THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

En Sciences de la Mer

École doctorale GAIA

Unité mixte de recherche MARBEC
Laboratoire Halieutique Méditerranée, Ifremer

Intégrité des habitats benthiques du plateau continental face aux perturbations physiques naturelles et aux arts trainants : quelles méthodes d'observations ? Comment suivre le retour vers un bon état écologique ?

Présentée par Cyrielle JAC
Le 10 décembre 2020

Sous la direction de Sandrine VAZ et Nicolas DESROY
Et le co-encadrement de David MOUILLOT

Devant le jury composé de

Nadia AMEZIANE, Professeure, MNHN	Présidente
Olivier BRIVOIS, Cadre scientifique des EPIC, BRGM	Examinateur
Pascal LAFFARGUE, Cadre scientifique des EPIC, Ifremer	Examinateur
Mireille HARMELIN-VIVIEN, Directeur de recherche, MIO	Rapporteur
Hervé LE BRIS, Professeur, Agrocampus Ouest	Rapporteur
Sandrine VAZ, Cadre scientifique des EPIC, Ifremer, UMR MARBEC	Directrice de thèse
Nicolas DESROY, Cadre scientifique des EPIC, Ifremer	Co-directeur de thèse
David MOUILLOT, Professeur des universités, Université de Montpellier, UMR MARBEC	Co-encadrant de thèse

UNIVERSITÉ DE MONTPELLIER

Résumé

L'Union Européenne a élaboré, en 2008, la Directive Cadre Stratégie pour le Milieu Marin (DCSMM) dans le but d'atteindre le Bon Etat Ecologique des eaux marines. En reliant les changements observés aux pressions subies, cette directive se définit comme un outil destiné à mieux contrôler les facteurs de dégradation du milieu et à en tirer les conséquences. Plusieurs descripteurs sont définis dans le cadre de la DCSMM et notamment les descripteurs 1, portant sur la diversité biologique des fonds marins et 6, portant sur l'intégrité des fonds (c'est-à-dire sur la qualité de leurs structures et de leurs fonctions). La pêche aux arts traînants (chalut et drague) étant la principale source de perturbation des fonds du plateau continental, étudier son impact est indispensable. Cependant, ses effets sont dépendants de plusieurs critères comme le type d'engin utilisé, la distribution spatiale et temporelle de l'effort de pêche, les habitats ciblés et le degré de perturbation naturelle existant dans la zone. Ainsi, l'objectif général de cette thèse est d'évaluer l'impact des activités de pêche aux arts trainants dans des contextes hydrodynamiques et sédimentaires variés. Quatre zones ont été considérées : le sud de la mer du Nord, la Manche, le Golfe du Lion et la partie est de la Corse. Pour suivre l'impact d'une pression anthropique sur un écosystème, il est nécessaire de déterminer les indicateurs et la méthode d'échantillonnage la plus appropriée. La comparaison d'une quinzaine d'indices et de trois méthodes d'échantillonnage a montré que l'échantillonnage de la mégafaune benthique au chalut scientifique était particulièrement efficace pour suivre l'impact des arts traînants sur les communautés benthiques et que l'imagerie vidéo pouvait-être une méthode alternative non destructive relativement intéressante pour les fonds grossiers. Les indices basés sur la sensibilité des espèces au chalutage, déterminée à l'aide de leurs traits biologiques, sont apparus comme les plus pertinents pour suivre l'effet des arts traînants sur les communautés benthiques. L'utilisation de ces indicateurs a également permis de proposer un cadre conceptuel d'effet, de déterminer des seuils d'impact et de cartographier l'état écologique des habitats benthiques, lié à la pression de pêche aux arts trainants, dans les quatre zones étudiées.

L'évaluation combinée de l'effet de l'abrasion et de différents paramètres environnementaux sur ces indices a permis de mettre en avant que les principaux facteurs structurant les communautés benthiques ne sont pas les mêmes dans les zones étudiées. En effet, ce sont majoritairement les processus physiques (marée, houle...) qui structurent les communautés benthiques en Manche alors que ce sont majoritairement des paramètres en lien avec la croissance des espèces (disponibilité en nourriture, température…) qui influent sur la distribution et la composition des communautés benthiques méditerranéennes. L'abrasion est également apparue comme un facteur structurant ces communautés benthiques et un des indices précédemment sélectionné a permis de différencier les effets de l'environnement des effets du chalutage dans les zones où l'abrasion influent significativement sur les indices.

Mots clés : Mégafaune benthique, méthode d'échantillonnage, impact de la pêche, sensibilité, facteurs environnementaux, bon état écologique

Abstract

In 2008, the European Union drew up the Marine Strategy Framework Directive (MSFD) with the aim of achieving Good Environmental Status of marine waters. By linking the changes observed to the pressures experienced, this directive is defined as a tool designed to better control environmental degradation factors and to assess their implications. Several descriptors are defined within the framework of MSFD, in particular descriptors 1 relating to the biological diversity of the seabed and 6 relating to the integrity of the seabed (*i.e.* the quality of its structures and functions). As dragging (trawling and dredging) is the main source of disturbance of continental shelf seabed, it is essential to study its impact. However, its effects depend on several criteria such as the type of gear used, the spatial and temporal distribution of fishing effort, the targeted habitats and the degree of natural disturbance existing in the area. The general objective of this thesis is to evaluate the impact of trawling activities in various hydrodynamic and sedimentary contexts and design a generalized assessment framework. Four zones were considered: the southern North Sea, the English Channel, the Gulf of Lion and the eastern part of Corsica. To monitor the impact of anthropogenic pressure on an ecosystem, it is necessary to determine which indicators and which sampling methods are the most appropriate. The comparison of fifteen indices and three sampling methods showed that sampling of the benthic megafauna with scientific trawls was particularly effective for monitoring the trawling impact on benthic communities and that video imaging could be a relatively interesting non-destructive alternative method for coarse bottoms. Indices based on species sensitivity to trawling, appeared to be the most relevant for monitoring the effect of trawling on benthic communities. A conceptual approach to detect effect thresholds and impacts was developed and, as a result, the ecological status, linked to the fishing pressure, of the four study areas could be determined and mapped.

The evaluation of the effect of abrasion and various environmental parameters on these indices highlighted that the main factors structuring the benthic communities are not the same in all study areas. It is mainly physical processes (tide, swell...) which structure the benthic communities in the English Channel whereas it is mainly parameters linked to species growth (availability of food, temperature...) which influence the distribution and composition of Mediterranean benthic communities. Abrasion has also emerged as a structuring factor of these benthic communities. One of the previously selected indices was able, in areas where abrasion significantly influences the indices, to differentiate environmental effects from the effects of trawling.

Key words : Benthic megafauna, sampling methods, fishing impact, sensitivity, natural drivers, good environmental status

Remerciements

Cette thèse a été co-financée par l'Institut Français pour l'exploitation de la Mer, la région Occitanie et l'Union Européenne (DG-ENV projet IDEM - Implementation of the MSFD to the Deep Mediterranean Sea; contract EU No 11.0661/2017/750680/SUB/ENV.C2). Elle a été réalisée dans le cadre du projet EC2CO BENTCHAL.

Une thèse, ce n'est pas, comme on peut l'entendre ou se l'imaginer, un travail solitaire mais plutôt une aventure partagée où certaines personnes font figure de pilier. Je me dois donc de débuter ces remerciements en m'adressant à mes deux directeurs de thèse qui se sont partagé « ma garde » durant ces trois ans et sans qui ce projet n'aurait pas vu le jour et n'aurait pas pu être mené à bien. En fin de master 2, lorsque je commençais à jeter un coup d'œil en direction d'une thèse, ce qui me semblait le plus important était le sujet de thèse. Je sais aujourd'hui que même si le sujet reste quelque chose d'important (on est d'accord que je me serais pas épanouie avec une thèse sur le plancton – désolée guillaume – ou pire sur un écosystème terrestre !), il est indispensable d'être bien encadré ! Et je dois dire que sur ce point, je ne regrette absolument pas mon petit coup de poker en débutant une thèse avec des encadrants que je n'avais jamais eu l'occasion de rencontrer auparavant. Merci Nicolas d'avoir accepté de partager ton bureau (extrêmement grand et bien rangé) pendant près d'un an avec quelqu'un qui ne voue pas un culte aux polychètes. J'ai autant appréciée nos discussions sur une grande variété de sujets en rapport avec la mer, que ta précieuse et indispensable aide pour l'identification de la faune benthique. Sandrine, un grand merci pour tout le temps que tu as su m'accorder et notamment au travers d'un grand nombre de corrections de documents en tout genre. Ton aisance à l'oral et ta grande pédagogie m'ont impressionnée pendant ces trois ans et j'espère arriver, un jour, à égaler ta capacité de transmission d'informations complexes. Ces quelques phrases ne peuvent pas exprimer toute ma gratitude envers vous mais encore merci pour votre présence et votre soutien au cours de ces trois dernières années.

Je tiens également à remercier David Mouillot, co-encadrant de cette thèse, pour ses différents conseils toujours très pertinents et qui malgré un emploi du temps extrêmement chargé a su se rendre disponible lorsque j'en avais besoin.

Je souhaite également remercier les membres du jury, Nadia Améziane, Hervé Le Bris, Mireille Harmelin-Vivien, Pascal Laffargue et Olivier Brivois qui ont accepté d'évaluer mon travail.

Lors de ma thèse, j'ai eu la chance d'avoir deux ports d'attache très différents mais pourtant extrêmement complémentaires : le LERBN à Dinard et le LHM – UMR MARBEC à Sète. Mise à part le fait que cela à engendrer de nombreux déménagements, cela fait surtout deux fois plus de personnes à remercier.

Je commence donc par les Bretons et je tiens à exprimer ma gratitude à tous mes collègues du LERBN de Dinard qui ont su m'accueillir à bras ouverts et m'ont fait oublier le manque de soleil ! Un grand merci à Claire Rollet, la cheffe de station, qui a toujours pris le temps de s'assurer que tout allait bien pour moi et que je ne reste pas toute la nuit au dessus de ma loupe binoculaire à tenter d'identifier de minuscules polychètes. Je tiens également à remercier grandement Julie Dardanelli pour toute son aide sur les diverses questions administratives mais également pour son éternelle bonne humeur. Merci à Françoise pour les nombreuses discussions sur la voile qui m'ont permis de continuer à faire mûrir mes projets futurs. Un grand merci à Manuel Rouquette pour ses nombreux coups de mains sur les bases de données benthos, mais également pour nos discussions très animées sur le formol. Un très grand merci à Aurélie, que ce soit pour sa participation à mon comité de thèse, l'aide gigantesque qu'elle m'a fourni sur les identifications mais également pour mes papilles gustatives qui ont fortement appréciées ses talents de pâtissière. Merci à Louis Costes pour les heures passées à traiter une partie des échantillons de granulométrie utilisés dans cette thèse. (Et puis c'est toujours agréable d'avoir un autre intechos dans le labo avec qui discuter pêche, plongée et photo!) Profite bien de Tahiti ! Un grand merci à Alexandre Robert qui avec son optimiste constant n'a jamais cessé de m'encourager. En étant un des seuls du labo à maitriser R et à aussi bien connaitre la problématique du chalut en France, tu étais comme un phare au milieu du crachin breton et tu m'as permis de me réorienter lorsque je déviais un peu de mon chemin ! Je souhaite également remercier les deux merveilleuses stagiaires qui m'ont permis de me sentir beaucoup moins seule au labo et d'arrêter d'écouter France Culture 10 heures par jour : Jessica et Marie. Vous avez fait un travail monstre d'identification, merci beaucoup ! Merci aussi à Julien, Aurore, Aurélie, Patrick et à tous les collègues du CRESCO que j'apercevais de temps en temps de l'autre côté des portes battantes…. Enfin un grand merci à tous les copains côté Museum sans qui cette année au pays des crêpes et du kouign-amann n'aurait pas été la même : Maxime, Salomé, Valentin, Benjamin, Emma, Quentin, Nicolas et Laetitia.

Du côté de Sète, je souhaiterais tout d'abord remercier Angélique Jadaud, Louisa Metral et Blandine Brisset pour leur accueil sur MEDITS et pour les nombreuses discussions que j'ai pu avoir avec chacune d'entre elles. Merci également à Isabelle Cherret pour ses petites attentions quotidiennes et les discussions très enrichissantes que l'on a pu avoir. Je tiens également à remercier Antoine Duparc pour son aide précieuse en modélisation mais également ses conseils en escalade ! Merci aux doctorants de l'année précédente (pardon aux docteurs !) : Marine, Kilian et Quentin. Sans vous je serais toujours en train de me battre avec les procédures de l'ED ! Un énorme merci à Yoluène, Marie et Géraldine pour leur soutien sans faille durant cette année 2020 qui fut pleine de changements et de remise en question. Merci de m'avoir aidé à me changer les idées ! Enfin merci à tous les doctorants, stagiaires, post-docs que j'ai pu croiser : Miriam, Njara, Alex, Aurélien, Alex, Guillaume, Quentin & Quentin, Bastien, Chloé ... pour n'en citer que quelques-uns.

J'aimerais également remercier grandement Céline Labrune qui, dès le début de ma thèse a su me faire confiance pour le déploiement du Pagure en mer et qui m'a été d'un grand soutien pour les différents articles. Je t'apprécie énormément que ce soit humainement et professionnellement et j'espère sincèrement être amené à refaire du terrain avec toi, que ce soit en méditerranée ou sous des latitudes plus clémentes ! Merci également à Lyvia et Laurène pour les nombreux échanges au sujet de la vidéo… C'était d'un grand réconfort de pester un peu toutes ensemble contre les vidéos et de ne pas se sentir seule devant les problèmes d'analyses. Bien évidemment, un grand merci à toutes les deux pour tous les autres moments que l'on a partagé ensemble et pour votre soutien en cette année particulière. Laurène, un énorme merci pour le travail gargantuesque que tu as fait en relisant avec une grande attention l'ensemble de ce manuscrit, alors que tu venais à peine de terminer le tien !

Je tiens également à remercier mes amis « d'avant la thèse », qui m'ont pas beaucoup vu ces trois dernières années mais qui ont toujours été présents, que ce soit dans les coups durs mais également dans tous les grands moments. Un grand merci à vous qui même d'aussi loin que vous êtes n'avez jamais cessé d'être à mes côtés. Caroline, Victoria, Juliette et Anna encore merci d'avoir toujours été là et à n'importe quelle heure ! Promis, le 10 décembre marquera pour vous la fin des discussions (ok… monologues) interminables sur la thèse et les problèmes liés chalutage en France !

En dernier lieu, je souhaite remercier ma famille pour avoir éveillé en moi cette passion pour la mer, mais également pour m'avoir soutenu tout au long de mes études dans chacun de mes choix même si ceux-ci m'ont poussé à vivre de nombreuses fois à des milliers de kilomètres de vous. Merci maman d'avoir tout fait pour que je fasse les études qui me plaisaient, d'avoir corrigé chaque année des documents avec un vocabulaire inconnu pour toi et de m'avoir encouragé et soutenue dans cette aventure folle qu'est une thèse. Enfin un énorme merci à toi Romaric qui m'a été d'une immense aide au cours de cette difficile année 2020. Et puis quoi de mieux pour des frères et sœurs que de partager la même passion ! Ce n'est pas grâce à ma thèse qu'on pourra enfin faire un article Jac & Jac, alors je compte sur toi maintenant ! Je ne sais pas de quoi sera fait notre avenir mais j'espère sincèrement que cela sera sur la même île du pacifique (il y a plein des requins dans le Pacifique ;)) et peut-être même dans le même labo… Bonne chance à toi qui, on ne sait jamais, te lancera peut-être dans quelques mois dans la grande aventure qu'est une thèse en écologie marine.

Table des matières

Introduction générale

1. Evaluation des impacts anthropiques : objectif majeur du XXIème siècle

Les zones côtières sont le lieu d'un grand nombre d'activités humaines : transport maritime, production d'énergie marine renouvelable, extraction de matière première, pêche, aquaculture, tourisme… Ces différentes activités peuvent avoir des conséquences néfastes pour le milieu marin en appauvrissant la biodiversité, en dégradant les habitats ou encore en générant des contaminations par des substances dangereuses... A ces pressions directement liées aux activités maritimes s'ajoutent celles générées par les activités terrestres, qui peuvent avoir des impacts négatifs importants sur le milieu marin en fonction de leur nature, leur échelle et leur localisation. L'agriculture peut par exemple entraîner un apport de substances nutritives dans le milieu et augmenter l'eutrophisation en zone côtière (Jessen et al. 2015), la croissance démographique, une augmentation de l'exploitation des ressources marines… À ces pressions s'ajoutent les effets liés au changement climatique comme l'acidification de l'océan ou l'augmentation de la température de l'eau (Halpern et al. 2008). Jusqu'en 2008, et la mise en place d'une politique européenne globale de protection de l'environnement marin, les mesures visant à contrôler ces différentes pressions étaient élaborés secteur par secteur, avec pour effet un manque de cohérence entre les politiques, les législations, les programmes et les plans d'action au niveau régional, national, européen et international (Fabri and Andral 2011).

1.1. La Directive Cadre Stratégie Milieu Marin (DCSMM) : un tournant dans la politique de préservation des habitats ?

La directive Cadre Stratégie pour le Milieu Marin (ou Marine Strategy Framework Directive – MSFD), élaborée en 2008 par l'Union Européenne, définit une politique européenne globale de protection de l'environnement marin des eaux placées sous la direction des états membres (sauf l'outre-mer), axée sur une approche écosystémique. L'objectif de cette directive est de maintenir ou d'atteindre un bon état écologique (BEE, ou GES en anglais) pour un certain nombre de composantes de l'écosystème marin dont les habitats benthiques (EC 2008). Le bon état écologique est défini, dans ce cadre, comme « l'état écologique des eaux marines tel que celles-ci conservent la diversité écologique et le dynamisme d'océans et de mers qui soient propres, en bon état sanitaire et productifs, et que l'utilisation du milieu marin soit durable, sauvegardant ainsi le potentiel de celui-ci aux fins des utilisations et activités des générations actuelles et à venir » (Ministère de la transition écologique et solidaire 2019). Cette directive définit onze descripteurs des utilisations humaines de l'écosystème marin, chacun étant décliné en critères et en normes méthodologiques pour déterminer le bon état écologique (Table 1).

Table 1: Descripteurs et critères définis dans la Directive Cadre Stratégie Milieu Marin (d'après Ministère de la transition écologique et solidaire 2019)

Descripteurs	Critères
D1. Biodiversité	D1C1. Taux de mortalité par captures accidentelles
	D1C2. Abondance des populations
	D1C3. Caractéristiques démographiques des populations
	D1C4. Distribution spatiale des populations
	D1C5. Habitat des espèces
	D1C6. Caractéristiques du type d'habitat pélagique
	D6C4. Etendue de la perte du type d'habitat benthique
	D6C5. Etendue des effets néfastes sur l'état du type d'habitat benthique
D2. Espèces non indigènes	D2C1. Espèces non indigènes nouvellement introduites
	D2C2. Espèces non indigènes établies
	D2C3. Effets néfastes dus à la présence d'espèces non indigènes
D.3 Espèces commerciales	D3C1. Taux de mortalité par pêche
	D3C2. Biomasse du stock reproducteur
	D3C3. Structuration des populations par âge/taille
D4. Réseau trophique	D4C1. Diversité des espèces de la guilde trophique
	D4C2. Abondance dans les guildes trophiques
	D4C3. Distribution des tailles de guilde trophique
	D4C4. Productivité de guilde trophique
D5. Eutrophisation	D5C1. Concentration en nutriments
	D5C2. Concentration en chlorophylle a
	D5C3. Blooms d'algues nuisibles
	D5C4. Limite photique (transparence) de la colonne d'eau
	D5C5. Concentration en oxygène dissous
	D5C6. Abondance des macroalgues opportunistes
	D5C7. Communautés de macrophytes des habitats benthiques
	D5C8. Communautés de macrofaune des habitats benthiques
D6. Intégrité des fonds marins	D6C1. Perte physique des fonds marins
	D6C2. Perturbation physique des fonds marins
	D6C3. Effets néfastes dus aux perturbations physiques
D7.Changements hydrographiques	D7C1. Modification permanente des conditions hydrographiques
	D7C2. Effets néfastes dus à la modification permanente des conditions hydrographiques
D8. Contaminants	D8C1. Contaminants dans l'environnement
	D8C2. Effets des contaminants sur les espèces et les habitats
	D8C3. Episodes significatifs de pollution aiguë
	D8C4. Effets des épisodes significatifs de pollution aiguë
D9. Questions sanitaires	D9C1. Contaminants dans les produits de la mer destinés à la consommation humaine
	D9C2. Contamination microbiologique pathogène
D.10 Déchets marins	D10C1. Déchets (hors micro-déchets)
	D10C2. Micro-déchets
	D10C3. Déchets intégrés
	D10C4. Effets néfastes des déchets
D11. Bruit sous-marin	D11C1. Bruit impulsif anthropique
	D11C2. Bruit continu anthropique à basse fréquence

Sur les onze descripteurs définis dans la directive MSFD, deux d'entre eux concernent l'habitat benthique : le descripteur 1 (biodiversité) et le descripteur 6 (intégrité des fonds marins). Les critères 1 et 2 du descripteur 6 (D6C1, D6C2) sont consacrés à l'évaluation de l'étendue spatiale de la perte physique ou de la perturbation des fonds marins. Le critère D6C3 se concentre sur l'établissement de valeurs seuils de pression pour les effets néfastes des perturbations physiques. Enfin, les critères D6C4 et D6C5 permettent d'évaluer l'étendue de la « perte » ou de « l'altération » de la communauté benthique et doivent fixer la proportion maximale admissible de perte d'habitat et évaluer le statut de chaque habitat à cet égard (EC 2008, 2017a). La perturbation physique des fonds est définie par des changements temporaires de leur nature par rapport à un état de référence (non impacté ou moins impacté). La perte physique d'habitat est quant à elle définit comme tout altération permanente de l'habitat (par exemple au niveau 2 de EUNIS) provoquée par l'homme et dont le rétablissement est impossible sans une nouvelle intervention humaine. Ces définitions proposées par le CIEM (ICES 2019a, 2019b) font cependant encore débat et sont toujours en cours de discussion au niveau européen (Vaz, 2020, comm. pers.).

Un habitat est défini ici comme un environnement particulier qui se distingue par ses caractéristiques physico-chimiques (structure du sol, salinité, température, exposition aux courants…) et les espèces qui lui sont associées, dans un espace géographique observable. Bien que la nature soit continue et non linéaire, il convient de définir des typologies afin de faciliter l'analyse et la classification de réalités complexes comme les habitats. La typologie EUNIS (European Nature Information System qui remplace CORINE Biotope) mise au point par l'Agence Européenne de l'Environnement est un système de description visant l'exhaustivité, qui tend à constituer un standard au niveau européen (Galparsoro et al. 2012). Cette typologie est notamment utilisée dans le cadre de la DCE. Celle-ci a l'avantage de prendre en compte tous les habitats : des habitats naturels aux habitats artificiels, des habitats terrestres aux habitats d'eau douce et marins. Elle a une structure hiérarchique fondée sur 11 grands types de milieux parmi lesquels figurent les habitats marins (A). Chacun de ces grands types de milieux peut être subdivisé jusqu'à 7 niveaux inférieurs, basés sur des critères relatifs aux facteurs environnementaux qui influencent les communautés. Au total, la classification compte ainsi 5 282 unités (Louvel-Glaser et al. 2013). Les principaux critères retenus pour les habitats côtiers correspondent à une succession de critères abiotiques (étage, substrat, exposition, salinité) puis biotiques avec les espèces structurantes et les communautés associées (Bajjouk et al. 2015). Malgré les progrès techniques, dresser une cartographie précise et globale des habitats des fonds marins reste un défi du fait de leur difficulté d'accès et de l'immensité des mers. EUSeaMap est un des huit projets du programme européen EMODnet (European Marine Observation and Data Network), qui vise à améliorer la connaissance de l'environnement marin. Il a pour mission d'établir une carte des habitats benthiques des eaux européennes suivant la typologie EUNIS en assemblant et harmonisant les données géographiques marines existantes dans les Etats membres de l'Union européenne. Il est toutefois impossible de mettre en place de telles techniques pour cartographier les fonds marins européens dans leur ensemble. Pour être exhaustif, EUSeaMap s'appuie donc sur une approche de cartographie dite à « basse résolution » qui repose principalement sur la description des facteurs environnementaux caractérisant les habitats (Populus et al. 2017).

1.2. Méthodes d'évaluation

Pour chacun des critères développés dans la directive, chaque Etat membre doit élaborer des indices quantitatifs et des valeurs seuils afin d'observer les progrès réalisés en matière de bon état écologique (Rice et al. 2012). Ces indicateurs, qualitatifs ou quantitatifs sont définis comme des attributs spécifiques à chaque critère et servent à déterminer si un critère répond au bon état écologique ou dans quelle mesure il s'en écarte. L'utilisation d'indicateurs, courante dans le cadre de programmes de gestion ou d'évaluation (telle la DCE en France qui a recours à un certain nombre d'indicateurs), permet de limiter le nombre de paramètres à mesurer en ne retenant que les plus représentatifs des aspects fonctionnels et structurels de l'écosystème étudié. Ainsi, l'évaluation de l'état écologique peut dériver de mesures directes sur un composant particulier de la biodiversité (indicateurs d'état) ou indirectes, en mesurant les pressions anthropiques dominantes (indicateurs de pression). Dans ce dernier cas, les impacts des pressions sur la biodiversité doivent être connus. Pour évaluer l'état d'un écosystème, des indicateurs simples (comme par exemple le nombre d'espèces dans une communauté benthique) ou plus complexes (comme l'indice de Shannon) peuvent être employés (Pedel et al. 2013). Cependant pour certains critères, et notamment ceux concernés dans cette étude, il est nécessaire de développer des indices appropriés capables de détecter les changements par rapport aux perturbations anthropiques (OSPAR 2012; Rice et al. 2012; Leonardsson et al. 2015; van Loon et al. 2018).

Pour les critères ne disposant d'aucune valeur seuil, les Etats membres ont pour obligation de les définir. Ces valeurs seuils représentent le niveau de perturbation au-delà duquel le critère n'est plus considéré comme en bon état écologique (Sub-GEnS, Figure 1).

La définition de ces valeurs seuils a donc pour but d'aider les Etats membres à évaluer le niveau de l'état écologique. Elle doit répondre à différentes exigences (EC 2017a):

- Refléter, le cas échéant, le niveau de qualité et *de facto* l'importance d'un effet défavorable pour un critère donné ;
- Etre définie en lien avec une condition de référence ;
- Etre cohérente avec la législation de l'Union Européenne ;
- Etre établie à une échelle géographique appropriée pour rendre compte des diverses caractéristiques biotiques et abiotiques des régions, sous-régions et subdivisions ;
- Etre établie sur la base du principe de précaution et prendre en compte les risques potentiels pour l'environnement marin ;
- Tenir compte de la nature dynamique des écosystèmes marins et de leurs éléments, qui peuvent évoluer dans le temps et l'espace au gré des variations climatiques et hydrologiques, des relations entre proies et prédateurs et d'autres facteurs environnementaux ;

- Traduire le fait que les écosystèmes marins, s'ils se sont détériorés, ne peuvent pas nécessairement revenir à un état antérieur spécifique mais reviennent plutôt à un état correspondant aux conditions physiographiques, géographiques, climatiques et biologiques qui prévalent.

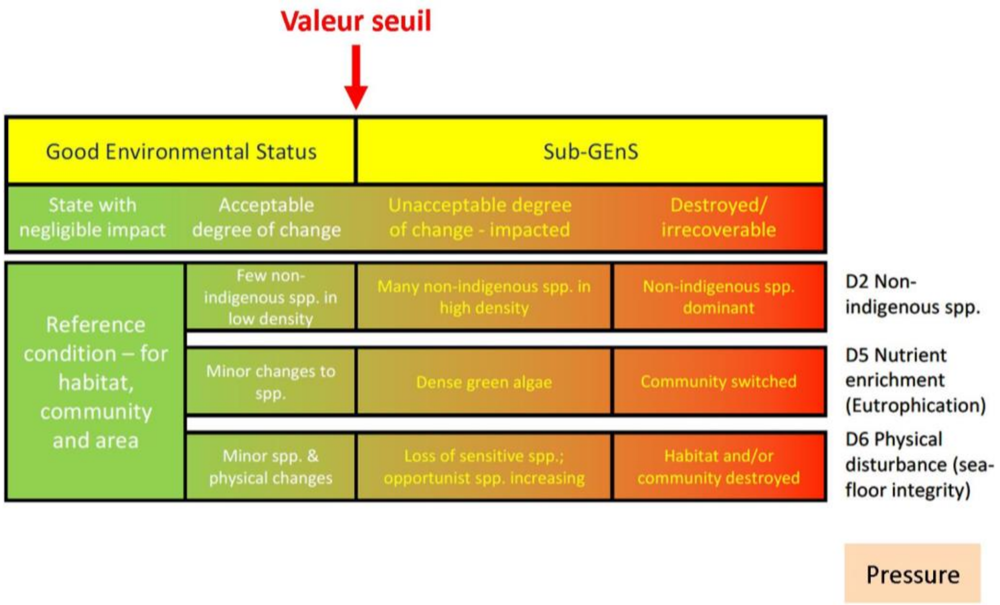


Figure 1: Relation conceptuelle entre le bon état écologique (GES) et les conditions post-GES (Sub-GEnS), telle qu'exprimée par les effets négatifs des différentes pressions (d'après OSPAR 2012)

2. Les arts traînants : principale source de perturbation du plateau continental en Europe

2.1. Description des engins

2.1.1. Le chalut

Le chalut est un filet remorqué par un ou deux bateaux à une vitesse comprise entre 2 et 4 nœuds (Prado and Dremiere 1990) pendant plusieurs heures, sur une distance d'environ 20 km, à des profondeur maximale de 800 m depuis son interdiction à des profondeurs plus importantes en Europe (EC 2016). Il existe deux grands types de chaluts: les chaluts à panneaux et les chaluts à perche, le premier étant le plus communément utilisé (Eigaard et al. 2016). Le filet est de forme conique avec la partie antérieure plus large qui constitue l'ouverture par laquelle les poissons et les crustacés sont capturés. De lourds panneaux, reliés aux treuils du chalutier par des câbles en acier nommés « funes », sont disposés de chaque côté du chalut pour assurer l'écartement horizontal du filet. Le cul-de-chalut, avec un maillage plus fin, permet de concentrer les prises et de les décharger. Tout le long du filet, des ralingues (cordages peu extensibles) permettent de conserver la forme du chalut lors de son remorquage. Pour maintenir le chalut sur le fond, des lests sont disposés au niveau du bourrelet situé sur la face ventrale. Ce bourrelet peut être équipé de chaines ou de rouleaux en métal ou en caoutchouc (Figure 2) en fonction de la nature du sédiment chaluté. Dans certains cas, la face ventrale peut également être équipée de chaines pour extraire les espèces du sédiment.

Les dimensions de chacune des parties varient selon la taille, la puissance des chalutiers mais également des espèces ciblées (Valdemarsen et al. 2007). Même si la pénétration du filet et des panneaux est dépendante des caractéristiques du chalut utilisé et du type de sédiment, les panneaux peuvent creuser une tranchée pouvant aller jusqu’à 35 centimètres de profondeur dans certains sédiments (Lucchetti and Sala 2012; Table 2).

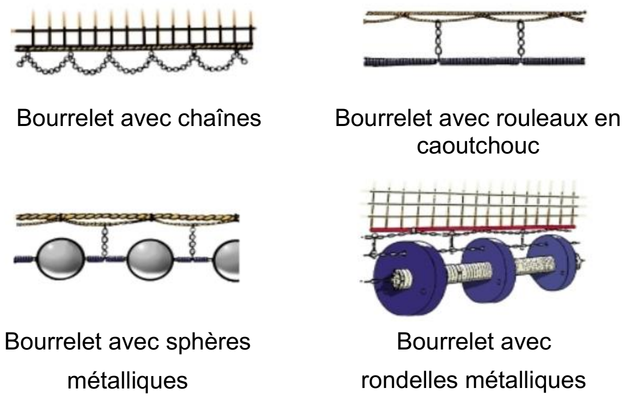


Figure 2: Différents types de bourrelets en tête de chalut

Table 2: Profondeur de pénétration (en cm) des principaux composants des chaluts et des dragues dans différents types de sédiments (d'après Eigaard et al. 2016)

Engins	Composantes	Sédiment grossier	Sable	Vase	Sédiments mixtes
Chalut à panneaux	Funes et entremises		0-2	0	
	Bras		0-2	2-5	
	Chaînes gratteuses (racasseurs)	2-5	2-5		2-5
	Panneaux	5-10	0-10	≤ 15-35	10
	Bourrelet		3-15	10-15	
	Train de pêche		0-2	0-10	1-8
Chalut à perche	Patins	≤ 5-10	≤ 5-10	≤ 5-10	≤ 5-10
	Chaînes gratteuses (racasseurs)	≤ 3-10	≤ 3-10	≤ 10	≤ 3
	Train de pêche		1-8		0
Drague	Train de pêche		1-15	6	

Dans certains cas, un chalutier peut tracter deux chaluts à panneaux, on parle de chaluts jumeaux. Un chalut peut aussi être tracté par deux chalutiers; on parle dans ce cas de chaluts bœufs (Figure 3).

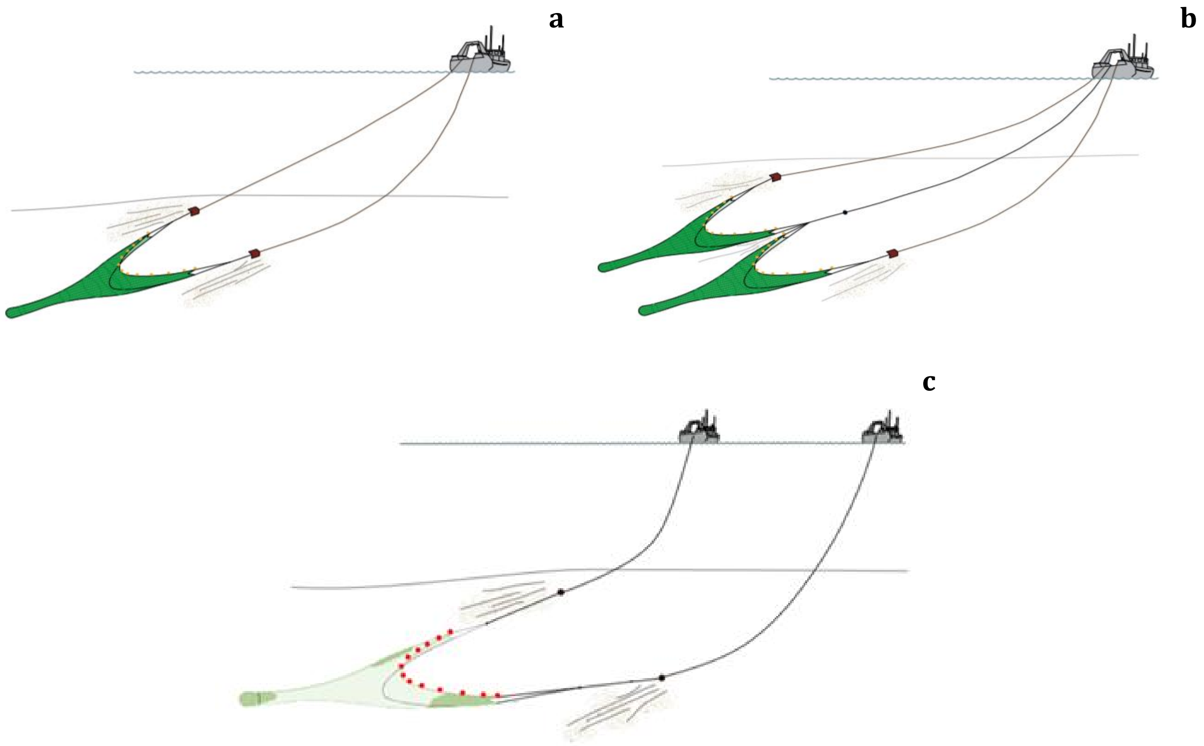


Figure 3: Chalut de fond à panneaux (a) jumeaux (b) bœufs (c)

Si le chalutage à perche (Figure 4) existe depuis les années 1400, c'est à partir des années 1960 que le nombre de bateau utilisant cette méthode de pêche a augmenté (Linnane et al. 2000). Le chalut est fixé sur une armature rigide (métallique dans la plupart du temps) qui assure l'ouverture horizontale et verticale du filet. Dans les eaux européennes, l'ouverture verticale du chalut à perche est d'environ 1 mètre et l'ouverture horizontale varie entre 4 et 12 mètres (Valdemarsen et al. 2007; Eigaard et al. 2016). Le chalut à perche est lourdement lesté pour permettre un bon contact avec le fond et est remorqué à une vitesse comprise entre 2.5 et 7 nœuds (Eigaard et al. 2016). Des chaines sont disposées à l'avant du filet dans la partie inférieure pour remuer le sédiment devant le chalut et ainsi capturer les poissons enfouis. Même si la profondeur de pénétration du chalut à perche est variable en fonction du poids de l'engin, de la vitesse de remorquage et du type de substrat, elle peut atteindre près de 10 cm (Paschen et al. 2000; Depestele et al. 2016; Table 2).

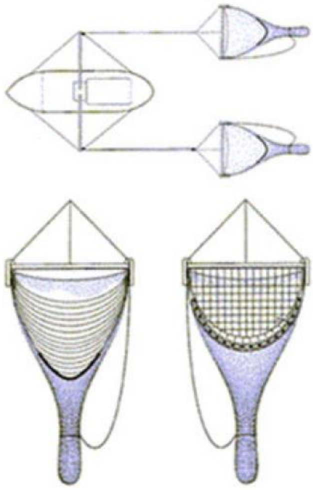


Figure 4: Chalut à perche (d'après Eigaard et al. 2016)

2.1.2. La drague

Les dragues sont utilisées pour capturer des mollusques, principalement la coquille Saint-Jacques, les moules ou les huitres. Elles sont constituées de filets en forme de poche, dont une partie est parfois constituée d'anneaux métalliques, fixés à une armature métallique (Figure 5). Cette barre de traction mesure entre 0.75 et 3 mètres dans le Nord de l'Europe (Eigaard et al. 2016) et au maximum 3 mètres en Méditerranée depuis 2014 pour les navires français (Ministère de l'écologie du développement durable et de l'énergie 2013a). Un maximum de 14 filets peuvent-être fixés sur chaque barre et les bateaux peuvent en tracter soit une à l'arrière, soit une de chaque côté à une vitesse d'environ 2 à 2.5 nœuds (Prado and Dremiere 1990).
Suivant le type de coquillage ciblé, la barre est munie d'une lame formant un racloir ou de dents métalliques qui ratissent le fond. La taille maximale des barres, le nombre de dents ou leur espacement est règlementé dans différentes pêcheries présentes dans les zones étudiées dans ce travail (Ministère de l'écologie du développement durable et de l'énergie 2010, 2013a). Suivant le type de sédiments et les caractéristiques des dragues utilisées, cet engin peut créer des sillons d'une profondeur maximale de 15 cm (Lucchetti and Sala 2012; Table 2).

Figure 5: Drague à coquille Saint-Jacques (crpbn.fr)

2.2. L'importance des arts trainants en Europe

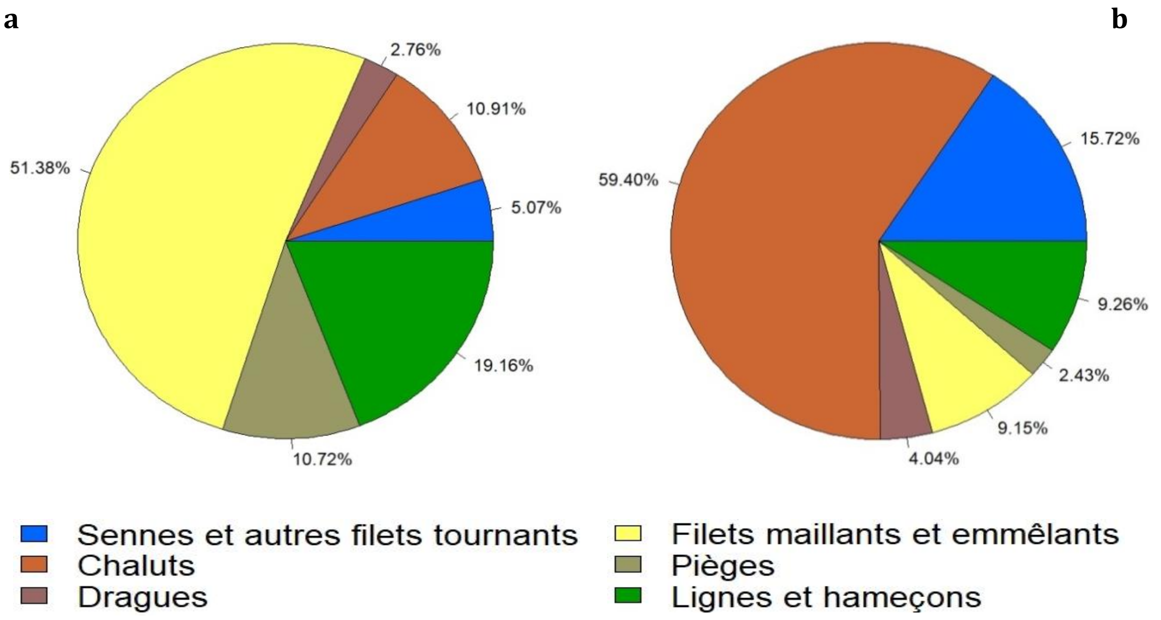


Figure 6: Proportion annuelle européenne du nombre de bateau pour chaque type d'engin entre 2011 et 2019 (a) et des captures (en tonnes) pour chaque type d'engin entre 2015 et 2019 (b)
(https://ec.europa.eu /eurostat/fr/web/fisheries/data)

En Europe, les bateaux équipés de chaluts ou de dragues représentent seulement 20%des navires de pêches présents dans les zones de pêches européennes. Cependant en termes de captures, les drageurs et les chalutiers prélèvent environ 60% de la biomasse de totale collectées par les engins de pêches (Figure 6). Bien que la pêche et notamment les arts trainants existent en Europe depuis de nombreuses années (Linnane et al. 2000; Thurstan et al. 2010), les captures annuelles de poissons, crustacés eet mollusques ont fortement variées pendant les 70 dernières années. C'est notamment le cas en France où le tonnage maximal de capture a été atteint en 1975, après une augmentation importante et quasiment continue entre 1950 et 1975 (Figure 7). Depuis les années 80, le tonnage des captures liées à la pêche est en déclin et à même atteind en 2009-2010 des valeurs proches de celle de 1950. Pendant les dix dernières années, le volume totale de capture semble légèrement réaugmenté mais reste relativement loin des quantitées pêches dans les années 70-80. La presssion de pêche et notamment des arts trainants est donc continuelle depuis des décennies mais tend doucement à diminuer, notamment grâce à la mise en place de plan de sortie de flotte (Ministère de l'écologie du développement durable et de l'énergie 2013b; Ministère de l'agriculture et de l'alimentation 2017).

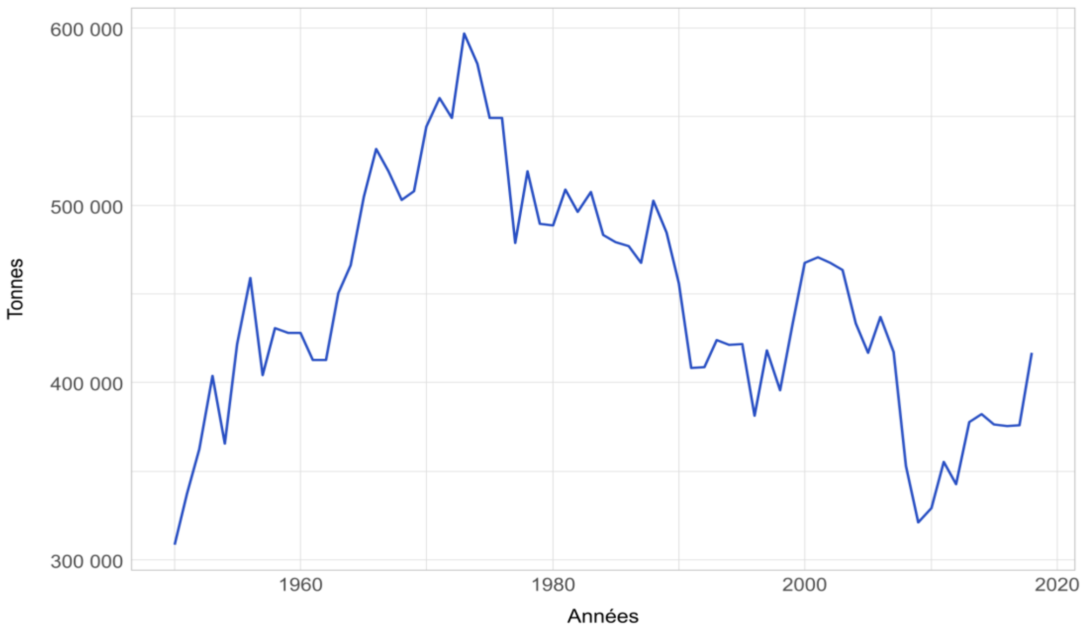


Figure 7: Evolution des captures de crustacés, mollusques et poissons par les bateaux français (1950-2019)
(FAO - Fisheries and Aquaculture Information and Statistics Branch - 11/12/2020)

2.3. Effets des arts traînants sur les habitats benthiques

Les différents engins décrits précédemment n'exercent pas des pressions identiques sur les habitats benthiques à cause de leurs différences d'emprises sur le fond ou de pénétration dans le sédiment. Plusieurs autres paramètres peuvent également influer sur la profondeur de pénétration des engins de pêche comme le type de sédiment (la pénétration est généralement plus importante dans les fonds vaseux), les dimensions et le poids de l'engin ainsi que la vitesse de remorquage et la façon dont l'engin est utilisé (Black and Parry 1999). En effet, avec l'augmentation de la vitesse de remorquage, l'empreinte de l'engin sur le fond tend à diminuer (Fonteyne 2000) alors que la surface de la zone balayée, quant à elle, augmente. La présence d'accessoires comme des chaines ou des dents métalliques sur les engins peut par ailleurs augmenter le degré de perturbation exercé sur le fond (Linnane et al. 2000; Martín et al. 2014). Du fait des surfaces couvertes et de la récurrence des passages, les arts traînants façonnent les habitats benthiques en influant sur leur composition, leur texture et leur morphologie, à des échelles spatiales très variables (Martín et al. 2014). Ainsi, l'utilisation de sonar à balayage latéral a permis de mettre en évidence, dans des sédiments vaseux, une altération physique du sédiment après le passage d'un engin traînant (Friedlander et al. 1999; Smith et al. 2007; Lucchetti and Sala 2012; Palanques et al. 2014) et cela même plus d'un an après le passage de l'engin (Tuck et al. 1998; Palanques et al. 2001). Le passage répété d'un chalut peut également entrainer une diminution de la complexité de l'habitat benthique en altérant les structures topographiques générées par des processus naturels ou par des organismes (Watling and Norse 1998). Ceci se traduit, à grande échelle, par une homogénéisation des fonds (Veale et al. 2000; Thrush and Dayton 2002). De plus, dans certaines conditions hydrodynamiques, le remorquage répété d'engin de pêche sur le fonds peut conduire à des modifications de granulométrie et de qualité du tri du sédiment (Palanques et al. 2001; Brown et al. 2005; Trimmer et al. 2005; Mengual et al. 2016).

Les frottements du filet et des panneaux contre le fond induisent également une remise en suspension du sédiment superficiel (Churchill 1989; Palanques et al. 2001, 2014; Ferré et al. 2005; Madron et al. 2005) qui peut avoir pour conséquence d'augmenter localement la turbidité (Churchill 1989; Palanques et al. 2001; Madron et al. 2005), de libérer des contaminants (Bradshaw et al. 2012) ou de la matière organique enfouis dans les sédiments (Pusceddu et al. 2005), voire de modifier les processus biogéochimiques ayant lieu à l'interface eau-sédiment (Sciberras et al. 2016). Concernant l'augmentation de la turbidité locale, Palanques et al (2001) ont observé une turbidité supérieure à la normale plus de quatre jours après le passage d'un chalut. Le type de sédiments chalutés influe significativement sur les dimensions du panache de remobilisation sédimentaire généré par le passage du chalut. De ce dernier point de vue, de Madron et al (2005) ont observé au sein de sédiments fins, des panaches de plus de 4 m de hauteur et 190 m de largeur environ 30 minutes après le passage de l'engin. D'un point de vue biogéochimique, plusieurs études ont mis en évidence l'effet de la remise en suspension des sédiments, causé par les arts traînants, sur le cycle des nutriments et la reminéralisation de la matière organique. Le cycle de la silice semble par exemple impacté par les arts traînants à la fois de façon immédiate avec une diminution de la concentration en silicate dans l'eau interstitielle (Falcão et al. 2003) mais également de manière plus durable, avec une diminution de la concentration en silicate dans la couche superficielle des sédiments vaseux le long d'un gradient d'intensité de chalutage (Sciberras et al. 2016). Ces phénomènes peuvent-être expliqués par une augmentation du gradient de diffusion causé par la remise en suspension de la couche supérieure des sédiments par les arts traînants (Warnken et al. 2003). L'augmentation de concentration en chlorophylle a et en ammonium des sédiments profonds (à 5 cm de profondeur) observée le long d'un gradient d'intensité de chalutage (Sciberras et al. 2016) et l'augmentation du taux de sulfato-réduction dans les sites les plus chalutés (Trimmer et al. 2005) peuvent-être liés à l'enfouissement de la matière organique induit par le chalutage récurrent, dans les states sédimentaires profondes. Les impacts des arts traînants sur la biogéochimie sont tout de même très dépendants des conditions environnementales comme l'hydrodynamisme ou la nature des sédiments (Warnken et al. 2003; Trimmer et al. 2005; Sciberras et al. 2016) mais également du type d'engin utilisé (Tiano et al. 2019).

2.4. Effets des arts traînants sur la faune

2.4.1. Les communautés ichtyologiques

La pêche, indépendamment de la technique utilisée affecte les communautés de poissons par le prélèvement plus ou moins sélectif d'espèces cibles, par les prises accessoires d'espèces non ciblées et par la modification de l'habitat. Ainsi le chalutage peut-être responsable d'une diminution de la biomasse et de l'abondance des espèces cibles mais également de la communauté totale (Rijnsdorp et al. 1996), d'une diminution de la diversité en espèce (Greenstreet and Hall 1996) et d'une modification des structures de taille (Jennings et al. 1999). Ceci est cependant dépendant du cycle de vie de chaque espèce et des interactions trophiques entre les espèces (Bianchi et al. 2000). Ainsi, l'interdiction du chalutage dans le golfe de Castellammare (Nord-ouest de la Sicile) a entrainé une augmentation de 120% l'abondance de pieuvre musquée (*Eledone moschata*) et une augmentation d'environ 500% de l'abondance du grondin *Lepidotrigla cavillone* (Pipitone et al. 2000). Le type d'engin utilisé et notamment le type de maille dont est constitué le cul de chalut peut également avoir une influence sur l'impact du chalutage sur les communautés ichtyologiques (Stergiou et al. 1997). En effet, en fonction de la forme de la maille des culs de chaluts (losange ou carrée) et de la distance inter-nœuds, la proportion d'espèces non commerciales présentes dans la capture totale varie significativement. Des expériences en laboratoire ont également montré que, chez certaines espèces, les blessures engendrées par le chalut combinées à l'épuisement induit par la fuite peuvent entraîner une mortalité d'environ 10% des individus (Soldal et al. 1993).

Les arts traînants peuvent également impacter de manière indirecte les communautés icthyologiques. En effet, Hiddink et al (2011) ont montré que le chalutage peut avoir une influence négative sur la condition corporelle de certaines espèces cibles comme la plie *Pleuronectes platessa*, en induisant une diminution de l'abondance de leurs proies, majoritairement des invertébrés benthiques du groupe des annélides polychètes.

2.4.2. Les communautés d'invertébrés benthiques

Au sein d'une communauté benthique, les espèces peuvent êtres classifiées suivant différents critères : leur taille, leur position vis-à-vis du sédiment et leur mobilité (Figure 8). Ainsi pour la taille, il peut être fait une distinction entre la méiofaune (*ie.* taille comprise entre 0.1 et 1 mm), la macrofaune (*i.e.* taille comprise entre 1 mm et 1 cm) et la mégafaune (*i.e.* taille supérieur à 1 cm). Concernant la position des espèces par rapport au sédiment, on peut différencier l'endofaune (*i.e.* les espèces qui vivent à l'intérieur du sédiment) et l'épifaune (*i.e.* celles qui vivent sur le sédiment).

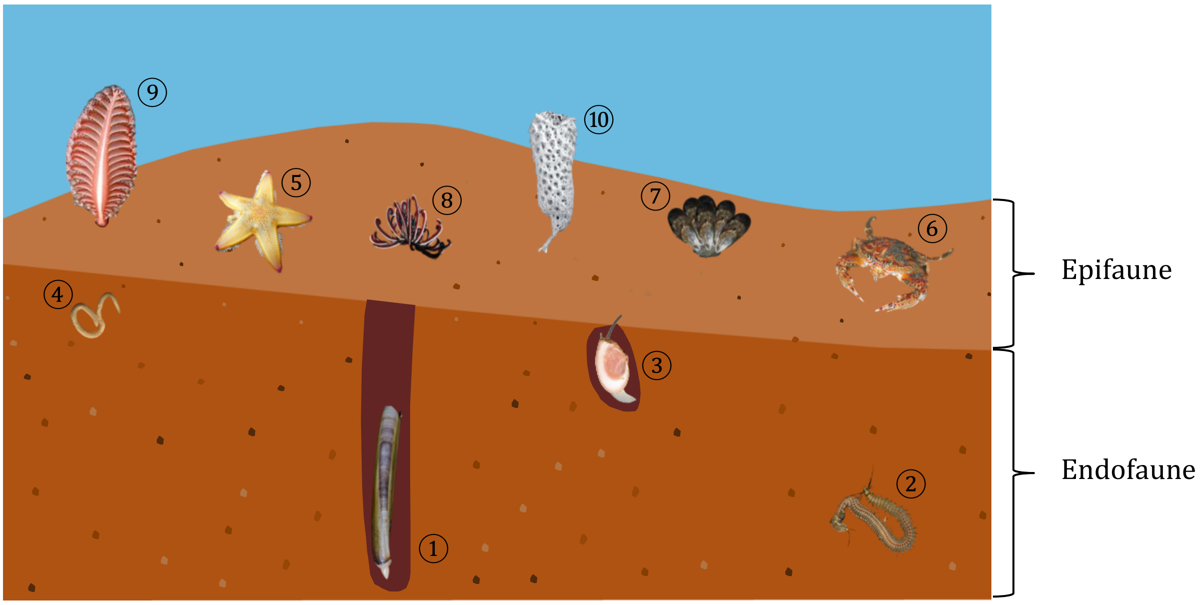


Figure 8: Catégorisation des différentes espèces de la macro ou mégafaune benthique

1. *Ensis ensis* (mobile et enfouissementt profondément). 2. *Nereis sp.* (sédentaire et enfouissement profond). 3. *Abra sp.* (mobile et enfouissement peu profond). 4. *Lumbricalis sp.* (mobile et enfouissement peu profond). 5. *Asterias sp.* (mobile et émergente). 6. *Liocarcinus sp.* (mobile et émergent). 7. *Mytilus sp.* (sessile et émergente). 8. *Antedon sp.* (mobile et érigé). 9. *Pennatula rubra* (sessile et érigée). 10. *Sycon sp.* (sessile et érigée)

Concernant les espèces appartenant à l'endofaune, certaines vivent profondément enfouies dans le sédiment comme par exemple le couteau *Ensis ensis* alors que d'autres vivent dans les premiers centimètres du sédiment. C'est le cas de certains polychètes comme ceux du genre *Lumbricalis* ou les bivalves du genre *Abra*. Pour les espèces appartenant à l'épifaune, il faut différencier les espèces érigées comme la pénatule rouge Pennatula rubra de celles vivant posées sur le sédiment comme les étoiles de mer. Enfin les espèces sont soient mobiles, les crabes par exemple, ou sessiles, les moules ou les spongiaires par exemple (Figure 8).

Impacts physiques

Les invertébrés benthiques sont particulièrement impactés par les arts traînants puisqu'un certain nombre d'entre eux vont être prélevés ou abîmés par l'engin de pêche (Kaiser and Spencer 1996). Des fissures sur la couche externe de la coquille du couteau *Enisis siliqua*, attribuées au dragage répété, ont par exemple été mises en évidence au Portugal (Gaspar et al. 1994). Les étoiles de mers (*Asterias rubens*, *Astropecten irregularis*) et les ophiures (*Ophiura ophiura*) subissent également de nombreuses lésions. Ainsi après 2h de chalutage, plus de 40% des ophiures n'ont plus aucun bras (Kaiser and Spencer 1995). Bergman and Van Santbrink (2000) ont également mis en évidence qu'un seul trait de chalut à perche (entre 4 et 12 m de large) peut induire un taux de mortalité de 68% chez certains bivalves comme *Gari fervensis* et compris entre 10 et 40% chez certains oursins comme *Echinocardium cordatum*. En mer de Bering, une diminution de l'abondance de certaines éponges (*Craniella zetlandica*, *Axinella sp.*, *Phakellia sp.*), de certains cnidaires comme *Funiculina quadrangularis*, de l'oursin *Spatangus purpureus* ou du polychète *Ditrupa arietina* a été observée le long d'un gradient d'intensité de chalutage (Buhl-mortensen et al. 2016). Toutes les espèces ne sont pas impactées de façon homogène par les arts traînants et les espèces sessiles, les espèces à longue durée de vie et/ ou de grande taille ainsi que les espèces suspensivores seraient les plus vulnérables au passage d'un chalut sur le fond (Tillin et al. 2006; de Juan et al. 2007; Kenchington et al. 2007).

A l'inverse, d'autres espèces peuvent bénéficier de l'effet du chalutage comme par exemple les polychètes, dont certaines espèces voient leur biomasse augmenter dans les zones modérément exploitées (Hiddink et al. 2008) grâce à leurs taux de croissance et de reproduction élevés qui leur confèrent la capacité à soutenir des taux de mortalité importants. Cependant, d'autres études suggèrent qu'à des niveaux très élevés de chalutage, l'abondance et la biomasse des petits organismes, dont les polychètes, peuvent diminuer (Jennings et al. 2002; Queirós et al. 2006; Reiss et al. 2009). En fonction de leur régime alimentaire, certains organismes peuvent-être favorisés par le chalutage grâce à une plus grande disponibilité alimentaire dans les zones impactées. Les espèces déposivores peuvent par exemple bénéficier de l'enrichissement du sédiment en matière organique (Frid et al. 2000) alors que les prédateurs-charognards bénéficient, pour leur part, de l'augmentation du nombre d'espèces blessées ou tuées par le chalut (Groenewold and Fonds 2000; Rumohr and Kujawski 2000; Bergmann et al. 2002; Bozzano and Sarda 2002). A cause de son manque de sélectivité, la pêche aux arts traînants génère beaucoup de prises accessoires et donc une grande quantité de rejets en mer (Costa et al. 2008; Diamond and Beukers-Stewart 2011).

L'obligation de débarquement concernant certaines espèces de poissons (EC 2017b, 2018) tend cependant à diminuer le volume rejeté. Malgré tout, Kaiser and Spencer (1996) ont observé des agrégations de charognards juste après le passage d'un chalut et émis l'hypothèse que les charognards se nourrissent sur les rejets de la pêche. Cependant la part des rejets dans leur alimentation semble être variable. Catchpole et al. (2006) ont estimé que, pendant la période de pêche, les rejets contribuent à près d'un tiers de l'énergie nécessaire prédateurs-charognards alors que Kaiser and Hiddink (2007) suggèrent que la production des prédateurs-charognards ne serait soutenue par les rejets de la pêche qu'à hauteur de 3 jours par an.

Impacts sur la structure des communautés benthiques

La pression de chalutage, en diminuant l'abondance et la biomasse de certaines espèces mais également en favorisant l'apparition ou le développement d'autres, induit de manière indirecte des modifications de la structure des communautés benthiques. A long terme, le chalutage est donc susceptible de modifier la composition taxonomique des communautés benthiques de la macrofaune [> 1 mm ; (Frid et al. 2000; Mangano et al. 2014)] ou de la mégafaune [> 10 mm ; Buhl-mortensen et al. 2016)]. Différentes études ont mis en avant un changement de la composition taxonomique des communautés benthiques le long d'un gradient d'intensité de chalutage, sur des sites exploités depuis plusieurs dizaines d'années en mer du Nord (Reiss et al. 2009) et au nord-est de la mer d'Irlande (Hinz et al. 2009). Une diminution de la richesse spécifique des communautés benthiques et de la biomasse de la macrofaune ont également été observées le long de ce même gradient d'intensité de chalutage (Hinz et al. 2009; Reiss et al. 2009).

Impacts sur le fonctionnement de la communauté

En plus d'entraîner des changements de la structure des communautés benthiques, les arts traînants peuvent modifier le fonctionnement de l'écosystème benthique. Parmi les populations d'espèces relativement impactées par le chalutage, certaines sont des espèces ingénieurs au rôle fonctionnel clef (Coleman and Williams 2002). C'est le cas par exemple du polychète *Sabellaria spinulosa* qui, grâce à sa capacité à construire des structures récifales plus ou moins étendues, permet à un grand nombre d'espèces de s'établir dans des zones à prédominance sédimentaire où elles ne se trouveraient pas autrement, et dont les récifs peuvent-être totalement ou partiellement détruit par les engins de pêche traînants. C'est également le cas de certains spatangues qui, grâce à leur activité de bioturbation et de bio-irrigation, jouent un rôle essentiel dans plusieurs processus biogéochimiques ayant lieu à l'interface eau-sédiment (Lohrer et al. 2004, 2005; Mermillod-blondin et al. 2006; Meysman et al. 2006) et dont l'abondance et la biomasse sont fortement réduites dans les zones chalutées (Bergman and Van Santbrink 2000; Jennings et al. 2002; Buhl-mortensen et al. 2016; Pommer et al. 2016). D'autres espèces, connues pour influer sur la concentration des sédiments en carbone inorganique comme *Brissopsis lyrifera* ou *Amphiura chiajei*, voient leur densité réduite sous l'effet du chalutage (Olsgard et al. 2008). Ainsi, en supprimant ou en réduisant l'abondance de certaines de ces espèces clefs, le chalutage peut fortement impacter le fonctionnement des écosystèmes benthiques sans pour autant en réduire drastiquement la diversité spécifique.

Différentes études ont mis en évidence des modifications de la production secondaire macro et mégabenthique induites par les arts traînants (Jennings et al. 2001b; Hermsen et al. 2003; Reiss et al. 2009). Hiddink et al. (2006) ont suggéré qu'en mer du Nord, la production secondaire benthique pourrait être réduite de 21% dans les zones chalutées par rapport aux zones d'exclusion de pêche aux arts traînants. Cependant, ces résultats sont à nuancer car l'impact de ces méthodes de pêche sur la production secondaire benthique peut être variable géographiquement, selon la sensibilité des espèces composant la communauté benthique. Par exemple, dans le sud de la mer du Nord, la production secondaire est principalement assurée par des espèces peu sensibles au chalutage alors que dans la partie nord, elle est conduite par des espèces sensibles aux arts traînants (Bolam et al. 2014).

Les arts traînants, en impactant de façon inégale les différentes espèces benthiques (de Juan et al. 2007; Kenchington et al. 2007; van Denderen et al. 2015), peuvent engendrer, sans forcément que la richesse spécifique soit fortement affectée, une érosion de la diversité fonctionnelle de la communauté (Figure 9a), des modifications dans les fonctions remplies par la communauté (Figure 9b) ou une nouvelle répartition des fonctions dans cette communauté (Figure 9c). Ces différents cas de figure dépendent principalement des caractéristiques fonctionnelles de la communauté benthique initiale. Ainsi, dans le cas d'une réduction du nombre de fonctions dans la communauté, en réponse à une pression exercée par les arts traînants, la richesse fonctionnelle de la nouvelle communauté sera fortement réduite et seules les fonctions peu ou pas vulnérables à cette pression seront conservées dans la communauté. Dans le cas d'un déplacement de l'espace fonctionnel, le phénomène identique se produit mais avec, en complément, l'arrivée de nouveaux individus dans la communauté benthique qui entraîne l'apparition de traits biologiques originaux. La communauté originale est ici remplacée par une communauté fonctionnellement adaptée à la perturbation (ou au degré de perturbation subie). Enfin, dans le cas où seule la redondance fonctionnelle est affectée par la perturbation (c'est-à-dire que le nombre d'individus portant les mêmes fonctions est fortement réduit), la richesse fonctionnelle de la communauté est maintenue mais son fonctionnement devient particulièrement sensible à une nouvelle diminution de la diversité en espèces. La redondance fonctionnelle, existant lorsque différentes espèces ou groupes d'espèces remplissent des fonctions similaires, peut permettre d'éviter la perte du fonctionnement des écosystèmes après une diminution de la diversité des espèces (Guillemot et al. 2011).

Ainsi, pour observer l'effet des arts traînants sur la structure fonctionnelle des communautés benthiques, de nombreuses études se sont basées sur l'utilisation de traits biologiques des espèces qui sont des proxys des fonctions écosystémiques (Bremner et al. 2003b; Tillin et al. 2006; de Juan et al. 2007; Kenchington et al. 2007).

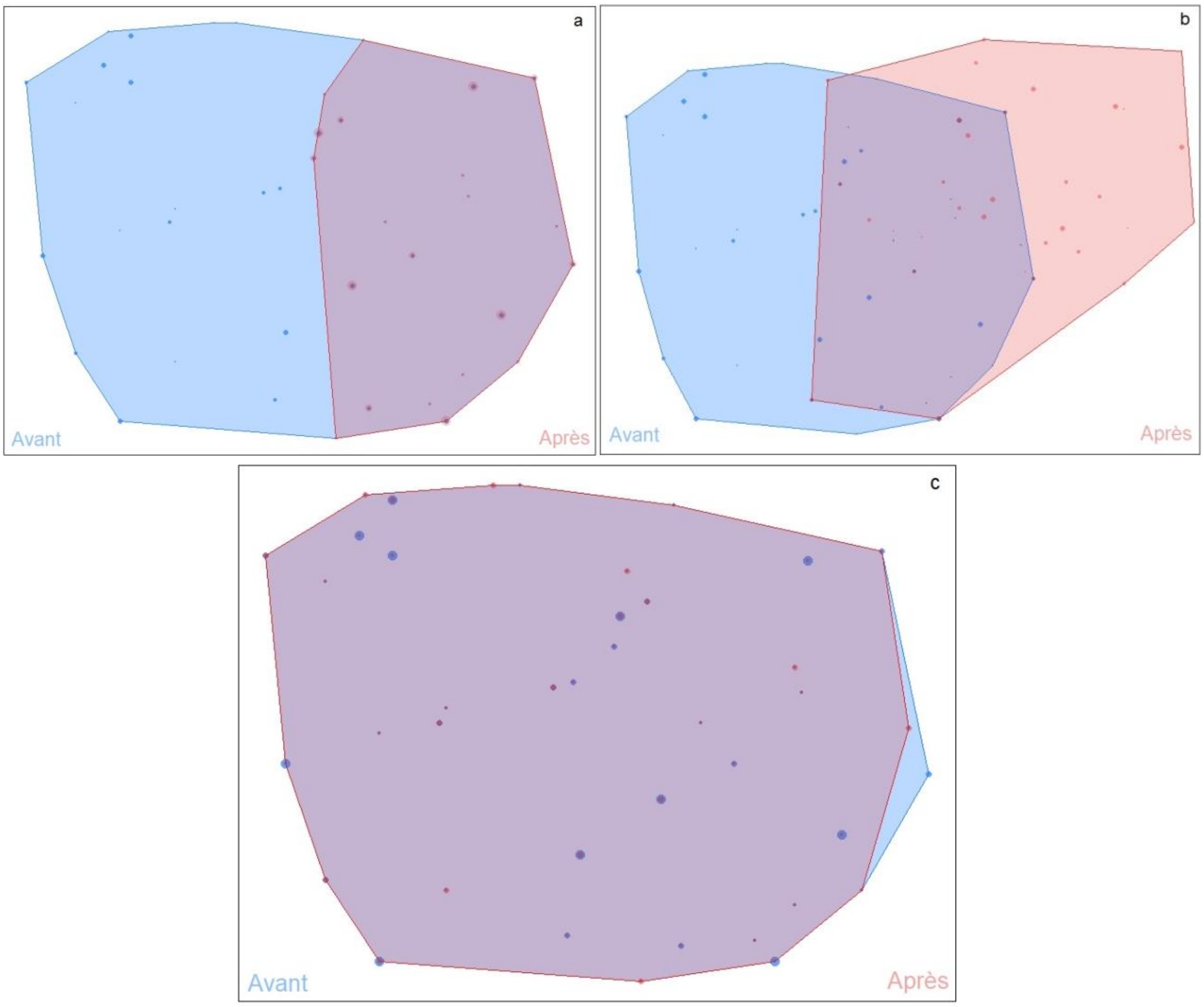


Figure 9: Schéma théorique des changements potentiels de la structure fonctionnelle d'une communauté benthique après une perturbation. L'espace fonctionnel de la communauté avant (bleu) et après perturbation (rouge) est représenté ici en deux dimensions, où les axes sont des caractéristiques synthétiques extraites d'une analyse en composantes principales. Les individus (points) sont positionnés dans l'espace fonctionnel en fonction de la valeur de leurs caractéristiques respectives. La taille des cercles est proportionnelle à l'abondance relative des individus avant et après la perturbation, en bleu et en rouge respectivement. (a) La perturbation entraine une réduction de la richesse fonctionnelle (=une réduction de l'espace fonctionnel). (b) La perturbation entraine le déplacement de l'espace fonctionnel (des fonctions de la communauté originale ont disparu et sont remplacées par de nouvelles). (c) La richesse fonctionnelle n'est que très peu affectée par la perturbation, mais celle-ci induit des modifications de la redondance fonctionnelle (= modifications de la taille des cercles après la perturbation).

Des effets dépendants du type d'habitat

En plus d'être liés au type d'engin utilisé, à l'intensité et la distribution de l'effort de pêche et à la présence d'espèces sensibles (Mengual et al. 2016; Rijnsdorp et al. 2016a), les effets des arts traînants sont également dépendants de l'habitat considéré (Kaiser et al. 2006; Diesing et al. 2013; van Denderen et al. 2015). Une étude menée par Queirós et al. (2006) en mer du Nord et en Mer d'Irlande a permis de mettre en avant des différences de sensibilité aux arts traînants entre les communautés benthiques des sédiments vaseux et sableux, avec notamment un effet négatif sur la biomasse dans les zones vaseuses et aucun effet significatif en zones sableuses. Ces différences semblent-être liées à une différence dans la composition des communautés benthiques car la granulométrie, tout comme d'autres paramètres environnementaux (disponibilité en nourriture, lumière, hydrodynamisme, topographie locale…) influence la composition de la communauté benthique (Hiddink et al. 2006; Gray and Elliott 2009; Buhl-Mortensen et al. 2010; van Denderen et al. 2014; Couce et al. 2020). Dans tout habitat, les espèces présentes ont des adaptations ou des modes de vie qui leur permettent de se développer dans cet environnement et donc une résilience inhérente à un certain niveau de perturbation physique naturelle (Kaiser et al. 2002). Différentes études ont mis en évidence que le degré de perturbation naturelle que subit une communauté benthique peut influer sur sa sensibilité aux arts traînants. Ainsi, les habitats sablonneux peu profonds balayés par les courants de marées et les vagues présentent des communautés benthiques adaptées à des taux élevés de mortalité et de perturbations naturelles (Diesing et al. 2013). Hiddink et al. (2006) ont, grâce à l'utilisation d'un modèle basé sur la taille pour évaluer les effets du chalutage sur la faune benthique dans différents habitats, constaté que les impacts du chalutage étaient plus importants dans les zones où les niveaux de perturbation naturelle étaient faibles. A l'inverse, ils ont observé que les impacts du chalutage étaient limités dans les zones présentant un taux élevé de perturbations naturelles. Diesing et al. (2013) ont, quant à eux, mis en avant que la perturbation liée à la pêche était toujours plus importante que l'effet des perturbations naturelles dans les sédiments vaseux alors qu'à l'inverse, dans les sédiments grossiers, la perturbation naturelle était plus importante que l'effet de la pêche dans 50% des cas. Les sédiments vaseux et les habitats circalittoraux vaseux apparaissent, dans leur étude, comme les habitats les plus sensibles aux arts traînants car peu soumis à des perturbations naturelles. Enfin, van Denderen et al. (2015) ont observé que les traits biologiques des organismes benthiques dans les zones chalutées étaient similaires à ceux présents dans les zones où les perturbations naturelles sont importantes. Ils ont notamment observé une diminution des filtreurs et des espèces longévives avec l'augmentation de la pression de pêche ou du degré de perturbation naturelle. L'ensemble de ces études montre donc que les espèces vivant dans des zones où les perturbations naturelles sont importantes seront plus à même de résister à un niveau donné de chalutage que celles vivant dans des zones où les perturbations naturelles sont relativement faibles.

3. Méthodes d'évaluation de l'effet du chalutage sur les communautés benthiques

3.1. Echantillonnage

La très grande majorité des études effectuées au cours de ces dernières années sur l'impact des arts traînants sur les communautés benthiques ont utilisé des bennes pour échantillonner la faune benthique (Table 3). Leur principal intérêt est d'échantillonner quantitativement la faune, c'est-à-dire de prélever sur une surface de sédiment connue, qui varie généralement entre 0.05 et 0.25m^2 selon le type de benne utilisée (Eleftheriou 2013). La plus communément utilisée est la benne van Veen (van Veen 1933; Figure 10). Le choix de la benne dépendra des conditions environnementales mais également du type de sédiment à échantillonner.

Dans la majorité des études portant sur la macrofaune benthique des sédiments fins, la benne Van Veen est la plus utilisée, alors que la benne Hamon est privilégiée pour l'étude des sédiments grossiers (Boyd et al. 2006; Bolam et al. 2008).

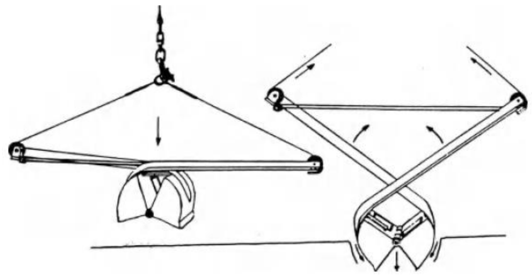


Figure 10: Benne Van Veen (Eleftheriou 2013)

Quel que soit le type de benne, cet échantillonnage n'apparaît pas très adapté aux espèces appartenant à l'épifaune [particulièrement sensibles aux arts traînants (Bradshaw et al. 2001; Lambert et al. 2011; van Denderen et al. 2015)], notamment à cause de la faible surface échantillonnée qui ne permet pas de quantifier convenablement l'abondance d'espèces mobiles ou réparties de manière sporadique (Rees 2009; Eleftheriou 2013). Les carottiers, également très utilisés dans les études s'intéressant à l'effet du chalutage sur les communautés benthiques (Table 3), ne permettent pas non plus d'échantillonner efficacement les espèces épibenthiques (Rees 2009). Des engins traînants comme le chalut (principalement chalut à perche) ou des dragues peuvent donc être utilisés en complément des bennes (Table 3) car, bien qu'ils ne donnent que des données dites « semi-quantitatives », ils sont plus appropriés pour l'échantillonnage de ces espèces (Rees 2009). L'échantillonnage au chalut est généralement réalisé à l'aide de chaluts à perche de 2 à 3 mètres de largeur), traînés à une vitesse relativement faible (autour de 1 nœud) durant un temps assez court (généralement 5 minutes) (Jennings et al. 2001a; Tillin et al. 2006; Rees 2009). La surface d'échantillonnage est généralement comprise entre 10 et 100 m^2 (Rees 2009) pour les dragues et aux alentours de 500 m^2 pour les chaluts (Jennings et al. 2001a; Tillin et al. 2006; Lambert et al. 2011), ce qui paraît toutefois faible au regard des dizaines de km^2 balayés à chaque trait de chalut commercial.

L'utilisation de données issues des chalutages scientifiques effectués sur l'ensemble du plateau continental pourrait donc être une bonne alternative pour étudier l'impact des arts traînants sur les communautés benthiques. Les macro- et méga-invertébrés benthiques (commerciaux et non-commerciaux) sont régulièrement identifiés lors des relevés scientifiques effectués dans toutes les eaux européennes dans le cadre du programme pluriannuel de collecte de données de la politique commune de la pêche. L'utilisation de ces données semble tout à fait pertinente car 1) elles représentent la fraction de la faune benthique la plus directement touchée par les arts traînants, 2) elles intègrent la composition des assemblages sur de grandes surfaces (3-4 km) et sont plus représentatives de la structure des habitats à plus grande échelle (Foveau et al. 2017) et 3) elles représentent de manière satisfaisante l'état *in situ* des assemblages naturels (Rees 2009).

Néanmoins, toutes ces méthodes d'échantillonnage sont dites "destructrices" et peuvent avoir un impact durable sur la biodiversité benthique, qui, bien que clairement négligeable par rapport aux impacts de la pêche, devrait tendre à être réduit (Trenkel et al. 2019). Ces dernières années, l'imagerie sous-marine a été de plus en plus utilisée pour observer la macrofaune et notamment l'épifaune benthique (Rees 2009), mais également pour étudier la diversité des habitats benthiques (Mallet and Pelletier 2014). En plus d'être non-destructive, l'imagerie sous-marine permet d'acquérir rapidement une grande quantité d'informations sur des sites qui peuvent être difficiles à échantillonner (en raison de la profondeur, des caractéristiques du fond marin ou de la topographie) par des engins classiques comme les bennes ou les carottiers (Taormina et al. 2020). Cependant, la qualité des données issues d'un recensement visuel des espèces est fortement dépendante des conditions environnementales (en particulier la turbidité) et de la résolution des images (liée aux contraintes techniques et notamment au type de caméra utilisé). Cela se traduit généralement par une réduction du niveau d'identification taxonomique des individus, ce qui peut entraîner une diminution de la quantité et de l'utilité des informations contenues dans les données obtenues (Flannery and Przeslawski 2015). Malgré ces contraintes et limites, les données collectées par échantillonnage vidéo, étant exprimées en d'abondance, peuvent être utilisées pour suivre l'impact des arts traînants sur les communautés benthiques au même titre que les données issues d'un échantillonnage classique à la drague ou au chalut. A ce jour, encore très peu de travaux portant sur ce sujet ont eu recours à l'utilisation de système vidéo (Table 3).

Table 3: Méthodes d'échantillonnage utilisées dans les principales études portant sur l'impact du chalutage sur les communautés benthiques

Références	Zone d'étude	Benne	Carottier	Drague	Chalut	Vidéo
Bergman and Van Santbrink 2000	Mer du Nord	X	X	X		
Pranovi et al. 2000	Mer Adriatique		X			X
Sanchez et al. 2000	Mer Méditerranée	X				
Smith et al. 2000	Mer Méditerranée	X	X		X	X (descriptif)
Jennings et al. 2001a	Mer du Nord			X	X	
Kenchington et al. 2001	Atlantique Nord-Est	X				
Duplisea et al. 2002	Mer du Nord			X		
Queirós et al. 2006	Mer du Nord et mer d'Irlande	X	X			
Tillin et al. 2006	Mer du Nord				X	
de Juan et al. 2007	Mer Méditerranée	X		X		
Olsgard et al. 2008	Mer du Nord	X				
Grizzle et al. 2009	Atlantique Nord-Est	X	X			X
Hinz et al. 2009	Mer d'Irlande	X			X	
Reiss et al. 2009	Mer du Nord	X				
Svane et al. 2009	Australie				X	
Atkinson et al. 2011	Atlantique Sud-Ouest	X			X	
Shirmohammadi et al. 2012	Golfe Persique	X				
Bolam et al. 2014	Manche et Mer du Nord	X	X			
Mangano et al. 2014	Mer Tyrrhénienne	X				
van Denderen et al. 2015	Mer du Nord et mer d'Irlande	X	X			
Buhl-mortensen et al. 2016	Mer de Barents					X
Muntadas et al. 2016	Mer Méditerranée	X		X		
Pommer et al. 2016	Mer du Nord		X			
Sciberras et al. 2016	Mer d'Irlande		X			
Lambert et al. 2017	Mer d'Irlande	X			X	
van Loon et al. 2018	Mer du Nord	X	X			
McLaverty et al. 2020	Mer du Nord	X				

3.2. Indicateurs

Dans le cadre du suivi de l'impact des arts traînants sur les communautés benthiques du plateau continental, un grand nombre d'indicateurs ont déjà été proposés. Ceux-ci peuvent être différenciés en trois grands types: les indicateurs de diversité taxonomique, les indicateurs fonctionnels et les indicateurs de sensibilité à la pression de pêche.

3.2.1. Indicateurs de diversité

Les indices de diversité taxonomiques, comme l'abondance ou la biomasse par espèces (ou de certaines espèces clés), la richesse spécifique (SR), l'indice de Shannon (H' ; Shannon and Weaver 1963), l'indice de Pielou (J' ; Pielou 1969), l'indice de Simpson (λ ; Simpson 1949) ou encore l'indice de Margalef (d ; Margalef 1958) ont été régulièrement utilisés comme indicateurs de l'impact du chalutage sur les communautés benthiques (Sanchez et al. 2000; Jennings et al. 2001a; Kenchington et al. 2001; Schratzberger et al. 2002; Shirmohammadi et al. 2012; van Loon et al. 2018; Rabaoui et al. 2019). Cependant leur utilisation présente certains désavantages comme par exemple le fait que ces indices peuvent être influencés par certains paramètres environnementaux pas toujours dissociables de l'effet du chalutage (*e.g.* le taux de fraction fine dans le sédiment) ou encore le fait qu'ils sont sensibles à la structure de la communauté [*e.g.* indice de Margalef (Boyle et al. 1990)].

3.2.2. Indicateurs fonctionnels

D'autres indicateurs, développés et utilisés par différents pays dans le cadre de la Directive Cadre sur l'Eau (DCE) pour suivre l'état des communautés macrobenthiques, ont également été proposés pour évaluer l'impact des arts traînants sur les communautés benthiques. A cette fin, Rabaoui et al. (2019) ont étudié l'effet du chalutage et de la saison sur l'indice AMBI (Borja et al. 2000), utilisé dans le cadre de la DCE pour l'évaluation de la qualité des communautés d'invertébrés benthiques des côtes Méditerranéenne françaises (Ministère de la transition écologique et solidaire 2018). De même les évolutions du DKI (Henriksen et al. 2014), dérivé de l'indice AMBI utilisé au Danemark, et du BQI (Leonardsson et al. 2009), retenu en Suède, le long d'un gradient de chalutage ont été étudiées par Gislason et al. (2017). Seul l'indice BQI semble être en mesure de mettre en avant des modifications dans les communautés benthiques le long d'un gradient de chalutage. Cependant, l'utilisation de cet indice nécessite le calcul d'une valeur de sensibilité de chaque espèce qui ne peut être obtenue qu'avec au minimum vingt échantillons pour chaque espèce provenant de zones non perturbées.

3.2.3. Indicateurs de sensibilité au chalutage

L'ensemble des espèces benthiques n'étant pas impactés de la même façon par les arts traînants, différents indicateurs prenant en compte le degré de sensibilité des espèces au chalutage ont été développés. C'est le cas par exemple de l'indice TDI (Trawling Disturbance Impact; de Juan and Demestre 2012), de l'indice de vulnérabilité (T ; Certain et al. 2015) ou encore du BESITO (Benthos Sensitivity Index to Trawling Operations ; González-Irusta et al. 2018). L'un des principaux inconvénients de ces méthodes est la nécessité d'obtenir un certain nombre d'informations pour chacune des espèces permettant de définir leur sensibilité à la pression de pêche.

3.2.4. Modélisations

Des approches de modélisation ont également été développées pour étudier l'effet du chalutage sur les communautés benthiques. La méthode du RBS (Relative Benthic Status ; Pitcher et al. 2017) permet par exemple de modéliser l'état écologique de la faune benthique à partir d'un nombre restreint d'informations : le taux de mortalité dû au chalut et le taux de croissance par espèce. D'autres méthodes reposent sur la reconstruction de biomasses (Lambert et al. 2011) ou la composition de la longévité d'une communauté benthique (Rijnsdorp et al. 2016b), les espèces à durée de vie importante (lié à un faible taux de croissance et une maturité à un âge plus avancé) ayant un taux de résilience plus faible et étant donc sensibles à la mortalité induite par la pêche. Cependant, pour la mise en œuvre de ces différentes méthodes, il est nécessaire d'avoir plusieurs informations qui peuvent être parfois difficiles à obtenir : la longévité de chaque espèce ou taxon et des informations, réelles ou reconstruites, sur la composition de la communauté à son état de référence (biomasse, composition de la longévité, taille maximale…).

Pour l'ensemble des indices présentés ici, aucune comparaison systématique de leur sensibilité ou spécificité n'a été effectuée. Des tests, permettant notamment de différencier l'effet de différents gradients environnementaux et du chalutage, devraient être réalisés pour s'assurer que ces indices peuvent être utilisés dans le cadre d'un suivi de l'impact des arts traitants sur les communautés benthiques du plateau continental. A ce jour, aucun indicateur n'a été sélectionné dans le cadre de la DCSMM pour permettre ce suivi, et ce sur l'ensemble des plateaux continentaux européens.

4. Objectifs de la thèse et démarche adoptée

L'objectif général de cette thèse est d'étudier l'impact des activités de pêche aux arts traînants sur les communautés benthiques. L'effet du chalutage étant différent selon les habitats et dépendant du degré de perturbation naturelle auquel sont exposées les communautés benthiques, quatre secteurs ont été considérés dans cette étude :

- la partie sud de la mer du Nord, mer épicontinentale soumise à un hydrodynamisme modéré à fort (localement) et où les sédiments sont majoritairement fins ;
- la Manche, bassin épicontinental soumis à un très fort hydrodynamisme et où les fonds sont essentiellement grossiers ;
- le Golfe du Lion, grand plateau continental où l'hydrodynamisme est relativement faible et où les fonds sont dominés par des sédiments fins ;
- la partie est de la Corse, où l'hydrodynamisme est relativement faible et où les fonds sont majoritairement détritiques.

L'objectif de ce projet a été traité au travers de deux questions :

1. Comment suivre l'état écologique des habitats benthiques du plateau continental ?
2. L'influence de différents paramètres environnementaux, dont l'hydrodynamisme, peut-il masquer les effets de la pêche aux arts traînants, selon les habitats considérés ?

5. Plan de la thèse

Le manuscrit a été rédigé à partir d'articles soumis et/ou acceptés dans des revues internationales durant la période de doctorat. Les articles n'ont pas été intégrés directement dans le corps du manuscrit mais replacés au sein de chaque chapitre afin de rendre le document cohérent et éviter les répétitions concernant les données et méthodes utilisées.

Trois articles ont été soumis, deux sont actuellement sous presse et un est accepté :

(1) Jac C., Desroy N., Certain G., Foveau A., Labrune C., Vaz S. 2020. Detecting adverse effect on seabed integrity. Part 1: Generic sensitivity indices to measure the effect of trawling on benthic mega-epifauna. Ecological Indicators. *In press*. https://doi.org/10.1016/j.ecolind.2020.106631

(2) Jac C., Desroy N., Certain G., Foveau A. Labrune C., Vaz S. 2020. Detecting adverse effect on seabed integrity. Part 2: How much of seabed habitats are left in good environmental status by fisheries? Ecological Indicators. *In press*. https://doi.org/10.1016/j.ecolind.2020.106617

(3) Jac C., Desroy N., Duchêne J-C., Foveau A., Labrune C., Vaz S. Assessing the impact of trawling on benthic megafauna: comparative study of video surveys versus scientific trawling. ICES Journal of Marine Science. *In press.* 10.1093/icesjms/fsab033

Le chapitre 1 présente les données et les méthodes qui ont été utilisées au cours du travail de thèse. Ses deux premières parties sont consacrées à la description des différentes zones d'étude et des campagnes d'observation scientifique. Les chapitres 2, 3 et 4 portent sur l'analyse de différentes méthodes d'échantillonnage pour suivre l'impact des arts traînants sur les communautés benthiques du plateau continental. Le chapitre 5 concerne le développement d'une méthode permettant de définir l'état écologique des habitats benthiques par rapport à la pression de pêche aux arts trainants dans les eaux européennes. Enfin, le chapitre 6 vise à déterminer l'influence de l'environnement naturel et de l'abrasion sur les différents indices de suivi du chalutage étudiés lors de ce travail de thèse. Le chapitre 2 est basé sur l'article (1), le chapitre 3 sur l'article (3) et le chapitre 5 sur l'article (2).

Chapitre I : Méthodes générales

1. Sites d'étude

1.1. Le Golfe du Lion

Le Golfe du Lion, situé au Nord-Ouest de la Méditerranée entre Marseille et le Cap Creus (Figure 11), est le plus grand plateau continental du bassin Nord-Méditerranéen.

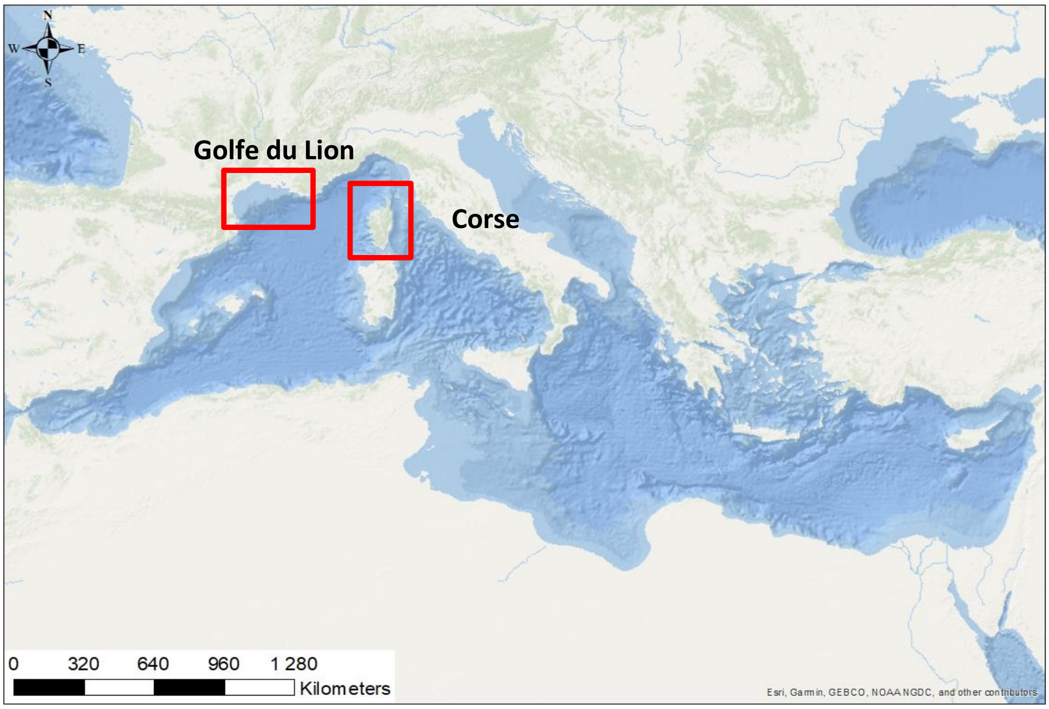


Figure 11: Carte de la mer Méditerranée

1.1.1. Bathymétrie

D'une profondeur moyenne de 90 mètres, le Golfe du Lion se prolonge par un talus abrupt entaillé par de nombreux canyons sous-marins. Ce talus se situe à proximité de l'isobathe 160 m (Figure 12) et constitue une frontière entre la zone côtière et la plaine abyssale.

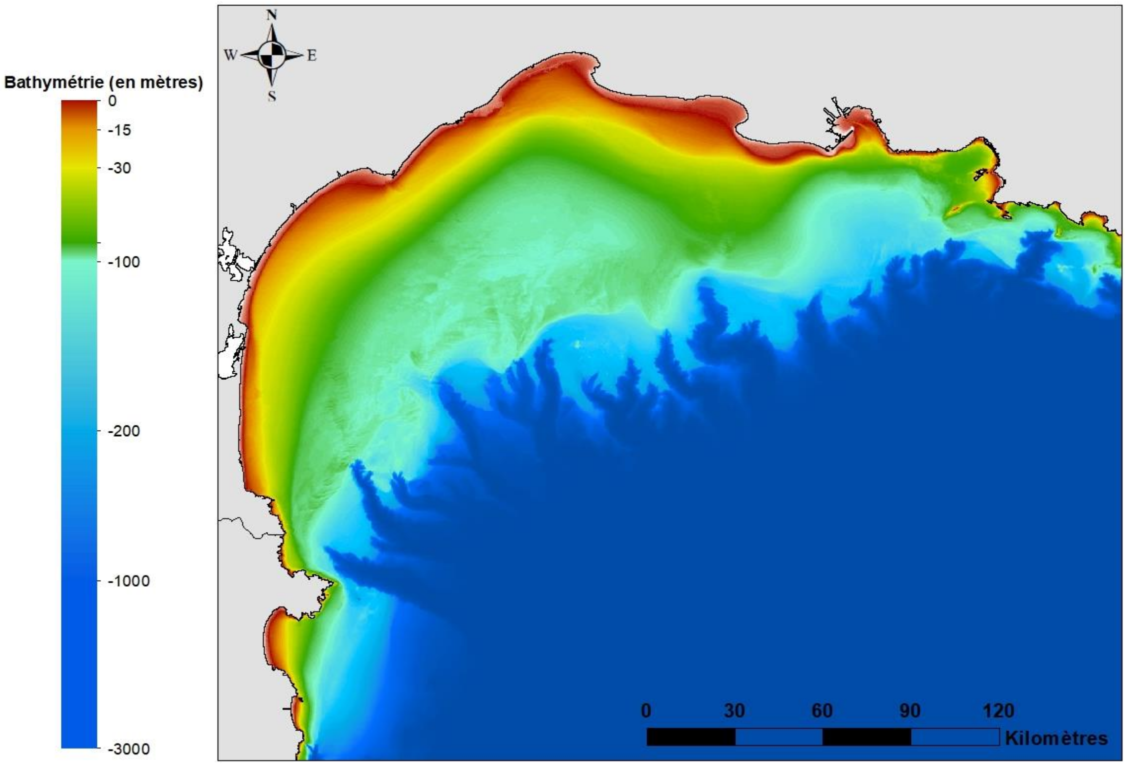


Figure 12: Bathymétrie du Golfe du Lion (SHOM, 2015)

1.1.2. Hydrodynamisme

Du fait du régime micro-tidal de la mer Méditerranée, la circulation des masses d'eau dans le Golfe du Lion est fortement influencée par les conditions atmosphériques (vents et flux de chaleur principalement), les apports fluviaux et le courant liguro-provençal (LPC). Ce courant (d'une puissance allant de 25 à 50 $cm.s^{-1}$) entraîne en surface les eaux moins salées de l'Atlantique (entrées par le détroit de Gibraltar) de la mer de Ligure aux côtes Catalanes (Figure 13). Présent toute l'année, il est tout de même sujet à une importante variabilité saisonnière, liée à l'évaporation et aux changements de température de l'eau mais également au vent, qui joue sur sa position et son intensité. Un second paramètre régit la dynamique des masses d'eau dans le Golfe du Lion : les apports fluviaux et majoritairement ceux du Rhône qui représentent 95 % des apports fluviaux dans la zone (Bourrin and Durrieu de Madron 2006). La différence de densité entre l'eau douce provenant des fleuves et l'eau salée de la mer entraîne des mouvements de masse d'eau avec un écoulement de l'eau douce en surface jusqu'à sa dilution par les processus de mélange vertical. L'absence de fortes marées dans le Golfe du Lion, entraîne une dilution relativement lente des eaux du Rhône avec l'eau adjacente. La distribution spatiale de cette zone de dilution, où les gradients de salinité contraignent la circulation, est très variable en fonction des régimes de vents (Demarcq and Wald 1984). Ainsi, le vent à un rôle très important dans la circulation des masses d'eau du Golfe du Lion puisqu'en plus d'influer sur les autres mécanismes susceptibles d'influencer la circulation au niveau du plateau, il peut également provoquer un mouvement des couches superficielles générant différents schémas de circulation et aussi participer à la création de phénomènes locaux d'upwellings ou de downwellings (Millot 1990).

Concernant les houles dans le Golfe du Lion, la majorité d'entre elles sont générées par des vents de terre (Mistral ou Tramontane) et sont donc fréquentes mais de faibles amplitudes [hauteur < 1m et période < 5s ; (Guizien 2009; Ferrer 2010)]. Cependant, des tempêtes peuvent ponctuellement générer des houles d'amplitude plus importante, principalement entre octobre et mars. L'orientation du littoral n'étant pas la même à l'est ou à l'ouest du Golfe, une importante variabilité spatiale du régime de houle existe dans cette zone (Guizien 2009).

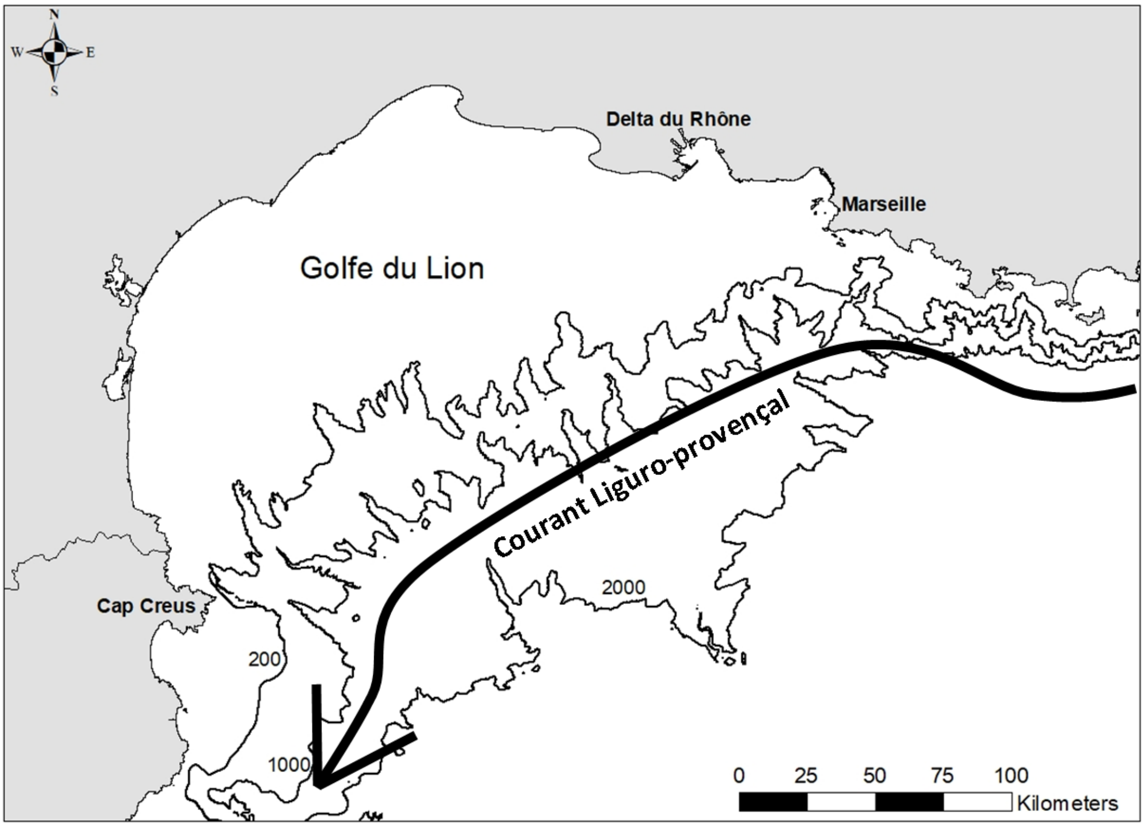


Figure 13: Circulation principale dans le Golfe du Lion

1.1.3. Couverture sédimentaire

La grande majorité (environ 95% des apports solides) des apports sédimentaires dans le Golfe du Lion proviennent du Rhône (Bourrin and Durrieu de Madron 2006) et près de 90 % de ces sédiments rejetés sont piégés sur le plateau (Durrieu De Madron et al. 2000). Ainsi, la nature des fonds du Golfe du Lion (Figure 14) est relativement hétérogène (http://www.emodnet.eu, EUseamap), avec un étroit cordon sableux (A5.46 et A5.23) sur le plateau interne, un dépôt vaseux sur le plateau médian (A5.38 et A5.39) et un plateau externe recouvert de sédiments hétérogènes où vases et sables se mélangent (A5.47). Dans le Golfe du Lion, la remise en suspension naturelle des sédiments est principalement causée par les vagues lors des tempêtes et n'est effective que sur le plateau interne, à une profondeur inférieure à 35 mètres (Guillén et al. 2002 ; Ferré et al. 2005).

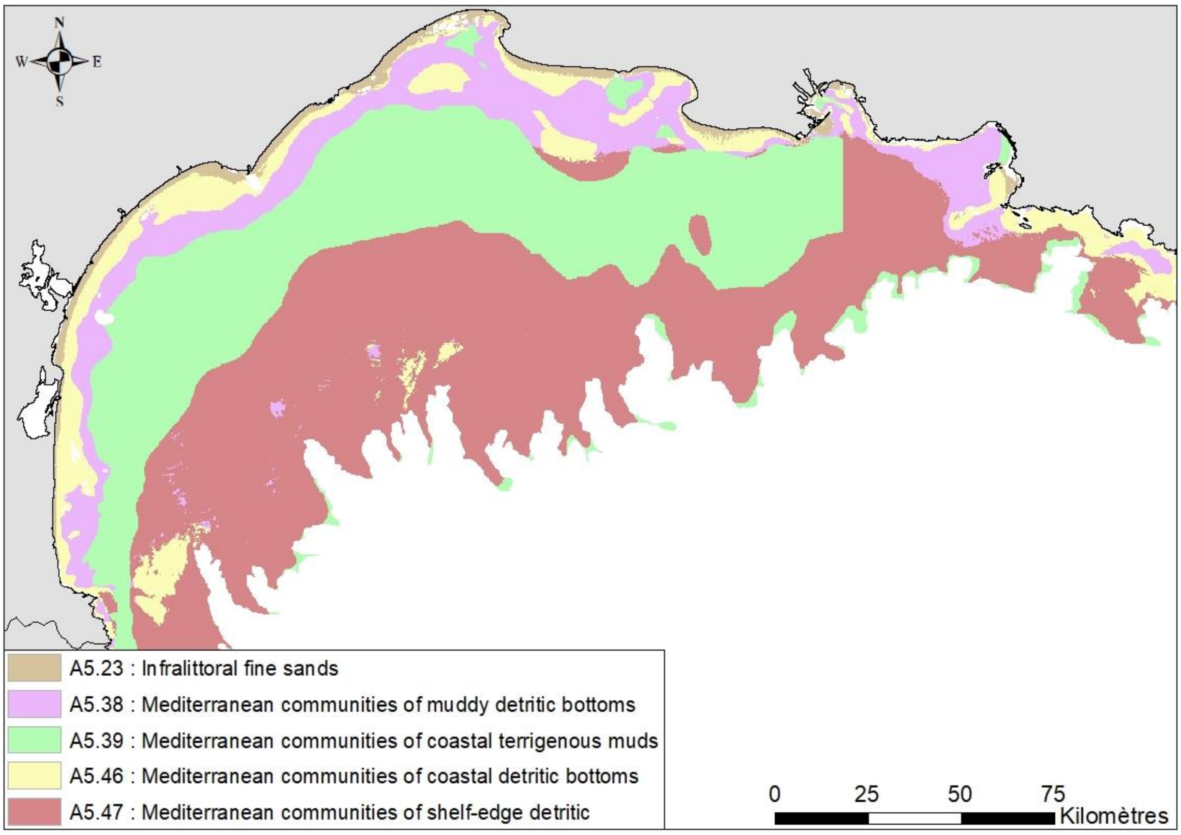


Figure 14: Principaux habitats benthiques du Golfe du Lion (http://www.emodnet.eu, EUseamap)

1.1.4. Communautés benthiques

Dans le Golfe du Lion, plusieurs études ont portées sur l'identification des communautés benthiques présentes au sein des différents types sédimentaires. Ainsi Guille en 1970 à mis en avant, dans la partie catalane du Golfe du Lion, l'existence de huit communautés distinctes entre 4 et 125 m de profondeur (Table 4), toutes associées aux fonds sableux ou vaseux. De l'autre côté du Golfe du Lion, une autre classification des commuanautés benthiques côtières à été développée par Picard (1965). Seuls les travaux de Reyss (1971) ont portés sur les assemblages benthiques en deçà de 150 mètres de profondeur. Ses travaux ont ainsi eprmis d'identifiées cinq communautés (Table 4). Plus récemment, Labrune et al. (2007b) ont proposé une terminologie permettant la correspondance entre les communautés décrites par Guille (1970) et Picard (1965). Trois assemblages benthiques entre 4 et 70 mètres ont ainsi été identifiés en lien avec la granulométrie (Table 4). Ils ont également montré que la composition de ces assemblages a évolué depuis les travaux de Guille et de Picard avec notamment des modifications des espèces dominantes.

Table 4: Communautés benthiques du golfe du Lion le long d'un gradient de profondeur

Profondeur		**Guille (1970)**	**Labrune *et al.* (2007b)**
4 à 46 m		Communauté des sables grossiers et fins graviers à *Branchiostoma lanceolatum*	
4 à 25 m		Communauté des sables fins à *Spisula subtruncata*	Sables fins infralittoraux
20 à 33 m		Faciès de transition des sables vaseux à *Nephtys hombergii*	
30 à 42.5 m	Communauté des fonds envasés à *Amphiura filiformis*	Faciées des vases sableuses à *Scoloplos armiger*	Vases sableuses littorales
40 à 90 m		Sous-communauté des vases à *Nucula sulcata*	Vases terrigènes côtières
30 à 72 m		Sous-communauté du détritique envasé à *Timoclea ovata*	
88 à 125 m		Sous-communauté du détritique du large à *Auchenoplax crinita*	
		Reys (1971)	
150 à 220 m		Fonds à *Salmacina dysteri* Ou Sables vaseux à *Maldane glebiflex* et *Haploops dellavallei*	
200 à 300 m		Fonds à *Leptometra phalangium* Ou Vases sableuses à *Praxilella gracilis* et *Lumbrineris fragilis*	
200 à 400 m		Fonds à *Caryophyllia clavus* et *Sarcodychyon catenata* Ou Graviers envasés	
300 à 350 m		Fonds à *Ophiocantha setosa* et *Ophiothrix fragilis* Ou Fonds détritiques très envasés à *Ophiocantha* et *Anapagurus*	
300 à 1000 m		Vases profondes à *Kophobelemnon* et *Funiculina*	

1.2. La côte est de la Corse

La Corse est une île située à l'est de la Méditerranée occidentale, au large de la France métropolitaine et de l'Italie et au Nord de la mer Tyrrhénienne (Figure 11).

1.2.1. Bathymétrie

L'est de la Corse est caractérisé par un plateau continental relativement étroit, dont la largeur varie entre 5 km au Nord et 25 km au Sud et dont le haut du talus se situe entre 110 et 120 m (Bellaiche et al. 1994). Ce plateau continental est suivi d'une pente continentale abrupte incisée de canyons sinueux. La profondeur augmente rapidement avec la distance à la côte et atteint environ 900 m dans la zone centrale, entre la Corse et l'Italie (Figure 15).

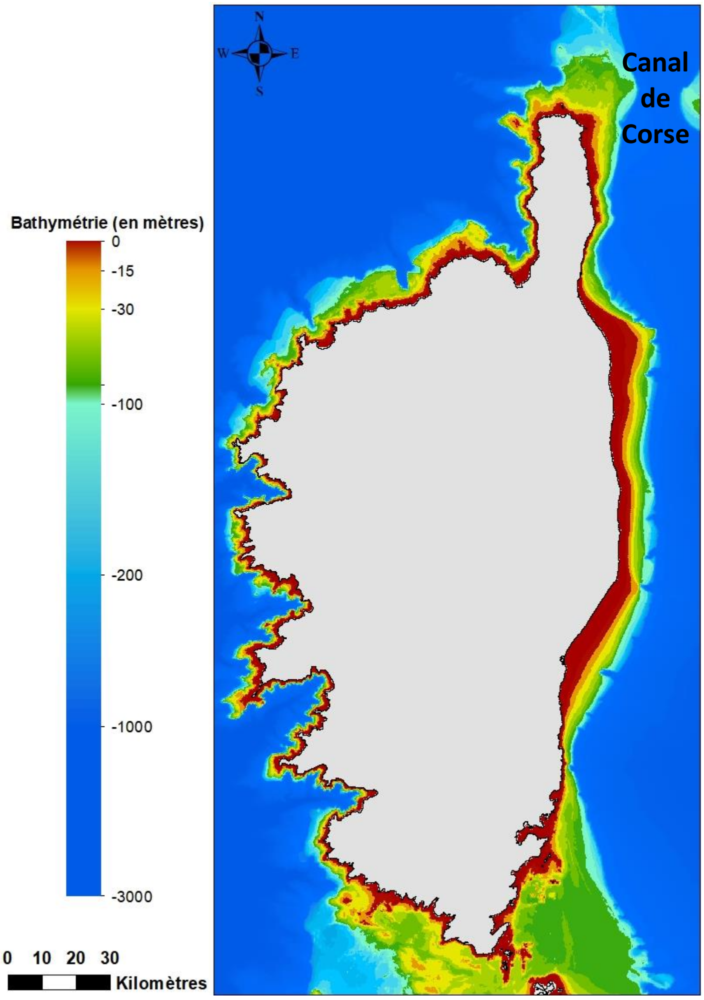


Figure 15: Bathymétrie de la Corse (SHOM, 2015)

1.2.2. Hydrodynamisme

La courantologie dans la partie est de la Corse est caractérisée par un courant remontant le long des côtes italiennes et dont une petite partie va franchir le canal Corse (situé entre l'Italie et la Corse) et ainsi alimenter le LPC (Guihou 2013). Ce courant Est-corse a une forte variabilité saisonnière.

Le flux hivernal, environ trois fois plus élevé en hiver qu'en été (La Violette 1994), génère un apport d'eaux « chaudes » (le courant Est-Corse étant à l'abri des forts vents continentaux froids) hivernales dans le bassin Ligure (Millot and Wald 1980; Crepon et al. 1982). Ces apports en eaux « chaudes » permettent au LPC d'être identifié par sa signature thermique en surface, plus chaude que celle des eaux du plateau et du large.

1.2.3. Couverture sédimentaire

La grande majorité du littoral côtier de la côte orientale de la Corse est constituée de sédiments mixtes et de débris coquilliers (A5.46 et A5.47 ; Figure 16). En zone très côtière, la pente extrêmement progressive permet le développement important d'herbiers de posidonie qui s'étendent dans certains cas jusqu'à environ 5 km du rivage (Pasqualini et al. 1998). Plus au large, les habitats profonds sont majoritairement constitués de vases (A5.38, A6.51 et A6.511 ; http://www.emodnet.eu/seabed-habitats).

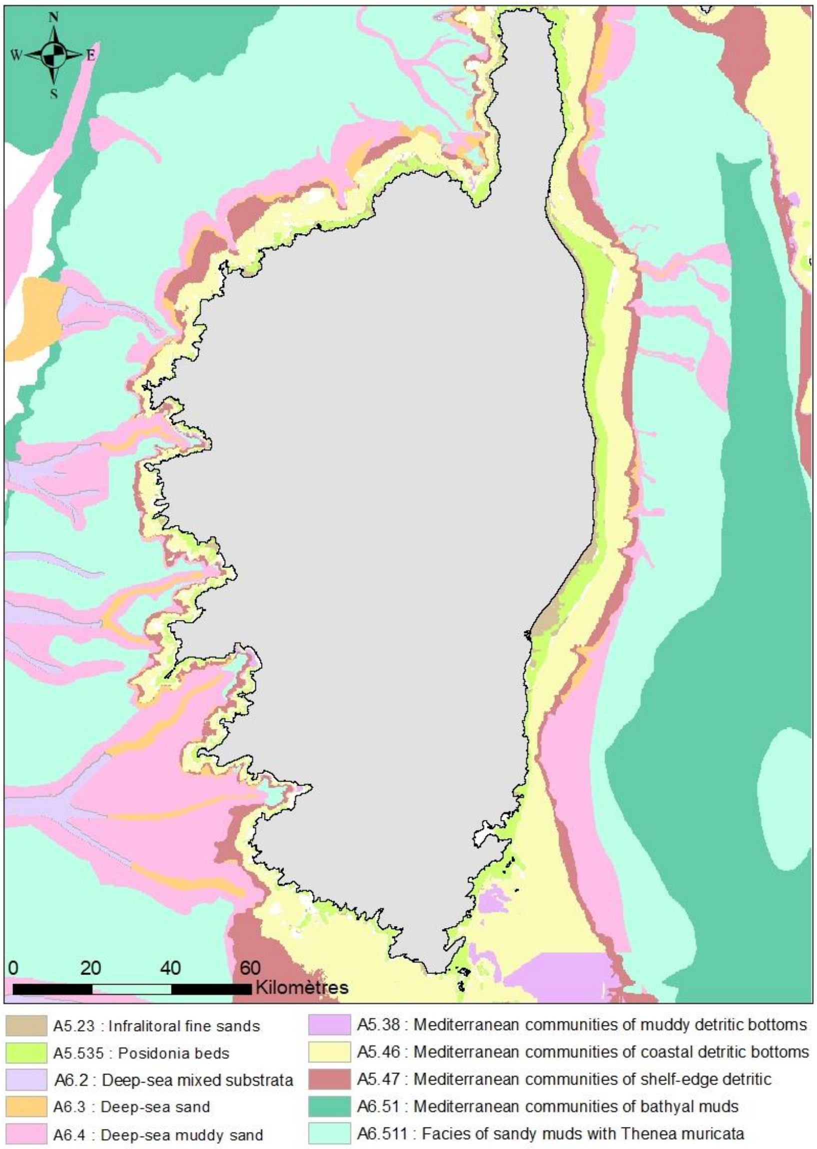


Figure 16: Principaux habitats benthiques de la Corse (http://www.emodnet.eu, EUseamap)

1.2.4. Communautés benthiques

A ce jour, aucune description des assemblages benthiques de la partie Est de la corse n'a été réalisée. Ainsi les habitats dans cette zone n'ont été définis que part des critères abiotiques tel que la nature du sédiment, la présence ou non de posidonie et la bathymétrie.

1.3. La Manche

La Manche (Figure 17) est une plateforme épicontinentale, située entre la France et l'Angleterre et qui s'étend suivant un axe NE-SW. Longue d'environ 700 km depuis le Pas-de Calais jusqu'à l'extrémité ouest de la Manche, sa largeur varie entre 30 km au niveau du détroit du Pas-de-Calais et 180 km dans sa partie occidentale (Larsonneur et al. 1982).

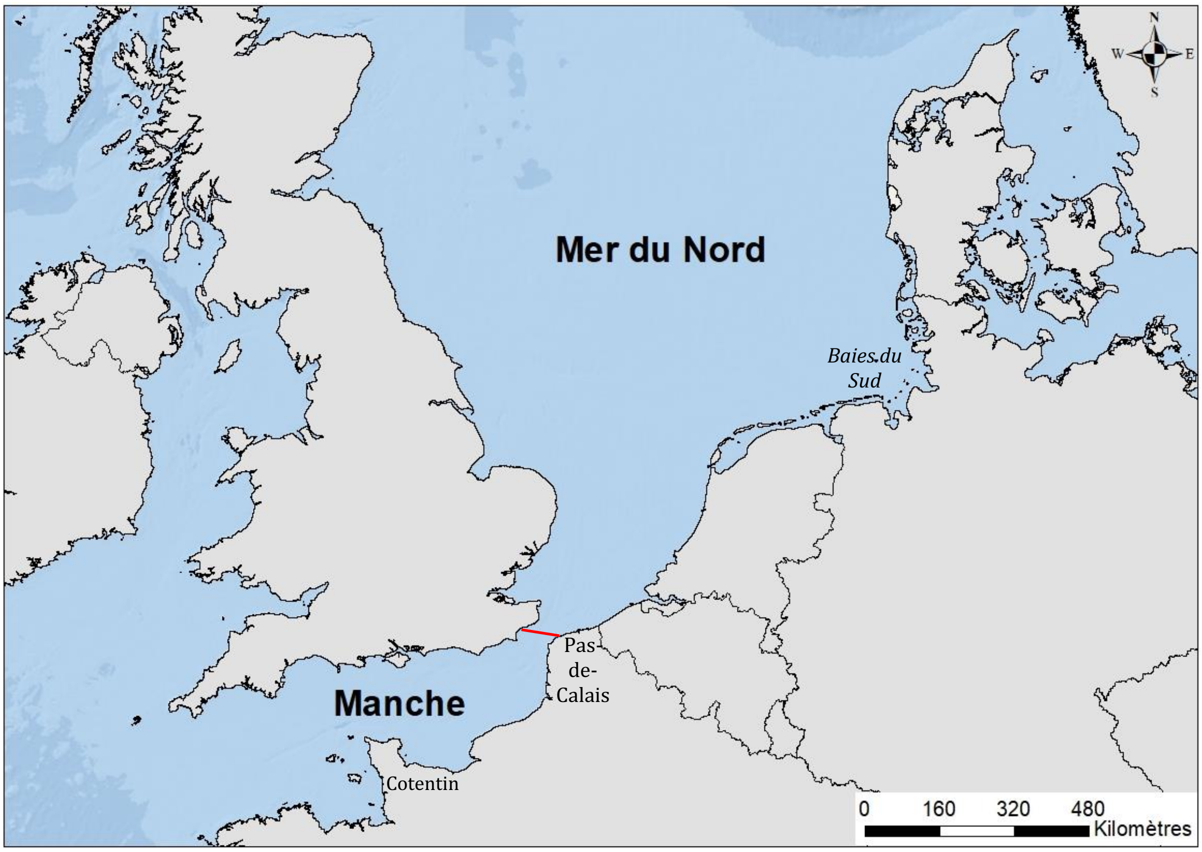


Figure 17: Carte de la Manche et de la mer du Nord

1.3.1. Bathymétrie

La Manche est caractérisée par une profondeur dépassant rarement 100 m (Figure 18). Dans sa partie ouest, mise à part au niveau de la fosse des Casquets qui a une profondeur d'environ 170 m, les fonds les plus importants se situent à la jonction avec les mers celtiques où le plateau continental présente une pente douce jusqu'au talus. A l'est de la presqu'île du Cotentin, les profondeurs dépassent rarement les 50 m. La délimitation entre la Manche et la Mer du Nord se situe sur la ligne joignant Leathercote Point (51° 10′ 02″ N, 1° 24′ 08″ E) au phare de Walde (50° 59′ 40″ N, 1° 54′ 55″ E).

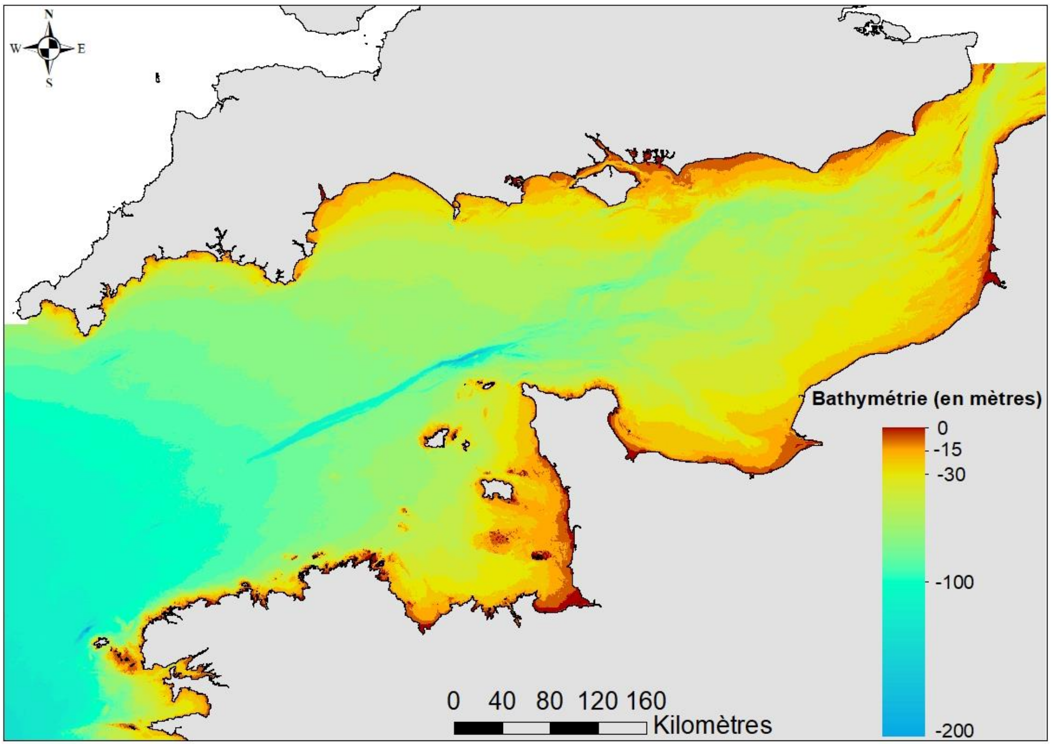


Figure 18: Bathymétrie de la Manche (SHOM, 2015)

1.3.2. Hydrodynamisme

Le mouvement des masses d'eau en Manche est principalement causé par les forts courants de marée existant dans cette zone. Le courant de marée se propage d'ouest en est, de sorte que la zone ouest est à marée haute lorsque la région est est à marée basse et inversement. C'est cette oscillation des masses d'eau qui induit les forts courants de marée observés. Avec un marnage moyen de 6 à 10 mètres mais pouvant atteindre 15.5 m autour des îles Anglo-Normandes, les vitesses de surface peuvent dépasser 3 nœuds au large du Cotentin, au Nord de la Bretagne et au centre du détroit du Pas-de-Calais et atteindre 6-8 nœuds au large du Cap de la Hague (Larsonneur et al. 1982). Les eaux étant généralement peu profondes et la bathymétrie souvent irrégulière, les courants de marée créent des courants à long terme appelées résidus de marée (Salomon 1990). La vitesse de ces courants diminue vers l'ouest, dans la mer Celtique mais également dans les baies ou à l'approche du détroit du Pas-de-Calais. Près des côtes, ces courant engendrés sont généralement giratoires et tournent dans le sens des aiguilles d'une montre et la résiduelle de marée est quasiment nulle (Salomon and Breton 1993).

Les vents peuvent également parfois induire une dérive importante. Même si les déplacements qu'ils engendrent habituellement sont relativement faibles (en hiver les vents dominants d'ouest induisent un courant d'est rarement supérieur à 0.2 nœuds), à l'occasion de certaines tempêtes, ce courant peut augmenter au point de masquer l'effet des marées (Larsonneur et al. 1982; Salomon 1990). Cependant, le vent changeant régulièrement de direction et de vitesse, une partie de son effet disparaît sur des échelles de temps importantes, alors que la marée est permanente (Salomon 1990).

Un autre facteur peut induire des mouvements des masses d'eau dans la Manche : la houle (majoritairement des secteurs Sud-Ouest à Nord-Ouest). La hauteur moyenne est cependant différente selon la provenance de la houle (2 m pour les houles d'ouest et environ 1 m pour les houles de nord ; Guillou 2007).

Le vent et la houle ont cependant des influences sur le mouvement des masses d'eau jusqu'à une profondeur relativement faible. Ainsi, lorsque la profondeur est supérieure à quelques mètres et en absence de conditions de tempête, les courants de marées deviennent le principal facteur contrôlant le mouvement (Dyer 1986). Les vagues et le vent ont donc un effet sur les fonds, uniquement dans les zones peu profondes ou pendant les tempêtes (Grochowski et al. 1993).

1.3.3. Couverture sédimentaire

La Manche est très largement dominée par des habitats sublittoraux de sédiments grossiers (A5.13, A5.14 et A5.15 ; Figure 19) en réponse aux fortes contraintes de cisaillement exercées par les courants de marée et la houle (Coggan and Diesing 2011). Pour ces mêmes raisons, les sables très fins (A5.2) et les sédiments vaseux (A5.3) sont très peu abondants et sont restreints aux baies abritées ou aux estuaires (Grochowski et al. 1993; Coggan and Diesing 2011). Quelques zones rocheuses sont présentes le long des côtes (principalement anglaise) et autour de l'île de Wight et des îles anglo-normandes (Grochowski et al. 1993). Enfin, en Manche Occidentale, des zones relativement éparses de sédiments mixtes (A5.4) sont présentes.

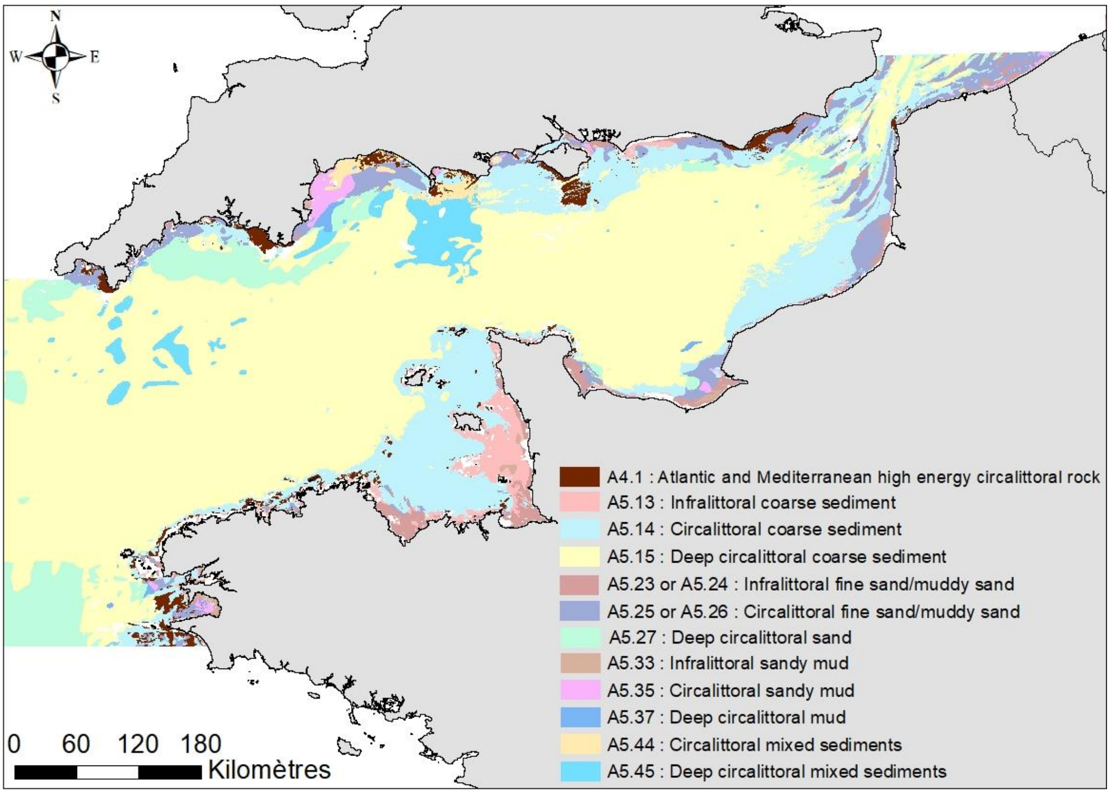


Figure 19: Principaux habitats benthiques en Manche (http://www.emodnet.eu, EUseamap)

1.3.4. Communautés benthiques

En Manche, plusieurs études réalisées dans les années 60-80 ont permis d'identifier les communautés benthiques présentent dans cette zone (Holme 1961, 1966; Cabioch and Gentil 1975; Cabioch and Glaçon 1977; Cabioch et al. 1977). Ainsi sept assemblages distincts en Manche (Table 5) ont été mis en avant par ces travaux. Cinq d'entre eux correspondent à des typologies sédimentaires bien définis.

Table 5: Assemblages benthiques identifiés en Manche dans les années 1971-1976 (d'après Foveau 2009)

Assemblages	Espèces caractéristiques	Espèces principales	Sédiments et profondeur moyenne
I	*Anapagurus hyndmanni* *Galathea intermedia* *Pilumnus hirtellus* *Buccinum undatum* *Calliostoma zizyphinum* *Gibbula tumida* *Ocenebra erinacea* *Lepidonotus squamatus*	*Ophiothrix fragilis* *Psammechinus miliaris* *Pisidia longicornis*	Sédiments grossiers 33.4 m
II		*Nucula nitidosa* *Asterias rubens* *Pisidia longicornis*	Sables graveleux 24.8 m
III	*Eumida sanguinea* *Gattyana cirrhosa* *Nepthys hombergii* *Pectinaria (Lagis) koreni* *Mya truncata* *Phaxas pellucidus* *Ophiura ophiura*	*Owenia fusiformis* *Pectinaria (Lagis) koreni* *Abra alba*	Sables (+/- graveleux) 10.2 m
IV	*Bathyporeia elegans* *Gastrosaccus spinifer*	*Nepthys cirrosa* *Spiophanes bombyx* *Gastrosaccus spinifer*	Sables dunaires 13.9 m
V	*Branchiostoma lanceolatum*	*Ophiura albida* *Echinocyamus pusillus* *Branchiostoma lanceolatum*	Graviersensablés 24.9 m
VI		*Spatangus purpureus* *Glycera gigantea* *Ampelisca spinipes*	
VII		*Ampelisca brevicornis* *Ampelisca tenuicornis* *Nucula nitidosa*	

Pour compléter ces travaux et suite à la présence de pression anthropique croissante, une étude plus récente a été réalisée par Foveau (2009) en Manche orientale. Cette étude à permis d'identifier 18 assemblages benthiqus différents dont six ont pu être mis en lien avec des caractéristiques environnementales (Table 6).

Table 6: Principaux assemblages benthiques identifiés en Manche orientale par Foveau (2009)

Assemblages	Espèces caractéristiques	Espèces principales	Sédiments et profondeur moyenne
I	*Anchialina agilis* *Eulalus pusiolus* *Gnathia varax* *Siriella jaltensis* *Arabella (Arabella iricolor)* *Asclerocheilus intermedius* *Dipolydora giardi* *Glycera capitata* *Glycera gigantea* *Harmothoe impar* *Laonice cirrata* *Lumbrineris gracilis* *Nereis pelágica* *Orbinia (Orbinia) sertulata* *Peteloproctus terricolus* *Pista elongata* *Sabella pavonina* *Thelepus cincinnatus* *Dosinia exoleta* *Gari depressa* *Goodallia triangularis* *Jujubinus montagui* *Leptochiton scabridus* *Limatula subauriculata*	*Galathea intermedia* *Pisidia longicornis* *Ampharete baltica*	Graviers ensablés 41.0 m
II	*Galathea squamifera* *Calliostoma granulatum*	*Corophium sextonae* *Pisidia longicornis* *Ophiothrix fragilis*	Cailloutis 29.1 m
III	*Lumbrineriopsis paradoxa*	*Echinocyamus pusillus* *Ophiothrix fragilis* *Notomastus latericeus*	Sables graveleux à graviers ensablés 36.4 m
IV	*Sthenelais limicola*	*Spiophanes bombyx* *Magelona filiformis* *Eumida*	
V		*Nepthys cirrosa* *Spiophanes bombyx* *Ophelia borealis*	Sables 16.7 m

VI	*Macrochaeta helgolandica* *Schistomeringos caeca* *Trypanosyllis (Trypanosyllis) coelica* *Ampelisca pectenata*	*Hesionura elongata* *Pisione remota* *Glycera lapidum*	
VII	*Magelona mirabilis* *Phyllodoce (Anaitides) lineata* *Nucula sulcata*	*Spiophanes bombyx* *Nepthys cirrosa* *Notomastus latericeus*	Sables graveleux 27.7 m
VIII	*Protodorvillea kefersteini*	*Polygordius lacteus* *Pisione remota* *Branchiostoma lanceolatum*	
IX		*Ophelia borealis* *Glycera lapidum* *Nepthys cirrosa*	Sables légèrement graveleux 20.8 m
X	*Clymenura clypeata* *Eteone foliosa* *Gnathia maxillaris*	*Echinocyamus pusillus* *Ophiothrix fragilis* *Ophiura albida*	
XI	*Archidoris pseudoargus* *Doto fragilis* *Gastrochaena dubia* *Onchidoris bilamellata* *Gammaropsis lobata* *Lysianassa ceratina* *Macropodia linaresi* *Tryphosella sarsi* *Phyllodoce (Anaitides) mucosa*	*Echinocyamus pusillus* *Ophiura albida* *Pisidia longicornis*	
XII		*Ophelia borealis* *Ophiura albida* *Echinocyamus pusillus*	
XIII		*Soocarnes erythrophtalmus* *Polygordius lacteus* *Glycera lapidum*	
XIV	*Jassa falcata* *Pandalus montagui*	*Ophiothrix fragilis* *Pisidia longicornis* *Caprellidae*	
XV		*Urothoe brevicornis* *Nepthys cirrosa* *Glycera lapidum*	
XVI	*Bodotria arenosa* *Caprella linearis* *Urothoe poseidonis* *Trivia arctica*	*Corophium sextonae* *Caprella linearis* *Ophiura albida*	
XVII	*Ampelisca diadema* *Demonax branchyona* *Epitonium clathrus*	*Ophiura albida* *Paraonis fulgens* *Nassarius reticulatus*	
XVIII	*Proceraea aurantiaca* *Syllis prolifera*	*Psammechinus miliaris* *Ophiura albida* *Pisidia longicornis*	

1.4. La partie sud de la mer du Nord

La mer du Nord (Figure 17) est une des plus grandes mers épicontinentales au monde. Elle est entourée par sept pays (le Royaume-Uni, la France, la Belgique, les Pays-Bas, l'Allemagne, le Danemark et la Norvège). Ses limites sont au sud, la partie la plus étroite du détroit du Pas-de-Calais, à l'est, une ligne rejoignant Hantsholm (au Danemark) à Lindesnaes (en Norvège), au nord, une ligne entre les îles Shetland et la côte norvégienne en suivant le parallèle 61°00' Nord et à l'ouest, une ligne rejoignant l'Ecosse (Dunnet Head) à Horse Island (îles Shetland).

A large échelle, la mer du Nord apparaît comme un système « homogène», pourtant à plus petite échelle, des différences notables existent entre la partie Nord et la partie Sud. Ainsi, seules les caractéristiques de la partie sud de la mer du Nord sont présentées dans cette étude.

1.4.1. Bathymétrie

Avec une moyenne de 70 mètres de profondeur, la mer du Nord est relativement peu profonde. Si la profondeur n'est que de 20 à 40 m dans les baies du sud et allemandes, elle augmente vers le nord jusqu'à 100/150 m près du 58°N (Huthnance 1991). La partie sud de la mer du Nord, peu profonde, abrite de nombreux bancs de sable s'élevant à moins de 10 m de la surface (Figure 20).

La mer du Nord est par ailleurs le lieu d'interactions importantes entre les influences océaniques (marée, oscillation de l'Atlantique Nord, système de basse pression de l'Atlantique Nord) et continentales (apports d'eau douce, flux de chaleur…), créant ainsi un régime physique et biogéochimique très spécifique (Sündermann and Pohlmann 2011).

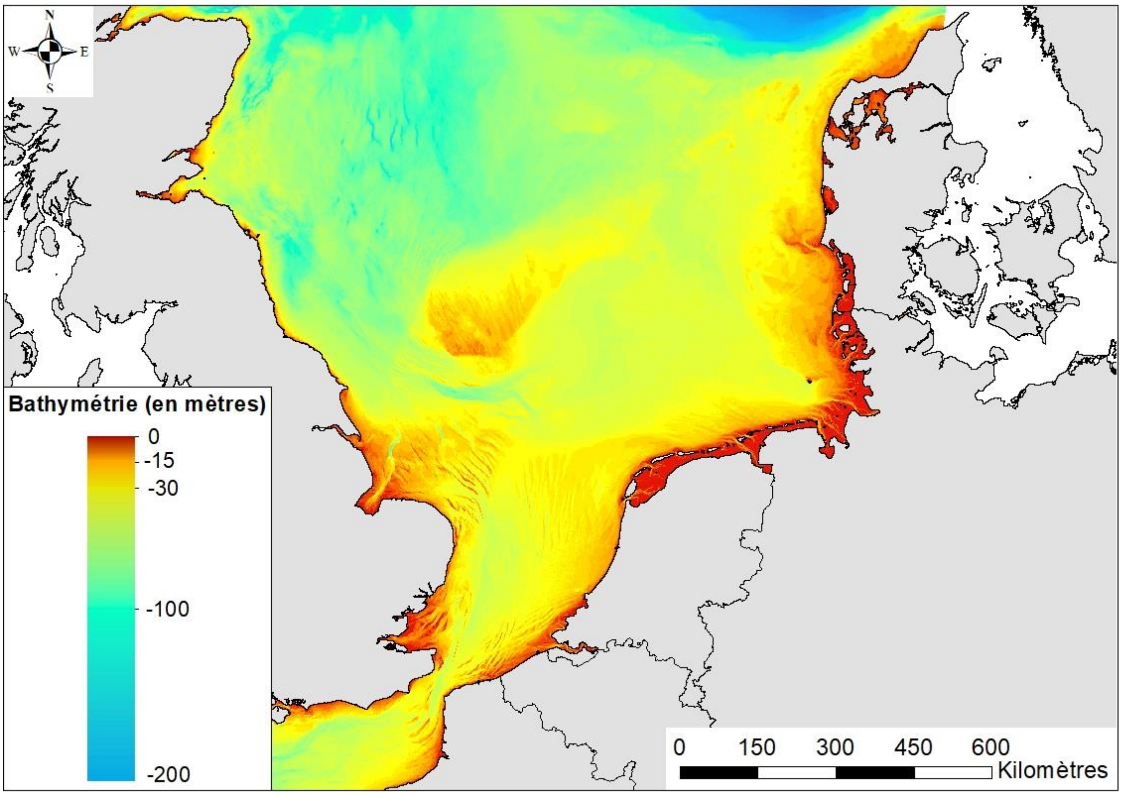


Figure 20: Bathymétrie de la partie sud de la mer du Nord (SHOM, 2015)

1.4.2. Hydrodynamisme

L'hydrodynamisme en mer du Nord est principalement régi par les marées semi-diurnes et notamment dans sa partie sud. Les vitesses de courants induites par la marée sont variables d'une zone à l'autre, avec des valeurs dépassant généralement 0.5 $m.s^{-1}$ au sud et près des côtes anglaises et de l'Ecosse et pouvant dépasser 1.2 $m.s^{-1}$ dans le détroit du Pas-de-Calais et au large de l'East Anglia (Huthnance 1991). Même si le courant de marée est le facteur principal influençant le mouvement des masses d'eau en mer du Nord, d'autres paramètres jouent sur la circulation générale notamment dans la partie sud de la mer du Nord : le vent, la topographie, les apports fluviaux et les entrées d'eau provenant de la Manche (Rodhe 1998).

1.4.3. Couverture sédimentaire

La partie sud de la mer du Nord est très largement dominée par les sables fins à moyens (A5.2 ; Figure 21), mais la présence de sédiments plus ou moins grossiers (A5.15) dans certaines zones, comme le détroit du Pas-de-Calais ou devant la côte est de l'Angleterre, est à noter. L'extrême sud de la mer du Nord, à proximité du Pas de Calais, est caractérisée par la présence de nombreux bancs de sable et champs de dunes (Le Bot 2001).

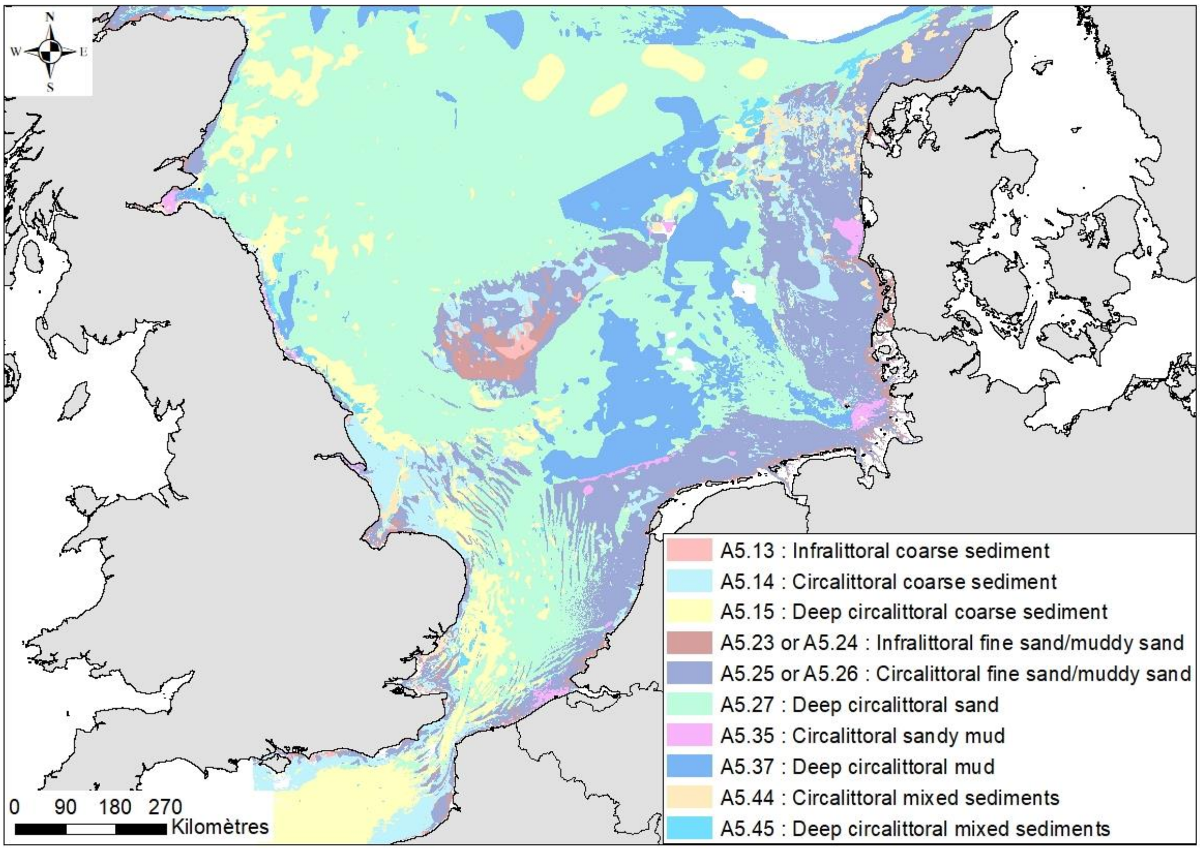


Figure 21: Principaux habitats benthiques dans la partie sud de la mer du Nord
(http://www.emodnet.eu, EUseamap)

1.4.4. Communautés benthiques

En mer du Nord, plusieurs études ont été réalisées dans les années 80 pour identifier les différentes commuanutés benthiques présentent dans cette zone (Kingston and Rachor 1982; Salzwedel et al. 1985; Kröncke and Bergfeld 2003). Plus récemment, les travaux de Kröncke et al. (2011) ont comparés les communautés identifiées dans les travaux de Künitzer et al. (1992) de celles décritent par Vanden Berghe et al. (2007). Ces travaux ont mis en évidence des évolutions dans la composition des communautés benthiques de la mer du Nord (Table 7 & 8) que ce soit en terme d'abondance ou de dominance des espèces ou de distribution spatiale de ces communautés (Kröncke et al. 2011 ; Figure 22).

Table 7: Principaux assemblages de macrofaune benthique dans le sud de la mer du Nord en 1986 (d'après Kröncket et al. 2011)

Assemblages	Espèces caractéristiques	Espèces dominantes
B	*Myriochele spp.* *Capitella spp.* *Goniada spp.* *Levinsenia gracilis*	*Myriochele spp.* *Capitella spp.* *Ampelisca spinipes* *Levinsenia gracilis*
C	*Amphiura filiformis* *Phoronida* *Scoloplos armiger*	*Amphiura filiformis* *Phoronida* *Scoloplos armiger* *Eudorellopsis deformis*
D1	*Bathyporeia spp.* *Magelona spp.* *Spiophanes spp.* *Tellina spp.* *Polinices spp.* *Phoronida* *Harpinia antennaria*	*Bathyporeia spp.* *Magelona spp.* *Spiophanes spp.* *Tellina spp.* *Phoronida*
D2	*Amphiura filiformis* *Mysella bidentata* *Pholoe baltica*	*Amphiura filiformis* *Mysella bidentata* *Pholoe baltica* *Myriochele spp.*
E3	*Ophelia borealis* *Amphiura filiformis* *Scoloplos armiger*	*Ophelia borealis* *Amphiura filiformis* *Scoloplos armiger*
E4	*Amphiura filiformis* *Scoloplos armiger* *Nemertina*	*Amphiura filiformis* *Scoloplos armiger* *Myriochele spp.* *Spiophanes spp.*
F1	*Mysella bidentata* *Pholoe baltica* *Nemertina*	*Mysella bidentata* *Pholoe baltica*
F2	*Ophelia borealis* *Bathyporeia spp.*	*Ophelia borealis* *Bathyporeia spp.* *Magelona spp.* *Spisula spp.* *Pisione remota*

Table 8: Principaux assemblages de macrofaune benthique dans le sud de la mer du Nord en 2000 (d'après Kröncket et al. 2011)

Assemblages	Espèces caractéristiques	Espèces dominantes
H	*Aoinides paucibranchiata* *Ophelia borealis*	*Aoinides paucibranchiata* *Spio spp.* *Goodallia triangularis* *Branchiostoma lanceolata*
I	*Spiophanes spp.* *Nepthys cirrosa* *Bathyporeia spp.* *Spio spp.*	*Spiophanes spp.* *Nepthys cirrosa* *Bathyporeia spp.* *Gastrosaccus spinifer* *Urothoe poseidonis*
K	*Pomatocerus spp.* *Nemertina* *Cauleriella spp.*	*Pomatocerus spp.* *Lanice concheliga* *Pectinaria spp.* *Pisidia longicornis*
L1	*Spiophanes spp.* *Amphiura filiformis* *Magelona spp.* *Phoronida* *Pholoe baltica*	*Spiophanes spp.* *Amphiura filiformis* *Magelona spp.* *Mysella bidentata*
L2	*Spiophanes spp.* *Magelona spp.* *Bathyporeia spp.* *Tellina spp.*	*Spiophanes spp.* *Magelona spp.* *Bathyporeia spp.* *Tellina spp.* *Phoronida* *Spisula spp.*
M1	*Spiophanes spp.* *Amphiura filiformis* *Scoloplos armiger* *Paramphinome jeffreysii*	*Spiophanes spp.* *Amphiura filiformis* *Myriochele spp.*
M2	*Myriochele spp.* *Paramphinome jeffreysii* *Spiophanes spp.* *Goniada spp.*	*Myriochele spp.* *Paramphinome jeffreysii* *Spiophanes spp.*
N	*Harpinia antennaria* *Nepthys hombergii* *Notomastus spp.*	*Amphiura filiformis* *Myriochele spp.* *Corbula gibba* *Abra alba*

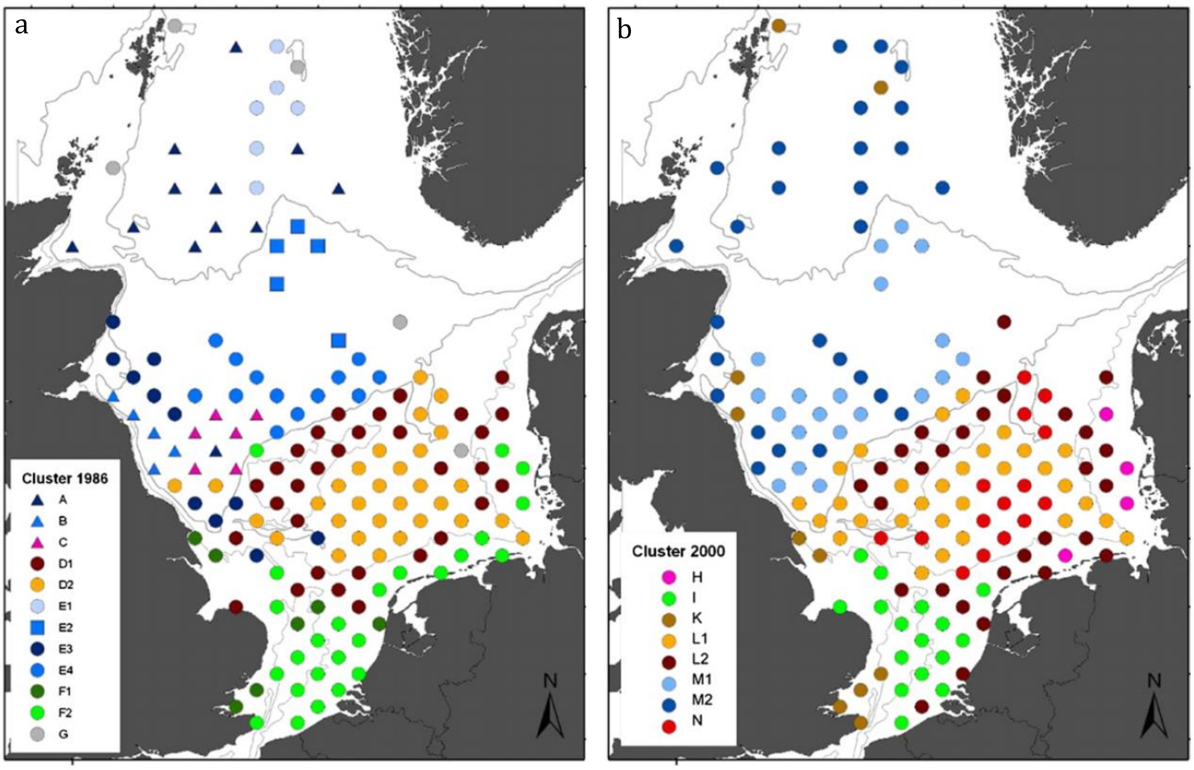


Figure 22: Distribution spatiale des communautés de macrofaune en 1986 (a) et en 2000 (b)
(Kröncke et al. 2011)

2. Données de chalutage scientifique

Chaque année, des campagnes scientifiques de chalutage de fond sont réalisées sur l'ensemble des façades maritimes françaises afin d'évaluer l'état des stocks des poissons démersaux. La faune benthique, considérée comme une prise accessoire du chalut, est collectée lors de ces campagnes et les espèces sont triées, identifiées, comptées et pesées. Les données de trois de ces campagnes (MEDITS – MEDIterranean Trawl Survey, IBTS – International Bottom Trawl Survey et CGFS – Channel Ground Fish Survey) ont été utilisées lors de ce travail. La partie ouest de la Manche étant échantillonnée par la campagne CGFS que depuis 2016, les données issues de la campagne CAMANOC (ChAlutage en MANche OCcidentale) réalisée en Manche en 2014 ont également été utilisées dans cette étude.

2.1. MEDITS

Réalisée en mer Méditerranée (dans le Golfe du Lion et en Corse), cette campagne scientifique de chalutage benthique (MEDITS, Jadaud et al. 1994) est effectuée chaque année en juin depuis 1994, mais la faune benthique n'est collectée que depuis 2012. L'engin d'échantillonnage utilisé est un chalut de fond adapté pour travailler à toutes les profondeurs (10 - 800 m) et qui est composé de quatre panneaux, avec un maillage étiré de 20 mm au niveau du cul de chalut. Le plan d'échantillonnage est stratifié par strate de profondeur et réparti de manière uniforme sur l'ensemble de la zone (Figure 23). Les traits, réalisés de jour, sont d'une durée de 30 minutes à 3 nœuds au-dessus de 200 m et de 60 minutes à la même vitesse en dessous de 200 m (MEDITS 2017). En raison du changement de la durée du chalutage au-delà de 200 m de profondeur et de la transition de la zone photique à la zone aphotique, seules les données échantillonnées entre 0 et 200 mètres ont été utilisées dans cette étude, soit un total de 448 stations (environ 54 stations dans le Golfe du Lion et 10 en Corse échantillonnées chaque année entre 2012 et 2018 ; Table 9).

Table 9: Nombre d'échantillonnage effectués chaque année lors des différentes campagnes

Années	MEDITS	IBTS	CGFS	CAMANOC
2008			98	
2009		50	98	
2010		75	92	
2011		87	99	
2012	65	84	89	
2013	63	85	93	
2014	64	82	94	40
2015	64	90	90	
2016	64	72	81	
2017	64	70	66	
2018	64	66	115	

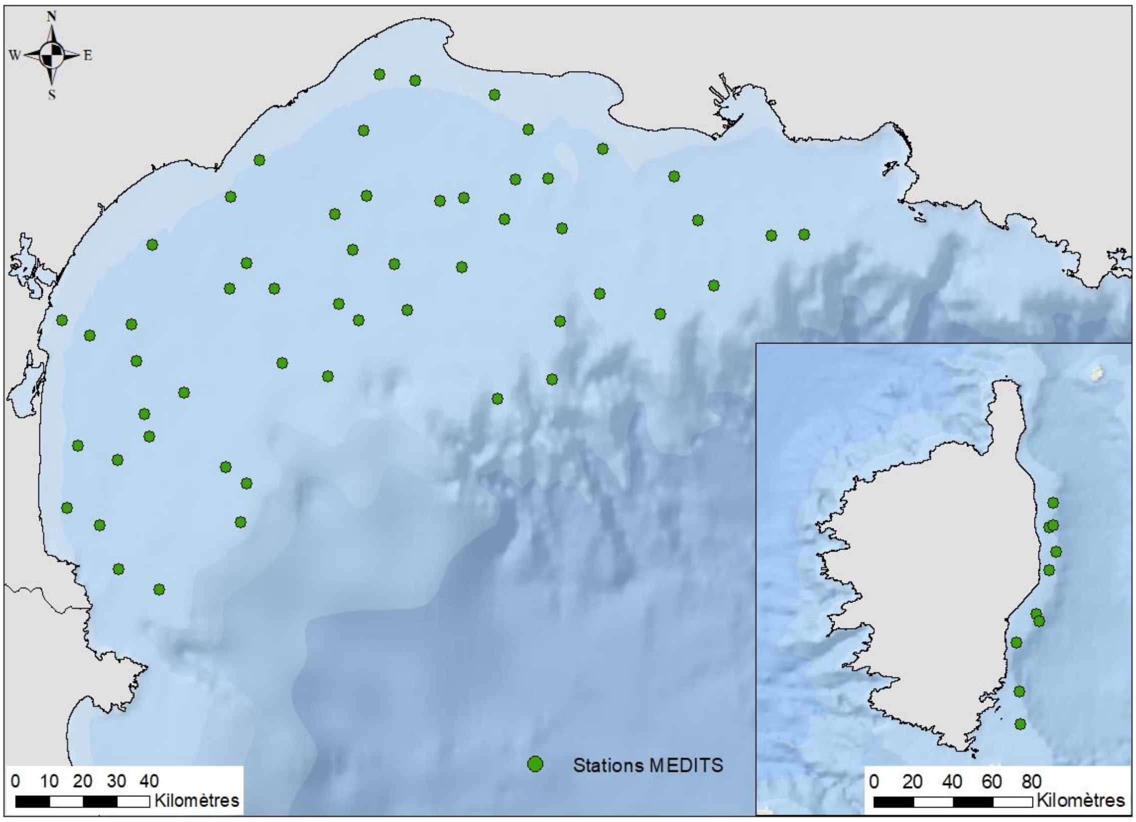


Figure 23: Emplacement des stations MEDITS dans le Golfe du Lion et sur la côte Est de la corse

2.2. International Bottom Trawl Survey

La campagne IBTS (International Bottom Trawl Survey) est réalisée chaque année en janvier/février depuis 1970 (Auber 1992) dans la partie sud de la mer du Nord et la partie est de la Manche. Cependant, la faune benthique n'est identifiée et collectée que depuis 2009. L'engin d'échantillonnage utilisé est un chalut de fond à grande ouverture verticale (VHVO) avec un maillage étiré de 20 mm au niveau du cul du chalut. Le plan d'échantillonnage est stratifié sur la base de rectangles statistiques du CIEM, avec une station par rectangle de 30'x60' pour assurer une bonne couverture de la zone d'étude (Figure 24). Chaque année, les rectangles devant être échantillonnés sont les mêmes, mais les traînes de chalut réalisées au sein de ces rectangles sont aléatoirement sélectionnées. Les traits sont effectués de jour, pendant 30 minutes à 4 nœuds (ICES 2015, 2017a). Entre 2009 et 2018, 761 traits de chaluts ont été réalisés pendant cette campagne (Table 9).

2.3. Channel Ground Fish Survey

La campagne CGFS (Channel Ground Fish Survey) se déroule chaque année dans la partie est de la Manche au mois d'octobre depuis 1988 (Coppin and Travers-Trolet 1989). L'engin d'échantillonnage est le même que celui utilisé lors de la campagne IBTS : un chalut de fond à grande ouverture verticale (VHVO) avec un maillage étiré de 20 mm au niveau du cul du chalut. Le plan d'échantillonnage est basé sur les rectangles statistiques du CIEM, avec une station par maille de 15'x15' (soit 8 stations par rectangle statistique) pour assurer une bonne couverture de la zone d'étude (Figure 24). Les emplacements des traînes de chalut ont été initialement choisis à l'aide de plans de pêche professionnels ou trouvés par prospection, et les stations ont été maintenues fixes depuis 1988 (ICES 2017a). Entre 2008 et 2018, 1015 stations ont été échantillonnées lors de cette campagne (Table 9).

2.4. Campagne Manche Occidentale

La campagne CAMANOC (Campagne Manche Occidentale) a eu lieu en septembre/octobre 2014 dans la partie ouest de la Manche (Verin and Travers-Trolet 2014). Contrairement aux campagnes présentées précédemment, CAMANOC est une campagne pluridisciplinaire visant à échantillonner l'ensemble de l'écosystème (plancton, invertébrés benthiques, poissons et céphalopodes, oiseaux marins…). Ainsi des prélèvements à la drague Rallier du Baty ainsi que des transects vidéo ont été réalisés en plus du déploiement d'un chalut spécifique pour les fonds durs. Au total 40 traînes de chalut ont été réalisées, dans le bassin occidental lors de cette campagne, choisies parmi des traînes de pêcheries chalutières sur la base d'une stratification bathy-sédimentaire (Figure 24 ; Table 9).

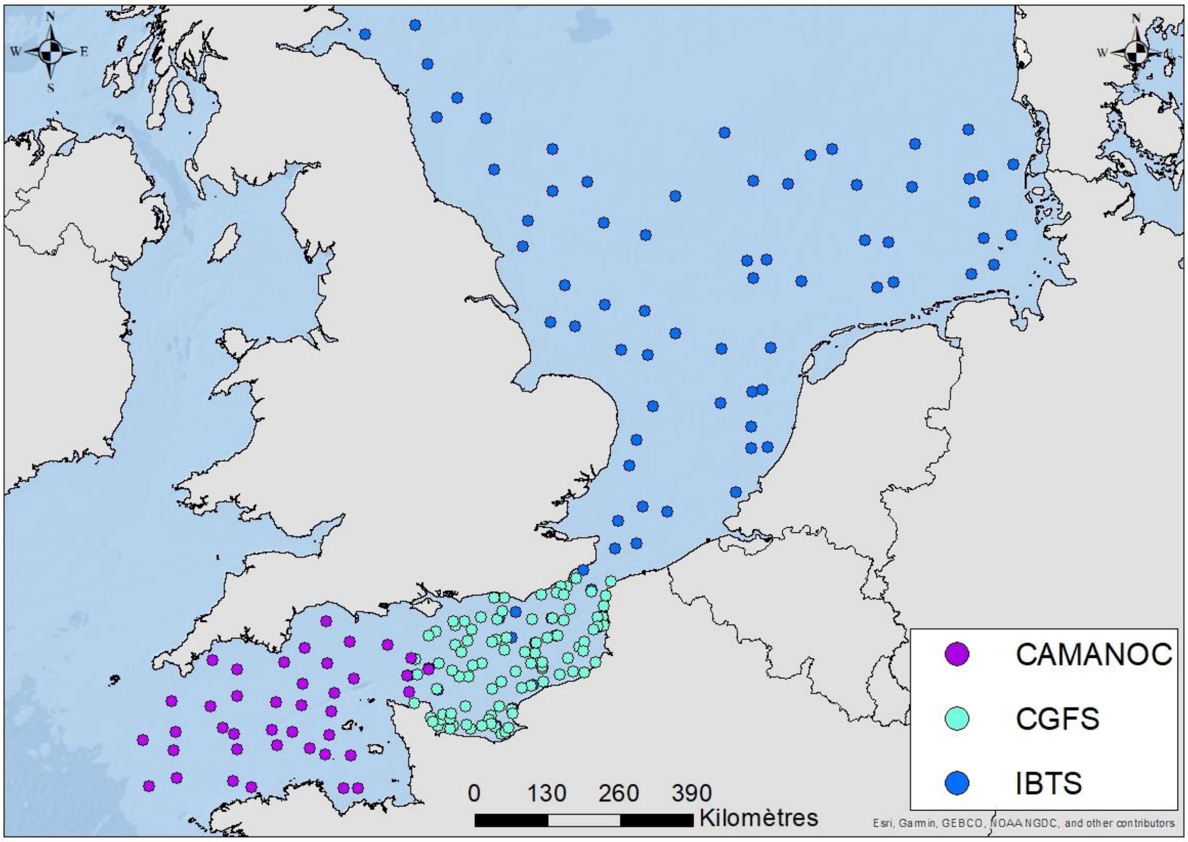


Figure 24: Emplacement des stations échantillonnées durant les campagnes CGFS, IBTS et CAMANOC en 2014

3. Préparation des données biologiques

3.1. Ensemble des jeux de données

L'ensemble des espèces commerciales (*Homarus gammarus*, *Crangon crangon*, *Maja brachydactyla*, *Pecten maximus*, *Aequipecten opercularis*, *Palaemon serratus*, *Nephrops norvegicus*, *Buccinum undatum*, *Cancer pagurus*, *Aristaeomorpha foliacea*, *Aristeus antennatus*, *Parapeneus longisrostris*, *Bolinus brandaris*) et les céphalopodes ont été retirés des jeux de données utilisés dans ce travail car ces espèces peuvent-être ciblées par les pêcheries et ne sont donc pas indépendantes de la répartition spatiale de l'effort de pêche aux arts traînants.

3.2. Données biologiques issues des campagnes de chalutage scientifique

La totalité des espèces benthiques sont pesées lors des campagnes de chalutage scientifique mais seules les espèces non coloniales peuvent-être dénombrées. Ainsi, pour travailler sur l'ensemble de la faune benthique capturée et pas uniquement sur les espèces non coloniales, les données de chalutage scientifique utilisées dans ce travail ont été des données de biomasse. La surface échantillonnée à l'aide du chalut n'étant pas toujours la même, les données ont été normalisées et exprimées en $g.km^{-2}$.

Afin de limiter les erreurs d'identification et les biais dus à l'expertise taxonomique variable des déterminateurs présents lors des campagnes de chalutage scientifique, certains taxa ont été agrégés à des niveaux taxonomiques supérieurs en suivant la méthode proposée par Foveau *et al.* (2017).

Pour être maintenue à son niveau taxonomique initial, une espèce donnée devait être observée dans 90 % des années échantillonnées (5 ans pour MEDITS, 8 ans pour IBTS et 9 ans pour CGFS), sous peine d'être agrégée itérativement à un niveau taxonomique supérieur (genre, famille, ordre, classe, embranchement) jusqu'à ce qu'elle remplisse ce critère. Par exemple, l'ascidie *Molgula appendiculata,* observée seulement pendant deux années, a été agrégée au genre *Molgula* qui lui a été observé chaque année. Si, après application de ce traitement, un embranchement donné était observé dans moins de 90% des années échantillonnées, il a alors été retiré des analyses (Foveau et al. 2017). Dans la plupart des cas, le taxon supprimé en raison d'incertitudes sur les caractéristiques taxonomiques ou fonctionnelles représentait moins de 10 % de la biomasse/l'abondance totale échantillonnée. Toutefois, si les taxa supprimés représentaient plus de 25% de l'abondance ou biomasse totale d'une ou de plusieurs stations échantillonnées, alors celles-ci ont été supprimées du jeu de données pour la suite des analyses.

4. Traits biologiques de sensibilité

L'ensemble des espèces benthiques ne sont pas affectées de la même manière par les arts traînants en raison de leurs caractéristiques biologiques. Ainsi, cinq traits biologiques ont été retenus dans cette étude pour caractériser les réponses potentielles des organismes à l'abrasion physique (de Juan et al. 2007; Bolam and Eggleton 2014; Foveau et al. 2017). Ces traits sont (i) la position des organismes dans le sédiment, (ii) le mode d'alimentation, (iii) la capacité de mobilité, (iv) la taille adulte et (v) la fragilité des organismes ou sa capacité de régénération. Chaque trait a été subdivisé en de multiples "modalités" afin d'englober la gamme des attributs possibles de tous les taxa.

Pour permettre de réaliser des analyses quantitatives, une valeur a été attribuée à chaque modalité, variant d'une sensibilité faible (0) à une sensibilité élevée [3 (Table 10 ; Foveau et al. 2019)]. Les valeurs attribuées dans les cinq catégories ont été additionnées pour chaque taxon (les taxa très vulnérables atteignent donc un score maximum de 15) et cette valeur a été considérée comme un indice de sensibilité de l'espèce (SI) spécifique aux perturbations induites par le chalutage (Foveau et al. 2017).

Dans le cas où un taxon a été agrégé à un niveau taxonomique supérieur, des valeurs ont été attribués au groupe en utilisant la valeur la plus élevée observée dans ce groupe pour chaque trait sous réserve de valider deux conditions: l'écart type entre les valeurs présentes au sein d'un même trait doit être inférieur à 1,5 et l'écart type de la somme des SI des différents taxa regroupés dans ce groupe doit être inférieur à 2,5 (Foveau et al. 2017). Lorsque ces deux conditions n'ont pas été respectées, le groupe taxonomique a été retiré de l'analyse. Dans les cas où les groupes supprimés représentaient plus de 25 % de la biomasse totale de la station échantillonnée, la station a été retirée de l'ensemble des données. Des matrices traits-espèces ont été produites, pour chaque jeu de données utilisé dans ce travail, pour permettre le calcul d'indices basés sur les traits biologiques des espèces (Foveau et al. 2019).

Table 10: Traits biologiques de sensibilité à l'abrasion et scores associés

Scores de sensibilité	Position	Mode d'alimentation	Mobilité	Taille	Fragilité
0	Enfouissement profond	Nécrophage	Très mobile (nage)	Petite (<5 cm)	Coquille dure, vermiforme, régénérescence possible
1	Enfouissement en surface (premiers centimètres)	Déposivore et prédateur	Mobile (rampante)		Flexible
2	Surface		Sédentaire	Moyenne (5-10 cm)	Sans protection
3	Emergent	Filtreur	Sessile	Grande (>10 cm)	Coquille ou structure fragile

5. Indices biotiques

Trois types d'indices biotiques ont été étudiés dans ce travail : (i) des indices de diversité taxonomique; (ii) des indices de diversité fonctionnelle et (iii) des indices de sensibilité fonctionnelle spécifiquement construits pour détecter les impacts physiques sur les communautés benthiques.

5.1. Les indices de diversité taxonomique

Richesse spécifique

La Richesse spécifique (SR) se définit comme le nombre d'espèces rencontrées à chacune des stations (Stirling & Wilsey, 2001).

Indice de Margalef

L'indice de Margalef (Eq. 1) est basé sur l'hypothèse d'une relation linéaire entre le nombre d'espèces et le logarithme du nombre total d'individus (Margalef 1958). Plus la valeur de cet indice est élevée, plus le nombre d'espèces observées est important.

$$(1) \quad d = \frac{SR - 1}{ln(N)}$$

Où *RS* est le nombre d'espèces et *N* le nombre total d'individus observés

Indice de Shannon

L'indice de Shannon (Eq. 2) permet de quantifier l'hétérogénéité de la biodiversité d'un milieu d'étude et est sensible aux espèces rares. Sa valeur varie toujours entre 0 (une seule espèce) et le logarithme en base 2 de la richesse spécifique [lorsque toutes les espèces ont la même abondance (Shannon & Weaver, 1949)].

$$(2) \quad H' = -\sum_{i=1}^{SR} p_i . log_2(p_i)$$

Où $p_i=n_i/N$ représente la proportion d'abondance d'une espèce i (n_i étant le nombre d'individus de l'espèce et N le nombre total d'individus observés)

Indice de Pielou

L'indice de Pielou (Eq. 3) est le rapport entre l'indice de Shannon (H') et le logarithme en base 2 de la richesse spécifique (Pielou 1969). Il permet de mesurer la répartition des individus au sein des espèces, indépendamment de la richesse spécifique. Il varie de 0 (lorsqu'il y a dominance d'une des espèces) à 1 (lorsqu'il y a équi-répartition des individus entre les espèces).

$$(3) \quad J' = \frac{H'}{log_2(SR)}$$

Indice de Simpson

L'indice de Simpson (Eq. 4 ; Simpson 1949) exprime la probabilité que deux individus échantillonnés de façon aléatoire et indépendante au sein d'une communauté appartiennent à la même espèce. Ainsi, plus l'indice est faible, plus la station analysée est diversifiée.

$$(4) \quad \lambda = \frac{\sum_{i=1}^{SR} n_i\,(n_i - 1)}{N(N-1)}$$

Où n_i est le nombre d'individus de l'espèce i et N le nombre total d'individus observés

L'ensemble de ces indices ont été calculés en utilisant le package Vegan 2.5-2 (Oksanen et al. 2019).

5.2. Les indices de diversité fonctionnelle

Ces indices ont été utilisés parce qu'ils mettent en évidence les variations de certaines fonctions spécifiques (comme le mode d'alimentation par exemple) au sein des communautés benthiques (Mouillot et al. 2013a). Avant de calculer les indices de diversité fonctionnelle, une analyse des correspondances multiples (ACM) par zone d'étude a été effectuée avec le package PCAmixdata 3.1 (Chavent et al. 2017) sur les matrices traits-espèces car la classification des traits est catégorielle alors que les indices fonctionnels ont été construits pour des traits ayant des modalités quantitatives et continues (Villéger et al. 2008). Les scores de l'ACM ont été combinés avec les matrices de biomasse ou d'abondance des espèces pour calculer quatre indices fonctionnels (Mouillot et al. 2013a).

<u>Richesse fonctionnelle</u>

La richesse fonctionnelle (FRic) représente le volume maximal de l'espace fonctionnel occupé par la communauté (Villéger et al. 2008). Plus formellement, cette mesure quantifie le volume à l'intérieur de l'enveloppe de l'espace fonctionnel contenant toutes les espèces appartenant à la communauté.

La richesse fonctionnelle n'est influencée que par l'identité des espèces (leur abondance ne compte pas) et plus particulièrement par les espèces dont les traits fonctionnels sont les plus extrêmes et délimitent l'enveloppe de l'espace fonctionnel. Ainsi, plus la richesse fonctionnelle est élevée, plus la diversité fonctionnelle de l'assemblage est importante.

<u>Divergence fonctionnelle</u>

L'indice de divergence fonctionnelle (FDiv, Eq.10) permet de quantifier si les abondances les plus élevées sont proches des limites de l'espace fonctionnel. Cet indice varie entre 0, lorsque les espèces très abondantes sont très proches du centre de gravité de l'espace fonctionnel occupé et 1 lorsque les espèces très abondantes sont très éloignées du centre de gravité (Villéger et al. 2008).
Premièrement, les coordonnées du centre de gravité Gv (g1, g2,..., gT) des espèces V formant les sommets de l'enveloppe de l'espace fonctionnel sont calculées (Eq. 5).

$$(5) \quad g_k = \frac{1}{V}\sum_{i=1}^{V} x_{ik}$$

Où x_{ik} sont les coordonnées de l'espèce *i* pour le trait *k[1,T]*

Ensuite, pour chaque espèce S, la distance euclidienne au centre de gravité (Eq. 6) et la distance moyenne des espèces S au centre de gravité (Eq. 7) sont définies.

$$(6) \quad dG_i = \sqrt{\sum_{k=1}^{T} (x_{ik} - g_k)^2}$$

$$(7) \quad \overline{dG} = \frac{1}{S} \sum_{i=1}^{S} dG_i$$

Puis, la somme des déviances de l'abondance pondérée *(Δd)* et des déviances de l'abondance relative pondérée *(Δ|d|)* par rapport à la distance du centre de gravité sont calculées suivant les équations 8 et 9.

$$(8) \quad \Delta d = \sum_{i=1}^{S} w_i \times (dG_i - \overline{dG})$$

$$(9) \quad \Delta|d| = \sum_{i=1}^{S} w_i \times |dG_i - \overline{dG}|$$

La divergence fonctionnelle (FDiv) est ensuite calculée comme dans l'équation 10.

$$(10) \quad FDiv = \frac{\Delta d + \overline{dG}}{\Delta|d| + \overline{dG}}$$

<u>Equitabilité fonctionnelle</u>

L'équitabilité fonctionnelle (FEve) peut être définie comme l'homogénéité de la distribution de l'abondance des espèces dans l'espace fonctionnel (Mason et al. 2005). Cet indice varie entre 0 et 1 et n'est pas biaisé par la richesse spécifique. Plus les abondances principales appartiennent à des espèces fonctionnellement proches, plus l'indice est faible (Villéger et al. 2010).

Afin de transformer la distribution des espèces d'un espace fonctionnel multidimensionnel en une distribution selon un axe unique, un « arbre couvrant minimum », qui lie tous les points contenus dans un espace multidimensionnel avec la somme minimale des longueurs de branches, est utilisé (Villéger et al. 2010). En premier lieu, pour chaque branche de l'arbre, la longueur est divisée par la somme des abondances des deux espèces liées par la branche (Eq. 11).

$$(11) \quad EW_l = \frac{dist(i,j)}{w_i + w_j}$$

Où *EW* est l'équitabilité pondérée, *dist(i,j)* la distance euclidienne entre l'espèce *i* et *j* (impliquées dans la branche l), w_i et w_j l'abondance relative des espèces *i* et *j*

Pour chacune de ces branches, la valeur EW_l est divisée par la somme des valeurs EW pour l'arbre afin d'obtenir l'équitabilité pondérée partielle (PEW ; Eq. 12).

$$(12) \quad PEW_l = \frac{EW_l}{\sum_{l=1}^{S-1} EW_l}$$

Si la distribution d'abondance est parfaitement homogène le long de l'arbre, tous les EW_l seront égaux et toutes les valeurs du PEW_l seront égales à $1/S\text{-}1$ (Villéger et al. 2008).

L'indice d'équitabilité fonctionnelle est donc calculé suivant l'équation 13.

$$(13) \quad FEve = \frac{\sum_{l=1}^{S-1} min(PEW_l \frac{1}{S-1}) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$$

Spécialisation fonctionnelle

Le degré de spécialisation (Spe) d'une espèce peut être défini comme la distance euclidienne de cette espèce au centroïde de l'espace fonctionnel lorsque toutes les espèces de l'assemblage sont représentées dans un espace fonctionnel en fonction de leur valeur pour chacun des traits étudiés. Ainsi, les espèces dites « généralistes » se trouvent au centre de l'espace fonctionnel et les espèces « spécialistes » en périphérie (Mouillot et al. 2013a). L'indice de spécialisation fonctionnelle (Fspe ; Eq. 14), calculé à partir du degré de spécialisation de chaque espèce, varie entre 0 et 1 en fonction du nombre d'espèces spécialistes présentes dans l'écosystème considéré.

$$(14) \quad Fspe = \frac{\sum_{i=1} Abrel_i Spe_i}{Spe_{max}}$$

Où $Abrel_i$ est l'abondance relative de l'espèce *i*, Spe_i le degré de spécialisation de l'espèce *i* et Spe_{max}, le degré de spécialisation maximale

5.3. Indices de sensibilité fonctionnelle

Les indices de sensibilité fonctionnelle ont été conçus pour détecter des impacts particuliers sur les communautés. Contrairement aux indices de diversité fonctionnelle pour lesquels chaque modalité au sein d'un même trait se voit attribuer un poids égal, la notation semi-quantitative des traits indique la sensibilité potentielle de chaque espèce à une pression donnée. Les indices de sensibilité fonctionnelle intègrent donc cette notation dans leur calcul. Cinq indices de ce type, pouvant-être utilisés dans le cadre du suivi de l'impact du chalutage sur les communautés benthiques ont été utilisés dans ce travail. Seuls trois d'entre eux ont été spécifiquement développés pour détecter l'impact du chalutage (TDI, mTDI, pTDI).

Indice AMBI

L'indice AMBI a été développé pour caractériser la réponse des communautés benthiques des substrats mous aux perturbations naturelles ou anthropogéniques, en particulier l'eutrophisation, dans les environnements côtiers (Borja et al. 2000). Bien que cet indice ne soit pas approprié pour étudier l'effet des pressions physiques, car il a été construit pour traiter principalement de l'effet de l'enrichissement organique sur les communautés benthiques, il a été testé dans cette étude en raison de son utilisation régulière dans les études de la faune benthique, en particulier dans le cadre de la directive-cadre sur l'eau (van Hoey et al. 2015). Dans cette méthode, la macrofaune benthique est classée en cinq groupes écologiques de polluo-sensibilité (Table 11).

Table 11: Groupes écologiques de polluo-sensibilité (d'après Hily, 1984)

Groupes	Type d'espèces	Caractéristiques	Groupes trophiques
I	Sensibles à une hypertrophisation	Largement dominantes en conditions normales Disparaissent les premières lors de l'enrichissement du milieu Dernières à se réinstaller	Suspensivores, carnivores sélectifs et quelques déposivores tubicoles de subsurface
II	Indifférentes à une hypertrophisation	Espèces peu influencées par une augmentation de la quantité de MO	Carnivores et nécrophages peu sélectifs
III	Tolérantes à une hypertrophisation	Naturellement présentes dans les vases mais, leur prolifération étant stimulée par l'enrichissement du milieu, elles sont le signe d'un déséquilibre du système	Déposivores tubicoles de surface profitant du film superficiel chargé de MO
IV	Opportunistes de second ordre	Cycle de vie court (souvent <1 an) proliférant dans les sédiments réduits	Déposivores de subsurface
V	Opportunistes de premier ordre	Prolifèrent dans les sédiments réduits sur l'ensemble de leur épaisseur jusqu'à la surface	Déposivores

La proportion de chaque groupe écologique présent (GI à GV) est ensuite pondérée par le poids de sa contribution dans la représentation du niveau de perturbation (Eq. 15).

$$(15) \quad AMBI = \{(0 \times \%GI) + (1.5 \times \%GII) + (3 \times \%GIII) + (4.5 \times \%GIV) + (6 \times \%GV)\}/100$$

Où $\%G_i$ est l'abondance relative du groupe *i* dans l'échantillon

Cet indice varie entre 0 (lorsque la zone considérée est en bon état écologique) et 7 (lorsque la zone est azoïque et donc en très mauvais état écologique).

Trawling Disturbance Impact

L'indice « Trawling Disturbance Impact" (TDI ; de Juan and Demestre 2012) est basé sur l'utilisation du score de sensibilité des espèces (SI) défini précédemment dans ce chapitre. Ainsi, les espèces sont réparties en cinq groupes suivant leur SI (Table 12).

Table 12: Groupes de sensibilité au chalutage et gamme de score correspondante (d'après de Juan and Demestre, 2012)

Groupes	Scores (SI)	Vulnérabilité au chalutage	Organismes
1	0 - 4	Très faible vulnérabilité, voire effet bénéfique	Petits crustacés, Paguridae, gastéropodes
2	5 - 7	Faible vulnérabilité	Bivalves fouisseurs, étoiles de mer, crabes nageurs
3	8 - 10	Vulnérabilité modérée	Petites ascidies, poissons, grands bivalves
4	11 - 13	Forte vulnérabilité	Bryozoaires, éponges, grandes ascidies
5	14 - 15	Très forte vulnérabilité	Gorgones et grandes éponges

Le TDI (Eq. 16) est calculé avec l'abondance (ou la biomasse) de chacun des groupes (G1 à G5) par rapport à l'abondance (ou la biomasse totale).

$$(16)\quad TDI = \frac{Log1 \times Log(G1+1) + Log2 \times Log(G2+1) + Log4 \times Log(G3+1) + Log8 \times Log(G4+1) + Log16 \times Log(G5+1)}{Log(N+1)}$$

Où *G1-G5* sont les abondances (ou la biomasse) de chaque groupe fonctionnel et *N* l'abondance (ou la biomasse) totale de la station échantillonnée

Le TDI modifié

Le TDI modifié (mTDI) proposé par Foveau et al. (2017) est également basé sur l'indice de sensibilité des espèces (Eq. 17). Il varie entre 0 (pas d'espèces vulnérables) et 15 (seules des espèces très vulnérables sont présentes dans la zone).

$$(17)\quad mTDI = \sum_{1}^{N} \frac{B_i}{B_n} \times SI_i$$

Avec B_i l'abondance (ou la biomasse) du taxon i, *Bn* l'abondance (ou la biomasse) totale de la station échantillonnée et SI_i le score de vulnérabilité de l'espèce i

Le TDI partiel

Le TDI partiel (pTDI) a été développé dans le but de détecter de manière plus efficace l'effet du chalutage sur les communautés benthiques, en se concentrant uniquement sur les espèces sensibles (SI>7). Son calcul est basé sur celui du mTDI (Eq. 18).

$$(18) \quad pTDI = \sum_{1}^{N} \frac{B_{ij}}{B_n} \times SI_{ij}$$

Avec B_{ij} l'abondance (ou biomasse) du $i^{ème}$ taxon de la liste j des taxa sensibles, SI_{ij} du $i^{ème}$ taxon de la liste j des taxa sensibles et B_n l'abondance (ou biomasse) totale de la station échantillonnée.

L'indice de vulnérabilité modifié

L'indice de vulnérabilité modifié (mT), basé sur l'indice développé par Certain *et al.* (2015), est un indice généraliste permettant de suivre n'importe quelle pression à condition que des informations sur les traits de sensibilité spécifiques à cette pression soient disponibles.

Pour le calcul de l'indice de vulnérabilité modifié (mT), les scores de toutes les modalités des traits biologiques sont rééchelonnés entre 0,25 (faible sensibilité) et 1 (forte sensibilité). Un sixième trait est utilisé pour le calcul du mT : le statut de protection de chaque espèce (Foveau et al. 2019). Ainsi, un score de 1 est attribué i) aux espèces présentes dans le Golfe du Lion et répertoriées sur la liste des espèces marines vulnérables de la mer Méditerranée (OCEANA 2016) et ii) aux espèces présentes en Manche/Mer du Nord et répertoriées sur la liste OSPAR des espèces et habitats menacés et/ou en déclin (OSPAR 2008). Les six traits sont par la suite séparés entre les facteurs directs et indirects (nommés respectivement facteurs de vulnérabilité et de sensibilité par Certain et al. 2015). Ainsi, les facteurs directs sont des mesures relatives d'éléments contrôlant la probabilité d'être affecté par un type de pression donné, le chalutage dans cette étude. Les facteurs indirects sont, quant à eux, des mesures relatives d'éléments décrivant l'état de conservation des espèces et leur sensibilité indirecte aux perturbations (par exemple, les filtreurs peuvent être perturbés par la remise en suspension des sédiments due au chalutage). Ensuite, pour les deux types de facteurs, une hiérarchie est établie entre les facteurs primaires qui contrôlent directement la sensibilité et les facteurs d'aggravation qui peuvent ne pas être importants en soi, mais qui peuvent aggraver une sensibilité préexistante. La classification des facteurs utilisée dans notre étude est détaillée dans la 13.

Table 13: Facteurs direct et indirect et leur classification hiérarchique

Facteurs	Description	Type de facteur	Hiérarchie
F_1	Position	Direct	Primaire
F_2	Mobilité	Direct	Primaire
F_3	Taille	Direct	Primaire
F_4	Fragilité	Direct	Aggravation
F_5	Mode d'alimentation	Indirect	Primaire
F_6	Statut de protection	Indirect	Primaire

La composante directe de l'indice, t_i, de chaque taxon individuel i, est obtenue en appliquant l'équation (19) avec $a_i = F_{i1} \times F_{i2} \times F_{i3}$, $g_i = F_{i4}$ et $\gamma = 0{,}5$. La composante indirecte de l'indice, s_i, du taxon i est obtenue en appliquant l'équation (19) avec $a_i = (F_{i5} + F_{i6})/2$ et $g_i = 0$.

$$(19) \quad t_i = a_i^{\,1-g_i/(g_i+\gamma)}$$

L'indice de vulnérabilité modifié (mT) est ensuite calculé suivant l'équation 20.

$$(20) \quad mT = -\sum_{i=1}^{N} \frac{Bri}{t_i \times s_i}$$

Avec Bri la biomasse relative (ou l'abondance relative) du taxon i et N le nombre total de taxon (ou le poids des taxa) dans la station échantillonnée.
Cet indice augmente lorsque la sensibilité des assemblages augmente.

L'ensemble des calculs et analyses statistiques de cette étude ont été réalisés avec R version 3.6.3 (R Core Team 2020).

6. Données d'effort de pêche

L'abrasion induite par la pêche aux arts traînants sur les fonds marins, exprimée en ratio de surface abrasée par an ($SAR.y^{-1}$), a été calculée en agrégeant annuellement les trajectoires de pêche et le type d'engin utilisé, selon la méthodologie d'Eigaard et al. (2016). Dans la Manche et le sud de la mer du Nord, la distribution spatiale et temporelle de la pêche de fond a été estimée à partir des données du système de surveillance des navires (VMS) pour les engins traînants (chalutiers à perche, dragueurs et chalutiers à panneaux) sur la période 2009-2017 avec une résolution de 3'x3' (ICES 2019c). Les données, en accès libre, ont été téléchargées en mars 2019 sur le site web d'OSPAR (https://www.ospar.org), où elles sont référencées sous l'intitulé "OSPAR Bottom Fishing Intensity – Surface".

Pour la zone française de la Méditerranée, une approche similaire a été adoptée en utilisant les données VMS disponibles, agrégées mensuellement (entre 2009 et 2017) sur une grille de 1'x1' [durée de pêche en heure par pays, mois, classe de longueur de navire et type d'engin (Jac and Vaz 2018)]. Les variabilités intra-annuelles (uniquement en mer Méditerranée où des données mensuelles sur l'abrasion étaient disponibles) et inter-annuelles de la distribution de l'abrasion sur la période disponible ont été explorées par le biais de corrélations des paires et se sont avérées statistiquement négligeables. Afin de ne pas sous-estimer les impacts passés et de refléter le temps (probablement long) nécessaire au rétablissement des espèces sensibles, une valeur d'abrasion proche de la valeur maximale observée sur la série disponible (90ème percentile) a été utilisée. Ce percentile 90 a été choisi pour filtrer les valeurs les plus extrêmes qui peuvent être liées à des erreurs de mesure ou de calcul. Des cartes représentant le percentile 90 interannuel de l'abrasion ont été réalisées pour chacune des zones étudiées, avec une résolution de 3'x3' en Manche et dans le sud de la mer du Nord et une résolution de 1'x1' en mer Méditerranée (Figure 25).

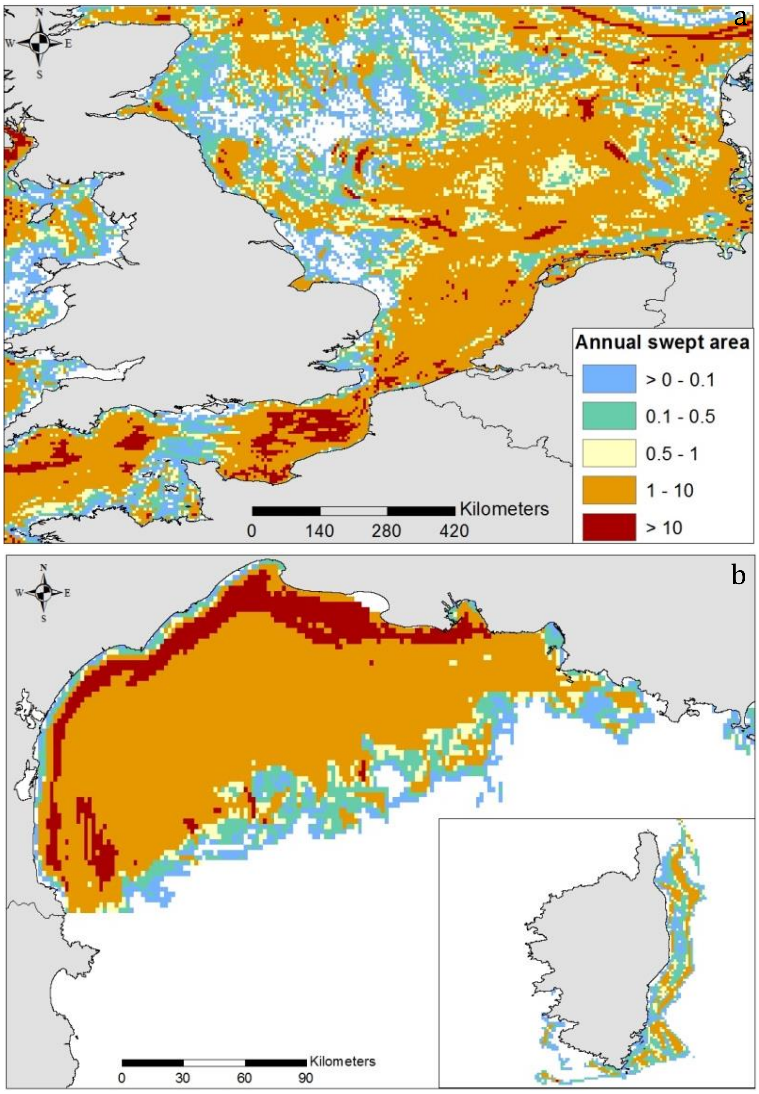


Figure 25: Percentile 90 interannuel de l'abrasion en Manche et dans le sud de la mer du Nord entre 2009 et 2017 (a) et dans le Golfe du Lion entre 2009 et 2017 (b)

Inter Chapitre

Le premier chapitre de cette thèse était une présentation de toutes les méthodes communes aux chapitres suivants. D'autres méthodes, spécifiques à chaque chapitre seront quant à elles développées dans les parties correspondantes.

L'ensemble des plateaux continentaux européens sont soumis à une forte pression de chalutage. Les communautés benthiques présentes sur ces plateaux continentaux peuvent, quant à elles, être spécifiques dans certaines zones en lien avec les conditions environnementales et les habitats locaux. Ainsi, il est nécessaire que les indicateurs permettant de suivre l'impact du chalutage soient suffisamment génériques pour être utilisés dans l'ensemble des eaux européennes malgré les différences de composition et de structure des communautés benthiques.

Dans le deuxième chapitre, la pertinence de l'utilisation de différents indices pouvant être utilisés comme indicateurs de l'impact du chalutage sur les communautés benthiques a été évaluée dans les quatre zones étudiées au cours de cette thèse.

Chapitre II: Generic sensitivity indices to measure the effect of trawling on benthic mega-epifauna

Ce chapitre est basé sur un article sous presse dans la revue *Ecological Indicators.*

Jac C., Desroy N., Certain G., Foveau A., Labrune C., Vaz S. 2020. Detecting adverse effect on seabed integrity. Part 1: Generic sensitivity indices to measure the effect of trawling on benthic mega-epifauna. Ecological Indicators. *In press*. https://doi.org/10.1016/j.ecolind.2020.106631

Résumé de la publication en français

La faune benthique des plateaux continentaux européens est une composante de l'écosystème marin gravement impactée, principalement en raison de l'intense activité de chalutage de fond. L'effet du chalutage dépend de la répartition spatiale et temporelle de l'abrasion, du type d'habitat, de l'intensité des perturbations naturelles et de l'engin de pêche utilisé. Dans ce cadre, il est urgent d'identifier ou de développer des indices susceptibles de mesurer l'effet du chalutage.

Afin de considérer cette question, les prises accessoires de faune benthique, collectées lors des campagnes de chalutage scientifique menées chaque année dans toutes les eaux européennes dans le cadre du programme pluriannuel de collecte de données de la politique commune de la pêche, ont été utilisées.

Les données sur les invertébrés benthiques utilisées dans cette étude ont été recueillies lors de campagnes scientifiques au chalut de fond couvrant la Manche, la mer du Nord et le nord-ouest de la Méditerranée. Les ratios de surface balayée dérivés des données VMS ont été utilisés pour quantifier l'intensité de l'abrasion induite par la pêche sur les fonds marins. Quinze indices ont été étudiés : des mesures de diversité taxonomique, des indices de diversité fonctionnelle et des indices fonctionnels, les deux derniers étant basés sur les caractéristiques de sensibilité des espèces à l'abrasion. Leurs propriétés, telles que leur capacité à détecter l'effet du chalutage, leur comportement statistique ou leur capacité à informer sur la structure des communautés, ont été analysées. Parmi eux, quatre indices spécifiques à la détection de l'effet de la pêche basés sur des caractéristiques biologiques sont apparus comme répondant le mieux à ces exigences : le « Trawling Disturbance Index » (TDI), le modified-Trawling Disturbance Index », le « partial-Trawling Disturbance Index » (pTDI) et le « modified sensitivity index » (mT). Des cartes de la distribution de la sensibilité des fonds marins, mises en avant par chacun de ces quatre indices, ont été produites. Ce travail a mis en évidence la nécessité d'utiliser des indices spécifiques pour surveiller l'effet du chalutage sur les communautés benthiques, mais aussi la nécessité de l'utilisation de différents indices, adaptés, pour effectuer cette surveillance dans l'ensemble des eaux européennes.

1. Introduction

Numerous studies have shown that bottoms trawls damage biogenic structure, disturb seabed sediments and affect the structure and the functioning of the benthic invertebrate community mainly by changing the species composition (Collie et al. 2000; Rumohr and Kujawski 2000; Thrush and Dayton 2002; Hiddink et al. 2006; Rijnsdorp et al. 2018). The differences in species composition between trawled and un-trawled area indicate that each benthic species has different degree of sensitivity (Hiscock et al. 1999; Borja et al. 2003; Foveau et al. 2017) to trawling pressure. Most studies to evaluate the impact of fishing activities on benthic communities are conducted relatively nearshore with restricted spatial coverage (Brind'Amour et al. 2014) and focused mainly on the infauna, with a sampling realized with grabs, boxcorers or dredges (van Loon et al. 2018). Benthic data from scientific bottom trawl surveys carried out in all European waters in the frame of the Common Fishery Policy Data Collection Multiannual Program could be used to study the impact of trawling on the benthic mega-epifauna because 1) they represent the benthic fauna fraction the more directly affected by bottom-contacting fishing and 2) they integrate assemblages' composition over large areas (3-4 km) and are more representative of larger scale habitat structure (Foveau et al. 2017).

Many indices exist and detect differences or changes in the benthic fauna community in relation to anthropogenic pressure, but not all are effective for physical disturbance like trawling impact. Several univariate indices such as species richness, community biomass, Shannon index (Shannon and Weaver 1963), Margalef diversity (Margalef 1958), Pielou evenness (Pielou 1969) and Simpson index (Simpson 1949) have already been tested for assessing effects of trawls on benthic communities (Schratzberger et al. 2002; Svane et al. 2009; Atkinson et al. 2011; van Loon et al. 2018). Despite variable results in the literature, the use of diversity indices can highlight the disruptive effect of fishing on benthic communities (Blanchard et al. 2004). Other indices, specific to the trawling pressure and based on biological traits of benthic species like the Trawl Disturbance Indicator (TDI, de Juan and Demestre 2012) and the vulnerability index (Certain et al. 2015) appear as good candidates to evaluate trawling impact. Species' responses to trawling is believed to be mainly determined by their biological traits (Bremner et al. 2003; de Juan et al. 2009). The selected biological traits (mobility, fragility, position on substrata, average body size and feeding mode), were chosen because they determine individual sensitivity to trawling and they can be easily related to other concepts such as recovery capacity and vulnerability. In the present study, species vulnerability is understood as resulting from both species sensitivity and its exposure level to the disturbance. Finally, modelling approaches were developed to study the effect of trawling on benthic community like the Relative Benthic Status method (RBS; Pitcher et al. 2017), based on longevity or composition of benthic community (Eigaard et al. 2017; Rijnsdorp et al. 2018) or method based on biomass reconstruction (Lambert et al. 2011).

In view of the quantity of existing indices, previous studies have listed different requirements to inform on indicators quality and to classify potential indicators to be used for the assessment of the trawling impact on benthic communities (Queiros et al. 2016; ICES 2017a). Thus indices must: reflect features of ecosystems that are relevant for structure and function (requirement 1: Theoretical basis), be sensitive to changes in trawling (requirement 2: Sensitivity), provides rapid and reliable feedback on the consequences of management (requirement 3: Responsiveness). The quality of sampling method (requirement 5) and the nature and quality of data (requirement 6: Quality of underlying data) must also be taken into account in the indices selection process. Finally, the existence of reference state (requirement 7), the cost of method (requirement 8: Cost effectiveness) and the cross regional applicability (requirement 9) were the three other requirements proposed to evaluate the quality of an indicator.

The aims of this chapter were to (a) list or define indices susceptible to measure the effect of trawling on benthic fauna that can be used in all European waters (b) test different properties of these indices and in particular their ability to relate to trawling intensity and to measure assemblages structures and (c) identify a suitable set of indices to be used for monitoring trawling impact on benthic communities in the frame of the MSFD requirements.

2. Material and methods

2.1. Study areas

See Chapter I for English Channel and Gulf of Lion descriptions

2.2. Biotic indices investigated

Three types of sensitivity indices were investigated: 1) taxonomic diversity metrics; 2) functional diversity indices and 3) functional sensitivity indices specifically constructed to detect impacts on benthic communities. The effect of trawling on the biomass of the community was also studied.

Five common taxonomic diversity indices were calculated: species richness (SR, the total number of taxon), Margalef index, Shannon diversity (H'), Pielou evenness (J') and Simpson index (Λ). The first two focus on species or individuals richness while the others are weighted by abundance or biomass to assess equitability between species (J') or give more or less influence to rare species (H' and Λ). These indices were calculated in R, using the vegan 2.5-2 package (Oksanen et al. 2019) and by using individual biomass.

Functional Richness (FRic, Cornwell et al. 2006; Villeger et al. 2008), Functional Specialization (Fspe; Bellwood et al. 2006, Villeger et al. 2010), Functional Evenness (FEve; Mason et al. 2005) and Functional Divergence (FDiv; Mason et al. 2005) were investigated using the species-traits matrix described earlier. These indices were used because they highlight variation in specific function among benthic communities (Mouillot et al. 2013a).

Functional sensitivity indices are designed to detect particular impacts on communities. In contrast to functional diversity indices for which each trait level is given equal weight, semi-quantitative trait scoring indicates the potential sensitivity of each species to a given pressure. Functional sensitivity indices therefore integrate this scoring in their calculation.

The tested indices were: AZTI Marine Biotic Index (AMBI), Trawling Disturbance Index (TDI), modified TDI (mTDI), partial TDI (pTDI) and the modified vulnerability Index (mT). TDI-derived indices were developed specifically to detect trawling impact, while mT is issued from a general framework allowing to address any pressure as long as specific sensitivity traits were available to detect it.

All of these indices were calculated as described in Chapter 1 and from biomass data.

2.3. Methods of indices evaluation and selection

In order to find which indices were most appropriate to monitor the impact of trawling on benthic communities, five different tests were carried out while distinguishing different surveys and geographic basins. The two first tests ensured that the index reflects the abrasion pressure. Thus, spearman correlation tests (Hollander and Wolfe 1973) were conducted to determine the correlation level between indices and abrasion in each area studied. Similarity, their spatial distribution was also tested with the calculation of an index of difference in spatial pattern (Lee et al., 2010). This indicator varies between 0 (same spatial pattern) and 1 (many differences in the spatial patterns). Three complementary tests were carried out to discriminate the indices having good correlations with abrasion. The percentage of variance of the community structure explained by each index was determined by performing a redundancy analysis (RDA; van den Wollenberg 1977) on the community biomass matrix and using each index in turn as sole constraining factor. The statistical behavior, and more particularly the nature of the distribution, of each index was also studied with the calculation of their skewness and kurtosis (Groeneveld and Meeden 1984) because a normal distribution of the index will facilitate the use of this index for further statistical regression approaches.

In order to simplify the assessment of all indices properties, a qualitative scoring scheme was used. For each study area and property studied, a score was attributed to each index by dividing its test value by the maximum test value obtained for this property in this area. For example, if the maximum value of spearman correlation in the Gulf of Lion was 0.5 for the TDI, the biomass that has a correlation value of 0.25, has a score of 0.25/0.5=0.5. In the particular case of the Lee index which decreases when spatial similarity increases, the minimum test value was divided by higher test values. For skewness and kurtosis tests, when their values were between - 1 and 1, a score of 1 was assigned for that index in the study area, conversely, a score of 0 was assigned if theirs values were outside these bounds. Scores were then summed over areas for each index and as the study considers four areas, the maximal score by index was 4.

A total score was computed summing each index scores over each of the five properties investigated. A ponderation of 2 was applied for the two major properties, spearman correlation test and Lee spatial correlation index, as they were the main focus of the present study. So, the maximal total score per index was 28. Once a total score per index was computed, indices could be ranked according to their performance and those with the highest score were selected.

Spearman correlation between each selected indices was also studied to better understand the differences between them. Selected indices relations to abrasion by zones were illustrated using boxplot over abrasion classes. After log- or arcsin transformation of indices that do not have a normal distribution, each index were locally averaged over time and subjected to a variographic analysis and interpolated using ordinary kriging in R using package geoR 1.7-5.2.1(Ribeiro Jr and Diggle 2018). Kriged estimates were mapped to illustrate the distribution pattern of seabed sensitivity captured through each of the four indices.

3. Results

3.1. Which is the best index to study the impact of trawling in three contrasted areas?

Table 14: Results of spearman correlation tests and spatial correlation index for each index in the four studied areas. GoL = Gulf of Lion. CGFS + CAM = CGFS and CAMANOC surveys * indicates that p<0.05 ; ** indicates that p<0.01; *** indicates that p<0.001 ; ns indicates no significant difference. Grey shading indicates best scores

Indices	Spearman correlation test					Spatial correlation (Lee index)				
	GoL	Corsica	IBTS	CGFS + CAM	Score	GoL	Corsica	IBTS	CGFS + CAM	Score
Community biomass	-0.15**	-0.05	0.001	0.26***	1.28	0.71	0.58	0.76	0.66	2.37
Species richness	0.13*	0.31**	0.10**	0.09**	1.77	0.31	0.44	0.49	0.42	3.82
Margalef index	0.13*	0.32**	0.10**	0.11**	1.86	0.31	0.44	0.49	0.42	3.82
Shannon index	0.24**	0.13	0.01	-0.02	1.10	0.32	0.47	0.52	0.43	3.65
Pielou Index	0.21**	0.07	-0.10**	-0.11**	1.40	0.32	0.48	0.53	0.43	3.62
Simpson index	0.19**	0.15	-0.01	-0.03	1.01	0.32	0.46	0.52	0.42	3.61
FRic	0.19**	0.36**	0.09*	0.15**	2.44	0.38	0.58	0.58	0.56	3.02
FDiv	0.08	-0.01	-0.14*	-0.21**	1.00	0.30	0.54	0.56	0.41	3.55
FEve	0.21**	-0.07	0.01	-0.11**	1.11	0.30	0.56	0.57	0.42	3.50
FSpe	0.14**	0.28*	0.03	0.05	1.41	0.30	0.53	0.54	0.41	3.60
AMBI	-0.26**	0.36**	0.003	-0.08**	1.99	0.42	0.57	0.58	0.52	3.02
TDI	-0.33**	0.07	-0.35***	-0.34***	3.08	0.32	0.56	0.57	0.47	3.34
mTDI	-0.31**	-0.08	-0.28**	-0.32***	2.80	0.31	0.52	0.53	0.42	3.59
pTDI	-0.26**	-0.09	-0.35***	-0.37***	3.01	0.30	0.72	0.72	0.61	2.87
mT	-0.34**	-0.01	-0.22**	-0.30***	2.47	0.29	0.50	0.50	0.37	3.86

Results of the evaluation of the indices relationships to abrasion both in terms of ranked values or spatial pattern are presented in table 14 for each studied area. Over all studied areas, the four indices which present the highest spearman correlation values (higher total score) are the TDI, the mTDI, the pTDI and the mT. For other indices, the Spearman correlation was often not significant, in particular in the North Sea (IBTS data) or even counter-intuitively reversed in Corsica. For the Lee index, all indices showed fairly similar results excepted species richness, Margalef index and mT for which values were slightly better. The spatial correlation between indices and abrasion is lower in Corsica and in the North Sea (IBTS data) than in other areas.

The measure of percentage of variance of the community structure explained by each index and skewness and kurtosis tests are presented in table 15. Almost all indices had a close to normal distribution in at least 3 of the 4 studied areas; only community biomass, FRic and FSpe did not. The percentage of community structure variance explained by each index is very variable from one area to the next. Apart from FRic and FEve, all indices based on biological traits better explained the community structure (higher score).

The total scores were computed by summing all scores for each type of test (Table 14 & 15). According to this result, the four better performing indices were TDI, mTDI, pTDI, and mT.

Table 15: Results of RDA and normality tests for each index in the four studied areas.
GoL = Gulf of Lion; CGFS + CAM = CGFS and CAMANOC surveys. Grey shading indicates best scores

Indices	Percentage of variance of the community structure explained					Skewness					Kurtosis					Total score
	GoL	Corsica	IBTS	CGFS + CAM	Score	GoL	Corsica	IBTS	CGFS + CAM	Score	GoL	Corsica	IBTS	CGFS + CAM	Score	
Community biomass	4.8	19.8	0.4	0.9	1.17	5	1.8	17.07	11.45	0	31.24	2.60	365.71	166.16	0	8.47
Species richness	1.3	14.5	2.9	0.9	1.13	0.48	0.91	0.89	0.73	4	-0.19	-0.02	0.64	-0.45	4	20.31
Margalef index	1.4	14.5	2.9	0.9	1.13	0.48	0.91	0.89	0.72	4	-0.19	-0.02	0.64	0.66	4	20.49
Shannon index	12.0	15.7	2.0	1.5	1.94	-0.75	0.03	-0.19	-0.09	4	-0.27	-0.72	-0.64	-0.45	4	19.44
Pielou Index	13.0	17.5	1.0	1.2	1.88	-0.95	-0.41	-0.25	-0.37	4	0.046	-0.73	-0.4	-0.33	4	20.28
Simpson index	11.0	16.2	1.4	1.4	1.79	-1.47	-0.54	-0.74	-0.78	3	1.39	-0.60	-0.36	-0.21	3	17.03
FRic	1.8	5.8	1.4	0.6	0.63	1.33	2.06	1.26	4.34	0	2.43	3.57	-0.41	32.40	1	12.55
FDiv	7.3	20.8	0.7	5.6	2.17	-0.43	-0.61	1.26	-0.27	3	-0.50	-0.16	-0.41	-0.65	4	18.27
FEve	2.4	0.7	0.4	0.6	0.35	0.14	-0.076	2.10	0.25	3	0.08	-0.40	2.43	0.23	3	15.57
FSpe	8.1	32.7	3.4	6.3	3.12	0.11	-0.61	2.28	1.53	2	-0.39	-0.75	8.73	1.85	2	17.14
AMBI	6.1	17.2	6.2	5.5	2.82	0.44	0.65	0.76	0.95	4	-0.46	-0.48	0.20	1.39	3	19.84
TDI	8.1	16.1	6.4	4.4	2.79	-0.14	-0.34	1.19	0.73	3	0.10	-0.77	0.35	-0.25	4	22.63
mTDI	11.9	13.5	6.1	4.2	2.93	-0.10	-0.32	1.56	0.96	3	-0.75	-0.40	1.75	0.68	3	21.68
pTDI	7.8	12.5	2.5	6.5	2.37	-0.05	-0.44	1.10	0.67	3	-0.55	0.36	0.04	-0.75	4	21.13
mT	13.0	8.5	5.4	2.7	2.53	0.32	-0.35	-0.40	1.45	3	-0.32	0.19	0.11	5.63	3	21.19

All TDI derived indices were very correlated by construction as were species richness to Margalef indices or Shannon, Pielou and Simpson indices (Appendix A). Moreover, since the strength of the relationship to abrasion is given precedence over the other investigated properties, it is only natural that the best performing indices end up mechanically correlated with each other (and with abrasion).

3.2. Indices' behavior along abrasion gradient

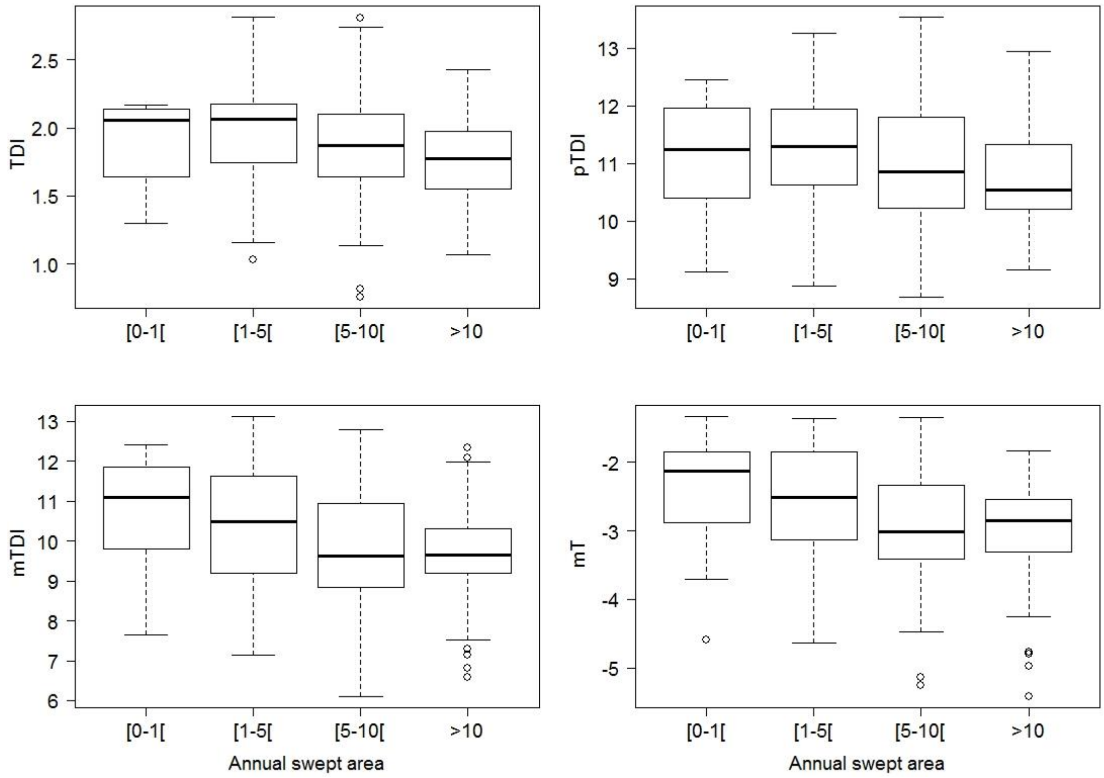


Figure 26: Values of the four selected indices by class of abrasion in the Gulf of Lion

For all indices and studied areas, overall values of indices appeared to decrease with abrasion (Figure 26, 27, 28 & 29) which was already revealed by significantly negative (although weak) correlation between the indices and abrasion (Table 14). For the majority of indices, variations of index values in abrasion class were very high as for example for the pTDI (in CGFS and CAMANOC surveys; Figure 29) where the index varies between 0.07 and 15 for an abrasion below 1 and between 0.006 and 14 for an abrasion higher than 10.

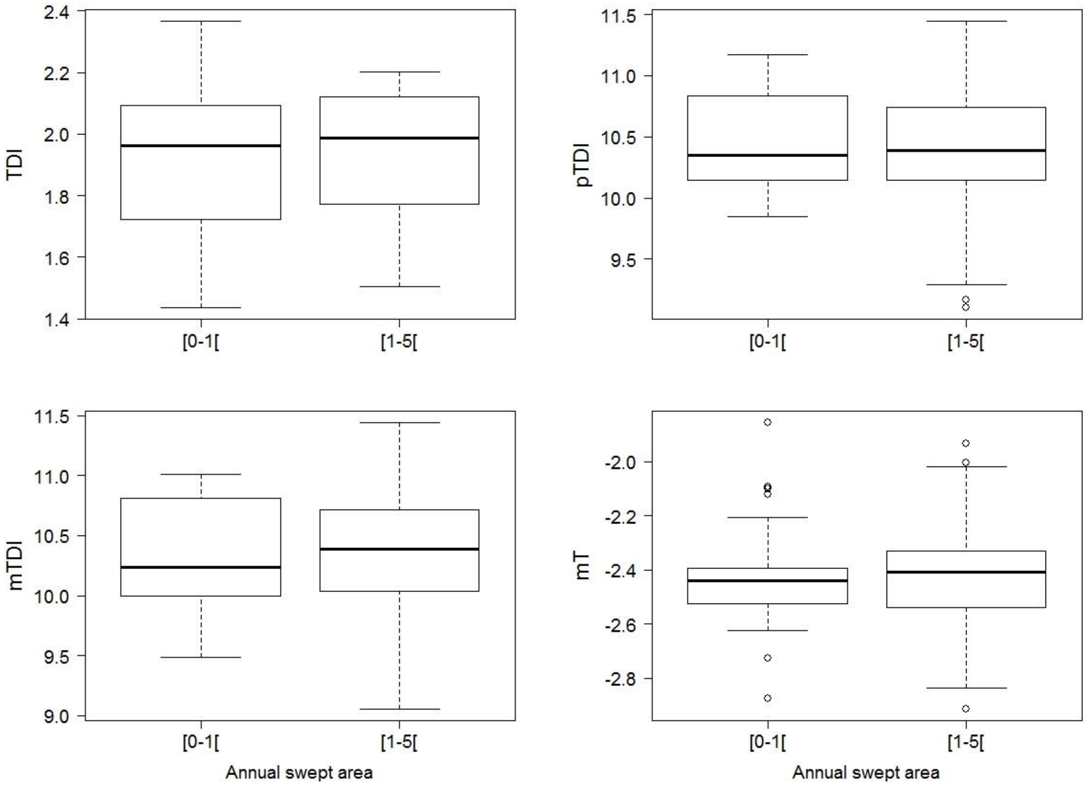


Figure 27: Values of the four selected indices by class of abrasion in Corsica

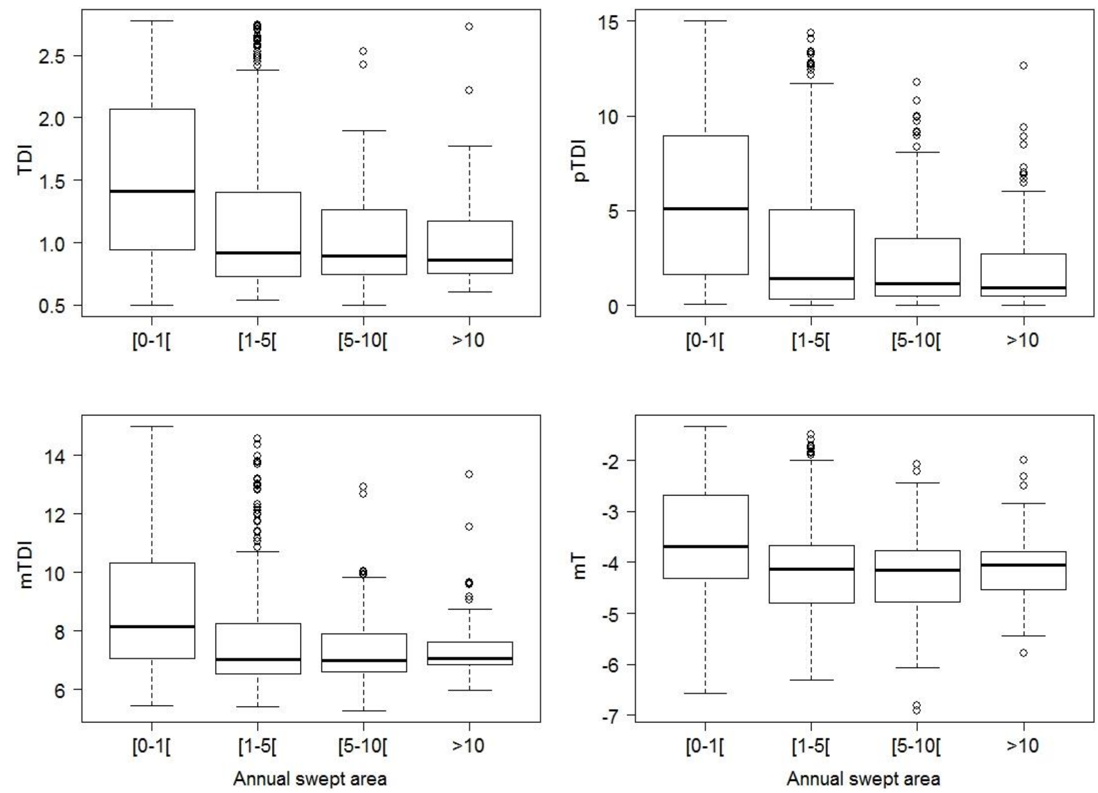


Figure 28: Values of the four selected indices by class of abrasion for the IBTS data (eastern English Channel and southern North Sea)

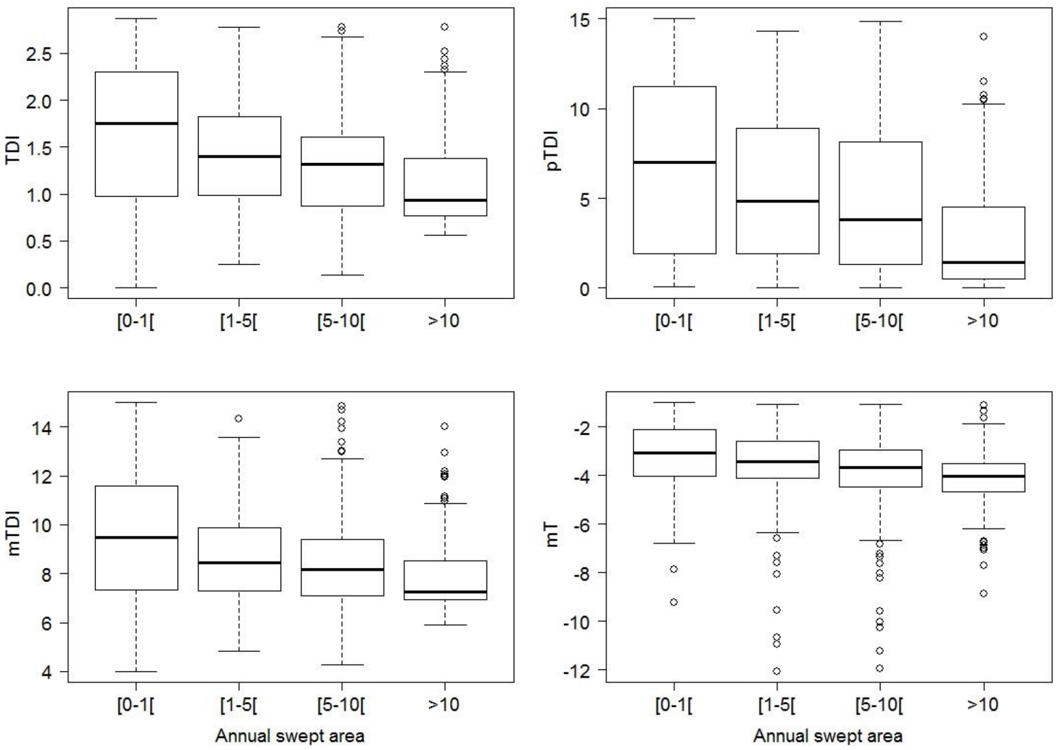


Figure 29: Values of the four selected indices by class of abrasion for the CGFS and CAMANOC data (English Channel)

3.3. Spatial distribution of the trawling sensitivity of benthic communities

The distribution patterns of the trawling sensitivity of the benthic communities, in the Gulf of Lion, were almost the same for the four indices (Figure 30). Thus, the degree of sensitivity of the communities was positively correlated with the distance to the coast, with communities that were not very sensitive to trawling in the coastal zone (lower values of the indices) and communities that were much more sensitive offshore (higher values of the indices).

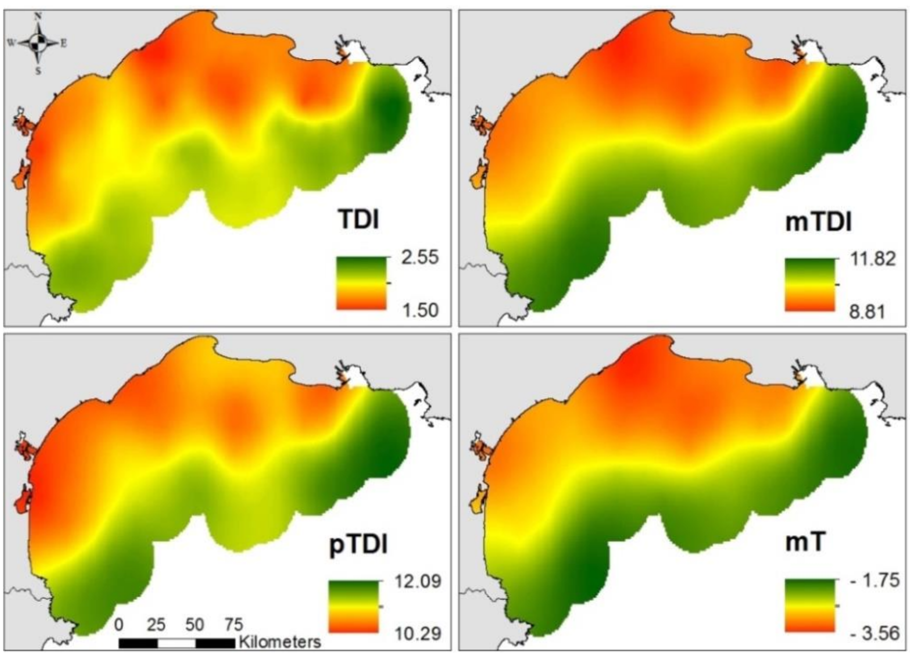


Figure 30: Distribution pattern of benthic sensitivity to trawling in the Gulf of Lion (MEDITS data)

In the North Sea, despite small differences, distribution patterns of the trawling sensitivity of benthic communities were substantially the same for the four indices (Figure 31). Benthic ecosystems of the South and the East part of the North Sea appeared particularly impacted by the trawling and so not very sensitive (lower values of the indices). Values of indices were high only in a small area in the West of the North Sea making it particularly vulnerable to trawling, with the presence of species considered to be sensitive to trawling.

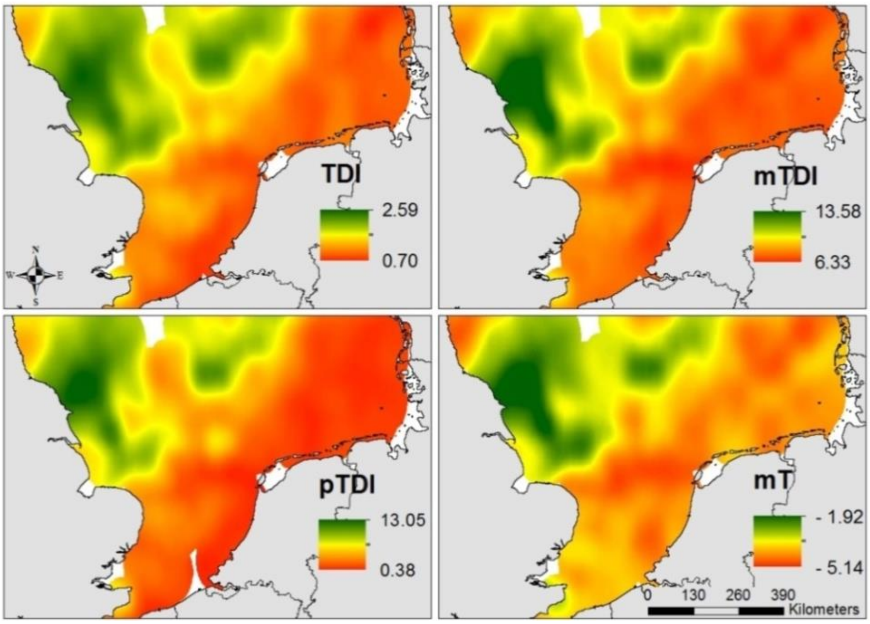


Figure 31: Distribution pattern of benthic sensitivity to trawling in the southern North Sea (IBTS data)

Concerning the English Channel, three of the four indices (TDI, mTDI, mT) had low values in the Eastern Channel and the northern part of the Western Channel (Figure 32), reflecting areas already heavily impacted by trawling. Except around Plymouth, the Western English Channel looks particularly sensitive to trawling, as highlighted by the pTDI results.

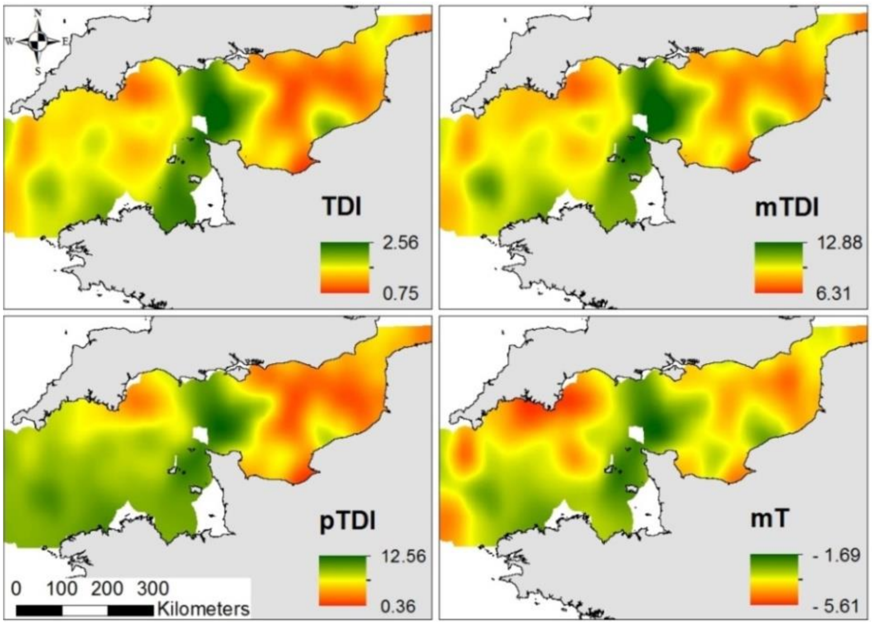


Figure 32: Distribution pattern of benthic sensitivity to trawling in the English Channel (CGFS and CAMANOC data)

4. Discussion

Most of the studies focusing on benthic communities use grab or box-corer for sampling (Engel and Kvitek 1998; Kenchington et al. 2001; Atkinson et al. 2011; Rijnsdorp et al. 2018; van Loon et al. 2018). These methods only sample a small area at a time (generally about between 0.1 and 0.5 m^2) whereas trawling methods sample large-scale benthic communities. Grab and core methods mainly collected infauna species (Rumohr 1999) and do not effectively sample the larger epifauna and megafauna component of the seabed (Bergman and Van Santbrink 2000). Therefore, biomass and abundance of species such as sponges, hydrozoans, sea stars or crabs are underestimated despite their strong sensitivity to trawling (de Juan and Demestre 2012). Although it is often considered a non-quantitative method (Eleftheriou 2013), bottom trawls may be appropriate to investigate the effect of trawling. This method allows capturing the benthic fauna fraction which is the most directly affected by bottom fishing : the epifauna (Rumohr 1999; Reiss et al. 2006; Foveau et al. 2017). The use of this sampling technique also allows the observation of benthic assemblages over large areas, in agreement with the large-scale distribution of abrasion. Benthic invertebrates forming a significant proportion of by-catch in the trawl fisheries (Reiss et al. 2006; Foveau et al. 2017), scientific bottom trawling surveys carried out yearly in different countries for the purpose of the Common Fishery Policy may be a useful and cost-effective way to obtain a large amount of good quality data over a wide spatial extent and potentially long temporal range.

As numerous studies on trawling impact showed that organisms’ responses to disturbance depend on their biological traits (Thrush et al. 1998; Blanchard et al. 2004; de Juan et al. 2007; Kenchington et al. 2007; Strain et al. 2012), the selection of traits used in the calculation of functional indices is an important step in the process. The utilization, in our study, of a set of biological traits known to respond positively or negatively to trawling disturbances (Thrush et al. 1998; de Juan et al. 2007; Gray and Elliott 2009), allows to better monitor the effect of trawling on benthic ecosystems. For example, the feeding mode of the species induces different responses to trawling, since burrowing scavengers may benefit from trawling disturbance or discards, whereas filter feeders can be highly affected by increased sediment resuspension (de Juan et al. 2007). Other traits could reflect the resilience of species and might be used as indicators of trawling disturbance such as the species longevity (Rijnsdorp et al. 2018), the reproduction mode or the dispersion mechanisms (Bremner et al. 2006). However, the lack of information about these biological traits for a large number of species did not allow us to include them in indices calculations. Moreover, some of these traits, such as longevity, are probably environment specific and may need to be locally adapted which further complicate their use for generic index calculation.

One of the aims of this study was to select a generic index capable of detecting the effect of trawling on benthic communities in all European waters. The combination of five selection properties allowed us to select four indices (TDI, pTDI, mTDI and mT index) responding to the fishing pressure. These four indices are highly correlated at large scale since they are based on the same set of biological traits and were chosen for their significant correlation to abrasion. However, the lower correlations between mT and the TDI derived indices indicate that their mathematical formulation still matters. As a result, their usefulness may be zone-dependent since the correlation between mT and abrasion seems stronger than that of TDI derivatives in the Gulf of Lion and vice versa in the English Channel/southern North Sea. Therefore, although closely related, it seems difficult to select only one of these for impact assessment and their behavior at habitat scale needs to be investigated. Despite their apparently significant relationship to abrasion in most studied areas (except in Corsica), large observation variability resulted in weak correlation values. This very large variability probably resulted from the fact that benthic habitats were not differentiated in this study, and that trawling does not have the same impact on all seabed habitats, particularly because bottom-trawl catchability depends on the nature of the bottom (Reiss et al. 2006). Tracking trawl effects on benthic communities, for example, should be done at a finer resolution (*e.g.* EUNIS Level 4) choosing which index is the most sensitive in the studied area (in application to the precautionary approach).

As for the other indices tested, despite their potential relevance to other aspects, they do not appear to be relevant for monitoring the effect of trawling on benthic communities. The fact that all retained indices were based on biological traits indicated that taxonomic indices (Shannon, Pielou…) or community biomass were weakly relevant to monitor the effect of trawling. Even if many anterior studies found a negative effect of trawling on the biomass of benthic community (Collie et al. 2000b; Jennings et al. 2001b; Queirós et al. 2006), it does not always relate linearly to trawling pressure, especially with polychaetes (Hiddink et al. 2011). In the present study, the absence of significant negative correlation seemed consistent across most of the studied areas. The biomass of the community is known to be influenced by the nature of sediments and particularly silt and clay contents (Queirós et al. 2006; Hinz et al. 2009). It is therefore possible that, due to the lack of differentiation between habitats, the variance of biomass is too high at basin scale to detect anything about the effect of trawling. Such responsiveness sensitivity may hinder the operational use of this measure.

Concerning diversity indices, the great disparity of indices' responses to the effect of fishing between studied areas is also consistent with existing literature. Previous studies have shown a negative influence of fishing on Shannon, Pielou and Simpson index (Smith et al. 2000; Shirmohammadi et al. 2012). On the opposite, others could not detect any significant effect (Svane et al. 2009; Atkinson et al. 2011), or even evidenced a positive effect of abrasion on the Simpson index (Shirmohammadi et al. 2012) and on the Pielou index for a few months of the year in the Mediterranean Sea (Smith et al. 2000). Heterogeneity in these results highlights that the effect of trawling on species number or biomass is unclear, but rather appears to modify functional components of benthic communities, with for example a decrease of epifaunal sedentary suspension feeders in trawled areas (de Juan et al. 2007). Except for the FRic, the functional indices calculated in this study did not appear to respond to trawling activities in all studied areas. The positive correlation between FEve and FSpe and abrasion in the Mediterranean suggests that trawling leads to an increase and dominance (in terms of biomass) of specialized species. In the opposite, the negative correlation between FDiv and FEve and the abrasion in the southern North Sea suggests that increased trawling induced a dominance of functionally close generalist species (close to center of gravity of functional space). Functional indices are, in essence, sensitive to the trait composition of the benthic community which may result in change in the index response to trawling depending on the trait composition of each area. Such information is valuable, from an ecological point of view, to anticipate trawl-induced change in a given community, but does not satisfy the requirements of a general index of sensibility, as its interpretation remains strongly context-dependent. Concerning the functional richness (FRic), the positive correlation with the abrasion in all studied areas suggests that trawling led to an increase of the functional diversity of the benthic community by attracting for example different scavengers (Collie et al. 2000b; Thrush and Dayton 2002). However, regarding its poor scores obtained for other properties, this index is also a poor candidate to evaluate the effect of trawling on benthic communities.

Based on biological traits known to be influenced by trawling, the four retained indices (TDI, mTDI, pTDI and mT index) were specific to the trawling effect. This suggests that it seems illusory to find a generic indicator able to respond to all the pressures experienced by benthic habitats and, therefore, that the study of the ecological status of seabed must rely on several indicators specific to each type of impact. In addition, the different effectiveness of indices between study areas suggests the systematic use of a set of indices, the combination of which should provide information on the ecological status of the area in terms of fishing pressure.

Unlike the results obtained in the other three zones, very low correlations are observed between tested indices and trawling effort in Corsica. The lack of significant relationship between the majority of the indices and the abrasion may be explained by the limited number of data available in this area. Furthermore, abrasion being relatively low over the whole of Corsica (Jac and Vaz 2018), the benthic communities were sampled on a low abrasion gradient (less than 5 vs. 0.08 to 29.15 in the Gulf of Lion). It seemed unlikely that there would be a change in indices values over such a reduced abrasion gradient, especially since the small number of samples would tend to exacerbate the natural variability at the same abrasion intensity. Absence of relation between selected indices and low abrasion range might indicate that the effect of trawling on the benthic community is undetectable at these levels. Thus, relation between indices and trawling effort appeared not to be linear over the entire abrasion range and the likely presence of thresholds seems to be emerging.

Sensitivity indices proposed here to satisfactorily assess the effect of trawling meet many of the requirements suggested in previous studies (Queirós et al. 2016; ICES 2017b) :

1. They are based on biological traits known to be affected by trawling. This agrees with the first requirement (Theoretical basis), which directly reflects the changes that trawling induces on the community, through the change in the proportion of each trait in the community.
2. This makes these indices particularly sensitive to the trawling pressure (requirement 2: sensitivity).
3. The use of yearly scientific trawl surveys' data allows us to respond positively to several criteria such as data quality (requirement 6) and the repeatability of the method (requirement 5).

4. The four selected indices present consistent and significant changes as a result of a pressure change (third requirement: responsiveness), since the resilience of the species after reducing or removing abrasion depend on their biological characteristics. Lambert et al (2014) showed that in high current areas, species with low mobility would have a faster recovery time than other species. Considered as a very important requirement for the species' sensitivity to trawling, the increase of low-mobility species biomass, due to a reduction of abrasion, leads to an increase in the value of indices.

5. The acquisition of data is done with limited costs (requirement 8) since the surveys already exist and the identification and the measurements (weighing and counting) are mostly carried out on board.

6. Although it is often very difficult to distinguish the effect of a physical pressure, such as trawling, from the effect of the environment on benthic communities, these indicators can be considered as specific (requirement 4: specificity) as they use known biological traits providing specific information on the species' sensitivity to trawling.

7. The use of four contrasted study areas in this work allows us to conclude positively on the cross regional applicability (requirement 9).

8. Finally, even if this is not mentioned in the requirements, the fact that the four indices are negatively correlated to abrasion makes them easily interpretable.

Inter Chapitre

Le deuxième chapitre de cette thèse a permis de confirmer l'intérêt des données de faune benthique collectées dans le cadre des campagnes de chalutage scientifique menées chaque année dans les eaux européennes pour suivre l'impact des arts traînants sur les communautés benthiques. Il a permis d'identifier quatre indices, basés sur la sensibilité des espèces, susceptibles d'être utilisés comme indicateurs de la perturbation liée aux arts traînants.

L'ensemble de la faune benthique n'étant pas affectée de la même manière par le chalutage, la méthode d'échantillonnage peut grandement influer sur la capacité des indices à détecter l'impact du chalutage. Ainsi, il est nécessaire d'évaluer quelle méthode d'échantillonnage est la plus pertinente pour suivre l'impact des arts traînants sur les communautés benthiques.

Dans le troisième chapitre, les caractéristiques des communautés benthiques, estimées à partir d'un chalut scientifique et d'une drague, en Manche et dans le Golfe du Lion, ont été comparées d'un point de vue taxonomique mais également fonctionnel. La pertinence de l'utilisation de ces deux méthodes d'échantillonnage dans le cadre d'un suivi de l'impact des arts traînants sur les communautés benthiques a été évaluée en comparant la capacité de détection de plusieurs indices.

Chapitre III: Dredge sampling can be used to monitor the effect of trawling on benthic communities?

Jac C., Vaz S., Foveau A., Desroy N. Assessing the impact of trawling on benthic macrofauna: comparative study of dredge sampling versus scientific trawling. *In preparation.*

Résumé du chapitre en français

La faune benthique est particulièrement impactée par la pression exercée par les arts traînants sur les plateaux continentaux européens. Cependant, l'ensemble de la communauté benthique ne semble pas être affectée de la même manière par cette pression, l'impact étant plus important sur les espèces de l'épifaune. A ce jour, la plupart des études sur les communautés benthiques ont été menées à petite échelle en ciblant principalement l'endofaune avec des échantillonnages réalisés à l'aide de bennes ou de carottiers. Dans ce cadre, l'utilisation des données benthiques provenant des relevés scientifiques au chalut de fond effectués dans toutes les eaux européennes dans le cadre du programme pluriannuel de collecte de données de la politique commune de la pêche semble être une bonne alternative pour étudier l'impact des activités de pêche à grande échelle. Toutefois, le déploiement d'un chalut scientifique peut-être contraignant et la capturabilité dépend fortement de la nature du fond marin et des adaptations des engins qui en résultent. En raison de sa capacité à échantillonner une grande diversité d'habitat benthique et sa facilité de déploiement, la drague Rallier du Baty pourrait être une bonne alternative pour surveiller l'impact du chalutage sur les communautés benthiques. Une étude des différences taxonomiques et fonctionnelles entre les communautés échantillonnées au moyen du chalut et de cette drague a été réalisée. L'influence de l'abrasion et du type de sédiment sur neuf indices pouvant être utilisés pour suivre l'effet du chalutage sur les communautés benthiques et calculés à l'aide des données de drague, a été étudiée dans deux zones d'étude distinctes. Parmi ces indices, seul l'un d'entre eux était significativement influencé par l'abrasion dans les deux zones : la richesse spécifique. L'efficacité de ces indices pour surveiller l'effet du chalutage a été évaluée et comparée entre les données issues du chalutage scientifique et de la drague. Ce travail a mis en évidence que l'échantillonnage à l'aide de la drague ne semble pas pertinent pour surveiller l'effet du chalutage sur les communautés benthiques dans les eaux européennes.

1. Introduction

Many studies on benthic fauna are conducted with restricted spatial coverage (Brind'Amour et al. 2014) and focused mainly on infauna (Eleftheriou 2013) using grabs and boxcorers as sampling methods (Queirós et al. 2006; van Denderen et al. 2015; van Loon et al. 2018). In addition to capturing only a portion of the benthic fauna, these methods of sampling, very well adapted to soft sediments, are more difficult to deploy over coarser sediments where penetration is more limited (Eleftheriou 2013). In addition, the sampling of benthic fauna using grabs or boxcorer does not seem very relevant to monitor the impact of trawling or dredging on benthic communities, which have a large-scale impact on a wide variety of habitats, including mixed or coarse sediments (Eigaard et al. 2017). Several studies have also indicated that epifaunal species are particularly affected by this type of fishing because these devices are designed specifically to physically disturb surface sediments (Kaiser et al. 1996; Thrush et al. 1998; Collie et al. 2000a; Hinz et al. 2011).

Although providing relative rather than absolute abundance data (Jennings et al. 2001a), fishing dredges and/or trawls are regularly used to study the impact of trawling on benthic communities (Jennings et al. 2001b; Duplisea et al. 2002; Svane et al. 2009). The use of these two types of gears presents several interests, such as the fact that they can sample relatively large areas (over areas of m^2 to 10s m^2) of the sea bottom (Jennings et al. 2001a), but also that they can capture some species of benthic epifauna (Muntadas et al. 2016) by penetrating in the few first centimeters of the sediment. As such, trawling appears to be a particularly relevant sampling method for assessing the impact of towed fishing gears on benthic communities throughout European waters. The use of benthic data from scientific bottom trawl surveys carried out in all European waters in the frame of the Common Fishery Policy Data Collection Multiannual Program allowed to study the impact of fishing activities on large scale (Foveau et al. 2017; Chapter II).

To optimize the collection of benthic fauna (*i.e.* epifauna and infauna), the majority of studies using trawl or dredge sampling methods also use other techniques such as grab sampling. Indeed, dredging or trawling was generally used to collect epifauna while grabs were used to sample infauna (de Juan et al. 2007; Atkinson et al. 2011; Muntadas et al. 2016) and in some studies the combination of these sampling techniques allowed both megafauna (trawl and dredges samples) and macrofauna (grabs samples) to be collected (Bergman and Van Santbrink 2000; Smith et al. 2000). Many types of scientific dredges have been developed to sample different habitat types and thus collect a wide variety of species (Eleftheriou 2013). For example, Clarke (1972) used a dredge to sample in mixed boulder and mud sediments while Bergman and van Santbrink (1994) have developed a dredge that allows a satisfactory quantitative collection of the larger-sized epifauna and infauna of low abundance on soft sediments. The Rallier du Baty anchor dredge seems particularly adapted to sample a wide variety of benthic habitats (Gentil 1976).

As such, sampling by scientific dredges could be a good alternative or at least complement to trawling method because 1) data are more representative of the diversity of benthic community (dredge collecting both infaunal and epifaunal species belonging to mega and macrofauna), and 2) the analysis of samples at the laboratory allows to limit identification errors and increase the level of taxonomic identification which greatly increase the amount and usefulness of information contained in the resulting data. When dredge sampling is used, the quality of the data is highly dependent on the grain size of the seafloor: on rather coarse sediments, the dredge will tend to bounce, whereas it will tend to silt up very quickly in soft sediments. In these two cases, the dredge will only partially collect the benthic macrofauna present in the area. However, these limits are similar to those existing for trawl sampling, which is nonetheless classically used to generate abundance or biomass data, and allows indicators of ecological status or pressure to be calculated for the purpose of fishery management.

To monitor trawling impact on benthic communities, it is necessary to observe changes in the benthic community. Different types of indices can be used (Chapter I & II; Jac et al. 2020) to study the evolution of benthic communities along the pressure intensity gradient. The work presented in Chapter 2 suggested that functional sensitivity indices are better suited to monitor the effect of trawling on benthic megafauna.

The aims of this study were to (a) list or determine indices susceptible to detect the effect of trawling on benthic fauna with scientific dredge sampling method (b) compare the capacity of two sampling methods (scientific dredge and trawl) to monitor the impact of fishing on benthic communities' at large scale in different habitat.

2. Methods

2.1. Study areas

See Chapter I for English Channel and Gulf of Lion descriptions

2.2. Biological data

2.2.1. Surveys

Two sampling surveys with both trawl and scientific dredge were carried out in the Gulf of Lion and in the eastern part of the English Channel.

In the Gulf of Lion, 10 stations (Figure 33a) were sampled with these two gears in September 2018 during the EPIBENGOL survey (Vaz 2018a). The trawl used was the same as the one used during the MEDITS surveys (Chapter I) and the dredge used was a Rallier du Baty anchor dredge of 0.65 m diameter designed to penetrate all types of soft bottoms from mud to cobbles (Le Loc'h 2004). This dredge was dragged onto the seabed for 1 min in the Gulf of Lion (because of the rapid silting of the dredge) at 1.5 knots.

In the English Channel, 16 stations were sampled using both gears (trawl and dredge) (Figure 33b). The Rallier du Baty dredge was dragged for 5–10 min at 1.5 knots.

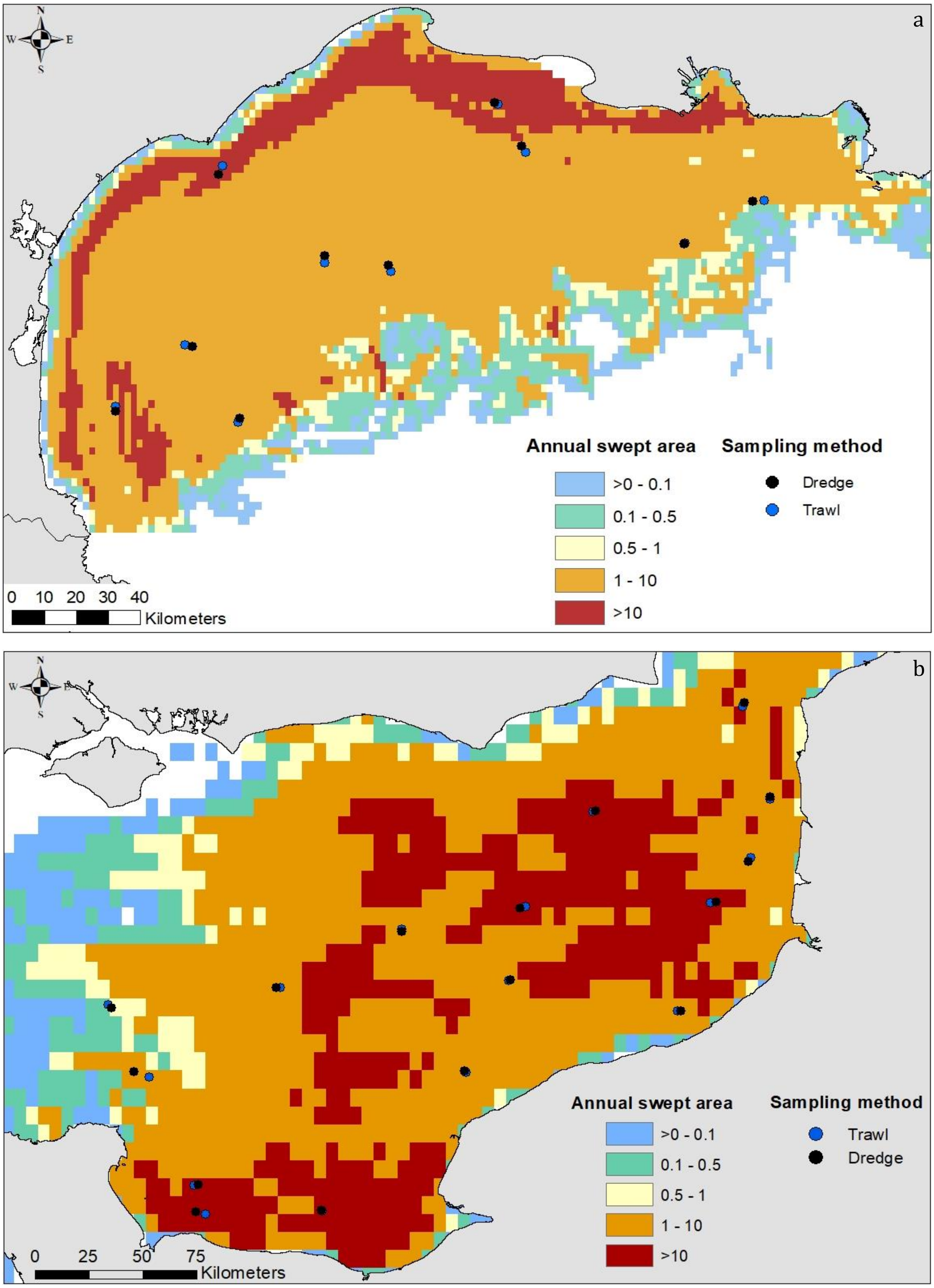


Figure 33: Location of trawl and dredge stations in the Gulf of Lion (a) and in the English Channel (b). The annual swept area was 90th inter-annual percentile of the abrasion in during the period 2009-2017

Since the surface of the area sampled by the dredge is reduced compared to those of the trawl (smaller opening and reduced dragging time), three dredge samples were taken along the trawl transect at each station (beginning, center and end of the transect). Each dredge allowed collecting 50L of sediment but only 10L was sorted to extract the benthic fauna.

Samples of 10L sub-sampled in dredges were sieved through a 1mm square mesh size to only select the benthic macrofauna. Sieved samples were then fixed in 4% borax-buffered formaldehyde in ambient seawater and preserved in 70% ethanol after their identification. At the laboratory, all animals were identified to the lowest taxonomic level possible and count. Colonial species such as sponges or hydrozoans were weighed since individuals could not be counted. Data from the three dredges were then summed to provide a better representation of the benthic communities present throughout the transect sampled by the trawl. Analyses were then based on a total aggregated 30L sample.

2.2.2. Dredge data

Data from the dredge were composed of both abundance (for countable species) and biomass data (for colonial species). Abundance and biomass semi-quantitative classes were designed to combine both type of data and compute a single sensitivity index per station, taking all available species into account. The distribution of biomass or abundance data roughly followed a Poisson distribution and a base 10 logarithmic classification was used (Table 16). As biomass values were divided into 6 classes while abundance values were only divided into 4 classes, a rescaling of the biomass classifier had to be carried out so that both data classification schemes were comparable and could be merged. The indices were then calculated using these transformed semi-quantitative abundance and biomass data. As the data collected in the English Channel and the Gulf of Lion were of the same order of magnitude, the same classification was used in both areas.

Table 16: Description of abundance and biomass semi-quantitative classifications

Abundance classes	Abundance	Biomass classes	Biomass (in g)
1	]0-1]	0.67	]0-0.001]
2	]1-10]	1.33	]0.001-0.01]
3	]10-100]	2	]0.01-0.1]
4	]100-1000]	2.67	]0.1-1]
		3.33	]1-10]
		4	]10-100]

2.2.3. Trawling data

For scientific trawl data, biotic indices were calculated using biomass data, as in all other chapters.

All indices were calculated with R version 3.6.3 (R Core Team 2020).

2.3. Abrasion data

Abrasion values at each sampled station (Table 17) of the two studied areas were extracted from swept surface area ratio per year (SAR.y^{-1}) distribution maps (Figure 33).

2.4. Habitat data

For each sample collected with the dredge, a sediment sample was taken to determine the sediment type at each station (three samples were therefore collected per station). After being washed with freshwater to remove salt, sediment samples were stored in an oven for 48 hours at 60°C. The different fractions of sediment were separated using sieves (27 different mesh; from 4 cm to 63 µm) stacked on an automatic sieve shaker left for shaking for 20 min. Each sieve's residual and the fraction less than 63 µm were weighed. Values obtained for the three samples of the same station were then added together to obtain a single value by size fraction that represented the station. The contribution of each size fraction (*i.e.* gravel, sand and mud) was calculated at each station to determine the sediment type at each station using the Folk diagram (Folke 1954) and the package G2Sd version 2.1.5 (Gallon and Fournier 2015). Three sedimentary types were identified for each of the two study areas (Table 17). In the following analyses the sediment type is referred to as the habitat.

Table 17: Range of abrasion sampled for each of the sediment types identified in the two study areas

Area	Sediment type	Sampled abrasion range (SAR.y^{-1})	Number of stations
Gulf of Lion	**All type**	**2.06 – 5.87 – 10.68**	**10**
	Fine silt	9.04 – 9.12 – 10.68	3
	Coarse silt	2.06 – 3.24 – 4.79	4
	Fine sand	5.19 – 5.76 – 5.97	3
English Channel	**All type**	**0.63 – 11.22 – 72.34**	**16**
	Sand	3.40 – 14.12 – 72.34	7
	Very fine gravel	3.10 – 11.22 – 19.02	6
	Gravel	0.63 – 3.96 – 4.71	3

2.5. Data analysis

2.5.1. Biotic indices

All the indices presented in Chapter I and studied in Chapter II, except those that could not be calculated with the available data (community biomass and abundance and Margalef index), were used in this chapter to evaluate the capacity of dredge sampling to monitor the impact of trawling on benthic communities.

2.5.2. Selection of indices immune to semi-quantitative abundance transform

In the Gulf of Lion, all the individuals collected by dredging were counted, as they were not colonial. These data allowed us verify that the semi-quantitative categorization of the abundance data did not significantly influence the behavior of biotic indices. In this study area, all indices were calculated with abundance data but also with transformed abundance data (semi-quantitative abundance classes). Each index was calculated with the two types of data and the Pearson correlation between them was evaluated. Only indices with a correlation value higher than 0.90 were selected for the following analyses. The lack of complete biomass dataset did not allow applying the same validation procedure to the semi-quantitative biomass transform.

2.5.3. Comparison between the two sampling methods

Community description

For each sampling method and in the two study areas, the number of sampled taxa was counted and the proportions of each taxonomic level, evaluated to better understand the differences in catchability between the two gears. Similarly to trawls, dredges primarily collect epifauna or surface burrowing fauna, but they can also capture more deeply buried infauna in some sediment types (Eleftheriou 2013). The proportions of species belonging to the different categories of the trait "Position of organisms in the sediment" were studied for each sampling method in the two studied areas.

The diameter of the circular dredge used being reduced and the dredging time, relatively short, the area sampled with the dredge is smaller than the area sampled by the trawl. The Rallier du Baty anchor dredge is also less effective than the trawl for catching mobile species. The proportion of mobile vs not mobile species collected with the two sampling methods was investigated in both studied areas. The proportion of each modality of other biological traits was not studied because the diversity of these traits within the community was not supposed to vary between the two sampling methods.

Monitoring of trawling impact

An assessment of the relevance of each of the sampling methods for monitoring the impact of trawling on benthic communities was carried out. In each area and for the two sampling methods, generalized linear models (GLM) were used to investigate which variables (abrasion and sediment type) significantly influenced the previously selected indices. The most significant variables were selected for each GLM by forwarding procedure based on the Akaike Information Criterion using the MASS package 7.3-51.5 and the goodness of fit of the model was assessed by performing a $\chi 2$ test between the null and the selected model. For each index, adjusted R-squared values were compared between sampling methods to evaluate which gear is most appropriate to monitor the trawling impact on benthic communities.

3. Results

3.1. Is rescaled abundance compatible with indices calculations?

The use of classes for species abundance has led to significant changes in the calculation of some indices (Table 18). For example, correlations between indices calculated using abundance or rescaled abundance appeared relatively weak for Pielou and Simpson indices. The majority of the indices, however, seemed to be hardly affected by the conversion of abundances in semi-quantitative abundance classes, as shown by correlation values up to 0.90. Consequently, the proposed rescaling method was used in further analyses but only indices with a correlation value superior to 0.90 were considered. In the absence of similar data in the English Channel and for biomass transformation, these Gulf of Lion abundance results had to be extrapolated to the rest of the study. Graphic illustrations of these correlations were presented in Appendix B (Figure B.1, B.2 & B.3).

Table 18: Correlation between indices calculated with the abundance data and indices calculated with scaled abundance

Index	Correlation
Species richness (SR)	1
Shannon index (H')	0.69
Pielou index (J')	0.16
Simpson index (D)	0.23
FRic	1
FDiv	0.84
FSpe	0.90
FEve	0.96
AMBI	0.90
TDI	0.91
mTDI	0.91
pTDI	1
mT	0.91

3.2. Differences in the sampled community between the two sampling method

In the English Channel, despite a significantly larger area sampled by trawling than by dredging, a greater number of taxa were observed in the dredge samples (Table 19). A total of 281 taxa representing 145 families of 68 orders distributed in 10 phyla were observed in dredge samples and 60 taxa representing 40 families of 24 orders and 8 phyla were sampled by trawling. Only 28 taxa were common to both sampling methods.

On the opposite, in the Gulf of Lion, a higher number of taxa were collected by trawl with 99 taxa representing 76 families (38 orders and 9 phyla) against 92 taxa distributed in 53 families (24 orders and 5 phyla) collected with dredges. Only 14 taxa were common to the two sampling methods.

Table 19: Number of taxa by sampling method and areas

	Gulf of Lion		English Channel	
Taxonomic level	**Dredge**	**Trawl**	**Dredge**	**Trawl**
Taxon	92	99	281	60
Species	79	73	257	43
Genus	72	78	195	38
Family	53	76	145	40
Order	24	38	60	24
Phylum	9	9	10	8

For dredge samples, the identification of individuals in the laboratory has allowed the identification of more than 85% of the taxa at species level in the Gulf of Lion and more than 91% in the English Channel. Despite identification to the species level being more frequent with dredge sampling, more than 75% of the taxa were at least identified at genus level, at which indices are calculated, regardless of the type of sampling (Figure 34).

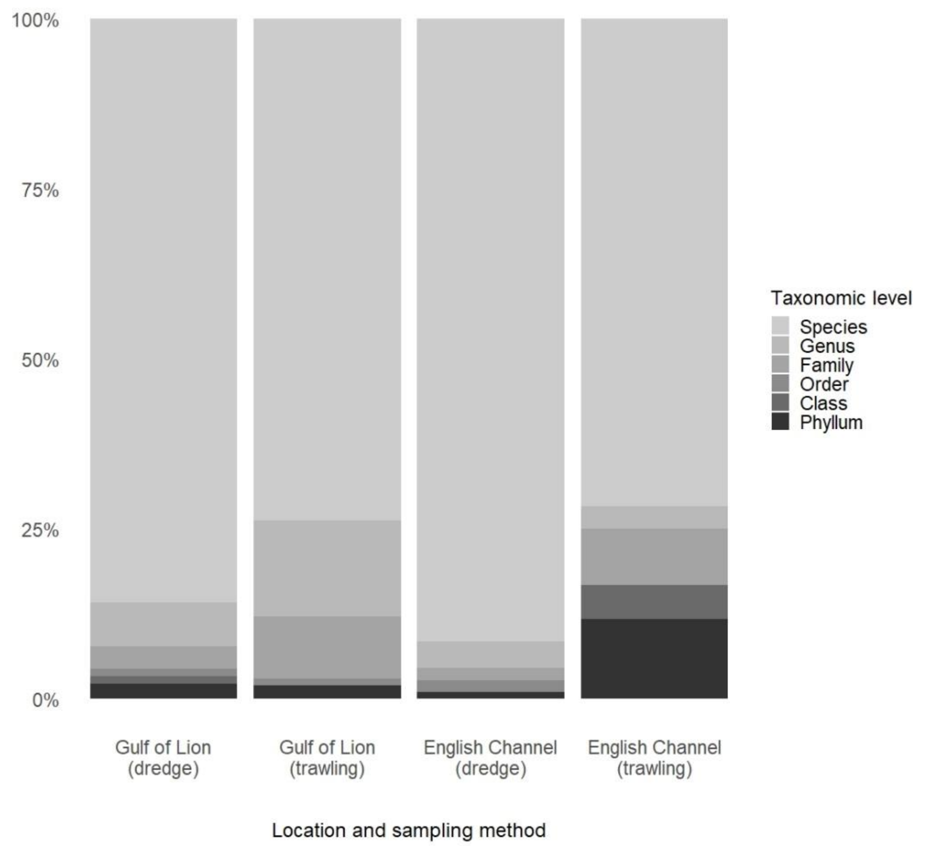


Figure 34: Proportion of each taxonomic level identified with the two sampling method in the two studied areas

Whatever the studied area considered, taxa non-sensitive to trawling (SI ≤ 7) were, in proportion to total catch, mostly found in samples collected by dredges. More than 75% of the taxa collected by dredging in the Gulf of Lion and about 60% of those in the English Channel are considered as non-sensitive species (Figure 35). In samples collected by trawl, these groups represent approximately 45% of the species collected in both areas. The distribution of taxa within the different sensitivity groups appears to be more homogeneous in samples collected by trawl compared to those collected by dredge.

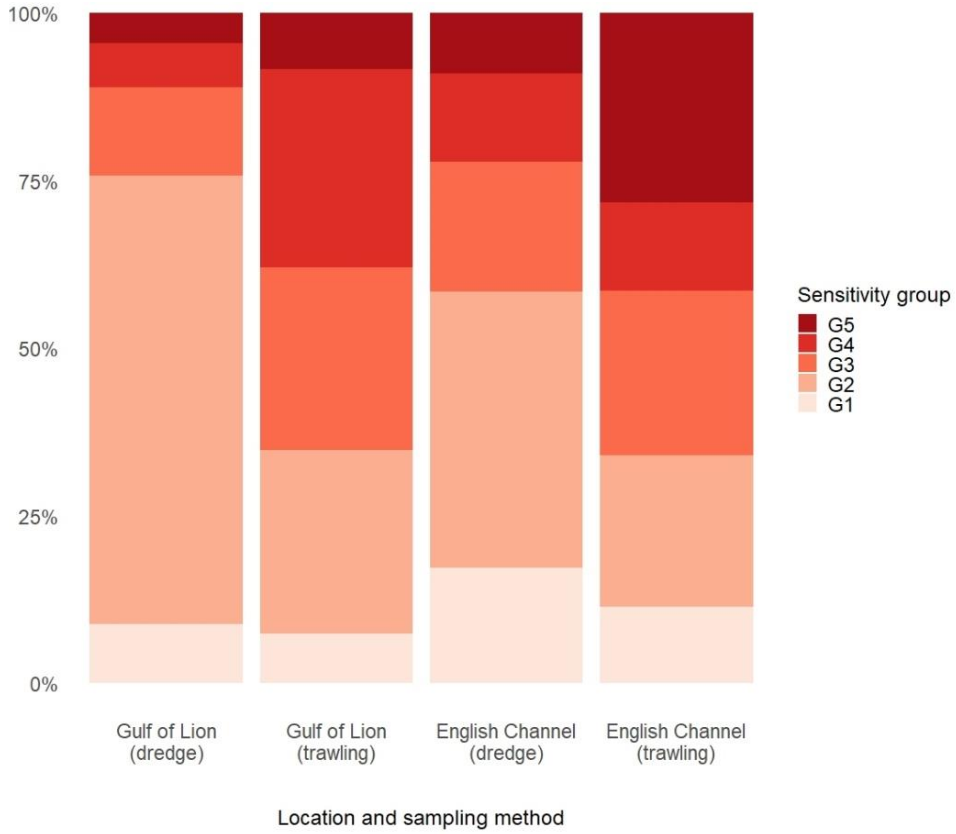


Figure 35: Proportion of taxa belonging to each sensitivity group for each sampling method

G1: SI≤4; G2: 5≤SI≤7; G3: 8≤SI≤10; G4: 11≤SI≤13; G5: SI≥14

Looking at the sensitivity of the ten most represented taxa in terms of biomass or abundance in each sampling method, it appears that these results were very contrasted between the Gulf of Lion and the Channel (Table 20). In the Gulf of Lion, nine of the ten dominant dredge caught taxa were considered not sensitive to trawling while only three of those caught with the trawl were so. The majority of the dominant taxa in the dredge collected assemblage were polychaetes while the trawl assemblage was dominated by Echinoderms (*Parastichopus regalis, Astropecten irregularis pentacanthus, Ocnus planci* and *Leptometra sp.)* and Cnidarians (*Funiculina quadrangularis*, *Alcyonium palmatum* and *Cavernularia pusilla*). In the English Channel, only three dredged taxa and five trawled taxa out of the ten dominant ones were considered as non-trawl-sensitive. However, the dominant taxa in dredge samples seemed less sensitive than those caught by trawl as their average sensitivity score was 8.4 as opposed to 9.2 for those collected by trawl.

Table 20: Dominant taxa observed with the two sampling methods in the two studied areas and their sensitivity score (SI; Foveau et al. 2019). Green shading indicates that the species is considered less sensitive to trawling (SI ≤ 7).

Areas	Devices	Species	SI
Gulf of Lion	Dredge	*Marphysa bellii*	6
		Notomastus latericeus	6
		Aponuphis brementi	6
		Glycera tridactyla	6
		Goneplax rhomboides	8
		Alpheus glaber	6
		Callianassa subterranea	6
		Sternapsis scutata	4
		Amphicteis sarsi	6
		Drilonereis filum	5
	Trawling	*Funiculina quadrangularis*	14
		Parastichopus regalis	12
		Astropecten irregularis pentacanthus	8
		Liocarcinus depurator	6
		Ocnus planci	10
		Alcyonium palmatum	15
		Turitella communis	5
		Cavernularia pusilla	13
		Galeodea rugosa	7
		Leptometra sp.	14
English Channel	Dredge	*Pisidia longicornis*	8
		Galathea intermedia	8
		Hydrallmania falcata	15
		Spirobranchus triqueter	8
		Balanus crenatus	10
		Psammechinus miliaris	7
		Ophiothrix fragilis	11
		Ampelisca spinipes	4
		Nucula nucleus	5
		Spirobranchus lamarckii	8
	Trawling	*Psammechinus miliaris*	7
		Asterias rubens	7
		Ophiothrix fragilis	11
		Pagurus bernhardus	3
		Alcyoniidae	15
		Alcyonium digitatum	15
		Necora puber	6
		Pyuridae	10
		Flustra foliacea	15
		Pagurus prideaux	3

Regardless of the area, the dredge caught a higher proportion of infaunal species compared to the trawl (Figure 36). For example, in the Gulf of Lion, respectively about 17% and 68% of the species collected by trawl and dredge were burrowers. In this area, the majority of dredge collected species were infaunal while the vast majority of those collected by trawling lived on the sediment surface. In the English Channel, although a greater proportion of infaunal species have been caught with the dredge than in the trawl, collected species were mainly epifaunal.

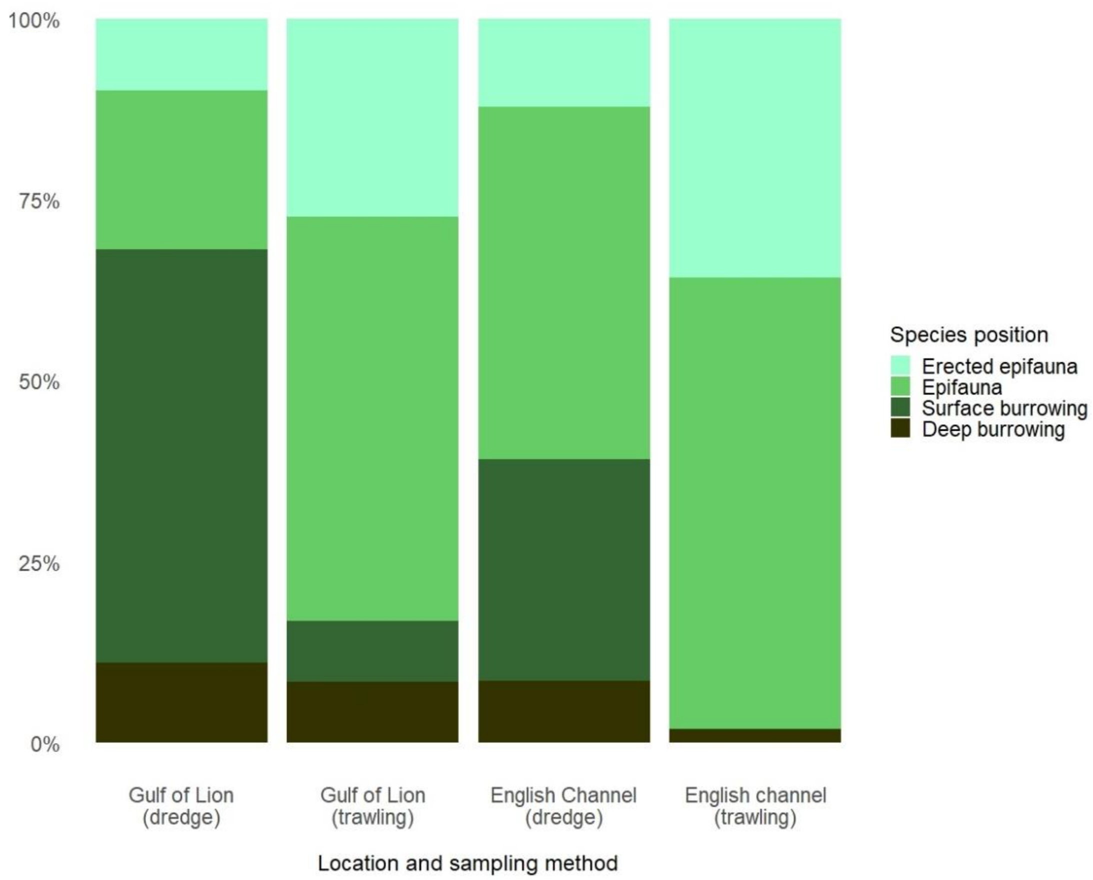


Figure 36: Proportion of each position category by sampling method in the two studied areas

3.3. Monitoring of trawling impact

Only a few indices correlated significantly with abrasion, whether calculated with dredge or trawl data (Table 21). In the English Channel, using dredge data, abrasion was significantly related to three indices (S, FSpe and AMBI), whereas, based on trawl data, this was only the case for TDI. No index seemed influenced by habitat types in this area. In the Gulf of Lion, using dredge data, only S and mT were related to abrasion whereas, based on trawl data, this was the case for all functional sensitivity indices and AMBI. Moreover, habitat had a significant influence on AMBI when using dredge data and on FRic with trawl data.

Although species richness (SR) was significantly influenced by abrasion in the dredge data, this relationship was positive in the Gulf of Lion and negative in the Channel.

Only the mT index, in the Gulf of Lion was related to abrasion regardless of the sampling method.

Table 21: Outcomes of the stepwise selection procedure on the generalized linear models.
GoL = Gulf of Lion. E.C = English Channel. * indicates that p<0.05 ; ** indicates that p<0.01 ; *** indicates that p<0.001; n.s indicates no significant effect. No explanatory variable indicates that the null model was selected.

		Dredge			Trawling		
Indices	**Area**	**Explanatory variable**	**Significance (and regression coefficient for abrasion)**	**Adjusted-R^2**	**Explanatory variable**	**Significance (and regression coefficient for abrasion)**	**Adjusted-R^2**
SR	GoL	Habitat Abrasion	** 0.17***	0.69	-	-	-
	E.C	Abrasion	- 0.03**	0.45	-	-	-
FRic	GoL	-	-	-	Habitat	*	0.48
	E.C	-	-	-	-	-	-
FSpe	GoL	Habitat Abrasion	*** n.s	0.70	-	-	-
	E.C	Abrasion	4.6.10-3***	0.55	-	-	-
FEve	GoL	-	-	-	-	-	-
	E.C	-	-	-	-	-	-
AMBI	GoL	Habitat	**	0.64	Abrasion Habitat	0.20* n.s	0.53
	E.C	Abrasion	- 0.01*	0.29	-	-	-
TDI	GoL	-	-	-	Abrasion	- 0.05*	0.35
	E.C	-	-	-	Abrasion Habitat	-0.01** n.s	0.48
mTDI	GoL	-	-	-	Abrasion	- 0.66**	0.85
	E.C	-	-	-	-	-	-
pTDI	GoL	-	-	-	Abrasion	- 0.47**	0.83
	E.C	-	-	-	-	-	-
mT	GoL	Abrasion	- 0.21*	0.54	Abrasion	- 0.31*	0.71
	E.C	-	-	-	-	-	-

4. Discussion

4.1. Is rescaled abundance compatible with indices calculations?

Most colonial species are particularly sensitive to trawling as they are often filter feeders, erected, sessile and fragile (Foveau et al. 2019). In addition, colonial epifauna is ecologically important because many taxa, such as sponges or hydroids, generate three-dimensional microhabitats that increase the structural complexity of the benthic environment (Asch and Collie 2008). Their consideration in monitoring the impact of trawling is particularly important. However, individual enumeration within a colony is impossible and only colony fragments are usually collected with both trawl or dredge. As a consequence, colonial species collected have to be weighed rather than counted as would non-colonial species. To overcome this problem, some studies proposed to estimate abundance from the biomass of colonial species (Bradshaw et al. 2002). The lack of information concerning the weight/number relationship for many of these species makes this approach impractical. In the present work, a semi-quantitative classification method to compare and merge abundance and biomass data was preferred to an approximate method of abundance estimation.

Based on abundance in the Gulf of Lion, three indices of taxonomic diversity (Shannon, Pielou and Simpson) and one index of functional diversity (FDiv) were particularly affected by the data transformation proposed. Such results are not surprising as they are related to the characteristics of each index:

- Shannon index is sensitive to rare species (Peet 1974), but the use of a limited number of classes (four in the present study) for abundance data lead to a decrease in the importance of rare species.

- Concerning the Pielou index, as it takes into account the distribution of individuals between species, the limited number of classes will have a significant influence on its calculation. The calculation of this index also takes into account the Shannon index (Pielou 1969), which explains the very low correlation observed between the index calculated using abundance data and that calculated using abundance classes.

- The Simpson's index measures the probability that two individuals belong to the same species (Simpson 1949), so the use of a scaled abundance leads to a modification of this index by reducing the differences in abundance between species.

- Finally, the functional divergence index (FDiv) relates to how abundance is distributed within the volume of functional trait space occupied by species (Villéger et al. 2008). Thus, as for the Simpson's index, the classification of abundances into only four classes leads to a decrease in the differences in abundance between species and thus significantly modifies the values of the index.

Conversely, the values of three indices (SR, FRic and pTDI) were not at all influenced by the type of data used. Species and functional richness being influenced only by the identity of the species present (Stirling and Wilsey 2001; Villéger et al. 2008), these results were consistent. Concerning the pTDI, the lack of influence of the type of data on the index results and the observation of a slightly lower correlation for mTDI suggest that for sensitive species, the use of abundance classes is equally successful.

The efficiency of this method could only be evaluated in the Gulf of Lion and only with abundance data. These results had to be extrapolated to the English Channel and to the biomass data, assuming that the same trend would hold in this area. The validity of this working hypothesis will need to be further verified in the future although appropriate average species weight observations per habitat may be even more preferable.

4.2. Differences between fauna sampled

The Rallier du Baty anchor dredge and the scientific trawl used in this work have technical characteristics that do not necessarily result in the capture of the same benthic species. This was confirmed by the few number of common taxa between the two sampling methods (28 taxa in the English Channel and only 14 in the Gulf of Lion). The mesh sizes of the two gears were not similar, therefore the dredge allowed the capture of all individuals larger than 1 mm, whereas only individuals larger than 1-2 cm may be retained in the trawl (ICES 2017a; MEDITS 2017). Although the dredge should collect a greater diversity of taxa than the trawl, it was only observed in the English Channel where nearly five times more species were sampled by dredge. In contrast, in the Gulf of Lion, the trawl collected slightly more taxa (99 vs. 92) than the dredge. These differences are probably due to the homogeneity of the habitat and the highly muddy nature of the sediments in the Gulf of Lion. As the dragging time was further reduced, compared to the English Channel, because of the rapid silting of the dredge, the surface sampled with the dredge was greatly reduced in the Gulf of Lion. As suggested by the benthic assemblage collected, composed mostly of burrowing species, the dredge may penetrate quite deeply into the mud when deployed and may rapidly be silted. Consequently, the dredge was unable to capture many of the over-dispersed epifauna. On the opposite, the trawl, penetrating the muddy sediments of the Gulf of Lion only by few centimeters at most (Eigaard et al. 2016) and being equipped with a 10mm mesh size in the cod-end (MEDITS 2017), captured only a small proportion of infaunal species such as polychaetes.

In the English Channel, even if the proportion of infauna was higher in dredge than in trawl samples, the majority of sampled species belonged to epifauna. The number of infaunal species collected with the trawl was very low. Such differences between the Gulf of Lion and the English Channel seem to be linked to the sediment type, the depth of penetration of trawl or dredge being lower in coarse sediments (such as those of the English Channel) than in muddy sediments [such as the Gulf of Lion; (Eigaard et al. 2016)].

Finally, regardless of the studied areas, the proportion of sensitive species to trawling was always higher in the benthic communities sampled with the trawl than the dredge. Infaunal species such as polychaetes being less exposed and therefore sensitive to the effects of trawling (Jennings et al. 2001b), these results seems coherent.

4.3. Taxonomic identification of individuals

Whatever the study area considered, the ratio of individuals identified at species level is higher in dredge samples than in trawl. This is particularly marked in the English Channel, where nearly 91% of the 281 taxa collected by dredge were identified down to the species level, compared with 71% of the 60 taxa sampled with the trawl. These differences are due to the examination of each individual by experts at the laboratory, under binocular magnifiers (Althaus et al. 2015). The species richness may be underestimated by trawl sampling because several individuals, morphologically very close, may be grouped under the same taxa even though they belong to different species. For approaches based on the use of functional traits, the genus level is often sufficient to define the biological characteristics of individuals (Brind'Amour et al. 2009; Foveau et al. 2017). In this study, the rate of identification at the level of the genus appeared satisfactory (more than 75%) for both sampling methods in the two studied areas.

4.4. Which sampling method to monitor the trawling impact in the two studied areas?

The type of gear used (trawl, dredge, grab…) can influence the type (*e.g.* epifauna *vs.* infauna or crustaceans *vs*. Alcyonidae) and number of species collected (Jørgensen et al. 2011) and influence the potential detection of impacts. This study has highlighted differences between dredges and trawls in their ability to monitor the effect of trawling on benthic communities. Indeed, the comparison of different indices calculated with the data from the two types of sampling revealed a great heterogeneity of results. Only one index based on dredge data, species richness, was significantly influenced by abrasion in the two areas studied. However, the relationship between this index and abrasion was not significant for the data collected with the trawl. This difference could be due to the type and number of species collected with each gear. Few taxa were common to both sampling methods and the proportion of infauna and epifauna species was different between the sampling methods. Epifauna and infauna are not affected in the same way by dredging (Lambert et al. 2017). Thus, these compositional differences may explain the differences observed between trawl and dredge sampling.

Results obtained with each gear were very different between the two study areas and probably because the habitats and benthic communities sampled were very different.

4.4.1. Gulf of Lion

In the Gulf of Lion, sediment type (habitat variable) had a significant influence on the benthic communities sampled, whether dredged or trawled. Some indices such as AMBI with dredge data or functional richness (FRic) with trawl data only seemed related to sediment type. Soft-bottom macrofauna being largely controlled by abiotic factors such as depth or granulometry (Labrune et al. 2008), these results are not surprising. In addition, the habitat effect was mostly detected in the dredge data, strongly dominated by infaunal species. The distribution of polychaete assemblages, strongly influenced by grain size, in the Gulf of Lion (Labrune et al. 2007a) could explain these results. In all cases, the absence of a significant effect of abrasion for these two indices, while it was observed with other indices, suggests that these indices are not adapted to follow the impact of towed fishing gears and that the effect of abrasion could be masked by the habitat effect as has already been observed in areas of high natural disturbance (Stokesbury and Harris 2006; Sciberras et al. 2013).

The absence of significant influence of abrasion on taxonomic and functional diversity indices calculated with trawl data, while observed in Chapter 2 (Jac et al. 2020a), suggests that either the amount of data used in this study is insufficient to allow these indices to detect an impact, or that the abrasion range sampled may not be sufficient. Although the available dataset size may not be large enough to detect abrasion impact with certain indices, functional sensitivity indices based on biological traits (TDI, mTDI, pTDI and mT), derived from trawl data, were found to be significantly related to abrasion. This indicated that even on such a limited gradient, they were able to detect functional changes in the assemblage composition that could be linked to fishery pressure. These four particular indices were found particularly relevant for large scale studies (Jac et al. 2020a).

However, only two indices calculated with dredge data were significantly influenced by the abrasion: species richness and mT. With respect to species richness, the lack of significant influence of abrasion when trawl data were used suggested that, for this index, dredge data are more relevant to monitor trawling impact. However, the significant influence of granulometry on this index will require monitoring this impact habitat by habitat (as is suggested for trawl data in the Chapter II; Jac et al. 2020a). In addition, the relationship between this index and abrasion seemed quite counter-intuitive because the number of species increased along the abrasion gradient. Several hypotheses can explain this. Firstly, various studies have observed, under certain conditions, an increase in the biomass of the infauna, and in particular for the polychaetes, along a trawling gradient (Jennings et al. 2001b, 2002; Hiddink et al. 2008). This was mainly linked to a decrease in competition and predation with the large epifauna species particularly affected by trawling. Since the dredge in the Gulf of Lion captured mainly infauna, the apparent increase of species richness along the abrasion gradient may in fact reflect the decrease of epifauna species. In addition, previous studies reported that the species richness of polychaetes decreased when trawling pressure was very high (Hiddink et al. 2008). In spite of particularly high (> 2 SAR.y-1) abrasion values in the Gulf of Lion, such decrease was not observed in the dredge data. This could result from the small number of stations sampled that did not allow for the detection of the species richness decrease in areas where abrasion is very high. Finally, as the direct effect of other environmental factors affecting the diversity of the benthic fauna has not been studied in this work, it is conceivable that abrasion is in fact strongly correlated with an environmental gradient, such as depth, having a strong influence on the production of the species of the infauna and in particular the polychaetes. The diversity of confusing factors that may explain the observed relationship of species richness to abrasion mostly stresses the need for further studies to better understand what process is related to this increase in species richness along the abrasion gradient in the Gulf of Lion.

Although based on the same biological traits, only mT, among all functional indices, detected a significant influence of trawling on benthic communities. These differences may be due either to the way in which biological traits are taken into account in the calculation of indices, and in particular the hierarchy of the traits (Certain et al. 2015), or by the addition of the protection status of the species in the calculation of this index. The vast majority of protected species in the Mediterranean belong to the epifauna [*e.g.* sponges, sea pens, corals; (OCEANA 2016)], and the dredge has overwhelmingly captured infauna. It seems therefore unlikely that it was the addition of the "protection status" factor that induced the observed differences between mT and other functional indices. Consequently, the mathematical combination of biological traits used by mT appears to perform better than those of the other functional indices with respect to the dredge data.

Although dredge based mT detected a significant influence of abrasion on benthic communities, the adjusted r-square was higher with the trawl data than with that of the dredge data, suggesting that scientific trawling may be more robust to monitor trawling impact on benthic communities when using this particular index.

In addition, with the exception of mT, no significant relationship between abrasion and other functional sensitivity indices could be found using dredge data indicating that these indices are unable to detect the impact of trawling on benthic communities.

This resulted from the fact that the proportion of sensitive species captured by dredge hardly varied along the abrasion gradient. The sampled abrasion gradient being quite high, the absence of trawl-sensitive species could be related to their over-dispersed nature and to the unsustainable fishing pressure exerted over them. Such sensitive species could still be found in the trawl data which seems to indicate that the sampled assemblages were different.

4.4.2. English Channel

In the English Channel, no common index could be significantly related to abrasion while using both data types. These results are most likely due to the large differences (taxonomic and functional) between the benthic communities sampled with the two different gears studied. The dredge collected nearly five times more species than the trawl and about 45% of these species belonged to the infauna compared to less than 2% in trawl samples. As a result a greater proportion of the species caught with the trawl were considered sensitive. These notable differences are probably related to the type of substrate sampled and the way each gear samples each substrate. In the English Channel, sampled substrates were relatively coarse. However, the trawl penetrates with difficulty into coarse sediments (Eigaard et al. 2016), thus it catches mainly epifauna attached to gravels and pebbles. The dredge will tend to sample the bottom in successive jumps (Foveau 2009) and will potentially sink deeper if it hits an area of finer sediment between coarser areas. Moreover, the round shape of the Rallier du Baty dredge and its rather small opening diameter (0.65 cm) compared to the trawl opening, may limit the collection of coarse gravel and thus associated fixed epifauna.

No significant influence of sediment type on the studied indices was observed in the English Channel, either with dredge data or scientific trawl data whereas the distribution of benthic macrofauna in this area is known to be linked to complexes interaction between temperature, current and grain size (Cabioch et al. 1977). Several hypotheses can explain this lack of habitat effect. Firstly, the distinction between the different habitats considered in this work may not be sufficiently marked for the associated benthic communities to be different from one another. Another possibility is that the granulometry based sediment classification may not be sufficiently representative as a number of methodological biases may have taken place. For instance, the granulometry was carried out from sediment samples taken by the dredge. However, the eastern English Channel is dominated by gravelly-sandy sediments (Vaslet et al. 1979) and the dredge may over sample soft sediment while bouncing over coarser ones hence the lack of representativeness in the data. The amount of very fine sediments may also be influenced by this sampling method because when the dredge "Rallier du Baty" is raised, the finest sediments may be washed out by the water circulating in the pocket (Foveau 2009) resulting in an underestimation of the finest sediment fractions. Finally, the fishing effort, and therefore abrasion, being very variable depending on the habitats considered (Eigaard et al. 2017), a part of the abrasion influence (for the indices significantly influenced by the abrasion) may actually be mirroring the granulometry effect. Another likely possibility is that the lack of habitat effect is related to the limited amount of data available (only 16 sampled stations). The number of sampled stations per habitat was perhaps too low to detect significant differences between these habitats.

Concerning the trawl data, most functional indices but TDI could not be related to abrasion in contrast to what was observed in the English Channel (CGFS data) in Chapter II (Jac et al. 2020a). This result highlights the fact that the dataset used may indeed be too limited in size and abrasion gradient contrast to detect impact. Indeed, more than 1000 stations were used in the analyses performed in Chapter II (Jac et al. 2020a) compared to 16 here. Regarding abrasion, although the sampled range is almost the same (0.63 to 72.34 SAR.y^{-1} here vs. 0 to 74.15 SAR.y^{-1} in Chapter II), the stations are not distributed in the same way along this gradient since the median is 11.22 SAR.y^{-1} here versus 6.65 SAR.y^{-1} in Chapter II (Jac et al. 2020a, 2020b). Thus, these results seem to indicate that, in the present work, the number of stations sampled with the scientific trawl and their distribution along the abrasion gradient is insufficient to satisfactorily detect the effects of trawling. As the dredge stations were matched to the trawl stations, it is conceivable that the low detection of the trawling effect in the dredge data is also related to these sampling biases.

Unlike in the Mediterranean, the species richness was negatively and significantly influenced by the abrasion in this area. These results are the opposite of those observed with the trawl data in Chapter II (Jac et al. 2020a) where the species richness increased in all areas, including the English Channel, along the abrasion gradient. The sampling differences discussed above may partly explain these results. However, the lack of detection of an trawling effect on benthic communities in the trawl data combined with the detection of an effect on the dredge data is contrary to what was observed by Hiddink et al. (2006). The relationships between species richness and abrasion thus appear to be particularly complex and variable depending on a large number of parameters such as the area sampled, the type of data, and the abrasion gradient sampled. The use of this index thus seems little adapted to follow the impact of towed gears on the benthic communities.

Nonetheless, a significant relationship between the functional specialization index calculated with the dredge data and abrasion indicated that there was a marked change in the abundance in either generalist or specialist species abundance (Mouillot et al. 2013a) along the abrasion gradient. Trawling selectively affects benthic species according to their biological characteristics (Lambert et al. 2014; Foveau et al. 2017) and generally induces a decrease in the abundance of sessile, long-lived and filter-feeding species (Kenchington et al. 2001; Tillin et al. 2006) whereas other more opportunistic species such as polychaetes may be only slightly impacted (Kaiser et al. 2006). The significant evolution of the degree of specialization of species along the abrasion gradient does not appear surprising because only highly specialized species (*e.g.* species living deep in the sediment, not very fragile, carnivorous) will be able to maintain themselves despite a very high trawling rate. As the abrasion influence on the functional specialization was not observed in the trawl data, it would seem that these variations only concern the proportion of the benthic community sampled by the dredge in the English Channel. As this index has the highest value of adjusted r-square, it seems to be the most relevant index to be used to monitor the trawling impact in the Channel using data from dredge sampling.

In conclusion, when using dredge data, only species richness could detect a significant effect of abrasion in the two studied areas. However, the relationship between this index and abrasion was positive in the Gulf of Lion and negative in the English Channel. In addition, this index is hardly specific to the investigated pressure, and requires to carefully consider the habitat effect on this index. Thus, the species richness may not be considered as a generic index and an improvement of knowledge concerning its link to abrasion in each of the study areas is necessary. It therefore does not seem to be an appropriate index for monitoring the impact of trawling on benthic communities.
In contrast with trawled data, the proportion of the benthic community caught by dredges, being largely composed of infauna and species weakly or not sensitive to trawling, indices directly based on species sensitivity scoring do not seem to be able to satisfactorily reflect the effects of trawling over the entire benthic community. A recent study has shown that the size of individuals has an influence on the response of a number of indicators to the effect of trawling and that large benthic megafauna seemed to be more impacted by trawling than small benthic fauna (McLaverty et al. 2020). As the dredge collects mainly macrofauna, it may not be the most suitable gear to monitor this impact.
However, these different findings need to be confirmed by further studies, because inconsistencies between the results found here and those obtained in Chapter II (Jac et al., 2020a) suggests that there may be insufficient data to draw a definitive conclusion. Further sampling, better distributed within the different existing habitats in the two study areas and along the abrasion gradient, should be considered to confirm these results.

Inter Chapitre

Le troisième chapitre de cette thèse a permis de démontrer que la drague Rallier du Baty n'est pas un engin d'échantillonnage pertinent dans le cadre du suivi de l'impact des arts traînants sur les communautés benthiques. La faune benthique collectée à l'aide de cet engin d'échantillonnage, principalement constituée de petites espèces appartenant à l'endofaune, ne semble pas répondre de façon cohérente à la pression de chalutage. Ce chapitre a également permis de mettre en avant l'importance du nombre de points échantillonnés et de leur répartition le long du gradient d'abrasion pour évaluer au mieux l'impact du chalutage sur les communautés benthiques des plateaux continentaux.

L'utilisation de méthodes d'échantillonnage dites "destructives" comme la drague et le chalut peut sembler incompatible avec un suivi régulier de l'impact d'une pression anthropique, comme le chalutage, sur les habitats benthiques. L'imagerie vidéo, en se concentrant principalement sur la macro-épifaune sessile connue pour être particulièrement sensible à l'impact des arts traînants, pourrait être une méthode d'échantillonnage très efficace pour suivre l'impact du chalutage tout en ayant un impact écologique négligeable sur les communautés benthiques.

Dans ce quatrième chapitre, les caractéristiques taxonomiques et fonctionnelles des communautés benthiques observées à la vidéo et collectées au chalut ont été comparées. La pertinence de l'utilisation de ces deux méthodes d'échantillonnage dans le cadre d'un suivi de l'impact des arts traînants sur les communautés benthiques a été évaluée en comparant la capacité de détection de plusieurs indices calculés à l'aide des données collectées au chalut scientifique et des observations vidéo.

Chapitre IV: Can towed video sampling be used to monitor the effect of trawling on benthic communities?

Ce chapitre est basé sur un article sous presse dans la revue *ICES Journal of Marine Science.*

Jac C., Desroy N., Duchêne J-C., Foveau A., Labrune C., Lescure L., Vaz S. Assessing the impact of trawling on benthic megafauna: comparative study of video census surveys scientific trawling. ICES Journal of Marine Science. *In press.* 10.1093/icesjms/fsab033

Résumé de la publication en français

L'importante activité des arts traînants sur les plateaux continentaux européens impacte sévèrement la faune benthique. Toutes les espèces de la communauté benthique ne sont toutefois pas affectées de la même manière par cette pression et les espèces épibenthiques semblent être particulièrement impactées par l'abrasion des fonds marins induite par le chalutage. La plupart des études menées sur les communautés benthiques ont été conduites à petite échelle et ont eu recours à des méthodes d'échantillonnage destructives (comme les bennes, les carottiers et les dragues) collectant principalement l'endofaune. Utiliser les données benthiques provenant des relevés scientifiques au chalut de fond effectués dans toutes les eaux européennes dans le cadre du programme pluriannuel de collecte de données de la politique commune de la pêche semble donc être une bonne alternative pour étudier l'impact des activités de pêche à grande échelle. Toutefois, la capturabilité du chalut dépend fortement de la nature du fond marin et des adaptations des engins qui en résultent. En raison de sa nature non destructive et de sa capacité à se concentrer sur la macro-épifaune benthique, l'échantillonnage à l'aide d'un système vidéo remorqué est également à considérer pour estimer l'impact du chalutage sur les communautés benthiques. Une étude des différences taxonomiques et fonctionnelles entre les communautés échantillonnées au moyen du chalut et de la vidéo a donc été réalisée. L'influence des caractéristiques du système vidéo (*e.g* qualité de l'image) et de l'abrasion sur neuf indices pouvant-être utilisés pour suivre l'effet du chalutage sur les communautés benthiques, a été étudiée. Parmi ceux-ci, trois indices spécifiques à la détection des effets de la pêche basés sur des caractéristiques biologiques sont apparus comme les indices les plus performants avec des données vidéo : le modified-Trawling Disturbance Index » (mTDI le « partial-Trawling Disturbance Index » (pTDI) et le « modified sensitivity index » (mT). L'efficacité de ces indices pour surveiller l'effet du chalutage a été évaluée et comparée entre les données issues du chalutage scientifique et de l'échantillonnage vidéo. Ce travail a mis en évidence que l'échantillonnage vidéo peut être une bonne alternative, ou tout du moins une méthode complémentaire, aux méthodes d'échantillonnage destructives pour surveiller l'effet du chalutage sur les communautés benthiques.

1. Introduction

Most studies evaluating the anthropogenic impacts such as fishing activities on benthic communities use sampling methods such as grabs, box-corers or dredges which are mainly focused mainly on the infauna (Eleftheriou 2013; van Loon et al. 2018). Usually, these samplings are conducted with restricted spatial coverage and relatively nearshore (Brind'Amour et al. 2014). To study the impact of fishing activities on a large scale, benthic data from scientific bottom trawl surveys carried out in all European waters in the frame of the Common Fishery Policy Data Collection Multiannual Program seem to be a good alternative (Foveau et al. 2017; Chapter II). Nevertheless, all these sampling methods are "destructive" and may have a lasting impact on benthic biodiversity, which, although clearly negligible in comparison to fisheries impacts, should be reduced (Trenkel et al. 2019). In recent years, underwater imagery has been increasingly used to observe megafauna and habitat diversity (Mallet and Pelletier 2014). These methods allow rapid acquisition of a large amount of information on sites that may be difficult to sample (due to depth, seafloor characteristic or topography) with classic methods (Taormina et al. 2020). In addition, marine imagery is non-destructive (Mallet and Pelletier 2014). Five main techniques were developed to monitor marine biodiversity: remote underwater video (RUV), baited remote underwater video (BRUV), towed video (TOWV), diver-operated video (DOV) and remote operating vehicle imaging (ROV). However, these methods are not applied to assess the same compartments of the marine ecosystem (Brind'Amour et al. 2014). Only DOV, ROV and TOWV techniques may be deployed to evaluate the abundance of benthic species or to study the benthic substrate/habitat (Rooper and Zimmermann 2007; Mallet and Pelletier 2014; Sheehan et al. 2016; Mérillet et al. 2017). When using visual census, the quality of data is strongly dependent on environmental conditions (especially turbidity) and image resolution (resulting from technical constraints). This often results in reduced taxonomic identification levels which may decrease the amount and usefulness of the information contained in the resulting data (Flannery and Przeslawski 2015). Notwithstanding these limitations, visual observations enable the production of large amounts of information, whether taxonomical, functional, or environmental, which can be used to assess the ecological status of a site or the effect of certain pressures on a community. The data collected by video sampling may indeed be used to calculate indicators of ecological status or pressures just as well as the data usually derived from classical sampling such as grabs or trawl.

In order to monitor trawling impact on benthic communities, it is necessary to observe changes in the benthic community and particularly in the benthic megafauna, which seems more appropriate than smaller fauna to detect the effect of trawling (McLaverty et al. 2020). Different indices could be used to track the modification of benthic community along the pressure intensity gradient: taxonomic diversity metrics, functional diversity indices and functional sensitivity indices. The first will provide information on the differences in species richness and their relative dominance, homogeneity or rarity in the community. The two later are based on biological traits sensitive to physical abrasion induced by fishing (size, position, mobility, fragility, feeding mode) and thus provide information on function changes within the benthic community and on changes in sensitive species abundance (in the case of functional diversity indices and functional sensitivity indices). Previous work suggests that indices in the latter category are better suited to monitor the effect of trawling on benthic mega-epifauna (Chapter II; Jac et al. 2020a). (Jac et al. 2020a). Although recent studies have shown the usefulness of indices based on the longevity of benthos (Rijnsdorp et al. 2018; Hiddink et al. 2020), there is too little information existed on the mega-epifauna studied here to use this particular trait.

The aims of this study were to (a) list or determine indices that may detect the effect of trawling on benthic fauna with a towed video sampling method (b) compare the ability of two sampling methods (video and trawling) to monitor the impact of fishing on benthic communities on a large scale.

2. Material and methods

2.1. Surveys

In the English Channel, all the videos used for this study were acquired between 2014 and 2019 during CGFS and IBTS surveys. In the Gulf of Lion, the videos were collected between 2016 and 2018 during EPIBENGOL (Vaz 2018a), VIDEO GALION (Vaz 2016, 2017), APPEAL MED (Labrune 2018) and IDEM VIDEO (Vaz 2018b). For two trawl surveys (EPIBENGOL, CGFS), video transect was carried out just before the trawl haul. After verifying that the trawl's mean position was less than 2km away from that of the video transect, they were considered paired with the corresponding video transect. The video transects, collected during dedicated video surveys (VIDEO GALION, APPEAL MED and IDEM VIDEO) or opportunistically during a bottom trawl survey (IBTS), were paired to trawl stations that were both less than 2km distant and mostly less than a year apart in time (Table 22). A total of 24 videos in the English Channel and 28 videos in the Gulf of Lion were analyzed but only 22 in each area could be paired with trawl stations.

Table 22: Characteristics of paired stations

Pag 1 = Pagure 1; Pag2 = Pagure 2

Study area	Video (year – campaign – device	Trawl (year – campaign)	Number of video transect paired to trawl	Number of video transect un-paired to trawl
Gulf of Lion	2018 – EPIBENGOL – Pag 2	2018 – EPIBENGOL	6	-
	2017 – VIDEOGALION - Pag 1	2017 – MEDITS	11	-
		2016 – MEDITS	3	-
	2016 – VIDEOGALION – Pag 1	2016 – MEDITS	2	-
	2018 – APPEAL MED	-	-	2
	IDEM VIDEO	-	-	3
English Channel	2019 – CGFS – Pag 2	2019 – CGFS	4	-
	2016 – CGFS – Pag 2	2016 – CGFS	11	-
		2015 – CGFS	2	-
		2011– CGFS	1	-
	2014 – IBTS – Pag 1	2015 – CGFS	2	-
		2013 – CGFS	1	2
		2014 – CGFS	1	-

Discrepancies in the number of videos per year and areas resulted from the fact that no dedicated survey could be carried out in the English Channel where the video system had to be deployed opportunistically. In contrast, dedicated surveys could be deployed in the Gulf of Lion. In order to match a video transect with a corresponding trawl haul, an unbalanced design had to be tolerated.

2.1.1. Towed video systems

Two Towed video systems were used to carry out video transects of approximatively 500 meters length (15 min at maximum 1kt) in different locations in the Gulf of Lion and English Channel. The first device (Pagure 1; Figure 37) was a large stainless steel sled (length: 1500 mm, width: 1700 mm, height: 1250 mm, weight: 340 kg, about 100kg in water using 272L floats) equipped with an anodized aluminum housing that can hold a camera (here, a Panasonic HC-V700 or a GoPro Hero 4 or 5), a pair of LED lights (underwater LED SeaLite® Sphere, SLS 5100, 20/36 V, 5000 Lumens or SLS 5150, 20/36 V, 9000 Lumens) fixed on each side of the camera, two laser pointers (SeaLasers® 100 Dualmount, wavelength 532 nm Green) placed 100 mm from each other and two subCtech Li-Ion PowerPacks (25Ah, 24V) to power the lights and lasers (Sheehan et al. 2016).

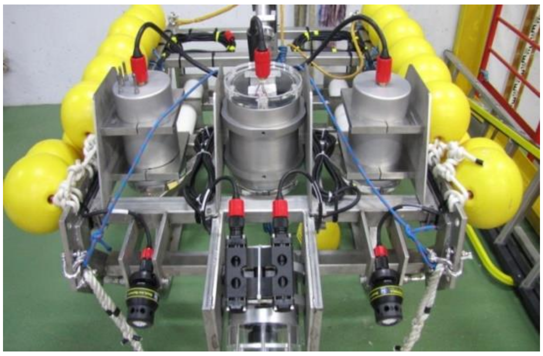


Figure 37: Photography of Pagure 1

The second device (Pagure 2; Figure 38) is larger (length: 2000 mm, width: 1100 mm, height: 740 mm, weight: 450 kg, 30 to 100kg in water using 272-380L floats depending on currents and bottom hardness). Some equipment was also different between the small device and this larger device: the camera (here, Panasonic HC-V700 or Sony PXW-Z90), four LED lights (a pair of each light listed above) powered by an additional battery (subCtech Li-Ion PowerPack, 70Ah, 25.2V).

Figure 38: Photography of Pagure 2

As the exact position of the video system during the haul was not known, the transect positions were trigonometrically back-calculated using GPS coordinates, vessel bearing and dimension, sounded depth and towing cable length along the 15 min transect.

2.1.2. Video image analysis

Analyses of the videos were performed image by image with the Avinotes software, specially developed by J.C. Duchêne to annotate video images. Between 700 and up to a maximum of 1200 video frames (approximately half of transect) were analyzed depending on video quality. For each transect, a visual evaluation of the image quality was performed with a classification system taking into account parameters related to sledge deployment (system stability and traction speed) and water turbidity (Table 23). A quality score, varying from good (3) to bad (9) image quality, was determined for each video transect by summing up the scores for each parameter.

Table 23 : Image quality classification parameters and their associated scores

Scores	Moving Speed	Stability	Turbidity
1	Constant speed and approximately less than 1 knot over the entire transect	The camera is correctly oriented (towards the bottom) over at least 1200 consecutive images.	The entire vision field is clearly visible
2	A few accelerations of the device but the average speed remain around 1 knot.	The camera is correctly oriented for 1200 non-consecutive images	Far vision field blur and many suspended particles but counting windows can still be analyzed
3	Approximately 50% of the transect images are not analyzable	The camera is correctly oriented over less than 1200 images over the entire transect.	Degraded identification and counting conditions in counting windows

A visual determination of sediment type (boulders, gravel, mixed sediments, sand and muds) was also carried out for each video transect.

Using laser pointers materializing a counting window on each image, it was possible to know the surface of the seabed sampled on each image. Special care was taken during the manual creation of this window so that it would not overlap from one image to another and create an overestimation of the sampled surfaces. On each image, all organisms present in the counting window were identified to the highest taxonomic level possible (Figure 39) and their abundance recorded even for colonial species for which the number of colonies was determined. The surface sampled per profile was then determined by multiplying the average area of the counting windows by the number of images analyzed. The average areas of the counting window were slightly different between the two towed video system with an average of 1032 cm^2 for the Pagure 1 and 1588 cm^2 for the Pagure 2. Data were standardized according to the average counting window area and expressed in $ind.m^{-2}$.

Taxonomically and morphologically similar organisms, like the crinoids *Leptometra sp*. and *Antedon sp*. which could not be distinguished at species or even genus level, were grouped at family level as Antedonidae.

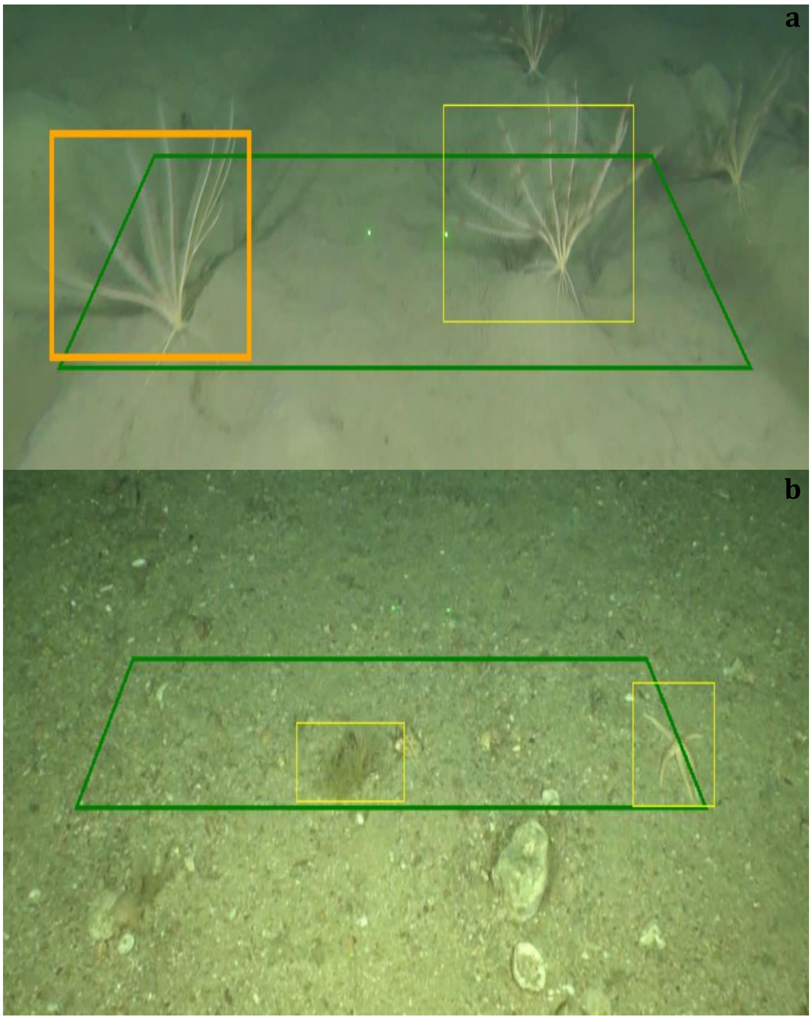


Figure 39: Example of organisms identified and counted in the counting window (green line) with video device.
(a) Two individuals of Antedonidae in a sampling area of 1531 cm^2. (b) On the right, a starfish of the genus *Henricia* and on the left, a colony of hydrozoans , in a sampling area of 2748 cm^2.

2.2. Abrasion and habitat data

The abrasion value at each sampled station (Table 24) of the two studied areas were determined from maps (Figure 25 & 40) of swept surface area ratio per year ($SAR.y^{-1}$), based on VMS data (Chapter I).

Table 24: Abrasion ranges of the sampled stations in the two studied areas.
The three abrasion values represent the minimum value, median and maximum value.

	Gulf of Lion	English Channel
Sampled abrasion range ($SAR.y^{-1}$)	0.08 – 4.65 – 20.87	0.29 – 10.92 – 72.34
Abrasion range ($SAR.y^{-1}$) of paired stations	0.08 – 4.91 – 20.87	0.29 – 8.73 – 72.34

In the Gulf of Lion, the visual determination of sediment type did not reveal different habitats, mainly because of small differences in granulometry that are difficult to observe on video. The different habitat types were therefore defined by EUNIS level 3 (Populus et al. 2017; www.emodnet.eu). Stations were categorized in two habitats: Sublittoral mud (A5.3) which includes the subtidal cohesive sandy muds and Sublittoral mixed sediments (A5.4) which includes a range of sediments, including heterogeneous muddy and gravelly sands (Figure 14 & 40).

In the English Channel, the absence of significant variation in depth between the stations allowed this factor to be disregarded in the characterization of sampled habitats. Thus, habitats were categorized, based on the visual definition of sediment type observed, into two classes: coarse or mixed sediments (sediments composed of mud, sand, gravel in variable proportions; Figure 36).

Paired trawl stations were assigned the same habitat types as those determined in video transect as in videos.

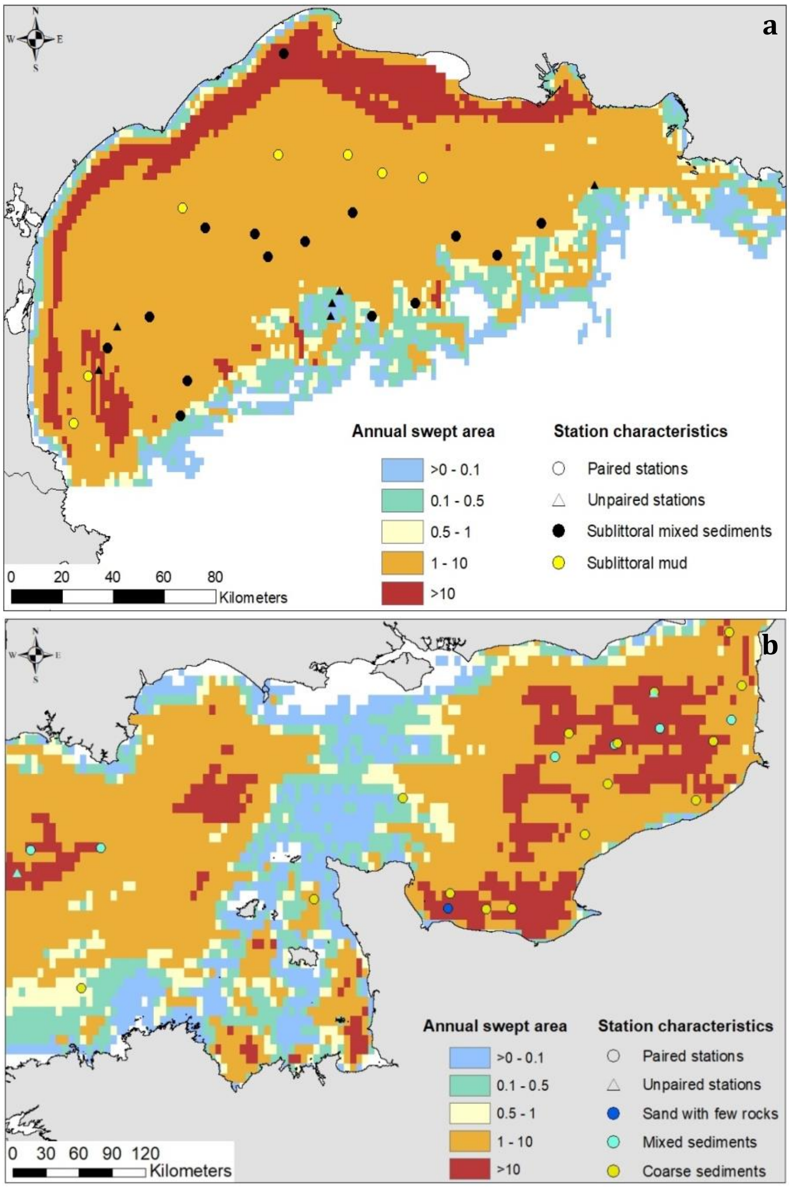


Figure 40: Location and sedimentary characteristics of video stations in the Gulf of Lion (a) and in the English Channel (b). The annual swept area was 90th inter-annual percentile of the abrasion in during the period 2009-2017

2.3. Biotic indices investigated

Four common taxonomic diversity indices were calculated: species richness (SR), Shannon diversity, Pielou evenness and Simpson index. These indices were calculated in R, using the vegan 2.5-2 package (Oksanen et al. 2019). The four functional sensitive indices (TDI, mTDI, pTDI and mT) were also calculated.

None of the other indices presented in Chapter 1 were calculated in this chapter because the low diversity of taxon on several video transects results either in an impossibility to calculate these indices [for example a minimum of 6 taxa is required to calculate functional indices because the number of species must be higher than the number of traits (Villéger et al. 2008)] or in a decrease in the robustness of these indices [it is the case for Margalef index or AMBI (Grall and Coïc 2006)].

For trawling data, the results of chapter 2 showed that functional sensitivity indices were the best indices to evaluate the impact of trawling on benthic communities but, in this chapter, only the indices selected based on video data were also recalculated with scientific trawl data for comparison purpose.

2.4. Data analyses

2.4.1. Indices evaluation and selection for video derived data

To find the most appropriate indices, generalized linear models (GLM) were used to investigate which variables (abrasion, habitat, camera type, device type and image quality) influenced the indices calculated with video data (using all video data available here). As benthic communities do not respond equally to trawling in different habitats (Kaiser et al. 1998), the interaction between habitat and abrasion was also included in GLMs. For each GLM, the variables were selected using forward procedure based on the Akaike Information Criterion using the MASS package 7.3-51.5 (Ripley et al. 2019). The goodness of fit of the model was assessed by performing a $\chi 2$ test between the null and the selected model.

Indices were first retained if no variables related to the video system specification (camera, video system and image quality) influenced the model. These indices were then selected if the regression coefficient for abrasion was negative and significant.

2.4.2. Comparison between the two sampling methods

To assess the relevance of each of the two sampling methods to monitor the impact of trawling on benthic communities, only paired stations were used for the following analyses.

Community description

For each sampling method in the two study areas, the number of sampled taxa was counted, and the proportion of each taxonomic level was evaluated to better understand the differences in catchability between the two methods. Underwater video techniques usually allow to observe only large (> 5 cm) epifauna (Mérillet et al. 2017). The diversity of biological traits sampled with trawling and video was evaluated by comparing functional spaces of all studied areas. Functional space can be defined as a multidimensional space where the axes are functional traits along which species are placed according to their functional trait values (Mouillot et al. 2013a). Thus a Multiple Correspondence Analysis (MCA) was performed in each area on the species-traits matrix, with the package PCAmixdata 3.1 (Chavent et al. 2017) to build a multidimensional functional space with axes corresponding to synthetic traits summarizing several raw traits.

In order, to identify, differences in the structure of the communities sampled with each of the two methods, the proportion of species belonging to the different categories of the trait "Position of organisms in the sediment" was studied. This analysis was not conducted on the other biological traits because the diversity of these traits within the community is not expected to vary as a result of the sampling methods.

Monitoring of trawling impact

An assessment of the relevance of each of the sampling methods for monitoring the impact of trawling on benthic communities was carried out using statistical regression and tests (only paired stations were used for the following analyses). In each area and for the two sampling methods, generalized linear models (GLM) were used to investigate which variables (abrasion and habitat), influenced previously selected indices. Interaction between habitat and abrasion was also included in GLMs. The most significant variables were selected for each GLM using forward procedure based on the Akaike Information Criterion using the MASS package 7.3-51.5 and the goodness of fit of the model was assessed by performing a $\chi 2$ test between the null and the selected model. For each index, the regression coefficient for abrasion and the R-squared values were compared between the different sampling methods to evaluate which is the most appropriate for monitoring trawling impacts on benthic communities.

3. Results

3.1. Indices evaluation and selection for video derived data

All indices considered in this study were not influenced by the same variables even if, in many cases, the habitat effect was significant (Table 25). Characteristics of the video system used (device or camera type and image quality) were selected in models, only for few indices like SR, Shannon or Abundance. Meanwhile, only sensitivity indices (TDI, mTDI, pTDI and mT) were significantly influenced by the abrasion. As TDI was also influenced by a variable related to the video system (camera type) which is not a desirable property, it was not selected for further analysis. Graphic representation of relationship between the three selected sensitivity indices and abrasion were performed (Figure 41 & 42).

Table 25: Variables retained by the model selection procedure for each index over the totality of the analyzed videos (Gulf of Lion and English Channel). Grey shading indicates indices meeting the selection criteria (negative relationship between abrasion and lack of significant relationship to image quality)

Indices	Selected explanatory variables	Regression coefficient for abrasion (and significance level)
SR	~ Device+ Image quality + Habitat + Abrasion	- 0.012
Shannon	~ Habitat + Device	-
Simpson	~ Habitat	-
Pielou	~ Habitat	-
Abundance	~ Habitat + Camera + Device	-
TDI	~ Abrasion + Camera	- 0.092***
mTDI	~ Abrasion	- 1.989***
pTDI	~ Abrasion	- 0.036***
mT	~ Abrasion + Habitat	- 0.012***

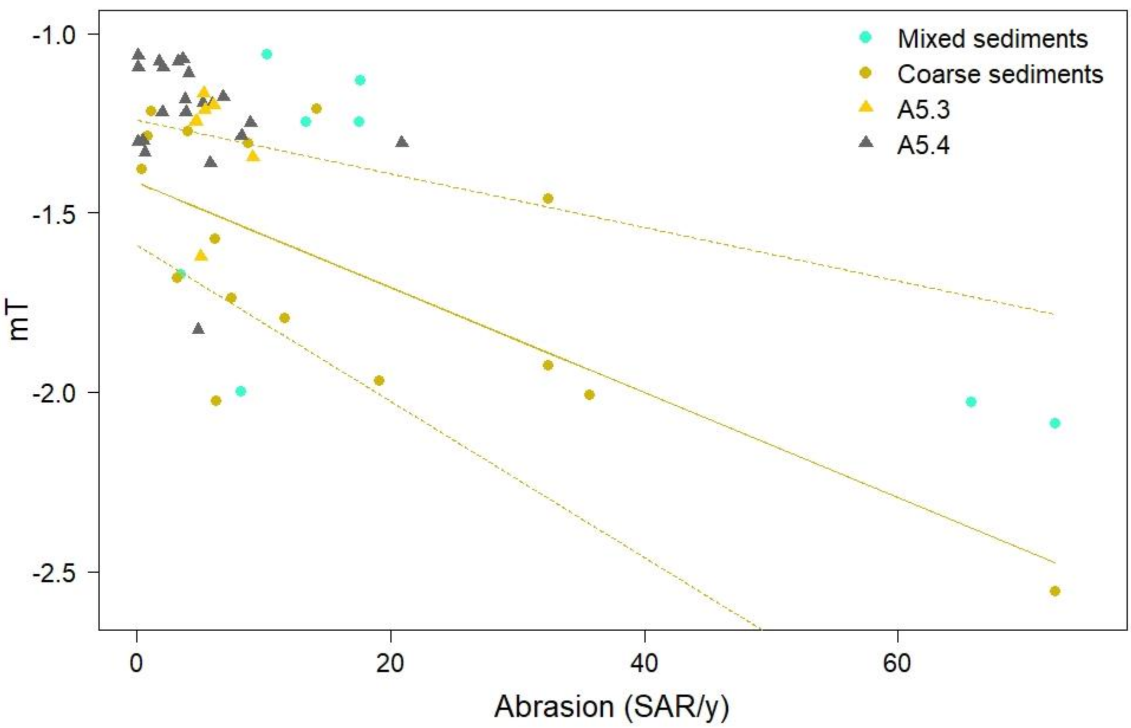


Figure 41: Relationships between mT index and fishery abrasion in all habitats.

The relationship was significant and negative only for habitat "Coarse sediments" (gold line and 95% confidence interval in dashed line). ● Stations in the in the English Channel; ▲ Stations in the Gulf of Lion.

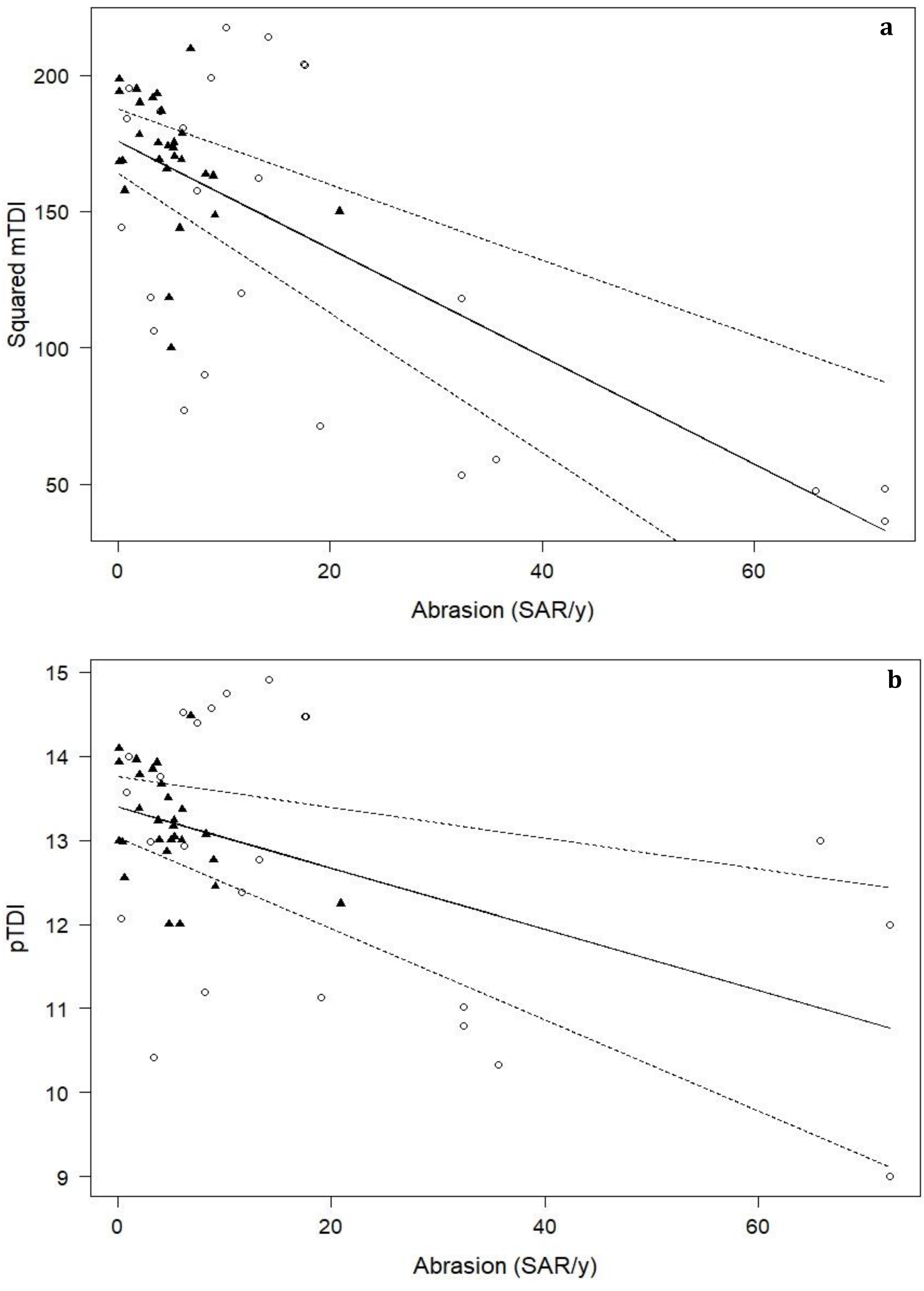


Figure 42: Relationships between mT index and fishery abrasion in all habitats.

The relationship was significant and negative only for habitat "Coarse sediments" (gold line and 95% confidence interval in dashed line). ● Stations in the in the English Channel; ▲ Stations in the Gulf of Lion.

3.2. Differences in the sampled community between the two sampling method

In both study areas and using both sampling devices, it was not always possible to identify the encountered organisms at species level. The total number of taxa therefore indicated the number of different organism types distinguished at the lowest taxonomic level possible.

In the English Channel, despite a significantly larger area sampled by trawling than by video (Table C.1), a greater number of taxa were observed by video (Table 26). A total of 88 taxa representing 53 families, 28 orders and 8 phyla were observed on video and 74 taxa representing 44 families, 26 orders and 8 phyla were sampled by trawling. Only 29 species were found with both sampling methods.

On the opposite, in the Gulf of Lion, a high number of taxa were collected by trawl with 134 taxa representing 89 families, 39 orders and 10 phyla against 39 taxa representing 27 families, 19 orders and 7 phyla observed on video. Only 19 taxa were common to the two sampling methods.

Table 26: Number of taxa by sampling method and areas

Taxonomic level	Areas	Trawl	Video
Taxon	Gulf of Lion	134	39
	English Channel	74	88
Species	Gulf of Lion	92	14
	English Channel	54	50
Genus	Gulf of Lion	96	26
	English Channel	49	57
Family	Gulf of Lion	89	27
	English Channel	44	53
Order	Gulf of Lion	39	19
	English Channel	26	28
Phylum	Gulf of Lion	10	7
	English Channel	8	8

Looking at the sensitivity of the most represented (> 5% of the total abundance or biomass) taxa in terms of biomass or abundance in each area, it appears that these results were very contrasted between the sampling methods (Table 27). Indeed, very few species in video data are considered as non-sensitive while almost half of the species dominating the trawl-collected assemblage were non-sensitive. In the English Channel, three species were dominant in video and trawl data (*Ophiothrix fragilis*, *Psammechinus miliaris* and *Alcyonium digitatum*). In the Gulf of Lion, the dominant taxa observed by video were Cnidarians (Antedon sp., *Funiculina quadrangularis* and *Cavernularia pusilla)* while the trawl samples were dominated by Echinoderms (*Gracilechinus acutus*, *Parastichopus regalis* and *Astropecten irregularis pentachanthus*) and Cnidarians (*Antedon sp.* and *Funiculina quadrangularis*).

Table 27: Dominant taxa observed with the two sampling methods in the two studied areas and their sensitivity score (SI; Foveau et al. 2019). Green shading indicates that the species is considered less sensitive to trawling (SI ≤ 7).

Areas	Device	Species	SI
English Channel	Video	*Ophiothrix fragilis*	*11*
		Mytilus sp.	*11*
		Sertularia sp.	*15*
		Psammechinus miliaris	*7*
		Alcyonium digitatum	*15*
		Porifera	14
	Trawling	*Asterias rubens*	*7*
		Psammechinus miliaris	*7*
		Necora puber	*6*
		Ophiothrix fragilis	*11*
		Alcyonium digitatum	*15*
Gulf of Lion	Video	*Antedon sp.*	*13*
		Funiculina quadrangularis	*14*
		Cavernularia pusilla	*13*
	Trawling	*Gracilechinus acutus*	*10*
		Parastichopus regalis	*12*
		Antedon sp.	*13*
		Funiculina quadrangularis	*14*
		Liocarcinus depurator	*6*
		Astropecten irregularis pentacanthus	*8*

Despite identification to the species level more frequent by trawl than by video, more than 65% of the taxa were identified to the genus level regardless of the type of sampling (Figure 43a).

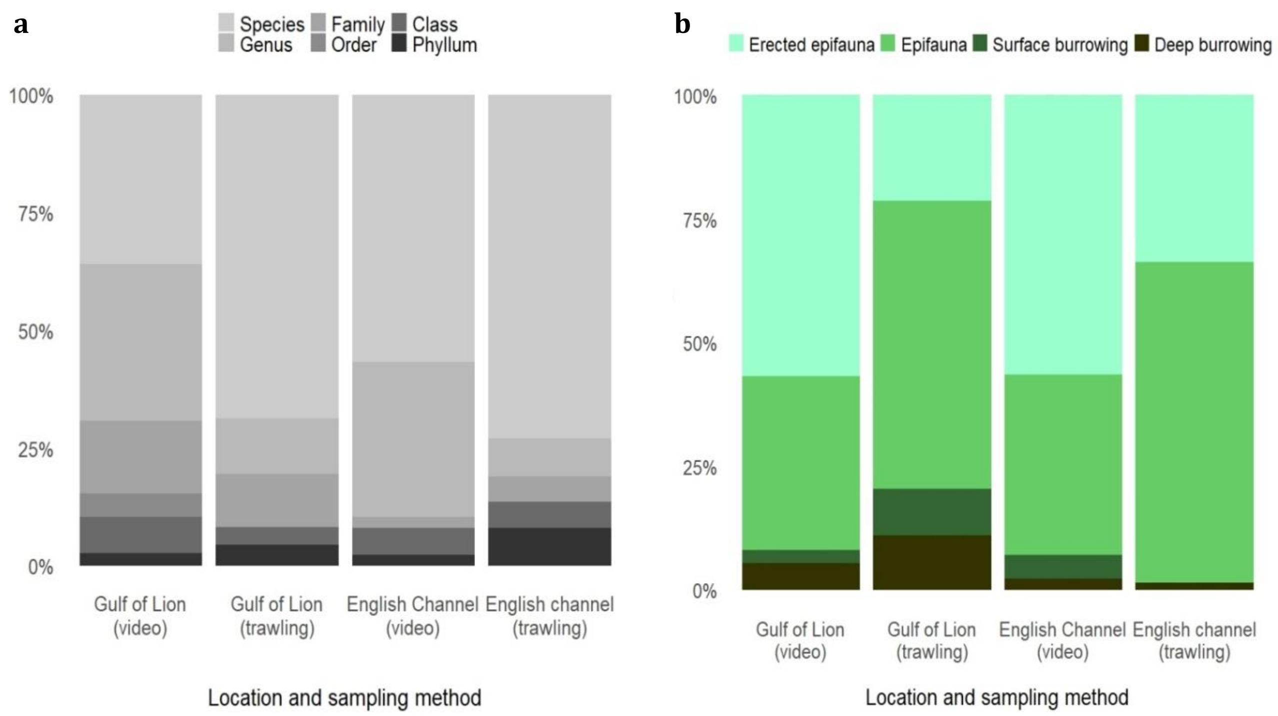


Figure 43 : Proportion of each taxonomic level identified (a) and category of position with the two sampling method in the two studied areas (b)

The proportion of sampled infauna represents less than 20% of the sampled taxa regardless of the type of sampling. The main difference observed between trawling and video results from the type of epifauna observed, particularly in the Gulf of Lion (Figure 43b) : more than 55% of the fauna observed by video and less than 35% of that sampled by trawl were erected epifauna (34 % in the English Channel and 21% in the Gulf of Lion).

Individuals caught by trawl have a greater functional diversity than those observed on video, particularly in the Gulf of Lion (Figure 44).

In the English Channel, only very few differences are observed between trawl and video sampling functional spaces. However, the dominant taxa were different for each sampling type. For trawling, the assemblage of taxa was dominated by individuals that are small, mobile, living at the surface or in the first few centimeters of sediment, which are not fragile and are mainly scavengers or deposit feeders/predators. For video sampling, the taxon assemblages observed were dominated by sessile individuals, emerging, fragile and mainly filter feeders, but also by medium-sized and flexible taxa.

In the Gulf of Lion, the trawl caught mostly large, unprotected, sedentary and burrowing individuals also some sessile, emerging, fragile and mainly filter feeders while no particular taxa dominance was observed by video. Moreover, highly mobile individuals are totally absent from the videos in this area.

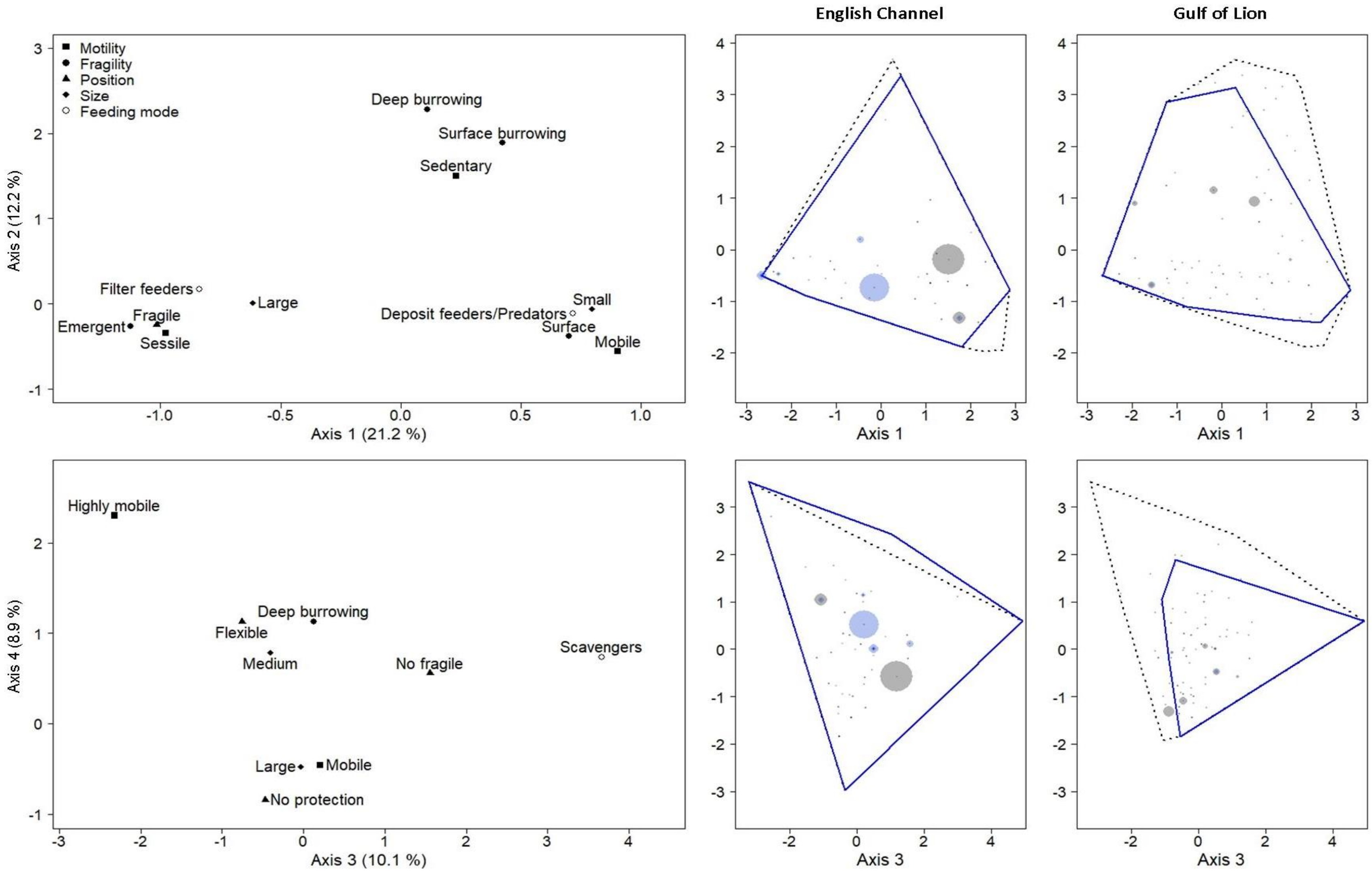


Figure 44: Multiple Correspondence Analyses of the functional traits of the different taxa observed on video and/or sampled by scientific trawling and functional space for axes 1-2 (21.2% and 12.2% variance) and axes 3-4 (10.1% and 8.9% variance) for trawl sampling (dotted polygon) and video sampling (blue line) in the English Channel and in the Gulf of Lion. The species are represented by points of diameter proportional to their density (blue points) for video sampling and their biomass (grey points) for trawling sampling.

3.3. Monitoring of trawling pressure: comparison between the two sampling methods

The comparative analysis of the influence of abrasion and habitat on selected indices computed from both sampling types is presented in the table 28 for each studied area.

In the Gulf of Lion, whatever the gear used or the index studied, abrasion never seems to significantly influence the index.

In the English Channel, results are more contrasted. For the mTDI, habitat had a significant influence on the index with trawl sampling whereas it was the abrasion that had an influence with video sampling. For pTDI, no significant relationship was observed with habitat or abrasion and in the case of video sampling but habitat had a significant influence on the index when using trawl sampling. Finally, for the mT, the two sampling methods allowed to detect significant relationships to abrasion and the R-squared was higher when using the video derived data

Table 28: Outcomes of the stepwise selection procedure on the generalized linear models.
GoL = Gulf of Lion. E.C = English Channel. * indicates that P<0.05 ; ** indicates that P<0.01 ; *** indicates that P<0.001; n.s indicates no significant effect. No explanatory variable indicates that the null model was selected.

		Video			**Trawling**		
Indices	**Areas**	**Explanatory variable**	**Significance**	**$AdjR^2$**	**Explanatory variable**	**Significance**	**$AdjR^2$**
mTDI	GoL	-	-	-	Abrasion Habitat	n.s *	0.86
	E.C	Abrasion	***	0.61	Habitat	**	0.79
pTDI	GoL	Abrasion	n.s	0.29			
	E.C	Abrasion	n.s	0.07	Habitat	**	0.57
mT	GoL	-	-	-	Habitat Abrasion	* n.s	0.26
	E.C	Abrasion	***	0.87	Abrasion Habitat	* n.s	0.80

4. Discussion

4.1. Differences in catchability

In the two geographic areas studied here, although the difference in sampling area between trawl and video was similar, the differences in catchability between the two sampling methods were very different. The number of taxa observed with the video was slightly higher than the taxa caught with the trawl (88 vs. 74) in the English Channel and lower (39 vs. 134) in the Gulf of Lion. Several parameters may explain these differences.

First of all, the higher proportion of infauna in trawl samples collected in the Gulf of Lion can be explained by the sediment type. The Gulf of Lion is characterized by the presence of soft sediments (Populus et al. 2017 ; www.emodnet.eu), whereas bottoms sampled in the English Channel have a higher granulometry and are sometimes even composed of blocks (Coggan and Diesing 2011).

As trawl penetration is lower in coarse sediments than in fine sediments (Eigaard et al. 2016), the gear catchability of the infauna is greater in areas of fine sediments. Reflecting these substrate differences, the trawls used in the English Channel and the Gulf of Lion were different (ICES 2015; MEDITS 2017), which may have increased the difference in the catchability of benthic fauna between these two gears. The gear used in the Gulf of Lion has a greater catchability of infauna than that of English Channel. In contrast, results obtained in the English Channel seem to indicate that in coarse sediment areas, video allows the observation of a greater diversity of species than does the trawl, probably because the trawl catchability of epibenthic species fixed on boulders is relatively low. Finally, the habitat type plays a major role on the species density and occupancy. Epifaunal species number and density were much higher on coarse habitats while it often exhibited overly dispersed distribution on bare soft sediments. This mostly explains the difference in diversity observed between the two areas for comparable surface sampled and also the differences between video and trawled observations in the Mediterranean.

Secondly, two slightly different devices were used for video transects and even though they were both used in both areas, the majority of transects in the Gulf of Lion was performed with a smaller device than in the English Channel, where a larger device was mostly used. Although the size of the observed areas is known to influence the number of species sampled (Crist and Veech 2006), no significant difference was found in the sampled surfaces with both video systems. Yet, the use of different devices had significant effect on the estimation of species richness, Shannon diversity and abundance and may partly explain the difference in diversity observed by video sampling between the two areas. Moreover, although neither sampling techniques are suited to capture infauna, the fact that much more could be caught by trawl in soft sediments may explain the differences in species diversity between trawl and video sampling in the Gulf of Lion.

4.2. Taxonomic identification of individuals

Regardless of the study area, the proportion of individuals identified at the species level is higher with trawls than with videos. This is particularly marked in the Gulf of Lion, where nearly 70% of the 134 taxa collected by trawls were identified down to the species level, compared with 36% of the 39 taxa observed on the video transects. One of the main disadvantages of using video alone is that identification at species level is particularly difficult (Flannery and Przeslawski 2015). Species-level identification often requires sampling of specimens coupled with magnifier observations and expert knowledge (Althaus et al. 2015). Determination of taxa as sponge species for which the differences between two species may require the examination of the spicules cannot be differentiated on video images. The species richness of a site may be underestimated if the species count was only done on video because several individuals may be grouped under the same taxa even though they belong to different species. However, for approaches based on the use of functional traits, the genus level is often sufficient to define the biological characteristics of individuals (Brind'Amour et al. 2009; Foveau et al. 2017). In this study, the rate of identification at the level of the genus appeared to be relatively close between the two sampling methods (70% of observed taxa for the video compared with 80% of taxa sampled with the trawl in the Gulf of Lion and 89% for the video compared with 82% for the trawl in the English Channel). Identification difficulties, intrinsic to video imagery, seem to have relatively little influence on approaches based on species biological traits. However, to overcome these methodological limitations, a “short list” only focusing on relevant sensitive species may be used to perform video analysis.

4.3. Functional diversity

The taxonomic diversity of a community does not always reflect the diversity of its functional structure (Törnroos and Bonsdorff 2012), which is defined as the quantification of the position that different species occupy in the ecosystem (Mouillot et al. 2013b). When several species perform similar functions, the reduction in species diversity may not have any influence on the functional structure of the community (Mouillot et al. 2014). In the English Channel, despite a greater number of species observed by video than by trawling, the species communities observed by both gears had a similar functional space. Therefore, despite a relatively different number of species, video observed or trawl sampled communities supported about the same number of biological traits. Despite this very significant overlap between the two functional spaces, notable differences in the type of dominant species could be highlighted with species assemblage dominated by mobile, living at the surface and mainly predator species for the trawl sampling and dominated by sessile, emergent, fragile and mainly filter-feeding species but also by medium sized and flexible species in video observations. In the Gulf of Lion, contrary to what was observed in the English Channel, the number of species collected and the proportion of infauna species was higher in the community sampled by trawl than that observed on video. As a result, the fauna collected by the trawl also had greater functional diversity (measured as functional space) than that observed by video.

Several parameters could explain the differences between the two sampling methods. Firstly, the dominance of emergent species and the lack of burrowing species on video transects in both areas are easily explained as video observations are limited to the surface of the sediment. In contrast, for the trawl data, in the English Channel, the dominance of mobile species living at the surface could be due to the relatively low penetration of the trawl in coarse sediments, hence resembling that of the video data. The opposite is observed in the Gulf of Lion where the trawl may penetrate much deeper the fine muddy sediments (Eigaard et al. 2016), thus resulting in higher infaunal diversity. Finally, with the video system moving at a maximum of 1 knot with an observation field around 1.3 meters wide, mobile species capable to move fast or to quickly retract in the sediment can escape detection while, with a towing speed of 3-4 knots and about 20 meters horizontal opening (ICES 2015; MEDITS 2017), very few mobile invertebrates or overly dispersed species may avoid capture by trawling. Regarding these results, the two sampling methods seemed complementary. The video device allowed to observe mainly fixed epifauna, regardless of the habitat sampled, this portion of the benthic community appearing, in the present work, relatively poorly sampled by the trawl on coarse habitats. Conversely, trawling was able to capture a greater diversity of infauna species on soft bottoms where this portion of the benthic community is dominant.

4.4. Indices evaluation and selection for video derived data

The procedure for selecting the factors influencing the different indices showed all of the taxonomic diversity indices tested (RS, Shannon, Simpson, Pielou and abundance) were influenced by the type of habitat. Only the species richness was influenced by the abrasion. Although the sampling method differs, these results are partly consistent with those presented in the meta-analysis carried out by Hiddink et al. (2020). Pielou and Shannon did not respond significantly to trawling, as opposed to the species richness. However, as the type of video gear also has an influence on species richness, this index does not seem to be appropriate for studying the effect of trawling on benthic communities when sampling is carried out using towed video. Hiddink et al. (2020) also found that abundance was strongly influenced by trawling, however, this was not found to be the case in the present study. This difference probably stems from the fact that the benthic community observed is not the same since video sampling only allows us to observe a particular portion of the benthic fauna: the erected megafauna.

For the sensitivity indices, only the mT was influenced by this factor. Since both study areas were included in this analysis, the habitat effect is likely more of a "geographical" effect than an effect of the type of sediment sampled. The number of taxa observed was more than twice as high in the English Channel than in the Gulf of Lion (88 vs. 39). The absence of influence of the habitat factor and therefore of the "geographical" effect, on three functional sensitive indices suggested that despite a greater taxonomic diversity in the English Channel compared to the Gulf of Lion, the response of benthic communities' sensitivity to trawling was not significantly different between the two areas.. For the mT index, the habitat factor influence could be related to the addition of the species protection status factor, not taken into account in the calculation of the other functional sensitive indices. Some species are protected in only one of the two study areas. This is the case for sponges of the genus *Tethya sp.*, protected in the Mediterranean Sea (OCEANA 2016) but not in the English Channel (OSPAR 2008). In addition, of all the individuals observed in the Gulf of Lion, 12 of the 39 observed taxa had a protected status, whereas in the Channel, this concerns only 4 of the 88 taxa. Taking into account emblematic species significantly impacted the mT index values and caused a differentiation between the two study areas. As benthic communities do not respond in the same way to trawling in different habitats (Kaiser et al. 1998), the habitat influence on the tested indices was not considered problematic here.

Two criteria allowed to select video derived indices that could monitor the trawling effects on benthic communities in the two areas studied: the presence of a significant negative influence of abrasion on the index and the absence of influence of device characteristics. Only three indices met both of these criteria: mTDI, pTDI and mT. A previous study based on scientific trawl data also suggested that these indices could be used to monitor the effect of trawl pressure on benthic communities in the English Channel, the North Sea, the Gulf of Lion and Corsica (Jac et al. 2020a, 2020b; Chapter II & V). As these three indices are based on the same set of biological characteristics and are selected for their significant correlation with abrasion, they are highly correlated. However, Jac et al (2020a; Chapter II) showed that, depending on the area studied, the same indices do not have the highest correlation with abrasion. Thus, although they are closely related, it seems difficult to select only one of them for the assessment of the impact of trawling on benthic communities. Monitoring the effects of trawling on benthic communities should therefore be carried out at a finer resolution (e.g. EUNIS level 4) by choosing the most sensitive index in the area studied (in application of the precautionary approach).

4.5. Monitoring of trawling pressure based on video transects?

In the Gulf of Lion, no significant influence of abrasion was detected on the three functional sensitive indices calculated with trawling data but significant influence of the habitat type was detected on mT and mTDI. These results, correlated with the lack of a significant effect of habitat on the pTDI index, suggest that the differences between habitat types were primarily related to low-sensitivity species as only the most sensitive species were included in the pTDI calculation (Jac et al. 2020a; Chapter II). This could also explain the absence of habitat effects on indices calculated from video derived data, since the species considered most sensitive are generally those of the fixed epifauna (Foveau et al. 2019) which are the species mainly observed on videos. These different results indicate that habitat affects mainly species with lower sensitivity (*i.e.* mobile species or infauna species) and has little to no influence on video observations. The results obtained by Labrune et al. (Labrune et al. 2008) indicating that there are clear links between polychaete assemblages and both bathymetry (between 10 and 50 meters in their study) and sediment grain size in the Gulf of Lion, tend to support this hypothesis.

The lack of relationship between abrasion and the different indices for the two sampling methods could be explained by the small number of stations sampled and the unbalanced distribution of these stations along the abrasion gradient. Jac et al. (2020a) found a significant effect of abrasion for habitats A5.46 (Mediterranean communities of coastal detritic bottoms) and A5.47 (Mediterranean communities of shelf-edge detritic),- grouped here as A5.4 - with a larger and better distributed dataset along the abrasion gradient (abrasion vary between 0 and 20.77 $SAR.y^{-1}$ with a median of 2.69 $SAR.y^{-1}$). Their results suggest that an increase in the number of stations sampled, particularly in areas of low abrasion, could enable the detection of a significant and negative relationship between the indices studied and abrasion. For the habitat A5.3 (sublittoral mud), results were consistent with those of Jac et al. (2020a) which pointed out the lack of a significant relationship between abrasion and the different indices in habitats A5.38 (Mediterranean communities of muddy detritic bottoms) and A5.39 (Mediterranean communities of coastal terrigenous muds), They interpreted this lack of relationship as reflecting that the original communities of these habitats had already been completely replaced by communities adapted to trawling. Thus, in the present study, as 50% of the sampling was carried out in areas with abrasion levels higher than 4 $SAR.y^{-1}$, the lack of relationship between the indices and the level of abrasion most likely also reflects the replacement of the original communities by communities fully adapted to trawling.

In the English Channel, results obtained with scientific trawl data appeared similar to those obtained in the Gulf of Lion. Habitat had a significant effect on two of the three indices (mTDI and pTDI) like in the Gulf of Lion. Contrary to what was observed in the Gulf of Lion, mT was significantly influenced by abrasion, even though habitat was still a selected parameter, but not significant in the model. The different response of the mT index from those of mTDI and pTDI could again be explained by the addition of the "protection status" factor in the calculation of mT or by the different computation of biological traits between the mT and TDI-derived indices (Certain et al. 2015; Foveau et al. 2017; Jac et al. 2020a). The relatively lower r^2 for the relationship between pTDI and abrasion than for mTDI (0.59 vs. 0.80) seemed to indicate that, as in the Gulf of Lion, habitat mainly affects species with low sensitivity.

The relationships between the video-derived indices and the parameters studied (abrasion and habitat) contrasted with those obtained with trawl sampling. For the three indices, the habitat parameter was not selected in any model and abrasion had a highly significant influence on mTDI and mT. The fraction of the benthic community that could be observed in the video appeared to be particularly sensitive to abrasion and regardless of the habitat studied. However, a great similarity between the functional spaces of the communities sampled with the two methods was observed. Differences in the behaviour of the indices in relation to the parameters studied could be explained by the metrics used in the two sampling methods, biomass data for trawling and abundance data for video. However, since trawl catches sessile epifauna with difficulty, their biomass may be underestimated in relation to their abundance in the area and thus induce differences in the behaviour of the indices between the two sampling methods. Furthermore, the absence of habitat effect on the video indices suggests that the abundance of the species observed in the video is not significantly influenced by the habitat type. Results obtained with data from scientific trawling seemed to indicate that habitat had an effect mainly on species with low sensitivity. This therefore suggests that the portion of the benthic community not observed in the video (mobile species, small individuals, etc.) and potentially not very sensitive to trawling may differ from one habitat to another.

In conclusion, data collected from the video sampling seemed to detect a significant negative effect of abrasion while avoiding the effect of habitat type in the English Channel. The use of a towed video method appears more reliable than the use of benthic megafauna data collected during scientific trawling surveys to monitor the effect of trawling on benthic communities in coarse and mixed sediments. As the strength of the relationship (as measured by r^2) between mT and abrasion appeared higher than that of mTDI, mT seemed to be the most appropriate index in this type of environment. However, in the Gulf of Lion, where the sediments are relatively fine, no method was conclusive to assess the effect of trawling on benthic communities because, in most cases, and although generally high, abrasion could not be related to the indices. Video sampling therefore seems particularly interesting for habitats consisting mainly of hard substrates (gravel, boulders, shell sands, etc.). On soft sediment, this methodology may require a much larger observation effort (larger surface observed) and both an increase in the number of stations sampled and a stronger abrasion gradient to verify its usefulness. A recent study has shown that the size of individuals has an influence on the response of a number of indicators to the effect of trawling. Large benthic megafauna seemed to be more impacted by trawling than small benthic fauna and less impacted by various environmental parameters such as depth or granulometry (McLaverty et al. 2020). Towed video, mainly sampling the large benthic megafauna in a non-destructive way, appears to be a good tool for monitoring the effect of trawling on benthic communities. Future work should be considered to determine whether size measurements of benthic megafauna' individuals, on video images, could become useful indices to monitor the effect of trawling on benthic communities.

Inter Chapitre

Le quatrième chapitre de cette thèse a permis de constater que l'imagerie vidéo peut être une méthode d'échantillonnage pertinente pour suivre l'impact des arts traînants sur les communautés benthiques attachées aux sédiments grossiers. Les résultats issus de ce chapitre ont également confirmé la pertinence, déjà soulignée au chapitre II, des indicateurs basés sur la sensibilité des espèces au chalutage, pour suivre l'impact des arts traînants sur les communautés benthiques des plateaux continentaux.

Dans le cadre de la DCSMM, les indicateurs doivent permettre d'évaluer l'état écologique de différentes composantes de l'écosystème marin. Pour le descripteur portant sur l'intégrité des habitats benthiques, le pourcentage d'habitat étant impacté ou à l'inverse en bon état écologique doit être déterminé.

L'objet de ce cinquième chapitre est donc de développer une méthodologie permettant de connaître, pour chaque habitat, la superficie et l'état des habitats impactés par les arts traînants.

Chapitre V: How much of seabed habitats are left in good environmental status by fisheries?

Ce chapitre est basé sur un article sous presse dans la revue *Ecological Indicators*

Jac C., Desroy N., Certain G., Foveau A. Labrune C., Vaz S. 2020. Detecting adverse effect on seabed integrity. Part 2: How much of seabed habitats are left in good environmental status by fisheries? Ecological Indicators. *In press*. https://doi.org/10.1016/j.ecolind.2020.106617

Résumé de la publication en français

En mettant en relation les changements observés et les pressions subies, la Directive Cadre Stratégie pour le Milieu Marin vise à mieux contrôler les facteurs de dégradation de l'environnement et à gérer leurs conséquences dans les eaux européennes. Plusieurs descripteurs sont définis dans le cadre de cette directive, notamment les descripteurs 1 relatif à la diversité biologique des fonds marins et 6, relatif à l'intégrité des fonds marins (c'est-à-dire la qualité de leurs structures et de leurs fonctions). Pour chaque descripteur, des indicateurs et des valeurs seuils doivent être définis. Une nouvelle approche conceptuelle pour définir et détecter les seuils d'intégrité des fonds marins est proposée ici. Le chalutage de fond étant la principale source de perturbation du plateau continental, il est important d'évaluer son impact sur l'habitat benthique. L'objectif de cette étude est de proposer une méthodologie pour déterminer les valeurs seuils de "bon état écologique" pour chaque type d'habitat présent dans trois sous-régions DCSMM très contrastées (la mer du Nord, la Manche et la mer Méditerranée). Les impacts du chalutage dépendent de la distribution spatiale et temporelle de l'effort de pêche, des engins de pêche, de l'intensité des perturbations naturelles et des types d'habitats. Les structures des communautés benthiques présentes dans ces zones ont été étudiées à l'aide des données sur les prises accessoires d'invertébrés benthiques non commerciales recueillies lors des campagnes scientifiques françaises de chalutage de fond. Les ratios de surface balayée dérivés des données VMS ont été utilisés pour quantifier l'intensité de l'abrasion induite par la pêche sur le fond marin. Une approche de modélisation a été utilisée pour déterminer les valeurs seuils d'abrasion sur chaque habitat de niveau 4 de la classification EUNIS. Les valeurs, au-delà desquelles le chalutage a un effet néfaste sur les communautés benthiques, ont été déterminées pour chaque habitat. Cela a permis d'évaluer et de cartographier l'état écologique de chacun des habitats et de déterminer le pourcentage de chaque habitat touché par le chalutage. La méthode proposée ici pour évaluer l'impact du chalutage sur les communautés benthiques a mis en évidence que la grande majorité des sous-régions étudiées ont subi un impact négatif ou ont été irrémédiablement altérées en raison de l'impact du chalutage sur les fonds marins.

1. Introduction

On the eleven descriptors defined in the MSFD, two of them specifically concern the benthic habitat: the descriptor 1 (biodiversity) and the descriptor 6 (seabed integrity). Criteria 1 and 2 of the descriptor 6 (D6C1, D6C2) are dedicated in evaluating the spatial extent of the physical loss or disturbance of seabed. The criteria D6C3 focuses on establishing pressure thresholds values for the adverse effects of physical disturbance. Finally, D6C4 and D6C5 must allow the assessment of the extent of benthic community "loss" or "alteration" and should set maximum admissible proportion of habitat loss and evaluate the status of each habitat in that respect (EC 2008, 2017a).

The information of these criteria requires the development of transparent indices, allowing for a scientifically defensible assessment of the environmental status of the seabed. Since each type of pressure will result in either habitat disturbance or total physical destruction, it is expected that they will affect benthic communities in different ways. It seems therefore more appropriate to address each pressure effect separately and to develop specific indices and thresholds. In Europe, dredging and bottom trawling occur over large surfaces of the continental shelf and are the principal source of the anthropogenic disturbance to seabed habitats (Hiddink et al. 2007; Halpern et al. 2008; CNDCSMM 2019). Based on an extensive assessment methodology, four indices were identified in the Chapter II to monitor the impact of trawling and could probably be used in all European waters. These were computed using benthic community data from scientific bottom trawl surveys which enable to work on a large spatial scale but also to focus on the epifauna, unlike other sampling methods such as grab or box-corer that perform small-scale sampling, mainly of the infauna (Rumohr 1999; Foveau et al. 2017). The set of indices retained were all based on species biological traits that are known to shape species sensitivity to physical abrasion such as that generated by bottom trawling.

The distribution and composition of benthic assemblages are known to be dependent of environmental conditions such as depth, hydrodynamism and granulometry (Gray and Elliott 2009) or trawling pressure (Eigaard et al. 2017). Therefore, the evaluation of trawling impact on benthic community must be carried out by habitat type. As a great diversity of seabed habitats is present in the continental shelf of European waters, the development of an index that can be used in all European waters requires its evaluation in contrasted habitats, subjected to important gradient of trawling effort. Thus, a pan-european habitat map in a reasonably standardized typology is necessary to evaluate the relevance of each tested index at the scale of each MFSD sub-regions. A generic and hierarchical habitat classification of European Waters was developed by the European Nature Information System (EUNIS; http://www.emodnet.eu) and is currently available. This typology is based on a hierarchical classification of habitats allowing access, for the marine domain, to levels of precision ranging from the type of substrate to the precise identification of benthic stands, defined by the presence of characteristics species, while integrating the exposure level and depth (Galparsoro et al. 2012). Many studies on trawling impact have used EUNIS level 3 (Eigaard et al. 2017; van Loon et al. 2018) which takes into account depth, sediment grain size, light and hydrodynamism.

The characterization of GES, with regard to the impact of trawling, requires the definition of thresholds for each habitat type that may be trawled. Threshold values correspond to values below which no negative effect of the impact source (trawling in this study) can be observed on the community (here the benthic community). Thus, beyond this value, the observed effect results from the abrasion. Existence of these threshold values is linked to the community resistance to trawling. The more a community is resistant to the pressure; the more the pressure threshold value from which a negative effect may be observed will be high. Threshold can also be defined as the point at which small changes in a driver (fishing intensity for example) may produce large responses in the ecosystem (Groffman et al. 2006). It is therefore important to define the threshold at which GES is met as the use of trends-based targets gives no clear indication of the status achieved (EC 2008).

The aims of this chapter were to propose a methodology based on four functional indices proposed earlier in chapter II to determine GES threshold values for each habitat type present in three contrasted MFSD sub-regions: Western Mediterranean Sea, North Sea and English Channel. Maps representing the environmental status of these sub-regions were produced as a result of the application of this methodology.

2. Material and methods

2.1. Fishing impact, biological and habitat data

See Chapter I for descriptions

2.2. Evaluation of ecological state of benthic habitats

2.2.1. Determination of threshold values by habitat and biogeographical area

Depending on habitat types, benthic communities do not respond in the same way to trawling (Kaiser et al. 1998). Thus, based on EUNIS marine habitat description, the relationship between indices and abrasion was studied separately in each habitat type. Indices were centered and standardized (rescaled to have a mean of zero and a standard deviation of one) using the robustHD package 0.5.1 (Alfons 2016) and abrasion values were squared or log-transformed to improve their statistical distribution. However this relationship is not expected to be linear over the entire abrasion range and "abrupt" changes in slope may occur when certain abrasion intensity thresholds are exceeded (Figure 45). The identification of the abrasion values where these changes appeared allows detecting trawling intensity thresholds for each habitat. Thus, below a given abrasion intensity threshold, no significant relationship between the index and fishing induced abrasion may be detected and therefore no significant relationship will be detected. Under this abrasion limit, this seabed habitat may therefore be considered un-impacted or achieving GES in respect to bottom fishing physical impact. Conversely, when the area is severely trawled, one should not expect to observe a significant relationship between the index and fishing induced abrasion because the benthic community has shifted toward an adapted assemblage to this level of disturbance and has stabilized in a trawling induced semi-natural climax. A benthic community withstanding such level of abrasion may be considered as fully altered and therefore lost. Between these two extreme states, modification of species composition is on-going and communities should therefore be considered as adversely impacted. For more resistant communities, the GES would be maintained to a higher pressure value than that of a non-resistant community. Similarly, in that case, the second threshold corresponding to habitat loss may be reached at higher pressure level. The kinetics of change may also be different so that the resulting curve could also have a different slope. For very sensitive communities, the first threshold may not even exist.

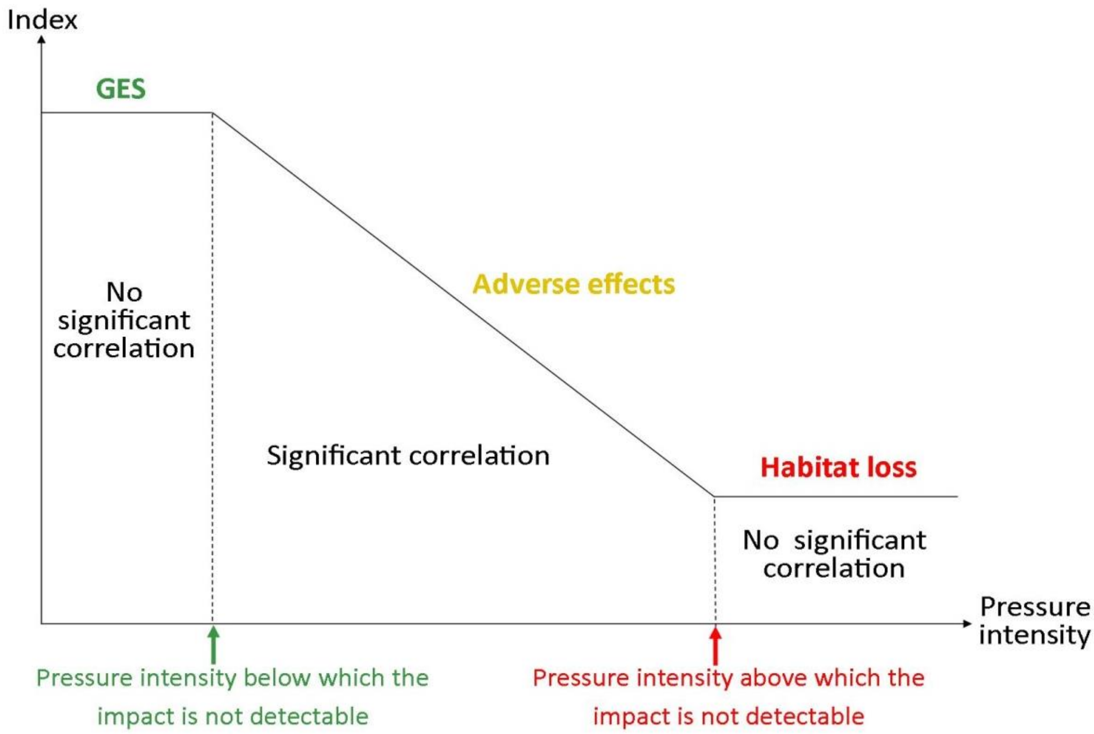


Figure 45 : Schematic relationship between any given index and pressure intensity and its corresponding ecological status

For each habitat, the detection of breakpoints and the determination of the corresponding abrasion threshold values required several steps. Thus, the type of relationship using statistical linear regressions (generalized linear models with Gaussian link function or segmented linear regression) between transformed abrasion values and standardized indices was studied, on each habitat, with a modelling approach consisting into fitting five models: two "simple" models (linear and null models) and three segmented models corresponding to a part (only one breakpoint) or all (two break points) of the theoretical relationship (Figure 46). The first step in selecting the "best model" was to check if the slope was negative or null, any other models being excluded. The presence of breakpoints was then evaluated using a specific statistical test (Davies 2002). In case of significant presence of breakpoints, "simple" models (linear and null) were excluded. Finally, the adjusted R squared (Yin and Fan 2001) was used to evaluate which model has the best explanatory power in each habitat as it penalizes more broken-line models than would the R-squared. All of these analyses were carried out with the Segmented R package 0.5-3.0 (Muggeo 2019) using R version 3.6.3 (R Core Team 2020). For each EUNIS habitat category, these models were therefore fitted to predict indices values from abrasion in the Western Mediterranean Sea, the English Channel and the southern North Sea and, when they could be detected, compute their associated thresholds.

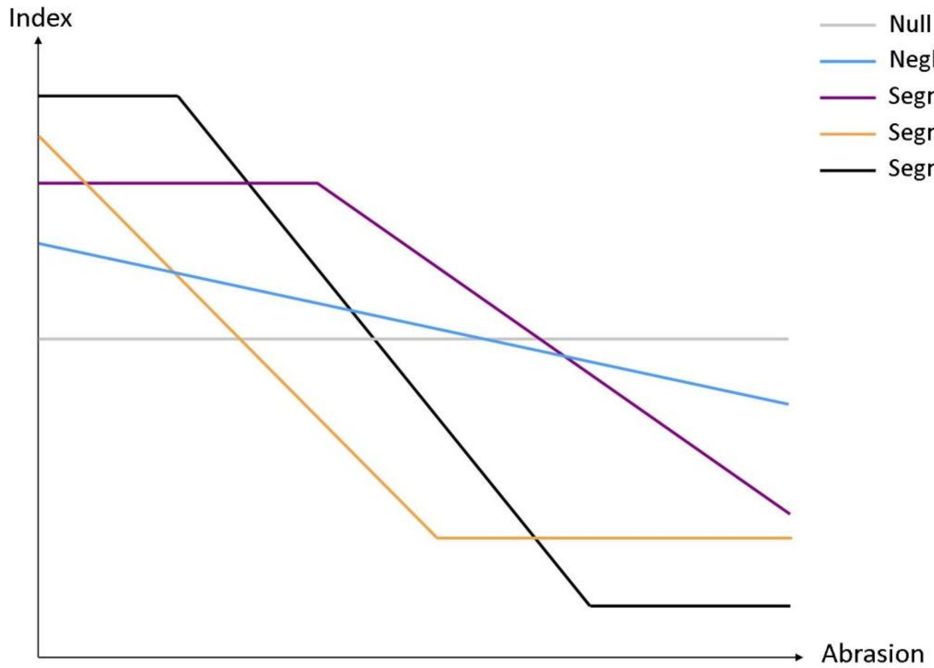


Figure 46 : Schematic representation of different models tested

2.2.2. Assessment approach for determining habitat disturbance and loss

MFSD criteria D6C3 and D6C4 require evaluating the percentage of surface where benthic communities were altered or lost by trawling. Depending on the respective responses of the four chosen indices, a composite indicator is proposed here. Based on a precautionary approach, and in case different threshold values were detected by different indices, this indicator will select the most conservative abrasion thresholds to classify habitat status based on specific EUNIS habitat susceptibility to fishing induced abrasion. This indicator is computed as follow:

For any given habitat, null abrasion values over the available period resulted in these areas being automatically considered in GES in respect to fishing physical impact (ICES 2018). The GES can be assessed until a pressure threshold from which a significant negative relationship between any selected indices and abrasion is detected (Segment 1 and 2 ; Figure 46). Above this threshold value or when the relationship is negative and significant over an entire non-null abrasion range (Neglinear ; Figure 46), it is considered that the trawling pressure has adverse effects on the benthic communities. If the habitat abrasion gradient exceeds that of the observed range, habitat ecological status would be “adverse effect” or “habitat loss” for the highest values outside the observed range. In contrast, the detection of a negative significant relationship below a given pressure threshold value and followed by an absence of significant relationship (Segment 2 and 3 ; Figure 46) would indicate that the habitat is lost. Indeed, the absence of relationship indicates that original communities were replaced by communities fully adapted to fishing. Moreover, in that case, if the existing abrasion values exceed that of the observed range, habitat ecological status is also defined as "habitat loss" for the highest values even if unobserved. The failure to detect any relationship between any index and non-null abrasion values when the observed abrasion range is very high (>1) indicates that the habitat is "probably habitat loss".

Any other un-sampled abrasion value for a given habitat or any unstudied habitats were labelled as "undetermined" status. If sampling occurs in different seasons, precautionary approach requires to keep the most "robust" season (with the higher number of observations per habitat) and, when quality and quantity of the available data were similar between seasons, the most sensitive season (with the lowest threshold value per habitat) was considered.

The conversion of habitat distribution and abrasion maps into ecological status categories ("GES", "adverse effect", "adverse effect or habitat loss", "probably habitat loss", "habitat loss", "undetermined") following the proposed assessment approach was conducted and proportion of habitat falling in each category was computed.

2.2.3. Uncertainty maps

To evaluate the degree of uncertainty of the approach developed in this work, the relative mean absolute model error (RMAE) was calculated by habitat as:

$$RMAE = \frac{MAE}{|\max(a) - \min(a)|}$$

Where max(a) is the maximum observed value of the "best" index in the studied habitat, min(a) the minimum observed value of the "best" index in the studied habitat and the mean absolute error (MAE) is calculated as:

$$MAE = \frac{\sum_{i=1}^{n} |p_i - a_i|}{n}$$

With p_i the i^{th} predicted value of the index, a_i the i^{th} observed value of the index and n the number of index value in the studied habitat

The spatial distribution of the RMAE was mapped for each habitat investigated and for the indices used, a value of 1 corresponding to the maximum possible prediction error. The RMAE can therefore be interpreted as a percentile of model uncertainty. Based on a precautionary approach and when several indices were significantly correlated with abrasion, the maximal uncertainty (higher RMAE) by habitat was conserved. For illustration purpose, the value of the RMAE was classified into very low uncertainty (0-0.1), low uncertainty (0.1-0.2), moderate uncertainty (0.2-0.5), high uncertainty (0.5-0.75) and very high uncertainty (0.75-1).

3. Results

3.1. Representativeness of available observation

Four habitats in the western Mediterranean, four in the southern North Sea and four in the English Channel were sufficiently sampled and investigated here.

In the Mediterranean area, two habitat types were sampled only in the Gulf of Lion (Table 29) : A5.38 (Mediterranean communities of muddy detritic bottoms), A5.39 (Mediterranean communities of coastal terrigenous muds). Two other habitats were sampled in both the Gulf of Lion and in Corsica (Table D.1): A5.46 (Mediterranean communities of coastal detritic bottoms) and A5.47 (Mediterranean communities of shelf-edge detritic). Although no observations were made in areas of low abrasion value in habitats A5.38 and A5.39, the abrasion range sampled seems very similar to the abrasion range experienced by each of these two habitats.

In the southern North Sea, IBTS observations covered eight habitats (Table D.2) but only four were found sufficiently sampled to be taken into account (Table 29). These were A5.15 (Deep circalittoral coarse sediment), A5.25/26 (Circalittoral fine sand/muddy sand), A5.27 (Deep circalittoral sand) and A5.37 (Deep circalittoral mud). Even if very high abrasion values were not sampled for all habitats, the abrasion range sampled seemed representative to that experienced by each habitat in the North Sea.

In the English Channel, observations were available for two seasons which were kept separated in the following analyses. In autumn, CGFS and CAMANOC surveys' data were used and covered twelve different habitat types. Seven habitats were re-sampled in winter during the IBTS survey (Table D.3).

A great diversity of habitats has been sampled in the Channel but only five habitats in autumn and two in winter were found sufficiently sampled to be studied in more detailed (Table 29). These were A5.14 (Circalittoral coarse sediment) and A5.15 (Deep circalittoral coarse sediment) for the two seasons and A5.23/24 (Infralittoral fine sand/muddy sand), A5.25/26 (Circalittoral fine sand/muddy sand) and A5.27 (Deep circalittoral sand) for the autumn. Despite higher sampling effort in areas of high abrasion values than that of low abrasion, the abrasion range sampled seemed representative of the abrasion withstood by each habitat in the English Channel for the two sampled seasons.

Table 29: Abrasion ranges of the main habitats sampled in the different areas studied and the number of survey carried out in these habitats. The three abrasion values represent the minimum value, the median and the maximum value. GoL = Gulf of Lion

Area	Habitats	Number of observations	Number of station with null abrasion	Abrasion range ($SAR.y^{-1}$)	Sampled abrasion range ($SAR.y^{-1}$)
GoL	A5.38	49	0	0 – 10.79 – 38.18	2.70 – 17.22 – 29.15
	A5.39	129	0	0 – 5.59 – 29.66	2.06 – 5.25 – 13.79
GoL & Corsica	A5.46	80	9	0 – 3.35 – 28.49	0 – 1.00 – 20.77
	A5.47	182	0	0 – 2.14 – 20.22	0.08 – 3.62 – 11.07
Southern North Sea	A5.15	108	11	0 – 1.15 – 32.70	0 – 3.43 – 16.51
	A5.25/26	121	0	0 – 1.61 – 51.27	0.11 – 2.02 – 11.14
	A5.27	226	10	0 – 0.98 – 62.76	0 – 1.17 – 16.15
	A5.37	84	0	0.004 – 1.30 – 26.47	0.60 – 1.74 – 13.41
English Channel (Autumn)	A5.14	264	3	0 – 0.86 – 36.72	0 – 4.60 – 29.58
	A5.15	495	0	0 – 3.40 – 78.71	0.03 – 14.00 – 74.15
	A5.25/26	140	0	0 – 1.51 – 33.40	0.03 – 3.75 – 21.42
	A5.27	42	0	0.05 – 2.98 – 35.67	1.29 – 11.98 – 26.14
English Channel (Winter)	A5.14	60	1	0 – 0.86 – 36.72	0 – 5.29 – 29.58
	A5.15	71	0	0 – 3.40 – 78.71	1.55 – 10.41 – 72.34

3.2. Mediterranean habitats

The multi-indices and multi-model approach proposed to identify threshold values was applied to each of the four habitats in the French part of the Mediterranean Sea (Gulf of Lion and Corsica; Table 30).

No significant correlation between indices and abrasion was detected on habitats A5.38 and A5.39 in the Gulf of Lion (Figure E.1 & E.2; Table E.1 & E.2). On these habitats, the observed range of abrasion was high, an abrasion value above 2 meaning that the surface of the habitat was entirely swept by trawling at least twice a year. In contrast, negative impacts of the trawling on the benthic community were detected on the two other sampled habitats although no threshold value could be highlighted. On the habitat A5.47, two indices (mTDI and mT) detected a negative significant correlation over all the sampled abrasion range (Figure E.4; Table E.4) while a single index (mT) detected such relationship on habitat A5.46 (Figure E.3; Table E.3).

On these four habitats, the variance explained by all models for each index seemed very low with a maximal value of adjusted R-squared of 0.05 (Table E.1, E.2, E.3 & E.4).

Table 30: Correlation between indices and abrasion, and the type of model selected for each Mediterranean habitats.* indicates that p< 0.05; ** indicates that p< 0.01; *** indicates that p<0.001; - indicates that there is no negative significant correlation. The lack of value next to an asterisk means that the correlation is significant and negative on the entire abrasion range and that no breakpoint could be found. GoL = Gulf of Lion. Grey shading indicates the index choose for this habitat.

Habitats	TDI	mTDI	pTDI	mT	Selected model	AdjR²
A5.38 (GoL)	-	-	-	-	Null	0
A5.39 (GoL)	-	-	-	-	Null	0
A5.46 (Corsica+GoL)	-	-	-	*	Neglinear	0.04
A5.47 (Corsica+GoL)	-	**	-	**	Neglinear	0.05

3.3. North Sea habitats

Significant negative relationship between the values of the index and abrasion was detected on all observed habitats (Table 31). Threshold values of 5.90 to 6.52 above which the fishing impact was no longer detectable were determined in habitat A5.15 for most indices (Figure E.5; Table E.5). For the three other habitats, the relationship between indices and abrasion was negative and significant over the entire sampled abrasion range even though the observed range of habitat A5.27 included ten apparently un-impacted stations (Figure E.6). On habitats A5.25/26, a significant relationship to abrasion was detected with all indices, except the mT index but no threshold could be found (Figure E.7; Table E.7). In contrast, on habitat A5.37, only the mT index detected an impact over the entire abrasion range (Figure E.8; Table E.8). On two habitats (A5.25/26 and A5.37), the variance explained by all models for each indices was very low, with a maximal value of adjusted R-squared of 0.07 for the model neglinear on the relationship between the TDI and the abrasion on the habitat A5.25/26 (Table E.6 & E.8). For the two others habitats, the variance explained by all models were relatively higher with a maximum adjusted R-squared of 0.18 for the neglinear model on the habitat A5.27 (Table E.5 & E.7).

Table 31: Correlation between indices and abrasion, and the type of model selected for each habitats in the southern North Sea. * indicates that p< 0.05; ** indicates that p< 0.01; *** indicates that p<0.001; - indicates that there is no negative significant correlation. Values in red represent the trawl intensity above which impact of fishing is not detectable. The lack of value next to an asterisk means that the correlation is significant and negative on the entire abrasion range but no breakpoints could be found. Grey shading indicates the index choose for this habitat.

Habitats	TDI	mTDI	pTDI	mT	Selected model	AdjR²
A5.15	***	6.52**	5.91**	5.90*	Segmented2	0.09
A5.25/26	**	*	**	-	Neglinear	0.07
A5.27	***	***	***	***	Neglinear	0.18
A5.37	-	-	-	*	Neglinear	0.06

3.4. English Channel habitats

The impact of trawling has been detected on all studied habitats (Table 32). On habitat A5.14 and A5.25/26, most indices detected an impact over all the sampled abrasion range but no threshold values were found even though very high abrasion values were also sampled in both cases and three un-impacted observation were available in the A5.14 (Figure E.9 & E.11; Table E.9 & E.11). Threshold values beyond which the fishing impact was no longer detectable were determined for two indices (mTDI and TDI) for the habitat A5.15 (Figure E.10; Table E.10). On habitat A5.27, over which sampled abrasion was quite high, only pTDI and mTDI were able to detect a negative effect of trawling over the entire range of abrasion (Figure E.11; Table E.11). Variance explained by all models were relatively low at three of the four habitats (Table E.9, E.11 & E.12) with a maximum adjusted R-squared of 0.10 for the neglinear model on the habitat A5.25/26. But for the habitat A5.15, models seemed to better explain the variance (maximum adjusted R-squared of 0.29 for neglinear models and 0.28 for Segment2 models; Table E.10).

Table 32: Correlation between indices and abrasion, and the type of model selected for each habitats in English Channel in September/October. * indicates that p< 0.05; ** indicates that p< 0.01; *** indicates that p<0.001; - indicates that there is no negative significant correlation. Values in red represent the trawl intensity above which impact of fishing is not detectable. The lack of value next to an asterisk means that the correlation is significant and negative on the entire abrasion range but no breakpoint could be found. Grey shading indicates the index choose for this habitat.

Habitats	TDI	mTDI	pTDI	mT	Selected model	AdjR²
A5.14	*	*	**	-	Neglinear	0.03
A5.15	12.34**	12.34***	***	***	Segment2	0.27
A5.25/26	**	***	***	***	Neglinear	0.21
A5.27	-	*	*	-	Neglinear	0.20

In winter, based on IBTS observations, only two habitats were sufficiently covered to be studied and trawling impact was detected over each of them (Table 33). In habitat A5.15, two of the four indices are no longer able to detect the effect of trawling above an abrasion intensity of about 71.10 for the mT and 18.13 for the pTDI (Figure E.14; Table E.14). No lower bond threshold values were found even though one un-impacted observation (null abrasion) was available. For habitat A5.14, this impact appeared detectable over the whole range of abrasion sampled and no threshold value could be found in spite of the very high observed abrasion values (Figure E.13; Table E.13).

Table 33: Correlation between indices and abrasion, and the type of model selected for each habitats in English Channel in January/February. * indicates that $p< 0.05$; ** indicates that $p< 0.01$; *** indicates that $p<0.001$. Values in red represent the trawl intensity above which impact of fishing is not detectable. The lack of value next to an asterisk means that the correlation is significant and negative on the entire abrasion range but no breakpoint could be found. Grey shading indicates the index choose for this habitat.

Habitats	TDI	mTDI	pTDI	mT	Selected model	$AdjR^2$
A5.14	**	**	***	***	Neglinear	0.22
A5.15	***	***	18.13*	71.10*	Segment2	0.32

3.5. Evaluation of habitat disturbance and loss

The study of the relationship between each index and the abrasion allowed determining the ecological state of each habitat linked to the trawl fishing pressure in the three studied areas (Table 34, 35 & 36). Thus, in the Gulf of Lion, only very small areas were considered in GES (maximum 10 % of the habitat for A5.39). On more than three quarters of the surface of habitats A5.38 and A5.39, which cover together about 50% of the studied area, original benthic communities were considered to be replaced by communities perfectly adapted to the impact of fishing (Figure 47; Table 34). Conversely, in Corsica, no habitat was classified as lost and about 40% of the studied habitat surface was in GES. In the two Mediterranean areas studied, undetermined ecological status on the investigated habitats resulted from lack of observations on the entire range of existing abrasion, but concerned less than 10% of each habitat (except for habitat A5.38). Although habitats A5.46 and A5.47 were jointly assessed in Corsica and in the Gulf of Lion to increase both the number of observations and the abrasion range, they were reported separately to better illustrate the assessment of the ecological status of habitats in Corsica (Table 34).

Table 34: Ranges of abrasion values (in SAR.y-1) corresponding to the different ecological status in the Mediterranean habitats. GoL = Gulf of Lion

Habitats	Area	GES	Undetermined	Adverse effects	Adverse effects or habitat loss	Probably habitat loss
A5.38	GoL	0	]0 - 2.70[			≥ 2.70
A5.39		0	]0 - 2.06[			≥ 2.06
A5.46		0		]0 - 20.77]	]20.77 - 28.49]	
A5.47			[$8{\times}10^{-4}$ - 0.08[	[0.08 - 11.07]	]11.07 - 20.22]	
A5.46	Corsica	0		]0 - 5.74		
A5.47		0	]0 - 0.08[	[0.08 - 3.46]		

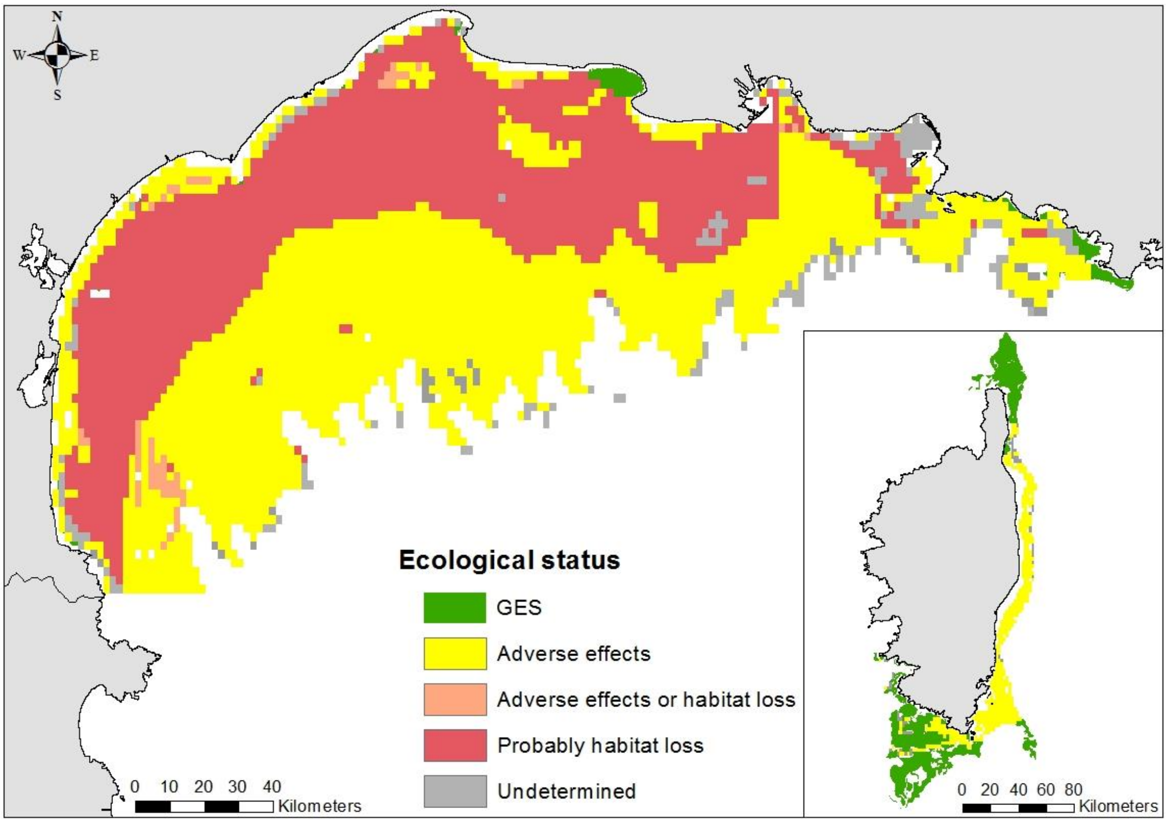


Figure 47 : Ecological status of benthic habitats linked to the trawl fishing pressure in the Western Mediterranean Sea

Table 35: Proportion of the Golf of Lion (GoL) and Corsica habitats in each of the ecological status category

Ecological status	A5.38 (GoL)	A5.39 (GoL)	A5.46 (GoL)	A5.47 (GoL)	A5.46 (Corsica)	A5.47 (Corsica)
GES	3 %	10 %	5 %	-	46 %	32 %
Adverse effects	-	-	89.4 %	96.4 %	54 %	62.5 %
Adverse effect or habitat loss	-	-	5.6 %	1.8 %	-	-
Probably habitat loss	77 %	83.7 %	-	-	-	-
Undetermined	20 %	6.3 %	-	1.8 %	-	5.5 %

Table 36: Ranges of abrasion values (in SAR.y-1) corresponding to the different ecological status in the North Sea habitats

Habitats	GES	Undetermined	Adverse effects	Adverse effects or habitat loss	Habitat loss
A5.15	0		]0 - 5.90]		> 5.90
A5.25/26	0	]0 - 0.11[	[0.11 - 11.14]	]11.14 - 51.27]	
A5.27	0		]0 - 16.15]	]16.15 - 62.76]	
A5.37		[0.004 - 0.60[	[0.60 - 13.41]	]13.41 - 26.47]	

In the South of the North Sea, a majority of habitats was considered as impacted (adverse effects) but not lost (Figure 48; Table 36) and only very few small and scattered areas were considered as lost (less than 5% of each habitat). Since an important part of the North Sea is apparently untrawled, many areas were considered in GES, especially in the western part. As a result, about 51.5% of the habitat A5.15 was considered in GES in respect to fishing physical impact to the seabed (Table 37). Undetermined ecological status represented from 4% in habitat A5.25/26 to almost 13% of habitat A5.37.

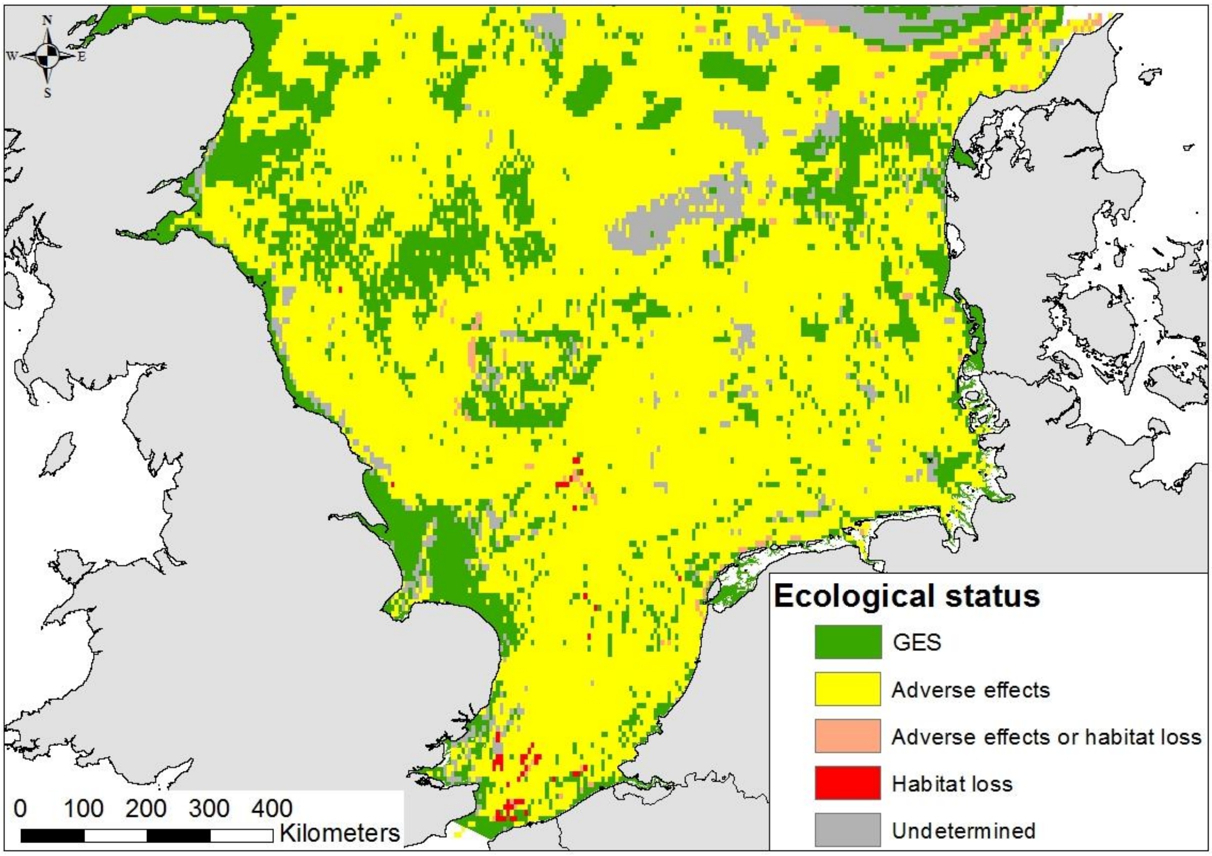


Figure 48 : Ecological status of benthic habitats linked to the trawl fishing pressure in the southern North Sea

Table 37: Proportion of southern North Sea habitats in each of the ecological status category

Ecological status	A5.15	A5.25/26	A5.27	A5.37
GES	51.5 %	0.5 %	6 %	-
Adverse effects	45 %	93.6 %	93.4 %	86.5 %
Adverse effects or habitat loss	-	2 %	0.6 %	0.7 %
Habitat loss	3.5 %	-	-	-
Undetermined	-	3.9 %	-	12.8 %

Table 38: Ranges of abrasion values (in SAR.y-1) corresponding to the different ecological status in the English Channel in autumn and winter according to abrasion

Habitats	Season	GES	Undetermined	Adverse effects	Adverse effects or habitat loss	Habitat loss
A5.14	Autumn	0		]0 - 29.58]	]29.58 - 36.72]	
A5.15		0	]0 - 0.03[	[0.03 - 12.34]		> 12.34
A5.25/26		0	]0 - 0.03[	[0.03 - 21.42]	]21.42 – 33.40]	
A5.27			[0.05 - 1.29[	[1.29 - 26.14]	]26.14 - 35.67]	
A5.14	Winter	0		]0 - 29.58]	]29.58 - 36.72]	
A5.15		0	]0 - 0.03[	[0.03 - 18.13]		> 18.13

For the two habitats sampled in the English Channel in autumn and in winter, only few differences were observed in the habitat A5.15, with a threshold after an abrasion of 12.34 in autumn and 18.13 in winter (Table 38).

In autumn in the English Channel, only small coastal areas were found in GES and 9% of habitat A5.15 was classified as "habitat loss" (Figure 51; Table 37 & 38). In this particular case study, the proportion of inadequately sampled habitats seemed quite substantial and resulted in a large amount of grey areas. In addition, the ecological status of nearly 3.6% of the studied habitats could not be determined with, in particular, 14.5% of habitat A5.27 and 8.4% of habitat A5.25/26 labelled as undetermined.

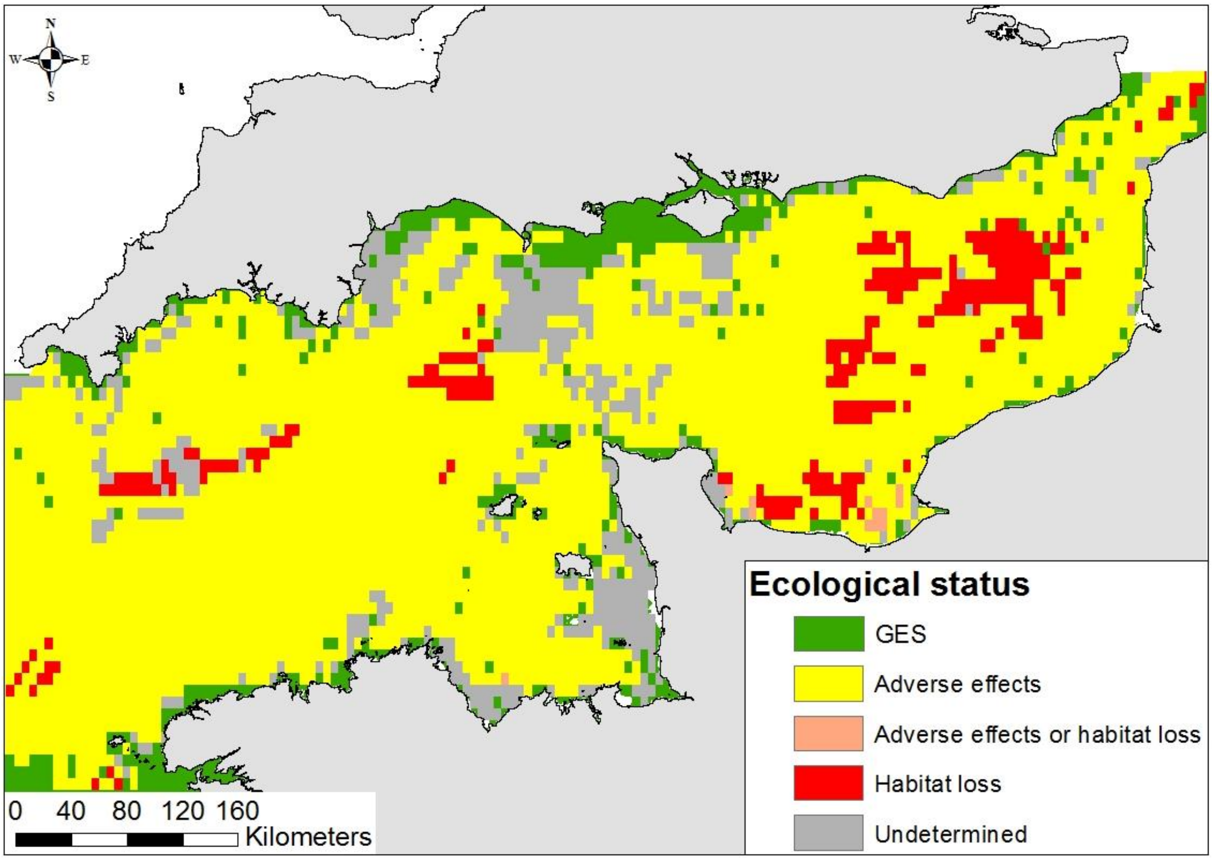


Figure 49 : Ecological status of benthic habitats linked to the trawl fishing pressure in the English Channel

Table 39: Proportion of English Channel habitats in each of the ecological status in autumn

Ecological status	A5.14	A5.15	A5.25/26	A5.27
GES	15.5 %	0.5 %	8 %	-
Adverse effects	84.3 %	88.0 %	77.4 %	83.5 %
Adverse effects or habitat loss	0.2 %	-	6.2 %	2.0 %
Habitat loss	-	9.0 %	-	-
Undetermined	-	2.5 %	8.4 %	14.5 %

3.6. Uncertainty representation

Modeled uncertainties were different between habitats and areas but were relatively low in most areas particularly in the English Channel and in Corsica (Figure 50). In the southern North Sea, models uncertainties were higher in the West while in the Gulf of Lion, the uncertainties were higher ($0.2 < RMAE \leq 0.5$) for the most offshore habitats. Note that the areas where abrasion was zero are classified in the category “Very low uncertainties”.

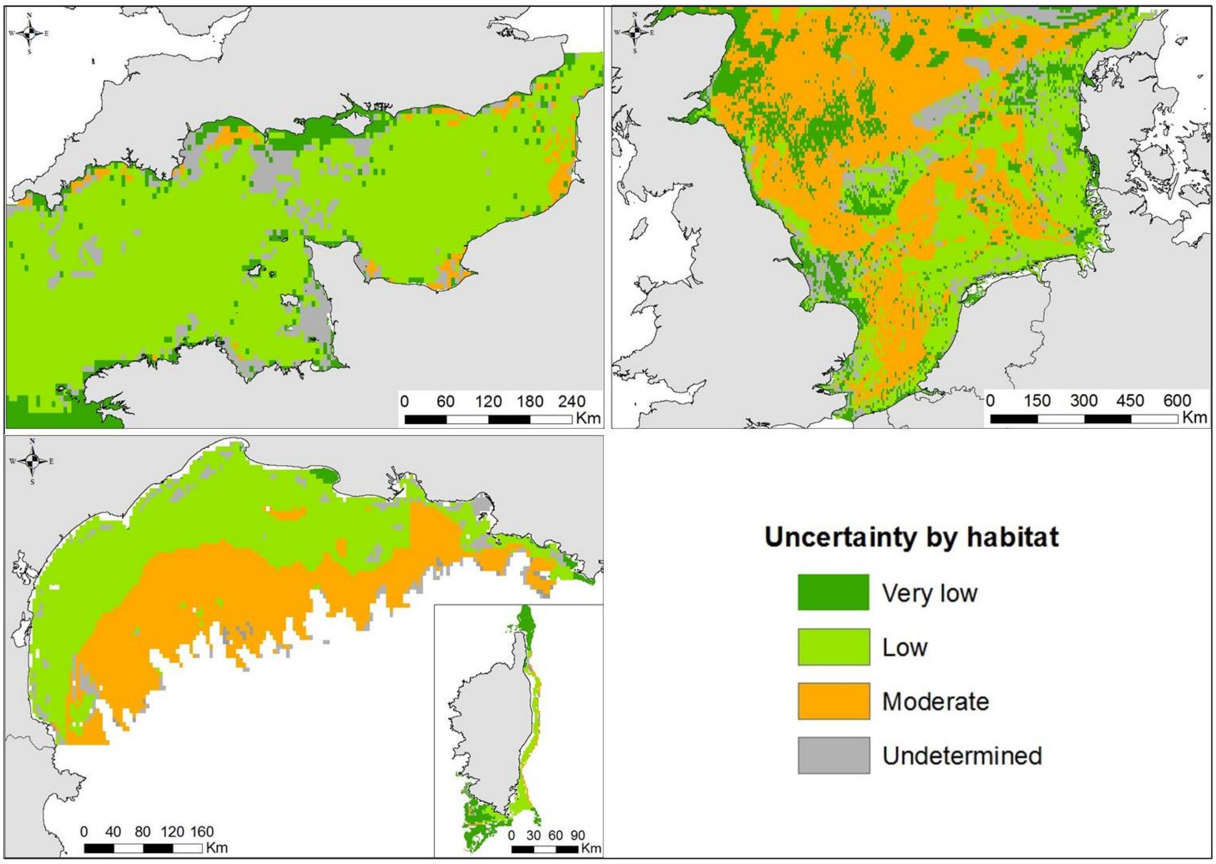


Figure 50: Models uncertainties by habitat in the three studied areas.
Very low correspond to 0≤RMAE≤0.1; Low correspond to 0.1<RMAE≤0.2; Moderate correspond to 0.2<RMAE≤0.5

4. Discussion

4.1. Method uncertainties

4.1.1. Data variance

In the majority of the habitats sampled in this study, the variance explained by models seemed low as is often the case with noisy data. This variability mostly resulted from inter-annual variations due to the pooling of several years of surveys together. Inter-annual variations could be due to several factors: the natural variability of each population (quality of recruitment and different growth between years), the separation time between the last fisher trawling operation and the scientific haul or even location inaccuracy of the haul station across years. Working at habitat level increased the effect of temporal over spatial variability of the benthic communities in the three studied areas. Although this should increase model uncertainty, it appeared relatively moderate in most instances due to relatively low mean absolute error between modeled predictions and observations. However, other sources of uncertainties such as errors in the calculation of abrasion values or in modeled habitat classification should also be taken into account in the present approach.

4.1.2. VMS data

The use of VMS data for the calculation of abrasion induces a certain number of uncertainties. Firstly, VMS positioning is required only for vessels of 12 m or longer (EC 2009) since 2012, and 15 m or longer before that. The trawling operations carried out by smaller vessels are therefore not taken into account in the abrasion data and it is conceivable that the coastal areas considered in GES are actually trawled or dredged by the small vessels in particular in estuaries or bays. As a consequence, some areas, in particular coastal areas, may be wrongly considered as untrawled and therefore in GES. Moreover, the signal frequency is limited to once every two hours (Shepperson et al. 2018), which further reduces the accuracy and spatial resolution of the abrasion values (ICES 2018). The use of aggregated VMS data (3'x3' in the English Channel/southern North Sea and 1'x1' in the Mediterranean Sea) does not allow us to have the precise location of the trawl hauls and induces potential errors on the allocation of abrasion values to the different sampled stations. However, if the distribution of fishing activities is random within each grid cells, the compilation of several years of abrasion strongly reduces this bias by making the distribution of the abrasion homogenous within the cell (Ellis et al. 2014; Eigaard et al. 2017). Despite all these potential sources of biais, no uncertainty assessment method for the abrasion calculation has been proposed. Nevertheless, the generalization of the use of VMS to all professional fishing vessels and the increase of the signal frequency to less than 30 minutes would make it possible to overcome these methodological biases in the near future which seems preferable to systematically excluding near shore areas from the assessment. Finally, the English Channel, the southern North Sea and the Mediterranean Sea have been subjected to industrial trawling for decades (Englehard 2008; Hidalgo et al. 2009; Thurstan et al. 2010) and in the present study, the data on abrasion only concern the 2009-2017 period. As a result, there is no certainty that areas considered untrawled are pristine areas or fully recovered from past trawling disturbances.

4.1.3. EUNIS classification

The use of EUNIS habitat classification and predictive maps also leads to uncertainties. Indeed, boundaries between habitats classes can be uncertain or habitats can be wrongly described due to erroneous description and classification of the continuous physical variables such as substrate types or energy classes. To evaluate uncertainties specific to each area, a confidence assessment method was already developed by Populus et al. (2017) to obtain a classification in three levels (low, moderate, high) of the habitat type confidence (https://www.emodnet-seabedhabitats.eu).

The assessment of the total uncertainty of the method proposed in the present study would require combining the error arising from three sources of uncertainties: model error, abrasion calculation error and EUNIS classification confidence levels. Currently, only the uncertainty maps of the models developed in this study, and maps of EUNIS habitat uncertainties exist and provide a partial overview of the overall uncertainty.

4.2. Variation in threshold values

Habitat response to fishing pressure was shown to vary with geographic basins and even seasons. Indeed, the habitat A5.15 was sampled in the North Sea and the English Channel but was considered lost after an abrasion threshold of 5.90 in the North Sea and 12.34 in the English Channel. Several reasons may explain these differences.

Firstly, although this habitat was classified in the same way in EUNIS, it is possible that benthic communities slightly differ between the two basins. Indeed, in this habitat, for instance, two main facies are defined in the EUNIS classification: A5.151 (facies with *Glycera lapidium*, *Thyasira spp.* and *Amythasides macroglossus*) and A5.152 (facies with *Hesionura elongata* and *Protodorvillea keferteini*). Only the consideration of the level 5 of EUNIS could confirm this hypothesis and may explain these differences. Additionally, the apparently higher trawling resistance of the benthic communities of habitat A5.15 in the English Channel compared to the North Sea could also be due to differences in hydrodynamics between the two basins. Many studies have shown that natural disturbance due to waves and tides increases the resilience of benthic communities to fishing disturbance (Diesing et al. 2013; van Denderen et al. 2015) in at least two ways. Firstly, the resilience can be increased by selecting for fast-growing opportunistic species which quickly recolonize disturbed areas and can reach sexual maturity before the next disturbance event (Pianka 1970). Second, species that display traits that pre-adapt them to withstand the disturbance may have an advantage in naturally disturbed habitats (Diesing et al. 2013). The intense hydrodynamism in the English Channel relative to the North Sea can therefore result in more resistance of the English Channel's benthic communities to trawling and therefore the value of fishing intensity causing habitat to be "lost" is higher. To verify this, the Kostylev approach (Kostylev and Hannah 2007; Foveau et al. 2017) could be used to combine a pool of environmental layers explicitly linked to relevant ecological processes known to affect the seabed. These, such as salinity, temperature, oxygen saturation, sediment grain size or friction velocity at seabed may in turn be used to predict and map habitat sensitivity. The combination of both EUNIS and process-driven sensitivity would certainly enable a better distinction of these habitats.

Circalittoral coarse sediment (A5.15) was sampled in autumn and in winter in the eastern English Channel and sensitivity difference was highlighted between the two seasons. This habitat seemed less sensitive to trawling in winter than autumn (habitat considered lost from a value of 12.34 abrasion in autumn to 18.13 in winter). It is very likely that this resulted from differences in the number of observations available for each season. The study of the seasonal effect on the sensitivity of benthic habitat to trawling requires to use similar sampling station set for each season and may also require monthly VMS data and was clearly out of the scope of this study. The most "robust" season, i.e. with the largest sample size on each habitat, was chosen to build the assessment of habitat disturbance and loss. As all habitats of the English Channel were largely sampled in autumn, this season was chosen for the assessment of the ecological status of the benthic habitats of this area.

More importantly, this study has highlighted how different indices performance may vary amongst habitats and/or abrasion range. Although the four indices used were closely related by construction, they displayed different abilities to describe benthic communities' sensitivity to trawling as a result of the inequal weighting given to different biological traits present in these communities. These indices sensitivity appeared somehow dependent of each community overall traits' composition. The approach proposed here, based on precautionary principle, may easily be extended to another set of complementary indices that may be more suited for different habitats, abrasion range, biotic data type or to investigate another type of pressure altogether.

4.3. On the difficulty to find and sample low abrasion reference areas: a methodological bolt

In the French part of the Mediterranean Sea, there was no clear relationship between abrasion and any of the four selected indices in muddy habitats (A5.38 and A5.39). For these, there was no observation located in low abrasion areas and sampling was carried out in areas with abrasion levels higher than 2. These values being high (the surface being totally swept twice a year), we assume that the original communities of these habitats have already been completely replaced by communities adapted to trawling, which would justify the lack of relationship between indices and abrasion levels. These particularly severe results may be explained by the particular environmental conditions prevailing of this geographical area. Firstly, as the hydrodynamics is relatively low in the continental shelf of the Gulf of Lion (absence of tide or high current), benthic communities are not naturally adapted to disturbances and would therefore be very sensitive to any additional physical disturbance such as trawling. Similarly, the oligotrophic nature of the Mediterranean Sea (Estrada 1996) could also lead to higher fragility of benthic habitats to trawling than would be in more productive environments such as the English Channel or the North Sea. In fact, oligotrophy results in low species abundance and smaller individuals biomasses (Smith et al. 2000), which reduces community resilience. Finally, the accuracy of the habitat maps may also be questioned as differences in assemblage of benthic communities are known to exist between the East and West of the Gulf of Lion (Labrune et al. 2007, 2008). These differences being related to the sediment granulometry, the use of a more accurate habitat map or the use of the Kostylev habitat approach (Kostylev and Hannah 2007) may possibly correct this bias in the future.

The absence of pressure free, ideally pristine, areas for most habitats in the different basins investigated prevents the use of a method based on an observed reference state to contrast and monitor the trawling disturbance. Indeed, only few stations (a maximum of 11 stations by habitats and 33 stations in total) were sampled in un-impacted areas in the four surveys available and this may be explained in two ways.

Firstly, as in many other geographical areas (Nilsson and Ziegler 2007; Baird et al. 2015), the totality of the trawlable habitats of the European shelves is trawled (*e.g.* habitat A5.27 in the English Channel and A5.37 in the North Sea) and, therefore, no reference area exists for these habitats. In this case, the creation of protected areas where trawling is banned may possibly allow, after a certain delay (probably very long), the restoration of the original community that may then be used as reference.

Secondly, the small number of stations sampled in untrawled areas is due to gaps in the sampling design of the chosen surveys. Indeed, scientific trawl surveys are not dedicated to the study of the effect of trawling but to the evaluation of fish stocks, so sampling is not carried out according to an abrasion gradient but following a random stratified sampling scheme deemed relevant for each area and the targeted stocks (MEDITS 2017). The addition of complementary observations to existing scientific trawl surveys in untrawled or lesser trawled habitats such as A5.15 in the English Channel or A5.38 in the Gulf of Lion would enable to investigate their original communities and set reference states. The increase in the number of observations could also reduce the surface of indeterminate status areas that represented more than 10% of the total area of some habitats (*e.g.* A5.37 in the North Sea and A5.27 in the English Channel).

4.4. Non-linear impact of trawling on benthic fauna

The response of benthic fauna community structure to environmental impacts is often non-linear with increasing change above a threshold value of the impact factor (Josefson et al. 2008). Trawling seems to non-linearly impact benthic fauna according to the fishing intensity (Hiddink et al. 2008, 2011) and/or the season (Kaiser et al. 1998). In this work, it was considered that relationship between indices (*i.e.* sensitivity of benthic community) and abrasion is segmented and composed of two threshold values between which trawling impacts negatively and significantly the benthic fauna. It has been hypothesized that below a certain annual value of abrasion (probably extremely low) the sensitivity of the community (and therefore the value of the index) does not vary significantly. Between this value and the absence of abrasion, benthic community is considered in a good ecological status. Beyond this threshold value of abrasion, the pressure is strong enough to progressively alter the benthic community (decrease of index values), in particular by inducing a decrease in trawl-sensitive species by minimizing their ability to recover. This process could be considered as a physical disturbance (change to the seabed from which it can recover if the activity causing the disturbance pressure ceases; ICES 2018) and define “adverse effects” in the ecological classification of the seabed in this study. In addition to affect benthic communities, especially epifauna, trawling results in a change in physical habitat. In fact, trawling induces changes (i) in grain size, with an increase in coarse sediment and a decrease in mud (Palanques et al. 2014; Mengual et al. 2016), (ii) an increase in the organic carbon content in the first centimeters of sediments (Palanques et al. 2014) and (iii) a flattening of the bottom topography by eliminating natural irregular feature such as ripples, bioturbation mounds, biogenic reefs or seagrass mats (Fonteyne 2000). Such physical modifications of the bottom may also modify original benthic communities, which may be, in very heavily trawled areas, completely replaced by others, perfectly adapted to these disturbances. Consequently, beyond a certain abrasion value, the index cannot respond negatively to the increase in abrasion and the original habitat (biotic and abiotic) may be considered as lost because it is a permanent modification of the seabed that can last a very long time, even after stopping trawling (ICES 2018).

4.5. Towards the restoration of benthic habitats?

Restoration of benthic habitat is a long process as reported by Sheehan et al. (2013) which observed a partial recolonization of the epifauna, three years after trawling ban in the western English Channel, Tuck et al. (1998) which showed that 18 months were necessary to the recovering of infaunal communities in Scottish Sea lochs and Desprez (2000) and Sardá et al. (2000) which underlined recovery delays between one to three years for macrobenthic invertebrates like molluscs, crustaceans and echinoderms (in the eastern English Channel and Catalan western Mediterranean respectively). However, the complete recovery of original communities, including slow growing species such as sponges or cold water corals may take several years or decades. Determining recovery time is very important for the management of the marine ecosystem and complementary studies are required on benthic recolonization of areas where trawling is permanently banned.

The assessment of the ecological status of benthic habitats not only provides information on the integrity of the seabed to date, but can also provide some clues about its evolution. Indeed, areas where the habitat is considered as lost will not have the same capacity to return at the GES than impacted areas (adverse effects category) when fishing pressure is reduced or removed. The habitat type (Collie et al. 2000b), the ecological connectivity of the areas (Eno et al. 2013) and the diversity of responses between different species to disturbance (Muntadas et al. 2016) also play an important role in the resilience of benthic communities. The presence of a large number of small areas considered in good ecological state in the English Channel and in the North Sea would appear beneficial for all the benthic habitats of these two zones. The existence of untrawled areas and the important productivity of these two marine basins will allow some species to withstand the impacts of trawling through recruitment or regeneration processes (Osman and Whitlatch 1998; Pranovi et al. 1998; Frid et al. 2000). Although the interruption of trawling would certainly lead to environmental status improvement, all habitats will not necessarily return to GES at the same speed. In the worst case scenarios, areas where the original community is fully replaced by a fishery adapted community (habitat loss), if too isolated from a potential source original population, could potentially never regain their original state even with complete trawling exclusion.

4.6. Extension of the approach to coastal areas and other pressures

In the present study, only the specific effect of fishing disturbance on the seabed was taken into account. A large part of the European continental shelf surface is exclusively submitted to the fishery induced abrasion pressure and the present work offers an operational and cost-efficient method to evaluate its impact on seabed integrity in the frame of the MFSD. The assessment of the ecological status of benthic habitats should also account for other anthropogenic physical pressures such as aggregate extraction, placement of physical structures (oil and gas extraction, renewable energy, harbours and coastal defense, tourism/recreation, road and rail transportation, pipelines and cables, wrecks, artificial reefs…), or dredge disposal (ICES 2019a) to provide a full picture of the ecological status of the benthic habitats in studied areas. In coastal areas, the impact of other pressures, also including pollution and eutrophication may largely exceed that of fishing and prevent habitat restoration even if fishery pressure is lessened. The threshold detection approach, developed in this work, could be applied to other pressure types (with indicators specific to these pressures) and could thus respond to this need. However, a pressure and habitat-by-habitat approach, using the most appropriate observed biological data, seems more relevant and defensible than a global approach. Using ecological status classification of benthic habitats for each pressure and aggregating them would allow a general assessment (combining all pressures) of the ecological states of the seabed. The development of methodologies to aggregate environmental status resulting from different types of pressure and to account for potential cumulative effects of these impacts are necessary to monitor the sea-floor integrity as a whole.

Finally, this work meets different criteria of the MSFD because pressure thresholds values for the adverse effects of physical disturbance were defined (D6C3) and an assessment of the extent of benthic community "loss" or "alteration" was realized (D6C4 and D6C5). In all investigated areas, the percentage of habitat impacted by trawling pressure seems to exceed the recommended 30% of the total surface while only a few habitats exceed the value of 5% of lost habitat (Unknow 2016). Decrease of impacted surfaces is recommended, but this should not be done at the cost of increasing habitat loss surfaces as a result of fishing effort displacement. It necessary should be assorted of an overall bottom trawl effort reduction.

In conclusion, the establishment of the MSFD by the European Union in 2008 requires the development methodological standards for determining the good environmental status. Trawling appearing as one of the strongest pressures on the seabed, the definition of thresholds for each habitat type that may be trawled is required. However, the absence of sampling on certain habitat or poor sampling distribution along the abrasion gradient, for some habitat, showed the necessity to increase the sampling effort especially in low and high abrasion areas. The evaluation of the impact of trawling on benthic communities highlighted that the vast majority of the investigated sub-regions were adversely impacted or lost as a result of seabed impacting trawling.

Inter Chapitre

Le cinquième chapitre de cette thèse a permis d'évaluer le pourcentage de chaque type d'habitat considéré comme définitivement altéré, impacté ou en bon état écologique. Une cartographie de l'état écologique des habitats benthiques des quatres zones d'étude a également été réalisée.

Différents paramètres environnementaux peuvent régir la composition et la distribution des communautés benthiques. Or, l'effet du chalutage sur ces communautés dépend de leur structure. Par exemple, les espèces capables de résister à d'importantes perturbations naturelles comme la houle ou les courants de marée peuvent être plus à même de résister aux impacts physiques dus aux arts traînants que les espèces se développant dans des zones où l'hydrodynamisme est moins important. L'effet du chalutage peut donc être confondu avec l'effet de différents facteurs environnementaux. Il est donc nécessaire d'évaluer distinctement leurs effets.

Dans le sixième chapitre, les différents paramètres influant sur la structure des communautés benthiques ont été déterminés pour trois des quatre zones étudiées au cours de cette thèse. La capacité de quatre indices basés sur la sensibilité des espèces au chalutage à distinguer les effets de l'environnement et des arts traînants sur les communautés benthiques a été évaluée dans le but de proposer un indicateur dont la réponse est indépendante des effets de l'environnement

Chapitre VI: Does environmental variability mask the effect of trawling on benthic communities?

Jac C., Desroy N., Foveau A., Vaz S. Does environmental variability mask the effect of trawling on benthic communities? *In preparation.*

Résumé du chapitre en français :

Différents paramètres environnementaux comme la température, la profondeur ou encore l'hydrodynamisme influent sur la composition et la distribution des assemblages benthiques. Or, l'impact du chalutage sur les communautés benthiques dépend de leur composition puisque l'ensemble des espèces n'ont pas le même degré de sensibilité aux arts traînants. De plus, le chalutage peut avoir, sur les espèces benthiques, des effets similaires à un certain nombre de perturbations naturelles comme par exemple une augmentation locale de la turbidité. Ainsi, les espèces adaptées à ces perturbations naturelles peuvent-être résistante à un certain niveau de chalutage. Cette étude porte sur l'évaluation de l'influence conjointe des paramètres environnementaux et de la pression de chalutage sur quatre indices de sensibilité fonctionnelle dans trois zones environnementalement différentes. Les différents paramètres environnementaux influant sur le comportement de ces indices ont été identifiés dans chacune des zones d'étude. Ces paramètres ont été divisés en deux groupes en fonction du type d'influence qu'ils ont sur la communauté benthique. Le premier, « Scope for Growth » (SfG) est en lien avec la résilience des espèces alors que le second « Disturbance » (Dist) concerne leur résistance aux pressions physiques. L'influence seule et combinée avec l'abrasion de ces deux groupes de paramètres sur les indices a permis de mettre en avant que la distribution des espèces benthiques en Manche est principalement liée aux perturbations physiques et donc à leur résistance alors que c'est principalement les paramètres liées à la résilience des communautés qui influent sur la répartition de la faune benthique en Méditerranée. Seul l'indice pTDI a permis de distinguer l'effet de l'abrasion de l'effet de l'environnement dans les deux zones où le chalutage avait un effet significatif sur les indices de sensibilité fonctionnelle. La composition et la distribution des communautés benthiques de Corse, quant à elles, ne semblaient pas être influencées par la pression de pêche aux arts traînants.

1. Introduction

Physical disturbances generated by bottom trawl are known to induce changes such as reduced benthic habitat complexity (Watling and Norse 1998), increased local turbidity and enhanced release of the organic matter normally buried in the sediments (Palanques et al. 2001). Trawling also leads to mortality in benthic invertebrates and thus affect the structure and the functioning of the benthic invertebrate community (Collie et al. 2000b; Rijnsdorp et al. 2018).

Benthic species have different degrees of sensitivity to trawling depending on their biological characteristics and in particular their recovery rates (Hiscock et al. 1999; Lambert et al. 2014; Foveau et al. 2017). Further studies have shown that opportunistic species such as polychaetes (Kaiser et al. 2006) were less affected by trawling while the abundance of some sessile, long-lived and filter-feeding species decreased after a certain level of trawling (Kenchington et al. 2001; Tillin et al. 2006). Response of benthic community to trawling depends on the pre-fished composition of the community (Kaiser et al. 2002).

The composition and the distribution of benthic assemblages are strongly influenced by physico-chimical drivers (Hall et al. 1994) such as for example, salinity or bottom-water temperature and depth (Rees et al. 1999). Other factors such as the amount of organic carbon (Eleftheriou and Basford 1989) and the chlorophyll a concentration (Heip et al. 1992) can also influence the composition of benthic communities at regional scale. However, the influence of these different parameters on benthic assemblages can vary geographically.

Hydrodynamic parameters such as shear bedstress (current induced shear pressure on seabed) and sediment grain size (Couce et al. 2020) can also play a role in the distribution and structure of benthic assemblages. Benthic communities are also strongly affected by the natural disturbance induced, for example, by currents, waves or storms (Thistle 1981). Natural disturbance has the potential to erode seabed sediment, causing resuspension of organic matter (Morris and Howarth 1998) and affecting settlement of new invertebrate recruits (Hunt and Scheibling 1997). As trawling itself is known to have fairly similar consequences, species adapted to natural disturbances may also be resistant to trawling (Kaiser 1998). Many species in shallow tidal and wave-swept sandy habitats are well adapted to high rates of disturbance-induced mortality (Diesing et al. 2013) and therefore have potentially greater resistance to additional fishing disturbance. Thus, several studies have focused on comparing the effect of natural disturbances and trawling in benthic habitats. Hiddink et al. (2006) have, for example, demonstrated that trawling impacts were greatest in areas with low levels of natural disturbance and limited in areas with high degree of natural disturbance. Van Denderen et al. (2015) observed a decrease in filter feeders and long-lived species with an increase of the fishing pressure or of the degree of natural disturbance. These different results suggest that the effect of trawling on benthic communities could potentially be intertwined with natural disturbances in areas where these are significant.

Process-driven seafloor habitat sensitivity (PDS) has been defined from the method developed by Kostylev and Hannah (2007) which takes into account physical disturbance and "Scope for Growth" as structuring factors of benthic communities. It is a conceptual model that relates species biological traits and general metabolic requirement to environmental properties.

The "Disturbance" axis reflects the magnitude of habitat change or destruction (*i.e.* the stability of habitats over time), solely as a result of the natural processes that influence the seabed and are responsible for the selection of biological traits (Foveau et al. 2017). It can be related to the potential natural resistance of the community to physical disturbance. The "Scope for Growth" axis takes into account environmental stresses inducing a physiological cost to organisms and limiting their growth and reproductive potential. This axis estimates the remaining energy available for the species growth and reproduction [the energy spent on adapting itself to the environment being already taken into account; (Kostylev and Hannah 2007)]. It can be linked to the metabolic theory of ecology and the potential natural resilience of communities. Following this framework, maps of the physical environment can be converted into a map of benthic habitat types, each supporting communities of species with specific sensitivity to human pressures (which are here considered as potentially excessive additional stresses to natural processes).

When comparing the effects of abrasion and trawling, the environmental variables selected should best reflect the level of natural disturbance to benthic species. In habitats with low natural disturbance, surface sediments are little altered by natural processes (wave and tidal current). This allows the establishment of a high diversity of sessile and erect species that are known to be very sensitive to trawl abrasion (Foveau et al. 2017). Several proxies of natural physical disturbances can be used such as bottom current velocity or wave height. The growth of benthic species is strongly influenced by the food supply but also by other parameters such as water temperature value (Phillips 2005) and stability. Different growth proxies can be used such as temperature, food availability or chlorophyll a concentration. Habitats that are naturally undisturbed and where the cost to growth and reproduction of species is high are often composed of species that feed in suspension, have a long life span and slow growth and are therefore particularly sensitive to trawling (Bradshaw et al. 2003; Kostylev and Hannah 2007).

The implementation of the MSFD requires tools able to detect and monitor the effects of anthropogenic impacts on benthic communities, such as the four functional sensitivity indices identified in Chapter II (Jac et al. 2020a). They should be ideally insensitive to natural variability (Kröncke and Reiss 2010). However, since functional sensitivity indices are based on a set of biological traits known to be sensitive to trawling but also to most kinds of natural physical disturbances (van Denderen et al. 2015), they are likely to respond equally to both pressure types. It seems necessary to try to dissociate the effect of fishing and natural disturbance on the behaviour of each of these indices but also to see whether the influence of these parameters differs according to the habitats sampled, as perhaps suggested by the study of Diesing et al. (2013).

Aims of this study were to (a) identify the environmental forcing that influence the behaviour of the functional sensitivity indices in three different areas and (b) Assess the joined influence of these environmental parameters and trawl disturbance on these indices.

2. Methods

2.1. Study areas

See Chapter I for English Channel, Gulf of Lion and Corsica descriptions

2.2. Fishing impact data

See Chapter I for descriptions

2.3. Environmental data

Based on previous studies (Vaz and Llpasset 2016; Foveau et al. 2017) and the framework developed in the Kostylev habitat approach, environmental parameters being known to influence the composition and resilience of benthic communities to physical pressures were considered in this study. In the present work, it was considered that benthic community composition is mainly linked to physical constraints ("Disturbance axis") such as friction on the seabed due to tidal currents or stress induced by the waves. These parameters will mainly influence the composition of the community in epifauna/infauna and fragile/flexible species. The resilience of benthic community ("SfG" axis) depends mainly on metabolic constraints such as nutrition, osmotic, thermal or hyperbaric regulation. It will therefore be influenced by temperature (and in particular strong variations in temperature), salinity, oxygen concentration, depth or food availability.

2.3.1. English Channel

The English Channel is a shallow epicontinental platform subject to strong tidal currents. In the area studied in this work, there was no or very little stratification and the oxygen saturation was nearly maximal due to shallow depths and mixed waters masses (Foveau et al. 2017). The following environmental factors were used to reflect the main ecological characteristics of the benthic habitats in the English Channel:

Variables related to the community resilience (or Scope for Growth)

The secondary production and therefore the growth rate of benthic species is correlated with temperature, particularly in shallow areas (Tumbiolo et al. 1994). Seasonal increase in temperature can induce a temporary increase in the metabolic rate of some benthic species (Brockington and Clarke 2001). Thus, different temperature proxies were used in this study (SST, Ta and Ti).

<u>SST:</u> NOAA satellite data of the monthly mean (from 2000 to 2006) sea surface temperature, with a spatial resolution of 1.2 km.

<u>Ta:</u> the standard deviation between monthly mean temperature (using NOAA satellite data) within a year (calculated for each year from 2000 to 2006 and averaged) as a proxy of seasonal temperature variation.

Ti: the standard deviation of average annual temperatures between years (using NOAA satellite data from 2000 to 2006) as a proxy of inter-annual temperature variation.

Food availability: data of Particular Organic Carbon, considered as food for benthic fauna, calculated from monthly means [from 1998 to 2006; (Pingree and Griffiths 1980)] of satellite-derived chlorophyll-a data, with a 1.2 km spatial resolution (Foveau et al. 2017).

Salinity: mean salinity (calculated from issues of ECOMARS-3D model for year 2000 to 2006, monthly, with a spatial resolution of 4 km and a temporal resolution of six hours (Foveau et al. 2017). Salinity has an influence on the distribution and diversity of benthic species since each species has a salinity preference (Gogina and Zettler 2010). Changes in salinity significantly affect different physiological processes such as active intracellular transport, feeding rate or absorption, respiration and excretion of nutrients (Schmidt-Nielsen 1997) and in particular osmoregulation (Kinne 1971). Thus, variations in salinity lead to changes in the amount of energy allocated to different metabolic processes and individual production (Normant and Lamprecht 2006).

Variables related to the natural physical disturbance

Wave stress: data were obtained from NORGAS model and compiled for years 2007 to 2009. The model has temporal resolution of 3 hours. Significant period and height data were calculated from the 90th percentile (Rivier 2010a; Foveau et al. 2017). Waves may generate sediment resuspension (Morris and Howarth 1998). Thus, in areas with high wave action, the abundance of filter feeders may be reduced.

Seabed stress: it was the friction of water masses on the bottom, due to the diurnal tide (Aldridge and Davies 1993). With an initial resolution of 1/8° of longitude by 1/12° of latitude (referenced WGS 1984 datum), bed shear stress was interpolated to create a continuous raster of $1km^2$ resolution (Carpentier et al. 2009). Tidal currents may impose direct physical stress on epifaunal communities (Warwick and Uncles 1980). In areas with high seabed stress the benthic community can be composed of species with a low sensitivity to trawling.

Friction velocity: data were estimated using data of wave generated currents and seabed stress (methods calculation was presented in Foveau et al. 2017). In areas subjected to high friction velocity, benthic communities will be mainly composed of species that are not very sensitive to trawling (non-filtering and resistant to physical impacts). The friction velocity was calculated as:

$$Friction\ velocity = (wave\ generated\ currents) + (seabed\ stress)$$

with wave generated currents calculated from the depth, peak wave period and wave height parameters and the seabed stress were assumed to be collinear with wave generated currents.

Depth: bathymetric data were obtained from MNT data of SHOM (SHOM 2015). The resolution was about 100m and the MNT was vertically referenced to the sea mean level. In the English Channel, the waves have an influence on bottoms down to about 30 m (Grochowski and Collins 1994). Beyond this depth, only tidal currents disturb the bottom (Dyer 1986).

Sediments: sediments were categorized in 5 classes (Mud, Fine Sand, Coarse Sand, Pebbles, and Gravels) relative to the average mean grain size of surficial sediments (Foveau et al. 2017). Macrofauna distribution is mainly related to the nature of the sediment (Dauvin et al. 2017). In the English Channel, diversity hotspots of sessile epifauna are in gravel and pebbles sediments (Foveau et al. 2013). Higher number of sensitive species to trawling may be observed in the areas with high average mean grain size of superficial sediments.

2.3.2. Gulf of Lion and Corsica

Unlike in the English Channel, Mediterranean waters are often very stratified and much deeper. Salinity being hardly varying at the scale of this study, it was chosen to not consider it here. Following environmental factors were used to reflect the main ecological characteristics of the benthic habitats in the Gulf of Lion and in Corsica:

Variables related to the community resilience (or Scope for Growth)

Temperature is one of the main factors to explain seasonal patterns of growth, reproduction, and abundance in Mediterranean benthic suspension feeders (Boero and Fresis 1986). Seasonal variations of temperature can also impact the structure of benthic community. With global change, water temperature tends to increase and particularly in the Mediterranean Sea due to its relatively small volume. Warming of these waters can induce several episodic events of mass mortalities affecting species of cold-water affinity as it was reported in Mediterranean Sea from 1983 (Rivetti et al. 2014). Different temperature proxies were therefore used in this study (SST, Ta and Ti).

SST: average bottom temperature calculated from monthly model predictions (MyOcean (http://marine.copernicus.eu/) of bottom temperatures from 1994 à 2014.

Ta: standard deviation of bottom temperature between monthly averages (over 1994 to 2014) as a proxy of seasonal temperature variation.

Ti: standard deviation of bottom temperature between yearly averages (from 1994 to 2014) as a proxy of inter-annual temperature variation.

Depth: bathymetric data expressed as average water depth on a 1/16 * 1/16 arc minute of longitude and latitude (ca 115 * 115 meters) resolution were obtained from EMODnet Bathymetry Consortium (2018). Depth is linked to the stratification, the food availability for benthic fauna and the temperature. The body size of some individuals of benthic macrofauna can increase with increasing water depth (Albertelli et al. 1999). This parameter is therefore a good proxy of the benthic fauna growth and development.

Stratification: average absolute difference between surface and 30 (± 5) m depth density over 20 years. Density was calculated using data of salinity and temperature covering the 1994-2014 period (MyOcean (http://marine.copernicus.eu/)). High Pressure International Equation of State of Seawater (Millero et al. 1980) was used to compute sea water density. Details on computation of density seawater at high pressure from temperature and salinity was presented in Vaz and Llpasset (2020). Mediterranean Sea is characterized by a strong stratification of the water column in summer, due to high water column stability and high temperatures. This stratification is responsible for the exhaustion of dissolved surface nutrients. Furthermore, particle sinking results in a severe depletion of suspended food resources (Estrada 1996). Energetic constraints due to high metabolic activity and prolonged low levels of food can affect suspension-feeder like sponges or gorgonians (Coma and Ribes 2003) that are considered as sensitive species to trawling impact.

Chlorophyll a concentration: maximum concentration of surface chlorophyll obtained from monthly satellite observations from 1998 to 2014 (MyOcean (http://marine.copernicus.eu/)). Chlorophyll a concentration is used as a proxy of the primary production (Huot et al. 2007) and thus the energy available for the growth and development of the benthic fauna.

Food availability: Benthic animals are organized structurally, numerically and by feeding mode in relation to food availability (Rosenberg 1995). Benthic suspension feeder's dynamics are particularly influenced by the existence, in Mediterranean Sea, of a common energy shortage phenomenon mainly related to low food availability (Coma and Ribes 2003).

To calculate the food availability, only surface chlorophyll a was available as a reliable proxy of primary production. In order to account for the negative effect that both depth and stratification may have on this food source for the benthic communities, following Kostylev and Hannah (2007) the food availability was computed as:

$$Fa = F - stratification$$

$$F = \log\left(\frac{Chla}{depth}\right)$$

Oxygen saturation: average percent of dissolved oxygen from 1999 to 2014 (using data of monthly model predictions MyOcean (http://marine.copernicus.eu/)). Methods details were presented in Vaz and Llpasset (2020).

Within benthic communities, there is large variation in tolerance to hypoxia and anoxia between the different species (Nilsson and Rosenberg 1994). For example, under severe hypoxia small worms are better able to satisfy their metabolic demands with more efficient aerobic metabolism using the small amount of available oxygen than would large worms. Hypoxia persistence can cause a metabolic switching in favour of near anaerobic or anaerobic pathways (Diaz and Rosenberg 1995). One of the main impacts of very low oxygen concentration is the fact that to protect themselves, mobile species will tend to move and burrowing species will tend to emerge from the sediment (Nilsson and Rosenberg 1994). Thus, the resilience of communities to the impact of trawling is relatively related to oxygen saturation.

Variables related to the natural physical disturbance

Seabed shear stress (SBS): data were estimated using hydrodynamic models (based on current data, wave significant height, peak frequency, peak direction and bathymetry) limited to the north-west Mediterranean in 2001 and June 2007 to April 2009 (limited to wave data available) (Rivier 2010b, 2010a). Current fields were generated using 3D MEDNOR hydrodynamic model with a 1x1km spatial resolution and 3h time resolution. Wave data and bathymetry were estimated using the MED01DEG model at 0.1° spatial resolution over 3h time steps. The methodology is detailed in Rivier 2010a. Rugosity length was set to 0.1 mm.

In areas subject to high seabed shear stress, the assemblage of benthic community will be mainly composed of species that are not very sensitive to trawling (non-filtering and resistant to physical impacts).

Sediment grain size: Benthic communities in the Gulf of Lion are clearly spatially structured by granulometry (Bonifácio 2015). SHOM sediment map in the French Mediterranean waters (Garlan 2011) was used to obtain sediment distribution, grain size range (mm) per sediment group and % fraction of each main sediment group (Rock, pebble, pebble and gravel, gravel, sand, sand and fine sand, fine sand, mud, silt and clay). Römkens et al. (1997) equation enabling the estimation of average grain size from sediment typology and fraction was applied to obtain modelled seabed sediment average grain size (Vaz and Llpasset 2020).

2.4. Biological data

2.4.1. Surveys

Benthic invertebrate by-catch data derived from scientific bottoms trawl surveys occurring in the English Channel and in French Mediterranean waters were used in this work: CGFS and CAMANOC in the English Channel and MEDITS in the Gulf of Lion and in Corsica (Table 40). Survey protocols and data pre-processing are detailed in Chapter I.

Table 40: Number of stations sampled per year at the three study areas for which all environmental data were available

Years	English Channel	Gulf of Lion	Corsica
2008	89		
2009	84		
2010	85		
2011	92		
2012	78	48	10
2013	88	47	10
2014	121	48	10
2015	82	48	10
2016	70	48	10
2017	57	47	10
2018	94	47	10

2.4.2. Biotic indices

It was demonstrated in Chapters II (Jac et al. 2020a) and III that functional sensitivity indices seemed to be the most suitable for monitoring the effect of trawling on benthic communities, particularly with scientific trawl data. Only these indices (TDI, mTDI, pTDI and mT – computation detailed in chapter I) were used in this chapter.

2.5. Abrasion data

The fishery induced abrasion value (described in detail in chapter I) at each sampled station (Table 41) of the three studied areas were determined from maps (chapter I; Figure 25) of swept surface area ratio per year ($SAR.y^{-1}$).

Table 41: Abrasion ranges of the sampled stations in the three studied areas.
The three abrasion values represent the minimum value, median and maximum value.

	Gulf of Lion	Corsica	English Channel
Sampled abrasion range ($SAR.y^{-1}$)	0.08 – 4.81 – 20.69	0.00 – 0.11 – 2.03	0.00 – 7.47 – 74.15

2.6. Data analyses

Functional sensitivity indices that did not have a normal distribution were log- or square root transformed prior to analyses. To explore the relationship between the different explanatory variables, correlation matrices were computed.

2.6.1. Initial selection of environmental parameters

Since multicollinearity between the variables had to be avoided as much as possible for model construction, the calculation of the variance inflation factor (VIF) for each predictor variables was performed with the car R package 3.0-9 (Fox et al. 2019) after a generalized linear model (GLM). The lack of multicollinearity results in a small VIF and a VIF value that exceeds 10 indicates a problematic amount of collinearity (Lin 2008). The variables with too high VIF were iteratively removed, since the presence of multicollinearity implies that the information that this variable provides about the response is redundant in the presence of the other variables (Bruce and Bruce 2017).

2.6.2. Model of environmental influence on indices

To evaluate the influence of natural variability on functional sensitivity indices, generalized additive models (GAM) were used to investigate which environmental variables influenced the indices variations. As the available variable used to describe environmental conditions differed between the studied areas, separate models were developed for each study area. Since benthic community sampling was conducted over several years and benthic assemblages may change between years (independently of the environmental factors tested here), the "year" factor was also added in these models. Gaussian models with an identity link were built with a spline function and third degree of smoothing for all variables. For each GAM, the most significant variables were selected using forward procedure based on the Akaike Information Criterion (AIC; Akaike 1974) using the MASS package 7.3-51.5 (Ripley et al. 2019).

A variance partitioning procedure was used to distinguish the effect of inter-annual variation from the effect of variables related to resilience process and those related to disturbance impact using the model explained deviance. This procedure was used to quantify the marginal (when alone) contribution and conditional (when dropped) contribution of each type of process following the procedure described in Lehmann et al. (2002).

2.6.3. Study of abrasion influence on indices

Since the relationship between abrasion and functional sensitivity indices is not always linear over the entire abrasion range (Chapter V; Jac et al. 2020b), GAMs were used to study the influence of abrasion on each of the indices in the three studied areas.

2.6.4. Natural variability *vs.* abrasion

In order to understand the influence that environmental conditions (and the inherent inter-annual variations) and abrasion can have, separately and jointly, on the functional sensitivity indices, additional GAMs were carried out. In each studied area and for each indices, models were performed with environmental variables previously selected and the abrasion (if it was previously found to have a significant influence on the index).

For each index in each study area, the percentages of deviance explained by each of the three models (only environmental parameters, only abrasion, and all variables) were compared to determine whether natural variability (distinguishing between disturbance and resilience variables) overlapped with the effect of abrasion (and thus trawling) on benthic communities.

3. Results

3.1. Environmental parameters selection

In the three studied areas, strong correlations were observed between several environmental parameters. Thus, in the Gulf of Lion, the different temperature parameters (SST, Ti, Ta) were highly correlated (> 0.81). Ti was also strongly positively correlated to oxygen concentration and negatively correlated with depth. A high positive correlation between chlorophyll a concentration and stratification was also observed in this area. In Corsica, only the temperature parameters (SST, Ti and Ta) were strongly correlated. In the English Channel, salinity and food availability were strongly correlated (> - 0.87) but were also highly correlated with depth and Ta (Appendix F).

3.1.1. Gulf of Lion

The majority of parameters had variance inflation factor (VIF) superior to 10 when all environmental variables were retained (Table 42). All environmental variables had a VIF< 10 after the iterative removal of Ti, stratification and oxygen saturation.

Table 42: Variance inflation factor (VIF) of each environmental co-variable in the Gulf of Lion and variable removal effect. Grey shading indicates parameters with VIF>10. Ta = standard deviation between monthly mean temperature within a year; Ti = standard deviation of average annual temperature between years.

Environmental parameters	VIF	VIF	VIF	VIF
Ti	28.33	-	-	-
Ta	16.41	11.10	10.24	4.83
Stratification	15.72	14.39	-	-
Depth	15.56	13.10	10.25	9.71
Oxygen saturation	14.21	14.11	11.70	-
Chlorophyll a concentration	11.09	9.63	4.49	1.82
Food availability	9.35	8.41	4.14	2.56
SST	5.86	4.43	4.38	4.05
Seabed stress	2.79	2.77	2.50	2.41
Sediment size	2.44	2.40	2.06	1.85
Year	1.01	1.01	1.01	1.00

3.1.2. Corsica

The variance inflation factor was initially greater than 10 for almost all environmental variables (Table 43). All environmental variables had a VIF< 10 after the iterative suppression of the temperature, chlorophyll a concentration and intra-annual temperature variability (Ta) data.

Table 43: Variance inflation factor (VIF) of each environmental co-variable in Corsica and variable removal effect. Grey shading indicates parameters with VIF>10. Ta = standard deviation between monthly mean temperature within a year; Ti = standard deviation of average annual temperature between years.

Environmental parameters	VIF	VIF	VIF	VIF
Temperature	447.62	-	-	-
Ti	275.78	13.68	9.75	2.51
Ta	76.70	19.26	10.33	-
Chlorophyll a concentration	25.96	21.06	-	-
Food availability	23.98	19.75	5.35	3.73
Stratification	20.27	9.72	3.84	3.08
Oxygen saturation	13.29	13.27	5.29	4.98
Depth	14.16	9.27	8.71	5.11
Sediment size	1.44	1.30	1.19	1.13
Seabed stress	1.40	1.38	1.37	1.35
Year	1.31	1.26	1.23	1.22

3.1.3. English Channel

None of the environmental parameters studied in the English Channel had a variance inflation factor (VIF) greater than 10 (Table 44). Thus, all these environmental variables were retained for further analysis.

Table 44: Variance inflation factor (VIF) of each environmental co-variable in the English Channel.
SST = mean of the sea surface temperature; Ta = standard deviation between monthly mean temperature within a year; Ti = standard deviation of average annual temperature between years.

Environmental parameters	VIF
Food availability	7.68
Salinity	4.60
SST	1.87
Ta	4.43
Ti	1.91
Wave stress	3.03
Friction velocity	6.42
Seabed stress	1.05
Depth	6.74
Sediments	4.97
Year	1.26

3.2. Influence of environmental parameters on indices

3.2.1. Gulf of Lion

Over the eight environmental variables studied in the Gulf of Lion, only depth was removed from all developed models (Table 45). The chlorophyll a concentration, the intra-annual variation of temperature (Ta) and the year parameter were retained in each GAM. SBS was also retained for all indices except the TDI. As in the English Channel, the models selected highlighted the complexity and non-linearity of the relationships between the different indices and environmental variables (Figure G.1, G.2, G.3 & G.4).

Table 45: Model selected for each sensitivity index in the Gulf of Lion.
Chla = concentration in Chlorophyll a; Ta = standard deviation between monthly mean temperature within a year; SBS = Seabed stress; Sed = sediment size. "s" corresponds to spline function.

Indices	Selected explanatory variables	AdjR²	Explained deviance (%)
TDI	s(Ta, 3) + Chla + s(Sed, 3) + Year	0.45	47.0
mTDI	s(Ta, 3) + s(Fa, 3) + Chla + s(SST, 3) + SBS + s(Sed, 3) + Year	0.52	54.2
pTDI	Ta + Chla + s(SST, 3) + s(SBS, 3) + Year	0.34	35.9
mT	s(Ta, 3) + Chla + s(Fa, 3) + SBS + s(Sed, 3) + Year	0.53	55.3

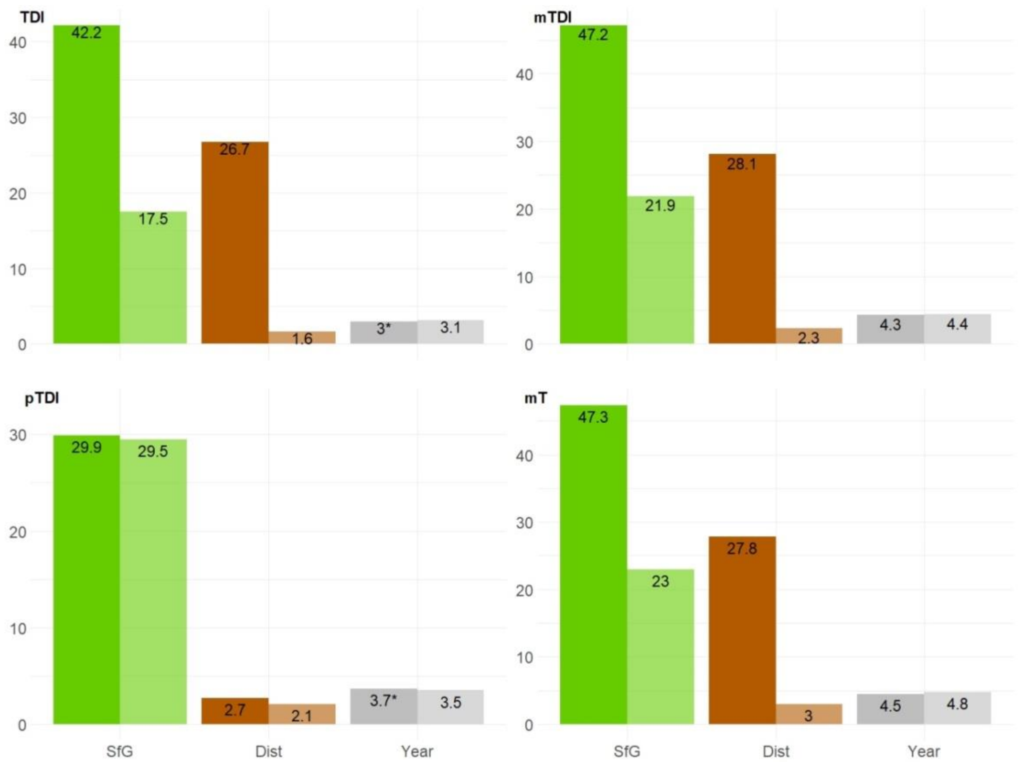


Figure 51: Percentage of deviance explained by each group of variables (SfG, Dist or Year) for each sensitivity index in the Gulf of Lion. SfG = Scope for Growth; Dist= Disturbance. Colored histogram= marginal contribution; histogram with transparency= conditional contribution. * indicate that the effect of this variable alone was not significant. Unexplained deviation for each of the indices (TDI: 53%, mTDI: 45.8%, pTDI: 64.1%, mT: 44.7%).

In the Gulf of Lion, the proportion of deviance explained by "Scope for Growth" and "Disturbance" parameters was high (>35%) and similar between the mTDI and the mT and even if values stayed relatively high, they were lower for TDI and pTDI (Figure 51; Table 45). In addition, for each index, the deviance explained by SfG parameter was always higher (for both marginal and conditional contributions) than the one explained by Dist parameter. Finally, overlap effects were very important in the gulf of Lion because differences between marginal and conditional contributions were high for each parameter.

3.2.2. Corsica

Over the eight environmental variables studied in Corsica, only the year parameter was removed from all models (Table 46). FA, SBS and the sediments grain size (Sed) were also retained for TDI derivatives and the mT. The stratification parameter was also retained for all indices except the mTDI. As before, the models selected highlighted the complexity and non-linearity of the relationships between the different indices and environmental variables (Figure G.5, G.8, G.11& G.14).

Table 46: Model selected for each sensitivity index in Corsica.
Fa = Food availability; Ti = standard deviation of average annual temperature between years; stratif = Stratification; O_2 sat = oxygen saturation; SBS = Seabed stress; Sed = sediment size. "s" corresponds to spline function.

Indices	Selected explanatory variables	AdjR²	Explained deviance (%)
TDI	Fa + s(Ti, 3) + s(O_2 sat, 3) + s(stratif, 3) + s(SBS, 3) + s(Sed, 3)	0.33	43.1
mTDI	Fa + O_2 sat + s(SBS, 3) + Depth + s(Sed, 3)	0.37	42.7
pTDI	s(Fa, 3) + s(Ti, 3) + s(stratif, 3) + s(SBS, 3) + Depth + s(Sed, 3)	0.37	45.2
mT	s(stratif, 3) + Depth	0.31	33.5

The proportion of deviance explained by environmental variables was high (>33%) and relatively close for TDI and its derivatives. The value for mT was lower even though it remained relatively high (Figure 52; Table 46). As in the Gulf of Lion, for each index, the deviance explained by SfG parameter was always higher (for both marginal and conditional contributions) than the one explained by Dist parameter. Only the SfG parameter (stratification and depth) ever seemed to have an influence on the mT. Over 55% of the deviance of each index was left unexplained by the environment. Moreover, the variables seemed to have a more structuring effect when they were all together in the general model than when the SfG and Dist variables were separated (conditional contribution), where they explained less variance and for some of them were not significant (Figure G.6, G.7, G.9, G.10, G.12 & G.13).

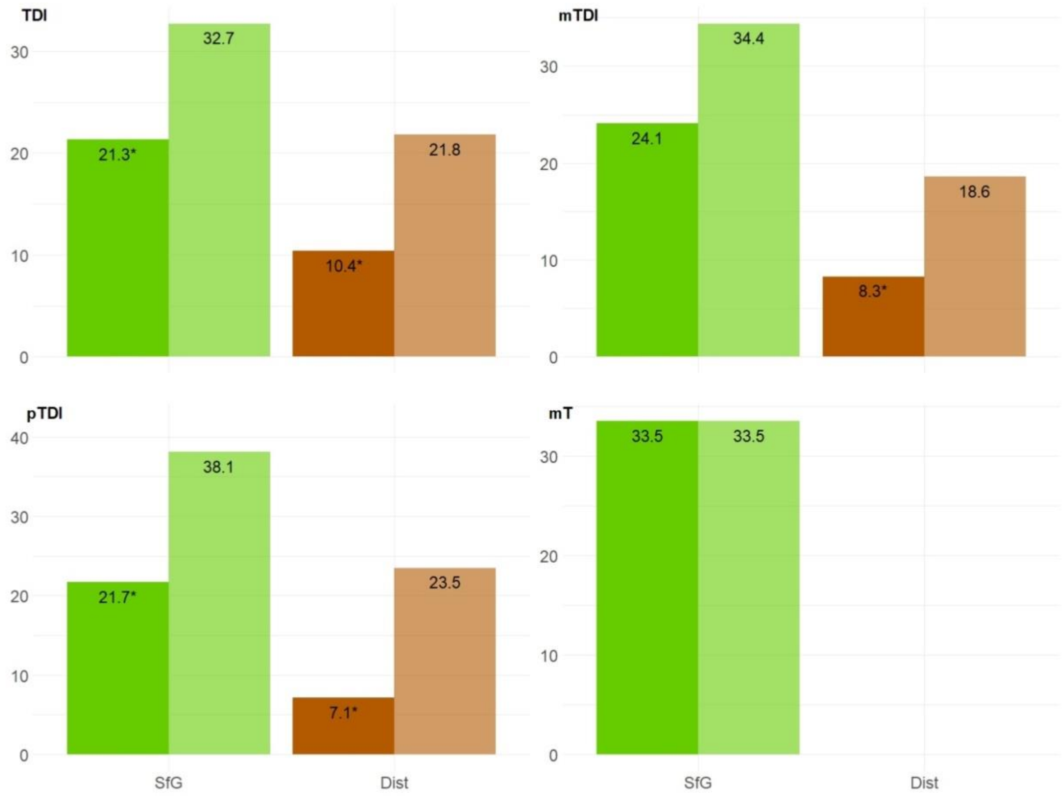


Figure 52: Percentage of deviance explained by each group of variables (SfG, Dist or Year) for each sensitivity index in Corsica. SfG = Scope for Growth; Dist= Disturbance. Colored histogram= marginal contribution; histogram with transparency= conditional contribution. * indicate that the effect of this variable alone/one variable was not significant. Unexplained deviation for each of the indices (TDI: 56.9%, mTDI: 57.3%, pTDI: 54.8%, mT: 66.5%).

3.2.3. English Channel

Over the 11 environmental variables studied in the English Channel, only the sea surface temperature (SST) was consistently removed from all tested models (Table 47). Food availability (Fa), salinity, annual variation of temperature (Ti), friction velocity (FV), seabed stress (SBS) and type of sediment (Sed) were retained in all GAMs developed. The year and wave stress parameters were also retained for two indices: TDI and pTDI. Overall, the selected models highlighted the complexity and non-linearity of the relationships between the different indices and environmental variables (Figure G.15, G.16, G.17 & G.18).

Table 47: Model selected for each sensitivity index in the English Channel.

Fa = Food availability; Ta = standard deviation between monthly mean temperature within a year; Ti = standard deviation of average annual temperature between years; FV = Friction velocity; SBS = Seabed stress; Sed = sediment type. "s" corresponds to spline function.

Indices	Selected explanatory variables	$AdjR^2$	Explained deviance (%)
TDI	s(Fa, 3) + s(Salinity, 3) + Ti + s(FV, 3) + s(Wave stress, 3) + s(SBS, 3) + Sed + Year	0.25	27.1
mTDI	s(Fa, 3) + s(Salinity, 3) + Ti + s(FV, 3) + s(SBS, 3) + Sed	0.23	23.8
pTDI	s(Fa, 3) + s(Salinity, 3) + s(Ta, 3) + Ti + s(FV, 3) + s(Wave stress, 3) + s(SBS, 3) + Sed + Year	0.32	33.4
mT	s(Fa, 3) + s(Salinity, 3) + s(Ti, 3) + s(FV, 3) + s(SBS, 3) + Sed	0.22	22.8

In the English Channel, the deviance proportion explained by "Scope for Growth" and "Disturbance" parameters was relatively similar for the different indices, with the exception of the pTDI where the explained deviance by SfG parameters was higher than for other indices. More precisely, the marginal contribution of the Dist parameter was greater than that of the SfG parameter for each index except pTDI. However, for all indices, the inverse was observed for the conditional contributions. From 66 to 77% of the deviance of each index was left unexplained by the studied variables (Figure 53; Table 47).

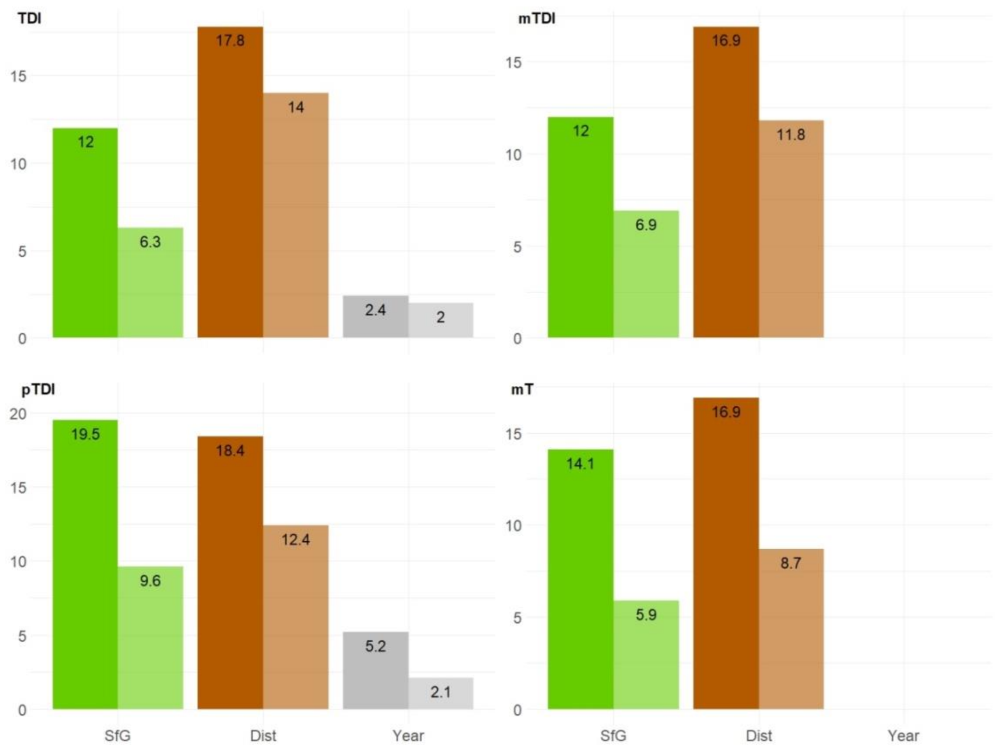


Figure 53: Percentage of deviance explained by each group of variables (SfG, Dist or Year) for each sensitivity index in the English Channel. SfG = Scope for Growth; Dist= Disturbance. Colored histogram= marginal contribution; histogram with transparency= conditional contribution. Unexplained deviation for each of the indices (TDI: 72.9%, mTDI: 76.2%, pTDI: 66.6%, mT: 77.2%).

3.3. Abrasion influence on indices

In the English Channel, the proportion of deviance explained by abrasion was higher for pTDI than for the other indices (Table 48). In the Gulf of Lion, values of deviation explained by abrasion were very similar for TDI and mTDI, lower for pTDI while it was higher for mT. The shape of relationship between abrasion and index, in both the Gulf of Lion (Figure 54), and the English Channel (Figure 56) was similar and generally decreasing with abrasion for the four sensitivity indices. In contrast, no significant relationship between abrasion and indices was observed in Corsica (Figure 55).

Table 48: Evaluation of the influence of abrasion (SAR.y-1) on sensitivity indices in the three studied areas

Areas	Indices	AdjR^2	Explained deviance (%)
Gulf of Lion	TDI	0.16	16.7
	mTDI	0.16	16.6
	pTDI	0.12	12.5
	mT	0.18	18.9
Corsica	TDI	-	-
	mTDI	-	-
	pTDI	-	-
	mT	-	-
English Channel	TDI	0.13	13.2
	mTDI	0.12	11.8
	pTDI	0.16	15.9
	mT	0.09	9.3

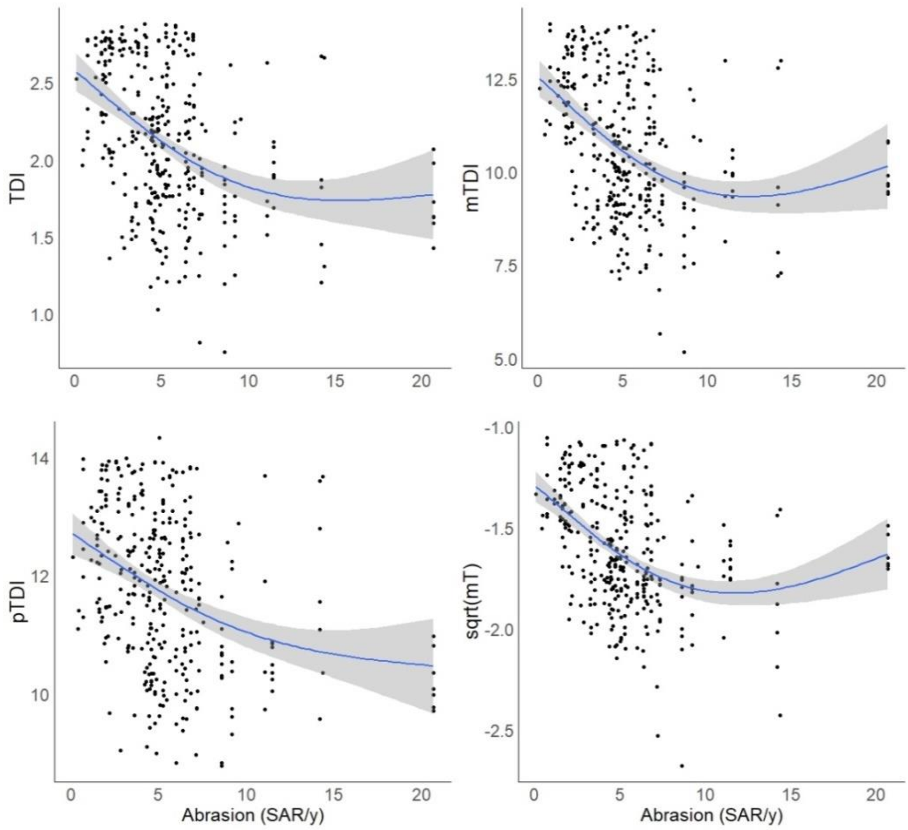


Figure 54: Relationship between abrasion (SAR.y-1) and functional sensitivity indices in the Gulf of Lion

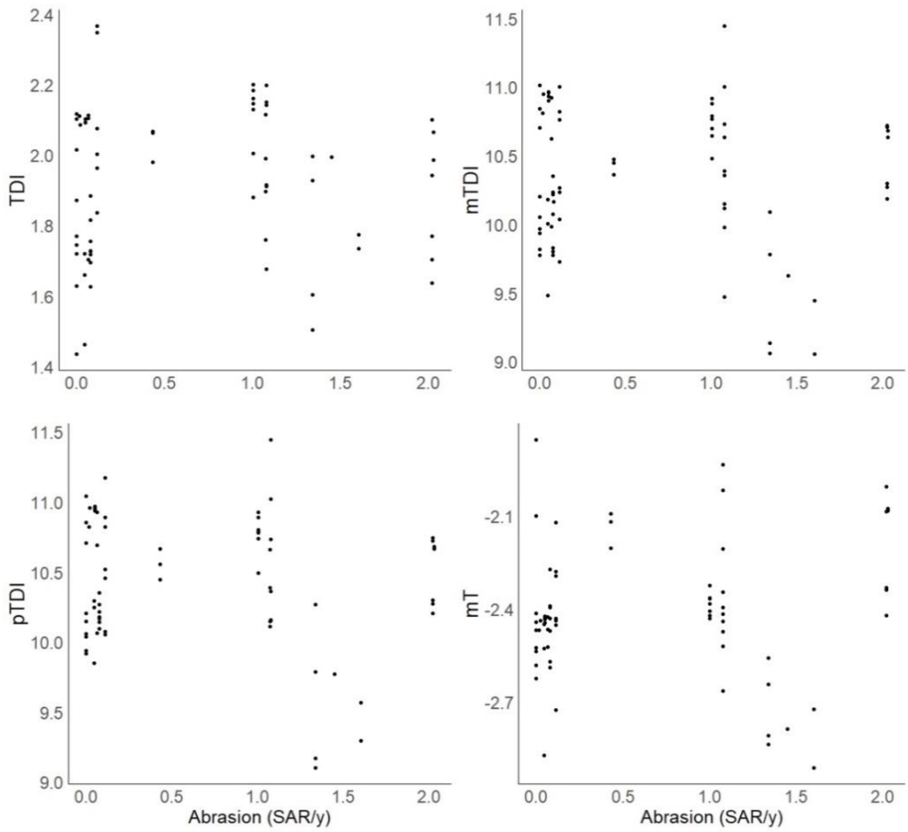


Figure 55: Absence of significant relationship between abrasion (SAR.y-1) and functional sensitivity indices in Corsica

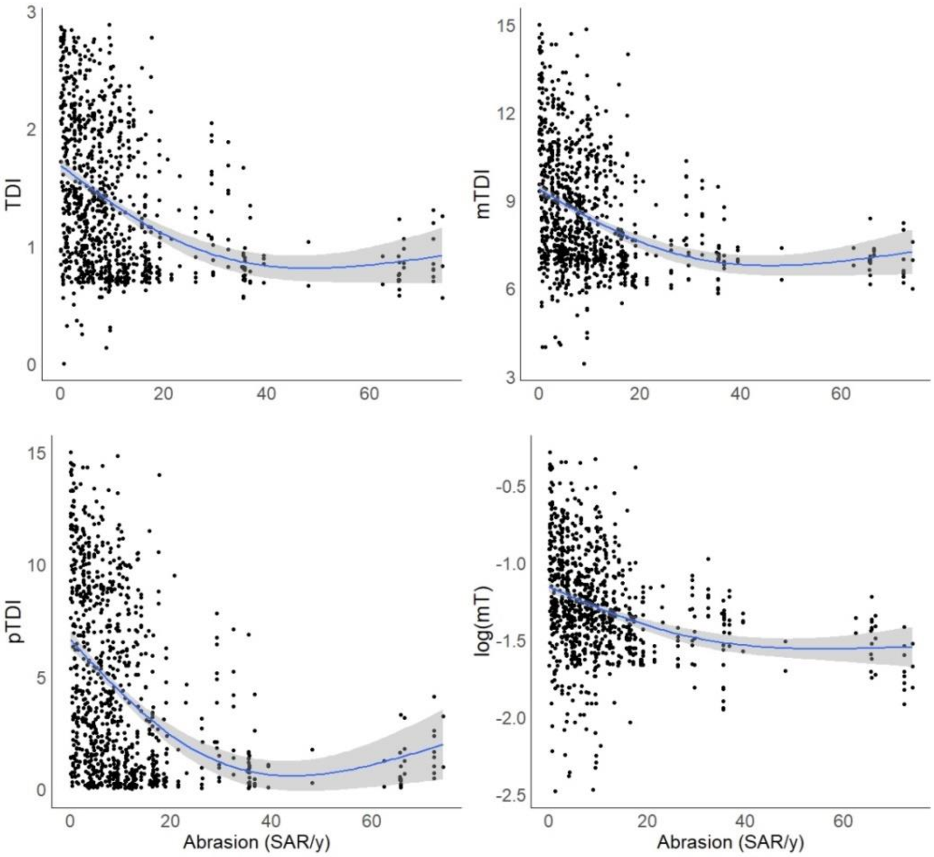


Figure 56: Relationship between abrasion (SAR.y^{-1}) and sensitivity indices in English Channel

3.4. Natural variability *vs.* abrasion

In view of the results obtained for Corsica in the part 3.3, the analysis combining environment and abrasion effects was not relevant. These analyses were only carried out in the other two study areas.

3.4.1. Gulf of Lion

In the Gulf of Lion, abrasion was retained by the selection model procedure only for the pTDI (Table 49) and its addition added little explanatory value to the model (Figure 57). For other indices only the initial environmental parameters were retained. However, the percentage of deviance explained by environment and/or abrasion was relatively low for pTDI compared to the other indices. Around 50% of the deviance of each index was not explained by the studied parameters.

Table 49: Evaluation of the combined influence of previously selected environmental parameters and abrasion on sensitivity indices in the Gulf of Lion. Chla = concentration in Chlorophyll a; Ta= standard deviation between monthly mean temperature within a year; SBS = Seabed stress; Sed = sediment size. "s" corresponds to spline function.

Indices	Selected explanatory variables	AdjR²	Explained deviance (%)
TDI	s(Ta, 3) + Chla + s(Sed, 3) + Year	0.45	47.0
mTDI	s(Ta, 3) + s(Fa, 3) + Chla + s(SST, 3) + SBS + s(Sed, 3) + Year	0.52	54.2
pTDI	s(Abrasion, 3) + Ta + Chla + s(SST, 3) + s(SBS, 3) + Year	0.35	37.7
mT	s(Ta, 3) + Chla + s(Fa, 3) + SBS + s(Sed, 3) + Year	0.53	55.3

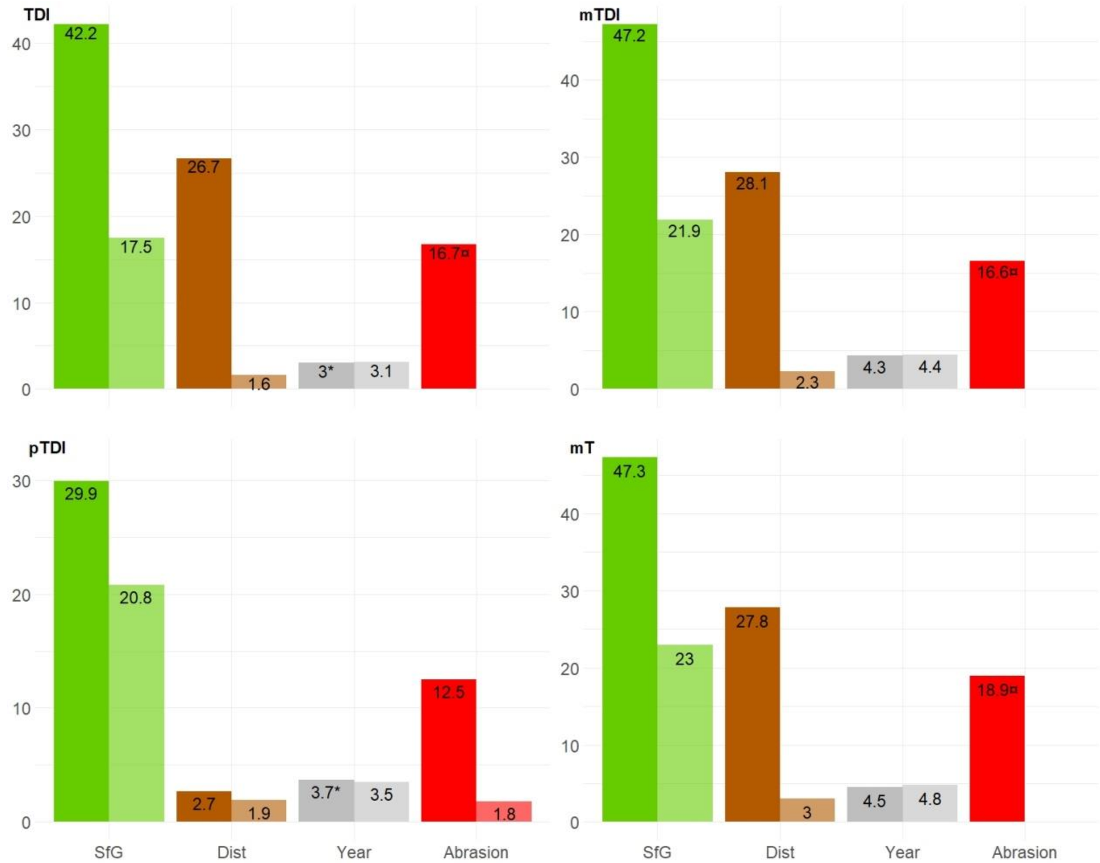


Figure 57: Percentage of deviance explained by each group of variables (SfG, Dist, Year or Abrasion) for each sensitivity index in the Gulf of Lion. SfG = Scope for Growth; Dist= Disturbance. Colored histogram= marginal contribution; histogram with transparency= conditional contribution. ¤ indicate that the effect of this variable alone was significant but not with the other variables in the model; * indicate that the effect of this variable alone was not significant. Unexplained deviation for e20ach of the indices (TDI: 53%, mTDI: 45.8%, pTDI: 62.3%, mT: 44.7%).

3.4.2. English Channel

In the English Channel, the abrasion and several environmental variables were retained in all GAMs (Table 50). For all indices, environmental variables retained were the same as for models without abrasion (Table 47). The deviance explained by environmental parameters and/or abrasion was higher for the pTDI than for the other indices (Figure 58). For each index, the deviance explained by abrasion alone was quite high (marginal effect > 9%) but very low when other variables were taken into account. In all cases, from 6.4 to 11.6% of the variation explained by abrasion was found to also overlap with the environment effect. Over 62% of the deviance of each index was left unexplained by the environment or the abrasion.

Table 50: Evaluation of the combined influence of previously selected environmental parameters and abrasion on sensitivity indices in the English Channel. Fa = Food availability; Ti = standard deviation of average annual temperature between years; FV = Friction velocity; SBS = Seabed stress. Sed = sediment type. "s" corresponds to spline function.

Indices	Selected explanatory variables	AdjR²	Explained deviance (%)
TDI	s(Abrasion, 3) + Fa + s(Salinity, 3) + Ti + s(FV, 3) + s(Wave stress, 3) + s(SBS, 3) + Sed + Year	0.29	31.2
mTDI	S(Abrasion, 3)+ s(Fa, 3) + s(Salinity, 3) + Ti + s(FV, 3) + s(SBS, 3) + Sed	0.26	27.5
pTDI	s(Abrasion, 3) + s(Fa, 3) + s(Salinity, 3) + s(Ta, 3) + Ti + s(Wave stress, 3) + s(FV, 3) + s(SBS, 3) + + Sed + Year	0.36	37.7
mT	s(Abrasion, 3) + Fa + s(Salinity, 3) + Ti + s(FV, 3) + s(SBS, 3) + Sed	0.24	25.5

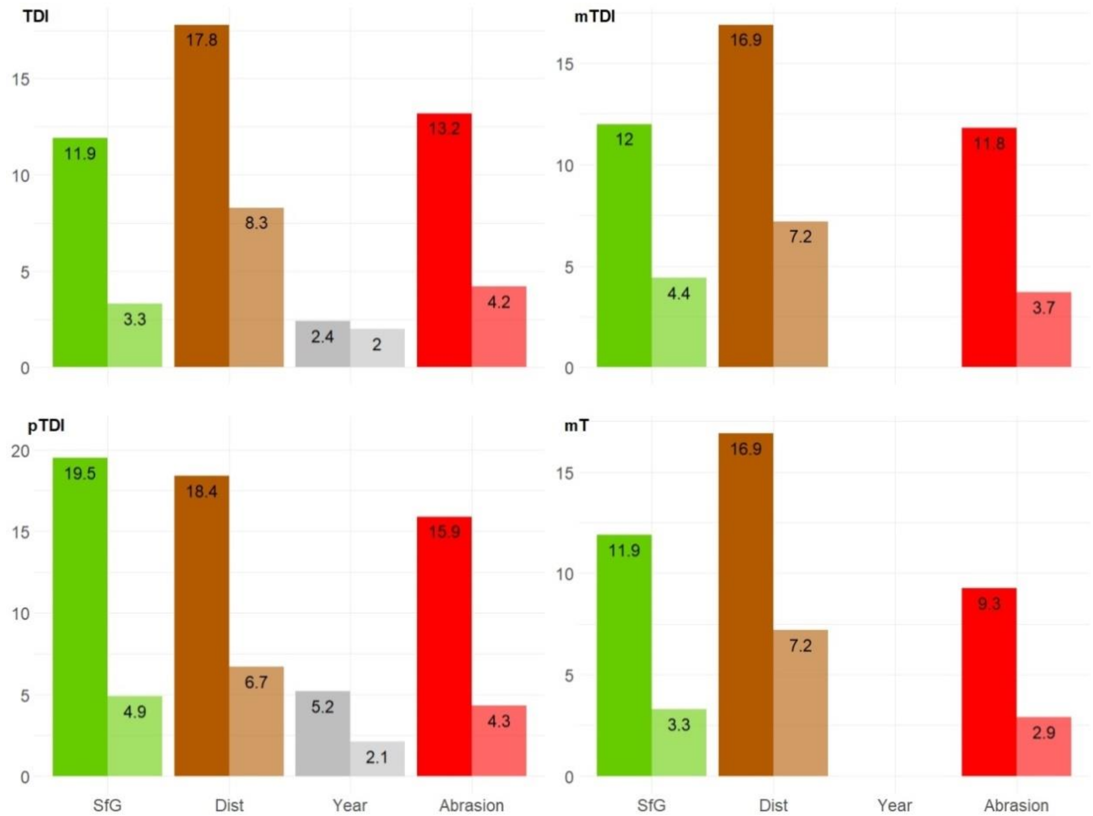


Figure 58: Percentage of deviance explained by each group of variables (SfG, Dist, Year or Abrasion) for each sensitivity index in the English Channel. SfG = Scope for Growth; Dist= Disturbance. Colored histogram= marginal contribution; histogram with transparency= conditional contribution. Unexplained deviation for each of the indices (TDI: 68.8%, mTDI: 72.5%, pTDI: 62.3%, mT: 74.5%).

4. Discussion

4.1. Which environmental parameters drive the composition of benthic communities?

Distribution and composition of benthic communities is known to be strongly influenced by environmental conditions (Hall et al. 1994). However, regional differences in the nature of the forcing factors could be observed. Even if the environmental parameters studied here were, initially, almost the same in the different study areas, the composition of the different benthic communities seemed to be governed by different environmental drivers. In the English Channel, food availability, salinity, inter-annual temperature variation, friction velocity, seabed stress and sediment type were the main factors influencing the composition of benthic communities. Environmental variables making up the "Disturbance" axis had a greater effect than the others on the different indices tested. In this zone, the benthic communities seem to be particularly structured by their potential natural resistance to physical disturbance and in particular their ability to withstand wave and tidal currents (friction velocity, seabed stress). Bremner et al. (2006) found that “SfG axis” variables such as salinity and SST had the greatest influence on the biological traits of benthic species in the English Channel and Irish Sea. However, they did not study exactly the same environmental variables as in this work and used a larger number of biological traits. More precisely, in the present work, index values tended to be positively correlated with the friction velocity or the seabed stress and negatively with the wave stress. These results seem counter-intuitive as they suggest that more trawl-sensitive species are found in areas where the natural physical impact on the bottom is greater.

In the Gulf of Lion and Corsica, the main environmental parameters that influenced the benthic composition were different from those in the English Channel and were the concentration of chlorophyll a, the intra-annual temperature variations, the FA, the SBS and the sediment size in the Gulf of Lion and the depth, the FA, the stratification, the oxygen saturation, the inter-annual temperature, the SBS and the sediment size in Corsica. In both zones, despite a non-negligible influence of the different parameters related to the "Disturbance" axis, parameters related to the metabolism of benthic species (Chl a concentration Ti, FA, depth) mostly influenced the different indices. In these two areas, the distribution of benthic communities seemed to be mainly influenced by the availability of resources necessary for their growth and development than by physical processes. As the Mediterranean is a microtidal sea with relatively low swell amplitudes in the Gulf of Lion (Guizien 2009), these results seem coherent. In addition, regarding the oligotrophy of the Mediterranean Sea (Rosenberg et al. 2003), the availability of food (and the chlorophyll a concentration in the Gulf of Lion) was logically a factor limiting the growth and development of benthic communities. Even though the Gulf of the Lion and Corsica are relatively close, several factors influencing the composition of benthic communities were different, which confirms the usefulness of studying these two areas separately. These differences may reflect the different hydrodynamic and geomorphological conditions between the two areas. The Gulf of Lion is a continental shelf where the depth is relatively shallow (90m on average; SHOM 2015) and where the circulation of water masses is mainly linked to regional winds (Millot 1990). Conversely, east Corsica is composed of a relatively narrow continental shelf followed by a steep continental slope (the depth increases rapidly with distance to the coast; SHOM 2015) hence the marked effect of depth on the structure of benthic communities in this zone.

More surprisingly, within the same area, indices did not seem to be influenced by the same environmental variables. For example, in the English Channel, a significant influence of the wave stress and year factor was observed on TDI and pTDI, whereas this was not the case for the other indices. Since these indices are calculated on the same biological data and based on the same biological traits (Foveau et al. 2019), these results suggested that certain index calculation methods may mask the influence of some environmental variables. The deviance explained by these parameters differed between indices with a higher value for pTDI than for other indices in all areas except in the Gulf of Lion. As this index only takes into account the species most sensitive to trawling (Chapter I, Jac et al. 2020a), these results suggested that the distribution of these species in the English Channel and in Corsica was particularly influenced by the environmental parameters studied in this work. In these two zones, the deviance explained by environmental parameters (conditional contribution) related to resilience (scope of growth) appeared to be greater for pTDI than for the other indices. In the Gulf of Lion, even if the deviance explained was lower for the pTDI than other indices, the deviance explained by SfG parameters (conditional contribution) was also higher for the pTDI than for other indices. This may suggest that the distribution of species considered sensitive to trawling is more dependent on factors related to resilience than other species of the benthic community. Resilience capacity even appeared to be the main factor structuring the species sensitive to trawling in Corsica and the Gulf of Lion. In the present work, the species particularly sensitive to trawling were filter feeders, sessile, large, fragile and belonged to the epifauna. The availability of food is known to be, in certain areas, a factor limiting the development of filter feeders with low mobility such as *Amphiura filiformis* (Rosenberg 1995). Bremner et al. (2006) showed that there is a link between the flexibility of the species, their position in the sediment and a number of environmental factors such as salinity or temperature. Finally, the size of benthic species can also be related to productivity (Romero-Wetzel and Gerlach 1991). The important influence of environmental parameters related to species resilience on species sensitive to trawling observed here appears to be consistent with previous findings.

In the Gulf of Lion, the low value of explained deviance for the pTDI could suggest that other factors, environmental or not, than those studied could better explain the distribution of these species. As the distribution of trawl-sensitive species appears to be particularly driven by their resilience capacity (SfG), it is likely that these missing factors are related to this parameter. Bremner et al. (2006) showed that fish abundance (and thus predation) could have a significant effect on a large number of functional traits. Proxies of the trophic relationships existing in studied areas could allow a better understanding of the factors influencing the distribution, in the Gulf of Lion, of species considered sensitive to trawling.

Regardless of index type or study area, the majority of environmental variables appeared to have a complex and non-linear relationship with the indices. When all areas and indices are combined, only the Chlorophyll a concentration had a negative linear relationship with functional sensitivity indices. This may result from the fact that many species exhibit asymmetric responses (or, although less frequently, multimodal patterns) along environmental gradients (Anderson 2008). These results confirm the interest and even the need to use splines and generalized additive models (GAMs) in the present study, to better understand the effect of natural variables on the functional sensitivity indices studied.

4.2. Abrasion

It is generally accepted that trawling has an impact on benthic communities and that not all species are equally sensitive to it (Kaiser et al. 1998; Sanchez et al. 2000; Queirós et al. 2006). Chapter II (Jac et al. 2020a) showed that four functional sensitivity indices, based on biological traits known to respond to trawl disturbance (Bremner et al. 2006; Gray and Elliott 2009; Bolam et al. 2014), responded significantly and negatively along a gradient of abrasion intensity and to different degrees depending on the area. In the present study, all functional sensitivity indices were significantly influenced by abrasion, except in Corsica where no significant influence of the abrasion was observed. The explained deviance was quite low for all the indices (< 20%) and relatively different between some indices within the same studied area. The higher explained deviance did not result from the use of the same index in the two studied areas. In the English Channel, as for the environmental parameters, the abrasion explained a larger part of the variance of the pTDI than that of the other indices whereas in the Gulf of Lion this index has the lowest value of explained deviance. These results show that in the English Channel, the biomass of species sensitive to trawling is particularly influenced by the abrasion [whereas it does not seem to be the case in the Gulf of Lion (lower value of explained deviance for pTDI)]. Finally, among the various environmental parameters studied those related to natural physical disturbance (Dist) had the greatest influence on indices. This suggests that, in the English Channel, benthic communities are essentially structured by physical disturbances. In the Gulf of Lion, physical disturbance and abrasion do not appear to be sources of significant stress for benthic communities and therefore do not appear as strongly structuring parameters.

In the Gulf of Lion, abrasion seemed to explain a larger part of the variance of mT than of the other functional sensitivity indices whereas the contrary has been observed in the English Channel. Compared to TDI and its derivatives, a factor has been added to the method of calculating mT: the protection status of the species (see Chapter I for details). The large difference in the influence of abrasion on mT and other indices could be related to this factor. This difference could also come from the method of combining the different biological traits used. In the calculation of the mT: a hierarchy is made between the different traits by separating primary and secondary factors and then, those having direct and indirect effect. The addition of the factor "protection status" in the calculation of TDI and its derivatives could allow the validation of one or the other of these hypotheses.

4.3. Natural variability *vs.* abrasion

4.3.1. English Channel, an area under multiple stressors

In some cases, where natural disturbances are very high, the effect of trawling on benthic communities may be very limited or even undetectable (Kaiser et al. 1998; van Denderen et al. 2015). In the English Channel, the addition of abrasion in the different GAMs did not result in removing the significant influence of one of the environmental variables. Abrasion itself seemed to have a significant influence on the index regardless of the index of functional sensitivity studied. Effect of abrasion is not fully overlapping with that of the environmental variables. The deviance explained by models including both abrasion and the various environmental parameters is higher, whatever the index studied, than models containing only abrasion or only environmental factors. This indicates that, in the English Channel, contrary to what has been observed by Stokesbury and Harris (2006) in the Atlantic or by Sciberras et al. (2013) in Cardigan Bay (Wales), natural disturbances, although strong (large swell and strong tidal currents), do not fully mask the impact of trawling on benthic communities. The fact that, for each index, the value of the deviance explained in the final model was not equal to the sum of the deviance explained by the environment and that explained by fishing indicated that there was still an overlap between the effect of fishing and the effect of environmental parameters on benthic communities. As shown in Kaiser (1998), trawl disturbance seems to affect benthic communities in a similar way to natural disturbance but to also induce specific changes, not fully masked by that of the environmental parameters.

In summary, in the English Channel, indices were not influenced in the same way by environmental parameters and abrasion which was consistent with previous results. The composition and distribution of benthic communities is governed by environmental conditions but also by fishing effort (or abrasion) and species most sensitive to trawling are the most suited to detect this effect. As a result, the pTDI index seemed to be the most appropriate to detect the effect of specific abrasion (not overlapped with the environment) in this study area.

4.3.2. Gulf of Lion, too late to say?

In the absence of tidal currents, the Gulf of Lion is subjected to a calm hydrodynamic regime and is dominated mainly by fine sediments (Ferré et al. 2008). Thus, since the benthic communities are not subjected to major natural physical disturbances, their composition and distribution should be particularly affected by the abrasion induced by trawling (Kaiser 1998). Following this hypothesis, abrasion should have a significant influence on all indices, independently (or with little overlap) of environmental conditions. It appeared that in models combining abrasion and environmental parameters, abrasion specific effects could only be detected when using pTDI.

Two hypotheses may emerge from the absence of significant relationship between abrasion and the chosen indices when environmental parameters are taken into account. Firstly, the significant effect of abrasion observed on its own is entirely shared with one or several environmental variables. The correlation matrix indicated that abrasion was not fully correlated to one variable but slightly correlated (> 0.60) with several variables (the three proxies of temperature and depth). The effect of abrasion may not be distinguished from the effect of the combination of these variables. The second hypothesis is that the significance of the observed abrasion is in fact only related to the environment. Consequently, there is no real effect of fishing on the benthic communities of the Gulf of Lion.

The use of the available *in situ* observations alone does not permit to confirm either of these hypotheses with certainty. A significant effect of abrasion on pTDI could be detected when food availability and sediment size variables were removed. This suggests that abrasion does have a significant effect on the distribution of trawl-sensitive species, but, when considering the entire benthic community, this effect is masked by variations in these environmental parameters. Given that trawling has been present in the area for a very long time and at extremely high intensities (Jac and Vaz 2018), it is conceivable that trawling has lead to long-term changes in a number of environmental parameters such as sediment characteristics' (Brown et al. 2005; Trimmer et al. 2005). Original communities might have been replaced by fully adapted benthic communities (Chapter V; Jac et al. 2020b). These semi-natural communities are therefore only shaped by local environmental variations.

In order to verify these hypotheses, it is necessary to monitor benthic communities along a wider abrasion gradient, containing in particular unfished areas. Since no untrawled areas are currently sampled within the framework of scientific bottoms trawl surveys, cruises dedicated to monitoring the effect of trawling on benthic communities should be implemented. In the case where no unfished area may be left [as it seems to be the case in the Gulf of Lion (Jac and Vaz 2018)], a temporary closure of certain zones to fishing may allow to monitor the evolution of the environment (granulometry for example) and of the benthic communities, and observe (or not) a return to original communities.

The significant influence of the year on all the indices studied shows an inter-annual variability in the composition of benthic communities in the Gulf of Lion. This was also reported by Labrune et al. (2007), who suggested that these changes could be cyclic and potentially linked to regional climatic variations.

4.4. Corsica, too little to say?

Contrary to what has been observed in other study areas, no significant relationship between the four indices and the abrasion was observed in Corsica. This was suspected as abrasion values are relatively low over the whole Corsica (Chapter I). Benthic communities were consistently sampled in areas with low levels of fishing. As discussed in Chapter II (Jac et al. 2020a), the chosen indices did not appear to be able to detect the effect of trawling on benthic communities at such low levels of abrasion. An environmental effect, mainly related to the resilience of communities (SfG), was however detected by the indices. Moreover, the absence of a significant effect for most of the environmental variables when taken separately (marginal contribution), whereas they had a significant effect in the overall model, indicated either an overfitting adjustment of the model or important underlying interactions (antagonistic or synergistic effects) between environmental parameters related to unknown processes. The latter, often referred to as the Simpson's paradox, may result in drawing the wrong conclusions and requires complementary data to be solved (Pearl 2014). In view of these results, no conclusion can be made on the relationship between functional sensitivity indices and the environment in this area. Finally, the absence of a significant effect of the year factor suggested that, contrary to what was observed in the two other study areas, the benthic communities sampled in Corsica were relatively similar between the different years reflecting little natural or anthropogenic variability present in Corsica.

In conclusion, in the different study areas, benthic communities did not seem to be structured by the same environmental factors. In the English Channel, environmental parameters related to the resistance of species to natural physical disturbances were those which mainly influence the benthic communities whereas in the Mediterranean, these were the parameters related to the resilience of the communities.

Abrasion also appeared as a variable structuring benthic community in the English Channel whereas this was not observed in Corsica. In the Gulf of Lion, only one index was able to differentiate between the abrasion effect and the various environmental variables. In the two zones where an abrasion effect could be detected, the species considered sensitive to trawling seemed to better respond to abrasion and the different environmental variables related to their resilience. The pTDI index seems quite appropriate to evaluate the effect of abrasion and the environment, and more particularly parameters related to growth and resilience of benthic species.

Discussion générale, conclusions et perspectives

L'ambition de ce projet doctoral était d'étudier les effets des activités de pêche aux arts traînants sur les communautés benthiques, dans quatre secteurs différents en termes d'hydrodynamisme et de couverture sédimentaire. Les questions de recherche auxquelles cette étude a tenté de répondre sont les suivantes :

1. Comment suivre l'état écologique des habitats benthiques du plateau continental ?
2. L'influence de différents paramètres environnementaux, dont l'hydrodynamisme, peut-il masquer les effets de la pêche aux arts traînants, selon les habitats considérés ?

Le premier objectif de cette discussion générale est de synthétiser les avantages et inconvénients des différentes méthodes d'échantillonnage et d'analyse des données pour suivre l'impact du chalutage sur les communautés benthiques du plateau continental. La deuxième partie vise à proposer une évaluation de l'état écologique des habitats benthiques. Enfin des perspectives scientifiques sont proposées en dernière partie de cette discussion.

1. Suivre l'impact du chalutage sur les communautés benthiques

1.1. Quelle méthode d'échantillonnage ?

Cette thèse propose la première évaluation de l'intérêt de trois méthodes d'échantillonnage de la faune benthique (le chalutage scientifique, la drague et la vidéo tractée) pour suivre l'impact des arts traînants sur les communautés benthiques. L'utilisation "classique" d'engins, tels que les bennes ou les carottiers (Jørgensen et al. 2011; Eleftheriou 2013), pourtant quantitatifs mais n'échantillonnant que des surfaces réduites, n'est pas pertinente pour suivre l'impact de perturbation telle que celle des arts traînants opérant sur de larges surfaces. De surcroît, la faune ciblée – principalement de l'endofaune détritivore de petite taille (Jørgensen et al. 2011; Bolam et al. 2014) - est peu impactée par le chalutage. Ces méthodes ne semblent donc pas adaptées pour étudier l'effet du chalutage sur les communautés benthiques, car elles ne prélèvent pas efficacement les grandes espèces de l'épifaune généralement peu abondantes (Bolam et al. 2014) mais particulièrement sensibles aux arts traînants (Bradshaw et al. 2003; van Denderen et al. 2015). De plus, les bennes comme les carottiers ne peuvent pas être déployés sur des fonds durs ou des sédiments grossiers alors même que ces types d'habitats sont régulièrement chalutés dans les eaux européennes (Eigaard et al. 2017). La sélection d'une méthode d'échantillonnage dans le cadre d'un suivi d'une pression anthropique doit donc reposer sur trois aspects : la sensibilité de la faune échantillonnée à la pression étudiée, la possibilité de déployer l'engin dans une grande diversité d'habitats et enfin la mise en œuvre opérationnelle (temps d'analyses, coûts opérationnels…).

1.1.1. Performance des engins

Le chalutage scientifique

Les résultats issus des chapitres II, III et IV ont permis de mettre en avant les principaux avantages et inconvénients inhérents à l'utilisation d'un chalut scientifique pour évaluer l'impact des arts traînants sur les communautés benthiques. L'un des principaux intérêts de l'utilisation de données collectées au chalut scientifique lors des campagnes de pêche annuelles est sa capacité à représenter de manière satisfaisante la structure de la faune benthique à large échelle spatiale (Foveau et al. 2017). En effet, les chalutiers professionnels opérant à très large échelle (traits de plus de 20 km à 4 nœuds), échantillonner la faune benthique sur des surfaces du même ordre de grandeur semble pertinent et nécessaire. Bien que plus efficace sur les fonds meubles (avec notamment une meilleur représentativité de la diversité de la faune benthique présente), cet engin peut également être déployé sur des fonds grossiers, ce qui permet de suivre l'impact des arts traînants sur les ensemble des habitats pouvant être ciblés. Les données issus du chalut sont considérées comme semi-quantitatives à condition que les coordonnées GPS du début et de la fin du trait soient enregistrées (Doré et al. 2015), ce qui permet alors de calculer de façon précise la surface balayée et la densité ou les rendements au km² des espèces capturées. Or ces informations sont toujours disponibles et particulièrement précises dans le cadre de chalutages scientifiques.

Ce travail a permis de mettre en avant que l'identification des espèces directement sur le bateau après la capture permettait tout de même d'identifier plus de 70% des taxa au niveau de l'espèce et près de 80% au niveau du genre, ce qui semble satisfaisant pour la réalisation d'analyses basés sur les traits biologiques. Bien que le chalut s'enfonce de quelques centimètres dans les sédiments meubles (Eigaard et al. 2016), la grande majorité de la faune benthique capturée, durant les différentes campagnes de pêche scientifique, appartient à l'épifaune (environ 90% des taxa collectés en Manche et plus de 75% de ceux capturés dans le Golfe du Lion). C'est probablement une des raisons pour lesquelles un grand nombre d'indices calculés avec les données de chalutage répondaient significativement à l'abrasion et ce, dans toutes les zones étudiées exceptée la corse (Chapitre II ; Jac et al. 2020a). En Corse, les résultats obtenus ne semblent pas être liés à l'engin utilisé pour l'échantillonnage mais plutôt à une pression de pêche très faible et à une mauvaise répartition de l'échantillonnage le long du gradient d'intensité de l'abrasion. Ces travaux suggèrent que lorsque l'effort de pêche (et donc l'abrasion) est très fort ou très faible, la portion de la communauté benthique collectée à l'aide du chalut ne répond pas ou plus à la pression.

Le principal désavantage de cette méthode d'échantillonnage est sa nature destructive. En effet, l'utilisation répétée de chalut scientifique dans une zone peut avoir un impact négatif sur la biodiversité (Trenkel et al. 2019), ce qui peut sembler peu cohérent dans un contexte d'évaluation d'impacts et mise en place de stratégies de conservation.

Drague

La drague peut être considérée comme un engin intermédiaire entre les bennes et les chaluts. En effet, bien que cet engin capture principalement de petites espèces de l'endofaune comme les polychètes, qui n'est pas le compartiment qui répond le mieux à l'effet des arts traînants (Jennings et al. 2002), près de 40% des taxa collectés sur les fonds grossiers appartenaient à l'épifaune. Le second avantage principal de la drague est sa polyvalence : elle est capable d'échantillonner des fonds meubles aux fonds durs. Même si ces points positifs pourraient faire de la drague une méthode d'échantillonnage appropriée pour suivre l'impact des arts traînants sur la faune benthique, peu d'indices calculés avec les données issues de la drague étaient significativement influencés par l'abrasion. La communauté échantillonnée à l'aide de la drague ne semble donc pas répondre de manière satisfaisante au chalutage. Bien que le nombre de stations échantillonnées à la drague ne permet pas d'assurer avec certitude l'inefficacité de la drague pour suivre l'impact des arts traînants sur les communautés benthique, son utilisation dans ce cadre semble peu pertinente. La représentativité spatiale de cette méthode ne semble également pas pleinement satisfaisante : la drague prélève la faune de manière très locale (même si dans cette étude, trois prélèvements de drague ont été effectués le long de chaque transect de chalut scientifique). La limitation spatiale de l'échantillonnage à l'aide de drague est encore plus prononcée dans les sédiments particulièrement vaseux à cause du remplissage très rapide de l'engin. Enfin, comme le chalut scientifique, cette méthode de prélèvement est dite « destructive ». Même si elle est semi quantitative (le volume de sédiments récolté par la drague est connu), il reste cependant difficile d'estimer la surface échantillonnée à la drague, le trait étant plus ou moins long en fonction de la nature du sédiment et de l'envasement de la drague (Doré et al. 2015).

Vidéo

Depuis plusieurs années, l'imagerie vidéo est régulièrement utilisée pour étudier la diversité des habitats benthiques ou observer la mégafaune marine (Mallet and Pelletier 2014). Grâce à leur nature non destructive, mais également leur capacité à échantillonner une grande diversité d'habitat, les méthodes s'appuyant sur l'imagerie vidéo semblent prometteuses pour un grand nombre de travaux portant sur l'évaluation des impacts anthropiques. Les systèmes vidéo tractés sont particulièrement intéressants pour suivre l'impact des arts traînants sur les communautés benthiques puisqu'ils peuvent-être déployés à large échelle (déploiement sur 500 mètres minimum dans le cadre de cette étude). Les résultats issus du chapitre IV montrent que la vidéo tractée permet d'échantillonner en grande majorité des espèces de la macro-épifaune benthique – compartiment particulièrement sensible aux impacts du chalutage (Bradshaw et al. 2003; van Denderen et al. 2015). Le système s'est montré particulièrement efficace pour observer la mégafaune benthique, que ce soit sur les sédiments grossiers en Manche ou les sédiments fins dans le Golfe du Lion. Seule la turbidité est apparue comme une réelle limite environnementale à l'utilisation de ce système. Enfin, l'utilisation d'un système vidéo tracté pour suivre l'effet des arts traînants sur les communautés benthiques est particulièrement pertinente dans les sédiments mixtes ou grossiers alors qu'elle semble moins adaptée dans les sédiments fins (dans le cas d'un nombre de stations échantillonnées très limité).

Un des principaux inconvénients de l'utilisation de systèmes vidéo réside dans le fait qu'il est, la plupart du temps, difficile d'identifier les individus jusqu'à l'espèce (Flannery and Przeslawski 2015). Cependant dans le cadre de l'utilisation d'indices basés sur des traits fonctionnels, ces difficultés d'identification semblaient avoir relativement peu d'influence puisque près de 70% des taxas observés ont été identifiés au minimum au niveau du genre, niveau qui est généralement suffisant pour définir les caractéristiques biologiques des individus (Brind'Amour et al. 2009; Foveau et al. 2017).

Bien que la capacité de la méthode d'échantillonnage à détecter l'impact des arts traînants sur les communautés benthiques soit le principal facteur permettant de considérer cette méthode comme viable pour un suivi à long terme de l'évolution de perte d'intégrité des habitats benthiques causé par le chalutage, le volet « faisabilité opérationnelle » doit également être pris en compte.

1.1.2. Opérationnalité des engins

Malgré l'absence de données précises quantitatives, la mise en œuvre de chacune des méthodes est discutée dans cette partie et synthétisée dans la table 51.

Le chalutage scientifique

Le principal avantage de l'utilisation du chalut scientifique réside dans le fait qu'il est annuellement déployé dans les quatre zones étudiées dans ce travail, dans la cadre des campagnes d'évaluation des stocks des poissons benthiques ou démersaux (MEDITS, CGFS et IBTS). Un important jeu de données contenant plusieurs années de suivi est déjà constitué à ce jour (Vaz et al. 2019). Le caractère opportuniste de ces collectes de faune benthique est donc particulièrement intéressant. L'identification des individus à bord permet de limiter le temps alloué à l'identification des espèces. Même si parfois ce temps restreint dédié à l'identification des espèces entraîne une diminution de la précision taxonomique, il apparaît que ces données sont relativement fiables et que l'identification au genre ou à la famille sont de bons substituts pour l'identification des espèces dans les analyses de communautés benthiques (Brind'Amour et al. 2014). En cas de difficulté répétée à identifier une espèce, il est également possible de conserver l'espèce pour ensuite pouvoir l'identifier en laboratoire. Cependant, la mise en place d'une identification systématique de l'ensemble de la macrofaune benthique capturée lors des campagnes de chalutage de fonds nécessite tout de même la présence à bord de personnel formé à l'identification du benthos dans le but de diminuer au maximum les potentielles erreurs d'identification.

Drague

D'un point de vue opérationnel, même si la drague Rallier du Baty est relativement facile à déployer en mer, c'est le processus d'analyse et d'identification des individus collectés qui apparaît plus contraignant. Tout d'abord, après avoir rincé et tamisé les échantillons, ceux-ci sont conservés dans une solution contenant de formaldéhyde à 4% pour éviter la dégradation des tissus. Le volume d'échantillons conservés à chaque drague étant approximativement de 10L, l'une des principales contraintes de l'utilisation de la drague est la nécessité d'avoir d'importants moyens de stockage, que ce soit en mer sur le bateau mais également au retour en laboratoire. De plus, avant le tri et l'identification des individus, les échantillons doivent donc être rincés abondamment à l'eau claire afin d'en retirer l'excédent de formol. En plus d'être relativement chronophage, cette étape du traitement des échantillons issus de la drague nécessite une prise en charge adaptée des déchets formolés. Enfin, les étapes de tri des individus et d'identification des espèces à la loupe binoculaire sont particulièrement chronophages et notamment pour les sédiments constitués de débris coquilliers dans lesquels il est parfois difficile de repérer les individus très petits. Ainsi, dans le cadre de cette étude, le temps nécessaire au tri d'un échantillon variait entre 1 et 17 heures avec une moyenne de 7h par échantillon. Doré et al. (2015) ont estimé que le temps de traitement des échantillons issus de la drague Rallier du Baty variait entre quelques heures et quelques jours de travail en fonction du type de sédiment, de la richesse spécifique de l'échantillon et de la taille des mailles du tamis utilisé.

Vidéo

Le principal inconvénient de l'utilisation de la vidéo est le temps d'analyse qui peut être relativement long (Mallet and Pelletier 2014). Doré et al. (2015) ont estimé qu'il faut en moyenne 2 à 3 fois le temps d'enregistrement pour analyser une vidéo. Dans le cadre de ce travail, l'identification de l'ensemble des individus sur un transect vidéo a pris entre 2 et 5 heures. Malgré cette contrainte temporelle, l'utilisation d'imagerie vidéo est particulièrement intéressante car il est possible de revenir sur une analyse ou d'analyser plusieurs fois le transect, par exemple pour évaluer les biais d'identification liés aux observateurs (Pelletier et al. 2012). L'existence de deux points lasers sur les images permet également d'obtenir des données quantitatives (puisque la surface est connue), mais également de réaliser un certain nombre de mesures comme la taille de certaines espèces par exemple. Enfin, le déploiement en mer de cette technique nécessite tout de même des conditions particulières puisque la houle et une vitesse trop importante ou peu régulière entraîne une diminution de l'exploitabilité des vidéos.

Table 51: Synthèse de la pertinence des trois méthodes d'échantillonnage selon différents critères.
✓ indique que la méthode répond au critère ; ✓ indique que la méthode répond en partie au critère ; × indique que la méthode ne répond pas au critère
Le nombre de « + » font référence à une quantité d'espèce dans chaque catégorie

Méthode	Type de sédiment			Taille de la faune prélevée		Position de la faune prélevée		Niveau d'identification			Qualification des données		Détection de l'effet du chalutage
	Fin	Mixte	Grossier	Macrofaune	Mégafaune	Endofaune	Epifaune	Espèce	Genre	Famille	Quantitatives	Semi-quantitatives	
Chalutage scientifique	✓	✓	✓	×	✓	+	++	++	+	+	×	✓	✓
Drague Rallier du Baty	✓	✓	✓	✓	×	++	+	+++	+		×	✓	✓
Vidéo tractée	✓	✓	✓	×	✓	+	+++	+	+	+	✓	×	✓

1.2. Quels indicateurs ?

Suivre l'impact d'une pression anthropique ou évaluer les conséquences de la mise en place de mesures de gestion de cet impact nécessite l'utilisation d'indicateurs. Concernant l'impact des arts traînants sur les communautés benthiques, un grand nombre d'indicateurs a déjà été proposé comme l'abondance, la biomasse, la richesse en espèces, certains indices de diversité et des méthodes basées sur les traits biologiques des espèces benthiques (Rijnsdorp et al. 2016a; van Loon et al. 2018; Rabaoui et al. 2019). De récentes études ont tenté d'identifier l'indicateur susceptible de détecter au mieux l'effet de la pression des arts traînants sur les communautés benthiques. La première de ces études, réalisée par van Loon et al. (2018) est basée uniquement sur des échantillons récoltés à la benne en mer du Nord. Différents indices benthiques (sept différents et onze au total en comptant les combinaisons d'indices) non spécifiques à la pression de chalutage ont été testés et c'est l'indice de Margalef qui est apparu le plus à même de suivre l'impact du chalutage sur les communautés benthiques. Hiddink et al. (2020) ont quant à eux analysé 41 études, réparties sur le continent Nord-Américain ou en Europe, comparant les communautés benthiques dans les zones chalutées à celles de sites témoins et examiné sept indicateurs potentiels dont l'abondance et la biomasse par taxon et pour la communauté entière ou encore l'indice de Shannon. Cette étude a montré que la biomasse de la communauté apparaissait être le meilleur indice pour suivre l'impact des arts traînants sur les communautés benthiques. Les différences observées entre ces deux études proviennent probablement en partie du fait qu'elles ne comparent pas exactement les mêmes indicateurs, mais également qu'elles ne se basent pas sur les mêmes critères pour évaluer l'intérêt et l'efficacité des indices.

Le ou les indices proposés comme indicateurs de l'impact du chalutage sur les communautés benthiques devraient répondre à une série d'exigences qui ont été énoncées dans différents travaux (Queirós et al. 2016; ICES 2017b; Hiddink et al. 2020).

Parmi toutes ces exigences, deux semblent essentielles: la sensibilité et la spécificité de l'indice à la pression. La réponse des différents indices à ces deux exigences est discutée dans cette partie et synthétisée dans la table 52 pour les autres critères.

Le travail réalisé au cours de cette thèse s'inscrit ainsi parfaitement dans les démarches actuelles de propositions d'indicateurs pour suivre l'impact des arts traînants. L'intérêt de quinze indices et de trois méthodes d'échantillonnage a été évalué dans quatre zones d'études hydrodynamiquement différentes afin de déterminer si ces différents indices sont sensibles et spécifiques à la pression de pêche quelle que soit la zone étudiée et la méthode d'échantillonnage utilisée.

1.2.1. Sensibilité des indices aux arts traînants

Les travaux réalisés dans le chapitre II ont ainsi montrés qu'aucun des indices testés n'était en mesure de détecter l'effet du chalutage dans l'ensemble des quatre zones d'études. Plusieurs indices sont apparus significativement sensibles à l'impact des arts traînants mais neuf l'étaient dans au moins trois zones et pour seulement il n'y avait pas d'inversion du sens de la corrélation entre les différentes zones. Parmi les trois grandes catégories d'indice étudiées dans ce travail (indices de diversité taxonomique, de diversité fonctionnelle et basés sur le degré de sensibilité des espèces), ce sont les indices appartenant à la troisième catégorie (TDI, mTDI, pTDI et mT) qui étaient le plus corrélé à l'abrasion (critère « réactivité » de la table 48). Les résultats du chapitre IV confirment ces résultats et mettent en avant que ces indices peuvent également être utilisés dans le cadre d'une surveillance non-destructive des communautés benthiques comme la vidéo sous-marine. Les résultats des différents chapitres de cette thèse ont également mis en avant que ces indices n'étaient pas en mesure de détecter l'impact du chalutage sur les communautés benthiques lorsque la pression était trop faible (*i.e.* en Corse) ou lorsque la répartition des échantillonnages le long du gradient d'abrasion n'était pas satisfaisante. L'importante corrélation à l'abrasion de ces indices de sensibilité, combinée à leur réponse à un certain nombre d'exigences mentionnées précédemment (Queirós et al. 2016; ICES 2017b; Hiddink et al. 2020), font de ces différents indices de très bons candidats pour suivre l'impact des arts traînants sur les communautés benthiques dans le cadre de la DCSMM.

Les résultats obtenus dans le Chapitre II (Jac et al. 2020a), relatifs à l'indice de Margalef et la biomasse totale de la communauté vont à l'encontre de ceux obtenus par van Loon et al. (2018) et Hiddink et al. (2020), qui ont désigné ces deux indices comme les plus pertinents pour évaluer l'impact des arts traînants sur les communautés benthiques. Dans le chapitre II, bien qu'une corrélation significative et positive entre l'indice de Margalef et l'abrasion ait été observée dans l'ensemble des zones étudiées elle n'était supérieure à celles entre les indices de sensibilité et l'abrasion que pour une seule zone : la Corse. Même si ces différences peuvent être liées aux méthodes d'échantillonnage différentes de celles des travaux de van Loon et al. (2018), il semble que l'indice de Margalef soit apparu pertinent dans leurs travaux principalement car aucun indice de sensibilité n'a été étudié.

En ce qui concerne la biomasse totale de la communauté benthique, les résultats obtenus dans le cadre de cette thèse (Chapitre II) ne confirment pas l'intérêt de cet indice pour suivre l'effet du chalutage sur les communautés benthiques mis en avant dans les travaux de Hiddink et al. (2020). Un effet de l'abrasion sur la biomasse de la communauté a été observé dans seulement deux des quatre zones d'étude (Manche et Golfe du Lion) et la relation entre l'indice et l'abrasion était en plus inverse entre les deux zones (positif en Manche et négatif dans le Golfe du Lion). L'utilisation de cet indice, dont la relation à la pression observée semble très variable, paraît donc peu généralisable à l'ensemble des eaux européennes.

1.2.2. Spécificité des indicateurs à la pression de pêches aux arts traînants

La spécificité d'un indicateur à la pression qu'il suit peut dépendre de deux critères : sa capacité à répondre principalement à cette pression donnée et sa capacité à être indépendant des variations environnementales [ou que l'effet de ces variations soit quantifiable (Hiddink et al. 2020)].

Une réponse spécifique à l'abrasion ?

Parmi les différents indices étudiés lors de ces travaux de thèse, un certain nombre n'était pas en mesure de répondre spécifiquement à la pression de chalutage (Table 48). C'est le cas par exemple de:

1. l'indice AMBI, habituellement utilisé pour suivre l'eutrophisation en zone côtière, mais qui peut également permettre de détecter l'effet d'une contamination aux métaux lourds (Borja et al. 2003).
2. la richesse spécifique qui peut être impactée par une multitude d'autres pressions anthropiques comme les pollutions organiques (Simboura et al. 1995; Tabatabaie and Amiri 2011) ou métalliques (Rygg 1985).
3. l'indice de Margalef, identifié par van Loon et al. (2018) comme indice pertinent pour suivre l'impact des arts traînants sur les communautés benthiques, qui semble répondre à des phénomènes d'eutrophisation du milieu (Salas et al. 2006; Teixeira et al. 2008).

L'utilisation d'indices basés sur un ensemble de traits biologiques connus pour être impactés par la pression devant être évaluée permet d'assurer au maximum la spécificité de la réponse de ces indices. Différentes caractéristiques biologiques des espèces benthiques peuvent les rendre vulnérables au chalutage, comme par exemple leur mode d'alimentation ou leur capacité à se mouvoir. Une dizaine de traits biologiques ayant un effet sur la réponse des espèces à la pression de chalutage a ainsi été proposé dans différents travaux (de Juan et al. 2007; Bolam et al. 2017). Chaque trait étant ensuite subdivisé en deux à six modalités fonctionnelles. Même si l'utilisation d'une approche fonctionnelle permet de suivre plus spécifiquement une pression, elle entraîne un certain nombre de biais méthodologiques. Tout d'abord, très peu d'études expérimentales ont été réalisées sur la physiologie des espèces benthiques. Ainsi un grand nombre de ces caractéristiques biologiques sont attribuées à dire d'experts (de Juan and Demestre 2012). Certaines espèces peuvent adopter plusieurs caractéristiques biologiques appartenant au même trait fonctionnel. C'est par exemple le cas des Ophiuroidae qui peuvent être à la fois filtreuses, déposivores ou même prédatrices (Warner 1982). Ainsi, attribuer à chaque espèce une seule caractéristique biologique par trait peut entraîner une surestimation ou à l'inverse une sous-estimation de la sensibilité de cette espèce au chalutage. Pour pallier ce biais, plusieurs auteurs ont recours à la méthode de « codage flou » (Chevenet et al. 1994) qui permet d'attribuer un score (généralement entre 0 et 3) à chacune des modalités de chaque traits afin de traduire l'affinité de l'espèce pour chacune des caractéristiques biologiques des traits (Bolam and Eggleton 2014; Bolam et al. 2014). Enfin plusieurs de ces traits, comme par exemple la taille maximale ou encore la longévité, peuvent varier d'une zone à l'autre.

Bien que les approches fonctionnelles puissent-être basées sur l'utilisation d'un seul et unique trait (e.g. la longévité ; Rijnsdorp et al. 2018), ces travaux de thèse prennent en compte cinq traits: la position de l'espèce, son mode d'alimentation, sa mobilité, sa taille maximale et sa fragilité (Foveau et al. 2019). Ainsi, chaque espèce est caractérisée par une combinaison d'attributs de traits, également appelée « syndrome de traits » (Tardy 2015) Le long d'un gradient de pression, certains traits de réponse peuvent-être covariants, formant ainsi un syndrome de réponse (Raffard et al. 2017). Dans le cadre de ces travaux de thèse, les indices calculés à l'aide de la combinaison des cinq traits réponses précédement cités (*i.e.* mobilité, taille maximale, fragilité, mode d'alimentation et position), sont donc basé sur ce concept, et leur utilisation semble donc d'autant plus pertinente. Malgré leur spécificité à la pression de chalutage, les huit indices calculés à l'aide de ces traits fonctionnels ont eu des réponses différentes à l'abrasion en fonction des zones étudiées et de la méthode d'échantillonnage (Chapitre II & III). En ce qui concerne les données de chalutage scientifique (Chapitre II), seuls les quatre indices de sensibilité et la richesse fonctionnelle ont été en mesure d'observer des changements dans les communautés benthiques le long d'un gradient d'abrasion. Même si des modifications dans la richesse des fonctions de la communauté benthique se dessinent le long du gradient d'abrasion, c'est principalement le degré de sensibilité des espèces qui évolue. L'attribution d'un score de sensibilité à chaque caractéristique biologique en fonction de sa vulnérabilité au chalutage (de Juan and Demestre 2012; Foveau et al. 2019) permet de suivre au mieux cette évolution. Cependant, la sélection de ces traits fonctionnels et l'attribution du score de sensibilité à chacune des modalités a été réalisée sur la base de connaissances actuelles sur la réponse de la faune benthique aux perturbations du chalutage (de Juan et al. 2009) et ne prend pas en compte les caractéristiques *in situ* de l'animal. Par exemple pour le trait « Taille », un score de 3 (forte sensibilité) sera affectée aux *Funiculina quadrangularis* (car leur taille maximale est supérieure à 10 cm ; http://atlasbenthal.ifremer.fr) quelle que soit la taille de l'individu collecté. De telles approximations peuvent entraîner une surestimation de la sensibilité de la communauté dans certaines zones. Enfin, ces traits biologiques ont été sélectionnés comme proxy de la sensibilité de l'épifaune et ne sont pas forcément adaptés à l'endofaune, ce qui pourrait en partie expliquer la faible détection de l'effet du chalutage par indices basé sur la sensibilité des espèces avec un échantillonnage issu de la drague (Chapitre III).

Les différences dans la réponse des quatre indices de sensibilité fonctionnelle observées tout au long de ces travaux de thèse suggèrent que la méthode de combinaison des différents traits fonctionnels est essentielle pour définir une réponse des indices à l'abrasion. Certaines combinaisons sont ainsi plus sensibles que d'autres dans certaines zones ou en fonction de la méthode d'échantillonnage.

Dépendance aux variations environnementales

La composition et la distribution des communautés benthiques sont fortement influencées par différents paramètres environnementaux comme la salinité, la température, la profondeur (Hall et al. 1994; Rees et al. 1999) ou encore la granulométrie (Couce et al. 2020). Pour qu'un indicateur soit considéré comme spécifique à la pression étudiée, ces changements ne doivent pas être fondés sur une variation environnementale (Hiddink et al. 2020). Au vue des liens étroits entre les assemblages benthiques et une multitude de paramètres environnementaux, cette exigence semble quelque peu utopique, surtout pour les indicateurs basés sur une approche fonctionnelle, car certains traits biologiques des espèces benthiques sont influencés par différentes variables environnementales (Bremner et al. 2006). Ainsi, un bon indicateur d'impact doit présenter une forte réponse à la pression étudiée et n'inclure que de faibles effets des variations de l'environnement (Maxwell and Jennings 2005). Il est donc nécessaire que l'indicateur puisse refléter distinctement les variations causées par la pression étudiée et celles causées par l'environnement (Hiddink et al. 2020). Dans ce cadre, Gislason et al. (2017) ont suggéré d'inclure les facteurs environnementaux ainsi que les effets aléatoires des années dans les analyses d'évaluation des indices, afin d'identifier l'impact de la pression anthropique souhaitée (le chalutage dans cette thèse) sur un fond de variation naturelle substantielle.

En ce qui concerne l'impact des arts traînants sur les communautés benthiques, l'environnement peut influer, soit sur la composition de la communauté (et donc potentiellement sur l'abondance ou non d'espèces considérées comme sensibles à cette pression), soit sur sa résilience. La première étape du processus d'évaluation de l'effet de l'environnement sur les indices doit donc se concentrer sur le choix des variables environnementales étudiées mais également sur l'effet qu'elles peuvent avoir sur les communautés benthiques. Le chapitre VI a ainsi permis de mettre en avant que, dans des zones hydrologiquement différentes (la Méditerranée et la Manche dans ce cas-là), ce ne sont pas exactement les mêmes variables qui structurent les communautés benthiques (c'est le cas des courants de marée par exemple). En Méditerranée, le développement des communautés benthiques semble limité par des facteurs influant sur le métabolisme des espèces (disponibilité en nourriture, température de l'eau…) alors qu'en Manche il est principalement lié à la capacité des espèces à résister aux impacts physiques (courant de marée et de houle majoritairement). Les processus d'évaluation de l'effet des facteurs environnementaux sur les indices doivent donc être réalisés à une grande échelle pour limiter l'influence des variations très locales sur les communautés benthiques, mais surtout à une échelle en cohérence avec l'influence des paramètres environnementaux majeurs pouvant influer sur les communautés benthiques.

Les quatre indices utilisés (précédemment sélectionnés pour leur sensibilité et leur spécificité à la pression de chalutage) n'ont pas tous été en mesure de distinguer l'effet de la pêche et l'effet des différentes variables environnementales sur les communautés benthiques. Dans le Golfe du Lion, seul l'indice pTDI, prenant en compte uniquement les espèces les plus sensibles au chalutage, a permis de différencier l'effet de l'abrasion et de celui des perturbations naturelles. Cet indice a également permis en Manche de différencier l'effet de la pêche au chalut sur les communautés benthiques de celles des variations liées à l'environnement et des changements aléatoires liées à l'année.

En conclusion, les différents travaux sur la sensibilité et la spécificité des indices à la pression de chalutage ont permis de mettre en avant l'intérêt des indices basés sur les traits fonctionnels des espèces mais ont également démontré la capacité de ce type d'indice à distinguer l'effet de la pêche et de l'environnement sur les communautés benthiques.

L'effet de l'environnement sur les deux indices mis en avant par les travaux de van Loon et al. (2018) et Hiddink et al. (2020), à savoir l'indice de Margalef et la biomasse totale de la communauté, ne semble pas, à ce jour, encore avoir été étudié. L'utilisation de l'indice de Margalef pour étudier d'autres pressions environnementales ne semble pas en cohérence avec la nécessité que l'indicateur soit spécifique à la pression étudiée. En ce qui concerne la biomasse de la communauté, l'absence de sensibilité de cet indicateur dans certaines des zones échantillonnées lors de ces travaux de thèse couplée à des relations inversées le long du gradient d'abrasion selon les zones rend cet indice peu pertinent dans le cadre d'un suivi de l'impact des arts traînants lorsque l'échantillonnage a été réalisé à l'aide d'un chalut scientifique. Malgré une sensibilité légèrement inférieure aux autres indices de sensibilité fonctionnelle dans certaines zones étudiées, la spécificité du pTDI à la pression de chalutage et sa capacité à distinguer l'effet de l'abrasion et de l'environnement font de cet indice un candidat idéal pour suivre l'impact des arts traînants sur les communautés benthiques dans le cadre de la DCSMM. En se concentrant uniquement sur les espèces les plus sensibles, l'utilisation de cet indice permet une réduction du temps de collecte des données, ce qui peut être un avantage non négligeable dans le cadre de la mise en place d'un suivi régulier de l'effet de la pression de chalutage sur les communautés benthiques.

Table 52: Synthèse des avantages et inconvénients des diféérents indices selon plusieurs critères proposés par Queiros et al. (2016) et ICES (2017b).
✓ indique que la méthode répond au critère ; ✓ indique que la méthode répond en partie au critère ; × indique que la méthode ne répond pas au critère. Le nombre de « + » font référence à la valeur de la corrélation entre la presseion et l'indice pour le critère réactivité et à la durée d'analyse

Indices	Reflète les changements dans la communauté	Sensibilité	Réactivité	Spécificité	Temps d'analyse (coût limité)	Applicabilité	Interprétabilité
Biomasse	✓	✓	+	×	+	×	✓
Richesse spécifique	✓	✓	++	×	+++	✓	✓
Indice de Margalef	✓	✓	++	×	+++	✓	✓
Indice de shannon	✓	×	+	×	+++	×	✓
Indice de Pielou	✓	✓	+	×	+++	×	✓
Indice de Simpson	✓	×	+	×	+++	×	✓
FRic	✓	✓	++	✓	++	✓	✓
FDiv	✓	✓	+	✓	++	×	✓
FEve	✓	✓	+	✓	++	×	✓
FSpe	✓	✓	+	✓	++	✓	✓
AMBI	✓	✓	++	×	+++	×	✓
TDI	✓	✓	+++	✓	++	✓	✓
mTDI	✓	✓	+++	✓	++	✓	✓
pTDI	✓	✓	+++	✓	++	✓	✓
mT	✓	✓	+++	✓	++	✓	✓

1.2.3. Le cas particulier des zones à faible abrasion : l'exemple de la Corse

Dans l'ensemble des travaux réalisés au cours de cette thèse, la Corse s'est particulièrement démarquée des autres secteurs étudiés. Alors qu'elle est géographiquement assez proche du Golfe du Lion, les caractéristiques de ces deux zones d'études sont pourtant loin d'être identiques. Au-delà des différences dans les caractéristiques environnementales (bathymétrie, hydrodynamisme et nature sédimentaire des fonds…) entre ces deux zones (Chapitre I & VI), la pression de pêche est le principal facteur de divergence entre ces deux zones. En effet, alors qu'une pression relativement forte est présente dans le Golfe du Lion, celle-ci est beaucoup plus faible en Corse (Jac and Vaz 2018). La nature opportuniste de l'échantillonnage réalisé dans cette thèse a d'autant plus accentué ces différences, avec une abrasion médiane échantillonnée (tout habitat confondu) de 5.02 SAR.y^{-1} dans le Golfe du Lion contre 0.11 SAR.y^{-1} en Corse. De ce fait, les différents résultats obtenus pour cette zone ont très souvent été contradictoires avec ceux obtenus pour les autres zones étudiées.

Dans le chapitre II, aucune relation significative n'a pu être mise en évidence entre les indices de sensibilité fonctionnelle et l'abrasion. A l'exception de l'AMBI qui était dans cette zone positivement corrélé à l'abrasion, seuls les indices touchant à la richesse taxonomique (SR et indice de Margalef) ou fonctionnelle (FRic) varient significativement le long du gradient d'abrasion. Deux hypothèses distinctes émergent de ces résultats :

1. L'effet de l'abrasion détectée par ces indices est en réalité lié à divers processus naturels dont les variations sont confondues avec celle de l'abrasion. Ceci pourrait par ailleurs expliquer l'absence totale de réponse significative des indices basés sur la sensibilité des espèces au chalut, reportée aux chapitres II et VI. L'absence de forte corrélation entre l'abrasion et les différents paramètres environnementaux étudiés (Annexe E) indique que l'effet de l'abrasion n'est pas, dans cette zone, confondu avec ceux qui ont été pris en compte dans cette étude et qui sont connus pour influencer la distribution et la structure des communautés benthiques à large échelle comme par exemple la disponibilité en nourriture ou la stratification.

2. Lorsque les niveaux d'abrasion et de perturbations naturelles sont très faibles (communauté stable et diversifiée), les indices de richesses taxonomique et fonctionnelle sont sensibles aux variations de l'abrasion. Ces indices pourraient donc permettre de détecter le premier seuil et donc d'identifier jusqu'à quel niveau d'abrasion les communautés benthiques dans ces environnements stables restent en bon état écologique.

2. Définir l'état écologique des habitats benthiques

Dans le cadre de la DCSMM, l'étendue spatiale de la perte physique ou de la perturbation des fonds marins (D6C1 et D6C2) ainsi que l'étendue de la perte ou de l'altération de la communauté benthique (D6C3, D6C4 et D6C5) doit être évaluée (EC 2008, 2017a). Le chapitre V propose donc une méthode permettant d'évaluer la proportion perdue ou altérée pour les principaux habitats échantillonnés dans les quatre zones étudiées.

L'ensemble des travaux repose sur l'hypothèse de l'existence d'une relation non-linéaire (et même segmentée) sur l'ensemble de la gamme de pression entre la pression de pêche et l'état des communautés benthiques et donc la réponse détectée par les indicateurs. Ceci suggère qu'en deçà d'une certaine valeur d'abrasion, la capacité de résilience des communautés benthiques suffit à compenser les pertes causées par le chalutage, mais que dès lors que cette valeur est dépassée un impact négatif sur les communautés benthiques est observé (diminution des valeurs de l'indicateurs). Lorsqu'une deuxième valeur seuil est dépassée (abrasion importante), les communautés benthiques originelles sont remplacées par des communautés adaptées et l'augmentation de la pression n'entraîne plus de conséquences néfastes sur cette communauté (pas de variations de l'indicateur). Bien que ce type d'approche n'ait, à ce jour, pas été utilisée dans le cadre de l'évaluation de l'impact du chalutage sur les communautés benthiques, plusieurs études portant sur des sujets variés comme la gestion des pêcheries ou l'état biologique d'un cours d'eau se sont basées sur cette relation théorique (Allan 2004; Rice 2009; Koops et al. 2012).

La mise en évidence de relation linéaire négative jusqu'à une certaine valeur d'abrasion, suivie par une relation linéaire constante confirme l'intérêt de l'utilisation de cette approche. Cependant, l'existence de la première valeur seuil, qui représente le passage entre le bon état écologique et le moment où la communauté benthique est altérée, n'a été observée dans aucune des zones étudiées. Plusieurs hypothèses pourraient expliquer cette absence de détection de la première valeur seuil :

1. L'échantillonnage opportuniste, donc non régulier le long du gradient d'abrasion ne permet pas la détection de ce premier seuil (échantillonnage trop déséquilibré vers les zones à forte abrasion).

2. La présence du chalutage dans ces différentes zones depuis de très nombreuses années (Thurstan et al. 2010; Farrugio 2013) a entraîné une dégradation générale de l'état écologique des communautés benthiques (notamment liée à un potentiel déplacement de l'effort de pêche entre les décennies) et, à ce jour, aucun habitat benthique ne peut être considéré en bon état écologique.

3. L'état écologique des habitats benthiques est dégradé par une ou plusieurs autres pressions anthropiques dans les zones à faibles abrasion et c'est cette dégradation que les indices détectent.

Dans le Golfe du Lion, une influence de l'abrasion sur l'indice a été mise en évidence pour deux habitats sur les quatre échantillonnés. Comme l'abrasion était relativement forte (> 2 $SAR.y^{-1}$) dans les zones où l'échantillonnage a été réalisé, cette absence de relation a été considérée comme l'absence de réponse de la communauté totalement adaptée au chalutage qui a remplacé celle originelle. Ceci démontre les limites de la méthode utilisée lorsque le gradient d'abrasion échantillonné ne comprend que de fortes valeurs. Il est impératif que l'ensemble du gradient d'abrasion existant au sein d'un habitat soit échantillonné pour évaluer au mieux la proportion d'habitat perdu ou altéré.

La commission OSPAR a proposé en 2017 une méthodologie pour évaluer l'étendu spatial des dommages causés aux principaux habitats et espèces de la zone OSPAR (OSPAR Commission 2017). Afin d'obtenir le pourcentage d'habitat impacté par le chalutage, les cartes de sensibilité des habitats benthiques (basées sur les travaux de Tillin et al. 2010 et de Tillin and Tyler-Walters 2013) et de l'abrasion entre 2010 et 2015 ont été combinées. La perturbation a ensuite été classifiée sur une échelle de 1 à10 où les valeurs de 5 à 10 correspondent à des zones très perturbées et 0 à 4 à des zones faiblement perturbées. Ces travaux ont démontré que 72% de la surface des habitats benthiques de la Manche sont perturbés contre 68 % en mer du Nord et qu'il existait, dans ces deux régions, des zones peu voire pas du tout perturbées. La méthode utilisée dans le cadre de cette thèse donne des résultats légèrement supérieurs avec, en Manche, 86.6% des habitats benthiques impactés et, en mer du Nord, 90.5%. A ces surfaces s'ajoutent 6.8% des habitats, considérés comme perdus en Manche et 0.13% en mer du Nord. Bien qu'il existe des différences entre ces deux méthodes, certainement liées au fait que la classification proposée par la méthode OSPAR est de dix niveaux alors que celle utilisée durant cette thèse n'en comporte que quatre, elles montrent toutes deux l'importance de l'impact du chalut sur l'état écologique des habitats benthiques des plateaux continentaux européens.

3. Quel avenir pour les habitats benthiques des plateaux continentaux européens ?

Lorsqu'un écosystème est affecté par des pressions anthropiques, il peut, s'il a une certaine capacité de résistance aux perturbations, montrer initialement peu de réaction à une pression croissante. Cependant, au-delà d'un certain point, le changement peut devenir rapide et aboutir à un état de l'écosystème radicalement différent. De même, l'importance de sa résilience conditionnera sa capacité de reconstitution après l'arrêt de la pression. Ainsi, en fonction des capacités conjuguées de résilience et de résistance de ces écosystèmes, la diminution de la pression, n'engendre pas toujours leur retour à l'état initial. L'ensemble des trajectoires possibles (continues linaires ou non, ou présentant des discontinuités fortes, voir catastrophiques) de l'évolution d'une communauté en réponse à un stress ou une perturbation ont été décrites dans de nombreux travaux (Figure 59 ; Andersen et al. 2009; Ducrotoy 2010; Fauchard 2010; Shade et al. 2012; Selkoe et al. 2015).

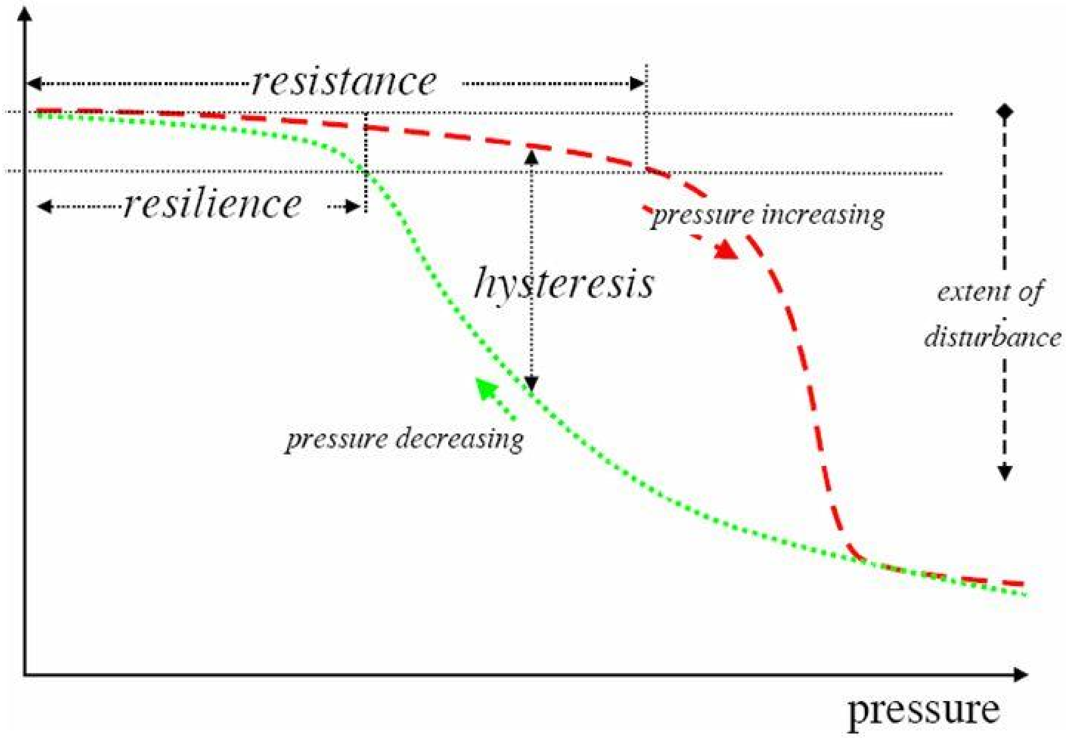


Figure 59: Réponse schématique des écosystèmes à une perturbation temporaire (modifié d'après Tett et al. 2007)

L'ensemble des travaux réalisés au cours de cette thèse semble suggérer qu'une diminution ou un arrêt de la pression physique liée aux arts trainants n'aura pas des conséquences similaires sur cette trajectoire dans l'ensemble des zones étudiées. En effet, la zone manche/mer du Nord étant marquée par un hydrodynamisme fort et étant relativement très productive (https://www.emodnet.eu/en/map-week-chlorophyll-concentration), la résistance naturelle de certaines communautés leur permet d'endurer des pressions de pêche non négligeables et une diminution des perturbations physiques dans cette zone pourrait conduire à une récupération satisfaisante des communautés à la faveur d'une résilience suffisante des habitats benthiques. Cependant, les résultats de cette thèse ne permettent pas de conclure si la résilience des communautés suivra le même schéma que leur disparition ou si un phénomène d'hystérèse (retard de la trajectoire de récupération du fait d'une trop faible résilience) sera observé (Figure 59).

En Méditerranée, l'absence d'habitats benthiques en bon état écologique dans le Golfe du Lion dans des zones où l'abrasion est faible ou intermédiaire semble suggérer une faible résistance des communautés benthiques naturellement peu perturbées par l'hydrodynamisme régional. En outre, la forte diminution du nombre de chalut dans le Golfe du Lion depuis les années 2000 (EU Fleet Register, SIH, 2020) pourraient indiquer que l'effort de pêche et donc l'abrasion étaient relativement plus importants auparavant. De plus, la Méditerranée est relativement oligotrophique (https://www.emodnet.eu/en/map-week-chlorophyll-concentration) et les communautés benthiques présentent dans cette zone semblent, naturellement structurées par des variables environnementales liées à la résilience (Chapitre 5). La capacité de résilience semble donc être un facteur limitant pour ces communautés. L'absence de zones en bon état écologique peut donc également traduire une faible résilience des communautés benthiques dans le Golfe du Lion.

Ainsi, la présence d'un phénomène d'hystérèse dans le Golfe du Lion semble envisageable et les résultats obtenus peuvent également suggérer une rupture catastrophique de l'état écologique des habitats benthiques sans retour possible à leur état initial (Figure 60).

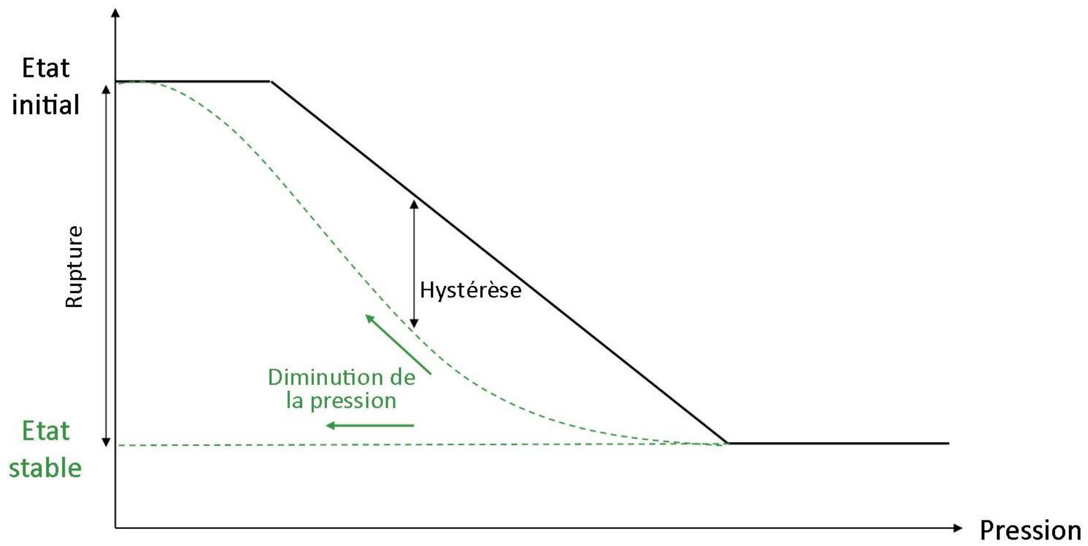


Figure 60: Evolution théorique des habitats benthiques du Golfe du Lion

Afin de mieux comprendre les processus engendrés par une diminution ou un arrêt de la pêche aux arts trainants, des travaux sur la résilience des communautés benthiques s'imposent dans les quatre zones d'études. L'observation de l'évolution des communautés dans des zones où les arts trainants auraient été exclus semble être nécessaire pour pouvoir statuer sur la réversibilité de l'impact du chalutage dans les eaux européennes.

4. Perspectives

4.1. Amélioration des méthodes et protocoles d'échantillonnage

4.1.1. Protocoles d'échantillonnage

Les données traitées durant ces travaux de thèse ont été récoltées de manière opportuniste, lors de campagnes n'ayant pas pour objectif spécifique d'étudier l'impact du chalutage sur les communautés benthiques. Bien que ce caractère opportun soit un des principaux intérêts de l'utilisation des données issues du chalutage scientifique puisqu'il ne nécessite pas la mise en place d'une nouvelle campagne, c'est également une des principales limites des travaux présentés ici. Comme cela a été démontré tout au long du manuscrit, l'absence d'un échantillonnage régulier le long du gradient d'abrasion pose quelques difficultés pour comprendre l'effet que peut avoir le chalutage dans certaines zones. Pour pallier à ce manque, des points d'échantillonnage supplémentaires, situés dans des habitats peu échantillonnés ou dans des zones peu abrasées et dans une large gamme de profondeur (jusqu'à 800 m), devraient être ajoutés aux grilles d'échantillonnage des campagnes annuelles de chalutage scientifique. L'effort d'échantillonnage en Corse devrait également être revu à la hausse pour tenter de mieux comprendre ce qui est à l'origine des réponses observées dans cette zone.

En ce qui concerne les deux autres méthodes d'échantillonnage utilisées dans cette étude, à savoir la vidéo sous-marine tractée et la drague, un échantillonnage plus important et mieux réparti le long du gradient d'abrasion permettrait également de pouvoir confirmer les résultats obtenus.

Les conclusions dégagées avec l'indice basé uniquement sur les espèces les plus sensibles à la pression de pêche étant satisfaisant que ce soit d'un point de vue de la sensibilité ou de la spécificité à l'impact du chalutage, l'augmentation du nombre de point d'échantillonnage pourrait être combinée à une diminution des espèces à surveiller. Il pourrait être envisagé d'utiliser, pour les analyses, une liste d'espèces restreinte ne contenant que les espèces les plus sensibles au chalutage, dont celles qui sont classées sur la liste OSPAR des espèces et habitats menacés et/ou en déclin (OSPAR 2008) et la liste des espèces marines vulnérables de la mer Méditerranée (OCEANA 2016).

4.1.2. Vidéo sous-marine

Avec la nécessité de réduire au maximum l'impact des activités de recherche sur l'écosystème marin, l'utilisation de vidéo sous-marine semble être une bonne alternative. Le faible nombre de transect vidéo analysés n'a fourni qu'un aperçu partiel de l'intérêt de la vidéo pour suivre l'impact des arts traînants. Les résultats, plutôt satisfaisants, obtenus sur les habitats grossiers devraient en faire une méthode de choix pour le suivi de l'impact du chalutage sur ce type d'habitat.

L'un des principaux freins à l'utilisation de la vidéo, quel que soit le système utilisé (ROV, BRUV, TOWN…), est le temps d'analyse nécessaire au traitement des images collectées. Cependant, avec le nombre croissant de recherches sur les algorithmes d'apprentissage automatique (Romero-Ramirez et al. 2016; Piechaud et al. 2019; Han et al. 2020), l'identification semi-automatisée, voire automatisée des espèces devrait voir le jour dans quelques années et ainsi réduire grandement le temps d'analyse.

De plus, un certain nombre de vidéos n'ont pas pu être analysées ou n'ont été analysées qu'en partie à cause des « sauts » que l'engin vidéo faisait sur le fond et de la mauvaise qualité des images. En effet, lorsque la houle est trop importante, le câble tractant le système à tendance à le tirer vers le haut. Cette difficulté est inhérente à tous les engins tractés le long d'un câble. L'utilisation d'un ROV autonome filmant toujours à la même distance du fond et à vitesse constante (Lopez-Garrido et al. 2020) pourrait permettre de s'affranchir de la plupart des limites liées au déploiement d'un système tracté et ainsi augmenter la proportion de vidéo analysable. Ceci permettrait également d'augmenter la précision sur l'évaluation de la surface échantillonnée.

4.2. Optimisation et développement de nouveaux indicateurs

Les résultats obtenus montrent l'intérêt de l'utilisation d'indices basés sur la sensibilité des espèces au chalutage pour suivre l'impact des arts traînants sur les communautés benthiques du plateau continental. Ces travaux n'ont porté que sur cinq traits biologiques, alors que plus d'une dizaine ont déjà été identifiés comme pouvant jouer un rôle dans la sensibilité des espèces au chalutage (de Juan et al. 2007; Bolam et al. 2017). L'ajout de nouveaux traits comme le type de développement larvaire de l'espèce (planctonique ou benthique) pourrait permettre d'augmenter la sensibilité et la spécificité des indices mis en avant par ces travaux de thèse mais également d'observer potentiellement une modification de l'espace fonctionnel le long du gradient d'abrasion. En effet, même si un resserement de l'espace fonctionnel autour des modalités basses (0-1) et donc une diminution de la richesse le long du gradient d'abrasion était attendu (Figure 9), ceci n'a pas été mis en évidence lors de ces travaux de thèse. Ces modifications fonctionnelles peuvent potentiellement concerner des traits qui n'ont pas été pris en compte dans ces travaux de thèse. L'ajout de nouveaux traits pourrait permettre de confirmer cette hypothèse.Comme quelques doutes persistent sur le degré de sensibilité de certaines espèces (les ascidies par exemple), des expérimentations sur la capacité de résistance d'un certain nombre d'espèces au chalutage sont nécessaires afin de confirmer ou infirmer la haute sensibilité d'une espèce.

Les différences observées entre les indices basés sur les traits fonctionnels suggèrent que la méthode de combinaison des traits biologiques à une influence sur la capacité de l'indice à détecter l'effet de l'abrasion. Des études complémentaires devraient être réalisées à ce sujet pour mieux comprendre mathématiquement et écologiquement ce phénomène, mais également pour déterminer s'il n'existe pas de meilleure combinaison de ces traits qui pourrait augmenter la sensibilité de l'indice au chalutage et notamment dans les zones où l'abrasion est faible.

Dans les zones de faible abrasion, l'absence de détection d'un impact du chalutage pourrait être en lien avec la capacité de résilience des espèces et notamment les espèces sensibles. Il est en effet envisageable que lorsque la zone est abrasée moins d'une fois par an, un certain nombre d'espèces ait le temps de recoloniser la zone et d'apparaître dans les échantillons récoltés. Elles seront donc présentes dans la zone mais potentiellement de plus petite taille (car le temps dont elles disposent pour leur croissance entre deux coup de chalut est relativement court) que dans les zones non pêchées. L'utilisation de la biomasse des individus permet en partie de s'affranchir de cette possibilité, puisque le poids des espèces est lié à leur taille et donc à leur croissance. Cependant, cette relation n'est pas linéaire et variable entre les espèces (Al-Adhub and Bowers 1977; Pihl and Rosenberg 1982; Ceccherelli and Rossi 1984). La précision de la balance utilisée lors des campagnes de chalutage scientifique ne permet, de surcroît, pas de détecter de légères variations de biomasse chez certaines espèces ayant une très faible biomasse mais qui sont pourtant extrêmement sensibles (hydraires). Des mesures morphométriques pourraient toutefois être réalisées sur certaines espèces sensibles, comme *Funiculina quadrangularis*, *Virgularia mirabilis* ou encore plusieurs espèces d'éponge, et être comparées le long du gradient d'abrasion. Cependant, tout comme la biomasse, la taille des espèces peut-être fortement liée à certains facteurs environnementaux comme la disponibilité en nourriture (Taghon and Greene 1992; Witbaard 1996) ou la température de l'eau (Nair and Anger 1979). Pour utiliser les variations morphométriques des espèces sensibles comme indicateur de l'impact du chalutage, il est indispensable d'être en mesure de déterminer précisément comment l'environnement influe sur ce paramètre.

En Méditerranée, seuls les échantillons prélevés à moins de 200 mètres de profondeur ont été utilisés dans cette étude. Les arts trainants sont cependant autorisés jusqu'à 1000 mètres (EC 2011).

Ainsi, une étude plus approfondie devrait être réalisée pour les espèces profondes pour déterminer si les mêmes traits biologiques et les mêmes indices peuvent-être utilisés pour évaluer l'impact du chalutage dans ces zones.

4.3. Evaluation globale de l'état écologique des habitats benthiques ?

Seul l'impact physique lié à la pression des arts traînants a été étudié au cours de cette thèse. Cependant, même si le chalutage est considéré comme la principale pression que subissent les habitats benthiques des plateaux continentaux (Hiddink et al. 2007; Halpern et al. 2008), d'autres activités sont tout aussi, voire même plus, impactantes à petite échelle spatiale. C'est le cas par exemple de l'extraction de granulats marins, de l'installation de câble sous-marin ou encore de la poldérisation (La Rivière et al. 2015; Taormina et al. 2018). La méthode proposée dans le chapitre V (Jac et al. 2020b) pour évaluer l'état écologique des habitats benthiques pourrait être appliquée à ces différentes pressions. Les cartes d'état écologique des habitats benthiques liées à chacune de ces pressions peuvent être par la suite combinées pour obtenir une cartographie générale de l'état écologique des communautés benthiques des plateaux continentaux européens. Cependant, plusieurs de ces pressions anthropiques sont susceptibles de s'exercer simultanément sur un habitat, elles sont donc concomitantes et peuvent donc interagir entre elles et avoir des effets additifs, synergiques ou antagonistes (Griffith et al. 2012; Ocaña et al. 2019). L'effet de ces pressions concomitantes devrait donc être déterminé pour permettre une évaluation la plus complète de l'état écologique des habitats benthiques.

4.4. Vers une réduction et/ou une modification spatiale de l'effort de pêche ?

Ces travaux de thèse ont démontré, conformément aux résultats obtenus par la commission OSPAR (OSPAR Commission 2017), qu'une très large majorité des habitats benthiques de la Manche, la mer du Nord et du Golfe du Lion sont, à ce jour, néfastement impactés par les arts traînants. Une partie de ceux-ci est même considérée comme perdue, avec une disparition totale de la communauté originelle. Ces conclusions sont alarmantes et il semble nécessaire que des mesures permettant la diminution des impacts du chalutage sur les habitats benthiques soient mises en place. Ces mesures de gestion de la pression exercée par les arts traînants sur les communautés benthiques peuvent être classées en quatre grandes catégories (McConnaughey et al. 2020) :

1. les mesures techniques
2. le contrôle spatial de l'effort de pêche
3. l'implémentation de quotas
4. le contrôle et la réduction de l'effort de pêche

Concernant les mesures techniques, un grand nombre de modifications des engins de chalutage pourraient les rendre plus sélectifs (comme l'utilisation d'un maillage plus grand ou de mailles carrées), ou réduire leur contact physique avec le fond et leur pénétration dans le sédiment (Hammond et al. 2013; Smeltz et al. 2019). Cependant, ces modifications ne doivent pas se faire en faveur d'engins dont l'ensemble des impacts sur les communautés benthiques n'ont pas encore été évalués, comme c'est le cas pour les chaluts électriques pour lesquels les connaissances sur l'effet de l'électricité sur les organismes marins restent à ce jour encore limitées (Soetaert et al. 2015; Soetaert 2016).

Différentes mesures peuvent permettre de contrôler spatialement l'effort de pêche aux arts traînants. Tout d'abord des zones d'exclusion de chalutage peuvent être mises en place comme cela a déjà été réalisé en Méditerranée (Ministère de l'agriculture et de l'alimentation 2018), au Qatar (Walton et al. 2018) ou autour de Madère, des Açores et des îles Canaries (EC 2005). L'interdiction de chalutage dans certaines zones entraîne généralement le développement d'autres méthodes de pêche ayant un impact plus faible sur les communautés benthiques comme les palangres (Suuronen et al. 2012). Ce changement de méthode de pêche peut, tout en minimisant l'impact sur les habitats benthiques, toutefois impacter d'autres communautés qui n'étaient jusqu'ici pas touchées, comme c'est le cas pour les oiseaux avec la palangre (Montevecchi 2001). De plus, l'interdiction totale du chalutage dans une zone peut potentiellement avoir un impact social non négligeable comme cela a été observé lors de l'interdiction du chalutage en Indonésie (Endroyono 2017) ou au Venezuela (McConnaughey et al. 2020).

La seconde méthode pour contrôler spatialement l'effort de pêche peut être de limiter ou d'interdire l'expansion spatiale des arts traînants, en fermant les zones qui sont actuellement très faiblement ou pas pêchées. L'avantage de cette méthode est d'éviter les effets négatifs potentiellement importants sur les habitats et les communautés benthiques liés au déplacement de l'effort de pêche vers des zones qui n'étaient pas encore exploitées (Dinmore et al. 2003). Ce type de réglementation a d'ailleurs été mise en place pour limiter le développement de la pêche en eaux profondes en Atlantique (EC 2016) et en Méditerranée (EC 2011). Pour obtenir de meilleurs résultats, cette méthode doit être couplée à une limitation de l'effort de pêche et/ou la mise en place de quotas afin de garantir que les populations soient exploitées de manière durable (McConnaughey et al. 2020). Cette méthode ne semble cependant pas très adaptée dans différentes zones comme en dans le Golfe du Lion où les zones très peu pêchées (Jac and Vaz 2018) sont rares et situées principalement au large [en lien avec la réglementation limitant le nombre d'heure de pêche à 15h par jour (Ministère de l'agriculture et de l'alimentation 2019)] sur des habitats différents de ceux en zone plus côtière (SHOM 2015). De telles options permettraient de préserver en partie un seul type d'habitat dans le Golfe du Lion.

Une autre solution peut-être la création de zones de pêche définies par la profondeur ou la distance à la côte. La répartition de l'effort peut être basée sur la taille des navires ou le tonnage brut, ce qui, dans certains cas, permet de séparer efficacement les différents engins de pêche. (McConnaughey et al. 2020). En Croatie par exemple, onze zones de pêche ont été établies (Mackelworth et al. 2010) et la pêche aux arts traînants est interdite à moins de 1 mn des côtes.

Dans la zone méditerranéenne française, le chalutage est interdit à moins de 3 milles nautiques de la côte (Ministère de l'écologie du développement durable et de l'énergie 2013c). Cette interdiction, également appliquée aux autres façades maritimes françaises, souffre pourtant de trop nombreuses exceptions.

Généralement, le chalutage est interdit sur les habitats facilement perturbés et dont la résilience est lente, comme les herbiers marins ou les zones coralliennes (Neckles et al. 2005; Kaiser et al. 2018; McConnaughey et al. 2020). Cependant, ces zones d'interdiction de chalutage pourraient être étendues aux zones où la densité d'espèces sensibles au chalutage, comme les funicules ou les pennatules, est importante. Cela nécessite une bonne connaissance de l'écologie de ces espèces et notamment d'établir une cartographie précise de leur répartition spatiale (Greathead et al. 2014).

Enfin, la dernière solution pouvant permettre de limiter spatialement l'effort de pêche est la création d'aires marines protégées dans lesquelles le chalutage serait interdit. Si ces zones de protection couvrent différents habitats benthiques, cela peut permettre qu'une petite portion de chaque habitat benthique soit maintenue en bon état écologique. De telles initiatives pourraient permettre une meilleure résilience de l'ensemble de l'habitat, en augmentant potentiellement le taux de recrutement des espèces benthiques.

La mise en place de quotas sur les prises accessoires (invertébrés benthiques) ou sur les habitats pourrait également permettre une réduction de l'impact des arts traînants sur les communautés benthiques. En ce qui concerne les invertébrés benthiques, des quotas de capture pourraient être mis en place avec, par exemple, un déplacement de plusieurs miles nautiques dans le cas où la biomasse d'espèces sensibles dans le trait dépasse le quota fixé. Une méthode semblable a été mise en place au Canada, imposant aux navires de signaler toute capture de coraux ou d'éponges supérieure à 20 kg par trait (Wallace et al. 2015). Un règlement similaire est envisagé en Méditerranée pour les espèces indicatrices d'écosystèmes marins vulnérables (GFCM 2019). Bien que cette méthode puisse être particulièrement efficace, elle nécessite le déploiement d'un grand nombre d'observateurs sur l'ensemble des chalutiers pêchant dans les eaux françaises ce qui engendre d'importants coûts de mise en place et de fonctionnement.

Pour limiter les coûts inhérents à la mise en œuvre de cette méthode, un système de quotas par habitat, donc le contrôle est basé sur les données VMS peut-être mis en place. Ainsi, chaque bateau pourrait utiliser son quota, soit en pêchant longtemps sur un habitat peu sensible, soit en pêchant sur une durée très courte dans un habitat sensible (Batsleer et al. 2018; McConnaughey et al. 2020). Néanmoins, cette méthode de quotas, qui laisse la possibilité aux bateaux de pêcher dans les zones considérées comme très sensibles aux arts traînants, devrait être couplée avec un contrôle spatial très fin de l'effort de pêche. La conséquence directe risque malheureusement d'être l'augmentation de l'effort de pêche dans les zones peu sensibles. Des mesures de réduction globale de l'effort de pêche devraient donc être envisagées en complément de la mise en place de ces quotas. Le principal désavantage de cette méthode est la nécessité d'avoir une cartographie à haute résolution de la sensibilité des habitats, qui, à ce jour, n'existe pas pour l'ensemble des plateaux continentaux européens. Des études à l'échelle européenne devraient donc être envisagées pour la création de ces cartes.

Enfin la dernière mesure pouvant être mise en place, et généralement en complément d'une autre méthode, est la réduction globale de l'effort de pêche. Des régulations à plusieurs niveaux peuvent-être mises en place comme la limitation de la capacité de pêche de chaque chalutier (tonnage du navire, puissance moteur…) ou la réduction du nombre de jours autorisé à la pêche. En méditerranée française, ce nombre s'établit désormais à moins de 200 jours par an et la longueur des bateaux ne peut excéder 26 mètres pour une puissance maximale de 316 kW (Ministère de l'écologie du développement durable et de l'énergie 2013c). Ces mesures sont cependant toujours insuffisantes pour permettre une exploitation durable des ressources et pour permettre de préserver les habitats benthiques et doivent être encore durcies dnans le cadre de la politique commune des pêches (EC 2019) et assorties de fermeture temporaires de zones (Ministère de l'agriculture et de l'alimentation 2019).

Une multitude de mesures peuvent donc être mises en place pour assurer l'intégrité des fonds marins européens, tout en conservant la totalité ou une partie de la flotte de chalutiers européens. L'ensemble de ces mesures peuvent être adoptées individuellement ou en combinaison avec d'autres, mais des études locales doivent impérativement être menées pour prendre en compte des particularités régionales et ainsi mettre en place les mesures les plus adaptées aux territoires concernés.

Références

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Automat Contr 19:716–723

Al-Adhub AHY, Bowers AB (1977) Growth and breeding of Dichelopandalus bonnieri in Isle of Man waters. J Mar Biol Assoc United Kingdom 57:229–238

Albertelli G, Covazzi-Harriague A, Danovaro R, Fabiano M, Fraschetti S, Pusceddu A (1999) Differential responses of bacteria, meiofauna and macrofauna in a shelf area (Ligurian Sea, NW Mediterranean): Role of food availability. J Sea Res 42:11–26

Aldridge JN, Davies AM (1993) A high-resolution three-dimensional hydrodynmic tidal model of the Esatern Irish Sea. J Phys Oceanogr 23:207–224

Alfons A (2016) Package “robustHD”. https://cran.r-project.org/web/packages/robustHD/.

Allan JD (2004) Landscapes and riverscapes: The influence of land use on stream ecosystems. Annu Rev Ecol Evol Syst 35:257–284

Althaus F, Hill N, Ferrari R, Edwards L, Przeslawski R, Schönberg CHL, Stuart-Smith R, Barrett N, Edgar G, Colquhoun J, Tran M, Jordan A, Rees T, Gowlett-Holmes K (2015) A standardised vocabulary for identifying benthic biota and substrata from underwater imagery: The CATAMI classification scheme. PLoS One 10:1–18

Andersen T, Carstensen J, Hernández-García E, Duarte CM (2009) Ecological thresholds and regime shifts: approaches to identification. Trends Ecol Evol 24:49–57

Anderson MJ (2008) Animal-sediment relationships re-visited: Characterising species’ distributions along an environmental gradient using canonical analysis and quantile regression splines. J Exp Mar Bio Ecol 366:16–27

Asch RG, Collie JS (2008) Changes in a benthic megafaunal community due to disturbance from bottom fishing and the establishment of a fishery closure. Fish Bull 106:438–456

Atkinson LJ, Field JG, Hutchings L (2011) Effects of demersal trawling along the west coast of southern Africa: Multivariate analysis of benthic assemblages. Mar Ecol Prog Ser 430:241–255

Auber A (1992) IBTS : International Bottom Trawl Survey. https://doi.org/10.18142/17.

Ayma A, Aguzzi J, Canals M, Lastras G, Bahamon N, Mecho A, Company JB (2016) Comparison between ROV video and Agassiz trawl methods for sampling deep water fauna of submarine canyons in the Northwestern Mediterranean Sea with observations on behavioural reactions of target species. Deep Res Part I Oceanogr Res Pap 114:149–159

Baird SJ, Hewitt J, Wood BA (2015) Benthic habitat classes and trawl fishing disturbance in New Zealand waters shallower than 250 m. New Zealan:

Bajjouk T, Guillaumont B, Michez N, Thouin B, Croguennec C, Populus J, Louvel-Glaser J, Gaudillat V, Chevalier C, Tourolle J, Hamon D (2015) Classification EUNIS, Système d’information européen sur la nature : Traduction française des habitats benthiques des Régions Atlantique et Méditerranée. Vol. 2. Habitats subtidaux & complexes d’habitats. IFREMER/DYNECO/AG/15-02/TB2. Japanese Account Today 237

Batsleer J, Marchal P, Vaz S, Vermanrd Y, Rijnsdorp AD, Poos JJ (2018) Exploring habitat credits to manage the benthic impact in a mixed fishery. Mar Ecol Prog Ser 586:167–179

Bellaiche G, Droz L, Gaullier V, Pautot G (1994) Small submarine fans on the eastern margin of Corsica: Sedimentary significance and tectonic implications. Mar Geol 117:177–185

Bellwood D, Wainwright P, Fulton C, Hoey A (2006) Functional versatility supports coral reef biodiversity. Proc R Soc B Biol Sci 273:101–107

Vanden Berghe E, Rees HL, Eggleton JD (2007) NSBP 2000 data management. In: Rees H.L., Eggleton J.D., Rachor E., Vanden Berghe E. (eds) Structure and dynamics of the North Sea benthos. ICES Cooperative research report, pp 7–22

Bergman MJN, van Santbrink JW (1994) A new benthos dredge ('triple-D’) for quantitative sampling of infauna species of low abundance. Netherlands J Sea Res 33:129–133

Bergman MJN, Van Santbrink JW (2000) Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. ICES J Mar Sci 57:1321–1331

Bergmann M, Wieczorek SK, Moore PG, Atkinson RJA (2002) Discard composition of the Nephrops fishery in the Clyde Sea area , Scotland. Fish Res 57:169–183

Bianchi G, Gislason H, Graham K, Hill L, Jin X, Koranteng K, Manickchand-Heileman S, Payá I, Sainsbury K, Sanchez F, Zwanenburg K (2000) Impact of fishing on size composition and diversity of demersal fish communities. ICES J Mar Sci 57:558–571

Black KP, Parry GD (1999) Entrainment, dispersal, and settlement of scallop dredge sediment plumes: field measurements and numerical modelling. Can J Fish Aquat Sci 56:2271–2281

Blanchard F, Leloc F, Hily C, Boucher J (2004) Fishing effects on diversity , size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. Mar Ecol Prog Ser 280:249–260

Boero F, Fresis E (1986) Zonation and evolution of a rocky bottom hydroid community. PSZNI Mar Ecol 7:123–150

Bolam SG, Coggan RC, Eggleton J, Diesing M, Stephens D (2014) Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. J Sea Res 85:162–177

Bolam SG, Eggleton J, Smith R, Mason C, Vanstaen K, Rees H (2008) Spatial distribution of macrofaunal assemblages along the English Channel. J Mar Biol Assoc United Kingdom 88:675–687

Bolam SG, Eggleton JD (2014) Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. J Sea Res 88:47–58

Bolam SG, Garcia C, Eggleton J, Kenny AJ, Buhl-Mortensen L, Gonzalez-Mirelis G, van Kooten T, Dinesen G, Hansen J, Hiddink JG, Sciberras M, Smith C, Papadopoulou N, Gumus A, Van Hoey G, Eigaard OR, Bastardie F, Rijnsdorp AD (2017) Differences in biological traits composition of benthic assemblages between unimpacted habitats. Mar Environ Res 126:1–13

Bonifácio P (2015) Étude de l'état actuel et des variations temporelles de la composition de la macrofaune benthique des substrats meubles du Golf du Lion, Méditerranée Occidentale. Université de Bordeaux

Borja A, Franco J, Pérez V (2000) A marine Biotic Index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Mar Pollut Bull 40:1100–1114

Borja A, Muxika I, Franco J (2003) The application of a Marine Biotic Index to different impact sources affecting soft-bottom benthic communities along European coasts. Mar Pollut Bull 46:835–845

Le Bot S (2001) Morphodynamique de dunes sous-marines sous influence des marées et des tempêtes: processus hydro-sédimentaires et enregistrement: exemple du Pas-de-Calais. Université des Sciences et Technologies de Lille

Bourrin F, Durrieu de Madron X (2006) Contribution to the study of coastal rivers and associated prodeltas to sediment supply in Gulf of Lions (NW Mediterranean Sea). Vie Milieu 56:307–314

Boyd SE, Barry J, Nicholson M (2006) A comparative study of a 0.1 m^2 and 0.25 m^2 Hamon grab for sampling macrobenthic fauna from offshore marine gravels. J Mar Biol Assoc United Kingdom 86:1315–1328

Boyle TP, Smillie GM, Anderson JC, Beeson DR (1990) A sensitivity analysis of nine diversity and seven similarity indices. Res J Water Pollut Control Fed 62:749–762

Bozzano A, Sarda F (2002) Fishery discard consumption rate and scavenging activity in the northwestern Mediterranean Sea. ICES J Mar Sci 59:15–28

Bradshaw C, Collins P, Brand AR (2003) To what extent does upright sessile epifauna affect benthic biodiversity and community composition? Mar Biol 143:783–791

Bradshaw C, Tjensvoll I, Sköld M, Allan IJ, Molvaer J, Magnusson J, Naes K, Nilsson HC (2012) Bottom trawling resuspends sediment and releases bioavailable contaminants in a polluted fjord. Environ Pollut 170:232–241

Bradshaw C, Veale LO, Brand AR (2002) The role of scallop-dredge disturbance in long-term changes in Irish Sea benthic communities: A re-analysis of an historical dataset. J Sea Res 47:161–184

Bradshaw C, Veale LO, Hill AS, Brand AR (2001) The effect of scallop dredging on Irish Sea benthos: Experiments using a closed area. Hydrobiologia 465:129–138

Bremner J, Frid CLJ, Rogers SI (2003a) Assessing Marine Ecosystem Health: The long-term effects of fishing on functional biodiversity in North Sea benthos. Aquat Ecosyst Heal Manag 6:131–137

Bremner J, Rogers S, Frid C (2003b) Assessing functional diversity in marine benthic ecosystems: A comparison of approaches. Mar Ecol Prog Ser 254:11–25

Bremner J, Rogers SI, Frid CLJ (2006) Matching biological traits to environmental conditions in marine benthic ecosystems. J Mar Syst 60:302–316

Brind'Amour A, Laffargue P, Morin J, Vaz S, Foveau A, Le Bris H (2014) Morphospecies and taxonomic sufficiency of benthic megafauna in scientific bottom trawl surveys. Cont Shelf Res 72:1–9

Brind'Amour A, Rouyer A, Martin J (2009) Functional gains of including non-commercial epibenthic taxa in coastal beam trawl surveys: A note. Cont Shelf Res 29:1189–1194

Brockington S, Clarke A (2001) The relative influence of temperature and food on the metabolism of a marine invertebrate. J Exp Mar Bio Ecol 258:87–99

Brown EJ, Finney B, Dommisse M, Hills S (2005) Effects of commercial otter trawling on the physical environment of the southeastern Bering Sea. Cont Shelf Res 25:1281–1301

Bruce P, Bruce A (2017) Practical statistics for data scientists. Sebastopol

Buhl-mortensen L, Ellingsen KE, Buhl-mortensen P, Skaar KL, Gonzalez-mirelis G (2016) Trawling disturbance on megabenthos and sediment in the Barents Sea: chronic effects on density, diversity, and composition. ICES J Mar Sci 73:i98–i114

Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ, Raes M (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Mar Ecol 31:21–50

Cabioch L, Gentil F (1975) Distribution des peuplements benthiques dans la partie orientale de la Baie de Seine. Compte rendu l'académie des Sci Paris 280:571–574

Cabioch L, Gentil F, Glaçon R, Retière C (1977) Le macrobenthos des fonds meubles de la Manche: distribution générale et écologie. In: Keegan B.F., Ceidigh P.O., Boaden P.J.S. (eds) Biology of Benthic Organisms. Pergamon Press, Oxford, pp 115–128

Cabioch L, Glaçon R (1977) Distribution des peuplements benthiques en Manche Orientale, du cap d'Antifer à la Baie de Somme. Compte rendu l'académie des Sci Paris 285:209–213

Callaway R, Alsvåg J, De Boois I, Cotter J, Ford A, Hinz H, Jennings S, Kröncke I, Lancaster J, Piet G, Prince P, Ehrich S (2002) Diversity and community structure of epibenthic invertebrates and fish in the North Sea. ICES J Mar Sci 59:1199–1214

Carpentier A, Martin CS, Vaz S (2009) Channel Habitat Atlas for marine Resource Management, final report (CHARM phase II). INTERREG 3a Program

Catchpole T, Science A, Frid CLJ (2006) Importance of discards from the English Nephrops norvegicus fishery in the North Sea to marine scavengers. Mar Ecol Prog Ser 313:215–226

Ceccherelli VU, Rossi R (1984) Settlement, growth and production of the mussel Mytilus galloprovincialis. Mar Ecol Prog Ser 16:173–184

Certain G, Jorgensen LL, Christel I, Planque B, Bretagnolle V (2015) Mapping the vulnerability of animal community to pressure in marine systems: disentangling pressure types and integrating their impact from the individual to the community level. ICES J Mar Sci 72:1470–1482

Chabanet P, Loiseau N, Join J, Ponton D (2012) VideoSolo, an autonomous video system for high-frequency monitoring of aquatic biota, applied to coral reef fishes in the Glorioso Islands (SWIO). J Exp Mar Bio Ecol 430–431:10–16

Chavent M, Kuentz-Simonet V, Labenne A, Saracco J (2017) Multivariate Analysis of Mixed Data: The R Package PCAmixdata.

Chevenet F, Dolédec S, Chessel D (1994) A fuzzy coding approach for the analysis of long-term ecological data. Freshw Biol 31:265–309

Churchill JH (1989) The effect of commercial trawling on sediment resuspension and transport over the Middle Atlantic Bight continental shelf. Cont Shelf Res 9:841–864

Clarke AH (1972) The Arctic Dredge, a benthic biological sampler for mixed boulder and mud substrates. J Fish Res Board Canada 29:1503–1505

CNDCSMM (2019) Synthèse de l'évaluation de l'atteinte du bon état écologique au titre du descripteur 6 "Intégrité des fonds marins" (critères D6C1, D6C2 et D6C3) par façade maritime.

Coggan R, Diesing M (2011) The seabed habitats of the central English Channel: A generation on from Holme and Cabioch, how do their interpretations match-up to modern mapping techniques? Cont Shelf Res 31:132–150

Coleman FC, Williams SL (2002) Overexploiting marine ecosystem engineers : potential consequences for biodiversity. Trends Ecol Evol 17:40–44

Collie JS, Escanero GA, Valentine PC (2000a) Photographic evaluation of the impacts of bottom fishing on benthic epifauna. ICES J Mar Sci 57:987–1001

Collie JS, Hall SJ, Kaiser MJ, Poiner IANR (2000b) A quantitative analysis of fishing impacts on shelf-sea benthos. J Anim Ecol 69:785–798

Coma R, Ribes M (2003) Seasonal energetic constraints in Mediterranean benthic suspension feeders: Effects at different levels of ecological organization. Oikos 101:205–215

Coppin F, Travers-Trolet M (1989) CGFS : Channel Ground Fish Survey. https://doi.org/10.18142/11.

Cornwell WK, Schwilk DW, Ackerly DD (2006) A trait-based test for habitat filtering: Convex hull volume. Ecology 87:1465–1471

Costa ME, Erzini K, Borges TC (2008) Bycatch of crustacean and fish bottom trawl fisheries from southern Portugal (Algarve). Sci Mar 72:801–814

Couce E, Engelhard GH, Schratzberger M (2020) Capturing threshold responses of marine benthos along gradients of natural and anthropogenic change. J Appl Ecol 57:1137–1148

Crepon M, Wald L, Monget JM (1982) Low-frequency waves in the Ligurian Sea during December 1977. J Geophys Res 87:595–600

Crist TO, Veech JA (2006) Additive partitioning of rarefaction curves and species-area relationships: Unifying α-, β- and γ-diversity with sample size and habitat area. Ecol Lett 9:923–932

Cruz ICS, Kikuchi RKP, Leão ZMAN (2008) Use of the video transect method for characterizing the Itacolomis reefs, Eastern Brazil. Brazilian J Oceanogr 56:271–280

Dauvin JC, Lucas S, Navon M, Lesourd S, Mear Y, Poizot E, Alizier S (2017) Does the hydrodynamic, morphometric and sedimentary environment explain the structure of soft-bottom benthic assemblages in the Eastern Bay of Seine (English Channel)? Estuar Coast Shelf Sci 189:156–172

Davies R (2002) Hypothesis testing when a nuisance parameter is present only under the alternative: linear model case. Biometrika 89:484–489

Demarcq H, Wald L (1984) La dynamique superficielle du panache du Rhône d'après l'imagerie infrarouge satellitaire. Oceanol acta 7:159–162

van Denderen P, Bolam S, Hiddink J, Jennings S, Kenny A, Rijnsdorp A, van Kooten T (2015) Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. Mar Ecol Prog Ser 541:31–43

van Denderen P, Hintzen N, Rijnsdorp A, Ruardij P, van Kooten T (2014) Habitat-Specific Effects of Fishing Disturbance on Benthic Species Richness in Marine Soft Sediments. Ecosystems 17:1216–1226

Depestele J, Ivanovic A, Degrendele K, Esmaeili M, Polet H, Roche M, Summerbell K, Teal LR, Vanelslander B, Neill FGO (2016) Measuring and assessing the physical impact of beam trawling. ICES J Mar Sci 73:i15–i26

Desprez M (2000) Physical and biological impact of marine aggregate extraction along the French coast of the Eastern English Channel: Short-and long-term post-dredging restoration. ICES J Mar Sci 57:1428–1438

Diamond B, Beukers-Stewart BD (2011) Fisheries discards in the North Sea: Waste of resources or a necessary evil ? Rev Fish Sci 231–245

Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanogr Mar Biol an Annu Rev 33:245–303

Diesing M, Stephens D, Aldridge J (2013) A proposed method for assessing the extent of the seabed significantly affected by demersal fishing in the Greater North Sea. ICES J Mar Sci 70:1085–1096

Dinmore TA, Duplisea DE, Rackham BD, Maxwell DL, Jennings S (2003) Impact of a large-scale area closure on patterns of fishing disturbance and the consequence for benthic communities. ICES J Mar Sci 60:371–380

Doré A, Horellou A, Herard K, Touroult J (2015) ZNIEFF MARINES - Pratiques et mise en oeuvre sur les substrats meubles. Rapport SPN 2015 - 9.

Ducrotoy JP (2010) Ecological restoration of tidal estuaries in north western Europe: An adaptive strategy to multi-scale changes. Plankt Benthos Res 5:174–184

Dunbrack R, Zielinski R (2003) Seasonal and diurnal activity of sixgill sharks (Hexanchus griseus) on a shallow water reef in the Strait of Georgia , British Columbia. Can J Zool 81:1107–1111

Duplisea DE, Jennings S, Warr KJ, Dinmore TA (2002) A size-based model of the impacts of bottom trawling on benthic community structure. Can J Fish Aquat Sci 59:1785–1795

Durrieu De Madron X, Abassi A, Heussner S, Monaco A, Aloisi JC, Radakovitch O, Giresse P, Buscail R, Kerherve P (2000) Particulate matter and organic carbon budgets for the Gulf of Lions (NW Mediterranean). Oceanol Acta 23:717–730

Dyer KR (1986) Coastal and estuarine sediment dynamics. New York

EC (2005) Council regulation (EC) No. 1568/2005 of 20 September 2005 amending regulation (EC) No 850/98 as regards the protection of deep-water coral reefs from the effects of fishing in certain areas of the Atlantic Ocean. Off J Eur Union L252:2–3

EC (2008) Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). Off J Eur Union 19–40

EC (2009) Council Regulation (EC) No. 1224/ 2009 of 20 November 2009 establishing a Community control system for ensuring compliance with the rules of the common fisheries policy, amending Regulations (EC) No 847/96, (EC) No 2371/2002, (EC) No 811/2004, (EC) No 768. Off J Eur Union L343:1–50

EC (2011) Regulation (EU) No 1343/2011 of the european parliament and of the council of 13 december 2011 on certain provisions for fishing in the GFCM (General Fisheries Commission for the Mediterranean) Agreement area and amending council regulation (EC) No 1967/2. Off J Eur Union L347:44–61

EC (2016) Regulation (EU) 2016/2336 of the european parliament and of the council of 14 December 2016 establishing specific conditions for fishing for deep-sea stocks in the north-east Atlantic and provisions for fishing in international waters of the north-east At. Off J Eur Union L354:1–19

EC (2017a) Commission decision (EU) 2017/848 of 17 May 2017 laying down criteria and methodological standards on good environmental status of marine waters and specifications and standardised methods for monitoring and assessment, and repealing Decision 2010/477/EU. Off J Eur Union L125:43–73

EC (2017b) Commission Delegated Regulation (EU) No 1396/2014 of 20 October 2016 establishing a discard plan for certain small pelagic fisheries in the Mediterranean Sea. Off J Eur Union L14:4–8

EC (2018) Commission delegated regulation (EU) 2018/2035 of 18 October 2018 specifying details of implementation of the landing obligation for certain demersal fisheries in the North Sea for the period 2019-2021. Off J Eur Union L327:17–26

EC (2019) Council regulation (EU) 2019/2236 of 16 December 2019 fixing for 2020 the fishing opportunities for certain fish stocks and groups of fish stocks applicable in the Mediterranean and Black Seas. Off J Eur Union L336:14–25

Eigaard OR, Bastardie F, Breen M, Dinesen GE, Hintzen NT, Laffargue P, Mortensen LO, Nielsen JR, Nilsson HC, O'Neill FG, Polet H, Reid DG, Sala A, Sköld M, Smith C, Sorensen TK, Tully O, Zengin M, Rijnsdorp AD (2016) Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J Mar Sci 73:i27–i43

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P, Catarino R, Dinesen GE, Egekvist J, Fock HO, Geitner K, Gerritsen HD, González MM, Jonsson P, Kavadas S, Laffargue P, Lundy M, Gonzalez-Mirelis G, Nielsen JR, Papadopoulou N, Posen PE, Pulcinella J, Russo T, Sala A, Silva C, Smith CJ, Vanelslander B, Rijnsdorp AD (2017) The footprint of bottom trawling in European waters: Distribution, intensity, and seabed integrity. ICES J Mar Sci 74:847–865

Eleftheriou A (2013) Methods for the study of marine benthos.

Eleftheriou A, Basford DJ (1989) The macrobenthic infauna of the offshore northern north sea. J Mar Biol Assoc United Kingdom 69:123–143

Ellis N, Pantus F, Pitcher CR (2014) Scaling up experimental trawl impact results to fishery management scales - a modelling approach for a "hot time." Can J Fish Aquat Sci 71:733–746

EMODnet Bathymetry Consortium (2018) EMODnet Digital Bathymetry (DTM 2018).

Endroyono (2017) Overview of the trawl fisheries socio-economic conditions in Indonesia after the second trawl ban. In: Siar S.V., Suuronen P., Gregory R. (eds) FAO fisheries and aquaculture proceedings. The Food and Agriculture Organization of the United Nations, Rome, pp 3–37

Engel J, Kvitek R (1998) Effects of otter trawling on a benthic community in Monterey Bay Nation. Conserv Biol 12:1204–1214

Englehard GH (2008) One hundred and twenty years of change in fishing power of English North Sea trawlers. In: Payne A., Cotter J., Potter T. (eds) Advances in Fisheries Science: 50 years on from Beverton and Holt. pp 1–25

Eno N, Frid C, Hall K, Ramsay K, Sharp R, Brazier D, Hearn S, Dernie K, Robinson K, Paramor O, Robinson L (2013) Assessing the sensitivity of habitats to fishing: From seabed maps to sensitivity maps. J Fish Biol 83:826–846

Estrada M (1996) Primary production in the northwestern Mediterranean. Sci Mar 60:55–64

Fabri M-C, Andral B (2011) Appui à la mise en œuvre de la Directive Cadre Stratégie pour le Milieu Marin - DCSMM.

Falcão M, Gaspar MB, Caetano M, Santos MN, Vale C (2003) Short-term environmental impact of clam dredging in coastal waters (south of Portugal): Chemical disturbance and subsequent recovery of seabed. Mar Environ Res 56:649–664

Farrugio H (2013) Fisheries in the Gulf of Lions.

Fauchard P (2010) Predator-prey reversal: a possible mechanism for ecosystem hysteresis in the North Sea? Ecology 91:2191–2197

Ferré B, Durrieu de Madron X, Estournel C, Ulses C, Le Corre G (2008) Impact of natural (waves and currents) and anthropogenic (trawl) resuspension on the export of particulate matter to the open ocean. Application to the Gulf of Lion (NW Mediterranean). Cont Shelf Res 28:2071–2091

Ferré B, Guizien K, Durrieu De Madron X, Palanques A, Guillén J, Grémare A (2005) Fine-grained sediment dynamics during a strong storm event in the inner-shelf of the Gulf of Lion (NW Mediterranean). Cont Shelf Res 25:2410–2427

Ferrer P (2010) Morphodynamique à multi-échelles du trait de côte du Golfe du Lion depuis le dernier optimum climatique. Université de Perpignan Via Domitia

Flannery E, Przeslawski R (2015) Comparison of sampling methods to assess benthic marine biodiversity: Are spatial and ecological relationships consistent among sampling gear?

Folke RL (1954) The distinction between grain size and mineral composition in sedimentary rock nomenclature. J Geol 62:344–356

Fonteyne R (2000a) Physical impact of beam trawls on seabed sediments. In: Kaiser M.J., De Groot S.J. (eds) Effects of fishing on non-target species and habitats. Blackwell Science, Oxford, pp 15–36

Fonteyne R (2000b) Physical impacts of beam trawls on seabed sediments. In: Kaiser M.J., Groot S.J. (eds) Effects of fishing on non-target species and habitats. Blackweel Science, Oxford, pp 12–36

Foveau A (2009) Habitats et communautés benthiques du bassin oriental de la Manche: état des lieux au début du XXIe siècle. Lille 1

Foveau A, Desroy N, Dauvin JC, Dewarumez JM (2013) Distribution patterns in the benthic diversity of the eastern English Channel. Mar Ecol Prog Ser 479:115–126

Foveau A, Jac C, Llpasset M, Guillerme C, Desroy N, Vaz S (2019) Updated biological traits' scoring and protection status to calculate sensitivity to trawling on mega-epibenthic fauna. https://doi.org/10.17882/59517.

Foveau A, Vaz S, Desroy N, Kostylev VE (2017) Process-driven and biological characterisation and mapping of seabed habitats sensitive to trawling. PLoS One 12:1–30

Fox J, Weisberg S, Price B, Adler D, Bates D, Baud-Bovy G, Bolker B, Ellison S, Firth D, Friendly M, Gorjanc G, Graves S, Heiberger R, Krivitsky P, Laboissiere R, Maechler M, Monette G, Murdoch D, Nilsson H, Ogle D, Ripley B, Venables W, Walker S, Winsemius D, Zeileis A, R-Core (2019) car: Companion to applied regression.

Frid CLJ, Harwood KG, Hall SJ, Hall JA (2000) Long-term changes in the benthic communities on North Sea fishing grounds. ICES J Mar Sci 57:1303–1309

Friedlander AM, Boehlert GW, Field ME, Mason JE, Gardner J V., Dartnell P (1999) Sidescan-sonar mapping of benthic trawl marks on the shelf and slope off Eureka, California. Fish Bull 97:786–801

Gallon RK, Fournier J (2015) G2Sd: Grain-Size Statistics and Description of Sediment.

Galparsoro I, Connor DW, Borja Á, Aish A, Amorim P, Bajjouk T, Chambers C, Coggan R, Dirberg G, Ellwood H, Evans D, Goodin KL, Grehan A, Haldin J, Howell K, Jenkins C, Michez N, Mo G, Buhl-mortensen P, Pearce B, Populus J, Salomidi M, Sánchez F, Serrano A, Shumchenia E, Tempera F, Vasquez M (2012) Using EUNIS habitat classification for benthic mapping in European seas: Present concerns and future needs. Mar Pollut Bull 64:2630–2638

Garlan T (2011) Sédimentologie - Méditerrannée occidentale. https://sextant.ifremer.fr/Donnees/Catalogue#/metadata/e4f891f7-e495-4a9b-b557-5c2c6c653a2d.

Gaspar MB, Richardson CA, Monteiro CC (1994) The effects of dredging on shell formation in the razor clam Ensis siliqua from Barrinha, southern Portugal . J Mar Biol Assoc United Kingdom 74:927–938

Gentil F (1976) Distribution des peuplements benthiques en baie de somme. Université de Paris VI

GFCM (2019) Resolution GFCM/43/2019/6 on the establishment of a set of measuures to protect vulnerable marine ecosystems formed by cnidarian (coral) communities in the Mediterranean Sea. 1–7

Gislason H, Bastardie F, Dinesen GE, Egekvist J, Eigaard OR (2017) Lost in translation? Multi-metric macrobenthos indicators and bottom trawling. Ecol Indic 82:260–270

Gogina M, Zettler ML (2010) Diversity and distribution of benthic macrofauna in the Baltic Sea. Data inventory and its use for species distribution modelling and prediction. J Sea Res 64:313–321

González-Irusta JM, De La Torriente A, Punzón A, Blanco M, Serrano A (2018) Determining and mapping species sensitivity to trawling impacts: The BEnthos Sensitivity Index to Trawling Operations (BESITO). ICES J Mar Sci 75:1710–1721

Grall J, Coïc N (2006) Synthèse des méthodes d'évaluation de la qualité du benthos en milieu côtier.

Gray J, Elliott M (2009) Ecology of marine sediments: from science to management. Oxford University Press, New York

Greathead C, González-Irusta JM, Clarke J, Boulcott P, Blackadder L, Weetman A, Wright PJ (2014) Environmetal requirements for three sea pen species: a relevance to distribution and conservation. ICES J Mar Sci 72:576–586

Greenstreet SPR, Hall SJ (1996) Fishing and the ground-fish assemblage structure in the North-Western North Sea: An analysis of long-term and spatial trends. J Anim Ecol 65:577

Griffith GP, Fulton EA, Gorton R, Richardson AJ (2012) Predicting interactions among fisging, ocean warming, and ocean acidification in a marine system with whole-ecosystem models. Conserv Biol 26:1145–1152

Grizzle RE, Ward LG, Mayer LA, Malik MA, Cooper AB, Abeels HA, Greene JK, Brodeur MA, Rosenberg AA (2009) Effects of a large fishing closure on benthic communities in the western Gulf of Maine: Recovery from the effects of gillnets and otter trawls. Fish Bull 107:308–317

Grochowski NTL, Collins MB (1994) Wave activity on the sea-bed of the English Channel. J Mar Biol Assoc United Kingdom 74:739–742

Grochowski NTL, Collins MB, Boxall SR, Salomon JC (1993) Sediment transport predictions for the English Channel, using numerical models. J Geol Soc London 150:683–695

Groeneveld RA, Meeden G (1984) Measuring Skewness and Kurtosis. Stat 33:391–399

Groenewold S, Fonds M (2000) Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. ICES J Mar Sci 57:1395–1406

Groffman PM, Baron JS, Blett T, Gold AJ, Goodman I, Gunderson LH, Levinson BM, Palmer MA, Paerl HW, Peterson GD, Poff NLR, Rejeski DW, Reynolds JF, Turner MG, Weathers KC, Wiens J (2006) Ecological thresholds: The key to successful environmental management or an important concept with no practical application? Ecosystems 9:1–13

Guihou K (2013) Étude de la dynamique du Courant Nord au large de Toulon, à l'aide de modèle, observations in-situ et données satellites. Université de Toulon

Guille A (1970) Bionomie benthique du plateau continental de la côte catalane française. II. Les communautés de la macrofaune. Vie Milieu 21:149–280

Guillemot N, Kulbicki M, Chabanet P, Vigliola L (2011) Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. PLoS One 6:1–15

Guillén J, Jiménez JA, Palanques A, Gracia V, Puig P, Sánchez-Arcilla A (2002) Sediment resuspension across a microtidal, low-energy inner shelf. Cont Shelf Res 22:305–325

Guillou N (2007) Rôles de l'hétérogénéité des sédiments de fond et des interactions houle-courant sur l'hydrodynamique et la dynamique sédimentaire en zone subtidale - applications en Manche orientale et à la pointe de la Bretagne. Université de Bretagne Occidentale

Guizien K (2009) Spatial variability of wave conditions in the gulf of lions (NW mediterranean sea). Vie Milieu 59:261–270

Hall SJ, Raffaelli D, Thrush SF (1994) Patchiness and disturbance in shallow water benthic assemblages. In: Giller P.S., Hildrew A.G., Raffaelli D. (eds) Aquatic Ecology: Scale, Pattern and Process. Blackwell Scientific Publications, London, pp 333–375

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan H., Madin EM., Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. Science (80-) 319:948–953

Hammond CF, Conquest LL, Rose CS (2013) Using reflex action mortality predictors (RAMP) to evaluate if trawl gear modifications reduce the unobserved mortality of Tanner crab (Chionoecetes bairdi) and snow crab (C. opilio). ICES J Mar Sci 70:1308–1318

Han F, Yao J, Zhu H, Wang C (2020) Marine organisme detection and classification from underwater vision based on the deep CNN method. Math Probl Eng 1–11

Heip C, Basford D, Craeymeersch JA, Dewarumez JM, Dorjes J, De Wilde P, Duineveld G, Eleftheriou A, Herman PMJ, Niermann U, Kingston P, Kiinitzer A, Rachor E, Rumohr H, Soetaert K, Soltwede T (1992) Trends in biomass, density and diversity of north sea macrofauna. ICES J Mar Sci 49:13–22

Henriksen P, Josefson AB, Hansen JW, Krause-Jensen D, Dahl K, Dromph KM (2014) Danish contribution to the EU Water Framework Directive intercalibration phase 2.

Hermsen JM, Collie JS, Valentine PC (2003) Mobile fishing gear reduces benthic megafaunal production on Georges Bank. Mar Ecol Prog Ser 260:97–108

Hidalgo M, Massutí E, Guijarro B, Moranta J, Ciannelli L, Lloret J, Oliver P, Stenseth NC (2009) Population effects and changes in life history traits in relation to phase transitions induced by long-term fishery harvesting: European hake (Merluccius merluccius) off the Balearic Islands. Can J Fish Aquat Sci 66:1355–1370

Hiddink JG, Jennings S, Kaiser MJ (2007) Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. J Appl Ecol 44:405–413

Hiddink JG, Jennings S, Kaiser MJ, Queirós AM, Duplisea DE, Piet GJ (2006) Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Can J Fish Aquat Sci 63:721–736

Hiddink JG, Johnson AF, Kingham R, Hinz H (2011) Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. J Appl Ecol 48:1441–1449

Hiddink JG, Kaiser MJ, Sciberras M, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Parma AM, Suuronen P, Rijnsdorp AD, Jennings S (2020) Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. J Appl Ecol 57:1199–1209

Hiddink JG, Rijnsdorp AD, Piet G (2008) Can bottom trawling disturbance increase food production for a commercial fish species? Can J Fish Aquat Sci 65:1393–1401

Hinz H, Prieto V, Kaiser MJ (2009) Trawl disturbance on benthic communities: Chronic effects and experimental predictions. Ecol Appl 19:761–773

Hinz H, Tarrant D, Ridgeway A, Kaiser MJ, Hiddink JG (2011) Effects of scallop dredging on temperate reef fauna. Mar Ecol Prog Ser 432:91–102

Hiscock K, Jackson A, Lear D (1999) Assessing seabed species and ecosystems sensitivities. Existing approaches and development.

van Hoey G, Bonne W, Salas F (2015) Intercalibration report for benthic invertebrate fauna of the North East Atlantic Geographical intercalibration group for coastal waters (NEA 1/26). ILVO Meded

Hollander M, Wolfe DA (1973) Kendall and Spearman tests. Nonparametric Statistical Methods. John Wiley & Sons, New York, pp 185–194

Holme NA (1961) The bottom fauna of the English Channel. Part I. J Mar Biol Assoc United Kingdom 41:397–461

Holme NA (1966) The bottom fauna of the English channel. Part II. J Mar Biol Assoc United Kingdom 46:401–493

Hunt HL, Scheibling RE (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Mar Ecol Prog Ser 155:269–301

Huot Y, Babin M, Bruyant F, Grob C, Twardowski MS, Claustre H (2007) Does chlorophyll a provide the best index of phytoplankton biomass for primary productivity studies ? Biogeosciences Discuss 707–745

Huthnance JM (1991) Physical oceanography of the North Sea. Ocean Shorel Manag 16:199–231

ICES (2015) Manual for the International Bottom Trawl Surveys.

ICES (2017a) Manual of the IBTS North Eastern Atlantic Surveys. http://doi.org/10.17895/ices.pub.3519.

ICES (2017b) Report of the Workshop to evaluate regional benthic pressure and impact indicator(s) from bottom fishing (WKBENTH).

ICES (2017c) EU request on indicators of the pressure and impact of bottom-contacting fishing gear on the seabed , and of trade-offs in the catch and the value of landings.

ICES (2018) Interim Report of the Working Group on fisheries benthic impact and trade-offs (WGFBIT).

ICES (2019a) Workshop to evaluate and test operational assessment of human activities causing physical disturbance and loss to seabed habitats (MSFD D6C1, C2 and C4). ICES Sci reports 1:77

ICES (2019b) Workshop to evaluate and test operational assessment of human activities causing physical disturbance and loss to seabed habitats (MSFD D6 C1, C2 and C4) (WKBEDPRES2). ICES Sci reports 1:1–87

ICES (2019c) OSPAR request on the production of spatial data layers of fishing intensity/pressure. ICES Tech Serv

Jac C, Desroy N, Certain G, Foveau A, Labrune C (2020a) Detecting adverse effect on seabed integrity . Part 1 : Generic sensitivity indices to measure the effect of trawling on benthic mega-epifauna. Ecol Indic 117:

Jac C, Desroy N, Certain G, Foveau A, Labrune C, Vaz S (2020b) Detecting adverse effect on seabed integrity. Part 2: How much of seabed habitats are left in good environmental status by fisheries? Ecol Indic 117:

Jac C, Vaz S (2018) Abrasion superficielle des fonds par les arts trainants - Méditerranée (surface swept area ratio). https://doi.org/10.12770/8bed2328-a0fa-4386-8a3e-d6d146cafe54.

Jadaud A, Souplet A, Bertrand J (1994) MEDITS. https://doi.org/10.18142/7.

Jennings S, Dinmore TA, Duplisea DE, Warr KJ, Lancaster JE (2001a) Trawling disturbance can modify benthic production processes. J Anim Ecol 70:459–475

Jennings S, Greenstreet SPR, Reynolds JD (1999) Structural change in an exploited fish community: A consequence of differential fishing effects on species with contrasting life histories. J Anim Ecol 68:617–627

Jennings S, Nicholson MD, Dinmore TA, Lancaster JE (2002) Effects of chronic trawling disturbance on the production of infaunal communities. Mar Ecol Prog Ser 243:251–260

Jennings S, Pinnegar J, Polunin N, Warr K (2001b) Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. Mar Ecol Prog Ser 213:127–142

Jessen C, Bednarz VN, Rix L, Teichberg M, Wild C (2015) Marine eutrophication. In: Armon R.H., Hänninen O. (eds) Environmental Indicators. Springer, Dordrecht, pp 1–1068

Jørgensen LL, Renaud PE, Cochrane SKJ (2011) Improving benthic monitoring by combining trawl and grab surveys. Mar Pollut Bull 62:1183–1190

Josefson AB, Hansen JLS, Asmund G, Johansen P (2008) Threshold response of benthic macrofauna integrity to metal contamination in West Greenland. Mar Pollut Bull 56:1265–1274

de Juan S, Demestre M (2012) A Trawl Disturbance Indicator to quantify large scale fishing impact on benthic ecosystems. Ecol Indic 18:183–190

de Juan S, Demestre M, Thrush S (2009) Defining ecological indicators of trawling disturbance when everywhere that can be fished is fished: A Mediterranean case study. Mar Policy 33:472–478

de Juan S, Thrush SF, Demestre M (2007) Functionnal changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). Mar Ecol Prog Ser 334:117–129

Juhel JB, Vigliola L, Wantiez L, Letessier TB, Meeuwig JJ, Mouillot D (2019) Isolation and no-entry marine reserves mitigate anthropogenic impacts on grey reef shark behavior. Sci Rep 9:1–11

Kaiser MJ (1998) Significance of Bottom-Fishing Disturbance. Conserv Biol 12:1230–1235

Kaiser MJ, Clarke KR, Hinz H, Austen MCV, Somerfield PJ, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. Mar Ecol Prog Ser 311:1–14

Kaiser MJ, Collie JS, Hall SJ, Jennings S, Poiner IR (2002) Modification of marine habitats by trawling activities: Prognosis and solutions. Fish Fish 3:114–136

Kaiser MJ, Edwards DB, Armstrong PJ, Radford K, Lough NEL, Flatt RP, Jones HD (1998) Changes in megafaunal benthic communities in different habitats after trawling disturbance. ICES J Mar Sci 55:353–361

Kaiser MJ, Hiddink JG (2007) Food subsidies from fisheries to continental shelf benthic scavengers. Mar Ecol Prog Ser 350:267–276

Kaiser MJ, Hill AS, Ramsay K, Spencer BE, Brand AR, Veale LO, Prudden K, Rees EIS, Munday BW, Ball B, Hawkins SJ (1996) An estimate of fishing gear disturbance intensities in the Irish Sea: a comparison of beam trawling and scallop dredging. Aquat Conserv Mar Freshw Ecosyst 6:269–287

Kaiser MJ, Hormbrey S, Booth JR, Hinz H, Hiddink JG (2018) Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear. J Appl Ecol 55:1060–1070

Kaiser MJ, Spencer BE (1995) Survival of by-catch from a beam trawl. Mar Ecol Prog Ser 126:31–38

Kaiser MJ, Spencer BE (1996) The effects of beam-trawl disturbance on infaunal communities in different habitats. J Anim Ecol 65:348–358

Kenchington EL, Kenchington TJ, Henry LA, Fuller S, Gonzalez P (2007) Multi-decadal changes in the megabenthos of the Bay of Fundy: The effects of fishing. J Sea Res 58:220–240

Kenchington ELR, Prena J, Gilkinson KD, Gordon Jr. DC, MacIsaac K, Bourbonnais C, Schwinghamer PJ, Rowell TW, McKeown DL, Vass WP (2001) Effects of experimental otter trawling on the macrofauna of a sandy bottom ecosystem on the Grand Banks of Newfoundland. Can J Fish Aquat Sci 58:1043–1057

Kingston PF, Rachor E (1982) North sea level bottom communities. ICES CM 41:1–16

Kinne O (1971) Marine Ecology. A comprehensive, integrated treatise on life in oceans and coastal waters. Wiley-Interscience, John Wiley & Sons, London

Koops MA, Koen-Alonso M, Smokorowski KE, Rice JC (2012) A Science-based interpretation and framework for considering the contribution of the relevant fish to the ongoing productivity of commercial, recreational or aboriginal fisheries. DFO Can Sci Advis Secreteriat Res Doc

Kostylev VE, Hannah CG (2007) Process-driven characterization and mapping of seabed habitats. Spec Pap - Geol Assoc Canada 47:171–184

Kröncke I, Bergfeld C (2003) North sea benthos: a review. Senckenbergiana Maritima 33:205–268

Kröncke I, Reiss H (2010) Influence of macrofauna long-term natural variability on benthic indices used in ecological quality assessment. Mar Pollut Bull 60:58–68

Kröncke I, Reiss H, Eggleton JD, Aldridge J, Bergman MJN, Cochrane S, Craeymeersch JA, Degraer S, Desroy N, Dewarumez J, Duineveld GCA, Essink K, Hillewaert H, Lavaleye MSS, Moll A, Nehring S, Newell R, Oug E, Pohlmann T, Rachor E, Robertson M, Rumohr H, Schratzberger M, Smith R, Vanden E, Dalfsen J Van, Hoey G Van, Vincx M, Willems W, Rees HL (2011) Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. Estuar Coast Shelf Sci 94:1–15

Künitzer A, Basford D, Craeymeersch JA, Dewarumez J-M, Dörjes J, Duineveld GCA, Eleftheriou A, Heip C, Herman P, Kingston P, Niermann U, Rachor E, Rumohr H, De Wilde PAJ (1992) The benthic infauna of the North Sea: species distribution and assemblages. ICES J Mar Sci 49:127–143

Labrune C (2018) APPEAL MED. https://doi.org/10.17600/18000598.

Labrune C, Grémare A, Amouroux JM, Sardá R, Gil J, Taboada S (2007a) Assessment of soft-bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey. Estuar Coast Shelf Sci 71:133–147

Labrune C, Grémare A, Amouroux JM, Sardá R, Gil J, Taboada S (2008) Structure and diversity of shallow soft-bottom benthic macrofauna in the Gulf of Lions (NW Mediterranean). Helgol Mar Res 62:201–214

Labrune C, Grémare A, Guizien K, Amouroux JM (2007b) Long-term comparison of soft bottom macrobenthos in the Bay of Banyuls-sur-Mer (north-western Mediterranean Sea): A reappraisal. J Sea Res 58:125–143

Lambert GI, Jennings S, Kaiser MJ, Davies TW, Hiddink JG (2014) Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. J Appl Ecol 51:1326–1336

Lambert GI, Jennings S, Kaiser MJ, Hinz H, Hiddink JG (2011) Quantification and prediction of the impact of fishing on epifaunal communities. Mar Ecol Prog Ser 430:71–86

Lambert GI, Murray LG, Hiddink JG, Hinz H, Lincoln H, Hold N, Cambiè G, Kaiser MJ (2017) Defining thresholds of sustainable impact on benthic communities in relation to fishing disturbance. Sci Rep 7:1–15

Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G, Watson DL (2010) Cost-efficient sampling of fish assemblages: Comparison of baited video stations and diver video transects. Aquat Biol 9:155–168

Larsonneur C, Boysse P, Auffret J -P (1982) The superficial sediments of the English Channel and its western approaches. Sedimentology 29:851–864

Lee J, South AB, Jennings S (2010) Developing reliable, repeatable, and accessible methods to provide high-resolution estimates of fishing-effort distributions from vessel monitoring system (VMS) data. ICES J Mar Sci 67:1260–1271

Lehmann A, Overton JM, Leathwick JR (2002) GRASP: generalized regression analysis and spatial prediction. Ecol Modell 157:189–207

Leonardsson K, Blomqvist M, Magnusson M, Wikström A, Rosenberg R (2015) Calculation of species sensitivity values and their precision in marine benthic faunal quality indices. Mar Pollut Bull 93:94–102

Leonardsson K, Blomqvist M, Rosenberg R (2009) Theoretical and practical aspects on benthic quality assessment according to the EU-Water Framework Directive - Examples from Swedish waters. Mar Pollut Bull 58:1286–1296

Lin FJ (2008) Solving multicollinearity in the process of fitting regression model using the nested estimate procedure. Qual Quant 42:417–426

Linnane A, Ball B, Munday B, Marlen B Van, Fonteyne R (2000) A review of potential techniques to reduce the environmental impact of demersal trawls. Irish Fish Investig 7:1–43

Le Loc'h F (2004) Structure, fonctionnement, évolution des communautés benthiques des fonds meubles exploités du plateau continental Nord Gascogne. Université de Bretagne occidentale

Lohrer AM, Thrush SF, Gibbs MM (2004) Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature 431:2–5

Lohrer AM, Thrush SF, Hunt L, Hancock N, Lundquist C (2005) Rapid reworking of subtidal sediments by burrowing spatangoid urchins. J Exp Mar Bio Ecol 321:155–169

van Loon WMGM, Walvoort DJJ, van Hoey G, Vina-Herbon C, Blandon A, Pesch R, Schmitt P, Scholle J, Heyer K, Lavaleye M, Phillips G, Duineveld GCA, Blomqvist M (2018) A regional benthic fauna assessment method for the Southern North Sea using Margalef diversity and reference value modelling. Ecol Indic 89:667–679

Lopez-Garrido PH, Barry JP, Gonzalez-Gordillo JI, Escobar-Briones E (2020) ROV's video recording as a tool to estimate variation in megabenthic epifauna diversity and community composition in the Guaymas basin. Front Mar Sci 7:1–16

Louvel-Glaser J, Gaudillat V, Poncet L (2013) EUNIS, European Nature Information System, système d'information européean sur la nature. Classification des habitats. Habitats terrestres et d'eau douce.

Lucchetti A, Sala A (2012) Impact and performance of mediterranean fishing gear by side-scan sonar technology. Can J Fish Aquat Sci 69:1806–1816

Mackelworth P, Holcer D, Jovanovic J, Fortuna C (2010) Marine conservation and assesion: the future for the Croatian Adriactic. Environmetal Manag 47:644–655

Madron XD De, Ferré B, Corre G Le, Grenz C, Conan P, Buscail R, Bodiot O (2005) Trawling-induced resuspension and dispersal of muddy sediments and dissolved elements in the Gulf of Lion (NW Mediterranean). Cont Shelf Res 25:2387–2409

Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952-2012). Fish Res 154:44–62

Mangano MC, Kaiser MJ, Porporato EMD, Lambert GI, Rinelli P, Spanò N (2014) Infaunal community responses to a gradient of trawling disturbance and a long-term Fishery Exclusion Zone in the Southern Tyrrhenian Sea. Cont Shelf Res 76:25–35

Margalef R (1958) Information theory in ecology. Int J Gen Syst 3:36–71

Martín J, Puig P, Palanques A, Giamportone A (2014) Commercial bottom trawling as a driver of sediment dynamics and deep seascape evolution in the Anthropocene. Anthropocene 7:1–15

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional and functional evenness divergence: the primary of functional components diversity. Oikos 111:112–118

Maxwell D, Jennings S (2005) Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish. J Appl Ecol 42:25–37

McConnaughey RA, Hiddink JG, Jennings S, Pitcher CR, Kaiser MJ, Suuronen P, Sciberras M, Rijnsdorp AD, Collie JS, Mazor T, Amoroso RO, Parma AM, Hilborn R (2020) Choosing best practices for managing impacts of trawl fishing on seabed habitats and biota. Fish Fish 21:319–337

McLaverty C, Eigaard OR, Gislason H, Bastardie F, Brooks ME, Jonsson P, Lehmann A, Dinesen GE (2020) Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance. Ecol Indic 110:1–13

MEDITS (2017) MEDITS - International Bottom Trawl Survey in the Mediterranean : Instruction Manual Version 9.

Mengual B, Cayocca F, Le Hir P, Draye R, Laffargue P, Vincent B, Garlan T (2016) Influence of bottom trawling on sediment resuspension in the 'Grande-Vasière' area (Bay of Biscay, France). Ocean Dyn 66:1181–1207

Mérillet L, Mouchet Ma, Robert M, Salaun M, Schuck L, Vaz S, Kopp D (2017) Using underwater video to assess megabenthic community vulnerability to trawling in the Grande Vasière (Bay of Biscay). Environ Conserv 45:163–172

Mermillod-blondin F, Rosenberg R, Fluviaux H, Claude U, Lyon B (2006) Ecosystem engineering : the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. Aquat Sci 68:434–442

Meysman FJR, Galaktionov OS, Gribsholt B, Middelburg JJ (2006) Bioirrigation in permeable sediments : Advective pore-water transport induced by burrow ventilation. Limnol Oceanogr 51:142–156

Millero FJ, Chen C, Bradshaw A, Schleicher K (1980) A new high pressure equation. Deep Res 27:255–264

Millot C (1990) The Gulf of Lions' hydrodynamics. Cont Shelf Res 10:885–894

Millot C, Wald L (1980) The effects of Mistral wind on the Ligurian current near Provence. Oceanol Acta 3:399–402

Ministère de l'agriculture et de l'alimentation (2017) Arrêté du 26 juillet 2017 relatif à la mise en oeuvre d'un plan de sortie de flotte pour les navires de 6 à 18 mètres pêchant la langoustine au moyen d'un chalut en zone GSA8 en Méditerranée. J Off la République Française

Ministère de l'agriculture et de l'alimentation (2018) Arrêté du 23 avril 2018 portant création de zones de pêche à accès réglementé dans le Golfe du Lion (GSA 7). J Off la République Française

Ministère de l'agriculture et de l'alimentation (2019) Arrêté du 20 décembre 2019 portant modification de l'arrêté du 28 février 2013 portant adoption d'un plan de gestion pour la pêche professionnelle au chalut en mer Méditerranée par les navires battant pavillon français. J Off la République Française

Ministère de l'écologie du développement durable et de l'énergie (2010) Arrêté du 15 juillet 2010 réglementant l'usage et les caractéristiques de la drague pour la pêche des coquilles Saint-Jacques dans les eaux françaises des zones CIEM IV, VII et VIII. J Off la République Française

Ministère de l'écologie du développement durable et de l'énergie (2013a) Arrêté du 12 avril 2013 portant modification de certaines dispositions applicables à la pêche professionnelle à la drague en Méditerranée par les navires battant pavillon français. J Off la République Française

Ministère de l'écologie du développement durable et de l'énergie (2013b) Arrêté du 2 avril 2013 relatif à la mise en oeuvre d'un plan de sortie de flotte pour les navires pêchant au chalut en Méditerranée. J Off la République Française

Ministère de l'écologie du développement durable et de l'énergie (2013c) Arrêté du 28 février 2013 portant adoption d'un plan de gestion pour la pêche pofessionnelle au chalut en mer Méditerranée par les navires battant pavillon français. J Off la République Française

Ministère de la transition écologique et solidaire (2019) Arrêté du 9 septembre 2019 relatif à la définition du bon état écologique des eaux marines et aux normes méthodologiques d'évaluation. J Off la République Française

Montevecchi WA (2001) Interactions between fisheries and seabirds. In: Schreiber E.A., Burger J. (eds) Biology of Marine Birds. CRC Press, Washington DC, pp 527–558

Morris AW, Howarth MJ (1998) Bed stress induced sediment resuspension (SERE 88/89). Cont Shelf Res 18:1203–1213

Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013a) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–177

Mouillot D, Villeger S, Parravicini V, Kulbicki M, Arias-Gonzalez JE, Bender M, Chabanet P, Floeter SR, Friedlander A, Vigliola L, Bellwood DR (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc Natl Acad Sci 111:13757–13762

Mouillot, Graham, Villéger, Mason, Bellwood (2013b) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–177

Muggeo V (2019) Package "segmented". https://cran.r-project.org/web/packages/segmented/.

Muntadas A, De Juan S, Demestre M (2016) Assessing functional redundancy in chronically trawled benthic communities. Ecol Indic 61:882–892

Nair KKC, Anger K (1979) Experimental studies on the life cycle of Jassa falcata (Crustacea, Amphipoda). Helgoländer wiss Meeresunters 32:444–452

Neckles HA, Short FT, Barker S, Kopp BS (2005) Disturbance of eelgrass Zostera marina by commercial mussel Mytilus edulis harvesting in Maine: Dragging impacts and habitat recovery. Mar Ecol Prog Ser 285:57–73

Nilsson HC, Rosenberg R (1994) Hypoxic response of two marine benthic communities. Mar Ecol Prog Ser 115:209–218

Nilsson P, Ziegler F (2007) Spatial distribution of fishing effort in relation to seafloor habitats in the Kattegat, a GIS analysis. Ann Zool Fennici 17:421–440

Normant M, Lamprecht I (2006) Does scope for growth change as a result of salinity stress in the amphipod Gammarus oceanicus? J Exp Mar Bio Ecol 334:158–163

Ocaña FA, Pech, Daniel, Simões N, Hernandez-Avila I (2019) Spatial assessment of the vulnerability of benthic communities to multiple stressors in the Yucatan Continental Shelf, Gulf of Mexico. Ocean Coast Manag 181:1–9

OCEANA (2016) Developing a list of Vulnerable Marine Ecosystems. 4

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHM, Wagner H (2019) Package "vegan": Community ecology package. http://vegan.r-forge.r-project.org/

Olsgard F, Schaanning MT, Widdicombe S, Kendall MA, Austen MC (2008) Effects of bottom trawling on ecosystem functioning. J Exp Mar Bio Ecol 366:123–133

Osman RW, Whitlatch RB (1998) Local control of recruitment in an epifaunal community and the consequences to colonization processes. Hydrobiologia 375–376:113–123

OSPAR (2008) List of threatened and/or declining species and habitats.

OSPAR (2012) MSFD Advice Manual on Biodiversity Approaches to determining good environmental status , setting of environmental targets and selecting indicators.

OSPAR Commission (2017) Intermediate assessment 2017: Extent of physical damage to predominant and sepcial habitats.

Palanques A, Guillén J, Puig P (2001) Impact of bottom trawling on water turbidity and muddy sediment of an unfished continental shelf. Limnol Oceanogr 46:1100–1110

Palanques A, Puig P, Guillén J, Demestre M, Martín J (2014) Effects of bottom trawling on the Ebro continental shelf sedimentary system (NW Mediterranean). Cont Shelf Res 72:83–98

Paschen M, Ritcher U, Köpnick W (2000) TRAPESE - trawl penetration in the seabed. Final report EI Contract 96-006.

Pasqualini V, Pergent-Martini C, Clabaut P, Pergent G (1998) Mapping of Posidonia oceanica using aerial photographs and side scan sonar: Application off the Island of Corsica (France). Estuar Coast Shelf Sci 47:359–367

Pearl J (2014) Comment: Understanding Simpson's paradox. Am Stat 68:8–13

Pedel L, Fabri M-C, Menot L, Van den Beld I (2013) Mesure de l'état écologique des habitats benthiques du domaine bathyal à partir d'imagerie optique.

Peet RK (1974) The Measurement of Species Diversity. Annu Rev Ecol Syst 5:285–307

Pelletier D, Leleu K, Mallet D, Mou-Tham G, Hervé G, Boureau M, Guilpart N (2012) Remote high-definition rotating video enables fast spatial survey of marine underwater macrofauna and habitats. PLoS One 7:1–13

Phillips NE (2005) Growth of filter-feeding benthic invertebrates from a region with variable upwelling intensity. Mar Ecol Prog Ser 295:79–89

Pianka E (1970) On r- and K-Selection. Am Nat 104:592–597

Picard J (1965) Recherches qualitatives sur les biocénoses marines des substrats meubles dragables de la région marseillaise. Rech Trav Stn Mar Endoume 31:5–137

Piechaud N, Hunt C, Culverhouse PF, Foster NL, Howell KL (2019) Automated identification of benthic epifauna with computer vision. Mar Ecol Prog Ser 615:15–30

Pielou E (1969) An introduction to mathematical ecology. Wiley-Iterscience, New York

Pihl L, Rosenberg R (1982) Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, Western Sweden. J Exp Mar Bio Ecol 57:273–301

Pingree RD, Griffiths DK (1980) Currents driven by a steady uniform wind stress on the shelf seas around the British Isles. Oceanol acta 3:227–236

Pipitone C, Badalamenti F, D'Anna G, Patti B (2000) Fish biomass increase after a four-year trawl ban in the Gulf of Castellammare (NW Sicily, Mediterranean Sea). Fish Res 48:23–30

Pitcher CR, Ellis N, Jennings S, Hiddink JG, Mazor T, Kaiser MJ, Kangas MI, McConnaughey RA, Parma AM, Rijnsdorp AD, Suuronen P, Collie JS, Amoroso R, Hughes KM, Hilborn R (2017) Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a simple quantitative risk assessment method applicable to data-limited fisheries. Methods Ecol Evol 8:472–480

Pommer CD, Olesen M, Jhansen ØLS (2016) Impact and distribution of bottom trawl fishing on mud-bottom communities in the Kattegat. Mar Ecol Prog Ser 548:47–60

Populus J, Vasquez M, Albrecht J, Manca E, Agnesi S, Al Hamdani Z, Andersen J, Annunziatellis A, Bekkby T, Bruschi A, Doncheva V, Drakopoulou V, Duncan G, Inghilesi R, Kyriakidou C, Lalli F, Lillis H, Mo G, Muresan M, Salomidi M, Sakellariou D, Simboura M, Teaca A, Tezcan D, Todorova V, Tunesi L (2017) EUSeaMAP : A European broad-scale seabed habitat map.

Prado J, Dremiere PY (1990) Fisherman's workbook. Fishing News Books, Oxford

Pranovi F, Giovanardi O, Franceschini G (1998) Recolonization dynamics in areas disturbed by bottom fishing gears. Hydrobiologia 375–376:125–135

Pranovi F, Raicevich S, Franceschini G, Farrace MG, Giovanardi O (2000) Rapido trawling in the northern Adriatic Sea: Effects on benthic communities in an experimental area. ICES J Mar Sci 57:517–524

Pusceddu A, Fiordelmondo C, Polymenakou P, Polychronaki T, Tselepides A, Danovaro R (2005) Effects of bottom trawling on the quantity and biochemical composition of organic matter in coastal marine sediments (Thermaikos Gulf, northwestern Aegean Sea). Cont Shelf Res 25:2491–2505

Queirós AM, Hiddink JG, Kaiser MJ, Hinz H (2006) Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. J Exp Mar Bio Ecol 335:91–103

Queirós AM, Strong JA, Mazik K, Carstensen J, Bruun J, Somerfield PJ, Bruhn A, Ciavatta S, Flo E, Bizsel N, Özaydinli M, Chuševe R, Muxika I, Nygård H, Papadopoulou N, Pantazi M, Krause-Jensen D (2016) An objective framework to test the quality of candidate indicators of good environmental status. Front Mar Sci 3:1–21

R Core Team (2017) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

R Core Team (2020) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

Rabaoui L, Lin YJ, Roa-Ureta RH, Dagoy J, Joydas T V., Borja A, Muxika I, Franco J, Al-Abdulkader K, Loughland R, Alnazry H, Qurban MA (2019) Recovery of benthic communities from small-scale shrimp trawling: Evidence from using ecological indices over a short temporal scale. Ecol Indic 99:299–309

Raffard A, Lecerf A, Cote J, Buoro M, Lassus R, Cucherousset J (2017) The functional syndrome: linking individual trait variability to ecosystem functioning. Proc R Soc B Biol Sci 284:

Rees HL (2009) Guidelines for the study of the epibenthos of subtidal environments. ICES Tech Mar Environ Sci 42:1–88

Rees HL, Pendle MA, Waldock R, Limpenny DS, Boyd SE (1999) A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas. ICES J Mar Sci 56:228–246

Reiss H, Greenstreet SPR, Sieben K, Ehrich S, Piet GJ, Quirijns F, Robinson L, Wolff WJ, Kröncke I (2009) Effects of fishing disturbance on benthic communities and secondary production within an intensively fished area. Mar Ecol Prog Ser 394:201–213

Reiss H, Kröncke I, Ehrich S (2006) Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments. ICES J Mar Sci 63:1453–1464

Reyss D (1971) Les canyons sous-marins de la mer catalane, le rech du cap et le rech lacaze-duthiers. III. Les peuplements de macrofaune benthique. Vie Milieu 12:529–613

Ribeiro Jr PJ, Diggle PJ (2018) Package "geoR". https://cran.r-project.org/web/packages/geoR/.

Rice J, Arvanitidis C, Borja A, Frid C, Hiddink JG, Krause J, Lorance P, Ragnarsson SÁ, Sköld M, Trabucco B, Enserink L, Norkko A (2012) Indicators for sea-floor integrity under the European Marine Strategy Framework Directive. Ecol Indic 12:174–184

Rice JC (2009) A generalization of the three-stage model for advice using the precautionary approach in fisheries, to apply broadly to ecosystem properties and pressures. ICES J Mar Sci 66:433–444

Rijnsdorp AD, Bastardie F, Bolam SG, Buhl-Mortensen L, Eigaard OR, Hamon KG, Hiddink JG, Hintzen NT, Ivanović A, Kenny A, Laffargue P, Nielsen JR, O'Neill FG, Piet GJ, Polet H, Sala A, Smith C, Van Denderen PD, Van Kooten T, Zengin M (2016a) Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. ICES J Mar Sci 73:i127–i138

Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, van Denderen PD, van Kooten T (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. Ecol Appl 28:1302–1312

Rijnsdorp AD, Bolam SG, Garcia C, Hintzen N, Van Denderen PD (2016b) Impact of Bottom Trawling on Sea Bed Integrity. 48:

Rijnsdorp AD, Buys AM, Storbeck F, Visser EG (1998) Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES J Mar Sci 55:403–419

Rijnsdorp AD, Van Leeuwen PI, Daan N, Heessen HJL (1996) Changes in abundance of demersal fish species in the North Sea between 1906-1909 and 1990-1995. ICES J Mar Sci 53:1054–1062

Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D (2019) MASS: support functions and datasets for venables and Ripley's MASS. R package version 7.3-51.5. Available from https://CRAN.R-project.org/package=MASS. R Top Doc

Rivetti I, Fraschetti S, Lionello P, Zambianchi E, Boero F (2014) Global warming and mass mortalities of benthic invertebrates in the Mediterranean Sea. PLoS One 9:1–12

Rivier A (2010a) Evaluation de l'action de la houle et du courant sur les fonds marins dans le cade de la réalisation de cartographie d'habitats marins.

Rivier A (2010b) North West Mediterranean modeled seabed shear stress (90th percentile). https://sextant.ifremer.fr/record/e7f839fc-ae46-4607-8892-63b5b5c5342e/.

La Rivière M, Aish A, Gauthier O, Grall J, Guérin L, Janson A-L, Labrune C, Thibaut T, Thiébaut É (2015) Méthodologie pour l'évaluation de la sensibilité des habitats benthiques aux pressions anthropiques. 1–52

Rodhe J (1998) The Baltic and North Seas: a process-oriented review of the physical oceanography. In: Robinson A.R., Brink K.H. (eds) The global coastal ocean. Cambridge, Massachusetts and London, pp 699–732

Romero-Ramirez A, Grémare A, Bernard G, Pascal L, Maire O, Duchêne J-C (2016) Development and validation of a video analysis software for marine benthic applications. J Mar Syst 162:4–17

Romero-Wetzel MB, Gerlach SA (1991) abundnace, biomass, size-distribution and bioturbation potential of deep-sea macrozoobenthos on the Voring Plateau (1200-1500m, Norwegian Sea). Meeresforschung 33:247–265

Römkens MJM, MYoung RA, Poesen JWA, MCCool DK, El-Swaify SA, Bradford JM (1997) Soil erodibility factor (K). In: Renard K.G., Foster G.R., Weesies G.A., McCool D.K., Yoder D.C. (eds) Predicting soil erosion by water: a guide to conservation planning with the revised universal soil equation (RUSLE). US Department of Agriculture, Washington DC, pp 65–99

Rooper CN, Zimmermann M (2007) A bottom-up methodology for integrating underwater video and acoustic mapping for seafloor substrate classification. Cont Shelf Res 27:947–957

Rosenberg R (1995) Benthic marine fauna structured by hydrodynamic processes and food availability. Netherlands J Sea Res 34:303–317

Rosenberg R, Grémare A, Amouroux JM, Nilsson HC (2003) Benthic habitats in the northwest Mediterranean characterised by sedimentary organics, benthic macrofauna and sediment profile images. Estuar Coast Shelf Sci 57:297–311

Roussiez V, Aloisi JC, Monaco A, Ludwig W (2005) Early muddy deposits along the Gulf of Lions shoreline: A key for a better understanding of land-to-sea transfer of sediments and associated pollutant fluxes. Mar Geol 222–223:345–358

Rumohr H (1999) Soft bottom macrofauna: Collection, treatment, and quality assurance of samples. ICES Tech Mar Environ Sci 27:1–20

Rumohr H, Kujawski T (2000) The impact of trawl fishery on the epifauna of the southern North Sea. ICES J Mar Sci 57:1389–1394

Rygg B (1985) Effect of sediment copper on benthic fauna. Mar Ecol Prog Ser 25:83–89

Salas F, Marcos C, Neto JM, Patrício J, Pérez-Ruzafa A, Marques JC (2006) User-friendly guide for using benthic ecological indicators in coastal and marine quality assessment. Ocean Coast Manag 49:308–331

Salomon J (1990) Role of instantaneous and long-term water movements on the recruitment and life of benthic fauna in the English Channel. La mer 28:211–217

Salomon JC, Breton M (1993) An atlas of long-term currents in the Channel. Oceanol Acta 16:439–448

Salzwedel H, Rachor E, Gerdes D (1985) Benthic communities in the German Bight. Veröffentlichungen des Instituts für Meeresforsch Bremerhaven 20:199–267

Sanchez P, Demestre M, Ramon M, Kaiser MJ (2000) The impact of otter trawling on mud communities in the northwestern Mediterranean. ICES J Mar Sci 57:1352–1358

Sardá R, Pinedo S, Gremare A, Taboada S (2000) Changes in the dynamics of shallow sandy-bottom assemblages due to sand extraction in the Catalan Western Mediterranean Sea. ICES J Mar Sci 57:1446–1453

Schmidt-Nielsen K (1997) Animal physiology: Adaptation and environment. Cambridge University Press, Cambridge

Schratzberger M, Dinmore TA, Jennings S (2002) Impacts of trawling on the diversity, biomass and structure of meiofauna assemblages. Mar Biol 140:83–93

Sciberras M, Hinz H, Bennell JD, Jenkins SR, Hawkins SJ, Kaiser MJ (2013) Benthic community response to a scallop dredging closure within a dynamic seabed habitat. Mar Ecol Prog Ser 480:83–98

Sciberras M, Parker R, Powell C, Robertson C, Kröger S, Bolam S, Geert Hiddink J (2016) Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments. Limnol Oceanogr 61:2076–2089

Selkoe KA, Blenckner T, Caldwell MR, Crowder LB, Erickson AL, Essington TE, Estes JA, Fujita RM, Halpern BS, Hunsicker ME, Kappel C V., Kelly RP, Kittinger JN, Levin PS, Lynham JM, Mach ME, Martone RG, Mease LA, Salomon AK, Samhouri JF, Scarborough C, Stier AC, White C, Zedler J (2015) Principles for managing marine ecosystems prone to tipping points. Ecosyst Heal Sustain 1:1–18

Shade A, Peter H, Allision SD, Baho DL, Berga M, Bürgmann H, Huber DH, Langenheder S, Lennon JT, Martiny JBH, Matulich KL, Schmidt TM, Handelsman J (2012) Fundamentals of microbial community resistance and resilience. Front Microbiol 3:1–19

Shannon CE, Weaver W (1963) The mathematical theory of communication. Univ Illinois Press 1–131

Sheehan E V., Vaz S, Pettifer E, Foster NL, Nancollas SJ, Cousens S, Holmes L, Facq JV, Germain G, Attrill MJ (2016) An experimental comparison of three towed underwater video systems using species metrics, benthic impact and performance. Methods Ecol Evol 7:843–852

Shepperson JL, Hintzen NT, Szostek CL, Bell E, Murray LG, Kaiser MJ (2018) A comparison of VMS and AIS data: The effect of data coverage and vessel position recording frequency on estimates of fishing footprints. ICES J Mar Sci 75:988–998

Shirmohammadi M, Doustshenas B, Mediseh D, Simin S, Sakhaei N (2012) Impacts of Trawling on Distribution and Diversity of Gastropods in the Persian Gulf : the Bahrakan Fishing Area. J Persian Gulf 3:37–45

SHOM (2015) MNT bathymétrique de façade.

Simboura N, Zenetos A, Panayotidis P, Makra A (1995) Changes in benthic community structure along an environmental pollution gradient. Mar Pollut Bull 30:470–474

Simpson EH (1949) Measurement of Diversity. Nature 163:688–688

Smeltz TS, Harris BP, Olson J V., Sethi SA (2019) A seascape-scale habitat model to support management of fishing impacts on benthic ecosystems. Can J Fish Aquat Sci 76:1836–1844

Smith C, Papadopoulou KN, Diliberto S (2000) Impact of otter trawling on an eastern Mediterranean commercial trawl fishing ground. ICES J Mar Sci 57:1340–1351

Smith CJ, Banks AC, Papadopoulou KN (2007) Improving the quantitative estimation of trawling impacts from sidescan-sonar and underwater-video imagery. ICES J Mar Sci 64:1692–1701

Soetaert M (2016) Laboratory study of the impact of repetitive electrical and mechanical stimulation on brown shrimp Crangon crangon. Mar Coast Fish Dyn Manag Ecosyst Sceince 8:404–411

Soetaert M, Decostere A, Polet H, Verschueren B, Chiers K (2015) Electrotrawling: A promising alternative fishing technique warranting further exploration. Fish Fish 16:104–124

Soldal AV, Engås A, Isaksen B (1993) Survival of gadoids that escape from a dermersal trawl. ICES Mar Sci Symp 196:122–127

Stergiou KI, Politou CY, Christou ED, Petrakis G (1997) Selectivity experiments in the NE Mediterranean: The effect of trawl codend mesh size on species diversity and discards. ICES J Mar Sci 54:774–786

Stirling G, Wilsey B (2001) Empirical Relationships between Species Richness, Evenness, and Proportional Diversity. Am Nat 158:286–299

Stokesbury KDE, Harris BP (2006) Impact of limited short-term sea scallop fishery on epibenthic community of Georges Bank closed areas. Mar Ecol Prog Ser 307:85–100

Strain EMA, Allcock AL, Goodwin CE, Maggs CA, Picton BE, Roberts D (2012) The long-term impacts of fisheries on epifaunal assemblage function and structure, in a Special Area of Conservation. J Sea Res 67:58–68

Sündermann J, Pohlmann T (2011) A brief analysis of North Sea physics. Oceanologia 53:663–689

Suuronen P, Chopin F, Glass C, Løkkeborg S, Matsushita Y, Queirolo D, Rihan D (2012) Low impact and fuel efficient fishing-Looking beyond the horizon. Fish Res 119–120:135–146

Svane I, Hammett Z, Lauer P (2009) Impacts of trawling on benthic macro-fauna and -flora of the Spencer Gulf prawn fishing grounds. Estuar Coast Shelf Sci 82:621–631

Tabatabaie T, Amiri F (2011) Evaluation of the impact of industrial sewage pollution on marine benthic communities. J Water Supply Res Technol - AQUA 60:364–374

Taghon GL, Greene RR (1992) Utilization of deposited and suspended particulate matter by benthic "interface" feeders. Limnol Oceanogr 37:1370–1391

Taormina B (2019) Potential impacts of submarine power cables from marine renewable energy projects on benthic communities. Université de Bretagne Occidentale

Taormina B, Bald J, Want A, Thouzeau G, Lejart M, Desroy N, Carlier A (2018) A review of potential impacts of submarine power cables on the marine environment: Knowledge gaps, recommendations and future directions. Renew Sustain Energy Rev 96:380–391

Taormina B, Marzloff MP, Desroy N, Caisey X, Dugornay O, Metral Thiesse E, Tancray A, Carlier A (2020) Optimizing image-based protocol to monitor macroepibenthic communities colonizing artificial structures. ICES J Mar Sci 77:835–845

Tardy F (2015) Caractérisation fonctionnelle des stratégies de compétition pour les ressources aériennes et souterraines au sein d'une gamme d'espèces végétales: application à la régulation biologique des adventices par les plantes de services dans l'agrosystème bananie. Université de Montpellier

Teixeira H, Salas F, Neto JM, Patrício J, Pinto R, Veríssimo H, García-Charton JA, Marcos C, Pérez-Ruzafa A, Marques JC (2008) Ecological indices tracking distinct impacts along disturbance-recovery gradients in a temperate NE Atlantic Estuary - Guidance on reference values. Estuar Coast Shelf Sci 80:130–140

Tesi T, Miserocchi S, Goñi MA, Langone L (2007) Source, transport and fate of terrestrial organic carbon on the western Mediterranean Sea, Gulf of Lions, France. Mar Chem 105:101–117

Tett P, Gowen R, Mills D, Fernandes T, Gilpin L, Huxham M, Kennington K, Read P, Service M, Wilkinson M, Malcolm S (2007) Defining and detecting undesirable disturbance in the contaxt of marine eutrophication. Mar Pollut Bull 55:282–297

Thistle D (1981) Natural Physical Disturbances and Communities of Marine Soft Bottoms. Mar Ecol Prog Ser 6:223–228

Thrush SF, Dayton PK (2002) Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. Annu Rev Ecol Syst 33:449–473

Thrush SF, Hewitt JE, Cummings VJ, Dayton PK, Cryer M, Turner SJ, Funnell GA, Budd RG, Milburn CJ, Wilkinson MR (1998) Disturbance of the marine benthic habitat by commercial fishing: Impacts at the scale of the fishery. Ecol Appl 8:866–879

Thurstan RH, Brockington S, Roberts CM (2010) The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nat Commun 1:1–6

Tiano JC, Witbaard R, Bergman MJN, Van Rijswijk P, Tramper A, Van Oevelen D, Soetaert K, Degraer S (2019) Acute impacts of bottom trawl gears on benthic metabolism and nutrient cycling. ICES J Mar Sci 76:1917–1930

Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Mar Ecol Prog Ser 318:31–45

Tillin HM, Hull S, Tyler-Walters H (2010) Development of a sensitivity matrix (pressures-MCZ/MPA features).

Tillin HM, Tyler-Walters H (2013) Assessing the sensitivity of subtidal sedimentary habitats to pressures associated with marine activities. Phase 1 Report: Rationale and proposed ecological groupings for Level 5 biotopes against which sensitivity assessments would be best undertaken.

Törnroos A, Bonsdorff E (2012) Developing the multitrait concept for functional diversity: Lessons from a system rich in functions but poor in species. Ecol Appl 22:2221–2236

Trenkel VM, Vaz S, Albouy C, Amour AB, Duhamel E, Laffargue P, Romagnan JB, Simon J, Lorance P (2019) We can reduce the impact of scientific trawling on marine ecosystems. Mar Ecol Prog Ser 609:277–282

Trimmer M, Petersen J, Sivyer DB, Mills C, Young E, Parker ER (2005) Impact of long-term benthic trawl disturbance on sediment sorting and biogeochemistry in the southern North Sea. Mar Ecol Prog Ser 298:79–94

Tuck ID, Hall SJ, Robertson MR, Armstrong E, Basford DJ (1998) Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. Mar Ecol Prog Ser 162:227–242

Tumbiolo ML, Downing JA, Tumbiolo ML, Downing JA, Nazionale C, Vaccara VL (1994) An empirical model for the secondary production in marine benthic invertebrate populations. Mar Ecol Prog Ser 114:165–174

Unknow (2016) Guidance for assessments under article 8 of the Marine Strategy Framework directive - Part 1 : Intergration of assessements results.

Valdemarsen JW, Jorgensen T, Engas A (2007) Options to mitigate bottom habitat impact of dragged gears. FAO Fish Tech Pap 506:29p

Vaslet D, Larsonneur C, Auffret J-P (1979) Les sédiments superficiles de la Manche 1/500 000.

Vaz S (2016) VIDEO GALION. https://doi.org/10.17600/16001100.

Vaz S (2017) VIDEO GALION. https://doi.org/10.17600/17013500.

Vaz S (2018a) EPIBENGOL. https://doi.org/10.17600/18000589.

Vaz S (2018b) IDEM VIDEO. https://doi.org/10.17600/18000654.

Vaz S, Auber A, Coppin F, Desroy N, Foveau A, Goascoz N, Lazard C, Le Roy D, Martin J, Quinquis J, Rouquette M, Travers-Trolet M, Verin Y (2019) Benthic invertebrates' by-catches in Ifremer bottom trawl surveys in the English Channel and southern Notrh Sea: 2006-2018.

Vaz S, Llpasset M (2016) Mediterranean process-driven seafloor habitat sensitivity in French waters. https://sextant.ifremer.fr/Donnees/Catalogue#/metadata/e377df42-6436-4b63-ae9b-730a49d7de47

Vaz S, Llpasset M (2020) Modelled seabed sediment average grain size in French Mediterranean waters. https://sextant.ifremer.fr/record/5b62e0c9-05ab-4b86-bd04-282fec733f87/.

Veale LO, Hill AS, Hawkins SJ, Brand AR (2000) Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats. Mar Biol 137:325–337

van Veen J (1933) Onderzoek naar het zandtransport von rivieren. Ing 48:151–159

Verin Y, Travers-Trolet M (2014) CAMANOC cruise. https://doi.org/10.17600/14001900.

Villéger S, Mason H, Mouillot D (2008) New multidimensional functional diversity indices for a multifacted framework in functional ecology. Ecology 89:2290–2301

Villéger S, Ramos Miranda J, Flores Hernández D, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol Appl 20:1512–1522

La Violette PE (1994) Overview of the major forcings and water masses of the Western Mediterranean Sea. Seasonal and interannual variability of the Western Mediterranean Sea. AGU, Whashington D.C., pp 1–11

Wallace S, Turris B, Driscoll J, Bodtker K, Mose B, Munro G (2015) Canada's pacific groundfish trawl habitat agreement: A global first in an ecosystem approach to bottom trawl impacts. Mar Policy 60:240–248

Walton MEM, Hayes J, Al-Ansi M, Abdallah M, Al Maslamani I, Al-Mohannadi M, Al-Shaikh I, D'Urban Jackson T, Szostek C, Egerton J, Kaiser MJ, Le Vay L (2018) Towards spatial management of fisheries in the Gulf: Benthic diversity, habitat and fish distributions from Qatari waters. ICES J Mar Sci 75:178–189

Warner GF (1982) Food and feeding mechanisms: Ophiuroidea. In: Jangoux M., Lawrence J.M. (eds) Echinodern nutrition. A.A. Ballkema, Rotterdam, pp 199–210

Warnken KW, Gill GA, Dellapenna TM, Lehman RD, Harper DE, Allison MA (2003) The effects of shrimp trawling on sediment oxygen consumption and the fluxes of trace metals and nutrients from estuarine sediments. Estuar Coast Shelf Sci 57:25–42

Warwick R, Uncles R (1980) Distribution of benthic macrofauna associations in the Bristol Channel in relation to tidal stress. Mar Ecol Prog Ser 3:97–103

Watling L, Norse EA (1998) Disturbance of the seabed by mobile fishing gear : A comparison to forest clearcutting. Conserv Biol 12:1180–1197

Watson DL, Harvey ES, Fitzpatrick BM, Langlois TJ, Shedrawi G (2010) Assessing reef fish assemblage structure: How do different stereo-video techniques compare? Mar Biol 157:1237–1250

Witbaard R (1996) Growth variations in Artica islandica L. (Mollusca): a reflection of hydrography-related food supply. ICES J Mar Sci 53:981–987 van den Wollenberg A (1977) Redundancy analysis. An alternative for canonical correlation analysis. Psychometrika 42:207–219

Yin P, Fan X (2001) Estimating r2 shrinkage in multiple regression: A comparison of different analytical methods. J Exp Educ 69:203–224

Appendix A. Correlation between indices

Table A.1: Spearman correlations between tested indices

Biom = Community Biomass. SR = Species richness. H' = Shannon index, S'= Pielou index. λ = Simpson index. * indicates that p<0.05; ** indicates that p<0.01; *** indicates that p<0.001. Grey shading indicates best correlations

	Biom	SR	Margalef index	H'	S'	λ	FRic	FDiv	FEve	FSpe	AMBI	TDI	mTDI	pTDI	mT	Abrasion
Biom	1	0.45***	0.46***	-0.06***	-0.40***	-0.11***	0.25***	-0.03	-0.23***	-0.05**	0.05**	0.03	0.09***	0.03	0.15***	0.09
SR		1	1***	0.59***	0.07***	0.47***	0.70***	-0.11***	-0.04	-0.06*	0.04	0.32***	0.30***	0.36***	0.26***	0.16
Margalef index			1	0.58***	0.07***	0.47***	0.71***	-0.11***	-0.03	-0.06*	0.03	0.33***	0.31***	0.37***	0.26***	0.16
H'				1	0.79***	0.97***	0.38***	-0.03	0.19***	0.03	-0.08**	0.33***	0.25***	0.35***	0.13***	0.14
S'					1	0.86***	0.09***	0.01	0.27***	0.07***	-0.10***	0.24***	0.14***	0.24***	0.02	0.07
λ						1	0.31***	-0.04	0.17***	0.04	-0.08**	0.28**	0.20***	0.29***	0.08***	0.13
FRic							1	-0.01	0.04	0.25***	0.01	0.27**	0.25***	0.34***	0.22***	-0.02
FDiv								1	0.26***	0.75***	-0.13***	0.03	0	0.07*	-0.04	-0.16
FEve									1	0.21***	-0.07**	0.16***	0.13***	0.21***	0.08**	-0.07
FSpe										1	-0.24***	-0.04	-0.08***	0.02	-0.12***	-0.13
AMBI											1	-0.05	0	-0.07**	0.05*	-0.15
TDI												1	0.96***	0.96***	0.84***	-0.30
mTDI													1	0.91***	0.93***	-0.27
pTDI														1	0.78***	-0.27
mT															1	-0.24

Appendix B. Correlation between indices calculated using abundance and scaled abundance

1. Taxonomic diversity indices

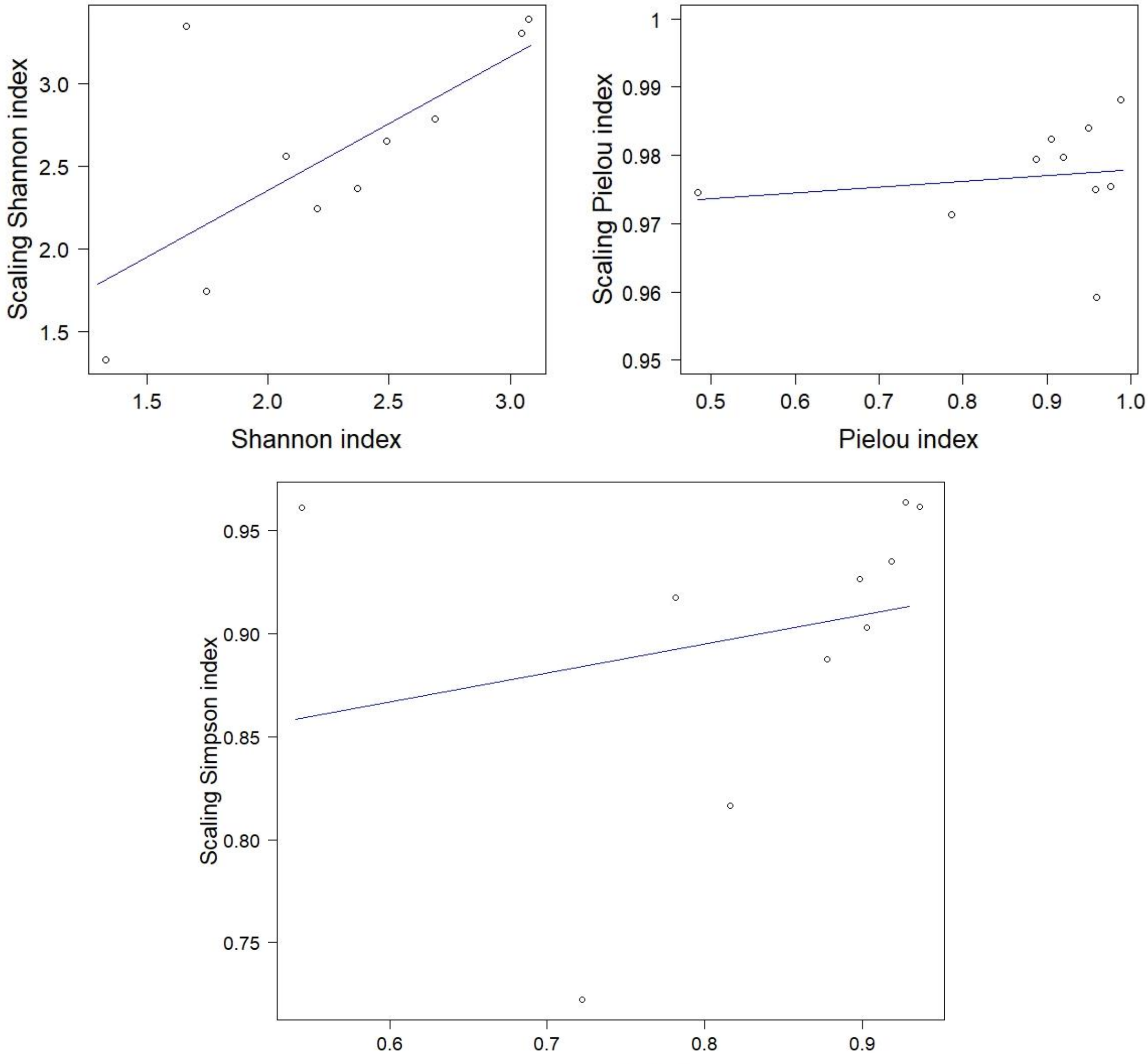


Figure B.1: Relationship between taxonomic diversity index calculated with abundance data and scaled abundance data in the Gulf of Lion

2. Functional diversity indices

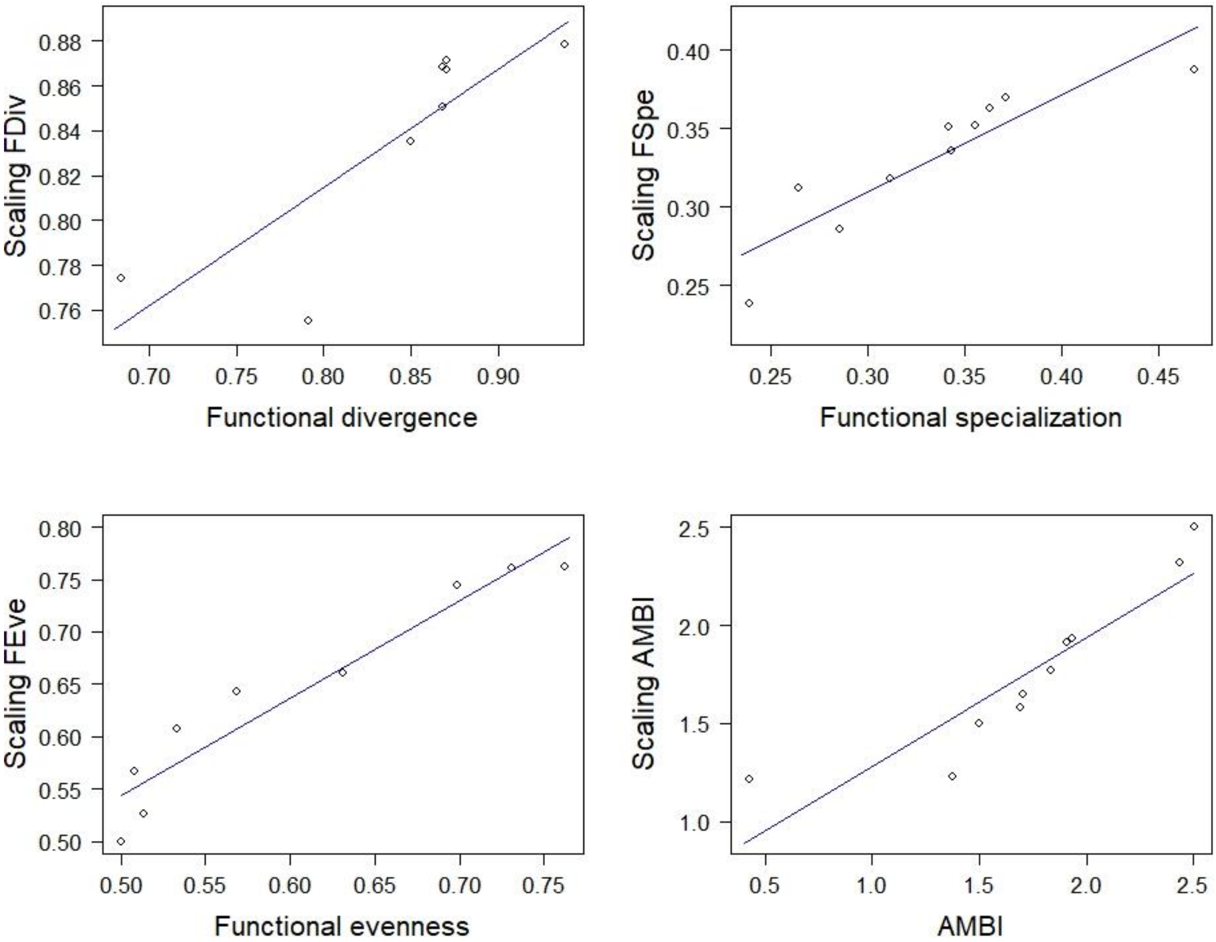


Figure B.61: Relationship between functional diversity index calculated with abundance data and scaled abundance data in the Gulf of Lion

3. Functional sensitivity indices

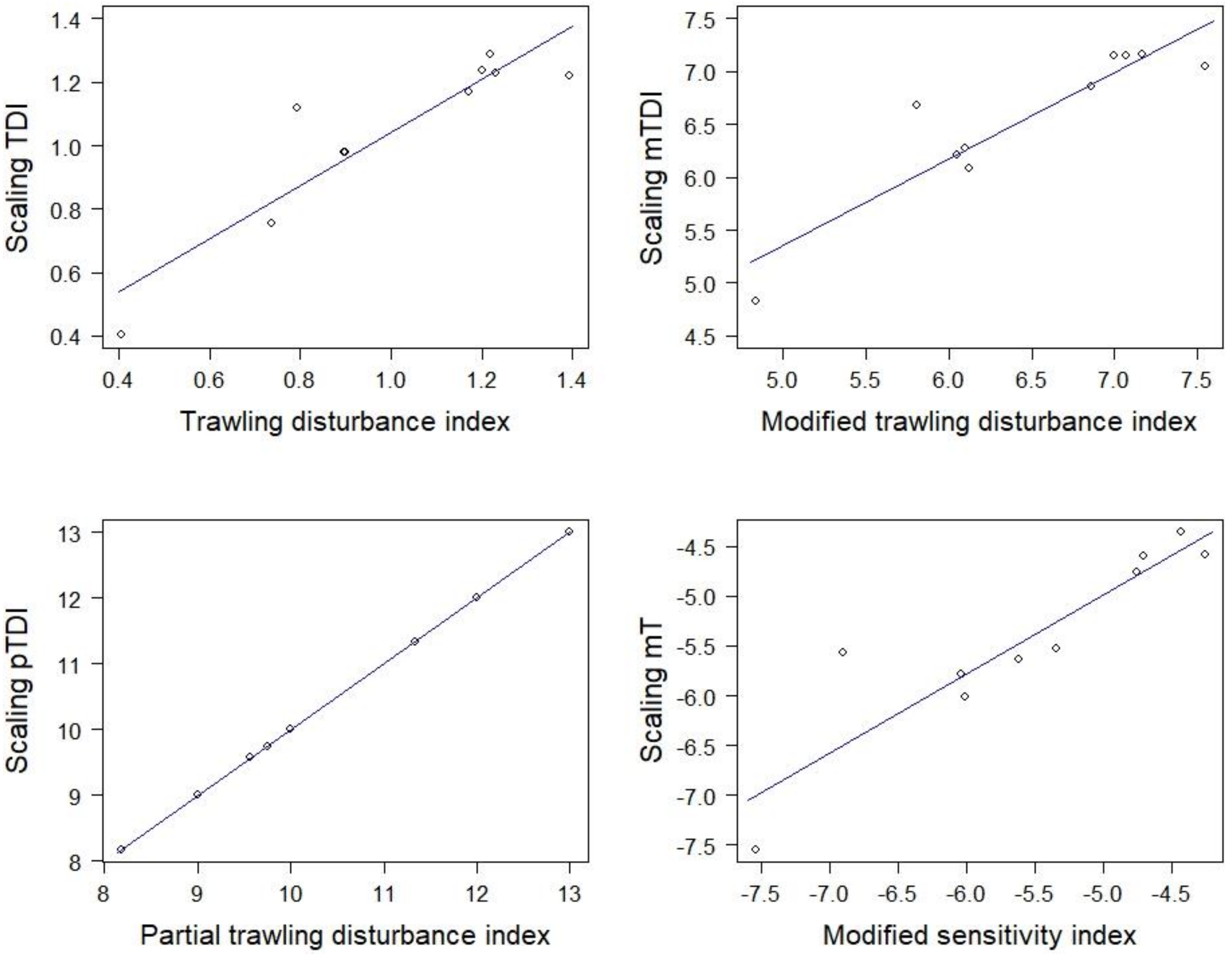


Figure B.62: Relationship between functional sensitivity index calculated with abundance data and scaled abundance data in the Gulf of Lion

Appendix C. Sampled surface

Table C.1: Sampled surface by the two observations methods in the Gulf of Lion and the English Channel.

The three abrasion values represent the minimum value, the mean and the maximum value.

	Video		Trawl	
	Gulf of Lion	English Channel	Gulf of Lion	English Channel
Sampled surface (in km^2)	0.004 - 0.012 - 0.018	0.005 - 0.012 - 0.020	0.204 - 0.239 - 0.265	0.162 - 0.226 - 0.254

Appendix D. Details on habitat sampled

Table D.1: Number of MEDITS' observations in each habitat and corresponding abrasion ranges.
The three abrasion values represent the minimum value, the median and the maximum value in the Gulf of Lion (GoL) and eastern Corsica. Grey shading indicates habitats sufficiently covered by the available observation (more than 40 observations). A5.46 and A5.47 in GoL and Corsica had to be merged.

Habitats	Areas	Number of observations	Number of un-trawled stations	Abrasion range ($SAR.y^{-1}$)	Sampled abrasion range ($SAR.y^{-1}$)
A5.38	GoL	49	0	0 – 10.79 – 38.18	2.70 – 17.22 – 29.15
A5.39		129	0	0 – 5.59 – 29.66	2.06 – 5.25 – 13.79
A5.46		24	0	0 – 4.02 – 28.49	0.20 – 3.81 – 20.77
A5.47		170	0	8×10^{-4} – 3.49 – 20.22	0.08 – 3.64 – 11.07
A5.46	Corsica	56	9	0 – 0.34 – 5.74	0 – 0.11 – 2.03
A5.47		12	0	0 – 0.15 – 3.46	0.08 – 0.75 – 2.03

Table D.2: Number of IBTS' observations in each North Sea habitat and corresponding abrasion ranges.
The three abrasion values represent the minimum value, the median and the maximum value. Grey shading indicates habitats sufficiently covered by the available observation (more than 40 observations)

Habitats	Number of observations	Number of un-trawled stations	Abrasion range ($SAR.y^{-1}$)	Sampled abrasion range ($SAR.y^{-1}$)
A5.13	7	0	0 – 1.91 – 8.42	1.59 – 1.98 – 2.14
A5.14	15	0	0 – 0.62 – 31.53	0.0001 – 1.06 – 7.64
A5.15	108	11	0 – 1.15 – 32.70	0 – 3.43 – 16.51
A5.25/26	121	0	0 – 1.61 – 51.27	0.11 – 2.02 – 11.14
A5.27	226	10	0 – 0.98 – 62.76	0 – 1.17 – 16.15
A5.37	84	0	0.004 – 1.30 – 26.47	0.60 – 1.74 – 13.41
A5.44	1	0	0 – 0.15 – 5.45	0.007
A5.45	3	0	0.002 – 0.95 – 18.24	6.94 – 7.08 – 7.08

Table D.3: Number of observations in each English Channel habitat and corresponding abrasion ranges for the two sampling season. The three abrasion values represent minimum, median and maximum value. Grey shading indicates habitats with a good representativeness in the sampling (more than 40 observations)

Habitats	Season	Number of observations	Number of un-trawled stations	Abrasion range ($SAR.y^{-1}$)	Sampled abrasion range ($SAR.y^{-1}$)
A4.1	Autumn	9	0	0 – 0.14 – 5.16	0.98 – 1.06 – 1.06
A4.2		2	0	0 – 0.17 – 6.20	0.30 – 0.75 – 1.20
A5.13		2	0	0 – 1.09 – 25.21	5.47 – 6.22 – 6.97
A5.14		264	3	0 – 0.86 – 36.72	0 – 4.60 – 29.58
A5.15		495	0	0 – 3.40 – 78.71	0.03 – 14.00 – 74.15
A5.23/24		29	0	0.04 – 2.69 – 22.58	0.65 – 6.21 – 14.10
A5.25/26		140	0	0 – 1.51 – 33.40	0.03 – 3.75 – 21.42
A5.27		42	0	0.05 – 2.98 – 35.67	1.29 – 11.98 – 26.14
A5.33		3	0	0.008 – 1.81 – 16.40	9.29
A5.35		4	0	6×10^{-4} – 0.21 – 116	1.16 – 6.46 – 9.29
A5.37		11	0	0.76 – 1.71 – 16.88	2.61 – 2.61 – 5.91
A5.45		5	0	0 – 3.55 – 18.46	2.50 – 2.90 – 8.85
A4.2	Winter	1	0	0 – 0.17 – 6.20	1.20
A5.13		1	0	0 – 1.09 – 25.21	6.97
A5.14		60	1	0 – 0.86 – 36.72	0 – 5.29 – 29.58
A5.15		71	0	0 – 3.40 – 78.71	1.55 – 10.41 – 72.34
A5.25/26		10	0	0 – 1.51 – 32.09	0.46 – 1.16 – 8.52
A5.27		5	0	0.05 – 2.98 – 35.67	9.41 – 18.83 – 26.14
A5.37		3	0	0.76 – 1.71 – 16.88	2.61

Appendix E. Details on selected models in each studied areas

1. Mediterranean Sea

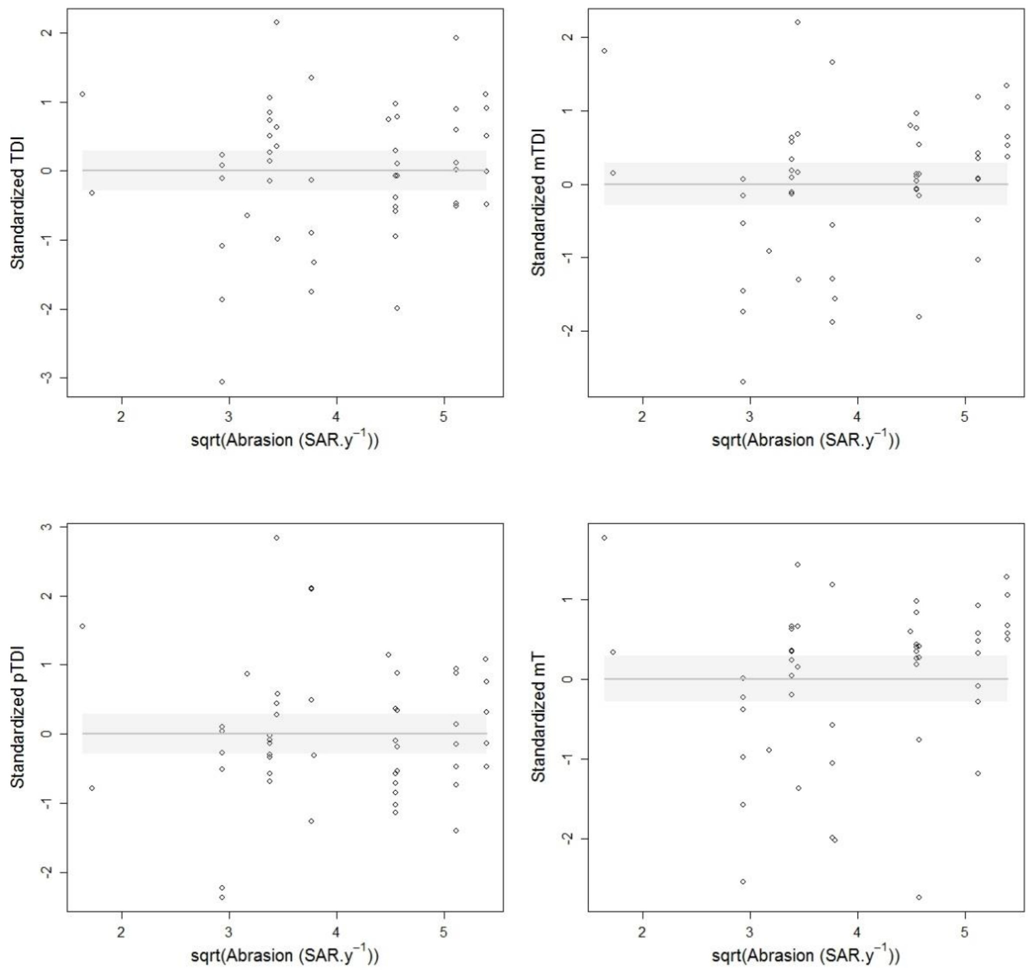


Figure E.1: Indices modelled relationships to fishery abrasion in habitat A5.38: Mediterranean communities of muddy detritic bottoms. Null models (grey lines and 95% confidence interval in grey shading) were the only fitting models for all indices. No negative significant relationship and no thresholds could be detected.

Table E.1: Summary of the modelling results in the habitat A5.38
Grey shading indicates the index and the model selected for this habitat

Indices	Models	Slope	AdjR²	RMAE
TDI	Null	-	0	0.14
	Neglinear	0.13	-	-
mTDI	Null	-	0	0.15
	Neglinear	0.18	0.01	-
pTDI	Null	-	0	0.14
	Neglinear	0.02	-	-
mT	Null	-	0	0.17
	Neglinear	0.18	0.01	-

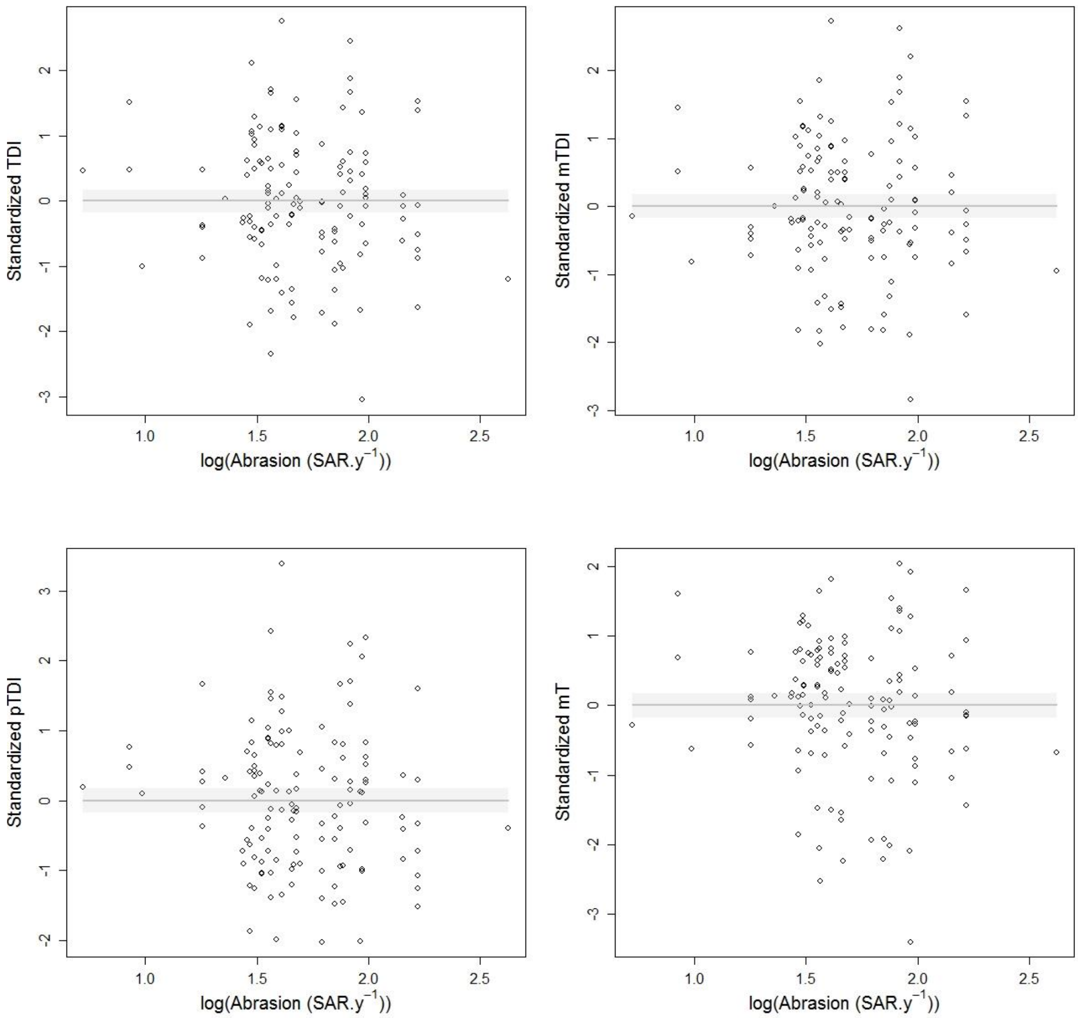


Figure E.2: Indices modelled relationships to fishery abrasion in habitat A5.39: Mediterranean communities of coastal terrigenous muds. Null models (grey lines and 95% confidence interval in grey shading) were the only fitting models for all indices. No negative significant relationship and no thresholds could be detected.

Table E.2: Summary of the modelling results in the habitat A5.39

Grey shading indicates the index and the model selected for this habitat

Indices	Models	Slope	AdjR²	RMAE
TDI	Null	-	0	0.13
	Neglinear	-0.35	2.10^{-3}	-
mTDI	Null	-	0	0.14
	Neglinear	-0.18	-	-
pTDI	Null	-	0	0.15
	Neglinear	-0.30	-	-
mT	Null	-	0	0.14
	Neglinear	-0.42	0.01	-

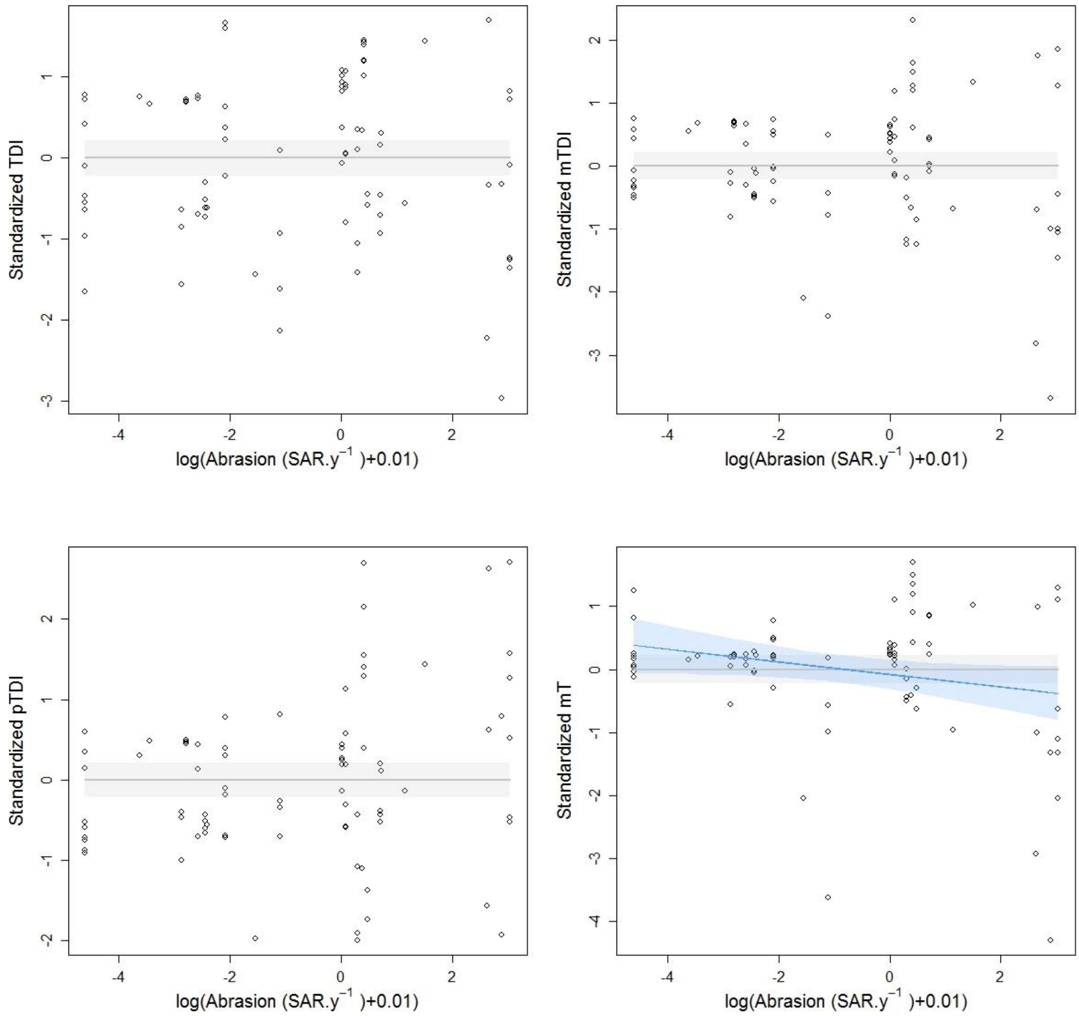


Figure E.3: Indices modelled relationships to fishery abrasion in habitat A5.46: Mediterranean communities of coastal detritic bottoms. Null models (grey lines and 95% confidence interval in grey shading) were the only fitting models for TDI, mTDI and pTDI but neglinear model (blue line and 95% confidence interval in blue shading) was more suited for mT index. No significant thresholds could be detected.

Table E.3: Summary of the modelling results in the habitat A5.46

Grey shading indicates the index and the model selected for this habitat.
* indicates that p<0.05 ; ** indicates that p<0.01

Indices	Models	Slope	AdjR²	RMAE
TDI	Null	-	0	-
	Neglinear	-0.02	-	-
mTDI	Null	-	0	-
	Neglinear	-0.05	-	-
pTDI	Null	-	0	-
	Neglinear	0.10*	0.04	-
mT	Null	-	0	-
	Neglinear	- 0.10*	0.04	0.11

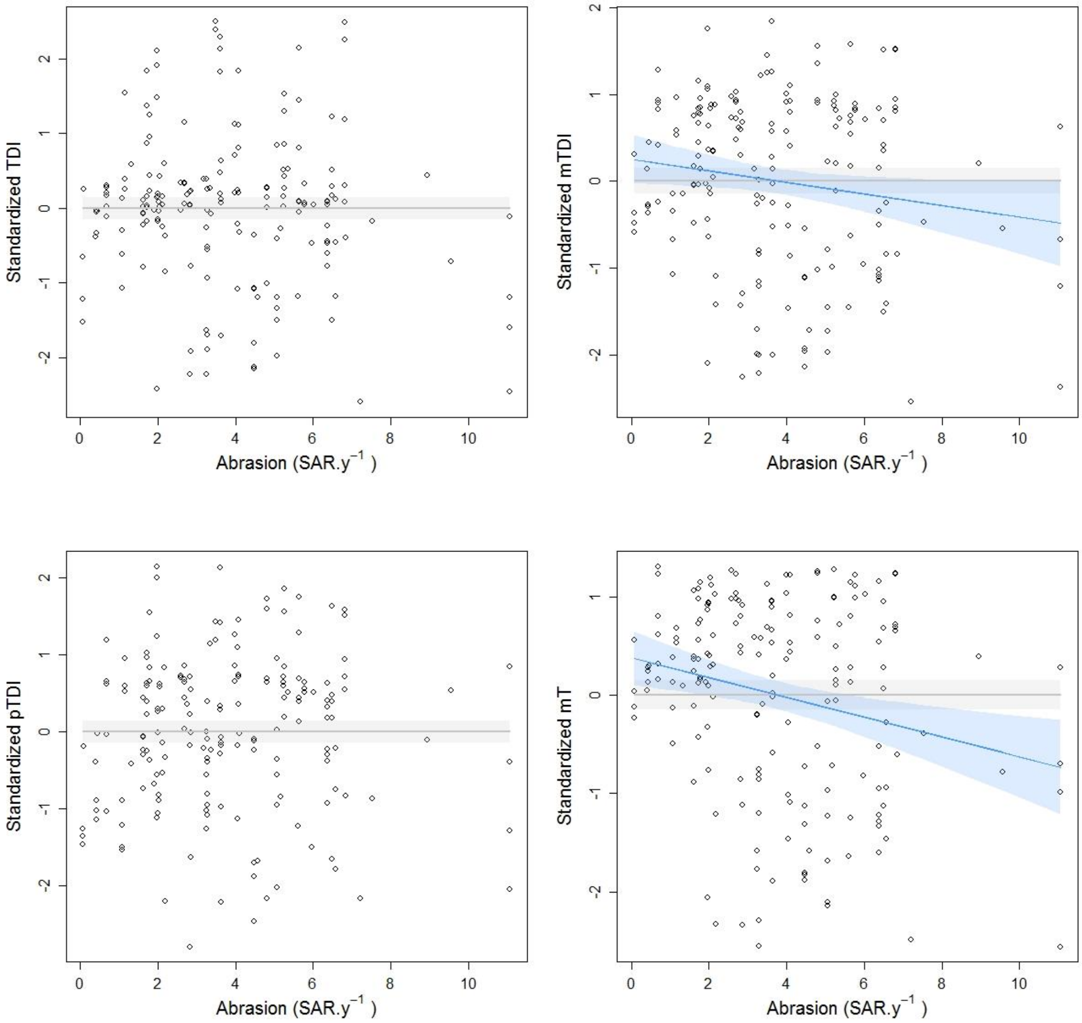


Figure E.4: Indices modelled relationships to fishery abrasion in habitat A5.47: Mediterranean communities of coastal detritic bottoms. Null models (grey lines and 95% confidence interval in grey shading) were the only fitting models for TDI and pTDI but neglinear models (blue lines and 95% confidence interval in blue shading) were more suited for mTDI and mT index. No significant thresholds could be detected.

Table E.4: Summary of the modelling results in the habitat A5.47

Grey shading indicates the index and the model selected for this habitat.
* indicates that p<0.05; ** indicates that p<0.01

Indices	Models	Slope	AdjR²	RMAE
TDI	Null	-	0	-
	Neglinear	-0.05	7.10^{-3}	-
mTDI	Null	-	0	-
	Neglinear	-0.09**	0.04	0.19
pTDI	Null	-	0	-
	Neglinear	0.01	-	-
mT	Null	-	0	-
	Neglinear	- 0.10**	0.05	0.21

2. North Sea

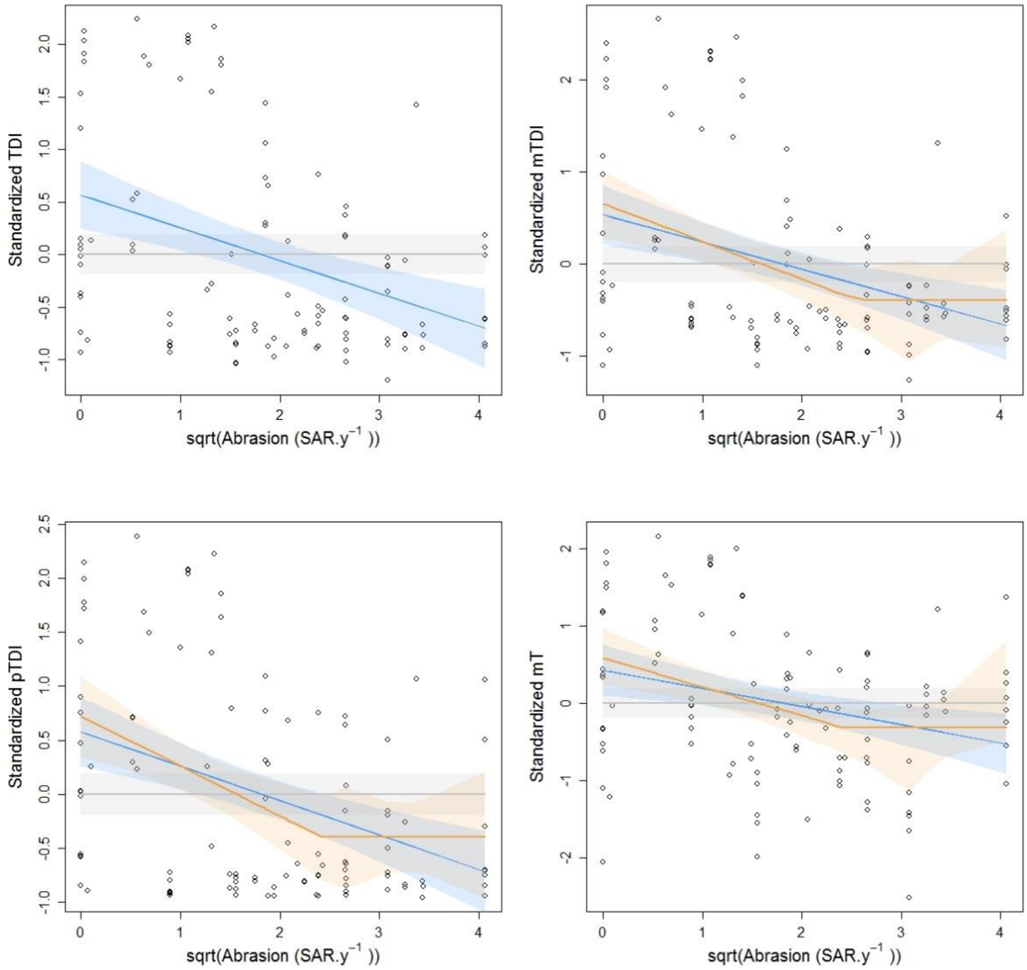


Figure E.5: Indices modelled relationships to fishery abrasion in habitat A5.15: Deep circalittoral coarse sediment. Null models (grey lines and 95% confidence interval in grey shading) and neglinear models (blue lines and 95% confidence interval in blue shading) fitted for all indices but segmented2 (orange lines and 95% confidence interval in orange shading) model was more suited for mTDI, pTDI and mT.

Table E.5: Summary of the modelling results in the habitat A5.15

Grey shading indicates the index and the model selected for this habitat. * indicates that p<0.05; ** indicates that p<0.01 ; *** indicates that p<0.001

Indices	Models	Slope	Threshold 1	Threshold 2	AdjR²	RMAE
TDI	Null	-	-	-	0	-
	Neglinear	-0.31***	-	-	0.14	-
mTDI	Null	-	-	-	0	-
	Neglinear	-0.29***	-	-	0.12	-
	Segment2	-0.41**	-	6.52**	0.13	-
pTDI	Null	-	-	-	0	-
	Neglinear	-0.32***	-	-	0.14	-
	Segment2	-0.46**	-	5.91**	0.15	-
mT	Null	-	-	-	0	-
	Neglinear	-0.23*	-	-	0.07	-
	Segment2	-0.37*	-	5.90*	0.09	0.16

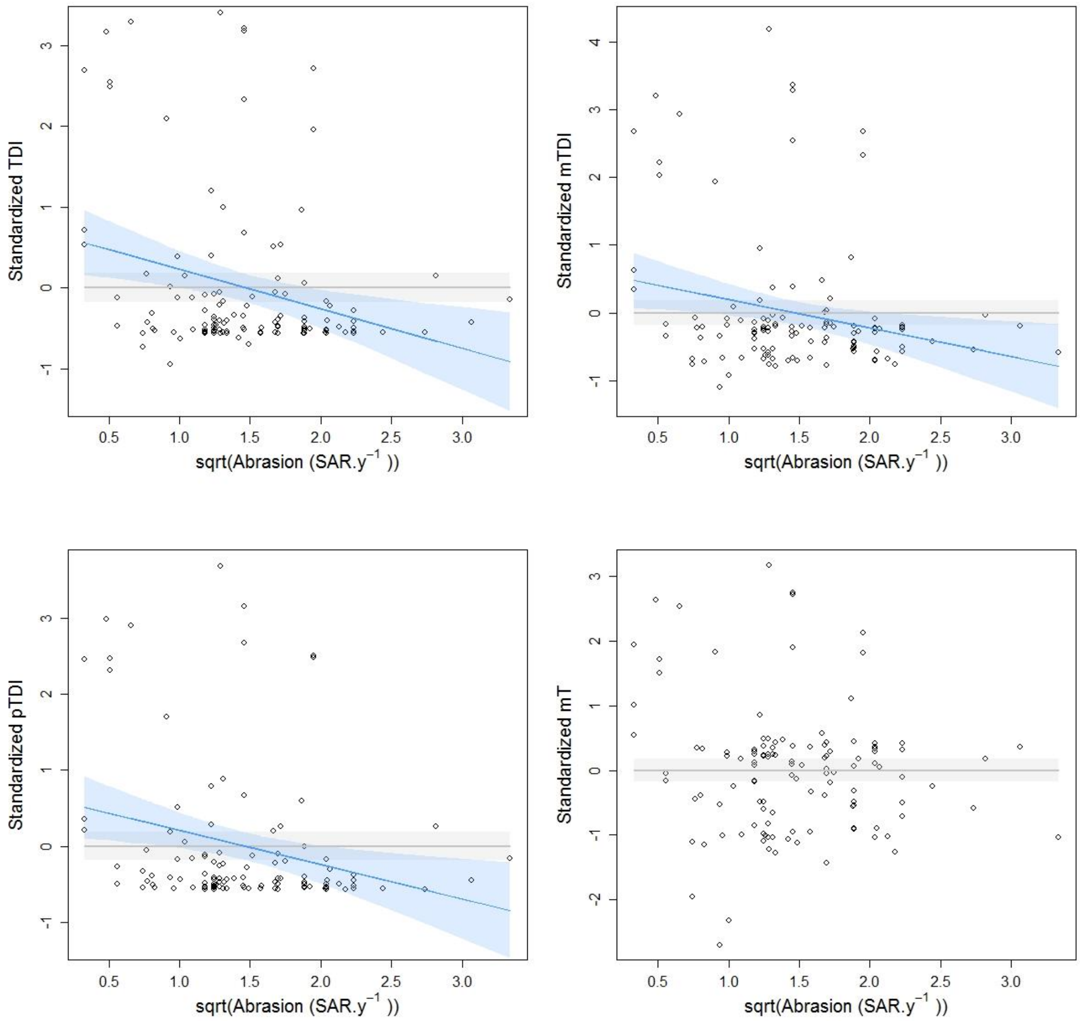


Figure E.6: Indices modelled relationships to fishery abrasion in habitat A5.25/26: Circalittoral fine sand/muddy sand. Null model (grey lines and 95% confidence interval in grey shading) was the only fitting model for mT but neglinear models (blue lines and 95% confidence interval in blue shading) were more suited for TDI, mTDI and pTDI. No significant thresholds could be detected.

Table E.6: Summary of the modelling results in the habitat A5.25/26

Grey shading indicates the index and the model selected for this habitat.
* indicates that p<0.05 ; ** indicates that p<0.01 ; *** indicates that p<0.001

Indices	Models	Slope	AdjR²	RMAE
TDI	Null	-	0	-
	Neglinear	-0.49**	0.07	0.15
mTDI	Null	-	0	-
	Neglinear	-0.42*	0.05	-
pTDI	Null	-	0	-
	Neglinear	-0.45**	0.06	0.15
mT	Null	-	0	-
	Neglinear	- 0.24	0.01	-

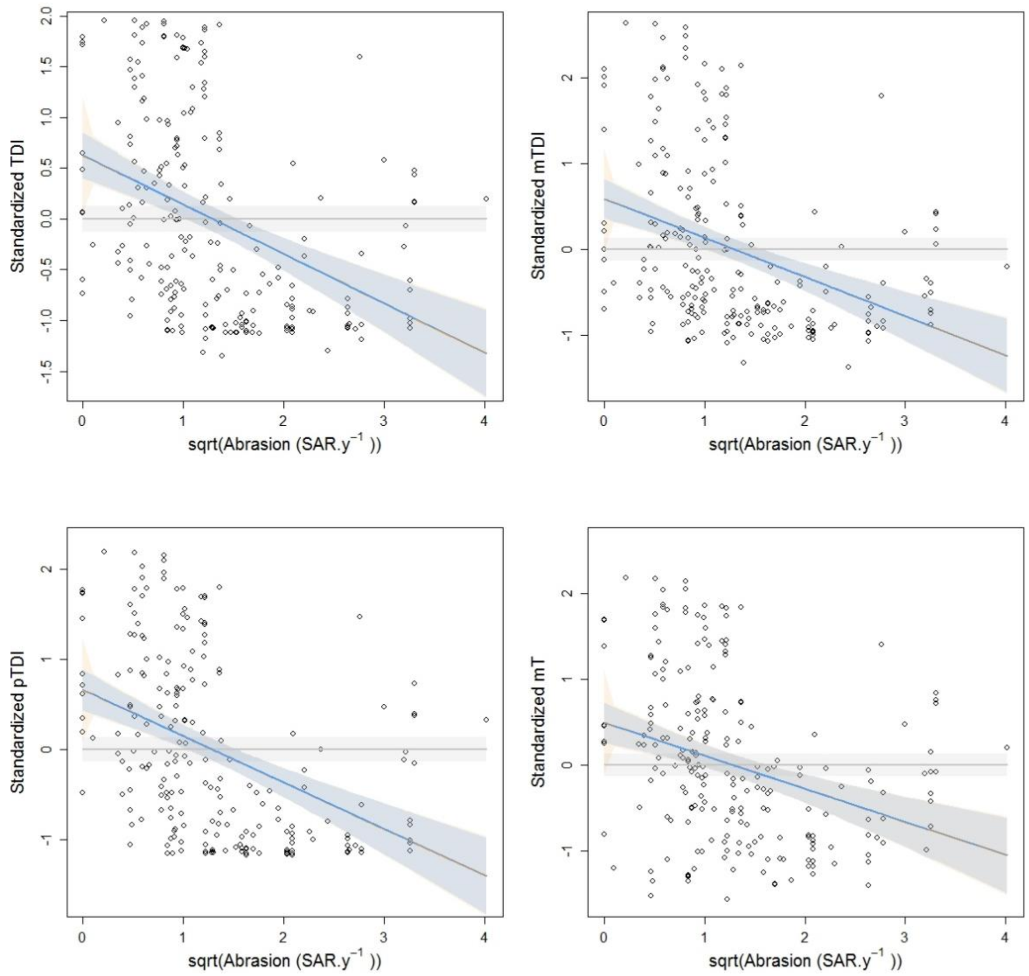


Figure E.7: Indices modelled relationships to fishery abrasion in habitat A5.27: Deep circalittoral mud.
Null models (grey lines and 95% confidence interval in grey shading), neglinear (blue lines and 95% confidence interval in blue shading) and segment1 (orange) models fitted all indices. In all cases neglinear and segment1 models were so similar that their graphic representation fully overlapped but neglinear models were more suited (higher adjusted R-squared) for all of these. Significant threshold could be detected in all cases but were not retained here.

Table E.7: Summary of the modelling results in the habitat A5.27
Grey shading indicates the index and the model selected for this habitat. * indicates that p<0.05; ** indicates that p<0.01; *** indicates that p<0.001

Indices	Models	Slope	Threshold 1	Threshold 2	AdjR²	RMAE
TDI	Null	-	-	-	0	-
	Neglinear	-0.49***	-	-	0.15	-
	Segment1	-0.48***	3.10^{-3}***	-	0.15	-
mTDI	Null	-	-	-	0	-
	Neglinear	-0.46***	-	-	0.13	-
	Segment1	-0.44***	$1.6.10^{-5}$***	-	0.13	-
pTDI	Null	-	-	-	0	-
	Neglinear	-0.51***	-	-	0.18	0.23
	Segment1	-0.49***	1.10^{-6}***	-	0.17	-
mT	Null	-	-	-	0	-
	Neglinear	-0.39***	-	-	0.09	-
	Segment1	-0.37***	3.10^{-4}***	-	0.09	-

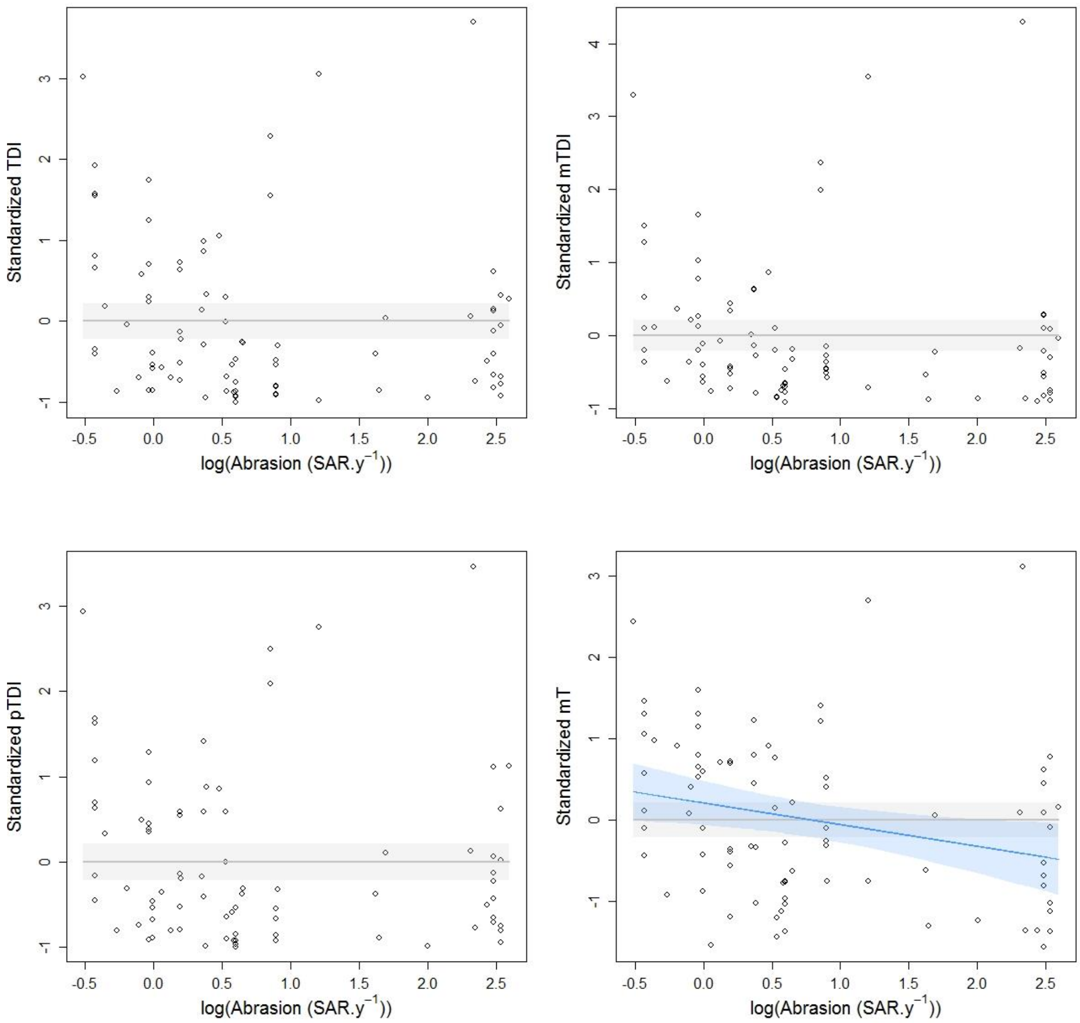


Figure E.8: Indices modelled relationships to fishery abrasion in habitat A5.37: Deep circalittoral mud.
Null model (grey lines and 95% confidence interval in grey shading) fitted all indices but neglinear models (blue lines and 95% confidence interval in blue shading) were more suited for mT. No significant thresholds could be detected.

Table E.8: Summary of the modelling results in the habitat A5.37

Grey shading indicates the index and the model selected for this habitat.
* indicates that p<0.05; ** indicates that p<0.01; *** indicates that p<0.001

Indices	Models	Slope	AdjR²	RMAE
TDI	Null	-	0	-
	Neglinear	-0.15	0.01	-
mTDI	Null	-	0	-
	Neglinear	-0.16	0.01	-
pTDI	Null	-	0	-
	Neglinear	-0.10	-	-
mT	Null	-	0	-
	Neglinear	-0.27*	0.06	0.17

3. English Channel

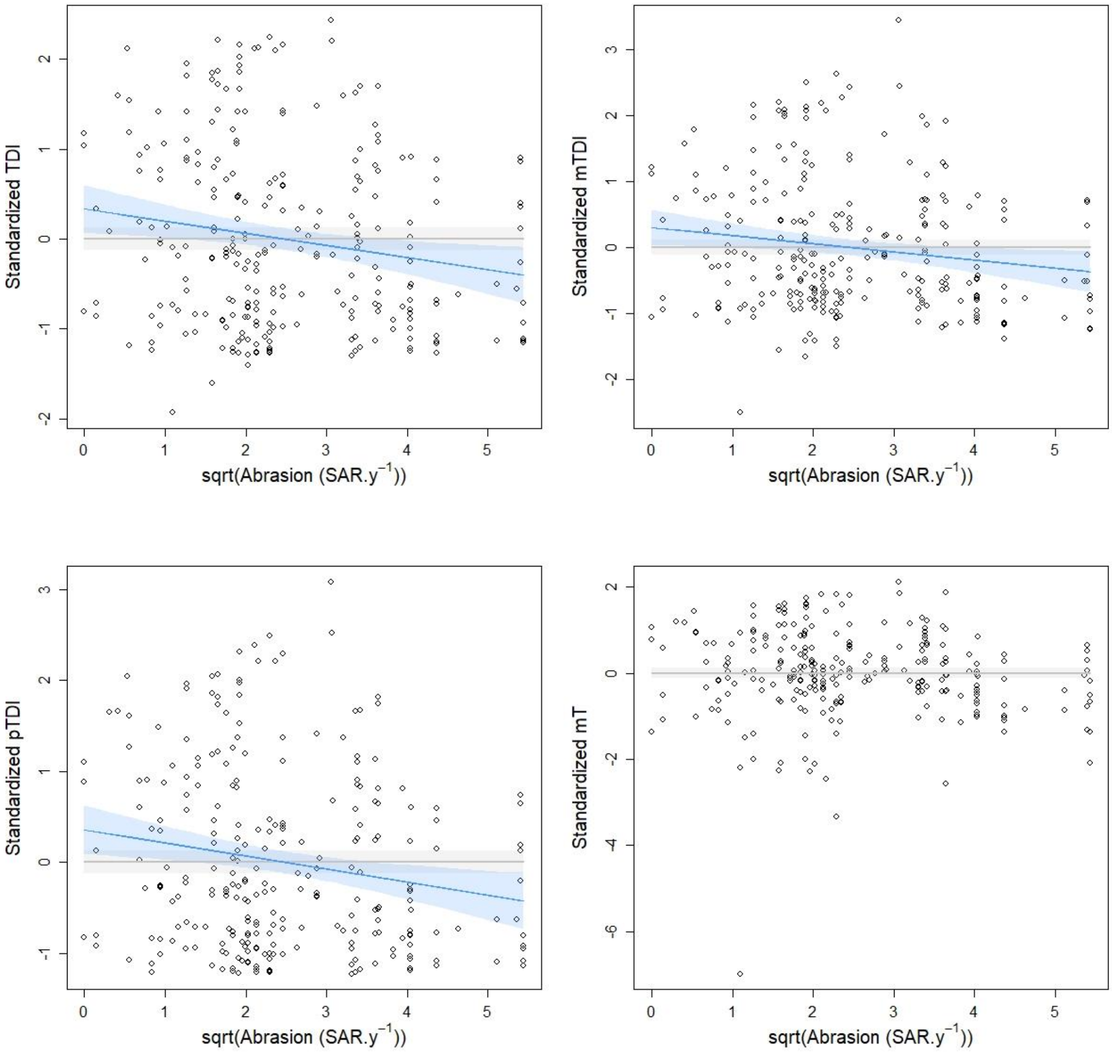


Figure E.9: Indices modelled relationships to fishery abrasion in habitat A5.14 (in autumn): Circalittoral coarse sediment. Null model (grey lines and 95% confidence interval in grey shading) was the only fitting model for mT index and neglinear models (blue lines and 95% confidence interval in blue shading) were more suited for TDI, mTDI and pTDI. No significant thresholds could be detected.

Table E.9: Summary of the modelling results in the habitat A5.14 in autumn

Grey shading indicates the index and the model selected for this habitat.
* indicates that p<0.05 ; ** indicates that p<0.01

Indices	Models	Slope	AdjR²	RMAE
TDI	Null	-	0	-
	Neglinear	-0.13**	0.02	0.19
mTDI	Null	-	0	-
	Neglinear	-0.12*	0.02	-
pTDI	Null	-	0	-
	Neglinear	-0.14**	0.03	0.19
mT	Null	-	0	-
	Neglinear	- 0.08	6.10^{-3}	-

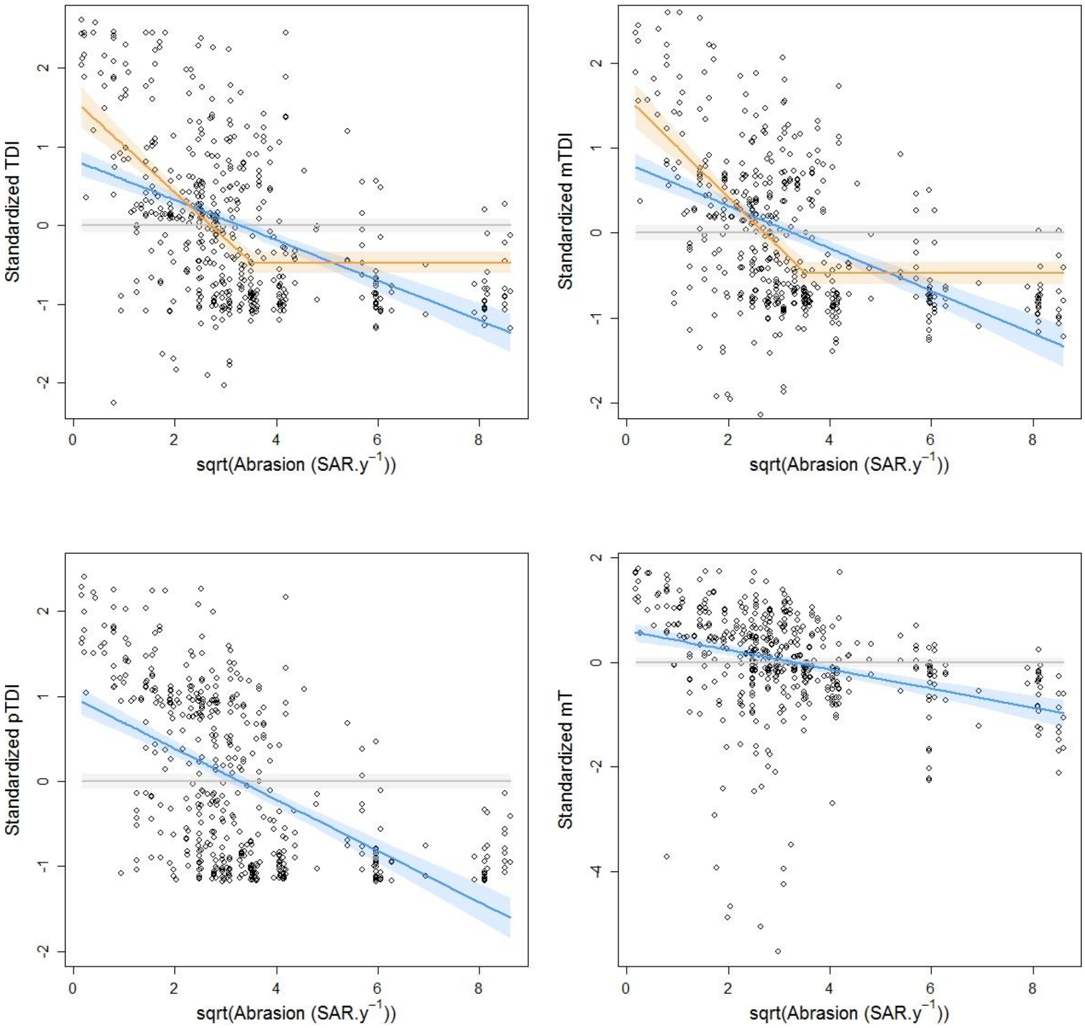


Figure E.10: Indices modelled relationships to fishery abrasion in habitat A5.15 (in Autumn): Deep circalittoral coarse sediment. Null models (grey lines and 95% confidence interval in grey shading) and neglinear models (blue lines and 95% confidence interval in blue shading) fitted for all indices but segment2 models (orange lines and 95% confidence interval in orange shading) were more suited for TDI and mTDI indices.

Table E.10: Summary of the modelling results in the habitat A5.15 in Autumn

Grey shading indicates the index and the model selected for this habitat. ** indicates that $p<0.01$; *** indicates that $p<0.001$

Indices	Models	Slope	Threshold 1	Threshold 2	AdjR²	RMAE
TDI	Null	-	-	-	0	-
	Neglinear	-0.26***	-	-	0.21	-
	Segment2	-0.59***	-	12.34**	0.28	-
mTDI	Null	-	-	-	0	-
	Neglinear	-0.25***	-	-	0.20	-
	Segment2	-0.58***	-	12.34***	0.27	0.15
pTDI	Null	-	-	-	0	-
	Neglinear	-0.30***	-	-	0.29	-
mT	Null	-	-	-	0	-
	Neglinear	-0.18***	-	-	0.10	-

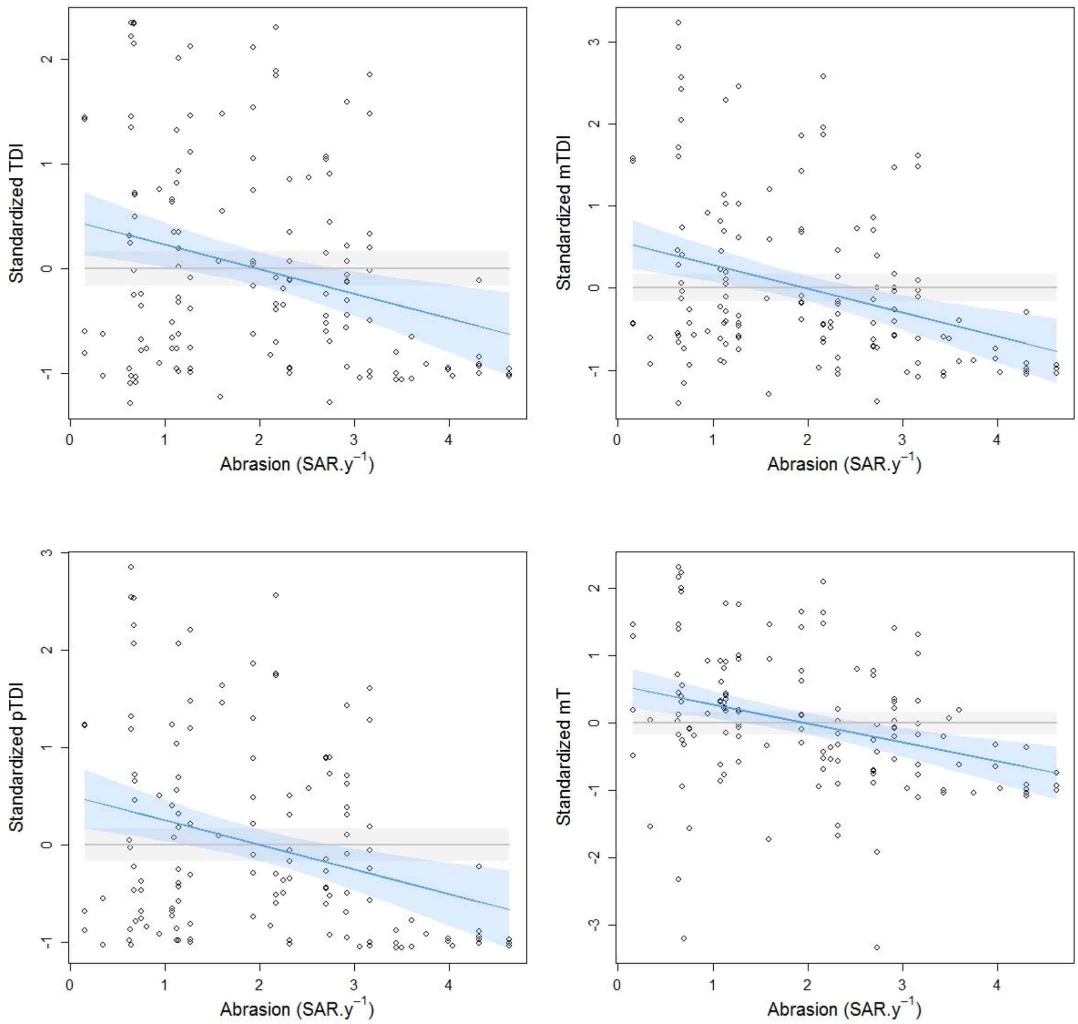


Figure E.11: Indices modelled relationships to fishery abrasion in habitat A5.25/26: Circalittoral fine sand/muddy sand. Null models (grey lines and 95% confidence interval in grey shading) and neglinear models (blue lines and 95% confidence interval in blue shading) fitted all indices but neglinear models were more suited in all case. No significant thresholds could be detected.

Table E.11: Summary of the modelling results in the habitat A5.25/26

Grey shading indicates the index and the model selected for this habitat.
** indicates that p<0.01; *** indicates that p<0.001

Indices	Models	Slope	AdjR²	RMAE
TDI	Null	-	0	-
	Neglinear	-0.24**	0.07	0.21
mTDI	Null	-	0	-
	Neglinear	-0.29***	0.10	0.15
pTDI	Null	-	0	-
	Neglinear	-0.25***	0.08	0.20
mT	Null	-	0	-
	Neglinear	-0.28***	0.10	0.12

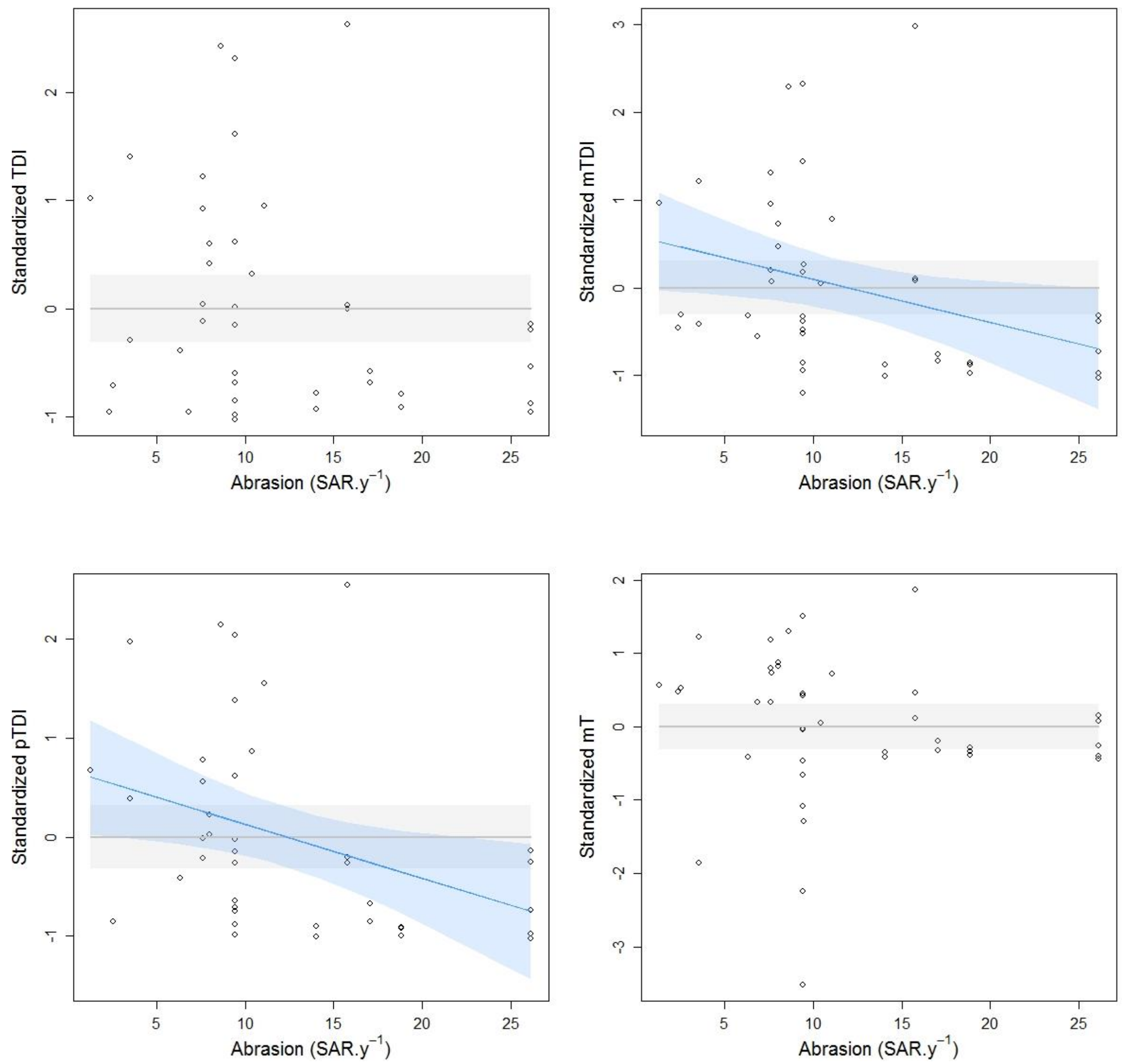


Figure E.12: Indices modelled relationships to fishery abrasion in habitat A5.27: Deep circalittoral sand.
Null models (grey lines and 95% confidence interval in grey shading) were the only fitting models for TDI and mT indices but neglinear model (blue lines and 95% confidence interval in blue shading) was more suited for mTDI and pTDI indices. No significant thresholds could be detected.

Table E.12: Summary of the modelling results in the habitat A5.27

Grey shading indicates the index and the model selected for this habitat. *indicates that $p<0.05$

Indices	Models	Slope	AdjR²	RMAE
TDI	Null	-	0	-
	Neglinear	-0.04	0.04	-
mTDI	Null	-	0	-
	Neglinear	-0.04*	0.08	0.17
pTDI	Null	-	0	-
	Neglinear	-0.05*	0.11	0.20
mT	Null	-	0	-
	Neglinear	-0.02	-0.01	-

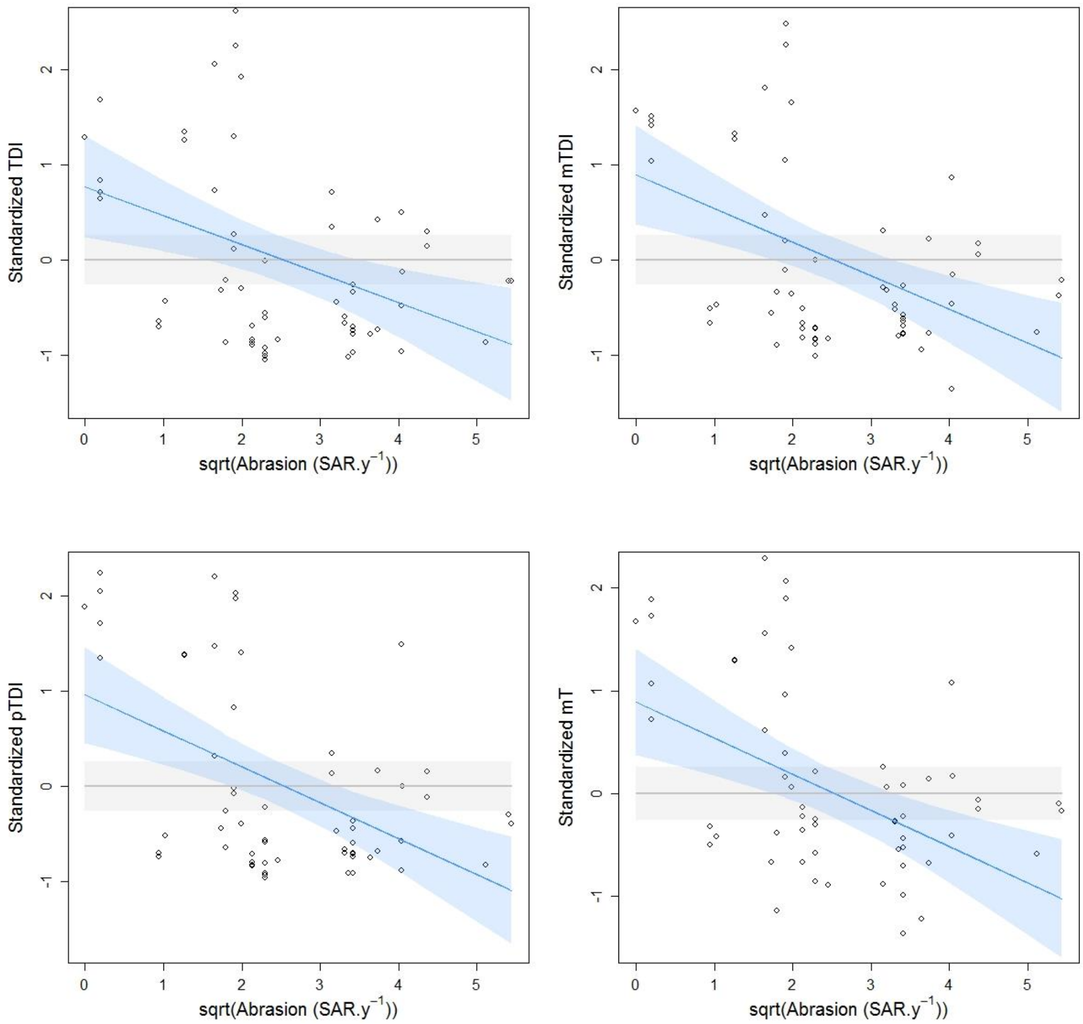


Figure E.13: Indices modelled relationships to fishery abrasion in habitat A5.14 (in Winter): Circalittoral coarse sediment. Null models (grey lines and 95% confidence interval in grey shading) and neglinear models (blue lines and 95% confidence interval in blue shading) fitted all indices but neglinear models were more suited in all case. No significant thresholds could be detected.

Table E.13: Summary of the modelling results in the habitat A5.14 in winter

**indicates that $p<0.01$; ***indicates that $p<0.001$

Indices	Models	Slope	AdjR²	RMAE
TDI	Null	-	0	-
	Neglinear	-0.31**	0.14	-
mTDI	Null	-	0	-
	Neglinear	-0.23**	0.08	-
pTDI	Null	-	0	-
	Neglinear	-0.38***	0.22	-
mT	Null	-	0	-
	Neglinear	- 0.35***	0.19	-

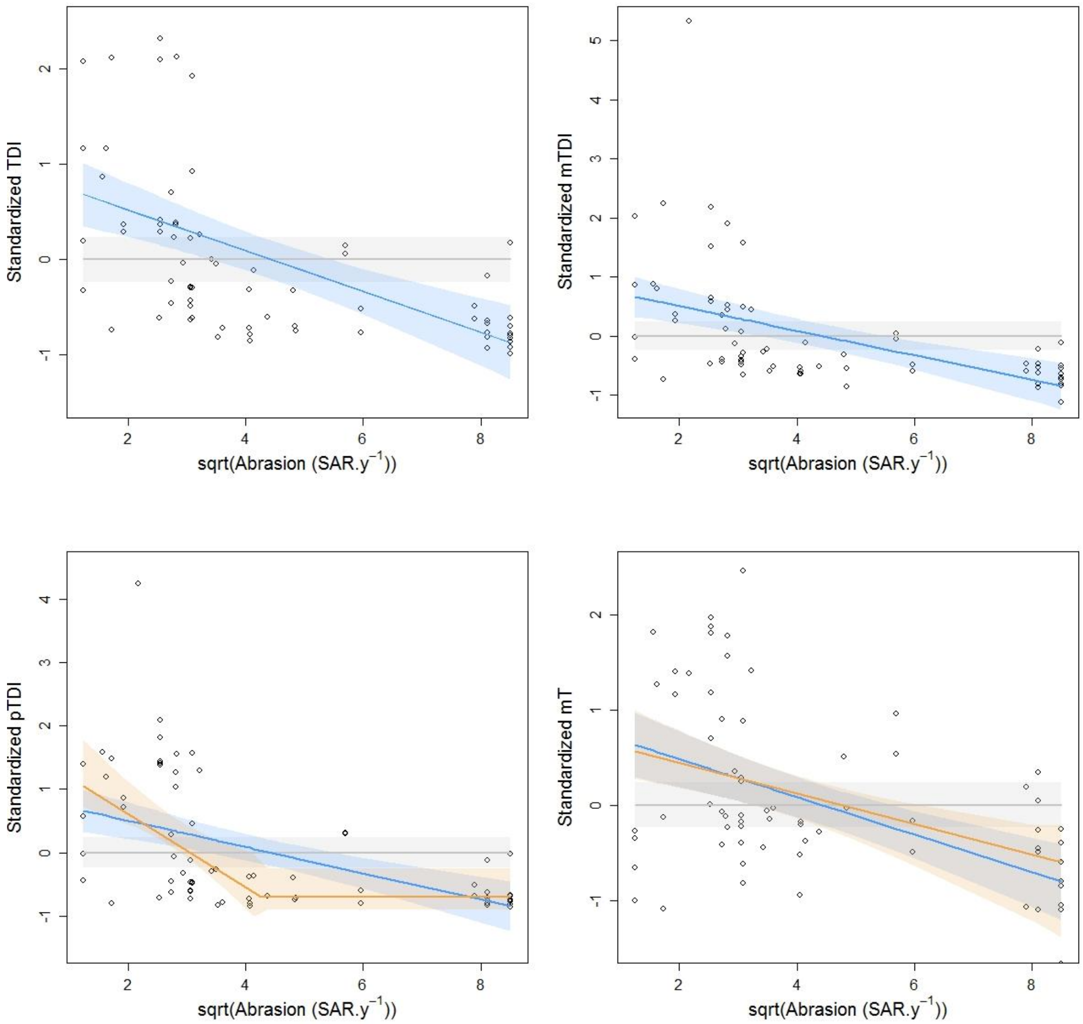


Figure E.14: Indices modelled relationships to fishery abrasion in habitat A5.15 (in Winter): Deep circalittoral coarse sediment. Null models (grey lines and 95% confidence interval in grey shading) and neglinear models (blue lines and 95% confidence interval in blue shading) fitted for all indices but segment2 models (orange lines and 95% confidence interval in orange shading) were more suited for pTDI and mT indices.

Table E.14: Summary of the modelling results in the habitat A5.15 in winter

*indicates that p<0.05; **indicates that p<0.01; ***indicates that p<0.001

Indices	Models	Slope	Threshold 1	Threshold 2	AdjR²	RMAE
TDI	Null	-	-	-	0	-
	Neglinear	-0.21***	-	-	0.28	-
mTDI	Null	-	-	-	0	-
	Neglinear	-0.20***	-	-	0.24	-
pTDI	Null	-	-	-	0	-
	Neglinear	-0.21***	-	-	0.26	-
	Segment2	-0.60**	-	18.13*	0.32	-
mT	Null	-	-	-	0	-
	Neglinear	-0.20***	-	-	0.23	-
	Segment2	-0.16**	-	71.1*	0.22	-

Appendix F. Correlation matrix between environmental variables

1. Gulf of Lion

Table F.1: Correlation matrix between environmental variables and abrasion in the Gulf of Lion.
Fa = Food availability; Chla = concentration in Chlorophyll a; Ta = standard deviation between monthly mean temperature within a year; SBS = Seabed stress. Grey shading indicates best correlations

Parameters	Fa	SST	Chla	Ta	Ti	Stratification	Oxygen saturation	SBS	Depth	Sediment size
Fa	-	-	-	-	-	-	-	-	-	-
SST	0.33	-	-	-	-	-	-	-	-	-
Chla	0.35	0.34	-	-	-	-	-	-	-	-
Ta	0.37	0.81	0.32	-	-	-	-	-	-	-
Ti	0.39	0.83	0.35	0.92	-	-	-	-	-	-
Stratification	0.07	0.37	0.85	0.42	0.45	-	-	-	-	-
Oxygen saturation	0.41	0.62	0.08	0.81	0.84	0.16	-	-	-	-
SBS	0.20	0.22	0.14	0.17	0.33	0.30	0.14	-	-	-
Depth	-0.45	-0.71	-0.43	-0.78	-0.88	-0.52	-0.68	-0.48	-	-
Sediment size	-0.14	-0.52	-0.45	-0.62	-0.61	-0.53	-0.51	-0.03	0.51	-
Abrasion	0.38	0.63	0.33	0.60	0.70	0.38	0.53	0.44	-0.73	-0.42

2. Corsica

Table F.2: Correlation matrix between environmental variables and abrasion in Corsica.

Fa = Food availability; Chla = concentration in Chlorophyll a; Ta = standard deviation between monthly mean temperature within a year; SBS = Seabed stress. Grey shading indicates best correlations

Parameters	Fa	SST	Chla	Ta	Ti	Stratification	Oxygen saturation	SBS	Depth	Sediment size
Fa	-	-	-	-	-	-	-	-	-	-
SST	0.07	-	-	-	-	-	-	-	-	-
Chla	0.77	- 0.27	-	-	-	-	-	-	-	-
Ta	0.26	0.92	-0.10	-	-	-	-	-	-	-
Ti	0.23	0.96	-0.14	0.99	-	-	-	-	-	-
Stratification	-0.51	-0.49	-0.29	-0.74	-0.69	-	-	-	-	-
Oxygen saturation	0.79	0.40	0.40	0.59	0.52	-0.65	-	-	-	-
SBS	0.47	0.14	0.42	0.31	0.27	-0.30	0.45	-	-	-
Depth	-0.71	-0.38	-0.21	-0.49	-0.49	0.38	- 0.78	-0.12	-	-
Sediment size	-0.01	0.03	-0.06	0.02	0.02	0.12	0.04	-0.02	-0.11	-
Abrasion	0.24	0.18	0.29	0.32	0.28	-0.50	0.22	0.27	-0.10	-0.38

3. English Channel

Table F.3: Correlation matrix between environmental variables and abrasion in the English Channel.
Fa = Food availability; Chla = concentration in Chlorophyll a; Ta = standard deviation between monthly mean temperature within a year; FV = Friction velocity; SBS = Seabed stress. Grey shading indicates best correlations

Parameters	Fa	Salinity	SST	Ta	Ti	Wave stress	FV	SBS	Depth
Fa	-	-	-	-	-	-	-	-	-
Salinity	-0.87	-	-	-	-	-	-	-	-
SST	0.25	-0.44	-	-	-	-	-	-	-
Ta	0.93	-0.83	0.10	-	-	-	-	-	-
Ti	-0.18	0.17	-0.45	-0.06	-	-	-	-	-
Wave stress	0.60	-0.45	-0.03	0.66	-0.14	-	-	-	-
FV	-0.08	0.07	0.16	-0.05	-0.24	0.12	-	-	-
SBS	-0.46	0.40	0.18	-0.47	-0.18	-0.44	0.78	-	-
Depth	-0.90	0.80	-0.27	0.14	0.14	-0.65	0.04	0.45	-
Abrasion	-0.06	-0.14	0.09	-0.07	0.35	-0.17	-0.40	-0.25	0.12

Appendix G. Details on selected models in each studied areas

1. Gulf of Lion

a. Trawling Disturbance Index (TDI)

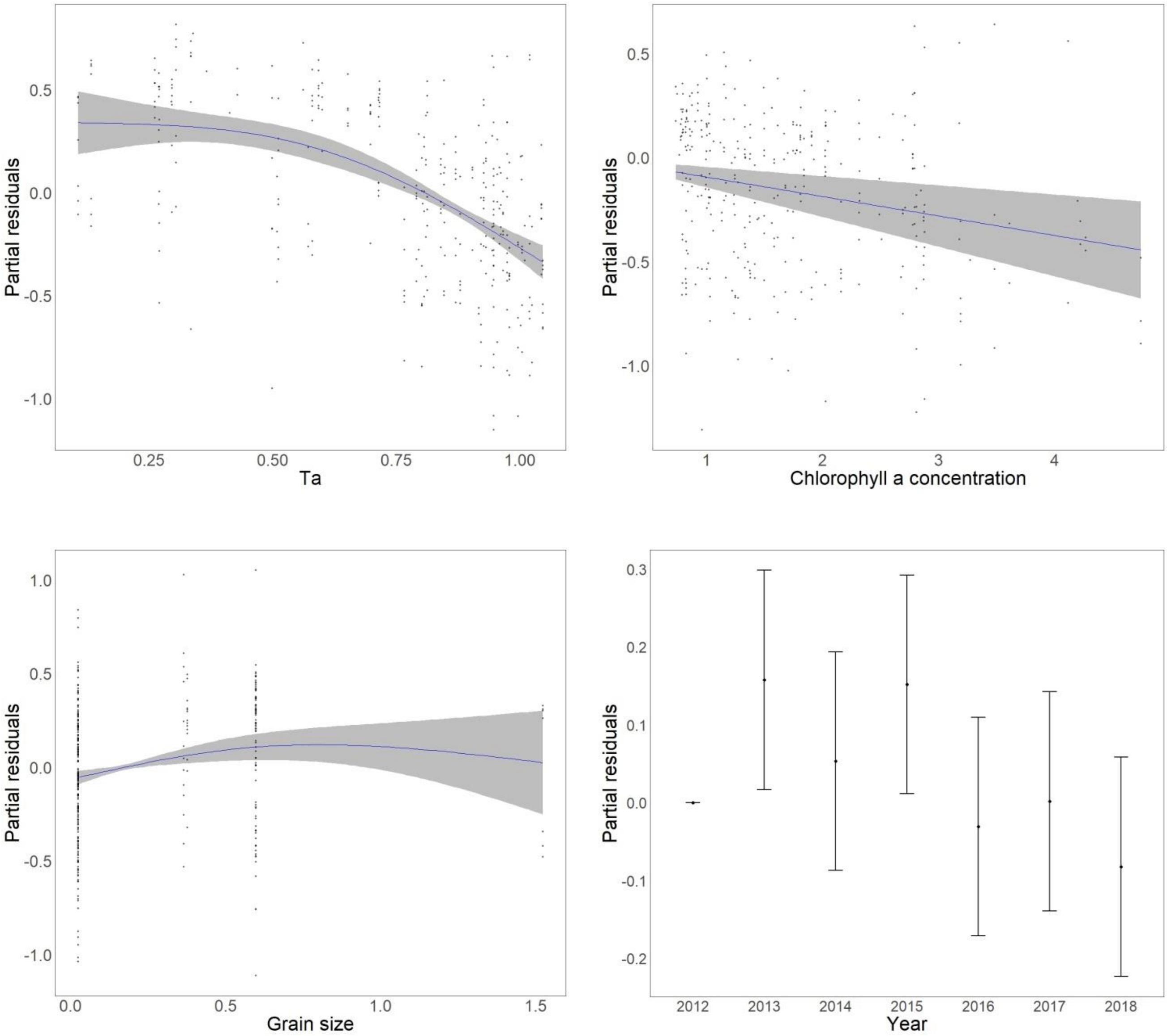
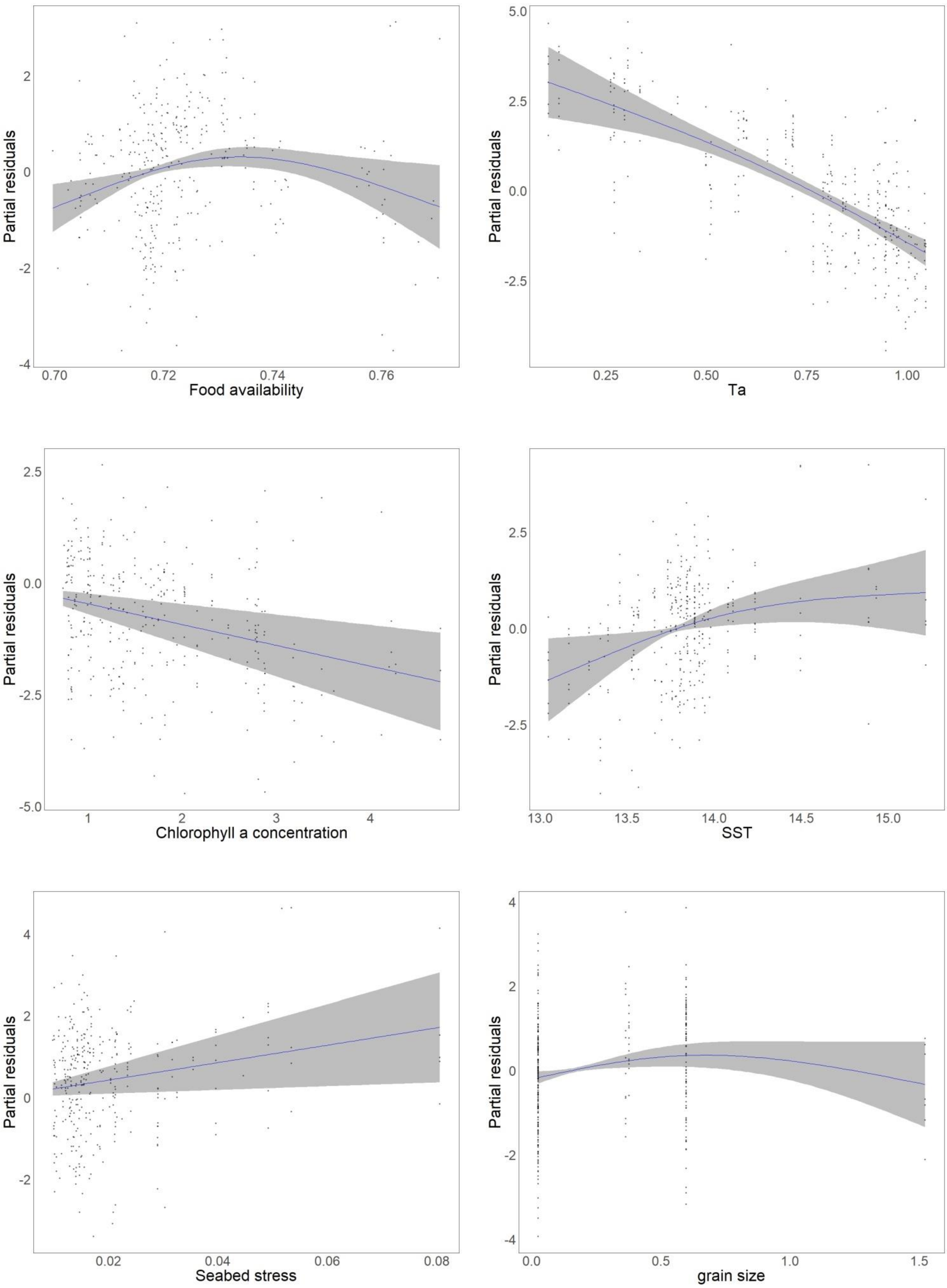


Figure G.1: Modelled relationships between environmental variables and TDI in the Gulf of Lion.
Grey shading represent the 95% confidence interval

b. Modified-TDI (mTDI)



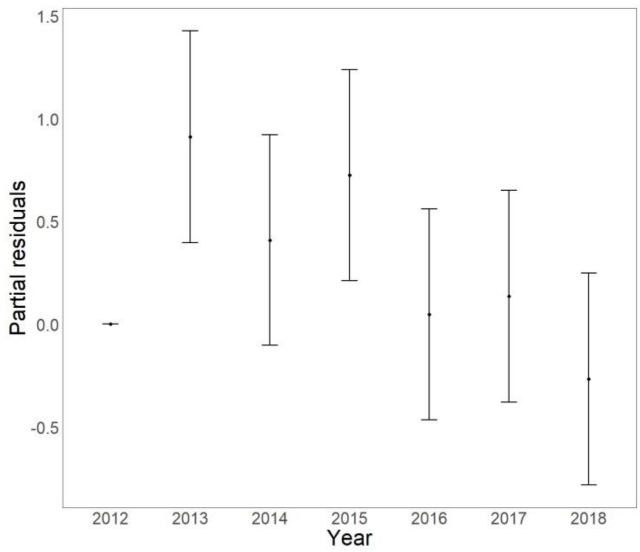


Figure G.2: Modelled relationships between environmental variables and mTDI in the Gulf of Lion.
Grey shading represent the 95% confidence interval

c. Partial-TDI (pTDI)

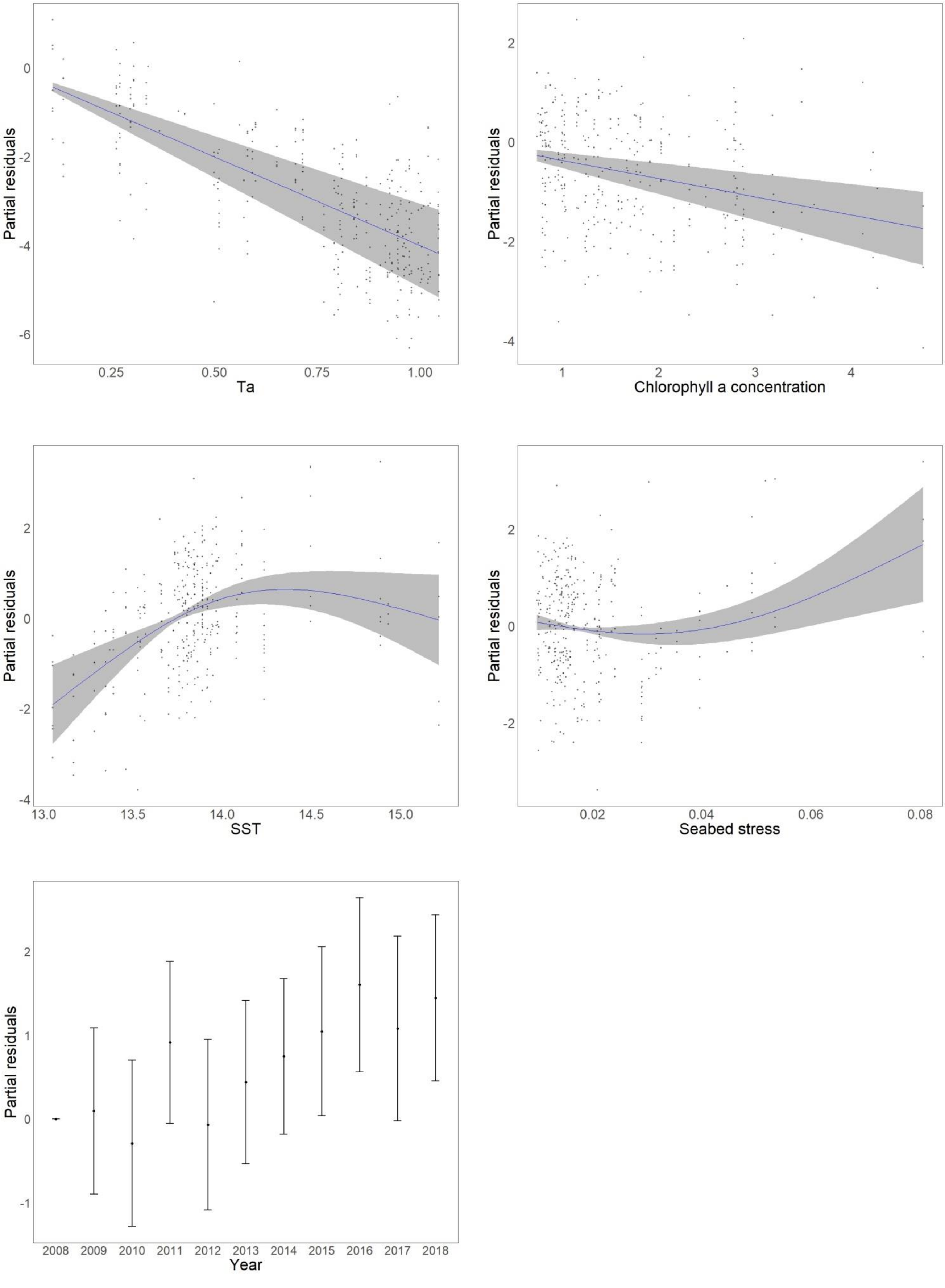


Figure G.3: Modelled relationships between environmental variables and pTDI in the Gulf of Lion.

Grey shading represent the 95% confidence interval

d. mT

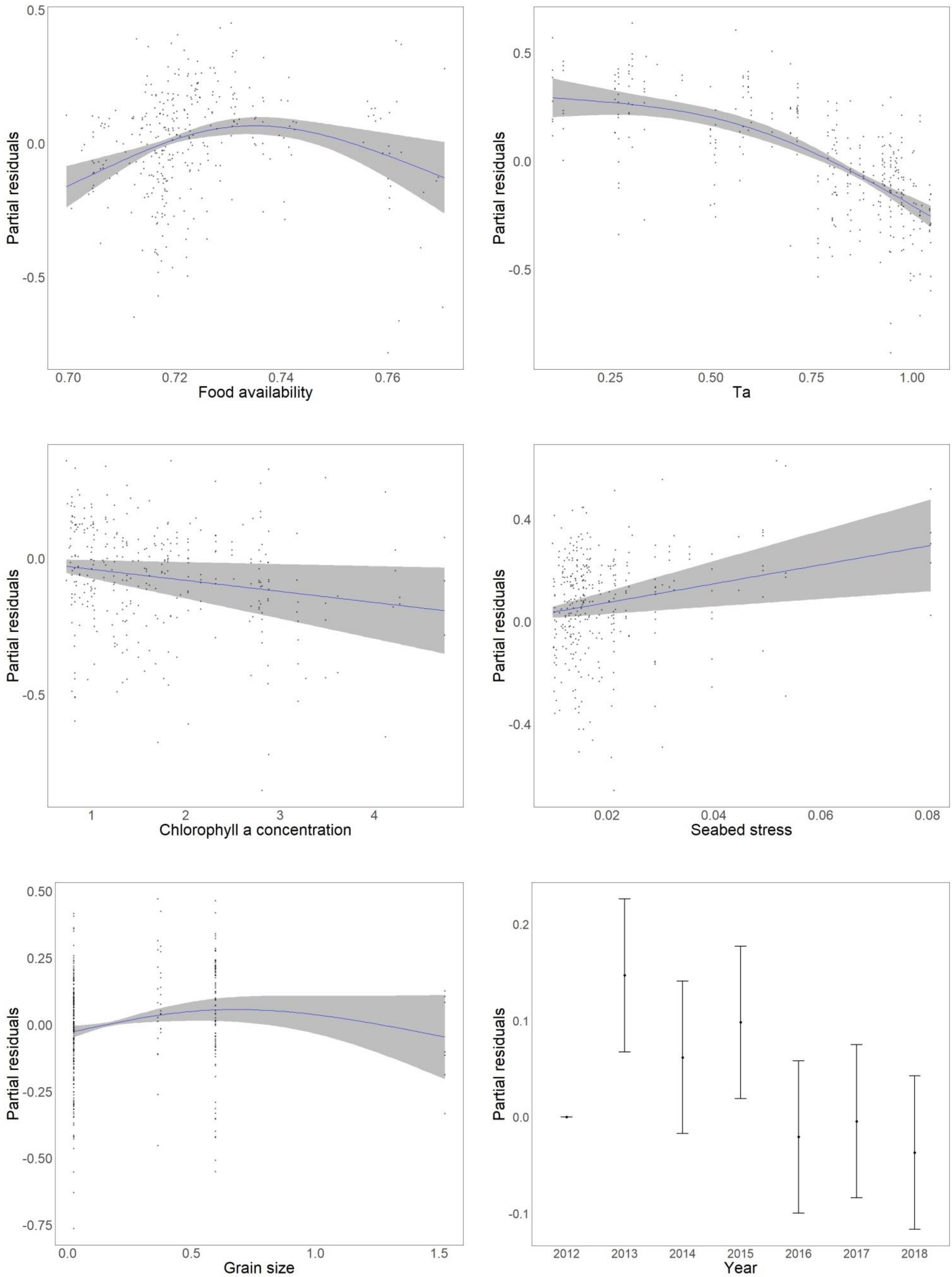


Figure G.4: Modelled relationships between environmental variables and mT in the Gulf of Lion.
Grey shading represent the 95% confidence interval

3. Corsica

a. Trawling Disturbance Index (TDI)

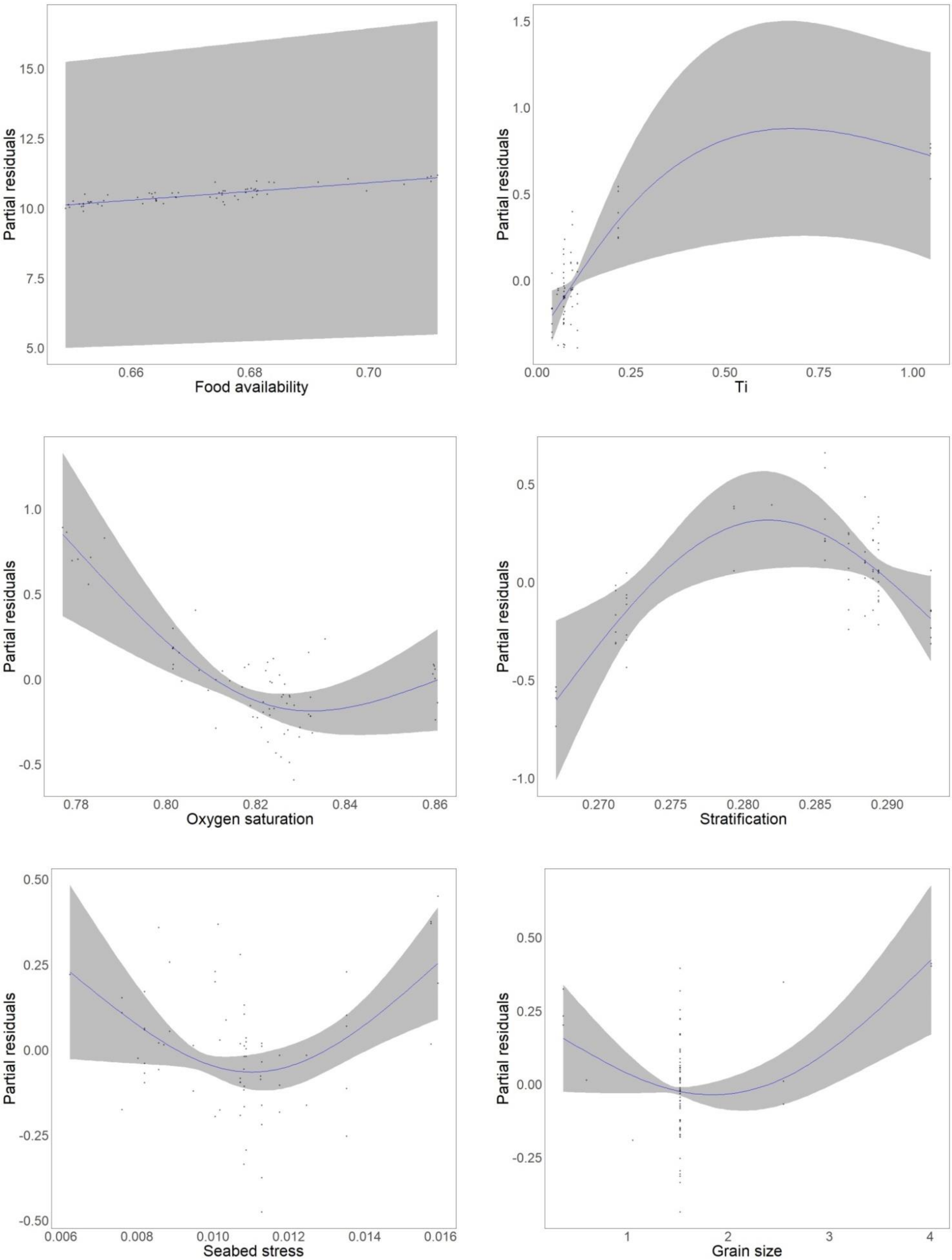


Figure G.5: Modelled relationships between environmental variables and TDI in Corsica.
Grey shading represent the 95% confidence interval

Marginal effects – Scope of Growth:

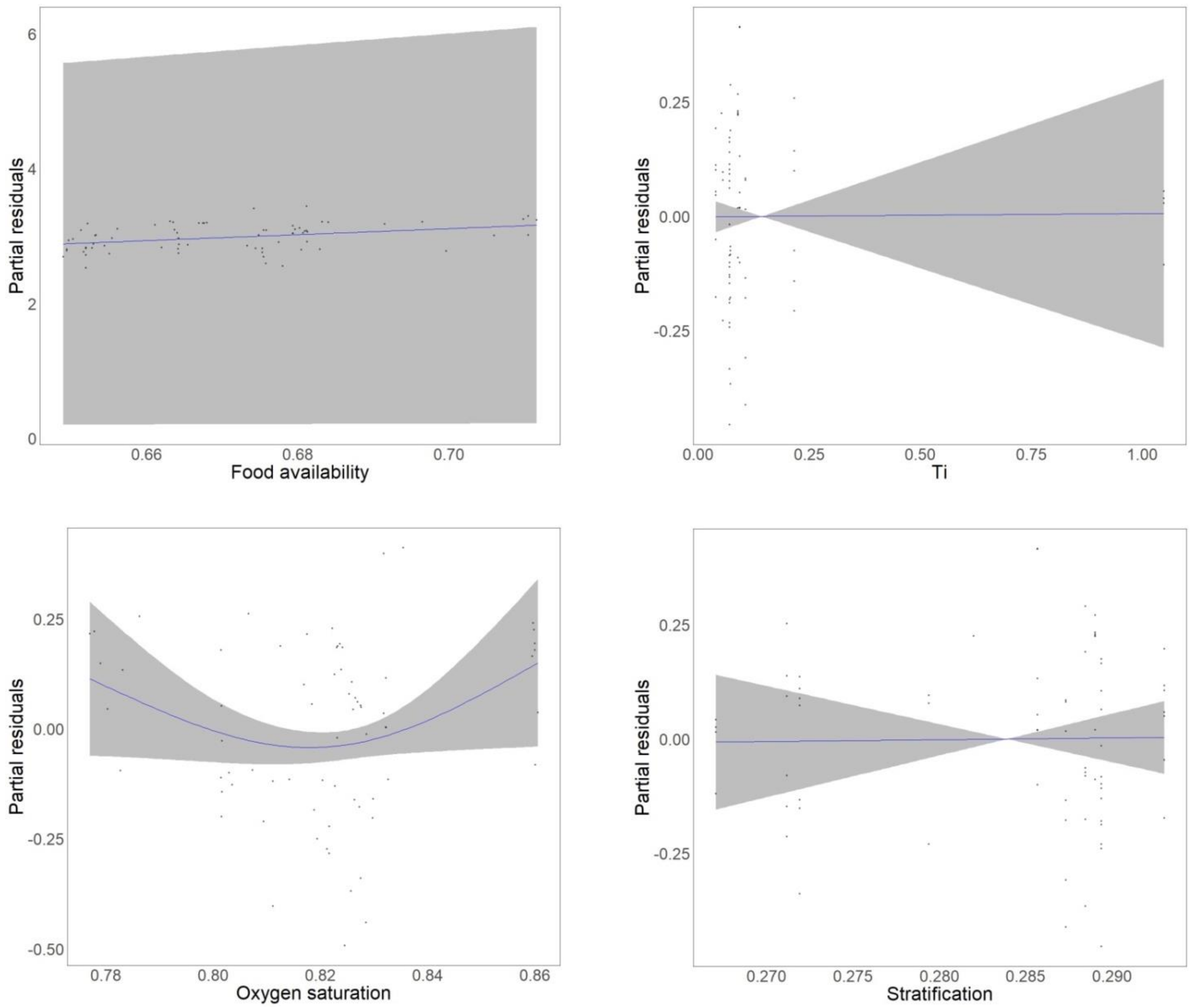


Figure G.6: Modelled relationships between environmental variables (linked to the SfG) and TDI in Corsica.
Grey shading represent the 95% confidence interval

Marginal effects – Dist:

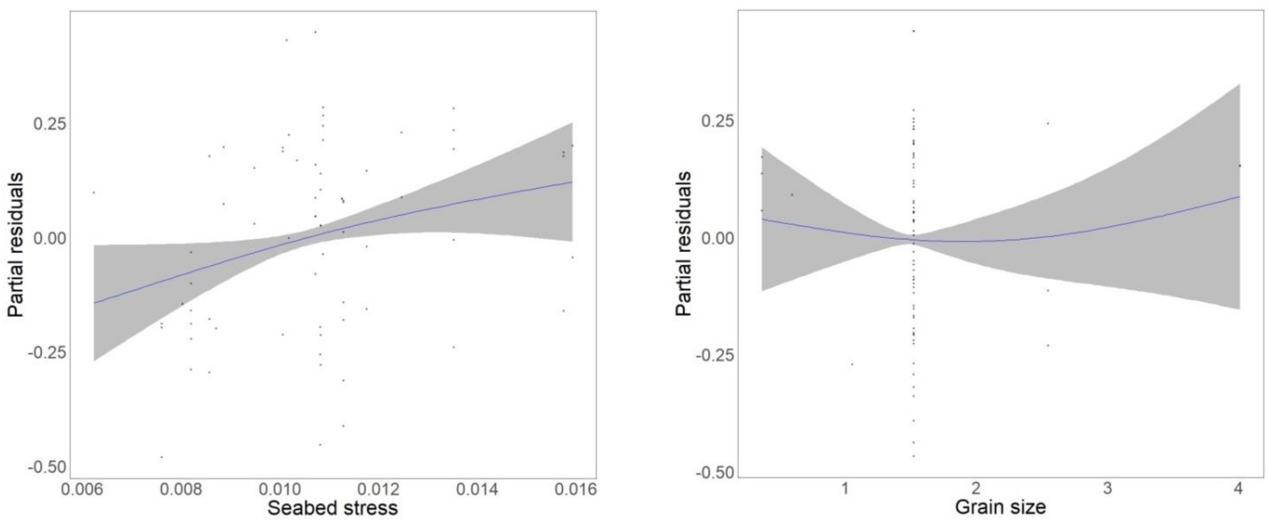


Figure G.7: Modelled relationships between environmental variables (linked to the Dist) and TDI in Corsica.
Grey shading represent the 95% confidence interval

b. Modified-TDI (mTDI)

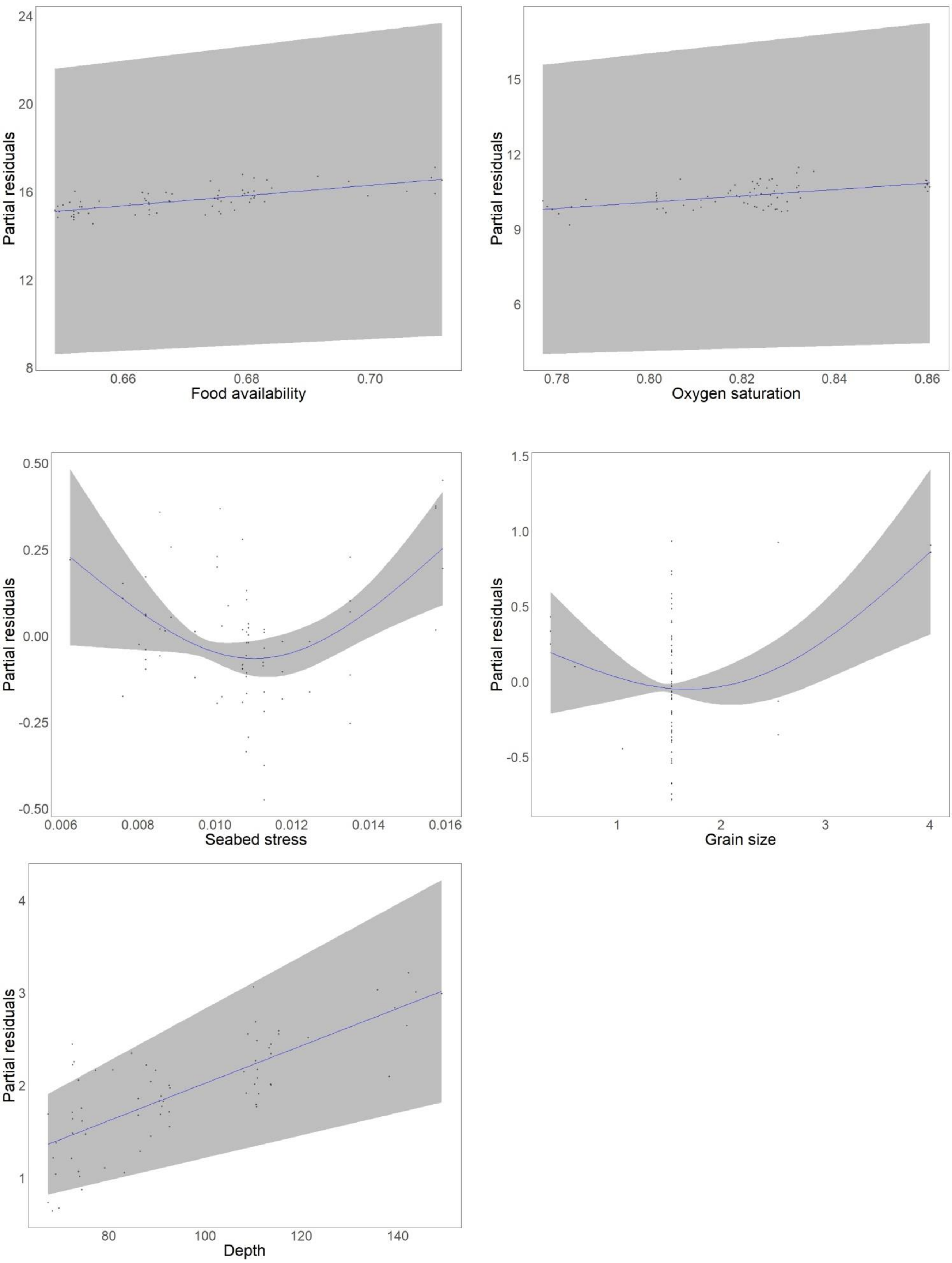


Figure G.8: Modelled relationships between environmental variables and mTDI in Corsica.
Grey shading represent the 95% confidence interval

Marginal effects – Scope of Growth:

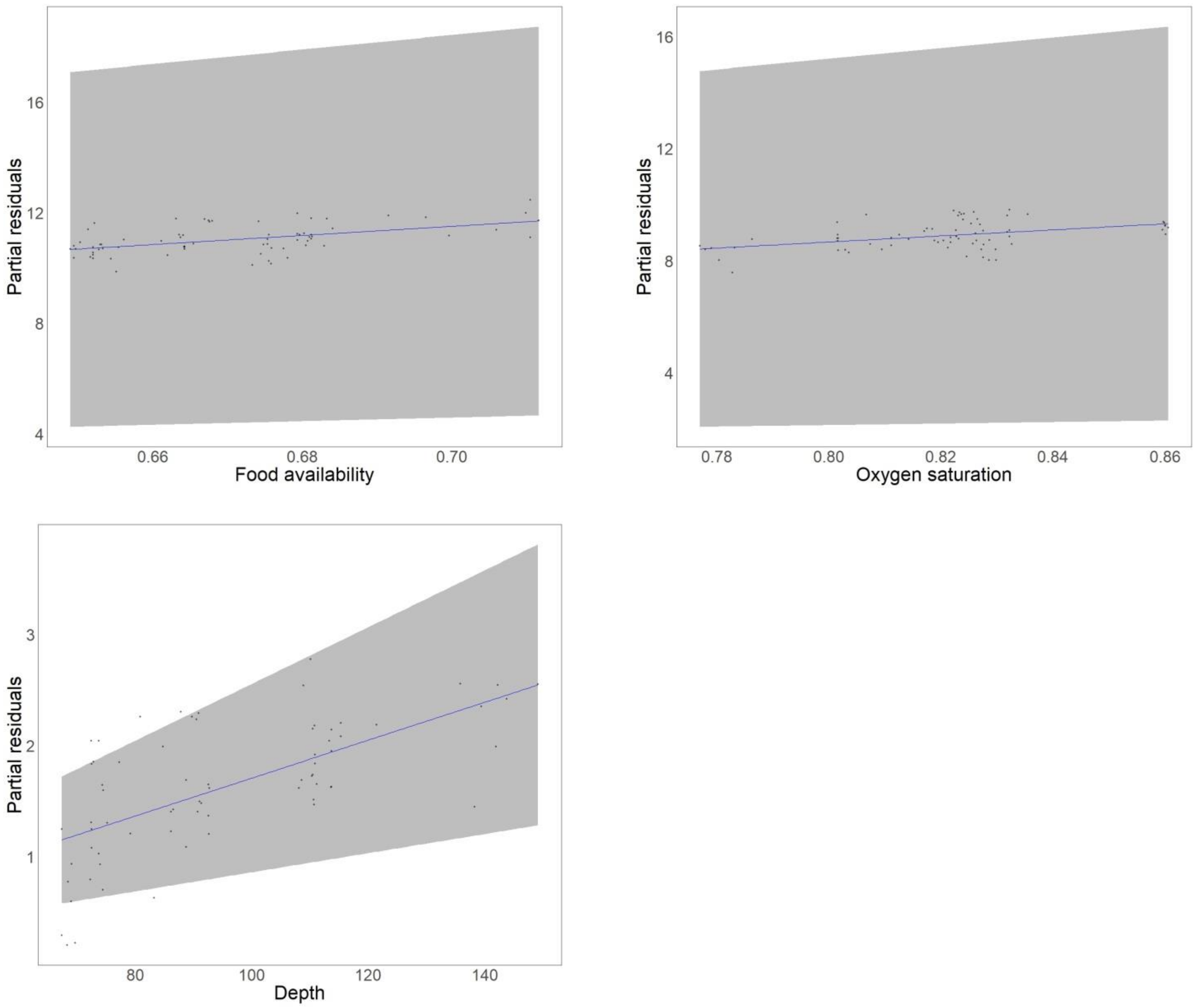


Figure G.9: Modelled relationships between environmental variables (linked to the SfG) and mTDI in Corsica.
Grey shading represent the 95% confidence interval

Marginal effects – Dist:

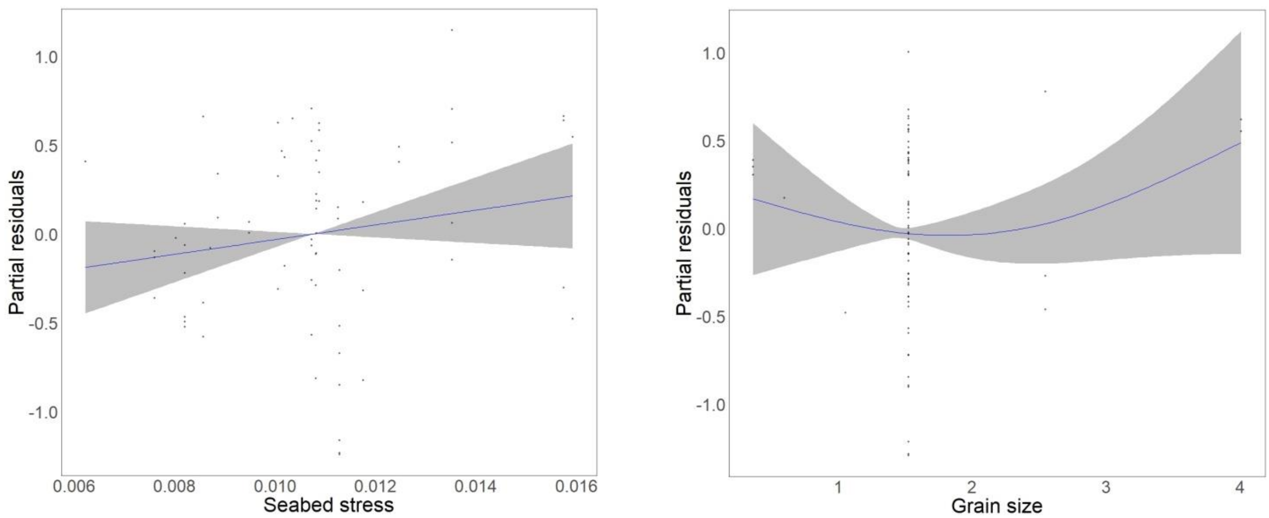


Figure G.10: Modelled relationships between environmental variables (linked to the Dist) and mTDI in Corsica.
Grey shading represent the 95% confidence interval

c. Partial-TDI (pTDI)

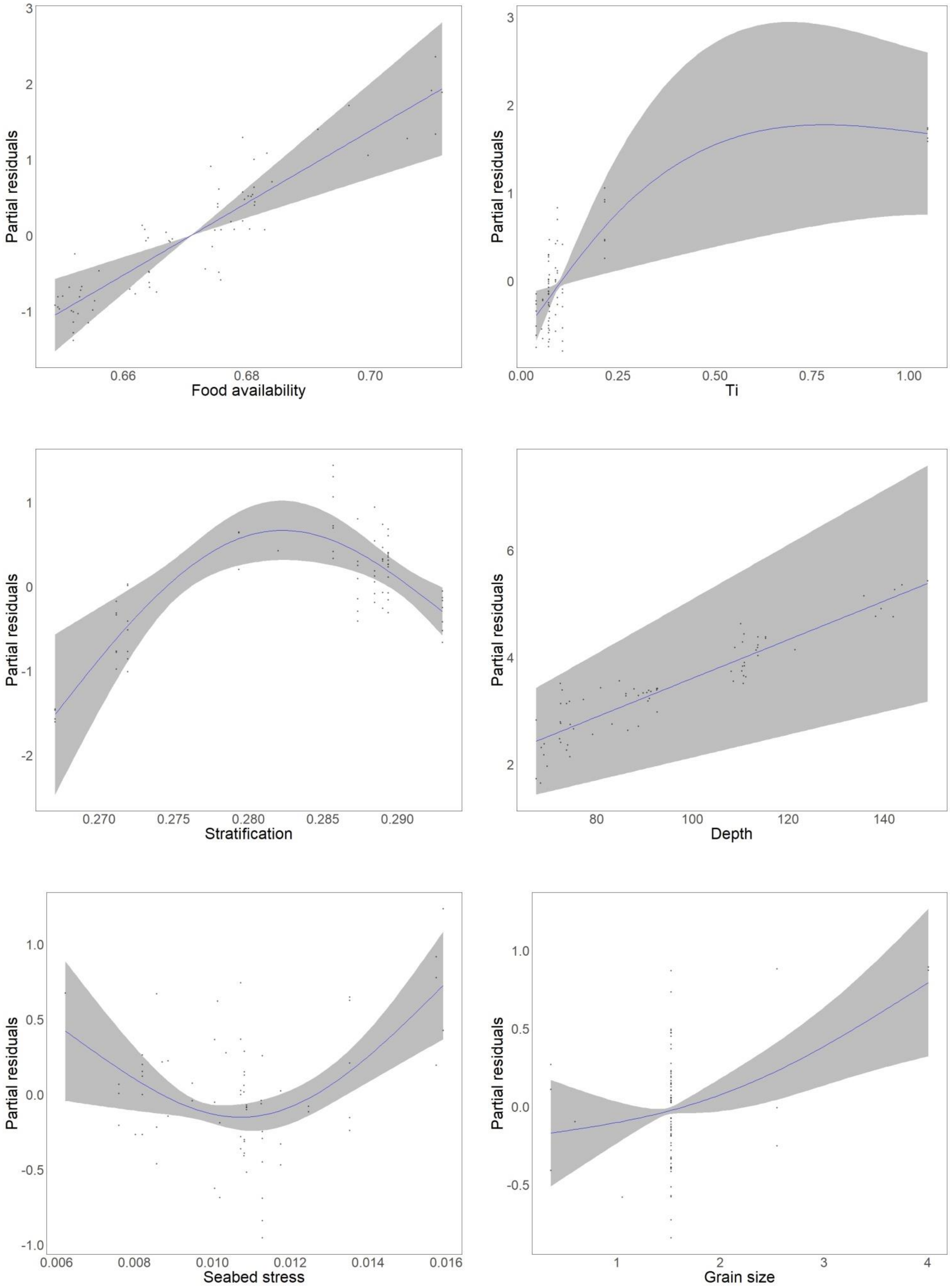


Figure G.11: Modelled relationships between environmental variables and pTDI in Corsica.
Grey shading represent the 95% confidence interval

Marginal effects – Scope of Growth:

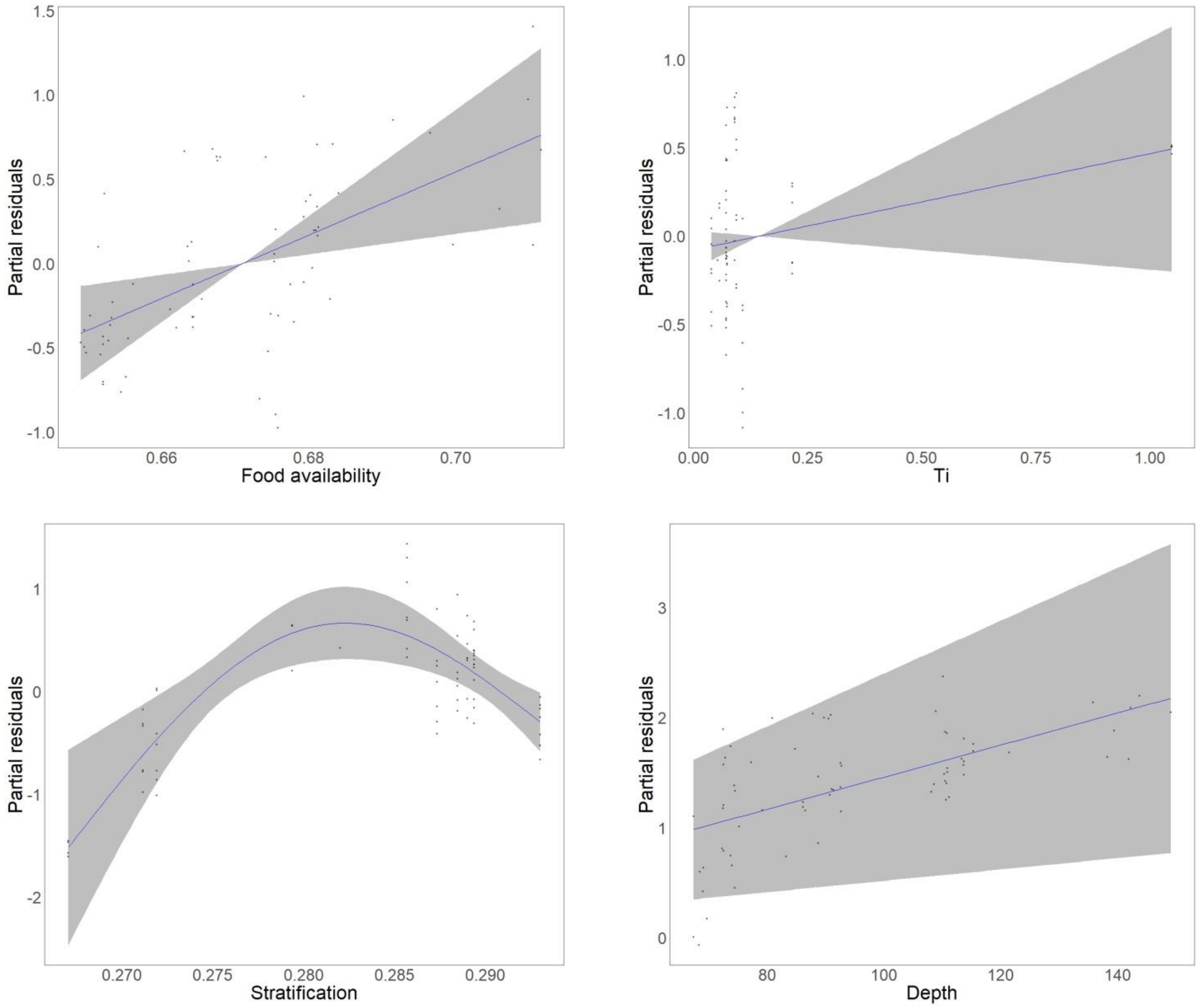


Figure G.12: Modelled relationships between environmental variables (linked to the SfG) and pTDI in Corsica. Grey shading represent the 95% confidence interval

Marginal effects – Dist:

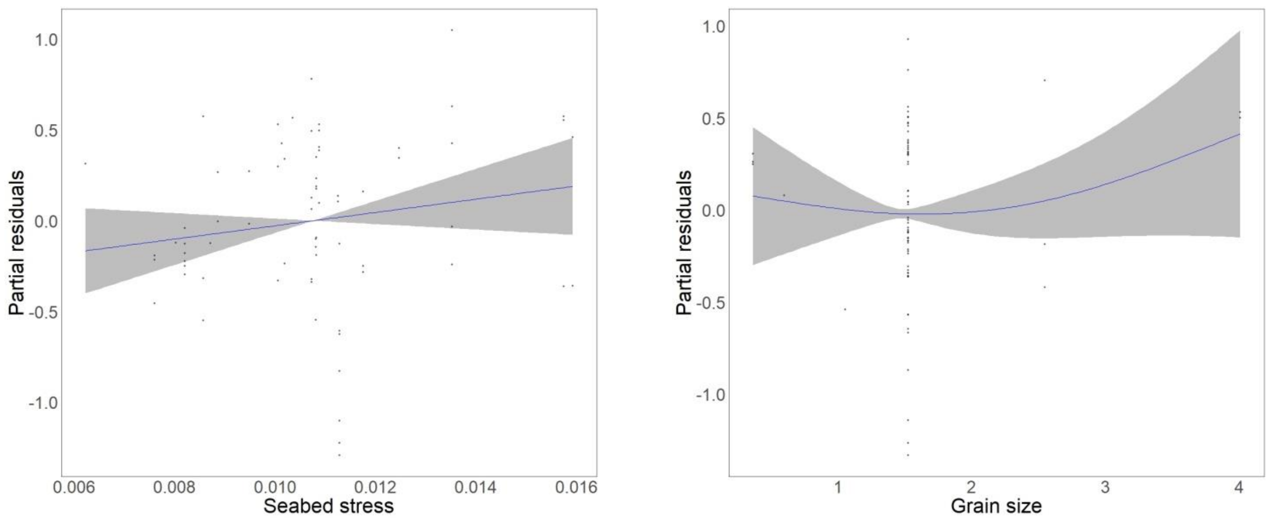


Figure G.13: Modelled relationships between environmental variables (linked to the Dist) and pTDI in Corsica. Grey shading represent the 95% confidence interval

d. mT

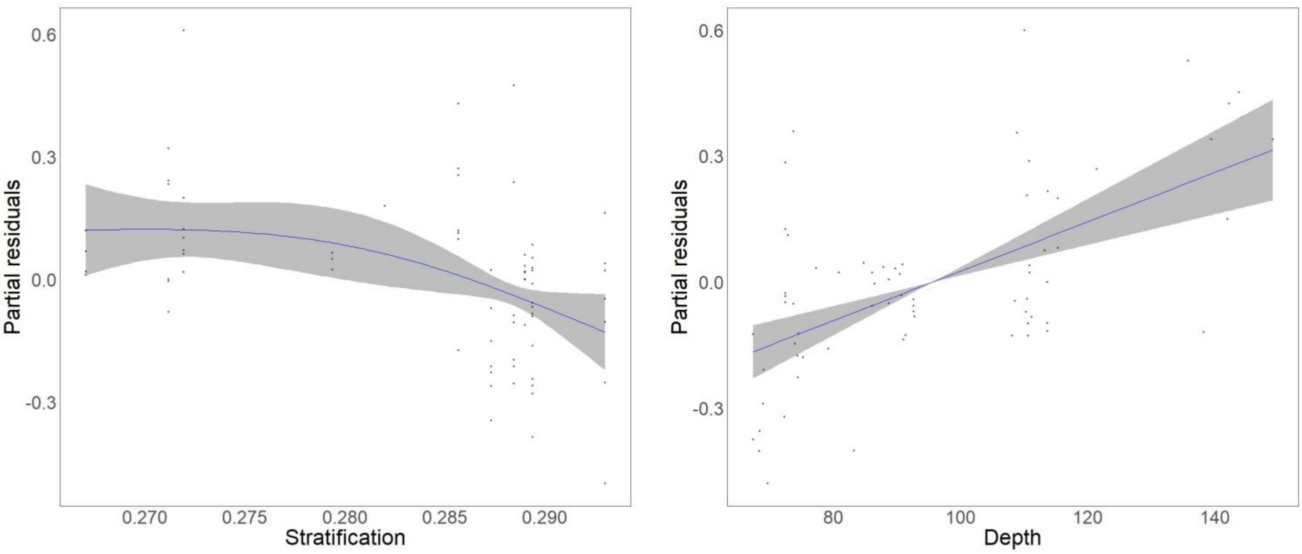
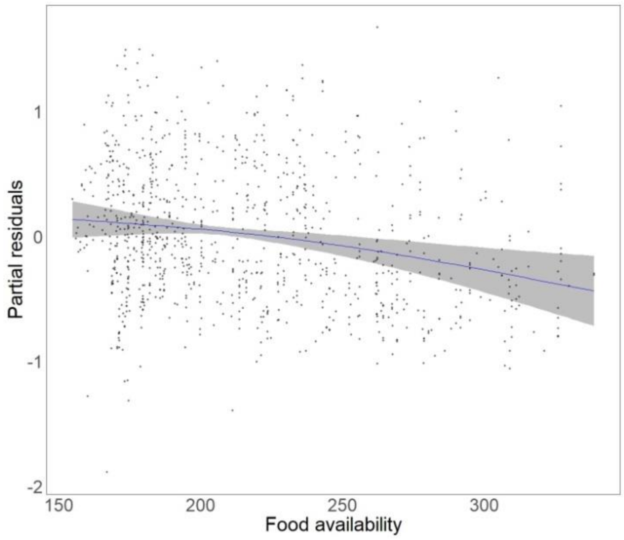
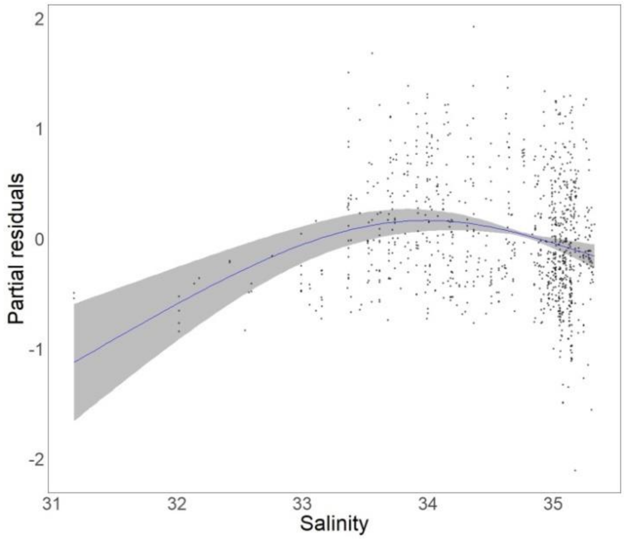


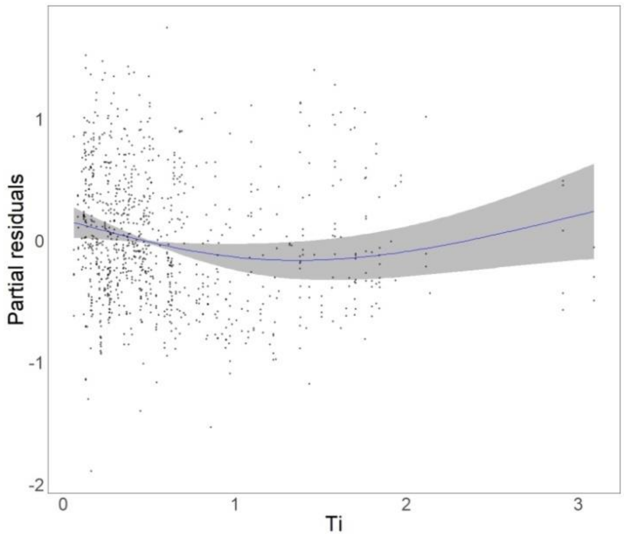
Figure G.14: Modelled relationships between environmental variables and mT in Corsica.
Grey shading represent the 95% confidence interval

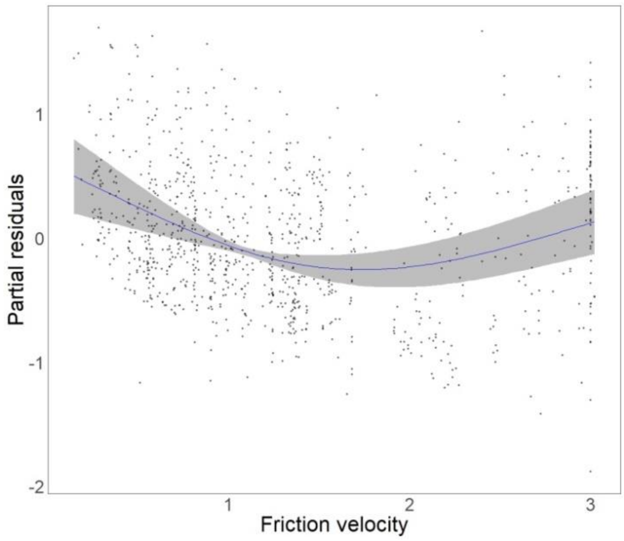
3. English Channel

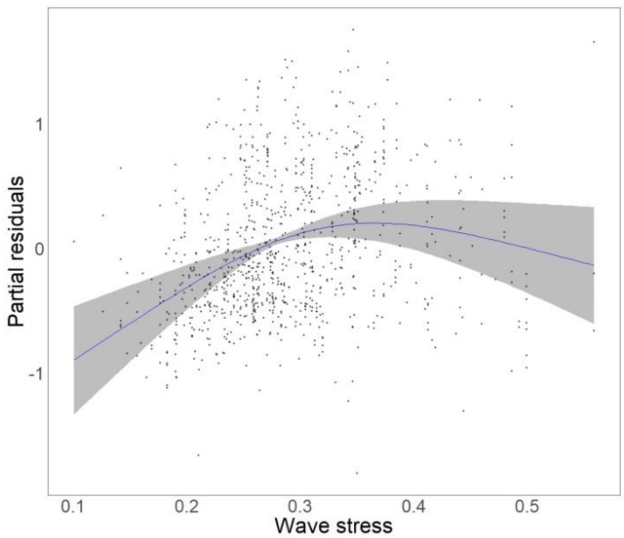
a. Trawling Disturbance Index (TDI)

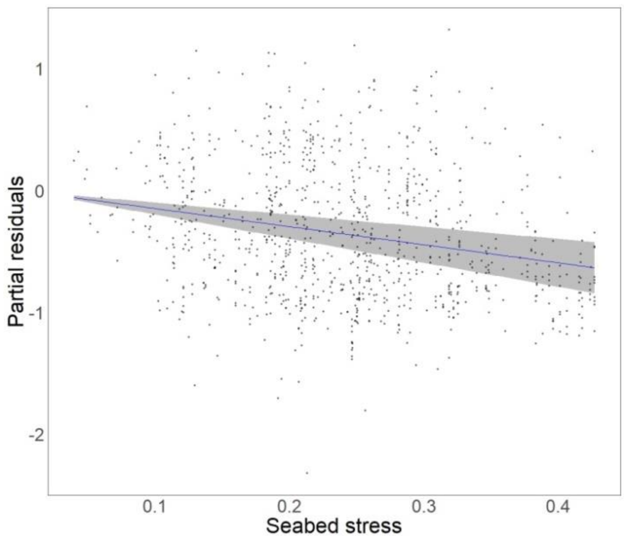












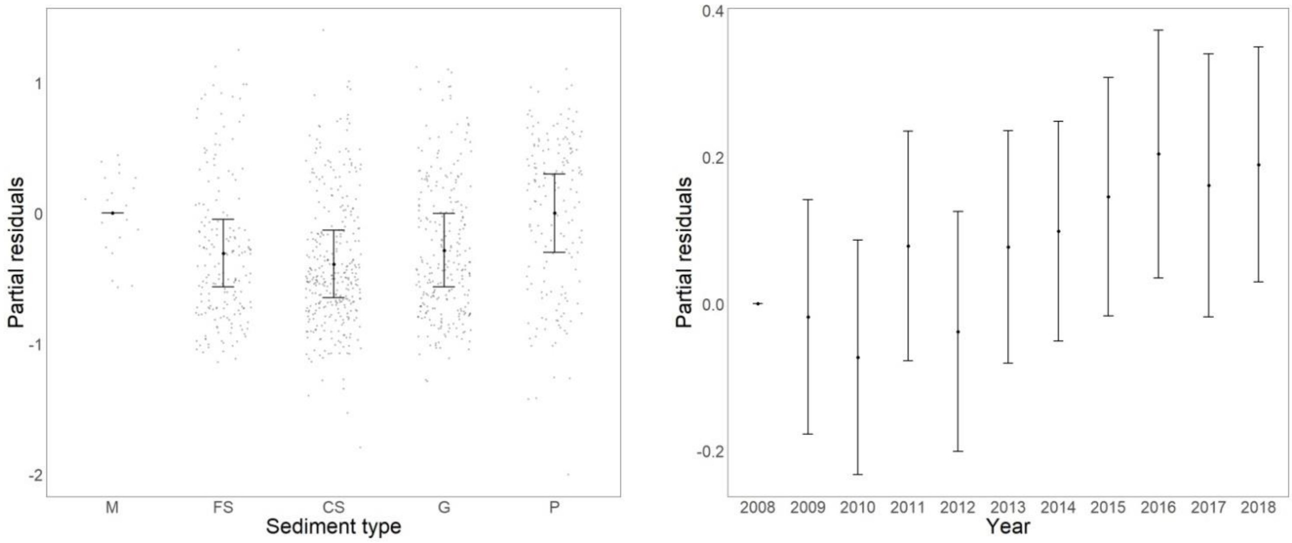
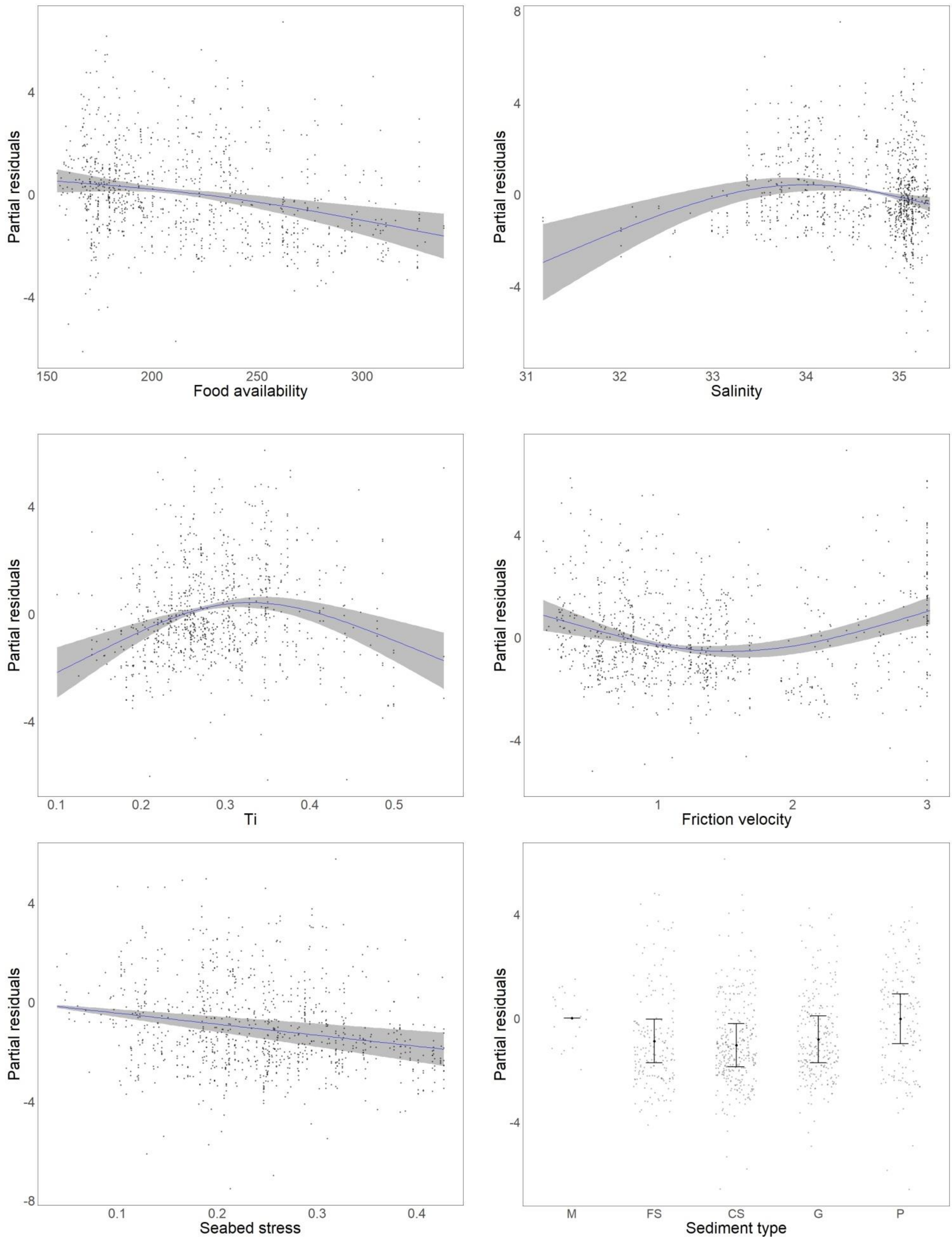


Figure G.15: Modelled relationships between environmental variables and TDI in the English Channel.
Grey shading represent the 95% confidence interval

b. Modified-TDI (mTDI)



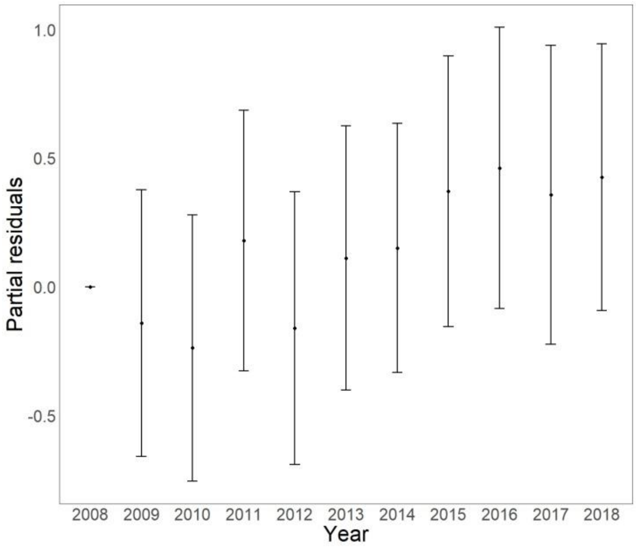
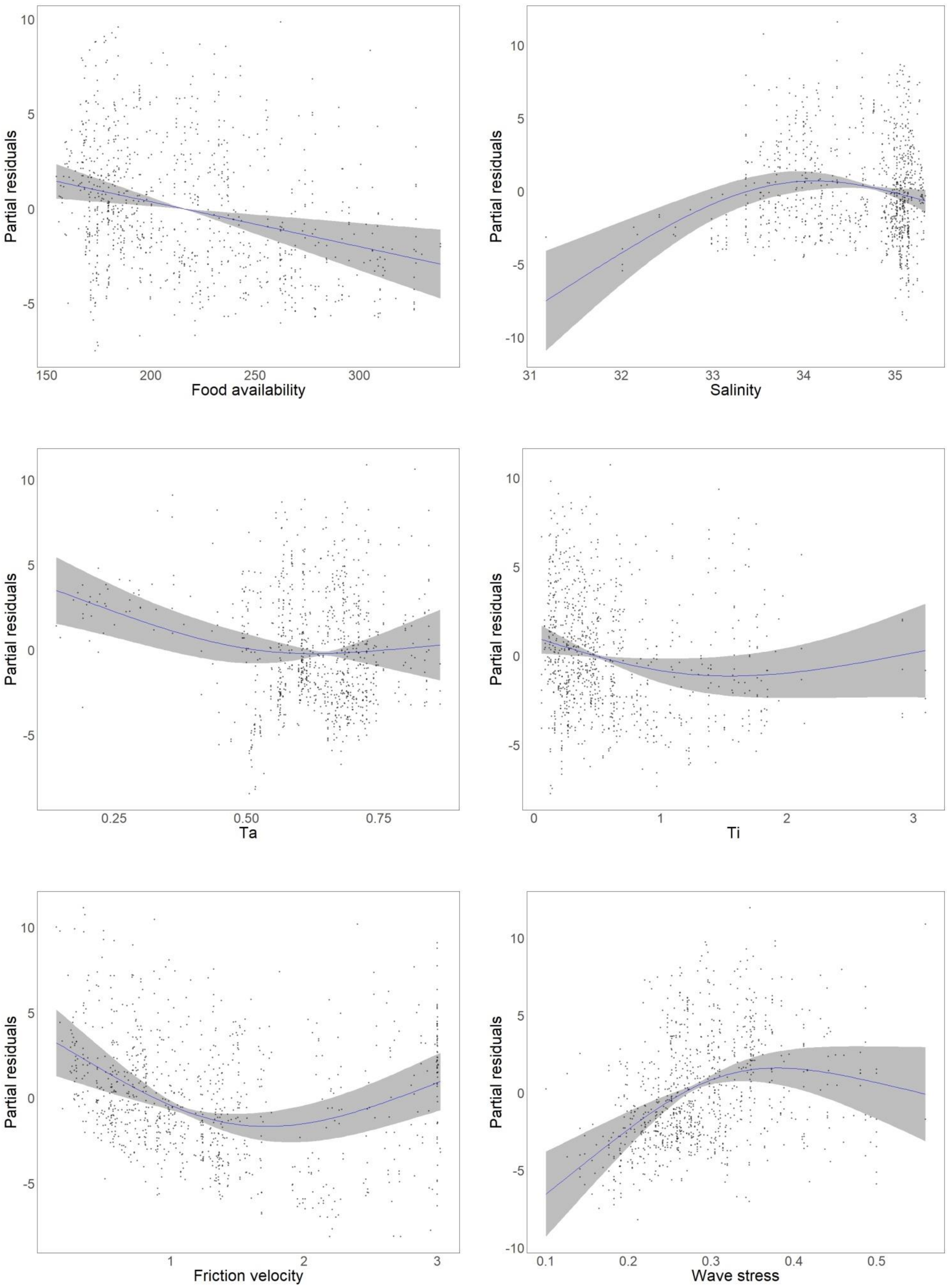


Figure G.16: Modelled relationships between environmental variables and mTDI in the English Channel.
Grey shading represent the 95% confidence interval

c. Partial-TDI (pTDI)



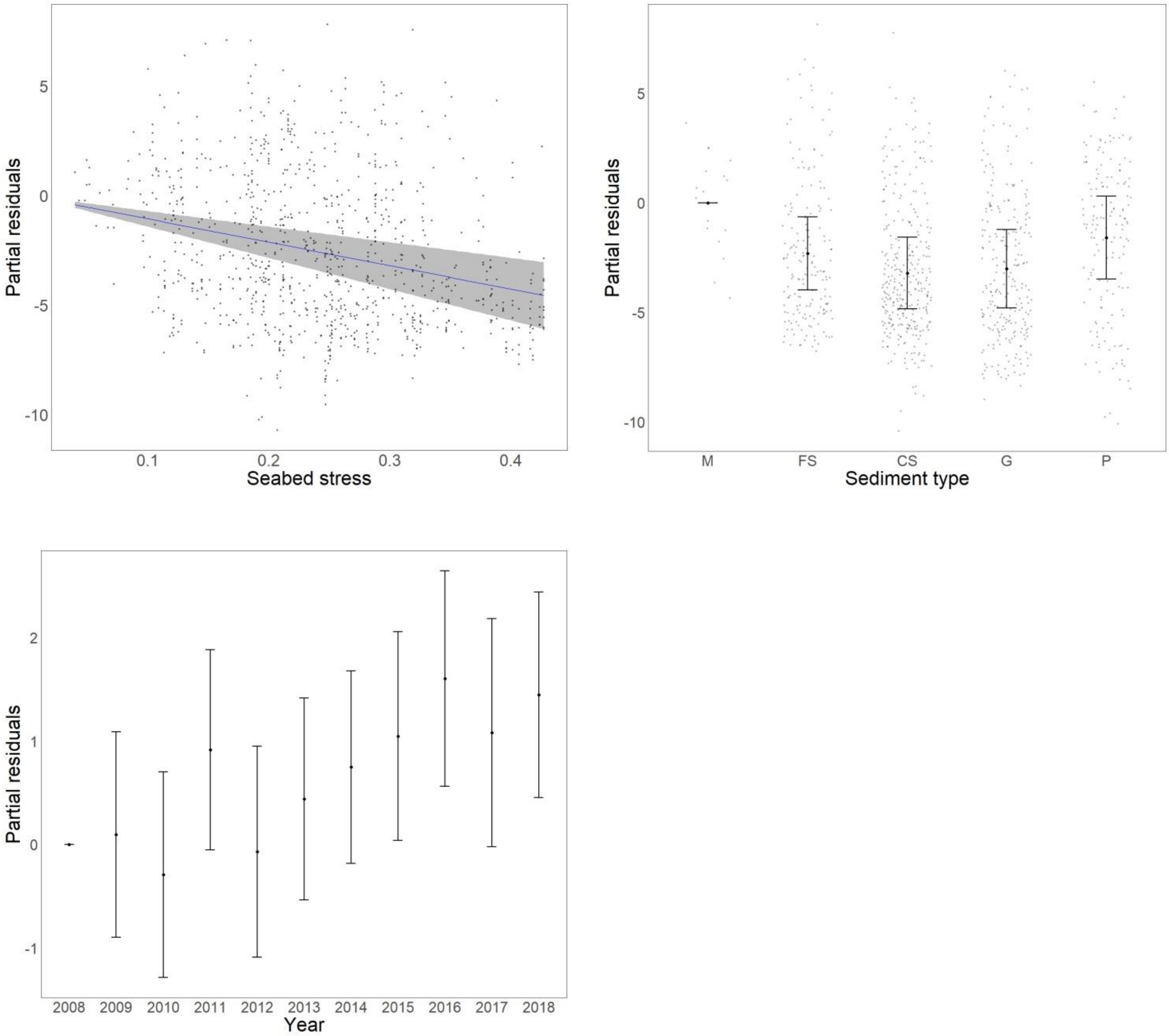


Figure G.17: Modelled relationships between environmental variables and pTDI in the English Channel.
Grey shading represent the 95% confidence interval

d. mT

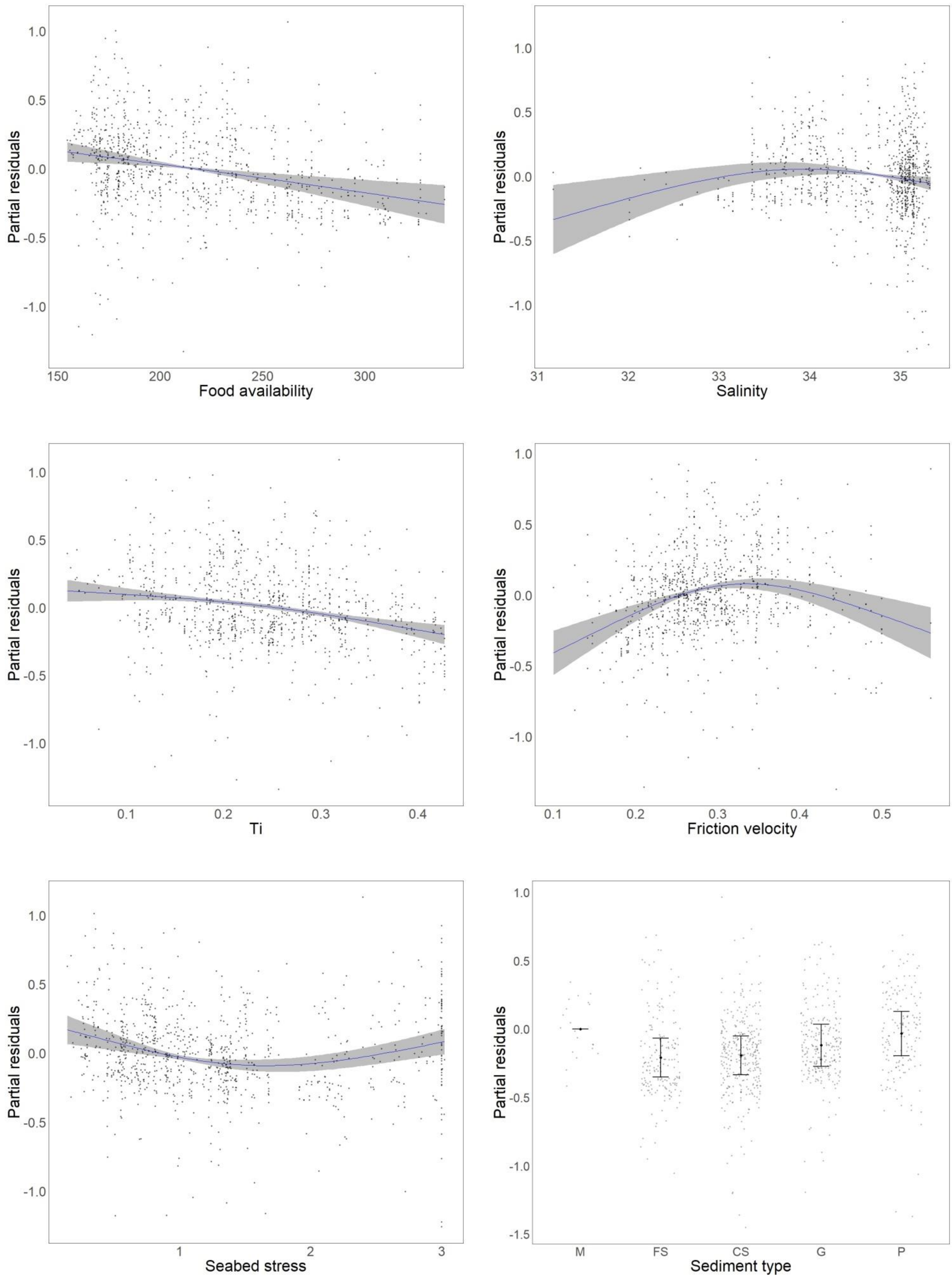


Figure G.18: Modelled relationships between environmental variables and mT in the English Channel.

Appendix H. Detecting adverse effect on seabed integrity. Part 1: Generic sensitivity indices to measure the effect of trawling on benthic mega-epifauna

Ecological Indicators

Cyrielle Jac, Nicolas Desroy, Grégoire Certain, Aurélie Foveau, Céline Labrune, Sandrine Vaz

Detecting adverse effect on seabed integrity. Part 1 : Generic sensitivity indices to measure the effect of trawling on benthic mega-epifauna

Cyrielle JAC[a]*, Nicolas Desroy[b], Gregoire Certain[a], Aurélie Foveau[b], Céline Labrune[c], Sandrine Vaz[a]

[a] MARBEC, Univ Montpellier, Ifremer, IRD, CNRS, Sète, France
[b] Ifremer, Laboratoire Environnement et Ressources Bretagne Nord, 38 Rue du Port Blanc, 35800 Dinard, France
[c] Sorbonne Université, CNRS, Laboratoire d'Ecogéochimie des Environnements Benthiques, LECOB UMR 8222, F-66650 Banyuls-sur-Mer, France
* corresponding author : cyrielle.jac@ifremer.fr

Abstract

The benthic fauna of European continental shelves is a severely impacted community, mostly due to intense bottom trawling activity. Trawling effect may be dependent on the spatial and temporal distribution of abrasion, the habitat type including natural perturbation intensity and the fishing gear used. Nonetheless, there is an urgent need to identify or develop indices likely to measure the effect of trawling. For this purpose benthic fauna by-catch monitored in scientific trawl surveys carried out in all European waters in the frame of the Common Fishery Policy Data Collection Multiannual Program may be used. Benthic invertebrates data used in this study were collected during scientific bottom trawl surveys covering the English Channel, the North Sea and the North-West Mediterranean. Swept area ratios derived from VMS data were used to quantify the intensity of fishery induced abrasion on the seabed. Fifteen indices were investigated: taxonomic diversity metrics, functional diversity indices and functional indices, the two later based on sensitivity traits to physical abrasion. Their properties, such as their capacity to detect trawling effect, their statistical behavior or their ability to inform on community structure, were investigated. Among them, fours indices specific to fishery effect detection based on biological traits appeared to be the best performing benthic indices regarding these requirements: Trawling Disturbance Index (TDI), modified-Trawling Disturbance Index (mTDI), partial-Trawling Disturbance Index (pTDI), modified sensitivity index (mT). Maps of the distribution pattern of seabed sensitivity captured through each of these four indices were produced. This work has highlighted the need to use specific indices to monitor the effect of trawling on benthic communities but also that the use of different indices may be necessary to carry out this monitoring in all European waters.

Keywords: Benthic sensitivity, Trawling effect, Indices, Seabed integrity, MFSD

1. Introduction

The European Union drew up the Marine Strategy Framework Directive (MSFD) in 2008 to achieve or to maintain good environmental status in the marine environment in 2020 at the latest. To control degradation factors and manage the consequences, the MSFD is divided in descriptors and criteria for which indicators and threshold values must be defined. Two of these descriptors, biodiversity (D1) and seabed integrity (D6) require that the human impact on benthic habitats is assessed regularly.

Bottom trawling and dredging are the most widespread source of anthropogenic disturbance occurring on over large surfaces of continental shelf benthic habitats (Hiddink et al.

2007; Halpern et al. 2008). Before the early 2000s, abrasion was derived from UE logbook that compiled information of fishing skippers, but records of fishing locations were not always reliable and were only confirmed for a small proportion of vessels by ship- or air-based surveillance (Lee et al. 2010). The development of satellite-based vessel monitoring systems (VMS) has revolutionized the knowledge of the spatial and temporal distribution of abrasion, providing large-scale high-resolution information of European fishing activity for largest fishing vessels (Lee et al. 2010; Eigaard et al. 2016). VMS data inform on the time spent to fish per area and time units (Lee et al. 2010). Knowing that differences in the gear and boat characteristics between activities (otter trawls, twin trawls, Danish seines, beam trawls or dredges) cause different benthic impacts, the utilization of total swept area ratio, per area and time unit better reflects fishing impact on seabed than the number of fishing hour (Eigaard et al. 2016, 2017). In Europe, the footprint of bottom impacting fishing on the continental shelf varies between 53-99% per habitat type of the seafloor down to 200m (Eigaard et al. 2017), with patchy spatial and temporal distributions (Rijnsdorp et al. 1998, 2018; van Denderen et al. 2015).

Numerous studies have shown that bottoms trawls damage biogenic structure, disturb seabed sediments and affect the structure and the functioning of the benthic invertebrate community mainly by changing the species composition (Collie et al. 2000b; Rumohr and Kujawski 2000; Thrush and Dayton 2002; Hiddink et al. 2006; Rijnsdorp et al. 2018). The differences in species composition between trawled and un-trawled area indicate that each benthic species has different degree of sensitivity (Hiscock et al. 1999; Borja et al. 2003; Foveau et al. 2017) to trawling pressure. Most studies to evaluate the impact of fishing activities on benthic communities are conducted relatively nearshore with restricted spatial coverage (Brind'Amour et al. 2014) and focused mainly on the infauna, with a sampling realized with grabs, boxcorers or dredges (van Loon et al. 2018). Benthic data from scientific bottom trawl surveys carried out in all European waters in the frame of the Common Fishery Policy Data Collection Multiannual Program could be used to study the impact of trawling on the benthic mega-epifauna because 1) they represent the benthic fauna fraction the more directly affected by bottom-contacting fishing and 2) they integrate assemblages' composition over large areas (3–4 km) and are more representative of larger scale habitat structure (Foveau et al. 2017).

Many indices exist and detect differences or changes in the benthic fauna community in relation to anthropogenic pressure, but not all are effective for physical disturbance like trawling impact. Several univariate indices such as species richness, community biomass, Shannon index (Shannon and Weaver 1963), Margalef diversity (Margalef 1958), Pielou evenness (Pielou 1969) and Simpson index (Simpson 1949) have already been tested for assessing effects of trawls on benthic communities (Schratzberger et al. 2002; Svane et al. 2009; Atkinson et al. 2011; van Loon et al. 2018). Despite variable results in the literature, the use of diversity indices can highlight the disruptive effect of fishing on benthic communities (Blanchard et al. 2004). Other indices, specific to the trawling pressure and based on biological traits of benthic species like the Trawl Disturbance Indicator (TDI, de Juan and Demestre 2012) and the vulnerability index (Certain et al. 2015) appear as good candidates to evaluate trawling impact. Species' responses to trawling is believed to be mainly determined by their biological traits (Bremner et al. 2003a; de Juan et al. 2009). The selected biological traits (mobility, fragility, position on substrata, average body size and feeding mode), were chosen because they determine individual sensitivity to trawling and they can be easily related to other concepts such as recovery capacity and vulnerability. In the present study, species vulnerability is understood as resulting from both species sensitivity and its exposure level to the disturbance. Finally, modelling approaches were developed to study the effect of trawling on benthic community like the Relative Benthic Status method (RBS; Pitcher et al. 2017), based on longevity or composition of benthic community

(Eigaard et al. 2017; Rijnsdorp et al. 2018) or method based on biomass reconstruction (Lambert et al. 2011).

In view of the quantity of existing indices, previous studies have listed different requirements to inform on indicators quality and to classify potential indicators to be used for the assessment of the trawling impact on benthic communities (Queirós et al. 2016; ICES 2017b). Thus indices must: reflect features of ecosystems that are relevant for structure and function (requirement 1: Theoretical basis), be sensitive to changes in trawling (requirement 2: Sensitivity), provides rapid and reliable feedback on the consequences of management (requirement 3: Responsiveness). The quality of sampling method (requirement 5) and the nature and quality of data (requirement 6: Quality of underlying data) must also be taken into account in the indices selection process. Finally, the existence of reference state (requirement 7), the cost of method (requirement 8: Cost effectiveness) and the cross regional applicability (requirement 9) were the three other requirements proposed to evaluate the quality of an indicator.

The aims of this study were to (a) list or define indices susceptible to measure the effect of trawling on benthic fauna that can be used in all European waters (b) test different properties of these indices and in particular their ability to relate to trawling intensity and to measure assemblages structures and (c) identify a suitable set of indices to be used for monitoring trawling impact on benthic communities in the frame of the MSFD requirements.

2. Methods

2.1. Study areas

The present study was performed in four different areas affected by contrasted and sometimes intense trawling pressure: the Gulf of Lion, the Eastern coast of Corsica, the English Channel and the southern North Sea.

The Gulf of Lion, situated in the NW Mediterranean, is a wave-dominated continental shelf incised by a number of submarine canyons and characterized by a micro-tidal regime (Tesi et al. 2007). Fine sediments (sand and mud) represent the majority of sedimentary types present in this area (Roussiez et al. 2005).

The Eastern coast of Corsica closes the north of the Tyrrenean Sea and is defined by a relatively small shelf, which width varies from 5 km in the north to over 25 km in the South. Depth increases rapidly with distance to the coast and reaches about 900m in the central zone, between Corsica and Italy (http://www.emodnet.eu/bathymetry). Seabed is constituted of detritic sediments on the shelf and of mixed sandy to coarse sediment on the slope that are gradually replaced by deep-sea muddy sands and muds (http://www.emodnet.eu/seabed-habitats). This area is at present relatively sheltered from many anthropogenic threats such as intensive fishery.

The English Channel is a shallow epicontinental sea situated between France and England, subjected to megatidal currents (Larsonneur et al. 1982; Salomon 1990). Depth does not exceed 120m, except in the Hurd Deep in the western basin, and seabed is constituted of fine sediments (fine sand and mud) in bays and estuaries and coarser sediments in offshore areas or area more exposed to tidal currents (Larsonneur et al. 1982).

The North Sea is an extensive epicontinental sea surrounded by seven states (United Kingdom, France, Belgium, Netherlands, Germany, Denmark and Norway). The regime is macrotidal and depth increases northwards with a mean of 70m (Huthnance 1991). Seabed composition is dominated by sandy substrates, with locally some areas of muddy or mixed sediments (Diesing et al. 2013).

2.2. Biological data

Benthic fauna's samples, considered as bye-catch, were opportunistically collected and monitored (Callaway et al. 2002; Reiss et al. 2006; Brind'Amour et al. 2009, 2014) during four scientific bottom-trawling surveys. For each survey, species were sorted, identified, counted and weighed.

In the Mediterranean Sea, Mediterranean International Trawl Surveys (MEDITS , Jadaud et al. 1994) is conducted yearly in June since 1994 but benthic fauna is studied only since 2012. The sampling gear used is a bottom trawl made of four panels, well adapted for work in all depths (10 – 800 m), with a 20 mm stretched mesh size at the cod-end. The sampling scheme is stratified by depth evenly distributed over the whole study area. Hauls are 30 minutes long at 4 knots above 200 meters and 60 minutes long at the same speed below 200m (MEDITS 2017). Due to the change in trawling duration beyond 200 m depth and the transition from photic to aphotic zone, only data sampled between 0 and 200 m were used in this study (448 stations in total, including approximately 54 stations in the Gulf of Lion and 10 in Corsica sampled each year from 2012 to 2018; Table 1).

In the English Channel and the North Sea, three scientific trawling cruise are carried out: International Bottom Trawl Surveys (IBTS) yearly in January/February since 1970 (Auber 1992), Channel Ground Fish Surveys (CGFS) yearly in October since 1988 (Coppin and Travers-Trolet 1989) and CAMANOC in September 2014 (Verin and Travers-Trolet 2014). For all three surveys, the sampling gear used is a Very High Vertical Opening bottom trawl with a 20 mm stretched mesh size at the cod-end. The sampling is randomly stratified evenly distributed over the whole study area and hauls are carried out during daytime for 30 minutes at 4 knots (ICES 2015, 2017a).

Data from CAMANOC and CGFS surveys were merged as the sampling occurred at the same period and in the same area: the English Channel. A total of 1055 stations sampled in September/October (CGFS and CAMANOC, 2008-2018) and 761 stations in January/February (IBTS, 2009-2018) were used in this study (Table 1).

Table 53 : Number of observations used in this study

	SURVEY (number of trawls)			
Year	MEDITS (Gulf of Lion and Eastern coast of Corsica)	IBTS (English Channel and southern North Sea)	CGFS (English Channel)	CAMANOC (English Channel)
2008			98	
2009		50	98	
2010		75	92	
2011		87	99	
2012	65	84	89	
2013	63	85	93	
2014	64	82	94	40
2015	64	90	90	
2016	64	72	81	
2017	64	70	66	
2018	64	66	115	

2.3. Data preparation

Commercials species (*Homarus gammarus*, *Crangon crangon*, *Maja brachydactyla*, *Pecten maximus*, *Aequipecten opercularis*, *Palaemon serratus*, *Nephrops norvegicus*, *Buccinum undatum*, *Cancer pagurus*, *Aristaeomorpha foliacea*, *Aristeus antennatus*, *Parapeneus longisrostris*, *Bolinus brandaris)* and cephalopods were removed from the dataset because they may be targeted by the fishery. As a result, abrasion distribution may not be independent from the presence of these species.

Biomass data were preferred to abundance data, as abundance could not be estimated for a number of colonial species such as hydroids or sponges. Data were standardized according to trawling swept area and expressed in g.km^{-2}.

To limit identification errors or biais due to the irregular presence of expert scientific staff, some taxons were aggregated at higher taxonomic levels. The following procedure was used: to be kept at its initial taxonomic level, a given species had to be observed in 90% of the sampled years (5 years for MEDITS, 8 years for IBTS and 9 years for CGFS), otherwise it was iteratively aggregated at higher taxonomic level (genus, family, order, class, phylum) until it fulfilled this criteria. For example, the ascidian *Molgula appendiculata,* observed only 2 years, was aggregated into the genus *Molgula*, which was observed every year. If, after applying this treatment, a given phylum was observed in less than 90% of the sampled years, it was removed from the analyses (Foveau et al. 2017).

2.4. Biological sensitivity trait*s*

Following on previous studies, a set of five biological traits were selected to characterize potential responses of organisms to physical abrasion (de Juan and Demestre 2012; Bolam and Eggleton 2014; Foveau et al. 2017). These traits are (i) position of organisms in the sediment; (ii) feeding mode; (iii) mobility capacity; (iv) adult size and (v) fragility of the structure of organisms. Each trait was subdivided into multiple “modalities” to encompass the range of possible attribute of all taxa. To allow quantitative analysis, a score was assigned to each modality, varying from low sensitivity (0) to high sensitivity (3) (Table 2 ; Foveau et al. 2019). When a taxon was aggregated at higher taxonomic level, scores were assigned to the group using the highest value observed in this group for each trait after that the homogeneity of each modality’s score was investigated. The standard deviation of any given index score had to be below 1.5 and that of the sum of scores had to be below 2.5 (Foveau et al. 2017). In the opposite case, the taxonomic group was removed from the analysis. When the deleted taxon represented more than 25% of the total station’s biomass, the station was removed from the dataset. A species-traits matrix was produced for each survey in order to compute functional indices

Table 54 : Biological sensitivity traits to physical abrasion and associated scores

Scores	Position in the sediment	Feeding mode	Mobility	Adult size	Fragility
0	Deep burrowing	Scavengers	Highly mobile (swimming)	Small (<5 cm)	Hard shell, burrow, vermiform, regeneration
1	Surface burrowing (first cm)	Deposit feeders/predators	Mobile (crawling)		Flexible
2	Surface		Sedentary	Medium (5-10 cm)	No protection
3	Emergent	Filter feeders	Sessile (attached)	Large (>10 cm)	Fragile shell/structure

In most cases, deleted taxon due to taxonomic or functional trait uncertainties accounted for less than 10% of the total biomass sampled. However, in some station, deletions represent more than 25% of biomass. They cause differences in the number of stations used for the calculation of the different type of indices (Table 3).

Table 3: Number of stations used for indices calculations in each studied area.
Calculation of univariates indices were performed with all available data (all sampling stations). GoL = Gulf of Lion

Type of indices	MEDITS - GoL	MEDITS - Corsica	IBTS	CGFS + CAMANOC
Taxonomic diversity indices	378	70	761	1055
AMBI	373	68	711	1031
Functional indices	372	68	721	1006

2.5. Fishing impact data

To compute the abrasion induced by fishery over the seabed, expressed as swept surface area ratio per year, fishing trajectories and gear type were used and aggregated yearly following Eigaard et al. (2016) methodology. In the English Channel and southern North Sea, the spatial and temporal distribution of bottom fishing was estimated from Vessel Monitoring System (VMS) data for ground-towed gears (beam trawlers, dredgers and otter trawlers) over the 2009-2017 period over a 3'x3' resolution (ICES 2019c). The data was readily available and downloaded in March 2019 through OSPAR website (https://www.ospar.org), in which they are referenced as "OSPAR Bottom Fishing Intensity – Surface".

For the French part of Mediterranean Sea, a similar approach was taken using available VMS data aggregated monthly (between 2009 and 2017) on a 1'x1' grid (fishing duration in hour by country, month, vessel length class and gear type) (Jac and Vaz,2018).

Intra-annual (only in the Mediterranean Sea where monthly abrasion data were available) and inter-annual variabilities of abrasion distribution over the available period were explored through pair-wise correlations and found to be statistically negligible. It was then decided to use the highest (90^{th} percentile) abrasion value over the entire available time series at each location to avoid overlooking past impacts and reflect the probably long recovery time needed for sensitive species. This 90^{th} percentile was chosen to filter out the most extreme values that may be related to measurement or computation errors. As a result, a map of 90^{th} inter-annual percentile of the abrasion in each study area was computed over the respective available period of time for each area, at 3'x3' resolution in the English Channel and southern North Sea and at 1'x1' resolution in Mediterranean Sea (Figure 1).

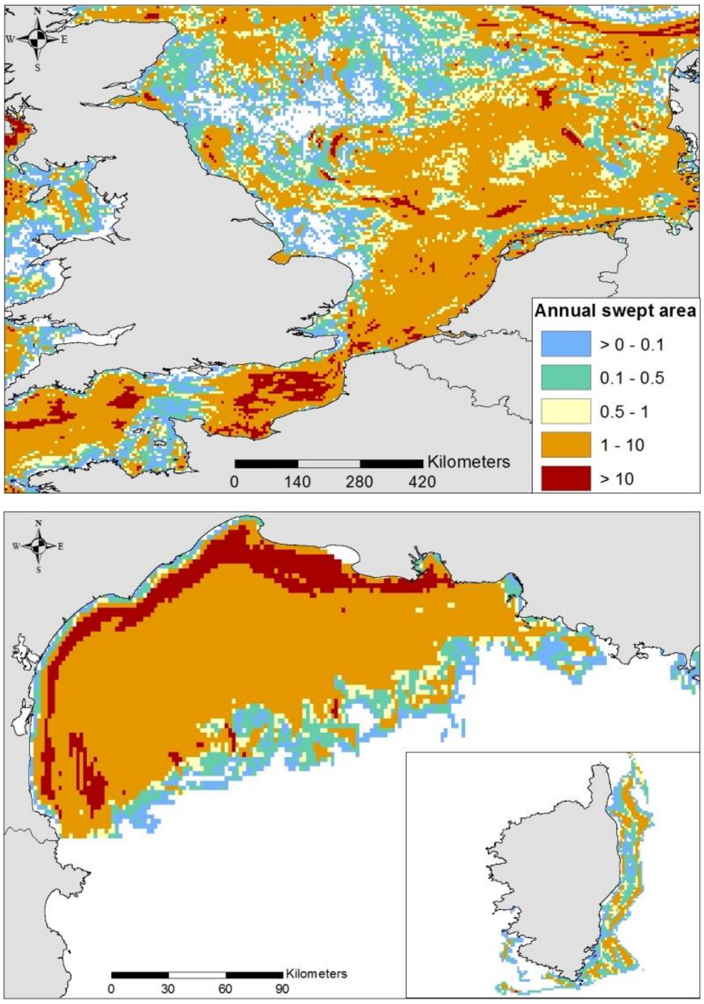


Figure 1: 90^{th} inter-annual percentile of the abrasion in the English Channel and southern North Sea during the period 2009-2017 (a) and in the Gulf of Lion during the period 2009-2017 (b)

2.6. Biotic Indices

Three types of sensitivity indices were investigated: 1) taxonomic diversity metrics; 2) functional diversity indices and 3) functional sensitivity indices specifically constructed to detect impacts on benthic communities. The effect of trawling on the biomass of the community was also studied.

Five common taxonomic diversity indices were calculated: species richness (S, the total number of taxon), Margalef index (Margalef 1958), Shannon diversity (H', Shannon and Weaver 1963), Pielou evenness (J', Pielou 1969) and Simpson index (λ, Simpson 1949). The first two focus on species or individuals richness while the others are weighted by abundance or biomass to assess equitability between species (J') or give more or less influence to rare species (H' and λ). These indices were calculated in R, using the vegan 2.5-2 package (Oksanen et al. 2019) and by using individual biomass.

Functional Richness (FRic, Cornwell et al. 2006; Villéger et al. 2008), Functional Specialization (Fspe; Bellwood et al. 2006, Villéger et al. 2010), Functional Evenness (FEve; Mason et al. 2005) and Functional Divergence (FDiv; Mason et al. 2005) were investigated using the species-traits matrix described earlier. These indices were used because they highlight variation in specific function among benthic communities (Mouillot et al. 2013a). Before calculating functional diversity indices, Multiple Correspondence Analysis (MCA) was performed with package PCAmixdata 3.1 (Chavent et al. 2017) on the species-traits matrix because the traits are categorical and functional indices were designed for continuous traits (Villéger et al. 2008). Scores from MCA were used with species biomass matrix to calculate functional indices (Mouillot et al. 2013a). Functional richness (FRic) allows quantifying the amount of function available in assemblages (there is a positive correlation between the value of the index and the number of functions). Functional Specialization (FSpe) quantify the specialization degree of species based on the assumption that generalist are at the center of the functional space while specialist are on the periphery. This metric quantify the radial distribution of species on the functional space, the higher the index is, the more specialized species are (Mouillot et al. 2013a). Functional evenness (FEve) may be defined as the homogeneity of the distribution of biomass in the functional space. FEve varies between 0 (main species in term of biomass have same functions) and 1 (main species in term of biomass are functionally different) (Villéger et al. 2010). Functional divergence (FDiv) quantifies if the main species in term of biomass are near to the limits of the multidimensional volume of the functional traits space. This metric varies between 0 (main species in term of biomass are close to center of gravity of functional space) and 1 (main species in term of biomass species are very far from the center of gravity (Villéger et al. 2008).

Functional sensitivity indices are designed to detect particular impacts on communities. In contrast to functional diversity indices for which each trait level is given equal weight, semi-quantitative trait scoring indicates the potential sensitivity of each species to a given pressure. Functional sensitivity indices therefore integrate this scoring in their calculation. The tested indices were: AZTI Marine Biotic Index (AMBI ; Borja et al. 2000), Trawling Disturbance Index (TDI; de Juan and Demestre 2012), modified TDI (mTDI, Foveau et al. 2017), partial TDI (pTDI) and the modified vulnerability Index (mT; modified from Certain et al. 2015). TDI-derived indices were developed specifically to detect trawling impact, while mT is issued from a general framework allowing to address any pressure as long as specific sensitivity traits were available to detect it.

AMBI was developed to characterize the response of benthic communities of soft substrates to natural or anthropogenic disturbances, particularly the eutrophication, in coastal environments (Borja et al. 2000). Although this index is not appropriate to study the effect of physical pressures, as it was built to deal mainly with the effect organic enrichment on benthic communities, it was tested in this study because of its large use in studies of benthic fauna, particularly in the framework of the Water Framework Directive (van Hoey et al. 2015). It uses the percentages of abundance of each ecological group (G1 to G5; from sensitive to highly opportunistic species) which are known to differ according to the level of disturbance (Eq. 1).

$$(1)\quad AMBI = \frac{(0 \times \%G1) + (1.5 \times \%G2) + (3 \times \%G3) + (4.5 \times \%G4) + (6 \times \%G5)}{100}$$

For calculating TDI, mTDI and pTDI, scores of the five categories of sensitivity traits (Table 2) were summed for each species and this value is considered as the species sensitivity index (SI) to trawling disturbance. Thus, highly vulnerable species could have a maximum score of 15.

For the TDI (Eq. 2), species are distributed into five groups according to SI: group 1, SI ranged from 0 to 4; group 2, SI = 5-7; group 3, SI = 8-10, group 4, SI = 11-13 and group 5, SI = 14-15. The biomass of each group was calculated as the sum of biomass of all taxa within each group.

$$(2)\quad TDI_x = \frac{Log1 \times Log(G1_x+1) + Log(G2_x+1) + Log4 \times Log(G3_x+1) + Log8 \times Log(G4_x+1) + Log16 \times Log(G5_x+1)}{Log(N_x+1)}$$

where $G1_x$-$G5_x$ were the total biomasses of each group in the x^{th} observation and N_x the total biomass of the x^{th} observation

Another indice based on the species sensitivity was proposed by Foveau et al. (2017), the mTDI (Eq.3).

$$(3)\quad mTDI_x = \sum_1^{N_x} \frac{Bi_x}{Bn_x} \times SI_i$$

with N_x, the number of taxons in the x^{th} observation; Bi_x, biomass of the i^{th} taxon in the x^{th} observation; Bn_x, summed biomass of the x^{th} observation and SI_i, the sensitivity index (SI) of the i^{th} taxon

To focused only on sensitive species (SI >7) and thus try to better detect the effect of trawling, a further modification of mTDI was proposed (pTDI ; Eq. 4).

$$(4)\quad pTDI_x = \sum_1^{N_x} \frac{Bij_x}{Bn_x} \times SI_{ij}$$

with Bij_x, biomass of the i^{th} taxon of the list j of sensitive taxon (SI>7) in the x^{th} observation; and SI_{ij}, SI of the i^{th} taxon of the list j of vulnerable taxon, ; Bn_x, summed biomass of the x^{th} observation (including all observed taxa)

Values of these three indices are high when the biomass is dominated by sensitive species and decrease as they are replaced by less sensitive species in the assemblage.

For the calculation of the modified vulnerability Index (mT), the scores of all modalities were rescaled between 0.25 (low sensitivity) and 1 (high sensitivity) (Certain et al. 2015). A sixth trait was used for the calculation of mT: the protection status of each species. A score of 1 was attributed for species indexed on the Vulnerable Marine Ecosystems in Mediterranean Sea list (OCEANA 2016) and presents on the OSPAR list of threatened and/or declining species and habitats (OSPAR 2008). A score of 0.5 was attributed for all other species. The six traits were separated between direct and indirect factors. Although named vulnerability and sensibility factors respectively by Certain et al. (2015), they were renamed in this study to avoid confusion with the earlier definitions of these terms. Direct factors are relative measures of elements controlling the probability of being impacted by a given pressure type, trawling in our case. Indirect factors are relative measures of elements describing the conservation status of species and their indirect sensitivity to disturbance (e.g. filter feeders can be disturbed by the resuspension of sediments due to trawling).Then, for both type of factors, a hierarchy was established between primary factors that directly control the sensitivity and aggravation factors that may not be important on their own, but may worsen pre-existing sensitivity. The factor classification used in our study is detailed in Table 4.

Table 4: Direct and indirect factors and their hierarchical classification

	Short description	Factor type	Factor hierarchy
F_1	Position in the sediment	Direct	Primary
F_2	Mobility	Direct	Primary
F_3	Adult size	Direct	Primary
F_4	Fragility	Direct	Aggravation
F_5	Feeding mode	Indirect	Primary
F_6	Protection status	Indirect	Primary

The direct component of the index, t_i, of each individual taxon i, is obtained by applying equation (5) with $a_i = F_{i1} \times F_{i2} \times F_{i3}$, $g_i = F_{i4}$ and $\gamma = 0.5$. The indirect component of the index, s_i, of the i^{th} taxon is obtained by applying equation (5) with $a_i = (F_{i5} + F_{i6})/2$ and $g_i = 0$.

$$(5) \quad t_i = a_i^{\,1 - g_i/(g_i + \gamma)}$$

The modified vulnerability Index (mT_x) in then calculated as in equation (6).

$$(6) \quad mT_x = \ -\sum_{i=1}^{N_x} \frac{Bri_x}{t_i \times s_i}$$

with Bri_x, relative biomass of the i^{th} taxon of the station x and Nx the total number of taxon of the station x. This index tends to increase as the assemblage sensitivity increases.

All index calculations were performed using R version 3.4.2 (R Core Team 2017).

2.7. Indices evaluation and selection

In order to find which indices were most appropriate to monitor the impact of trawling on benthic communities, five different tests were carried out while distinguishing different surveys and geographic basins. The two first tests ensured that the index reflects the abrasion pressure. Thus, spearman correlation tests (Hollander and Wolfe 1973) were conducted to determine the correlation level between indices and abrasion in each area studied. Similarity, their spatial distribution was also tested with the calculation of an index of difference in spatial pattern (Lee et al., 2010). This indicator varies between 0 (same spatial pattern) and 1 (many differences in the spatial patterns). Three complementary tests were carried out to discriminate the indices having good correlations with abrasion. Thus, the percentage of variance of the community structure explained by each index was determined by performing a redundancy analysis (RDA; van den Wollenberg 1977) on the community biomass matrix and using each index in turn as sole constraining factor. The statistical behavior, and more particularly the nature of the distribution, of each index was also studied with the calculation of their skewness and kurtosis (Groeneveld and Meeden 1984) because a normal distribution of the index will facilitate the use of this index for further statistical regression approaches.

In order to simplify the assessment of all indices properties, a qualitative scoring scheme was used. For each study area and property studied, a score was attributed to each index by dividing its test value by the maximum test value obtained for this property in this area. For example, if the maximum value of spearman correlation in the Gulf of Lion was 0.5 for the TDI, the biomass that has a correlation value of 0.25, has a score of 0.25/0.5=0.5. In the particular case of the Lee index which decreases when spatial similarity increases, the minimum test value was divided by higher tests values. For skewness and kurtosis tests, when their values were between -1 and 1, a score of 1 was assigned for that index in the study area, conversely, a score of 0 was assigned if theirs values were outside these bounds. Scores were then summed over areas for each index and as the study considers four areas, the maximal score by index was 4. A total score was computed summing each index scores over each of the five properties investigated. A ponderation of 2 was applied for the two major properties, spearman correlation test and Lee spatial correlation index, as they were the main focus of the present study. So, the maximal total score per index was 28. Once a total score per index was computed, indices could be ranked according to their performance and those with the highest score were selected.

Spearman correlation between each selected indices was also studied to better understand the differences between them. Selected indices relations to abrasion by zones were illustrated using boxplot over abrasion classes. After log- or arcsin transformation of indices that do not have a normal distribution, each index were locally averaged over time and subjected to a variographic analysis and interpolated using ordinary krigging in R using package geoR 1.7-5.2.1(Ribeiro Jr and Diggle 2018). Kriged estimates were mapped to illustrate the distribution pattern of seabed sensitivity captured through each of the four indices.

3. Results

Results of the evaluation of the indices relationships to abrasion both in term of ranked values or spatial pattern are presented in the table 5 for each studied areas. Over all studied areas, the four indices which present the highest spearman correlation values (higher total score) are the TDI, the mTDI, the pTDI and the mT. For other indices, the Spearman correlation was often not significant, in particular in the North Sea (IBTS data) or even counter-intuitively reversed in Corsica. For the Lee index, all indices showed fairly similar results excepted Species richness, Margalef index and mT for which values were slightly better. The spatial correlation between indices and abrasion is lower in Corsica and in the North Sea (IBTS data) than in other areas.

Table 5: Results of spearman correlation tests and spatial correlation index for each index in the four studied areas. GoL = Gulf of Lion. CGFS + CAM = CGFS and CAMANOC surveys * indicates that P<0.05 ; ** indicates that P<0.01 ; *** indicates that P<0.001; ns indicates no significant difference. Grey shading indicates best scores

Indices	**Spearman correlation test**					**Spatial correlation (Lee index)**				
	GoL	Corsica	IBTS	CGFS + CAM	Score	GoL	Corsica	IBTS	CGFS + CAM	Score
Community biomass	-0.15**	-0.05	0.001	0.26***	1.28	0.71	0.58	0.76	0.66	2.37
Species richness	0.13*	0.31**	0.10**	0.09**	1.77	0.31	0.44	0.49	0.42	3.82
Margalef index	0.13*	0.32**	0.10**	0.11**	1.86	0.31	0.44	0.49	0.42	3.82
Shannon index	0.24**	0.13	0.01	-0.02	1.10	0.32	0.47	0.52	0.43	3.65
Pielou Index	0.21**	0.07	-0.10**	-0.11**	1.40	0.32	0.48	0.53	0.43	3.62
Simpson index	0.19**	0.15	-0.01	-0.03	1.01	0.32	0.46	0.52	0.42	3.61
FRic	0.19**	0.36**	0.09*	0.15**	2.44	0.38	0.58	0.58	0.56	3.02
FDiv	0.08	-0.01	-0.14*	-0.21**	1.00	0.30	0.54	0.56	0.41	3.55
FEve	0.21**	-0.07	0.01	-0.11**	1.11	0.30	0.56	0.57	0.42	3.50
FSpe	0.14**	0.28*	0.03	0.05	1.41	0.30	0.53	0.54	0.41	3.60
AMBI	-0.26**	0.36**	0.003	-0.08**	1.99	0.42	0.57	0.58	0.52	3.02
TDI	-0.33**	0.07	-0.35***	-0.34***	3.08	0.32	0.56	0.57	0.47	3.34
mTDI	-0.31**	-0.08	-0.28**	-0.32***	2.80	0.31	0.52	0.53	0.42	3.59
pTDI	-0.26**	-0.09	-0.35***	-0.37***	3.01	0.30	0.72	0.72	0.61	2.87
mT	-0.34**	-0.01	-0.22**	-0.30***	2.47	0.29	0.50	0.50	0.37	3.86

The measure of percentage of variance of the community structure explained by each index and skewness and kurtosis tests are presented in table 6. Almost all indices had a close to normal distribution in at least 3 of the 4 studied areas; only community biomass, FRic and FSpe did not. The percentage of community structure variance explained by each index is very variable from one area to the next. Apart from FRic and FEve, all indices based on biological traits better explained the community structure (higher score).

The total scores were computed by summing all scores for each type of test (Table 5 & 6). According to this result, the four better performing indices were TDI, mTDI, pTDI, and mT.

Table 6: Results of RDA and normality tests for each index in the four studied areas
GoL = Gulf of Lion; CGFS + CAM = CGFS and CAMANOC surveys. Grey shading indicates best scores

Indices	Percentage of variance of the community structure explained					Skewness					Kurtosis					Total score
	GoL	Corsica	IBTS	CGFS +CAM	Score	GoL	Corsica	IBTS	CGFS +CAM	Score	GoL	Corsica	IBTS	CGFS + CAM	Score	
Community biomass	4.8	19.8	0.4	0.9	1.17	5	1.8	17.07	11.45	0	31.24	2.60	365.71	166.16	0	8.47
Species richness	1.3	14.5	2.9	0.9	1.13	0.48	0.91	0.89	0.73	4	-0.19	-0.02	0.64	-0.45	4	20.31
Margalef index	1.4	14.5	2.9	0.9	1.13	0.48	0.91	0.89	0.72	4	-0.19	-0.02	0.64	0.66	4	20.49
Shannon index	12.0	15.7	2.0	1.5	1.94	-0.75	0.03	-0.19	-0.09	4	-0.27	-0.72	-0.64	-0.45	4	19.44
Pielou Index	13.0	17.5	1.0	1.2	1.88	-0.95	-0.41	-0.25	-0.37	4	0.046	-0.73	-0.4	-0.33	4	20.28
Simpson index	11.0	16.2	1.4	1.4	1.79	-1.47	-0.54	-0.74	-0.78	3	1.39	-0.60	-0.36	-0.21	3	17.03
FRic	1.8	5.8	1.4	0.6	0.63	1.33	2.06	1.26	4.34	0	2.43	3.57	-0.41	32.40	1	12.55
FDiv	7.3	20.8	0.7	5.6	2.17	-0.43	-0.61	1.26	-0.27	3	-0.50	-0.16	-0.41	-0.65	4	18.27
FEve	2.4	0.7	0.4	0.6	0.35	0.14	-0.076	2.10	0.25	3	0.08	-0.40	2.43	0.23	3	15.57
FSpe	8.1	32.7	3.4	6.3	3.12	0.11	-0.61	2.28	1.53	2	-0.39	-0.75	8.73	1.85	2	17.14
AMBI	6.1	17.2	6.2	5.5	2.82	0.44	0.65	0.76	0.95	4	-0.46	-0.48	0.20	1.39	3	19.84
TDI	8.1	16.1	6.4	4.4	2.79	-0.14	-0.34	1.19	0.73	3	0.10	-0.77	0.35	-0.25	4	22.63
mTDI	11.9	13.5	6.1	4.2	2.93	-0.10	-0.32	1.56	0.96	3	-0.75	-0.40	1.75	0.68	3	21.68
pTDI	7.8	12.5	2.5	6.5	2.37	-0.05	-0.44	1.10	0.67	3	-0.55	0.36	0.04	-0.75	4	21.13
mT	13.0	8.5	5.4	2.7	2.53	0.32	-0.35	-0.40	1.45	3	-0.32	0.19	0.11	5.63	3	21.19

All TDI derived indices were very correlated by construction as were Species richness to Margalef indices or Shannon, Pielou and Simpson indices (Table S1). Moreover, since the strength of the relationship to abrasion is given precedence over the other investigated properties, it is only natural that the best performing indices end up mechanically correlated with each other (and with abrasion).

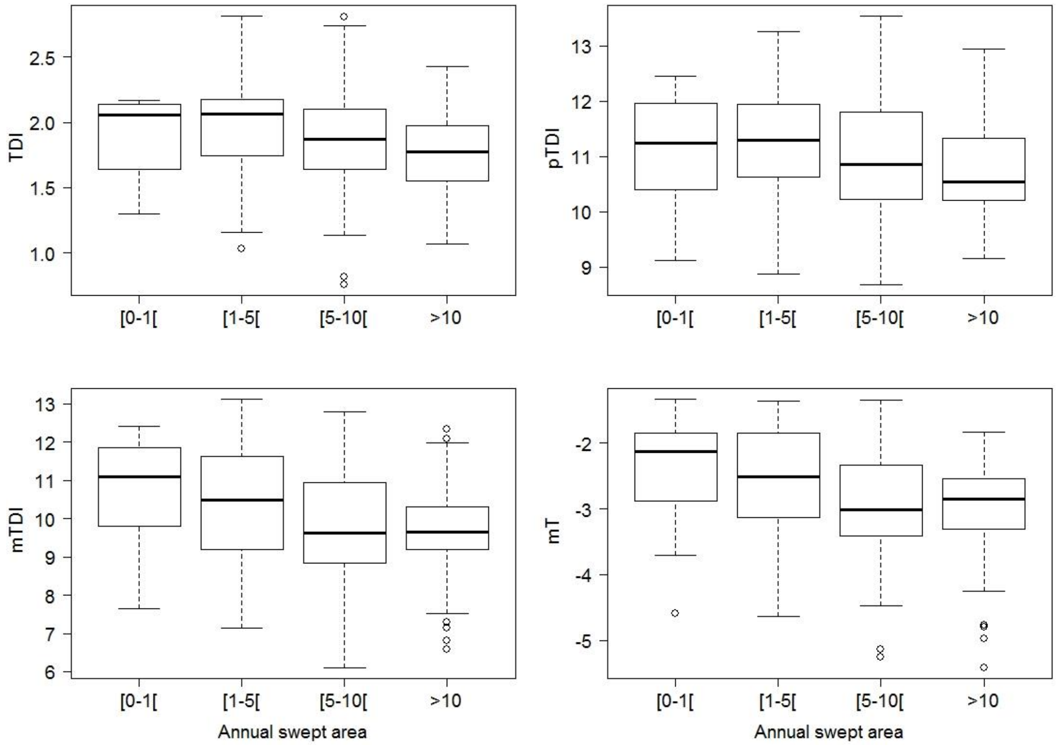


Figure 2: Values of the four selected indices by class of abrasion in the Gulf of Lion

For all indices and studied areas, overall values of indices appeared to decrease with abrasion (Figure 2, 3, 4 & 5) which was already revealed by significantly negative (although weak) correlation between the indices and abrasion (Table 5). For the majority of indices, variations of index values in abrasion class were very high as for example for the pTDI (in CGFS and CAMANOC surveys; Figure 5) where the index varies between 0.07 and 15 for an abrasion below 1 and between 0.006 and 14 for an abrasion higher than 10.

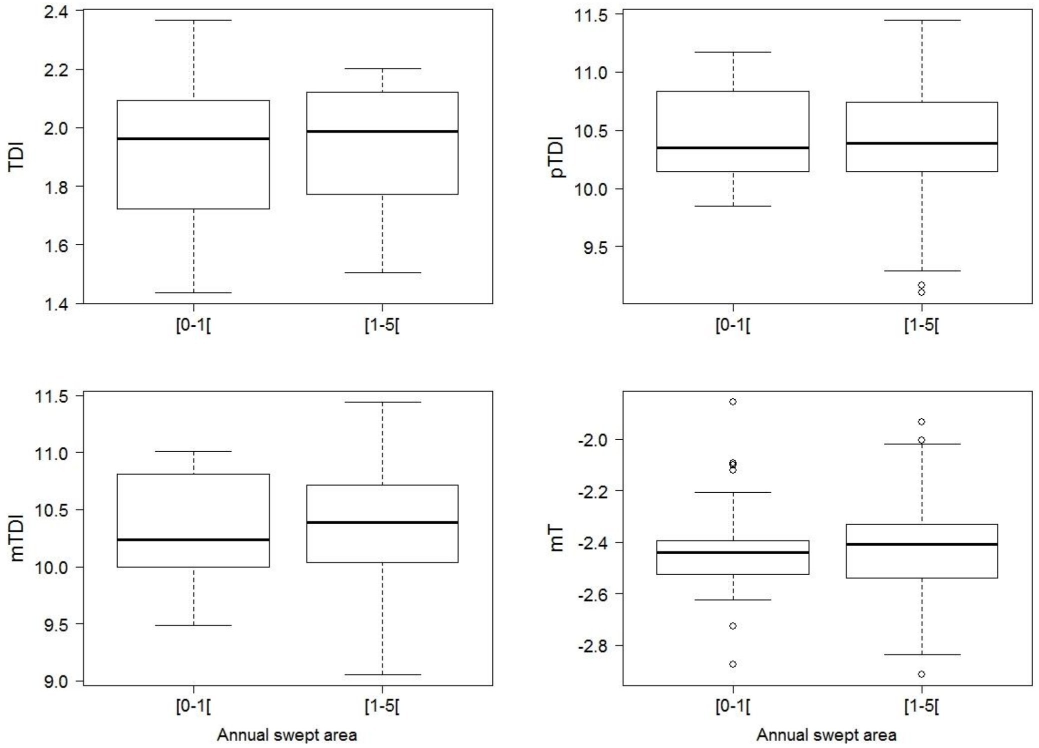


Figure 3: Values of the four selected indices by class of abrasion in Corsica

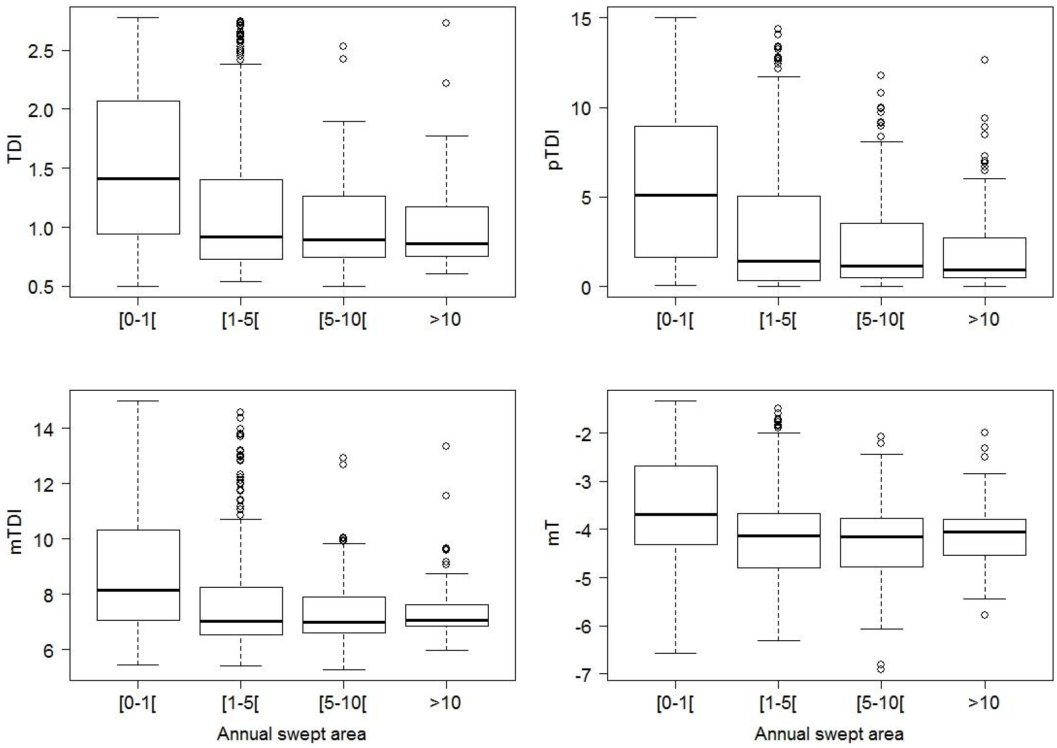


Figure 63: Values of the four selected indices by class of abrasion for the IBTS data (eastern English Channel and southern North Sea)

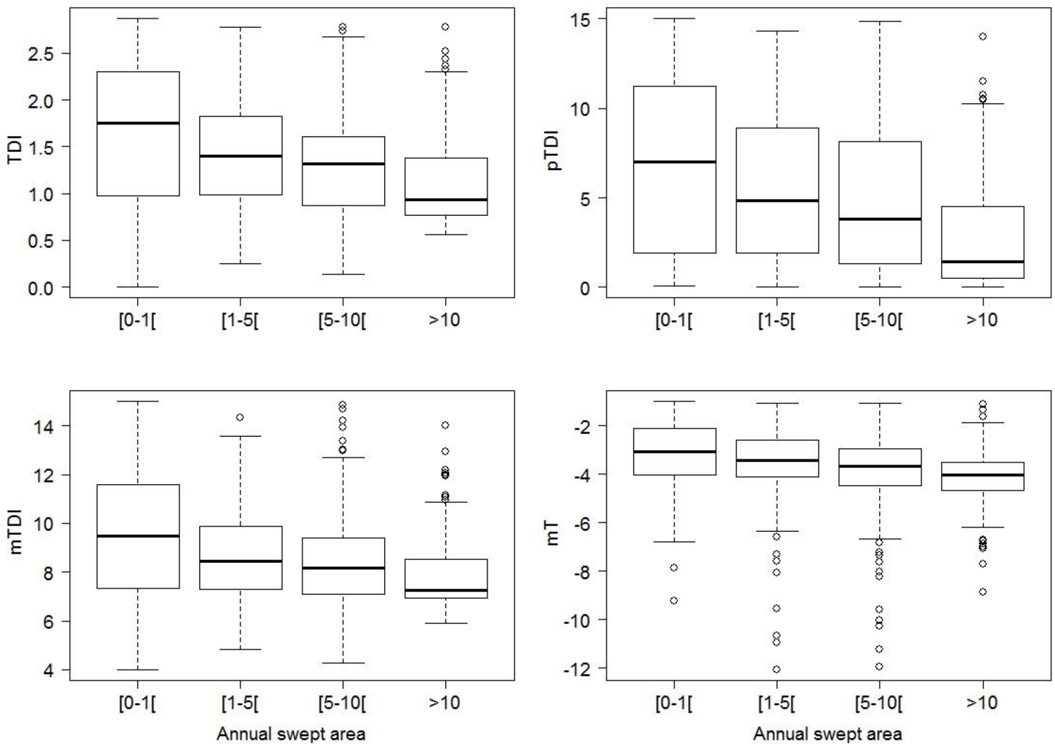


Figure 5: Values of the four selected indices by class of abrasion for the CGFS and CAMANOC data (English Channel)

The distribution patterns of the trawling sensitivity of the benthic communities, in the Gulf of Lion, were almost the same for the four indices (Figure 6). Thus, the degree of sensitivity of the communities was positively correlated with the distance to the coast, with communities that were not very sensitive to trawling in the coastal zone (lower values of the indices) and communities that were much more sensitive offshore (higher values of the indices).

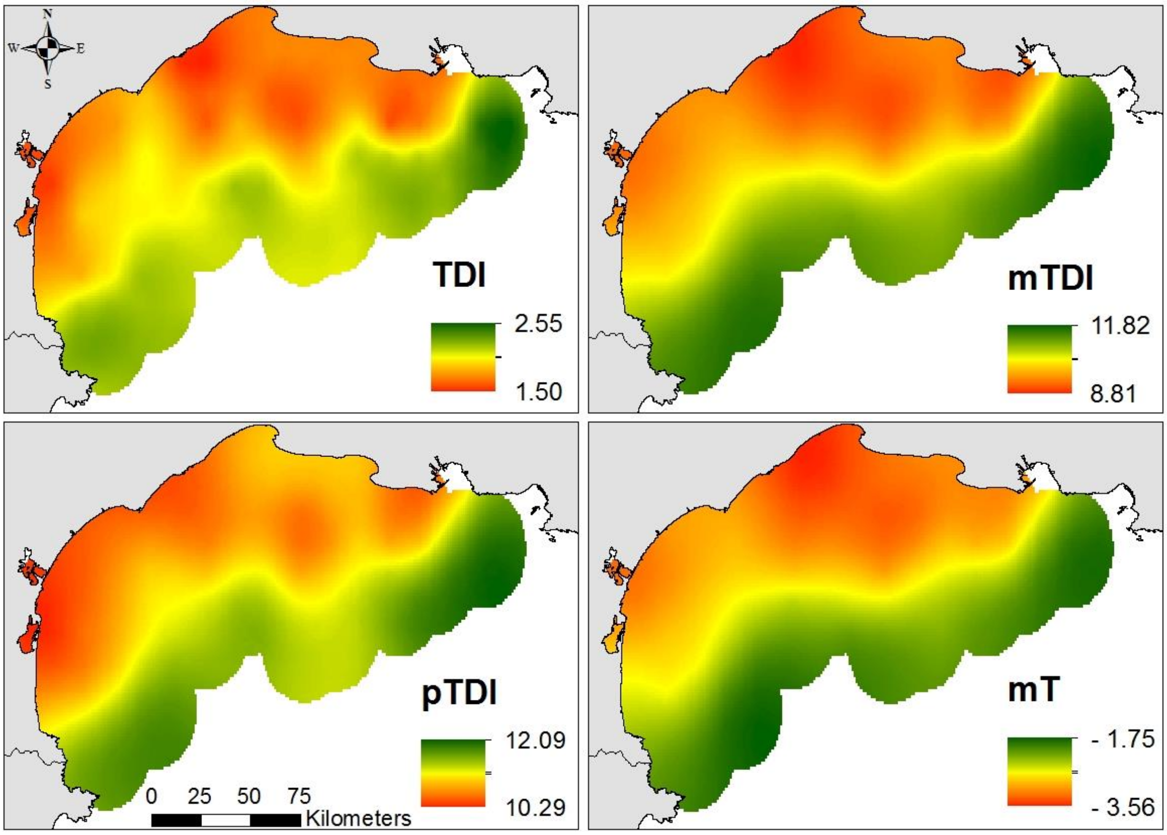


Figure 6: Distribution pattern of benthic sensitivity to trawling in the Gulf of Lion (MEDITS data)

In the North Sea, despite small differences, distribution patterns of the trawling sensitivity of benthic communities were substantially the same for the four indices (Figure 7). Benthic ecosystems of the South and the East part of the North Sea appeared particularly impacted by the trawling and so not very sensitive (lower values of the indices). Values of indices were high only in a small area in the West of the North Sea making it particularly vulnerable to trawling, with the presence of species considered to be sensitive to trawling.

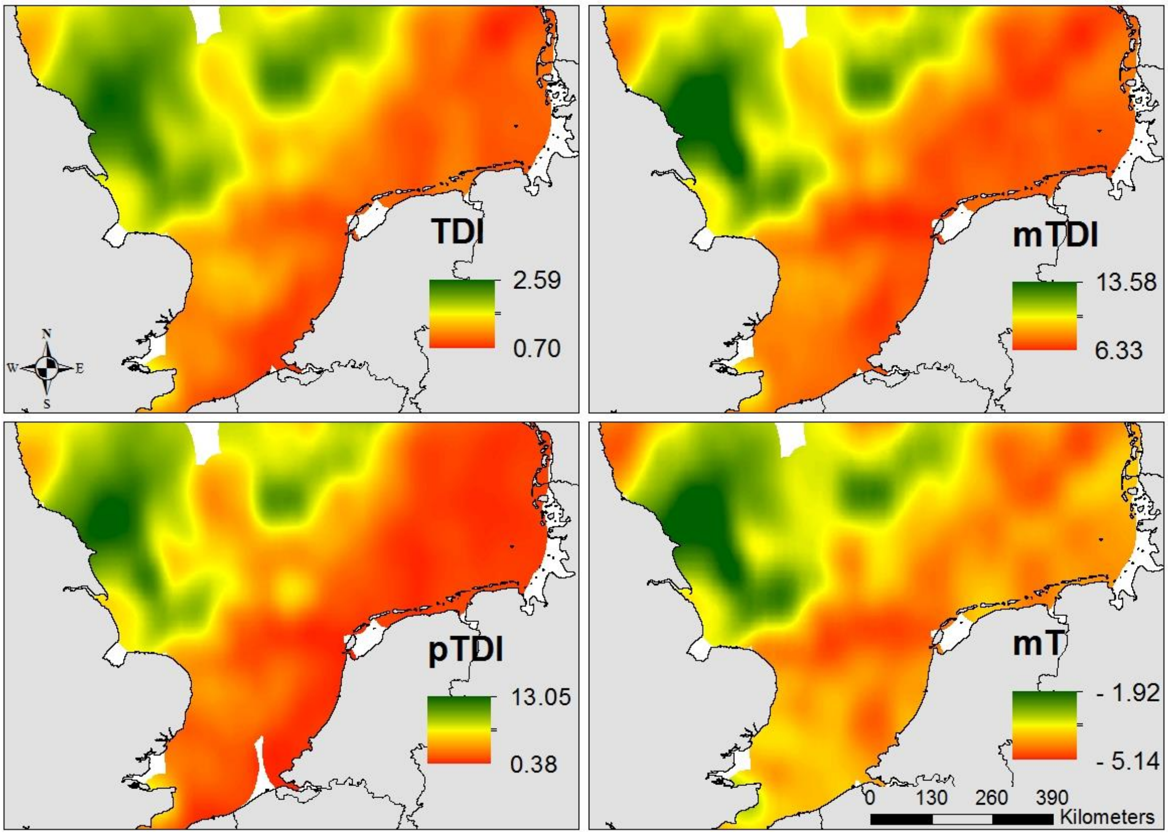


Figure 64: Distribution pattern of benthic sensitivity to trawling in the southern North Sea (IBTS data)

Concerning the English Channel, three of the four indices (TDI, mTDI, mT) had low values in the Eastern Channel and the northern part of the Western Channel (Figure 8), reflecting areas already heavily impacted by trawling. Except around Plymouth, the Western English Channel looks particularly sensitive to trawling, as highlighted by the pTDI results.

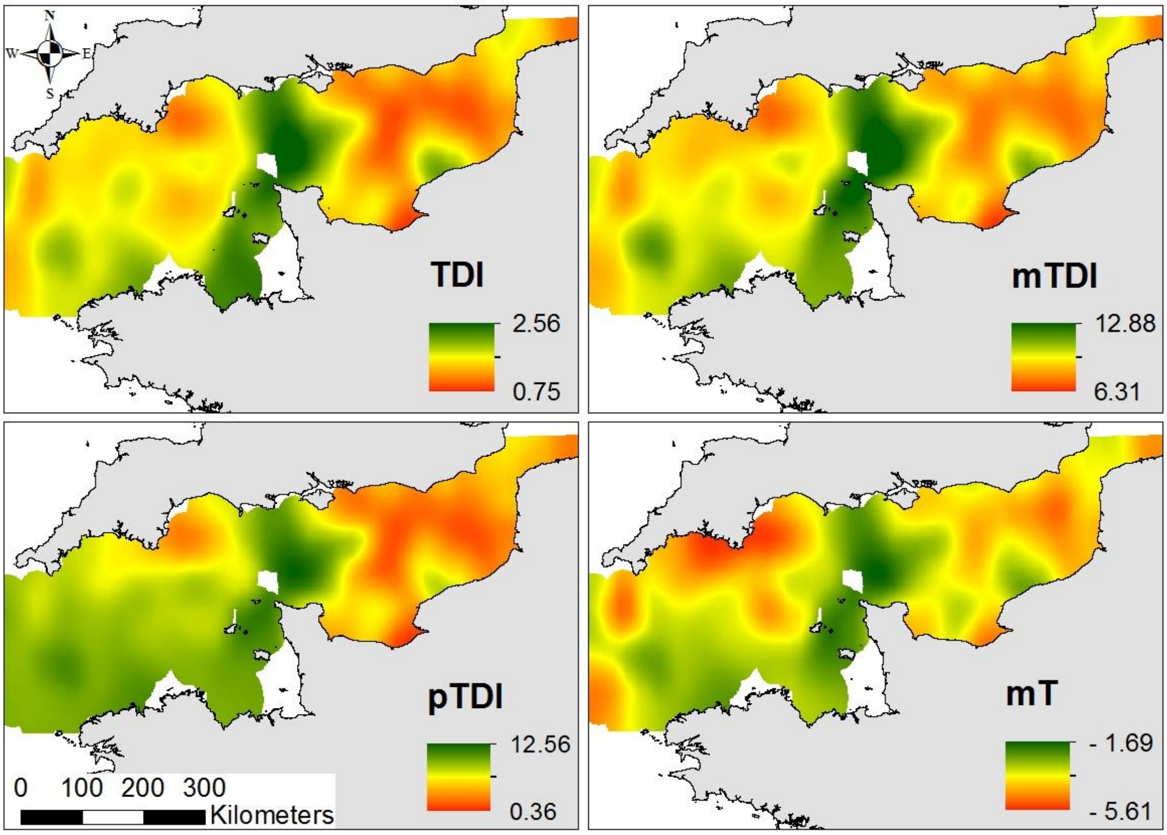


Figure 8: Distribution pattern of benthic sensitivity to trawling in the English Channel (CGFS and CAMANOC data)

4. Discussion

Most of the studies focusing on benthic communities use grab or box-corer for sampling (Engel and Kvitek 1998; Kenchington et al. 2001; Atkinson et al. 2011; Rijnsdorp et al. 2018; van Loon et al. 2018). These methods only sample a small area at a time (generally about between 0.1 and 0.5 m²) whereas trawling methods sample large-scale benthic communities. Grab and core methods mainly collected infauna species (Rumohr 1999) and do not effectively sample the larger epifauna and megafauna component of the seabed (Bergman and Van Santbrink 2000). Therefore, biomass and abundance of species such as sponges, hydrozoans, sea stars or crabs are underestimated despite their strong sensitivity to trawling (de Juan and Demestre 2012). Although it is often considered a non-quantitative method (Eleftheriou 2013), bottom trawls may be appropriate to investigate the effect of trawling. This method allows capturing the benthic fauna fraction which is the more directly affected by bottom fishing : the epifauna (Rumohr 1999; Reiss et al. 2006; Foveau et al. 2017). The use of this sampling technique also allows the observation of benthic assemblages over large areas, in agreement with the large-scale distribution of abrasion. Benthic invertebrates forming a significant proportion of by-catch in the trawl fisheries (Reiss et al. 2006; Foveau et al. 2017), scientific bottom trawling surveys carried out yearly in different countries for the purpose of the Common Fishery Policy may be a useful and cost-effective way to obtain a large amount of good quality data over a wide spatial extent and potentially long temporal range.

As numerous studies on trawling impact showed that organisms' responses to disturbance depend on their biological traits (Thrush et al. 1998; Blanchard et al. 2004; de Juan et al. 2007; Kenchington et al. 2007; Strain et al. 2012), the selection of traits used in the calculation of functional indices is an important step in the process. The utilization, in our study, of a set of biological traits known to respond positively or negatively to trawling disturbances (Thrush et al. 1998; de Juan et al. 2007; Gray and Elliott 2009), allows to better monitor the effect of trawling on benthic ecosystem. For example, the feeding mode of the species induces different responses to trawling, since burrowing scavengers may benefit from trawling disturbance or discards, whereas filter feeders can be highly affected by increased sediment resuspension (de Juan et al. 2007). Other traits could reflect the resilience of species and might be used as indicators of trawling disturbance such as the species longevity (Rijnsdorp et al. 2018), the reproduction mode or the dispersion mechanisms (Bremner et al. 2006). However, the lack of information about these biological traits for a large number of species did not allow us to include them in indices calculations. Moreover, some of these traits, such as longevity, are probably environment specific and may need to be locally adapted which further complicate their use for generic index calculation.

One of the aims of this study was to select a generic index capable of detecting the effect of trawling on benthic communities in all European waters. The combination of five selection properties allowed us to select four indices (TDI, pTDI, mTDI and mT index) responding to the fishing pressure. These four indices are highly correlated at large scale since they are based on the same set of biological traits and were chosen for their significant correlation to abrasion. However, the lower correlations between mT and the TDI derived indices indicate that their mathematical formulation still matters. As a result, their usefulness may be zone-dependent since the correlation between mT and abrasion seems stronger than that of TDI derivatives in the Gulf of Lion and vice versa in the English Channel/southern North Sea. Therefore, although closely related, it seems difficult to select only one of these for impact assessment and their behavior at habitat scale needs to be investigated. Despite their apparently significant relationship to abrasion in most studied areas (except in Corsica), large observation variability resulted in weak correlation values. This very large variability probably resulted from the fact that benthic habitats were not differentiated in this study, and that trawling does not have the same impact on all seabed habitats, particularly because bottom-trawl catchability depends on the nature of the bottom (Reiss et al. 2006). Thus, tracking trawl effects on benthic communities, for example, should be done at a finer resolution (*e.g.* EUNIS Level 4) choosing which ever index is the most sensitive in the studied area (in application to the precautionary approach).

As for the other indices tested, despite their potential relevance to other aspects, they do not appear to be relevant for monitoring the effect of trawling on benthic communities. The fact that all retained indices were based on biological traits indicated that taxonomic indices (Shannon, Pielou…) or community biomass were weakly relevant to monitor the effect of trawling. Even if many anterior studies found a negative effect of trawling on the biomass of benthic community (Collie et al. 2000b; Jennings et al. 2001b; Queirós et al. 2006), it does not always relate linearly to trawling pressure, especially with polychaetes (Hiddink et al. 2011). In the present study, the absence of significant negative correlation seemed consistent across most of the studied areas. The biomass of the community is known to be influenced by the nature of sediments and particularly silt and clay contents (Queirós et al. 2006; Hinz et al. 2009). It is therefore possible that, due to the lack of differentiation between habitats, the variance of biomass is too high at basin scale to detect anything about the effect of trawling. Such responsiveness sensitivity may hinder the operational use of this measure.

Concerning diversity indices, the great disparity of indices' responses to the effect of fishing between studied areas is also consistent with existing literature. Previous studies have shown a negative influence of fishing on Shannon, Pielou and Simpson index (Smith et al. 2000; Shirmohammadi et al. 2012). On the opposite, others could not detect any significant effect

(Svane et al. 2009; Atkinson et al. 2011), or even evidenced a positive effect of abrasion on the Simpson index (Shirmohammadi et al. 2012) and on the Pielou index for a few months of the year in the Mediterranean Sea (Smith et al. 2000). Heterogeneity in these results highlights that the effect of trawling on species number or biomass is unclear, but rather appears to modify functional components of benthic communities, with for example a decrease of epifaunal sedentary suspension feeders in trawled areas (de Juan et al. 2007). Except for the FRic, the functional indices calculated in this study did not appear to respond to trawling activities in all studied areas. The positive correlation between FEve and FSpe and abrasion in the Mediterranean suggests that trawling leads to an increase and dominance (in terms of biomass) of specialized species. In the opposite, the negative correlation between FDiv and FEve and the abrasion in the southern North Sea suggests that increased trawling induced a dominance of functionally close generalist species (close to center of gravity of functional space). Functional indices are, in essence, sensitive to the trait composition of the benthic community which may result in change in the index response to trawling depending on the trait composition of each area. Such information is valuable, from an ecological point of view, to anticipate trawl-induced change in a given community, but does not satisfy the requirements of a general index of sensibility, as its interpretation remains strongly context-dependent. Concerning the functional richness (FRic), the positive correlation with the abrasion in all studied areas suggests that trawling led to an increase of the functional diversity of the benthic community by attracting for example different scavengers (Collie et al. 2000b; Thrush and Dayton 2002). However, regarding its poor scores obtained for other properties, this index is also a poor candidate to evaluate the effect of trawling on benthic communities.

Based on biological traits known to be influenced by trawling, the four retained indices (TDI, mTDI, pTDI and mT index) were specific to the trawling effect. This suggests that it seems illusory to find a generic indicator able to respond to all the pressures experienced by benthic habitats and, therefore, that the study of the ecological status of seabed must rely on several indicators specific to each type of impact. In addition, the different effectiveness of indices between study areas suggests the systematic use of a set of indices, the combination of which should provide information on the ecological status of the area in terms of fishing pressure.

Unlike the results obtained in the other three zones, very low correlations are observed between tested indices and trawling effort in Corsica. The lack of significant relationship between the majority of the indices and the abrasion may be explained by the limited number of data available in this area. Furthermore, abrasion being relatively low over the whole of Corsica (Jac and Vaz 2018), the benthic communities were sampled on a low abrasion gradient (less than 5 vs. 0.08 to 29.15 in the Gulf of Lion). It seemed unlikely that there would be a change in indices values over such a reduced abrasion gradient, especially since the small number of samples would tend to exacerbate the natural variability at the same abrasion intensity. Absence of relation between selected indices and low abrasion range might indicate that the effect of trawling on the benthic community is undetectable at these levels. Thus, relation between indices and trawling effort appeared not to be linear over the entire abrasion range and the likely presence of thresholds seems to be emerging.

Sensitivity indices proposed here to satisfactorily assess the effect of trawling meet many of the requirements suggested in previous studies (Queirós et al. 2016; ICES 2017b) :

1) They are based on biological traits known to be affected by trawling. This agrees with the first requirement (Theoretical basis), which directly reflects the changes that trawling induces on the community, through the change in the proportion of each trait in the community.

2) This makes these indices particularly sensitive to the trawling pressure (requirement 2: sensitivity).

3) The four selected indices present consistent and significant changes as a result of a pressure change (third requirement: responsiveness), since the resilience of the species after reducing or removing abrasion depend on their biological characteristics. Lambert et al (2014) showed that in high current areas, species with low mobility would have a faster recovery time than other species. Considered as a very important requirement for the species' sensitivity to trawling, the increase of low-mobility species biomass, due to a reduction of abrasion, leads to an increase in the value of indices.

4) The use of yearly scientific trawl surveys' data allows to respond positively to several criteria such as data quality (requirement 6) and the repeatability of the method (requirement 5).

5) The acquisition of data is done with limited costs (requirement 8) since the surveys already exist and the identification and the measurements (weighing and counting) are mostly carried out on board.

6) Although it is often very difficult to distinguish the effect of a physical pressure, such as trawling, from the effect of the environment on benthic communities, these indicators can be considered as specific (requirement 4: specificity) as they use known biological traits providing specific information on the species' sensitivity to trawling.

7) The use of four contrasted study areas in this work allows us to conclude positively on the cross regional applicability (requirement 9).

8) Finally, even if this is not mentioned in the requirements, the fact that the four indices are negatively correlated to abrasion makes them easily interpretable.

5. Conclusions

The establishment of the MSFD by the European Union in 2008 requires the development of indicators to assess and to monitor the effect of human pressures on the marine environment. Trawling appearing as one of the strongest pressure on the seabed, the development of indices to study its impact was necessary. Evaluation of the efficiency of fourteen different indices showed the necessity to use indices specific to trawling to detect its effect on benthic habitat in very contrasted regions. However, their detection power varied geographically and although closely related, it seems difficult to select and recommend only one of them. In conclusion, to monitor the effect of trawling on benthic communities in all European waters, these indices would need to be systematically screened and the locally most suitable one chosen for impact assessment.

Acknowledgement

The authors are grateful to the projects leaders of MEDITS, CGFS, IBTS and CAMANOC scientific surveys, the scientific staff and vessel crews who participated to these surveys. This study was supported by the EC2CO National Program on Coastal Environments (Bentchal) and the DG ENV project IDEM (Implementation of the MSFD to the Deep Mediterranean Sea; contract EU No 11.0661/2017/750680/SUB/EN V.C2). C. J. from MARBEC, Ifremer acknowledge support from the Occitanie region through its PhD research funding program.

References

Atkinson LJ, Field JG, Hutchings L (2011) Effects of demersal trawling along the west coast of southern Africa: Multivariate analysis of benthic assemblages. Mar Ecol Prog Ser 430:241–255

Auber A (1992) IBTS : International Bottom Trawl Survey. https://doi.org/10.18142/17.

Bellwood D, Wainwright P, Fulton C, Hoey A (2006) Functional versatility supports coral reef biodiversity. Proc R Soc B Biol Sci 273:101–107

Bergman MJN, Van Santbrink JW (2000) Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. ICES J Mar Sci 57:1321–1331

Blanchard F, Leloc F, Hily C, Boucher J (2004) Fishing effects on diversity , size and community structure of the benthic invertebrate and fish megafauna on the Bay of Biscay coast of France. Mar Ecol Prog Ser 280:249–260

Bolam SG, Eggleton JD (2014) Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. J Sea Res 88:47–58

Borja A, Franco J, Pérez V (2000) A marine Biotic Index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Mar Pollut Bull 40:1100–1114

Borja A, Muxika I, Franco J (2003) The application of a Marine Biotic Index to different impact sources affecting soft-bottom benthic communities along European coasts. Mar Pollut Bull 46:835–845

Bremner J, Frid CLJ, Rogers SI (2003) Assessing Marine Ecosystem Health: The long-term effects of fishing on functional biodiversity in North Sea benthos. Aquat Ecosyst Heal Manag 6:131–137

Bremner J, Rogers SI, Frid CLJ (2006) Matching biological traits to environmental conditions in marine benthic ecosystems. J Mar Syst 60:302–316

Brind'Amour A, Laffargue P, Morin J, Vaz S, Foveau A, Le Bris H (2014) Morphospecies and taxonomic sufficiency of benthic megafauna in scientific bottom trawl surveys. Cont Shelf Res 72:1–9

Brind'Amour A, Rouyer A, Martin J (2009) Functional gains of including non-commercial epibenthic taxa in coastal beam trawl surveys: A note. Cont Shelf Res 29:1189–1194

Callaway R, Alsvåg J, De Boois I, Cotter J, Ford A, Hinz H, Jennings S, Kröncke I, Lancaster J, Piet G, Prince P, Ehrich S (2002) Diversity and community structure of epibenthic invertebrates and fish in the North Sea. ICES J Mar Sci 59:1199–1214

Certain G, Jorgensen LL, Christel I, Planque B, Bretagnolle V (2015) Mapping the vulnerability of animal community to pressure in marine systems: disentangling pressure types and integrating their impact from the individual to the community level. ICES J Mar Sci 72:1470–1482

Chavent M, Kuentz-Simonet V, Labenne A, Saracco J (2017) Multivariate Analysis of Mixed Data: The R Package PCAmixdata.

Collie JS, Hall SJ, Kaiser MJ, Poiner IANR (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. J Anim Ecol 69:785–798

Coppin F, Travers-Trolet M (1989) CGFS : Channel Ground Fish Survey. https://doi.org/10.18142/11.

Cornwell WK, Schwilk DW, Ackerly DD (2006) A trait-based test for habitat filtering: Convex hull volume. Ecology 87:1465–1471

van Denderen P, Bolam S, Hiddink J, Jennings S, Kenny A, Rijnsdorp A, van Kooten T (2015) Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. Mar Ecol Prog Ser 541:31–43

Diesing M, Stephens D, Aldridge J (2013) A proposed method for assessing the extent of the seabed significantly affected by demersal fishing in the Greater North Sea. ICES J Mar Sci 70:1085–1096

Eigaard OR, Bastardie F, Breen M, Dinesen GE, Hintzen NT, Laffargue P, Mortensen LO, Nielsen JR, Nilsson HC, O'Neill FG, Polet H, Reid DG, Sala A, Sköld M, Smith C, Sorensen TK, Tully O, Zengin M, Rijnsdorp AD (2016) Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J Mar Sci 73:i27–i43

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P, Catarino R, Dinesen GE, Egekvist J, Fock HO, Geitner K, Gerritsen HD, González MM, Jonsson P, Kavadas S, Laffargue P, Lundy M, Gonzalez-Mirelis G, Nielsen JR, Papadopoulou N, Posen PE, Pulcinella J, Russo T, Sala A, Silva C, Smith CJ, Vanelslander B, Rijnsdorp AD (2017) The footprint of bottom trawling in European waters: Distribution, intensity, and seabed integrity. ICES J Mar Sci 74:847–865

Eleftheriou A (2013) Methods for the study of marine benthos. Wiley-Blackwell, Hoboken

Engel J, Kvitek R (1998) Effects of Otter Trawling on a Benthic Community in Monterey Bay Nation. Conserv Biol 12:1204–1214

Foveau A, Jac C, LIpasset M, Guillerme C, Desroy N, Vaz S (2019) Updated biological traits' scoring and protection status to calculate sensitivity to trawling on mega-epibenthic fauna. https://doi.org/10.17882/59517.

Foveau A, Vaz S, Desroy N, Kostylev VE (2017) Process-driven and biological characterisation and mapping of seabed habitats sensitive to trawling. PLoS One 12:1–30

Gray J, Elliott M (2009) Ecology of marine sediments: from science to management. Oxford University Press, New York

Groeneveld RA, Meeden G (1984) Measuring Skewness and Kurtosis. Stat 33:391–399

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan H., Madin EM., Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. Science (80-) 319:948–953

Hiddink JG, Jennings S, Kaiser MJ (2007) Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. J Appl Ecol 44:405–413

Hiddink JG, Jennings S, Kaiser MJ, Queirós AM, Duplisea DE, Piet GJ (2006) Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Can J Fish Aquat Sci 63:721–736

Hiddink JG, Johnson AF, Kingham R, Hinz H (2011) Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. J Appl Ecol 48:1441–1449

Hinz H, Prieto V, Kaiser MJ (2009) Trawl disturbance on benthic communities: Chronic effects and experimental predictions. Ecol Appl 19:761–773

Hiscock K, Jackson A, Lear D (1999) Assessing seabed species and ecosystems sensitivities.

van Hoey G, Bonne W, Salas F (2015) Intercalibration report for benthic invertebrate fauna of the North East Atlantic Geographical intercalibration group for coastal waters (NEA 1/26). ILVO Meded

Hollander M, Wolfe DA (1973) Kendall and Spearman tests. Nonparametric Statistical Methods. John Wiley & Sons, New York, pp 185–194

Huthnance JM (1991) Physical oceanography of the North Sea. Ocean Shorel Manag 16:199–231

ICES (2015) Manual for the International Bottom Trawl Surveys.

ICES (2017a) Report of the Workshop to evaluate regional benthic pressure and impact indicator(s) from bottom fishing (WKBENTH).

ICES (2017b) Manual of the IBTS North Eastern Atlantic Surveys.

ICES (2019) OSPAR request on the production of spatial data layers of fishing intensity/pressure. ICES Tech Serv

Jac C, Vaz S (2018) Abrasion superficielle des fonds par les arts trainants - Méditerranée (surface swept area ratio). https://doi.org/10.12770/8bed2328-a0fa-4386-8a3e-d6d146cafe54.

Jadaud A, Souplet A, Bertrand J (1994) MEDITS. https://doi.org/10.18142/7.

Jennings S, Pinnegar J, Polunin N, Warr K (2001) Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. Mar Ecol Prog Ser 213:127–142

de Juan S, Demestre M (2012) A Trawl Disturbance Indicator to quantify large scale fishing impact on benthic ecosystems. Ecol Indic 18:183–190

de Juan S, Demestre M, Thrush S (2009) Defining ecological indicators of trawling disturbance when everywhere that can be fished is fished: A Mediterranean case study. Mar Policy 33:472–478

de Juan S, Thrush SF, Demestre M (2007) Functionnal changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). Mar Ecol Prog Ser 334:117–129

Kenchington EL, Kenchington TJ, Henry LA, Fuller S, Gonzalez P (2007) Multi-decadal changes in the megabenthos of the Bay of Fundy: The effects of fishing. J Sea Res 58:220–240

Kenchington ELR, Prena J, Gilkinson KD, Gordon Jr. DC, MacIsaac K, Bourbonnais C, Schwinghamer PJ, Rowell TW, McKeown DL, Vass WP (2001) Effects of experimental otter trawling on the macrofauna of a sandy bottom ecosystem on the Grand Banks of Newfoundland. Can J Fish Aquat Sci 58:1043–1057

Lambert GI, Jennings S, Kaiser MJ, Hinz H, Hiddink JG (2011) Quantification and prediction of the impact of fishing on epifaunal communities. Mar Ecol Prog Ser 430:71–86

Larsonneur C, Boysse P, Auffret J -P (1982) The superficial sediments of the English Channel and its Western Approaches. Sedimentology 29:851–864

Lee J, South AB, Jennings S (2010) Developing reliable , repeatable , and accessible methods to provide high-resolution estimates of fishing-effort distributions from vessel monitoring system (VMS) data. ICES J Mar Sci 67:1260–1271

van Loon WMGM, Walvoort DJJ, van Hoey G, Vina-Herbon C, Blandon A, Pesch R, Schmitt P, Scholle J, Heyer K, Lavaleye M, Phillips G, Duineveld GCA, Blomqvist M (2018) A regional benthic fauna assessment method for the Southern North Sea using Margalef diversity and reference value modelling. Ecol Indic 89:667–679

Margalef R (1958) Information theory in ecology. Int J Gen Syst 3:36–71

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional and functional evenness divergence: the primary of functional components diversity. Oikos 111:112–118

MEDITS (2017) MEDITS - International Bottom Trawl Survey in the Mediterranean : Instruction Manual Version 9.

Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–177

OCEANA (2016) Developing a list of Vulnerable Marine Ecosystems.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHM, Wagner H (2019) Package "vegan": Community ecology package. http://vegan.r-forge.r-project.org/

OSPAR (2008) List of threatened and/or declining species and habitats.

Pielou E (1969) An introduction to mathematical ecology by EC Pielou.

Pitcher CR, Ellis N, Jennings S, Hiddink JG, Mazor T, Kaiser MJ, Kangas MI, McConnaughey RA, Parma AM, Rijnsdorp AD, Suuronen P, Collie JS, Amoroso R, Hughes KM, Hilborn R (2017) Estimating the sustainability of towed fishing-gear impacts on seabed habitats: a simple quantitative risk assessment method applicable to data-limited fisheries. Methods Ecol Evol 8:472–480

Queirós AM, Hiddink JG, Kaiser MJ, Hinz H (2006) Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats. J Exp Mar Bio Ecol 335:91–103

Queirós AM, Strong JA, Mazik K, Carstensen J, Bruun J, Somerfield PJ, Bruhn A, Ciavatta S, Flo E, Bizsel N, Özaydinli M, Chuševe R, Muxika I, Nygård H, Papadopoulou N, Pantazi M, Krause-Jensen D (2016) An objective framework to test the quality of candidate indicators of good environmental status. Front Mar Sci 3:1–21

R Core Team (2017) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

Reiss H, Kröncke I, Ehrich S (2006) Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments. ICES J Mar Sci 63:1453–1464

Ribeiro Jr PJ, Diggle PJ (2018) Package “geoR”. https://cran.r-project.org/web/packages/geoR/.

Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, van Denderen PD, van Kooten T (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. Ecol Appl 28:1302–1312

Rijnsdorp AD, Buys AM, Storbeck F, Visser EG (1998) Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES J Mar Sci 55:403–419

Roussiez V, Aloisi JC, Monaco A, Ludwig W (2005) Early muddy deposits along the Gulf of Lions shoreline: A key for a better understanding of land-to-sea transfer of sediments and associated pollutant fluxes. Mar Geol 222–223:345–358

Rumohr H (1999) Soft bottom macrofauna: Collection, treatment, and quality assurance of samples. ICES Tech Mar Environ Sci 1–20

Rumohr H, Kujawski T (2000) The impact of trawl fishery on the epifauna of the southern North Sea. ICES J Mar Sci 57:1389–1394

Salomon J (1990) Role of instantaneous and long-term water movements on the recruitment and life of benthic fauna in the English Channel. La mer 28:211–217

Schratzberger M, Dinmore TA, Jennings S (2002) Impacts of trawling on the diversity, biomass and structure of meiofauna assemblages. Mar Biol 140:83–93

Shannon CE, Weaver W (1963) The mathematical theory of communication. Univ Illinois Press 1–131

Shirmohammadi M, Doustshenas B, Mediseh D, Simin S, Sakhaei N (2012) Impacts of Trawling on Distribution and Diversity of Gastropods in the Persian Gulf : the Bahrakan Fishing Area. J Persian Gulf 3:37–45

Simpson EH (1949) Measurement of Diversity. Nature 163:688–688

Smith C, Papadopoulou KN, Diliberto S (2000) Impact of otter trawling on an eastern Mediterranean commercial trawl fishing ground. ICES J Mar Sci 57:1340–1351

Strain EMA, Allcock AL, Goodwin CE, Maggs CA, Picton BE, Roberts D (2012) The long-term impacts of fisheries on epifaunal assemblage function and structure, in a Special Area of Conservation. J Sea Res 67:58–68

Svane I, Hammett Z, Lauer P (2009) Impacts of trawling on benthic macro-fauna and -flora of the Spencer Gulf prawn fishing grounds. Estuar Coast Shelf Sci 82:621–631

Tesi T, Miserocchi S, Goñi MA, Langone L (2007) Source, transport and fate of terrestrial organic carbon on the western Mediterranean Sea, Gulf of Lions, France. Mar Chem 105:101–117

Thrush SF, Dayton PK (2002) Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. Annu Rev Ecol Syst 33:449–473

Thrush SF, Hewitt JE, Cummings VJ, Dayton PK, Cryer M, Turner SJ, Funnell GA, Budd RG, Milburn CJ, Wilkinson MR (1998) Disturbance of the marine benthic habitat by commercial fishing: Impacts at the scale of the fishery. Ecol Appl 8:866–879

Verin Y, Travers-Trolet M (2014) CAMANOC cruise. https://doi.org/10.17600/14001900.

Villéger S, Mason H, Mouillot D (2008) New multidimensional functional diversity indices for a multifacted framework in functional ecology. Ecology 89:2290–2301

Villéger S, Ramos Miranda J, Flores Hernández D, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol Appl 20:1512–1522

van den Wollenberg A (1977) Redundancy analysis. An alternative for canonical correlation analysis. Psychometrika 42:207–219

Appendix I. Detecting adverse effect on seabed integrity. Part 2: How much of seabed habitats are left in good environmental status by fisheries?

Ecological Indicators

Cyrielle Jac, Nicolas Desroy, Grégoire Certain, Aurélie Foveau, Céline Labrune, Sandrine Vaz

Detecting adverse effect on seabed integrity. Part 2: How much of seabed habitats are left in good environmental status by fisheries?

Cyrielle Jac[a]*, Nicolas Desroy[b], Gregoire Certain[a], Aurélie Foveau[b], Céline Labrune[c], Sandrine Vaz[a]

[a] MARBEC, Univ Montpellier, Ifremer, IRD, CNRS, Sète, France
[b] Ifremer, Laboratoire Environnement et Ressources Bretagne Nord, 38 Rue du Port Blanc, 35800 Dinard, France
[c] Sorbonne Université, CNRS, Laboratoire d'Ecogéochimie des Environnements Benthiques, LECOB UMR 8222, F-66650 Banyuls-sur-Mer, France

* corresponding author : cyrielle.jac@ifremer.fr

Abstract

By relating observed changes to the pressures suffered, the Marine Strategy Framework Directive intends to better control the factors of environmental degradation and to manage their consequences in European waters. Several descriptors are defined within the framework of the MSFD and in particular descriptor 1 relating to the biological diversity of the seabed and descriptor 6 relating to the seabed integrity (i.e. the quality of their structures and functions). For each descriptor, indicators and threshold values must be defined and a novel conceptual approach to define and detect seabed integrity thresholds is proposed here. Bottom trawling being the main source of shelf continental disturbance, it is important to evaluate its impact on benthic habitat. The goal of this study is to propose a methodology to determine "Good Ecological Status" threshold values for each habitat type present in three contrasted MSFD sub-region (North Sea, English Channel and Mediterranean Sea). Trawling impacts are dependent of the spatial and temporal distribution of the fishing effort, fishing gears, intensity of natural disturbances and habitat types. Benthic community structures present in these areas were studied using by-catch non-commercial benthic invertebrates data collected during French scientific bottom trawl surveys. Swept area ratios derived from VMS data were used to quantify the intensity of fishery induced abrasion on the seabed. A modeling approach was used to determine abrasion threshold values on each EUNIS level 4 habitat. The values, beyond which trawling has an adverse effect on benthic communities, have been determined for each habitat. This made it possible to assess and map the ecological status of each of the habitats and to determine the percentage of each habitat impacted by trawling. The method proposed here to evaluate the impact of trawling on benthic communities highlighted that the vast majority of the investigated sub-regions were adversely impacted or lost as a result of seabed impacting trawling.

Keywords: GES, Threshold values, Trawling impact, Indices, MSFD

1. Introduction

In 2008, the European Union drew up the Marine Strategy Framework Directive (MSFD) to achieve or to maintain "Good Environmental Status" (GES) in the marine environment (EC 2008). This directive sets out eleven descriptors of human uses of the marine ecosystem, each comprising a number of criteria and methodological standards for determining GES. Each member state must therefore develop quantitative indices and threshold values corresponding to each criteria to assess progress towards the GES (Rice et al., 2012). To measure the evolution of this environmental status, the evaluation of some criteria requires to develop appropriate indices able to detect changes in relation to anthropogenic disturbance (Leonardsson et al. 2009; OSPAR 2012; Rice et al. 2012; van Loon et al. 2018). On the eleven descriptors defined in the MSFD, two of them specifically concern the benthic habitat: the descriptor 1 (biodiversity) and the descriptor 6 (seabed integrity). Criteria 1 and 2 of the descriptor 6 (D6C1, D6C2) are dedicated in evaluating the spatial extent of the physical loss or disturbance of seabed. The criteria D6C3 focuses on establishing pressure thresholds values for the adverse effects of physical disturbance. Finally, D6C4 and D6C5 must allow the assessment of the extent of benthic community “loss” or “alteration” and should set maximum admissible proportion of habitat loss and evaluate the status of each habitat in that respect (EC 2008, 2017a).

The information of these criteria requires the development of transparent indices, allowing for a scientifically defensible assessment of the environmental status of the seabed. Since each type of pressure will result in either habitat disturbance or total physical destruction, it is expected that they will affect benthic communities in different ways. It seems therefore more appropriate to address each pressure effect separately and to develop specific indices and thresholds. In Europe, dredging and bottom trawling occur over large surfaces of the continental shelf and are the principal source of the anthropogenic disturbance to seabed habitats (Hiddink et al. 2007; Halpern et al. 2008; CNDCSMM 2019). Based on an extensive assessment methodology, it was possible to identify four indices (Jac et al., submitted) that respond to trawling impact and may probably be used in all European waters. These were computed using benthic community data from scientific bottom trawl surveys which enable to work on a large spatial scale but also to focus on the epifauna, unlike other sampling methods such as grab or box-corer that perform small-scale sampling, mainly of the endofauna (Rumohr 1999; Foveau et al. 2017). The set of indices retained were all based on species biological traits that are known to shape species sensitivity to physical abrasion such as that generated by bottom trawling.

The distribution and composition of benthic assemblages are known to be dependent of environmental conditions such as depth, hydrodynamism and granulometry (Gray and Elliott 2009) or trawling pressure (Eigaard et al. 2017). Therefore, the evaluation of trawling impact on benthic community must be carried out by habitat type. As a great diversity of seabed habitats is present in the continental shelf of European waters, the development of an index that can be used in all European waters requires its evaluation in contrasted habitats, subjected to important gradient of trawling effort. Thus, a pan-european habitat map in a reasonably standardized typology is necessary to evaluate the relevance of each tested index at the scale of each MFSD sub-regions. A generic and hierarchical habitat classification of European Waters was developed by the European Nature Information System (EUNIS; http://www.emodnet.eu/ntly available. This typology is based on a hierarchical classification of habitats allowing access, for the marine domain, to levels of precision ranging from the type of substrate to the precise identification of benthic stands, defined by the presence of characteristics species, while integrating the exposure level and depth (Galparsoro et al. 2012). Many studies on trawling impact have used EUNIS level 3 (Eigaard et al. 2017; van Loon et al. 2018) which takes into account depth, sediment grain size, light and hydrodynamism.

The characterization of GES, with regard to the impact of trawling, requires the definition of thresholds for each habitat type that may be trawled. Threshold values correspond to values below which no negative effect of the impact source (trawling in this study) can be observed on the community (here the benthic community). Thus, beyond this value, the observed effect results from the abrasion. Existence of these threshold values is linked to the community resistance to trawling. The more a community is resistant to the pressure; the more the pressure threshold value from which a negative effect may be observed will be high. Threshold can also be defined as the point at which small changes in a driver (fishing intensity for example) may produce large responses in the ecosystem (Groffman et al. 2006). It is therefore important to define the threshold at which GES is met as the use of trends-based targets gives no clear indication of the status achieved (EC 2008).

The aims of this study were to propose a methodology based on four functional indices proposed earlier by Jac et al. (submitted) to determine GES threshold values for each habitat type present in three contrasted MFSD sub-regions: Western Mediterranean Sea, North Sea and English Channel. Maps representing the environmental status of these sub-regions were produced as a result of the application of this methodology.

2. Methods

2.1. Fishing impact

Maps of 90th inter-annual (from 2009 to 2017) percentile of swept surface area ratio, based on VMS data (Eigaard et al. 2016; ICES 2019c), were used to determine the abrasion value at each sampled stations of the three studied areas (as detailed in Jac et al., submitted). Resolutions of these maps were different: 3'x3' in the English Channel and North Sea (https://www.ospar.org) and 1'x1' in Mediterranean Sea (Jac and Vaz 2018).

2.2. Biological data

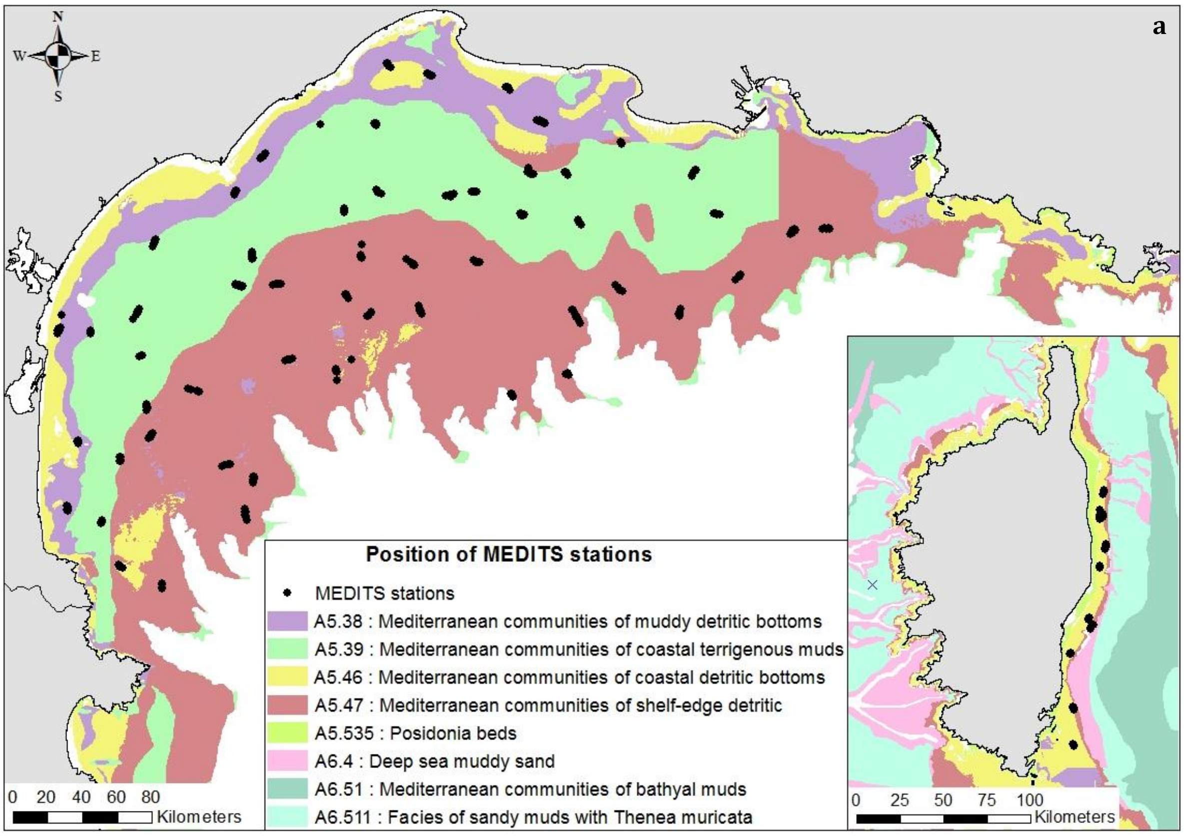
The benthic fauna studied in this work was collected, identified, counted and weighed during four scientific bottom trawling surveys: Mediterranean International Trawl Survey (MEDITS ; Jadaud et al. 1994), International Bottom Trawl Survey (IBTS ; Auber 1992), Channel Ground Fish Survey (CGFS ; Coppin and Travers-trolet 1989), Campagne Manche Occidentale (CAMANOC ; Verin and Travers-Trolet 2014) taking place in our study areas. These surveys are internationally coordinated and use standardized bottom trawls and fishing protocols. Three of these four surveys were performed in the English Channel and the North Sea: IBTS yearly in January/February since 1970, CGFS yearly in October since 1988 and CAMANOC in September 2014. MEDITS has been conducted each year in June since 1994 in the Mediterranean Sea. The data generated are mostly used in the frame of the Data Collection Program to support the implementation of the European Common Fisheries Policy (CFP). Benthic invertebrate species, considered as by-catch species, are either opportunistically or contractually monitored during these surveys since 2008 during CGFS surveys, 2009 during IBTS surveys and 2012 during MEDITS surveys (Callaway et al. 2002; Reiss et al. 2006; Brind'Amour et al. 2009, 2014). As the spatial repartition of abrasion is not independent of the presence of target species, commercial species (*Homarus gammarus*, *Crangon crangon*, *Maja brachydactyla*, *Pecten maximus*, *Aequipecten opercularis*, *Palaemon serratus*, *Nephrops norvegicus*, *Buccinum undatum*, *Cancer pagurus*, *Aristaeomorpha foliacea*, *Aristeus antennatus*, *Parapeneus longisrostris*, *Bolinus brandaris)* and cephalopods were removed from the dataset. Since it is impossible to estimate the number of individuals for colonial species such as sponges or hydrozoans, biomass data was preferred to abundance data. Data were standardized according to trawling swept area and expressed in $g.km^{-2}$. Finally, to limit identification errors, the procedure proposed by Foveau et al. (2017) to aggregate uncertain taxa at a higher identification level was used (Jac et al., submitted).

2.3. Indices computation

Four indices, all based on species biological traits specifically related to trawling sensitivity, were found to detect trawling impact in benthic community composition (Jac et al, 2020, submitted). These were the Trawling Disturbance Index (TDI; de Juan and Demestre 2012), the modified TDI (mTDI, Foveau et al. 2017), the partial TDI (pTDI, Jac et al. submitted), the modified Sensitivity to Trawling Index (mT; modified by Jac et al. submitted after Certain et al. 2015). Calculation methods of each of these indices were detailed in Jac et al., submitted.

2.4. Habitat data

Spatial repartition of the seabed habitats was obtained from the EUNIS layers level 4 as defined in EUNIS habitats classification of 2019 ; (http://www.emodnet.eu/abitat classes corresponding to sampled locations were extracted and assigned to each station (Figure 1). Only habitats sampled at least 40 times were retained for analysis. The IBTS survey is carried out in both the English Channel and the southern North Sea. As a result, habitats A5.14 and A5.15 of the English Channel were sampled twice each year (January/February with IBTS and September/October with CGFS). Analyses were therefore performed independently to allow the observation of seasonal differences on these habitats.



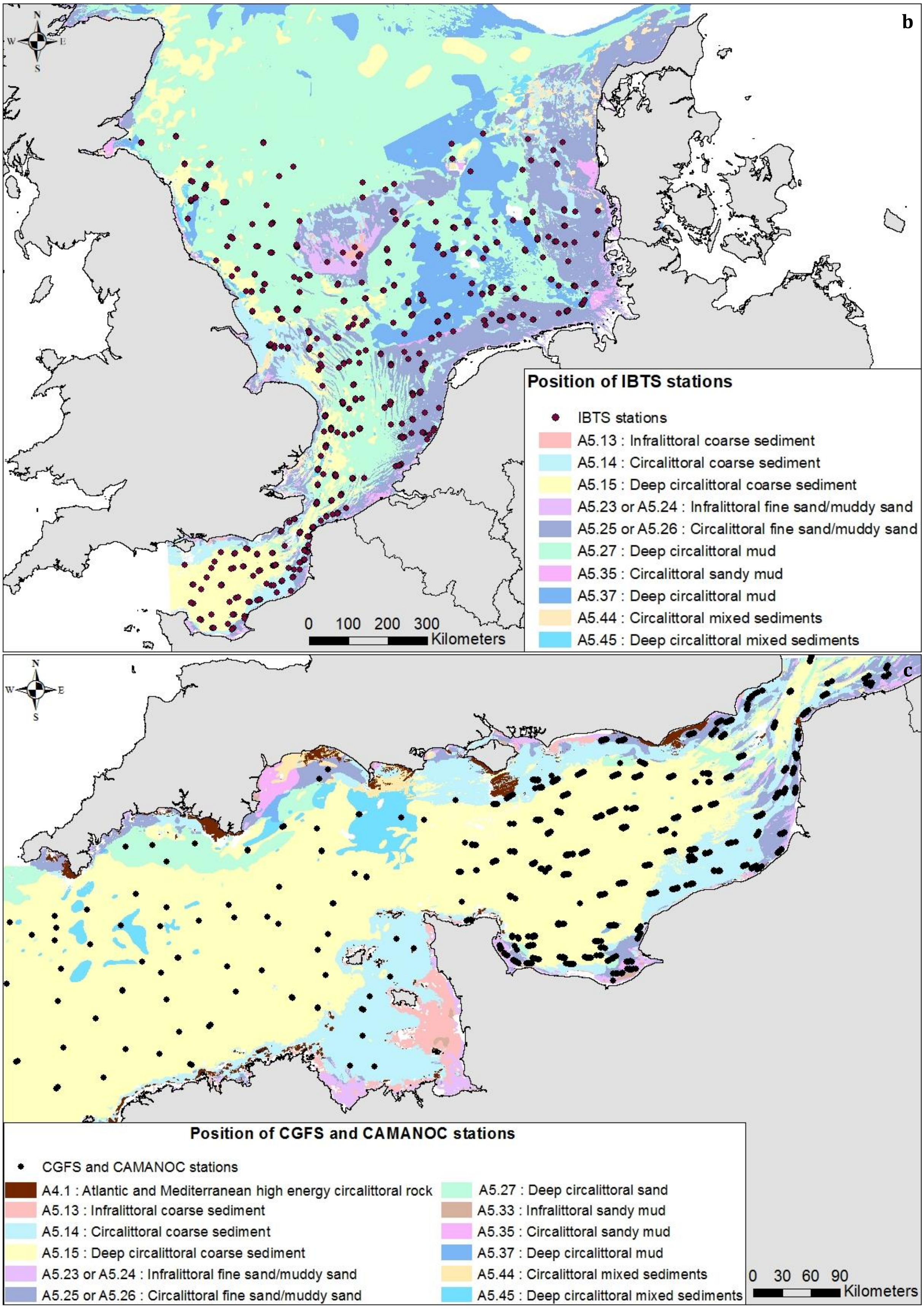


Figure 1: Location of sampled stations within different benthic habitats a. MEDITS stations in the Gulf of Lion and eastern Corsica b. IBTS stations in the southern North Sea and Eastern English Channel c. CGFS and CAMANOC stations in the English Channel

2.5. Data analysis

2.5.1. Determination of threshold values by habitat and biogeographical area

Depending on habitat types, benthic communities do not respond in the same way to trawling (Kaiser et al. 1998). Thus, based on EUNIS marine habitat description, the relationship between indices and abrasion was studied separately in each habitat type. Indices were centered and standardized (rescaled to have a mean of zero and a standard deviation of one) using the robustHD package 0.5.1 (Alfons 2016) and abrasion values were squared or log-transformed to improve their statistical distribution. However this relationship is not expected to be linear over the entire abrasion range and "abrupt" changes in slope may occur when certain abrasion intensity thresholds are exceeded (Figure 2). The identification of the abrasion values where these changes appeared allows detecting trawling intensity thresholds for each habitat. Thus, below a given abrasion intensity threshold, no significant relationship between the index and fishing induced abrasion may be detected and therefore no significant relationship will be detected. Under this abrasion limit, this seabed habitat may therefore be considered un-impacted or achieving GES in respect to bottom fishing physical impact. Conversely, when the area is severely trawled, one should not expect to observe a significant relationship between the index and fishing induced abrasion because the benthic community has shifted toward an adapted assemblage to this level of disturbance and has stabilized in a trawling induced semi-natural climax. A benthic community withstanding such level of abrasion may be considered as fully altered and therefore lost. Between these two extreme states, modification of species composition is on-going and communities should therefore be considered as adversely impacted. For more resistant communities, the GES would be maintained to a higher pressure value than that of a non-resistant community. Similarly, in that case, the second threshold corresponding to habitat loss may be reached at higher pressure level. The kinetics of change may also be different so that the resulting curve could also have a different slope. For very sensitive communities, the first threshold may not even exist.

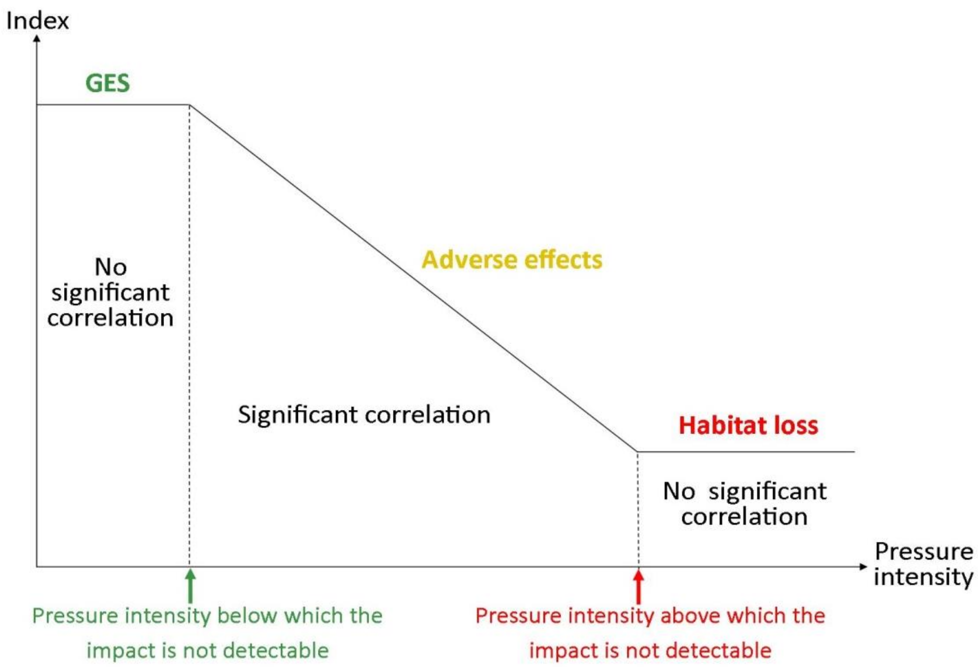


Figure 2: Schematic relationship between any given index and pressure intensity and its corresponding ecological status

For each habitat, the detection of breakpoints and the determination of the corresponding abrasion threshold values required several steps. Thus, the type of relationship using statistical linear regressions (generalized linear models with Gaussian link function or segmented linear regression) between transformed abrasion values and standardized indices was studied, on each habitat, with a modelling approach consisting into fitting five models: two “simple” models (linear and null models) and three segmented models corresponding to a part (only one breakpoint) or all (two break points) of the theoretical relationship (Figure 3). The first step in selecting the “best model” was to check if the slope was negative or null, any other models being excluded. The presence of breakpoints was then evaluated using a specific statistical test (Davies 2002). In case of significant presence of breakpoints, “simple” models (linear and null) were excluded. Finally, the adjusted R squared (Yin and Fan 2001) was used to evaluate which model has the best explanatory power in each habitat as it penalizes more broken-line models than would the R-squared. All of these analyses were carried out with the Segmented R package 0.5-3.0 (Muggeo 2019) using R version 3.4.2 (R Core Team 2017). For each EUNIS habitat category, these models were therefore fitted to predict indices values from abrasion in the Western Mediterranean Sea, the English Channel and the southern North Sea and, when they could be detected, compute their associated thresholds.

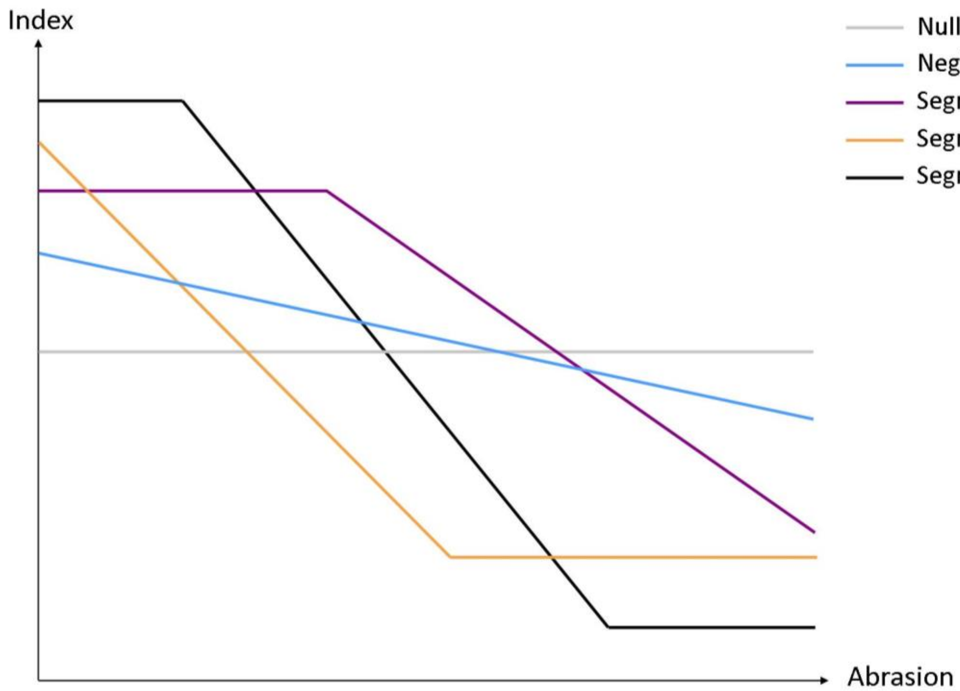


Figure 3: Schematic representation of different models tested

2.5.2. Assessment approach for determining habitat disturbance and loss

MFSD criteria D6C3 and D6C4 require evaluating the percentage of surface where benthic communities were altered or lost by trawling. Depending on the respective responses of the four chosen indices, a composite indicator is proposed here. Based on a precautionary approach, and in case different threshold values were detected by different indices, this indicator will select the most conservative abrasion thresholds to classify habitat status based on specific EUNIS habitat susceptibility to fishing induced abrasion. This indicator is computed as follow:

For any given habitat, null abrasion values over the available period resulted in these areas being automatically considered in GES in respect to fishing physical impact (ICES 2018). The GES can be assessed until a pressure threshold from which a significant negative relationship between any selected indices and abrasion is detected (Segment 1 and 2, Figure 3). Above this threshold value or when the relationship is negative and significant over an entire non-null abrasion range (Neglinear, Figure 3), it is considered that the trawling pressure has adverse effects on the benthic communities. If the habitat abrasion gradient exceeds that of the observed range, habitat ecological status would be “adverse effect” or “habitat loss” for the highest values outside the observed range. In contrast, the detection of a negative significant relationship below a given pressure threshold value and followed by an absence of significant relationship (Segment 2 and 3, Figure 3) would indicate that the habitat is lost. Indeed, the absence of relationship indicates that original communities were replaced by communities fully adapted to fishing. Moreover, in that case, if the existing abrasion values exceed that of the observed range, habitat ecological status is also defined as “habitat loss” for the highest values even if unobserved. The failure to detect any relationship between any index and non-null abrasion values when the observed abrasion range is very high (>1) indicates that the habitat is “probably habitat loss”.

Any other un-sampled abrasion value for a given habitat or any unstudied habitats were labelled as “undetermined” status. If sampling occurs in different seasons, precautionary approach requires to keep the most “robust” season (with the higher number of observations per habitat) and, when quality and quantity of the available data were similar between seasons, the most sensitive season (with the lowest threshold value per habitat) was considered.

The conversion of habitat distribution and abrasion maps into ecological status categories (“GES”, “adverse effect”, “adverse effect or habitat loss”, “probably habitat loss”, “habitat loss”, “undetermined”) following the proposed assessment approach was conducted and proportion of habitat falling in each category was computed.

2.6. Uncertainty maps

To evaluate the degree of uncertainty of the approach developed in this work, the relative mean absolute model error (RMAE) was calculated by habitat as:

$$RMAE = \frac{MAE}{|\max(a) - \min(a)|}$$

Where max(a) is the maximum observed value of the “best” index in the studied habitat, min(a) the minimum observed value of the “best” index in the studied habitat and the mean absolute error (MAE) is calculated as:

$$MAE = \frac{\sum_{i=1}^{n} |p_i - a_i|}{n}$$

With p_i the i^{th} predicted value of the index, a_i the i^{th} observed value of the index and n the number of index value in the studied habitat

The spatial distribution of the RMAE was mapped for each habitat investigated and for the indices used, a value of 1 corresponding to the maximum possible prediction error. The RMAE can therefore be interpreted as a percentile of model uncertainty. Based on a precautionary approach and when several indices were significantly correlated with abrasion, the maximal uncertainty (higher RMAE) by habitat was conserved. For illustration purpose, the value of the RMAE was classified into very low uncertainty (0-0.1), low uncertainty (0.1-0.2), moderate uncertainty (0.2-0.5), high uncertainty (0.5-0.75) and very high uncertainty (0.75-1).

3. Results

3.1. Representativeness of available observation

Four habitats in the western Mediterranean, four in the southern North Sea and four in the English Channel were sufficiently sampled and investigated here.
In the Mediterranean area, two habitat types were sampled only in the Gulf of Lion (Table 1): A5.38 (Mediterranean communities of muddy detritic bottoms), A5.39 (Mediterranean communities of coastal terrigenous muds). Two other habitats were sampled in both the Gulf of Lion and in Corsica (Table A.1): A5.46 (Mediterranean communities of coastal detritic bottoms) and A5.47 (Mediterranean communities of shelf-edge detritic). Although no observations were made in areas of low abrasion value in habitats A5.38 and A5.39, the abrasion range sampled seems very similar to the abrasion range experienced by each of these two habitats.

In the southern North Sea, IBTS observations covered eight habitats (Table A.2) but only four were found sufficiently sampled to be taken into account (Table 1). These were A5.15 (Deep circalittoral coarse sediment), A5.25/26 (Circalittoral fine sand/muddy sand), A5.27 (Deep circalittoral sand) and A5.37 (Deep circalittoral mud). Even if very high abrasion values were not sampled for all habitats, the abrasion range sampled seemed representative to that experienced by each habitat in the North Sea.

In the English Channel, observations were available for two seasons which were kept separated in the following analyses. In autumn, CGFS and CAMANOC surveys' data were used and covered twelve different habitat types. Seven habitats were re-sampled in winter during the IBTS survey (Table A.3).
A great diversity of habitats has been sampled in the Channel but only five habitats in autumn and two in winter were found sufficiently sampled to be studied in more detailed (Table 1). These were A5.14 (Circalittoral coarse sediment) and A5.15 (Deep circalittoral coarse sediment) for the two seasons and A5.23/24 (Infralittoral fine sand/muddy sand), A5.25/26 (Circalittoral fine sand/muddy sand) and A5.27 (Deep circalittoral sand) for the autumn. Despite higher sampling effort in areas of high abrasion values than that of low abrasion, the abrasion range sampled seemed representative of the abrasion withstood by each habitat in the English Channel for the two sampled seasons.

Table 1: Abrasion ranges of the main habitats sampled in the different areas studied and the number of survey carried out in these habitats.
The three abrasion values represent the minimum value, the median and the maximum value. GoL = Gulf of Lion

Area	Habitats	Number of observations	Number of station with null abrasion	Abrasion range ($SAR.y^{-1}$)	Sampled abrasion range ($SAR.y^{-1}$)
GoL	A5.38	49	0	0 – 10.79 – 38.18	2.70 – 17.22 – 29.15
	A5.39	129	0	0 – 5.59 – 29.66	2.06 – 5.25 – 13.79
GoL & Corsica	A5.46	80	9	0 – 3.35 – 28.49	0 – 1.00 – 20.77
	A5.47	182	0	0 – 2.14 – 20.22	0.08 – 3.62 – 11.07
Southern North Sea	A5.15	108	11	0 – 1.15 – 32.70	0 – 3.43 – 16.51
	A5.25/26	121	0	0 – 1.61 – 51.27	0.11 – 2.02 – 11.14
	A5.27	226	10	0 – 0.98 – 62.76	0 – 1.17 – 16.15
	A5.37	84	0	0.004 – 1.30 – 26.47	0.60 – 1.74 – 13.41
English Channel (Autumn)	A5.14	264	3	0 – 0.86 – 36.72	0 – 4.60 – 29.58
	A5.15	495	0	0 – 3.40 – 78.71	0.03 – 14.00 – 74.15
	A5.25/26	140	0	0 – 1.51 – 33.40	0.03 – 3.75 – 21.42
	A5.27	42	0	0.05 – 2.98 – 35.67	1.29 – 11.98 – 26.14
English Channel (Winter)	A5.14	60	1	0 – 0.86 – 36.72	0 – 5.29 – 29.58
	A5.15	71	0	0 – 3.40 – 78.71	1.55 – 10.41 – 72.34

3.2. Mediterranean habitats

The multi-indices and multi-model approach proposed to identify threshold values was applied to each of the four habitats in the French part of the Mediterranean Sea (Gulf of Lion and Corsica ; Table 2).
No significant correlation between indices and abrasion was detected on habitats A5.38 and A5.39 in the Gulf of Lion (Figure B.1 & B.2 ; Table B.1 & B.2). On these habitats, the observed range of abrasion was high, an abrasion value above 2 meaning that the surface of the habitat was entirely swept by trawling at least twice a year. In contrast, negative impacts of the trawling on the benthic community were detected on the two other sampled habitats although no threshold value could be highlighted. On the habitat A5.47, two indices detected a negative significant correlation over all the sampled abrasion range (Figure B.4 ; Table B.4) while a single index (mT) detected such relationship on habitat A5.46 (Figure S3 ; Table S3). On these four habitats, the variance explained by all models for each index seemed very low with a maximal value of adjusted R-squared of 0.05 (Table B.1, B.2, B.3 & B.4).

Table 2: Correlation between indices and abrasion, and the type of model selected for each Mediterranean habitats.* indicates that P< 0.05 ; ** indicates that P< 0.01 ; *** indicates that P<0.001 ; - indicates that there is no negative significant correlation. The lack of value next to an asterisk means that the correlation is significant and negative on the entire abrasion range and that no breakpoint could be found. GoL = Gulf of Lion. Grey shading indicates the index choose for this habitat.

Habitats	TDI	mTDI	pTDI	mT	Selected model	AdjR²
A5.38 (GoL)	-	-	-	-	Null	0
A5.39 (GoL)	-	-	-	-	Null	0
A5.46 (Corsica+GoL)	-	-	-	*	Neglinear	0.04
A5.47 (Corsica+GoL)	-	**	-	**	Neglinear	0.05

.

3.3. North Sea habitats

Significant negative relationship between the values of the index and abrasion was detected on all observed habitats (Table 3). Threshold values of 5.90 to 6.52 above which the fishing impact was no longer detectable were determined in habitat A5.15 for most indices (Figure B.5 ; Table B.5). For the three other habitats, the relationship between indices and abrasion was negative and significant over the entire sampled abrasion range even though the observed range of habitat A5.27 included ten apparently un-impacted stations (Figure B.6). On habitats A5.25/26, a significant relationship to abrasion was detected with all indices, except the mT index but no threshold could be found (Figure B.7 ; Table B.7). In contrast, on habitat A5.37, only the mT index detected an impact over the entire abrasion range (Figure B.8 ; Table B.8). On two habitats (A5.25/26 and A5.37), the variance explained by all models for each indices was very low, with a maximal value of adjusted R-squared of 0.07 for the model neglinear on the relationship between the TDI and the abrasion on the habitat A5.25/26 (Table B.6 & B.8). For the two others habitats, the variance explained by all models were relatively higher with a maximum adjusted R-squared of 0.18 for the neglinear model on the habitat A5.27 (Table B.5 & B.7).

Table 3: Correlation between indices and abrasion, and the type of model selected for each habitats in the southern North Sea. * indicates that P< 0.05 ; ** indicates that P< 0.01 ; *** indicates that P<0.001 ; - indicates that there is no negative significant correlation. Values in red represent the trawl intensity above which impact of fishing is not detectable. The lack of value next to an asterisk means that the correlation is significant and negative on the entire abrasion range but no breakpoints could be found. Grey shading indicates the index choose for this habitat.

Habitats	TDI	mTDI	pTDI	mT	Selected model	AdjR²
A5.15	***	6.52**	5.91**	5.90*	Segmented2	0.09
A5.25/26	**	*	**	-	Neglinear	0.07
A5.27	***	***	***	***	Neglinear	0.18
A5.37	-	-	-	*	Neglinear	0.06

3.3. English Channel habitats

The impact of trawling has been detected on all studied habitats (Table 4). On habitat A5.14 and A5.25/26, most indices detected an impact over all the sampled abrasion range but no threshold values were found even though very high abrasion values were also sampled in both cases and three un-impacted observation were available in the A5.14 (Figure B.9 & B.11; Table B.9 & B.11). Threshold values beyond which the fishing impact was no longer detectable were determined for two indices (mTDI and TDI) for the habitat A5.15 (Figure B.10; Table B.10). On habitat A5.27, over which sampled abrasion was quite high, only pTDI and mTDI were able to detect a negative effect of trawling over the entire range of abrasion (Figure B.11; Table B.11). Variance explained by all models were relatively low at three of the four habitats (Table B.9, B.11, B.12) with a maximum adjusted R-squared of 0.10 for the neglinear model on the habitat A5.25/26. But for the habitat A5.15, models seemed to better explain the variance (maximum adjusted R-squared of 0.29 for neglinear models and 0.28 for Segment2 models; Table B.10).

Table 4: Correlation between indices and abrasion, and the type of model selected for each habitats in English Channel in September/October. * indicates that P< 0.05 ; ** indicates that P< 0.01 ; *** indicates that P<0.001 ; - indicates that there is no negative significant correlation. Values in red represent the trawl intensity above which impact of fishing is not detectable. The lack of value next to an asterisk means that the correlation is significant and negative on the entire abrasion range but no breakpoint could be found. Grey shading indicates the index choose for this habitat.

Habitats	TDI	mTDI	pTDI	mT	Selected model	AdjR²
A5.14	*	*	**	-	Neglinear	0.03
A5.15	12.34**	12.34***	***	***	Segment2	0.27
A5.25/26	**	***	***	***	Neglinear	0.21
A5.27	-	*	*	-	Neglinear	0.20

In winter, based on IBTS observations, only two habitats were sufficiently covered to be studied and trawling impact was detected over each of them (Table 5). In habitat A5.15, two of the four indices are no longer able to detect the effect of trawling above an abrasion intensity of about 71.10 for the mT and 18.13 for the pTDI (Figure B.14; Table B.14). No lower bond threshold values were found even though one un-impacted observation (null abrasion) was available. For habitat A5.14, this impact appeared detectable over the whole range of abrasion sampled and no threshold value could be found in spite of the very high observed abrasion values (Figure B.13; Table B.13).

Table 5: Correlation between indices and abrasion, and the type of model selected for each habitats in English Channel in January/February. * indicates that P< 0.05 ; ** indicates that P< 0.01 ; *** indicates that P<0.001. Values in red represent the trawl intensity above which impact of fishing is not detectable. The lack of value next to an asterisk means that the correlation is significant and negative on the entire abrasion range but no breakpoint could be found. Grey shading indicates the index choose for this habitat.

Habitats	TDI	mTDI	pTDI	mT	Selected model	AdjR²
A5.14	**	**	***	***	Neglinear	0.22
A5.15	***	***	18.13*	71.10*	Segment2	0.32

3.5. Evaluation of habitat disturbance and loss

The study of the relationship between each index and the abrasion allowed determining the ecological state of each habitat in the three studied areas (Table 6, 8 & 10). Thus, in the Gulf of Lion, only very small areas were considered in GES (maximum 10 % of the habitat for A5.39). On more than three quarters of the surface of habitats A5.38 and A5.39, which cover together about 50% of the studied area, original benthic communities were considered to be replaced by communities perfectly adapted to the impact of fishing (Figure 4, Table 7). Conversely, in Corsica, no habitat was classified as lost and about 40% of the studied habitat surface was in GES. In the two Mediterranean areas studied, undetermined ecological status on the investigated habitats resulted from lack of observations on the entire range of existing abrasion, but concerned less than 10% of each habitat (except for habitat A5.38). Although habitats A5.46 and A5.47 were jointly assessed in Corsica and in the Gulf of Lion to increase both the number of observations and the abrasion range, they were reported separately to better illustrate the assessment of the ecological status of habitats in Corsica (Table 6).

Table 6: Ranges of abrasion values (in $SAR.y^{-1}$) corresponding to the different ecological status in the Mediterranean habitats

Habitats	Area	GES	Undetermined	Adverse effects	Adverse effects or habitat loss	Probably habitat loss
A5.38	GoL	0	]0 - 2.70[			≥ 2.70
A5.39		0	]0 - 2.06[			≥ 2.06
A5.46		0		]0 - 20.77]	]20.77 - 28.49]	
A5.47			[8×10^{-4} - 0.08[	[0.08 - 11.07]	]11.07 - 20.22]	
A5.46	Corsica	0		]0 - 5.74		
A5.47		0	]0 - 0.08[	[0.08 - 3.46]		

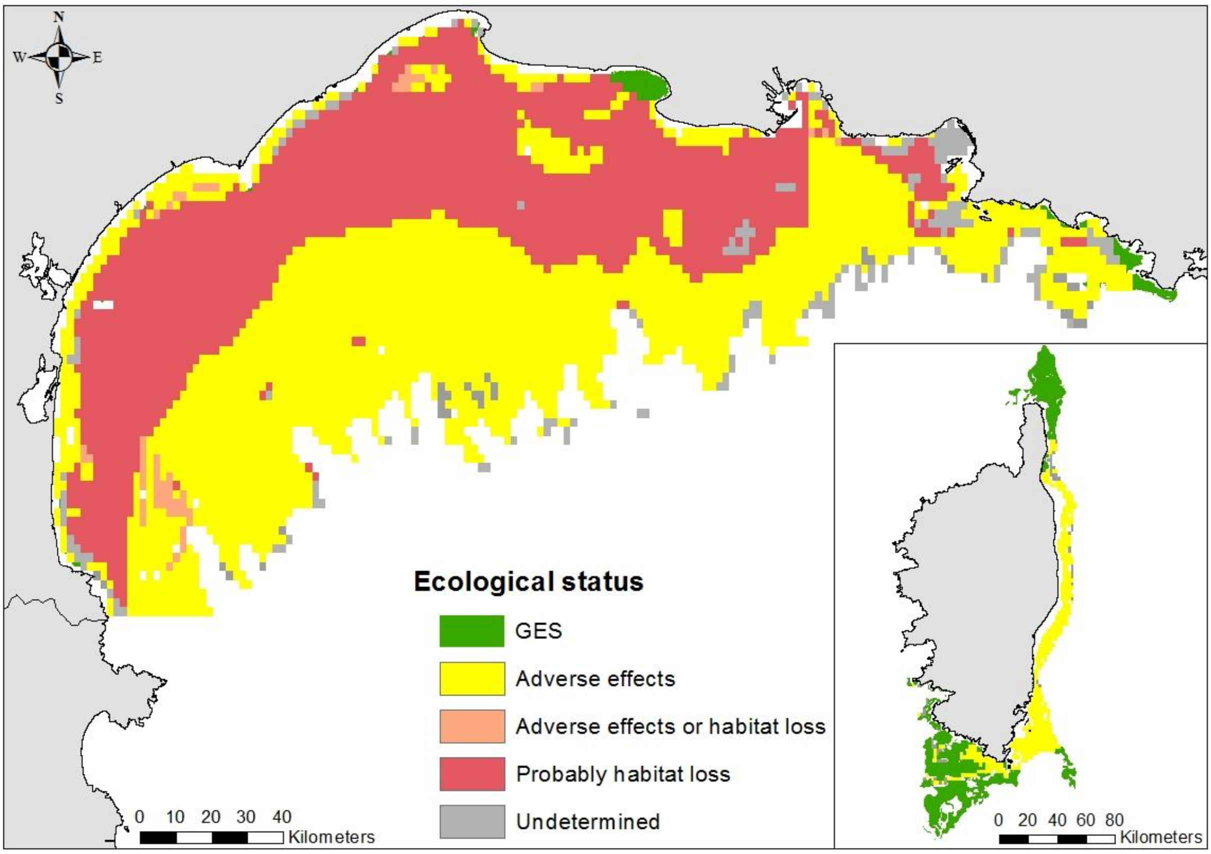


Figure 4: Ecological status of benthic habitats in the Western Mediterranean Sea

Table 7: Proportion of the Golf of Lion (GoL) and Corsica habitats in each of the ecological status category

Ecological status	A5.38 (GoL)	A5.39 (GoL)	A5.46 (GoL)	A5.47 (GoL)	A5.46 (Corsica)	A5.47 (Corsica)
GES	3 %	10 %	5 %	-	46 %	32 %
Adverse effects	-	-	89.4 %	96.4 %	54 %	62.5 %
Adverse effects or habitat loss	-	-	5.6 %	1.8 %	-	-
Probably habitat loss	77 %	83.7 %	-	-	-	-
Undetermined	20 %	6.3 %	-	1.8 %	-	5.5 %

Table 8: Ranges of abrasion values (in SAR.y^{-1}) corresponding to the different ecological status in the North Sea habitats

Habitats	GES	Undetermined	Adverse effects	Adverse effects or habitat loss	Habitat loss
A5.15	0		]0 - 5.90]		> 5.90
A5.25/26	0	]0 - 0.11[	[0.11 - 11.14]	]11.14 - 51.27]	
A5.27	0		]0 - 16.15]	]16.15 - 62.76]	
A5.37		[0.004 - 0.60[	[0.60 - 13.41]	]13.41 - 26.47]	

In the South of the North Sea, a majority of habitats was considered as impacted (adverse effects) but not lost (Table 8, Figure 5) and only very few small and scattered areas were considered as lost (less than 5% of each habitat). Since an important part of the North Sea is apparently untrawled, many areas were considered in GES, especially in the western part. As a result, about 51.5% of the habitat A5.15 was considered in GES in respect to fishing physical impact to the seabed (Table 9). Undetermined ecological status represented from 4% in habitat A5.25/26 to almost 13% of habitat A5.37.

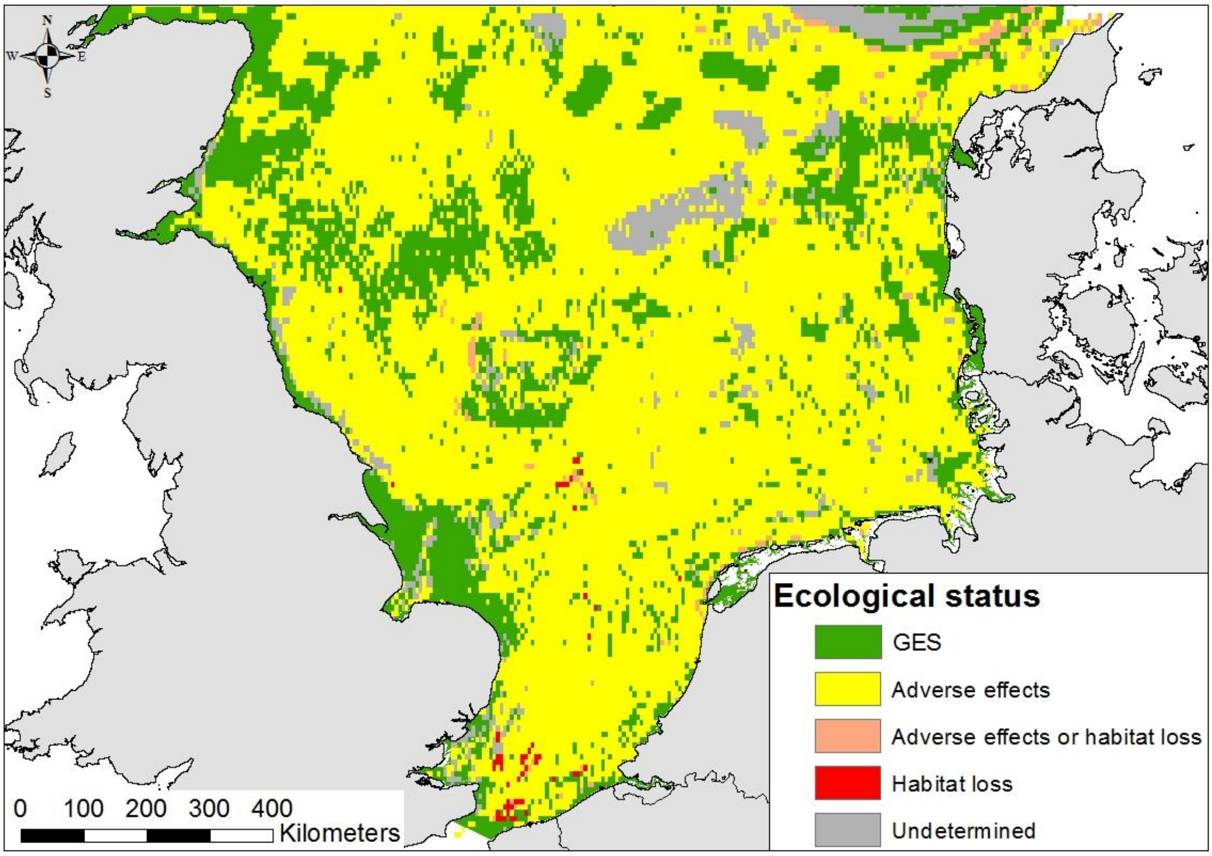


Figure 5: Ecological status of benthic habitats in the southern North Sea

Table 9: Proportion of southern North Sea habitats in each of the ecological status category

Ecological status	A5.15	A5.25/26	A5.27	A5.37
GES	51.5 %	0.5 %	6 %	-
Adverse effects	45 %	93.6 %	93.4 %	86.5 %
Adverse effects or habitat loss	-	2 %	0.6 %	0.7 %
Habitat loss	3.5 %	-	-	-
Undetermined	-	3.9 %	-	12.8 %

Table 10: Ranges of abrasion values (in SAR.y-1) corresponding to the different ecological status in the English Channel in autumn and winter according to abrasion

Habitats	Season	GES	Undetermined	Adverse effects	Adverse effects or habitat loss	Habitat loss
A5.14	Autumn	0		]0 - 29.58]	]29.58 - 36.72]	
A5.15		0	]0 - 0.03[	[0.03 - 12.34]		> 12.34
A5.25/26		0	]0 - 0.03[	[0.03 - 21.42]	]21.42 – 33.40]	
A5.27			[0.05 - 1.29[	[1.29 - 26.14]	]26.14 - 35.67]	
A5.14	Winter	0		]0 - 29.58]	]29.58 - 36.72]	
A5.15		0	]0 - 0.03[	[0.03 - 18.13]		> 18.13

For the two habitats sampled in the English Channel in autumn and in winter, only few differences were observed in the habitat A5.15, with a threshold after an abrasion of 12.34 in autumn and 18.13 in winter (Table10).

In autumn in the English Channel, only small coastal areas were found in GES and 9% of habitat A5.15 was classified as “habitat loss” (Table 10 & 11, Figure 6). In this particular case study, the proportion of inadequately sampled habitats seemed quite substantial and resulted in a large amount of grey areas. In addition, the ecological status of nearly 3.6% of the studied habitats could not be determined with, in particular, 14.5% of habitat A5.27 and 8.4% of habitat A5.25/26 labelled as undetermined.

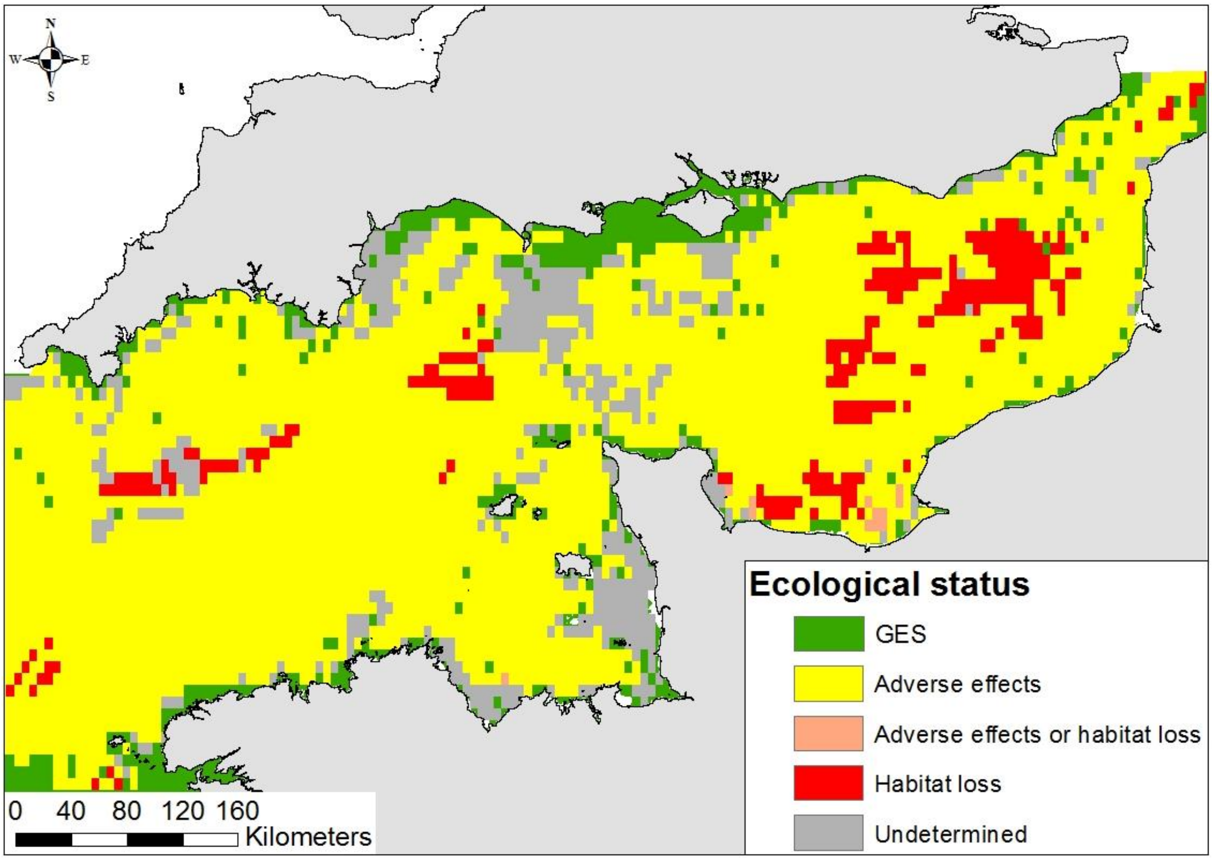


Figure 6: Ecological status of benthic habitats in the English Channel

Table 11: Proportion of English Channel habitats in each of the ecological status in autumn

Ecological status	A5.14	A5.15	A5.25/26	A5.27
GES	15.5 %	0.5 %	8 %	-
Adverse effects	84.3 %	88.0 %	77.4 %	83.5 %
Adverse effects or habitat loss	0.2 %	-	6.2 %	2.0 %
Habitat loss	-	9.0 %	-	-
Undetermined	-	2.5 %	8.4 %	14.5 %

3.6. Uncertainty maps

Modeled uncertainties were different between habitats and areas but were relatively low in most areas particularly in the English Channel and in Corsica (Figure 7). In the southern North Sea, models uncertainties were higher in the West while in the Gulf of Lion, the uncertainties were higher (0.2 < RMAE ≤ 0.5) for the most offshore habitats. Note that the areas where abrasion was zero are classified in the category “Very low uncertainties”.

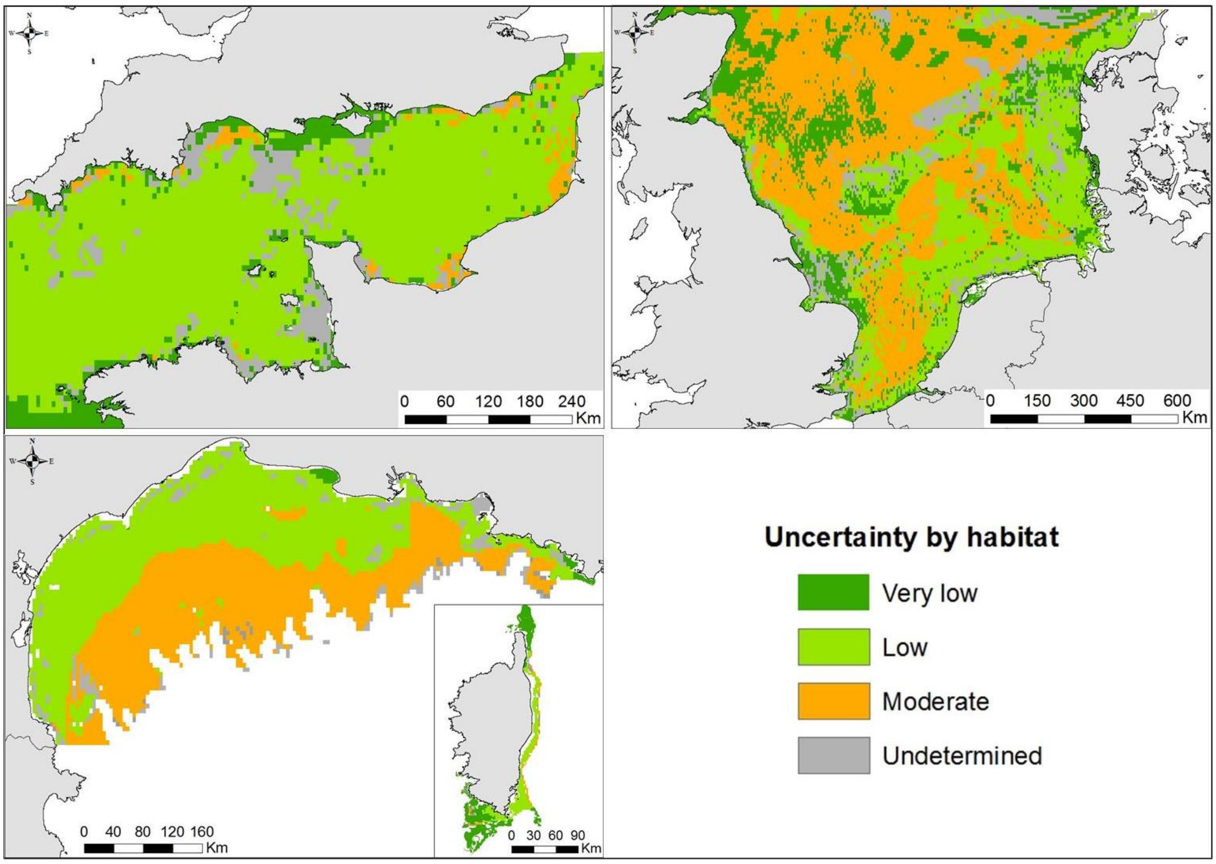


Figure 7: Models uncertainties by habitat in the three studied areas.
Very low correspond to 0≤RMAE≤0.1; Low correspond to 0.1<RMAE≤0.2; Moderate correspond to 0.2<RMAE≤0.5

4. Discussion

4.1. Method uncertainties

4.1.1. Data variance

In the majority of the habitats sampled in this study, the variance explained by models seemed low as is often the case with noisy data. This variability mostly resulted from inter-annual variations due to the pooling of several years of surveys together. Inter-annual variations could be due to several factors: the natural variability of each population (quality of recruitment and different growth between years), the separation time between the last fisher trawling operation and the scientific haul or even location inaccuracy of the haul station across years. Working at habitat level increased the effect of temporal over spatial variability of the benthic communities in the three studied areas. Although this should increase model uncertainty, it appeared relatively moderate in most instances due to relatively low mean absolute error between modeled predictions and observations. However, other sources of uncertainties such as errors in the calculation of abrasion values or in modeled habitat classification should also be taken into account in the present approach.

4.1.2. VMS data

The use of VMS data for the calculation of abrasion induces a certain number of uncertainties. Firstly, VMS positioning is required only for vessels of 12 m or longer (EC 2009) since 2012, and 15 m or longer before that. The trawling operations carried out by smaller vessels are therefore not taken into account in the abrasion data and it is conceivable that the coastal areas considered in GES are actually trawled or dredged by the small vessels in particular in estuaries or bays. As a consequence, some areas, in particular coastal areas, may be wrongly considered as untrawled and therefore in GES. Moreover, the signal frequency is limited to once every two hours (Shepperson et al. 2018), which further reduces the accuracy and spatial resolution of the abrasion values (ICES 2018). The use of aggregated VMS data (3'x3' in the English Channel/southern North Sea and 1'x1' in the Mediterranean Sea) does not allow us to have the precise location of the trawl hauls and induces potential errors on the allocation of abrasion values to the different sampled stations. However, if the distribution of fishing activities is random within each grid cells, the compilation of several years of abrasion strongly reduces this bias by making the distribution of the abrasion homogenous within the cell (Ellis et al. 2014; Eigaard et al. 2017). Despite all these potential sources of biais, no uncertainty assessment method for the abrasion calculation has been proposed. Nevertheless, the generalization of the use of VMS to all professional fishing vessels and the increase of the signal frequency to less than 30 minutes would make it possible to overcome these methodological biases in the near future which seems preferable to systematically excluding near shore areas from the assessment. Finally, the English Channel, the southern North Sea and the Mediterranean Sea have been subjected to industrial trawling for decades (Englehard 2008; Hidalgo et al. 2009; Thurstan et al. 2010) and in the present study, the data on abrasion only concern the 2009 – 2017 period. As a result, there is no certainty that areas considered untrawled are pristine areas or fully recovered from past trawling disturbances.

4.1.3. EUNIS classification

The use of EUNIS habitat classification and predictive maps also leads to uncertainties. Indeed, boundaries between habitats classes can be uncertain or habitats can be wrongly described due to erroneous description and classification of the continuous physical variables such as substrate types or energy classes. To evaluate uncertainties specific to each area, a confidence assessment method was already developed by Populus et al. (2017) to obtain a classification in three levels (low, moderate, high) of the habitat type confidence (https://www.emodnet-seabedhabitats.eu/ment of the total uncertainty of the method proposed in the present study would require combining the error arising from three sources of uncertainties: model error, abrasion calculation error and EUNIS classification confindence levels. Currently, only the uncertainty maps of the models developed in this study, and maps of EUNIS habitats uncertainties exist and provide a partial overview of the overall uncertainty.

4.2. Variation in threshold values

Habitat response to fishing pressure was shown to vary with geographic basins and even seasons. Indeed, the habitat A5.15 was sampled in the North Sea and the English Channel but was considered lost after an abrasion threshold of 5.90 in the North Sea and 12.34 in the English Channel. Several reasons may explain these differences.

Firstly, although this habitat was classified in the same way in EUNIS, it is possible that benthic communities slightly differ between the two basins. Indeed, in this habitat, for instance, two main facies are defined in the EUNIS classification: A5.151 (facies with *Glycera lapidium*, *Thyasira spp.* and *Amythasides macroglossus*) and A5.152 (facies with *Hesionura elongata* and *Protodorvillea keferteini*). Only the consideration of the level 5 of EUNIS could confirm this hypothesis and may explain these differences. Additionally, the apparently higher trawling resistance of the benthic communities of habitat A5.15 in the English Channel compared to the North Sea could also be due to differences in hydrodynamics between the two basins. Many studies have shown that natural disturbance due to waves and tides increases the resilience of benthic communities to fishing disturbance (Diesing et al. 2013; van Denderen et al. 2015) in at least two ways. Firstly, the resilience can be increased by selecting for fast-growing opportunistic species which quickly recolonize disturbed areas and can reach sexual maturity before the next disturbance event (Pianka 1970). Second, species that display traits that pre-adapt them to withstand the disturbance may have an advantage in naturally disturbed habitats (Diesing et al. 2013). The intense hydrodynamism in the English Channel relative to the North Sea can therefore result in more resistance of the English Channel's benthic communities to trawling and therefore the value of fishing intensity causing habitat to be "lost" is higher. To verify this, the Kostylev approach (Kostylev and Hannah 2007; Foveau et al. 2017) could be used to combine a pool of environmental layers explicitly linked to relevant ecological processes known to affect the seabed. These, such as salinity, temperature, oxygen saturation, sediment grain size or friction velocity at seabed may in turn be used to predict and map habitat sensitivity. The combination of both EUNIS and process-driven sensitivity would certainly enable a better distinction of these habitats.

Circalittoral coarse sediment (A5.15) was sampled in autumn and in winter in the eastern English Channel and sensitivity difference was highlighted between the two seasons. This habitat seemed less sensitive to trawling in winter than autumn (habitat considered lost from a value of 12.34 abrasion in autumn to 18.13 in winter). It is very likely that this resulted from differences in the number of observations available for each season. The study of the seasonal effect on the sensitivity of benthic habitat to trawling requires to use similar sampling station set for each season and may also require monthly VMS data and was clearly out of the scope of this study.

The most “robust” season, i.e. with the largest sample size on each habitat, was chosen to build the assessment of habitat disturbance and loss. As all habitats of the English Channel were largely sampled in autumn, this season was chosen for the assessment of the ecological status of the benthic habitats of this area.
More importantly, this study has highlighted how different indices performance may vary amongst habitats and/or abrasion range. Although the four indices used were closely related by construction, they displayed different abilities to describe benthic communities’ sensitivity to trawling as a result of the inequal weighting given to different biological traits present in these communities. These indices sensitivity appeared somehow dependent of each community overall traits’ composition. The approach proposed here, based on precautionary principle, may easily be extended to another set of complementary indices that may be more suited for different habitats, abrasion range, biotic data type or to investigate another type of pressure altogether.

4.3. On the difficulty to find and sample low abrasion reference areas: a methodological bolt

In the French part of the Mediterranean Sea, there was no clear relationship between abrasion and any of the four selected indices in muddy habitats (A5.38 and A5.39). For these, there was no observation located in low abrasion areas and sampling was carried out in areas with abrasion levels higher than 2. These values being high (the surface being totally swept twice a year), we assume that the original communities of these habitats have already been completely replaced by communities adapted to trawling, which would justify the lack of relationship between indices and abrasion levels. These particularly severe results may be explained by the particular environmental conditions prevailing of this geographical area.Firstly, as the hydrodynamics is relatively low in the continental shelf of the Gulf of Lion (absence of tide or high current), benthic communities are not naturally adapted to disturbances and would therefore be very sensitive to any additional physical disturbance such as trawling. Similarly, the oligotrophic nature of the Mediterranean Sea (Estrada 1996) could also lead to higher fragility of benthic habitats to trawling than would be in more productive environments such as the English Channel or the North Sea. In fact, oligotrophy results in low species abundance and smaller individuals biomasses (Smith et al. 2000), which reduces community resilience. Finally, the accuracy of the habitat maps may also be questioned as differences in assemblage of benthic communities are known to exist between the East and West of the Gulf of Lion (Labrune et al. 2007, 2008). These differences being related to the sediment granulometry, the use of a more accurate habitat map or the use of the Kostylev habitat approach (Kostylev and Hannah 2007) may possibly correct this bias in the future.
The absence of pressure free, ideally pristine, areas for most habitats in the different basins investigated prevents the use of a method based on an observed reference state to contrast and monitor the trawling disturbance. Indeed, only few stations (a maximum of 11 stations by habitats and 33 stations in total) were sampled in un-impacted areas in the four surveys available and this may be explained in two ways.
Firstly, as in many other geographical areas (Nilsson and Ziegler 2007; Baird et al. 2015), the totality of the trawlable habitats of the European shelves is trawled (eg. habitat A5.27 in the Channel and A5.37 in the North Sea) and, therefore, no reference area exists for these habitats. In this case, the creation of protected areas where trawling is banned may possibly allow, after a certain delay (probably very long), the restoration of the original community that may then be used as reference.
Secondly, the small number of stations sampled in untrawled areas is due to gaps in the sampling design of the chosen surveys. Indeed, scientific trawl surveys are not dedicated to the study of

the effect of trawling but to the evaluation of fish stocks, so sampling is not carried out according to an abrasion gradient but following a random stratified sampling scheme deemed relevant for each area and the targeted stocks (MEDITS 2017). The addition of complementary observations to existing scientific trawl surveys in untrawled or lesser trawled habitats such as A5.15 in the English Channel or A5.38 in the Gulf of Lion would enable to investigate their original communities and set reference states. The increase in the number of observations could also reduce the surface of indeterminate status areas that represented more than 10% of the total area of some habitats (eg. A5.37 in the North Sea and A5.27 in the English Channel).

4.4. Non-linear impact of trawling on benthic fauna

The response of benthic fauna community structure to environmental impacts is often non-linear with increasing change above a threshold value of the impact factor (Josefson et al. 2008). Trawling seems to non-linearly impact benthic fauna according to the fishing intensity (Hiddink et al. 2008, 2011) and/or the season (Kaiser et al. 1998). In this work, it was considered that relationship between indices (ie. sensitivity of benthic community) and abrasion is segmented and composed of two threshold values between which trawling impacts negatively and significantly the benthic fauna. It has been hypothesized that below a certain annual value of abrasion (probably extremely low) the sensitivity of the community (and therefore the value of the index) does not vary significantly. Between this value and the absence of abrasion, benthic community is considered in a good ecological status. Beyond this threshold value of abrasion, the pressure is strong enough to progressively alter the benthic community (decrease of index values), in particular by inducing a decrease in trawl-sensitive species by minimizing their ability to recover. This process could be considered as a physical disturbance (change to the seabed from which it can recover if the activity causing the disturbance pressure ceases ; ICES 2018) and define "adverse effects" in the ecological classification of the seabed in this study. In addition to affect benthic communities, especially epifauna, trawling results in a change in physical habitat. In fact, trawling induces changes (i) in grain size, with an increase in coarse sediment and a decrease in mud (Palanques et al. 2014; Mengual et al. 2016), (ii) an increase in the organic carbon content in the first centimeters of sediments (Palanques et al. 2014) and (iii) a flattening of the bottom topography by eliminating natural irregular feature such as ripples, bioturbation mounds, biogenic reefs or seagrass mats (Fonteyne 2000b). Such physical modifications of the bottom may also modify original benthic communities, which may be, in very heavily trawled areas, completely replaced by others, perfectly adapted to these disturbances. Consequently, beyond a certain abrasion value, the index cannot respond negatively to the increase in abrasion and the original habitat (biotic and abiotic) may be considered as lost because it is a permanent modification of the seabed that can last a very long time, even after stopping trawling (ICES 2018).

4.5. Towards the restauration of benthic habitats?

Restoration of benthic habitat is a long process as reported by Sheehan et al. (2013) which observed a partial recolonization of the epifauna, three years after trawling ban in the western English Channel, Tuck et al. (1998) which showed that 18 months were necessary to the recovering of infaunal communities in Scottish Sea lochs and Desprez (2000) and Sardá et al. (2000) which underlined recovery delays between one to three years for macrobenthic invertebrates like molluscs, crustaceans and echinoderms (in the eastern English Channel and Catalan western Mediterranean respectively). However, the complete recovery of original communities, including slow growing species such as sponges or cold water corals may take several years or decades. Determining recovery time is very important for the management of the marine ecosystem and complementary studies are required on benthic recolonization of areas where trawling is permanently banned.

The assessment of the ecological status of benthic habitats not only provides information on the integrity of the seabed to date, but can also provide some clues about its evolution. Indeed, areas where the habitat is considered as lost will not have the same capacity to return at the GES than impacted areas (adverse effects category) when fishing pressure is reduced or removed. The habitat type (Collie et al. 2000b), the ecological connectivity of the areas (Eno et al. 2013) and the diversity of responses between different species to disturbance (Muntadas et al. 2016) also play an important role in the resilience of benthic communities. The presence of a large number of small areas considered in good ecological state in the English Channel and in the North Sea would appear beneficial for all the benthic habitats of these two zones. The existence of untrawled areas and the important productivity of these two marine basins will allow some species to withstand the impacts of trawling through recruitment or regeneration processes (Osman and Whitlatch 1998; Pranovi et al. 1998; Frid et al. 2000). Although the interruption of trawling would certainly lead to environmental status improvement, all habitats will not necessary return to GES at the same speed. In the worst case scenarios, areas where the original community is fully replaced by a fishery adapted community (habitat loss), if too isolated from a potential source original population, could potentially never regain their original state even with complete trawling exclusion.

4.6. Extension of the approach to coastal areas and other pressures

In the present study, only the specific effect of fishing disturbance on the seabed was taken into account. A large part of the European continental shelf surface is exclusively submitted to the fishery induced abrasion pressure and the present work offers an operational and cost-efficient method to evaluate its impact on seabed integrity in the frame of the MFSD. The assessment of the ecological status of benthic habitats should also account for other anthropogenic physical pressures such as aggregate extraction, placement of physical structures (oil and gas extraction, renewable energy, harbours and coastal defense, tourism/recreation, road and rail transportation, pipelines and cables, wrecks, artificial reefs…), or dredge disposal (ICES 2019a) to provide a full picture of the ecological status of the benthic habitats in studied areas. In coastal areas, the impact of other pressures, also including pollution and eutrophication may largely exceed that of fishing and prevent habitat restoration even if fishery pressure is lessened. The threshold detection approach, developed in this work, could be applied to other pressures types (with indicators specific to these pressures) and could thus respond to this need. However, a pressure and habitat-by-habitat approach, using the most appropriate observed biological data, seems more relevant and defensible than a global approach. Using ecological status classification of benthic habitats for each pressure and aggregating them would allow a general assessment (combining all pressures) of the ecological states of the seabed. The development of methodologies to aggregate environmental status resulting from different types of pressure and to account for potential cumulative effect of these impacts are necessary to monitor the sea-floor integrity as a whole.

Finally, this work meets different criteria of the MSFD because pressure thresholds values for the adverse effects of physical disturbance were defined (D6C3) and an assessment of the extent of benthic community "loss" or "alteration" was realized (D6C4 and D6C5). In all investigated areas, the percentage of habitat impacted by trawling pressure seems to exceeds the recommended 30% of the total surface while only a few habitats exceed the value of 5% of lost habitat (Unknow 2016). Decrease of impacted surfaces is recommended, but this should not be done at the cost of increasing habitat loss surfaces as a result of fishing effort displacement. It necessary should be assorted of an overall bottom trawl effort reduction.

5. Conclusions

The establishment of the MSFD by the European Union in 2008 requires the development methodological standards for determining the good environmental status. Trawling appearing as one of the strongest pressure on the seabed, the definition of thresholds for each habitat type that may be trawled is required. However, the absence of sampling on certain habitat or poor sampling distribution along the abrasion gradient, for some habitat, showed the necessity to increase the sampling effort especially in low and high abrasion areas. The evaluation of the impact of trawling on benthic communities highlighted that the vast majority of the investigated sub-regions were adversely impacted or lost as a result of seabed impacting trawling.

Acknowledgement

The authors are grateful to, the projects leaders of MEDITS, CGFS, IBTS and CAMANOC scientific surveys, the scientific staff and vessel crews who participated to these surveys. This study was supported by the EC2CO National Program on Coastal Environments (Bentchal). This study has been supported by the DG ENV project IDEM (Implementation of the MSFD to the Deep Mediterranean Sea; contract EU No 11.0661/2017/750680/SUB/EN V.C2). C. J. from MARBEC, Ifremer acknowledge support from the Occitanie region through its PhD research funding program.

References

Alfons A (2016) Package “robustHD”. https://cran.r-project.org/web/packages/robustHD/.

Auber A (1992) IBTS : International Bottom Trawl Survey. https://doi.org/10.18142/17.

Baird SJ, Hewitt J, Wood BA (2015) Benthic habitat classes and trawl fishing disturbance in New Zealand waters shallower than 250 m. New Zealan:

Brind’Amour A, Laffargue P, Morin J, Vaz S, Foveau A, Le Bris H (2014) Morphospecies and taxonomic sufficiency of benthic megafauna in scientific bottom trawl surveys. Cont Shelf Res 72:1–9

Brind’Amour A, Rouyer A, Martin J (2009) Functional gains of including non-commercial epibenthic taxa in coastal beam trawl surveys: A note. Cont Shelf Res 29:1189–1194

Callaway R, Alsvåg J, De Boois I, Cotter J, Ford A, Hinz H, Jennings S, Kröncke I, Lancaster J, Piet G, Prince P, Ehrich S (2002) Diversity and community structure of epibenthic invertebrates and fish in the North Sea. ICES J Mar Sci 59:1199–1214

CNDCSMM (2019) Synthèse de l’évaluation de l’atteinte du bon état écologique au titre du descripteur 6 “Intégrité des fonds marins” (critères D6C1, D6C2 et D6C3) par façade maritime.

Certain G, Jorgensen LL, Christel I, Planque B, Bretagnolle V (2015) Mapping the vulnerability of animal community to pressure in marine systems: disentangling pressure types and integrating their imapct from the invidual to the community level. ICES J MAR Sci 72:1470-1482

Collie JS, Hall SJ, Kaiser MJ, Poiner IANR (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. J Anim Ecol 69:785–798

Coppin F, Travers-Trolet M (1989) CGFS : Channel Ground Fish Survey. https://doi.org/10.18142/11.

Davies R (2002) Hypothesis testing when a nuisance parameter is present only under the alternative: linear model case. Biometrika 89:484–489

de Juan S, Demestre M (2012) A Trawl Disturbance Indicator to quantify large scale fishing impact on benthic ecosystems. Ecol Indic 18:183-190

van Denderen P, Bolam S, Hiddink J, Jennings S, Kenny A, Rijnsdorp A, van Kooten T (2015) Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. Mar Ecol Prog Ser 541:31–43

Desprez M (2000) Physical and biological impact of marine aggregate extraction along the French coast of the Eastern English Channel: Short-and long-term post-dredging restoration. ICES J Mar Sci 57:1428–1438

Diesing M, Stephens D, Aldridge J (2013) A proposed method for assessing the extent of the seabed significantly affected by demersal fishing in the Greater North Sea. ICES J Mar Sci 70:1085–1096

EC (2008) Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). Off J Eur Union 19–40

EC (2009) Council Regulation (EC) No. 1224/ 2009 of 20 November 2009 establishing a Community control system for ensuring compliance with the rules of the common fisheries policy, amending Regulations (EC) No 847/96, (EC) No 2371/2002, (EC) No 811/2004, (EC) No 768. Off J Eur Union L343:1–50

EC (2017) COMMISSION DECISION (EU) 2017/848 of 17 May 2017 laying down criteria and methodological standards on good environmental status of marine waters and specifications and standardised methods for monitoring and assessment, and repealing Decision 2010/477/EU. Off J Eur Union 43–73

Eigaard OR, Bastardie F, Breen M, Dinesen GE, Hintzen NT, Laffargue P, Mortensen LO, Nielsen JR, Nilsson HC, O'Neill FG, Polet H, Reid DG, Sala A, Sköld M, Smith C, Sorensen TK, Tully O, Zengin M, Rijnsdorp AD (2016) Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J Mar Sci 73:i27–i43

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P, Catarino R, Dinesen GE, Egekvist J, Fock HO, Geitner K, Gerritsen HD, González MM, Jonsson P, Kavadas S, Laffargue P, Lundy M, Gonzalez-Mirelis G, Nielsen JR, Papadopoulou N, Posen PE, Pulcinella J, Russo T, Sala A, Silva C, Smith CJ, Vanelslander B, Rijnsdorp AD (2017) The footprint of bottom trawling in European waters: Distribution, intensity, and seabed integrity. ICES J Mar Sci 74:847–865

Ellis N, Pantus F, Pitcher CR (2014) Scaling up experimental trawl impact results to fishery management scales - a modelling approach for a "hot time." Can J Fish Aquat Sci 71:733–746

Englehard GH (2008) One hundred and twenty years of change in fishing power of English North Sea trawlers. In: Payne A., Cotter J., Potter T. (eds) Advances in Fisheries Science: 50 years on from Beverton and Holt. pp 1–25

Eno N, Frid C, Hall K, Ramsay K, Sharp R, Brazier D, Hearn S, Dernie K, Robinson K, Paramor O, Robinson L (2013) Assessing the sensitivity of habitats to fishing: From seabed maps to sensitivity mapsa. J Fish Biol 83:826–846

Estrada M (1996) Primary production in the northwestern Mediterranean. Sci Mar 60:55–64

Fonteyne R (2000) Physical impacts of beam trawls on seabed sediments. In: Kaiser M.J., Groot S.J. (eds) Effects of fishing on non-target species and habitats. Blackweel Science, Oxford, pp 12–36

Foveau A, Vaz S, Desroy N, Kostylev VE (2017) Process-driven and biological characterisation and mapping of seabed habitats sensitive to trawling. PLoS One 12:1–30

Frid CLJ, Harwood KG, Hall SJ, Hall JA (2000) Long-term changes in the benthic communities on North Sea fishing grounds. ICES J Mar Sci 57:1303–1309

Galparsoro I, Connor DW, Borja Á, Aish A, Amorim P, Bajjouk T, Chambers C, Coggan R, Dirberg G, Ellwood H, Evans D, Goodin KL, Grehan A, Haldin J, Howell K, Jenkins C, Michez N, Mo G, Buhl-mortensen P, Pearce B, Populus J, Salomidi M, Sánchez F, Serrano A, Shumchenia E, Tempera F, Vasquez M (2012) Using EUNIS habitat classification for benthic mapping in European seas : Present concerns and future needs. Mar Pollut Bull 64:2630–2638

Gray J, Elliott M (2009) Ecology of marine sediments: from science to management. Oxford University Press, New York

Groffman PM, Baron JS, Blett T, Gold AJ, Goodman I, Gunderson LH, Levinson BM, Palmer MA, Paerl HW, Peterson GD, Poff NLR, Rejeski DW, Reynolds JF, Turner MG, Weathers KC, Wiens J (2006) Ecological thresholds: The key to successful environmental management or an important concept with no practical application? Ecosystems 9:1–13

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan H., Madin EM., Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. Science (80-) 319:948–953

Hidalgo M, Massutí E, Guijarro B, Moranta J, Ciannelli L, Lloret J, Oliver P, Stenseth NC (2009) Population effects and changes in life history traits in relation to phase transitions induced by long-term fishery harvesting: European hake (Merluccius merluccius) off the Balearic Islands. Can J Fish Aquat Sci 66:1355–1370

Hiddink JG, Jennings S, Kaiser MJ (2007) Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. J Appl Ecol 44:405–413

Hiddink JG, Johnson AF, Kingham R, Hinz H (2011) Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition. J Appl Ecol 48:1441–1449

Hiddink JG, Rijnsdorp AD, Piet G (2008) Can bottom trawling disturbance increase food production for a commercial fish species? Can J Fish Aquat Sci 65:1393–1401

ICES (2018) Interim Report of the Working Group on fisheries benthic impact and trade-offs (WGFBIT).

ICES (2019a) OSPAR request on the production of spatial data layers of fishing intensity/pressure. ICES Tech Serv

ICES (2019b) Workshop to evaluate and test operational assessment of human activities causing physical disturbance and loss to seabed habitats (MSFD D6C1, C2 and C4). ICES Sci reports 1:77

Jac C, Vaz S (2018) Abrasion superficielle des fonds par les arts trainants - Méditerranée (surface swept area ratio). https://doi.org/10.12770/8bed2328-a0fa-4386-8a3e-d6d146cafe54.

Jac C, Desroy N, Certain G, Foveau A, Labrune C, Vaz S (2020). Detecting adverse effect on seabed integrity. Part 1: Generic sensitivity indices to measure effect of trawling on benthic mega-epifauna. Ecol Ind. In press

Jadaud A, Souplet A, Bertrand J (1994) MEDITS. https://doi.org/10.18142/7.

Josefson AB, Hansen JLS, Asmund G, Johansen P (2008) Threshold response of benthic macrofauna integrity to metal contamination in West Greenland. Mar Pollut Bull 56:1265–1274

Kaiser MJ, Edwards DB, Armstrong PJ, Radford K, Lough NEL, Flatt RP, Jones HD (1998) Changes in megafaunal benthic communities in different habitats after trawling disturbance. ICES J Mar Sci 55:353–361

Kostylev VE, Hannah CG (2007) Process-driven characterization and mapping of seabed habitats. Spec Pap - Geol Assoc Canada 171–184

Labrune C, Grémare A, Amouroux JM, Sardá R, Gil J, Taboada S (2007) Assessment of soft-bottom polychaete assemblages in the Gulf of Lions (NW Mediterranean) based on a mesoscale survey. Estuar Coast Shelf Sci 71:133–147

Labrune C, Grémare A, Amouroux JM, Sardá R, Gil J, Taboada S (2008) Structure and diversity of shallow soft-bottom benthic macrofauna in the Gulf of Lions (NW Mediterranean). Helgol Mar Res 62:201–214

Leonardsson K, Blomqvist M, Rosenberg R (2009) Theoretical and practical aspects on benthic quality assessment according to the EU-Water Framework Directive - Examples from Swedish waters. Mar Pollut Bull 58:1286–1296

van Loon WMGM, Walvoort DJJ, van Hoey G, Vina-Herbon C, Blandon A, Pesch R, Schmitt P, Scholle J, Heyer K, Lavaleye M, Phillips G, Duineveld GCA, Blomqvist M (2018) A regional benthic fauna assessment method for the Southern North Sea using Margalef diversity and reference value modelling. Ecol Indic 89:667–679

MEDITS (2017) MEDITS - International Bottom Trawl Survey in the Mediterranean : Instruction Manual Version 9.

Mengual B, Cayocca F, Le Hir P, Draye R, Laffargue P, Vincent B, Garlan T (2016) Influence of bottom trawling on sediment resuspension in the 'Grande-Vasière' area (Bay of Biscay, France).

Muggeo V (2019) Package "segmented". https://cran.r-project.org/web/packages/segmented/.

Muntadas A, De Juan S, Demestre M (2016) Assessing functional redundancy in chronically trawled benthic communities. Ecol Indic 61:882–892

Nilsson P, Ziegler F (2007) Spatial distribution of fishing effort in relation to seafloor habitats in the Kattegat, a GIS analysis. Ann Zool Fennici 17:421–440

Osman RW, Whitlatch RB (1998) Local control of recruitment in an epifaunal community and the consequences to colonization processes. Hydrobiologia 375–376:113–123

OSPAR (2012) MSFD Advice Manual on Biodiversity Approaches to determining good environmental status , setting of environmental targets and selecting indicators.

Palanques A, Puig P, Guillén J, Demestre M, Martín J (2014) Effects of bottom trawling on the Ebro continental shelf sedimentary system (NW Mediterranean). Cont Shelf Res 72:83–98

Pianka E (1970) On r- and K-Selection. Am Nat 104:592–597

Populus J, Vasquez M, Albrecht J, Manca E, Agnesi S, Al Hamdani Z, Andersen J, Annunziatellis A, Bekkby T, Bruschi A, Doncheva V, Drakopoulou V, Duncan G, Inghilesi R, Kyriakidou C, Lalli F, Lillis H, Mo G, Muresan M, Salomidi M, Sakellariou D, Simboura M, Teaca A, Tezcan D, Todorova V, Tunesi L (2017) EUSeaMAP : A European broad-scale seabed habitat map.

Pranovi F, Giovanardi O, Franceschini G (1998) Recolonization dynamics in areas disturbed by bottom fishing gears. Hydrobiologia 375–376:125–135

R Core Team (2017) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna

Reiss H, Kröncke I, Ehrich S (2006) Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments. ICES J Mar Sci 63:1453–1464

Rice J, Arvanitidis C, Borja A, Frid C, Hiddink JG, Krause J, Lorance P, Ragnarsson SÁ, Sköld M, Trabucco B, Enserink L, Norkko A (2012) Indicators for sea-floor integrity under the European Marine Strategy Framework Directive. Ecol Indic 12:174–184

Rumohr H (1999) Soft bottom macrofauna: Collection, treatment, and quality assurance of samples. ICES Tech Mar Environ Sci 1–20

Sardá R, Pinedo S, Gremare A, Taboada S (2000) Changes in the dynamics of shallow sandy-bottom assemblages due to sand extraction in the Catalan Western Mediterranean Sea. ICES J Mar Sci 57:1446–1453

Sheehan E V., Cousens SL, Nancollas SJ, Stauss C, Royle J, Attrill MJ (2013) Drawing lines at the sand: Evidence for functional vs. visual reef boundaries in temperate Marine Protected Areas. Mar Pollut Bull 76:194–202

Shepperson JL, Hintzen NT, Szostek CL, Bell E, Murray LG, Kaiser MJ (2018) A comparison of VMS and AIS data: The effect of data coverage and vessel position recording frequency on estimates of fishing footprints. ICES J Mar Sci 75:988–998

Smith C, Papadopoulou KN, Diliberto S (2000) Impact of otter trawling on an eastern Mediterranean commercial trawl fishing ground. ICES J Mar Sci 57:1340–1351

Thurstan RH, Brockington S, Roberts CM (2010) The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nat Commun 1:1–6

Tuck ID, Hall SJ, Robertson MR, Armstrong E, Basford DJ (1998) Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. Mar Ecol Prog Ser 162:227–242

Unknow (2016) Guidance for assessments under article 8 of the Marine Strategy Framework directive - Part 1 : Intergration of assessements results.

Verin Y, Travers-Trolet M (2014) CAMANOC cruise. https://doi.org/10.17600/14001900.

Yin P, Fan X (2001) Estimating r2 shrinkage in multiple regression: A comparison of different analytical methods. J Exp Educ 69:203–224

Appendix J. Assessing the impact of trawling on benthic megafauna: comparative study of video surveys versus scientific trawling

ICES Journal of Marine Science

Cyrielle Jac, Nicolas Desroy, Jean-Claude Duchêne, Aurélie Foveau, Céline Labrune, Lyvia Lescure, Sandrine Vaz

Assessing the impact of trawling on benthic megafauna: comparative study of video surveys versus scientific trawling

Cyrielle Jac[a], Nicolas Desroy[b], Jean-Claude Duchêne[c], Aurélie Foveau[b], Céline Labrune[d], Lyvia Lescure[d], Sandrine Vaz[a]

[a] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France
[b] LITTORAL-Unité littoral Ifremer, LITTORAL, F-35800 Dinard, France
[c] Université de Bordeaux 1, CNRS, UMR 5805 EPOC, Station Marine d'Arcachon, 2 rue du Pr Jolyet F-33120 Arcachon, France
[d] Sorbonne Université, CNRS, Laboratoire d'Ecogéochimie des Environnements Benthiques, LECOB UMR 8222, F-66650 Banyuls-sur-Mer, France

Abstract

Most studies about benthic community use small-scale sampling methods focused on the infauna such as grabs or box-corers. The benthic data collected by scientific trawl surveys in all European waters, in the frame of the Common Fishery Policy Data Collection Multiannual Program, can be used to study the impact of large-scale fisheries such as trawling. However, the catchability of trawls is very dependent on the nature of the seabed as well as resulting ground-gear adaptations. Due to its non-destructive nature and its ability to focus on benthic macro-epifauna, towed video sampling appears to be a good alternative to monitor the impact of trawling on benthic communities. In the present work, we studied the influence of fishery induced seabed abrasion and video characteristics on nine indices, which can be used to monitor the effect of trawling on benthic communities, was studied. Among them, three indices specific to fishery effect detection based on biological traits appeared to be the best performing benthic indices with video data: modified-Trawling Disturbance Index (mTDI), partial-Trawling Disturbance Index (pTDI) and modified sensitivity index (mT). The effectiveness of these indices to monitor the effect of trawling was evaluated and compared between trawl and video sampling. This work has highlighted that video sampling could be a good alternative, or at least a complementary method, to scientific trawling to monitor the effect of trawling on benthic communities in European waters.

Keywords: sampling methods; video; trawling effect; mega-epifauna, functional sensitivity indices

1. Introduction

Dredging and bottom trawling are carried out over large surfaces of the continental shelf and are the main sources of anthropogenic disturbance to seabed habitats (Hiddink et al. 2007; Halpern et al. 2008). However, in Europe, spatial and temporal trawl distributions may be very spatially patchy (Rijnsdorp et al. 1998, 2018) with a footprint of bottom fishing on the continental shelf that varies between 28 and 99% in the management areas of the Northeastern Atlantic and between 57 and 86% in the Mediterranean Sea (Eigaard et al. 2017). Although these values may be over-estimated depending on the data resolution chosen for the assessment, it remains incredibly high over most of the European continental shelves (Amoroso et al. 2018). These fishing methods are known to disturb seabed sediments, damage biogenic structure and, by changing the species composition, affect the structure and the functioning of the benthic communities (Collie et al. 2000; Rumohr and Kujawski 2000; Thrush and Dayton 2002; Hiddink et al. 2006, 2017; Rijnsdorp et al. 2018; Sciberras et al. 2018). On any given habitat, modifications of the species composition between trawled and un-trawled area are dependent of the pressure intensity (Jac et al. 2020a) and the sensitivity degree of each benthic species (Hiscock et al. 1999; Borja et al. 2003; Foveau et al. 2017) to trawling pressure.

Most studies evaluating the anthropogenic impacts such as fishing activities on benthic communities use sampling methods such as grabs, box-corers or dredges which are mainly focused mainly on the infauna (Eleftheriou 2013; van Loon et al. 2018). Usually, these samplings are conducted with restricted spatial coverage and relatively nearshore (Brind'Amour et al. 2014). To study the impact of fishing activities on a large scale, benthic data from scientific bottom trawl surveys carried out in all European waters in the frame of the Common Fishery Policy Data Collection Multiannual Program seem to be a good alternative (Foveau et al. 2017; Jac et al. 2020a). Nevertheless, all these sampling methods are "destructive" and may have a lasting impact on benthic biodiversity, which, although clearly negligible in comparison to fisheries impacts, should be reduced (Trenkel et al. 2019). In recent years, underwater imagery has been increasingly used to observe megafauna and habitat diversity (Mallet and Pelletier 2014). These methods allow rapid acquisition of a large amount of information on sites that may be difficult to sample (due to depth, seafloor characteristic or topography) with classic methods (Taormina et al. 2020). In addition, marine imagery is non-destructive (Mallet and Pelletier 2014). Five main techniques were developed to monitor marine biodiversity: remote underwater video (RUV), baited remote underwater video (BRUV), towed video (TOWV), diver-operated video (DOV) and remote operating vehicle imaging (ROV). However, these methods are not applied to assess the same compartments of the marine ecosystem (Brind'Amour et al. 2014). Only DOV, ROV and TOWV techniques may be deployed to evaluate the abundance of benthic species or to study the benthic substrate/habitat (Rooper and Zimmermann 2007; Cruz et al. 2008; Mallet and Pelletier 2014; Sheehan et al. 2016; Mérillet et al. 2017; Taormina 2019). When using visual census, the quality of data is strongly dependent on environmental conditions (especially turbidity) and image resolution (resulting from technical constraints). This often results in reduced taxonomic identification levels which may decrease the amount and usefulness of the information contained in the resulting data (Flannery and Przeslawski 2015). Notwithstanding these limitations, visual observations enable the production of large amounts of information, whether taxonomical, functional, or environmental, which can be used to assess the ecological status of a site or the effect of certain pressures on a community. The data collected by video sampling may indeed be used to calculate indicators of ecological status or pressures just as well as the data usually derived from classical sampling such as grabs or trawl.

In order to monitor trawling impact on benthic communities, it is necessary to observe changes in the benthic community and particularly in the benthic megafauna, which seems more appropriate than smaller fauna to detect the effect of trawling (McLaverty et al. 2020). Different indices could be used to track the modification of benthic community along the pressure intensity gradient: taxonomic diversity metrics, functional diversity indices and functional sensitivity indices. The first will provide information on the differences in species richness and their relative dominance, homogeneity or rarity in the community. The two later are based on biological traits sensitive to physical abrasion induced by fishing (size, position, mobility, fragility, feeding mode) and thus provide information on function changes within the benthic community and on changes in sensitive species abundance (in the case of functional diversity indices and functional sensitivity indices). Previous work suggests that indices in the latter category are better suited to monitor the effect of trawling on benthic mega-epifauna (Jac et al. 2020a). Although recent studies have shown the usefulness of indices based on the longevity of benthos (Rijnsdorp et al. 2018; Hiddink et al. 2020), there is too little information existed on the mega-epifauna studied here to use this particular trait.

The aims of this study were to (a) list or determine indices that may detect the effect of trawling on benthic fauna with a towed video sampling method (b) compare the ability of two sampling methods (video and trawling) to monitor the impact of fishing on benthic communities on a large scale.

2. Methods

2.1. Surveys

Each year, several scientific bottom trawl surveys occur in the English Channel and in the Gulf of Lion: the Channel Ground Fish Survey (CGFS; Coppin and Travers-Trolet 1989), the International Bottom Trawl Survey (IBTS ; Auber 1992) and the Mediterranean International Trawl Surveys (MEDITS ; Jadaud et al. 1994).

In the Gulf of Lion, the sampling gear used in MEDITS, during its yearly June survey, is a four panels' bottom trawl with a 20 mm stretched mesh size at the cod-end. The sampling scheme is stratified by depth evenly distributed over the whole study area. Hauls are carried out during daytime at 3 knots and are 30 minutes long above 200 meters and 60 minutes long below 200m (MEDITS 2017).

Based on MEDITS protocol but dedicated to the study of the benthic fauna, EPIBENGOL survey (Vaz 2018a) was carried out in September 2018 in the Gulf of Lion. During this survey, 10 stations were sampled with trawl and video.

In the English Channel, IBTS and CGFS are conducted yearly in January/February and October respectively. The sampling gear used is a Very High Vertical Opening bottom trawl with a 20 mm stretched mesh size at the cod-end. The sampling is randomly stratified and evenly distributed over the whole study area and hauls are carried out during daytime for 30 minutes at 4 knots (ICES 2015, 2017).

Benthic fauna samples, considered as by-catch, were sorted, identified, counted and weighed. Biomass data were chosen over abundance data because abundance was not estimated for several colonial species such as hydroids or sponges. Data were standardized according to trawling swept area and expressed in $g.km^{-2}$. In this study, only the trawls that could be paired with a co-located video transect were considered.

All the videos used for this study were acquired between 2014 and 2019 in the English Channel during CGFS and IBTS surveys, and between 2016 and 2018 in the Gulf of Lion during EPIBENGOL, VIDEO GALION (Vaz 2016, 2017), APPEAL MED (Labrune 2018) and IDEM VIDEO (Vaz 2018b). For two trawl surveys (EPIBENGOL, CGFS), video transect was carried out just before the trawl haul. After verifying that the trawl's mean position was less than 2km away from that of the video transect, they were considered paired with the corresponding video transect. The video transects, collected during dedicated video surveys (VIDEO GALION, APPEAL MED and IDEM VIDEO) or opportunistically during a bottom trawl survey (IBTS), were paired to trawl stations that were both less than 2km distant and mostly less than a year apart in time (Table 1). A total of 24 videos in the English Channel and 28 videos in the Gulf of Lion were analyzed but only 22 in each area could be paired with trawl stations.

Table 1: Characteristics of paired stations

Study area	Video (year – campaign – device)	Trawl (year – campaign)	Number of video transect paired to trawl	Number of video transect un-paired to trawl
English Channel	2019 – CGFS – Pag 2	2019 – CGFS	4	-
	2016 – CGFS – Pag 2	2016 – CGFS	11	-
		2015 – CGFS	2	
		2011– CGFS	1	
	2014 – IBTS – Pag 1	2015 – CGFS	2	2
		2013 – CGFS	1	
		2014 – CGFS	1	
Gulf of Lion	2018 – EPIBENGOL – Pag 2	2018 – EPIBENGOL	6	1
	2017 – VIDEOGALION - Pag 1	2017 – MEDITS	11	-
		2016 – MEDITS	3	
	2016 – VIDEOGALION – Pag 1	2016 – MEDITS	2	-
	2018 – APPEAL MED – Pag 2	-	-	2
	2018 - IDEM VIDEO – Pag 1	-	-	3

Pag 1 = Pagure 1; Pag 2 = Pagure 2

Discrepancies in the number of videos per year and areas resulted from the fact that no dedicated survey could be carried out in the English Channel where the video system had to be deployed opportunistically. In contrast, dedicated surveys could be deployed in the Gulf of Lion. In order to match a video transect with a corresponding trawl haul, an unbalanced design had to be tolerated.

2.1.1 Towed video systems

Two Towed video systems were used to carry out video transects of approximatively 500 meters length (15 min at maximum 1kt) in different locations in the Gulf of Lion and the English Channel.

The first device (Pagure 1) was a large stainless steel sled (length: 1500 mm, width: 1700 mm, height: 1250 mm, weight: 340 kg, about 100kg in water using 272L floats) equipped with an anodized aluminum housing that can hold a camera (here, a Panasonic HC-V700 or a GoPro Hero 4 or 5), a pair of LED lights (underwater LED SeaLite® Sphere, SLS 5100, 20/36 V, 5000 Lumens or SLS 5150, 20/36 V, 9000 Lumens) fixed on each side of the camera, two laser pointers (SeaLasers® 100 Dualmount, wavelength 532 nm Green) placed 100 mm from each other and two subCtech Li-Ion PowerPacks (25Ah, 24V) to power the lights and lasers (Sheehan et al. 2016).

The second device (Pagure 2) is larger (length: 2000 mm, width: 1100 mm, height: 740 mm, weight: 450 kg, 30 to 100kg in water using 272-380L floats depending on currents and bottom hardness). Some equipment was also different between the small device and this larger device: the camera (here, Panasonic HC-V700 or Sony PXW-Z90), four LED lights (a pair of each light listed above) powered by an additional battery (subCtech Li-Ion PowerPack, 70Ah, 25.2V).

As the exact position of the video system during the haul was not known, the transect positions were trigonometrically back-calculated using GPS coordinates, vessel bearing and dimensions, sounded depth and towing cable length along the 15 min transect.

2.1.2 Video image analysis

Analyses of the videos were performed image by image with the Avinotes software, specially developed by J.C. Duchêne to annotate video images. Between 700 and up to a maximum of 1200 video frames (approximately half of transect) were analyzed depending on video quality. For each transect, a visual evaluation of the image quality was performed with a classification system taking into account parameters related to sledge deployment (system stability and traction speed) and water turbidity (Table 2). A quality score, varying from good (3) to bad (9) image quality, was determined for each video transect by summing up the scores for each parameter.

Table 2 : Image quality classification parameters and their associated scores

Scores	Moving Speed	Stability	Turbidity
1	Constant speed and approximately less than 1 knot over the entire transect	The camera is correctly oriented (towards the bottom) over at least 1200 consecutive images.	The entire vision field is clearly visible
2	A few accelerations of the device but the average speed remain around 1 knot.	The camera is correctly oriented for 1200 non-consecutive images	Far vision field blur and many suspended particles but counting windows can still be analyzed
3	Approximately 50% of the transect images are not analyzable	The camera is correctly oriented over less than 1200 images over the entire transect.	Degraded identification and counting conditions in counting windows

A visual determination of sediment type (boulders, gravel, mixed sediments, sand and muds) was also carried out for each video transect.

Using laser pointers materializing a counting window on each image, it was possible to know the surface of the seabed sampled on each image. Special care was taken during the manual creation of this window so that it would not overlap from one image to another and create an overestimation of the sampled surfaces. On each image, all organisms present in the counting window were identified to the highest taxonomic level possible (Figure 1) and their abundance recorded even for colonial species for which the number of colonies was determined. The surface sampled per profile was then determined by multiplying the average area of the counting windows by the number of images analyzed. The average areas of the counting window were slightly different between the two towed video system with an average of 1032 cm² for the Pagure 1 and 1588 cm² for the Pagure 2. Data were standardized according to the average counting window area and expressed in ind.m^{-2}. Taxonomically and morphologically similar organisms, like the crinoids *Leptometra sp*. and *Antedon sp*. which could not be distinguished at species or even genus level, were grouped at family level as Antedonidae.

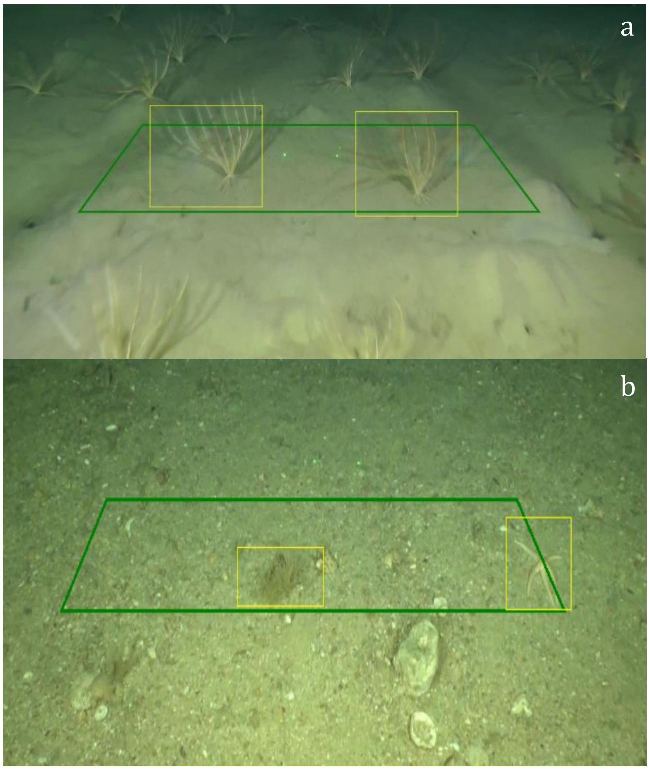


Figure 1: Example of organisms identified and counted in the counting window (green line) with video device.
a) Two individuals of Antedonidae in a sampling area of 1531 cm². b) On the right, a starfish of the genus Henricia and on the left, a colony of hydrozoan, in a sampling area of 2748 cm².

2.2. Abrasion and habitat data

The abrasion value at each sampled station (Table 3) of the two studied areas were determined from maps (Figure 2) of swept surface area ratio per year ($SAR.y^{-1}$), based on VMS data (Eigaard et al. 2016; ICES 2019). To avoid overlooking past impacts and reflect the probably long recovery time needed for sensitive species, the 90th inter-annual (from 2009 to 2017) percentile of swept surface area ratio was used [as detailed in Jac et al. (2020)]. Using this 90th percentile also allowed to filter out the most extreme values that may be related to measurement or computation errors. These maps' resolutions were different: 3'x3' in the English Channel (www.ospar.org.) and 1'x1' in the Gulf of Lion (Jac and Vaz 2018).

Table 3: Abrasion ranges of the sampled stations in the two studied areas.
The three abrasion values represent the minimum value, median and maximum value.

	English Channel	Gulf of Lion
Sampled abrasion range ($SAR.y^{-1}$)	0.29 – 10.92 – 72.34	0.08 – 4.65 – 20.87
Abrasion range ($SAR.y^{-1}$) of paired stations	0.29 – 8.73 – 72.34	0.08 – 4.91 – 20.87

In the Gulf of Lion, the visual determination of sediment type did not reveal different habitats, mainly because of small differences in granulometry that are difficult to observe on video. The different habitat types were therefore defined by EUNIS level 3 (Populus et al. 2017; www.emodnet.eu). Thus, stations were categorized in two habitats: Sublittoral mud (A5.3) which includes the subtidal cohesive sandy muds and Sublittoral mixed sediments (A5.4) which includes a range of sediments, including heterogeneous muddy and gravelly sands (Figure 2).

In the English Channel, the absence of significant variation in depth between the stations allowed this factor to be disregarded in the characterization of sampled habitats. Thus, habitats were categorized, based on the visual definition of sediment type observed, into two classes: coarse or mixed sediments (sediments composed of mud, sand, gravel in variable proportions).

Paired trawl stations were assigned the same habitat types as those determined in video transect as in videos.

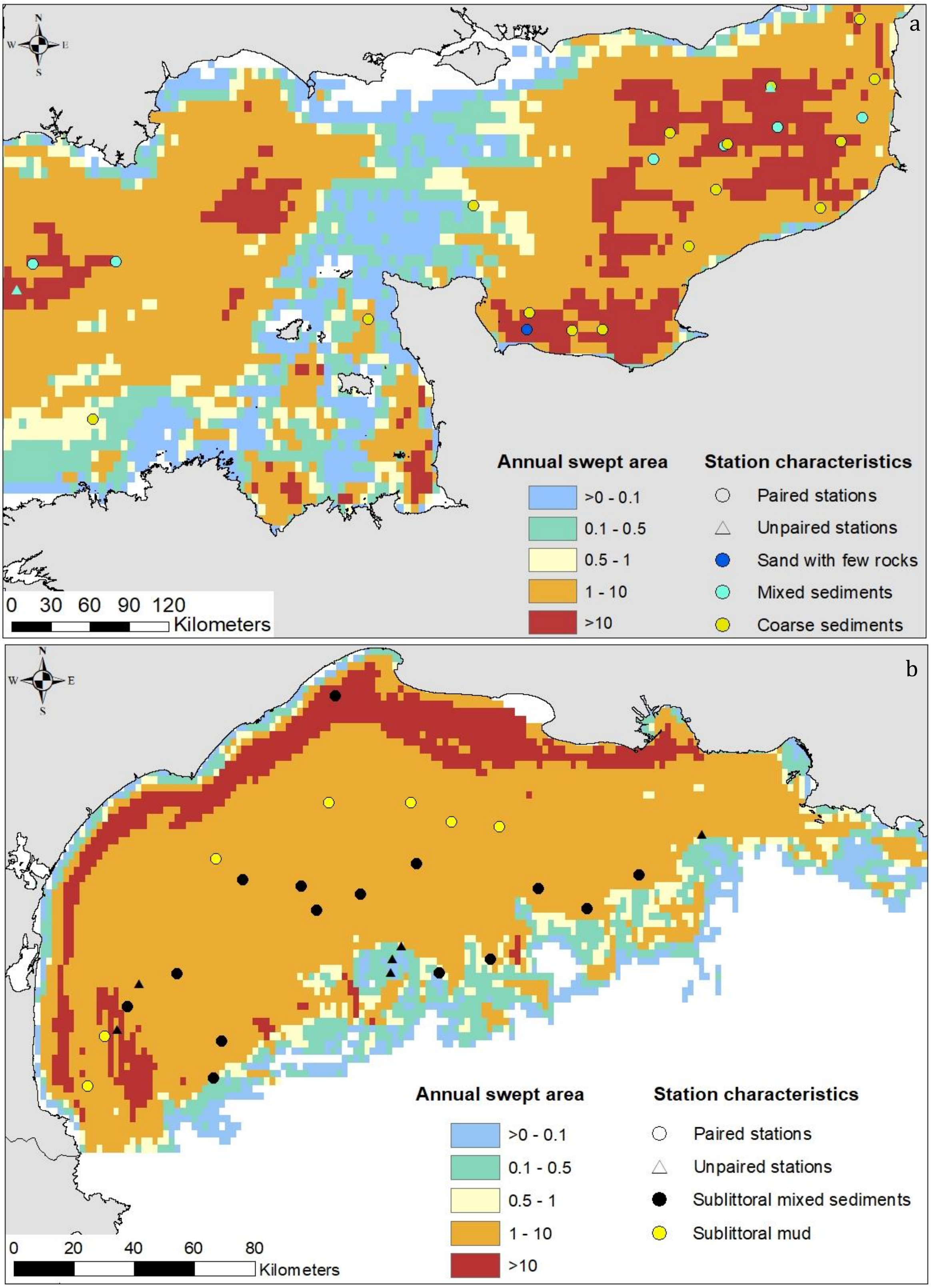


Figure 2: Location and sedimentary characteristics of video stations in the English Channel (a) and in the Gulf of Lion (b). The annual swept area was 90th inter-annual percentile of the abrasion in during the period 2009-2017

2.3. Biotic indices

As the spatial pattern of abrasion is not independent of the presence of target species, commercial species (*Homarus gammarus*, *Crangon crangon*, *Maja brachydactyla*, *Pecten maximus*, *Aequipecten opercularis*, *Palaemon serratus*, *Nephrops norvegicus*, *Buccinum undatum*, *Cancer pagurus*, *Aristaeomorpha foliacea*, *Aristeus antennatus*, *Parapeneus longisrostris*, *Bolinus brandaris*) and cephalopods have been removed from the two datasets.

To reduce misidentification errors, a procedure proposed by Foveau et al. (2017) to aggregate uncertain taxa at a higher identification level was applied.

Two types of sensitivity indices were investigated on video data: taxonomic diversity metrics and sensitivity indices specifically constructed to detect impacts on benthic communities. The effect of trawling on the species abundance was also studied.

Four common taxonomic diversity indices were calculated: species richness (SR, the total number of taxon), Shannon diversity (H'; Shannon and Weaver 1963), Pielou evenness (J'; Pielou 1969) and Simpson index (λ ; Simpson 1949). The last three are weighted by abundance to assess equitability between species (J') or give more or less influence to rare species (H' and λ). These indices were calculated in R, using the vegan 2.5-2 package (Oksanen et al. 2019).

Functional sensitivity indices, based on biological traits, were selected to characterize potential responses of organisms to physical abrasion (de Juan and Demestre 2012; Bolam et al. 2014; Foveau et al. 2017). These traits are (i) position of organisms in the sediment; (ii) feeding mode; (iii) mobility capacity; (iv) adult size and (v) fragility of the structure of organisms. Each trait was subdivided into multiple "modalities" to encompass the range of possible attributes of all taxa. To allow quantitative analysis, a score was assigned to each modality, varying from low sensitivity (0) to high sensitivity (3; Table 4). When some taxa had to be aggregated at higher taxonomic level, precautionary principle commended to assign, for each trait, the highest score values (higher sensitivity) observed within that particular taxonomical grouping following the procedure described by Jac et al. (2020). The calculated functional sensitive indices were: Trawling Disturbance Index (TDI; de Juan and Demestre 2012), modified TDI (mTDI; Foveau et al. 2017), partial TDI (pTDI; Jac et al. 2020) and the modified Sensitivity Index (mT; Jac et al. 2020). TDI-based indices were developed specifically to detect trawling impact, while mT is issued from a general framework allowing to address any pressure if specific sensitivity traits are available to detect it. Calculation methods of each of these indices were presented in Appendix 1. All indices were calculated with R version 3.5.1 (R Core Team 2017).

Concerning trawling data, a previous study investigated all the proposed indices and showed that functional sensitivity indices were the most useful to evaluate the impact of trawling on benthic communities (Jac et al. 2020a). Here, we chose to focus only on these indices which are more suited to video data, which were then also calculated using scientific trawl data for comparison purposes.

Table 4: Biological sensitivity traits to physical abrasion and associated scores (Foveau et al. 2019; Jac et al. 2020)

Scores	Position in the sediment	Feeding mode	Mobility	Adult size	Fragility
0	Deep burrowing	Scavengers	Highly mobile (swimming)	Small (<5 cm)	Hard shell, burrow, vermiform, regeneration
1	Surface burrowing (first cm)	Deposit feeders/predators	Mobile (crawling)		Flexible
2	Surface		Sedentary	Medium (5-10 cm)	No protection
3	Emergent	Filter feeders	Sessile (attached)	Large (>10 cm)	Fragile shell/structure

2.4. Data analyses

2.4.1 Indices evaluation and selection for video derived data

To find the most appropriate indices, generalized linear models (GLM) were used to investigate which variables (abrasion, habitat, camera type, device type and image quality) influenced the indices calculated with video data (using all video data available here). As benthic communities do not respond equally to trawling in different habitats (Kaiser et al. 1998), the interaction between habitat and abrasion was included in GLMs. For each GLM, the variables were selected using forward procedure based on the Akaike Information Criterion using the MASS package 7.3-51.5 (Ripley et al. 2019). The goodness of fit of the model was assessed by performing a $\chi 2$ test between the null and the selected model.

Indices were first retained if no variables related to the video system specification (camera, video system and image quality) influenced the model. These indices were then selected if the regression coefficient for abrasion was negative and significant.

2.4.2 Comparison between the two sampling methods

To assess the relevance of each of the two sampling methods to monitor the impact of trawling on benthic communities, only paired stations were used for the following analyses.

Community description

For each sampling method in the two study areas, the number of sampled taxa was counted, and the proportion of each taxonomic level was evaluated to better understand the differences in catchability between the two methods (only paired stations used for the following analysis). Underwater video techniques usually allow to observe only large (> 5 cm) epifauna (Mérillet et al. 2017). The diversity of biological traits sampled with trawling and video was evaluated by comparing functional spaces of all studied areas. Functional space can be defined as a multidimensional space where the axes are functional traits along which species are placed according to their functional trait values (Mouillot et al. 2013). Thus a Multiple Correspondence Analysis (MCA) was performed in each area on the species-traits matrix, with the package PCAmixdata 3.1 (Chavent et al. 2017) to build a multidimensional functional space with axes corresponding to synthetic traits summarizing several raw traits.

In order to identify differences in the structure of the communities sampled with each of the two methods, the proportion of species belonging to the different categories of the trait "Position of organisms in the sediment" was studied. This analysis was not conducted on the other biological traits because the diversity of these traits within the community is unlikely to vary between the two sampling methods.

Monitoring of trawling impact

An assessment of the relevance of each of the sampling methods for monitoring the impact of trawling on benthic communities was carried out using statistical regression and tests (only paired stations were used for the following analyses). In each area and for the two sampling methods, generalized linear models (GLM) were used to investigate which variables (abrasion and habitat), influenced previously selected indices. Interaction between habitat and abrasion was also included in GLMs. The most significant variables were selected for each GLM using forward procedure based on the Akaike Information Criterion using the MASS package 7.3-51.5 and the goodness of fit of the model was assessed by performing a $\chi2$ test between the null and the selected model. For each index, the regression coefficient for abrasion and the R-squared values were compared between the different sampling methods to evaluate which is the most appropriate for monitoring trawling impacts on benthic communities.

3. Results

3.1. Indices evaluation and selection for video derived data

All indices considered in this study were not influenced by the same variables even if, in many cases, the habitat effect was significant (Table 5). Characteristics of the video system used (device or camera type and image quality) were selected in models, only for few indices like SR, Shannon or Abundance. Meanwhile, only sensitivity indices (TDI, mTDI, pTDI and mT) were significantly influenced by the abrasion. As TDI was also influenced by a variable related to the video system (camera type) which is not a desirable property, it was not selected for further analysis. Graphic representation of relationship between the three selected sensitivity indices and abrasion were performed (Figure 3 & 4).

Table 5: Variables retained by the model selection procedure for each index over the totality of the analyzed videos (Gulf of Lion and English Channel). Grey shading indicates indices meeting the selection criteria (negative relationship between abrasion and lack of significant relationship to image quality)

Indices	**Selected explanatory variables**	**Regression coefficient for abrasion (and significance level)**
SR	~ Device+ Image quality + Habitat + Abrasion	- 0.013
Shannon	~ Habitat + Device	-
Simpson	~ Habitat	-
Pielou	~ Habitat	-
Abundance	~ Habitat + Camera + Device	-
TDI	~ Abrasion + Camera	- 0.092***
mTDI	~ Abrasion	- 1.972***
pTDI	~ Abrasion	- 0.036***
mT	~ Abrasion + Habitat	- 0.012***

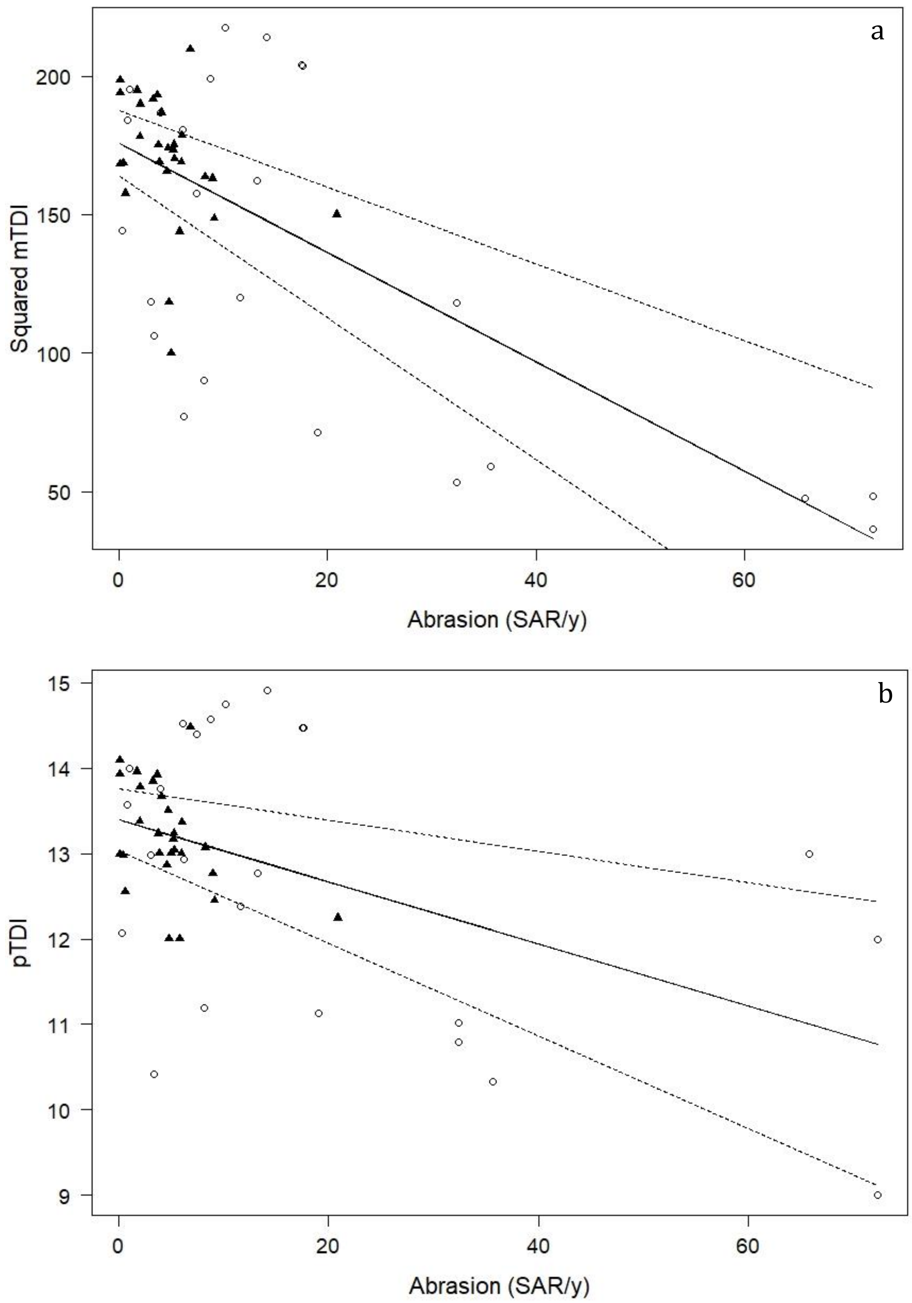


Figure 3: Relationships between fishery abrasion and a) squared mTDI index and b) pTDI index in all habitats. The relationship was significant and negative (black line and 95% confidence interval in dashed line) and no habitat/area influence was detected. ○ Stations in the English Channel; ▲ Stations in the Gulf of Lion.

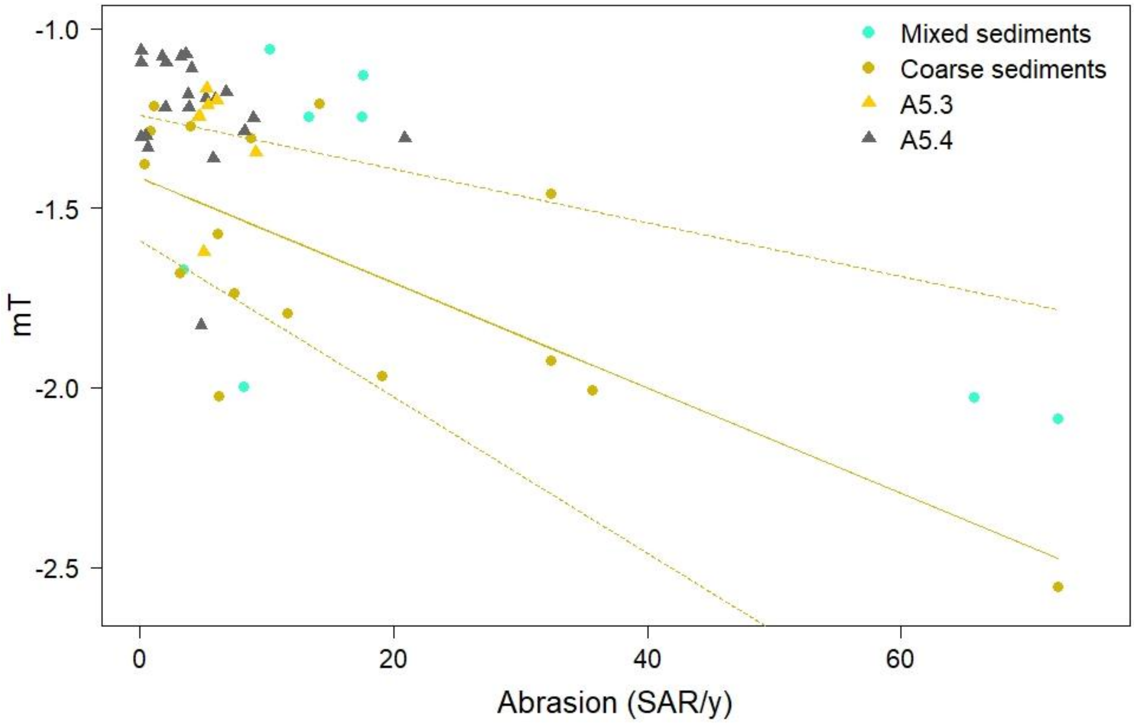


Figure 4: Relationships between mT index and fishery abrasion in all habitats. The relationship was significant and negative only for habitat “Coarse sediments” (gold line and 95% confidence interval in dashed line). ● Stations in the in the English Channel; ▲ Stations in the Gulf of Lion.

3.2. Differences in the sampled community between the two sampling method

In both study areas and using both sampling devices, it was not always possible to identify the encountered organisms at species level. The total number of taxa therefore indicated the number of different organism types distinguished at the lowest taxonomic level possible. In the English Channel, despite a significantly larger area sampled by trawling than by video (Table B.1), a greater number of taxa were observed by video (Table 6). A total of 88 taxa representing 53 families, 28 orders and 8 phyla were observed on video and 74 taxa representing 44 families, 26 orders and 8 phyla were sampled by trawling. Only 29 species were found with both sampling methods.

On the opposite, in the Gulf of Lion, a high number of taxa were collected by trawl with 134 taxa representing 89 families, 39 orders and 10 phyla against 39 taxa representing 27 families, 19 orders and 7 phyla observed on video. Only 19 taxa were common to the two sampling methods.

Table 6: Number of taxa by sampling method and areas

Taxonomic level	Areas	Trawl	Video
Taxon	English Channel	74	88
	Gulf of Lion	134	39
Species	English Channel	54	50
	Gulf of Lion	92	14
Genus	English Channel	49	57
	Gulf of Lion	96	26
Family	English Channel	44	53
	Gulf of Lion	89	27
Order	English Channel	26	28
	Gulf of Lion	39	19
Phylum	English Channel	8	8
	Gulf of Lion	10	7

Looking at the sensitivity of the most represented (> 5% of the total abundance or biomass) taxa in terms of biomass or abundance in each area, it appears that these results were very contrasted between the sampling methods (Table 7). Indeed, very few species in video data are considered as non-sensitive while almost half of the species dominating the trawl-collected assemblage were non-sensitive. In the English Channel, three species were dominant in video and trawl data (*Ophiothrix fragilis*, *Psammechinus miliaris* and *Alcyonium digitatum*). In the Gulf of Lion, the dominant taxa observed by video were Cnidarians (Antedon sp., *Funiculina quadrangularis* and *Cavernularia pusilla)* while the trawl samples were dominated by Echinoderms (*Gracilechinus acutus*, *Parastichopus regalis* and *Astropecten irregularis pentachanthus*) and Cnidarians (*Antedon sp.* and *Funiculina quadrangularis*).

Table 7: Dominant taxa observed with the two sampling methods in the two studied areas and their sensitivity score (SI; Foveau *et al.* 2019). Green shading indicates that the species is considered less sensitive to trawling (SI ≤ 7).

Areas	Device	Species	SI
English Channel	Video	*Ophiothrix fragilis*	*11*
		Mytilus sp.	*11*
		Sertularia sp.	*15*
		Psammechinus miliaris	*7*
		Alcyonium digitatum	*15*
		Porifera	14
	Trawling	*Asterias rubens*	*7*
		Psammechinus miliaris	*7*
		Necora puber	*6*
		Ophiothrix fragilis	*11*
		Alcyonium digitatum	*15*
Gulf of Lion	Video	*Antedon sp.*	*13*
		Funiculina quadrangularis	*14*
		Cavernularia pusilla	*13*
	Trawling	*Gracilechinus acutus*	*10*
		Parastichopus regalis	*12*
		Antedon sp.	*13*
		Funiculina quadrangularis	*14*
		Liocarcinus depurator	*6*
		Astropecten irregularis pentacanthus	*8*

Despite identification to the species level more frequent by trawl than by video, more than 65% of the taxa were identified to the genus level regardless of the type of sampling (Figure 5a).

The proportion of sampled infauna represents less than 20% of the sampled taxa regardless of the type of sampling. The main difference observed between trawling and video results from the type of epifauna observed, particularly in the Gulf of Lion (Figure 5b) : more than 55% of the fauna observed by video and less than 35% of that sampled by trawl were erected epifauna (34 % in the English Channel and 21% in the Gulf of Lion).

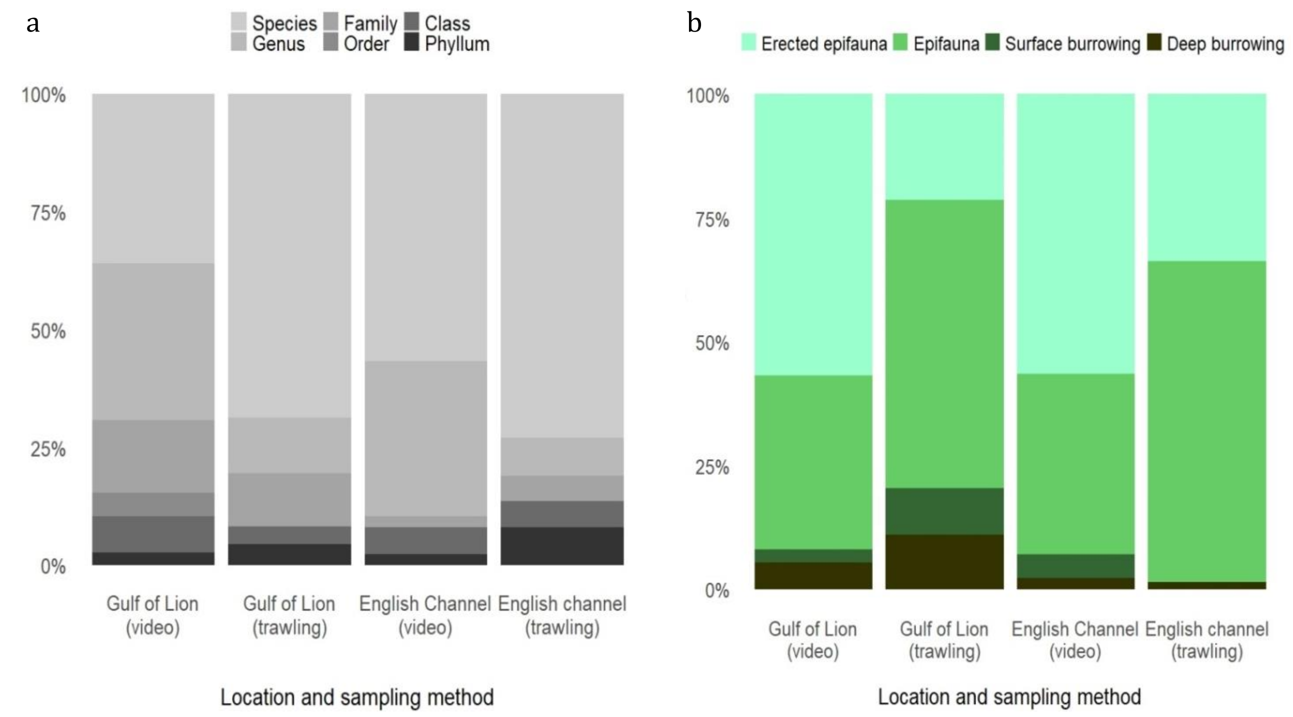


Figure 5: Proportion of each a) taxonomic level identified and b) category of position with the two sampling method in the two studied areas

Individuals caught by trawl have a greater functional diversity than those observed on video, particularly in the Gulf of Lion (Figure 6).

In the English Channel, only very few differences are observed between trawl and video sampling functional spaces. However, the dominant taxa were different for each sampling type. For trawling, the assemblage of taxa was dominated by individuals that are small, mobile, living at the surface or in the first few centimeters of sediment, which are not fragile and are mainly scavengers or deposit feeders/predators. For video sampling, the taxon assemblages observed were dominated by sessile individuals, emerging, fragile and mainly filter feeders, but also by medium-sized and flexible taxa.

In the Gulf of Lion, the trawl caught mostly large, unprotected, sedentary and burrowing individuals also some sessile, emerging, fragile and mainly filter feeders while no particular taxa dominance was observed by video. Moreover, highly mobile individuals are totally absent from the videos in this area.

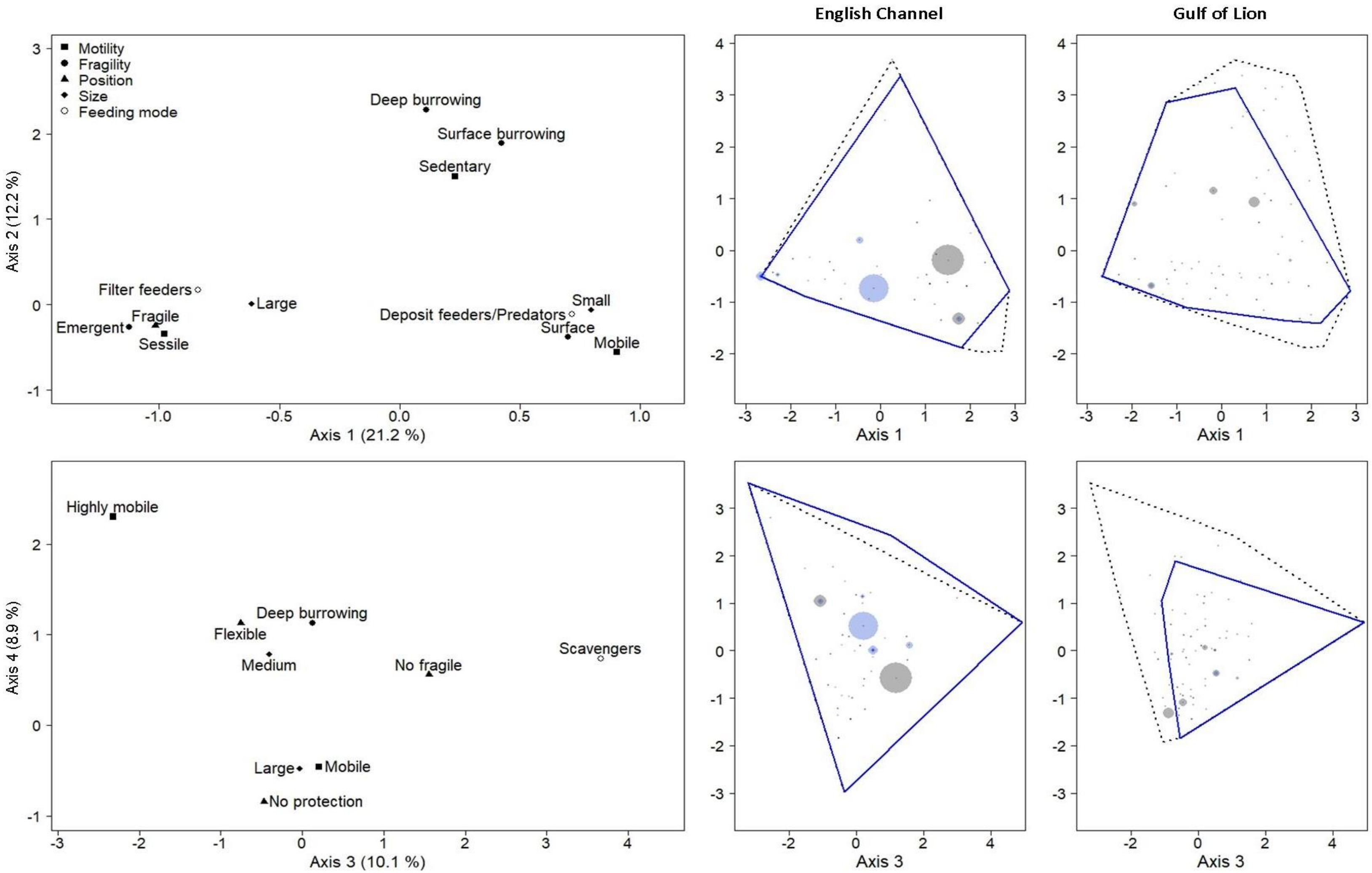


Figure 6. Multiple Correspondence Analyses of the functional traits of the different taxa observed on video and/or sampled by scientific trawling and functional space for axes 1-2 (21.2% and 12.2% variance) and axes 3-4 (10.1% and 8.9% variance) for trawl sampling (dotted polygon) and video sampling (blue line) in the English Channel and in the Gulf of Lion . The species are represented by points of diameter proportional to their density (blue points) for video sampling and their biomass (grey points) for trawling sampling.

3.3. Monitoring of trawling pressure: comparison between the two sampling methods

The comparative analysis of the influence of abrasion and habitat on selected indices computed from both sampling types is presented in the table 8 for each studied area.

In the Gulf of Lion, whatever the gear used or the index studied, abrasion never seems to significantly influence the index.

In the English Channel, results are more contrasted. For the mTDI, habitat had a significant influence on the index with trawl sampling whereas it was the abrasion that had an influence with video sampling. For pTDI, no significant relationship was observed with habitat or abrasion and in the case of video sampling but habitat had a significant influence on the index when using trawl sampling. Finally, for the mT, the two sampling methods allowed to detect significant relationships to abrasion and the R-squared was higher when using the video derived data

Table 8: Outcomes of the stepwise selection procedure on the generalized linear models. GoL = Gulf of Lion. E.C = English Channel. * indicates that $P<0.05$; ** indicates that $P<0.01$; *** indicates that $P<0.001$; n.s indicates no significant effect. No explanatory variable indicate that the null model was selected.

		Video			Trawling		
Indices	Areas	Explanatory variable	Significance	r^2	Explanatory variable	Significance	r^2
mTDI	E.C	Abrasion	***	0.63	Habitat	**	0.80
	GoL	-	-	-	Abrasion Habitat	n.s *	0.87
pTDI	E.C	Abrasion	n.s	0.12	Habitat	**	0.59
	GoL	Abrasion	n.s	0.16	-	-	-
mT	E.C	Abrasion	***	0.88	Abrasion Habitat	* n.s	0.82
	GoL	-	-	-	Habitat Abrasion	* n.s	0.33

4. Discussion

4.1. Differences in catchability

In the two geographic areas studied here, although the difference in sampling area between trawl and video was similar, the differences in catchability between the two sampling methods were very different. The number of taxa observed with the video was slightly higher than the taxa caught with the trawl (88 vs. 74) in the English Channel and lower (39 vs. 134) in the Gulf of Lion. Several parameters may explain these differences.

First of all, the higher proportion of infauna in trawl samples collected in the Gulf of Lion can be explained by the sediment type. The Gulf of Lion is characterized by the presence of soft sediments (Populus et al. 2017 ; www.emodnet.eu), whereas bottoms sampled in the English Channel have a higher granulometry and are sometimes even composed of blocks (Coggan and Diesing 2011). As trawl penetration is lower in coarse sediments than in fine sediments (Eigaard et al. 2016), the gear catchability of the infauna is greater in areas of fine sediments. Reflecting these substrate differences, the trawls used in the English Channel and the Gulf of Lion were different (ICES 2015; MEDITS 2017), which may have increased the difference in the catchability of benthic fauna between these two gears. The gear used in the Gulf of Lion has a greater catchability of infauna than that of English Channel. In contrast, results obtained in the English Channel seem to indicate that in coarse sediment areas, video allows the observation of a greater diversity of species than does the trawl, probably because the trawl catchability of epibenthic species fixed on boulders is relatively low. Finally, the habitat type plays a major role on the species density and occupancy. Epifaunal species number and density were much higher on coarse habitats while it often exhibited overly dispersed distribution on bare soft sediments. This mostly explains the difference in diversity observed between the two areas for comparable surface sampled and also the differences between video and trawled observations in the Mediterranean.

Secondly, two slightly different devices were used for video transects and even though they were both used in both areas, the majority of transects in the Gulf of Lion was performed with a smaller device than in the English Channel, where a larger device was mostly used. Although the size of the observed areas is known to influence the number of species sampled (Crist and Veech 2006), no significant difference was found in the sampled surfaces with both video systems. Yet, the use of different devices had significant effect on the estimation of species richness, Shannon diversity and abundance and may partly explain the difference in diversity observed by video sampling between the two areas. Moreover, although neither sampling techniques are suited to capture infauna, the fact that much more could be caught by trawl in soft sediments may explain the differences in species diversity between trawl and video sampling in the Gulf of Lion.

4.2. Taxonomic identification of individuals

Regardless of the study area, the proportion of individuals identified at the species level is higher with trawls than with videos. This is particularly marked in the Gulf of Lion, where nearly 70% of the 134 taxa collected by trawls were identified down to the species level, compared with 36% of the 39 taxa observed on the video transects. One of the main disadvantages of using video alone is that identification at species level is particularly difficult

(Flannery and Przeslawski 2015). Species-level identification often requires sampling of specimens coupled with magnifier observations and expert knowledge (Althaus et al. 2015). Determination of taxa as sponge species for which the differences between two species may require the examination of the spicules cannot be differentiated on video images. The species richness of a site may be underestimated if the species count was only done on video because several individuals may be grouped under the same taxa even though they belong to different species. However, for approaches based on the use of functional traits, the genus level is often sufficient to define the biological characteristics of individuals (Brind'Amour et al. 2009; Foveau et al. 2017). In this study, the rate of identification at the level of the genus appeared to be relatively close between the two sampling methods (70% of observed taxa for the video compared with 80% of taxa sampled with the trawl in the Gulf of Lion and 89% for the video compared with 82% for the trawl in the English Channel). Identification difficulties, intrinsic to video imagery, seem to have relatively little influence on approaches based on species biological traits. However, to overcome these methodological limitations, a "short list" only focusing on relevant sensitive species may be used to perform video analysis.

4.3. Functional diversity

The taxonomic diversity of a community does not always reflect the diversity of its functional structure (Törnroos and Bonsdorff 2012), which is defined as the quantification of the position that different species occupy in the ecosystem (Mouillot et al. 2013). When several species perform similar functions, the reduction in species diversity may not have any influence on the functional structure of the community (Mouillot et al. 2014). In the English Channel, despite a greater number of species observed by video than by trawling, the species communities observed by both gears had a similar functional space. Therefore, despite a relatively different number of species, video observed or trawl sampled communities supported about the same number of biological traits. Despite this very significant overlap between the two functional spaces, notable differences in the type of dominant species could be highlighted with species assemblage dominated by mobile, living at the surface and mainly predator species for the trawl sampling and dominated by sessile, emergent, fragile and mainly filter-feeding species but also by medium sized and flexible species in video observations. In the Gulf of Lion, contrary to what was observed in the English Channel, the number of species collected and the proportion of infauna species was higher in the community sampled by trawl than that observed on video. As a result, the fauna collected by the trawl also had greater functional diversity (measured as functional space) than that observed by video.

Several parameters could explain the differences between the two sampling methods. Firstly, the dominance of emergent species and the lack of burrowing species on video transects in both areas are easily explained as video observations are limited to the surface of the sediment. In contrast, for the trawl data, in the English Channel, the dominance of mobile species living at the surface could be due to the relatively low penetration of the trawl in coarse sediments, hence resembling that of the video data. The opposite is observed in the Gulf of Lion where the trawl may penetrate much deeper the fine muddy sediments (Eigaard et al. 2016), thus resulting in higher infaunal diversity. Finally, with the video system moving at a maximum of 1 knot with an observation field around 1.3 meters wide, mobile species capable to move fast or to quickly retract in the sediment can escape detection while, with a towing speed of 3-4 knots and about 20 meters horizontal opening (ICES 2015; MEDITS 2017), very few mobile invertebrates or overly dispersed species may avoid capture by trawling. Regarding these results, the two sampling methods seemed complementary. The video device allowed to observe mainly fixed epifauna, regardless of the habitat sampled, this portion of the benthic community appearing, in the present work, relatively poorly sampled by the trawl on coarse habitats. Conversely, trawling was able to capture a greater diversity of infauna species on soft bottoms where this portion of the benthic community is dominant.

4.4. Indices evaluation and selection for video derived data

The procedure for selecting the factors influencing the different indices showed all of the taxonomic diversity indices tested (RS, Shannon, Simpson, Pielou and abundance) were influenced by the type of habitat. Only the species richness was influenced by the abrasion. Although the sampling method differs, these results are partly consistent with those presented in the meta-analysis carried out by Hiddink et al. (2020). Pielou and Shannon did not respond significantly to trawling, as opposed to the species richness. However, as the type of video gear also has an influence on species richness, this index does not seem to be appropriate for studying the effect of trawling on benthic communities when sampling is carried out using towed video. Hiddink et al. (2020) also found that abundance was strongly influenced by trawling, however, this was not found to be the case in the present study. This difference probably stems from the fact that the benthic community observed is not the same since video sampling only allows us to observe a particular portion of the benthic fauna: the erected megafauna.

For the sensitivity indices, only the mT was influenced by this factor. Since both study areas were included in this analysis, the habitat effect is likely more of a "geographical" effect than an effect of the type of sediment sampled. The number of taxa observed was more than twice as high in the English Channel than in the Gulf of Lion (88 vs. 39). The absence of influence of the habitat factor and therefore of the "geographical" effect, on three functional sensitive indices suggested that despite a greater taxonomic diversity in the English Channel compared to the Gulf of Lion, the response of benthic communities' sensitivity to trawling was not significantly different between the two areas.. For the mT index, the habitat factor influence could be related to the addition of the species protection status factor, not taken into account in the calculation of the other functional sensitive indices. Some species are protected in only one of the two study areas. This is the case for sponges of the genus *Tethya sp.*, protected in the Mediterranean Sea (OCEANA 2016) but not in the English Channel (OSPAR 2008). In addition, of all the individuals observed in the Gulf of Lion, 12 of the 39 observed taxa had a protected status, whereas in the Channel, this concerns only 4 of the 88 taxa. Taking into account emblematic species significantly impacted the mT index values and caused a differentiation between the two study areas. As benthic communities do not respond in the same way to trawling in different habitats (Kaiser et al. 1998), the habitat influence on the tested indices was not considered problematic here.

Two criteria allowed to select video derived indices that could monitor the trawling effects on benthic communities in the two areas studied: the presence of a significant negative influence of abrasion on the index and the absence of influence of device characteristics. Only three indices met both of these criteria: mTDI, pTDI and mT. A previous study based on scientific trawl data also suggested that these indices could be used to monitor the effect of trawl pressure on benthic communities in the English Channel, the North

Sea, the Gulf of Lion and Corsica (Jac et al. 2020a, 2020b). As these three indices are based on the same set of biological characteristics and are selected for their significant correlation with abrasion, they are highly correlated. However, Jac et al (2020a) showed that, depending on the area studied, the same indices do not have the highest correlation with abrasion. Thus, although they are closely related, it seems difficult to select only one of them for the assessment of the impact of trawling on benthic communities. Monitoring the effects of trawling on benthic communities should therefore be carried out at a finer resolution (e.g. EUNIS level 4) by choosing the most sensitive index in the area studied (in application of the precautionary approach).

4.5. Monitoring of trawling pressure based on video transects?

In the Gulf of Lion, no significant influence of abrasion was detected on the three functional sensitive indices calculated with trawling data but significant influence of the habitat type was detected on mT and mTDI. These results, correlated with the lack of a significant effect of habitat on the pTDI index, suggest that the differences between habitat types were primarily related to low-sensitivity species as only the most sensitive species were included in the pTDI calculation (Jac et al. 2020a). This could also explain the absence of habitat effects on indices calculated from video derived data, since the species considered most sensitive are generally those of the fixed epifauna (Foveau et al. 2019) which are the species mainly observed on videos. These different results indicate that habitat affects mainly species with lower sensitivity (*i.e.* mobile species or infauna species) and has little to no influence on video observations. The results obtained by Labrune et al. (Labrune et al. 2008) indicating that there are clear links between polychaete assemblages and both bathymetry (between 10 and 50 meters in their study) and sediment grain size in the Gulf of Lion, tend to support this hypothesis.

The lack of relationship between abrasion and the different indices for the two sampling methods could be explained by the small number of stations sampled and the unbalanced distribution of these stations along the abrasion gradient. Jac et al. (2020a) found a significant effect of abrasion for habitats A5.46 (Mediterranean communities of coastal detritic bottoms) and A5.47 (Mediterranean communities of shelf-edge detritic),- grouped here as A5.4 - with a larger and better distributed dataset along the abrasion gradient (abrasion vary between 0 and 20.77 $SAR.y^{-1}$ with a median of 2.69 $SAR.y^{-1}$). Their results suggest that an increase in the number of stations sampled, particularly in areas of low abrasion, could enable the detection of a significant and negative relationship between the indices studied and abrasion. For the habitat A5.3 (sublittoral mud), results were consistent with those of Jac et al. (2020a) which pointed out the lack of a significant relationship between abrasion and the different indices in habitats A5.38 (Mediterranean communities of muddy detritic bottoms) and A5.39 (Mediterranean communities of coastal terrigenous muds), They interpreted this lack of relationship as reflecting that the original communities of these habitats had already been completely replaced by communities adapted to trawling. Thus, in the present study, as 50% of the sampling was carried out in areas with abrasion levels higher than 4 $SAR.y^{-1}$, the lack of relationship between the indices and the level of abrasion most likely also reflects the replacement of the original communities by communities fully adapted to trawling.

In the English Channel, results obtained with scientific trawl data appeared similar to those obtained in the Gulf of Lion. Habitat had a significant effect on two of the three indices (mTDI and pTDI) like in the Gulf of Lion. Contrary to what was observed in the Gulf of Lion, mT was significantly influenced by abrasion, even though habitat was still a selected parameter, but not significant in the model. The different response of the mT index from those of mTDI and pTDI could again be explained by the addition of the "protection status" factor in the calculation of mT or by the different computation of biological traits between the mT and TDI-derived indices (Certain et al. 2015; Foveau et al. 2017; Jac et al. 2020a). The relatively lower r^2 for the relationship between pTDI and abrasion than for mTDI (0.59 vs. 0.80) seemed to indicate that, as in the Gulf of Lion, habitat mainly affects species with low sensitivity.

The relationships between the video-derived indices and the parameters studied (abrasion and habitat) contrasted with those obtained with trawl sampling. For the three indices, the habitat parameter was not selected in any model and abrasion had a highly significant influence on mTDI and mT. The fraction of the benthic community that could be observed in the video appeared to be particularly sensitive to abrasion and regardless of the habitat studied. However, a great similarity between the functional spaces of the communities sampled with the two methods was observed. Differences in the behaviour of the indices in relation to the parameters studied could be explained by the metrics used in the two sampling methods, biomass data for trawling and abundance data for video. However, since trawl catches sessile epifauna with difficulty, their biomass may be underestimated in relation to their abundance in the area and thus induce differences in the behaviour of the indices between the two sampling methods. Furthermore, the absence of habitat effect on the video indices suggests that the abundance of the species observed in the video is not significantly influenced by the habitat type. Results obtained with data from scientific trawling seemed to indicate that habitat had an effect mainly on species with low sensitivity. This therefore suggests that the portion of the benthic community not observed in the video (mobile species, small individuals, etc.) and potentially not very sensitive to trawling may differ from one habitat to another.

In conclusion, data collected from the video sampling seemed to detect a significant negative effect of abrasion while avoiding the effect of habitat type in the English Channel. The use of a towed video method appears more reliable than the use of benthic megafauna data collected during scientific trawling surveys to monitor the effect of trawling on benthic communities in coarse and mixed sediments. As the strength of the relationship (as measured by r^2) between mT and abrasion appeared higher than that of mTDI, mT seemed to be the most appropriate index in this type of environment. However, in the Gulf of Lion, where the sediments are relatively fine, no method was conclusive to assess the effect of trawling on benthic communities because, in most cases, and although generally high, abrasion could not be related to the indices. Video sampling therefore seems particularly interesting for habitats consisting mainly of hard substrates (gravel, boulders, shell sands, etc.). On soft sediment, this methodology may require a much larger observation effort (larger surface observed) and both an increase in the number of stations sampled and a stronger abrasion gradient to verify its usefulness. A recent study has shown that the size of individuals has an influence on the response of a number of indicators to the effect of trawling. Large benthic megafauna seemed to be more impacted by trawling than small benthic fauna and less impacted by various environmental parameters such as depth or granulometry (McLaverty et al. 2020). Towed video, mainly sampling the large benthic megafauna in a non-destructive way, appears to be a good tool for monitoring the effect of trawling on benthic communities. Future work should be considered to determine whether size measurements of benthic megafauna' individuals, on video images, could become useful indices to monitor the effect of trawling on benthic communities.

Acknowledgement

The authors are grateful to the scientific officers of MEDITS, CGFS, IBTS, CAMANOC and APPEAL MED scientific surveys, the scientific staff and vessel crews of the TGIR – French Oceanographic Fleet who participated in these surveys. The authors thank the crew and captain of the professional fishing vessel Juliarth for the deployment of the video device during the GALION and IDEM surveys. This study was supported by the EC2CO National Program on Coastal Environments (Bentchal), the DG ENV project IDEM (Implementation of the MSFD to the Deep Mediterranean Sea; contract EU No 11.0661/2017/750680/SUB/EN V.C2) and French State Funding managed by France Energies Marines and the National Research Agency under the program "Investissements d'Avenir" (ANR-10-IEED-0006-25). C. J. from MARBEC, Ifremer acknowledges additional support from the Occitanie region through its PhD research funding program.

Author Contributions

Conceptualization: Nicolas Desroy and Sandrine VAZ
Methodology: Cyrielle Jac, Jean-Claude Duchêne and Lyvia Lescure
Software : Jean-Claude Duchêne
Validation : Cyrielle Jac
Formal Analysis : Cyrielle Jac
Investigation : Cyrielle Jac
Resources: Nicolas Desroy, Aurélie Foveau, Céline Labrune and Sandrine Vaz
Data Curation: Cyrielle Jac
Writing – Original Draft Preparation: Cyrielle Jac
Writing – Review & Editing: Nicolas Desroy, Jean-Claude Duchêne, Aurélie Foveau, Céline Labrune and Sandrine Vaz
Visualization: Cyrielle Jac
Supervision: Nicolas Desroy and Sandrine Vaz
Project Administration: Nicolas Desroy and Sandrine Vaz
Funding Acquisition: Nicolas Desroy and Sandrine Vaz

References

Althaus F, Hill N, Ferrari R, Edwards L, Przeslawski R, Schönberg CHL, Stuart-Smith R, Barrett N, Edgar G, Colquhoun J, Tran M, Jordan A, Rees T, Gowlett-Holmes K (2015) A standardised vocabulary for identifying benthic biota and substrata from underwater imagery: The CATAMI classification scheme. PLoS One 10:1–18

Amoroso RO, Pitcher CR, Rijnsdorp AD, McConnaughey RA, Parma AM, Suuronen P, Eigaard OR, Bastardie F, Hintzen NT, Althaus F, Baird SJ, Black J, Buhl-Mortensen L, Campbell AB, Catarino R, Collie J, Cowan JH, Durholtz D, Engstrom N, Fairweather TP, Fock HO, Ford R, Gálvez PA, Gerritsen H, Góngora ME, González JA, Hiddink JG, Hughes KM, Intelmann SS, Jenkins C, Jonsson P, Kainge P, Kangas M, Kathena JN, Kavadas S, Leslie RW, Lewise SG, Lundy M, Makin D, Martin J, Mazor T, Gonzalez-Mirelis G, Newman SJ, Papadopoulou N, Posen PE, Rochester W, Russok T, Salal A, Semmens JM, Silvan C, Tsoloso A, Vanelslander B, Wakefield CB, Wood BA, Hilborn R, Kaiser MJ, Jennings S (2018) Bottom trawl fishing footprints on the world's continental shelves. Proc Natl Acad Sci U S A 115:E10275–E10282

Auber A (1992) IBTS : International Bottom Trawl Survey. https://doi.org/10.18142/17.

Bolam SG, Coggan RC, Eggleton J, Diesing M, Stephens D (2014) Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. J Sea Res 85:162–177

Borja A, Muxika I, Franco J (2003) The application of a Marine Biotic Index to different impact sources affecting soft-bottom benthic communities along European coasts. Mar Pollut Bull 46:835–845

Brind'Amour A, Laffargue P, Morin J, Vaz S, Foveau A, Le Bris H (2014) Morphospecies and taxonomic sufficiency of benthic megafauna in scientific bottom trawl surveys. Cont Shelf Res 72:1–9

Brind'Amour A, Rouyer A, Martin J (2009) Functional gains of including non-commercial epibenthic taxa in coastal beam trawl surveys: A note. Cont Shelf Res 29:1189–1194

Certain G, Jorgensen LL, Christel I, Planque B, Bretagnolle V (2015) Mapping the vulnerability of animal community to pressure in marine systems: disentangling pressure types and integrating their impact from the individual to the community level. ICES J Mar Sci 72:1470–1482

Chavent M, Kuentz-Simonet V, Labenne A, Saracco J (2017) Multivariate Analysis of Mixed Data: The R Package PCAmixdata.

Coggan R, Diesing M (2011) The seabed habitats of the central English Channel: A generation on from Holme and Cabioch, how do their interpretations match-up to modern mapping techniques? Cont Shelf Res 31:132–150

Collie JS, Hall SJ, Kaiser MJ, Poiner IANR (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. J Anim Ecol 69:785–798

Coppin F, Travers-Trolet M (1989) CGFS : Channel Ground Fish Survey. https://doi.org/10.18142/11.

Crist TO, Veech JA (2006) Additive partitioning of rarefaction curves and species-area relationships: Unifying α-, β- and γ-diversity with sample size and habitat area. Ecol Lett 9:923–932

Cruz ICS, Kikuchi RKP, Leão ZMAN (2008) Use of the video transect method for characterizing the Itacolomis reefs, Eastern Brazil. Brazilian J Oceanogr 56:271–280

Eigaard OR, Bastardie F, Breen M, Dinesen GE, Hintzen NT, Laffargue P, Mortensen LO, Nielsen JR, Nilsson HC, O'Neill FG, Polet H, Reid DG, Sala A, Sköld M, Smith C, Sorensen TK, Tully O, Zengin M, Rijnsdorp AD (2016) Estimating seabed pressure from demersal trawls, seines, and dredges based on gear design and dimensions. ICES J Mar Sci 73:i27–i43

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P, Catarino R, Dinesen GE, Egekvist J, Fock HO, Geitner K, Gerritsen HD, González MM, Jonsson P, Kavadas S, Laffargue P, Lundy M, Gonzalez-Mirelis G, Nielsen JR, Papadopoulou N, Posen PE, Pulcinella J, Russo T, Sala A, Silva C, Smith CJ, Vanelslander B, Rijnsdorp AD (2017) The footprint of bottom trawling in European waters: Distribution, intensity, and seabed integrity. ICES J Mar Sci 74:847–865

Eleftheriou A (2013) Methods for the study of marine benthos.

Flannery E, Przeslawski R (2015) Comparison of sampling methods to assess benthic marine biodiversity: Are spatial and ecological relationships consistent among sampling gear?

Foveau A, Jac C, LIpasset M, Guillerme C, Desroy N, Vaz S (2019) Updated biological traits' scoring and protection status to calculate sensitivity to trawling on mega-epibenthic fauna. https://doi.org/10.17882/59517.

Foveau A, Vaz S, Desroy N, Kostylev VE (2017) Process-driven and biological characterisation and mapping of seabed habitats sensitive to trawling. PLoS One 12:1–30

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EM., Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. Science (80-) 319:948–953

Hiddink JG, Jennings S, Kaiser MJ (2007) Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. J Appl Ecol 44:405–413

Hiddink JG, Jennings S, Kaiser MJ, Queirós AM, Duplisea DE, Piet GJ (2006) Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Can J Fish Aquat Sci 63:721–736

Hiddink JG, Jennings S, Sciberras M, Szostek CL, Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2017) Global analysis of depletion and recovery of seabed biota after bottom trawling disturbance. Proc Natl Acad Sci U S A 114:8301–8306

Hiddink JG, Kaiser MJ, Sciberras M, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher CR, Parma AM, Suuronen P, Rijnsdorp AD, Jennings S (2020) Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. J Appl Ecol 57:1199–1209

Hiscock K, Jackson A, Lear D (1999) Assessing seabed species and ecosystems sensitivities. Existing approaches and development.

ICES (2015) Manual for the International Bottom Trawl Surveys.

ICES (2017) EU request on indicators of the pressure and impact of bottom-contacting fishing gear on the seabed , and of trade-offs in the catch and the value of landings.

ICES (2019) OSPAR request on the production of spatial data layers of fishing intensity/pressure. ICES Tech Serv

Jac C, Desroy N, Certain G, Foveau A, Labrune C (2020a) Detecting adverse effect on seabed integrity . Part 1 : Generic sensitivity indices to measure the effect of trawling on benthic mega-epifauna. Ecol Indic 117:

Jac C, Desroy N, Certain G, Foveau A, Labrune C, Vaz S (2020b) Detecting adverse effect on seabed integrity. Part 2: How much of seabed habitats are left in good environmental status by fisheries? Ecol Indic 117:

Jac C, Vaz S (2018) Abrasion superficielle des fonds par les arts trainants - Méditerranée (surface swept area ratio). https://doi.org/10.12770/8bed2328-a0fa-4386-8a3e-d6d146cafe54.

Jadaud A, Souplet A, Bertrand J (1994) MEDITS. https://doi.org/10.18142/7.

de Juan S, Demestre M (2012) A Trawl Disturbance Indicator to quantify large scale fishing impact on benthic ecosystems. Ecol Indic 18:183–190

Kaiser MJ, Edwards DB, Armstrong PJ, Radford K, Lough NEL, Flatt RP, Jones HD (1998) Changes in megafaunal benthic communities in different habitats after trawling disturbance. ICES J Mar Sci 55:353–361

Labrune C (2018) APPEAL MED. https://doi.org/10.17600/18000598.

Labrune C, Grémare A, Amouroux JM, Sardá R, Gil J, Taboada S (2008) Structure and diversity of shallow soft-bottom benthic macrofauna in the Gulf of Lions (NW Mediterranean). Helgol Mar Res 62:201–214

van Loon WMGM, Walvoort DJJ, van Hoey G, Vina-Herbon C, Blandon A, Pesch R, Schmitt

P, Scholle J, Heyer K, Lavaleye M, Phillips G, Duineveld GCA, Blomqvist M (2018) A regional benthic fauna assessment method for the Southern North Sea using Margalef diversity and reference value modelling. Ecol Indic 89:667–679

Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952-2012). Fish Res 154:44–62

McLaverty C, Eigaard OR, Gislason H, Bastardie F, Brooks ME, Jonsson P, Lehmann A, Dinesen GE (2020) Using large benthic macrofauna to refine and improve ecological indicators of bottom trawling disturbance. Ecol Indic 110:1–13

MEDITS (2017) MEDITS - International Bottom Trawl Survey in the Mediterranean : Instruction Manual Version 9.

Mérillet L, Mouchet Ma, Robert M, Salaun M, Schuck L, Vaz S, Kopp D (2017) Using underwater video to assess megabenthic community vulnerability to trawling in the Grande Vasière (Bay of Biscay). Environ Conserv 45:163–172

Mouillot D, Villeger S, Parravicini V, Kulbicki M, Arias-Gonzalez JE, Bender M, Chabanet P, Floeter SR, Friedlander A, Vigliola L, Bellwood DR (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proc Natl Acad Sci 111:13757–13762

Mouillot, Graham, Villéger, Mason, Bellwood (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–177

OCEANA (2016) Developing a list of Vulnerable Marine Ecosystems. 4

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHM, Wagner H (2019) Package "vegan": Community ecology package. http://vegan.r-forge.r-project.org/

OSPAR (2008) List of threatened and/or declining species and habitats.

Pielou E (1969) An introduction to mathematical ecology. Wiley-Iterscience, New York

Populus J, Vasquez M, Albrecht J, Manca E, Agnesi S, Al Hamdani Z, Andersen J, Annunziatellis A, Bekkby T, Bruschi A, Doncheva V, Drakopoulou V, Duncan G, Inghilesi R, Kyriakidou C, Lalli F, Lillis H, Mo G, Muresan M, Salomidi M, Sakellariou D, Simboura M, Teaca A, Tezcan D, Todorova V, Tunesi L (2017) EUSeaMAP : A European broad-scale seabed habitat map.

R Core Team (2017) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

Rijnsdorp AD, Bolam SG, Garcia C, Hiddink JG, Hintzen NT, van Denderen PD, van Kooten T (2018) Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. Ecol Appl 28:1302–1312

Rijnsdorp AD, Buys AM, Storbeck F, Visser EG (1998) Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES J Mar Sci 55:403–419

Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D (2019) MASS: support functions and datasets for venables and Ripley's MASS. R package version 7.3-51.5. Available from https://CRAN.R-project.org/package=MASS. R Top Doc

Rooper CN, Zimmermann M (2007) A bottom-up methodology for integrating underwater video and acoustic mapping for seafloor substrate classification. Cont Shelf Res 27:947–957

Rumohr H, Kujawski T (2000) The impact of trawl fishery on the epifauna of the southern North Sea. ICES J Mar Sci 57:1389–1394

Sciberras M, Hiddink JG, Jennings S, Szostek CL, Hughes KM, Kneafsey B, Clarke LJ, Ellis N, Rijnsdorp AD, McConnaughey RA, Hilborn R, Collie JS, Pitcher CR, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2018) response of benthic fauna to experimental bottom fishing: A global meta-analysis. Fish Fish 19:698–715

Shannon CE, Weaver W (1963) The mathematical theory of communication. Univ Illinois Press 1–131

Sheehan E V., Vaz S, Pettifer E, Foster NL, Nancollas SJ, Cousens S, Holmes L, Facq JV, Germain G, Attrill MJ (2016) An experimental comparison of three towed underwater video systems using species metrics, benthic impact and performance. Methods Ecol Evol 7:843–852

Simpson EH (1949) Measurement of Diversity. Nature 163:688–688

Taormina B (2019) Potential impacts of submarine power cables from marine renewable energy projects on benthic communities. Université de Bretagne Occidentale

Taormina B, Marzloff MP, Desroy N, Caisey X, Dugornay O, Metral Thiesse E, Tancray A, Carlier A (2020) Optimizing image-based protocol to monitor macroepibenthic communities colonizing artificial structures. ICES J Mar Sci 77:835–845

Thrush SF, Dayton PK (2002) Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. Annu Rev Ecol Syst 33:449–473

Törnroos A, Bonsdorff E (2012) Developing the multitrait concept for functional diversity: Lessons from a system rich in functions but poor in species. Ecol Appl 22:2221–2236

Trenkel VM, Vaz S, Albouy C, Amour AB, Duhamel E, Laffargue P, Romagnan JB, Simon J, Lorance P (2019) We can reduce the impact of scientific trawling on marine ecosystems. Mar Ecol Prog Ser 609:277–282

Vaz S (2016) VIDEO GALION. https://doi.org/10.17600/16001100.

Vaz S (2017) VIDEO GALION. https://doi.org/10.17600/17013500.

Vaz S (2018a) EPIBENGOL. https://doi.org/10.17600/18000589.

Vaz S (2018b) IDEM VIDEO. https://doi.org/10.17600/18000654.