taxons, les traits et les interactions) puisque certaines tendances ne sont visibles que d'un seul point de vue. Ce travail montre aussi l'importance de la prise en compte des interactions entre les espèces dans les plans de gestion car l'analyse des réseaux d'interaction donne une vision différente de la sensibilité des écosystèmes que celle donnée par leurs seules composantes.

Mots-clés : Approche écosystémique des pêches, dynamiques spatio-temporelles, traits d'histoire de vie, réseaux trophiques, gestion des ressources

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” Pour ce qui est de l’avenir, il ne s’agit pas de le prévoir, mais de le rendre possible. “

– Antoine de Saint Exupéry, *Citadelle*, 1948

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1 General introduction

1.1 Ecosystem functioning

Ecosystem functioning refers to the dynamics and the stability of biogeochemical flows through the biotic and abiotic components of an ecosystem, including the flow of material and energy (Díaz & Cabido, 2001; Naeem, 1998). This term covers many processes such as biomass production, trophic transfer through plants and animals, nutrient cycling, water dynamics or heat transfer (IPBES, 2019a). These *ecosystem processes* influence the benefits people obtain from ecosystems, *i.e. ecosystem services* (IPBES, 2019a). They are of diverse nature but 3 main kinds can be distinguished: *regulation and maintenance services* such as climate regulation through carbon sequestration in oceans; *provisioning services* as the provision of food through fishing and aquaculture and *cultural services* that include sport fishing, cruising and outdoors recreational activities (Costanza et al., 1997; Haines-Young & Potschin, 2018). In particular, the growth of human population, that should reach 9.7 billion people in 2050, leads to a growing demand in food. Fish consumption which currently contributes to 20% of the total animal protein intake, and provides animal protein to more than 3.3 billion people (FAO, 2020) is expected to further increase. To be able to maintain oceans productivity, it is of particular importance to understand what are the factor that influence their structure and functioning (Barbier, 2017).

There is now clear evidence that the loss of biodiversity strongly influences ecosystem functioning by altering *ecosystem processes*, such as biomass production, or the decomposition and the recycling of nutrients (Cardinale et al., 2012) (Fig. 1). The field of biodiversity and ecosystem functioning (BEF) was first developed with the pioneering experiment on grassland communities within the BIODEPTH project at Cedar Creek (Tilman & Downing, 1994). For 7

years, more than 200 plots were surveyed which enabled to show that greater diversity leads to greater productivity (i.e. production of biomass). The positive relationship between biodiversity and ecosystem functioning is now widely admitted (Cardinale et al., 2012; Tilman, Isbell, & Cowles, 2014). Following the development of BEF, the field of biodiversity and ecosystem services (BES) began to grow, based on the idea that ecosystem and their functioning provide essential benefits to humanity (Cardinale et al., 2012) (Fig. 1).

Conservation science had historically focused on biodiversity' intrinsic values, but was gradually enriched over the last 30 years by more utilitarian and anthropogenic arguments with the growing use of the ecosystem services concept (Mace, 2014; Robert et al., 2017). Following the way opened by the Millennium Ecosystem Assessment (2005) and the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), *ecosystem processes* and *ecosystem services* have been more and more integrated into policies and impact assessment, which calls for a more detailed vision of biodiversity. This first requires evaluating how biodiversity changes through space and time, which is rarely accounted for in environmental policies and conservation plans. For instance, the world stability is never used in the European Marine Strategy Framework Directive (EC, 2008).

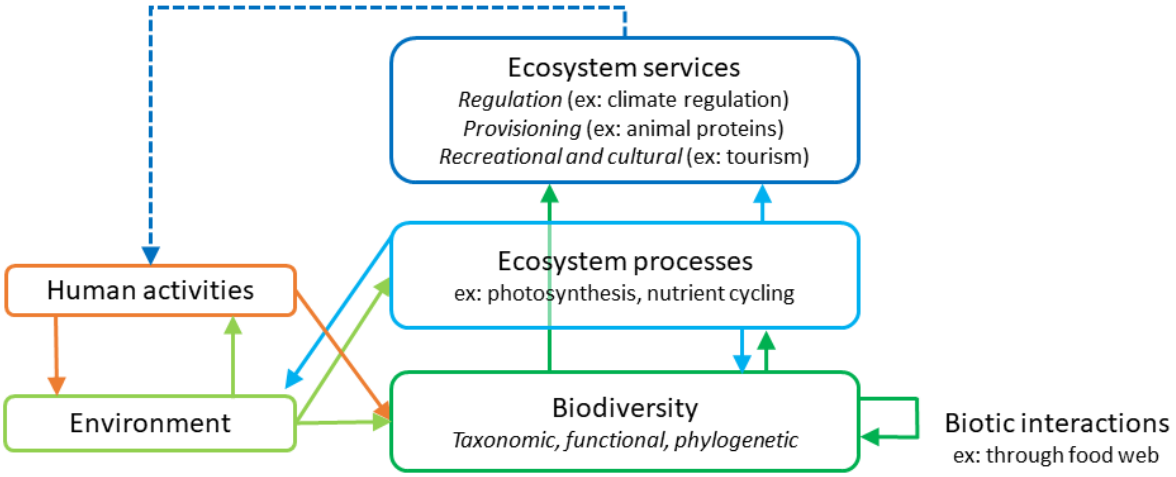

Figure 1: Synthesis graph of the causes and consequences of changes in biodiversity, modified from Diaz et al. 2006, Hooper et al. 2005, Vitousek et al. 1997 and Villeger 2008. Each arrow is a causal relationship.

This lack of consideration of the notion of stability may stem from the difficulty to define it. Indeed stability is originally a mathematical notion applying to systems unambiguously defined, unlike ecological systems (Grimm & Wissel, 1997). Following Mac Arthur (1955), stability could be divided into resistance and resilience. Resistance relates to the ability of a system to withstand a disturbance with little deviations from an average level, while resilience defines the capacity of a system to absorb changes and return to average level (Botton, Van Heusden, Parsons, Smidt, & Van Straalen, 2006; Craven et al., 2018). Applied in ecology, stability is currently defined in reference to a perturbation, that is to a change in the biotic or abiotic environment, leading to a loss of biomass, an alteration of the structure and/or dynamics of the community (Donohue et al., 2016; Kéfi et al., 2019; Rykiel, 1985). However, the relative importance of the different facets of biodiversity in the diversity-stability relationship needs further investigations (Craven et al., 2018).

1.2 The different facets of biodiversity

One of the main features of Earth is its incredible diversity of life forms. We estimate the number of eukaryote species to approximately 8.7 million (±1.3 million SE) among which only 1.2 million have been identified (Mora, Tittensor, Adl, Simpson, & Worm, 2011; Sweetlove, 2011). While diversity in marine ecosystems is estimated to be lower than on land (2.2 million eukaryotic species versus 6.5 millions), it remains largely unknown with an estimate of 91% of total marine species still to discover (Mora et al., 2011).

Biodiversity is a recent concept in the history of Sciences, defined at the Convention on Biological Diversity of Rio de Janeiro (1992) as "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems". Biodiversity thus refers to different levels of biological organization (genes, population, species and ecosystems), occurring at different geographical scales (local, regional, global). This definition recognizes explicitly three facets of biodiversity: intraspecies diversity (genetic diversity), interspecies diversity inside a community (taxon diversity) and diversity at the scale of the ecosystem (ecosystem diversity). Since the 1990's, technological advances and a gradual evolution of the study of species toward a more ecosystemic approach favoured the identification of other facets of biodiversity: phylogenetic as well as trait-based and functional diversity. Phylogenetic diversity is a measure of the amount of evolutionary history embodied in an assemblage (Chao, Chiu, & Jost, 2010) and can be a good proxy for ecological similarity between species (de Bello et al., 2015). Functional diversity concerns the range of functions organisms perform in communities and ecosystems (Díaz & Cabido, 2001) while trait-based diversity would refer to the diversity of species characteristics (Eros, Heino, Schmera, & Rask, 2009). Biodiversity has thus numerous dimensions that are not interchangeable but that are all threatened by human impacts (Cardinale

et al., 2012). In this work, I was mostly interested in the trait-based mechanisms behind species coexistence. For that reason, I will focus on the taxonomic and trait-based aspects of biodiversity in the following paragraphs.

1.2.1 Taxon diversity

Biodiversity has been, for long, investigated at the species' level and estimated with species richness (i.e. the number of species), which is the oldest and most intuitive measure of biodiversity (Magurran, 2004). Ecologists were also traditionally interested in the way abundance (or biomass) is distributed across these species, which led to the development of indices of species diversity that increase with both species' richness and abundance evenness. Ecosystem functioning is positively linked to species richness but with a saturating response as diversity increase (Hooper et al., 2005).

However, sometimes individuals cannot be identified at the species' level, but at lower taxonomic levels (genus, family, order…), gathered under the term taxa, which leads to measures of richness and diversity of taxa (i.e. taxon richness and diversity). Here I used the term of taxon diversity, the diversity of taxa at different taxonomic levels that has to be distinguished from taxonomic diversity, which is the pool of indices that explicitly account for the taxonomic distance between species.

Variations in abundance, extinction, colonization by foreign species or speciation are processes that shape taxon diversity. Due to anthropogenic activities, the species diversity has experienced one of the fastest decrease of Earth history over the past 50 years, with a human induced increase in species extinction rate by as much as 1,000 times compared to typical background rates (for mammals, amphibians and birds) (IPBES, 2019a; Millennium Ecosystem Assessment, 2005; Pimm et al., 2014). In the Anthropocene, biodiversity is marked by a decrease in species abundance and local or even global extinction of species causing a decrease in species diversity (Jackson et al., 2001). However, the abundance of certain species can also

locally increase, notably through predation release (Baum & Worm, 2009) or by colonising a humanly modified habitat that has been cleared from its original species (McGill, Enquist, Weiher, & Westoby, 2006). Local increases in richness can also be caused by climate change and the poleward displacement of species avoiding increased temperature (Cheung, Watson, & Pauly, 2013; Hawkins et al., 2003). Following the expansion of global trade, numerous species were introduced to ecosystems from which they were originally absent. Some of these species became invasive, which also provoked a homogenisation of biodiversity across ecosystems (Kortz & Magurran, 2019). Despite the historical efforts to measure it, species diversity remains incompletely known, with a strong bias toward the shallow and temperate ecosystems and taxa observable or used by humans (Millennium Ecosystem Assessment, 2005).

Taxon diversity measures are based on three main assumptions: (1) taxa are all equal in the sense that their relative abundance in an assemblage is the only factor that determines their importance in a diversity measure; (2) all individuals are equal; (3) taxa abundance has been recorded in appropriate and comparable units between taxa (Magurran, 2004). However, taxa, notably species, do not have the same biological characteristics (size, life span, habitat, metabolism, or behaviour) which leads to various ways of interacting with their environment. The importance of a taxon, in a diversity measure is thus not only determined by its abundance but it can also depend on its biological characteristics or traits, making the first assumption incorrect (Mouchet, Villéger, Mason, & Mouillot, 2010; Naeem, 1998).

1.2.2 Trait-based and functional diversity

Ecologists have been interested for a century in grouping together species with similar characteristics or traits to get a more synthetic view of ecosystem structure and functioning. For example, Raunkier in 1934 developed a classification of life forms of plants according to their way to survive over winter, and Grime in 1965 compared the role of adaptation of different flowering plants. Species traits can be defined as “any morphological, physiological or

phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization" (Violle et al., 2007). A difference can be made between traits in general and functional traits in particular, with the later defined by Violle et al. (2007) as "the morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance".

Functional diversity has been defined as "the value and range of those species and organismal traits that influence ecosystem functioning" (Tilman, 2001). Species' functional traits are associated with species ability to gain resources, disperse, reproduce, respond to loss and generally persist (Weiher et al., 2011) and thus strongly influence organism performance (McGill et al., 2006). A functional trait determines the response of an individual to abiotic or biotic factor (response traits) and /or its effects on ecosystem properties (effect traits) (Lavorel & Garnier, 2002).

Ecosystem functions have been proved to be linked to the presence or the diversity of certain traits (Cadotte, 2017). This raised some interest in describing which species were redundant in their traits but also which traits were complementary and favoured ecosystem functioning (Cardinale et al., 2012). However the mechanisms explaining how a trait contributes to a function were only recently elucidated for plants, i.e. complementarity is more important than competitive (fitness) difference in traits to explain species contribution to ecosystem function (Cadotte, 2017). Further investigation is still required for other phyla. The question of which traits to link to which ecosystem function remains central.

Following the development of functional ecology (less than 10 publications per year in 2003 to more than 200 in 2016 for plant, fish and bird together, Villéger *et al.*, 2017), a variety of traits have been used as functional traits: ecophysiological traits (resource uptake, metabolic rate), morpho-anatomical traits (presence of a shell, position of the eye), life-history traits

(longevity, fecundity), feeding traits (feeding guild, trophic level) or behavioural traits (sociability, migration). Among all these traits, rare are the ones being proper surrogate of a function, as can be specific leaf areas for photosynthesis for instance (Violle et al., 2007). In particular, life history traits indicate population dynamics and not an ecosystemic function. For that reason, in this work I will use the term trait-based (and not functional) when referring to the use of traits that are not explicitly linked with a function.

Traits have been used to study diverse phenomena, including (i) macroecological patterns, (ii) indicators for conservation, (iii) mechanisms of community assembly or (iv) maintenance of ecosystem functioning (Lefcheck, Bastazini, & Griffin, 2015).

(i) In the study of macroecological patterns, changes in diversity patterns can be outlined through changes in the trophic guild, as demonstrated by Pecuchet et al. (2019) in the Baltic sea, who reported a decrease in the relative abundance of piscivorous fish and an increase of ambush feeder copepods at the expense of feeding-current zooplankton.

(ii) The use of traits known to respond to certain pressure can enable to prioritize certain areas for conservation, notably sea mounts that gather intrinsically vulnerable deep water fish (Cheung, Watson, Morato, Pitcher, & Pauly, 2007).

(iii) Traits can be used to study co-occurrence patterns and evaluate the niche of the species. If the community exhibits a wider range of trait values than expected by chance, the so-called overdispersion in traits may highlight competitive exclusion processes that allow species with a niche overlap to co-exist (Cavender-Bares, Ackerly, Baum, & Bazzaz, 2004; Slingsby & Verboom, 2006).

(iv) To predict ecosystem functioning, trait-based diversity indices were proved to provide greater explanatory power than species richness or abundance (Gagic et al.,

2015). They are useful to assess which species exhibit some rare combination of traits that would hamper the functioning of ecosystems if lost (Leitão et al., 2016; Mouillot et al., 2013), or at the opposite, which species are redundant in their traits but not in their response to environmental drivers and therefore would maintain ecosystem functioning when facing environmental variations (Mouchet, 2010). In addition, as productivity is more related to certain combinations of traits than to species richness (Díaz & Cabido, 2001), this kind of integrative information provides insights into the dynamics of ecosystems, and is therefore potentially useful to implement management strategies.

Public and comprehensive database gathering traits are developing for all ecosystems, such as the CESTES database that gathers terrestrial, freshwater and marine traits (Jeliazkov et al., 2020) or more specialized ones like TRY on plant traits (Kattge et al., 2011), or for fish traits FishBase (Froese & Pauly, 2010) and Beukhof *et al.* (2019) data base in PANGAEA. However, the choice of the traits to include in a particular study has to be made with caution, as it will greatly influence the results (Lefcheck et al., 2015). Traits should be chosen carefully based on the hypothesis to be tested (McGill et al., 2006) and in relation with an ecosystem function of interest (Petchey & Gaston, 2006).

1.3 Environmental and human activities influence biodiversity

Marine biodiversity is structured according to natural gradients of latitude (highest marine diversity at mid latitudes while terrestrial diversity peaks at the equator), longitude (diversity decreases from west to east in the tropical Pacific and Atlantic) and depth (diversity decreases with depth) (Beaugrand, Kirby, & Goberville, 2020; Sala & Knowlton, 2006). In addition, biodiversity is higher in benthic than in pelagic systems, and higher near the coast than in open ocean since there is more diverse habitats (Gray, 1997). Chlorophyll a concentration and

temperature are important drivers of marine species distribution since they determine phytoplankton and zooplankton distribution (Calbet & Agustí, 1999) which in turn determines the distribution of species feeding on it (Beaugrand, Edwards, Brander, Luczak, & Ibanez, 2008). Extreme events such as storms, hurricanes or El Niño events are natural disturbances affecting biodiversity (Sala & Knowlton, 2006).

Although biodiversity was and is still influenced by natural causes, human's activities are currently the strongest drivers of these changes. In the past 60 years, human population has grown from 3 billion in 1960 to 7.7 billion in 2019 (United Nations, 2019). Over that period, the total global output of the world economy has increased by seven-fold (Roser, 2020) and is projected to grow a further three- to six-fold by 2050. These figures point toward a continued pressure on biodiversity since human population and its economic growth depend on biodiversity and the services it sustains (Pecl et al., 2017).

Coastal marine ecosystems have experienced biodiversity changes that can be grouped under five non-mutually exclusive direct environmental and anthropogenic drivers and ranked according to their historical succession: overexploitation, pollution, habitat change, species invasion and climate change (IPBES, 2019b; Jackson et al., 2001; Millennium Ecosystem Assessment, 2005). For marine ecosystem, direct exploitation (i.e. mainly fishing) had the largest impact, followed by land and sea-use changes including the coastal development for infrastructure and aquaculture (IPBES, 2019a). At the global scale, human activities are estimated to have already caused an increase of 1.0°C global warming compared to pre-industrial times and is likely to reach 1.5°C by 2030-2052 (IPCC, 2019), however its effects are still not visible in all ecosystems. In this thesis manuscript, I focussed on the impact of fishing and environmental drivers to detect the communities that would be the most sensitive to climate change.

1.3.1 Fishing

Oceans have been thought for a long time to be an endless source of food for humans. However, the past decades have demonstrated that marine populations can be severely depleted (FAO, 2020). From 1974 to 2017, the fraction of fish stock managed within the biologically sustainable level decreased from 90 to 65.8% at the global scale (FAO, 2020).

Unregulated fishing has induced worldwide species' depletion and even sometimes local extinctions (Myers & Worm, 2003; Pauly et al., 2002; Worm et al., 2006). Top predators were historically targeted, which led to a depletion of higher trophic levels. The collapse of the cod fisheries off the East coast of Newfoundland in the late 1980's, that never recovered since then and was indefinitely closed in 2003, is an emblematic illustration of overfishing. As a result, there were a transition in landings (i.e. a provisioning service) toward low trophic levels, short-lived invertebrates and planktivorous pelagic fish (Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998).

Beyond direct effect on target species, fishing affects many other species through by-catch, and has also indirect effects, causing modifications in the structure and functioning of the whole ecosystems (Jennings & Kaiser, 1998). The removal of high value top predators led to a decline of 0.05-0.10 trophic level of the catches per decades from 1970 to 2000 (Pauly et al., 2002). This "fishing down the food web" impacted ecosystems functioning through the reduction of the number and length of the links in the food web and their simplification (Pauly et al., 2002). The removal of top predators was reported to have cascading effects and to cause an increase of biomass in lower trophic levels through a release in predation, most of the time of invertebrates or low trophic level forage planktivourous fish. For instance, the overexploitation of cod in the Gulf of Main (Atlantic Ocean, east coast of North America) led to an increased abundance of small-bodied and commercially less important fish (sulpins Cottoidea, skates Rajidae, dogfishes Squalidae) and crustacean (lobster *Homarus americanus*,

crabs) and sea urchins (Pinnegar et al., 2000). Fishing has also been documented as the main driver of the observed increased efficiency in global biomass transfers from low to high trophic level (Maureaud et al., 2017)

Fishing not only affect species but also their habitats. Its global footprint has only recently been quantified. Industrial fishing occurs in >55% of ocean area and its spatial extent is over four times of the spatial extent of agriculture (Kroodsma et al., 2018). In particular, bottom trawl impacts more than 50% of the surface of certain European seas each year (Amoroso et al., 2018). It is one of the main sources of seabed disturbance worldwide, affecting the structure and the functioning of benthic communities (Kaiser et al., 2006) leading to the homogenization of the seafloor by the removal of habitat-forming species and the sieving of sediments (Mengual et al., 2016). In addition, dumped or lost fishing gears continue to impact ecosystem through ghost fishing (Garcia et al., 2003).

Finally, fishing effects on ecosystem functioning can also be considered from the point of view of traits. The identification of rare traits could be more frequently considered in fisheries management, as the overfishing of species with rare traits could alter the functioning of the ecosystem (Koutsidi, Tzanatos, Machias, & Vassilopoulou, 2016). Fishing is also responsible for intraspecific variations in biological traits. The selective removal of large individuals caused a decline in age and size at maturity of numerous species, such as cod, plaice, salmon or sardine (Morita & Fukuwaka, 2006; Rijnsdorp, 1993; Silva et al., 2013; Swain, Sinclair, & Hanson, 2007).

Facing overfishing growing consequences, management measures gradually evolved from single stock assessment to a more ecosystemic impact assessment (Link et al., 2010; Pauly et al., 2002). Historically, a focus has been given to species targeted by fishing but fishing also impacts non-target species. As species all interact in an ecosystem, the dynamic of these non-

commercial species influences the one of commercial species. To take into account the whole ecosystem including its biotic and abiotic components in fisheries management scenarios, the so-called ecosystem approach to fisheries was adopted by the FAO on the Reykjavik Conference in 2002 (Garcia et al., 2003).

The trend of total global fisheries capture has been stable since late-1980's (FAO, 2020). In the North East Atlantic, landings peaked in the late 1970's and stabilized in the 1990 at about 70% of the peak value. Since then, European Union has implemented fisheries policies that decreased fishing pressures through decline of fishing effort and the creation of temporary closed areas to fishing and marine protected areas (Walter, 2010). Stocks in this area show signs of recovery: their biomass increases and most of them are no longer classed as overfished. 79.3% of assessed stocks are within biologically sustainable levels in 2017 (in the North East Atlantic)(FAO, 2020; Fernandes & Cook, 2013a).

1.3.2 Synergistic effects of fishing and climate change

Climate change already affects marine ecosystems through the increase of water temperature, decrease of sea ice covering, changes in current circulation, greater upper ocean stratification, decrease in O_2 but also through increased acidification due to the growing amount of CO_2 dissolved in water bodies (Doney et al., 2012; Henson et al., 2017). Due to species physiological intolerance, a poleward displacement of marine species has been observed at a rate averaging 70 km per decade (Poloczanska et al., 2013), with a particular intensity at the poles, where temperature increase is the fastest (Fossheim et al., 2015). Changes have been particularly visible at biogeographic borders where many species reach their distributional limits. For instance in Europe, squat lobster *Gonoplax rhomboids* a Lusitanian-warm water species extended its range further into the North Sea that was previously inhabited by boreal-cold water species (Birchenough et al., 2015). Similarly, species richness of fishes increased into the North Sea over 1986-2008 (Hiddink & ter Hofstede, 2008).

Profound modification of ecosystem functioning can be expected following species displacement. In the Barents Sea for instance, the Arctic Fish community composed of small-sized bottom-dwelling benthivores is now mostly composed of larger, longer-lived and more piscivorous boreal species (Frainer et al., 2017). These physical and biological changes also lead to altered dispersal patterns through modification of currents, changes in species interactions such as the loss of zooxanthella in coral that provoke their bleaching (Doney et al., 2012) but also disruption in food webs. For example, boreal species moving northward in the Barents Sea tend to have higher degree of generalism than the arctic fish. This results in an increase of connectance and reduction in modularity resulting in a food web more prone to spread perturbations (Kortsch, Primicerio, Fossheim, Dolgov, & Aschan, 2015; Pecuchet et al., 2020).

In the context of increasing climate change impacts, it is essential to account for the potential synergistic effects of climate change and fishing. Indeed, climate could cause disruption of management plans and fisheries collapse. An example is the collapse of the lobster (*Homarus americanus*) fishery in the southern New England (United States) following a climate change induced increase in water temperature. During the same period, the neighbouring population in Gulf of Main sharply increased because of a good management through harvester-driven conservation effort to protect large individuals that are the more fecund (Le Bris et al., 2018). Conversely, fishing can impair the ability of a population to withstand climate change. For instance, truncation in age structure and the reduction of the proportion of large individuals in the total biomass could have consequences on recruitment as the largest individuals produce the most viable eggs (Planque et al., 2010). Truncation in age structure and hydro climatic variations could also lead to a temporal mismatch between fish life stage and their environmental requirements (Hidalgo et al., 2011).

Traits can help characterizing such shifts. For instance, the abundance of pelagic species with fast life-history strategy (broadcast spawning, small offspring size and early maturation) declined sharply in the late 1990's in the English Channel. This was associated with an increase in sea surface temperature caused by a warm phase of the Atlantic Multidecadal Oscillation, that likely exacerbated the historical effect of fishing (McLean, Mouillot, & Auber, 2018).

Fishing induced perturbations destabilize ecosystems and lead to reduced resilience (Planque et al., 2010), notably through the modification of food webs. They eventually cause regime shifts, as it has been documented in the North Sea (Kirby & Beaugrand, 2009; Kirby, Beaugrand, & Lindley, 2009). There, fishing and warming sea surface caused a decline in cod population that lead to an increase in adult decapods abundance. In return it triggered a higher mortality in bivalve populations which led to an increase of food for benthic detritivores and echinoderms (Kirby et al., 2009).

One driver can modify the composition of the community while the second gives the final impulse that provokes ecosystem change (Möllmann & Diekmann, 2012). The projection of climate change effects on regional conditions appears a key information to consider when implementing conservation measures, in order to increase the resilience of fisheries by maximizing the ability of species to adapt to future climate changes (Le Bris et al., 2018; Planque et al., 2010).

1.4 How to quantify the impact of environmental and anthropogenic drivers on biodiversity?

The following paragraphs describe the strategy chosen in this work, among the numerous possibilities to assess environmental and anthropogenic drivers of biodiversity, in relation with the specificities of the study area of this thesis.

1.4.1 Which data to characterize which aspect of biodiversity?

For a long time, fisheries have been managed stock by stock, but a fishery management accounting for the whole ecosystem and not only commercial species has gradually been implemented in the frame of the ecosystem approach to fisheries (Garcia et al., 2003). This change in paradigm has led to an increasing need of data, on various taxonomic group of species especially the poorly known ones, but also on the physical dynamics of the ecosystems. Scientific surveys, such as the European International Bottom Trawl Surveys (IBTS) can provide such data since they are conducted on a regular basis (yearly) since 1974 for the oldest program (ICES, 2012). They are independent of fishing effort and provide consistent time series since they follow a standardized protocol. These surveys historically aimed at providing data for stock assessments. Then, the monitoring protocol was gradually extended to non-commercial species and compartments of the ecosystems previously poorly sampled such as phyto and zooplankton or non-commercial benthos. Since the 2000-2010's, new methodologies of biodiversity sampling have been increasingly used such as underwater video or isotopic measurements.

The large amount of data generated provides stimulating perspectives of exploration of new aspects of biodiversity (non-commercial species, fragile benthic species, seascape components…) with different types of data (biomass from hauls, abundance from count on

videos, trophic level from isotopic analysis…). It can also raise some methodological questions on the more integrative way to extract the main trends of these various data source to characterize biodiversity dynamics in space and time. Diversity indices have proven to be good tools to extract main trends of biodiversity change (Granger et al., 2015). However, the choice of which indices to use for which aspects of biodiversity can be tricky. Indeed, the many different indices do not respond in the same way to biodiversity trends (such as uniform decline, proportional decline, rare species decline…) and do not show the same statistical robustness and sensitivity to biases in the dataset (Lamb et al., 2009; Santini et al., 2017). Common, simple multivariate analyses enable to summarize the spatial trends in abundance (or biomass) of numerous species (Johannesen et al., 2017) and also to keep the information at the species level (contrary to diversity indices). However, to study species dynamics in both space and time, under the influence of environmental and anthropogenic variables, the use of a more complex multivariate analysis can be discussed (see chapter 1). To explore various facets of biodiversity, datasets can be further enriched with traits or even phylogenetic information.

1.4.2 Explaining mechanisms causing biodiversity patterns

Once we understand which species co-occur in which environmental conditions and which traits can characterize their response to a pressure, we can understand the mechanisms causing the observed diversity patterns. Depending on the spatial scale, biodiversity varies differently. At global scale, biodiversity is mostly structured by latitudinal and elevation gradients, while at intermediate scales, immigration, regional extinction, speciation and biotic and abiotic interactions are likely to play important roles (Harrison & Cornell, 2007; Pavoine & Bonsall, 2011). The distribution of species at the scale of a region thus results from evolutionary history, interactions between them and with the environment. Species occurring in the same regional area share some similar evolutionary history and traits that enable them to

survive in that environment. Environmental filtering posits that only species having certain traits can survive in a given environment. Traits exhibited by species would thus be more similar than by chance under this scenario, which is called underdispersion in traits (Weiher & Keddy, 1995). Conversely, biodiversity patterns can also result from biotic interactions. Indeed, species with very similar traits would occupy the same niche and thus cannot coexist, according to the principle of competitive exclusion (Hardin, 1960). This principle is actually an enlarged view of the limiting similarity principle (MacArthur & Levins, 1967) which only concerns niche, with the notion of competitive ability/fitness (Mayfield & Levine, 2010). In this case, a phenomenon of overdispersion would be observed in traits linked to species niche (Moulton & Pimm, 1987) as illustrated by the well-known observation of MacArthur (1958) that different species of birds that co-exist have markedly different foraging strategies and clustering in traits linked to fitness to allow species coexistence.

1.4.3 Species respond to pressure: the notion of sensitivity and vulnerability

Sensitivity is generally defined as the likelihood of impairment, death or extinction of individuals, populations, ecosystem functions, communities or habitats in response to one or many stressors (Hewitt, Julian, & Bone, 2011). In this thesis, sensitivity will be mostly studied at the scale of the species, but also at the scale of the trophic network in link with the notion of robustness (see following section). It can be characterized based on traits known to reflect the potentiality of a species to resist or recover after disturbance. The notion of sensitivity can thus be based on those of resistance and resilience (La Rivière et al., 2016) but also on the size of distribution area, with species having a limited distribution range being more sensitive since they cannot avoid the perturbation (Pauly et al., 2002).

Depending on the pressure and on the nature of the traits used (qualitative or quantitative), a sensitivity index can be computed in different ways. For instance, to quantify

the sensitivity to global warming, it is common to use a Sensitivity Temperature Index (STI) which is the average temperature experienced by a species over its distribution range, or a Community Temperature Index (CTI) at the scale of the whole community (Devictor, Julliard, Couvet, & Jiguet, 2008; Thuiller, Lavorel, & Araújo, 2005). In this work, I was mostly interested in quantifying the sensitivity to fishing but approaches taken in this thesis could be applied to every environmental pressure.

Fishing harvests or impairs organisms and their capacity to recover depends on their population dynamics. This dynamic can be accurately modelled using life-history parameters (reproduction rate, recruitment, growing rate, age at maturity, fecundity, mortality rate…). However, these parameters are not documented for numerous marine species. Traits related to life history on the other hand are more broadly available, and can be used as proxies (Cheung, Pitcher, & Pauly, 2005; Le Quesne & Jennings, 2012; Wiedmann, Primicerio, Dolgov, Ottesen, & Aschan, 2014). For instance, the sensitivity of mobile pelagic, demersal and benthic fish, cephalopods and large commercial crustaceans can be studied with life history traits, such as maximum length, longevity, age at maturity, offspring size, reproductive guild or fecundity, which quantify their capacity to generate new individuals. Depending on the ecosystem compartment studied (benthic sessile or little mobile organisms), traits quantifying resistance can be more relevant to assess fishing sensitivity. For instance, de Juan and Demestre (2012) proposed a benthic sensitivity index based on fragility, position on the substratum, mobility, size and feeding mode. More recently, Rijnsdorp et al. (2018) recommended the use of longevity, which is an interesting trait to add to de Juan & Demestre's index (see chapter 2). The choice of the traits to include is also a function of data availability and the sampling methodology. Indeed, for benthic underwater video surveys, demographic parameters being scarcely available for benthic fauna, traits that can be assessed visually (e.g. position on the substratum, mobility) enable to overcome this limitation.

Investigation of the spatial and temporal variations of these sensitivity indices can be compared to environmental variables and are notably used to investigate the efficiency of management measures (see chapter 2). Nevertheless, a species can be sensitive to a perturbation but not exposed to it. The impact of a perturbation on a species is determined by its vulnerability to that perturbation (Halpern, Selkoe, Micheli, & Kappel, 2007) which is the susceptibility of a species to be impacted by external (natural or anthropogenic) factors (Cheung, Jones, Reygondeau, & Frölicher, 2018; Silvia de Juan et al., 2020). Following the simplified definition by the Intergovernmental Panel on Climate Change (IPCC) Vulnerability framework (IPCC, 2001), in this work I defined the vulnerability as the sensitivity crossed the exposure. The exposure to a perturbation can be defined as the probability of a hazard occurring (Weißhuhn, Müller, & Wiggering, 2018). Exposure of a species depends on its presence in an area when the perturbation occurs. The intensity of the perturbation could be for instance quantified by the abundance (or biomass) of the species affected (Cheung et al., 2018), the change in its projected distribution area (Thuiller et al., 2005) or the frequency of the perturbation (Hiddink et al., 2018). In the case of the fishing perturbation, exposure can be quantified with the amount of catch sustainably harvested (Halpern et al., 2012) or when data on the total biomass present is available, exposure can be defined as the fishing mortality (i.e. the biomass removed by fishing divided by the total biomass present, see Article 4). Proxy of fishing effort, such as the percentage of surface impacted by bottom fishing in a given area, could also be used (see Article 3).

1.4.4 Food webs as a tool to step up from species to ecosystem vulnerability

Moving from a species-centred view of biodiversity, functional ecology enables to group species together based on their trait similarities but interactions between species or groups have often been neglected in ecological studies (Bascompte, 2009). To fully understand

biodiversity patterns, the interaction network within which each species is embedded should be considered (Tylianakis et al., 2010). Indeed, networks enable to assess the consequences of a perturbation at the community level and to consider both its direct and indirect effects in a unique framework (Bascompte, 2009).

Food webs - defined as networks of trophic interactions - have a long history in ecology (Pimm, Lawton & Cohen, 1991). They have been described and studied for more than a century. The recent improvement in food-web data, with the increased number of highly resolved food webs, as well as new topological models and approaches borrowed from social sciences and general network theory contributed to bring back the focus on the structure of the networks at the beginning of the 2000s (Dunne, 2006). The structure of the network appears as an important property since it can contribute to biodiversity maintenance (Bastolla et al., 2009) but has also consequences on community dynamics and ecosystem functioning (Christensen et al., 1996; Pimm et al., 1991; Thompson et al., 2012). To be clear, a distinction has to be made between the food web structure and topology. Following Jordán and Scheuring (2004), I refer to topology to designate the existence of a trophic link between two species and I refer to structure to specify the direction or the weight of the link. Topological networks thus enable to understand species role in a community, to link species and ecosystem (Jordán & Scheuring, 2004; Thompson et al., 2012).

The stability of a network is greatly influenced by its topology (Tylianakis et al., 2010). The notion of network stability has many facets. In this manuscript, I will essentially work on the network robustness, as the capacity of a network to withstand species deletion. Several attributes of the network structure are relevant to the characterisation of food web robustness:

- Connectance is defined as the proportion of established interactions (L) relative to the possible ones (squared number of nodes S^2). Connectance is a good estimate of community sensitivity to a perturbation (Dunne, Williams, & Martinez, 2002b): low

level of connectance has been shown to promote the stability of the network (Thébault & Fontaine, 2010).

- Modularity characterises the compartmentalisation of a network. A module is a compartment that gathers species that more frequently interact with one another than with species outside the compartment (Pimm, 1979; Tylianakis et al., 2010). Modularity favours stability by restricting the spread of a perturbation outside a module (Delmas et al., 2019; Stouffer & Bascompte, 2010).
- Nestedness characterises the fact that the diet of the specialist species is a subset of the diet of more generalist species (Delmas et al., 2019). It has been hypothesised that a nested structure minimises competition among species and thus promotes a greater diversity (Bastolla et al., 2009). In addition, if a specialist species goes extinct, in a nested network, the remaining species would still have some species to interact with (Tylianakis et al., 2010).
- Mean shortest path length is the mean shortest food chain that connects each pair of species (Kortsch et al., 2018). The short chains have been reported to be more stable than the long ones but also to transmit a perturbation more quickly (Borrelli & Ginzburg, 2014; Williams, Berlow, Dunne, Barabási, & Martinez, 2002)

However, these are whole network-level metrics. Food web robustness could also be investigated at the species level, with metrics such as the number of their interaction partners (degree) or their centrality (Tylianakis & Morris, 2017). Centrality measures how influential a species is. Different types of centrality exist (Delmas et al., 2019), ranked from the most local to the most global view of the network:

(i) Degree centrality which is a count of the number of in and out links of a species.

(ii) Eigenvector centrality is comparable to a simulation of flow across edges, with each species influencing all of its partners simultaneously. Species that interact with numerous species, themselves interacting with numerous species have the highest eigenvector centrality.

(iii) Betweenness centrality describes if the species is located at the bridge between groups of species by quantifying how many paths go through it (i.e. how many times a species is between pairs of other species).

(iv) Closeness centrality measures the proximity of a species to all the other species of the network, based on the inverse mean shortest path length. It is thus a global measure that accounts for the entire network.

Mesoscale topology indices, i.e. neither local nor global, were presented as the most suited to assess species to community relation (Jordán, Liu, & Davis, 2006; Jordan & Scheuring, 2002). In addition, species do not all contribute in the same way to network topology and processes. Therefore, the removal of some species should have more consequences on the overall network than others would. One way to assess species influence on the network is to perform a removal experiment and analyse the effect of one species' extinction on the network structure through different indices (e.g. connectance, secondary extinctions, modularity, nestedness) (Estrada & Bodin, 2008).

Species' response to environmental and anthropogenic drivers can be characterised by their traits, notably through the notions of sensibility and vulnerability. It can be predicted which species would decrease in abundance and which ones will increase. Since food webs enable to study the potential spread of a perturbation from a species to the whole network (Dunne & Williams, 2009), they appear as a relevant tool to assess the sensitivity or vulnerability of the ecosystem. The use of trait-based approach to characterise species'

sensitivity and its integration to trophic ecology allows the study of the robustness of networks and appears as a promising field that I will explore in chapter 3. Indeed, despite a growing interest, there was no theory relating the functional composition of food webs to their properties and dynamics in 2016 (Gravel, Albouy, & Thuiller, 2016) and it appears that it is still currently the case. This is particularly true for the assessment of the sensitivity of food webs based on traits. Until now, two main research avenues have been explored:

- The position and the interactions that a species establish in a network can reflect its functional role (Delmas et al., 2019). Indeed, summary descriptors of the network topology such as the mean trophic level, the number of preys, the number of predators, the degree of omnivory, or the trophic guild can be considered as traits and used to assess food web robustness and develop indicators of ecosystem functioning (Cresson et al., 2019).
- Conversely, functional traits have rarely been integrated to the topology of the network. In chapter 3, I propose to do so in the context of extinction analysis where traits can be used to rank species according to certain properties that decide their rank in the deletion sequence. This enables to determine the species that would lead to the largest spread of a perturbation if affected.

1.5 Environmental and biotic characteristics and human activities in the study area: the Celtic Sea

1.5.1 Fishing and climate change in the Celtic Sea

The Celtic sea is a commercially important fishing ground for France, Ireland, the United Kingdom, Belgium and Spain mostly (Mateo et al., 2017). During the last decade, more than 420,000 tons were landed annually, mainly from French fleet (39% of the catches over 2010-2015), Irish (21%) and United Kingdom (18%) (Hernvann & Gascuel, 2020). It sustains an important fishery of pelagic fish such as mackerel *Scomber scombrus*, horse mackerel *Trachurus trachurus*, but also demersal fish such as hake *Merluccius merluccius*, haddock *Melanogrammus aeglefinus*, anglerfish *Lophius piscatorius*, megrim *Lepidorhombus whiffiagonis* and shellfish such as nephrops *Nephrops norvegicus* (Martinez, Ellis, Scott, & Tidd, 2013).

This area has been extensively fished for a century, with a maximum fishing effort reached in the late 1980's (Guénette & Gascuel, 2012). Bottom and pelagic trawls are the two main gears exerted in this area since they represent the largest effort (number of hours fished) and the largest landings (respectively a mean of 80% of total hours fished per year from 2012 to 2016 and a mean of 39.4% of the total landings, in tons per years, from 2012 to 2016). Bottom trawl has its highest values in the North of the Celtic Sea despite a decrease and a spread of the effort toward the South West of the area (Fig. 2). On the other hand, pelagic trawl has its largest values along continental slope in the South West of the area (Fig. 2).

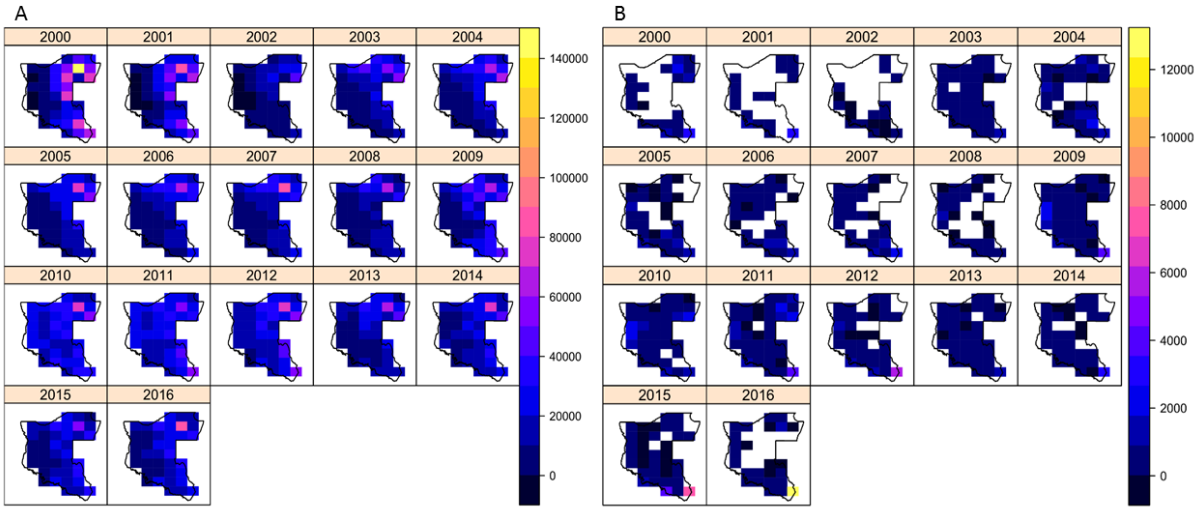

Figure 2: Fishing effort of bottom trawl (A) and pelagic trawl (B) in fishing hours per statistical rectangle per year from CSTEP new FDI data.

As in other fishing grounds with a long lasting fishing history, traditionally targeted large piscivorous fish, such as cod *Gadus morhua* and hake *Merluccius merluccius*, were the first stock to be depleted in the 1990's (Guénette & Gascuel, 2012; Hernvann & Gascuel, 2020; Martinez et al., 2013; Pinnegar, Jennings, O'Brien, & Polunin, 2002). Then fishing effort was reported toward lower trophic levels, on a few large fish species (i.e. angler fish *Lophius piscatorius* and *Lophius budegassa*) but also small demersal fish, crustaceans (i.e. edible crab *Cancer pagurus*, spider crab *Maja brachydactyla*) and cephalopods (Gascuel et al., 2016; Guénette & Gascuel, 2012; Hernvann & Gascuel, 2020). This temporal succession in target species is typical of the "fishing down the food-web" effect (Pauly et al., 1998) and suggests an alteration of the Celtic Sea trophic structure (Hernvann & Gascuel, 2020). The implementation of the European Common Fisheries Policy allows the recovery of some stocks in the Celtic Sea, i.e. whiting *Merlangius merlangus*, blue whiting *Micromestistius poutassou*, sole *Solea solea*, flounder *Pleuronectes platessa* and to a lesser extent cod *Gadus morhua* (Fernandes & Cook, 2013a; Hernvann & Gascuel, 2020). The sequential depletion of mackerel, then horse mackerel after 2000's let a vacant niche that likely benefited to boarfish that became the most fished

pelagic species (Hernvann & Gascuel, 2020; Martinez et al., 2013). This could also be linked to hydrodynamic changes and sea surface temperature (Tasker et al., 2008).

At the global scale, poleward movement of species and their implication on fisheries have been reported (Cheung et al., 2018). In the Celtic Sea, bottom temperature increased from 1993 to 2008 by 0.04°C/year (ter Hofstede, Hiddink, & Rijnsdorp, 2010). However, over the period studied here (2000-2016) at the scale of the Celtic Sea, no significant increase of bottom temperature was visible. Only at more local scale, I could observe that bottom temperature was increasing in the North East and decreasing in the South West of the Celtic Sea over 2000-2016, along the shelf border (see Paper 1, Fig. 8b).

1.5.2 Abiotic characteristics of the Celtic Sea

The area studied here, called the Celtic Sea, is located on the continental shelf, between the United Kingdom, Ireland and France (Fig. 3). It has to be distinguished from the Celtic Seas that encompass the North of the United Kingdom, the Irish Sea between the United-Kingdom and Ireland, the West and South of Ireland until the coasts of French Britany (ICES, 2018a).

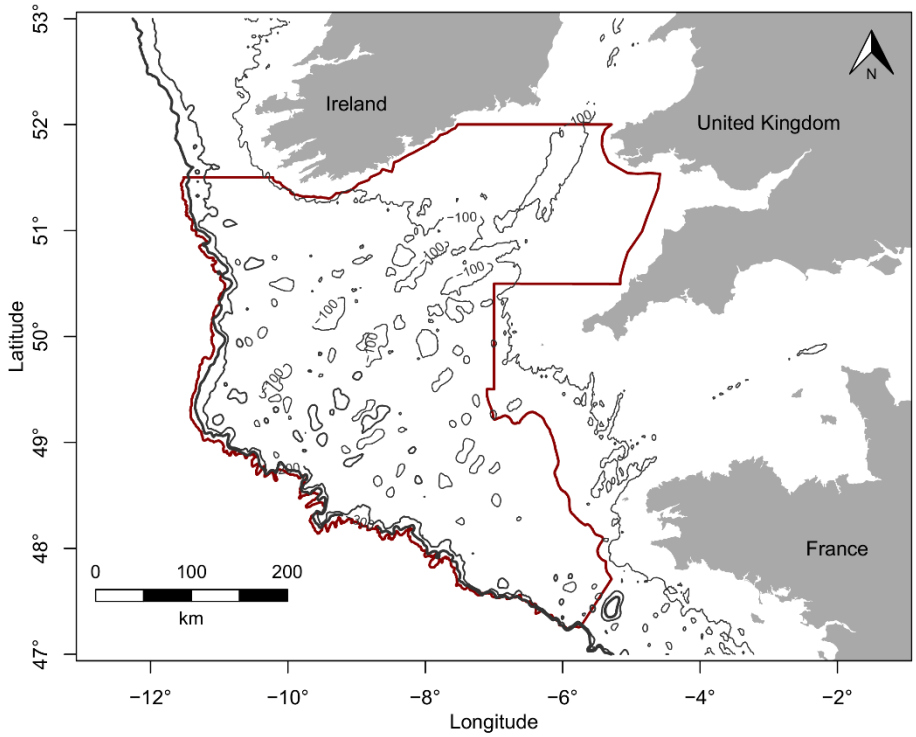

Figure 3: Limits of the Celtic Sea area studied in this thesis (in red) and bathymetry

The area of the Celtic Sea studied in this thesis is located at depth ranging from 57m to 340m (median of 139m) along a North-East to South-West slope. Sediments are mostly sandy and muddy, with large sand banks in the south and mud patch in the centre (Fig. 4), probably resulting from the circular bottom current around this central mud patch (Sharples, Ellis, Nolan, & Scott, 2013).

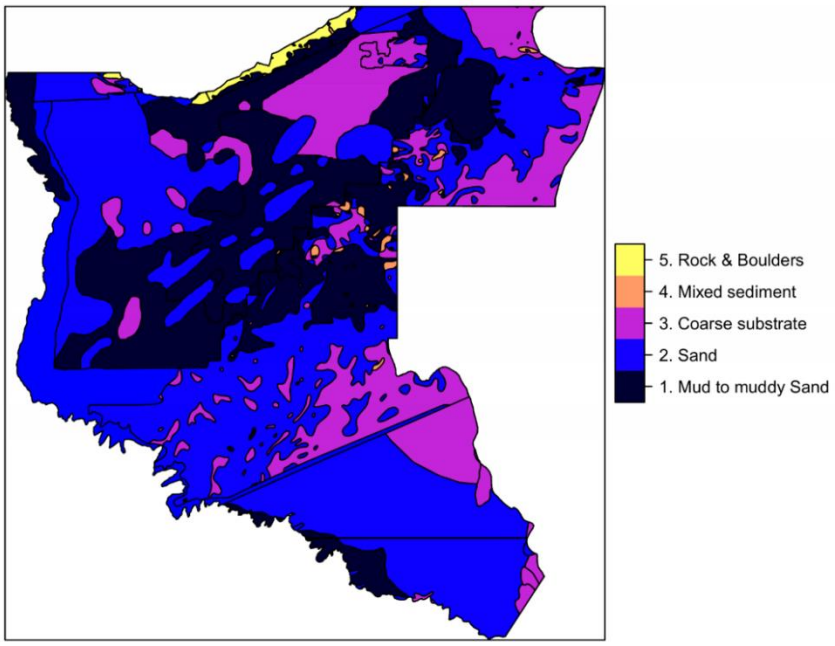

Figure 4: Sediment types in the Celtic Sea, From EmodNet data (updated in 2016) and SHOM data (updated in 2013).

Yearly average bottom temperature ranges from 9°C to 13°C, with the warmest temperatures in the deeper part of the area, in the south. Salinity is quite homogenous over the area (Fig. 5).

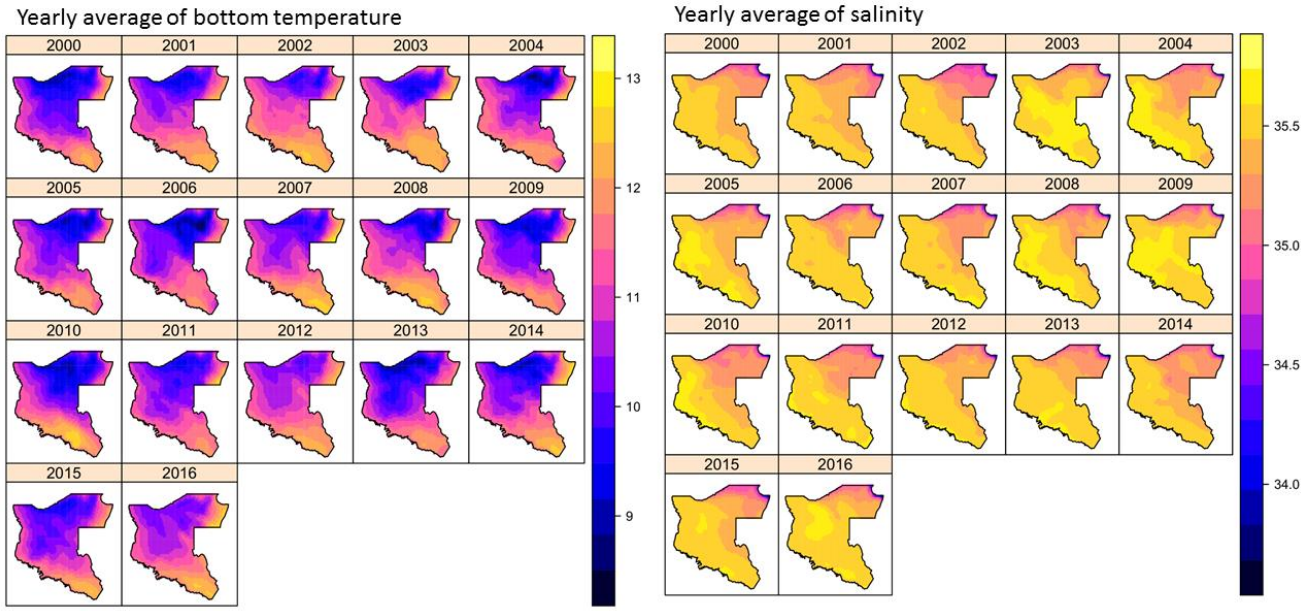

Figure 5: Yearly average of bottom temperature and salinity over the Celtic Sea, from IBI models in Copernicus

1.5.3 Biotic characteristics

The Celtic Sea waters are stratified from April to November then back to a fully mixed state, which fundamentally controls the cycles of primary production (Sharples, Scott, & Inall, 2013). A phytoplankton bloom usually occurs in April each year and is dominated by diatoms that consume the nitrogen of the surface layer. Primary production, approximated by chlorophyll a concentration, is relatively high (average over 2000-2016 of 0.36–1.63 mg/m^3) with the strongest values along the coast (Fig. 6) due to the presence of a mixing front (Sharples, Ellis, et al., 2013). This phytoplankton production feeds a zooplankton population which in turn sustains numerous fish species, notably commercial ones (Sharples, Ellis, et al., 2013).

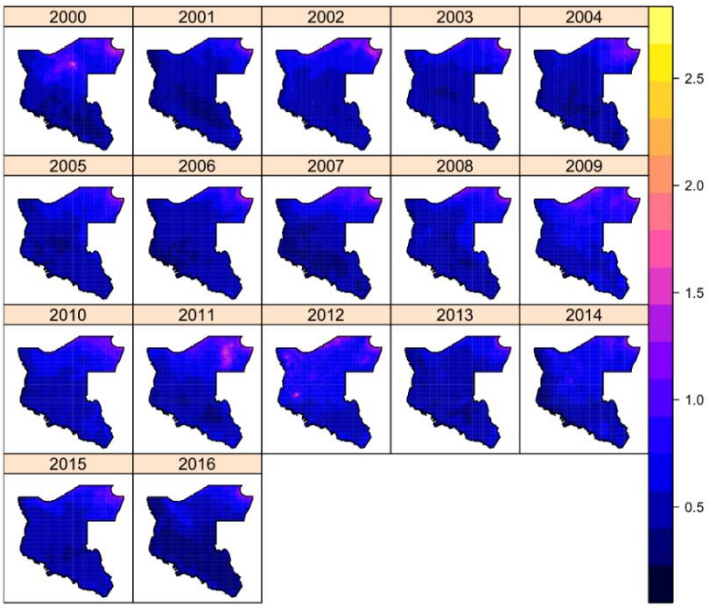

Figure 6: Chlorophyll a concentration (g/m3) extracted from Copernicus database

Depth, temperature and salinity were described as important structuring variables for numerous commercially important fish, such as blue whiting, whiting, megrim, gurnard, lesser-spotted dogfish and hake juveniles (Persohn, Lorance, & Trenkel, 2009).

According to Martinez, Ellis, Scott, & Tidd (2013), communities of fish in the Celtic Sea can be partitioned in four main areas (Fig. 7): (1) the deep parts and the outer shelf (dominated by hake, megrim, poor cod, blue whiting, and boarfish), (2) the central Celtic Sea (long-rough dab and megrim), (3) the North-East around Cornwall (horse mackerel, gadoids, lesser-spotted dogfish and squids) and (4) the shallow North, including part of the Bristol channel (whiting, lesser-spotted dogfish, horse mackerels, dab and plaice, sprat and herring, grey gurnard). Epibenthic spatial assemblages showed some similarities, with (1) deep parts over the shelf edge dominated by hormathid anemomes, sea spiders, Devonshire cup corals and swimming crabs. The central Celtic Sea (2) was characterized by the hermit crabs, shrimps and common starfishes. The area around Cornwall (3) was dominated by species cited in (2) as well as by brittle stars, shrimps and flying crabs. A southern assemblage, not present for fish, was composed of starfishes (Ellis et al., 2013).

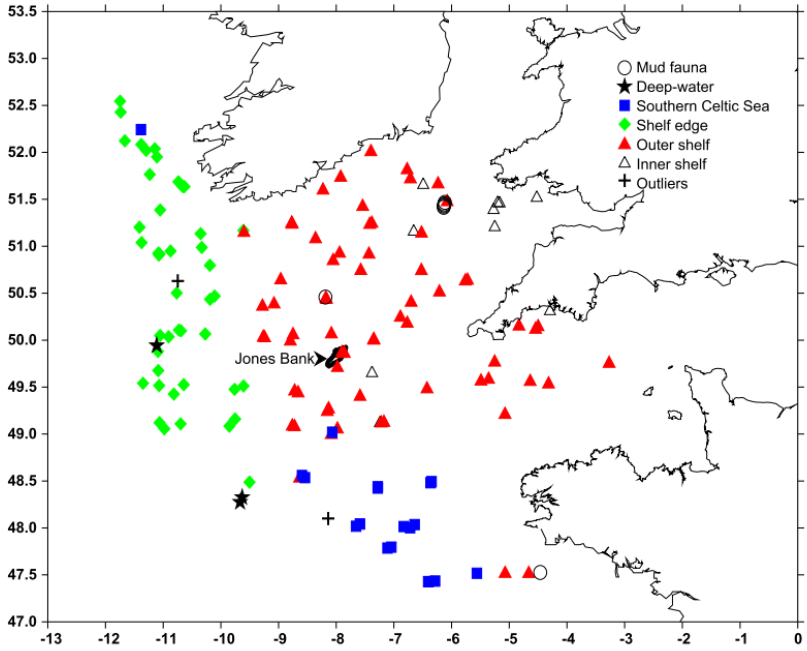

Figure 7: Distribution of demersal assemblages in the Celtic sea from multivariate analysis of 2m beam trawl catches from Ellis et al. 2013.

This area is located at the biogeographical border between two biogeographical areas. The Lusitanian region shelters warm water species, spanning from the south of the Bay of Biscay and Portuguese coasts while the boreal region houses more cold water species, ranging from the western Ireland to the south of Norway (Hátún et al., 2009; Tasker et al., 2008). These characteristics make the Celtic Sea a productive area, with a higher number of species than the adjacent ecoregions (ICES, 2018a). However, this also potentially makes some species in this area more vulnerable to environmental variations since they are at the limit of their range (Thomson et al., 2015).

1.5.4 Biotic data used in this thesis

The EVHOE ("Evaluation des ressources Halieutiques de l'Ouest de l'Europe") survey is carried out every year in November in the Celtic Sea as part of the European data collection framework program. I used data collected during these scientific campaigns to investigate the dynamics and the drivers of species communities in the Celtic Sea. EVHOE dataset suffers from several biases that needed to be corrected before analyses. First, only valid hauls (>20 min and no major damage) were retained. Then to standardize species abundance by the sampling surface, these surfaces had to be checked and re-computed, according to the distance covered by the haul and the length of the sweep line pennant (Cornou, 2017). Due to variations in the precision of taxonomic identification, some species had to be grouped at lower taxonomical levels than species level. I thus use the term taxa in chapters that include species grouped at higher taxonomical levels (Annexe A). What I called taxon diversity refers to diversity measures at the taxon level. Finally, to allow consistent spatial and temporal analysis, only taxa that occurred at more than 5% of the sampling sites in at least one EVHOE depth strata over the time series were kept for analysis and considered as correctly sampled (Annexe B). International bottom trawl surveys provide data about numerous classes of organisms (6 in the EVHOE surveys for instance Actinopterygii, Bivalvia, Cephalopoda, Elasmobranchii,

Holocephali, and Malacostraca) encompassing commercial and non-commercial taxa and enabling ecosystemic studies. However, fragile and small taxa and in particular macro and megabenthic taxa, such as hydrozoan, sea pens, crinoids or anemone, are poorly sampled by bottom trawl (Auster et al., 2011b).

Underwater video techniques (baited or non-baited, driver operated, towed…) are increasingly used to sample marine biodiversity (Mallet & Pelletier, 2014). In particular, towed underwater videos is easy to implement and enables a direct visualization of the seabed over large areas, of an order of magnitude of $100m^2$ (Mallet & Pelletier, 2014; Sheehan et al., 2016). This non-destructive technique, unlike bottom trawling, enables to visualize the seascape as well as fragile little mobile species, providing a complementary tool to bottom trawl surveys, leading to a broader understanding of ecosystems 'sensitivity to fishing. Indeed, these two methods appears complementary (Jac et al. 2020). For instance, two studies used data collected in the sand banks in the center of the Celtic Sea with both a baited camera and bottom trawling (namely Ellis et al., 2013; Martinez et al., 2013). Camera only picked up 28% of the species seen in the trawl (Martinez et al., 2013) but for benthos only, a higher species richness was observed with the camera than with the trawl (Ellis et al., 2013). During the EVHOE surveys, an underwater sledge with a camera was towed to sample macro and mega benthic species in 2014, 2016, 2018 and 2019.

Food web varies spatially. Samples of muscles, mantle, foot and gonads were also realized on board of the EVHOE surveys (and professional boats) as part of the EATME project to carry out isotopic analysis and determine the trophic position of species in the Celtic Sea.

1.6 Aims and problematics

The aim of that thesis is to assess the dynamics of the different facets of biodiversity and their main anthropogenic and environmental drivers, through the analysis of International Bottom Trawl Surveys time series by using robust statistical methods and frameworks. The questions associated to each facet of biodiversity studied here are summarized in Fig. 8.

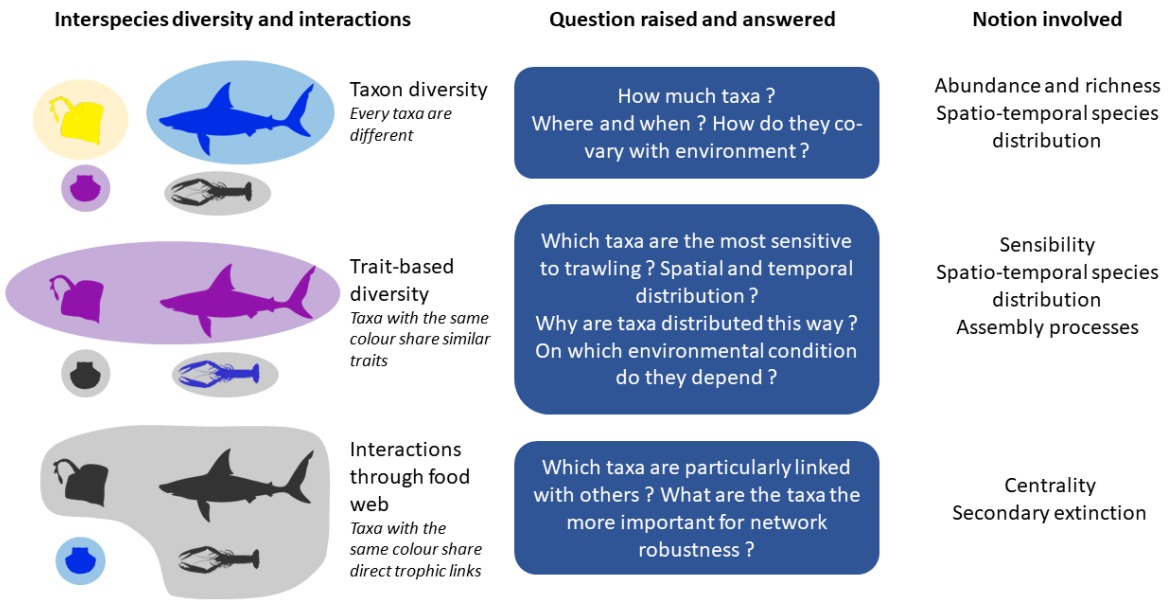

Figure 8: Schematic summary of the information brought by the different facets of biodiversity

More specifically, I investigated the following questions gathered in three chapters:

Knowing that fishing importance as a driver of the North East Atlantic has decreased since it peaked in the 80's, and that the effects of climate change, as well as periodic warming due to natural causes such as warm phases of the North Atlantic Oscillation (NAO) might have taken the lead as driving factors, I investigated:

(1) What are the spatio-temporal dynamics of taxon diversity in the Celtic Sea over 2000-2016 and the influence of environment and fishing on these dynamics?

Based on the results of (1), since fishing has a long history in the Celtic Sea and climate changes effects through the increase of bottom temperature are not significantly visible over the whole area, I focused on the study of the past and current effects of fishing and used life history traits known to respond to this variable. It can be noted that similar steps could be taken with other pressures. I further investigated:

(2) What assembly processes govern the distribution of life history strategies in the Celtic Sea? Can we link the increase of biomass of slow life history strategy species with the local decrease of fishing pressure? Can we see different sensitivity patterns if we consider a larger proportion of megabenthic species, known to be fragile?

Finally, networks of interactions offer a promising tool to scale up from species to the whole network. However, it is not clear whether the sensitivity to a given pressure at the level of species imply a low robustness of the network to this pressure. Because the increase in biomass of the sensitive species to fishing in the Celtic Sea might lead to further modification of the trophic network, I used fishing as an example of pressure to answer the following questions:

(3) What is the importance of sensitive species to fishing in the food web? What species are more susceptible to spread a perturbation to the whole network if affected? Is the food web in the Celtic Sea robust to fishing pressure?

To answer that last question, I propose a framework that scale up from species to ecosystem vulnerability to a given pressure (here fishing).

2 Chapter A

Environment outweighs the effects of fishing in regulating demersal community structure in an exploited marine ecosystem

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2.1 Preface

Previous studies over the Celtic Sea reported the important structuring effect of environment (depth, sediment and temperature) on communities (Ellis et al., 2013; Martinez et al., 2013). Fishing influenced this ecosystem, notably through the decrease in large fish and an increase in smaller ones (10-15cm), with a larger importance of fishing than temperature over 1987-2003 (Blanchard, Dulvy, Ellis, Pinnegar, & Jennings, 2003; Blanchard et al., 2005). However, there is a strong presumption that the importance of drivers of change in fish environment has changed in the recent years. Indeed, fishing effort decreased in the area formed by the Celtic Sea and the Bay of Biscay since the 1990's (Guénette & Gascuel, 2012) while the effects of climate change emerge from the background of natural variability in more and more ecosystems (Henson et al., 2017), for instance the Barents Sea (Fossheim et al., 2015). In the Celtic Sea a regional warming has been detected over 1993-2008 (ter Hofstede et al., 2010). However, no recent study on temperature trends nor on the structuring importance of other environmental and anthropogenic variables was available. More globally, bottom temperature and variation in fishing effort are rarely considered together in these exploited ecosystems. In addition, beyond a suspected shift in environmental drivers, a global study of the spatio-temporal dynamics in space and time of the megafaunal communities over the last decades was lacking to understand the recent dynamics of the area.

These caveats raised the need for an integrative study of the spatio-temporal dynamics of assemblages as well as their drivers over the last two decades. As early signs of regime shift might be perceptible only when considering numerous species at the same time (Möllmann, Müller-Karulis, Kornilovs, & St John, 2008), the use of data from an extensive bottom trawl survey enabled to include a large variety of taxa (i.e. fish, elasmobranchs, crustaceans, cephalopods and bivalves).

2.2 Introduction

Effects of climate change are increasingly visible in marine ecosystems worldwide (IPCC, 2014), and one of the largest concerns is maintaining fish populations and their habitats in states sufficiently stable to enable them to sustain a growing human population, as emphasized by the 14th Sustainable Development Goal of United Nations (Griggs, Nilsson, Stevance, & McCollum, 2017). Although coastal shelf seas represent only *ca.* 7% of the ocean surface area, they provide 30% of oceanic primary production and 90% of global fish catches (Jönsson, Salisbury, & Mahadevan, 2011; Pauly et al., 2002). These easily accessible areas have been exploited for centuries, and most have already experienced shifts in their biotic communities due to selective removal of target species (Guénette & Gascuel, 2012), leading to alternate stable states (Beisner, Haydon, & Cuddington, 2003) in which the importance of fishing pressure has progressively decreased. Indeed, progressive enforcement of fishing regulations in the past 40 years has lowered exploitation rates by decreasing fishing pressure in developed countries, notably in the North-East Atlantic (Fernandes & Cook, 2013a). The biomass of several important stocks increased from 2002-2011, indicating signs of recovery (Fernandes & Cook, 2013a); however, these metrics are based only on commercial species. This focus on commercial species has been widely contested by the need for a more systemic assessment of the health of ecosystems, as stressed by the Ecosystem-based Approach to Fisheries (Garcia et al., 2003), that implies including non-commercial species as well.

Today, the stability of these ecosystems continues to be challenged by climate change, whose impact is particularly visible in coastal ecosystems (Belkin, 2009) through the increase in temperature, increase in ocean acidification or change in pattern of primary production or fish distribution (Dulvy et al., 2008; Fabry, Seibel, Feely, & Orr, 2008; Fossheim et al., 2015; Henson et al., 2010). The first changes in marine communities attributable to climate change – increased bottom temperatures and modified fish distributions – were observed in the past 20

years (Dulvy et al., 2008). These changes can superimpose their effects on the many pressures already facing coastal ecosystems, from human activities (e.g. fishing, aquaculture, dredging, offshore structures, leisure, runoff from land) to natural perturbations such as the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) (Edwards, Beaugrand, Alheit, Helaouët, & Coombs, 2013; ICES, 2018a; Wakelin, Artioli, Butenschön, Allen, & Holt, 2015).

Managing exploited ecosystems in the context of the global climate change thus required accounting for synergistic effect of climate and fishing (Le Bris et al., 2018; Planque et al., 2010). Integrating multiple environmental drivers and ecosystem components simultaneously for a large number of species is necessary, especially to predict which species would be impacted the most by changes in several environmental variables acting in interaction. Among those other variables, primary productivity is particularly important to consider as it enables to account for the response of species to the input of energy in the system. In the context of an increasing number of reliable data sources that provide time series of environmental variables (such as the European Union's Copernicus marine environment monitoring service, Sotillo et al. 2015) and international marine surveys that sample increasingly larger areas of ecosystems, this goal becomes achievable.

Located on the continental shelf between France, Ireland and the United Kingdom (UK), the Celtic Sea lies at the biogeographical border between two faunal assemblages: warm-water species from the southern Bay of Biscay and Portuguese coasts and cold-water boreal species from western Ireland and the North Sea (Hátún et al., 2009). This geographical position leads to a higher number of species in the Celtic Sea (> 350 sampled during International Bottom Trawl Surveys) than in the surrounding seas but also implies that these species may be impacted more by environmental variations, since some are at the limits of their area of distribution (ICES, 2018a; Thomson et al., 2015). Regional warming has been detected in the whole Celtic

Sea, with the winter bottom temperature increasing significantly over the time series as studied by ter Hofstede, Hiddink, & Rijnsdorp (2010), i.e. from 1993 to 2008. This was most likely caused by the warm phase of the AMO in the late 1990s (McLean, Mouillot, Goascoz, Schlaich, & Auber, 2018). This increase in temperature coincided with expansion of warm-water fish from southern Portugal to northwestern Ireland (Quero, Du Buit, & Vayne, 1998). However, having a closer look at the time series, the temperature appears to have stabilized after 2002 (regression of bottom temperature on 2000-2016 showed non-significant trend: slope=-0.002, p-value=0.83). Local dynamics also have to be investigated as they might show different trends than the ones observed over the whole area. Primary production, approximated by chlorophyll a concentration, was relatively high (0.36-1.63 $mg.m^{-3}$) in the Celtic Sea (ICES, 2018a) but might decrease, according to simulations run under the A2 greenhouse-gas-emission scenario of the Intergovernmental Panel on Climate Change (Henson et al., 2010). The Celtic Sea is also an important fishing zone, intensively exploited by France, Ireland, the UK, Belgium and Spain since at least the 1950s (Guénette & Gascuel, 2012). It sustains an important fishery of more than 100 species, from algae to top-predator fishes (Mateo et al., 2017). After major changes occurred in the 1950-1970, a decreasing trend of fishing mortality has been reported since the mid-1990 for assessed benthic and demersal stocks (ICES, 2018b). Previous studies in the Celtic Sea described communities in relation to fishing and oceanographic variables, at relatively local geographical and temporal scales, around the banks in the center of the Sea (Martinez et al., 2013; Mateo et al., 2017; Sharples, Ellis, et al., 2013). However, the question of their long-term and large-scale variability remains to be addressed.

The Celtic Sea thus offers a good case study to investigate the synergistic importance of bottom temperature, fishing and primary productivity in driving communities of this North-Atlantic exploited shelf sea over the past 20 years. In particular, I aimed to assess whether taxa responded to spatial variations in bottom and pelagic trawl effort and in bottom temperature, or

to spatio-temporal variations in chlorophyll a concentration from 2000-2016. Knowing the relatively weak range of variations of the average bottom temperature (warm phase of the AMO) and fishing (stable or decreasing exploitation patterns) over the studied period at the regional scale of the Celtic Sea, we expected only minor temporal variations in these variables to manifest themselves at the assemblage level. However, we expected that spatial variations in these temperature and fishing variables and temporal variations at a local scale may still be important in driving the composition of specific species assemblages. We used a dataset of 1175 hauls from the International Bottom Trawl Survey EVHOE (Evaluation des ressources Halieutiques de l'Ouest de l'Europe). We considered 101 commercial and non-commercial taxa (i.e. fish, cephalopods, bivalves and crustaceans) to account for variation in the entire bentho-demersal ecosystem with the environment. We characterized the species assemblages from 2000-2016 as a function of depth, sediments, chlorophyll a, bottom temperature and fishing, where fishing and warming effects had already occurred. Since this relation may vary according to the spatial scale (deYoung et al., 2008), we studied two spatial scales: large scale (the entire Celtic Sea) and a finer scale (four sediment-depth strata). We characterized (1) temporal stability of relations between taxa and the environment and the possible presence of shifts in the relations, (2) average structuring of the community over this period and assemblages of taxa showing similar co-variation with climatic, anthropogenic and biological variables and (3) variation in this structure over the years and among sediment-depth strata.

2.3 Materials and methods

Sampling and taxa

We extracted data from the bottom trawl survey EVHOE, part of the International Bottom Trawl Survey (ICES 2015), that was conducted each year in the Celtic Sea in November from 2000-2016. The trawl was a 36/47 GOV (grande ouverture verticale) with a 20 mm net fitted in the codend, a horizontal opening of *ca.* 20 m and vertical opening of 4 m. A total of 53-84 hauls were performed each year according to a random stratified design based on depth strata. Hauls were conducted at 4 knots for 30 min. Our study used 1175 valid hauls. Due to less precise identification of certain taxa early in the time series, some species were grouped at a lower taxonomic level (hereafter, "taxon") (genus, for species of *Alloteuthis*, *Argentina*, *Arnoglossus*, *Gaidrosparus*, *Loligo*, *Munida*, *Mustelus*, *Octopus*, *Pomatoschistus* and *Sepiola*; family, for Ammodytidae and Gobiidae). Only the taxa that occurred at more than 5% of the sampling sites in at least one EVHOE depth strata over the time series were kept for analysis and considered as correctly sampled. A total of 101 taxa from 6 classes (Actinopterygii, Bivalvia, Cephalopoda, Elasmobranchii, Holocephali and Malacostraca) and 53 families were selected. We worked at the scale of the sampling stations and the biomasses were standardized per m^2 by dividing by the sampled area. The sampled area at each sampling site was computed from the geographic position at the beginning and the end of the haul that gave us the distance sampled, that we multiplied by the width of the net at each haul. Sampling sites were located at depths of 57-340 m (Fig. 1), mainly on sand and mud, with some mixed, coarse sediments and boulders.

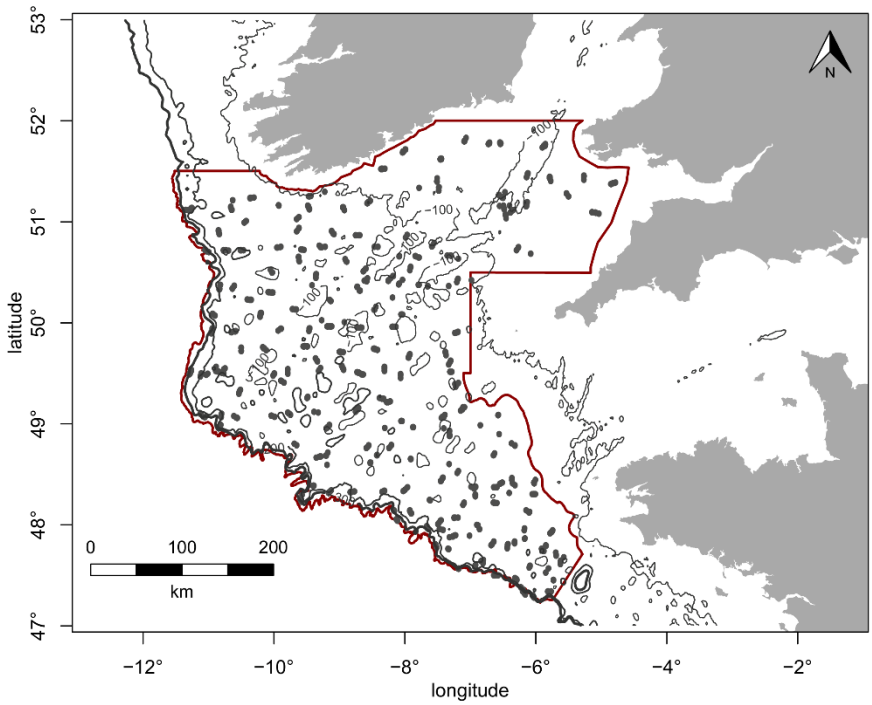


Figure 1 : Map of the study area (bounded by the red line) and the 1,175 sampling sites used (black dots)

Environmental and fishing variables

Based on the literature (Foveau, Vaz, Desroy, & Kostylev, 2017; Karakassis & Eleftheriou, 1997; Vaz, Carpentier, & Coppin, 2007), we selected variables known to influence Northern Atlantic sea shelf ecosystems and that characterize habitat (depth, sediments). We also selected variables to capture the driving of demersal communities by environment (bottom temperature and chlorophyll a concentration as a proxy for productivity) and human activities (fishing effort). These variables do not influence all taxa at the same time, neither with the same time lag. Due to the annual frequency of sampling and the differing life cycles of the 101 taxa, we assumed that annual means would be the most relevant values for the variables.

Depth was recorded at each sampling site, and sediment type (according to the Folk five-class classification) was extracted using a spatial join to EMODnet data

(https://www.emodnet-geology.eu). Because the sediment map provided by EMODnet did not cover the entire study area (93 of 1175 sampling sites missing), we obtained the missing values from France's Service Hydrographique et Océanographique de la Marine (SHOM) world sediment map (https://diffusion.shom.fr/loisirs/sedim-mondiale.html). Bottom temperature and chlorophyll a concentration were downloaded from Copernicus (http://marine.copernicus.eu/). Annual mean chlorophyll a concentrations were calculated from monthly means obtained from satellite observations at 1 km × 1 km resolution.

Annual mean bottom temperatures were calculated from the monthly mean Atlantic-Iberian Biscay Irish-Ocean Physics Reanalysis data product at 8 km × 8 km resolution. Information about fishing effort came from the New Fisheries Dependent Information from the EU's Scientific, Technical and Economic Committee for Fisheries (STECF) (https://stecf.jrc.ec.europa.eu/), which provided fishing effort for all European countries in hours fished and landings in tonnage, both per statistical rectangle (111.12 km × 55.56 km). Analysis was realized on fishing hours data while landings data were used to give insights during the interpretation step only (Appendix 3, Fig. S5, S7 and S9). We considered pelagic and bottom trawls since they represent the largest and second-largest landings, respectively. We hereafter refer to these variables as "environmental variables". To interpret outputs of the statistical analysis, we generated maps of yearly anomalies (pixel value of a given year – pixel mean value over the time series) for chlorophyll a, bottom temperature and bottom trawl effort (spatial coverage was insufficient for pelagic trawl effort) (Fig. 7a, 7b, 8a, and Appendix 2, Fig. S1 to S4) as well as a map of the slope of the regression of bottom temperature over time (Fig. 8b). We also assessed temporal evolution in fishing effort and landings of bottom and pelagic trawls (Appendix 3, Fig. S5 to S9).

Statistical analysis: STATICO

Ordination analyses are widely used to study relations between taxa and their environment (Thioulouse et al., 2004). Given the expected complexity of the relations between climatic, anthropogenic and biological variables, we chose STATICO analysis (Simier et al., 1999; Thioulouse et al., 2004) to identify potential relations between taxa biomass and environmental variables, without imposing causal relations. This method is particularly suited for analyzing both temporally stable and temporally variable relations between taxa and their environment (Thioulouse et al., 2004).

STATICO is based on two tables: a sites × taxa table, which provides biomass for each taxon at each site sampled, and a sites × environments table, which provides values for each environmental variable at each site. We defined the two tables for each year from 2000-2016. Although the sites sampled varied from year to year, the tables contained the same lists of taxa and environmental variables. As recommended by Rao (1995), we applied Hellinger's transformation to the biomass data to avoid placing undue emphasis on taxa with low frequencies when measuring similarities between samples. Bottom and pelagic trawl efforts were log-transformed because they had wide ranges. To avoid unbalanced sampling among sediment types, we recorded them as a numeric variable (1-5), with larger values representing larger particle size (1=Mud to muddy with muddy characterized by 100-10% mud, <90% sand and <5% gravel; 2=Sand; 3=Mixed sediment characterized by 95-10% mud, <90% sand and >=5% gravel; 4=Coarse substrate being either >=80% gravel or >=5% gravel and >=90% sand; 5=Rock & Boulders).

The first step of STATICO consists of co-inertia analysis that combines, for each year, the sites × taxa table with the sites × environments table, yielding a cross-covariance table. For each year, the cross-covariance table shows the environmental variables as rows, the taxa as columns and, as entries, the covariance between each taxon and environmental variable for all

sample sites. Each co-inertia analysis (for each year) was based on a normed principal component analysis (PCA) of the sites × taxa table and a normed PCA of the sites × environments table. Since this step assumes a linear relation between taxa biomass and environmental variables, we visually verified that the relation between each pair of taxon and environmental variable was roughly linear. The second step of STATICO consists of partial triadic analysis (PTA, Tucker 1966, Thioulouse et al. 2018) to analyze the series of cross-covariance tables over the years. The PTA has three steps:

(1) *Interstructure*. For each pair of years (i.e. each year with every other year), vectorial correlation coefficients *Rv* are calculated between their (environments × taxa) cross-covariance tables to identify similarities between these two tables. All pairwise *Rv* values are placed in a squared **Rv** matrix, which is diagonalized into eigenvectors and eigenvalues to define scores for the years that describe, in multidimensional space, similarities between their (environments × taxa) cross-covariance tables. The *interstructure* thus evaluates how similar the relationships between the biomass of taxa and the environmental variables have been over years. On the correlation circle, the length of the arrows associated with years on the first axis represented the weights used to calculate the weighted mean of the (environments × taxa) cross-covariance tables in the *compromise* analysis. The longer the arrow, the greater the contribution of a year to the *compromise*.

(2) *Compromise*. The first eigenvector of the interstructure analysis is used to weight the cross-covariance tables and calculate their weighted mean. A high weight for a given year indicates that this year is particularly representative of the relation between taxa and the environment during the time series. Conversely, a low weight means that the given year has unusual relations between taxa and the environment. Similar weights for all years indicate stable relations between taxa and the environment over the years. The structure of the averaged cross-covariance table is then calculated using a centered PCA, which yields

factorial maps with comparable scores for the taxa and environmental variables. The *compromise* thus assesses temporally stable relations between taxa biomass and environmental variables.

(3) *Intrastructure*. The rows (environmental variables) and columns (taxa) of each cross-covariance table for each year are projected onto the *compromise* space as supplementary elements (Thioulouse et al. 2018). To assess potential spatial patterns in taxa-environment relations, we projected the rows (sampling sites) of the initial sites × taxa and sites × environments tables onto the *compromise* space as supplementary elements. These projections provide an overview of annual variations in taxa-environment relations. The *intrastructure* thus assesses temporal changes in relations between taxa biomass and environmental variables, also called trajectories.

To obtain an integrated view of variations in taxa biomass and the environment, we clustered taxa according to their mean relation with the environment. We used k-means clustering on the taxa scores in the *compromise* space, and the optimal number of assemblages was determined by the Calinski-Harabasz criterion (Calinski & Harabasz, 1974). Clustering the taxa into assemblages and using the Hellinger transformation decreased some of the remaining sampling bias, such as fishing a school of one taxon in a given year. Analyzing the outputs of STATICO at the level of taxa assemblages instead of that of the taxa themselves also mitigated this kind of bias. To determine which environmental variables had the strongest relations with assemblages, we calculated Spearman correlation coefficients between annual mean *compromise* scores for taxa assemblages and the environmental variables.

Depth was correlated to bottom trawl (Spearman's rho= -0.46, p-value < 2.2e-16), pelagic trawl (Spearman's rho= 0.36, p-value < 2.2e-16) and bottom temperature (Spearman's rho= 0.60, p-value < 2.2e-16). However, the STATICO approach does not allow partialling out the effects of the variables, notably the ones that do not vary with time (i.e. depth and sediment

type). To evaluate the importance of stable environmental variables in the taxa-environment relation, we clustered sampling sites into strata according to depth and sediment type, using k-means clustering on Euclidean distance, determining the number of clusters according to the Calinski-Harabasz criterion. We analyzed temporal changes in taxa-environment relations for each stratum following Kidé et al. (2015). Indicator taxa for each site stratum were calculated based on the *IndVal* Species Indicator Value (Dufrêne & Legendre, 1997). For each indicator taxa, we identified its associated assemblage determined from the clustering of the STATICO *compromise* space. All statistical analyses were conducted in R (R Core Team, 2020).

2.4 Results

Interstructure analysis

The *interstructure* analysis measured the resemblance between the years in the relationship between taxa and the environmental variables (Fig. 2). The first axis of the *interstructure* space explained 70.8% of the correlations between years, and its second axis explained 18.1% (Fig. 2a). The similar length of arrows in the correlation circle indicated relative stability in the relation between taxa and the environment over the years (Fig. 2b). Nonetheless, some values of vectorial correlation coefficients *Rv* were moderate, indicating that some relations between taxa and environmental variables did vary for some years (Fig. 2c). The second axis of the *interstructure* distinguished two main periods: 2000-2002 and 2003-2016, the second of which could be subdivided into the periods 2003-2009 and 2010-2016 (Fig. 2b).

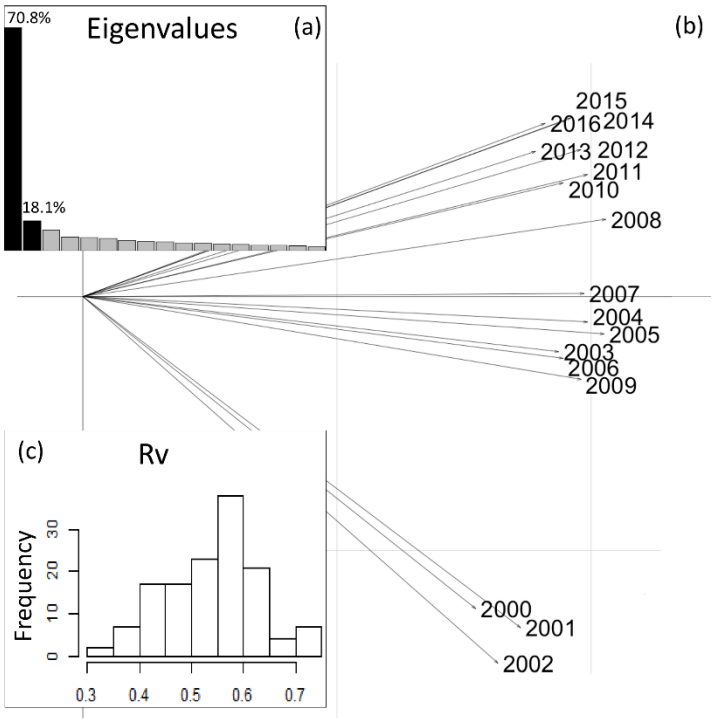


Figure 2: Interstructure analysis. (a) Eigenvalues of the Rv matrix (vectorial correlation in taxa–environment covariances between 2 years), (b) correlation circle with scores for years, and (c) histogram of all pairwise Rv values

Compromise analysis

The *compromise* analysis informed on the temporally stable part of the relationships between the taxa and the environmental variables. The first principal component of the *compromise* space, which explained 56.8% of total variation in the *compromise* space, was associated with depth, bottom temperature and pelagic trawl effort in its positive half and chlorophyll a and bottom trawl effort in its negative half (Fig. 3a). The second principal component explained 7.7% of total variation and was associated mostly with sediment type and bottom temperature (Fig. 3a).

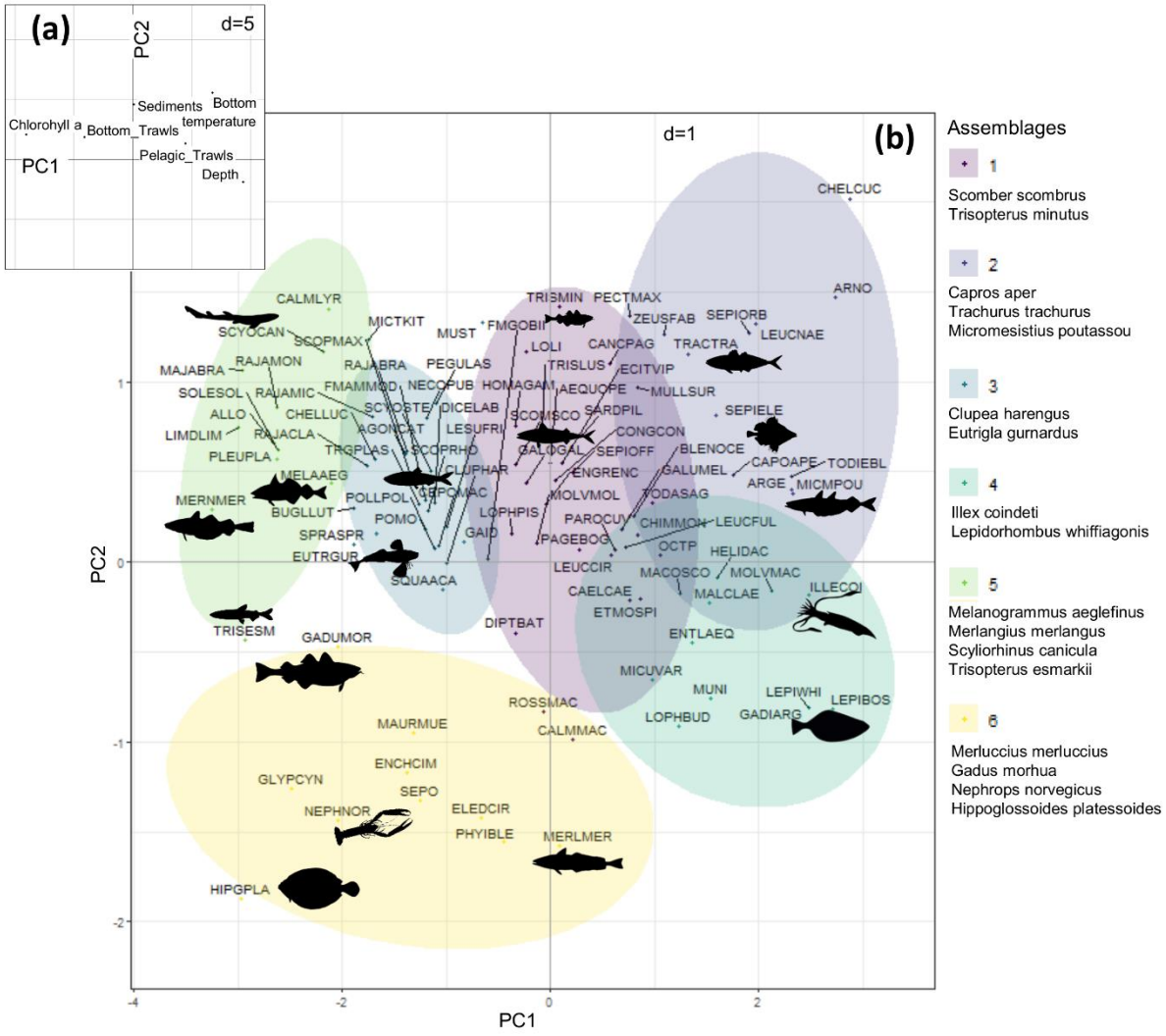


Figure 3: Compromise analysis. (a) Scores of the environmental variables. Parameter d shows the scale of the plot (width of a grid square). (b) Scores of the taxa clustered into six assemblages using k-means clustering. Taxa with the largest biomass in each assemblage are listed in the legend and displayed as silhouettes. Scientific names corresponding to taxa codes can be found in Appendix 1

Clustering of taxa scores on the first two axes of the *compromise* space yielded six assemblages (Fig. 3b, Appendix 4). Assemblage #1 lay near the center of the *compromise* space, with no distinct patterns, and is thus composed of generalist taxa. The biomass of this assemblage was dominated by mackerel *Scomber scombrus* and poor cod *Trisopterus minutus*. Assemblage #2,

in deeper areas, was associated with warm bottom temperature, high pelagic trawl effort, coarse sediments, low chlorophyll a concentration and low bottom trawl effort. Boarfish *Capros aper*, horse mackerel *Trachurus trachurus* and blue whiting *Micromesistius poutassou* had the largest biomass in this assemblage. Conversely, assemblage #3 was associated with shallow-to-medium depth, high chlorophyll a concentration, medium-high bottom trawl effort, low bottom temperature and low pelagic trawl effort. Atlantic herring *Clupea harengus* and grey gurnard *Eutrigla gunardus* had the largest biomass in this assemblage. Assemblages #1 and #3 contained more planktivorous species than the other assemblages. Assemblage #4 was found in environmental conditions similar to those of assemblage #2, but over finer sediments and in areas with colder bottom temperature. Shortfin squid *Illex coindeti* and megrim *Lepidorhombus whiffiagonis* had the largest biomass in this assemblage. Assemblage #5 was found in environmental conditions similar to those of assemblage #3, but with higher chlorophyll a concentration and higher bottom trawl effort. Commercial fish essentially dominated the biomass of this assemblage: haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus*, small-spotted catshark *Scyliorhinus canicula* and Norway pout *Trisopterus esmarkii*. Assemblage #6 also contained commercially important species, such as hake *Merluccius merluccius*, cod *Gadus morhua*, nephrops *Nephrops norvegicus* and American plaice *Hippoglossoides platessoides*, which were found in environmental conditions similar to those of assemblage #3, but over finer sediments and in areas with colder bottom temperature.

Intrastructure – Variation in the relative importance of structuring variables over 17 years

Overall, depth, chlorophyll a and temperature structured axis 1 the most for the entire time series (i.e. lay furthest from the center of the *compromise* space). The structuring effect of depth, sediment type and temperature remained relatively stable over the years (i.e. small

ellipses) (Fig. 4a). Conversely, chlorophyll a, bottom trawl effort and pelagic trawl effort varied most over the years (i.e. the largest ellipses) (Fig. 4b).

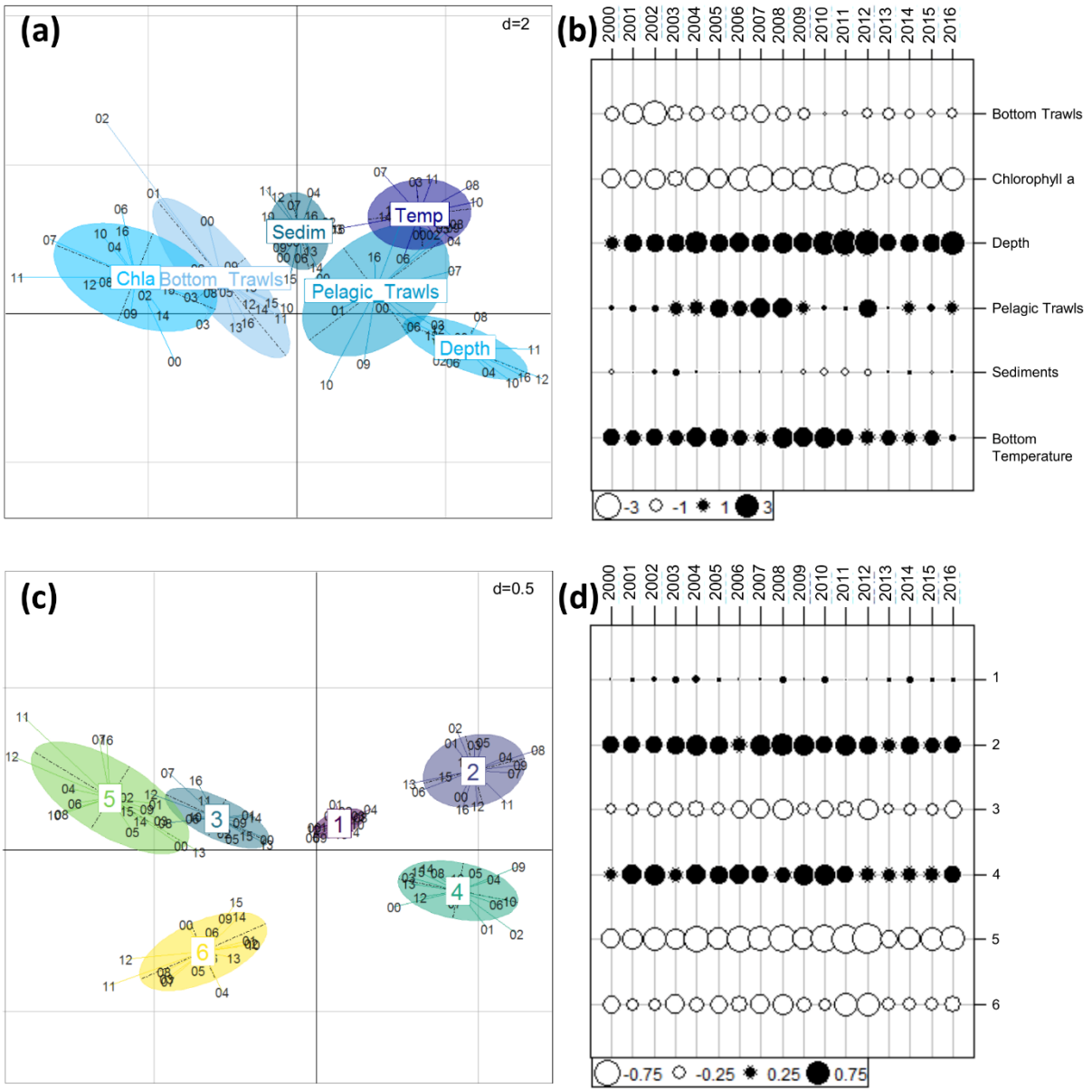


Figure 4: Intrastructure plots with (a) annual positions of environmental variables, (b) circles proportional to scores of the environmental variables on axis 1, (c) annual positions of taxa assemblages obtained after k-means clustering, and (d) circles proportional to scores of the assemblages on axis 1. Ellipses on plots (a) and (c) summarize the clouds of dots (years) weighted by their distance to the center of the ellipses (mean position over the years)

The structuring effect of bottom trawl effort on assemblages was strong in 2000, decreased slightly after 2002 and was weak from 2009-2016 (axis 1, Fig. 4a,b). Bottom trawl effort was exerted in area characterized by shallow depth with cold temperature, fine sediments and high chlorophyll a concentration from 2000-2002, then in area with less marked characteristics from 2002-2009. From 2010-2011, its association shifted toward greater depth and warmer temperature, after which it had less structuring effect (Fig. 4a,b).

Pelagic trawl effort had little structuring effect from 2000-2003 but was as important as depth, chlorophyll a and temperature from 2005-2008. After 2009, its structuring effect decreased strongly (Fig. 4b). Pelagic trawl effort was associated with great depth, warm temperature and low chlorophyll a concentration from 2005-2008 and again in 2012. Lastly, chlorophyll a had a strong structuring effect (especially in 2007 and 2011), except in 2003 and in 2013 (Fig. 4b). Temperature was particularly important in 2008 and 2010. After 2009, assemblages were thus driven essentially by depth, chlorophyll a and temperature.

The interpretation of the variations in the link with taxa biomass of depth and sediments, which values do not change over time, was not straightforward. Either the sampling was performed from significantly different sediment types and depths over the years, or taxa moved throughout the Celtic Sea, which would also have changed their relations with sediment type and depth. Since neither sampling depth nor sediment type differed significantly among years (Kruskal-Wallis Chi-squared = 10.88 and 37.83, respectively; p-value = 0.82 and 0.99, respectively), annual variations in the relations between taxa and sediment type or depth were most likely explained by the taxa moving among different sediment types and depths.

Intrastructure – temporal variability in assemblages in relation to environmental variables

Taxa maintained stable relations with the environment over the years (i.e. small ellipses in Fig. 4c,d). Assemblage #1 had less variation around its mean position in the *compromise*

space over the years than the other assemblages. Conversely, assemblage #5 varied the most (i.e. had the largest ellipse) and overlapped assemblage #3. These two assemblages co-varied positively with chlorophyll a concentration with no time lag (Table 1).

Table 1. Spearman correlation coefficients between yearly averaged scores of taxa and environmental variables on the first axis of the compromise *space for each assemblage. * $p < 0.05$.*

	Bottom trawl effort	Chlorophyll a	Depth	Pelagic trawl effort	Sediment type	Bottom temperature
1	0.069	0.137	-0.047	0.105	0.483	0.444
2	0.086	-0.561*	0.407	0.505*	-0.272	0.348
3	-0.017	0.806*	-0.630*	-0.618*	0.275	0.010
4	-0.147	-0.360	0.358	0.051	-0.059	0.397
5	-0.319	0.919*	-0.821*	-0.350	0.453	-0.125
6	0.000	0.360	-0.225	-0.434	0.282	0.113

When chlorophyll a had a strong structuring effect, the ellipses of these two assemblages also expanded toward higher chlorophyll a concentration in the *compromise* space. Conversely, when chlorophyll a had a strong structuring effect, assemblage #2 was associated with low chlorophyll a concentration. When pelagic trawl effort had a strong structuring effect, however, assemblage #2 was associated with high pelagic trawl effort, while assemblage #3 was associated with low pelagic trawl effort.

Spatio-temporal variability in assemblages and environmental variables

Sampling sites were clustered into four strata based on depth and sediment type. Stratum 1 consisted of a few sites (56) along the deepest border of the area (235-339.5 m deep) (Fig. 5) and was located in the part of the *compromise* space related to great depth, but also to warm bottom temperature and high pelagic trawl effort.

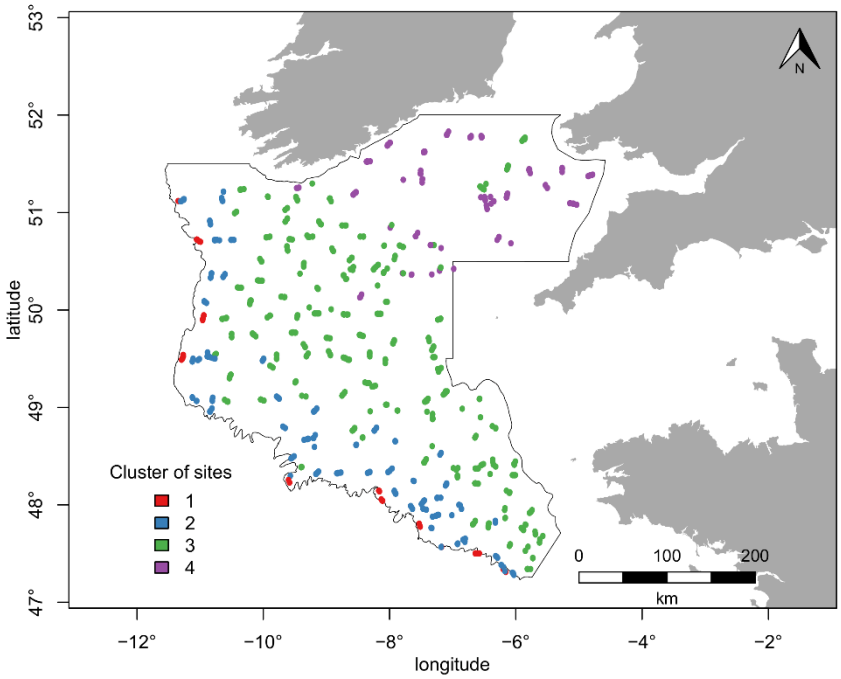


Figure 5 : Sampling sites in the Celtic Sea clustered based on depth and sediment type into four strata

There was no clear match between environmental and taxa trajectories at these sites (Fig. 6); thus, taxa at these sites were most likely influenced by other sources of variability than the environmental variables considered here. Stratum 2 consisted of shallower sites (155-229 m deep), also along the deepest border of the area, but with warmer bottom temperature and higher pelagic trawl effort than those of stratum 1. From 2001-2008 and 2012-2014, similar temporal variations between environmental variables and taxa suggested that variations in taxa biomass were related to dynamics of the environmental variables used in this study. From 2001-2008, pelagic trawl effort was most likely an important driver of assemblages at these sites, since it was an important driver of assemblages overall during this period and was exerted at these sites (Fig. 6 and 7a). Stratum 3 consisted of sites in the center of the Celtic Sea, where environmental and taxa trajectories showed the same move from the left to the right of the *compromise* space in 2006-2007 and 2009-2011, and then from the right to the left in 2007-2009 and 2011-2013 (Fig. 6).

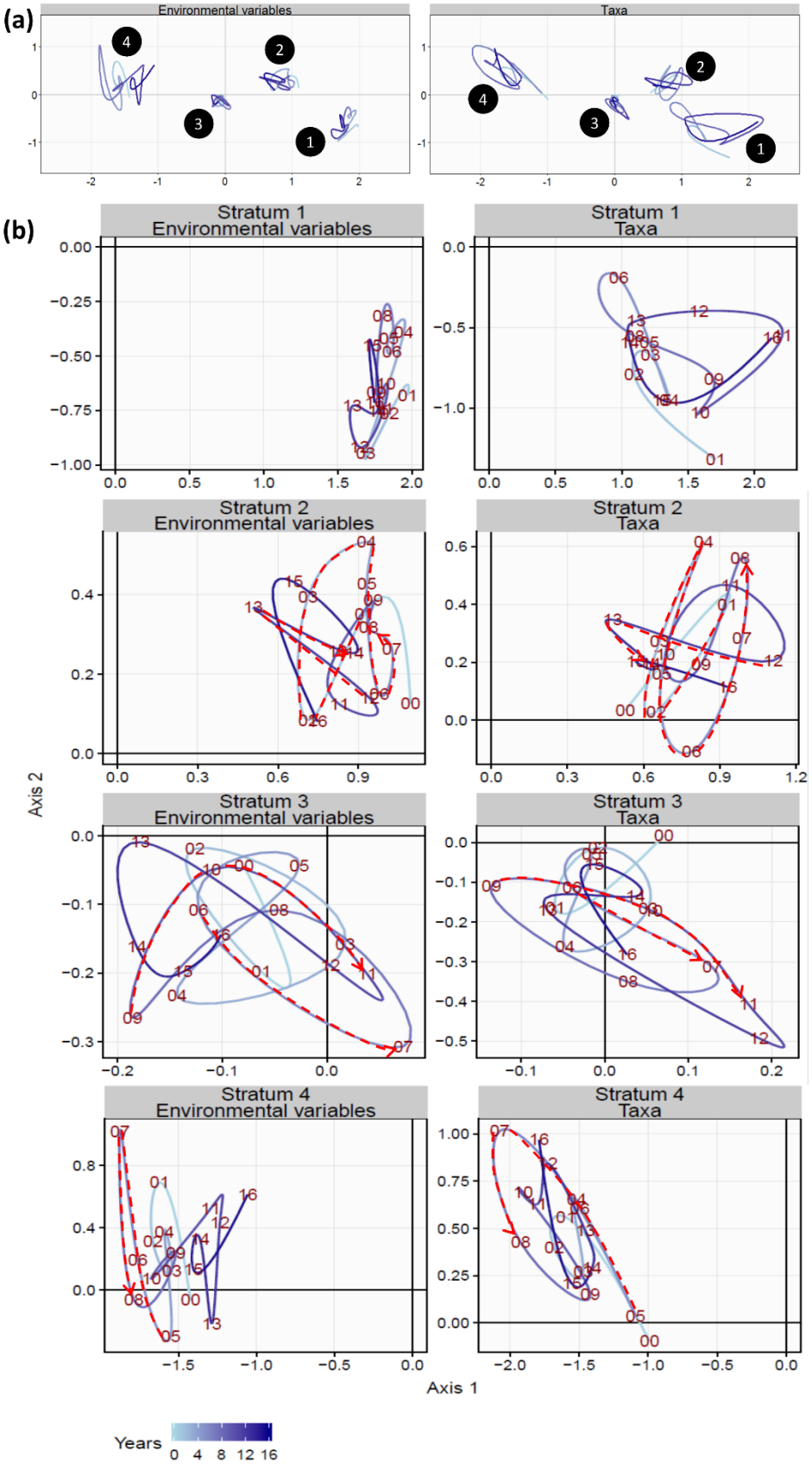


Figure 6 : Trajectory factor maps—projection of the four strata, clustered based on depth and sediment type, as supplementary elements in both factorial maps (environmental variables and

taxa) of the principal component analysis of the compromise space: (a) Overview of the position and extent of trajectories (in a gradient from light blue to dark blue) for each stratum. (b) Projection of the rows of the initial sites × environment stable (left column) and of the rows of the initial site × taxa table and (right column) into the compromise for each stratum. Labeled points indicate the mean position of taxa biomass or environmental variables for a given year. When the environment and taxa have the same trajectory (red dashed arrows), the environmental variables are considered to explain the variation in taxa biomass

These trajectories were most likely related to a relative increase in bottom temperature at these sites from 2006-2007 (Fig. 8a and Appendix 2, Fig. S3). From 2007-2009, the similar dynamics of environment and taxa were driven by a decrease in bottom temperature and a slight increase in chlorophyll a and bottom trawl effort in this stratum. From 2011-2013, a similar move toward the left of the *compromise* space was driven by a distinct decrease in mean bottom temperature (Fig. 6 and 8a). Finally, stratum 4 consisted of coastal sites and was located in the part of the *compromise* space related to high chlorophyll a concentration and high bottom trawl effort. Environmental trajectories of this stratum had a larger amplitude than those of the other strata (y-axis ranges in Fig. 6), which indicates the higher variability in this environment. These sites had similar trends from 2005-2009, but the dynamics were difficult to relate to variation in a particular environmental variable (Fig. 7, 8 and Appendix 2, Fig. S1 and S4). In addition, these sites are located in the part of the Celtic Sea where increase in bottom temperature has been the highest (+0.04°C/y) (Fig. 8b).

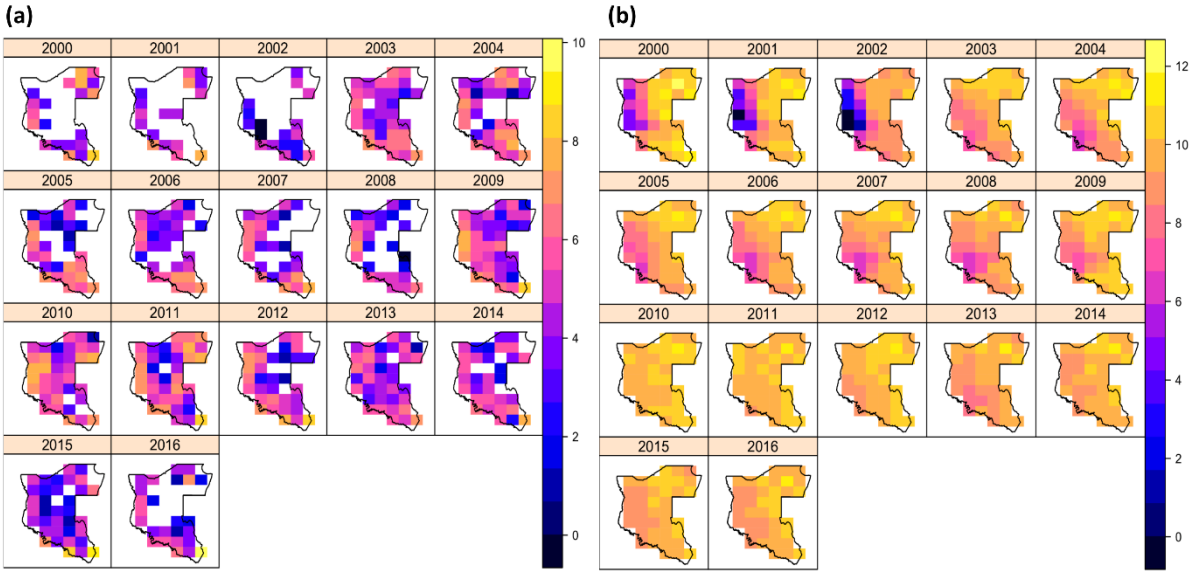


Figure 7 : (a) Pelagic trawl effort log(x + 1) and (b) bottom trawl effort log(x + 1), transformed as in the STATICO analysis (log(x + 1) hr fished per statistical rectangle). No pelagic trawl effort was recorded in white rectangles

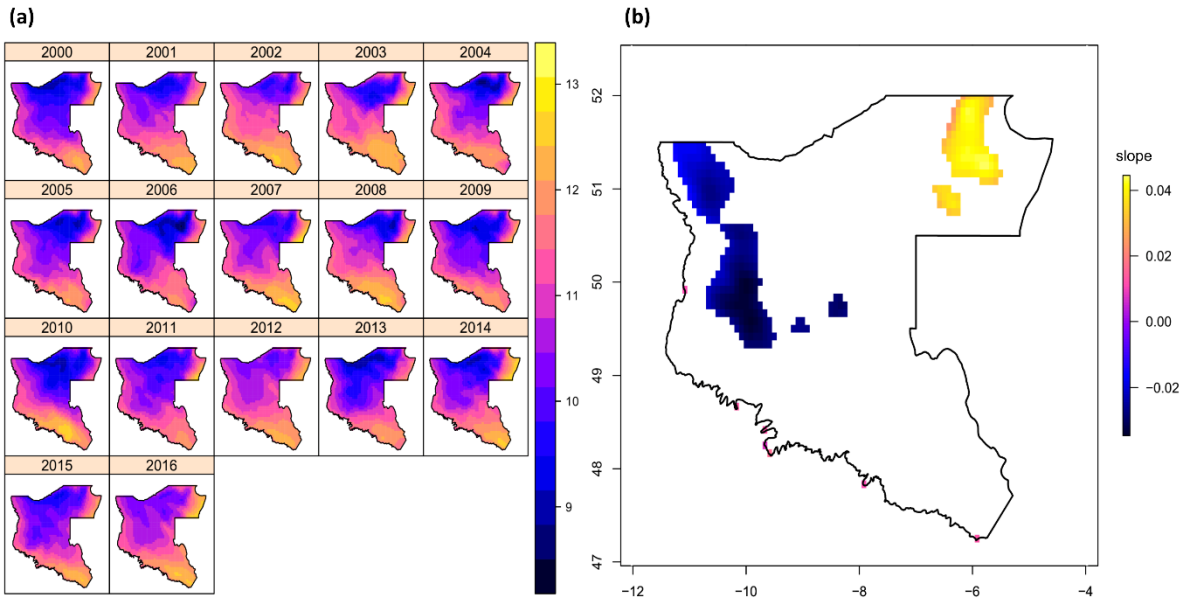


Figure 8 : (a) Spatio-temporal values of bottom temperature (°C) and (b) slope of the regression of bottom temperature over time (°C/year). Only pixels with p > .1 are plotted. See Appendix 2 for methodological details

For each stratum, we determined indicator taxa with the *IndVal* Species Indicator Value, which are the taxa found most often in that stratum, at all of its sites. The indicator taxa of strata 1 and 2, located on the deep border of the Celtic Sea, belonged to assemblages #4 and #2, respectively (Table 2), since these assemblages are found in the deepest part of the area (Fig. 2). Sites in stratum 3 (center of the Celtic Sea) hosted mixed assemblages since they had only one indicator taxon, poor cod *Trisopterus minutus*, which belonged to the generalist assemblage #1. Stratum 4 (coastal sites) consisted of indicator taxa that belonged to assemblages #3 and #5. Taxa from assemblages #1 and #6 were the indicator taxa of multiple strata. These assemblages had no distinct spatial distribution. Indicator taxa in a given stratum did not necessarily belong to the same assemblage and thus did not necessarily vary in the same way with the environment.

Table 2. Correspondence between indicator taxa of geographical strata based on depth and sediment type and those of assemblages defined in the compromise *space of STATICO (Fig. 2b). Scientific names corresponding to taxa codes can be found in Appendix 1. Taxa are ordered by decreasing values of* IndVal *Species Indicator Value index in each stratum.*

Taxon code	Depth and sediment-based stratum	STATICO assemblage
HELIDAC	1	4
ARGE		2
ILLECOI		4
MOLVMAC		4
LEPIBOS		4
MUNI		4
MALCLAE		4
GADIARG		4
TODIEBL		2
LEPIWHI		4
MERLMER		6
ARNO	2	2
CHELCUC		2
SEPIORB		2
ZEUSFAB		2

TRISMIN	3	1
MERNMER		5
EUTRGUR		3
LIMDLIM		5
TRISESM		5
SPRASPR		3
PLEUPLA		5
CLUPHAR		3
ALLO		5
CALMLYR	4	5
MELAAEG		5
SOLESOL		5
RAJAMON		5
SCYOCAN		5
MAJABRA		5
MICTKIT		3
HIPGPLA		6
SCOMSCO		1

2.5 Discussion

We investigated spatio-temporal dynamics of co-variations between the environment and taxa to determine whether the main environmental and anthropogenic trends in ecosystems in the Celtic Sea had influenced the biomass of taxa. Namely, if the reduced fishing mortality after the mid 90's (ICES, 2018b) has continued to shape the structure of the assemblage during a warmer regime since 2002. We distinguished six assemblages that illustrate different types of responses to environmental and fishing variables in the Celtic Sea and highlighted an overall stable relation between taxa and the environment over time. From 2000-2016, depth, chlorophyll a and bottom temperature were the main variables structuring assemblages in the Celtic Sea. In particular, we identified a relation between assemblages #2, #3 and #5 and chlorophyll a throughout the time series, highlighting a strong bottom-up influence for these assemblages.

Over the period studied, bottom and pelagic trawl efforts were less important than depth, chlorophyll a and temperature in structuring the assemblages. This finding echo the work of ter Hofstede et al. (2010) on species richness, who concluded that climate likely influenced species richness in the Celtic Sea more than fisheries did. The Celtic Sea has been intensively fished since the 1950s and thus has adapted to this driver, reaching a new steady state. The main shift in the Celtic Sea probably occurred before the 1980s, as indicated by a decrease in trophic levels (Guénette & Gascuel, 2012). Along the gradient of fishing effort, the most common effect of fishing documented on community structure is the removal of apex predators (Ellingsen et al., 2015; Stortini, Frank, Leggett, Shackell, & Boyce, 2018). Here, we investigate a period of relatively stable fishing scenario following a sharp increase (Guénette & Gascuel, 2012; ICES, 2018b); so no large shift resulting from the removal of a top predator was visible at the scale of our time series. Nevertheless, the level of fishing pressure in the Celtic Sea remains high, with only 29% of the stocks fished below the F_{MSY} (ICES, 2018b). Conversely, fishing seems to be the dominant driver of Northwest Atlantic ecosystems (Shackell, Bundy, Nye, & Link, 2012). This is most likely caused by the time series considered (1970-2008) compare to the one studied here (2000-2016).

Despite this overall stability, the relative importance of some structuring variables did change. In particular, bottom and pelagic trawl efforts had little effect on community composition after 2009, perhaps due to bottom trawl effort moving to deeper areas, thus sharply decreasing in coastal areas (Fig. 7b and Appendix 2, Fig. S4). This spatial movement of bottom trawl effort corresponds to a shift from targeting mostly nephrops *Nephops norvegicus* and whitefish species (*Merlangius merlangus, Melanogrammus aeglefinus*) to a larger share of anglerfish (*Lophius piscatorius* and *Lophius budegassa*) (Appendix 3, Fig. S7). For the taxa landed most often, pelagic trawl effort shifted after 2007 from horse mackerel *Trachurus trachurus* to boarfish Caproidae (Appendix 3, Fig. S9). This change in targeted taxa could

explain the decreased importance of fishing in structuring assemblages by shifting toward targeted taxa that do not co-vary with fishing effort.

Conversely, some environmental variables varied in their value but not in their structuring effect. For example, bottom temperature had an important and relatively stable structuring effect despite increasing by 0.04 °C/y from 2000-2016 in the northern Celtic Sea. Assemblages #3, #5 and especially #6, whose taxa co-varied negatively with bottom temperature, clearly differed from assemblage #2, whose taxa co-varied positively with bottom temperature. This difference may be related to the location of the Celtic Sea at the biogeographical boundary between warm-water Lusitanian taxa and cold-water boreal taxa (Ellis et al., 2013; Hátún et al., 2009). Assemblages #3, #5 and #6 contained commercially important taxa such as Atlantic herring *Clupea harengus* (#3), haddock *Melanogrammus aeglefinus* (#5), whiting *Merlangius merlangus* (#5), cod *Gadus morhua* (#6) and the American plaice *Hippogloissoides platessoides* (#6). These taxa may move northward in the coming years to avoid the increase in bottom temperature, which could change Celtic Sea communities and eventually fisheries. A similar northward movement was documented along the western coast of Scotland (ter Hofstede et al., 2010) of fish species considered to be cold-water boreal by Yang (1982). In addition, taxa from these assemblages may become less common in the Celtic Sea due to the predicted decrease in chlorophyll a concentration caused by climate change (Henson et al., 2010). Assemblage #2 contained warm-water taxa from the Bay of Biscay (Hátún et al., 2009), such as boarfish *Capros aper*, that have already begun and may continue to become more numerous and dominant in biomass due to the increase in temperature (Coad et al. 2014). Indeed, the number of warm-water species in the Celtic Sea has already increased (ter Hofstede et al., 2010), which makes it an area of special interest for studying potential replacement of cold-water taxa by warm-water taxa.

To characterize further the potential response of taxa to changes in environmental variables, a local scale must be considered. The more coastal sites in the northern Celtic Sea hosted taxa in assemblages #3 and #5 that co-varied negatively with temperature: whiting *Merlangius merlangus*, dab *Limanda limanda*, Norway pout *Trisopterus esmarkii*, sprat *Sprattus sprattus*, plaice *Pleuronectes platessa*, Atlantic herring *Clupea harengus*, haddock *Melanogrammus aeglefinus*, spotted ray *Raja montagui*, lemon sole *Microstomus kitt* and American plaice *Hippoglossoides platessoides*. Bottom temperature has increased the most in coastal areas (Fig. 8b), however, making these taxa susceptible to a decrease in biomass in the Celtic Sea. In addition, taxa located along the deepest border of the Celtic Sea, which co-varied positively with pelagic trawl effort throughout the time series, appeared to respond most to pelagic trawl effort from 2001-2008, which could reveal adaptation of the pelagic trawlers targeting taxa in this area. This response could help explain the spatial heterogeneity in taxa distribution already observed in the Celtic Sea (Dolder, Thorson, & Minto, 2018).

Despite overall stability of the relation between taxa and the environment in the Celtic Sea, variation in bottom temperature and bottom trawl effort showed spatial heterogeneity. Depending on the area considered, the environment and taxa did not always have the same trajectory over time. This difference highlights the complex influence of space and of the variables considered (i.e. chlorophyll a, bottom temperature, and bottom and pelagic trawl efforts). In addition, variables not considered in this study, such as salinity or current, could explain some variations in taxa biomass for the years with no visible match. Time lags not captured by the annual mean can also influence taxa dynamics. Long-lived taxa that feed on small fish can be influenced by variations in phytoplankton abundance over much longer timescales than the few days necessary to trigger a reaction in phytoplankton dynamics (Sharples, Ellis, et al., 2013). Larger-scale spatial patterns, such as the NAO or AMO, are also likely to influence these assemblages. The NAO warm phase results in more frequent storms

and precipitation in northern Europe. Since the late 1990s, this difference in atmospheric pressure has remained close to the average, except for a sharp decrease in 2010 (Edwards et al., 2013; Hátún et al., 2009; Hurrell, Kushnir, Ottersen, & Visbeck, 2003). The change in taxa' trajectories of strata could be related to the decrease in temperatures observed in 2011-2013 in the central Celtic Sea. In comparison, the AMO influences sea surface temperature and has a longer period of *ca.* 60-80 years. It has been in a positive phase since 1995, which is associated with warmer sea surface temperatures. It influences marine ecosystem dynamics strongly and, in particular, promotes growth of sardine *Sardina pilchardus* populations during its warm phases and Atlantic herring *Clupea harengus* populations during its cold phases (Edwards et al., 2013). These climatic phenomena superimpose their influences on global warming due to climate change, making it challenging to determine the relative influences of the AMO, NAO and global warming on the increase in temperature observed in the northern Celtic Sea. They have a complex influence on biological systems, which renders inference of their direct effects on taxa uncertain (Beaugrand, 2012). For these reasons, we focused only on regional variables whose influence on taxa could be identified.

Our integrated analysis enabled investigating spatio-temporal co-variations of taxa and the environment in a single analysis over 17 years for a large dataset of 101 taxa and six environmental variables. It summarized ecosystem dynamics to form assemblages of taxa with similar responses to environmental variations, which provided information about the most important structuring variables and average relations between taxa and the environment. Its strength lies in its ability to consider variations in the relations between taxa and the environment at different temporal and spatial scales, making the analysis an adaptive tool, and to study the relative effects of several environmental drivers. However, this statistical approach does not enable partialling out the effect of each variable.

Although the Celtic Sea is exploited greatly, its biotic assemblages are influenced mainly by depth, bottom temperature and chlorophyll a concentration. Indeed, only assemblage #3 significantly co-varied negatively with pelagic trawl effort. This result is consistent with that of Kidé et al. (2015), who analyzed the predominant role of chlorophyll a and sea surface temperature in structuring the ecosystem of another exploited fishing ground along the Mauritanian shelf. Studies at the ecosystem scale provide information about the relative importance of fishing effort as a structuring variable of ecosystems, which is necessary in the context of implementing more sustainable fishing practices. In the context of global warming, the response of commercial species to increased temperature also receives a great deal of attention, due to their potential changes in distribution and the resulting impacts on fisheries (Cheung et al., 2013). However, studies of the responses of a large number of species (i.e. commercial and non-commercial species) to simultaneous impacts of fishing effort and global warming remain scarce (but see Shackell, Bundy, Nye, & Link, 2012). In this study, we provided information about effects of variation in the spatial distribution of bottom and pelagic trawl effort in the Celtic Sea and the decrease in the importance of these two practices as structuring variables of communities after 2009. This study also provided information about the relative importance of fishing effort to the macro bentho-demersal diversity of an exploited fishing ground. Slight changes in the spatial distribution of fishing effort and the taxa targeted are thus likely to reduce the structuring effect of fishing effort on the entire ecosystem. Increased bottom temperature in the Celtic Sea has not yet changed assemblages of taxa but is likely to trigger substantial changes in their distributions in the coming years, especially cold-water commercial taxa such as hake, cod, nephrops and American plaice. These results could help select which species should have their dynamics simulated under variations in several environmental and fishing variables at the same time to provide information useful for managers and scientists.

Acknowledgement

We thank all those who made data sampling possible during the EVHOE surveys.

2.6 Supplementary material

Mean, minimum (1st quartile), maximum (99th quartile) and range (minimum – maximum) of the temperature preferendum (°C) of each of the 101 taxa in the study, calculated from native-range data in Aquamaps (https://www.aquamaps.org/). Quartiles were used to filter out abnormal values.

Scientific name	Code name	Mean	Min.	Max.	Range
Aequipecten opercularis	AEQUOPE	10.12	2.52	17.59	15.07
Agonus cataphractus	AGONCAT	8.89	3.20	12.01	8.81
Alloteuthis spp.	ALLO	11.27	2.51	17.82	15.30
Argentina spp.	ARGE	9.66	2.52	16.21	13.69
Arnoglossus spp.	ARNO	11.74	2.46	27.70	25.24
Blennius ocellaris	BLENOCE	12.58	2.52	18.31	15.78
Buglossidium luteum	BUGLLUT	10.79	3.84	16.52	12.69
Caelorinchus caelorhincus	CAELCAE	10.52	1.46	27.86	26.40
Callionymus lyra	CALMLYR	10.41	2.90	16.45	13.55
Callionymus maculatus	CALMMAC	9.62	3.16	15.46	12.31
Cancer pagurus	CANCPAG	9.46	2.59	13.34	10.74
Capros aper	CAPOAPE	10.96	2.52	17.85	15.33
Cepola macrophthalma	CEPOMAC	12.97	2.51	25.06	22.56
Aspitrigla cuculus	CHELCUC	10.20	2.72	15.78	13.05
Chelidonichthys lucerna	CHELLUC	10.19	3.12	19.12	16.00
Chimaera monstrosa	CHIMMON	8.52	2.06	15.19	13.13
Clupea harengus	CLUPHAR	5.48	-1.20	15.14	16.34
Conger conger	CONGCON	10.17	2.42	17.12	14.70
Dicentrarchus labrax	DICELAB	11.62	4.22	18.13	13.91
Dipturus batis	DIPTBAT	9.73	2.51	15.98	13.47
Echiichthys vipera	ECITVIP	10.51	6.83	16.63	9.80
Eledone cirrhosa	ELEDCIR	10.33	2.41	19.19	16.78
Enchelyopus cimbrius	ENCHCIM	6.73	-0.48	23.42	23.90
Engraulis encrasicolus	ENGRENC	11.71	2.37	27.54	25.16
Entelurus aequoreus	ENTLAEQ	8.14	2.52	12.85	10.33
Etmopterus spinax	ETMOSPI	9.77	0.64	26.74	26.11
Eutrigla gurnardus	EUTRGUR	9.50	3.20	15.42	12.22
Ammodytidae	FMAMMOD	9.22	3.23	13.36	10.13
Gobiidae	FMGOBII	11.18	3.37	19.25	15.88
Gadiculus argenteus	GADIARG	10.70	-0.17	16.79	16.95
Gadus morhua	GADUMOR	5.79	-1.03	12.10	13.13
Gaidropsarus spp.	GAID	9.09	2.53	15.18	12.65

Galeorhinus galeus	GALOGAL	11.16	1.22	24.87	23.65
Galeus melastomus	GALUMEL	10.44	2.49	17.23	14.74
Glyptocephalus cynoglossus	GLYPCYN	5.74	-1.05	12.89	13.95
Helicolenus dactylopterus	HELIDAC	10.02	1.16	27.23	26.07
Hippoglossoides platessoides	HIPGPLA	5.25	-1.07	10.97	12.04
Homarus gammarus	HOMAGAM	10.28	6.79	12.18	5.39
Illex coindetii	ILLECOI	11.09	2.26	27.54	25.28
Lepidorhombus boscii	LEPIBOS	11.20	2.52	16.19	13.67
Lepidorhombus whiffiagonis	LEPIWHI	9.54	3.15	14.68	11.53
Lesueurigobius friesii	LESUFRI	11.21	6.93	16.34	9.41
Leucoraja circularis	LEUCCIR	10.16	2.51	16.19	13.68
Leucoraja fullonica	LEUCFUL	10.14	2.86	15.07	12.21
Leucoraja naevus	LEUCNAE	9.91	2.58	15.88	13.30
Limanda limanda	LIMDLIM	8.80	4.01	12.14	8.13
Loligo spp.	LOLI	10.34	7.20	11.80	4.59
Lophius budegassa	LOPHBUD	10.70	2.52	15.55	13.03
Lophius piscatorius	LOPHPIS	11.05	2.38	26.04	23.66
Macroramphosus scolopax	MACOSCO	11.28	1.13	25.35	24.22
Maja brachydactyla	MAJABRA	10.78	6.68	15.07	8.39
Malacocephalus laevis	MALCLAE	8.38	1.38	25.16	23.77
Maurolicus muelleri	MAURMUE	7.60	-0.67	23.86	24.53
Melanogrammus aeglefinus	MELAAEG	4.79	-1.03	11.86	12.89
Merluccius merluccius	MERLMER	9.99	2.75	19.19	16.44
Merlangius merlangus	MERNMER	9.99	2.71	15.70	12.99
Micromesistius poutassou	MICMPOU	9.09	-0.73	16.22	16.95
Microstomus kitt	MICTKIT	9.02	3.22	12.01	8.79
Microchirus variegatus	MICUVAR	11.45	2.52	18.06	15.54
Molva macrophthalma	MOLVMAC	10.48	2.58	15.10	12.53
Molva molva	MOLVMOL	8.95	2.53	13.27	10.75
Mullus surmuletus	MULLSUR	10.77	2.64	19.28	16.64
Munida spp.	MUNI	9.64	3.86	12.60	8.74
Mustelus spp.	MUST	10.12	2.53	16.91	14.38
Necora puber	NECOPUB	10.78	6.68	15.07	8.39
Nephrops norvegicus	NEPHNOR	9.82	2.90	16.66	13.77
Octopus spp.	OCTP	13.10	1.42	28.37	26.95
Pagellus bogaraveo	PAGEBOG	11.48	2.46	19.19	16.73
Paromola cuvieri	PAROCUV	9.26	2.27	25.96	23.68
Pecten maximus	PECTMAX	9.88	6.26	15.52	9.26
Solea lascaris	PEGULAS	12.84	2.47	26.90	24.43
Phycis blennoides	PHYIBLE	10.49	2.51	16.10	13.59
Pleuronectes platessa	PLEUPLA	9.45	0.83	13.94	13.11
Pollachius pollachius	POLLPOL	10.24	6.45	13.00	6.55
Pomatoschistus spp.	POMO	9.48	2.56	15.24	12.69
Raja brachyura	RAJABRA	10.96	2.44	18.53	16.08
Raja clavata	RAJACLA	9.15	1.12	19.19	18.07
Raja microocellata	RAJAMIC	11.06	9.79	16.61	6.83
Raja montagui	RAJAMON	12.03	2.47	18.12	15.65
Rossia macrosoma	ROSSMAC	10.41	-0.87	19.40	20.28
Sardina pilchardus	SARDPIL	13.36	2.37	20.00	17.63
Scomber scombrus	SCOMSCO	6.78	-0.26	17.02	17.29
Scophthalmus maximus	SCOPMAX	8.74	3.41	15.80	12.39
Scophthalmus rhombus	SCOPRHO	9.87	4.40	16.34	11.95
Scyliorhinus canicula	SCYOCAN	12.14	2.38	25.95	23.57
Scyliorhinus stellaris	SCYOSTE	11.97	2.51	19.41	16.90
Sepia elegans	SEPIELE	11.95	2.29	25.34	23.05

Sepia officinalis	SEPIOFF	12.18	2.53	19.92	17.40
Sepia orbignyana	SEPIORB	11.95	2.29	25.34	23.05
Sepiola spp.	SEPO	8.75	6.91	10.58	3.67
Solea solea	SOLESOL	10.99	2.87	17.68	14.81
Sprattus sprattus	SPRASPR	9.55	3.69	16.24	12.55
Squalus acanthias	SQUAACA	8.66	0.28	24.70	24.42
Todarodes sagittatus	TODASAG	9.66	2.04	16.92	14.87
Todaropsis eblanae	TODIEBL	9.78	1.41	23.61	22.20
Trachurus trachurus	TRACTRA	11.15	2.43	20.17	17.74
Chelidonichthys lastoviza	TRGPLAS	13.51	3.30	27.48	24.18
Trisopterus esmarkii	TRISESM	8.57	2.80	11.32	8.52
Trisopterus luscus	TRISLUS	9.99	3.84	15.33	11.49
Trisopterus minutus	TRISMIN	9.23	4.27	12.15	7.88
Zeus faber	ZEUSFAB	11.83	1.16	25.20	24.04

APPENDIX 2

To facilitate interpretation of outputs of the statistical analysis, we calculated maps of anomalies (pixel value of a given year – pixel mean value over the time series) from mean values in the Celtic Sea from 2000-2016 for chlorophyll a, bottom temperature and bottom trawl effort (spatial coverage was insufficient for pelagic trawl effort). The gradient of mean chlorophyll a concentration was oriented from offshore (min. = 0.22 $mg.m^{-3}$) toward the coast, where it was the highest (max. = 2.95 $mg.m^{-3}$). The largest positive anomalies were recorded in the center of the Celtic Sea in 2000, 2009 and 2012 and in the north in 2011. Negative anomalies were observed in 2001, 2006, 2013 and 2016 throughout the Celtic Sea.

Annual mean bottom temperature varied from 8.5-14.6°C, with the warmest area located in the south, at greater depth. Positive thermic anomalies were observed in the center of the Celtic Sea in 2002 and 2003 and in the north in 2012, 2014 and 2016. Negative anomalies were observed in the center in 2000, 2010 and 2013 and in the north in 2010 and 2016 (see Appendix 2 Fig. S3). Finally, bottom temperature increased by 0.04 °C/y in the north from 2000-2016, which correspond to results of ter Hofstede et al. (2010) in the Celtic Sea from 1993-2008. Conversely, a decrease of 0.02 °C/y in the south may have been related to a decrease in the strength of the Gulf Stream.

Figure S1: Spatio-temporal values of chlorophyll a concentration (mg.m^{-3}).

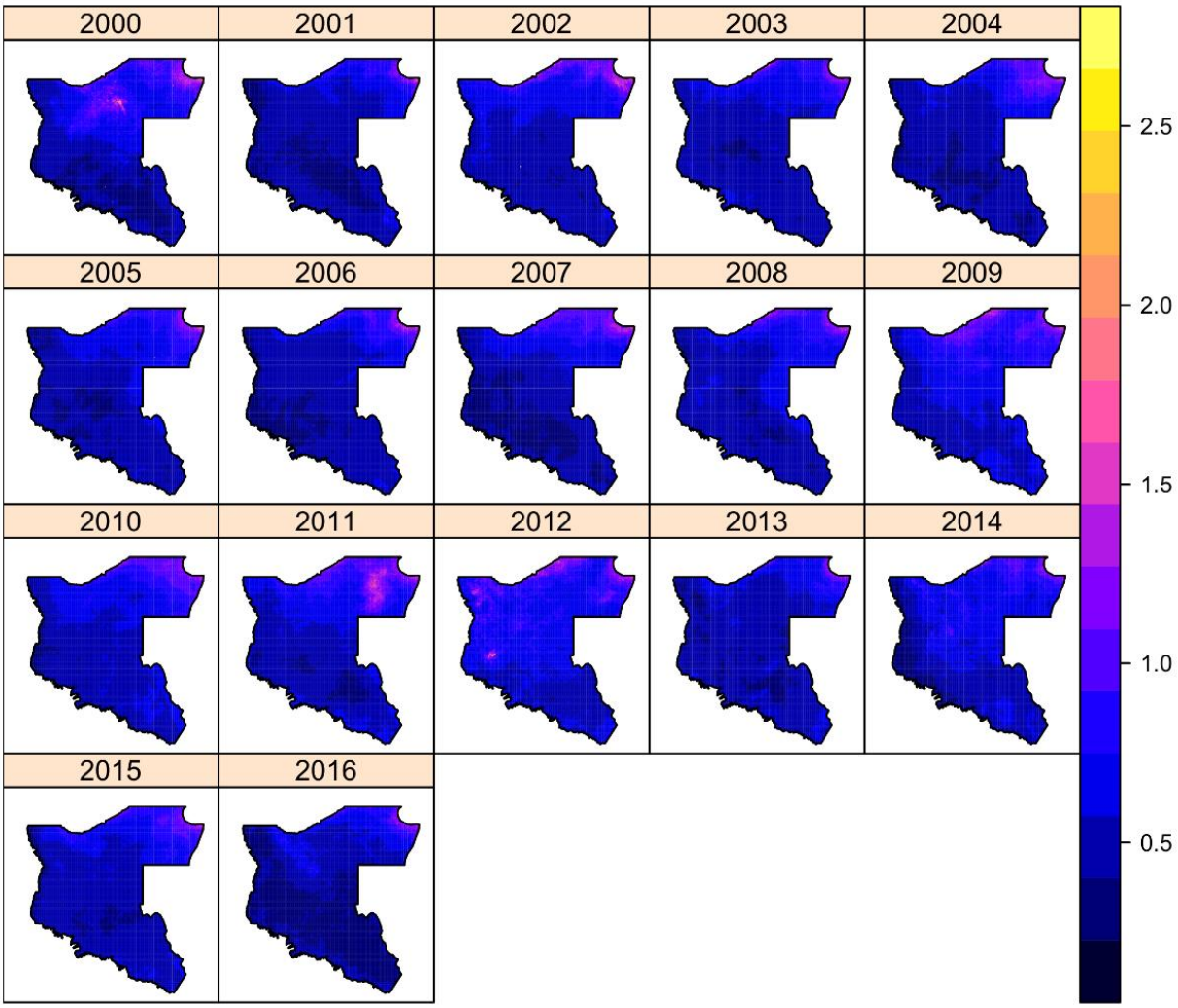


Figure S2: Spatio-temporal anomalies of chlorophyll a concentration (mg.m^{-3}).

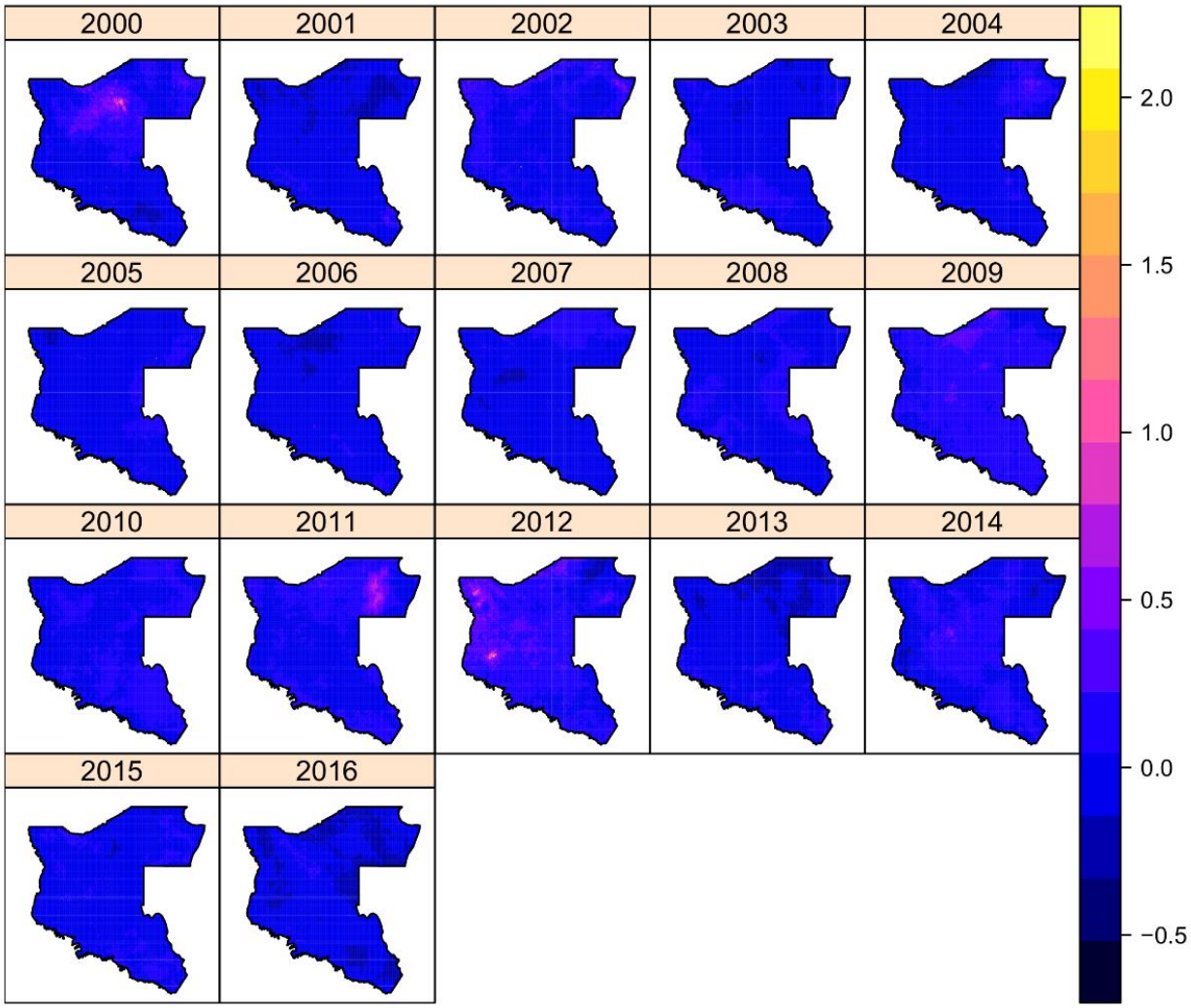


Figure S3: Spatio-temporal anomalies of bottom temperature (°C).

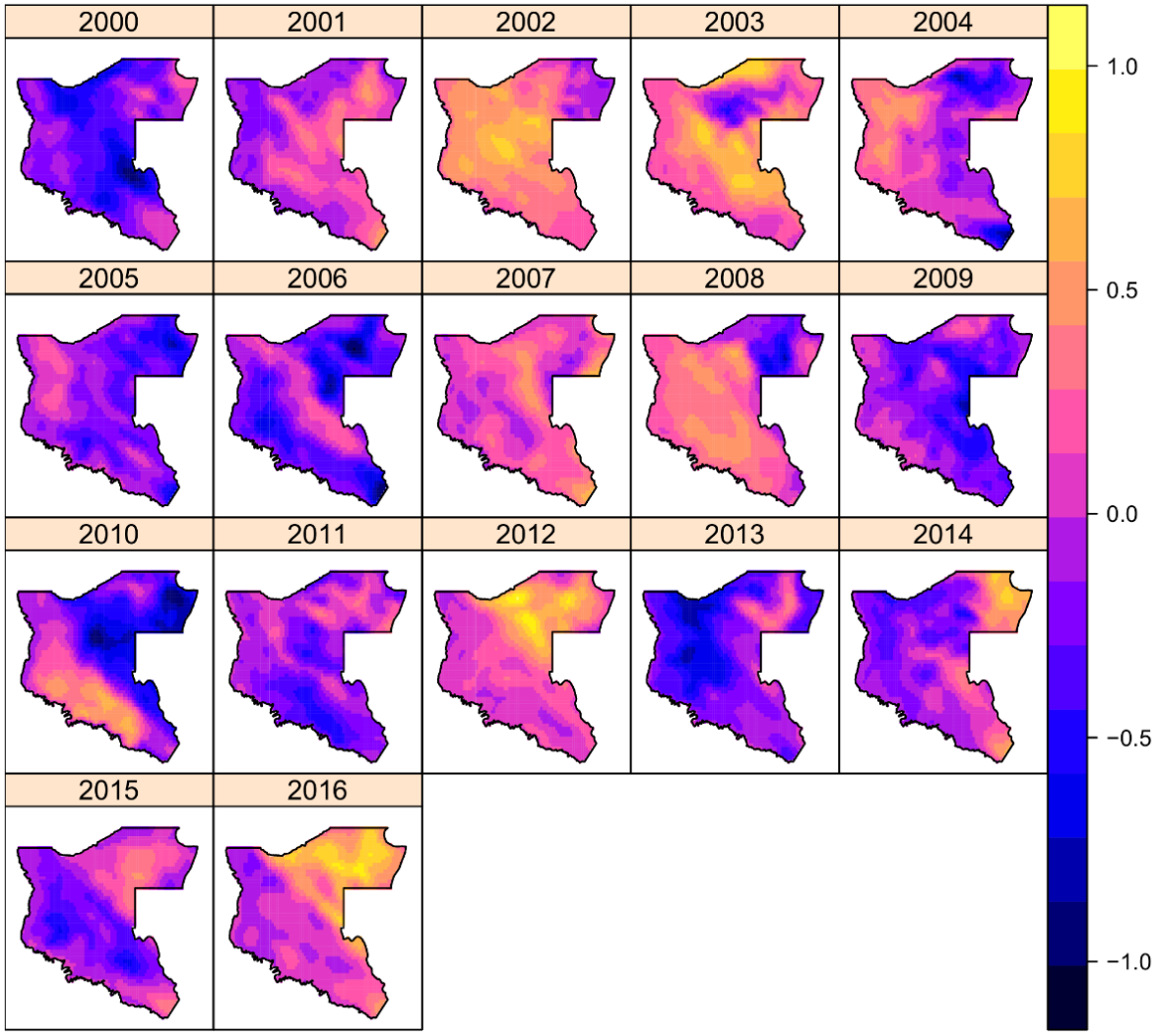
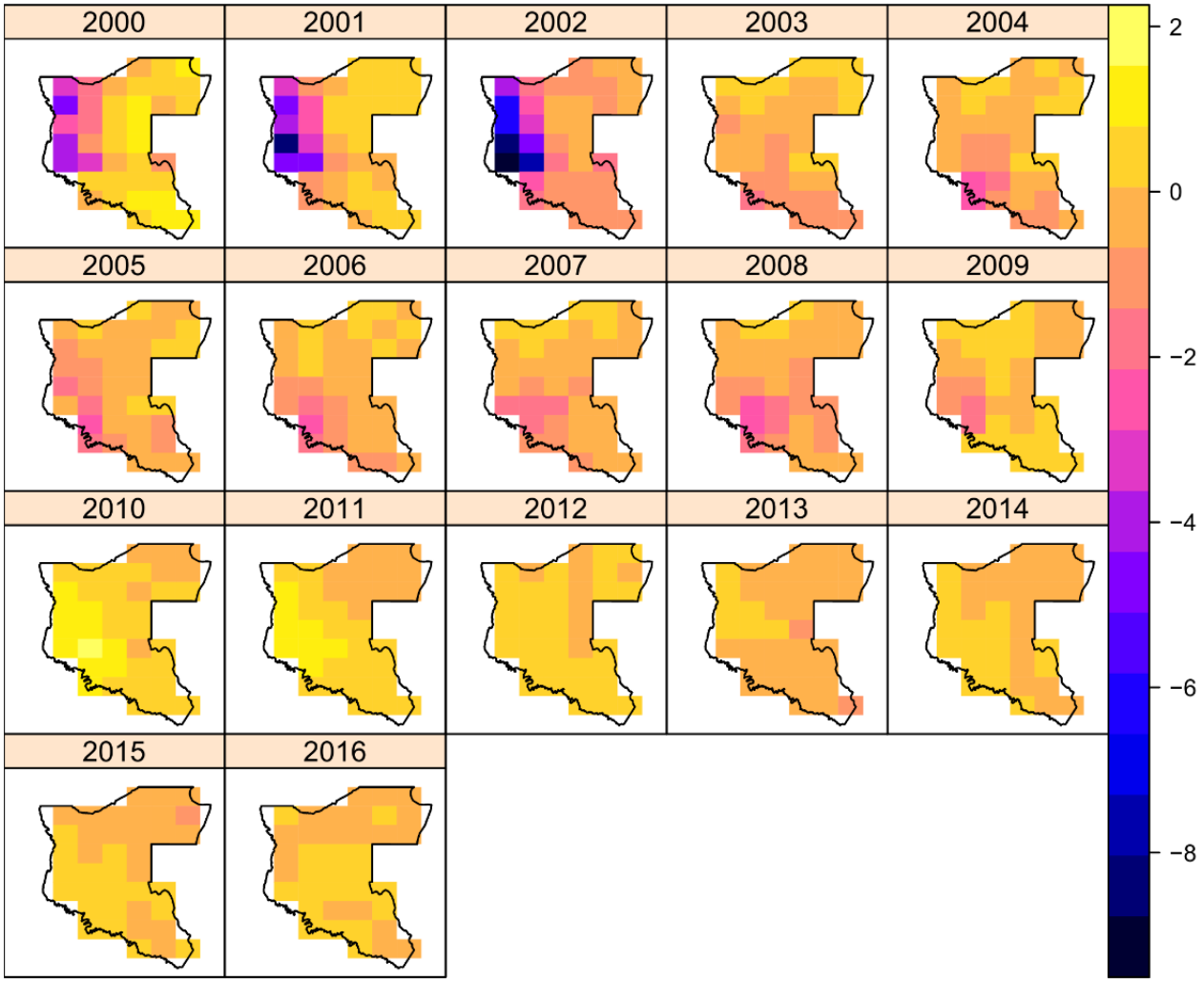


Figure S4: Spatio-temporal anomaly of bottom trawl effort log(x+1) transformed as in the STATICO analysis (log(x+1) hours fished per statistical rectangle).



APPENDIX 3: Fishing effort

To ease the interpretation of the relation between fishing effort and taxa, we used landing data (t per statistical rectangle (111.12 km × 55.56 km)) for the Celtic Sea from the Fisheries Dependent Information from the European Union's Scientific, Technical and Economic Committee for Fisheries (STECF) (https://stecf.jrc.ec.europa.eu/) to characterize the main taxa landed per year in bottom and pelagic trawls. Unfortunately, these data were only available from 2003-2016 (unlike fishing effort given in hours fished per statistical rectangle, that was available from 2000-2016). Pelagic trawls accounted for most landings (57.6%) from 2000-2016. The main taxa landed were the horse mackerel *Trachurus* spp., boarfishes Caproidae, mackerel *Scomber scombrus* and hering *Clupea harengus*. Pelagic trawl effort was exerted mostly along the deep border of the Celtic Sea and at its extreme north, between the United Kingdom and Ireland. Bottom trawls accounted for the second largest quantity of landings (i.e. 32.4% of total landings from 2003-2016) and the largest number of fishing hours in the Celtic Sea (i.e. 78.4% of total hours fished from 2000-2016). The highest efforts were exerted in the northern Celtic Sea. The main taxa landed in the Celtic Sea (in decreasing order of cumulative biomass landed from 2000-2016) were Lophiidae, *Lepidorhombus* spp., *Merlangius merlangus*, *Melanogrammus aeglefinus*, *Nephrops norvegicus*, *Rajidae*, *Merluccius merluccius and Gadus morhua* (Fig. S5). The decrease in total bottom trawl effort mentioned in the literature (ICES, 2018a) included western Ireland, which was not part of our study area. The decrease in bottom trawl effort is not visible in the Celtic Sea (Fig. 7b, Appendix 2, Fig. S4 and Appendix 3 Fig. S6), but the move of bottom trawl effort to deeper areas after 2009 is (Appendix 2, Fig. S4).

Figure S5: Cumulative biomass of the taxa landed by bottom trawls in the Celtic Sea from 2000-2016 (only taxa with biomass > 1000 t are shown) from SETFC data.

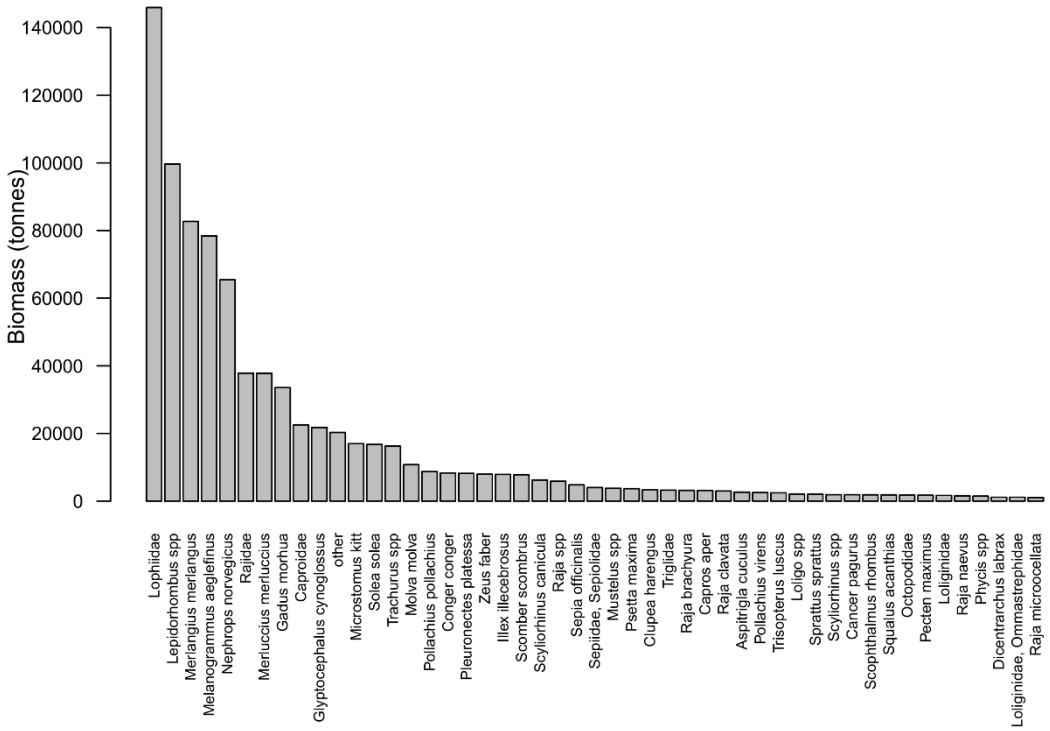


Figure S6: Temporal evolution of cumulative bottom trawl effort in the Celtic Sea from 2000-2016. Source: NewFDI data from STECF (cumulative hours fished per statistical rectangle).

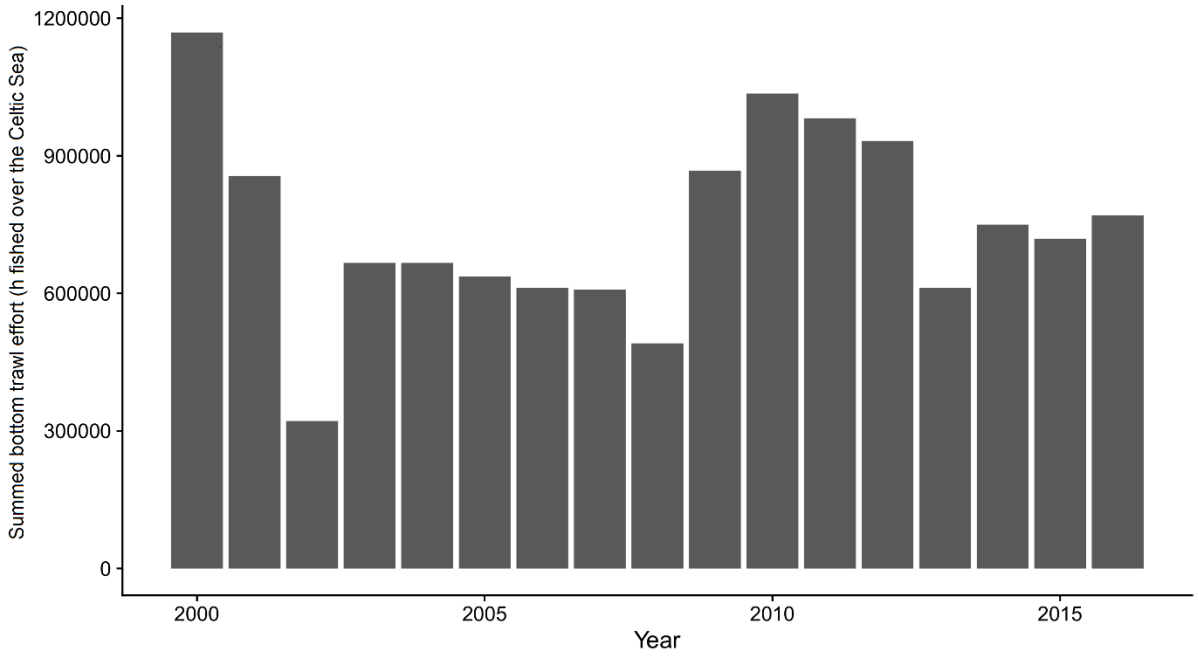


Figure S7: Landing composition of bottom trawls (in t per statistical rectangle) in the Celtic Sea from 2003-2016, for the taxa representing 95% of the total biomass landed.

Lophiidae increase in proportion after 2008, in accordance with the change in target taxa.

Data from the STECF are based on declaration made by the countries. Before 2009 and the commissioning of the electronic logbooks, a strong misreporting of the landings at the international level most likely skewed the available data, leading to a non-realistic increase of the landings after 2008.

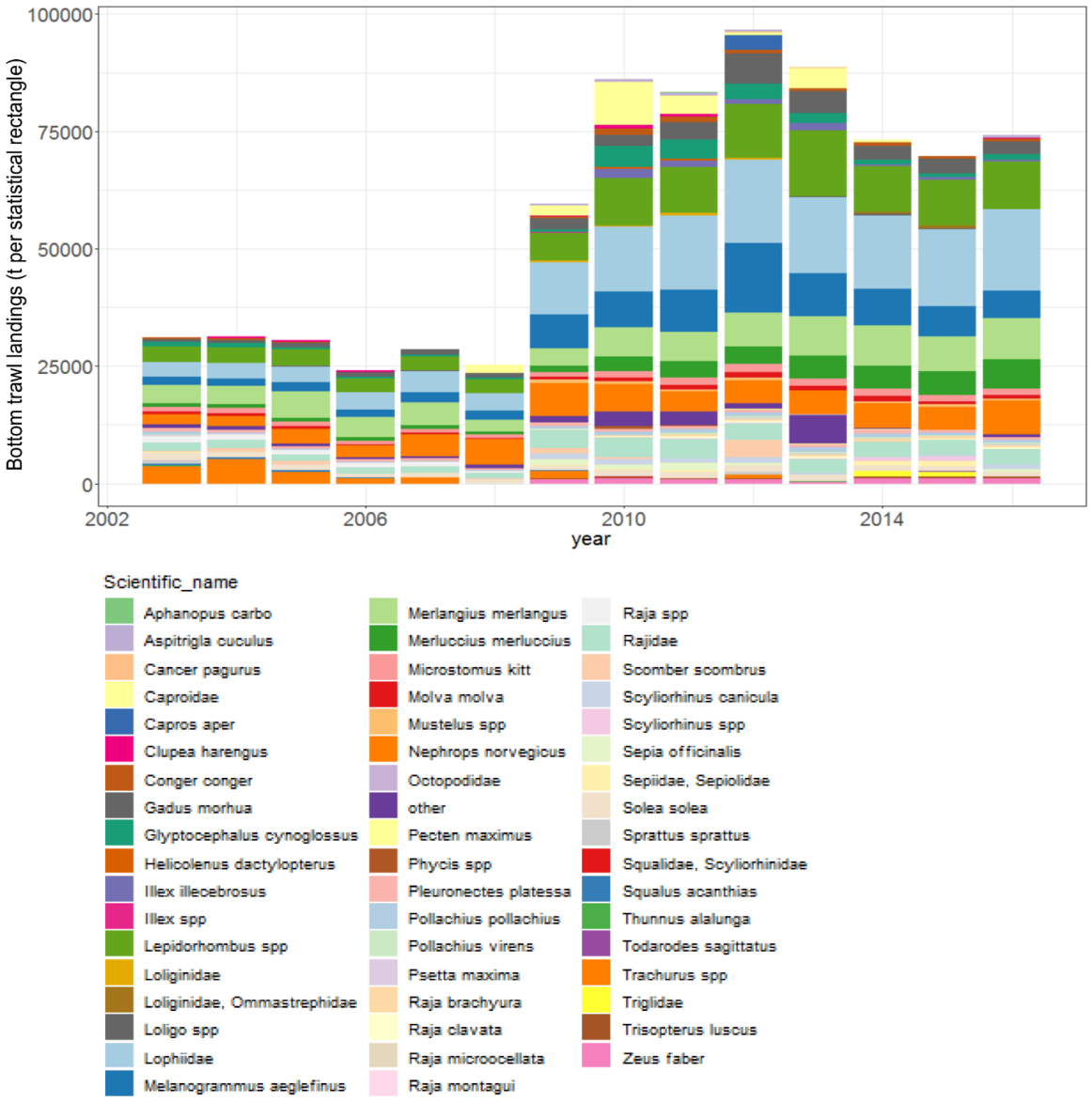


Figure S8: Temporal evolution of cumulative pelagic trawl effort in the Celtic sea from 2000-2016. Source: NewFDI data from STECF (cumulative hours fished per statistical rectangle)

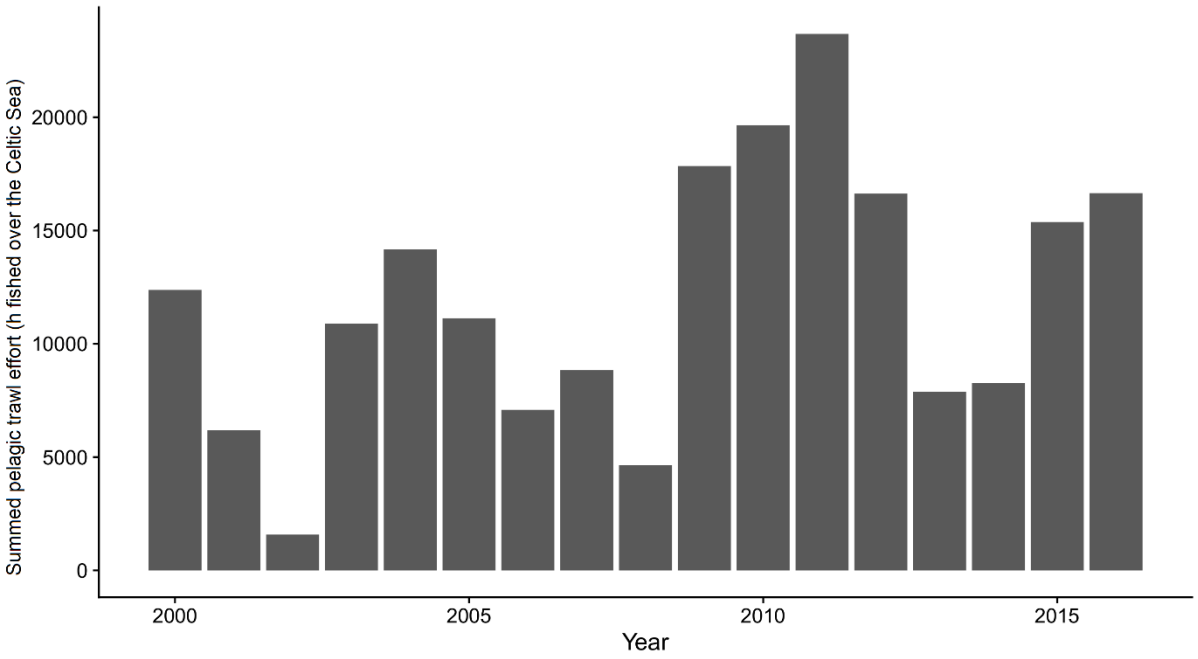
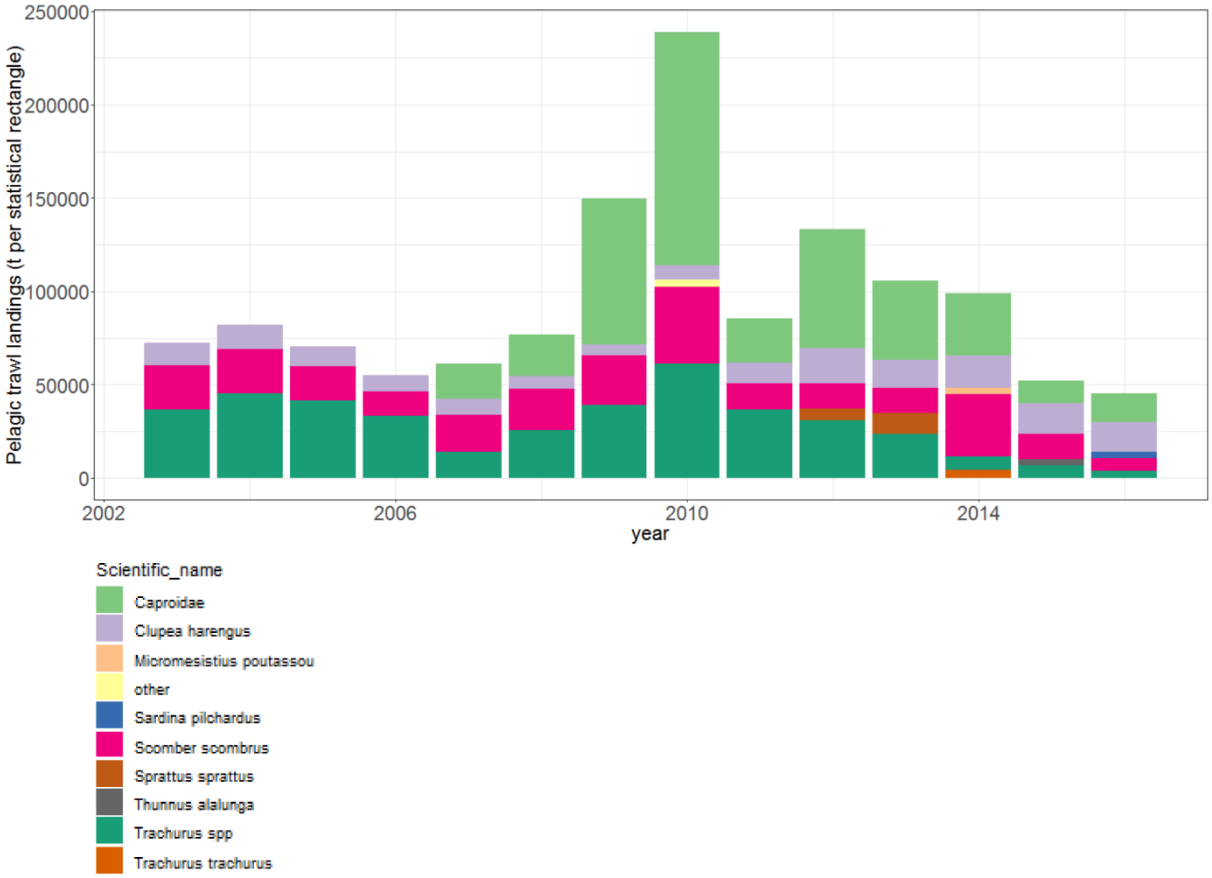


Figure S9: Landing composition of pelagic trawls (in t per statistical rectangle) in the Celtic Sea from 2003-2016, for the taxa representing 95% of the total biomass landed.



APPENDIX 4: *Composition of taxa assemblages clustered using k-means clustering on the two first axes of the compromise space.*

species_Rsuffi	Scientific name	Assemblage
SCOMSCO	*Scomber scombrus*	1
CHIMMON	*Chimaera monstrosa*	1
MOLVMOL	*Molva molva*	1
TRISMIN	*Trisopterus minutus*	1
PAROCUV	*Paromola cuvieri*	1
CANCPAG	*Cancer pagurus*	1
CALMMAC	*Callionymus maculatus*	1
TODASAG	*Todarodes sagittatus*	1
DIPTBAT	*Dipturus batis*	1
ETMOSPI	*Etmopterus spinax*	1
PECTMAX	*Pecten maximus*	1
TRISLUS	*Trisopterus luscus*	1
AEQUOPE	*Aequipecten opercularis*	1
LEUCFUL	*Leucoraja fullonica*	1
LEUCCIR	*Leucoraja circularis*	1
CONGCON	*Conger conger*	1
HOMAGAM	*Homarus gammarus*	1
LOLI	*Loligo* spp.	1
ROSSMAC	*Rossia macrosoma*	1
GALUMEL	*Galeus melastomus*	1
ECITVIP	*Echiichthys vipera*	1
CAELCAE	*Caelorinchus caelorhincus*	1
MULLSUR	*Mullus surmuletus*	1
LOPHPIS	*Lophius piscatorius*	1
GALOGAL	*Galeorhinus galeus*	1
PAGEBOG	*Pagellus bogaraveo*	1
ENGRENC	*Engraulis encrasicolus*	1
SEPIOFF	*Sepia officinalis*	1
BLENOCE	*Blennius ocellaris*	1
OCTP	*Octopus* spp.	1
SARDPIL	*Sardina pilchardus*	1
MICMPOU	*Micromesistius poutassou*	2
ARGE	*Argentina* spp.	2
TODIEBL	*Todaropsis eblanae*	2
LEUCNAE	*Leucoraja naevus*	2
CHELCUC	*Aspitrigla cuculus*	2
CAPOAPE	*Capros aper*	2
TRACTRA	*Trachurus trachurus*	2
ARNO	*Arnoglossus* spp.	2
ZEUSFAB	*Zeus faber*	2
SEPIELE	*Sepia elegans*	2

SEPIORB	*Sepia orbignyana*	2
CLUPHAR	*Clupea harengus*	3
SQUAACA	*Squalus acanthias*	3
SCOPMAX	*Scophthalmus maximus*	3
AGONCAT	*Agonus cataphractus*	3
MICTKIT	*Microstomus kitt*	3
GAID	*Gaidropsarus* spp.	3
RAJACLA	*Raja clavata*	3
FMAMMOD	Ammodytidae	3
POMO	*Pomatoschistus sp.*	3
EUTRGUR	*Eutrigla gurnardus*	3
SPRASPR	*Sprattus sprattus sprattus*	3
SCOPRHO	*Scophthalmus rhombus*	3
MUST	*Mustelus* spp.	3
CHELLUC	*Chelidonichthys lucerna*	3
POLLPOL	*Pollachius pollachius*	3
NECOPUB	*Necora puber*	3
BUGLLUT	*Buglossidium luteum*	3
RAJABRA	*Raja brachyura*	3
RAJAMIC	*Raja microocellata*	3
FMGOBII	Gobiidae	3
LESUFRI	*Lesueurigobius friesii*	3
DICELAB	*Dicentrarchus labrax*	3
SCYOSTE	*Scyliorhinus stellaris*	3
PEGULAS	*Solea lascaris*	3
CEPOMAC	*Cepola macrophthalma*	3
TRGPLAS	*Chelidonichthys lastoviza*	3
ENTLAEQ	*Entelurus aequoreus*	4
MALCLAE	*Malacocephalus laevis*	4
LEPIWHI	*Lepidorhombus whiffiagonis*	4
MUNI	*Munida* spp.	4
HELIDAC	*Helicolenus dactylopterus dactylopterus*	4
MOLVMAC	*Molva macrophthalma*	4
LOPHBUD	*Lophius budegassa*	4
GADIARG	*Gadiculus argenteus argenteus*	4
ILLECOI	*Illex coindetii*	4
LEPIBOS	*Lepidorhombus boscii*	4
MACOSCO	*Macroramphosus scolopax*	4
MICUVAR	*Microchirus variegatus*	4
MELAAEG	*Melanogrammus aeglefinus*	5
TRISESM	*Trisopterus esmarkii*	5
LIMDLIM	*Limanda limanda*	5
PLEUPLA	*Pleuronectes platessa*	5
MERNMER	*Merlangius merlangus*	5
CALMLYR	*Callionymus lyra*	5
MAJABRA	*Maja brachydactyla*	5

SOLESOL	*Solea solea*	5
ALLO	*Alloteuthis* spp.	5
RAJAMON	*Raja montagui*	5
SCYOCAN	*Scyliorhinus canicula*	5
HIPGPLA	*Hippoglossoides platessoides*	6
GLYPCYN	*Glyptocephalus cynoglossus*	6
GADUMOR	*Gadus morhua*	6
ENCHCIM	*Enchelyopus cimbrius*	6
MAURMUE	*Maurolicus muelleri*	6
SEPO	*Sepiola* spp.	6
NEPHNOR	*Nephrops norvegicus*	6
MERLMER	*Merluccius merluccius*	6
ELEDCIR	*Eledone cirrhosa*	6
PHYIBLE	*Phycis blennoides*	6

3 Chapter B

Patterns of sensitivity to fishing: different views of the Celtic Sea

3.1 Preface

Biological characteristics of species can inform on the links between species and their environment (Lavorel et al., 2008). Some traits, called effect traits, provide information on the way species contribute to ecological processes. Other traits, called response traits, characterise the way species respond to environmental and anthropogenic drivers (Lavorel & Garnier, 2002). Life history traits belong to the latter category. Life history traits approximate the demographic characteristics of a species and have been proven to respond to fishing pressure. At the scale of the North East Atlantic ecosystems, decrease in fishing effort was related to the increase in biomass of slow life history species (Pecuchet et al., 2017). In the previous chapter, I showed the decreased importance of fishing as a driver of Celtic Sea ecosystems communities since 2009, despite the average yearly effort remained the similar. Therefore, I was interested in elucidating whether any patterns of increase in biomass of slow life history species were visible at the scale of the Celtic Sea and if they could be related to local decrease in fishing effort and management measures. To answer that question, in a first part of this chapter, I investigated the distribution of life history traits (maximum length, longevity, age at maturity, offspring size, fecundity, reproductive guild) of fish and large benthos species based on bottom trawl surveys data. Assembly processes were used to characterise the mechanisms explaining the spatial patterns observed.

Nevertheless, it has been reported that fishing has a differential impact on species depending on their mobility or fragility for instance (S. de Juan & Demestre, 2012), with the most detrimental impact observed on species with a slow demographic turnover and low mobility (Tyler-Walters, Rogers, Marshall, & Hiscock, 2009). Bottom trawl, with a cod end fitted with a mesh as the one used in EVHOE surveys (20mm), does not enable to sample small (<20mm) or fragile organisms because their skeletons break during the haul. In a second part of this chapter, to propose a more complete view of the sensitivity patterns, we used underwater video footages to investigate the distribution of life history traits of fragile and sessile benthos, such as sea pens or crinoids, in regard of environmental and fishing drivers. In addition to life history traits, we used mobility and resistance traits as species could express a large range of ability to escape the net (from mobile migrating fish to fixed benthic invertebrates) and among the fixed organisms, not all have the same capacity to withstand a pass of a trawl (from a hard shell to a fragile skeleton).

3.2 Article 2

Biomass of slow life history species increases as local bottom trawl effort decreases in the Celtic Sea

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3.2.1 Introduction

Marine ecosystems experience multiple pressures, the most severe of which include climate change and fishing (Halpern et al., 2015). Climate change already affects the structure, functioning and adaptive capacity of ecosystems by modifying pH, temperature, oxygen concentration and food availability (Henson et al., 2017), which results in displacement of species toward higher latitudes and deeper waters (Cheung et al., 2013; Jorda et al., 2020). Its effects occur along with those of fishing (Rogers et al., 2019), which has notably caused a decrease in biomass and even local extinctions of species worldwide (Worm et al., 2006). It is widely acknowledged that a population's ability to recover from disturbance depends on its demographic dynamics, which are related to life history strategies (Le Quesne & Jennings, 2012; Wiedmann et al., 2014). Historically, life history strategies were characterised by their position along the continuum of r strategies (energy allocated to producing many offspring) vs. K strategies (energy allocated to producing a few extremely fit offspring) (Pianka, 1970). More recently, life history strategies of fish were described as a triangle: (i) an opportunistic strategy for small, short-lived and rapidly maturing fish; (ii) a periodic strategy for large, long-lived and highly fecund fish and (iii) an equilibrium strategy for intermediate-sized fish that produce a few large offspring for which they provide parental care (Pecuchet et al., 2018; Winemiller & Rose, 1992). These life history strategies can be summarised along a fast-slow continuum (Promislow & Harvey, 1990) that balances percentage of mortality and optimal size. Large and long-lived species that mature late and give birth to large offspring lie at the "slow" end of the continuum (Wiedmann et al., 2014). These species escape predation and have low non-human mortality rate, while the fast end is characterised by the opposite properties. Species with a slow life history strategy are thus particularly sensitive to additional mortality, such as that caused by anthropogenic pressures (e.g. fishing) (Kozlowski, 2006). Understanding their spatio-temporal distribution is thus particularly useful for ecosystem management (Le Quesne & Jennings, 2012).

Identifying and explaining how species are distributed has long been a core challenge in ecology. Evolutionary history, environmental variables and species interactions drive the spatio-temporal distribution of species (Mouchet, Burns, Garcia, Vieira, & Mouillot, 2013; Webb, Ackerly, McPeek, & Donoghue, 2002). Three major non-exclusive assembly rules explain biodiversity patterns (Kraft, Cornwell, Webb, & Ackerly, 2007): environmental filtering (Zobel, 1997), competitive exclusion (Hardin, 1960) and stochasticity (Hubbell, 2001). Environmental filtering implies strong biotic control, which results in the survival of species that have a narrow range of traits that enable them to endure environmental pressures. The principle of competitive exclusion assumes that species can coexist if they have different niche-related biological traits (Hardin, 1960). Thus, traits of species in an assemblage may be similar if they are selected via environmental filtering or different if they are selected via competitive exclusion. Conversely, neutral theory hypothesises that species coexist regardless of their biological traits due to stochastic events of dispersal, birth and death (Hubbell, 2001). The prevalence of one assembly rule over the others may depend on the scale considered. At the local scale, biotic and abiotic parameters can act on species simultaneously, and determining their relative importance remains challenging (Mouillot, Dumay, & Tomasini, 2007).

Assembly processes in exploited marine ecosystems have attracted attention only recently (Pecuchet, Törnroos, & Lindegren, 2016), as studies have historically focussed on freshwater and estuarine communities (Mouillot et al., 2007; Peres-Neto, 2004; Schmera, Erös, & Heino, 2013). The North East Atlantic fishing grounds have shown signs of over-exploitation since the 1970s (Gascuel et al., 2016), which caused species distribution to be driven by fishing in addition to environmental and habitat characteristics, such as temperature, depth and sediment (Foveau et al., 2017). We hypothesise that gradual enforcement of European Union (EU) fishing policies over the past 40 years that has decreased fishing pressure in the North East Atlantic (Fernandes & Cook, 2013a), may have helped the biomass of species with slow

life history traits to increase. However, temporal patterns of life history strategies of commercial and non-commercial taxa are rarely studied as a function of environmental or anthropogenic variables, and should be taken into account in management measures more frequently (Fromentin & Fonteneau, 2001; Matson & Gertseva, 2020).

The Celtic Sea has been extensively fished for decades with a peak of the number of species significantly exploited in the 1990's (Gascuel et al., 2016; Guénette & Gascuel, 2012). Fishing mortality has then decreased at the ecosystem scale since 2010 (Moullec, Gascuel, Bentorcha, Guénette, & Robert, 2017). Since a clear impact of climate change, such as an increase in bottom temperature, is not yet visible (Mérillet, Kopp, Robert, Mouchet, & Pavoine, 2020), fishing most likely remains a major influence of the distribution of life history strategies in the Celtic Sea. Based on a 17-year time series, we explore the influence of fishing on the spatio-temporal distribution of life history strategies in the bentho-demersal community by considering 101 commercial and non-commercial taxa. We assessed (i) which assembly processes and (ii) which environmental and anthropogenic variables drive the spatio-temporal distribution of life history traits and (iii) at the local scale, the relationship between the increase in species sensitive to fishing and the decreasing trend in bottom trawl fishing.

3.2.2 Materials and methods

Taxa biomass and life history traits

Data on species biomass were extracted from the EVHOE (*Evaluation des ressources Halieutiques de l'Ouest de l'Europe*) surveys, an International Bottom Trawl Survey (ICES, 2015) performed every November in the Celtic Sea. These surveys provide reliable and consistent data for evaluating the impact of fishing as they are independent from fishing effort and follow the same standardised protocol each year. EVHOE surveys use a 36/47 GOV (*Grande Ouverture Verticale*) net fitted with a 20 mm cod end mesh, with a horizontal opening

of ca. 20 m and a vertical opening of 4 m. Sampling hauls are performed at 4 knots for 30 min. From 2000-2016, the surveys performed 53-84 valid hauls per year, for a total of 1175 hauls. Due to variations in the accuracy of species identification, some species were grouped into higher taxonomic levels (hereafter, 'taxon'; genus, for species of *Alloteuthis*, *Argentina*, *Arnoglossus*, *Gaidrosparus*, *Loligo*, *Munida*, *Mustelus*, *Octopus*, *Pomatoschistus* and *Sepiola*; family, for Ammodytidae and Gobiidae). To identify temporal changes in taxa biomass, only those that occurred at more than 5% of the sampling sites in at least one EVHOE depth strata over the time series were kept for analysis and considered correctly sampled. This process identified a total of 101 taxa from six classes (Actinopterygii, Bivalvia, Cephalopoda, Elasmobranchii, Holocephali and Malacostraca). Biomass was standardised by the area sampled during each haul. Sampling sites were located at depths of 57-340 m (Fig. 1), mainly on sand, mud, mixed sediments, coarse sediments and boulders (level taken as a reference).

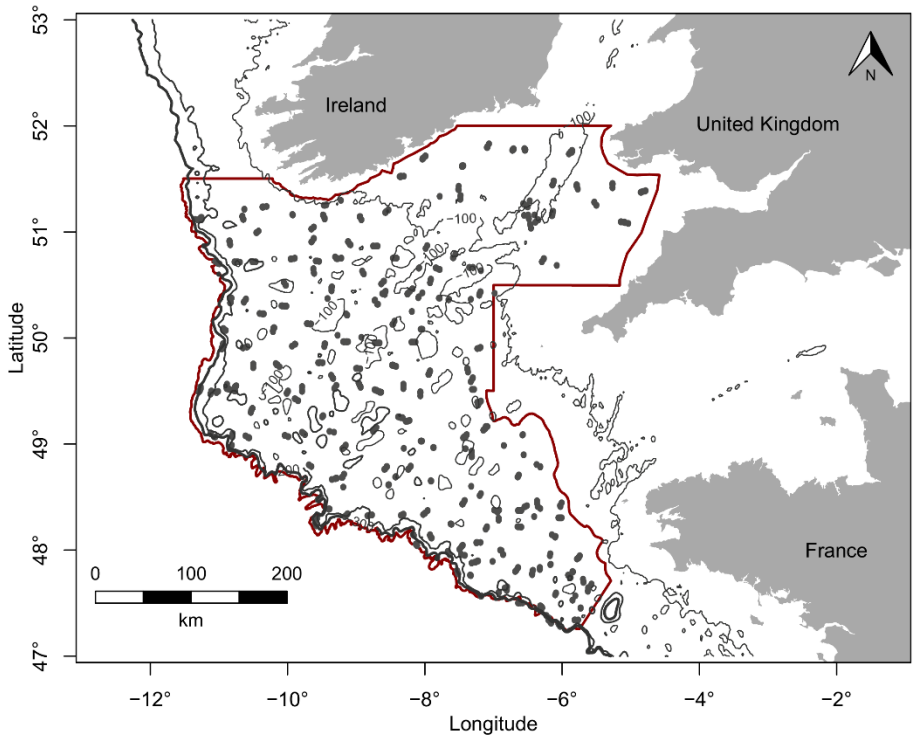


Figure 1: Map of sampling sites (grey dots) in the study area in the Celtic Sea.

We selected the following biological traits for their known response to fishing pressure: maximum length, longevity, age at maturity, offspring size, reproductive guild and fecundity (Le Quesne & Jennings, 2012; Shephard, Gerritsen, Kaiser, & Reid, 2012; Wiedmann et al., 2014). Values of these traits were extracted from the literature and the PANGAEA data library (Beukhof, Dencker, et al., 2019).

Community assembly processes

To identify community assembly processes related to life history traits, we calculated the community-weighted variance (CWV) according to Gaüzère et al., (2019) for the six life history traits. As CWV can be defined only for quantitative traits, levels of the two qualitative traits (bearer, guarder and non-guarder for reproductive guild; low, medium, high and very high for fecundity) were converted into quantitative values, with the highest values corresponding to the levels most sensitive to fishing (i.e. bearer and low). Assembly rules were assessed using a standard effect size (SES) by comparing the CWV to a null model based on random community assembly (i.e. 1000 random permutations of trait values among taxa). Negative SES values indicated underdispersion, meaning that the observed trait variability was lower than that expected by chance. Conversely, positive SES values indicated overdispersion and an observed trait variability higher than that expected by chance.

The SES was calculated for each sampling site as (1).

$$SES_i = \frac{x_{obs,i} - x_{th,i}}{SD_{th,i}} \quad (1)$$

with $x_{obs,i}$ the observed CWV at site i, $x_{th,i}$the mean of the null models at site i and $SD_{th,i}$ the standard deviation of the null models at site i. Inverse-distance-weighting interpolation was used only for graphical representation, and a histogram of SES values was created for each trait.

Life history trait distribution as a function of environmental and fishing variables

To relate the spatio-temporal distribution of traits to environmental and fishing variables, community-weighted means (CWM) were calculated using the "FD" package (Laliberté, Legendre, Shipley, & Laliberté, 2014) of R software (R Core Team, 2020). The CWM of quantitative traits (i.e. maximum length, longevity, age at maturity and offspring size) was the mean of trait values weighted by taxa biomass. For each qualitative trait (i.e. reproductive guild and fecundity), one CWM was calculated for each level of the trait as the proportion of the biomass of taxa exhibiting that level at each site. Before analysis, CWMs were log-transformed to reduce their variability. Like for CWV, inverse-distance-weighting interpolation was used only for graphical representation, and a histogram of CWMs was created for each trait.

We selected environmental and fishing variables known to influence Celtic Sea ecosystems, and more generally North Atlantic shelf ecosystems (Foveau et al., 2017; Mérillet et al., 2020). Depth was recorded at each sampling site. Sediment data according to Folk's 5-level classification system came from the EMODnet Geology Portal (https://www.emodnet-geology.eu). Data for the few (95) sampling sites that were not included in the EMODnet dataset were extrapolated from the SHOM database (https://diffusion.shom.fr/loisirs/sedim-mondiale.html). Bottom temperature data were downloaded from Copernicus (http://marine.copernicus.eu), from the monthly mean Atlantic-Iberian Biscay Irish-Ocean Physics Reanalysis data product at 8 km × 8 km resolution, while chlorophyll a data were extracted from monthly means obtained from satellite observations at 1 km × 1 km resolution. Fishing effort data were derived from the New Fisheries Dependent Information from the EU's Scientific, Technical and Economic Committee for Fisheries (https://stecf.jrc.ec.europa.eu), which provided data on fishing effort for all EU countries in hours fished per statistical rectangle (111.12 km × 55.56 km). We considered only bottom and pelagic trawls as they represented the largest mean percentages of total hours fished per year (80%) and total t of

landings per year (39.4%) from 2012-2016. These variables influence taxa at different frequencies and time lags. Nonetheless, as our community data were based on annual sampling, and the 101 taxa studied display a wide variety of life cycles, we assumed that annual means would be the most relevant values for the covariables.

In a preliminary step, a permutation test for Moran's I statistic (Moran, 1950) indicated that spatial autocorrelation was significant ($p = 0.001$) for all traits (maximum length ($I = 0.41$), longevity (0.24), age at maturity (0.41), offspring size (0.26), reproductive guild (0.33) and fecundity (0.28)); thus, spatial variables (i.e. latitude, longitude, latitude^2, longitude^2 and the latitude × longitude interaction) were included in the models. We studied the distribution of each CWM as a function of environmental variables (depth, sediment, chlorophyll a and temperature), fishing variables (bottom trawl, pelagic trawl) and time (year). Collinearity between variables was assessed with a variance inflation factor and a threshold of five.

The log-transformed CWMs calculated for quantitative traits (i.e. maximum length, longevity, age at maturity and offspring size) followed a Gaussian distribution and were modelled using generalised linear models (GLM). We built a full model and selected the best combination of explanatory variables using a stepwise procedure based on minimising the Akaike information criterion (AIC). As residuals of the best GLMs remained autocorrelated, simultaneous autoregressive (SAR) models were used. This family of models assumes that the response at each location is a function of the explanatory variables but also of neighbouring locations (Kissling & Carl, 2008). The spatial-error model, which is the most reliable SAR model, captures spatial autocorrelation that is not completely explained by the explanatory variables or that is an inherent property of the response variable. To implement these models, we used the *errorsarlm* function in the "SpatialReg" R package (R. Bivand & Piras, 2015). A full model was built, and the one with the lowest AIC was selected using the *dredge* function ("MuMIn" R package). We compared AIC, Nagelkerke R^2 (Nagelkerke, 1991), correlation

between observed and predicted values and autocorrelation in model residuals to determine the degree to which the SAR models improved upon results of the GLMs.

For qualitative traits (reproductive guild and fecundity), Dirichlet regressions were performed using the "DirichletReg" R package (Maier, 2014) with the same explanatory variables as for the quantitative traits (i.e. environmental, fishing, time and spatial). Dirichlet regression is used to model a dependent variable that is the sum of multiple components. Goodness-of-fit of the models was assessed with a specific Pearson χ^2 statistic, as described by Hijazi (2006). Statistical methods to capture spatial autocorrelation in the Dirichlet regression are not well developed, but the inclusion of spatial terms in the models partially compensated for it.

Temporal trends in the biomass of the taxa most sensitive to fishing

We used Hill-Smith analysis (Hill & Smith, 1976), which is principal component analysis that considers both quantitative and qualitative variables, to identify which taxa had the largest values – or level – of traits as CWM increased. To assess the sensitivity of each taxon comprehensively, all of the life history traits studied were included in the Hill-Smith analysis. The first axis of the Hill-Smith analysis, which explained the most variability in the distribution of life history traits across taxa, was used as a sensitivity score (the more negative the score, the more sensitive the taxa). Based on a histogram of the sensitivity scores, the 20 most sensitive taxa, which clustered apart from the other taxa, were examined in more detail.

In addition, a linear model with a Gaussian distribution was fitted to *log(x+1)*-transformed biomass of the 101 taxa, with year as the only explanatory variable. For each taxon, the coefficient of the year variable was extracted when significant ($p<0.05$). To characterise the relation between sensitivity and temporal trends of species' biomass, we computed correlation between sensitivity scores and significant slopes of the regressions of the biomass over time.

Then, to examine the temporal increase in CWMs of certain traits observed in the GLM analysis, we investigated (i) which taxa had the highest values – or level – of the traits whose CWMs increased over time and (ii) which taxa had an increase in biomass. We identified taxa among the 20 most sensitive that had experienced an increase in biomass. We focussed on temporal dynamics of the biomass of these taxa by plotting the slope of the regression of their biomass over time in each statistical rectangle. We graphically examined the spatial covariation of biomass and trends in fishing effort to assess whether the sampling sites with an increase in biomass of the most sensitive taxa also had experienced a decrease in bottom trawl effort.

3.2.3 Results

Assembly rules based on life history traits

Overall, most sampling sites had negative SES values (Fig. 2), which implies that variability in trait distribution was lower than that expected by chance (i.e. underdispersed traits). This result indicates that only a small portion of the entire range of each trait value was expressed at these sites. Few sampling sites had positive SES values (i.e. wider range of traits values than that expected by chance), indicating overdispersion (Fig. 2).

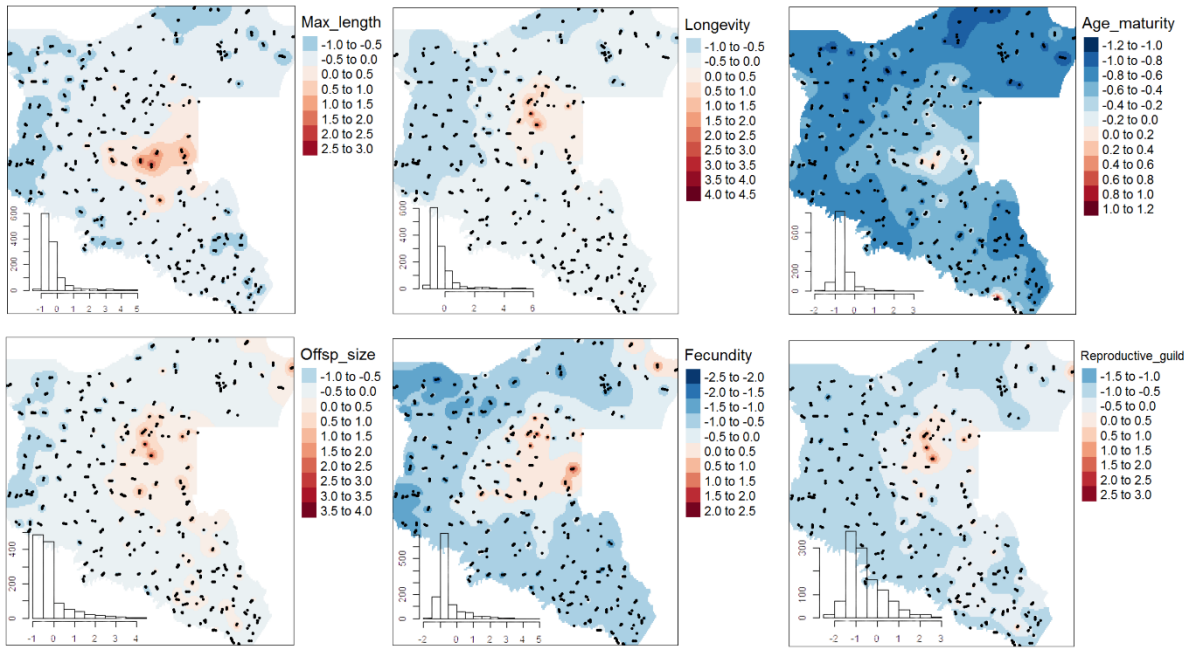


Figure 2: Maps of standard effect size of the community-weighted variance (CWV) of the six life history traits of 101 taxa in the Celtic Sea with their histograms. Positive values (in red) indicate overdispersion of the traits, while negative values (in blue) indicate underdispersion.

For all six traits, SES values were most negative along the north-western border and positive in the centre-east of the Celtic Sea. For offspring size, reproductive guild and fecundity, the North-East also had positive SES values, which suggests that it also had a wider range of trait values than that expected by chance.

Environmental drivers of the distribution of sensitivity traits

CWMs of maximum length, age at maturity and offspring size were highest in the centre-east of the Celtic Sea (Fig. 3), which had the widest range of trait values expressed (i.e. overdispersion), indicated by the most positive SES values (Fig. 2). Thus, taxa with low maximum length, age at maturity and offspring size were also present in the centre-east. Only longevity showed a slightly different pattern, with the narrowest range of trait values in the north and the widest in the south. For reproductive guild, two of the three levels (i.e. bearer and

guarder) had their highest proportions of biomass in the centre and extreme North-East of the Celtic Sea and were nearly absent elsewhere. Thus, all three reproductive guilds occurred in these two areas (Fig. 3), which agreed with the overdispersion observed there (Fig. 2). Similarly, three levels of the four fecundity levels (i.e. low, medium and very high) had some of their highest proportions of biomass in the centre and were nearly absent elsewhere, which led to overdispersion of the fecundity trait in the centre (Fig. 3).

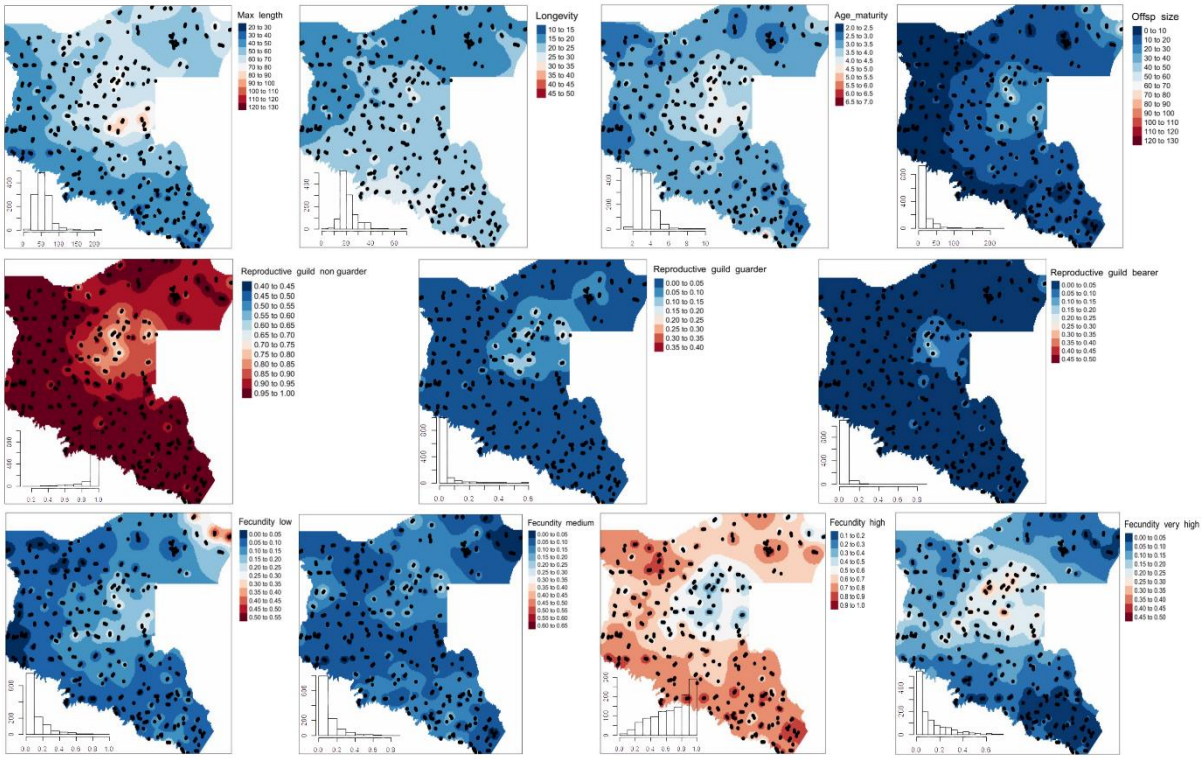


Figure 3: Maps of community-weighted means (CWMs) of the six life history traits of 101 taxa in the Celtic Sea. Each level of the two qualitative traits is represented separately. Maps also show histograms of the CWMs.

Table 1: Performance of the spatial autoregressive models and Dirichlet regression of community-weighted means. Asterisks identify the models selected.

Quantitative trait	Model	AIC	Nagelkerke R^2	Moran's test p-value	Correlation obs vs. predict	Correlation p-value
Max. length	SAR*	536	0.330	0.567	0.577	< 0.001
	GLM	546	0.343	0.001	0.573	< 0.001
Longevity	SAR*	-5.75	0.271	0.484	0.521	< 0.001
	GLM	-7.73	0.279	0.409	0.521	< 0.001
Age at maturity	SAR*	-187	0.235	0.574	0.496	< 0.001
	GLM	-149	0.215	0.001	0.458	< 0.001
Offspring size	SAR*	3444	0.263	0.593	0.523	< 0.001
	GLM	3481	0.391	0.001	0.494	< 0.001
Qualitative trait	Level	AIC	Dirichlet pearson χ^2	Moran's test p-value	Correlation obs vs. predict	Correlation p-value
Reproductive guild		-17351	3378	< 0.001		
	bearer			0.020	0.344	< 0.001
	guarder			0.001	0.452	< 0.001
	non-guarder			0.004	0.503	< 0.001
Fecundity		-9525	3879	< 0.001		
	low			0.001	0.446	< 0.001
	medium			0.001	0.318	< 0.001
	high			0.001	0.449	< 0.001
	very high			0.001	0.574	< 0.001

For SAR models, Moran's I indicated no residual autocorrelation ($p > 0.05$), which was not the case for the GLM (Table 1). SAR models also yielded stronger correlations between observed and predicted values and lower AICs, except for longevity. The Dirichlet regression model was significantly better than the null model for reproductive guild (χ^2=3378 and $p < 2.2\times10^{-16}$) and fecundity (χ^2=3879 and $p < 2.2\times10^{-16}$), although the residuals still displayed some spatial patterns (Moran's I test: $p < 0.01$), as spatial autocorrelation was not corrected for the Dirichlet regressions (Table 1).

Table 2: Estimates of explanatory variables (log transformed) in spatial autoregressive models (for quantitative traits) and the Dirichlet regression model (for qualitative traits) of community-weighted means. Only significant estimates are shown ($p<0.01$).

Trait	Depth	Sediment		Chlorophyll a	Bottom temp.	Bottom trawl	Pelagic trawl	Year	Lat.	Long.	Lat.^{2}	Long.^{2}	Lat. × Long.
Max. length	8.79 ×10^{-4}					-3.80 ×10^{-6}		6.44 ×10^{-3}	2.39 ×10^{-1}	2.03 ×10^{-1}	-1.48 ×10^{-1}	-6.83 ×10^{-2}	-4.84 ×10^{-2}
Longevity	-1.13 ×10-3	Coarse	-4.92 ×10^{-2}		6.81 ×10^{-2}	-1.14 ×10^{-6}	-1.05 ×10^{-5}		-8.24 ×10^{-2}	-4.10 ×10^{-3}		-7.71 ×10^{-2}	2.63 ×10^{-2}
		Mix	-2.73 ×10^{-1}										
		Mud	9.09 ×10^{-3}										
		Sand	5.06 ×10^{-2}										
Age at maturity	8.06 ×10-4	Coarse	-4.61 ×10^{-2}	-9.25 ×10^{-2}		-4.25 ×10^{-6}		4.83 ×10^{-3}	5.74 ×10^{-2}	1.29 ×10^{-1}	-6.67 ×10^{-2}	-6.33 ×10^{-2}	
		Mix	1.02 ×10^{-1}										
		Mud	1.06 ×10^{-1}										
		Sand	5.75 ×10^{-2}										
Offspring size						-1.45 ×10^{-5}		4.35 ×10^{-2}	3.22 ×10^{-1}	7.22 ×10^{-1}	-4.13 ×10^{-1}	-1.05 ×10^{-1}	
Reproductive guild													
bearer	-3.16 ×10^{-3}												
guarder					-1.74 ×10^{-1}			-3.65 ×10^{-2}		-1.77 ×10^{-1}	-1.75 ×10^{-1}	8.14 ×10^{-2}	
non-guarder	-1.63 ×10^{-2}	Coarse	2.68			1.16 ×10^{-5}	1.30 ×10^{-4}		-8.33 ×10^{-1}	-1.64	9.19 ×10^{-1}	2.05 ×10^{-1}	1.88 ×10^{-1}
		Sand	1.54										
Fecundity													
low	-2.49 ×10^{-3}	Mix	9.78 ×10^{-1}			-1.20 ×10^{-5}		1.70 ×10^{-2}		2.41 ×10^{-1}			
medium		Mix	1.30	-7.23 ×10^{-1}				-2.74 ×10^{-2}	1.58 ×10^{-1}		1.08 ×10^{-1}	-9.93 ×10^{-2}	
high	-7.59 ×10^{-3}					1.08 ×10^{-5}		-2.62 ×10^{-2}	-3.34 ×10^{-1}	-6.40 ×10^{-1}	3.54 ×10^{-1}	5.76 ×10^{-2}	-2.95 ×10^{-2}
very high		Mix	1.29	-5.68 ×10^{-1}	-1.94 ×10^{-1}	-5.87 ×10^{-6}			1.84 ×10^{-1}		-2.19 ×10^{-1}		-7.80 ×10^{-2}

The spatial variables (latitude, longitude, their quadratic effects and interaction) as well as bottom trawl effort, depth, sediment and year were significant drivers of most of the CWMs modelled (Table 2).

Depth appeared to influence the distribution of life history traits strongly. The relative biomass of taxa with large maximum length and high age at maturity increased in shallower areas (Table 2). Conversely, the relative biomass of taxa that are long-lived, bear their offspring (i.e. bearer) and have low fecundity, as well as that of non-guarder taxa and high fecundity taxa, tended to increase in deeper areas (Table 2). Sediment had a major influence on longevity, age at maturity, non-guarder taxa and three of the four fecundity levels (i.e. low, medium and very high) (Table 2).

All CWMs of the traits sensitive to fishing covaried negatively with bottom trawl effort (Table 2). Areas with little bottom trawl effort tended to have the highest relative biomass of large, long-lived taxa that have low fecundity, mature late and give birth to large offspring. The relative biomass of taxa with very high fecundity also decreased as bottom trawl effort increased. Conversely, areas with large bottom trawl effort had the highest relative biomass of taxa that guard their eggs and have high fecundity. In comparison, the spatial covariation of CWMs with pelagic trawl effort was significant only for the longevity trait and the non-guarder level. Pelagic trawl effort had a negative influence on the relative biomass of long-lived taxa but a positive influence on that of non-guarder taxa (Table 2).

Regarding temporal trends in CWMs in the Celtic Sea, the relative biomass of large taxa that mature late, have low fecundity and large offspring increased from 2000-2016. Conversely, the relative biomass of taxa that guard their eggs and have medium or high fecundity decreased from 2000-2016 (Table 2). As bottom temperature increased, the relative biomass of long-lived taxa increased, while that of non-guarder taxa and taxa with very high fecundity decreased.

Taxa with very high and medium fecundity tended to have lower relative biomass at sites with higher chlorophyll a concentration (Table 2).

Spatio-temporal pattern of slow living strategy taxa in relation to bottom trawling

Hill-Smith analysis of the selected life history traits enabled us to characterise the extent to which each taxon's combination of life history traits made it sensitive to fishing. The first axis (used as the sensitivity score) explained 34.3% of the total variability, while the second axis explained 15.2% (Fig. 4). The most sensitive taxa (i.e. large, long-lived taxa that mature late, bear their offspring and have low fecundity) had the lowest sensitivity scores. The 20 most sensitive taxa were selected and framed in red (Fig. 4). Of these taxa, 14 were elasmobranchs (i.e. sharks, rays and chimaeras) (Table S1).

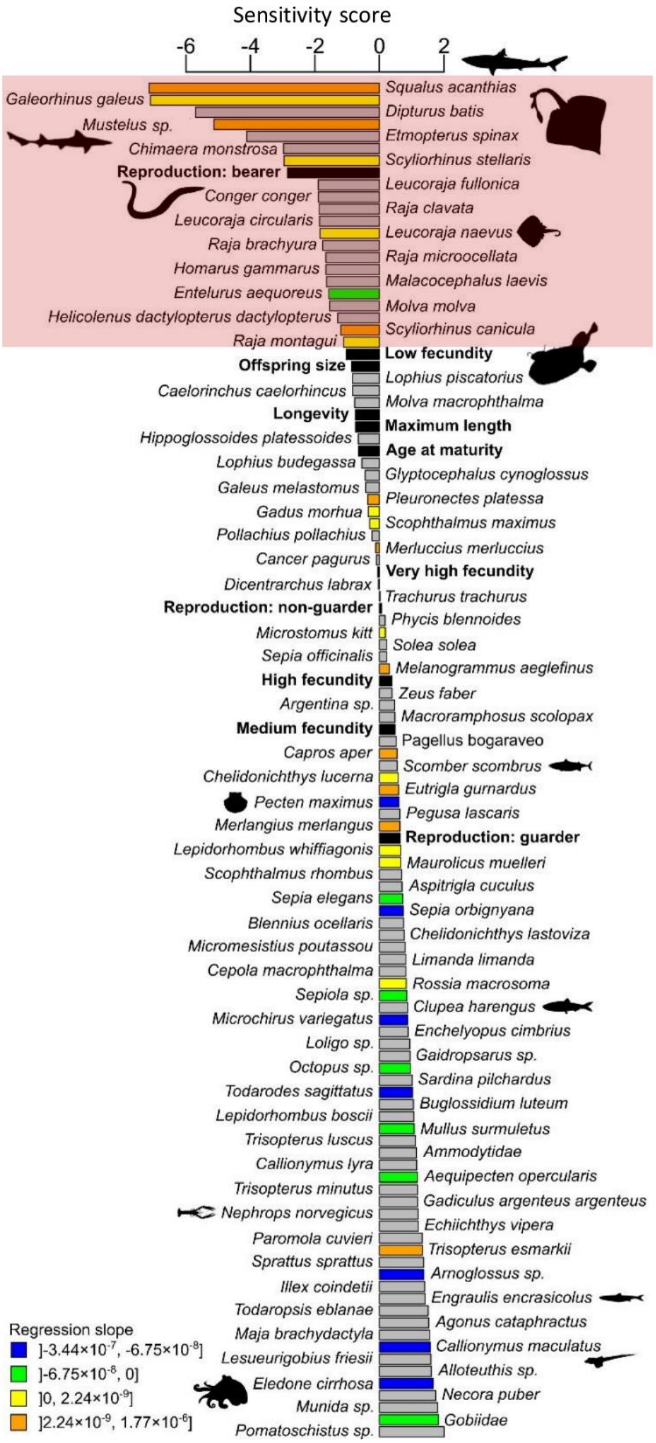
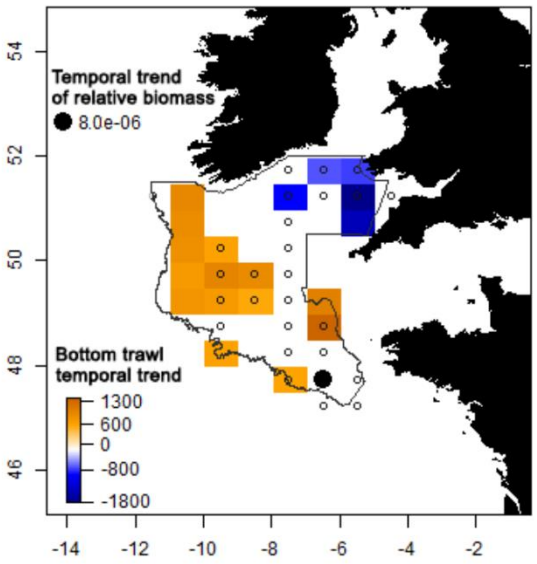


Figure 4: Sensitivity scores from Hill-Smith analysis of the six life history traits of 101 taxa in the Celtic Sea, ranked from most to least sensitive to fishing. Sensitivity scores of individual taxa coloured according to the quartile of the slope of the regression of biomass (g/m^2) from 2000-2016. Non-significant slopes ($p > 0.05$) are coloured grey. Mean sensitivity scores for all taxa with a given trait are coloured black. The first 20 most sensitive taxa are framed in red.

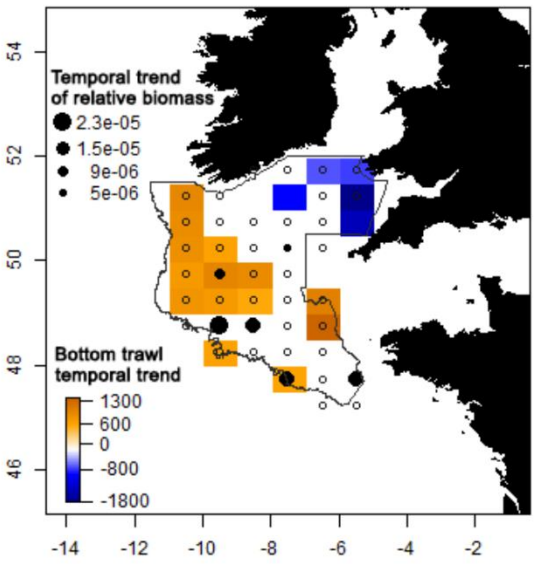
Among all taxa, the temporal trend in biomass significantly increased for 21 taxa, significantly decreased for 14 taxa and had no significant trend for 66 taxa (Table S1). Globally, biomass appeared to increase for slow life history taxa (lowest sensitivity scores) but to decrease for fast life history taxa (highest sensitivity scores). This is confirmed by the negative correlation between significant slope of the regression ($p<0.05$) of the biomass over time and sensitivity scores (Spearman's $\rho = -0.60$; $p < 0.001$). Taxa among the 20 most sensitive whose biomass increased were school shark *Galeorhinus galeus*, smooth-hounds *Mustelus* sp., cuckoo ray *Leucoraja naevus*, small-spotted catshark *Scyliorhinus canicula*, nursehound *Scyliorhinus stellaris* and spiny dogfish *Squalus acanthia*s.

Biomass of *Mustelus* sp., *S. canicula*, *S. stellaris* and, to a lesser extent *S. acanthia*s, increased significantly in the North-East of the Celtic Sea (Fig. 5), which experienced a significant decrease in bottom trawling, although the relationship was difficult to assess for *S. stellaris* because of its small range in the Celtic Sea (Fig. 5). Along the southern border of the Sea, biomass of *L. naevus* increased significantly, as did, to a lesser extent, those of *G. galeus*, *Mustelus* sp. and *S. canicula*. Along this border, biomass increased mostly in statistical rectangles with no significant trends in bottom trawling (Fig. 5).

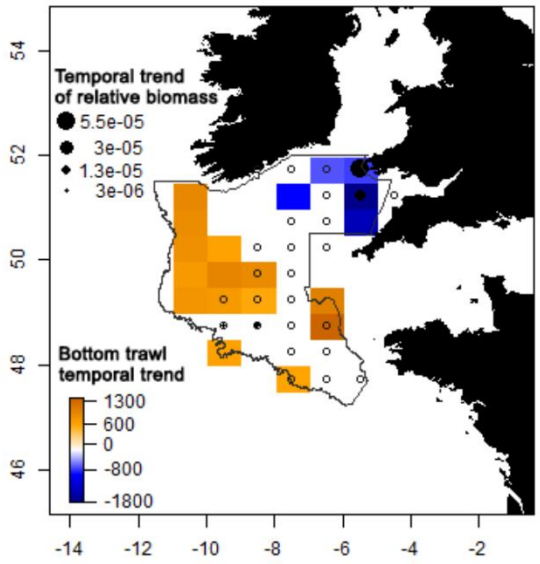
Galeorhinus galeus



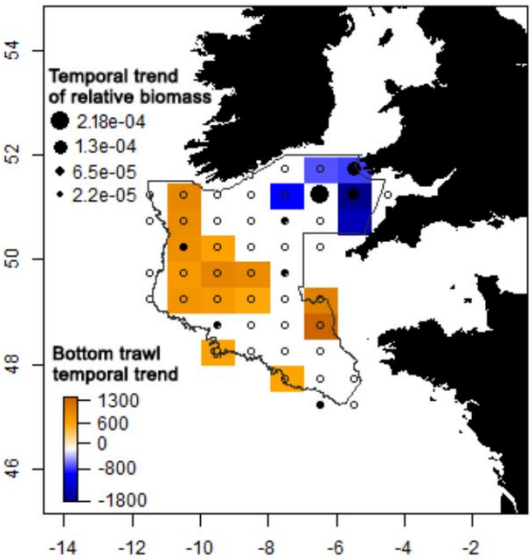
Leucoraja naevus



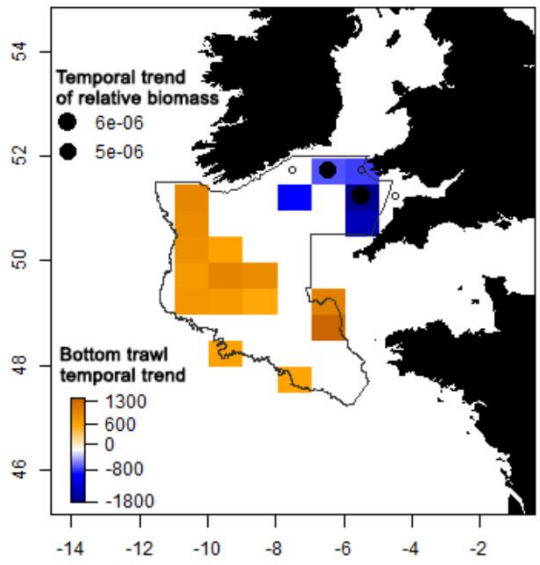
Mustelus sp.



Scyliorhinus canicula



Scyliorhinus stellaris



Squalus acanthias

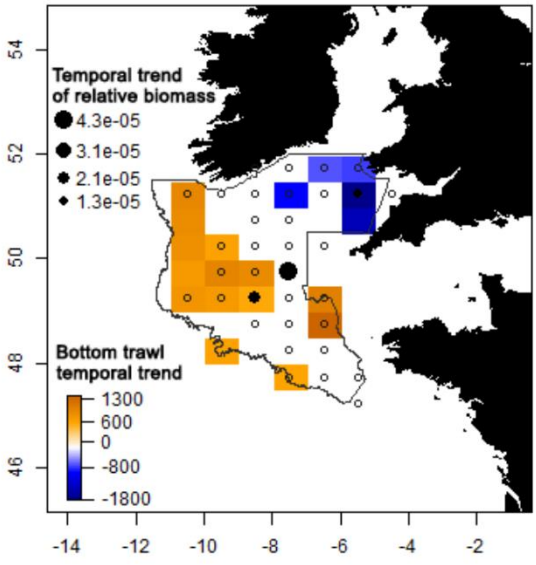


Figure 5: Map of the slope of the regression of biomass (g/m^2, black circles) in each statistical rectangle (111.12 km × 55.56 km) of the Celtic Sea from 2000-2016 for the taxa most sensitive to fishing whose biomass increased. Open circles represent the distribution of the taxa, and statistical rectangles are coloured according the slope of the regression of bottom trawl effort (hours per year within the rectangle) on time (only slopes with p <0.05 are coloured).

3.2.4 Discussion

To evaluate impacts of fishing on community structure, the distribution of life history traits that are sensitive to fishing was studied to identify assembly rules, as well as their environmental and anthropogenic drivers. At the scale of the Celtic Sea, life history traits show signs of underdispersion. This overall pattern is not surprising, as overdispersion may be detected more often at the local scale (i.e. sampling sites), where competition outweighs environmental filtering (Edgar et al., 2017; Mouchet et al., 2013). The underdispersion could also be related to having chosen traits that are influenced by abiotic filters (Weiher & Keddy, 1995), such as temperature and depth; for instance, maximum length of many fish tends to increase as depth increases (Macpherson & Duarte, 1991). At a finer scale, we observed both underdispersion and overdispersion in the Celtic Sea. Values of life history traits are more diverse than expected by chance in the centre-east and extreme North-East of the Sea, which suggests diversified life history strategies. This overdispersion of traits is driven by the co-occurrence of taxa with a slow living strategy, such as the common skate *Dipturus batis*, and a fast living strategy, such as the Atlantic horse mackerel *Trachurus trachurus* (Fig. 3). Three non-exclusive processes could explain the distribution of underdispersion and overdispersion in the Celtic Sea:

(i) *Competition among coexisting taxa fosters trait overdispersion.* Competition might lead to either competitive exclusion or to spatial and/or temporal avoidance among co-occurring taxa (Cahill, Kembel, Lamb, & Keddy, 2008; Mayfield & Levine, 2010). For instance, Norway lobster *Nephrops novergicus* and squat lobster *Munida* sp. compete for food and burrows in the Bay of Biscay (Loc'h & Hily, 2005). However, our analyses tested this process only weakly and thus cannot indicate whether it occurs at the scale of the entire community.

(ii) *Small-scale seascape heterogeneity provides a greater diversity of niches*, in agreement with the *habitat heterogeneity hypothesis* (Tews et al., 2004). We observed that sediments, which are generally homogenous throughout the Celtic Sea (mud and sand), tend to be patchier where overdispersion occurs (i.e. centre-east and extreme North-East). Life history traits define one of at least five dimensions of the species ecological niche (i.e. habitat, life history, trophic, defence and metabolic) Winemiller, Fitzgerald, Bower, & Pianka (2015)). The overdispersion of life history traits observed could thus indicate that sufficient resources exist to sustain diverse life history strategies.

(iii) *Increased trait dispersion is related to temporal changes in biomass distribution, which is related to a decrease in fishing pressure*. Overdispersion might occur when new taxa with different trait values arrive or due to changes in taxa biomass among trait values. For the Celtic Sea, we observed stability in the taxonomic structure of these communities despite spatio-temporal changes in environmental and anthropogenic pressures (Mérillet et al., 2020). Focusing on traits, we highlight that the biomass of slow life history taxa increased over time in the centre-east and extreme North-East, thereby increasing the frequency of these original trait values in the community and flattening the distribution of trait values. In the extreme North-

East, the biomass of sensitive taxa could have increased due to the decrease in fishing pressure. Sensitive taxa may be filtered from areas with intensive fishing, and a decrease in fishing pressure could allow more diverse taxa to coexist.

Among these three processes, the latter two are related to environmental filtering, but the second is related to seascape characteristics, while the third is related directly to anthropogenic pressure. We found no evidence of stochastic processes, at least at the scale of the Celtic Sea. Except for the centre-east and extreme North-East, the trait underdispersion of communities in the Celtic Sea lies at the fast end of the life history continuum. This underdispersion is often due to environmental (in a broad sense) filtering that selects taxa that can endure specific environmental conditions. Depth, sediments, year and bottom trawl effort are the variables that significantly drive of the largest number of traits and have thus a particularly structuring effect on their distribution. The dependence of the CWMs on variables that do not vary over time at a given site (i.e. depth and sediments) illustrates the structuring effects of habitat. For variable that vary over time, bottom trawl effort thus appears to be a severe condition that restricts the distribution of life history traits in the Celtic Sea, with a negative relationship with the biomass of slow life history strategy taxa.

We observed temporal variation in the biomass of slow life history strategy taxa that increased from 2000-2016 at the regional scale. More precisely, of the 21 taxa with an increase in biomass, 6 were also among the most sensitive to fishing: *G. galeus*, *Mustelus* sp., *L. naevus*, *S. canicula*, *S. stellaris* and *S. acanthia*s. As elasmobranchs, all six of these taxa have a slow life history strategy and thus are particularly sensitive to fishing (Shephard et al., 2012). At the scale of the Celtic Sea, bottom trawling was stable over the period studied (Mérillet et al., 2020), but this stability masks local differences that are visible at the scale of the statistical rectangle. Almost all significant increases in the biomass of these six elasmobranchs occurred in statistical rectangles in which bottom trawling decreased or showed no significant trend. This is

particularly clear for *Mustelus* sp., *S. canicula*, *S. stellaris* and *S. acanthia*s, whose population increases in these areas occurred most likely because local fishing pressure decreased. The biomass of taxa with a slow life history, especially elasmobranchs, is higher in the centre-east of the Celtic Sea, and the most of the increase in biomass of the six elasmobranchs occurred in adjacent areas: the extreme North-East and south-west. This pattern could be due to an increase in local population after a decrease in fishing pressure (in the North-East), but also to a replenishment from a population in the centre-east of the Celtic Sea (Green et al., 2014). As an open sea with relatively homogenous sediment, the Celtic Sea appears to be a seascape that large-bodied and mobile taxa can cross easily. We assume that the centre of the Celtic Sea could have functioned as a refuge and then a source for recolonization of the North-East when fishing pressure began to decrease. A similar recovery of a depleted population from adjacent areas in a fishing ground was observed for predatory fish on the North-West Atlantic shelf (Shackell, Fisher, Frank, & Lawton, 2012).

This increase in biomass of slow life history taxa agrees with the increase in equilibrium strategy taxa (e.g. elasmobranchs) observed at the European level (Pecuchet et al., 2017). In the Celtic Sea, this increase could be related to a local decrease in fishing pressure due to management practices. In 2009, the EU began to enforce its Common Fisheries Policy, which decreased overall fishing effort in EU seas (Walter, 2010). In this context, fishing effort was displaced from the North-East to the west and south-west of the Celtic Sea and decreased bottom trawl effort in certain statistical rectangles. It may also have benefited the prey of slow life history taxa, as demonstrated in Georges Bank, a formerly overexploited ecosystem east of Massachusetts, USA (Mayo, Fogarty, & M., 2014), although we did not observe an overall increase in biomass of small pelagic fish. However, this lack of evidence may have been due to incomplete sampling of pelagic communities. Moreover, the seasonal fishing closures of the Trevose Box (1st February until 31 March each year) prohibits fishing activity in three statistical

rectangles in the North-East Celtic Sea (30E4, 31E4 and 32E3). This seasonally closed area created in 2005 (European Commission, 2013; ICES, 2007) have most likely prompted the recovery observed in slow life history taxa and confirm the hypothesis of the benefits of this closure (Horwood, Nichols, & Milligan, 1998). Indeed, we observed the largest significant decrease in bottom trawl effort and increase in biomass for four of the six aforementioned elasmobranch taxa in this area. This area is also a known spawning ground and nursery for many species, including elasmobranchs (Potter, Claridge, Hyndes, & Clarke, 1997), and could, in addition to serving as a refuge for adults from fishing pressure, favour the replenishment of the population by increasing reproductive success.

Along with the increase in biomass of slow life history taxa, we observed that taxa with a decrease in biomass tended to be least sensitive to fishing and had fast life history traits (i.e. small maximum length, short-lived, early-maturing, small offspring, non-guarder and high or very high fecundity). This result is in line with the negative relationship between taxa with short lifespan and very high fecundity with bottom temperature and the increase in bottom temperature in the north of the Celtic Sea. This decrease in fast life history taxa was also observed in the English Channel after a warm phase of the Atlantic Multidecadal Oscillation (McLean, Mouillot, Lindegren, et al., 2018). Similarly, periodic strategy taxa in European seas have decreased over the past 30 years (Pecuchet et al., 2017). Fast life history taxa are highly responsive to an increase in temperature due to their short generation time (McLean, Mouillot, Lindegren, et al., 2018).

Assembly processes in the Celtic Sea are mostly explained by environmental filtering with a particular importance of fishing pressure. In this historical fishing ground, we clearly showed the negative relationship between fishing effort and the biomass of taxa exhibiting sensitive traits, but also the increase in biomass of the most sensitive taxa from 2000-2016, in

link with the creation of the Trevose box area closure. Rapid changes in the functional structure of the communities are expected in the future as climate change effects become more tangible and superimpose to fishing ones. Management measures leading to short-term improvement of the biomass of sensitive taxa to fishing or increase in water temperature are thus urgently needed (O'Leary et al., 2017). This study highlights potential positive dynamics for a group of sensitive species due to a local decrease in fishing pressure. Within two decades, mitigation measures, such as area closures that restrict fishing effort spatially or temporally could significantly increase the biomass of the most sensitive taxa. This positive response to recent EU policies could be a useful feedback for managers. However, a continual caution during ecosystem management of fishing grounds is requires, as commercially fished small pelagic taxa could experience a decrease in biomass in the future due to climate change.

Acknowledgement

We thank all those who made data sampling possible during the EVHOE surveys. This work is part of a PhD Thesis jointly funded by the French Institute for the Exploitation of the Sea (IFREMER) and the National Museum of Natural History (MNHN).

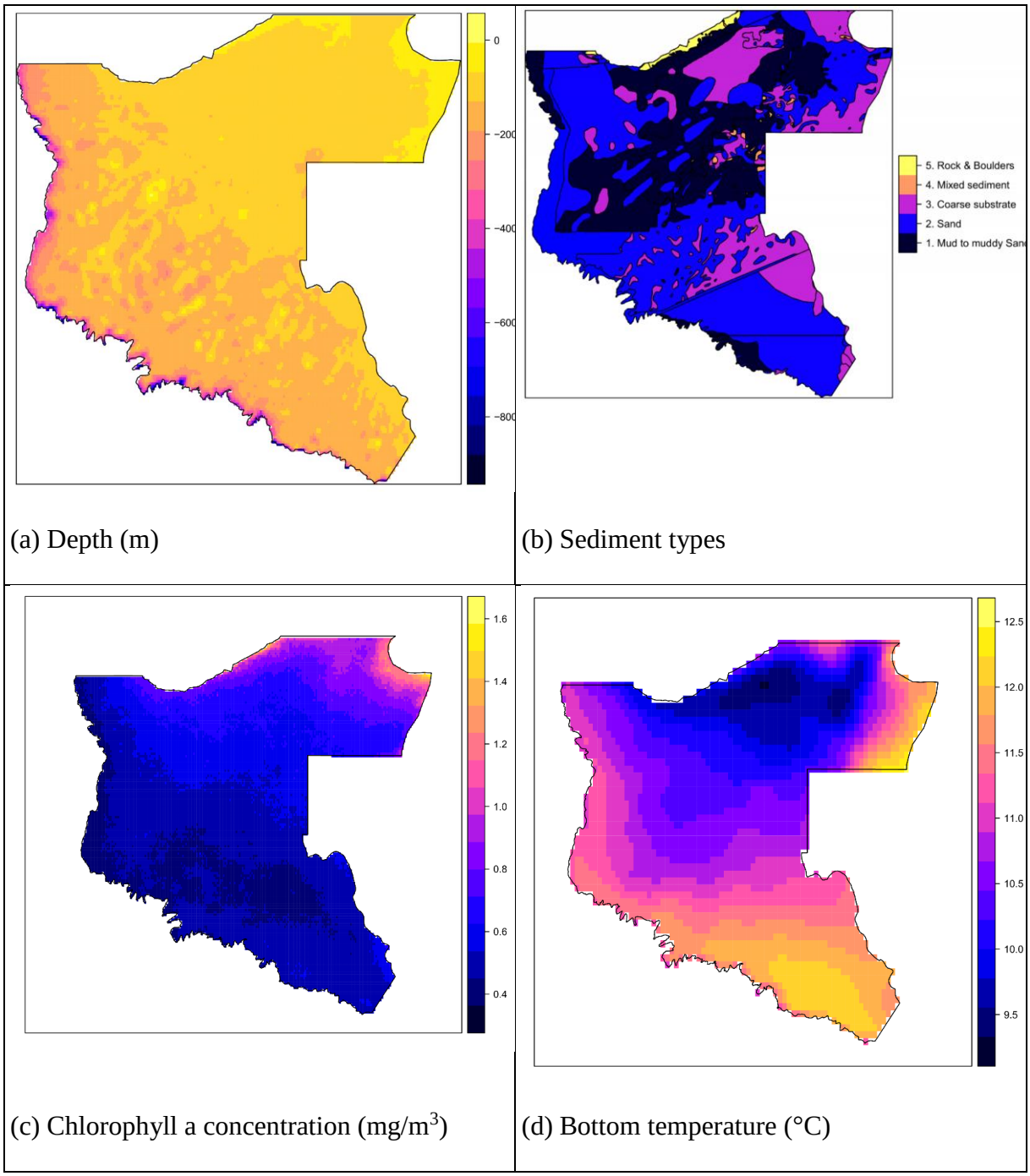
3.2.5 Supplementary materials

Table S1: Score of sensitivity to fishing (first axis of Hill-Smith analysis), direction of the change in biomass from 2000-2016, and the slope and p-value of the generalised linear model (GLM) of the regression of taxa biomass over time for the 35 taxa with significant changes in biomass ($p<0.05$) in the Celtic Sea. Taxa are listed from most to least sensitive.

Taxon	Latin name	Hill-Smith axis1	Biomass GLM slope	Biomass GLM p-value
SQUAACA	Squalus acanthias	-7.14	4.33×10-6	1.23×10-3
GALOGAL	Galeorhinus galeus	-7.10	6.85×10-7	1.90×10-2

MUST	Mustelus sp.	-5.13	2.57×10-6	7.40×10-4
SCYOSTE	Scyliorhinus stellaris	-2.96	2.11×10-7	1.66×10-3
LEUCNAE	Leucoraja naevus	-1.84	1.64×10-6	1.15×10-5
ENTLAEQ	Entelurus aequoreus	-1.57	-8.86×10-9	1.00×10-2
SCYOCAN	Scyliorhinus canicula	-1.20	1.32×10-5	5.80×10-6
RAJAMON	Raja montagui	-1.12	1.18×10-6	9.02×10-4
PLEUPLA	Pleuronectes platessa	-0.36	3.16×10-6	1.89×10-7
GADUMOR	Gadus morhua	-0.35	1.77×10-6	2.06×10-3
SCOPMAX	Scophthalmus maximus	-0.30	2.75×10-7	2.54×10-2
MERLMER	Merluccius merluccius	-0.11	7.56×10-6	1.04×10-4
MICTKIT	Microstomus kitt	0.19	4.21×10-7	1.32×10-3
MELAAEG	Melanogrammus aeglefinus	0.32	3.14×10-5	2.31×10-5
CAPOAPE	Capros aper	0.55	1.28×10-4	1.83×10-4
CHELLUC	Chelidonichthys lucerna	0.58	7.63×10-8	1.31×10-2
EUTRGUR	Eutrigla gurnardus	0.60	1.15×10-5	1.65×10-3
PECTMAX	Pecten maximus	0.61	-7.40×10-8	8.96×10-2
MERNMER	Merlangius merlangus	0.64	2.32×10-5	6.55×10-3
MAURMUE	Lepidorhombus whiffiagonis	0.66	2.24×10-9	2.21×10-2
LEPIWHI	Maurolicus muelleri	0.66	1.17×10-6	3.61×10-5
SEPIELE	Sepia elegans	0.73	-5.19×10-9	3.19×10-11
SEPIORB	Sepia orbignyana	0.75	-7.08×10-8	3.62×10-4
ROSSMAC	Rossia macrosoma	0.84	1.68×10-8	6.61×10-5
SEPO	Sepiola sp.	0.85	-3.74×10-8	2.45×10-6
MICUVAR	Microchirus variegatus	0.88	-2.87×10-7	8.91×10-5
OCTP	Octopus sp.	0.96	-4.16×10-9	4.13×10-2
TODASAG	Todarodes sagittatus	1.03	-1.21×10-7	2.04×10-7
MULLSUR	Mullus surmuletus	1.08	-6.05×10-8	1.17×10-2
AEQUOPE	Aequipecten opercularis	1.18	-6.41×10-8	1.78×10-2
TRISESM	Trachurus trachurus	1.34	9.09×10-6	3.65×10-2
ARNO	Arnoglossus sp.	1.38	-3.45×10-7	8.14×10-14
CALMMAC	Callionymus maculatus	1.58	-8.76×10-8	1.78×10-6
ELEDCIR	Eledone cirrhosa	1.67	-2.38×10-7	1.57×10-2
FMGOBII	Gobiidae	1.83	-4.28×10-10	1.32×10-2

Figure S1: Map of habitat characteristics ((a) depth and (b) sediment type) and environmental variables ((c) chlorophyll a concentration and (d) bottom temperature) in the Celtic Sea.



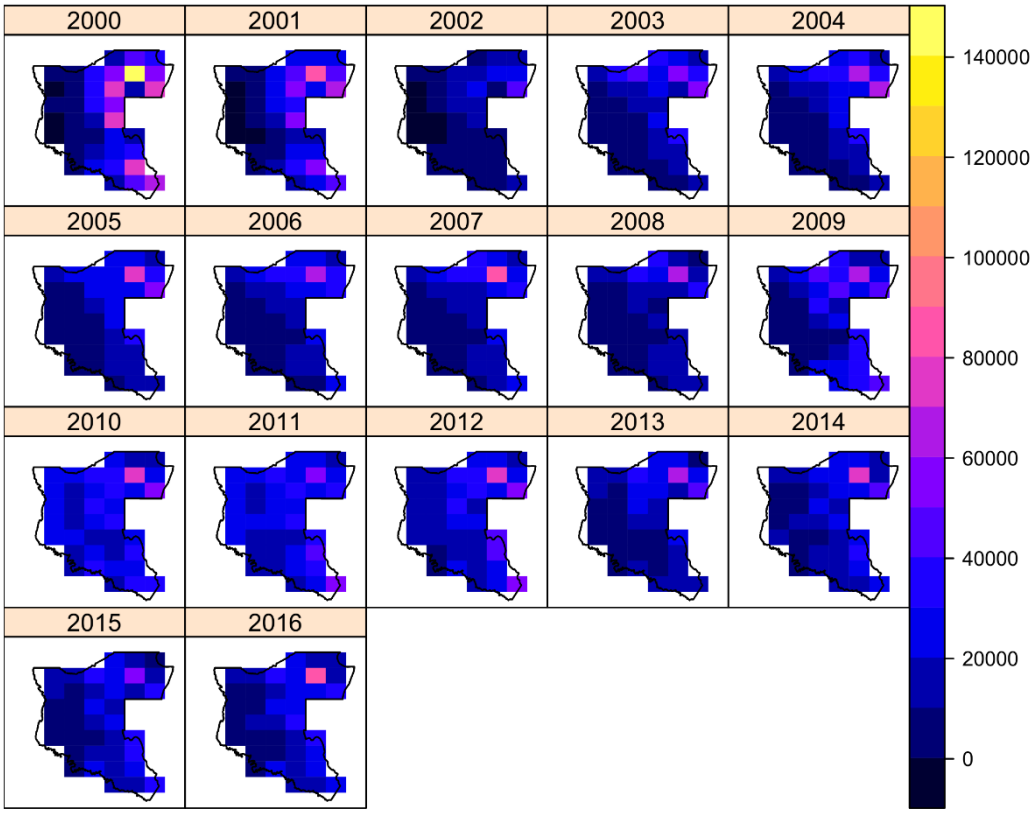
(a) Depth (m)

(b) Sediment types

(c) Chlorophyll a concentration (mg/m^3)

(d) Bottom temperature (°C)

Figure S2: Map of bottom trawl fishing effort (hours fished per statistical rectangle) from 2000-2016 in the Celtic Sea.



3.3 Article 3

Using biological traits to get insights on the bentho-demersal community sensitivity to trawling in the Celtic Sea

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Under review in ICES Journal of Marine Sciences as Dupaix, A., Merillet, L., Mouchet, M., Kopp, D., Robert, M. Sensitivity of megabenthic communities in the Celtic sea based on underwater video.

3.3.1 Introduction

One of the main goals of applied ecology is to understand the response of communities to pressures, whether natural or anthropogenic, in order to inform ecosystem management and conservation mitigation measures (Harrison & Cornell, 2008; McGill et al., 2006). To predict these responses to the drivers, it is important to assess the vulnerability of ecosystems to human activities, that are known to potentially jeopardise their structure and mode of functioning (Halpern et al., 2008). The vulnerability of marine ecosystems depends on their sensitivity, i.e. the degree to which an ecosystem will respond to a given pressure, as well as on their exposure, i.e. the extent and intensity of the pressure (ICES, 2017). Sensitivity can be broken down into the direct response of the ecological system to human pressure (resistance) and its capacity to recover (resilience), and can be characterized using biological traits (Bolam, Coggan, Eggleton, Diesing, & Stephens, 2014; Rijnsdorp et al., 2018; Tillin et al., 2006)

Assessing the sensitivity to perturbations of ecosystems located on continental margins is of particular interest for their management. Indeed, coastal shelf seas, which only represent 7% of the total ocean area, sustain the landing of 19 million tons of fish and invertebrates each year (Amoroso et al., 2018). These ecosystems are subject to several types of pressures of anthropic origin, the most important ones being fisheries (e.g. through direct catch or habitat modification), pollution (either land or ocean-based) and climate change (which exacerbates the impact of other factors, e.g. through ocean acidification and temperature modification) (Halpern et al., 2008; IPBES, 2019a). As far as fishing pressure is concerned, bottom trawling is responsible for almost a quarter of global wild marine landings (Amoroso et al., 2018), and for the highest human physical disturbance on marine ecosystems in continental shelves throughout the world (Foden, Rogers, & Jones, 2011; Watling, 2005). Trawling footprint shows strong variations between regions, with some regions concentrating most of the trawling activity. In European waters for example, in the Kattegat, it was estimated that nearly 100% of

benthic habitats are impacted by bottom trawling (Pommer, Olesen, & Hansen, 2016), and in the UK waters its footprint is estimated to account for up to 99% of the known effect of all human pressure on the seabed (Foden et al., 2011). Bottom trawling impacts bentho-demersal communities in several ways. First, its impact depends on the exposure, which is function of fishing gear characteristics, fishing intensity as well as population size (Hiddink et al., 2017). It is also influenced by the resistance of communities, which is determined by the physical (e.g. size, presence/absence of a shell) and behavioural (e.g. position on the substratum, mobility) characteristics of the species (Bolam et al., 2014; Mérillet et al., 2018). Finally, the resilience of bentho-demersal communities, mainly determined by the life-history of species (e.g. longevity, reproductive mode), also plays an important role in determining their response to trawling (Hiddink et al., 2019). The resilience is also determined by some behavioural traits, such as feeding mode (*e.g.* scavenger can benefit from organisms discarded by trawling when filter feeder will be highly vulnerable (de Juan, Demestre, & Thrush, 2009).

Several methods have been put forward for assessing species sensitivity (Bolam et al., 2014; de Juan, Thrush, & Demestre, 2007; de Juan, Demestre, & Thrush, 2009; González-Irusta, De la Torriente, Punzón, Blanco, & Serrano, 2018). For example, an integrated trait-based indicator developed by de Juan et al., 2009), based on 5 biological traits (size, position on the substratum, fragility, mobility and feeding mode) that describe species sensitivity to trawling, is particularly well adapted to describe the response of epibenthic communities to trawling disturbance. These studies mainly focussed on benthic organisms, without considering fish species which precludes a global assessment at the ecosystem level. When using traditional scientific fishing gear for sampling (otter trawl, beam trawl, dredge or box-corer), fragile species, such as sea pens or hydrozoans, could be broken, which hinders the correct counting and identification of individuals(Auster et al., 2011a). Finally, the catchability of some elusive, highly mobile species remains unknown when using such sampling methods. This study aimed

at assessing the sensitivity of the whole community living in the bentho-demersal habitat, and therefore needed a sampling method free of this sampling bias. A way of circumventing it, and to consider fragile species, is to use underwater video devices (Mallet & Pelletier, 2014). It has the advantage of allowing the direct visualization of the seabed over large areas and offers better accuracy for the evaluation of abundance and taxonomic richness (Buhl-Mortensen, Buhl-Mortensen, Dolan, & Gonzalez-Mirelis, 2015; Hewitt et al., 2011). However, this non-extractive sampling method depends on water turbidity and does not always enable the identification of taxa at the lowest taxonomic levels (Ninio, Delean, Osborne, & Sweatman, 2003). A way of by-passing this issue is to use biological traits which are easily measurable by using visual census, such as position, size, fragility, mobility or feeding type, as traits can be visually determined both both at the species level and at a higher taxonomic level (i.e. genus, family, class), if an organism cannot be reliably identified at the species level by visual census

In the framework of the implementation of the ecosystem approach to fisheries (Garcia et al., 2003), it is necessary to quantify the global sensitivity of an ecosystem to fishing, including both epibenthic invertebrates and demersal species, thanks to a methodology that makes it possible to properly sample fragile taxa. By analysing together fish species and taxa that had not yet been not sampled in traditional surveys, we aimed at unveiling previously unexplored patterns of sensitivity. The main goals of this study were i) to map the sensitivity of bentho-demersal communities to trawling, ii) to disentangle the relative influence of the environmental, geographical and fishing variables on the sensitivity of communities, iii) to analyse the distribution of each trait determining sensitivity and their spatial co-variations in response to environmental and fishing gradients. We used the Celtic Sea as a case study. This area located between France, Ireland and the United Kingdom is an important fishing ground for European fisheries, exploited since the 1950s for the fishing of over 100 species, ranging from algae to top-predator fish (Guénette & Gascuel, 2012). The Celtic Sea has been heavily

exploited since the 1950s, for the fishing of over 100 species, ranging from algae to top-predator fish (Guénette & Gascuel, 2012; Mateo et al., 2017).

3.3.2 Materials and methods

Sampling design

Sampling was conducted on board the R/V Thalassa in November 2014, 2016, 2018 and 2019 during the EVHOE annual survey (part of the International Bottom Trawl Survey, Garren, Laffargue, & Duhamel, 2019) which primarily aims at providing data for stock assessments purposes. Bottom trawl sampling sites are chosen according to a random stratified design based on depth strata, occurring at fixed sites since 2016. Video sampling sites were chosen among bottom trawl sampling sites to have a balanced number of sites sampled across various sediment types. A total of 54 transects were carried out in the Celtic Sea using a camera fixed on a sledge. The sledge was towed on the seabed at an average speed of ~1.5 knots for 20 minutes. Due to the low number of transects performed each year, the four years were considered as a single timeframe to provide a good spatial coverage of the area and allow statistical analysis. On each video, individuals were identified at the lowest taxonomic level possible within the first 15 valid minutes (a minute was considered valid when at least 30 seconds could be analysed). Individuals that could not be identified at the species level were grouped at higher taxonomic levels (hereafter taxon; e.g. genus, family, order, etc…). Every taxon identifiable on video footage and present in the benthic and demersal zones (i.e. both megabenthic invertebrates living on the sediment and fish species) were considered, in order to study the whole bentho-demersal community. The density of taxa was calculated for each site, standardizing by the surface of sampled area. Transect width was calculated using pictures captured every minute. Out of the 15 pictures obtained, 10 were sampled randomly. Two lasers, placed 0.10 m apart

were used to measure the width of the view field on each picture. Transect length was calculated using the GPS of the vessel and measured 475.0 m on average (sd = 106.3 m). Transect length and an annual median width value were then used to calculate the transect surface area. The use of an annual median width made it possible to account for minor modifications of the parameter of the sledge (camera type and angle for instance) from one year to the next, while having a width value obtained from a large sample of footages, which reduced the variability in the obtained value. The sampled area per transect was 779.6 m^2 on average (sd = 301.5 m^2).

Sensitivity score

We used the trawl disturbance indicator developed by de Juan et al. (2009) to characterize the sensitivity of taxa to trawling disturbance. The index combines five biological traits: mobility, size, feeding mode, fragility and position on the substratum. Since de Juan et al. (2009), several studies have highlighted that longevity also plays an important role in the characterization of sensitivity (Hiddink et al., 2019; Rijnsdorp et al., 2018). Longevity was therefore added to the calculation of the sensitivity score (Hiddink et al., 2019; Rijnsdorp et al., 2018). Trait values for each taxa were assigned using online databases (Beukhof, Dencker, et al., 2019; A. Foveau et al., 2020; Froese & Pauly, 2010; MarLIN, 2016; Palomares & Pauly, 2019) and expert knowledge. For each trait, scores ranging from 0 to 3 were assigned based on de Juan & Demestre (2012) methodology. Longevity scores were assigned following the classification of Hiddink et al., (2019) (*i.e.* 0: <1 year; 1: 1-3 years; 2: 3-10 years; 3: >10 years) (Supplementary Table 1). Trait scores were then summed to obtain a sensitivity score per taxa. The highest values of this score correspond to the most sensitive taxa (Supplementary Table 2). The Community Weighted Mean (CWM), as defined in Gaüzère et al. (2019), is the average of the local distribution of a trait in a community (i.e. the expected value of the trait of an individual chosen randomly from the community). In our study, the CWM was calculated for

each transect, using taxa densities and either sensitivity scores (for the first part of the statistical analysis) or each trait scores separately (for the second part).. It is calculated as follows, for a community of R taxa:

$$CWM = \sum_{i=1}^{R} p_i t_i$$

with p_i the density of taxon i, and t_i the value of the trait of taxon i (sensitivity score or individual trait score in our study).

Explanatory variables

We selected anthropogenic and environmental variables known to influence the structure and functioning of ecosystems in northeastern Atlantic seas, and more specifically in the Celtic Sea: depth, sediment type, surface chlorophyll a concentration (as a proxy for productivity), bottom temperature, bottom current velocity and fishing intensity (Foveau et al., 2017; Mérillet et al., 2020; Wiedmann et al., 2014). Depth was measured using a Marport device at each transect and ranged from 71 to 216m (Fig. 1.A). Sediment type was extracted from EMODnet database (http://www.emodnet-geology.eu) when available. Missing values (2 out of the 54 sampling sites) were obtained from the French *Service Hydrographique et Océanographique de la Marine* (SHOM) world sediment map and adapted to the EMODnet classification (https://diffusion.shom.fr/loisirs/sedim-mondiale.html). Five categories were used, according to the Folk classification system: Mud to muddy sands, Sand, Coarse substrate, Mixed sediment and Rock & boulders. The Celtic Sea offers a relatively complex habitat with a substratum that is mainly composed of three sediment types (sand, mud and coarse sediments) (Fig. 1.B). Chlorophyll a (Chlo) concentrations were obtained from the OceanColour products, based on satellite observations, at a 1 km x 1 km resolution. They were higher close to the English coast in the northeastern part of the area and decreased towards the end of the

continental shelf in the South-West (Fig. 1.C). Sea bottom temperature (SBT) and bottom current (BC) data, at a 8 km x 8 km resolution, were extracted from the IBI (Iberian Biscay Irish) Ocean Physics data product, which is based on the NEMO v3.6 ocean general circulation model (Madec, 2016). SBT displayed a latitudinal gradient with warmer waters close to the French coast and colder in the northern part of the area, close to the Irish coast (Fig. 1.D). BC was more homogeneous with an increase close to the coasts and close to the continental margin (Fig. 1.E). These three environmental variables (Chlo, BC and SBT) were downloaded from Copernicus (http://marine.copernicus.eu/). Annual mean values were estimated by averaging mean monthly values over the year preceding the sampling campaign. Depth, Sediment type, Chlo, BC and SBT will hereafter be referred to as "environmental variables".

The latitude, longitude and longitude × latitude interaction were obtained from the vessel GPS for each transect during the field campaign. These variables will hereafter be referred to as "geographical variables".

The International Council for the Exploration of the Sea, as a technical service of the OSPAR Convention (Convention for the Protection of the Marine Environment of the North-East Atlantic), produced spatial data layers on fishing intensity (ICES, 2018c) based on VMS data, at a 0.05° x 0.05° (approximately 5.5km x 5.5km) resolution for the *métiers* in contact with the seabed and thus likely to impact it (beam trawl, dredge, demersal seine and otter trawl). The total Surface Swept Area Ratio (SurfSAR), which is the proportion of the estimated swept area of the surface of each grid cell, was used as a proxy for fishing intensity. As these spatial data were only delivered up to 2017, the mean was calculated at every transect location (from 2013 to 2017) and used for 2018 and 2019, since, on visual inspection, fishing effort seemed stable through space and time (Supplementary Figure 1). The data showed a strong spatial heterogeneity at a small scale and no clear gradient of fishing intensity was observed. However,

the highest fishing intensities were observed in the northeastern region and lower intensities on the deeper continental shelf, close to the continental slope (Fig. 1.F).

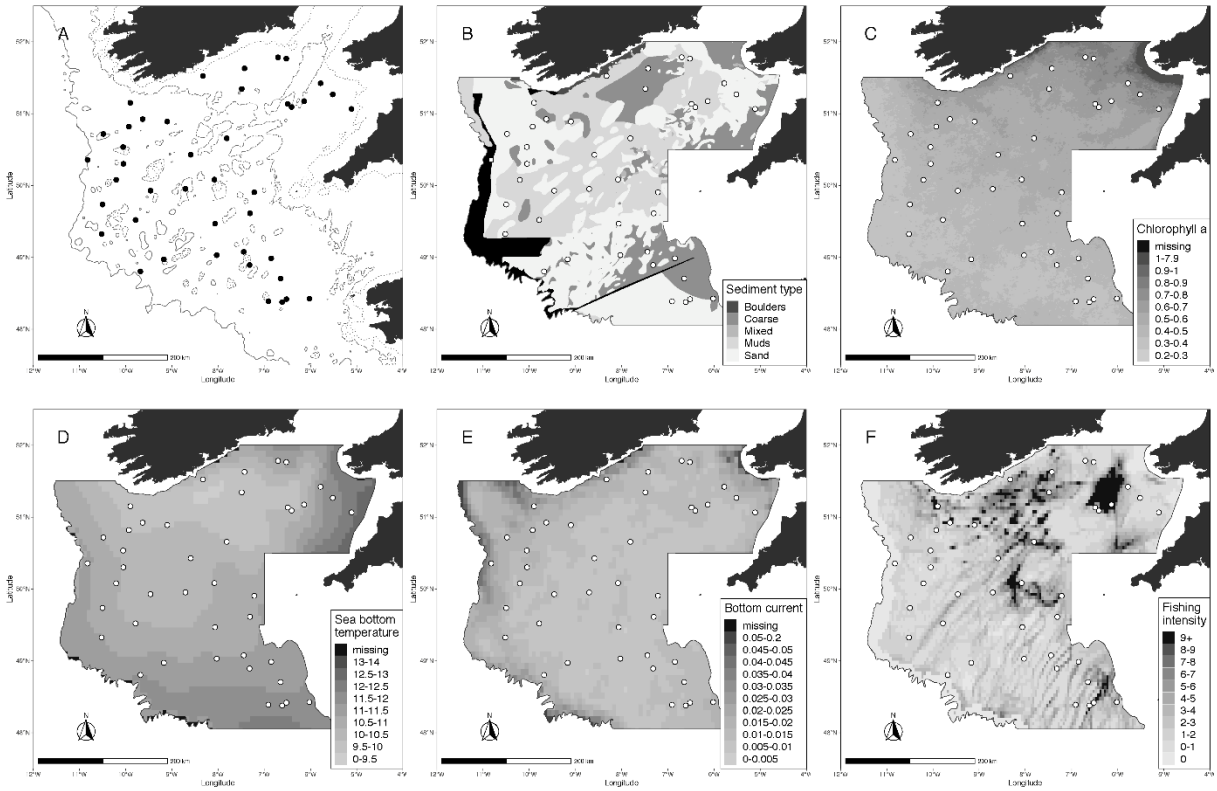

Figure 1: Maps of environmental variables and fishing intensity in the Celtic Sea. (A) Depth: 60, 100, and 200m isobaths (dotted, dashed and solid black lines respectively). (B) Sediment type, from EMODNet data, for all stations represented as white dots. The white square represents the transect for which the sediment type was missing in the EMODNet data and therefore adapted from SHOM data (classified as Sand). (C) Mean chlorophyll a concentration, expressed in mg.m^{-3}. (D) Mean sea bottom temperature, in °C. (E) Mean bottom current expressed in m.s^{-1}. The mean values, represented in maps (C) to (E) were calculated with the four datasets from which the data at transects was extracted (2014, 2016, 2018 and 2019). (F) Mean Surface Swept Area Ratio (SurfSAR) calculated with OSPAR data from 2013 to 2017. In every map, dots represent transect locations.

Statistical analysis

To test the relationship between explanatory variables and the CWM of the sensitivity score, a Generalized Linear Model (GLM) was performed, with a Gaussian link function. All quantitative variables were scaled to enable the comparison of their marginal effect on the sensitivity score, and geographical variables were centred in order to reduce multicollinearity (Legendre & Legendre, 1998). The collinearity among fishing intensity, environmental, and geographic variables was assessed using the Variance Inflation Factor (VIF), and a release threshold of 10 (Borcard, Gillet, & Legendre, 2011). As autocorrelation was detected in the data (Moran's I = 0.49, pval= 0.002) and because it improved the fit of the model (preliminary analysis, not shown), spatial terms were included in the model, i.e. longitude (Long), latitude (Lat), longitude × latitude (LongLat).

The best model was selected based on the lowest Akaike Information Criterion (AIC), which allows to select the model presenting the best trade-off between the goodness-of-fit and the number of model parameters (Borcard et al., 2011). The goodness-of-fit of the final model was assessed using an adjusted R^2 and a χ^2 statistic, and the spatial autocorrelation in the residuals was checked using a permutation test on Moran's I statistic, and the Gaussian distribution of the residuals was tested using a Shapiro-Wilk test.

To test covariations between environmental and fishing variables and the distribution of the different traits related with sensitivity while partialling out their interaction, a community weighted mean-redundancy analysis (CWM-RDA) was performed, using the CWMs of each trait (Mobility, Size, Feeding, Fragility, Position and Longevity) at the transects (Kleyer et al., 2012; Vandewalle et al., 2010). The CWM-RDA combines ordination methods with multi-linear regression in order to represent the traits as linear functions of the environment. It therefore analyses the relationship between a matrix of scaled trait CWMs and a matrix of scaled explanatory variables (Kleyer et al., 2012). The best CWM-RDA model was then selected based on the lowest AIC value and model, axis and variable significance were assessed using

permutation tests. The goodness-of-fit of the final model was assessed using an adjusted R^2. Transects were clustered using a K-means clustering algorithm on the RDA scores of the first two axes, and the optimal number of clusters was determined using the Calinski-Harabasz criterion. Explanatory variables and CWMs were then characterized at the transects of the different clusters, by performing Pearson's χ^2 tests between cluster values and overall values. As this characterization consisted in performing a total of 54 tests, a Bonferroni correction was performed on the p-values, and the tests were considered significant with adjusted p-values inferior to $\alpha = 0.05$.

All analyses were performed using the statistical software R v.3.6.3 (R Core Team, 2020) with the following packages and functions: "FD" v.1.0-12 (Laliberté et al., 2014); "car" v.3.0-7 (Fox & Weisberg, 2019); *stepAIC* function from "MASS" v.7.3-51.5. (Venables & Ripley, 2002); *moran.mc* from "spdep" v.1.1-3 (Bivand & Wong, 2018); *catdes* function from "FactoMineR" v.2.3 (Lê, Josse, & Husson, 2008).

3.3.3 Results

Sensitivity index and Community Weighted Means

A total of 23,243 individuals from 55 taxa were identified over the 825 minutes of observation (Supplementary Table 2). 95 % of these individuals belong to 20 taxa and the three most abundant taxa (*Actinauge spp.*, Hydrozoa and Polychaeta) comprised 54 % of all the observed individuals. Theoretical sensitivity score can range from 0 (all trait values set to zero) to 18 (all trait values at 3). Sensitivity scores per taxa ranged from 4 (*Munida spp.*, which is a small, deep-burrowing, scavenger taxon) to 17 (*Funiculina quadrangularis*, which is a fixed, filter feeding, emergent species with a size of more than 30 cm) in our study, with a median score of 11 (Supplementary Table 3).

Values of CWMs of the sensitivity score ranged from 9.0 to 14.7, with a median of 11.7 (sd = 1.19).. CWMs displayed a heterogeneous spatial distribution, with increasing values from the North-East to the South-West (Fig. 2). Smaller values, which indicate less sensitive communities, were observed in the area between Ireland and the UK. In the other part of the Celtic Sea, where more sensitive communities were observed, two sub-regions were visible, one with homogeneous values of sensitivity between transects, in the South-East, and another one with stronger sensitivity variations in the West (Fig. 2).

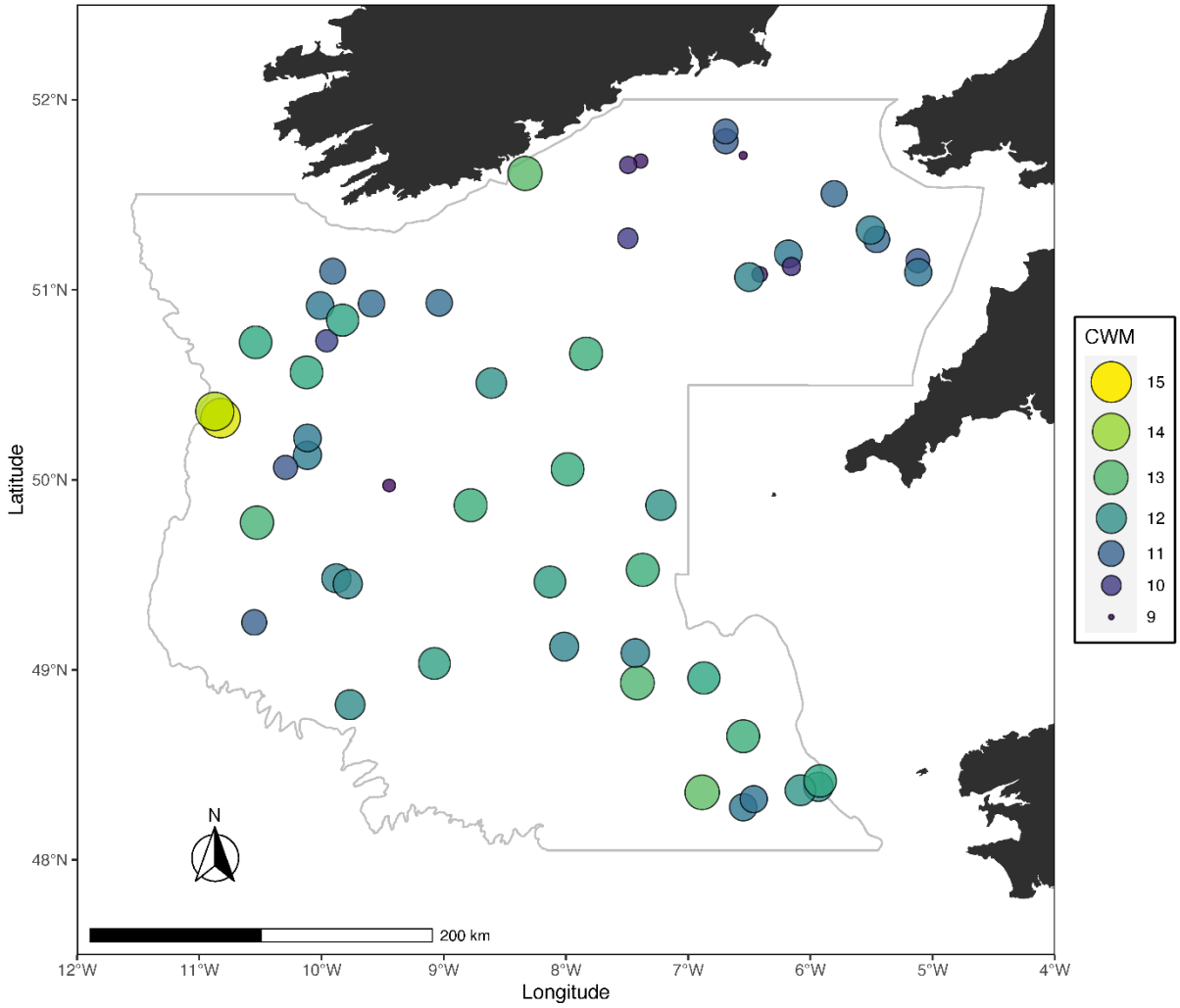

Figure 2: Community Weighted Means of the sensitivity score at transects. The position_jitter function from the package ggplot2 was used to slightly modify transect positions and facilitate visualization. The grey line represents the studied area.

Environmental drivers of sensitivity patterns

The model that elucidated best the spatial pattern of the CWM sensitivity score included depth, chlorophyll a, fishing intensity, latitude, longitude and latitude x longitude interaction (Table 1). The selected model accounted for ~ 60% of the observed variance (R^2_{step} = 0.58). The permutation test on Moran's I statistic showed no significant spatial autocorrelation in the residuals (*p-value* = 0.60) and residuals' distribution was not significantly different from a Gaussian distribution (Shapiro test: *p-value* = 0.09).

The GLM on CWM sensitivity score showed that sensitivity to trawling pressure of communities has a positive relationship with latitude (coefficient: 0.67; standard error: 0.25) and longitude (coefficient: 0.73; standard error: 0.21), but a negative effect of the longitude x latitude interaction (coefficient: -0.42; standard error: 0.18) showed an additional effect of an anisotropic gradient. Depth had the strongest influence on sensitivity scores, as its coefficient had the highest absolute value (3.83; standard error: 0.90), with an increase in depth being correlated with an increase in community sensitivity. The two most sensitive communities (sensitivity indexes: 14.3 and 14.7) were observed at the deepest transects (206 m and 216 m respectively), and the least sensitive (sensitivity index: 9.0) at the shallowest transect (71 m). The robustness of the correlation between depth and sensitivity was tested and showed little influence of these extreme points (results not shown). Both chlorophyll a concentration (i.e. productivity), and fishing intensity had a negative impact on the sensitivity of communities (coefficients -1.70; standard error: 0.65 and -0.61; standard error: 0.18 respectively).

Characterization of the different communities

The best CWM-RDA model selected, fitted on the CWM of each trait, is presented in Figure 3. Locations of a trait label correspond to a high score, *i.e*. close to 3, for the given trait (see Supplementary Table 2 for a detail of the scores for each trait). Angles between response variables (trait scores), explanatory variables (fishing intensity and environment), and between response and explanatory variables reflect their correlation (Borcard et al., 2011). The selected model included chlorophyll a concentration, depth, longitude, longitude x latitude interaction as well as fishing intensity, and accounted for 46.8 % of the total observed variance, with an adjusted R^2 of 0.41 (p-value = 0.001). The first two axes of the CWM-RDA were found to be significant (p-values = 0.001 and p-value = 0.003 respectively) and accounted for 36.5 % and 9.2 % of the observed variance. The first CWM-RDA axis was strongly correlated with chlorophyll a concentration (biplot score = 0.83), depth (-0.79) and longitude x latitude interaction (0.74) and showed lower correlations with longitude (0.35) and fishing intensity (0.33). The first CWM-RDA axis therefore represented a spatial gradient from deep transects with low chlorophyll a concentration and little fishing intensity, to shallower transects with high chlorophyll a concentration and higher fishing intensity. It allowed good discrimination of trait responses to explanatory variables. It showed correlations between mobility and feeding mode, and presented higher scores in deeper, less productive transects, which highlights the high proportion of sessile and filtering organisms in the deepest area. Fragility and position on the substratum also seemed correlated, since they presented higher scores in an intermediate position on the depth-chlorophyll gradient. Finally, the more long-lived taxa appear to be found in shallow and productive transects. The second CWM-RDA axis was strongly correlated with longitude (biplot score = -0.79) and showed correlation with depth (0.50) and fishing intensity (-0.39). It confirmed a geographical gradient of fishing intensity, visible in the data (Fig. 1.F), which increased towards shallower waters in the North-East. The discrimination of trait

responses to variables by the second axis was much lower than the one by the first axis. The second CWM-RDA axis showed a tendency to higher longevity and lower mobility towards the West as well as a tendency to more fragility, a higher position on the substratum and a larger size towards the East.

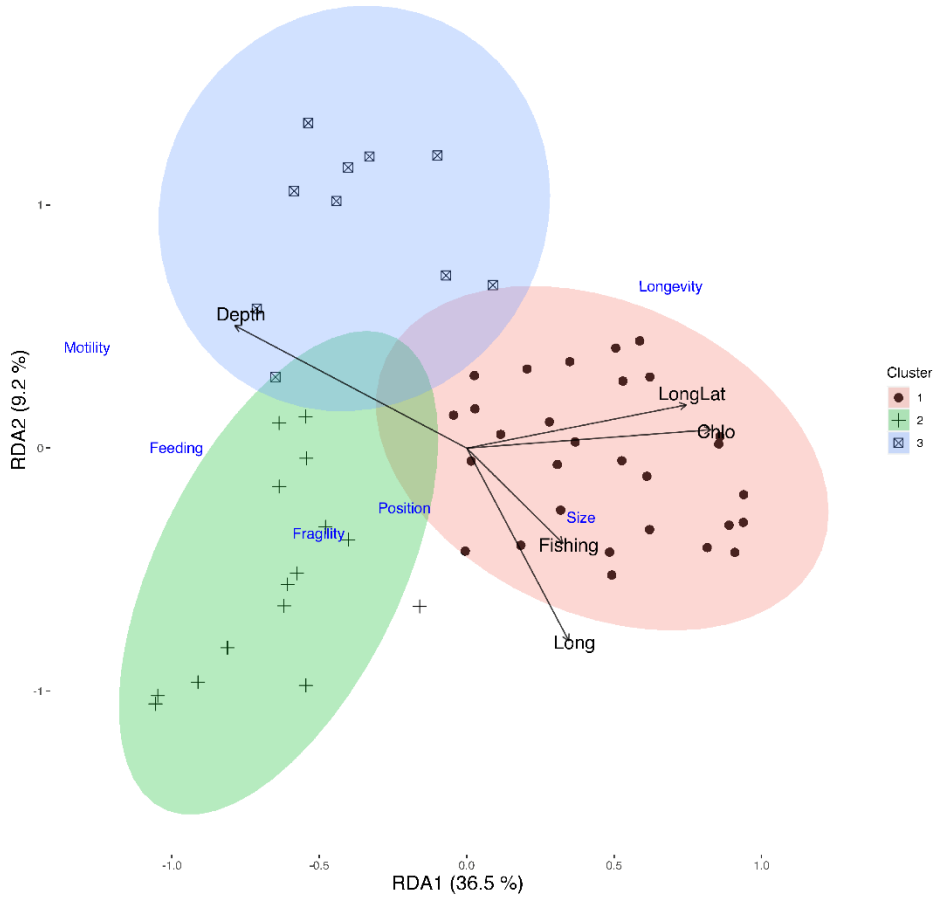

Figure 3: Biplot of the Community Weighted Mean-Redundancy Analysis, performed on trait scores CWMs, constrained by explanatory variables. Percentages on axis are the percentage of the total observed variance explained by the axis. Because traits are coded using increasing numeric numbers, the location of a trait label corresponds to high scores of the given trait. For example, motility and depth show a correlation, meaning that deeper transects present high motility sensitivity scores (i.e. a high proportion of sessile organisms – score = 3 – and a low proportion of mobile organisms – score = 0).

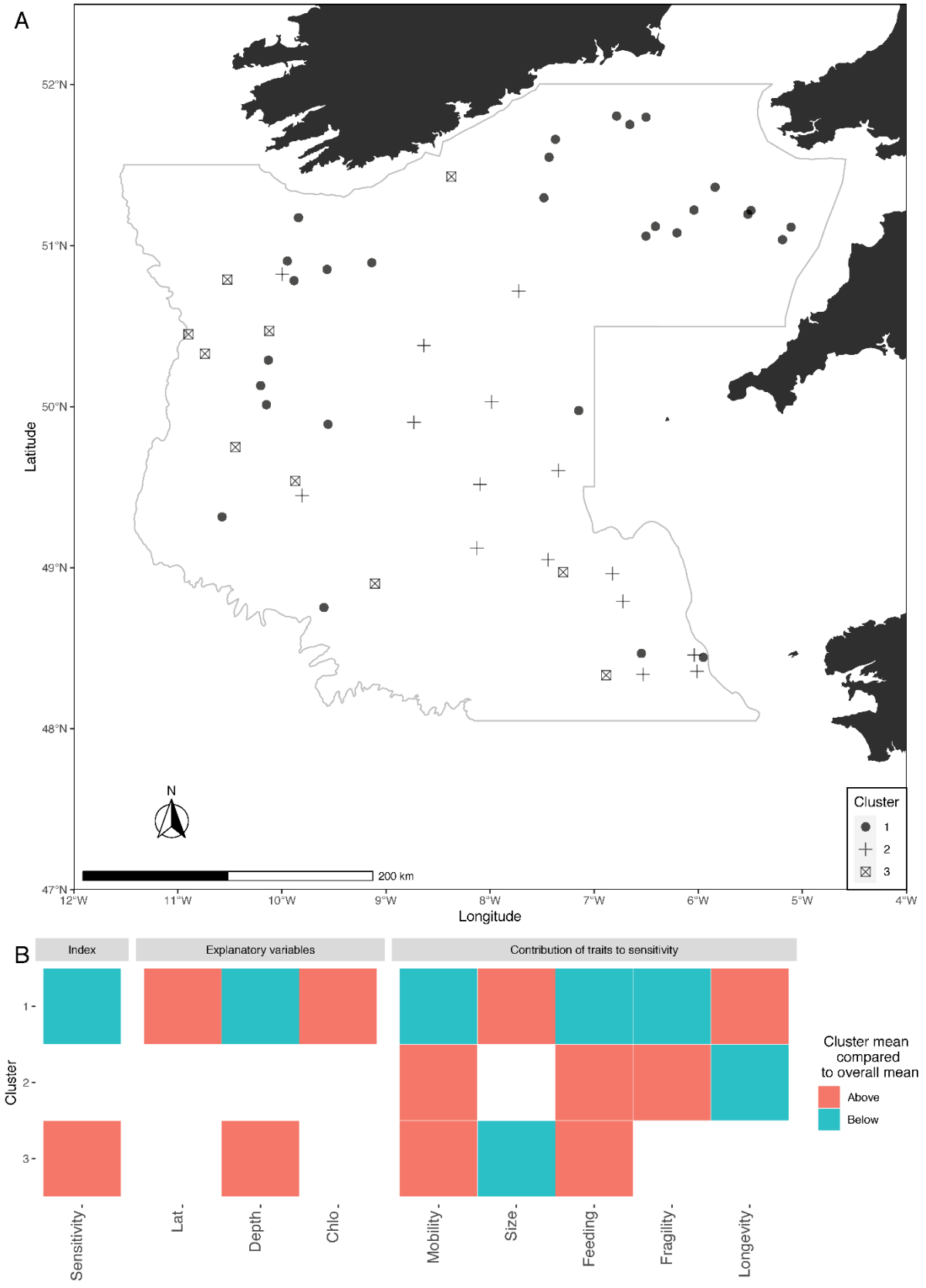

Figure 4: Characterization of the clustering performed on the RDA scores. (A) Map of the transects, point shapes represent the group in which the transect is clustered. (B) Mean values

of each cluster compared to overall mean values, for sensitivity, explanatory variables, and trait scores. Red cells represent higher mean cluster values, blue cells lower mean cluster values and white cells no significant difference (corrected p-value of Pearson's χ2 test > 0.05). Only the variables and traits for which a Pearson's χ2 test was significant for at least one cluster are represented.

The optimal number of clusters was three according to the Calinski-Harabasz criterion. The first cluster was separated from the two others according to the first CWM-RDA axis, and the second axis allowed the discrimination of clusters 2 and 3 (Fig. 3). The first cluster gathered the highest number of transects (*i.e.* 29 transects) and was significantly less sensitive to trawling (score = 10.8) than the overall mean (11.7; corrected p-value of the χ^2 test: 3.58×10^{-6}) (Fig. 4). It comprised all the communities sampled from transects between Ireland and the UK, and from other transects, mainly in the North-West (Fig. 4.A). It was composed of communities present in shallow waters, mainly in the North of the Celtic Sea, in an area with high primary production (significantly higher chlorophyll a concentrations) (Fig. 4.B). As expected from the CWM-RDA biplot, these communities presented lower sensitivity due to their mobility characteristics, suggesting a higher proportion of swimming and crawling organisms and a lower proportion of sessile organisms. It was also characterized by a lower proportion of fragile organisms, and of filter feeders. However, they were also characterized by high sensitivity due to size, as well as longevity, thus suggesting a higher proportion of long-lived taxa of a large body size (Fig. 5.A & 5.B, Supplementary Figure 2).

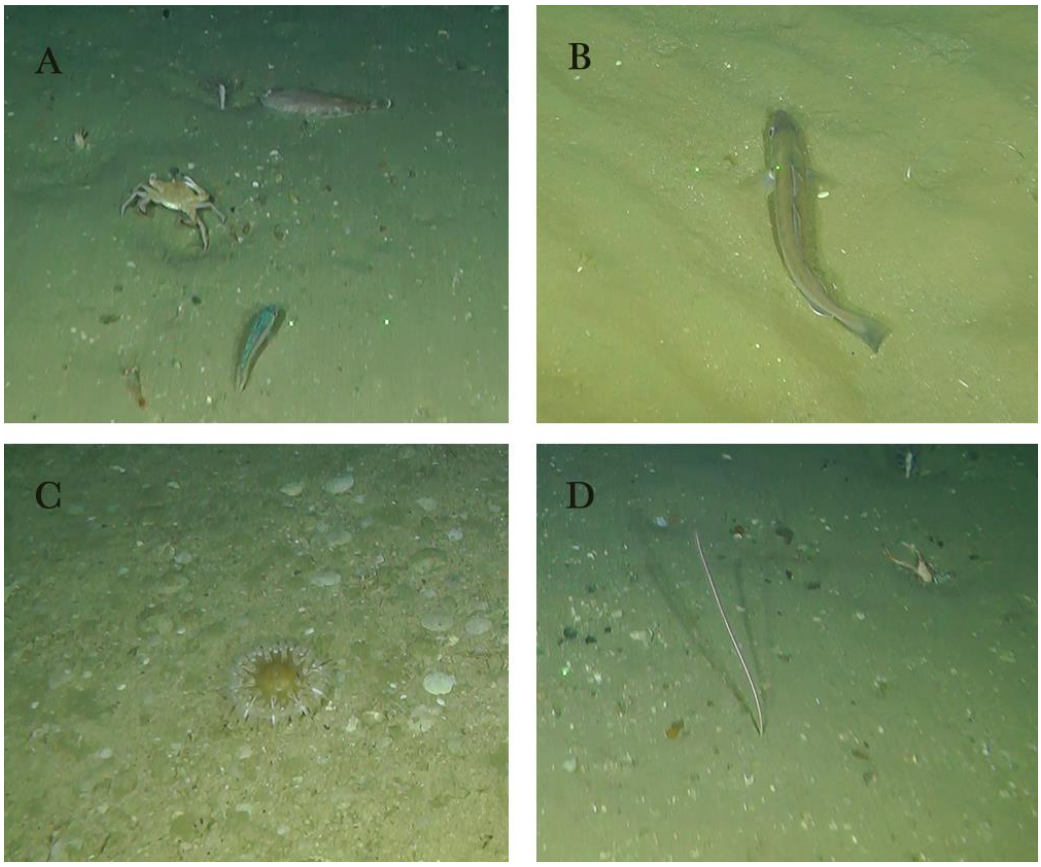

Figure 5: Images of representative communities or taxa found in the different clusters. Cluster 1 located mostly in the North-Eastern region, whose sensitivity tends to be lower than average for most traits, high proportion of highly mobile (A, Scomber scombrus, Pleuronectiforme; B, Merlangius merlangus) and deposit feeding taxa (A, Brachyura). Cluster 2 whose sensitivity tends to be slightly higher than average, with a high proportion of short-lived, sessile, filter-feeding organisms (C, Actiniaria). Cluster 3, whose sensitivity is above average, with a high proportion of emergent, sessile, filter-feeding (D, Funiculina quadrangularis) as well as small-sized taxa (D, Munida spp.).

The second cluster, composed of 15 transects, was slightly more sensitive (score = 12.3) than the overall mean (11.7), but insignificantly. It was mainly located in the South-East of the study area (Fig. 4.A). The communities clustered in this group presented low sensitivity in regard to longevity (more short-lived taxa) but they showed higher sensitivity due to mobility

(more sessile taxa), fragility (more fragile taxa), feeding mode (more filter-feeder taxa) and position on the substratum (emergent/demersal taxa) (Fig. 4.B & 5.C, Supplementary Figure 2).

The last cluster comprised 10 transects and the highest mean sensitivity (score = 13.0; corrected p-value of the χ^2 test: 2.23×10^{-3}). It included transects mainly located in the West of the study area, in deep waters (Figure 4). Similarly, to the second cluster, it was composed of communities characterized by higher sensitivity due to mobility (more sessile taxa) and feeding mode (more filter-feeder taxa) (Figures 4.B & 5.D). Its communities were also characterized by lower sensitivity due to size, hence a higher proportion of small organisms (Supplementary Figure 2).

3.3.4 Discussion

Characterizing the sensitivity of communities to trawling pressure and determining the underlying biological processes is of great interest among the diversity of ecosystem-based indicators. In this study, we characterized the sensitivity to trawling of bentho-demersal communities in the Celtic Sea, a very productive ecosystem for European fisheries, thus adapting an indicator developed by de Juan et al. (2009) by adding longevity. Using the Community Weighted Mean (CWM) of this sensitivity indicator and the CWMs of each trait individually, we characterized three community archetypes. The Celtic Sea can be partitioned into two main regions, a northeastern area close to the Irish Sea, and an area closer to the continental slope. The northeastern region, between Ireland and the UK, already observed in previous studies (Mateo et al., 2017; Mérillet et al., 2020) is dominated by communities whose sensitivity score tends to be lower than average for most traits. Its low sensitivity to trawling is explained by a high proportion of highly mobile, deposit-feeding organisms together with a low proportion of fragile organisms. The second region identified, which stretches along an arch

from the Irish coast to French Brittany, is more heterogeneous and presents transects from each of the three clusters. The two groups, encountered only in this area, present a similarity: higher sensitivity than in the northeastern part explained by the presence of a higher proportion of fixed and filter-feeding organisms. However, the most sensitive of these two groups is essentially located in the deepest waters and characterized by the presence of small-sized organisms while the other one is only slightly more sensitive than the overall mean (not significantly) and characterized by the presence of fragile but short-lived organisms.

Community sensitivity is mainly determined by a spatial gradient from shallow, productive areas in the Northeast to deep and less productive areas close to the continental slope, with the most sensitive communities being found in the deeper and less productive transects. These findings are consistent with (Pecuchet et al., 2018), who showed, in a study on the North Sea, that a depth-productivity gradient was an important factor that shaped the distribution of the life-history traits related to sensitivity of the community (e.g. feeding mode, size and fecundity). Deep communities are characterized by higher proportions of fixed, filter-feeding, and small body-sized organisms. Nevertheless, across many ecosystems, deep-water fish communities generally exhibit larger body sizes than inshore communities (Mindel, Webb, Neat, & Blanchard, 2016; Pecuchet et al., 2018). This pattern was not observed in our study probably because of the small depth range considered (from 71 m to 216 m) and the wide range of organism considered (benthos and fish). Indeed, the larger abundance of small sized organisms toward deeper area is caused by the presence of particular taxa in certain areas: small size filter-feeders such as Hydrozoa and *Caryophyllia spp*. in deep transects while shallower transects display a higher proportion of large size fish species. Sensitivity scores and CWM of traits may hence be driven by dense populations of a few taxa (e.g. crinoids in the Bay of Biscay, Mérillet et al., 2018). Finally, a lower level of natural disturbance in deeper transects could also explain the presence of more sensitive communities (Mengual et al., 2016).

Surface productivity also influences community sensitivity to trawling: communities present in productive areas are less sensitive, and characterized by highly mobile, deposit-feeding and long-lived organisms. However, productivity is usually linked with high proportions of filter-feeding and short-lived organisms (Pecuchet et al., 2017, 2018). The patterns observed here could result from the high trawling pressure exerted over the area that hampers the presence of filter feeding but not of deposit feeding organisms. In addition, the proxy for productivity used in this study is chlorophyll a concentration which represents productivity at sea surface. To the best of our knowledge, spatio-temporal index of benthic productivity is not available in our study area. However, through strong bentho-pelagic coupling over continental shelf, it is commonly accepted that surface productivity can have an indirect impact on bentho-demersal communities, especially invertebrates. Other factors which were not significant in our study, such as bottom current, could also influence seabed productivity and food availability for filter-feeding species, and hence influence the abundance of these species as well as community sensitivity (Foveau et al., 2017; Van Denderen et al., 2015). Moreover, an upwelling close to the shelf break in the Celtic Sea brings nutrients from deeper waters and could provoke a decoupling between surface productivity and food availability in the seabed (Joint et al., 2001; Pingree & Mardell, 1981; Sellers, Leung, & Torchin, 2020).

As expected community sensitivity was negatively impacted by fishing intensity, although to a lesser extent than environmental variables. Our results showed that areas subjected to high fishing pressure exhibit communities that are faintly sensitive to fishing. Indeed, the history of fishing disturbance is likely to influence abundance and species richness on a long-term basis (Sciberras et al., 2018), depending on the community recovery time, which could take more than 20 years for some species (Hiddink et al., 2017; Kaiser, Hormbrey, Booth, Hinz, & Hiddink, 2018). The Celtic Sea has been heavily exploited since the 1950s, with major

changes occurring in the 1950-1970s, followed by a decreasing trend of fishing mortality reported since the mid-1990s, with both fishing and environment acting as the main drivers on these ecosystems from 1985 onward (Guénette & Gascuel, 2012; Hernvann & Gascuel, 2020; ICES, 2018a; Mateo et al., 2017). Hence, in accordance with Mérillet et al. (2020) and (Hily, Le Loc'h, Grall, & Glémarec, 2008), our study strongly suggests that bentho-demersal communities were already shaped by a long history of mixed fisheries: areas of the Celtic Sea subject to high fishing pressure since the 1950s are now occupied by less sensitive communities, and present a lower proportion of; fixed and filter-feeding organisms. Similar results were also observed in other European seas, such as the Kattegat (Pommer et al., 2016). However, environmental and fishing variables act in synergy on community's sensitivity and sensitive taxa could also be naturally abundant in areas where fishing intensity is lower, because these areas could be too deep, or too rocky for example. Due to the absence of a known reference state, we cannot assess in detail the extent to which fisheries have shaped community composition and its sensitivity. In addition, the predictor variables used are averaged values in cells of size 1 km x 1 km to 8 km x 8 km depending on the variable. Hence, the value obtained for each transect might not reflect small-scale environmental conditions. Nevertheless, data at a finer scale were not available.

Most studies that assess the impact of environmental and fishing variables on community sensitivity in coastal waters, focused either on benthic communities (de Juan & Demestre, 2012; Jørgensen et al., 2019; Sciberras et al., 2018; Van Denderen et al., 2015) or on benthic and pelagic communities separately (Pecuchet et al., 2018). Considering bentho-demersal communities as we did in our study, may impair some signals often observed when focussing only on benthic communities. More precisely, sediment type seems to be an important factor which influences benthic community sensitivity (Bolam et al., 2014; Hily et al., 2008; Merillet et al., 2017). However, when including mobile fish species, less dependent on

substrate, we could not find any significant influence of sediments. Assessing fish and epibenthos sensitivity separately would have allowed to better focus on specific underlying mechanisms but would have led to a less global view of the ecosystem. This study considering both epibenthic invertebrates and fish allows to consider emergent and more integrated patterns.

Assessing community sensitivity as a whole is a stepping stone toward a more integrated ecosystem assessment of fishing impact. The implementation of an ecosystem approach to fisheries management necessitates opting for a more holistic understanding of the effects of fishing on community structure and ecosystem functioning (Garcia et al., 2003). It refers to several management goals and methods (Morishita, 2008), including multi-species management and the protection of vulnerable habitats (Jennings, 2005; OSPAR, 2018). Here, we implemented a multi-specific indicator, which included both benthic epifauna and fish species, and makes it possible to determine the most sensitive communities, and by extension to locate vulnerable habitats. This indicator focuses on only one aspect of vulnerability: the degree to which communities will respond to trawling pressure (ie. sensitivity) (ICES, 2017), can be assessed by calculating fishing effort, through vessel monitoring system (VMS) data, fishing gear characteristics and catch compositions. However, here community exposure to fishing pressure was not assessed in our study due to lack of spatial precision in the catch (landings and discards) data at international level and biomass estimates for non-commercial taxa. Moreover, accessibility to international fine scale VMS data and information on *métier* for research purposes are still challenging, despite recent advances (Skaar, Jørgensen, Ulvestad, & Engås, 2011)

The integrative indicator used here enabled to highlight several areas whose sensitivity to fishing was due to different components of the ecosystem (sessile filter feeders and large fishes). As a complementary tool, we better characterized the spatial patterns of sensitivity to trawling by considering the different traits separately. As the modified De Juan indicator could

thus be particularly useful in spatial planning, underwater video surveys should be largely deployed for better spatial and temporal coverage. Modelling its evolution in response to a homogeneous decrease in fishing intensity could allow the determination of spatial or temporal restrictions in fishing which would favour the conservation or the recovery of the most sensitive communities to fishing. It is then possible to predict the area where sensitivity would be the highest and infer where the fishing area closure would be the most interesting to place. If applied on a long-term basis, this methodology could provide valuable information on the temporal dynamics of communities' sensitivity in response to changes in fishing intensity and to climate change.

Acknowledgement

We thank all those who made data sampling possible during the EVHOE surveys.

3.3.5 Supplementary materials

Supplementary Table 1: List of transects per year with their corresponding coordinates. Some transects have the same rounded coordinates, but the realised video sampling haul was not exactly at the same location. We thus considered there were no repeatedly sampled transects.

Transect	Year	Long	Lat
1	2014	-5,7801	51,4225
2	2014	-6,1371	51,1741
3	2014	-6,4067	51,0902
4	2014	-6,5228	51,7655
5	2014	-9,8975	51,1510
6	2016	-5,1103	51,0654
7	2016	-5,5168	51,2675
8	2016	-6,0210	48,4255
9	2016	-6,1371	51,1741
10	2016	-6,4895	51,1342
11	2016	-6,7015	51,7843

12	2016	-7,2148	49,9046
13	2016	-7,4271	51,6295
14	2016	-7,4869	51,3447
15	2016	-9,9280	50,8193
16	2018	-6,0210	48,4255
17	2018	-6,5202	48,4173
18	2018	-6,6127	48,3770
19	2018	-6,7015	51,7843
20	2018	-7,3177	48,8928
21	2018	-8,3277	51,5247
22	2018	-8,5911	50,4278
23	2018	-9,4616	49,9274
24	2018	-9,6321	50,9233
25	2018	-9,7855	49,5207
26	2018	-9,9280	50,8193
27	2018	-10,0486	50,3014
28	2018	-10,2050	50,0783
29	2018	-10,4820	50,7173
30	2018	-10,4998	49,7353
31	2018	-10,5192	49,3240
32	2018	-10,8239	50,3556
33	2019	-5,1103	51,0654
34	2019	-5,5168	51,2675
35	2019	-6,0210	48,4255
36	2019	-6,6462	48,7049
37	2019	-6,8485	48,986
38	2019	-6,9100	48,3875
39	2019	-7,3083	49,6119
40	2019	-7,4271	51,6295
41	2019	-7,4433	49,0767
42	2019	-7,8118	50,6567
43	2019	-8,0292	49,0300
44	2019	-8,0648	49,469
45	2019	-8,0789	50,0828
46	2019	-8,7049	49,9524
47	2019	-9,0988	50,8894
48	2019	-9,1707	48,9718
49	2019	-9,6798	48,8031
50	2019	-9,7855	49,5207
51	2019	-9,9280	50,8193
52	2019	-10,0529	50,5352
53	2019	-10,2050	50,0783
54	2019	-10,8239	50,3556

Table S2: List of biological traits and assigned score in relation with sensitivity to trawling impact

Sensitivity score	Position	Feeding	Mobility	Size	Fragility	Longevity
0	Deep burrowing	Scavengers	Highly mobile, swimming	Small (<5cm)	Hardshell, vermiform, regeneration	<1year
1	Surface burrowing	Deposit feeders, predators, opportunistic scavengers	Mobile, crawling	Medium (5-10cm)	Softshell	1-3years
2	Surface	Planktonophage, filter feeders that can select their preys (eg. anemones)	Sedentary, can retract	Large (10-30cm)	No protection	3-10years
3	Emergent, demersal	Filter feeders	Sessile, attached	Very large (>30cm)	Fragile shell, structure	>10years

Table S3: Number of individuals, score by trait and sensitivity score per taxa

Taxa	Number of individuals	Motility	Size	Feeding	Fragility	Position	Longevity	Sensitivity
Actinauge spp.	4489	3	1	3	2	3	3	15
Hydrozoa	4247	3	1	3	3	3	0	13
Polychaeta	3963	2	2	1	2	2	2	11
Caryophyllia spp.	1911	3	0	3	2	2	3	13
Actiniaria	1215	3	1	3	2	2	3	14
Scomber spp.	1042	0	2	1	2	3	3	11
Paguroidea	972	1	0	0	0	2	2	5
Ophiuroidea	555	1	1	0	3	2	2	9
Pennatula phosphorea	542	3	2	3	2	2	3	15
Funiculina quadrangularis	515	3	3	3	2	3	3	17
Clupeiformes	424	0	2	2	2	3	3	12
Actinopterygii	410	0	1	2	2	3	3	11
Gastropoda	343	1	1	0	0	2	3	7

Asteroidea	341	1	2	0	2	2	2	9
Trachurus spp.	295	0	3	1	2	3	3	12
Crinoidea	204	3	0	3	3	2	2	13
Sabellidae	188	3	2	3	3	3	2	16
Pleuronectiformes	179	0	3	0	2	1	3	9
Lepidorhombus spp.	136	0	2	1	2	2	3	10
Caridea	119	1	0	1	1	2	2	7
Triglidae	116	0	2	1	2	2	3	10
Melanogrammus aeglefinus	115	0	3	1	2	3	3	12
Capros aper	113	0	2	2	2	3	3	12
Trisopterus spp.	111	0	2	1	2	3	2	10
Echinoidea	108	2	2	1	3	2	2	12
Decapodiformes	86	0	2	1	2	3	1	9
Argentina spp.	73	0	2	2	2	3	3	12
Brachyura	54	1	1	0	1	2	3	8
Micromesistius poutassou	51	0	2	2	2	3	3	12
Anthozoa	47	3	1	3	3	3	3	16
Scyliorhinus spp.	46	0	3	0	2	2	3	10
Octopodiformes	42	0	2	1	2	2	2	9
Munida spp.	23	1	0	0	1	0	2	4
Maurolicus muellieri	21	0	1	2	2	3	2	10
Veretillidae	21	3	2	3	2	3	3	16
Pectinidae	18	1	1	3	0	2	3	10
Alcyoniidae	16	3	1	3	3	3	3	16
Nephrops norvegicus	16	1	2	0	1	0	2	6
Merlangius merlangus	14	0	3	1	2	3	3	12
Lophius spp.	12	0	3	1	2	1	3	10
Bryozoa	7	3	0	3	3	3	2	14
Merluccius merluccius	7	0	3	1	2	3	3	12
Rajidae	5	0	3	1	2	1	3	10
Atrina spp.	4	2	2	3	3	0	3	13

Gadiculus argenteus	4	0	1	2	2	3	2	10
Selachii	4	0	3	1	2	2	3	11
Ascidiidae	3	3	1	3	3	3	2	15
Holothuria	3	2	2	3	2	2	2	13
Scalpellum scalpellum	3	3	0	3	3	2	0	11
Conger conger	2	0	3	0	2	2	3	10
Nudibranchia	2	1	1	1	2	2	0	7
Syngnathus spp.	2	0	2	1	2	2	1	8
Zeus faber	2	0	3	1	2	3	3	12
Maja spp.	1	1	2	0	1	2	2	8
Mullus surmuletus	1	0	2	1	2	3	3	11

Figure S1 : Fishing intensity in the Celtic Sea, obtained from the ICES. Total Surface Swept Area Ratio (SurfSAR) in 2014 (A), 2016 (B), and mean SurfSAR using yearly values from 2013 to 2017 (C). In every map, the dots represent the transects for which fishing intensity values were extracted from the given year.

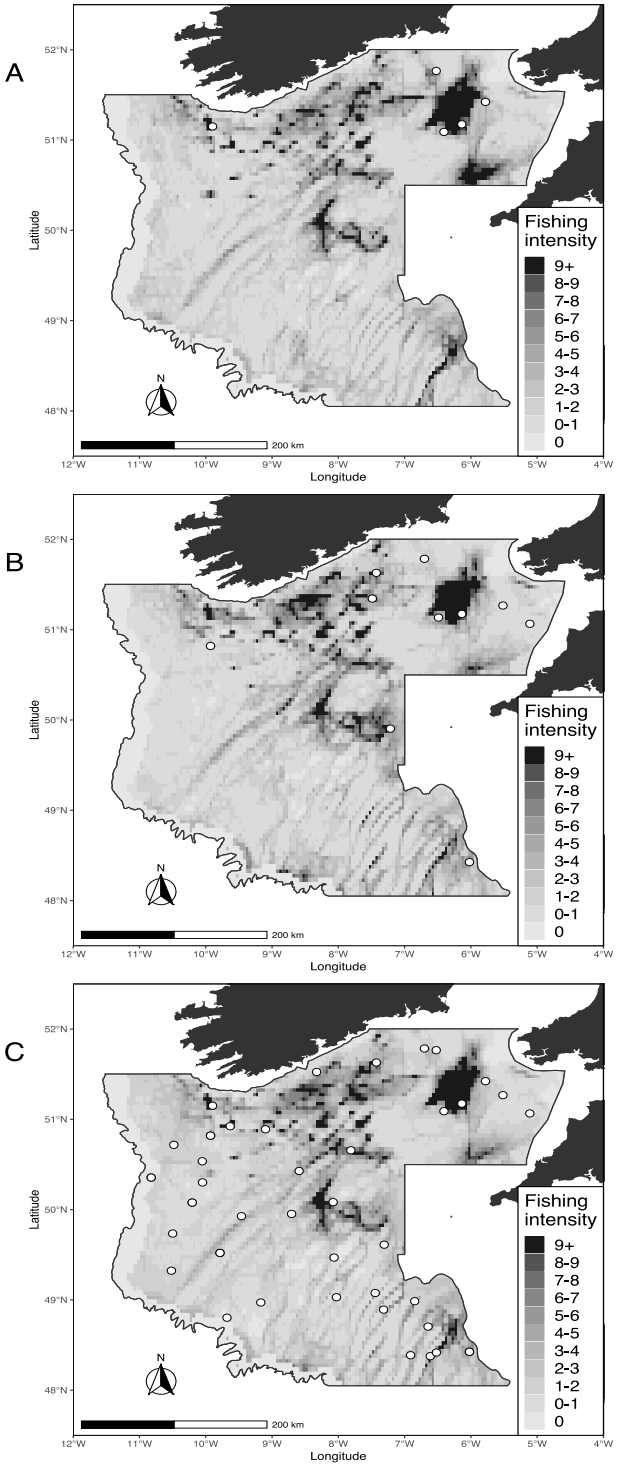

Figure S2 : Mean repartition of trait modalities in the three clusters. Categories corresponding to each modality are presented in Supplementary Table 1.

4 Chapter C

Trophic network in the Celtic Sea is robust to the loss of sensitive taxa to fishing but less robust to the loss of basal and the most exposed taxa

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4.1 Preface

The study of species interactions provides an important conceptual link between species communities and ecosystem functioning (Thompson et al., 2012). To ensure ecosystem integrity, a shift from a focus on the conservation of species, or functional groups, to the conservation of ecological networks is needed (Harvey et al., 2017). However, to prioritize conservation target, it is necessary to evaluate which species or functional group would be the more threaten by a perturbation and how this perturbation could spread to other components of the network. In particular, it is not clear whether sensitivity to a pressure at the level of species imply a lower robustness of the network to that pressure. In chapter 2, we showed that the biomass of taxa with slow life history traits has increased in the Celtic Sea, related to the implementation of an area closure. However, the Celtic Sea have been and is still heavily fished so we could wonder what is the importance of the most sensitive taxa to fishing at the scale of the network? In a first part of this chapter (Article 4), we investigated whether a perturbation at the level of the most sensitive taxa was susceptible to influence the entire network sensitivity, in the context of a fishing induced perturbation.

The spatial patterns of species and trait distribution have been widely studied in ecology, but few attention have been given to the spatial structure of trophic network so far (Gilarranz,

2020). Studying the spatial structure of networks would provide valuable information to disentangle the mechanisms through which communities function at the landscape level (Tylianakis & Morris, 2017). I distinguish two main features of the spatial structure of networks: (1) A network could vary through space, function of the species present at specific locations (Kortsch et al., 2018). Different areas are characterised by subset of the main network. (2) The structure of the network itself could have a spatial distribution, for instance with a larger biomass in a certain area of species with a certain topological characteristic (e.g. the more central species, or the ones with the highest number of preys…). Here, I was interested in the later type of spatial features (2). Groups of species that are more linked together than with other species in the network form a module, which is reported as a stabilising structure from where a perturbation would be less likely to reach the rest of the network (Thébault & Fontaine, 2010). Studying the spatial distribution of species in the same module could inform on the spatial scale a perturbation could spread. In a second part of this chapter, we present results on the spatial distribution of modules of the Celtic Sea network and discuss implication for management.

4.2 Article 4

Testing food web robustness against taxa' sensitivity in an exploited fishing ground

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In prepapration for submission in Current Biology as Mérillet, L., Robert, M., Hernvann, P.-Y., Pécuchet, L., Pavoine, S., Mouchet, M., Primicerio, R. and Kopp, D. Species traits and network topology drive the robustness of a marine food web to species removal.

4.2.1 Introduction

A shift in focus from species to ecological networks of interactions has recently been proposed as a necessary step in the adaptation of conservation goals to the maintenance of ecosystem integrity and the services ecosystems underpin (Harvey et al., 2017; Pecl et al., 2017; Scotti & Jordán, 2010). Ecological network enables to evaluate the vulnerability of ecosystems to a perturbation through the study of the changes in the structure of the network (Hattab et al., 2016; Robinson & Strauss, 2020; Stouffer & Bascompte, 2011; Tylianakis, Tscharntke, & Lewis, 2007). Its use to assess ecosystem state has increased in the recent years as it allows considering in a single framework the effects of fluctuation in species' abundance and their preys and predators, but also on indirectly linked species and the whole network itself (Jordán et al., 2006; Wallach et al., 2017).

The risk of network collapse can be characterized by its robustness to species extinction, namely its capacity to withstand the cascading perturbation generated by the removal of species (Dunne & Williams, 2009; Dunne, Williams, & Martinez, 2004; Jonsson, Berg, Pimenov, Palmer, & Emmerson, 2015). Human impact on ecosystems is intensifying and has already caused numerous collapses of species (Duarte et al., 2020). As ecosystems are being degraded at an unprecedented rate, the need to understand which perturbation sequences are expected to be more devastating than others has become pressing (Jonsson et al., 2015). The collapse of some well-connected species is expected to have a disproportionate impact on their ecosystems relatively to their biomass, and these species have to be identified (Jordán, 2009; Klemm, Serrano, Eguíluz, & Miguel, 2012; Worm & Paine, 2016). Central species with a large number of interactions, are likely to influence numerous species and thus have been defined as network hubs that should be prioritized for conservation (Curtsdotter et al., 2011). To identify these central species, mesoscale measures (i.e. intermediate level between the species (local) and the entire network (global)), such as eigenvector centrality, betweenness centrality or closeness

centrality have proven to be particularly suited for the assessment of species importance in the spread of a perturbation across the network (Estrada, 2007; Jordán, 2009).

Sensitivity and vulnerability assessment of species (defined as sensitivity added to exposure (IPCC, 2001)) have largely been conducted based on species traits (Le Quesne & Jennings, 2012; Tillin, Hull, & Tyler-walters, 2010; van Treeck, Van Wichelen, & Wolter, 2020). However, to evaluate properly the potential of a species to spread perturbation across the network, its centrality should be assessed alongside its sensitivity and exposure to a given pressure. Indeed, a species can be sensitive and vulnerable but not central, or it may be central but not sensitive nor vulnerable. In both cases, the species would not spread a perturbation across the network. In that sense, one can ask whether the robustness of the trophic network to the spread of a perturbation can be inferred from the sensitivity of its components.

To answer this question and shift the sensitivity assessment focus from species to ecological network, we propose a framework that examines network robustness to a given perturbation at the local (species), mesoscale and global (network) level, based on species traits and on the topology of the network. Specifically, we investigated the impact on the robustness of the network of the loss of the sensitive species, the exposed species and the central species.

We applied this framework to fishing pressure robustness of a trophic network from a historically exploited fishing ground, the Celtic Sea. Fishing impacts on the ecosystems are numerous, from decreased species abundance and depletion of higher trophic levels (Pauly & Palomares, 2005) to altered trophic networks as fishing pressure increases (Gilarranz, Mora, & Bascompte, 2016). At the species level, life history traits (e.g. maximum length, longevity or age at maturity) are good proxies of species' demographic characteristics and enable to characterize their sensitivity to fishing by ranking them along a "slow-fast" continuum of life history strategies (Le Quesne & Jennings, 2012). Fishing tends to favour small-sized, short-lived species that mature early and have a better capacity to recover after a fishing perturbation

(Jennings et al., 1998; Le Quesne & Jennings, 2012; Wiedmann et al., 2014). In the Celtic Sea, the intense development of fishing in the area during the second half of the 20th century until its climax in the late 1980's, deeply altered the ecosystem structure through the depletion of large demersal predators, i.e. cod, whiting, hake and sole (Guénette & Gascuel, 2012; Hernvann & Gascuel, 2020). Based on literature and isotopic measurements for 69 taxa (including fishes, elasmobranches, cephalopods, bivalves, and crustaceans), we assessed the vulnerability to fishing of both taxa and the trophic network structure. Specifically, we investigate whether (i) the most sensitive and the most exposed taxa to fishing are the most central; and whether (ii) the loss of sensitive, exposed or central taxa is the most detrimental for the network robustness. For a better understanding of the processes at play, we tested the robustness of the network against different species 'removal sequences, and notably assessed the importance of the number of predators and preys.

4.2.2 Materials and methods

Study area

The Celtic Sea is a shelf ecosystem (range depth 57-340m) located in Northwestern Europe. It is characterized by a gradient of sediments from shallow sand to mud habitats. It harbors a larger species richness than the surrounding area due to its position at the biogeographical border between warm water Lusitanian species and cold water Boreal ones (ICES, 2018a). For decades, the Celtic Sea has been an important fishing ground for European countries and fishing has been shaping its ecosystem (Hernvann & Gascuel, 2020). Importance of fishing driving the ecosystems have decreased after 2009 (Mérillet et al., 2020) but remains high, around 4000 thousand tons landed per years over 2000-2015 (Hernvann & Gascuel, 2020).

Food-web data

We studied the trophic network corresponding to the upper part of the Celtic Sea trophic network (TL>=2), defined at genus or species resolution and restricted to interactions between most abundant and common taxa observed during the scientific survey EVHOE (see Mérillet et al., 2020). Trophic links between taxa were taken from the literature review conducted in Hernvann et al. (2020), keeping the information at the taxon's level. We collected isotopic measurements for 69 taxa of the most commonly found in bottom trawls in the Celtic Sea (EATME project). We applied a lipid correction for the taxa with a C/N >3.5, following Sweeting, Polunin, & Jennings (2006). We then applied a baseline correction based on isotopic signatures of *Aequipecten opercularis*, using bottom temperature for δ13C (Barnes, Jennings, & Barry, 2009) and using bottom temperature and salinity correction for δ15N (Jennings & van der Molen, 2015). The performance of the correction was then checked by looking at the correlation between real and corrected values for other bivalves (i.e. *Pecten maximus*, *Aequipecten opercularis*, *Pseudamussium peslutrae* and *Pseudamussium clavatum*). Trophic levels TL of taxa i were computed from Post (2002) equation, as follows:

$$TL_i = \frac{\delta 15N_i - \delta 15N_{base}}{3.4} + TL_{base}$$

with δ15Ni the corrected δ15N value for the taxa i and δ15Nbase the mean of the δ15N base values of bivalves (TLbase = 2).

We computed several metrics informing on the structural properties of the network. Connectance (L/S2), computed from the number of links (L) and the number of species (S), gives information on how densely connected is trophic network. Our network of 69 species and 559 links has average values of connectance (0.12), with connectance ranging from 0 to 1, with 0 indicating the least possible number of interactions (Delmas et al., 2019). For a complete description of these metrics see Delmas et al. (2019) and Kortsch et al. (2018).

Vulnerability index: sensitivity and exposure to fishing

To quantify a taxon's sensitivity to fishing, we selected six traits widely used to characterize the life-history strategies of marine taxa: longevity, maximum length, reproductive guild, fecundity, age at maturity and size of the offspring (Jennings et al., 1998; Le Quesne & Jennings, 2012; Winemiller & Rose, 1992). Most of these traits came from PANGAEA database (Beukhof, Dencker, et al., 2019), but were completed by literature. We applied a Hill-Smith analysis (Hill & Smith, 1976), a multivariate analysis that enables to use both qualitative and quantitative traits, and gives the same weight to quantitative and qualitative traits (independently of the number of levels for a qualitative trait).

We used the proportion of biomass of a population that is exploited by fishing, to reflect the exposure to fishing. We expressed the exposure of a taxon i as the ratio between its removal by fisheries and its stock biomass in the study-area:

$$Exposure_i = \frac{C_i}{B_{tot,i}}$$

With C_i the biomass of the taxon i landed (i.e. catches) and discarded and $B_{tot,i}$ the total biomass present in the Celtic Sea (area 7e-j) in 2016. This ratio was directly available from the International Council for the Exploration of the Sea (ICES) working groups' reports for species whose stocks are assessed and have a spatial distribution relevant with our study area (ICES, 2020). For species without stock assessment, exposure was computed using the fishing mortality rates estimated for the corresponding functional groups by the Ecopath with Ecosim (EwE) Celtic Sea model (Hernvann et al., 2020). These rates are issued from the ratio of onshelf catches in ICES divisions 7e-j (official landings from STATLANT, (ICES, 2019) elevated by discard rates from the DISCARDLESS project, http://www.discardless.eu/) and biomass estimated for the corresponding area from the EwE mass balance equations. As EwE functional groups can gather several species with similar biological characteristics and trophic ecology,

the same exposure was attributed to our network's taxa when matching the EwE functional group.

Vulnerability of a taxon to fishing was defined as sensitivity added to exposure, following the simplified definition of the IPCC (IPCC, 2001). Finally, the proportion of each taxon relatively to the total biomass of all taxa in our dataset was computed to provide an order of magnitude of the proportion of the biomass that is sensitive or vulnerable to fishing pressure. To compute proportion of the total biomass represented by each taxon, we used EVHOE data in 2016 (Evaluation des ressources Halieutiques de l'Ouest de l'Europe,(Garren et al., 2019)). The biomass of each taxon was elevated to the depth-sediment strata, to account for the irregular sampling within a stratum, before computing the proportion.

Computation of a proxy of the flow of a perturbation across a network: the eigenvector centrality

The more connected a taxon is to the rest of the network, the more a perturbation affecting that taxon is likely to spread across the whole network (Delmas et al., 2019; Dunne, Williams, & Martinez, 2002a). To quantify the degree to which a taxon is connected to other highly connected species, we used the eigenvector centrality metric, which is akin to a simulation of flow across a network (Bonacich, 1987; Delmas et al., 2019). Taxa heavily connected to other highly connected taxa hence get higher scores of eigenvector centrality. Finally, to investigate whether there is a pattern of sensitivity and centrality across trophic pathways (pelagic for the lowest values of δ13C and benthic for the highest values) and trophic levels, a linear regression between sensitivity or eigenvector centrality and corrected values of δ13C or δ15N was realised (Fig. S1).

Quantifying the robustness of the food web to a perturbation

To evaluate the robustness of the network to taxa's extinction, we simulated primary extinctions of taxa (i.e. removal of taxa from the network) according to various removal sequences and monitored the values of connectance and accumulated secondary extinctions (i.e. the extinction caused by the removal of all the prey of one taxon). Connectance is a good estimate of community sensitivity to a perturbation, and large values of connectance favour the spread of a perturbation (Delmas et al., 2019; Martinez, 1992). On the other hand, secondary extinctions inform on robustness of the network, and is negatively correlated with it (Dunne et al., 2002a). These simulations of extinctions were done by removing taxa in five different orders: (1) Sensitivity, from the highest to the lowest sensitivity score, (2) Centrality, from taxa with the highest to the lowest eigenvector centrality values, (3) Exposure, from taxa with the highest to the lowest exposure to fishing pressure, (4) Prey, from taxa with the highest to the lowest number of prey and (5) Predator, from taxa with the highest to the lowest number of predators. The connectance and accumulated secondary extinctions generated in each of these 5 removal scenarios were compared to a random mode in which taxa are randomly selected and removed from the network. This random removal was iterated 500 times. We followed the same procedure for modularity and nestedness (Fig. S3). To compare the robustness of this network with other networks, we computed the R50, defined as the proportion of taxa that have to be removed to result in a total taxa's loss ≥50% of the species in the original web (Dunne et al., 2004).

All analyses were conducted in R 4.0.2 (R Core Team, 2020). The secondary extinction analysis was performed with modified functions from the NetworkExtinction package (Corcoran-Barrios, Avila-Thieme, Valdovinos, Navarrete, & Marquet, 2019).

4.2.3 Results

The Celtic Sea is characterized by a "slow-fast" continuum of life history, from small, short-lived taxa producing small offspring to large, long-lived taxa with large offspring (Beukhof, Frelat, et al., 2019; Pianka, 1970). Large, long-lived species with low reproductive output are typically the most sensitive to fishing pressure (Le Quesne & Jennings, 2012; Wiedmann et al., 2014; Winemiller & Rose, 1992). The most sensitive taxa to fishing are mostly elasmobranchs: sharks, spurdog *Squalus acanthias*, tope shark *Galeorhinus galeus* and smooth hound *Mustelus sp.* followed by rays, cuckoo ray *Leucoraja naevus*, thornback ray *Raja clavata*, blonde ray *Raja brachyura* and small-eyed ray *Raja microocellata*. Some large fishes also show high values of sensitivity such as European conger *Conger conger* and ling *Molva molva* (Fig. 1, axis 1).

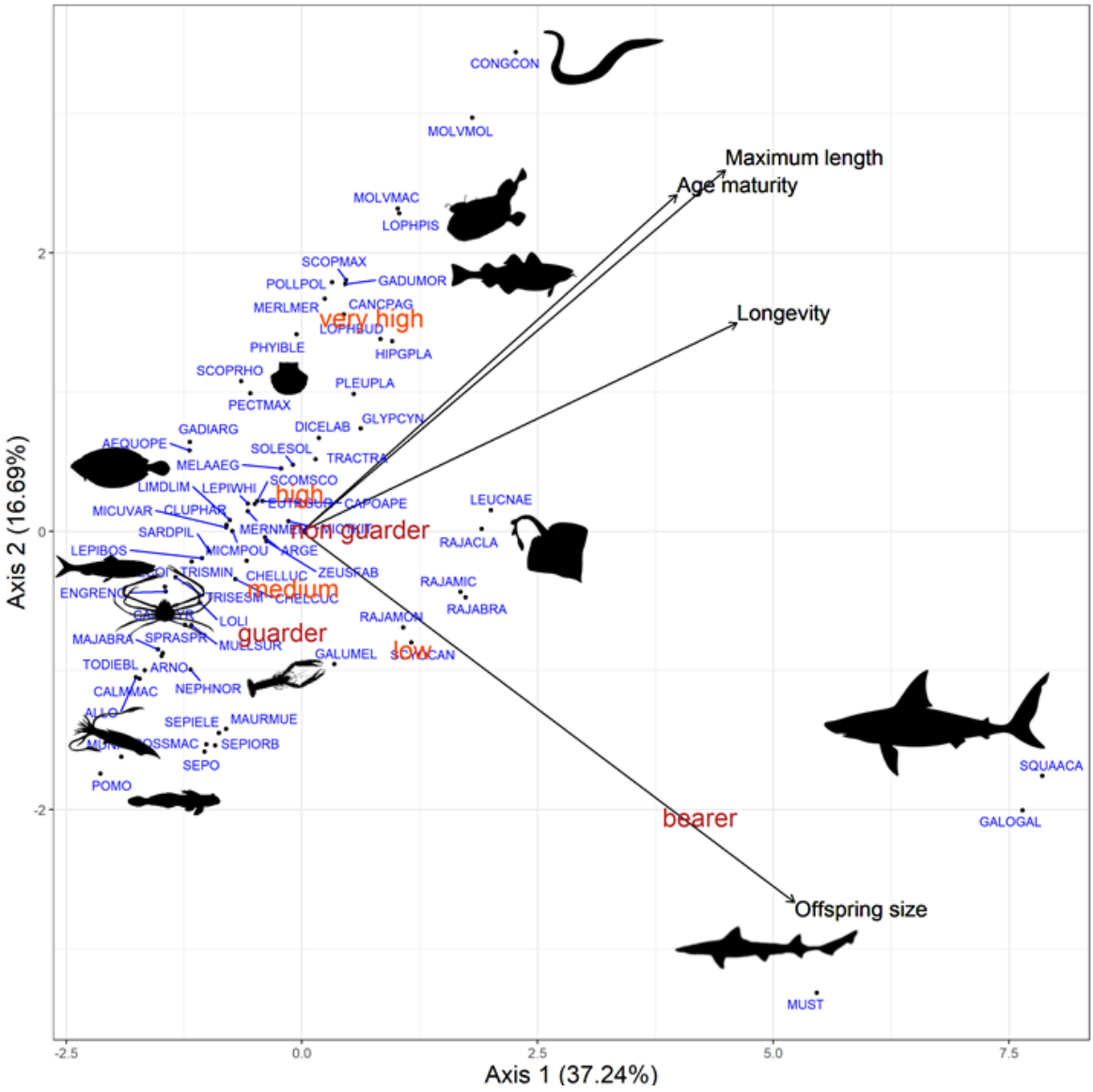


Figure 1: Factorial map of Hill Smith analysis on six functional traits related to a slow-fast gradient of life strategies: maximum length, longevity, offspring size, age at maturity, reproductive guild (modalities in brown) and fecundity (modalities in orange). The most sensitive taxa (right part) are characterized by high values of maximum length, longevity, age at maturity and offspring size and tend to bear their offspring. Full names of the taxa are given in Table S1.

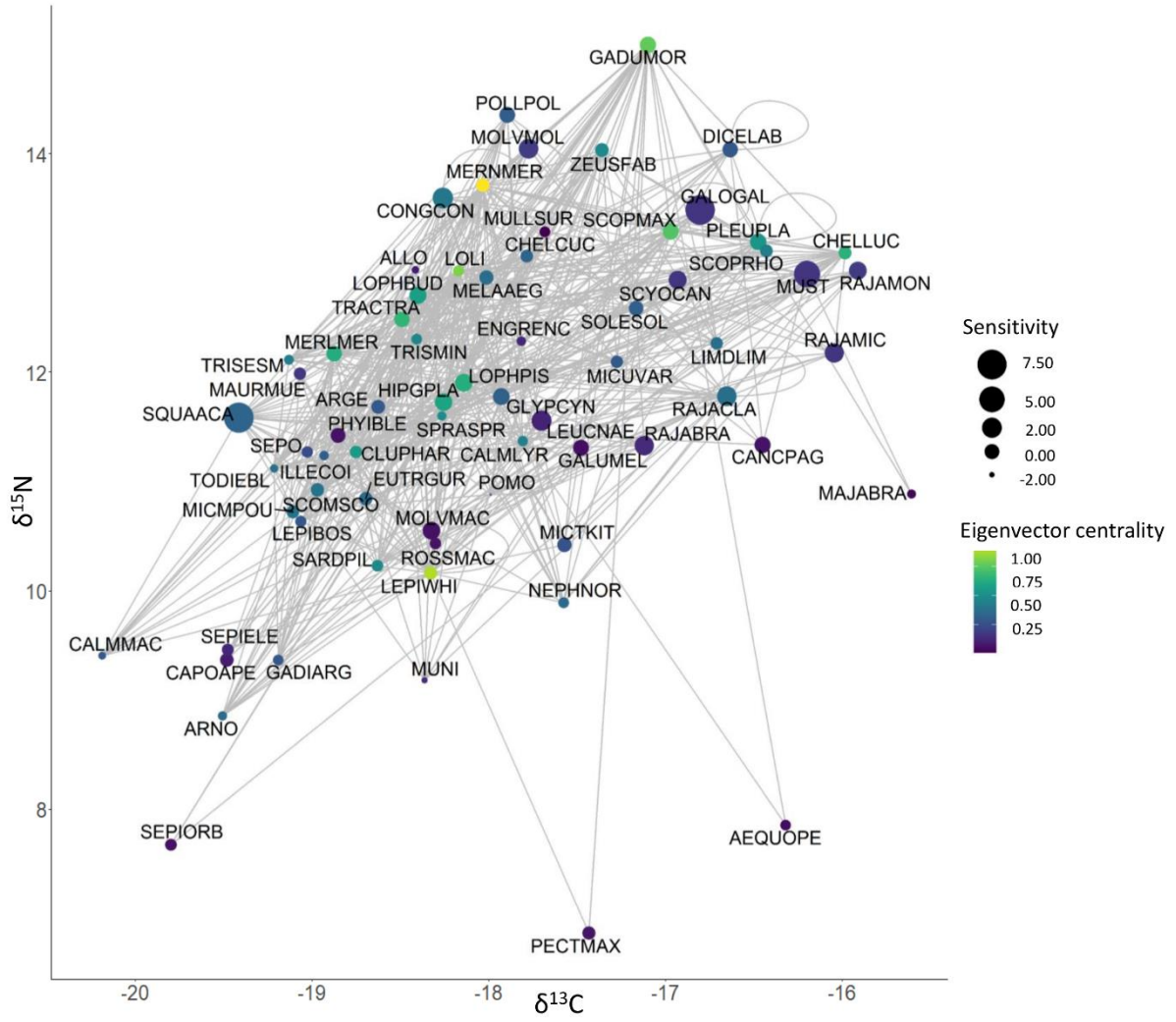


Figure 2: Representation of the trophic network of the Celtic Sea in the isotopic space with sensitivity to fishing (size of the dots) and centrality (colour scale from dark blue to light green). The isotopic space is defined by isotopic ratio of carbon 13C and nitrogen 15N. The nitrogen axis is consistent with species trophic level while the carbon axis discriminates pelagic (more negative) from benthic (less negative) pathways. Full names of the taxa are given in Table S1.

Highest values of eigenvector centrality (hereafter called centrality for simplicity) characterize highly connected taxa linked to taxa that are themselves highly connected. In the Celtic Sea, these are large piscivorous fishes, namely whiting *Merlangius merlangus*, megrim *Lepidorhombus whiffiagonis*, cod *Gadus morhua*, hake *Merluccius merluccius*, turbot

Scophthalmus maximus, and squid *Loligo sp.*. In our case, the most central species are not the most sensitive (Fig. 2). Notwithstanding this observation, taxa at high trophic levels tend to be more sensitive to fishing and more central than other species. Indeed, sensitivity tends to increase toward the top of the network (higher values of δ15N) and centrality increases with trophic levels (Appendix, Fig. S1).

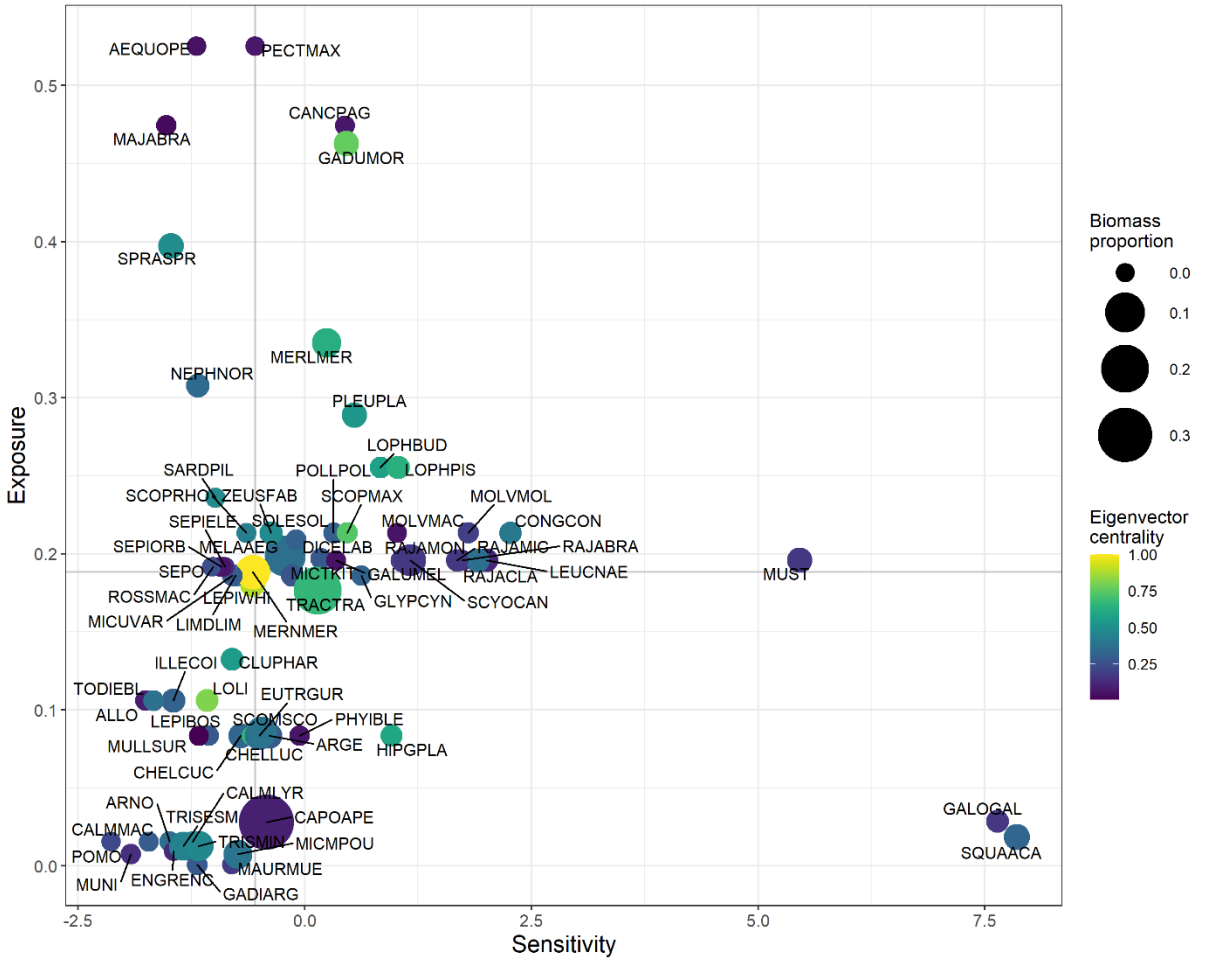


Figure 3: Summary plot of the vulnerability of taxa (sensitivity added to exposure), taxa biomass and the potentiality for the perturbation at the taxa's level to spread (eigenvector centrality). Solid lines depict median values of sensitivity and exposure. Taxa's relative biomass (each taxon's biomass is divided by the total biomass of the 69 studied taxa) is given as a proxy of their importance in trophic flux. Proportion lower than 0.1 are in the 0 category in the graph legend.

Vulnerable taxa are defined as both sensitive and exposed to fishing. In the Celtic Sea, we found no highly vulnerable taxon, i.e. no taxa in the top right corner (Fig. 3). However, some taxa had medium-high values of vulnerability: cod, edible crab *Cancer pagurus*, smooth-hound, and to a lesser extent hake, anglerfish *Lophius piscatorius*, European conger, European plaice *Pleuronectes platessa*, blackbellied anglerfish *Lophius budegassa* and ling (Fig. 3). In addition, three of these vulnerable taxa (cod, hake and anglerfish) have high values of centrality. These taxa, despite being central, are not accounting for a large proportion of the total biomass (Fig. 3), which suggests that whether these taxa are affected or favored by an external factor (i.e. environmental conditions or human pressures), it would have a low impact on the total biomass of the Celtic Sea.

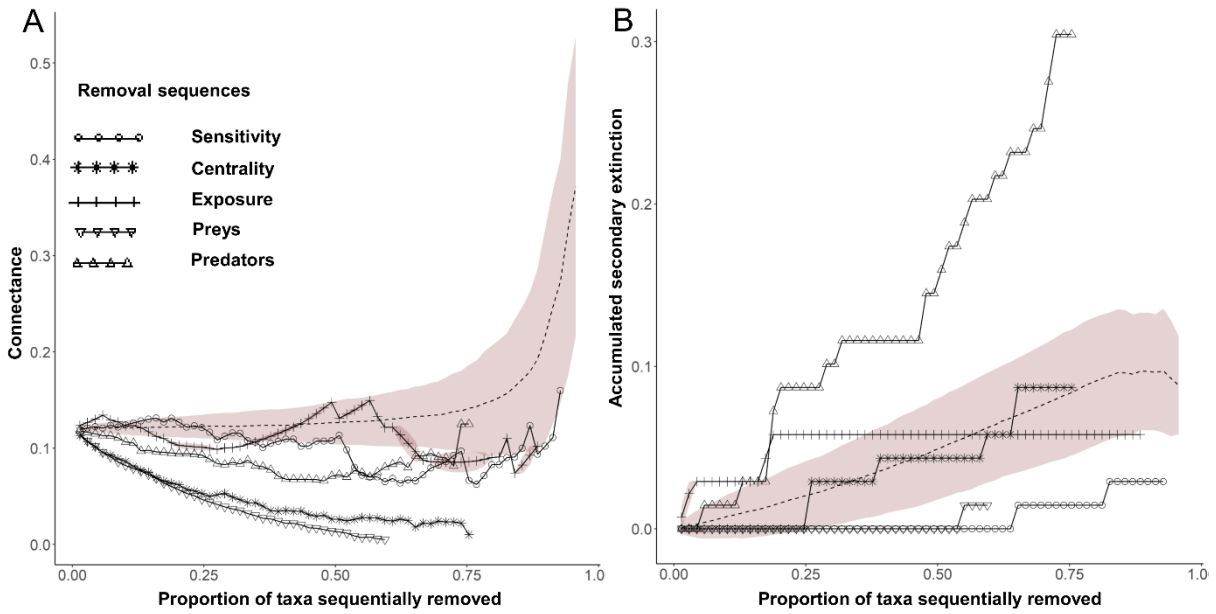


Figure 4: Connectance (A) and accumulated secondary extinctions (B) in response to the primary removal of taxa according to five different removal sequences: sensitivity = decreasing sensitivity to fishing, centrality = decreasing eigenvector centrality values, exposure = decreasing exposure to fishing, preys = decreasing number of prey, predators = decreasing number of predators. The shaded area represents the random model (500 iterations). Some taxa

have the same exposure score, so their order was randomly drawn (500 iterations), leading to a confidence interval (shaded area) on the exposure curve.

Simulating scenarios of species extinction sequences, we found that connectance (defined as the number of realized interactions in the network divided by the potential ones) is decreasing the fastest when the taxa are sequentially removed according to their number of preys (Preys removal sequence) and their influence (Centrality removal sequence) (Fig. 4A.). These removal scenarios are also responsible for the fastest collapse of the network (the remaining taxa are not linked together) after simulating the extinction of respectively 60% and 75% of the taxa of the network. These scenarios of taxa extinctions lead to a network with a lower connectance than if the taxa were deleted following a random sequence (Fig. 4A.). For these two removal sequences, values of modularity show the largest increase and values of nestedness the largest decrease (Fig. S2). Sequentially removing taxa with the highest number of predators (Predators removal sequence) provokes a less steady decrease of the connectance, but still with values lower than the model of random extinctions. The network collapses after the removal of 75% of the taxa. Conversely, the removal of only the 7% of the taxa that are the most exposed to fishing (Exposure removal sequence) leads to an increase in connectance, with values higher than the random model. Removing the taxa most sensitive to fishing (Sensitivity removal sequence) does not lead to variations in connectance different from the random model and causes the later collapse of the network, after removing 93% of the taxa (Fig. 4A.).

The removal of the first 7% of the most exposed taxa to fishing (Exposure removal sequence) causes the largest number of secondary extinctions (Fig. 4B.). Then, the simulated extinctions of taxa with the largest number of predators (Predators removal sequence) leads to the highest and fastest rate of secondary extinctions, higher than the null model, after the removal of 19% of the taxa. Removing taxa from the most to the least central (Centrality

removal sequence) produces secondary extinctions comparable to the random model (Fig. 4B.). Finally, removing the taxa with the largest number of preys (Preys removal sequence) and the most sensitive taxa (Sensitivity removal sequence) leads to the lowest number of accumulated secondary extinctions, even lower than the null model (Fig. 4B.).

A network is the most robust to node loss when the removal of taxa (primary removal) does not lead to secondary extinctions. The R50 robustness (Dunne et al., 2004) is defined as the proportion of taxa that has to be removed to reach the loss of ≥50% of the taxa in the original network. The larger the R50 is (maximum value of 50%), the more robust the network is. Here, the Sensitivity and Preys removal sequences lead to the most robust network (R50=50%), followed by the random model (46%), the Centrality removal sequence (46%), the exposure removal sequence (45%) and the Predator removal sequence (39%).

4.2.4 Discussion

Since the ecological role of taxa heavily depends on their position in the trophic network, we were interested in identifying whether the sensitivity and exposure of taxa to fishing pressure (i.e. vulnerability), completed by taxa's centrality, could have consequences on the robustness of the trophic network.

The secondary extinction analysis conducted here highlighted that the robustness of the Celtic Sea to fishing is not closely related to the sensitivity of its taxa to this pressure. This behaviour of the network results from the respective characteristics and feeding ecology of the taxa. Indeed, in the Celtic Sea, the most sensitive taxa are medium size elasmobranchs which are not top predators and have medium trophic levels (circa TL=3). Medium trophic levels taxa often have a high structural importance, with usually the largest values of centrality (Scotti & Jordán, 2010). However, we showed that this is not the case in the Celtic Sea were the most sensitive taxa are not the most central and are thus, if targeted, unlikely to spread a perturbation

to the whole network. Considering both the sensitivity and the exposure to fishing pressure, we showed that none of the taxa considered in this study is highly vulnerable to fishing, which could be linked to the long history of exploitation of the area (Guénette & Gascuel, 2012). The most vulnerable taxa include smooth hound, a sensitive and moderately exposed taxon, as well as large piscivorous taxa (cod, hake, anglerfishes, plaice, conger, ling) that are not very sensitive but are highly fished. Amongst these large piscivorous taxa, cod, anglerfish and hake are central taxa and are likely to propagate a perturbation to the whole network through top-down control. These species are important commercial stocks under quotas in the area, whose decrease should lead to significant cascading impacts in the trophic network.

The robustness of the Celtic Sea network to the removal of taxa with many preys and highly connected taxa was relatively high. The removal of taxa with many preys leads to the fastest collapse of the network, but only happens after removing 60% of the taxa, which is far from realistic conditions. Connectance decreases before the network collapses, making in a first instance the propagation of a perturbation less likely and the network more robust. Likewise, the network seems relatively robust to the removal of the most central taxa (decrease in connectance and a number of secondary extinctions similar to the one expected by chance). This finding contradicts the expected low robustness of a network facing the removal of its most connected taxa (Curtsdotter et al., 2011; De Visser, Freymann, & Olff, 2011; Dunne & Williams, 2009; Staniczenko, Lewis, Jones, & Reed-Tsochas, 2010) but see (Allesina & Pascual, 2009). The robustness of the network facing these two removal sequences is in line with the observed increase in modularity and decrease in nestedness (Fig. S2). Indeed, the increased modularity indicates an increased compartmentalisation, which is known to promote stability by restricting the spread of the perturbation outside the module (Thébault & Fontaine, 2010). On the other hand, a decrease in nestedness implies the removal of the redundant trophic interactions first (Nordstrom, Aarnio, Tornroos, & Bonsdorff, 2015), which translates here into

the removal of whiting *Merlangus merlangius*, megrim and squid *loligo sp.* that are preyed upon by generalist taxa.

The removal of taxa with many predators leads to the lowest robustness of the trophic network. Taxa with the largest number of predators here belong to intermediate trophic levels (between 3 and 3.5) namely herring *Clupea harengus*, sprat *Sprattus sprattus*, *sardine Sardina pilchardus*, dragonet *Callionymus lyra*, pouts *Trisopterus esmarkii* and *Trisopterus minutus* and horse mackerel *Trachurus trachurus* (Table S1). These forage species account for a large proportion of the biomass of the taxa considered in this study but also a large proportion in the catches (Hernvann & Gascuel, 2020; ICES, 2018b). These species are crucial for the network stability as their predators display medium to high trophic levels and are both benthic and pelagic. Hence, forage species allow the coupling between these two pathways, which has been shown to participate to trophic network stability and resilience (Blanchard, Law, Castle, & Jennings, 2011). In addition, if affected by a perturbation, these taxa heavily destabilize the network (Moullec et al., 2017).

The food-web topology reconstructed here integrates data from trophic studies covering a long time-span. Thus, the restructuration of the network due to changes in diets could not be investigated. Nonetheless, this makes the response of the network to removal-scenarios interpretable regarding the long-term history of the ecosystem. The relatively high robustness of the network to the removal of taxa with many preys could be one of the stability factors (with predation control of benthopelagic predator larvae by pelagic fish, Baum & Worm (2009)) of the more pelagic-dominated state of the ecosystem after the depletion of high trophic levels before 1980 (Hernvann & Gascuel, 2020).

Finally, the network has low robustness to the removal of the most exposed taxa at early stage of perturbation (i.e. when removing the 7% of the most exposed taxa). These highly exploited taxa are queen scallop *Aequipecten opercularis*, king scallop *Pecten maximus*, edible

crab, European spider crab *Maja brachydactyla*, cod, sprat and hake. This increase in connectance originates from a faster decrease in the number of potential interactions than in the realized ones and is due to these removed taxa having in general fewer feeding links than the averaged species in the network. This raised one of the limitations of network reconstruction, since the taxa considered were sampled with a bottom trawl that is not adapted to sample the basal components of the network (phyto and zooplankton are missing while benthos is underrepresented), as well as the top predators. Nevertheless, taxa included here are megafauna with the highest occurrence and account for most part of the network, enabling notably the survival of commercial taxa. These taxa are thus considered to provide a representative picture of the Celtic Sea ecosystems. Trophic levels were computed from local isotopic data collected in the Celtic Sea whereas the trophic links were taken from the literature. Thus, there might be a mismatch between the trophic position and the trophic links of some taxa with taxon feeding on taxon at slightly higher trophic level. However, because the computation the centrality score of one taxon is not based on data specific to our study area, it could be applied to other North-East Atlantic studies. In addition, we did not consider the fluxes of biomass between taxa, which could modulate our findings. Indeed, it might influence the spread of a perturbation, with a larger spread between taxa linked by a large flux of biomass.

Network theory has been identified as a helpful tool to support ecosystem-based fisheries management (Dee et al., 2017; Gaichas & Francis, 2008). Exposure and trait-based sensitivity metrics relative to fishing brought here a complementary information to the network analysis. Indeed, our study suggests that widely used mesoscale metrics such as centrality were not always adapted to prioritize species conservation to maintain the structure and the functioning of the network. On the contrary, our exposure metric highlighted that in some cases, the current fishing exploitation pressure should prevail on topology-based metrics, while sensitivity must be considered as it implies different abilities of species to tolerate various

exposure levels. Such metrics are particularly promising in the context of exploring potential new fishing management strategies. In particular, integrating the sensitivity to fishing, they could be used to investigate the risk of exploiting new species regarding to their own productivity potential (Zhou et al., 2019).

This study focused on fishing since this variable has a documented impact on taxa's biomass in the Celtic Sea, due to the long history of exploitation of this ecosystem (Hernvann & Gascuel, 2020). However, climate change will likely become the main driver of this ecosystem in the coming years. The framework proposed in this work could easily be adapted to assess species sensitivity to temperature or pH tolerance by selecting traits known to respond to these pressures. Ultimately, such a framework could be used in complement of management tools to indicate which taxon could impair ecological network structure and ecosystem functioning under increasing global change. It could also unravel early warnings about the loss of certain taxa that could jeopardize the Celtic Sea network more than their sensitivity at the taxon's level could suggest.

Acknowledgement

We are very grateful to M. Isadora Avila-Thieme for the enriching discussion on the results of the secondary extinction analysis. We also thank the whole EVHOE team as well as the professional boat that took part to the isotopic sampling.

4.2.5 Supplementary material

Table S1: Trophic network metrics for each taxon: Isotopic position (corrected values of δ15N and δ13C), trophic level, number of prey, number of predators, sensitivity to fishing estimated from life history traits, eigenvector centrality and exposure to fishing pressure.

Taxa	Latin names	$\delta^{15}N_{corr}$	$\delta^{13}C_{corr}$	TL	Number of preys	Number of predators	Sensitivity	Centrality	Exposure
AEQUOPE	*Aequipecten opercularis*	7.83	-16.35	2.285	0	2	-1.19	0.051	0.525
ALLO	*Alloteuthis* sp	12.90	-18.46	3.775	0	4	-1.759	0.085	0.106
ARGE	*Argentina* sp.	11.64	-18.67	3.407	1	12	-0.391	0.288	0.083
ARNO	*Arnoglossus* sp.	8.83	-19.56	2.578	2	12	-1.489	0.365	0.016
CALMLYR	*Callionymus lyra*	11.33	-17.85	3.315	1	22	-1.237	0.451	0.016
CALMMAC	*Callionymus maculatus*	9.38	-20.24	2.74	0	12	-1.719	0.296	0.016
CANCPAG	*Cancer pagurus*	11.30	-16.48	3.305	0	5	0.444	0.065	0.474
CAPOAPE	*Capros aper*	9.34	-19.53	2.729	0	4	-0.419	0.092	0.028
CHELCUC	*Chelidonichthys cuculus*	13.02	-17.83	3.812	3	11	-0.706	0.33	0.083
CHELLUC	*Chelidonichthys lucerna*	13.05	-16.01	3.821	20	10	-0.584	0.648	0.083
CLUPHAR	*Clupea harengus*	11.23	-18.80	3.286	2	26	-0.799	0.553	0.132
CONGCON	*Conger conger*	13.55	-18.30	3.968	19	3	2.27	0.408	0.213
DICELAB	*Dicentrarchus labrax*	13.99	-16.67	4.098	14	0	0.179	0.281	0.197
ENGRENC	*Engraulis encrasicolus*	12.24	-17.86	3.584	0	7	-1.446	0.125	0.009
EUTRGUR	*Eutrigla gurnardus*	10.81	-18.74	3.161	4	12	-0.501	0.357	0.083
GADIARG	*Gadiculus argenteus*	9.34	-19.24	2.728	2	11	-1.186	0.281	0.001
GADUMOR	*Gadus morhua*	14.95	-17.14	4.379	34	6	0.46	0.765	0.463
GALOGAL	*Galeorhinus galeus*	13.44	-16.84	3.936	10	0	7.642	0.163	0.029
GALUMEL	*Galeus melastomus*	11.27	-17.52	3.297	3	1	0.344	0.052	0.196
GLYPCYN	*Glyptocephalus cynoglossus*	11.74	-17.97	3.435	1	11	0.623	0.319	0.186
HIPGPLA	*Hippoglossoides platessoides*	11.69	-18.30	3.42	16	12	0.959	0.595	0.083
ILLECOI	*Illex coindetii*	11.20	-18.98	3.276	16	2	-1.451	0.313	0.106
LEPIBOS	*Lepidorhombus boscii*	10.60	-19.11	3.1	1	9	-1.059	0.283	0.083
LEPIWHI	*Lepidorhombus whiffiagonis*	10.13	-18.37	2.962	34	10	-0.575	0.887	0.18
LEUCNAE	*Leucoraja naevus*	11.52	-17.74	3.37	3	1	2.004	0.11	0.196
LIMDLIM	*Limanda limanda*	12.22	-16.74	3.578	0	16	-0.765	0.381	0.186
LOLI	*Loligo* sp.	12.89	-18.21	3.772	35	7	-1.078	0.809	0.106
LOPHBUD	*Lophius budegassa*	12.66	-18.45	3.707	29	4	0.835	0.571	0.255
LOPHPIS	*Lophius piscatorius*	11.86	-18.18	3.472	33	1	1.032	0.638	0.255
MAJABRA	*Maja sp.*	10.85	-15.63	3.173	0	2	-1.527	0.029	0.474
MAURMUE	*Maurolicus muelleri*	11.95	-19.12	3.496	0	7	-0.803	0.181	0.001
MELAAEG	*Melanogrammus aeglefinus*	12.82	-18.06	3.754	7	10	-0.218	0.366	0.199
MERLMER	*Merluccius merluccius*	12.13	-18.92	3.55	20	11	0.244	0.63	0.335
MERNMER	*Merlangius merlangus*	13.67	-18.08	4.003	35	16	-0.573	1	0.188

MICMPOU	*Micromesistius poutassou*	10.69	-19.16	3.126	4	15	-0.736	0.39	0.008
MICTKIT	*Microstomus kitt*	10.39	-17.61	3.038	0	9	-0.143	0.264	0.186
MICUVAR	*Microchirus variegatus*	12.06	-17.31	3.528	0	10	-0.801	0.291	0.186
MOLVMAC	*Molva macrophthalma*	10.52	-18.37	3.076	0	4	1.017	0.058	0.213
MOLVMOL	*Molva molva*	14.00	-17.82	4.1	5	4	1.805	0.188	0.213
MULLSUR	*Mullus surmuletus*	13.24	-17.72	3.877	0	1	-1.171	0.007	0.083
MUNI	*Munida* sp.	9.15	-18.41	2.674	0	9	-1.916	0.138	0.008
MUST	*Mustelus* sp.	12.86	-16.23	3.764	10	0	5.462	0.163	0.196
NEPHNOR	*Nephrops norvegicus*	9.86	-17.62	2.882	0	14	-1.18	0.351	0.308
PECTMAX	*Pecten maximus*	6.85	-17.48	1.996	0	2	-0.545	0.069	0.525
PHYIBLE	*Phycis blennoides*	11.38	-18.90	3.33	2	1	-0.055	0.06	0.083
PLEUPLA	*Pleuronectes platessa*	13.15	-16.51	3.85	12	12	0.55	0.538	0.289
POLLPOL	*Pollachius pollachius*	14.31	-17.94	4.191	11	4	0.32	0.303	0.213
POMO	*Pomatoschistus* sp.	10.84	-18.03	3.172	0	13	-2.138	0.225	0.016
RAJABRA	*Raja brachyura*	11.29	-17.16	3.303	6	1	1.737	0.132	0.196
RAJACLA	*Raja clavata*	11.74	-16.69	3.436	21	1	1.91	0.368	0.196
RAJAMIC	*Raja microocellata*	12.14	-16.07	3.552	7	1	1.681	0.165	0.196
RAJAMON	*Raja montagui*	12.89	-15.94	3.773	10	1	1.074	0.184	0.196
ROSSMAC	*Rossia macrosoma*	10.40	-18.35	3.041	0	4	-1.011	0.064	0.192
SARDPIL	*Sardina pilchardus*	10.20	-18.68	2.982	0	23	-0.985	0.477	0.236
SCOMSCO	*Scomber scombrus*	10.89	-19.02	3.184	4	16	-0.474	0.387	0.086
SCOPMAX	*Psetta maxima*	13.25	-17.01	3.878	21	9	0.47	0.738	0.213
SCOPRHO	*Scophthalmus rhombus*	13.07	-16.46	3.826	7	10	-0.643	0.432	0.213
SCYOCAN	*Scyliorhinus canicula*	12.80	-16.97	3.748	9	0	1.163	0.168	0.196
SEPIELE	*Sepia elegans*	9.43	-19.53	2.756	0	5	-0.881	0.124	0.192
SEPIORB	*Sepia orbignyana*	7.65	-19.85	2.232	0	3	-0.92	0.06	0.192
SEPO	*Sepiola sp.*	11.23	-19.08	3.286	0	11	-1.033	0.245	0.192
SOLESOL	*Solea solea*	12.55	-17.20	3.672	0	12	-0.096	0.313	0.209
SPRASPR	*Sprattus sprattus*	11.56	-18.31	3.383	0	24	-1.477	0.494	0.397
SQUAACA	*Squalus acanthias*	11.55	-19.47	3.378	22	0	7.855	0.333	0.019
TODIEBL	*Todaropsis eblanae*	11.08	-19.27	3.241	18	3	-1.666	0.373	0.106
TRACTRA	*Trachurus trachurus*	12.44	-18.54	3.642	16	17	0.146	0.667	0.176
TRISESM	*Trisopterus esmarkii*	12.07	-19.18	3.533	0	21	-1.34	0.439	0.013
TRISMIN	*Trisopterus minutus*	12.26	-18.45	3.589	2	20	-1.168	0.469	0.013
ZEUSFAB	*Zeus faber*	13.99	-17.40	4.096	27	0	-0.374	0.478	0.213

Figure S1: Regression of the Sensitivity and eigenvector centrality over corrected values of $\delta^{13}C$ *and* $\delta^{15}N$.

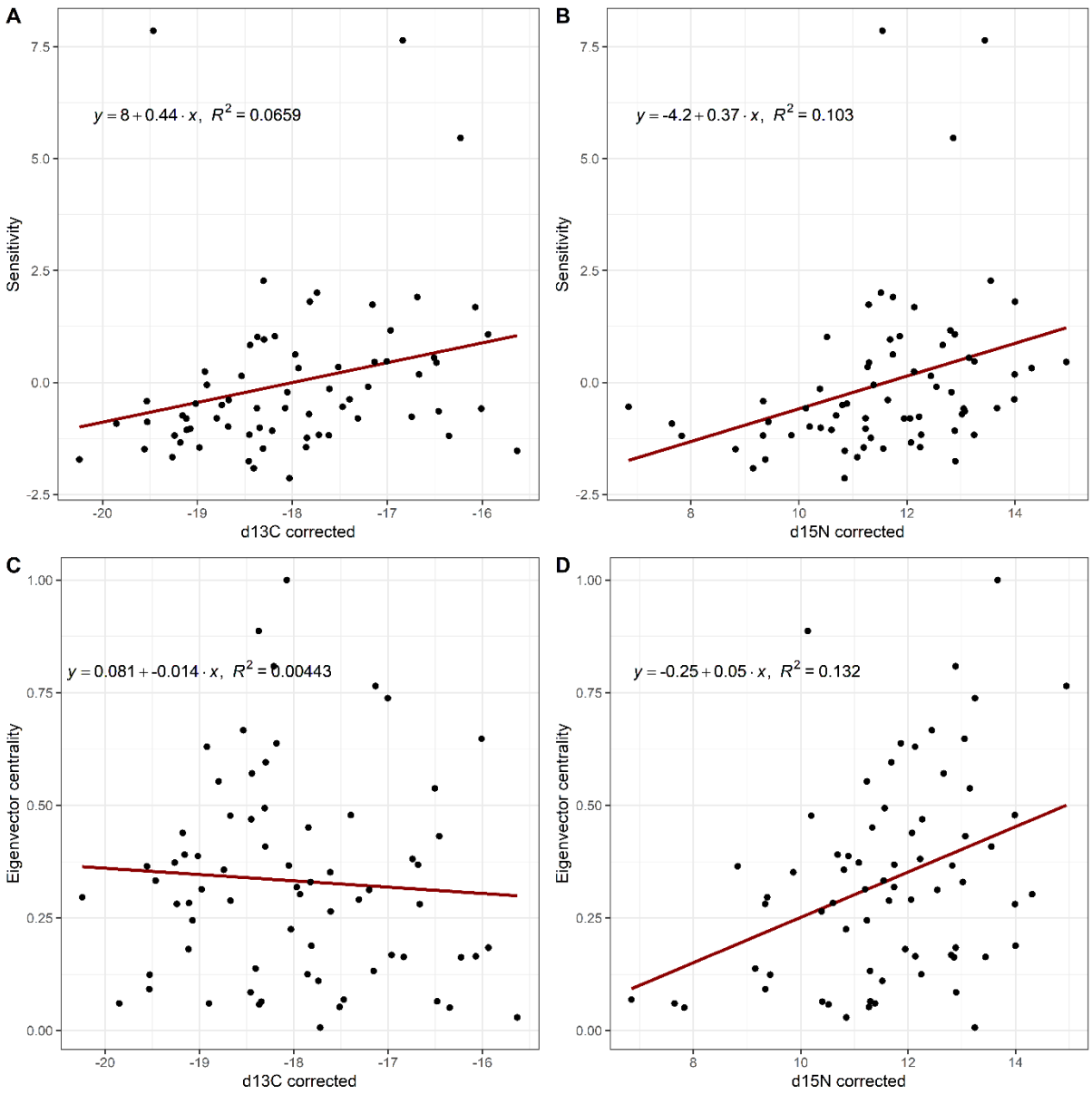
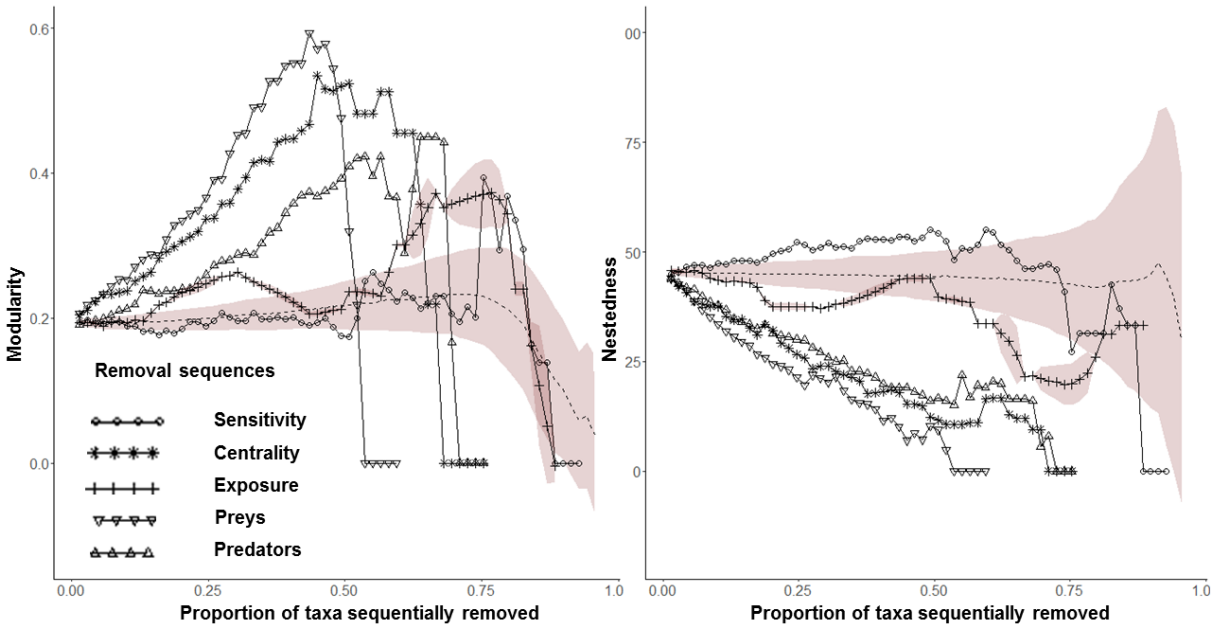


Figure S2: Modularity and nestedness trends in response to the primary removal of taxa according to five different removal sequences: Sensitivity= decreasing sensitivity to fishing, Centrality = decreasing eigenvector centrality values, Exposure = decreasing exposure to fishing, Preys = decreasing number of prey, Predators = decreasing number of predators

Modularity is positively associated with robustness, with perturbation spread hindered by the modules. Modularity of the Celtic Sea trophic network has low values (0.20) with modularity ranging from 0 (no modules) to 1 (strong community structure) with typical values usually spanning from 0.3 to 0.7 (Newman & Girvan, 2004). Finally, nestedness occurs when the diet of specialist is a subset of generalists. It has medium values in the Celtic Sea (45.31) with 0 indicating full complementarity of trophic links between taxa and 100 completely nested links (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008).



Values of modularity are negative when the number of links between taxa in a module is lower than expected by chance.

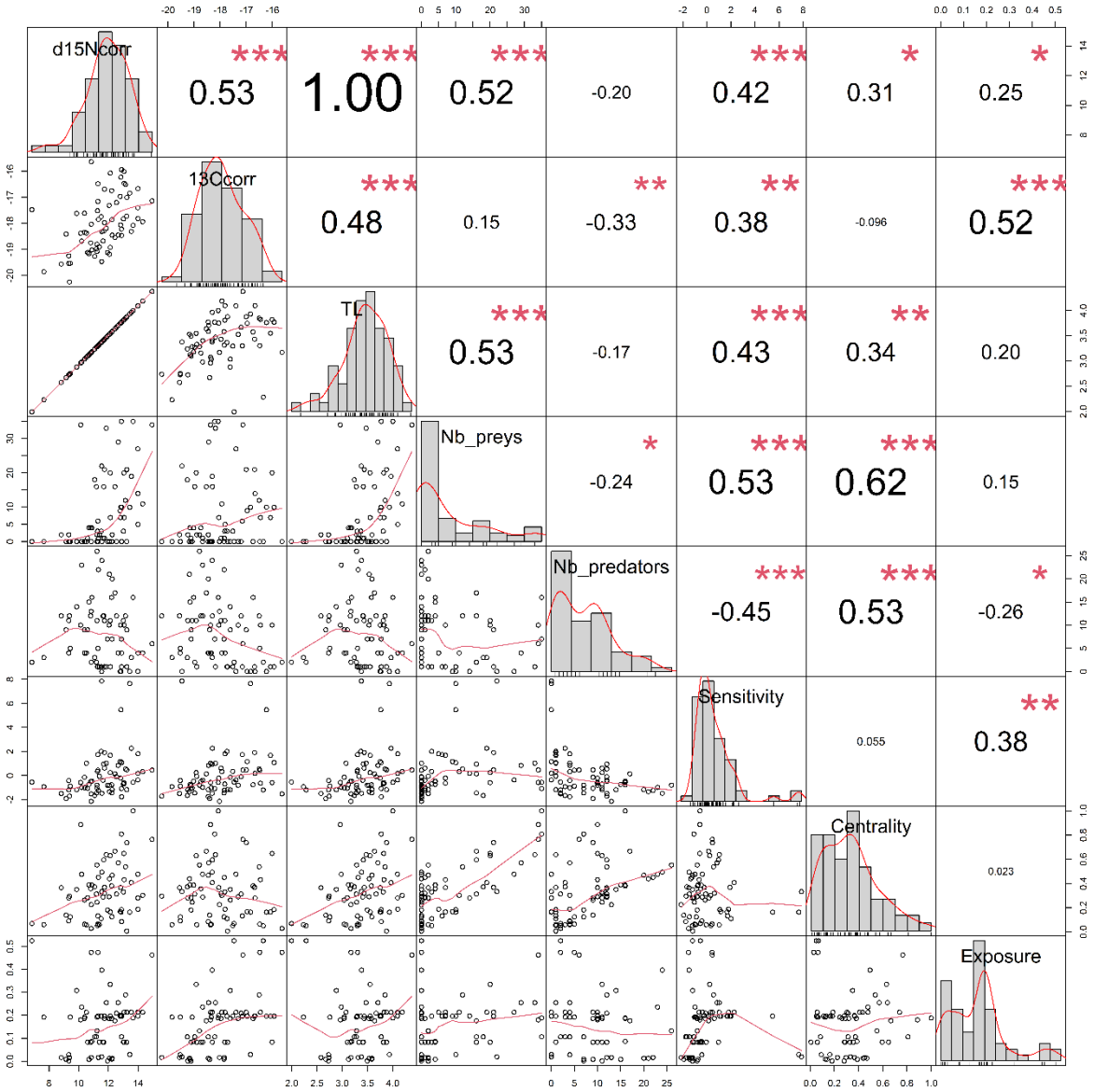
References:

Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A

consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. Oikos, 117(8), 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Newman, M. E. J., & Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics*, *69*(2 2), 1–15. https://doi.org/10.1103/PhysRevE.69.026113

*Figure S3: Correlation plots between trophic position characteristics and the metrics whose link with network robustness is investigated. The strength of the correlation is given by Spearman's correlation coefficients and supported by the level of significance (*** for p-value<0.001, ** for p-value<0.01, * for p-value<0.1). Taxa with the largest number of preys tend to have large values of centrality.*



4.3 Spatial aspect of the trophic network: the spatial patterns of modularity

4.3.1 Introduction

In the first part of this chapter (Article 4), we studied the Celtic Sea trophic network facing fishing disturbance from the sensitivity of the taxa to the robustness of the network. To characterize the robustness of the network, and its ability to retain the spread of a perturbation, modularity is a valuable metric (Grilli, Rogers, & Allesina, 2016; Robinson & Strauss, 2020; Stouffer & Bascompte, 2010; Thébault & Fontaine, 2010). It informs on the presence of subsystems which are more densely linked together than by chance (Delmas et al., 2019). Modularity has often been considered in the study of network structure but insufficiently to characterize the spatial structure of the network, which could yet bring crucial information on the spatial propagation of a great variety of elements, from diseases transmission to genes flow (Gilarranz, 2020). Based on the Celtic Sea trophic network (69 taxa), we investigated whether the modularity of the trophic network could characterize any spatial zonation of the Celtic Sea. In addition, since taxa inside a module are more linked together than with taxa outside, perturbation affecting a taxon in a module is more likely to propagate to taxa within the module than to taxa outside the module (Grilli et al., 2016). We thus investigated whether a module contains more sensitive or exposed taxa than the others.

4.3.2 Materials and methods

The same 69 taxa than the ones including in the first part of this chapter were used. These taxa are considered as present all over the Celtic Sea (but with a variable abundance across the area). Based on Newman & Girvan (2004) algorithm (using a spin-glass model simulating annealing), we attributed to each taxa a module and calculated the global modularity score of the network. Since no taxa in the Celtic Sea is highly vulnerable (highly sensitive and highly exposed), we studied separately the distribution of sensitivity and exposure across

modules. A post hoc non-parametric test (Kruskal-Wallis) was realised to test whether the sensitivity and the exposure were significantly different between modules. We then represented the spatial distribution of the biomass of each module, considering the belonging to a module as a trait and applying a CWM. Since we considered each module separately, this is equivalent to compute the biomass of taxa belonging to the module over the biomass of all taxa, at each site. For each module, values at each site were interpolated for graphical representation. Analyses were performed using the Ipgrah package (Csardi, 2013) in the R software (R Core Team, 2020).

4.3.3 Results

The network has a low global modularity score of 0.2. Three sub-systems could be distinguished, with a relatively balanced number of components: module 1 (20 taxa), module 2 (20 taxa), module 3 (29 taxa) (Fig. 1). The range of trophic levels is similar between modules, with the exception of module 3 that encompassed species with the lowest and the highest trophic levels (respectively king scallop, PECTMAX, and cod, GADUMOR).

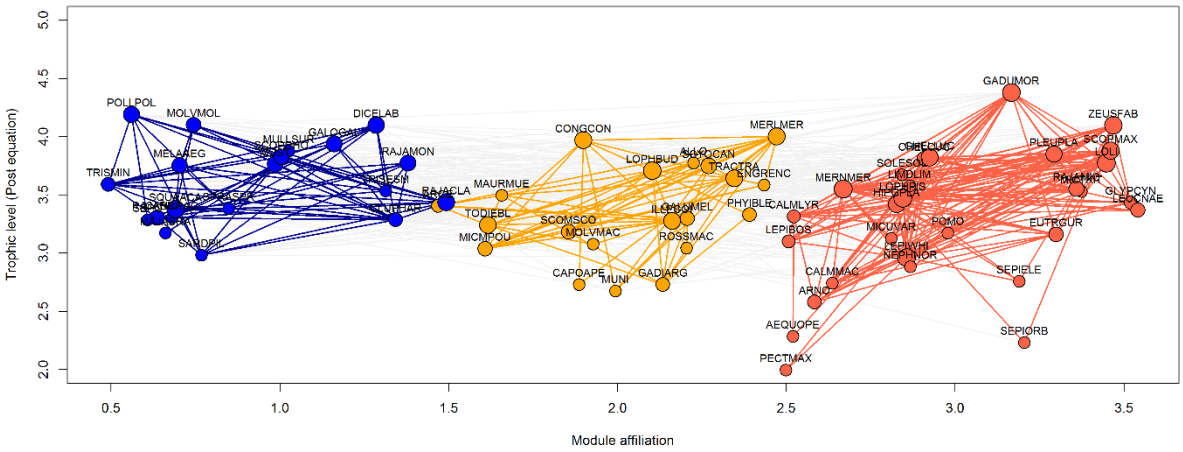


Figure 1: Composition of the 3 modules and their trophic levels. Position of taxa on the x-axis is realised according to their module affiliation and a uniform distribution to ensure maximum spanning between taxa for display purpose.

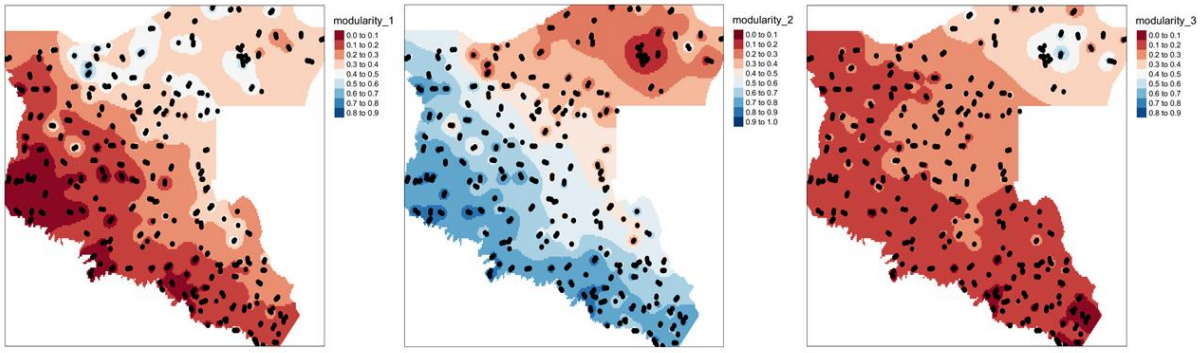


Figure 2: Interpolated map of the distribution of the biomass of each module in the Celtic Sea (the smallest values of biomass are in red and the highest in blue).

We observed that module 1 tended to gather slightly more sensitive taxa than modules 2 and 3, which may be caused by the presence of tope shark *Galeorhinus galeus* (GALOGAL), spurdog *Squalus acanthias* (SQUAACA) and rays in this group (Table S1). However there were no significant differences between any pair of group (Kruskal-Wallis rank sum test Chi-squared = 1.59, pval= 0.45) (Fig. 1). Similarly, module 1 tends to gather slightly more exposed taxa than module 2 and 3 with the presence of sprat *Spratus spratus*, edible crab *Cancer pagurus* and European spider crab *Maja sp.* (Fig.1 and Table S1). However, as for sensitivity, the difference of exposure between modules was not significant (Kruskal-Wallis rank sum test Chi-squared = 4.55, pval= 0.10). The largest biomass of taxa belonging to module 1 was found in the North of the Celtic Sea (Fig. 2). Module 2 gathered medium sensitivity and exposure taxa (Fig. 3), the largest biomass of which are encountered in the south of the Celtic Sea at high depth (Fig. 2). Finally, module 3 was composed of medium sensitivity but slightly higher exposure to fishing than module 2 (Fig. 3), with cod and queen scallop *Aequipecten opercularis*. The largest biomass of the taxa in this module are found in the extreme north of the Celtic Sea (Fig. 2).

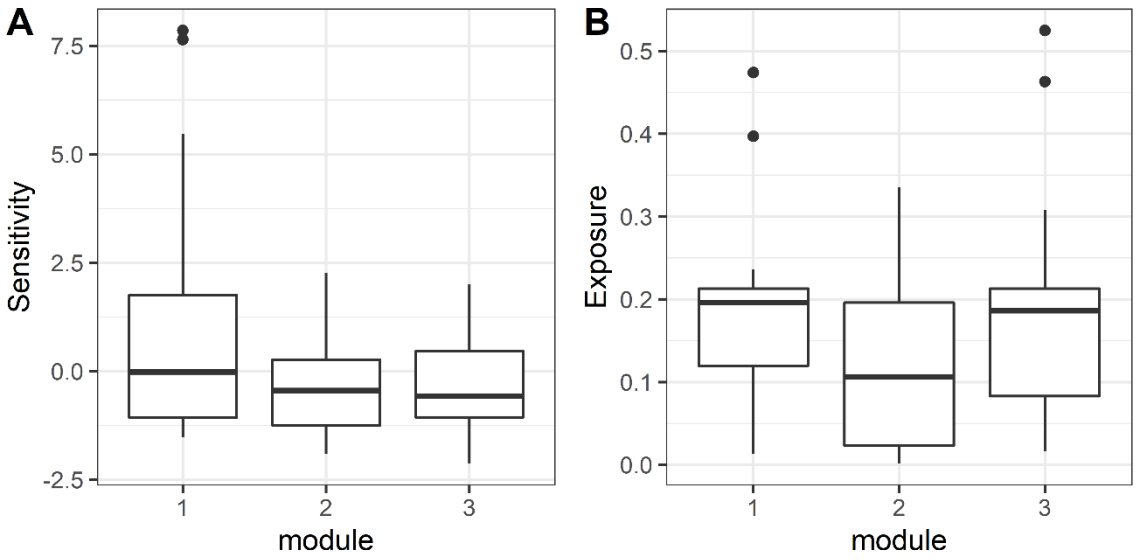


Figure 3: Boxplots of the sensitivity and exposure per module.

4.3.4 Discussion

Overall the trophic network of the Celtic Sea is weakly modular but its modules seem to be spatially segregated. Module 1 gathers the most sensitive and exposed taxa which makes this module the more likely to be affected by a perturbation like fishing-. Module 1 is located in an area that has been heavily trawled for years until the mid-2000's (Article 1). We could thus hypothesize that fishing had a strong impact on the taxa of this module, including the ones that were not highly sensitive or exposed since the fishing induced perturbation was likely to propagate within the module.

The trophic network of the Celtic Sea has a spatial structure with a neat partition between the North (modules 1 and 3) and the South (module 2) of the area. This suggests a relative spatial segregation of sub-network, with the spread of a perturbation between these areas that would be hampered by the presence of modules. Nevertheless, the low modularity of the network shows that the number of links shared by the taxa inside a module is not much larger than the number of links between taxa inside and outside the module. Some taxa could thus be grouped in another module without decreasing very much the ratio of the links with

taxa inside a module on the links with taxa outside, which would change the spatial structure observed.

Modularity in the Celtic Sea shows small values (0.2) compared to the usual range of modularity values of 0.3-0.7 for other networks (Newman & Girvan, 2004). The small values of modularity of the Celtic Sea network compared to other networks could reflect the fact that all taxa are well linked with each other but could also originate from the construction of the network using data from the literature. Indeed, a sampling reflecting the local trophic links, based on data collected only into the Celtic Sea (contrary to our trophic links which some of them come from adjacent ecosystems), could enable to remove links that do not occur in this area. Such spatial characterization of network could be further expended to provide spatial information on the scale at which conservation units should be implemented (Fletcher et al., 2013). In the case of the Celtic Sea, the closure area implemented in three ICES statistical rectangles in the North of the area would thus less likely to be beneficial for the South of the Celtic Sea.

4.3.5 Supplementary material

Table S1: Composition of the modules

Taxa	Latin names	Module
CANCPAG	*Cancer pagurus*	1
CLUPHAR	*Clupea harengus*	1
DICELAB	*Dicentrarchus labrax*	1
GALOGAL	*Galeorhinus galeus*	1
MAJABRA	*Maja* sp.	1
MELAAEG	*Melanogrammus aeglefinus*	1
MOLVMOL	*Molva molva*	1
MULLSUR	*Mullus surmuletus*	1
MUST	*Mustelus* sp.	1
POLLPOL	*Pollachius pollachius*	1
RAJABRA	*Raja brachyura*	1
RAJACLA	*Raja clavata*	1
RAJAMON	*Raja montagui*	1
SARDPIL	*Sardina pilchardus*	1

SCOPRHO	*Scophthalmus rhombus*	1
SEPO	*Sepiola* sp.	1
SPRASPR	*Sprattus sprattus*	1
SQUAACA	*Squalus acanthias*	1
TRISESM	*Trisopterus esmarkii*	1
TRISMIN	*Trisopterus minutus*	1
ALLO	*Alloteuthis* sp	2
ARGE	*Argentina* sp.	2
CAPOAPE	*Capros aper*	2
CONGCON	*Conger conger*	2
ENGRENC	*Engraulis encrasicolus*	2
GADIARG	*Gadiculus argenteus*	2
GALUMEL	*Galeus melastomus*	2
ILLECOI	*Illex coindetii*	2
LOPHBUD	*Lophius budegassa*	2
MAURMUE	*Maurolicus muelleri*	2
MERLMER	*Merluccius merluccius*	2
MICMPOU	*Micromesistius poutassou*	2
MOLVMAC	*Molva macrophthalma*	2
MUNI	*Munida* sp.	2
PHYIBLE	*Phycis blennoides*	2
ROSSMAC	*Rossia macrosoma*	2
SCOMSCO	*Scomber scombrus*	2
SCYOCAN	*Scyliorhinus canicula*	2
TODIEBL	*Todaropsis eblanae*	2
TRACTRA	*Trachurus trachurus*	2
AEQUOPE	*Aequipecten opercularis*	3
ARNO	*Arnoglossus* sp.	3
CALMLYR	*Callionymus lyra*	3
CALMMAC	*Callionymus maculatus*	3
CHELCUC	*Chelidonichthys cuculus*	3
CHELLUC	*Chelidonichthys lucerna*	3
EUTRGUR	*Eutrigla gurnardus*	3
GADUMOR	*Gadus morhua*	3
GLYPCYN	*Glyptocephalus cynoglossus*	3
HIPGPLA	*Hippoglossoides platessoides*	3
LEPIBOS	*Lepidorhombus boscii*	3
LEPIWHI	*Lepidorhombus whiffiagonis*	3
LEUCNAE	*Leucoraja naevus*	3
LIMDLIM	*Limanda limanda*	3
LOLI	*Loligo* sp.	3
LOPHPIS	*Lophius piscatorius*	3
MERNMER	*Merlangius merlangus*	3
MICTKIT	*Microstomus kitt*	3
MICUVAR	*Microchirus variegatus*	3
NEPHNOR	*Nephrops norvegicus*	3
PECTMAX	*Pecten maximus*	3
PLEUPLA	*Pleuronectes platessa*	3
POMO	*Pomatoschistus* sp.	3

RAJAMIC	*Raja microocellata*	3
SCOPMAX	*Psetta maxima*	3
SEPIELE	*Sepia elegans*	3
SEPIORB	*Sepia orbignyana*	3
SOLESOL	*Solea solea*	3
ZEUSFAB	*Zeus faber*	3

5 Discussion

The management of marine ecosystems based on a holistic knowledge of their different components still requires a large amount of data: at the species level for the ones that are poorly known, on the species biological characteristics (traits), on the way these species interact and on the past, current and future dynamics of abiotic environmental conditions. In parallel, the increased availability of complementary data sources such as time series and projection of environmental variables (e.g. temperature, salinity, current, chlorophyll a concentration) or traits for an increasing number of species makes the implementation of the ecosystem approach to fisheries possible. It also raises conceptual and methodological challenges in integrating concepts from other research fields (e.g. bioinformatics, social sciences).

Gathering the data necessary for ecosystem approach to fisheries management is the first step. The International Bottom Trawl Surveys (IBTS) led by the European Union and founded by DCF data collection framework offers the opportunity to collect some of those data. However, the practical way data are analysed and used for decision-making purposes to formulate management strategies is complex to implement. The findings of my thesis illustrate how trends of biodiversity at the scale of the species and the network of their interactions could enable to develop ecosystem indicators and conservation targets (see conclusion part 1) but also to monitor management effectiveness (e.g. Article 2 that showed increased biomass of sensitive taxa after the creation of a seasonal closure area). Such results could be integrated in ecosystem assessment approach (IEA; Fig. 1) that is the current methodological framework that enables an effective implementation of the concept of ecosystem approach to fisheries in Europe (Levin et al., 2009; Möllmann et al., 2014; Walther & Möllmann, 2014). It aims at providing a simple roadmap to managers and policy makers. At the European level, the International Council for the Exploration of the Sea (ICES) hosts a steering group in charge of guiding and supporting

Expert Groups that develop ecosystem assessment methods and contribute to ecosystem overview reports (DePiper et al., 2017). In the United States, the fisheries management councils are also increasingly interested in the outputs from these integrated ecosystem assessment (Levin et al., 2009). In the following paragraph, I would discuss how my results could inform decision making processes and what remains to be done.

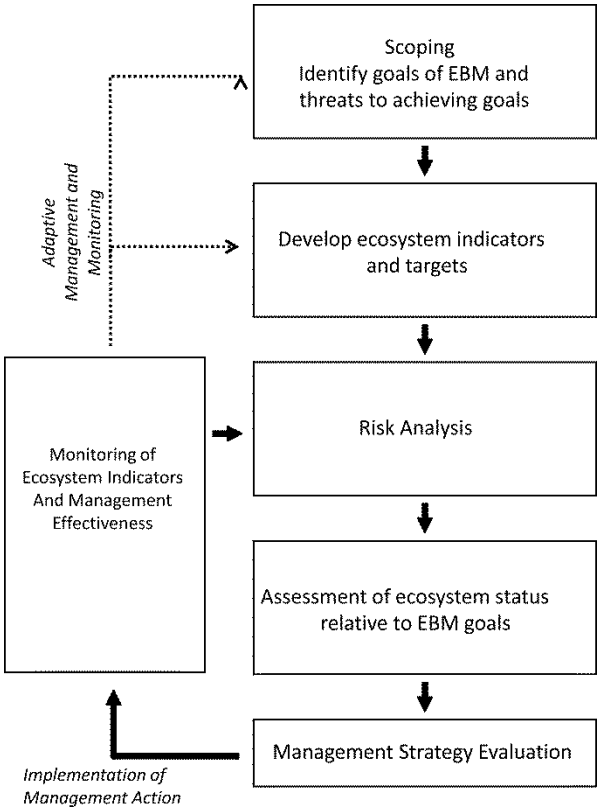


Figure 1: Schema of the five steps of Integrated Ecosystem Assessment from Levin et al. (2009). EBM is the abbreviation for ecosystem-based management.

5.1 Assessing drivers of communities in space and time: the combination of different facets of biodiversity enables to understand the past and draw the future trajectories

Fishing has shaped ecosystems in the North East Atlantic for a century, leading to several ecosystem shifts with a depletion of high trophic levels. Since it peaked in the 80's, fishing effort is decreasing. At the scale of the Celtic Sea, I could not show a decrease in the yearly average number of fished hours from 2000 to 2016. This global trend hide local disparities. For instance, I showed that at the scale of statistical rectangles in the Celtic Sea map, there was a decrease in bottom trawl fishing effort in the North East of the Celtic Sea and an increase in the South West that could be linked with change in fishing practices from targeting white fishes (cod *Gadus morhua*, hake *Merluccius merluccius*, and whiting *Merlangius merlangus*) to anglerfishes. I showed that bottom and pelagic trawl efforts had little effect on community composition after 2009 (Article 1). From 2000 to 2016, environmental variables (i.e. depth, chlorophyll a concentration and bottom temperature) were the main structuring variables for communities of demersal and benthic megafauna.

However, different information came from the use of traits. When focusing on sensitive taxa, as we did for bentho-demersal mega fauna sampled by bottom trawl (Article 2) and by underwater video (Article 3), we can see an importance of fishing as a structuring variable, even after 2009. For fish and large benthos from bottom trawl surveys data, I showed that depth, sediment and bottom trawl fishing explained the distribution of the largest number of life history traits considered (Article 2). For data from underwater video analysis that also include sessile and fragile organisms, the distribution of the biomass of sensitive taxa was mostly driven by depth, chlorophyll a and fishing, as well as spatial variables (Article 3). This indicates, first, that the indices of sensitivity we used and built were efficient at capturing the distribution of the sensitive taxa to fishing. This also suggests that only the distributions of the most sensitive

taxa present in the Celtic Sea are dependent on fishing toward the end of the period considered here.

These trends are visible at the scale of the Celtic Sea but this thesis also revealed more local phenomena (Fig. 2). Sediments and depth characteristics create four distinct zones (Fig. 5, Article 1). Environmental conditions and topology of the trophic network highlight a clear partition of the Celtic Sea between the North and the South of this diagonal (zones 1 and 2 versus zone 3 to 5 in Fig. 2). The South of the diagonal toward the continental slope (zone 1 and 2, Fig. 2) gathers the clusters 1 and 2 of the EVHOE sampling sites (Article 1, Fig. 5) and corresponds to the zone where the taxa of the module 2 of the trophic network have their largest biomasses (Article 3, Fig. 3). This area is characterised by deep and warm water taxa that tend to have more trophic interactions together than with the rest of the taxa present in the Celtic Sea. Communities in this area are homogenous, except at the extreme western border of the continental slope where few sampling sites gather the most sensitive communities characterized by the sea pen *Funiculina quadrangularis* (Article 3, Fig.2). Conversely, the North of this diagonal could be distinguished in 3 subareas (zones 3, 4 and 5, Fig. 2):

(1) one with the largest biomass of taxa in module 1 (Article 3, Fig. 3) (zone 3, Fig. 2);

(2) one with cold water taxa, under high concentration of chlorophyll a, and historically the more exposed to bottom trawl (zone 4, Fig. 2). In this area, the decrease in bottom trawl effort after 2009 and the creation of a seasonal area closure leads to the increase in elasmobranchs biomass (Article 2), but it also hosts the least sensitive benthic communities (Article 3). This area gathers the largest biomass of taxa from module 3, meaning that taxa that tend to have more trophic interactions together than with the rest of the area;

(3) one that has the largest biomass of sensitive taxa in the centre of the Celtic Sea (Article 2, Fig. 2 and 3) covering the 3 trophic network modules (Article 3, Fig. 3) (zone 5, Fig. 2). This

area is composed of mixed communities, with both slow and fast life history strategy taxa (Article 2, Fig. 2 and 3).

I can see that studying the different facets of the biodiversity gave a more precise view of the communities compare to what was previously known on the Celtic Sea communities (see Introduction, Fig. 7).

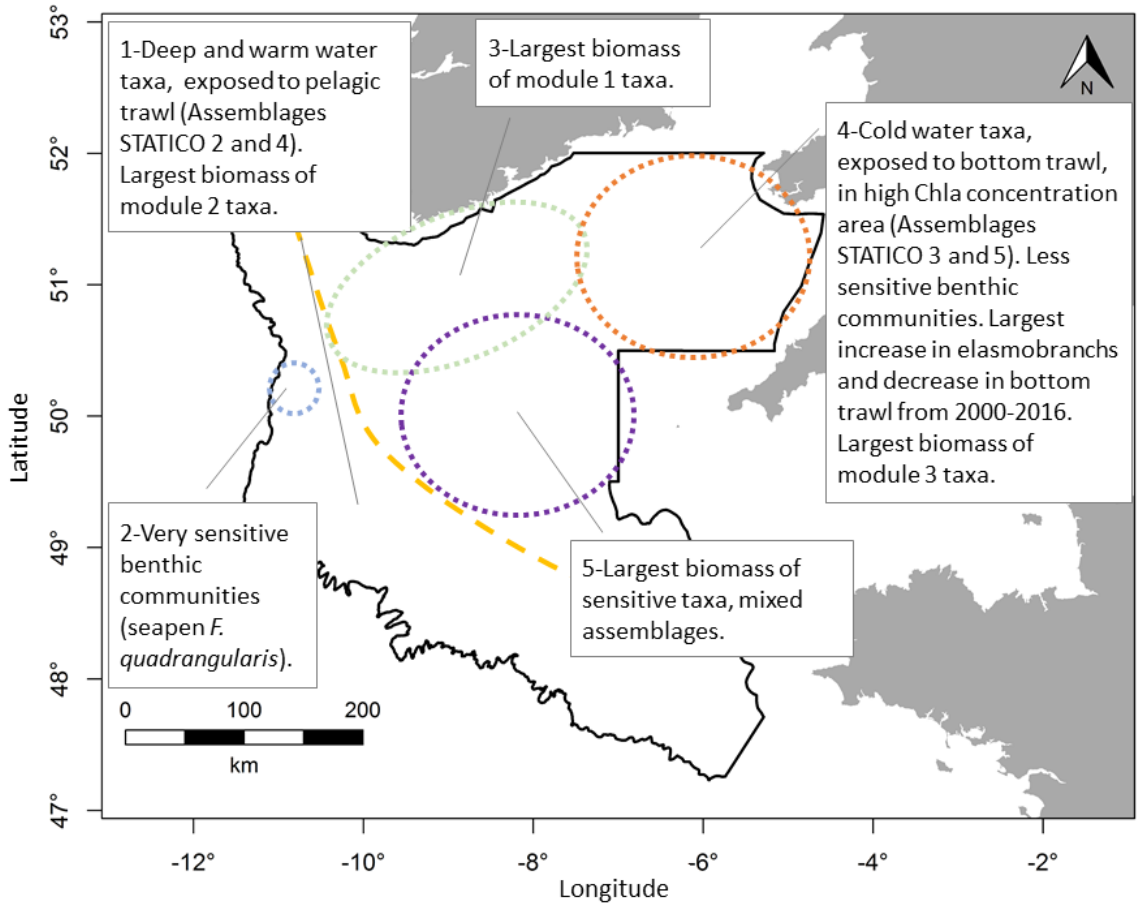


Figure 2: Summary of the characteristics of the distinct area of the Celtic Sea from the different facets of the biodiversity studied. The black line shows the limit of the area sampled by the EVHOE survey. The yellow dashed line separates the North and the South of the Celtic Sea. The dotted lines delineate the sub zones.

In the last 20 years, the effects of climate change became visible. It could be seen through modified fish distribution (Dulvy et al., 2008) superimposed to natural climate variations such

as the Atlantic Multidecadal Oscillation (AMO) that was in a warm phase in the late 1990's (McLean, Mouillot, Goascoz, et al., 2018). The main challenge faced by fishery managers in the North East Atlantic is now to assess the importance of fishing and climate change and their synergistic effects. This has to be done while accounting for the fact that climate change would affect populations that are already under fishing pressure.

Findings from the taxon and trait facets of the biodiversity as well as the interactions between taxa through trophic network inform on the possible future trajectory of the area under climate change scenarios. The area in the North-East of the Celtic Sea (area 4, Fig. 2) would face the largest number of changes. Historical bottom trawl fishing had most likely led to the depletion of sensitive benthic taxa in this area. Over 2000-2016, this area has experienced a significant increase in bottom temperature and is thus expected to face the fastest increase in temperature in the coming years. This area gathers cold-water commercial taxa, i.e. Atlantic herring *Clupea harengus*, whiting *Merlangius merlangus*, haddock *Melanogrammus aeglefinus* and American plaice *Hippoglossoides platessoides*. These species thus have to be particularly carefully monitored and changes in the Celtic Sea fisheries are to be planned as these species will likely move northward or toward deeper areas with increasing sea temperature as an effects of climate change. More generally, taxa that guard their offspring and have very high fecundity showed a negative relationship of their biomass with bottom temperature (Table 2, Article 2). The only taxon that exhibits these two traits is the edible crab *Cancer pagurus*, whose distribution is thus thought to be largely impacted. This taxon is also among the ones whose deletion would lead to the lowest robustness of the trophic network (Table S1, Article 4). Other taxa that lead to the lowest robustness of the network will also be impacted by climate change among the taxa that guard their offspring (i.e. European spider crab *Maja brachydactyla*) and among the taxa that have very high fecundity (i.e. queen scallop *Aequipecten opercularis*, king scallop *Pecten maximus*, cod and hake) (Appendix A). The trophic network of the Celtic Sea

would thus face some significant changes in the coming years when climate change impacts on bottom temperature will become more significant. Conversely, when considering benthic and fixed organisms (from underwater video) we did not show a significant relationship with temperature (Table 1, Article 3). It thus appears that benthic organisms in the Celtic Sea would be able to cope with a certain increase in bottom temperature in link with climate change even though most of them are fixed or little mobile and cannot move to avoid increased water temperature.

In addition, primary production is projected to decrease in the North East Atlantic by 50% by 2099 under the scenario Representative Concentration Pathway (RCP) 8.5 (Kwiatkowski et al., 2019). The North East of the Celtic Sea (Area 4, Fig. 2) gathers taxa that positively co-vary with chlorophyll a concentration and are thus particularly at risk. In addition, the decrease in primary production will affect first the most basal components of the trophic network that are very likely to spread this perturbation to the whole network, given the low robustness of the Celtic Sea food web to the simulated loss of its most basal components.

Putting together the different views of the communities brought by the study of taxon-diversity, trait-based diversity and interactions of taxa through trophic network highlights the complementarity of these approaches. Joining these approaches could allow developing indicators and targets to feed in an IEA approach. For instance, the STATICO approaches and notably its temporal trajectories (mean annual position of the ecosystem in the space of the environmental variables or in the space of taxa) part would provide indication on a potential increase or decrease in biomass of a large number of species in relation with environmental modifications. Targets could be set as a portion of the multivariate space in which are drawn the trajectories. The pool of species studied with this approach could be restricted to the one the most sensitive, or vulnerable to a given pressure, or the ones that are the most influential in the network of interaction between species. In addition, the spatial information gathered in Fig. 2

could feed a spatial planning process. It could be proposed in the coming years to implement closure area in where the most exposed taxa are present. The spatial aspect of the trophic network would be beneficial to consider creating such closure area.

5.2 A traits-based approach to explain assembly processes and explore the consequences of management measures

Bottom trawl and underwater video samplings gave a slightly different view of the distribution of sensitivity patterns in the Celtic Sea. For the sensitivity to fishing computed from bottom trawl surveys data, the most sensitive areas were located in the Centre East of the Celtic Sea, due to the presence of slow life history strategy taxa (mostly elasmobranchs). Instead, sensitivity computed from the underwater video data reached its highest values in the South, but also along the Western border of the area due to the presence of fixed and filter-feeders organisms with high sensitivity values (Fig. 2, Article 3). In particular, the highest value of sensitivity was reached in the deepest area, along the Western border and was caused by the presence of the sea pens *Funiculina quadrangularis*. This species is considered as one of the species of greatest conservation importance in the OSPAR regions II and III (Greater North Sea and Celtic Seas) (Clark et al., 2014). *F. quadrangularis* is found in areas of fine mud heavily bioturbated, at water depth ranging from 15-200m (OSPAR, 2008). This species is thus indicative of a particular biotope, identified as a "Seapen and burrowing megafauna" habitat by OSPAR and known to be very sensitive to fishing. However, there has been no detailed mapping of this habitat, making it very difficult to quantify its decline (OSPAR, 2008). Absence of *F. quadrangularis* from Norway lobster *Nephrops norvegicus* trawling ground in the centre of the Celtic Sea, despite it is a suitable habitat (OSPAR, 2008), raises the question of its presence before fishing exploitation. Conversely, the sea pen *Pennatula phosphorea* was

observed in the whole North of the Bay of Biscay. This is a favourable habitat for this species that was thought to have been depleted because of intensive trawling, but that can retract (Merillet et al., 2017). This questions the validity of the classification of some areas, as little sensitive, whereas they could harbour some sensitive species if they were undisturbed. This also highlights the fact that sensitivity assessment to bottom trawl should take into account the largest range of organisms possible and be based on data originating from various sources in order to get the broadest possible view of the ecosystem.

The use of traits to understand assembly patterns is a common practice that starts to be increasingly used in the marine ecosystems (Beauchard, Veríssimo, Queirós, & Herman, 2017; Kraft, Valencia, & Ackerly, 2008; Mouillot et al., 2007; Pecuchet et al., 2016). Applying this method to the Celtic Sea showed a global underdispersion in life history traits over this area, with the presence of slow life history traits most likely hampered by fishing pressure through a process of environmental filtering. Overdispersion observed in the centre of the Celtic Sea is due to the presence of both fast and slow life history taxa. However, in this case, overdispersion could not be related to any competitive exclusion process. Overdispersion was due to the presence of the same taxa than over the rest of the area plus slow life history taxa. The most likely hypothesis to explain this pattern is a combined effect of relaxed fishing pressure and greater diversity of niches via small-scale spatial heterogeneity in the centre of the Celtic Sea. This stresses the fact that overdispersion in traits should not always be associated with competitive exclusion when studying assembly processes. It could also be related to environmental filtering at small scale, as it is likely the case here.

The increased knowledge of the trait-environment relationship has opened the way to a large use of trait-based approaches to monitor ecological status of ecosystems, communities and

populations (Beauchard et al., 2017). Life history traits in particular have been widely studied and their relationships with fishing pressure have been documented by numerous studies (Jennings et al., 1998; Le Quesne & Jennings, 2012; Wiedmann et al., 2014). For instance, Pecuchet *et al.* (2017) showed an increase in the biomass of opportunistic species (highly fecund, short lived and small) and equilibrium species (long-lived and low fecund) in link with a decrease of fishing effort and an increase of temperature. This is in line with the increase, I observed in the Celtic Sea, in the biomass of large species that tend to mature late and have small offspring (Article 2). Trait-based approaches provide a systematic understanding of the main trends of biodiversity in response to environmental and anthropogenic drivers and can thus be used to evaluate the efficiency of management strategies. Looking at the local temporal trends of fishing effort and biomass of the most sensitive taxa, I showed that the increase in biomass occurred in local areas where seasonal fishing closure was implemented since 2005. This highlights the benefice of local management measures in less than two decades to increase the biomass of slow life history taxa.

However it can be difficult to transcribe management goals into traits indicators (Laughlin, 2014). Some relationships have already been extensively studied in the literature, such as the one between life history traits and fishing pressure (Jennings et al., 1998; Le Quesne & Jennings, 2012; Stevens, Bonfil, Dulvy, & Walker, 2000; Wiedmann et al., 2014) and can be considered as established. However, one major limitation of the use of a large number of traits in a trait-based approach in community ecology to evaluate ecosystem functioning for marine fish and benthos is the lack of clear relationship between traits and their response to pressure but also their effect on the biotic and abiotic components of the ecosystems (Pecuchet, 2017). Many pressure-trait relationships are still to be explored. For instance, traits such as sociability, migration, gonochorism or spawning period could reflect the adaptability of organisms to a fast changing environment. Migrating species could be more prone to travel long distance to find a

more suitable habitat. Species living in a group could have more difficulties to find their preys in a sufficient quantity to feed the whole group, or inversely could be favoured by efficient predation strategy. Species that have more than one biological sex or that can spawn at different time of the year could adapt more easily their reproduction to changing environment.

The spatial scale at which the analysis is conducted is also determinant. Indeed, the failure to detect a relationship between species distribution and traits at a global scale could be caused by traits operate within local and regional context (Costello et al., 2015; Vermeij & Leighton, 2003). Traits could vary between different locations for the same species. It is thus particularly important to account for intraspecific variations. Studies that account for intraspecific trait variability are still scarce (but see Blanck and Lamouroux, 2007), especially in the study of exploited marine ecosystems. Nevertheless, the development of comprehensive databases also contributes to alleviate this gap. For instance, Beukhof *et al.* (2019) released a database in the PANGAEA repository that gathers different values of traits for one fish species, according to the large marine ecosystem they were sampled in.

Well documented trait-pressure relationships could then be used to feed multispecies trait-based models to apply ecosystem fisheries approach (Barnett et al., 2019). The first trait-based approaches to inform fishery models dates back to two decades ago with the study of the differential response of r- and K-selected tuna species facing various levels of exploitation (Fromentin & Fonteneau, 2001). Trait information can thus be integrated to fisheries management through trait-based models. Other traits can also be used, such as size distribution. For example, “size-spectrum models” express the state of the community by a distribution of abundance of traits instead of taxonomic units and thus reduces the number of parameters necessary to run the model and more generally to inform data-poor stock assessments (Barnett et al., 2019). Reference points are conceptual criteria which capture the management objective

of the fisheries and are often based on stock-recruitments relationships (Heino et al., 2013). More development of trait-based reference points, e.g. the shape of the size distribution could also be developed and could enable to overcome the lack of data for certain species (Barnett et al., 2019). Candidate traits would be the ones likely to influence fitness, being directly linked to management outcomes or that are known proxies for biological processes (Barnett et al., 2019) and tool such as the probability for maturing at a certain age and size could be more often used (Olsen et al., 2004). Fishing induced evolution of life history traits could be used to monitor the state of one population and included to update the reference points (Heino et al., 2013). In the cod population off Labrador and Newfoundland for instance, life history traits continually shifted toward early maturation at small size before the collapse of the population (Olsen et al., 2004). Multivariate analysis of a chosen set of traits could also be used to support fisheries management since it summarises the multiple facets of traits of a species' pool (Beauchard et al., 2017). This approach is still poorly used in fisheries sciences and when applied was restricted to a small number of traits (Rijnsdorp et al., 2016, but see Koutsidi et al., 2020).

Traits enable to group species with similar characteristics together to better understand ecosystem functioning. However, to scale up to ecosystem level consequences of the dynamics observed at the species level, interactions between species have to be taken into account.

5.3 A step up from species to ecosystem sensitivity: integrating traits into food webs

Species interact together and a perturbation affecting one species is susceptible to spread to the entire ecosystem. Networks enable to assess the consequences of a perturbation at the community level and to consider both its direct and indirect effects (Bascompte, 2009). The

integration of trait-based approach to trophic network analysis to generate a more mechanistic understanding of ecosystem robustness to a perturbation is a promising field (Pecuchet, 2017; Thompson et al., 2012). In 2016, Gravel, Albouy and Thuiller noted a gap in theory relating functional composition of food webs to their dynamics and properties. This lack has to be overcome as there is a growing interest in the conservation of ecological networks to maintain ecological functions (Harvey et al., 2017). In particular, it was not clear whether the sensitivity of species implies the sensitivity of the trophic network to a given pressure. In this work, I proposed a simple framework that enables to scale up from a trait-based computed sensitivity at the species level to the sensitivity of the whole food web.

The Celtic Sea has been historically exploited by fishing, with a constant increase in fishing pressure from 1950 to early 2000's (Hernvann & Gascuel, 2020). Its trophic network has been modified, with a decrease in the biomass of high trophic level and emblematic species. The depletion of hake, cod, whiting and megrim, which are important predators and were driving the trophic network through top down effect, leads to a shift toward a more pelagic-dominated ecosystem (Hernvann & Gascuel, 2020). Using our framework, I investigated the possibility for a fishing induced perturbation to spread through the trophic network of the Celtic Sea.

The steps of the framework could be summarised as follow:

1- Based on life history traits (maximum length, longevity, age at maturity, offspring size, fecundity and reproductive guild), I quantified species sensitivity to fishing.

2- I crossed this information on sensitivity with species' centrality, to quantify the potential for a fishing induced perturbation to spread across the food web. In particular, I used the eigenvector centrality, a mesoscale centrality measure, to quantify how influential each species was.

3- A species can be sensitive to a perturbation but not exposed to it. Following a simplified definition of the IPCC (2001) vulnerability framework, I quantified vulnerability as

sensitivity crossed exposure. Exposure can be quantified by different metrics. For instance, catch level (Hobday et al., 2011), fishing event frequency (Halpern et al., 2007), or as here by fishing mortality defined as the biomass present over the area divided by the biomass of catch (that includes landings and discards).

4- To scale up to the network level, a secondary extinction analysis was performed based on deletion sequences from the previous steps and its effects on the connectance of the network.

These steps enabled us to conclude that the most influential species (i.e. the ones with the highest eigenvector centrality) in the Celtic Sea were not the most sensitive to fishing, nor the most vulnerable (Article 4). Following the definition of robustness, as the proportion of primary extinction events that lead to a particular proportion of total extinction (primary and secondary extinction) (Dunne et al., 2002a), the network appeared to be the least robust to the deletion of basal species (i.e. species with the highest number of predators) and the 7% of the most exposed species. The most exposed species are queen scallop, king scallop, edible crab, European spider crab, cod, sprat *Spratus spratus* and hake, which includes both basal and emblematic commercial species (Article 4). The largest threat for the robustness of the Celtic Sea trophic network amongst the scenario considered here would thus be to increase the catch of the taxa that have the largest ratio of biomass exploited over total biomass present in the area.

It was established in the literature that the removal of the most connected taxa lead to the lowest robustness of the network (Curtsdotter et al., 2011; Dunne & Williams, 2009). I found contradictory results since the removal of the taxa with the largest centrality leads to a number of secondary extinction similar to the one expected by chance (Fig. 4, Article 4). Some specificity in the topology of the Celtic Sea network explain this result. This could be explained by the small number of taxa with very large centrality values (i.e. with very large number of prey and predators). The robustness of the network when removing central taxa can also be

linked with the observed increased compartmentalization, i.e. increased modularity of the network, since modularity is known to promote network stability (Stouffer & Bascompte, 2011; Thébault & Fontaine, 2010). Removing the most central taxa thus reinforces the structure of the modules, with taxa sharing more links with taxa inside the module than outside. The robustness most likely also originates from the fact that the deletion of the most central taxa causes the removal of redundant trophic interactions first, as suggested by the decrease of the nestedness (Nordstrom et al., 2015). The remaining taxa still have taxa to feed on after the removal of the most central ones.

To my knowledge, there was a lack of approaches associating ecological network with a trait dataset to assess taxa' sensitivity to fishing pressure and the robustness of the network to perturbations. The steps at different levels, from local (i.e. taxa) to global (i.e. network) including mesoscale permit to understand the mechanisms causing to the patterns observed at the network level. The simple framework proposed here is easily applicable since it requires few data: life history traits are available for many species while more and more trophic networks are published.

Nevertheless, this approach does not include any spatial aspects, whereas the study of the spatial patterns of networks is a promising field for taxa conservation notably as it informs on the scale a perturbation could spread between components of the network (Gilarranz, 2020). In the Celtic Sea, I showed that the topology of the trophic network creates three subsystems. Each of these subsystems have a distinct spatial distribution, which imply that a perturbation affecting one of these subareas would less likely to spread to others. Spatial patterns of modularity however do not imply a that a perturbation would be totally restricted to one module as the modularity in the Celtic Sea is low, meaning that for taxa in the module the number of links with taxa inside the module is not very high compared to the number of links with taxa outside.

Finally, this framework has been used in the case of the Celtic Sea with the example of sensitivity to fishing pressure but could easily be extended to other pressure such as climate change. The use of temperature related traits could be proposed, such as species temperature index (STI) which is the species 'climate envelope or its equivalent when including several species, i.e. community temperature index (CTI) (Devictor et al., 2008; Thuiller et al., 2005).

5.4 A roadmap to navigate the questions raised by the ecosystem approach to fisheries management and the various kinds of data available

This work considered taxon and trait-based diversity but also the interactions between species that enables to enrich our view of ecosystem dynamics. I proposed the use of several statistical approaches to answer questions in link with the change in variable driving fishing ground in the North East Atlantic and the implementation of ecosystem approach to fisheries, making the most out of the IBTS data. The data necessary to answer some of these questions as well as the analysis proposed are summarised in the roadmap graph below (Fig. 3). This highlights the complementarity of these different source of data as well as their necessity to reach more advanced conclusions on the state of health of the ecosystems. For instance, the sensitivity of the species could be crossed with the trophic network topology to infer if species sensitive to a given pressure would spread the perturbation to the entire network.

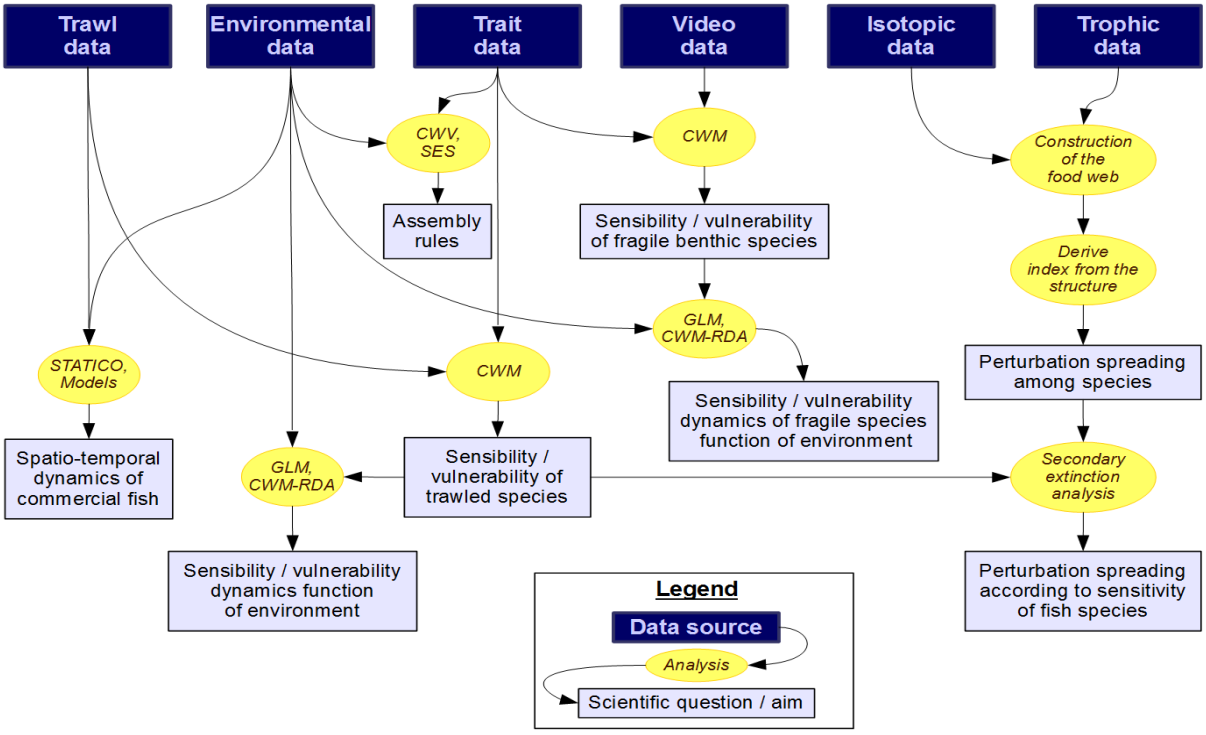


Figure 3: Road map of the question answered from the different kinds of data available from International Bottom Trawl Surveys and example of the analysis to use

6 Perspectives

6.1 Enlarging the focus on the Celtic Sea to study the effects of climate change in the North-East Atlantic region with IBTS data

The natural perspective of this thesis will be a characterisation of the effects of climate change and its cumulative effect with fishing. Interesting future questions to answer would be:

(1) Will the most sensitive taxa to climate change, notably the cold-water taxa present in the North of the Celtic Sea, disappear due to increased temperature that would exceed their thermic range?

(2) What taxa will arrive in the Celtic Sea?

(3) What will be the consequences in term of traits distribution? How the functional turnover would be impacted by species arrival and disappearance?

(4) What will be the consequences of removing the most sensitive species to increasing temperature for the trophic network? What will be the differences with removing the most sensitive to fishing and to both fishing and climate change? Which taxa would be the most influent? Would that be different ones than before?

To alleviate the effects of the increase in temperature, species either migrate northward (in the northern hemisphere) or toward deeper area. In the Celtic Sea, the latitudinal gradient is stronger than the bathymetric one in driving temperature, which means that the deepest areas located in the West and South are also the warmest (Fig. 8a, Article 1). I could thus expect a northward migration of the species more than a migration toward deeper area. Rate of migration of marine species in the last decade were in average of 72.0 ± 13.5km decade^{-1} (Poloczanska et al., 2013). To characterise the effects of climate change, it would be interesting to consider a larger area than the Celtic Sea. Indeed, as it is not an enclosed sea this would enable to better

follow the change in distribution of species, including early signs of northward migration of some species that are not at the moment in the Celtic Sea.

International Bottom Trawl Surveys are conducted across Europe according to a standardized protocol and are publicly available. Grouping these data sources together would provide a highly resolved regional view of the dynamics of a large number of species. This could allow to predict ecological but also social and economic consequences at the scale of the Atlantic North-East region (Poloczanska et al., 2016).

A metanalysis could be conducted at the scale of the Atlantic North-East region. The importance of the different environmental and anthropogenic drivers could be examined over the last two decades to state whether the decrease in importance of fishing as a structuring variable of communities could be seen in all European ecosystems and when this shift happens. This could also show that some European ecosystem are already without doubt driven by the warming induced by climate change, as it is the case in the Barents Sea (Fossheim et al., 2015). Similarly, pattern of life history traits could be investigated across European waters, as well as the changes induced by species shifts in distribution on trophic networks. A particular focus on the areas that have gained or lost species could be done to assess the consequences at the level of the network.

In this context of changes in species composition, it would be interesting to apply species turnover indices (Baselga, 2010). Beta diversity is the variation in species composition of an assemblage and can be partitioned between two components: nestedness (the species composition of some sites is a subset of others) and turnover (replacement of some species by others) (Baselga, 2007). Those indices have been further extended to account for functional composition of communities (Siefert, Ravenscroft, Weiser, & Swenson, 2013; Villéger, Grenouillet, & Brosse, 2013). Such functional beta diversity indices could be used at the scale of the North East Atlantic to account for changes in distribution of species exhibiting a large

thermal range or that are generalist feeders (indicate adaptability to abrupt changes in link with climate change), or an increase in slow life history taxa (following fishing pressure decrease).

These indices as well as other functional diversity indices (functional richness, evenness and divergence) were tested during the thesis but did not revealed any changes at the scale of the Celtic Sea and during the period considered (2000-2016). This could be linked with the restricted set of taxa studied here. Indeed, this thesis focussed on the 101 taxa that occurred in more than 5% of the sampling site over 2000-2016. This filters out all the rare species that could have led to the modification of functional structure through time. Evaluation of species turnover might thus be done on a dataset including less frequent or rare species.

In addition, most of the analysis conducted in this thesis (Article 1, 2 and 4) were realised based on bottom trawl data. The comparison between the sensitivity patterns from bottom and underwater video data highlight the different view of the ecosystem these different types of data provide. Considering a large number of ecosystem components requires to integrate various datasets with heterogeneous properties (temporal and/or spatial resolution for instance). On IBTS, haul samplings could be more often complemented, in the future, by underwater video footages in order to sample additional species such as fragile species but also observe seascape and the regular association of certain species together. For instance, some species were observed aggregated several times (e.g. brittle star *Ophiura ophiura* on sea anemones *Actinauge sp.*). In addition, to get a broader view of ecosystem, including rare species and other compartment than benthic and demersal megafauna, the use of other sampling tools could be proposed on board of the scientific surveys. For instance eDNA would enable to detect rare species that are poorly sampled by trawl or video (Rees, Maddison, Middleditch, Patmore, & Gough, 2014). Grab sampling would provide information on the benthic infauna, which gathers many the basal components of the trophic network, while plankton filtering mesh informs on zoo and phytoplankton presence.

6.2 Trait-based analysis and future improvements

The increased use of the trait-based approach to understand biodiversity patterns and ecosystem functioning in marine community ecology and fisheries sciences still needs to address several challenges. The lack of intraspecific variation has already been largely reported in previous studies. The development of comprehensive and publicly available databases is the first step to overcome this issue. As repositories now exist, it is now time to conduct a joint sampling effort to begin to reference intraspecific variations in traits in space and time. Such initiative could be conducted on board of the IBTS, since numerous individuals of the same species are captured every year. A unified sampling protocol at the European scale could enable to measure a large number of parameters on more than the main commercial species, on which few traits are already measured (e.g. weight, length, maturity state, sex). These new parameters could include, for instance, gonad weight (for a certain maturity state) which I could relate to the total body weight and the weight of one egg, as a proxy of fecundity, since weight-fecundity relationship is not known for all species. Other traits related to food acquisition (e.g. eye size and position or oral gape size, position and shape), nutrient assimilation (length of the gut) or to locomotion (cauda fin ratio, pectoral fin ratio, or caudal peduncle throttling) could also be measured (Villéger et al., 2017). In particular, nutrient assimilation could be linked to the role of fish in nutrient cycling (Villéger et al., 2017) and thus easily linked to an ecosystem function.

The intraspecific variations of these traits would be a valuable input into models to predict fish population dynamics. Indeed, parameters that control growth and mortality for instance, vary through years and individuals. Analytical solution such as advances in state-space models that enable to predict time-varying parameter or add additional random-effects by allowing slopes to vary through time (Barnett et al., 2019) could enable to overcome this issue. However, they do not bring a clear overview of why traits (or parameters) vary trough individuals and time. Implementing trait measurements for a larger number of parameters and

over a larger number of species would provide enough data to be able to understand the patterns of intraspecific variations and their main spatio-temporal drivers and try and predict them at the European scale. Measurements on 10-20 individuals randomly sampled across sites could be enough and would not require too much additional work compared to the measurements already realised on a regular basis.

The trait-based approach has also the potential to provide management indicators for numerous species, notably the one poorly studied for which demographic parameters are scarce. For instance, a multivariate analysis that integrates time, biomass of species and their traits would give an overview of the composition in trait of the community. The STATICO analysis could be modified to realise this analysis (Fig. 1). The first step could show any temporal shift in distribution of biomass or abundance across the different traits. The second step could provide an overview of which trait is exhibited at which site. Finally, in the last step, I could project the species in the compromise space of traits to have a yearly averaged position (forming trajectories) that would inform on which trait (or level of trait) has an increasing or decreasing biomass through time. The trajectories can offer an easy characterisation of the functional shift in the structure.

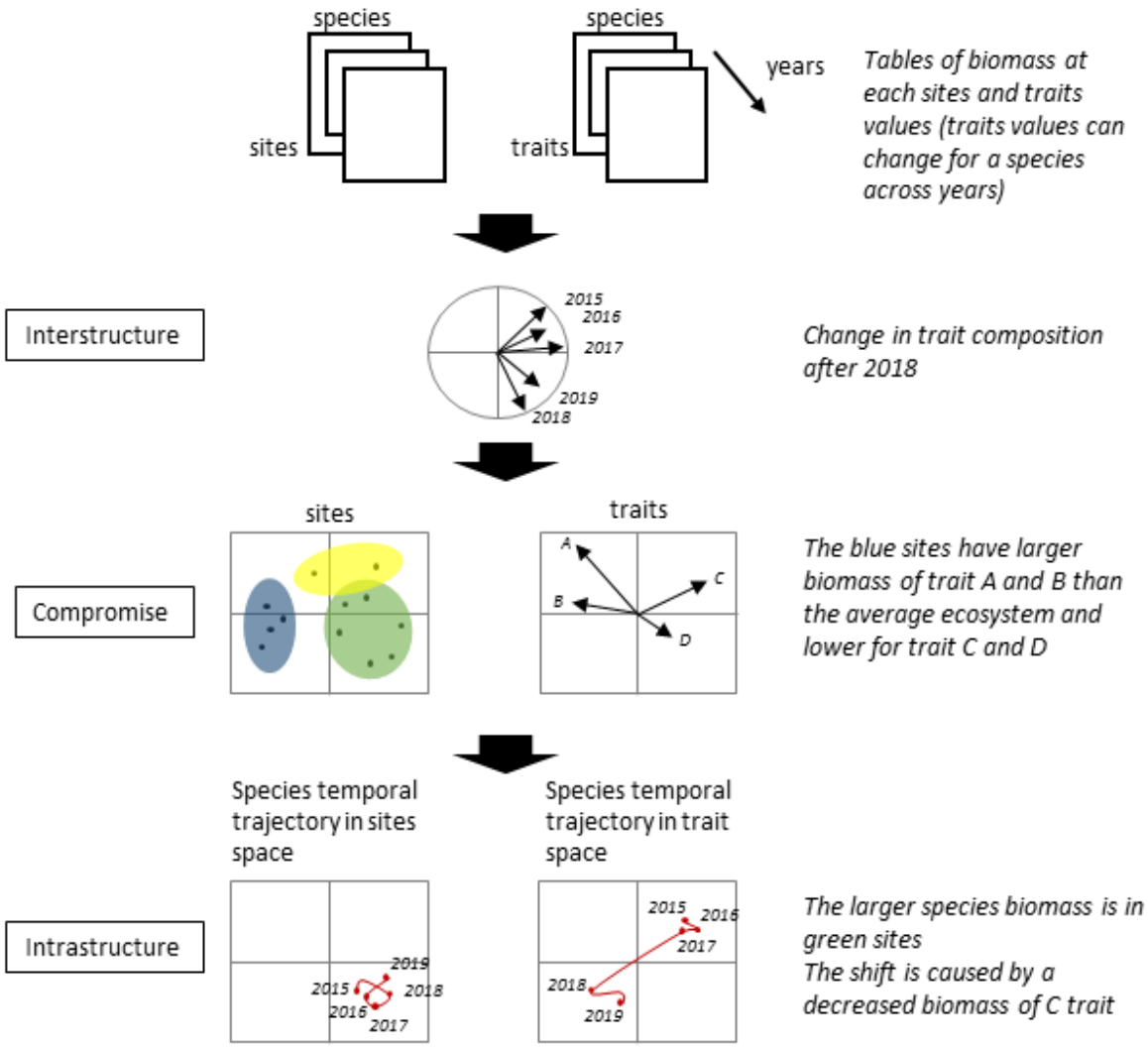


Figure 1: Proposition of modification of the STATICO analysis to include traits. The interstructure correlation circle identifies which years have similar composition in species and traits. The compromise summarizes the mean structure of the sites and the traits over all species. Sites can be grouped according to their composition in species (compromise left panel). The intrastructure is the projection of the species in the compromise space of sites (intrastructure left panel) and traits (intrastructure right panel).

In the context of the decrease in fishing pressure and the climate change predicted effects leading to temperature increase and primary productivity decrease, changes in relative biomass expressing certain traits is expected. In the Celtic Sea, in link with fishing pressure decrease, I showed an increase in slow life history. Increase in temperature would most likely modify the distribution of species according to their thermic *preferenda* but could also modify food assimilation. Indeed, the gradient of a larger biomass of herbivory fish toward low latitudes could be linked to the effect of temperature on physiology, with herbivorous fish that cannot meet the energetic demand in temperate waters (Behrens & Lafferty, 2007). I could wonder whether the increase in temperature would modify the biomass of herbivores in the Celtic Sea. This hypothesis could be tested with the modified STATICO method presented in this section. However, knowing that the primary productivity is predicted to decrease, this could generate contradictory trends in the biomass of herbivorous species.

6.3 Further development of integrating traits into trophic networks

Until now, traits in food webs from a topological point of view have been used to (1) group species in functional groups and study the flux between these compartments (Giraldo et al., 2017); (2) predict the prey-predator interactions (Spitz, Ridoux, & Brind'Amour, 2014) and potential changes in trophic networks (Pecuchet et al., 2020) with size being a major factor structuring these interactions and the traits of predators being more important than preys' ones in determining the interaction (Brose et al., 2019); (3) derive traits from the structure of the network, such as trophic level or number of prey and predators (Cresson et al., 2019). In parallel, the notions of sensitivity and vulnerability have attracted a great deal of attention in the recent years as environment faces fast changes that have to be understood, foreseen and minimised. However, there is still a lack of mechanistic insights in the current use of functional traits with

trophic networks. Given the diversity of these approaches, it appears difficult to integrate them all under a unified theory that would relate composition in traits of trophic networks with their dynamics and properties. Here, I built a simple framework that relates the sensitivity and vulnerability of species to food web topology to evaluate the potentiality for a perturbation to spread. I apply this framework to investigate the potential perturbation of food web by fishing. However, further developments would be needed toward a more mechanistic way to quantify the spread of a perturbation through the food web. In particular, it will be important that this framework allow quantifying the sum of the intrinsic vulnerability of a species to a perturbation and the additional vulnerability that originates from the spread of the perturbation from another species. This could be done with methods such as dynamic deterministic effects propagation networks (DDEPN) used in genetics (Bender et al., 2011). This method enables to follow a chain of propagation of a signal in a network from several initially perturbed nodes (Bender et al., 2011). This publication provides a R code that could be modified to apply to species instead of protein. In addition, in this framework, the direction of the propagation of the perturbation as well as the intensity of the fluxes would have to be considered as in food webs it would be interesting to differentiate between top down and a bottom up effect (Fig. 2).

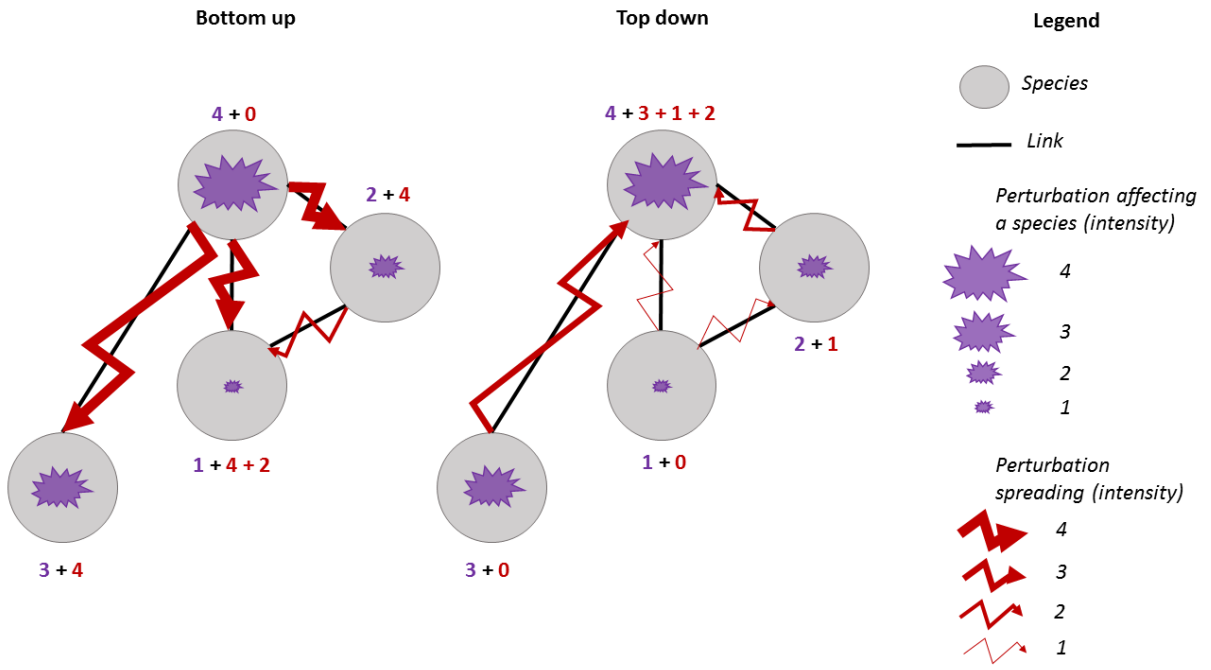


Figure 2: Example of quantification of the propagation of a perturbation through a food web. Both intrinsic taxa sensitivity (in violet) and the one resulting from the spread of the perturbation through the network (in red) are considered.

6.4 Species interactions networks beyond trophic interactions networks

Network analysis is one of the fastest growing disciplines in ecology (Borrett, Moody, & Edelmann, 2014) and is also applied to non-trophic interactions. In particular, Kéfi *et al.* (2016) contributed to open the way to the study of multiple types of interactions (multiplex networks) and showed that these interactions allow for higher species persistence and total biomass than expected by chance. Networks can also be used for a better understanding of assembly processes, as did Legras *et al.* (2019) that compared the co-occurrence network (based on species abundances) and the functional network (based on species trait values) to assess whether species belonging to a functional group belong to the same co-occurrence group. Finally, network can also be used to study ecosystem functioning through the consideration of trait

space. For instance, Siwicka, Thrush and Hewitt (2020) analysed a network where interactions were based on the co-occurrence of species in the trait space (i.e. how many traits any pair of species share), with a species × trait matrix as input data. They assess the density of connections between species in the trait space to inform on which species is likely to be impacted by environmental changes. More generally, analysis of network of interactions in different spaces simultaneously (trophic, taxonomic, functional, geographic) appears as a promising research field to answer the old community assembly and ecosystem functioning questions from a different perspective. Analysis of network of interactions (computed from co-occurrence notably) using graph theory as well as the position in a given space of the different entities could be used.

In the context of the development of a holistic view of the ecosystem this thesis showed the benefit of joining different views of diversity (taxon and trait based) since some patterns are only visible from one view. Interactions between species should be increasingly accounted for as their analysis provides a different view of ecosystem sensitivity than from its components alone.

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8 Appendix

Appendix A: List of the taxa from the EVHOE survey used in this thesis. The first column indicates their R-suffi codes in the Ifremer format. The last column gives the taxonomic level of aggregation.

Codes	Latin names	Taxonomic level
AEQUOPE	Aequipecten opercularis	Species
AGONCAT	Agonus cataphractus	Species
ALLO	Alloteuthis sp.	Genus
ARGE	Argentina sp.	Genus
ARNO	Arnoglossus sp.	Genus
BLENOCE	Blennius ocellaris	Species
BUGLLUT	Buglossidium luteum	Species
CAELCAE	Caelorinchus caelorhincus	Species
CALMLYR	Callionymus lyra	Species
CALMMAC	Callionymus maculatus	Species
CANCPAG	Cancer pagurus	Species
CAPOAPE	Capros aper	Species
CEPOMAC	Cepola macrophthalma	Species
CHELCUC	Aspitrigla cuculus	Species
CHELLUC	Chelidonichthys lucerna	Species
CHIMMON	Chimaera monstrosa	Species
CLUPHAR	Clupea harengus	Species
CONGCON	Conger conger	Species
DICELAB	Dicentrarchus labrax	Species
DIPTBAT	Dipturus batis	Species
ECITVIP	Echiichthys vipera	Species
ELEDCIR	Eledone cirrhosa	Species
ENCHCIM	Enchelyopus cimbrius	Species
ENGRENC	Engraulis encrasicolus	Species
ENTLAEQ	Entelurus aequoreus	Species
ETMOSPI	Etmopterus spinax	Species
EUTRGUR	Eutrigla gurnardus	Species
FMAMMOD	Ammodytidae	Family
FMGOBII	Gobiidae	Family
GADIARG	Gadiculus argenteus	Species
GADUMOR	Gadus morhua	Species
GAID	Gaidropsarus sp.	Genus
GALOGAL	Galeorhinus galeus	Species
GALUMEL	Galeus melastomus	Species
GLYPCYN	Glyptocephalus cynoglossus	Species
HELIDAC	Helicolenus dactylopterus	Species
HIPGPLA	Hippoglossoides platessoides	Species

HOMAGAM	Homarus gammarus	Species
ILLECOI	Illex coindetii	Species
LEPIBOS	Lepidorhombus boscii	Species
LEPIWHI	Lepidorhombus whiffiagonis	Species
LESUFRI	Lesueurigobius friesii	Species
LEUCCIR	Leucoraja circularis	Species
LEUCFUL	Leucoraja fullonica	Species
LEUCNAE	Leucoraja naevus	Species
LIMDLIM	Limanda limanda	Species
LOLI	Loligo sp.	Genus
LOPHBUD	Lophius budegassa	Species
LOPHPIS	Lophius piscatorius	Species
MACOSCO	Macroramphosus scolopax	Species
MAJABRA	Maja brachydactyla	Species
MALCLAE	Malacocephalus laevis	Species
MAURMUE	Maurolicus muelleri	Species
MELAAEG	Melanogrammus aeglefinus	Species
MERLMER	Merluccius merluccius	Species
MERNMER	Merlangius merlangus	Species
MICMPOU	Micromesistius poutassou	Species
MICTKIT	Microstomus kitt	Species
MICUVAR	Microchirus variegatus	Species
MOLVMAC	Molva macrophthalma	Species
MOLVMOL	Molva molva	Species
MULLSUR	Mullus surmuletus	Species
MUNI	Munida sp.	Genus
MUST	Mustelus asterias	Genus
NECOPUB	Necora puber	Species
NEPHNOR	Nephrops norvegicus	Species
OCTP	Octopus sp.	Genus
PAGEBOG	Pagellus bogaraveo	Species
PAROCUV	Paromola cuvieri	Species
PECTMAX	Pecten maximus	Species
PEGULAS	Pegusa lascaris	Species
PHYIBLE	Phycis blennoides	Species
PLEUPLA	Pleuronectes platessa	Species
POLLPOL	Pollachius pollachius	Species
POMO	Pomatoschistus sp.	Genus
RAJABRA	Raja brachyura	Species
RAJACLA	Raja clavata	Species
RAJAMIC	Raja microocellata	Species
RAJAMON	Raja montagui	Species
ROSSMAC	Rossia macrosoma	Species
SARDPIL	Sardina pilchardus	Species
SCOMSCO	Scomber scombrus	Species
SCOPMAX	Scophthalmus maximus	Species
SCOPRHO	Scophthalmus rhombus	Species
SCYOCAN	Scyliorhinus canicula	Species

SCYOSTE	Scyliorhinus stellaris	Species
SEPIELE	Sepia elegans	Species
SEPIOFF	Sepia officinalis	Species
SEPIORB	Sepia orbignyana	Species
SEPO	Sepiola sp.	Genus
SOLESOL	Solea solea	Species
SPRASPR	Sprattus sprattus sprattus	Species
SQUAACA	Squalus acanthias	Species
TODASAG	Todarodes sagittatus	Species
TODIEBL	Todaropsis eblanae	Species
TRACTRA	Trachurus trachurus	Species
TRGPLAS	Chelidonichthys lastoviza	Species
TRISESM	Trisopterus esmarkii	Species
TRISLUS	Trisopterus luscus	Species
TRISMIN	Trisopterus minutus	Species
ZEUSFAB	Zeus faber	Species

Appendix B: Aggregation of the species often misidentified on the EVHOE surveys

Species with identification issues		To be replaced with	
Latin names	**Codes**	**Latin names**	**Codes**
Maja Brachydactyla	MAJABRA	Maja Brachydactyla	MAJABRA
Maja Squinado	MAJASQU		
Ammodytes marinus	AMMOMAR	Ammodytes	FMAMMOD
Ammodytes tobianus	AMMOTOB		
Hyperoplus immaculatus	HYPEIMM		
Hyperoplus lanceolatus	HYPELAN		
Argentina silus	ARGESIL	Argentina	ARGE
Argentina sphyraena	ARGESPH		
Arnoglossus imperialis	ARNOIMP	Arnoglossus	ARNO
Arnoglossus laterna	ARNOLAT		
Gobiidae	FMGOBII	Gobiidae	FMGOBII
Gobius niger	GOBINIG		
Buenia jeffreysii	BUENJEF		
Gaidropsarus	GAID	Gaidropsarus	GAID
Gaidropsarus macrophthalmus	GAIDMAC		
Gaidropsarus mediterraneus	GAIDMED		
Gaidropsarus vulgaris	GAIDVUL		
Loligo forbesii	LOLIFOR	Loligo	LOLI
Loligo vulgaris	LOLIVUL		
Munida	MUNI	Munida	MUNI
Munida intermedia	MUNIINT		
Munida rugosa	MUNIRUG		
Mustelus	MUST	Mustelus	MUST
Mustelus asterias	MUSTAST		
Octopus	OCTP	Octopus	OCTP
Octopus vulgaris	OCTPVUL		
Syngnathus acus	SYNGACU	Syngnathus	SYNG
Syngnathus phlegon	SYNGPHL		
Pomatoschistus	POMO	Pomatoschistus	POMO
Pomatoschistus minutus	POMOMIN		
Pomatoschistus norvegicus	POMONOR		

Appendix B: Life history traits for each taxa and source of the information

Taxa	Latin name	Max length (cm)	Reproductive guild	Longevity (y)	Fecundity	Offspring size (cm)	Age at maturity (y)
AEQUOPE	*Aequipecten opercularis*	11	non.guarder	8	very_high	0,068	1
AGONCAT	*Agonus cataphractus*	21	non.guarder	3	medium	2	1
ALLO	*Alloteuthis sp.*	20,5	non.guarder	1	medium	0,22	1
ARGE	*Argentina sp.*	22	non.guarder	16	medium	1,91	6,4
ARNO	*Arnoglossus sp.*	19	non.guarder	7	medium	0,75	1,5
BLENOCE	*Blennius ocellaris*	17	guarder	6,4	low	1,16	2,5
BUGLLUT	*Buglossidium luteum*	14	non.guarder	13	medium	0,84	3
CAELCAE	*Caelorinchus caelorhincus*	48	non.guarder	28	medium	1,5	12,4
CALMLYR	*Callionymus lyra*	30	non.guarder	7	medium	0,9	2,5
CALMMAC	*Callionymus maculatus*	13	non.guarder	4	medium	0,7	1
CANCPAG	*Cancer pagurus*	27	guarder	20	very_high	0,401	10
CAPOAPE	*Capros aper*	18	non.guarder	26	high	0,4	3,3
CEPOMAC	*Cepola macrophthalma*	73	non.guarder	6,5	medium	0,72	2,4
CHELCUC	*Aspitrigla cuculus*	34	non.guarder	17	medium	1,5	3,5
CHELLUC	*Chelidonichthys lucerna*	56	non.guarder	15	medium	1,36	3,5
CHIMMON	*Chimaera monstrosa*	57	non.guarder	30	low	135	12
CLUPHAR	*Clupea harengus*	26	non.guarder	12,9	high	1,2	3,2
CONGCON	*Conger conger*	200	non.guarder	20	very_high	2,58	10
DICELAB	*Dicentrarchus labrax*	76	non.guarder	30	high	1,3	3
DIPTBAT	*Dipturus batis*	285	non.guarder	51	low	170	11
ECITVIP	*Echiichthys vipera*	15	non.guarder	14	high	1,2	1
ELEDCIR	*Eledone cirrhosa*	19	guarder	4	medium	7,2	2
ENCHCIM	*Enchelyopus cimbrius*	41	non.guarder	9	high	0,82	3
ENGRENC	*Engraulis encrasicolus*	21	non.guarder	5	high	1,5	1
ENTLAEQ	*Entelurus aequoreus*	60	bearer	7,5	low	1,2	2
ETMOSPI	*Etmopterus spinax*	60	bearer	57	low	80	5
EUTRGUR	*Eutrigla gurnardus*	36	non.guarder	21	high	1,35	2,8
FMAMMOD	*Ammodytidae*	19	non.guarder	7,7	medium	0,94	3,2
FMGOBII	*Gobiidae*	23	guarder	2,8	medium	1,04	1,2
GADIARG	*Gadiculus argenteus*	12	non.guarder	3	very_high	1	2
GADUMOR	*Gadus morhua*	116	non.guarder	25	very_high	1,52	2
GAID	*Gaidropsarus sp.*	11	non.guarder	8	very_high	0,78	2,8
GALOGAL	*Galeorhinus galeus*	195	bearer	57	low	280	5,5
GALUMEL	*Galeus melastomus*	54	non.guarder	8	low	42	3,5
GLYPCYN	*Glyptocephalus cynoglossus*	78	non.guarder	25	medium	1,16	7,9
HELIDAC	*Helicolenus dactylopterus*	33	non.guarder	43	high	2,8	13

HIPGPLA	*Hippoglossoides platessoides*	83	non.guarder	30	high	2,01	7,6
HOMAGAM	*Homarus gammarus*	65	guarder	72	medium	1,5	10
ILLECOI	*Illex coindetii*	37	non.guarder	1,5	high	2	0,8
LEPIBOS	*Lepidorhombus boscii*	35	non.guarder	13	high	1,1	1
LEPIWHI	*Lepidorhombus whiffiagonis*	47	non.guarder	16	high	1,1	2,8
LESUFRI	*Lesueurigobius friesii*	9	guarder	11	medium	1,8	2
LEUCCIR	*Leucoraja circularis*	120	non.guarder	20,3	low	60	6,4
LEUCFUL	*Leucoraja fullonica*	120	non.guarder	20,3	low	65	6,4
LEUCNAE	*Leucoraja naevus*	71	non.guarder	28	low	50	8,5
LIMDLIM	*Limanda limanda*	44	non.guarder	12	high	1,2	2,6
LOLI	*Loligo sp.*	93,7	non.guarder	1,5	medium	3,7	1
LOPHBUD	*Lophius budegassa*	93	non.guarder	21	high	1,8	8,2
LOPHPIS	*Lophius piscatorius*	140	non.guarder	24	very_high	2,7	4,5
MACOSCO	*Macroramphosus scolopax*	19	non.guarder	6	low	1	2
MAJABRA	*Maja brachydactyla*	22	guarder	7	high	0,735	2
MALCLAE	*Malacocephalus laevis*	60	non.guarder	42	medium	1,5	14,8
MAURMUE	*Maurolicus muelleri*	5	non.guarder	8	low	1,48	1
MELAAEG	*Melanogrammus aeglefinus*	76	non.guarder	20	high	1,38	2,6
MERLMER	*Merluccius merluccius*	86	non.guarder	20	very_high	0,97	3,4
MERNMER	*Merlangius merlangus*	46	non.guarder	20	high	1,14	2
MICMPOU	*Micromesistius poutassou*	29	non.guarder	20	high	1,16	1,9
MICTKIT	*Microstomus kitt*	67	non.guarder	23	medium	1,29	4
MICUVAR	*Microchirus variegatus*	25	non.guarder	14	high	1,2	3
MOLVMAC	*Molva macrophthalma*	108	non.guarder	23	very_high	1,05	6,5
MOLVMOL	*Molva molva*	200	non.guarder	25	very_high	1,05	6
MULLSUR	*Mullus surmuletus*	40	non.guarder	11	medium	0,87	1,5
MUNI	*Munida sp.*	10	guarder	8	medium	0,7	1
MUST	*Mustelus asterias*	129	bearer	11,9	low	280	4,9
NECOPUB	*Necora puber*	10,9	guarder	8	high	0,5	1
NEPHNOR	*Nephrops norvegicus*	24	guarder	10	medium	1,3	4,5
OCTP	*Octopus sp.*	120	guarder	2	high	2,5	1,3
PAGEBOG	*Pagellus bogaraveo*	53	non.guarder	20	high	1,2	2,5
PAROCUV	*Paromola cuvieri*	21,5	guarder	15	high	0,585	2
PECTMAX	*Pecten maximus*	21	non.guarder	20	very_high	0,07	2
PEGULAS	*Pegusa lascaris*	35	non.guarder	15	high	1,35	4
PHYIBLE	*Phycis blennoides*	50	non.guarder	20	very_high	0,84	3,5
PLEUPLA	*Pleuronectes platessa*	100	non.guarder	30	high	2,17	4
POLLPOL	*Pollachius pollachius*	130	non.guarder	15	very_high	1,16	2,5
POMO	*Pomatoschistus sp.*	6	guarder	2,4	medium	0,88	1
RAJABRA	*Raja brachyura*	115	non.guarder	15	low	90	5

RAJACLA	*Raja clavata*	139	non.guarder	15	low	65	6,1
RAJAMIC	*Raja microocellata*	88	non.guarder	24	low	75	5
RAJAMON	*Raja montagui*	77	non.guarder	18	low	60	3,8
ROSSMAC	*Rossia macrosoma*	8,5	non.guarder	1	low	3	0,9
SARDPIL	*Sardina pilchardus*	27	non.guarder	14	high	1,3	1,7
SCOMSCO	*Scomber scombrus*	50	non.guarder	21	high	1,15	2,2
SCOPMAX	*Scophthalmus maximus*	82	non.guarder	25	very_high	1	4
SCOPRHO	*Scophthalmus rhombus*	46	non.guarder	5,7	very_high	1,3	3
SCYOCAN	*Scyliorhinus canicula*	70	non.guarder	12	low	80	5
SCYOSTE	*Scyliorhinus stellaris*	170	non.guarder	19	low	160	5
SEPIELE	*Sepia elegans*	8,9	non.guarder	1,5	low	5	1,5
SEPIOFF	*Sepia officinalis*	49	non.guarder	2	low	14	2
SEPIORB	*Sepia orbignyana*	9,6	non.guarder	1,5	low	9	1
SEPO	*Sepiola sp.*	4,05	non.guarder	1,5	low	4,92	0,8
SOLESOL	*Solea solea*	60	non.guarder	26,4	high	1,28	2,9
SPRASPR	*Sprattus sprattus sprattus*	15	non.guarder	6	medium	1,1	2
SQUAACA	*Squalus acanthias*	110	bearer	75	low	260	8,8
TODASAG	*Todarodes sagittatus*	75	non.guarder	2	high	1,5	1,2
TODIEBL	*Todaropsis eblanae*	29	non.guarder	1	medium	2,5	1
TRACTRA	*Trachurus trachurus*	41	non.guarder	40	high	0,9	2,6
TRGPLAS	*Chelidonichthys lastoviza*	30	non.guarder	18	medium	1,35	3
TRISESM	*Trisopterus esmarkii*	21	non.guarder	5	high	1,14	1,7
TRISLUS	*Trisopterus luscus*	46	non.guarder	6	high	1,1	1,5
TRISMIN	*Trisopterus minutus*	24	non.guarder	8	high	1,04	2
ZEUSFAB	*Zeus faber*	59	non.guarder	18	medium	2	4

Résumé

Les écosystèmes marins font face à de nombreuses pressions dont les principales sont la pêche et le changement climatique. Ces pressions n'ont pas les mêmes conséquences sur les différentes facettes de la biodiversité, au niveau des taxons, des traits ou de leurs interactions et leur étude est nécessaire à la mise en place d'une approche écosystémique des pêches. La Mer Celtique est une zone de pêche très importante pour les pêcheries européennes et à une richesse spécifique supérieure aux zones adjacentes. Basé sur une série temporelle de 2000 à 2016, j'ai étudié les dynamiques spatio-temporelles de 101 espèces de l'écosystème. Sur cette période, la biodiversité taxonomique a été stable, et l'importance de la pêche comme variable structurante des communautés a diminué après 2009 devenant plus faible que l'environnement (profondeur, concentration en chlorophylle a et température). Suite à un relâchement local de la pression de pêche, la biomasse des espèces ayant des stratégies d'histoire de vie caractérisées par un faible taux de renouvellement, présentes dans le centre de la Mer Celtique, a augmenté. En particulier, l'augmentation de biomasse de 6 espèces d'élasmobranches a été mise en relation avec la création d'une zone de fermeture saisonnière à la pêche. Cette vision de la sensibilité à la pêche a été enrichie par des données provenant de l'exploitation de vidéos sous-marines. Cela a permis de mettre en évidence la présence de zones sensibles à l'Ouest de la Mer Celtique, le long du talus continental. De plus, l'étude des réseaux d'interactions qui lient les espèces, et en particulier des réseaux trophiques permettent de considérer les dynamiques de l'ensemble de l'écosystème à partir de ses composantes. En Mer Celtique, la sensibilité à la pêche des espèces n'implique pas la sensibilité du réseau à cette pression. Le réseau trophique est en revanche peu robuste à la perte des 7% des espèces les plus exploitées et des espèces basales.

Summary

Marine ecosystems face many pressures, the main ones being fishing and climate change. These pressures do not have the same consequences on the different facets of biodiversity, e.g. on taxa, traits and networks, and their study is necessary for the implementation of an ecosystem approach to fisheries. The Celtic Sea is a very important fishing area for European fisheries, with a specific richness greater than adjacent areas. Based on a time series from 2000 to 2016, I have studied the spatio-temporal dynamics of 101 species of the ecosystem. Over this period, taxonomic biodiversity was stable, and the importance of fishing as a structuring variable for communities decreased after 2009, and was lower than the environment (depth, chlorophyll a concentration and temperature). Following a local decrease in fishing pressure, the biomass of species with life history strategies characterised by a low renewal rate and present in the central Celtic Sea, increased. In particular, the increase in the biomass of six species of elasmobranchs has been linked to the creation of a seasonal fishing closure in the area. This vision of fishing sensitivity was enriched with data from the exploitation of underwater videos. This made it possible to highlight the presence of sensitive areas in the western Celtic Sea, along the continental slope. In addition, the study of interaction networks linking species, and in particular trophic networks, allowed considering the dynamics of the entire ecosystem based on its components. In the Celtic Sea, the sensitivity of species to fishing does not imply the sensitivity of the network to this pressure. On the other hand, the trophic network is not very robust to the loss of the 7% of the most exploited species and basal species.