# Long-term variations in the functional diversity of benthic communities in the English Channel

Lise Bacouillard

## To cite this version:

Lise Bacouillard. Long-term variations in the functional diversity of benthic communities in the English Channel. Biodiversity. Sorbonne Université, 2020. English. NNT : 2020SORUS071 . tel-03191322

**HAL Id: tel-03191322**
**https://tel.archives-ouvertes.fr/tel-03191322**

Submitted on 7 Apr 2021

# Sorbonne Université

École doctorale 227 MNHN - Sorbonne Université « Sciences de la nature et de l'homme: évolution et écologie »

*CNRS - Sorbonne Université, Station Biologique de Roscoff, UMR7144 - Adaptation et Diversité en Milieu Marin, EDYCO*

# Variations à long terme de la diversité fonctionnelle des communautés benthiques en Manche

Par **Lise Bacouillard**

Thèse de doctorat d'Écologie Marine

Dirigée par Éric Thiébaut

Présentée et soutenue publiquement le 18 Décembre 2020

Devant un jury composé de:

| | |
|---|---|
| Pr. Christine Dupuy<br>Université de La Rochelle | Rapportrice |
| Pr. Mathieu Cusson<br>Université du Québec à Chicoutimi | Rapporteur |
| Dr. Anik Brind'Amour<br>Ifremer Nantes | Examinatrice |
| Dr. François Charles<br>CNRS Banyuls-sur-Mer | Examinateur |
| Pr. Dominique Davoult<br>Sorbonne Université, Station Biologique de Roscoff | Examinateur |

*À Odette et Joël*

*Instigateurs de souvenirs alpins*

# Remerciements

Selon moi un travail de recherche ne peut se réaliser seul de son côté, il a besoin d'échanges et d'interactions pour se développer et grandir, un peu comme nous finalement. C'est pourquoi dans les quelques lignes qui suivent je tiens à remercier l'ensemble des personnes qui ont contribué à ce travail, à mon image donc de manière (très) concise.

Je remercie la région Bretagne et Sorbonne Université pour le financement de ce projet de thèse.

Je tiens à remercier sincèrement Éric pour son encadrement dans mon travail de thèse. Avoir un seul encadrant de thèse ce n'est pas forcément évident pour l'encadrant et l'encadré, donc merci pour la confiance que tu m'as accordée pour mener à bien ce projet. Malgré ton emploi du temps très chargé tu as toujours pu trouver du temps pour écouter mes questions, même les plus stupides, qui pouvaient surgir dans mon cerveau lors de mes moments de doutes (et il y en a eu) et pour y répondre, faire preuve de ta pédagogie appréciée depuis les cours de Master. La dernière année supplémentaire « surprise » que j'ai prise pour finir ma thèse n'a pas été facile donc merci pour ta patience lors de cette dernière année.

Je remercie l'ensemble des membres de mon jury qui ont accepté d'évaluer ma thèse : Christine Dupuy et Mathieu Cusson qui ont accepté le rôle de rapporteur, Anik Brind'Amour, François Charles, et Dominique Davoult qui ont accepté le rôle d'examinateur. Après avoir passé une année 2020 presque exclusivement à travailler de chez moi, loin d'un environnement scientifique stimulant, nos échanges lors de ma soutenance de thèse ont été un vrai plaisir.

Je remercie également les membres de mon comité de thèse, Jean-Claude Dauvin, Stanislas Dubois, François Rigal et Christophe Destombes qui m'ont apporté un regard différent sur mon travail et fait germer des idées nouvelles.

Toutes les personnes ayant contribué aux campagnes Pectow et au suivi Pierre Noire, sans qui les jeux de données sur lesquels repose ma thèse n'existeraient pas, méritent également d'être remercié. Ces jeux de données sont vraiment très précieux et je mesure ma chance d'avoir pu les exploiter.

Merci à Céline Houbin pour toute l'aide que tu as pu m'apporter aussi bien technique par ta connaissance des petites bêtes présentes dans mes jeux de données, pour tes cartes qui m'ont bien aidées, pour tes conseils couture … que morale. Merci à Pascal Riera pour ton aide et ta disponibilité sur l'aspect isotope dans lequel je me suis plongé assez tardivement.

Merci à Katja Geiger pour ton (immense) travail de Master 2 en amont de ma thèse. Tu m'as permis de commencer ma thèse sur de très bonnes bases et travailler avec toi ou après toi a toujours super facile. Merci à Raphaël pour sa contribution au chapitre IV lors de son stage de Master 2.

Je souhaite remercier ici l'ensemble des membres de l'équipe EDYCO (ex EFEB) que j'ai pu croiser pendant ma thèse ou lors de mes précédents stages. Vous m'avez toujours très bien accueilli et j'ai beaucoup apprécié les pauses café en votre compagnie (même si vous aviez parfois la flemme de venir me chercher au fond du couloir !).

Merci à Lucile, avec qui j'ai pu partager ces années de thèse car nous sommes arrivées et parties presque en même temps à la Station (bon ok, partie quand j'aurais dû partir). Te savoir quelque part dans la Station chantant des chansons nulles en pull de Noël m'a permis d'avoir un très bon environnement de travail. Et merci aux autres membres du groupe des L5, Lydia, Lucie, Louise, notamment pour les séances de sport à la salle qui sont devenues très attendues dans ma semaine grâce à vous. Merci à Caro de m'avoir aérer en sortie Percebes et pour sa vie très divertissante. Merci à mes compagnons doctorants de Roscoff et d'ailleurs avec qui j'ai pu partager mes malheurs (Auriane, Florian, Jean-Philippe, Zujaila, Dung, François…). Merci à la « team Brestois », camarades de promo de Master (Delphine, Elyne, Robin, Bastien, Julie) pour leur soutien moral lors ma dernière année de thèse. Merci aux autres que j'ai oublié ou qui ne se retrouvent pas dans les catégories sus-citées.

Enfin merci à ma famille et à Louis (et sa famille) pour leur soutien tout au long de mes années de thèse, surtout la dernière.

Pour finir, merci à notre cher ami Covid, qui n'a pas manquer de me rappeler tous les jours de 2020 qui si j'avais fini ma thèse en temps et en heure en 2019 ma fin de thèse aurait pu être bien moins laborieuse.

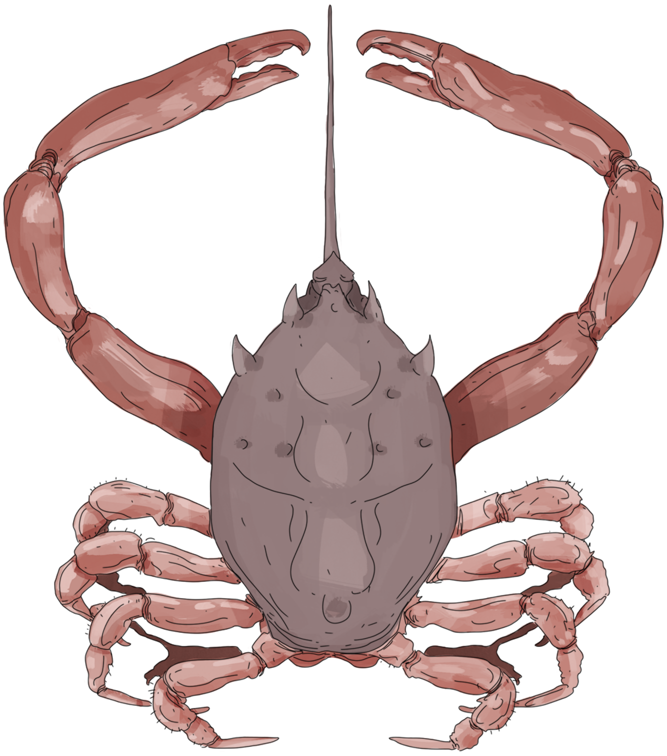
*Illustrations de premières pages de chapitre très gentiment réalisées par Mathilde Girard*

# Table des matières

# Table des figures

# Table des tableaux

# Introduction générale



# 1. Contexte général

Les pressions anthropiques croissantes, dont les principales sont le changement climatique, la surexploitation des ressources, les pollutions diverses et variées, la modification et la dégradation des habitats ou l'introduction d'espèces non-indigènes, vont avoir des effets cumulatifs importants sur les écosystèmes marins, tant benthiques que pélagiques (Halpern et al., 2008, 2015). A titre d'exemple, il est possible de mentionner les conséquences de l'acidification des océans sur la structure des communautés du phytoplancton (Dutkiewicz et al., 2015), les effets de diverses pressions anthropiques simultanées sur les écosystèmes très riches que sont les herbiers de zostère (Vieira et al., 2020), ou encore les impacts de la surpêche des individus de grande taille sur le fonctionnement des écosystèmes dont ils font partis (Shantz et al., 2020). La perte d'espèces en lien avec des activités humaines, donc une diminution de la diversité, peut modifier les performances des écosystèmes (Naeem et al., 1994). Toutefois, les effets des différentes pressions vont se traduire plus généralement par des modifications de la structure des communautés caractéristiques de ces écosystèmes qui se répercuteront sur leur fonctionnement et donc sur les différents services écosystémiques qu'ils peuvent fournir (Cardinale et al., 2012). Les zones fortement anthropisées comme les zones côtières sont particulièrement sensibles et sont soumises à des pressions spécifiques telles que la valorisation des terres, l'aménagement du littoral, le trafic maritime, la surpêche et les pollutions d'origine terrigène (Airoldi & Beck, 2007). Dans le cadre d'une préservation durable de leur intégrité et de leur fonctionnement, il existe un réel besoin d'évaluer la réponse des écosystèmes côtiers à l'ensemble de ces pressions et de mettre en place des outils de surveillance et de gestion adaptés.

Le maintien de la biodiversité et du bon fonctionnement des écosystèmes se retrouve dans diverses directives européennes spécifiques ou non au domaine marin: (1) la Directive Habitats Faune Flore (DHFF, 92/43/CEE), la Directive Cadre sur l'Eau (DCE, 2000/60/CE) et la Directive Cadre Stratégie pour le Milieu Marin (DCSMM, 2008/56/CE) (Fraschetti et al., 2018). Ces directives diffèrent par leurs objectifs ce qui permet d'agir sur le maintien de la biodiversité selon un large spectre d'initiatives. La DHFF s'intéresse tout particulièrement à la protection des espèces végétales et animales et des habitats d'intérêt communautaire par la mise en place d'un réseau de sites écologiques protégés à l'échelle européenne, les sites Natura 2000 dont les sites Natura 2000 en mer. Cette directive a pour objectif de maintenir une biodiversité élevée sur des sites précis à l'échelle de régions biogéographiques, terrestres ou aquatiques. La DCE quant à elle a été mise en place dans le but de maintenir ou restaurer le bon état écologique et chimique des masses d'eau en Europe (i.e. les eaux intérieures de surface, les eaux de transition, les eaux souterraines et les eaux côtières jusqu'à un mile nautique du trait de côte) en stimulant notamment la restauration des écosystèmes aquatiques, en réduisant la pollution de l'eau et en garantissant une utilisation durable de l'eau. L'évaluation de l'état écologique des masses d'eau s'appuie sur un programme de surveillance qui consiste en des suivis réguliers des paramètres physico-chimiques, et de la faune et de la flore aquatiques. Cette évaluation s'appuie sur des variables qui caractérisent la structure des écosystèmes (i.e. abondance des espèces, composition en espèces, présence de certaines espèces, …) (Borja et al., 2010, 2013) et sur la mise en place d'indicateurs de qualité. La DCSMM établit un cadre pour une politique communautaire dans le domaine marin et concerne les eaux côtières européennes - hors estuaires - jusqu'à la limite de la Zone Économique Exclusive (ZEE) située au maximum à 200 milles nautique au large. Au-delà d'une emprise spatiale différente, elle diffère de la DCE en ce sens qu'elle vise à maintenir un « bon état environnemental » des eaux marines en promouvant une approche plus intégrative et fonctionnelle de l'état de santé des écosystèmes marins (Borja et al., 2013). Elle prend donc en considération tout à la fois la structure, les fonctions et les processus qui régentent le fonctionnement des écosystèmes, et les conséquences des activités et pressions anthropiques sur ce fonctionnement. La définition du bon état environnemental au titre de cette directive s'appuie sur un programme de surveillance et l'utilisation de onze descripteurs qui incluent tout à la fois les propriétés des écosystèmes (e.g. descripteur 1 dédié à la biodiversité et descripteur 4 dédié aux réseaux trophiques) et les sources de perturbations (e.g. descripteur 5 consacré à l'eutrophisation et descripteur 8 consacré aux contaminants).

Les actions de gestion associées à ces directives se traduisent ainsi par la mise en place de programmes de surveillance qui reposent sur des suivis à long terme de différents compartiments des écosystèmes, notamment le compartiment benthique. En effet, le benthos est un compartiment particulièrement adapté à l'évaluation et à la caractérisation des perturbations anthropiques et peut être utilisé en tant que bio-indicateur des changements des conditions environnementales en raison de plusieurs de ces caractéristiques : (1) il possède pour la très grande majorité des espèces une faible mobilité au stade adulte ; (2) de nombreuses espèces sont longévives ; (3) il est composé de taxons très différents qui présentent une sensibilité variable face à une perturbation ; et (4) il joue un rôle important dans le fonctionnement des écosystèmes côtiers, au niveau du cycle du carbone et des éléments nutritifs (Dauvin et al., 2007a ; Snelgrove et al., 2014).

Au-delà de leur caractère opérationnel, les séries temporelles à long terme sont essentielles pour répondre à différentes questions plus fondamentales en écologie marine: (1) décrire et comprendre la dynamique à long terme de la diversité des communautés face aux variations des conditions environnementales ; (2) comprendre les effets de différentes sources de stress environnementaux et dégager la variabilité naturelle des effets des impacts anthropiques ; (3) fournir des données pour la construction de modèles prédictifs d'évolution des communautés marines ; (4) permettre le développement d'indicateurs écologiques pour évaluer l'état de santé des écosystèmes et (5) permettre la mise en place d'une approche écosystémique dans la gestion des milieux (Magurran et al., 2010 ; Duffy et al., 2013).

## 2. Les suivis de la biodiversité et du fonctionnement des écosystèmes

Selon l'article 2 de la Convention sur la Diversité Biologique (« Convention on Biological Diversity », CBD) signée en 1992 par 150 pays, la biodiversité ou diversité biologique est définie comme « la variabilité entre les organismes vivants de toute origine y compris, entre autres, les écosystèmes terrestres, marins et autres écosystèmes aquatiques et les composantes écologiques dont ils font partie ; cela comprend la diversité au sein des espèces, entre espèces et entre écosystèmes ». Différents auteurs ont proposé d'autres grilles de lecture pour évaluer et suivre l'état et l'évolution temporelle de la biodiversité face aux pressions anthropiques et contribuer à une meilleure gestion. Une première approche repose sur l'utilisation des variables essentielles de la biodiversité (« Essential Biodiversity Variables », EBV) qui prennent en compte l'ensemble des différentes dimensions de la biodiversité (Pereira et al., 2013). Ainsi, les variables essentielles de la biodiversité se répartissent en 6 classes distinctes: (1) la composition génétique, (2) les caractéristiques des populations (e.g. abondance et distribution), (3) les traits biologiques des espèces, (4) la composition des communautés, (5) la structure des écosystèmes et (6) la fonction des écosystèmes. Plus récemment, Lausch et al. (2016) ont proposé que la mesure de la biodiversité puisse se décomposer selon trois caractéristiques principales, i.e. la diversité taxonomique, la diversité structurelle et la diversité fonctionnelle qui sont mesurées à différents niveaux d'organisation du vivant, du niveau moléculaire au niveau des paysages en passant par ceux des individus, des populations et des écosystèmes (Figure 1A). Dans le même ordre d'idée, Cochrane et al. (2016) suggèrent d'adopter une approche pragmatique pour évaluer la biodiversité marine en mettant l'accent sur trois aspects différents en fonction des questions abordées: la biodiversité taxonomique structurelle, la biodiversité fonctionnelle et les réseaux trophiques qui résultent de trois fonctions écologiques majeures, i.e. la production primaire, la production secondaire et la reminéralisation de la matière organique, elles-mêmes intimement liées aux biodiversités taxonomique et fonctionnelle (Figure 1B).

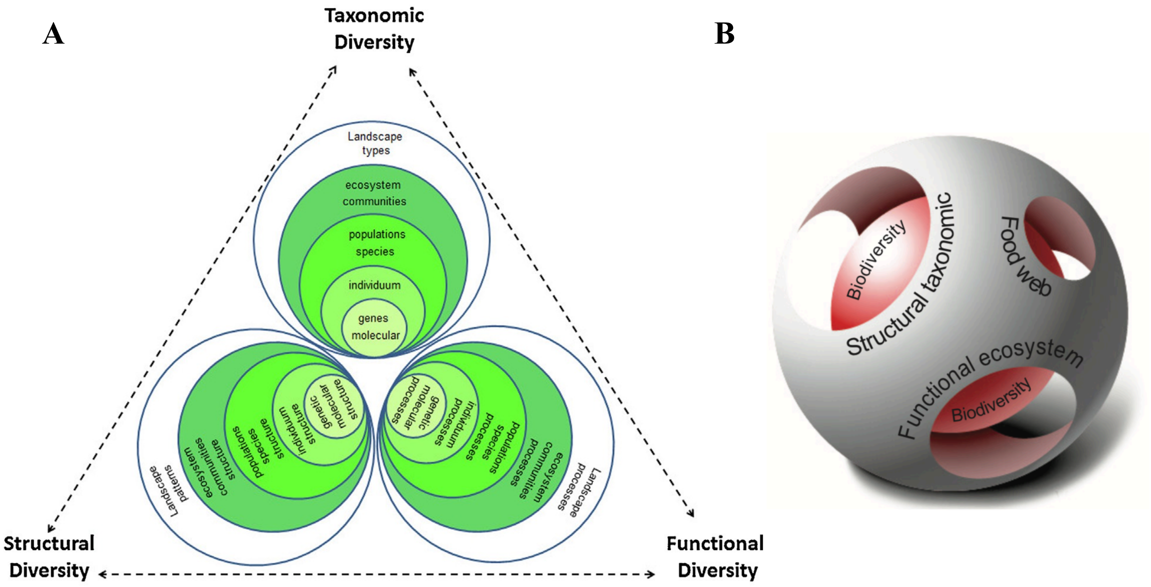


**Figure 1:** Représentation schématique des différentes facettes de la biodiversité à prendre en considération en fonction des questions abordées pour traiter de la réponse des écosystèmes marins aux pressions environnementales et anthropiques d'après (A) Lausch et al. (2016) et (B) Cochrane et al. (2016).

Indépendamment du niveau d'intégration du vivant, toute mesure de la biodiversité s'observera à différentes échelles spatiales et temporelles (Whittaker, 1960). Whittaker (1960, 1972) fut ainsi le premier à définir une terminologie toujours largement utilisée pour décrire les différentes échelles de la biodiversité même si différents ajustements ont pu être proposées depuis (voir par exemple Gray, 2000 ; Anderson et al., 2011). La diversité alpha correspond à la diversité au niveau d'un échantillon ou d'une communauté, la diversité beta au degré de variation de la diversité entre échantillons, et la diversité gamma à la diversité cumulée de plusieurs échantillons dans une région donnée (Whittaker, 1960). Dans le cas de la diversité beta, il est possible de distinguer deux concepts distincts: la variation de la structure de la communauté dans une région donnée et le taux de changement de la structure de la communauté le long d'un gradient spatial, temporel ou environnemental (Anderson et al., 2011). L'ensemble de ces échelles de la biodiversité a donné lieu au développement d'une multitude de méthodes de mesures (Gray, 2000 ; Carney, 2007 ; Anderson et al., 2011).

L'approche traditionnelle pour évaluer la réponse des écosystèmes aux pressions naturelles et anthropiques est basée sur la mesure des propriétés structurelles des communautés telles que l'identité des espèces, le nombre d'espèces, leurs abondances relatives, voire leurs biomasses. Elle se traduit généralement par l'utilisation d'indices de diversité spécifique tels que la richesse spécifique, l'indice de Shannon, l'indice de Simpson et l'indice de régularité de Piélou (Gray, 2000 ; Warwick et al., 2002 ; Johnston & Roberts, 2009 ; Urbina, 2016). Les indices de diversité sont traditionnellement utilisés pour mesurer la complexité d'une communauté. Des méthodes d'analyses multivariées exploratoires sont également traditionnellement utilisées pour décrire l'évolution de la composition et de la structure des communautés, qu'il s'agisse de méthodes de classification ou de méthodes d'ordination telles que le Cadrage Multidimensionnel paramétrique ou non paramétrique (« Multidimensional Scaling », MDS ou nMDS), l'Analyse Factorielle des Correspondances (AFC), l'Analyse en Composantes principales (ACP) ou l'Analyse en Coordonnées Principales (PCoA) (Jackson, 1993; Labat et al., 2005; Baldrighi et al., 2019). Cette approche qui met l'accent sur la composition taxonomique des communautés est utilisée lorsque la priorité est donnée aux politiques de conservation des espèces et des habitats. Lorsqu'elle est mise en œuvre pour également comprendre les incidences des changements de la biodiversité sur le fonctionnement des écosystèmes, elle part du postulat que les propriétés structurelles des communautés fournissent un indication indirecte du fonctionnement de l'écosystème bien qu'elles ne prennent pas en compte de manière explicite les traits biologiques qui gouvernent les processus écologiques. Cette méthode possède ainsi une capacité limitée à mettre en évidence des variations dans le fonctionnement de l'écosystème.

Une approche plus récente et plus en lien direct avec le fonctionnement d'un écosystème se base sur une mesure explicite de la diversité fonctionnelle en tant que proxy du fonctionnement de l'écosystème qui est alors la résultante des principales fonctions écologiques et de la résistance/résilience des communautés après une perturbation (Figure 2). La mesure de la diversité fonctionnelle repose sur ce que font les espèces présentes dans un écosystème et s'appuie sur la composition et les abondances relatives des traits fonctionnels des espèces. Un trait fonctionnel est une caractéristique phénotypique d'un organisme mesurable au niveau individuel qui va influencer les processus écosystémiques et ses réponses face à des facteurs environnementaux en impactant sa « fitness » (valeur adaptative) indirectement au travers de ses effets sur sa croissance, sa reproduction et sa survie (Naeem & Wright, 2003 ; Petchey & Gaston, 2006 ; Violle et al., 2007). Comme pour la diversité taxonomique, de nombreuses méthodes ont été proposées pour mesurer la diversité fonctionnelle à partir du calcul d'indices de diversité fonctionnelle (Mason et al., 2005 ; Villéger et al., 2008 ; Mouillot et al., 2013) ou de méthodes d'analyses multivariées (Bremner et al., 2006 ; Beauchard et al., 2017).

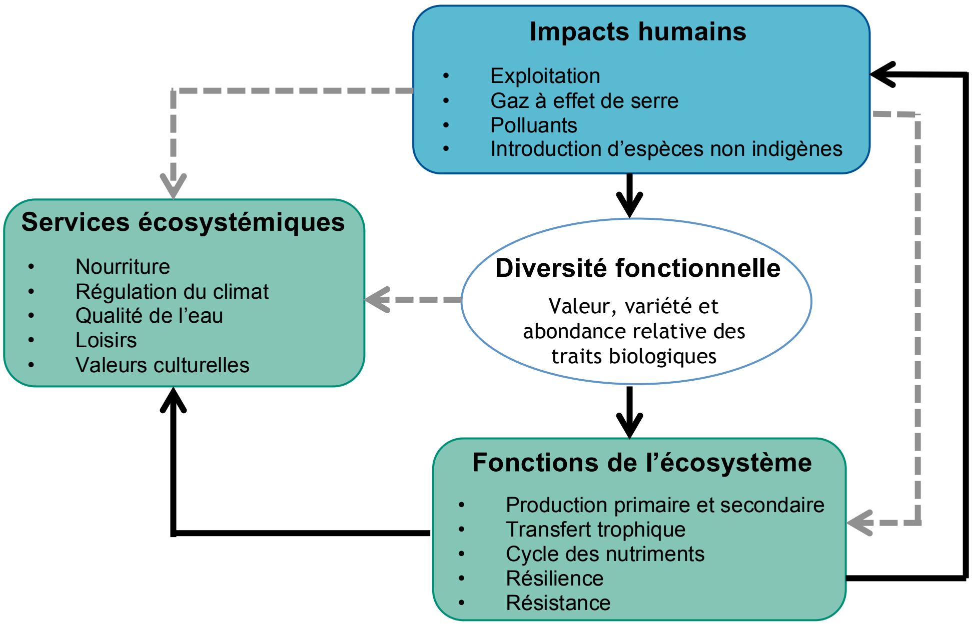


**Figure 2**: Schéma du concept général de l'approche fonctionnelle (modifié à partir de Díaz et al., 2007). Relations entre les diverses activités anthropiques potentiellement néfastes pour le milieu marin et la diversité fonctionnelle qui permet de faire le lien avec les fonctions écologiques gouvernées par les espèces, et les services écosystémiques qui en découlent.

Une troisième approche qui est à rapprocher d'une analyse des abondances relatives des différents groupes trophiques se base sur l'analyse des réseaux trophiques à partir de traceurs tels que les isotopes stables. Les isotopes stables du carbone et de l'azote ($\delta^{13}$C et $\delta^{15}$N) sont devenus un des outils les plus utilisés dans le domaine de l'écologie trophique pour identifier le régime alimentaire des espèces et étudier la structure d'un réseau trophique, à savoir qui mange qui, et les transferts d'énergie entre les sources et les consommateurs dans un écosystème (Sherr & Fry, 1984 ; Riera, 2006). Le principe général de l'utilisation des isotopes stables est que la composition isotopique d'un animal dépend de la composition isotopique de sa nourriture et d'un facteur d'enrichissement en isotopes lourds d'un consommateur par rapport à sa proie lors de chaque transfert trophique (DeNiro & Epstein, 1978, 1981 ; Minagawa & Wada, 1984 ; Post, 2002). Cet enrichissement s'explique physiologiquement, en particulier par la respiration et l'excrétion préférentielle des isotopes légers. Le $\delta^{13}$C subit un faible enrichissement trophique, de l'ordre de 1 ‰ mais varie fortement entre producteurs primaires en fonction des sources de carbone et d'azote minéral et de la voie métabolique utilisée pour réaliser la photosynthèse (Peterson & Fry, 1987 ; Riera, 2006). Il est ainsi utilisé pour identifier la contribution des différentes sources de matière organique dans le réseau trophique. Le $\delta^{15}$N présente un plus fort enrichissement, de l'ordre de 2,4‰ entre un producteur primaire et un consommateur primaire, et de 3,4‰ pour le $^{15}$N entre consommateurs de niveau trophique différent, et permet de mesurer le niveau trophique des espèces au sein du réseau (Carlier et al., 2007). Récemment, l'utilisation des isotopes stables a été étendue afin d'avoir une image de la structure du réseau trophique à l'échelle d'une communauté dans son ensemble, et de rendre compte quantitativement de sa complexité et de son évolution dans le temps ou dans l'espace. Les indices proposés décrivent la niche trophique réalisée d'une communauté et permettent de quantifier une diversité trophique comparable à la diversité fonctionnelle (Layman et al., 2007 ; Cucherousset & Villéger, 2015 ; Rigolet et al., 2015). Caractériser les réseaux trophiques en termes de longueur de chaîne, de diversité des sources ou de redondance trophique est essentiel pour mieux comprendre la résilience des écosystèmes en réponse à des perturbations anthropiques ou naturelles, et constitue donc un aspect important du fonctionnement global d'un écosystème (Cucherousset & Villéger, 2015 ; Silberberger et al., 2018).

Les trois approches évoquées succinctement ci-dessus représentent trois facettes de la biodiversité qui sont complémentaires pour évaluer la réponse fonctionnelle d'un écosystème aux pressions naturelles et anthropiques (Cochrane et al., 2016) (Figure 1). A titre d'exemple, la simulation de 1000 communautés benthiques générées artificiellement à partir de bases de données a montré que la simple mesure de la richesse spécifique parmi un panel d'indices de diversité spécifique, taxonomique et fonctionnelle néglige environ 88% de l'information réelle de la biodiversité (Lyashevska & Farnsworth, 2012). Par ailleurs, l'image que l'on peut avoir de l'organisation spatiale ou de l'évolution temporelle d'une communauté peut diverger fortement selon que l'on utilise la diversité spécifique ou la diversité fonctionnelle pour la décrire. Bremner et al. (2003) ont observé des différences dans les assemblages de la mégafaune épibenthique en Mer du Nord et en Manche et de leur distribution selon que ces derniers soient identifiés à partir de données sur la composition en espèces ou sur la composition en traits. De tels résultats suggèrent que les facteurs gouvernant la distribution des espèces et celle des traits diffèrent: la distribution des traits serait davantage influencées par les conditions environnementales locales que par des processus agissant à grande échelle. Il a été aussi mis en évidence que l'on pouvait avoir une image différente du rétablissement d'une communauté benthique après dragage en utilisant seulement la diversité spécifique ou la diversité fonctionnelle (Bolam, 2014). Une approche intégrative visant à combiner l'utilisation de la diversité fonctionnelle et de la diversité trophique peut également permettre de confronter la niche trophique théorique définie par les traits en lien avec la prise alimentaire et la niche trophique réalisée définie par les signatures isotopiques afin d'avoir une vision plus globale du fonctionnement d'un écosystème (Rigolet et al., 2015 ; Jones, 2017). La redondance fonctionnelle, dont l'intensité dépend de la relation entre diversité spécifique et diversité fonctionnelle, est un outil utile pour la prévision des conséquences des perturbations car une redondance écologique élevée implique que les fonctions des écosystèmes sont résistantes aux changements de diversité (Micheli & Halpern, 2005). Dans le cadre de la gestion des environnements côtiers il apparaît donc primordial de développer ces approches simultanément afin de définir des indicateurs fonctionnels opérationnels et d'évaluer la capacité des écosystèmes à délivrer certains services écosystémiques.

## 3. Les traits biologiques et la mesure de la diversité fonctionnelle

La mesure de la diversité fonctionnelle repose sur un certain nombre de termes qui ne font pas toujours consensus et sont amenés à créer de la confusion. Dans le cadre de cette thèse, le référentiel que nous suivrons est celui fourni dans le Tableau 1. La mesure de la diversité fonctionnelle est centrée autour de l'analyse des traits fonctionnels des espèces. Un trait fonctionnel correspond à une caractéristique phénotypique d'un organisme (i.e. caractéristiques morphologiques, comportementales et physiologiques), qui influence directement les processus écologiques et ses réponses face à des facteurs environnementaux en impactant sa valeur adaptative (« fitness ») indirectement au travers de ses effets sur sa croissance, sa reproduction et sa survie (Naeem & Wright, 2003 ; Petchey & Gaston, 2006 ; Violle et al., 2007). Un trait fonctionnel peut être défini comme un trait effet lorsqu'il détermine comment un organisme influence les propriétés de l'écosystème (ex: bioturbation) ou comme un trait réponse lorsqu'il détermine comment un organisme répond à une perturbation ou à un changement dans l'environnement (ex: durée de vie) (Lavorel & Garnier, 2002 ; Hooper et al., 2005). À travers une approche multi-traits, la diversité fonctionnelle peut être vue comme un bon proxy du fonctionnement d'un écosystème.

**Tableau 1**: Définitions des termes utilisés dans le cadre de cette thèse pour la mesure de la diversité fonctionnelle (Violle et al., 2007; Degen et al., 2018; Martini et al., in press).

| **Terme utilisé** | **Définition** |
|---|---|
| Processus écologiques | Transformation à petite échelle et translocation d'énergie et de matériel à travers l'écosystème en raison d'actions physiques, chimiques ou biologiques (ex : transport d'électron, photosynthèse) (Paterson et al., 2012). |
| Fonctions écologiques | Stocks et flux d'énergie et de matière au sein d'un système, ainsi que leur relative stabilité au cours du temps et leur capacité à se maintenir après une perturbation (ex : production primaire, cycle des nutriments, résistance/résilience …) (Paterson et al., 2012). |
| Services écosystémiques | Avantages socio-économiques retirés par l'homme de son utilisation durable des fonctions écologiques des écosystèmes (EFESE, 2017). |
| Fonctionnement de l'écosystème | Effets conjoints des processus qui maintiennent un écosystème (Reiss et al., 2009). |
| Diversité fonctionnelle | Variété et valeur des traits qui influencent le fonctionnement de l'écosystème (Tilman, 2001). |
| Trait biologique | Propriété bien définie et mesurable d'un organisme, en général au niveau individuel, et utilisé comparativement entre espèces (ex : taille, mobilité,…) (McGill et al., 2006 ; Reiss et al., 2009 ; Violle et al., 2007). |
| Trait fonctionnel | Composant du phénotype d'un organisme qui va influencer les processus écosystémiques et ses réponses face à des facteurs environnementaux en impactant sa « fitness » (valeur adaptative) indirectement au travers de ses effets sur sa croissance, sa reproduction et sa survie (Naeem & Wright, 2003 ; Petchey & Gaston, 2006 ; Violle et al., 2007). |
| Trait effet | Trait fonctionnel qui détermine comment un organisme influence les propriétés de l'écosystème (ex: bioturbation) (Lavorel & Garnier, 2002 ; Hooper et al., 2005). |
| Trait réponse | Trait fonctionnel qui détermine comment un organisme répond à une perturbation ou à un changement dans l'environnement (ex: durée de vie) (Lavorel & Garnier, 2002 ; Hooper et al., 2005). |

La mesure de la diversité fonctionnelle par les traits fonctionnels a été largement développée au cours des deux dernières décennies, dans un premier temps dans le domaine terrestre, en écologie des communautés végétales (Lavorel & Garnier, 2002 ; Wright et al., 2004 ; Diaz et al., 2007 ; Cadotte et al., 2009 ; Lavorel et al., 2013), ou des communautés d'invertébrés aquatiques (Usseglio-Polatera et al., 2000 ; Bonada et al., 2007 ; Paillex et al., 2013 ; Schmera et al., 2015 ; Ilarri et al., 2018) ou plus récemment en écologie des communautés d'insectes (Moretti et al., 2009 ; Yates et al., 2014) et d'oiseaux (de Arruda Almeida et al., 2018 ; Morelli et al., 2018), puis progressivement dans le domaine marin, en particulier pour les communautés de poissons (Mouillot et al., 2007 ; Mouchet et al., 2012 ; Villéger et al., 2012 ; Givan et al., 2017) ou planctoniques (Litchman & Klausmeier, 2008 ; Litchman et al., 2013 ; Pomerleau et al., 2015 ; Banas & Campbell, 2016). En écologie benthique, l'analyse par les traits biologiques (BTA) a été appliquée pour traiter diverses questions telles que la distribution d'assemblages en termes de composition des traits (Bremner et al., 2003; Hewitt et al., 2008), les relations entre les traits et les habitats (Bremner et al., 2006b; Törnroos & Bonsdorff, 2012; Rigolet et al., 2014) les effets des perturbations environnementales telles que la pollution (Paganelli et al., 2012), le chalutage et le dragage (Tillin et al., 2006; Bolam et al., 2014; Neumann et al., 2016) et l'extraction d'agrégats (Barrio Froján et al., 2011), les effets à long terme du changement climatique et de changement de régime (Neumann & Kröncke, 2011; Clare et al., 2015) ou encore l'évaluation de la santé des écosystèmes (Bremner, 2008; Dolbeth et al., 2013).

L'utilisation de cette approche, bien qu'en pleine expansion, reste encore limitée dans le domaine de l'écologie benthique pour de multiples raisons. (1) Ce compartiment comprend des espèces très différentes (morphologie, cycle de vie…) appartenant à de nombreux groupes phylogénétiques, comparé aux végétaux, aux insectes ou aux poissons. (2) Il existe un déficit de connaissances élémentaires sur l'auto-écologie de nombreuses espèces macrobenthiques. (3) L'accès à la donnée dans des bases de données en libre accès demeure extrêmement difficile. Une analyse récente de la disponibilité de l'information pour différents traits chez les poissons et les invertébrés benthiques des eaux britanniques montre de forte disparité entre ces deux groupes fonctionnels (Figure 3). Alors que l'information est disponible pour de nombreux traits chez plus de 75 % des espèces de poissons, seule la taille est un trait aisément disponible chez plus de 75% des espèces d'invertébrés. *A contrario*, de nombreux traits en lien avec le cycle de vie (longévité, mode de reproduction, fécondité, dispersion larvaire) ou le rôle trophique de l'espèce (méthode d'alimentation, régime alimentaire) ne sont renseignés dans les bases de données chez moins de 25% des invertébrés. L'absence d'accès aisé aux données rend la mesure de la diversité fonctionnelle très chronophage et nécessite des recherches auprès de multiples sources (base de données, articles sur espèces spécialisés, experts…). (4) Les liens entre trait et fonction ne sont pas systématiquement formalisés (Beauchard et al., 2017). (5) Pour de nombreux traits, l'information est semi-quantitative ou qualitative et n'intègre pas la variabilité inter-individuelle. Enfin, le manque d'échanges entre les deux communautés d'écologues terrestres et marins, qui n'est pas propre à l'étude de la diversité fonctionnelle, ralentit assurément l'appropriation de cette approche en écologie marine et plus spécifiquement en écologie benthique (Raffaelli et al., 2005).

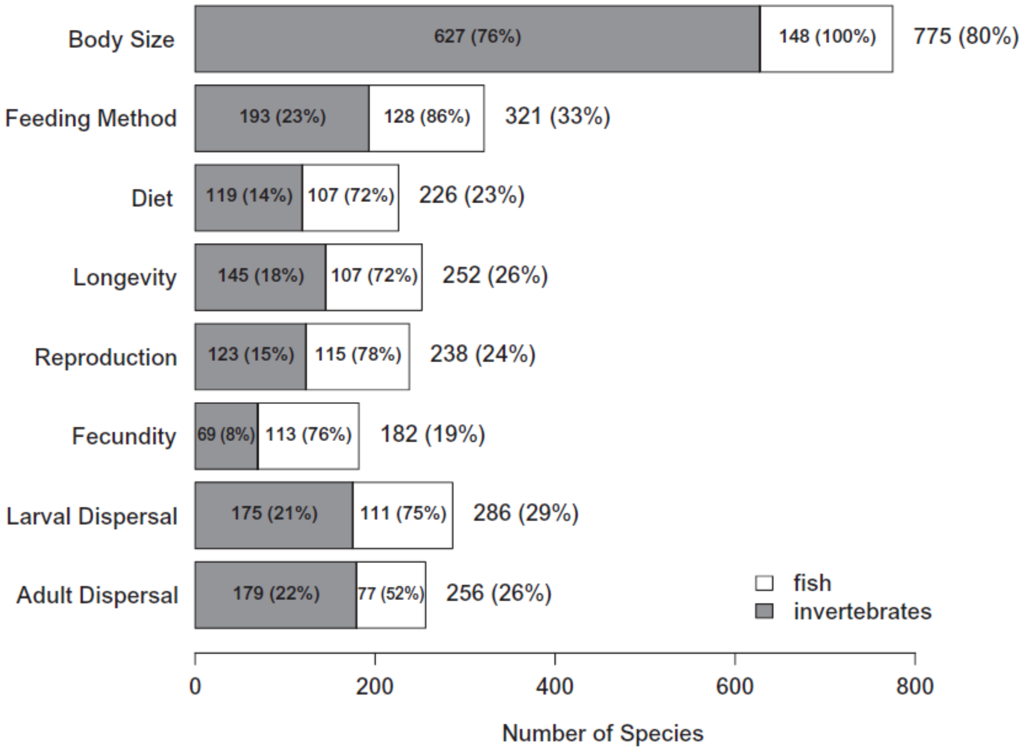


**Figure 3**: Disponibilité de l'information pour huit traits biologiques associés à des poissons et invertébrés de la faune marine britannique. Pour chaque trait, le nombre total d'espèces pour lesquelles la donnée est disponible ainsi que le pourcentage sont indiqués (Tyler et al., 2012).

Malgré l'existence d'études se focalisant sur des aspects méthodologiques liés à l'utilisation des traits en écologie benthique, comme par exemple la contribution d'un trait particulier à la mesure de la diversité fonctionnelle (Bremner, 2008), de nombreux points restent à approfondir (Schleuter et al., 2010 ; Maire et al., 2015 ; Beauchard et al., 2017): quels traits utiliser ? selon quels critères de sélection ? quel est le nombre de traits à retenir ? quel est le nombre de modalités des traits à choisir ? comment pondérer les traits au regard des abondances ou des biomasses des espèces ? comment intégrer les différences intra-spécifiques ? comment gérer les données manquantes ? De Bello et al. (2011) ont proposé deux méthodes basées sur la partition de la variance prenant en considération l'abondance relative des espèces pour quantifier l'effet sur la diversité fonctionnelle de la variabilité intra-spécifique au niveau des traits et ont souligné l'importance de cette variabilité sur la dynamique des communautés. La décomposition de la variance totale de la communauté en effets intra- et inter-spécifique peut être mise en œuvre d'une manière similaire à la décomposition de l'entropie quadratique sur la dissimilarité individuelle par paire (Pavoine & Dolédec, 2005). Le choix des traits et des modalités est large et devrait être guidé par les seuls objectifs de l'étude (Beauchard et al., 2017). Concernant le nombre de traits, il apparaît logique que l'utilisation d'un plus grand nombre de traits donnera l'image la plus fidèle du fonctionnement d'un écosystème. Cependant, certains traits peuvent être fortement corrélés et il est possible de limiter le nombre de traits en éliminant les traits qui pourraient réagir de la même manière face à un changement de conditions du milieu par exemple. Il est toutefois difficile actuellement de connaître les relations entre traits et de savoir comment ils réagissent (Bremner et al., 2006a). Par ailleurs, des simulations ont montré que le nombre de traits nécessaire à une bonne représentation de l'espace fonctionnel d'une communauté varie en fonction de la richesse spécifique et de la nature des traits (Maire et al., 2015). En pratique, le choix des traits et de leur nombre est pragmatique: il est souvent nécessaire de prendre en considération la disponibilité de la donnée et de trouver un compromis entre la qualité de l'information apportée et le temps passé à récolter cette information. Un groupe d'experts britanniques travaillant sur la diversité fonctionnelle des communautés benthiques de substrats meubles et rocheux a ainsi identifié 28 traits majeurs à potentiellement prendre en considération, traits recouvrant à la fois l'utilisation des ressources, les interactions trophiques, les interactions avec l'environnement ou le cycle de vie des espèces (Bremner, 2008). En Mer Baltique, Törnroos et Bonsdorff (2012) ont identifié pas moins de 25 traits distincts pour mesurer la diversité fonctionnelle des communautés benthiques de substrats meubles. Cependant selon une revue bibliographique réalisée à partir de 94 études traitant de l'usage des traits en écologie benthique de 2000 à 2019, il apparaît qu'en moyenne le nombre de traits utilisés soit de 9 (Figure 4). Au total 53 traits différents ont été mentionnés au moins une fois dans ces 94 études et dans une étude donnée entre 3 et 25 traits différents peuvent être utilisés.

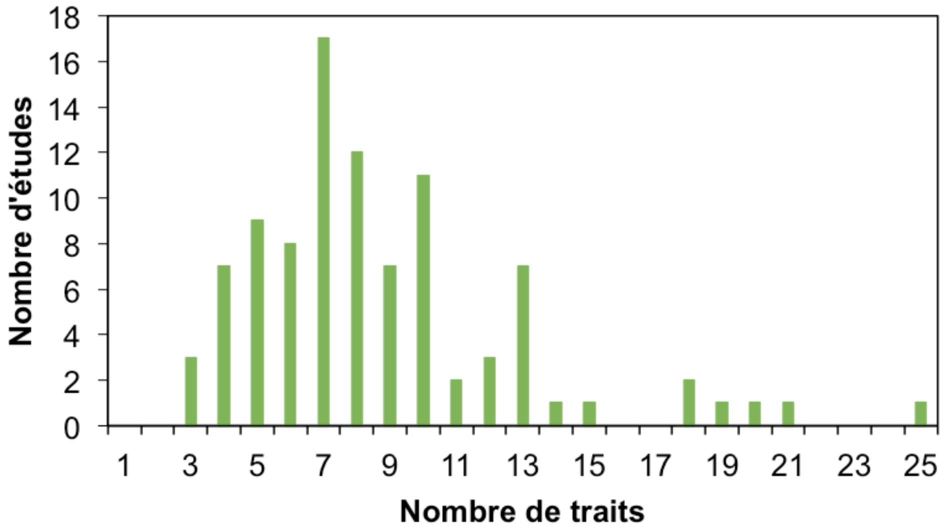


**Figure 4:** Nombre de traits utilisés par étude sur un total de 94 études.

Lorsque la mesure de la diversité fonctionnelle repose sur une pondération de l'importance relative des espèces, il convient également de se poser la question du critère à prendre en considération pour réaliser une telle pondération. S'agit-il de la réaliser au regard des densités des différentes espèces ou de leurs biomasses sachant que l'acquisition des données de biomasses est beaucoup plus longue que celle des données d'abondances. Les biomasses sont traditionnellement moins utilisées mais ce choix est en général guidé par des raisons pratiques et non écologiques. D'après notre revue bibliographique, la majorité des études traitant de l'usage des traits en écologie benthique sur la macrofaune utilisent des données d'abondances alors que les études sur la mégafaune utilisent de façon équivalente les deux types de données, les biomasses étant plus facile à acquérir sur de la mégafaune (Figure 5).

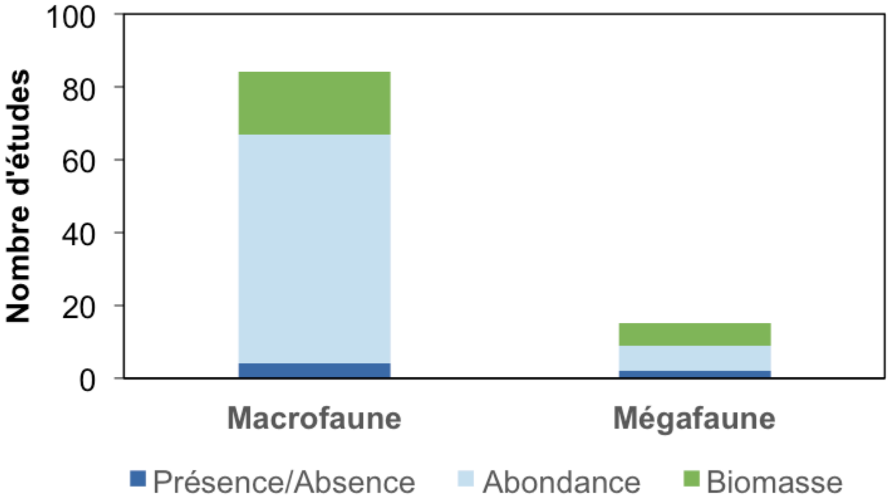


**Figure 5:** Nombre d'études traitant de l'usage des traits en écologie benthique sur la macrofaune ou la mégafaune en relation avec la nature des données utilisées (i.e. présence/absence, abondance, biomasse).

Comme pour les mesures de la diversité spécifique, la mesure de la diversité fonctionnelle s'effectue à travers l'utilisation d'indices de diversité fonctionnelle calculés à partir de matrices de traits fonctionnels qui ont pour objectifs de décrire l'occupation de l'espace multidimensionnel fonctionnel, c'est à dire l'espace crée par l'ensemble des traits par les espèces qui composent une communauté, qui a autant de dimensions que de traits. La multiplication récente du nombre d'indices (voir par exemple Mouillot et al., 2013) rend complexe l'interprétation des résultats acquis et pose plusieurs questions sur le choix des indices à sélectionner et sur leur degré de redondance (Mouchet et al., 2010). Un certain nombre d'études suggèrent néanmoins de prendre en compte au minimum trois aspects de la diversité fonctionnelle: la richesse, la régularité et la divergence (Mason et al., 2005; Villéger et al., 2008; Maire et al., 2015) dont la signification est reportée sur la Figure 6. Par ailleurs, Maire et al. (2015) suggèrent que l'entropie quadratique de Rao représente un mix entre la richesse fonctionnelle et la divergence fonctionnelle.

Dans le cadre de cette thèse, cinq indices différents de diversité fonctionnelle ont été sélectionnés et sont présentés dans le Tableau 2. Par ailleurs, les valeurs moyennes des traits pondérés de la communauté (« Community-Weighted Mean trait value », CWM) ont été calculés afin d'identifier les traits dominants d'une communauté et leur évolution temporelle.

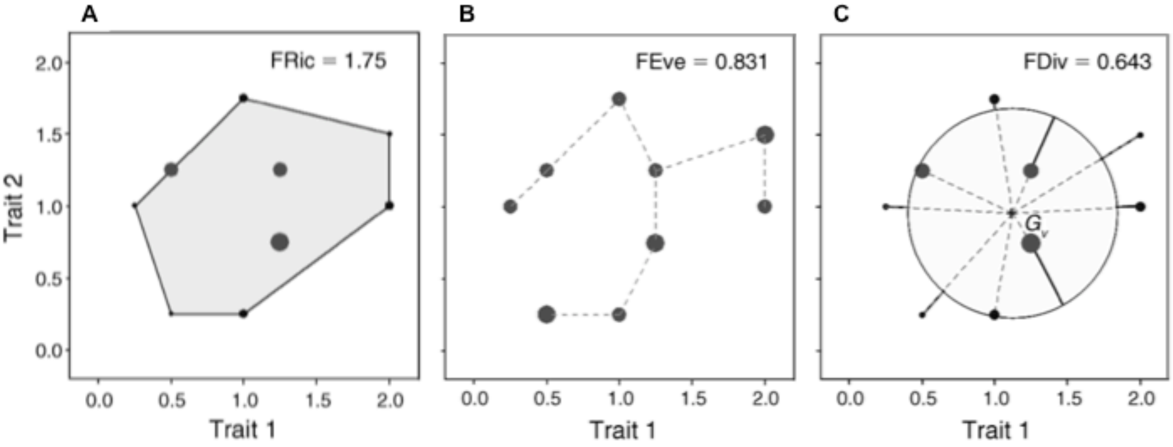


**Figure 6:** Représentation graphique de trois indices de diversité fonctionnelle dans l'espace multidimensionnel fonctionnel (FRic, FEve, FDiv). Par souci de simplification, deux traits et neuf espèces sont représentés. (A) Les limites de l'espace fonctionnel sont représentées par une ligne noire, les espèces sont représentées par des points noirs, leurs diamètres étant proportionnels à leurs abondances, et le volume de l'espace fonctionnel est coloré en gris. La richesse fonctionnelle (FRic) correspond à ce volume. (B) Arbre couvrant de poids minimal reliant les points. La régularité fonctionnelle (FEve) mesure la régularité de la répartition des points (espèces) le long de l'arbre et la régularité de leurs abondances. (C) Position du centre de gravité des sommets de l'espace fonctionnel (Gv). La divergence fonctionnelle (FDiv) représente la déviation par rapport au centre de gravité de l'espace fonctionnel (d'après Villéger et al., 2008).

**Tableau 2:** Indices de diversité fonctionnelle utilisés dans cette étude.

| **Indices** | **Abréviation** | **Mesure** | **Signification écologique** |
|---|---|---|---|
| Richesse fonctionnelle (Villéger et al., 2008) | FRic | Volume de l'espace fonctionnel. Ne dépend pas des abondances des espèces. | Une faible valeur indique que les espèces présentent peu de modalités de traits. |
| Régularité fonctionnelle (Villéger et al., 2008) | FEve | Régularité de la distribution des espèces dans l'espace fonctionnel à partir d'un arbre couvrant de poids minimal en prenant en compte à la fois la régularité des distances entre les espèces et la régularité de la distribution des abondances relatives des espèces. | Une faible valeur indique que la communauté est composée d'espèces regroupées dans des secteurs de l'espace fonctionnel (redondance et compétition), une valeur élevée indique une optimisation de l'espace fonctionnel (résilience). |
| Divergence fonctionnelle (Villéger et al., 2008) | FDiv | Écart des espèces à la distance moyenne au centre de gravité de l'espace fonctionnel pondéré par les abondances relatives des espèces. | Une faible valeur indique que les espèces dominantes se trouvent au centre de l'espace fonctionnel (espèces généralistes), une valeur élevée indique que les espèces dominantes se trouvent à la périphérie de l'espace fonctionnel (espèces spécialisées). |
| Dispersion fonctionnelle (Laliberté & Legendre, 2010) | FDis | Distance moyenne des espèces individuelles par rapport au centroïde de toutes les espèces de la communauté pondérée par les abondances relatives. | Une faible valeur indique une uniformisation dans les modalités de traits, une valeur élevée indique la présence d'espèces spécialisées. |
| Entropie quadratique de Rao (Botta-Dukát, 2005) | RaoQ | Somme des distances par paire d'espèces pondérée par les abondances relatives. | Une faible valeur indique une uniformisation dans les modalités de traits, une valeur élevée indique que les espèces diffèrent dans leurs traits. |

Des analyses multivariées permettent également de décrire la variabilité spatiale ou temporelle de la structure fonctionnelle des communautés benthiques (Bremner et al., 2006 ; Beauchard et al., 2017). Il peut s'agir de méthodes d'ordination comparables à celles appliquées dans l'étude des changements de structure taxonomique des communautés telles que certaines méthodes d'ordination (e.g. Cadrage multidimensionnel, nMDS ; Analyse en Composantes Principales, ACP) ou de méthodes spécifiquement dédiées à l'analyse des traits fonctionnels telle que l'Analyse des Correspondances Floue (« Fuzzy Correspondence Analysis », FCA) dans le cas de variables catégorielles (Chevenet et al., 1994).

## 4. La mesure de la diversité trophique

Des indices permettant de caractériser quantitativement différentes caractéristiques de la structure d’un réseau trophique dans l’espace isotopique $\delta^{13}C$-$\delta^{15}N$ ont été développés initialement par Layman et al. (2007). Les premiers indices rendent comptent de l’occupation de l’espace isotopique par les différentes espèces présentes au sein d’une communauté et incluent: (1) l’étendue des valeurs de $\delta^{13}C$ qui traduit la diversité des sources de nourriture (CR) ; (2) l’étendue des valeurs de $\delta^{15}N$ qui renseigne sur la longueur des chaînes trophiques et donc le nombre de niveaux trophiques (NR) ; (3) l’aire totale (TA) qui correspond à la surface de l’enveloppe convexe et mesure la richesse trophique ; (4) la distance moyenne au centroïde (CD) qui renseigne sur la diversité trophique moyenne des espèces qui composent une communauté. Le deux autres indices reflètent la position relative des espèces les unes par rapport aux autres dans l’espace isotopique et estiment le degré de redondance trophique. Il s’agit ainsi de la distance moyenne au plus proche voisin (MNND) et de l’écart-type de la distance au plus proche voisin (SDNND). L’aire totale TA étant particulièrement sensible au nombre d’espèces présentes dans une communauté et à la présence d’espèces rares possédant une signature isotopique originale, Jackson et al. (Jackson et al., 2011) ont proposé d’utiliser en lieu et place de cet indice une mesure de l’ellipse standard corrigée (SEAc). Si ces indices reflètent bien différentes propriétés d’un réseau trophique, ils accordent le même poids à l’ensemble des espèces présentes dans la communauté et ne prennent pas en considération le fait que les espèces sont inégalement réparties en termes d’abondance ou de biomasse au sein d’une communauté. Or, les espèces à forte biomasse sont supposées jouer un rôle fonctionnel plus important, en particulier en termes d’interactions trophiques ou de flux de matière et d’énergie dans l’écosystème. Afin de pallier à ces lacunes des indices proposés par Layman et al. (2007), des indices de diversité trophique s’inspirant des indices développés pour la mesure de la diversité fonctionnelle ont également été développés et permettent de prendre en considération l’importance relative des espèces en termes d’abondance ou de biomasse (Cucherousset & Villéger, 2015 ; Rigolet et al., 2015). La représentation graphique de certains de ces indices est reportée Figure 7. Ces indices permettent de quantifier différents aspects de la structure trophique à l’échelle d’une communauté, qu’il s’agisse de la richesse isotopique (IFr), de la régularité isotopique (IEve), de la divergence isotopique (IDiv) et de la dispersion isotopique (IDis) (Tableau 3).

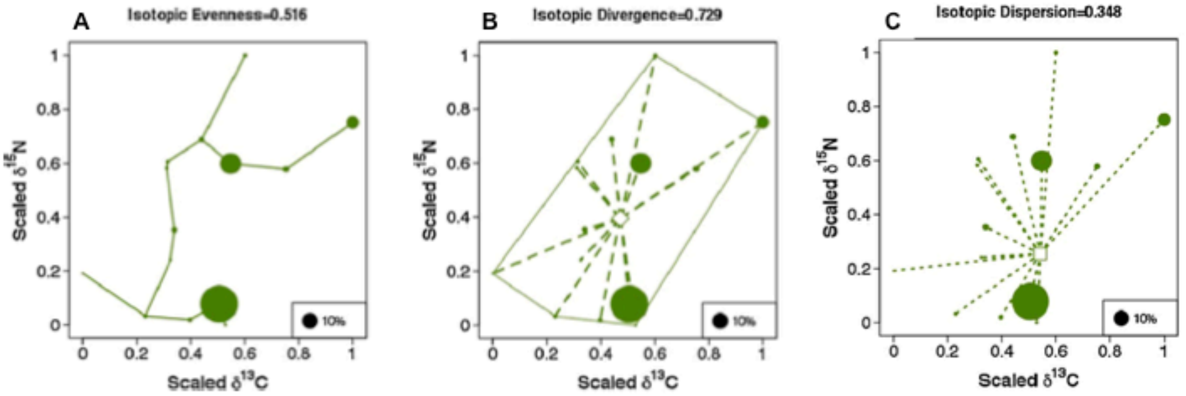


**Figure 7:** Représentation graphique de trois indices de diversité isotopique dans l'espace isotopique (IEve, IDiv, IDis). (A) La régularité isotopique (IEve) est la régularité des points (position et importance) le long de l'arbre le plus court reliant tous les points (dendrogramme vert). (B) La divergence isotopique (IDiv) mesure la distribution de l'importance des organismes à l'intérieur de l'enveloppe convexe (polygone vert) et est calculée en utilisant les distances entre les points et le centre de gravité des sommets de l'enveloppe convexe (lignes pointillées). (C) La dispersion isotopique (IDis) est la distance moyenne pondérée au centre de gravité de tous les points (carré vert) (d'après Cucherousset & Villéger, 2015).

**Tableau 3:** Indices de diversité trophique pondérés par les abondances ou les biomasses utilisés dans cette étude.

| **Indices** | **Abréviation** | **Mesure** | **Signification écologique** |
|---|---|---|---|
| Surface de l'enveloppe convexe (Layman et al., 2007) | TA | Volume de l'espace isotopique (richesse isotopique). | Une faible valeur indique que les espèces présentent peu de différence dans leur régime trophique, impliquant un faible degré d'utilisation des ressources trophiques disponibles dans le réseau qui possède alors une faible capacité à amortir les fluctuations environnementales. |
| Zone d'ellipse standard corrigée (Jackson et al., 2011) | SEAc | Mesure de la richesse isotopique. | Similaire à TA. |
| Surface de l'enveloppe convexe pondérée par ls biomasses (Rigolet et al., 2015) | $\text{Hull}_{\text{biom}}$ | Forme modifiée de TA pondérée par les biomasses relatives des espèces. | Similaire à TA. |
| Régularité isotopique (Cucherousset & Villéger, 2015; Rigolet et al., 2015) | IEve | Régularité de la distribution des biomasses dans l'espace isotopique à partir d'un arbre couvrant de poids minimal en prenant en compte à la fois la régularité des distances entre les espèces et la régularité de la distribution des poids relatif des espèces. | Une faible valeur indique que la communauté est composée d'espèces regroupées dans des secteurs de l'espace isotopique, impliquant une redondance trophique et une compétition pour les ressources. Une valeur élevée traduit une meilleure utilisation des ressources grâce à une complémentarité entre les espèces. |

| Indices | Abréviation | Mesure | Signification écologique |
|---|---|---|---|
| Distance moyenne au plus proche voisin (Layman et al., 2007) | MNND | Mesure le degré d'uniformité de la distribution des espèces au regard de leur plus proche voisin et fournit ainsi une mesure indirecte de la régularité isotopique. | Similaire à IEve. |
| Ecart-type de la distance moyenne au plus proche voisin (Layman et al., 2007) | SDNND | Mesure indirecte de la régularité isotopique. | Similaire à IEve. |
| Divergence isotopique (Cucherousset & Villéger, 2015; Rigolet et al., 2015) | IDiv | Écart des espèces à la distance moyenne au centre de gravité de l'enveloppe convexe pondéré par les biomasses des espèces. | Une valeur élevée indique que les espèces dominantes se trouvent à la périphérie de l'espace isotopique ce qui traduit une plus forte spécialisation trophique et une plus grande différentiation des niches isotopiques spécifiques au sein de la communauté. |
| Distance moyenne au centroïde (Layman et al., 2007) | CD | Distance moyenne de chaque espèce au centre de gravité du nuage de points dans l'espace isotopique $\delta^{13}C$ et $\delta^{15}N$, mesure de divergence isotopique. | Similaire à IDiv. |
| Dispersion isotopique (Cucherousset & Villéger, 2015; Rigolet et al., 2015) | IDis | Distance moyenne pondérée au centre de gravité pondéré par les biomasses des espèces. | Une valeur élevée indique que la plupart des espèces sont éloignées du centre de gravité de l'espace isotopique, une faible valeur indique une simplification du réseau trophique. |
| Similarité isotopique (Cucherousset & Villéger, 2015) | ISim | Rapport entre la surface de l'espace isotopique occupé conjointement par deux groupes d'espèces et la surface totale de l'espace isotopique occupée par les deux groupes d'espèces. | Une valeur élevée indique que les deux groupes d'espèces remplissent le même espace isotopique. |
| Emboîtement isotopique (Cucherousset & Villéger, 2015) | INess | Rapport entre la surface de l'espace isotopique occupé conjointement par deux groupes d'espèces et la surface minimale occupée par l'un des deux groupes d'espèces. | Maximal lorsque le groupe ayant la plus faible richesse isotopique remplit un sous-ensemble de l'espace isotopique occupé par le groupe ayant la plus grande richesse isotopique. |

# 5. Cadre de la thèse

## 5.1. La zone d'étude

La Manche représente l'espace maritime entre la Grande Bretagne au Nord et la France au Sud et constitue une zone de transition entre le système océanique atlantique chaud et tempéré et les systèmes continentaux boréaux de la mer du Nord et de la mer Baltique de l'Europe du Nord (Dauvin, 2012). De par sa situation géographique, elle est le siège de nombreuses activités humaines et donc soumise à d'intenses pressions anthropiques: surexploitation des ressources marines, eutrophisation, contamination par des polluants, urbanisation côtière, espèces invasives, etc. L'augmentation de ces activités dans les dernières décennies a naturellement conduit à l'augmentation du nombre de suivis, notamment benthiques, et d'études sur le statut de la diversité marine en Manche (Foveau et al., 2008 ; Hinz et al., 2011 ; Metcalfe et al., 2013). La Manche est divisée en deux bassins (Cabioch, 1968) (Figure 8): le bassin occidental (WBEC) et le bassin oriental (EBEC). Le bassin occidental est caractérisé par l'influence de l'océan Atlantique, une profondeur moyenne de 80 m et des eaux claires (Dauvin, 2012). Le bassin oriental est caractérisé par l'influence de l'estuaire de la Seine qui crée une zone dessalée proche de la côte appelée le « Fleuve côtier » (Dauvin, 2008) et une profondeur moyenne moins importante de 50 m. Ce bassin est plus impacté par les activités humaines que le bassin occidental du fait de la présence de ports importants et de l'estuaire de la Seine et de l'accumulation d'activités traditionnelles telles que la pêche, la navigation et l'émergence d'activités nouvelles telles que l'extraction ou l'installation de parcs éoliens (Dauvin, 2015).

Dans le cadre de cette thèse, deux jeux de données provenant de ces deux bassins ont été utilisés. Ces deux jeux de données sont contrastés de par leur provenance géographique, les pressions anthropiques qui les caractérisent, le type de suivi mis en place pour les obtenir, les conditions environnementales ou encore les espèces caractéristiques présentes.

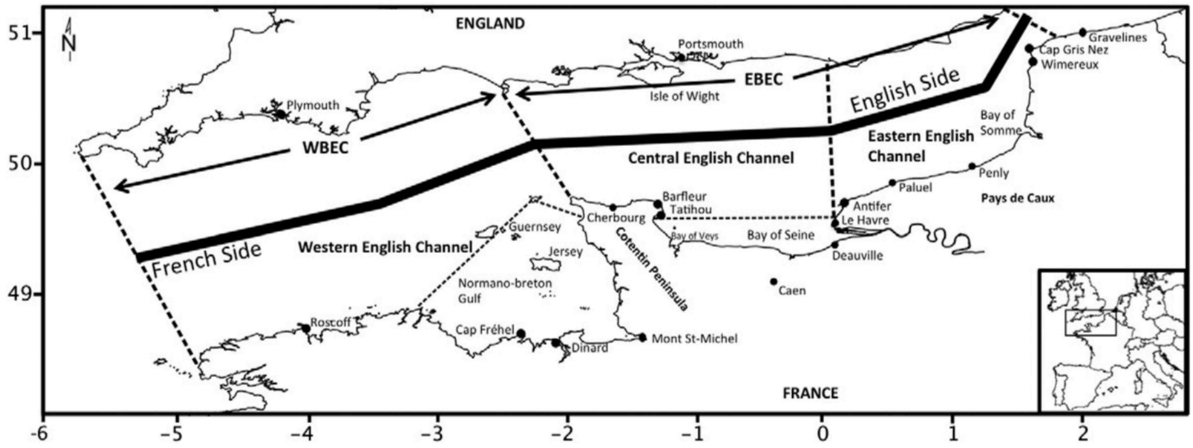


**Figure 8**: Carte de la Manche avec les deux bassins représentés: WBEC, bassin occidental ; EBEC, bassin oriental. Localisation de la Baie de Seine et de la baie de Morlaix proche de Roscoff (Dauvin, 2015).

Le premier jeu de données provenant du bassin oriental de la Manche est un suivi spatio-temporel à long-terme de la communauté benthique de sable fin plus ou moins envasés de la Baie de Seine orientale qui repose sur l'échantillonnage d'un réseau de 60 stations au cours de sept campagnes étalées sur une période de 28 ans, de 1988 à 2016 comprenant 221 espèces. La Baie de Seine est largement ouverte vers le Nord sur la partie centrale de la Manche avec une profondeur n'excédant pas 30 m. Elle comprend des zones sous mesure de protection Natura 2000. La Baie de Seine est caractérisée par des courants de marée semi-diurnes qui varient entre 1 et 3 nœuds et dont la vitesse diminue progressivement vers la partie orientale de la baie (Salomon and Breton, 1991). Ces courants, combinés à l'action des vagues, sont les principaux moteurs de la distribution des sédiments superficiels (Larsonneur et al., 1982 ; Marmin et al., 2016) et des communautés macrobenthiques (Cabioch & Gentil, 1975). La communauté de sable fin plus ou moins envasé à *Abra alba - Lagis koreni* est fortement structurée dans l'espace avec des noyaux d'abondance des espèces dominantes et des assemblages faunistiques distincts (Thiébaut et al., 1997 ; Baffreau et al., 2017 ; Dauvin et al., 2017). Thiébaut et al. (1997) ont démontré que la structure spatiale de la communauté résultait de la combinaison de plusieurs gradients environnementaux liés à la salinité, à la taille des particules sédimentaires et aux apports de matière organique. Cette communauté est largement impactée par la présence de l'estuaire de la Seine qui représente le plus grand estuaire macrotidal en Manche. La Baie de Seine orientale est exposée de longue date à de multiples perturbations anthropiques telles que le transport maritime, les travaux d'aménagement du port du Havre, la pêche, le dragage et le clapage de sédiment, la présence d'espèces non indigènes et de polluants terrestres relargués par la Seine (Dauvin, 2006). Au cours des dernières décennies, les plus importants changements environnementaux résultent de changement de la dynamique morphosédimentaire en relation avec les travaux d'aménagement portuaire (i.e. projet « Le Havre 2000 ») et de faibles débits de la Seine (Lesourd et al., 2001, 2016).

Le deuxième jeu de données provenant du bassin occidental de la Manche est un suivi stationnel à long-terme de la communauté de sable fin de la baie de Morlaix au site Pierre Noire (PN). Il repose sur l'échantillonnage d'une seule station deux fois par an (mars et octobre) sur une période de 40 ans, de 1977 à 2016 et comprend 250 espèces. Le site d'échantillonnage PN est une enclave de sables fins située à une profondeur de 17 m dans la partie Nord-Est de la Baie de Morlaix. Cette partie de la Manche occidentale étant caractérisée par de forts courants de marée, la colonne d'eau est homogène et ne présente pas de thermocline saisonnière. La communauté de sable fin est caractérisée par de fortes abondances d'Amphipodes du genre *Ampelisca*. À la différence de la communauté de sable fin de la Baie de Seine orientale, cette communauté n'est pas exposée à des pressions anthropiques chroniques fortes mais a été particulièrement impactée par le naufrage de l'Amoco Cadiz en 1978 au large de Portsall qui provoqua l'une des plus importantes marées noires (Dauvin, 1984). Des hydrocarbures piégés dans les sédiments de la baie de Morlaix ont été signalés seulement 2 semaines après le naufrage et ont été détectés jusqu'au printemps 1981 à des concentrations de 50 ppm (Cabioch et al., 1980). Cette perturbation ponctuelle et locale a eu des répercussions majeures sur la dynamique de la communauté avec une disparition quasi-totale des populations dominantes d'*Ampelisca* et un temps de récupération qui a excédé 10 ans (Dauvin, 1998 ; Poggiale & Dauvin, 2001).

## 5.2. La sélection des traits

Dans le cadre des mesures de la diversité fonctionnelle réalisées au cours du présent travail, huit traits fonctionnels ont été choisis pour leurs liens avec trois fonctions écologiques principales des communautés des fonds meubles, i.e. le cycle des nutriments, la production secondaire et la résistance/résilience, et leur relations avec des services écosystémiques identifiables. Ces traits avaient par ailleurs le mérite de pouvoir être renseignés à partir de la consultation de différentes bases de données et d'un examen approfondi de la littérature. Les traits choisis sont des traits qualitatifs donc difficiles à quantifier. Pour chaque trait un certain nombre de modalités a ainsi été défini afin de pouvoir quantifier parmi les espèces la proportion des traits fonctionnels choisis (Tableau 4). Les modalités représentent les différentes déclinaisons d'un trait que l'on peut retrouver parmi les espèces. Pour chaque espèce, l'appartenance aux différentes modalités est ensuite codée en codage flou avec un chiffre compris entre 0 et 3, afin de prendre en compte la variabilité intra-spécifique d'un trait. L'attribut 0 étant l'absence d'affinité d'une espèce pour une modalité et l'attribut 3 étant l'affinité maximale d'une espèce pour une modalité (Chevenet et al., 1994). Pour une espèce donnée et un trait donné la somme des affinités pour les modalités doit être égale à 3 (1-1-1 ou 1-2 ou 3 par exemple). Afin de donner le même poids à toutes les espèces et à tous les traits, le résultat des affinités pour les modalités est ensuite transformé en pourcentage (Chevenet et al., 1994).

**Tableau 4**: Présentation des huit traits fonctionnels utilisés dans ce travail, de leurs différentes modalités et de la justification du choix des traits (d'après Törnroos & Bonsdorff, 2012 ; van der Linden et al., 2016).

| **Trait fonctionnel** | **Modalités** | **Justification du choix du trait** |
|---|---|---|
| Taille maximale (cm) | Très petit (< 1 cm)<br>Petit (1-2 cm)<br>Petit-Moyen (3-10 cm)<br>Moyen (11-20 cm)<br>Moyen-Grand (> 20 cm) | Les espèces de petite taille peuvent caractériser des environnements très instables résultant de perturbations environnementales et/ou anthropiques imposées aux organismes (Mouillot et al., 2006). |
| Durée de vie | Court (< 2 ans)<br>Moyen (2-5 ans)<br>Long (> 5 ans) | La richesse et l'abondance des espèces à courte durée de vie augmentent à mesure que les perturbations s'intensifient (Pearson & Rosenberg, 1978). |
| Mode d'alimentation | Filtreur<br>Déposivore de surface<br>Déposivore de sub-surface<br>Prédateur - Charognard<br>Omnivore<br>Brouteur | Les modes d'alimentation déterminent les capacités de l'espèce à utiliser/ tolérer différentes conditions hydrodynamiques, le passage d'une dominance de filtreurs à une dominance de déposivores indiquant une réduction potentielle des conditions hydrodynamiques. Les brouteurs sont plus abondants dans les zones où les producteurs primaires sont nombreux, généralement dans les zones où la profondeur et l'hydrodynamisme sont faibles. Les prédateurs et les charognards seront associés à des zones à forte disponibilité de proies, et non spécifiquement à des perturbations hydrodynamiques (Rosenberg, 1995; Dolbeth et al., 2009). |
| Mode de reproduction | Sexuel<br>Asexuel | Le mode de reproduction peut servir d'indicateur pour le renouvellement d'une espèce. |
| Type de développement | Direct<br>Larve planctotrophique<br>Larve lecithotrophique | Le type de développement peut servir d'indicateur pour la réussite du recrutement. |

| Trait fonctionnel | Modalités | Justification du choix du trait |
|---|---|---|
| Mode de déplacement | Fouisseur<br>Rampeur<br>Nageur<br>Marcheur<br>Sessile<br>Constructeur de tube | Les espèces qui vivent dans des tubes ou enfouies sont potentiellement moins vulnérables aux fortes perturbations hydrodynamiques, aux conditions anoxiques et à la pollution de l'eau que les espèces se déplaçant librement, car ils peuvent se cacher dans leurs tubes ou leurs terriers fixes (Reise, 2002). Les espèces très mobiles peuvent plus facilement fuir une perturbation ponctuelle. |
| Bioturbation | Épifaune/ Pas d'effet<br>Transformateur superficiel<br>Biodiffuseur<br>Transporteur vers le haut<br>Transporteur vers le bas<br>Régénerateur | La bioturbation est un médiateur clé de nombreux processus géochimiques importants dans les systèmes marins (Queirós et al., 2013). |
| Tolérance à la perturbation (AMBI) | Sensible<br>Indifférent<br>Tolérant<br>Opportuniste de second ordre<br>Opportuniste de premier ordre | Permet de quantifier la résistance d'une espèce à un enrichissement organique. |

## 6. Objectifs de la thèse

En s'appuyant sur deux jeux de données distincts décrivant la dynamique à long terme des communautés de sédiments de sables fins de la Manche, en Baie de Seine orientale et en Baie de Morlaix (site Pierre Noire), les objectifs généraux de la thèse sont d'analyser la variabilité spatio-temporelle des différentes facettes de la biodiversité (diversité spécifique, diversité fonctionnelle et diversité isotopique) et de mettre en évidence leur complémentarité pour mieux décrire l'évolution à long terme des communautés benthiques côtières en réponse à différentes pressions anthropiques.

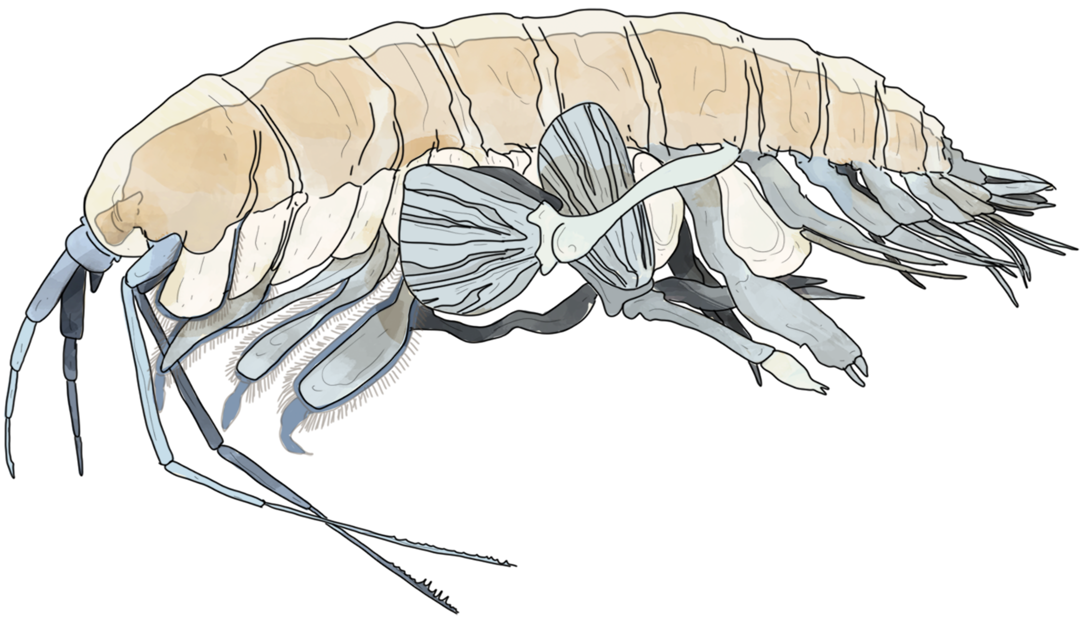
Le chapitre 1 décrit l'évolution à long terme de la diversité et de la structure de la communauté des sables fins de Pierre Noire en Baie de Morlaix en termes de composition spécifique et de composition en traits biologiques. Grâce à un suivi de 40 ans, il a permis de mettre en évidence deux changements de régime majeurs de nature différente, associés d'une part à la marée noire causée par les hydrocarbures de l'Amoco Cadiz en 1978, et d'autre part à une modification brutale de la communauté en réponse à des changements progressifs des conditions environnementales. Il montre des résultats très similaires entre diversité spécifique et diversité fonctionnelle mais souligne l'intérêt de l'approche par les traits pour mieux décrire les conséquences des changements de structure sur le fonctionnement de l'écosystème. Ce chapitre a donné lieu à la rédaction d'un article dont je suis second auteur et qui devrait être prochainement soumis à la revue Marine Pollution Bulletin.

Le chapitre 2 décrit l'évolution de l'organisation spatio-temporelle de la diversité spécifique et fonctionnelle de la communauté benthique des sables fins de la Baie de Seine orientale. S'appuyant sur une stratégie d'échantillonnage originale qui comporte un réseau de 60 stations échantillonnées tous les 3 ou 5 ans, nous nous sommes attachés dans ce chapitre à montrer comment différentes métriques décrivant la stabilité/variabilité d'une communauté (composition faunistique, abondance des espèces, organisation spatiale) variaient en fonction de l'échelle d'observation. Ce résultat nous a ainsi amené à proposer une nouvelle stratégie d'échantillonnage qui prenne en considération cette hétérogénéité spatiale des réponses de la communauté. Ce chapitre nous a aussi amené à souligner la stabilité relative remarquable de la communauté pourtant exposée à de nombreuses pressions. Il fait l'objet d'un article en premier auteur publié dans la revue Marine Environmental Research. Il est complété d'une section qui décrit en parallèle aux changements de diversité et de structure spécifique les changements de diversité fonctionnelle.

Alors que les dernières années ont été marquées par un intérêt croissant pour les mesures de la diversité fonctionnelle, cette mesure soulève de nombreuses questions méthodologiques sur le nombre de traits à utiliser, les traits à sélectionner, etc…. Nos travaux menés en Baie de Morlaix et en Baie de Seine orientale ont montré un fort niveau de concordance entre les résultats obtenus sur les mesures de la diversité spécifique et ceux obtenus sur les mesures de la diversité fonctionnelle, soulevant des interrogations sur la plus-value de cette approche au regard du caractère très chronophage de l'obtention des traits propres à chaque espèce. Dans des communautés dominées par un petit nombre d'espèces, cette forte concordance est à mettre en relation avec l'utilisation des densités pour pondérer le poids relatif des espèces. Dans le chapitre 3, nous nous sommes donc intéressés à l'impact qu'avait le choix de la méthode de pondération du poids des espèces (densités *vs* biomasses) sur la description de la variabilité spatiale (Baie de Seine orientale) ou temporelle (Baie de Morlaix) de la diversité fonctionnelle. Cette réflexion méthodologique se présente sous la forme d'une ébauche de note à publier dans les prochains mois dans le but d'améliorer le cadre méthodologique mis en œuvre dans l'analyse de la diversité fonctionnelle en écologie benthique.

Enfin, sur l'exemple de la Baie de Morlaix, le chapitre 4 permet d'aborder de manière exploratoire une autre approche fonctionnelle basée sur les traits isotopiques. Cette partie décrit en parallèle les changements inter-annuels de la structure de la communauté et de son réseau trophique grâce à l'utilisation d'un groupe de 13 indices de diversité isotopique. Ce chapitre nous a amené à considérer la pertinence et les limites de tels indices au regard d'une approche plus traditionnelle basée sur la mesure des propriétés structurelles des communautés.

# Chapter I : Long-term changes in the taxonomic and trait-based biodiversity and community structure of the macrobenthos in the Bay of Morlaix (western English Channel) over the last 40 years



# Chapitre I

Article en préparation en vue d'une soumission prochaine à Marine Pollution Bulletin

Éric Thiébaut[1], Lise Bacouillard[1], Jean-Claude Dauvin[2], Franck Gentil[1], Céline Houbin[3], Caroline Broudin[3], Paul J. S. Somerfield[4]

[1] Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR7144, Adaptation et Diversité en Milieu Marin, Place Georges Teissier, F-29680 Roscoff, France

[2] Normandie Université, UNICAEN, UMR6143, Laboratoire Morphodynamique Continentale et Côtière, 24 rue de Tilleuls, F-14000 Caen, France

[3] Sorbonne Université, CNRS, Station Biologique de Roscoff, FR2424, Place Georges Teissier, F-29680 Roscoff, France

[4] Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, United Kingdom

## ABSTRACT

Long-term series are an essential resource to assess temporal changes in biodiversity and disentangle the relative role of external and internal factors on community dynamics. In the Bay of Morlaix, benthic samples were collected at one station in a sandy community over a forty-year period (1977-2016) using the same sampling strategy. During this period, the community was exposed to a major oil spill but also to gradual changes in environmental conditions. Q-mode and r-mode analyses were performed to describe the trajectory of the community and identify taxa contributing to variation in faunal composition among years. A type 3 Similarities Profiles analysis was carried out to assess which species groups covariate coherently. In parallel, several indices based on the functional traits of the benthic macrofauna as well as multivariate analysis on the trait composition were computed. Over time, the long-term dynamics of the benthic community was marked by two major regime shifts of comparable intensity but of different origin. The first abrupt change was due to a major oil spill in 1978 and was followed by a low recovery period of about 12-15 years. The second regime shift was supposed to result from non-linear responses to slow environmental changes. Long-term patterns of taxonomic and trait-based variability of the benthic community structure in the bay of Morlaix were congruent, suggesting that changes in trait composition were principally linked to changes in the relative abundances of the different dominant species and that no process of substitution of one species by another within the same functional group occurred. The two regime shifts were characterized by changes in the relative proportions of suspension feeders and surface deposit-feeders, tube-dwellers and burrowers, and superficial modifiers and biodiffusors/conveyors with impact on the bentho-pelagic coupling and the sediment biogeochemistry. Our results highlight that benthic community may exhibit highly complex dynamics which cannot be easily assigned to one cause of change, raising the question of a reference status for ecosystem management.

## Keywords

Oil spill; Long-term time-series; English Channel; Species diversity; Functional diversity; Biological regime shifts

## I.1. Introduction

Marine coastal ecosystems currently experience multiple and increasing human activities including mainly overfishing, pollution and eutrophication, habitat losses and degradation, climate change and introduction of non-indigenous species (Halpern et al., 2015). The direct and indirect effects of these activities can greatly alter species composition, community structure and ecosystem functioning (Worm et al., 2006). In this context, multidecadal time-series are an essential tool to describe inter-annual and inter-decadal variability of marine ecosystems and to improve our knowledge on their complex dynamics, in particular to disentangle the effects of natural environmental drivers from the effects of anthropogenic disturbances (Magurran et al., 2010; Giron-Nava et al., 2017; Kröncke et al., 2019). The relative effects of these different factors may vary with time as it was reported from the Dove time-series in the North Sea where benthic communities responded to complex interactions between regional climate change, local environmental conditions, primary production and benthic-pelagic coupling, and intrinsic biotic feedbacks (Frid et al., 2009).

Among long-term changes of marine ecosystems, abrupt and persistent shifts in ecosystem structure and function are more and more documented in diverse marine ecosystems including their benthic components (deYoung et al., 2008). Although the terminology could vary among authors (e.g. regime shift, phase transition, abrupt community shift, biological shift), an ecological regime shift can be defined pragmatically as a substantial, dramatic and abrupt changes in the community structure that are persistent in time, encompassing multiple variables, and including key-structural species – independently from the mechanisms causing them (deYoung et al., 2004; Möllmann et al., 2015). On the other hand, regime shifts should occur on large geographic scales and encompass multiple trophic levels (deYoung et al., 2004). A regime does not represent a stable state but is characterized by fluctuations of the ecosystem around a given state meaning that a regime shift can be detected as an increasing rate of change in the biological variables. Although a regime shift can be the result of a sudden large external impact such as a massive accidental pollution or a storm, minor changes in environmental conditions (e.g. temperature in relation to climate change, nutrient concentrations in relation to eutrophication) can cause abrupt and catastrophic changes if a critical threshold is reached, the ecosystem moving from one dynamic regime, also called attractor, to another one (Scheffer & Carpenter, 2003; Conversi et al., 2015). A marine regime shift generally arises from multiple external drivers including anthropogenic ones (e.g. climate change, overexploitation) which interact with internal mechanisms (e.g. trophic interactions) (Conversi et al., 2015). On the other hand, Beaugrand (2015) showed that interactions between climate-induced temperature changes and the thermal niche of each species composing a community could explain regime shifts reported for copepods communities at the end of the 80s and 90s in the North Sea.

To understand to what extent coastal macrobenthic communities respond to short- and long- term changes in environmental drivers, traditional approaches have often been based on structural properties such as the number, identity, relative abundance and biomass of species (Pearson and Rosenberg, 1978; Gray et al., 1990; Warwick et al., 2002). These approaches have implicitly rested upon the insurance hypothesis, which assumes that increasing species biodiversity insures ecosystems against declines in their functioning caused by environmental fluctuations (Loreau, 2001). According to this hypothesis, species-rich systems should contain enough species to compensate for the decrease in the contribution of other species to ecosystem processes although the exact nature of the relationship between species diversity and ecosystem functions remains intensely debated (Stachowicz et al., 2007; Cardinale et al., 2012). On the other hand, these taxonomic approaches assume that changes in species composition and abundance reflect changes in ecosystem functioning although they did not address explicitly the role of each species on ecological processes. More recently, different authors proposed a trait-based approach which is based on the distribution of species functional traits strongly linked to multiple ecosystem processes (Díaz & Cabido, 2001; Lavorel & Garnier, 2002a). By measuring explicitly the functional diversity, i.e. the number, the type and the distribution of functional traits in a given ecosystem (Petchey & Gaston, 2006), this approach, also called biological trait analysis, assesses more directly the effects of natural and human-induced changes on the ecosystem functioning (Beauchard et al., 2017). In this context, a functional trait is any morphological, physiological or behavioural feature measurable at the individual level which impacts its fitness indirectly via its effect on growth, reproduction and survival (Violle et al., 2007). The use of biological traits analysis has grown exponentially since the early 2000s in marine environment, and especially for marine benthic communities (Beauchard et al., 2017). It has been applied to describe the distribution of benthic assemblages in terms of trait composition (Bremner et al., 2003; Hewitt et al., 2008), to analyse basic relationships between traits and habitats (Bremner et al., 2006b; Törnroos & Bonsdorff, 2012; Rigolet et al., 2014), to investigate the effects of environmental disturbances such as pollution (Paganelli et al., 2012), trawling and dredging (Tillin et al., 2006; Bolam, 2014; Neumann et al., 2016) and aggregate extraction (Barrio Froján et al., 2011), or to analyse the long-term effects of climate change and regime shift (Neumann & Kröncke, 2011;

Clare et al., 2015). It has also been used for conservation and management purpose including the assessment of ecosystem health (Bremner, 2008; Dolbeth et al., 2013).

In the western English Channel, the fine sand *Abra alba* community of the Bay of Morlaix is monitored since 1977 using the same methodology to understand the long-term changes in biodiversity of coastal benthic communities in response to natural and anthropogenic variability in environmental conditions (Dauvin, 1998). This community is remarkable at the scale of the Northwest European continental shelf by its very dense populations of amphipods from the genus *Ampelisca* with densities exceeding 40,000 ind.m$^{-2}$ (Dauvin, 1987; Poggiale and Dauvin, 2001). It was strongly altered by the spill of 223,000 tonnes of hydrocarbons from the Amoco Cadiz wreck in March 1978. The pollution resulted in the almost disappearance of the dominant *Ampelisca* populations and only a single species (i.e. *Ampelisca sarsi*) persisted but with very low densities (Dauvin, 1987). Because of the specific biological features of these amphipods (i.e. lack of pelagic larvae, low fecundity, isolated populations), recovery of the community took more than 15 years with the return to overall abundances almost equivalent to those preceding the oil spill from the middle of the 1990's (Dauvin, 1998). This period was also marked by the episodic proliferation of opportunistic polychaetes such as *Pseudopolydora pulchra* in 1982 and by the long-term effects of climate variability on the community dynamics (Ibanez et al., 1993; Fromentin et al., 1996, 1997; Dauvin, 1998). Beyond the rapid and abrupt change in the community structure due to the Amoco Cadiz oil spill, and its progressive recovery to the initial state, Fromentin et al. (1997) suggested that climatic events such as alternation of mild and cold winters with a cycle of seven-eight years could modify the relative abundance of species. Over a 15-year period, Dauvin et al. (1993) also reported decadal variations in *Abra alba* densities with maximal values in 1979-1980 and 1990-1991. However, these effects of regional climatic variables on the community structure were low in comparison with observations performed during the same period in the southern North Sea (Fromentin et al., 1997). Dauvin (1998) argued that the slow recovery of the community to its initial state indicated that an *Ampelisca*-dominated assemblage corresponded to the stable state of this community and that its stability could be related to the lower variability in the environmental conditions in the entrance of the western English Channel.

In the context of the Pierre Noire time series which is among the longest benthic time series in Europe, the aims of the present study were: (1) to analyse the long-term changes in the community structure over a 40-year period beyond the dramatic effects of the Amoco Cadiz oil spill to address the question of the long-term stability of this community; and (2) compare changes in taxonomic and functional diversity of the benthic community to assess the responses of these two different facets of diversity and the consequences of major changes in the community structure on ecosystem functioning.

## I.2. Materials and methods

### I.2.1. Study area

The sampling site Pierre Noire (PN) is located in the Bay of Morlaix along the French coasts of the Western English Channel (48°42,50’N; 3°51,96’W) at a depth of 17 m (Figure 9). It consists of fine sand sediment with a median particle size ranging between 150 and 190 µm. Because of strong tidal currents in this part of the western English Channel, the water column is homogeneous with no seasonal thermocline. The seasonal variations in hydrological parameters were low. Near-bottom water temperature varied between 8.0-11.0°C in March and 15.2-17.1 °C in September while salinity varied from 34.2-34.9 in spring to 35.1-35.6 in summer/autumn. Following the Amoco Cadiz oil spill in March 1978, hydrocarbons trapped in subtidal sediments of the Bay of Morlaix were reported just two weeks after the wreck (Cabioch et al., 1978). At Pierre Noire, hydrocarbons concentrations in the sediment reached 200 ppm in the summers of 1978 and 1979 and did not exceed 50 ppm after the winter of 1981 (Dauvin, 1984). The Pierre Noire site is currently a reference station in the French monitoring programme of benthic macrofauna according to Water Framework Directive.

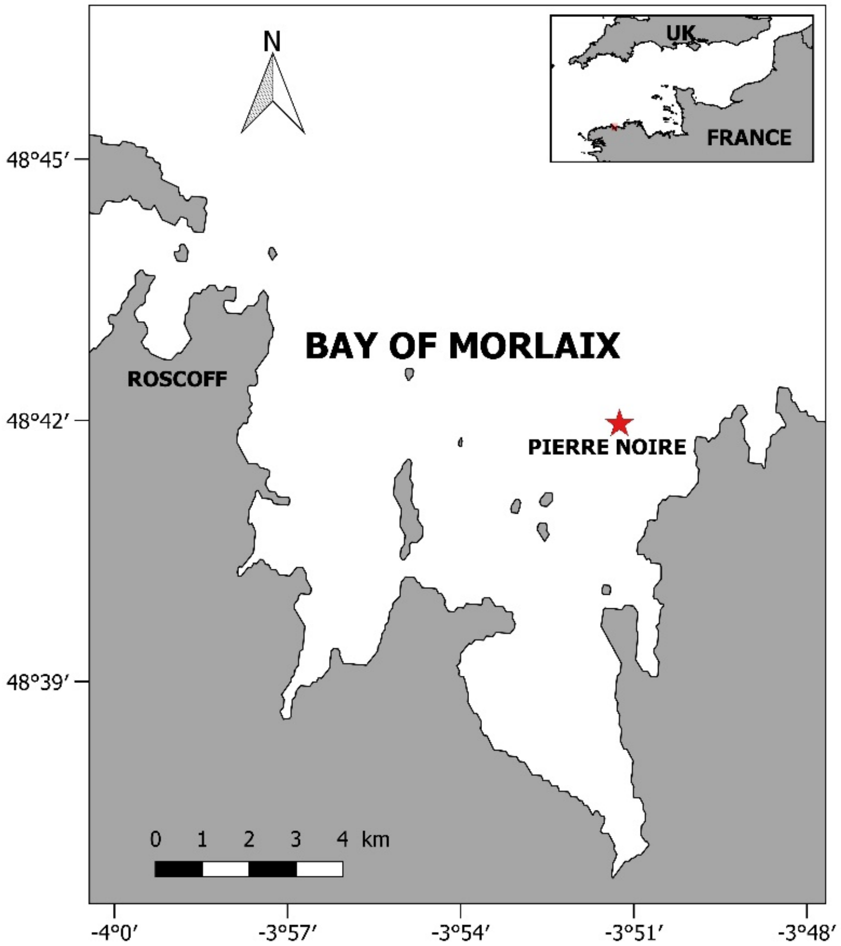


**Figure 9:** Location of the study area and the sampling station.

## I.2.2. Field sampling and laboratory analysis

To estimate species density and describe community structure, ten replicates samples using a Smith McIntyre grab were collected from 1977 to 2016 at two seasons, at the end of the winter (i.e. beginning of March), before the recruitment of most species, and at the end of summer (i.e. beginning of October), after the recruitment of most species. In 1977 and 1978, samples were collected in April. Samples were sieved on board through a 1 mm circular mesh and preserved in 10 % buffered formalin solution prior to later analysis. In the laboratory, organisms in the samples were sorted, counted and identified at the lowest taxonomic level, generally the species level. Species or taxa names were checked with the World Register of Marine Species (WORMS, http://www.marinespecies.org) on 16 July 2020. Although only three persons made species identification during the temporal survey, a peculiar attention was given to solve possible misidentifications and to take into account recent taxonomic revisions. In some cases, different species were merged at the genus or complex level. Data from replicate samples were pooled so that densities of the different taxa are expressed as number of individuals per $m^2$ to obtain a 'species by dates' matrix.

## I.2.3. Data analyses

### I.2.3.1. Macrofauna diversity and community structure

Macrofauna diversity at each sampling date was assessed using 'traditional' indices including the total abundance (N), the species richness, i.e. number of species per unit area (S), the Shannon-Weaver diversity index (H' using $\log_2$) and the Pielou's evenness (J'). The analysis of inter-annual changes in the community structure followed the statistical strategy proposed by Field et al. (1982) and combined an analysis of the relationships among samples, i.e. Q-mode analysis, and an analysis of patterns among variables, i.e. r-mode analysis. Year-to-year changes among samples were visualized from non-metric multidimensional scaling (n-MDS) plots based on Bray-Curtis similarity matrixes calculated from log-transformed abundances to decrease the contribution of the most abundant species. This analysis was performed separately on data collected in March and October. For the r-mode analysis, Similarity Profiles (SIMPROF) analyses of Type 2 and 3 were performed to address two different questions respectively (Somerfield & Clarke, 2013): (1) Are all species associated with each other? (2) Are some species coherently associated? Prior to conduct these analyses, some data pre-treatments were required. First, only species contributed to at least 2 % of total abundance in any one year were considered. Second, densities of the selected species were standardized, i.e. expressed as the percentage of the total abundances of each species in the complete dataset, to make values among species comparable. Third, a between-species resemblance matrix was built using the Index of Association (IA) which takes the value 100 when two species have exactly the same percentage abundances across the samples and the value 0 when they are found in completely different samples (Somerfield & Clarke, 2013).

To test the fact that all species are associated with each other in terms of standardized abundance through the time-series, a Type 2 SIMPROF test was used by randomizing species separately over all samples and by comparing the observed similarity profile with the profiles generated by randomization using the $\pi$ statistic. As the null hypothesis (i.e. no association among species) was rejected, species were then clustered using hierarchical agglomerative clustering and the different nodes were tested using a Type 3 SIMPROF test to identify groups of species which covariated coherently (Somerfield & Clarke, 2013). Changes in the relative abundances of the species within each group were plotted against time.

All analyses on macrofauna diversity and community structure were performed using PRIMER v7 (Clarke et al., 2014).

#### I.2.3.2. Biological trait analysis

To measure the changes in functional diversity of the fine sand community, eight relevant functional traits subdivided in 36 modalities which described adult morphology (i.e. maximum body size), life history (i.e. life span, reproductive mode and development type) and behaviour (i.e. feeding mode, movement type, sediment reworking type and tolerance to disturbance) were selected to reflect key ecosystem functions and processes (Tableau 5). Trait data were gathered from a variety of sources including publicly available databases such as the Biological Traits Information Catalogue (BIOTIC) developed by the Marine Life Information Network (http://www.marlin.ac.uk/biotc), Polytraits (http://polytraits.lifewatchgreece.eu) and the list of the AZTI Marine Biotic Index (AMBI) (http://ambi.azti.es), species identification guides (e.g. Hayward & Ryland, 2017), reviews on some traits like the sediment reworking type (Queirós et al., 2013), the reproduction (e.g. Rouse & Pleijel, 2006) or the feeding mode (Jumars et al., 2015), primary literature on species and expert knowledge. When data at the species level was missing, information was collected at the lowest taxonomic level, generally the genus or the family level. Each trait modality was scored using a fuzzy coding procedure on a 0 to 3 scale to include within species variability in trait expression (Chevenet et al., 1994). A score of ‘0’ indicates no affinity of a species to a trait modality and a score of ‘3’ indicates a high affinity to a trait modality. For a given trait, the sum of the scores of all modalities should be equal to 3. To give the same weight to each species and each functional trait in further analysis, affinity scores were standardized so that their sum for a given species and a given trait equals 1 (or 100%). Finally, the ‘species by traits’ matrix was combined with the ‘species by dates’ matrix to obtain a ‘traits by dates’ matrix.

**Tableau 5:** Functional traits and their modalities used to describe the long-term changes in the functional diversity of the Pierre Noire benthic community. The ecosystem functions and processes related to each trait are given according to Törnross & Bonsdorff (2012), Beauchard et al. (2017) and Degen et al. (2018). A code for each modality is given.

| **Functional trait** | **Trait modalities** | **Ecosystem functions and processes** |
|---|---|---|
| Maximum body size | Very small (< 1 cm) – A1<br>Small (1-2cm) – A2<br>Small-Medium (3-10 cm) – A3<br>Medium (11-20 cm) – A4<br>Medium-Large (> 20 cm) – A5 | Related to major physiological rates (e.g. oxygen demand, fecundity)<br>Secondary production<br>Nutrient cycling<br>Sensitivity to disturbance |
| Life span | Short (< 2 years) – B1<br>Medium (2-5 years) – B2<br>Long (> 5 years) – B3 | Reproductive success<br>Secondary production<br>Sensitivity to disturbance |
| Feeding mode | Filter-feeder – C1<br>Surface deposit-feeder – C2<br>Sub-surface deposit-feeder – C3<br>Predator – Scavenger – C4<br>Omnivore – C5<br>Grazer – C6 | Food acquisition<br>Benthic pelagic coupling |
| Reproductive mode | Sexual – D1<br>Asexual – D2 | Demographic resilience |
| Development type | Direct development – E1<br>Planktotrophic larva – E2<br>Lecithotrophic larva – E3 | Dispersal potential<br>Benthic pelagic coupling |
| Movement type | Burrower – F1<br>Crawler – F2<br>Swimmer – F3<br>Walker – F4<br>Sessile – F5<br>Tube dweller – F6 | Adult dispersal potential<br>Foraging mode<br>Benthic pelagic coupling<br>Nutrient cycling |
| Sediment reworking type | Epifauna/None – G1<br>Surficial modifiers – G2<br>Biodiffusors – G3<br>Upward conveyors – G4<br>Downward conveyors – G5<br>Regenerators – G6 | Benthic pelagic coupling<br>Sediment oxygenation<br>Nutrient cycling |
| Tolerance to disturbance (AMBI) | Sensitive – H1<br>Indifferent – H2<br>Tolerant – H3<br>Second-order opportunistic – H4<br>First-order opportunistic -H5 | Sensitivity to organic pollution |

A large number of functional diversity indices based on the distribution of species in the multidimensional functional space defined by traits has been developed during the last years (Villéger et al., 2008; Schleuter et al., 2010; Mouillot et al., 2013). Among these ones, we selected five different indices which cover several complementary facets of functional diversity. Functional richness (FRic) represents the amount of the functional space filled by the community and is independent of the species abundance (Villéger et al., 2008). Functional evenness (FEve) measures both the regularity of spacing between species and the evenness in the distribution of species abundance in the functional space (Villéger et al., 2008). A high functional evenness occurs when species and abundance are evenly distributed; this suggests an optimal use of resources and could result in a higher resilience. A low functional evenness suggests that the community is composed of clusters of species indicating some redundancy among species and competition. FEve is expected to decrease after a disturbance. Functional divergence (FDiv) measures how species abundance distribution is dispersed in the functional space (Villéger et al., 2008). FDiv is low when the most abundant species have functional traits that are closed to the centre of gravity of the functional space while FDiv is high when the most abundant species show extreme trait values, revealing a high degree of niche differentiation in the community. Functional dispersion (FDis) is the mean distance of species to the weighted centroid of all species in the functional space where weights correspond to the relative species abundance (Laliberté & Legendre, 2010). Rao's quadratic entropy (RaoQ) is a generalized form of the Simpson diversity index (and measures the average trait dissimilarity between two random individuals within the community (Leps et al., 2006). RaoQ is expected to be strongly correlated to FDis as both indices estimate the dispersion of species in trait space, weighted by their relative abundances. It reaches a maximum when species completely differ in their traits. All indices are expected to decrease after a disturbance (Mouillot et al., 2013; van der Linden et al., 2016). In addition, the community-weighted mean traits values (CWM) were calculated from the 'traits by dates' matrix. For each trait analysed separately, CWM values identify the dominant trait modalities in terms of relative abundances within the community and can be used to detect the trait responses to environmental changes and disturbance. The different indices were computed using the dbFD function of the FD package with R (Laliberté et al., 2014).

Finally, the 'traits by date' matrix was ordinated by means of a non-metric multidimensional scaling (n-MDS) based on a Bray-Curtis similarity matrix. As we would like to compare year-to-year changes among samples in terms of species composition and trait composition, the 'traits by date' matrix was calculated from $\log_{10}(x+1)$ transformed abundances of species.

# I.3. Results

## I.3.1. Long-term changes in local diversity

Species richness and total densities exhibited strong seasonal patterns with a minimum at the end of winter and a maximum at the end of summer (Figure 10). On the long-term, contrasted patterns were reported for the different indices. The species richness fluctuated largely from year to year, from 49 to 106 species in March and from 60 to 127 in October, with no clear long-term trend. The Amoco-Cadiz oil spill has a limited impact on species richness which decreased from a maximum of 89 in October 1977 to a maximum of 79 in October 1978. As of October 1979, species richness reached 92 species, a value that is higher than this reported in 1977. Conversely a major decline in total abundance was reported after the Amoco Cadiz oil spill due to the disappearance of most *Ampelisca* populations which largely dominated the benthic community in 1977 and a decline in the densities of other species like the polychaetes *Marphysa bellii* and *Nephtys* spp. (Tableau 6). Maximum abundances decreased by more than 90 % from 32,697 ind.m$^{-2}$ in October 1977 to 3,060 ind.m$^{-2}$ in October 1978 and remained low (< 10,000 ind.m$^{-2}$) until 1986 except in 1982 due to the proliferation of the polychaete *Polydora pulchra*. Abundances began to increase after 1986 to reach orders of magnitude comparable to 1977 by 1990. Since this year, maximum abundances fluctuated between 25,000 and 45,000 ind.m$^{-2}$ before a dramatic decline from 2003 to 2005. Maximum abundances were below 5,000 ind.m$^{-2}$ between 2006 and 2009 and have slightly increased since 2010 to vary around 5,000-7,500 ind.m$^{-2}$. This decrease in abundances was still related to a major reduction in the abundances of the *Ampelisca* populations and the other most abundant species (Tableau 6).

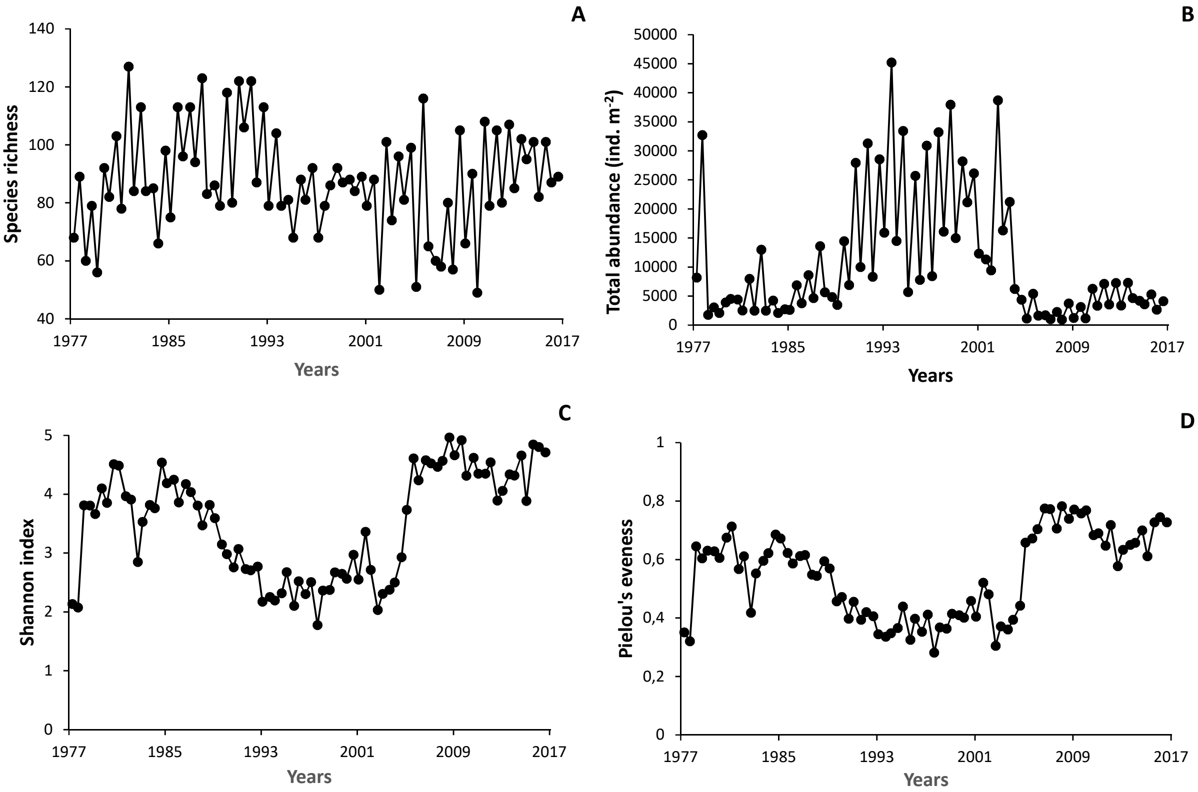


**Figure 10:** Long-term changes of 'traditional' diversity indices at the Pierre Noire station from 1977 to 2016. (A) Number of species per unit area; (B) Total abundance (ind. m$^{-2}$); (C) Shannon weaver index; (D) Pielous' evenness.

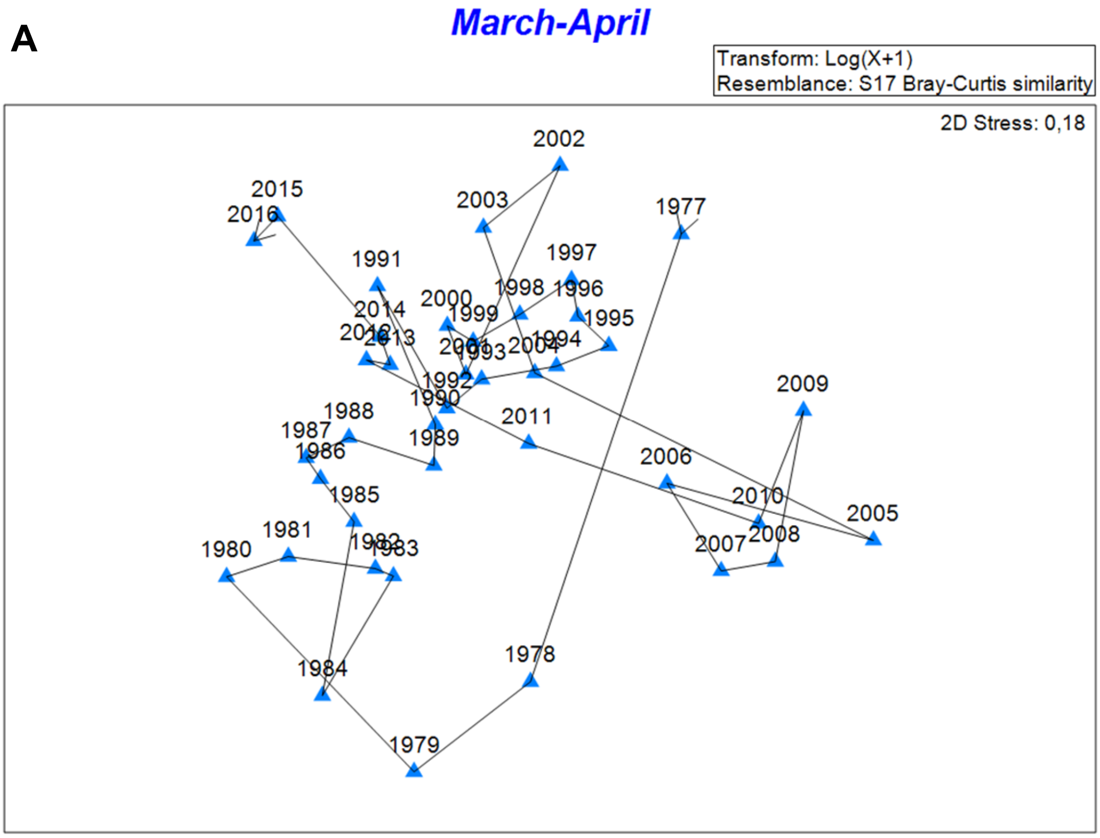
**Tableau 6:** Changes in the densities (ind.m$^{-2}$) of the ten most abundant species in March-April before and after the two major shifts in the community structure. For the first shift, densities were calculated the year before and two years after the Amoco Cadiz oil spill (1978-1979). For the second shift, mean densities were calculated for two periods of relative stability in the community structure: 1993-2004 and 2005-2010. The rank of each species for each period is given in bracket. Species for which densities decreased before and after the regime shift are given in bold.

| First abrupt shift | | | Second abrupt shift | | |
|---|---|---|---|---|---|
| Species | Mean densities 1977 | Mean densities 1978-1979 | Species | Mean densities 1993-2004 | Mean densities 2005-2010 |
| ***Ampelisca armoricana*** | 3436 (1) | 0 | ***Ampelisca sarsi*** | 4560.9 (1) | 218.7 (1) |
| ***Ampelisca sarsi*** | 3427 (2) | 187 (3) | ***Ampelisca armoricana*** | 3457.1 (2) | 123 (2) |
| *Paradoneis armata* | 327 (3) | 466 (1) | ***Ampelisca tenuicornis*** | 2295.6 (3) | 11.3 (23) |
| ***Marphysa bellii*** | 238 (4) | 87.5 (6) | ***Spio decoratus*** | 610.0 (4) | 60.2 (8) |
| ***Ampelisca tenuicornis*** | 120 (5) | 1 (49) | ***Paradoneis armata*** | 207.3 (5) | 79.7 (4) |
| ***Nephtys spp.*** | 82 (6) | 40.5 (9) | ***Marphysa bellii*** | 163.8 (6) | 85.3 (3) |
| *Aricidea pseudoarticulata* | 70 (7) | 125 (5) | ***Polydora flava*** | 77.9 (7) | 1 (71) |
| ***Hyalinoecia bilineata*** | 69 (8) | 31.5 (12) | ***Chaetozone sp.*** | 75.3 (8) | 35.8 (11) |
| *Spio decoratus* | 37 (9) | 318.5 (2) | ***Euclymene oerstedii*** | 74.5 (9) | 22.0 (15) |
| ***Euclymene oerstedii*** | 37 (10) | 12 (19) | ***Nephtys spp.*** | 71.8 (10) | 40 (10) |
| *Chaetozone sp.* | 18 (14) | 181 (4) | *Hyalinoecia bilineata* | 57.9 (14) | 72.5 (5) |
| *Scoloplos armiger* | 11 (21) | 62.5 (7) | *Scoloplos armiger* | 43.8 (17) | 66.5 (6) |
| *Aricidea cerrutii* | 4 (32) | 56 (8) | *Urothoe pulchella* | 49.6 (15) | 64.8 (7) |
| *Urothoe pulchella* | 8 (22) | 33.5 (10) | *Urothoe elegans* | 6.0 (43) | 43 (9) |

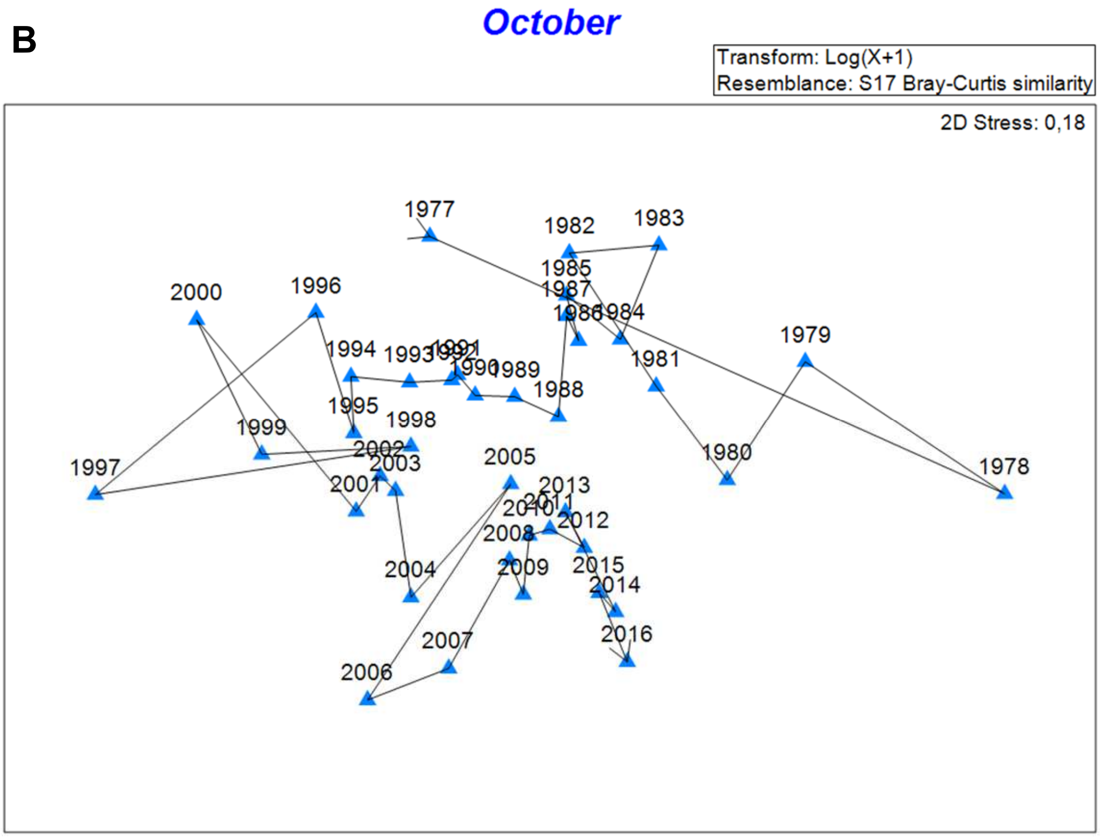
Changes in Shannon index and Pielou's evenness closely mirrored changes in total abundances and dominance patterns. Contrary to what is expected after a major pollution event, an increase in diversity was reported after the oil spill due to the disappearance of the dominant *Ampelisca* populations. The Shannon index increased from about 2 in 1977 to values ranging between 3.8 and 4.65 until 1988. In parallel to return to original abundances, low levels of diversity was measured from 1993 to 2005 before a step increase after 2005 following the second decline in total abundances.

### I.3.2. Long-term changes in community structure

The n-MDS ordination plots showed slightly different patterns of inter-annual changes in community structure depending on sampling months (Figure 11). In March-April, there was a major shift in the community structure just after the Amoco Cadiz oil spill between 1977 and 1978 (Figure 11A). It was then followed by a series of more or less important year-to-year changes from 1978 to early 1990s which corresponded to a slow and long recovery of the community to initial conditions. The period 1992-2004 appeared as a period of relative stability of the community with small changes between years except from 2001 to 2004. This period lies close to the first year of the survey suggesting a complete recovery of the community after the oil spill. In 2004 through 2005 there was a second abrupt shift in the community. Although this shift was characterized by a sharp decline in abundance comparable to that observed after the oil spill, it differed notably in terms of community structure (Tableau 6) and further dynamics. The first shift was marked by the near extinction of the populations of the three dominant *Ampelisca* species and the decline of some predatory polychaete species such as *Marphysa bellii* and *Nepthys* spp. but also by an increase in the abundance of some dominant polychaetes such as *Spio decoratus* and in a lesser extent *Paradoneis armata* and *Aricidea pseudoarticulata*. Densities of other less dominant species in 1977 such as the polychaetes *Chaetozone* sp. and *Scoloplos armiger* or the amphipod *Urothoe pulchella* also largely increased. Conversely, the second shift was characterized by a general decline in the densities of all ten most dominant species in the community over the period 1993-2004 and no extinction of *Ampelisca* population (Tableau 6). Only densities of less dominant species slightly increased. After the second shift, the community showed no sign of recovery to initial conditions and exhibited a complex dynamics with alternating periods of relative stability for some short periods (2005-2010; 2012-2014) and larger inter-annual changes.



March-April



October

**Figure 11:** Non-metric multidimensional scaling (n-MDS) ordination plots of macrofaunal community from 1977 to 2016 (A) in March and (B) in October showing the year-to-year changes in the species structure of the community. MDS plots are based on Bray-Curtis similarities after a log-transformation of species abundance.

In October, the n-MDS plot also showed the major shift in the community structure following the Amoco Cadiz oil spill and the slow recovery of the community over the next 10-15 years (Figure 11B). However, the second shift in the community structure corresponding to the second decline in abundances was not apparent. Since the early 90s, there was a serial pattern of community change with mostly relatively small changes between successive years, and sometimes more sudden changes (e.g. 1996-1997; 1997-1998; 2005-2008). This variability pattern over the last 25 years could reflect the large year-to-year variations in the magnitude of the summer recruitment of dominant species which could blur the long-term dynamics of the community.

### I.3.3. Species contribution to the long-term changes in the community structure

To assess which species contributed to the long-term changes in the community structure, only the March-April samples, which better reflect the long-term basic dynamics of the community, were taken into account. Fifty species were selected as dominant species, i.e. contributed to at least 2 % of total abundance in any one year. First, the results of the Type 2 SIMPROF test showed that the null hypothesis of no association among species should be rejected (Supplementary material). The group-average clustering of the 50 dominant species combined with Type 3 SIMPROF tests at each node identified 13 groups of 2 to 7 species which covariated coherently among years (Figure 12). Ten species had their own patterns of temporal variations. The different patterns of coherent variations among species are reported on Figure 13 for the seven groups which exhibited the most contrasted patterns. The first group included only two *Ampelisca* species, *A. armoricana* and *A. sarsi*, which were dominant in the community before the Amoco Cadiz oil spill, and from 1991 to 2004. The standardized abundances of these species were lower in 1996 and 1997. The other abundant *Ampelisca* species, *A. tenuicornis*, formed a distinct group on its own (data not shown) as this species was rare in 1977. The second group comprised three species of amphipods, *Bathyporeia* sp., *Urothoe pulchella* and *Ampelisca brevicornis*. Species in this group benefited from the decline of the *Ampelisca* species following the Amoco-Cadiz oil spill: their abundances increased during the 1980s before becoming very low again from 1994 onwards. However, no sharp increase in their abundance was observed during the second sharp decline in *Ampelisca* abundance in 2005. Within this group, the temporal variations of *A. brevicornis* slightly differed from those of *Bathyporeia* sp. and *Urothoe pulchella*. The third group of species was composed of two polychaetes, *Nepthys* spp. and *Spiophanes bombyx*, and one amphipod, *Perioculodes longimanus*. The abundances of species in this group also increased after the Amoco Cadiz oil spill, from 1978 to early 1990s. The fourth group was the largest one with seven species of polychaetes including *Ampharete lindstroemi*, *Aricidea* spp., *Marphysa bellii*, *Paradoneis armata* and *Spio decoratus*. These species showed cyclical patterns of temporal variations that were independent of the oil pollution and the second abrupt shift reported in 2005. Peaks in abundances were reported at a frequency of about ten years: 1979-1980, 1991-1993, 1999-2003 and 2011-2016. The fifth group comprised three species, the bivalve *Abra prismatica* and the polychaetes *Odontosyllis gibba* and *Scoloplos armiger*. The abundances of species in this group increased just after the Amoco Cadiz oil spill from 1978 to 1980-1981. Thereafter, they showed rather erratic dynamics with alternations of increase and decline over a few years. The sixth group included three polychaetes taxa, *Euclymene oerstedii*, *Hyalinoecia bilineata* and *Lumbrineridae*, whose abundance decreased after the Amoco Cadiz oil spill and then increased irregularly from 1986 to 2016. The last group was composed of six species, the bivalves *Abra alba*, *Nucula nitidosa* and *Tellina fabula*, the ophiurid *Acrocnida brachiata*, and the polychaetes *Praxillella affinis* and *Streblosoma bairdi*. These species increased to a dramatic peak at the end of the time-series before decreasing from 2014-2015.

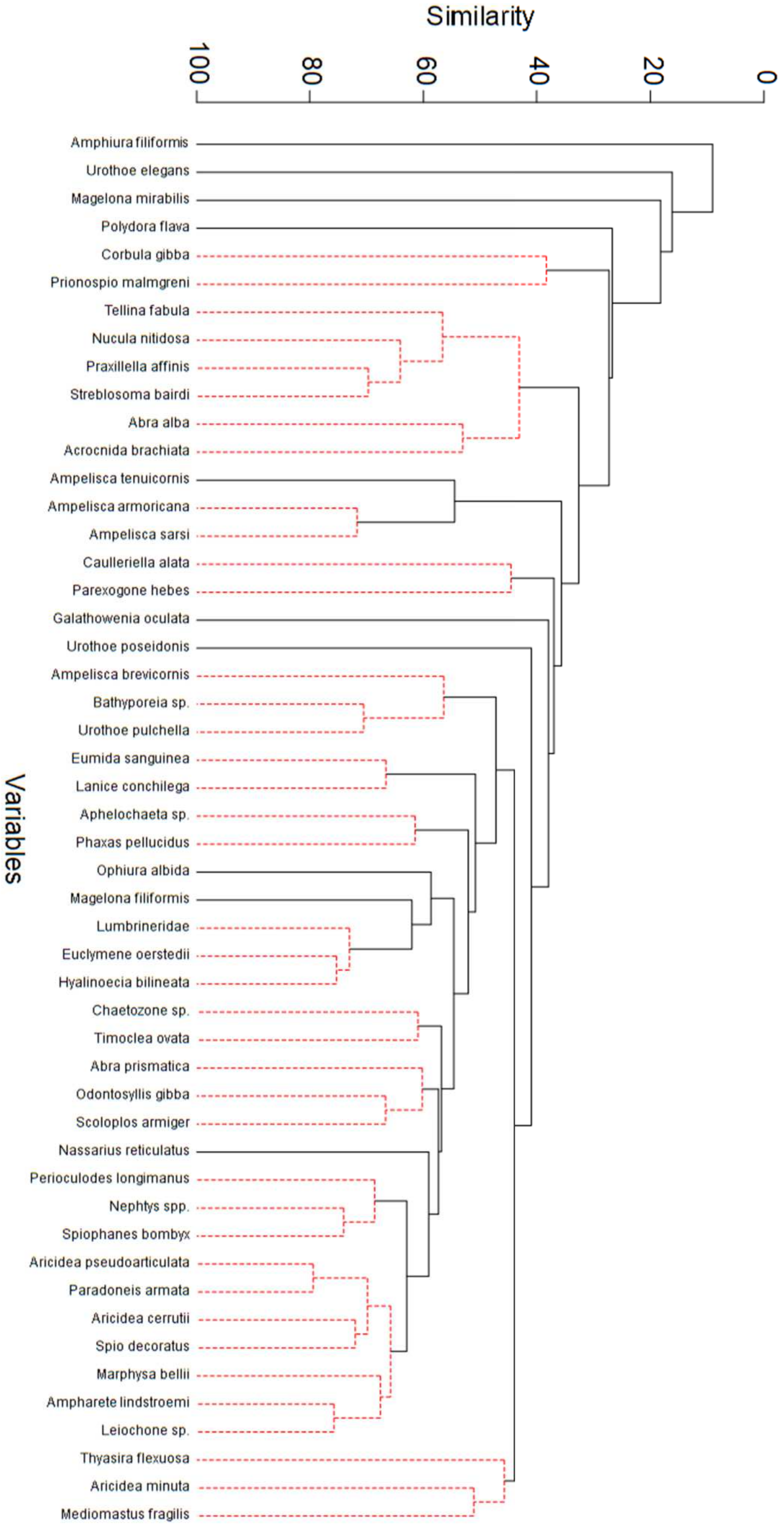


**Figure 12:** Dendrogram from group-average clustering of the 50 dominant species based on the Index of Association among species. Dashed lines indicate group of species which were not differentiated by Type 3 SIMPROF tests at the 5% level. Within these groups, the null hypothesis that all pairs of species are coherently associated cannot be rejected.

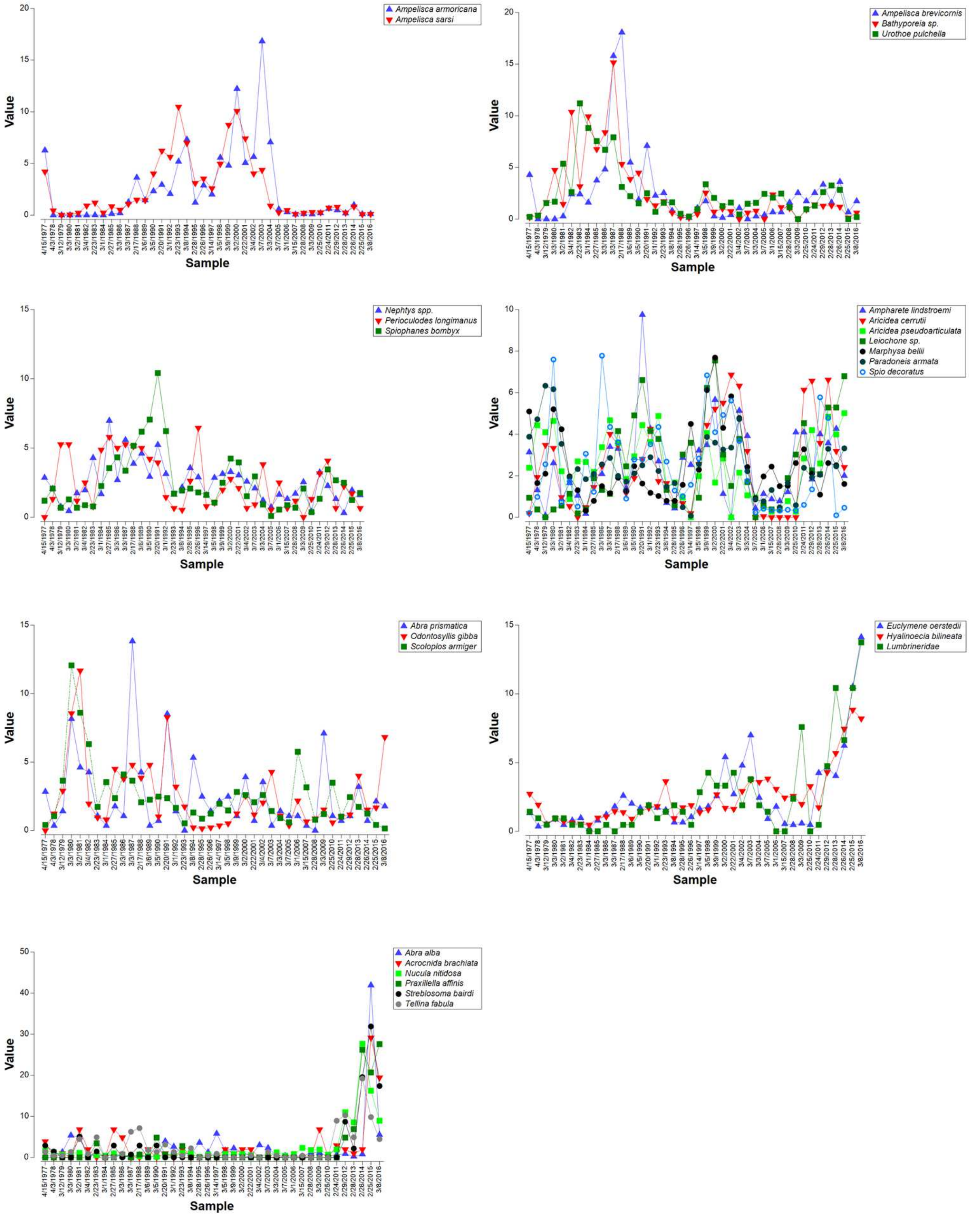


**Figure 13:** Long-term changes of the groups of species identified on **Figure 12** showing the consistency of species over time at the Pierre Noire station from 1977 to 2016. The y axes are the species-standardized abundances. Only six groups with contrasted patterns of coherent temporal variations are shown.

### I.3.4. Long-term changes in functional diversity

The different indices of functional diversity calculated only for the March samples showed contrasting temporal dynamics (Figure 14). As reported for the species richness to which it was significantly correlated ($r = 0.8272$; $p < 0.01$), functional richness (FRic) displayed large year-to-year variations with no long-term trend. Conversely, functional evenness (FEve) exhibited a remarkable stability over the long-term series. The functional dispersion (FDis) and the Rao's quadratic entropy (RaoQ) were strongly correlated with each other ($r = 0.9971$; $p < 0.001$) and with the Shannon diversity index ($r = 0.9672$ and $0.9708$ respectively; $p < 0.001$). Their year-to-year changes mirrored then the changes reported for the Shannon index and showed a pattern of temporal variation that was opposite to what was expected: they increased just after the perturbation caused by the Amoco Cadiz oil spill and remained at high values until 1987 before decreasing until 1993 when the community recovered. FDis and RaoQ were low from 1993 and 2004, and increased again from 2004 to 2007 during the second abrupt shift in the community structure. The parallel in the changes in FDis and RaoQ on the one hand, and the Shannon index on the other suggests that variations in these two indices of functional diversity were strongly impacted by variations in the abundance of the biological traits of *Ampelisca* species. Only the functional divergence (FDiv) had an original pattern of temporal variations that met the original assumptions: a decrease after the Amoco Cadiz oil spill and the second shift in the community structure. However, these two decreases occurred at different rates. While the decline after the oil spill was sudden, between 1977 and 1978, the second decline was gradual, from 2002 to 2017.

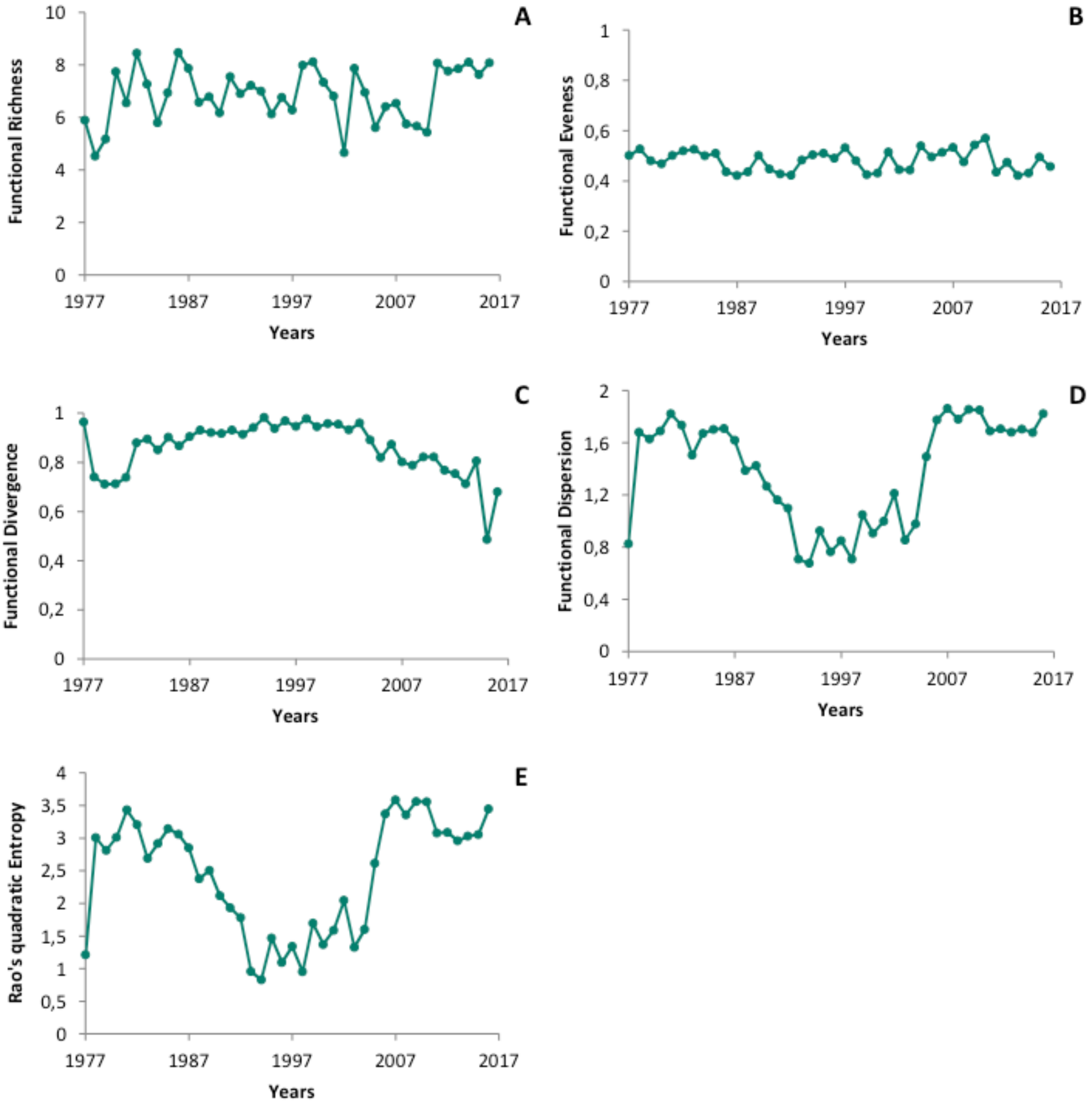


**Figure 14:** Long-term changes of the functional diversity indices at the Pierre Noire station from 1977 to 2016 for the March samples. (A) Functional richness; (B) Functional evenness; (C) Functional divergence; (D) Functional dispersion; (E) Rao's quadratic entropy.

Changes in the abundance of the different species over time were resulting in significant changes in the CWM values, i.e. the proportion of species abundance among modalities within each trait category (Figure 15). Before the oil spill, the community was mainly composed of very small (< 1 cm) to small (1-2 cm) species with a short life span (< 2 years) and a direct development. These species were filter-feeders, tube dwellers, surficial modifiers and sensitive to disturbance. The oil spill caused an increase in the maximum body size of the species, the community being dominated by small-medium (3-10 cm) species, and an increase in the life span with higher proportion of species with a medium life span. There was a switch from a community dominated by tubicolous suspension-feeders by a community dominated by burrowers and surface deposit-feeders. There was also a relative increase in the proportion of predators and scavengers. Finally, species sensitive to disturbance were largely replaced by tolerant species. From 1978 to early 1990s, the proportions of the different trait modalities within the community recovered to proportions close to that observed in 1977. The second major change observed in the community structure in the mid-2000s resulted in a more gradual change in the proportions of trait modalities within each trait category. A comparison of the two change periods (i.e. 1977-1978, mid-2000s) shows that they were quite similar in terms of functional composition. The major difference concerned the movement type. While the community was highly dominated by burrowers after the Amoco-Cadiz oil spill, it was composed in comparable proportions of burrowers and tube dwellers.

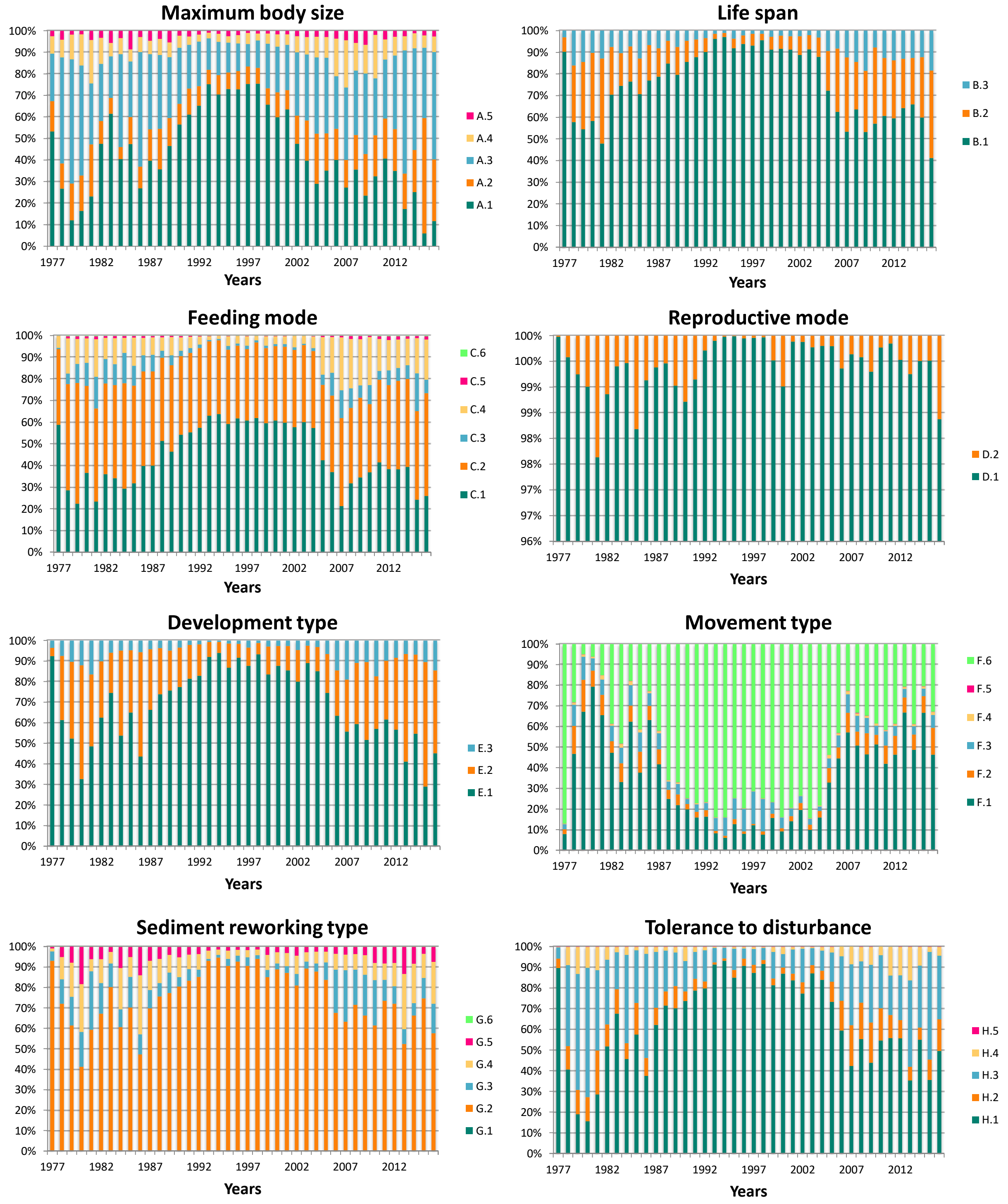


**Figure 15:** Long-term changes of community-weighted mean trait values at the Pierre Noire station from 1977 to 2016. The different modalities of the different traits are given in the **Tableau 5**.

The n-MDS ordination plot of functional trait composition of the benthic community confirmed the major changes in the functional composition of the community just after the oil spill in 1978-1980 and between 2003-2005 as well as the recovery period during the 1980s and early 1990s (Figure 16). After a period of relative stability between 2005 and 2010, the community changed again between 2010 and 2011. From 2011 to 2016, the functional structure of the community was closed to this from early 1980s.

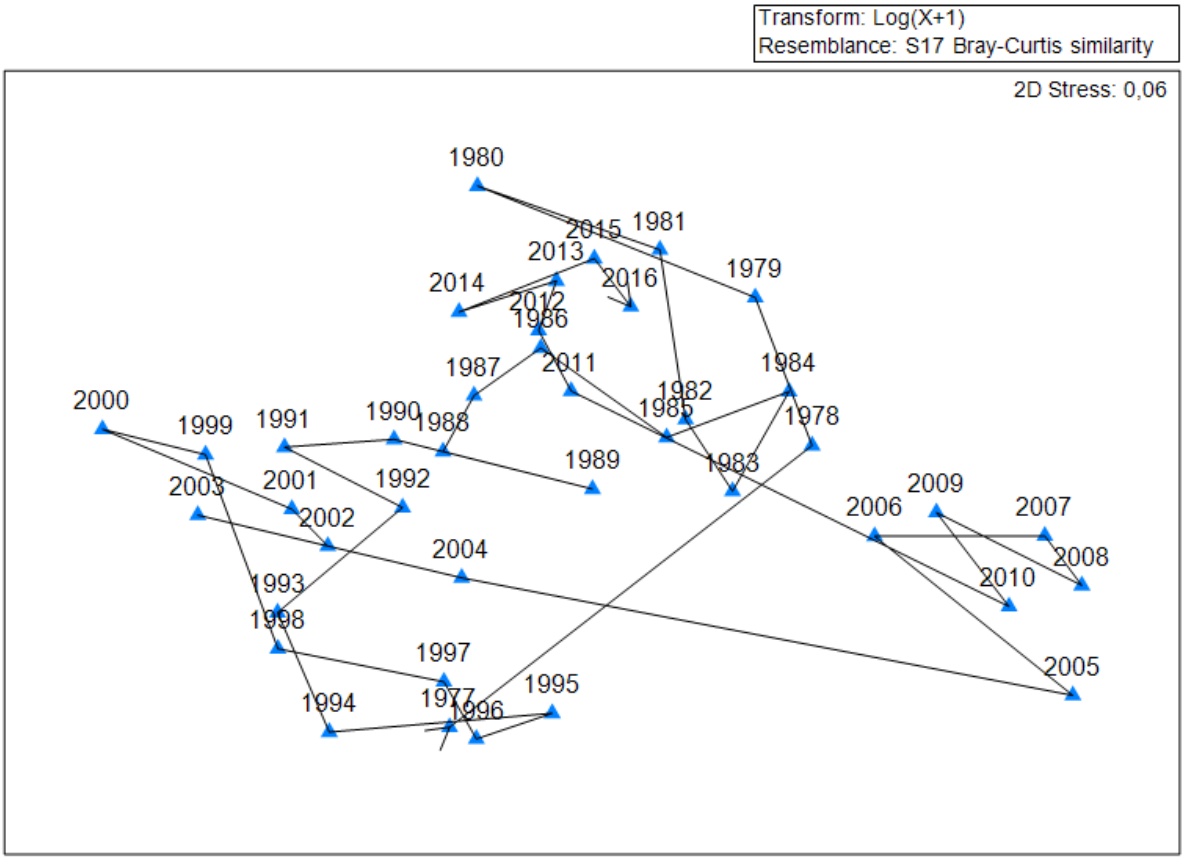


**Figure 16:** Non-metric multidimensional scaling (n-MDS) ordination plot of macrofaunal community in March from 1977 to 2016 showing the year-to-year changes in the functional structure of the community. MDS plot is based on Bray-Curtis similarities after a log-transformation of abundances of the different trait modalities.

## I.4. Discussion

Macrobenthic fine sand benthic communities in temperate shallow coastal waters are commonly characterized by large seasonal and year-to-year variations in their properties (i.e. composition, abundance and diversity) in response to local and regional drivers (Van Hoey et al., 2007). Seasonal predictable variations resulted from maxima in density and species richness at the end of summer and early autumn and minima at the end of winter and early spring before the recruitment of the dominant species. Conversely, inter-annual variations can be caused by unpredictable changes in weather conditions (e.g. storm events, cold winters), gradual environmental changes such as eutrophication or climate change, and accidental pollutions which altered species survivorship, reproductive output and biotic interactions (competition and predation). Along the French costs of the English Channel and the North Sea (bay of Morlaix, bay of Seine, southern Bight of the North Sea), Fromentin et al. (1997) reported that the different macrobenthic communities did not fluctuate in parallel over a 15-year period (1978-1992), suggesting that local conditions could play a major role on their temporal variations, in particular in the bay of Morlaix.

Long-term analysis of the benthic fine sand community in the Bay of Morlaix over the last 40 years highlighted two abrupt changes in community structure. These two changes displayed certain similarities, such as a dramatic reduction in densities and, as a consequence, a change in dominance patterns with an increase in specific diversity. However, the causes of these two changes and the temporal evolution of the community structure after the changes are fundamentally different. The first change resulting from the massive oil pollution of the Amoco Cadiz in the spring of 1978 has already been widely documented (Dauvin & Ibanez, 1986; Ibanez et al., 1993; Fromentin et al., 1996, 1997; Dauvin, 1998). It was thus characterized by the almost total disappearance of the *Ampelisca* populations that dominated the community, followed by a period of 2-3 years of rapid change of the community. This period was marked by an enrichment of organic matter in the sediment which favored biostimulation and the development of opportunistic polychaetes (*Spio decoratus, Caulleriella alata*) and surface deposit-feeders like the bivalve *Abra alba* (Ibanez et al., 1993). Our results also highlighted the dominance of some species just after the oil spill like *Abra prismatica*, *Scoloplos armiger*, *Spio decoratus*, *Marphysa bellii* and *Aricidea* spp. However, they suggested some of these species had more complex patterns of variation with cyclical fluctuations approximately every ten years. Recolonization by *Ampelisca* species took place after 1989 and the community progressively recovered. From early 1990s to 2004, abundances, species diversity and community structure showed weak year-to-year fluctuations. Despite a long recovery period of 12-15 years, which is largely explained by the demographic characteristics of amphipods (e.g. low fecundity, absence of larval phase), the return to a state close to the initial state and the long-term persistence of the community around this state for more than ten years are in all respects remarkable, whereas amphipods are very good indicators of environmental stress (de-la-Ossa-Carretero et al., 2012). They will lead Dauvin (1998) evoked the notion of “climax” for the amphipod-dominated state of the Pierre Noire fine sand community.

Beyond a sharp decline in total abundance and an increase in species diversity, the second abrupt change differed from the first one in a number of respects. First, in addition to the *Ampelisca*, the densities of most of the dominant species in the community decreased. Thus, some species that had been favored following pollution by the Amoco-Cadiz such as *Spio decoratus*, *Paradoneis armata* or *Chaetozone* sp. were declining. Only a few species of lesser importance such as *Urothoe pulchella* or *Scoloplos armiger* were increasing significantly. These differences in individual species responses were reflected in a different change in community structure. After 2005, the community showed no signs of recovery to a state close to that of the early 2000s. Densities remained extremely low, around 1000-1500 ind. $m^{-2}$ in March and 2000-6000 ind. $m^{-2}$ in October, and the community structure changed little between 2005 and 2010. After 2010, densities increased again to reach 3000-4000 ind. $m^{-2}$ in March and up to 7000 ind. $m^{-2}$ in October, and the community gradually changed from one year to the next. Since 2005, following the second shift, the community seemed to be characterized by an increase in structure variability over periods of a few years.

In a recent review on regime shifts, Dakos et al. (2015) identified 6 main mechanisms which can cause a regime shift: (1) a slow environmental change towards a tipping point; the shift is permanent and the recovery is possible only by restoring initial environmental conditions; (2) slow-fast cyclic transitions caused by the interactions between fast and slow variables and conducive to an alternation between two stable states; (3) a stochastic resonance with a swing between again two alternative states resulting from a combination of a periodic change in environmental conditions and stochastic perturbations; (4) noise-induced transitions in response to strong external disturbances which induced a shift to an alternative state; (5) long transient upon extreme events which strongly modified the state of the ecosystem without being trapped to an alternative state; (6) big stepwise changes in external conditions that will move the ecosystem to a new state. Although observed regime changes are typically the result of a combination of mechanisms acting at the same time, these definitions provide the conceptual framework to identify the relative role of mechanisms that had cause the two abrupt shifts in the Bay of Morlaix. Obviously, the shift observed after the Amoco Cadiz oil spill corresponds to a long transient in response to a major human disturbance and a slow recovery. Alternatively, the second shift seemed to be more the result of a non-linear community response to small changes in environmental conditions. Although we do not have continuous measurements of environmental variables since 1977 that would allow us to establish a direct link between the evolution of the benthic community and environmental forcing, no major extreme events (e.g. storm, heat wave, severe winter) were observed between 2004 and 2005 (see for instance the changes in the Sea surface temperature in the bay of Morlaix, Tréguer et al., 2014). Similarly, our results do not support the hypothesis of an alternation between two stable states.

Along the French Atlantic coasts, and more broadly along the western European coasts, various abrupt changes were reported for different compartments of the ecosystem at the end of 1990s and early 2000s, suggesting that the observations made in the Bay of Morlaix are part of a regional dynamic. In response to changes in regional climate and local atmospheric conditions, an increase in sea surface temperature and a decrease in nutrients and chlorophyll a concentration with subsequent effects on trophic food web were observed along the French Atlantic costs (Goberville et al., 2010). In the eastern English Channel a rapid and persistent structural change in the exploited fish community from strong to moderate dominance of small-bodied forage fish species with low temperature preferendum occurred in the mid-1990s in relation with a switch of the Atlantic Multidecadal Oscillation (Auber et al., 2015). In the southern North Sea, off the island off Nordeney, two major biological shifts of benthic communities were reported in response to climate changes during the mid-80s but also in early 2000s (Dippner et al., 2014). In the NE England, different studies suggested different results. Clare et al. (2017) reported only one major shift during the mid-80s in response to a shift in the pelagic primary production with different species reacting differently to changes in food supply and temperature. But in the same area, Frid et al. (2009) reported major changes at the end of the 80s but also at the turn of the millennium. These authors suggested that the dynamics of the community responded to different controlling factors at different temporal scales so that quasi-decadal (6–10 years) variations before a sudden shift were superimposed on a longer-term trend in the system. This diversity of specific responses should be compared with the observations made in the Bay of Morlaix where different species also showed different patterns of variation according to their environmental preferences and biotic interactions. Through the analysis of the year-to-year dynamics in a soft-bottom amphipod community in the western English Channel over a shorter period (2008-20014), Navarro-Barranco et al. (2017) described significant changes in the structure of the whole community in response to different environmental forcing. Abundance of amphipods was strongly correlated to bottom water temperatures while other species responded mainly to changes in phytoplankton biomass.

In parallel to analyses of changes in species diversity and taxonomic structures, understanding how long-term changes in diversity affect ecosystem functioning is of primary importance. In this context, changes in the functionality of an ecosystem is now more and more commonly addressed by incorporating information no species functional traits into the analyses (Clare et al., 2015; Meyer & Kröncke, 2019). In the present study, long-term patterns of taxonomic and trait-based variability of the benthic community structure in the bay of Morlaix were congruent and highlighted two major regime shifts in 1977-1978 after the Amoco Cadiz oil spill and in 2004-2005. Such a result differs markedly from observations made in the North Sea were trait composition did not vary significantly across periods that experienced significant changes in taxonomic composition (Clare et al., 2015). Clare et al. (2015) argued that this lack of alteration in trait composition resulted from a mechanism of abundance compensation by functionally similar benthic species acting as a buffer to changes in ecosystem functioning over time. Similar results were also reported in a Portuguese estuary where trait composition of subtidal macroinfauna persisted over time or recovered quickly (less than 5 years) after a restoration of environmental conditions (Veríssimo et al., 2012). Conversely, in the Bay of Morlaix, our results suggested that the changes in trait composition were principally linked to changes in the relative abundances of the different dominant species than to a process of substitution of one species by another within the same functional group. A shift in the taxonomic composition could cause a disruption in ecosystem functioning, the recovery of which depended to a large extent on the recovery of the taxonomic composition as reported following the first regime shift.

The sharp decline of the dense populations of *Ampelisca* during the two regime shifts caused a profound change in the trait composition of the community. In addition to changes in terms of life history traits of dominant species (e.g. life span, reproductive mode) and an increase of the proportion of tolerant species to disturbance, changes which will have a major impact on the bentho-pelagic coupling and the biogeochemistry of the sediment were also observed. In particular, there has been a reversal in the relative importance of suspension feeders and surface deposit-feeders. Following the Amoco Cadiz oil spill, this reversal can be explained on the one hand by the near disappearance of the *Ampelisca* populations due to their high sensitivity to hydrocarbons and on the other hand by biostimulation mechanisms resulting from an organic enrichment of the sediment (Dauvin & Ibanez, 1986; Ibanez et al., 1993). For the second regime shift, this reversal might reflect changes to the quantity and quality of detrital food supply that were proposed as a major cause of regime shifts reported in the North Sea. Another major consequence of the two regime shifts was the changes in traits involved in the community bioturbation potential (i.e. sediment reworking type, movement type) (Solan et al., 2004; Queirós et al., 2013). Tube dwellers and superficial modifiers were partly replaced by burrowers, biodiffusors and upward and downward conveyors, increasing the bioturbation potential. Although the lack of biomass data precludes the formal computation of the community bioturbation potential, one can expect that such changes alter nutrient cycling, carbon storage and organic matter decomposition (Solan et al., 2004, 2012).

The different complementary trait-based indices calculated to describe the different components of functional diversity clearly showed different long-term variability that were or were not consistent with what could be expected in response to a disturbance. They thus appeared to be more or less efficient in detecting changes in ecosystem functioning induced by the two regime shifts. Changes in functional richness were strongly correlated with changes in species richness as reported for different types of communities (Villéger et al., 2008; Schleuter et al., 2010). Both indices exhibited year-to-year variations without any clear temporal trend. The two regime shifts reported in the Bay of Morlaix were more the result of a change in species dominance patterns rather than a change in the number of species. Rao's quadratic entropy and Functional dispersion were also strongly correlated as expected since these two indices have a similar mathematical background (Laliberté & Legendre, 2010). However, contrary to the expectations following a disturbance, both indices increased after the Amoco Cadiz oil spill and the second regime shift in 2004-2005 as was also observed for an abundance-weighted diversity index like the Shannon diversity index. By addressing the performance of different trait-based indices in an estuarine environment, Van der Linden et al. (2016) reported similar results and highlighted that RaoQ and FDis should be interpreted with caution in communities dominated by a few species like the fine sand benthic communities in the Bay of Morlaix. By considering abundance to measure the amount of trait dissimilarity in a community, these indices give a differential weight to the traits of the dominance species and might provide a biased image of ecosystem functioning. Functional evenness was remarkably stable over the 40-year time-series and not informative. Finally, Functional Divergence (FDiv) decreased as expected in response to a disturbance (Mouillot et al., 2013). However, the rate of decrease was different for the two regime shifts confirming the differences in the mechanisms which caused them. It was sharp after the Amoco Cadiz oil spill and gradual after the second regime shift. A lower value of FDiv indicated that the most abundant species have functional traits closer to the centre of gravity of the functional space (Villéger et al., 2008). The community was then more dominated by more generalist species and that fewer ecological functions were achieved by the community. This change could have major consequences on the ecosystem functioning as several studies suggested that different functions are linked to ecological differences between species (i.e. the niche complementarity concept) which contributed to a better use of resources (Rigolet et al., 2015).

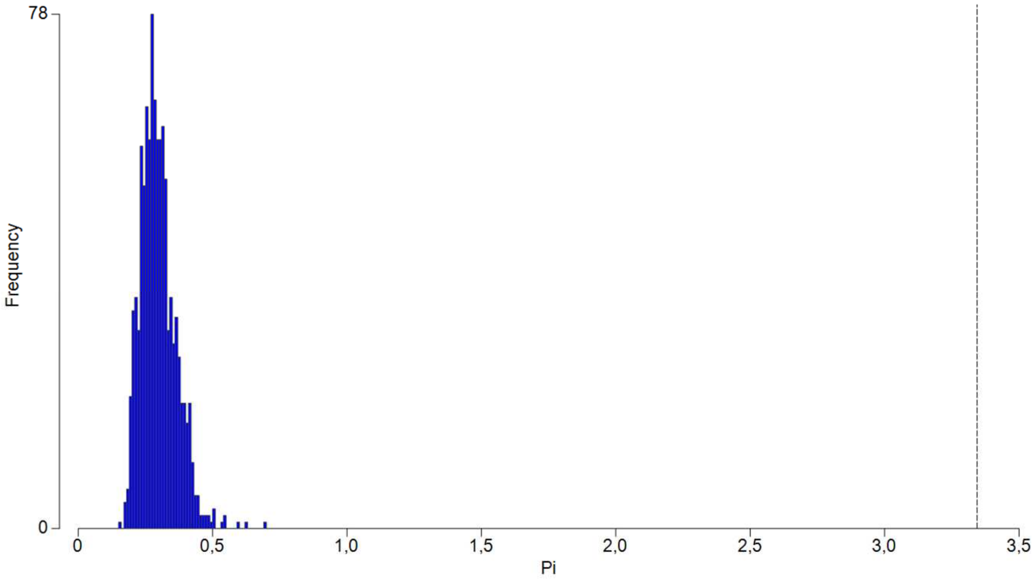
In the context of climate change and growing impact of anthropogenic activities on coastal areas, long-term research programs are key-programs to improve our knowledge on their dynamics and better predict their responses to natural and human-induced disturbances. The long-term time series in the Bay of Morlaix highlighted the complex temporal dynamics of marine benthic communities in coastal environments in terms of taxonomic and trait composition, diversity and structure. Over the last 40 years, the fine sand benthic community of the bay has been marked by two abrupt changes of comparable intensity but of different origin (a major oil spill vs. non-linear responses to slow environmental changes). A better understanding of the mechanisms involved in regime shift is also a critical element in many respects in assessing the ecosystem ecological status, the management of marine resources and coastal ecosystems, and the definition of monitoring programs (Kelly et al., 2015; Levin & Möllmann, 2015). Different issues can be then underlined. Regime shifts may cause an intrinsic decrease in the potential predictability of marine ecosystems and require the development of early warning indicators. Regime shifts induced by external forcing acting on a large scale (e.g. climate change) may call into question years of management efforts at local scales and raise questions about the interweaving of spatial and temporal scales in ecosystem management. Finally, the assessment of ecosystem health in the context of the European directives (Water Framework Directive, Marine Strategy Framework Directive) is based on the development of biotic indices which are compared to reference conditions which are expected to vary in response to shifting baselines. While the analysis of the first 20 years of the time-series suggested that the *Ampelisca*-dominated state was the reference state of the community, our recent results suggest that alternative states may occur in the absence of any apparent anthropogenic disturbance.

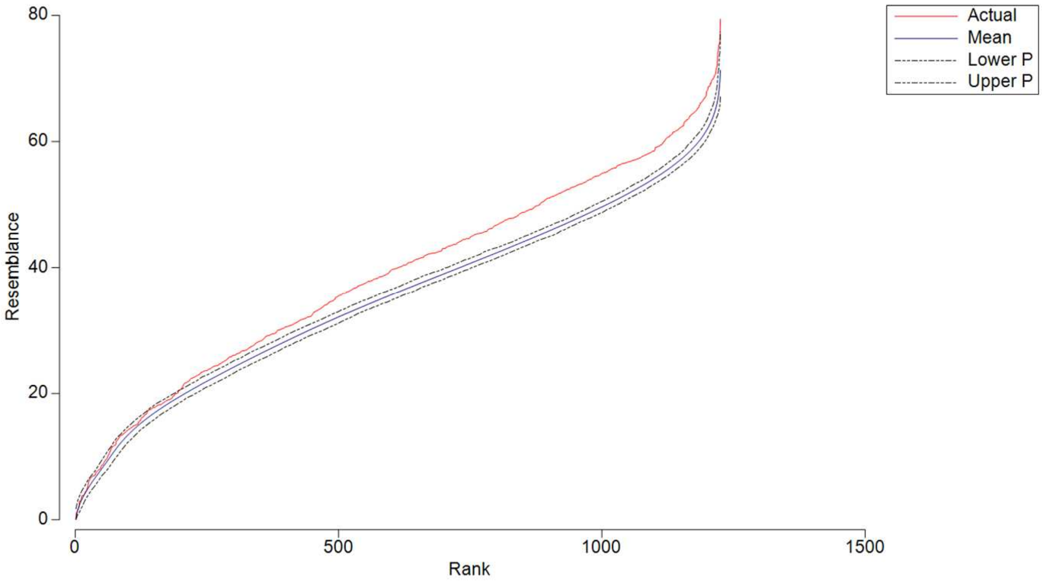
## Acknowledgements

The long-term monitoring program in the bay of Morlaix was successively supported by different contracts from the 'Réseau National d'Observation' coordinated by Ifremer and the REBENT programme funded by the 'Agence de l'Eau Loire Bretagne', the 'Région Bretagne' and the 'DREAL Bretagne'. This study forms part of the PhD thesis of Lise Bacouillard partly funded by the 'Région Bretagne'. The authors are grateful to the captains and the crews of the RV 'Mysis' and 'Neomysis' and all students and technicians who contribute to fieldwork and laboratory analyses.

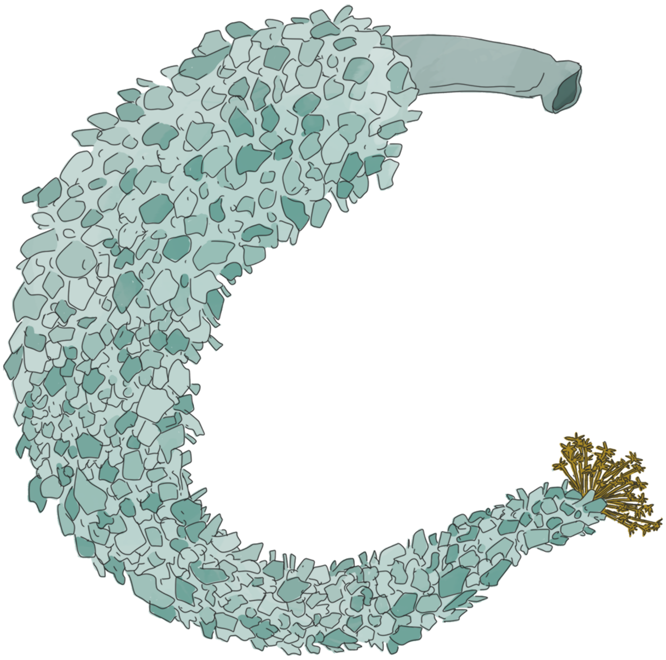
## Supplementary material

Results of the Type 2 SIMPROF test based on index of association among the fifty dominant species which contributed to at least 2 % of total abundance in any one year. The observed value of the statistic π (3.34) falls outside the distribution of values generated by 999 permutations representing null-hypothesis (i.e. no association among species) and is therefore highly significant ($p < 0.001$). In the Similarity Profile, continuous lines denote the observed profile, the full set of pairwise resemblances ordered from smallest to largest (y axis) plotted against their rank (x axis). Dashed lines are limits within which 99% of resemblances would be expected to fall, for any given rank, under the null hypothesis of no association amongst species.





# Chapter II : Long-term spatio-temporal changes of the muddy fine sand benthic community of the Bay of Seine (eastern English Channel)



# Chapter II

Article publié dans Marine Environmental Research

Lise Bacouillard[1], Noémie Baux[2, 3, 4], Jean-Claude Dauvin[2], Nicolas Desroy[5], Katja Juliana Geiger[1], Franck Gentil[1], Éric Thiébaut[1]

[1] Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR7144, Adaptation et Diversité en Milieu Marin, Place Georges Teissier, F-29680 Roscoff, France

[2] Normandie Université, UNICAEN, UMR6143, Laboratoire Morphodynamique Continentale et Côtière, 24 rue de Tilleuls, F-14000 Caen, France

[3] Normandie Université, UNICAEN, Laboratoire des Sciences Appliquées de Cherbourg, EA 4253, 50100 Cherbourg, France

[4] Conservatoire National des Arts et Métiers, INTECHMER, 50100 Cherbourg, France

[5] IFREMER, Station de Dinard, LER Bretagne Nord, 38 rue du Port Blanc, 35800 Dinard, France

## ABSTRACT

In the English Channel, the eastern Bay of Seine is exposed to numerous anthropogenic disturbances, in particular major changes in sediment dynamics, which are expected to greatly impact benthic communities. To assess the long-term effects of these stressors on the muddy fine sand benthic community, an original long-term monitoring program has been implemented since 1988. It is based on the sampling of a network of 60 stations during seven surveys over 28 years from 1988 to 2016. We investigate changes of species density, species composition and species diversity at different scales (α-diversity, β-diversity and γ-diversity). Contrary to results obtained in many coastal areas, our results showed a long-term persistence of the community in terms of species composition and structure although a general shift towards muddy sediment has resulted in increased colonisation by species associated with muddy habitats and a decrease in spatial beta diversity.

## Keywords

Benthic ecology; Coastal zone; Temporal variability; Species composition; Macrofauna; α-diversity; β-diversity; γ-diversity

## II.1. Introduction

Marine coastal ecosystems experience increasing pressures due to human activities including overexploitation of marine resources, eutrophication, contamination by organic and non-organic pollutants, coastal urbanization and introduction of non-indigenous species, which can overlap and interact with climate change (Airoldi & Beck, 2007; Halpern et al., 2008). The cumulative effects of these diverse pressures, which often vary in magnitude, spatial extent, temporal duration and frequency (Donohue et al., 2016), result in changes to the structure of marine communities (e.g. species richness, species composition, density and biomass of dominant species) which can alter ecosystem functioning and the delivery of ecosystem services (Cardinale et al., 2012; Gamfeldt et al., 2015). In this context, there is a growing need for analysis of long-term datasets to assess responses of communities to temporal changes in environmental conditions to facilitate management and conservation efforts (Magurran et al., 2010; Giron-Nava et al., 2017). Such datasets provide essential resources to address several issues: (1) describe and understand the complex long-term dynamics of community diversity in response to changing environmental conditions; (2) assess the effects of multiple stressors and disentangle the relative contributions of anthropogenic impacts and natural variability; (3) provide data for predictive models; (4) support the development of ecological indicators to evaluate the ecosystem; and (5) support the implementation of ecosystem-based management (Duffy et al., 2013).

For macrobenthic communities, two main strategies have been developed to monitor long-term ecological change over recent decades. The first approach consists of sampling one or multiple stations at a regular frequency, often yearly (e.g. Fromentin et al., 1997; Warwick et al., 2002; Frid et al., 2009; Clare et al., 2015), during several decades. It provides valuable information on the dynamics of macrobenthic communities and their drivers, but requires continuous and long-term financial and human support. Furthermore, it does not allow consideration of the spatial heterogeneity of environmental conditions or responses of macrobenthic communities. A second approach consists of sampling a network of stations after a long time interval, generally exceeding a decade, which allows rapid detection of major changes in macrobenthic macrofauna without being able to statistically infer the causes of the observed changes (Hinz et al., 2011; Kröncke et al., 2011; Callaway, 2016; Bonifácio et al., 2018). An original alternative approach, which has been implemented in the eastern Bay of Seine, combines both of these strategies and is based on long-term large-scale sampling of a network of stations (i.e. ~ 60 stations) at regular intervals (i.e. every five years) over a long period (i.e. 1988 to 2016). Thus, it enables the detection of interactive effects between spatial and temporal processes on the dynamic of macrobenthic communities.

Macrobenthic communities in the Bay of Seine were first described from data collected during early 1970s (Cabioch & Gentil, 1975; Gentil & Cabioch, 1997) which identified seven macrobenthic communities in relation to the spatial distribution of the sediment substrates: (1) the coarse gravel and pebbles community, (2) the sandy gravels and gravels community, (3) the *Branchiostoma lanceolatum* coarse sand community, (4) the *Ophelia borealis* - *Nephtys cirrosa* fine and medium clean sands community, (5) the *Abra alba* - *Lagis koreni* muddy fine sand community, (6) the heterogenous muddy mixed community and (7) the *Limecola balthica* community in estuarine muddy fine sand and mud. Since these pioneering works, studies on the *Abra alba* - *Lagis koreni* muddy fine sand community in the eastern part of the Bay of Seine showed that the community was distinctly structured in space with patchy distribution of most dominant species and the identification of distinct faunal assemblages (Thiébaut et al., 1997; Baffreau et al., 2017; Dauvin et al., 2017). Thiébaut et al. (1997) demonstrated that the spatial structure of the community resulted from the combination of several environmental gradients related to salinity, sediment grain size and food supply. These authors highlighted a relative stability of this spatial organization over a 5-year period. Over a longer period (1983-1992), the community structure at only one station was also relatively stable compared to other sandy communities in the western English Channel (Bay of Morlaix) and in the south of the North Sea (Gravelines area), despite the influence of alternative periods of cold and mild conditions on the densities of some species (Fromentin et al., 1997). More recently, the introduction of non-indigenous species and the arrival of species associated with muddy sediment were observed without an assessment of their impacts on the community structure (Dauvin et al., 2007b; Jourde et al., 2012). Thus, the non-indigenous razor clam *Ensis leei* (formerly *Ensis directus*) was first reported in 1998 and colonized the south-eastern coasts of the bay at moderate density (< 100 ind.m$^{-2}$; Dauvin et al., 2007). The polychaete *Melinna palmata* has been observed since 2002 and has rapidly extended its population to reach densities of 277 ind.m$^{-2}$ in March 2006 and between 625 and 2500 ind.m$^{-2}$ in September 2008 and September 2009 in parallel to the increased siltation rates of the bay (Dauvin et al., 2007b; Alizier, 2011). Likewise, another species inhabiting muddy sediment, the crab *Asthenognathus atlanticus*, was first sampled in 2008 (Jourde et al., 2012).

The concept of “stability/variability” is a focal point of ecological research that has received attention for decades by theoreticians and empiricists alike. Traditionally, stability was perceived as a binary measure based on the asymptotic stability of multispecies systems, with communities either stable or unstable (MacArthur, 1955). Recently, the concept of "multidimensional ecology stability" has emerged and multiple correlated or independent components of the stability were identified to capture the different aspects of the responses of communities to diverse disturbances, e.g. variability, persistence, resistance, resilience, or robustness (Donohue et al., 2013).

As described in Donohue et al. (2013), temporal variability at the population or community levels is commonly quantified as coefficient of variation (CV) of density or biomass, with high variability corresponding to low stability. The "compositional turnover" which represents the (temporal) beta diversity is the reciprocal of persistence and measures the extent of change in community composition over time. It can be quantified using Jaccard or Bray-Curtis similarity index depending if changes are addressed in terms of presence/absence or relative abundances of species. Furthermore, these different metrics of stability/variability can be calculated at different spatial scales to understand how temporal variation may differ from one site to another within a community. Therefore these different components allow assessing stability/variability appropriately at both a small or large scale, temporarily or spatially.

Using the study site of the eastern Bay of Seine, which is highly representative of urbanized coastal areas exposed to numerous anthropogenic threats (J.-C. Dauvin, 2008; Marmin et al., 2016; Tecchio et al., 2016; Baux et al., 2019), this study investigated the spatio-temporal changes of species density, species composition and species diversity at different scales ($\alpha$-diversity, $\beta$-diversity, $\gamma$-diversity) between 1988 and 2016. Based on the analysis of spatio-temporal data provided by the original long-term monitoring program of the muddy fine sand benthic community implemented in this area, we address two specific questions: (1) how did the benthic community vary through time and space according to the scale of observation (i.e. local station *vs*. whole community) and (2) what was the degree of correlation of the different components of the stability?

## II.2. Materials and methods

### II.2.1. Study area

Along the northwestern French coasts, the Bay of Seine forms a quadrilateral area of about 5000 km$^2$ largely open to the central English Channel in the north with a water depth never exceeding 30 m (Figure 17). Within the bay, semi-diurnal tidal currents range between 1 and 3 knots and their velocity gradually diminishes towards the eastern part of the bay

(Salomon & Breton, 1991). These currents combined with wave action are the main drivers for the distribution of superficial sediments (Larsonneur et al., 1982; Marmin et al., 2016) and macrobenthic communities (Gentil & Cabioch, 1997) resulting in an offshore-inshore gradient. Offshore sediments consist mainly of pebbles and gravels while coastal sediments are dominated by fine sand and muddy fine sand habitats. The shallow waters of the eastern part of the bay and the Seine estuary, the largest macrotidal estuary in the English Channel, are exposed to multiple anthropogenic disturbances such as maritime traffic, civil engineering works, fisheries, sediment dredging and dumping, and pollution (Dauvin, 2006). Since the middle of the 19th century, engineering works and dredging for the development of industrial and harbour activities have led to a decrease in the Seine river channel section, a lessening of the seawater exchanges and changes in the morpho-sedimentary dynamics (Le Hir et al., 2001; Lesourd et al., 2001, 2016). From the 70s to the 90s, an increase in fine-grained sedimentation in the subtidal shallow waters of the Bay of Seine in response to a downstream shift of the turbidity maximum has resulted in the evolution from sand-dominated seabed to one dominated by mud, with a threefold increase of the surface area covered by mud and sandy mud (Lesourd et al., 2001). More recently, following several years of low Seine river flows, a decrease in muddy area was reported in parallel to an increase in sandy mud and muddy sand mostly in front of the estuary, which has spread over the bay in the form of fine-grained sediment and been incorporated within the sandy fraction (Lesourd et al., 2016). The sediment dynamics within the bay is also influenced by the dumping, in the Northern Channel of the Seine estuary (Kannik) and North of the Cap de la Hève (Octeville), of 6-7 million m$^3$ per year (cumulated from two major harbours) of dredged material from Seine river and harbour basins (Marmin et al., 2016; Baux et al., 2019). In addition to the disturbances resulting from man-made modifications, the Seine estuary is placed among the most contaminated estuaries with high levels of heavy metals, particularly cadmium and lead, and organic contaminants (e.g. PAHs, PCBs, pesticides) which have highly variable effects on benthic organisms (J.-C. Dauvin, 2008; Fisson, 2014). The study site can be considered as highly disturbed before and since the beginning of the monitoring program in 1988. But, since 1988, it has undergone significant changes in terms of sedimentary dynamics in response to the "Port 2000" project, which corresponded to the large expansion of Le Havre harbour, aimed at making it a major crossroads for maritime trade and contributed to the increasing siltation rates of this part of the Bay of Seine (Tecchio et al., 2016).

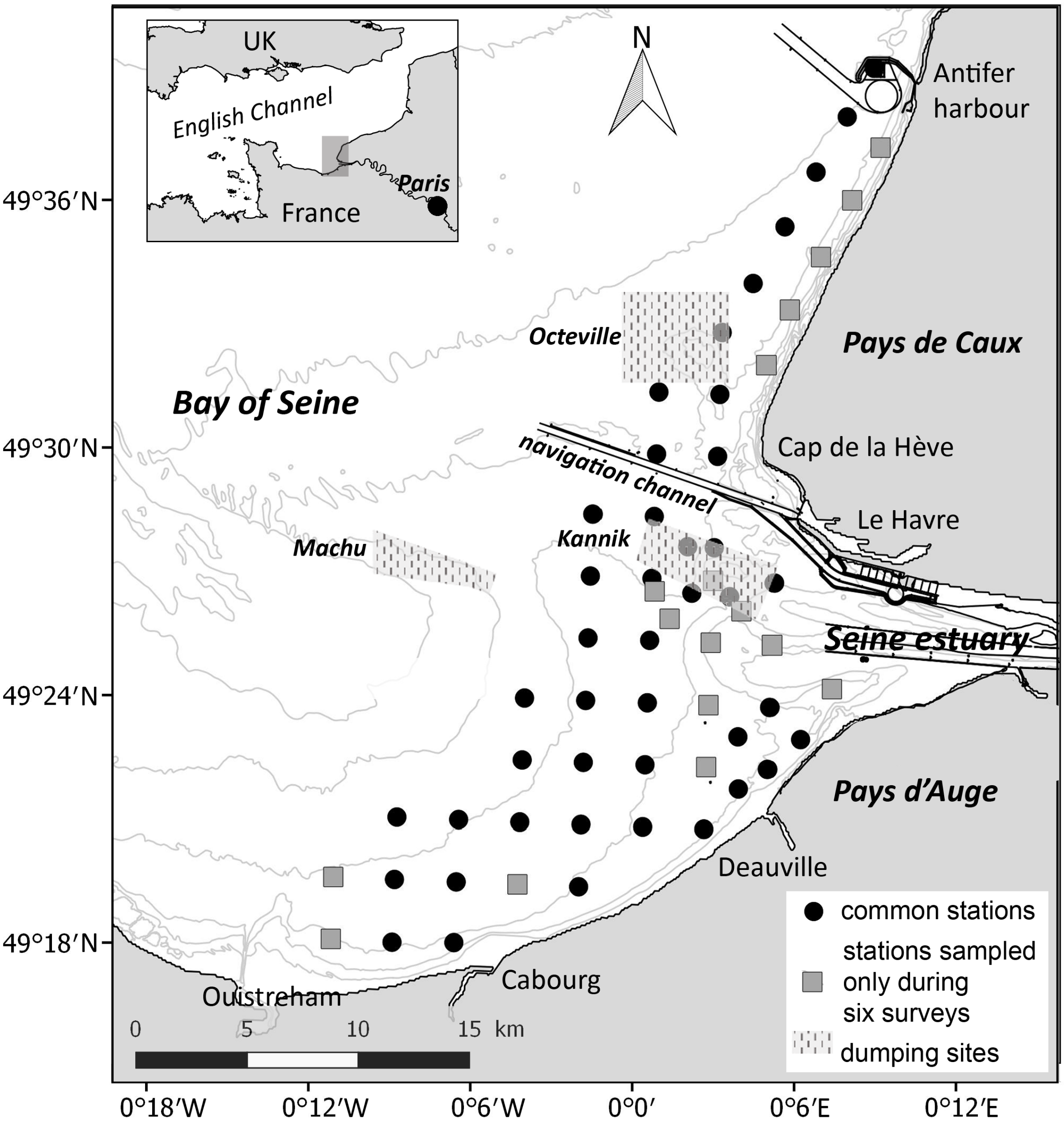


**Figure 17**: Location of the study area and of the 60 stations sampled between 1988 and 2016 during the seven sampling surveys in the eastern Bay of Seine. The black dots correspond to the 43 common stations sampled on every survey and the grey squares to the 17 stations sampled only during six surveys. The three dumping sites are indicated in grey line (Kannik, Machu, Octeville).

### II.2.2. Sampling and laboratory strategy

The macrofaunal distribution in the eastern part of the Bay of Seine was established during seven sampling surveys (named “PECTOW” surveys) carried out over 28 years (i.e. 1988, 1991, 1996, 2001, 2006, 2011 and 2016) during winter time (February/March) before the recruitment period of the dominant species. Sixty stations were sampled six or seven times from 1988 to 2016 with a total of 403 sampling station-period combinations: 43 stations were sampled on each of the seven surveys whilst 17 stations were sampled during only six surveys (Figure 17). At each station, two samples were collected using a 0.25 m$^2$ Hamon grab, except in 2016 where five samples were taken using a 0.1 $m^2$ Hamon grab for the same total sampling surface of 0.5 $m^2$. The Hamon grab has been used in previous studies undertaken within the Bay of Seine because it is effective in varied sedimentary environments, from mud to gravels (Eleftheriou & Moore, 2008), ensuring homogeneity in the protocol. An additional grab sample was collected for sediment grain analysis. Macrofauna was collected by sieving samples through a 2 mm circular mesh sieve on board, which is a sufficient mesh size to sample wintering adults of most macrofauna species (Thiébaut et al., 1997), and fixed with a 10% buffered formalin solution. Macrofaunal organisms were sorted and stored in 70% ethanol before being identified to the lowest possible taxa, generally to species level, and counted. Species or taxa names were checked against the World Register of Marine Species (WORMS, http://www.marinespecies.org) on February 2020. Densities of the different taxa are expressed as number of individuals per 0.5 $m^2$. Sediment samples of approximately 200 g were dried and sieved over sequentially arranged sieves following the Wentworth scale. Sediment type was then classified according to the silt content: fine sand (silt content < 5%), muddy fine sand (5% < silt content < 25%), sandy mud (25% < silt content < 75%) and mud (silt content > 75%) (Bachelet et al., 1997).

## II.2.3. Data analysis

### II.2.3.1. Temporal variability in species composition and densities

To quantify the temporal variability of species composition, the first 10 dominant taxa were identified for each survey. Then, the coefficient of variation (CV, i.e. the ratio of the standard deviation to the mean multiplied by 100) of their densities over time was used to describe the variability of species densities at two spatial scales, i.e. the scale of the bay and the scale of a local station, from the 43 common stations sampled on every survey. The CV at the scale of the bay was calculated using the mean and the standard deviation of the average species densities at the 43 common stations for the seven surveys. The CV at the scale of a local station was calculated using the mean and the standard deviation of species densities at each station for the seven surveys. The CV was calculated at stations for which densities were non-zero at least three times because three values are needed to calculate a standard deviation. Spatial variations in CVs at the scale of local stations provided information on the spatial heterogeneity of temporal variability in species densities.

### II.2.3.2. Gamma diversity

Gamma diversity (i.e. species diversity of the large sampling area; Whittaker, 1960) refers in this study to the total number of species sampled during each survey in the eastern Bay of Seine. For each survey, species accumulation curves were drawn after 999 permutations to describe its year-to-year variations.

### II.2.3.3. Alpha diversity

At each station for each survey, alpha diversity (i.e. species diversity in a sampling site) was calculated using species diversity indices that cover its different facets, i.e. richness, heterogeneity and evenness. These indices include species richness (S), Shannon-Weaver index (H') using $\log_2$ in its formulation, and Pielou's evenness (J'). The number of individuals per 0.5 $m^2$ (N) at each station was also calculated. To assess the variations in univariate indices among surveys, a Kruskal-Wallis non-parametric test was computed with R language (R Core Team, 2014). For those indices presenting a significant difference among surveys, a Dunn multiple comparison test was applied to identify which surveys are significantly different from the others (i.e. $p < 0.05$) (Zar, 1999).

### II.2.3.4. Beta diversity

To analyse the beta diversity (i.e. the degree of change in species composition/structure among sampling sites; Anderson et al., 2011), different analyses have been carried out depending on whether we have considered presence/absence or relative abundance data, and focused on the changes in species composition/structure among sites (i.e. spatial beta diversity) or among sampling dates at each sampling site (i.e. temporal beta diversity). The Jaccard distance was used to measure the "composition" component of beta diversity while the Bray-Curtis coefficient provided a measure of the "community structure" component of beta diversity (Donohue et al., 2013).

First, the spatio-temporal changes in community structure have been visualized from a Hierarchical Cluster Analysis (HCA) performed using the group average linkage method and the Bray-Curtis similarity index commonly used for benthic macrofauna (Field et al., 1982). Species densities were first $\log_{10}(x+1)$ transformed to reduce the contribution of the most abundant species. The resulting sub-clusters were tested using a type 1 "similarity profile" permutation test (i.e. SIMPROF test) to determine if they could be interpreted as distinct macrofaunal assemblages. The assemblages were first characterized with distinct species diversity indices (S, H’ and J’) and then with a Similarity Percentage analysis (SIMPER; Clarke, 1993) to determine which species contribute the most to the similarity between station-period combinations (i.e. one station sampled during a given survey) of a given assemblage. For this analysis, 11 station-periods out of the 403 sampling station-periods were identified as outliers and were excluded, leaving a total of 392 station-periods. These 11 station-periods corresponded to stations with very low species richness and low densities of individuals or dominance of a single species. The objective of this first analysis was to visualize the temporal changes in the spatial structure of the macrobenthic community at the scale of the eastern Bay of Seine, i.e. the spatial beta diversity.

Second, the changes in the community composition and structure over time at each station, i.e. the temporal beta diversity, were quantified using both the Jaccard similarity index calculated from species presence/absence data and the Bray-Curtis similarity index calculated from the $\log_{10}(x+1)$ transformed species densities. At each of the 43 common stations sampled on every survey and for both indices, a similarity matrix was generated between the seven surveys. One mean value of Jaccard and Bray-Curtis index was calculated from the corresponding similarity matrices at each of the 43 stations as a measure of the extent of change in the local community composition/structure over time. A high mean value indicated weak changes in the community composition/structure among surveys at the local scale while a low mean value showed large changes in the community composition/structure among surveys. Spatial variations in the mean value of similarity index at the scale of local stations documented the spatial heterogeneity of temporal variability in species composition/structure.

The proportion of variation in community structure related to sediment type was quantified using a Distance based Linear Model (DistLM) performed between the $\log_{10}(x+1)$ transformed species densities at each station-period and the sediment type data (i.e. fine sand, muddy fine sand, sandy mud, mud) at each station-period for a total of 390 station-periods. The analysis was performed using the Bray-Curtis similarity index for the species similarity matrix and by transforming the “sediment type” nominal variable into binary variables (Anderson et al., 2008).

All analyses on diversity were performed using PRIMER 7® and Permanova+ for Primer softwares (Anderson et al., 2008; Clarke et al., 2014).

## II.3. Results

### II.3.1. Sediment grain size analysis

From 1988 to 2001, the silt content was below 10 % in the majority of the study area except closest to the Seine estuary where it reached 25-50 % at some stations (Figure 18). Silt content increased slightly in 1996, especially along the coasts of Pays de Caux, where it reached 10-25 %. The increased siltation of the eastern Bay of Seine became apparent in 2006 with silt content exceeding 25 % in a high number of stations and 75 % at three stations directly in front of the estuary, off Cabourg and in Antifer harbour. While most stations were composed of fine sand and muddy fine sand between 1988 and 2001, with less than 15 % of stations with sandy mud or mud, by 2006 there had been a shift towards muddier sediments with more than 25 % of stations composed of sandy mud or mud. In 2011, the silt content tended to decrease but remained high in front of the Seine estuary and at some stations along the coasts of the Pays de Caux. Further a decreased siltation was observed in 2016. However, in contrast to earlier observations (1988 - 2001), silt content exceeded 10 % in most stations. The consistently high silt content in Antifer harbour reported in most surveys could be explained by the structure of the harbour, which traps fine sediments coming from the Seine estuary.

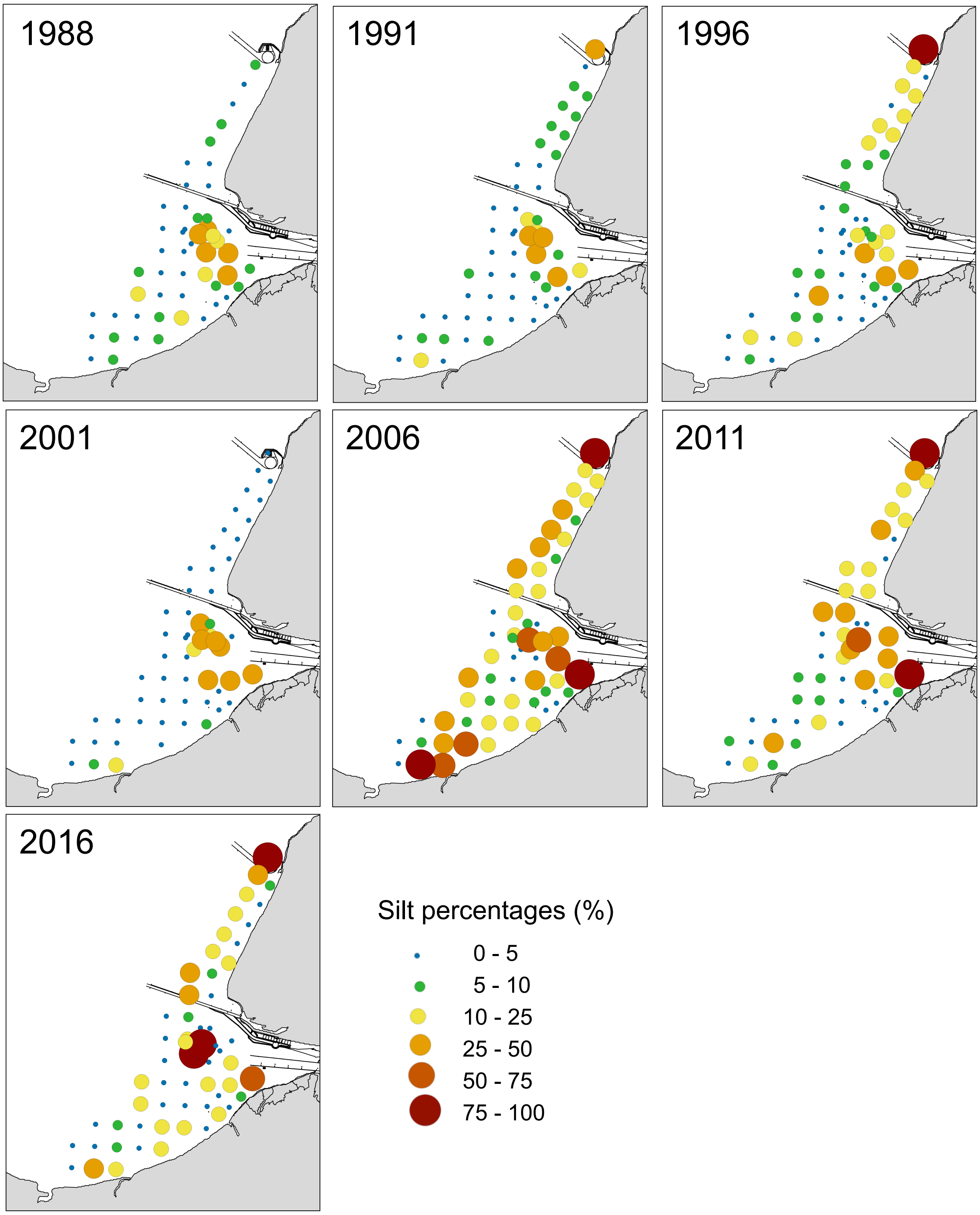


**Figure 18:** Spatial distribution of the silt percentages (%) within the sediment, in the eastern Bay of Seine for each survey.

### II.3.2. Species composition and densities

A total of 221 taxa belonging to nine phyla were reported during the survey period, including Annelida Polychaeta with 85 taxa (38 %), Arthropoda, mostly Malacostraca, with 69 taxa (33 %), Mollusca with 41 taxa (19 %) and Echinodermata with 12 taxa (5 %). The five other phyla were far less diverse: Cnidaria with four taxa, Sipuncula with three taxa, and

Chordata and Phoronida with only one taxon. Nemertea were not identified beyond phyla owing to difficulties in accurately identifying incomplete pieces of organisms. Of the 221 taxa, 40 were sampled only once during the seven surveys. Among the seven surveys, gamma diversity ranged from 90 taxa in 1988 to 158 taxa in 2016 and showed no temporal trend (Figure 19). The proportion of rare species per year (i.e. species found at one or two station-periods throughout the monitoring program) varied among years, following a temporal pattern close to that of the species accumulation curves, with 13 rare species reported in 2016 and 2006, 7 in 2011 and 2001, 5 in 1991, 4 in 1988 and 1 in 1996.

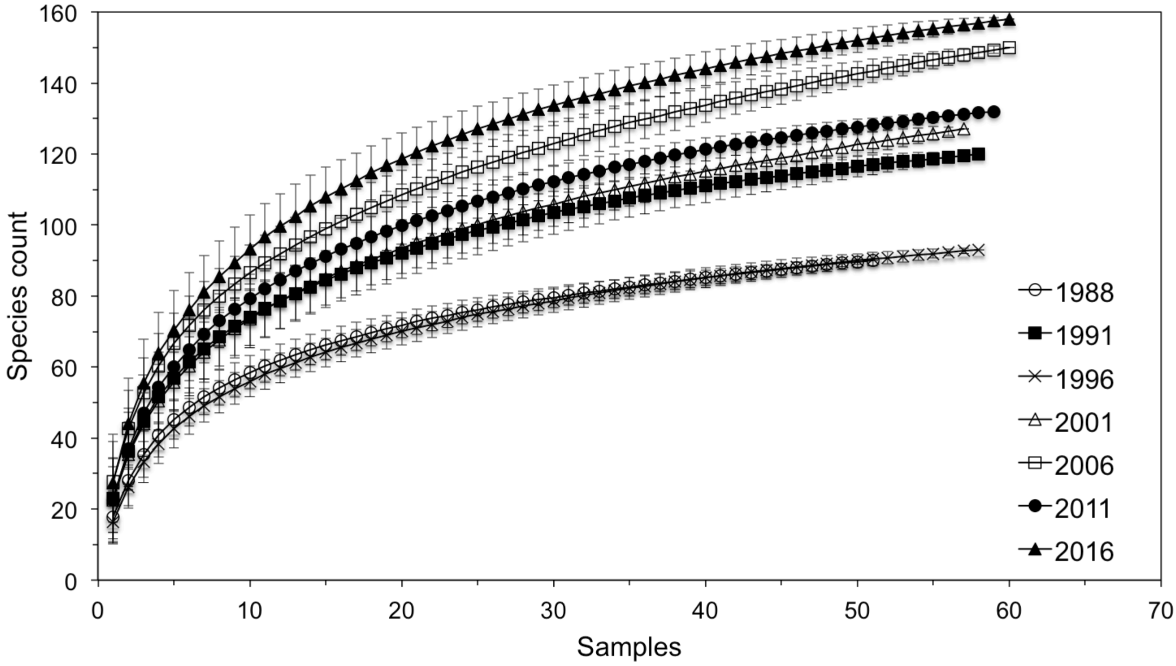


**Figure 19:** Species accumulation curves for the seven surveys performed in the eastern Bay of Seine from 1988 to 2016. Plotted values are mean values of 999 randomization of sample order.

Only twenty-one of the 221 taxa identified within the eastern Bay of Seine were ranked among the ten most abundant taxa in at least one survey (Tableau 7). Among the most abundant taxa, four species were common to the seven surveys (i.e. *Owenia fusiformis*, *Acrocnida brachiata*, *Lagis koreni* and *Nephtys hombergii*), two species six times (i.e. *Kurtiella bidentata* except in 2016 and *Abra alba* except in 2011), and one species five times (i.e. *Phaxas pellucidus* except in 1988 and 2006). These seven species represent the “typical” species of the *Abra alba* - *Lagis koreni* muddy fine sand community. *Owenia fusiformis* remained the most abundant species, except in 2001 and 2016 when it was ranked second, behind *Kurtiella bidentata* and *Phaxas pellucidus* respectively. The other taxa, which generally occurred in lower ranking positions, were (1) abundant only occasionally like

*Aphelochaeta marioni* in 2001, 2006 and 2016, or *Nucula nitidosa* in 2001 and 2006, (2) rather dominant at the beginning of the study period such as *Thyone fusus* and *Echinocardium cordatum* or (3) rather dominant at the end of the study period such as *Ampharete baltica, Magelona johnstoni* and *Melinna palmata*.

Regardless of the relative stability of the macrobenthic community in terms of species composition and relative densities of dominant species at the scale of the eastern Bay of Seine for the 28-year survey period, their average densities were highly variable over time, depending on the species. Thus, the CV of the most dominant species at the 43 common stations sampled on every survey ranged from 26% for *Lagis koreni* to 94% for *Phaxas pellucidus* (Tableau 7). The average densities of *Lagis koreni* varied by a factor of 2.2, from 13.0 ind.0.5m$^{-2}$ in 2011 to 29.2 ind.0.5m$^{-2}$ in 1988, while those of *Phaxas pellucidus* varied by a factor of 77.6, from 0.7 ind.0.5m$^{-2}$ in 1988 to 54.3 ind.0.5m$^{-2}$ in 2016. For the most abundant species, *Owenia fusiformis*, the CV reached 57% with average densities varying by a factor of 5.7, from 52.7 ind.0.5m$^{-2}$ in 2016 to 298.8 ind.0.5m$^{-2}$ in 1988.

**Tableau 7:** Rank of the 10 most abundant taxa (1 to 10), mean species density (M; ind.0.5m$^{-2}$) ± SE (Standard Error) for each sampling survey and all station-periods, and coefficient of variation (CV) of species densities (in %) at the scale of the bay only for the 43 common stations sampled on every survey.

| **Taxa** | **CV (%)** | **Sampling survey** | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1988 | | 1991 | | 1996 | | 2001 | | 2006 | | 2011 | | 2016 | |
| | | M | ±SE | M | ±SE | M | ±SE | M | ±SE | M | ±SE | M | ±SE | M | ±SE |
| *Owenia fusiformis* | 57 | 1 | | 1 | | 1 | | 2 | | 1 | | 1 | | 2 | |
| | | 298.8 | 74.7 | 214.8 | 50.1 | 90.3 | 21.2 | 64.6 | 15.3 | 190.9 | 51.5 | 153.5 | 46.4 | 52.7 | 14.0 |
| *Acrocnida brachiata* | 39 | 2 | | 3 | | 3 | | 5 | | 3 | | 5 | | 7 | |
| | | 39.3 | 8.9 | 46.2 | 10.6 | 27.1 | 7.9 | 23.0 | 8.0 | 37.4 | 11.3 | 20.2 | 7.4 | 10.0 | 2.6 |
| *Lagis koreni* | 26 | 4 | | 7 | | 4 | | 6 | | 5 | | 7 | | 4 | |
| | | 29.2 | 8.1 | 23.3 | 5.6 | 15.3 | 4.3 | 22.4 | 5.0 | 23.4 | 5.2 | 13.0 | 7.4 | 17.1 | 9.5 |
| *Nephtys hombergii* | 48 | 9 | | 6 | | 7 | | 10 | | 8 | | 9 | | 6 | |
| | | 5.6 | 0.9 | 26.1 | 3.1 | 9.3 | 1.3 | 11.2 | 1.6 | 15.0 | 2.2 | 11.7 | 1.8 | 10.4 | 1.5 |
| *Kurtiella bidentata* | 86 | 5 | | 2 | | 2 | | 1 | | 2 | | 3 | | - | |
| | | 17.7 | 6.7 | 109.7 | 39.5 | 28.4 | 11.8 | 121.1 | 35.5 | 148.4 | 48.5 | 28.2 | 8.6 | - | - |
| *Abra alba* | 78 | 6 | | 4 | | 6 | | 3 | | 9 | | - | | 5 | |
| | | 13.5 | 7.8 | 34.9 | 9.8 | 10.1 | 2.6 | 37.8 | 8.2 | 11.3 | 2.6 | - | - | 10.7 | 3.2 |
| *Phaxas pellucidus* | 94 | - | | 5 | | 5 | | 7 | | - | | 4 | | 1 | |
| | | - | - | 30.7 | 8.3 | 15.0 | 2.8 | 16.4 | 3.4 | - | - | 20.6 | 5.8 | 54.3 | 12.9 |
| *Aphelochaeta marioni* | 139 | - | | - | | - | | 4 | | 6 | | - | | 8 | |
| | | - | - | - | - | - | - | 34.6 | 8.7 | 19.6 | 8.1 | - | - | 9.2 | 2.4 |
| *Ampharete baltica* | 83 | - | | - | | - | | - | | 10 | | 6 | | 3 | |
| | | - | - | - | - | - | - | - | - | 10.3 | 2.7 | 16.9 | 5.0 | 19.8 | 3.8 |
| *Magelona johnstoni* | 159 | - | | - | | - | | - | | 4 | | 2 | | - | |
| | | - | - | - | - | - | - | - | - | 37.4 | 11.5 | 38.5 | 22.0 | - | - |
| *Magelona mirabilis* | 154 | - | | - | | 8 | | 9 | | - | | - | | - | |
| | | - | - | - | - | 6.3 | 2.0 | 12.5 | 3.6 | - | - | - | - | - | - |
| Nemertea | 131 | 3 | | - | | - | | - | | - | | 8 | | - | |
| | | 33.1 | 15.5 | - | - | - | - | - | - | - | - | 12.6 | 2.2 | - | - |
| *Nucula nitidosa* | 102 | - | | - | | - | | 8 | | 7 | | - | | - | |
| | | - | - | - | - | - | - | 14.3 | 5.4 | 17.9 | 5.2 | - | - | - | - |
| *Thyone fusus* | 74 | 8 | | 10 | | - | | - | | - | | - | | - | |
| | | 6.7 | 3.3 | 8.3 | 6.0 | - | - | - | - | - | - | - | - | - | - |
| *Echinocardium cordatum* | 53 | 10 | | - | | 9 | | - | | - | | - | | - | |
| | | 4.8 | 1.1 | - | - | 6.3 | 1.2 | - | - | - | - | - | - | - | - |
| *Melinna palmata* | 140 | - | | - | | - | | - | | - | | 10 | | 9 | |
| | | - | - | - | - | - | - | - | - | - | - | 9.7 | 3.0 | 8.5 | 1.5 |
| *Lanice conchilega* | 114 | 7 | | - | | - | | - | | - | | - | | - | |
| | | 11.5 | 9.7 | - | - | - | - | - | - | - | - | - | - | - | - |
| *Chaetozone gibber* | 113 | - | | 8 | | - | | - | | - | | - | | - | |
| | | - | - | 18.1 | 6.0 | - | - | - | - | - | - | - | - | - | - |
| *Fabulina fabula* | 98 | - | | 9 | | - | | - | | - | | - | | - | |
| | | - | - | 13.4 | 4.3 | - | - | - | - | - | - | - | - | - | - |
| *Sagartia troglodytes* | 37 | - | | - | | 10 | | - | | - | | - | | - | |
| | | - | - | - | - | 4.6 | 1.6 | - | - | - | - | - | - | - | - |
| *Corbula gibba* | 175 | - | | - | | - | | - | | - | | - | | 10 | |
| | | - | - | - | - | - | - | - | - | - | - | - | - | 7.8 | 2.1 |

At the local scale, the ranges of CV also differed between species (Figure 20). Some species such as *Nephtys hombergii* or *Thyone fusus* had a limited range of low values while other species such as *Melinna palmata* and *Magelona mirabilis* had a limited range of high values, suggesting that the temporal variations of their densities varied little in space between stations. Conversely, for other species like *Owenia fusiformis*, *Acrocnida brachiata* and *Echinocardium cordatum*, the CV showed a wide range of values among stations. There was no spatial consistency in the CV values of the mean densities for the most abundant species during the 28 years of the study period. For a given station, some species exhibited low temporal variations in their densities while other species showed high variations.

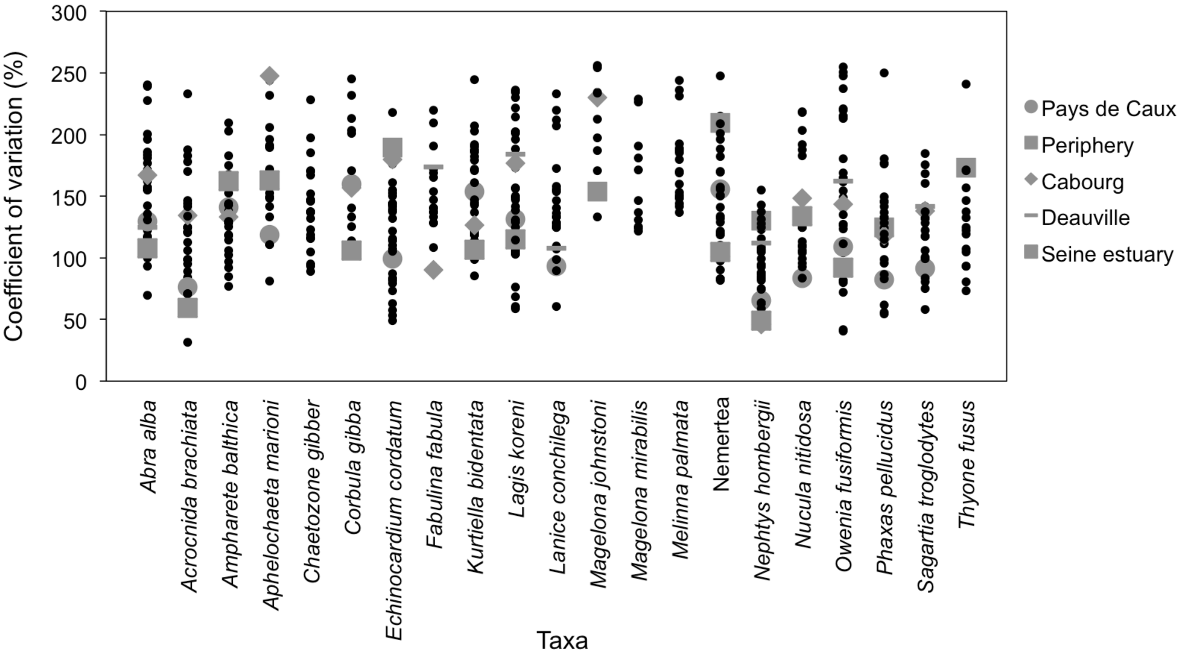


**Figure 20:** Coefficients of variation (CV) of species density (in %) calculated at each station for the 21 taxa ranked amongst the 10 most abundant species at least once, for each survey. The trend of CV values per station is given for five stations, each representative of different sectors of the study area.

### II.3.3. Changes in local diversity

The number of individuals and species diversity indices measured at each of the 403 sampling station-periods showed significant differences between years (Kruskal-Wallis test; N: $p < 0.01$; S: $p < 0.001$; H': $p < 0.001$; J': $p < 0.001$) (Figure 21). The number of individuals (N) varied between 1 and 4281 ind.0.5m$^{-2}$ with no temporal trend. There were no significant differences between the years 1988 and 1991 at the beginning of the study period and the years 2001, 2011 and 2016 at the end of the study period. N was significantly lower during 1996, compared to all other years and higher in 2006, compared to the two preceding and succeeding years. Maximal densities could locally exceed 2000 ind.0.5m$^{-2}$ except for the years 1996 and 2016. Species richness (S) ranged between 1 and 65 species and showed erratic variations with time. Dunn post-hoc tests indicated that S was significantly lower during years 1988 and 1996 compared to other surveys and significantly higher for the years 2006 and 2016. Intermediate values were reported for the years 1991, 2001 and 2011. Shannon index (H') varied between 0 and 5.07 while Pielou's evenness (J') varied between 0.07 and 0.97, both being significantly lower in 1988. H' and J' increased significantly between first and second surveys and remained constant for the last surveys (i.e. no significant differences between these last surveys).

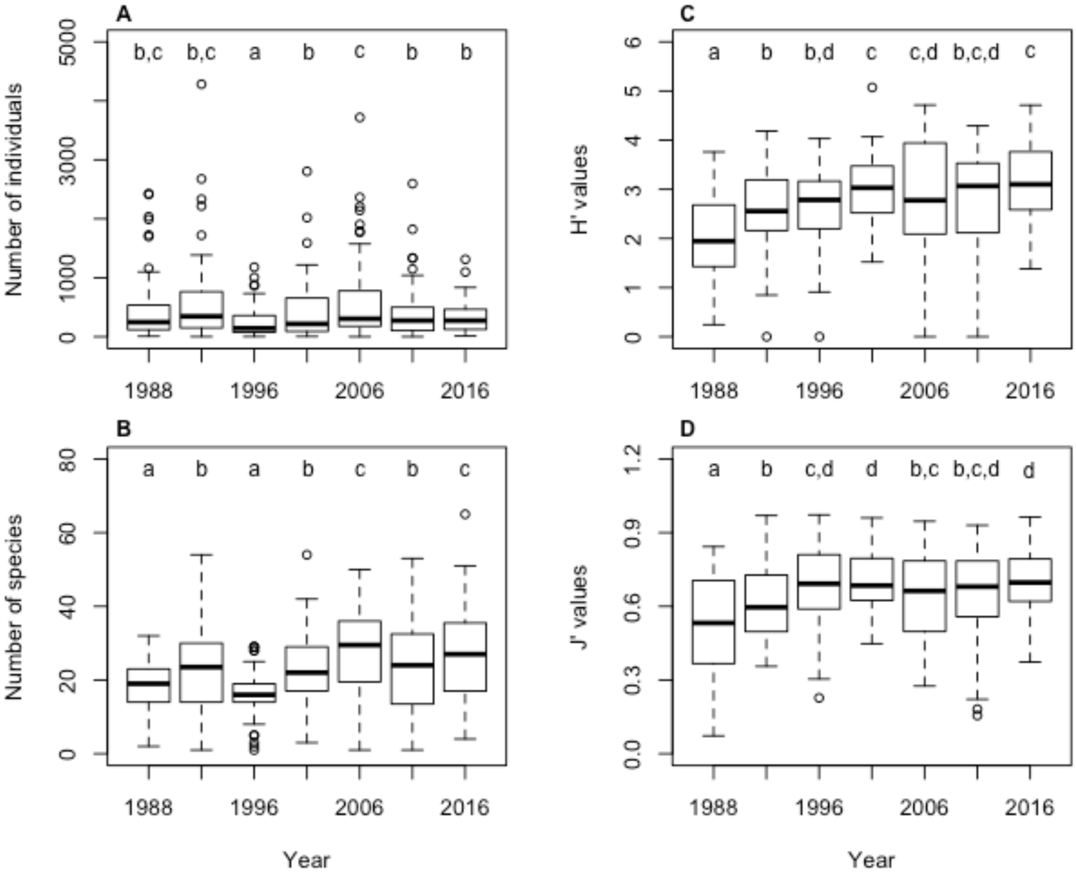


**Figure 21:** Boxplot representation of the species diversity indices calculated for each survey at each station: (A) Number of individuals (N); (B) Species richness (S); (C) Shannon-Weaver index (H'); (D) Pielou's evenness (J'). For each plot, similar letters (a, b, c and d) above each bar indicate no statistical differences among years following the Dunn tests ($p < 0.05$).

### II.3.4. Macrofaunal assemblages

On the basis of a compromise between the results of the SIMPROF test and the need to identify a limited number of assemblages on the 392 station-periods, five assemblages were identified from the HCA at a 21% similarity level (Figure 22): one major assemblage (IV) of 334 station-periods, two assemblages composed of about 20 station-periods (I, II), and two minor assemblages with only four and six station-periods respectively (III, V) (Tableau 8).

Four station-periods were isolated and not grouped within the five assemblages leaving a total of 388 station-periods spread across the assemblages. The main characteristics of these different assemblages and sub-assemblages and their spatial distribution are given in Tableau 8 and Figure 23. The results of the SIMPER analysis are provided in Tableau 9.

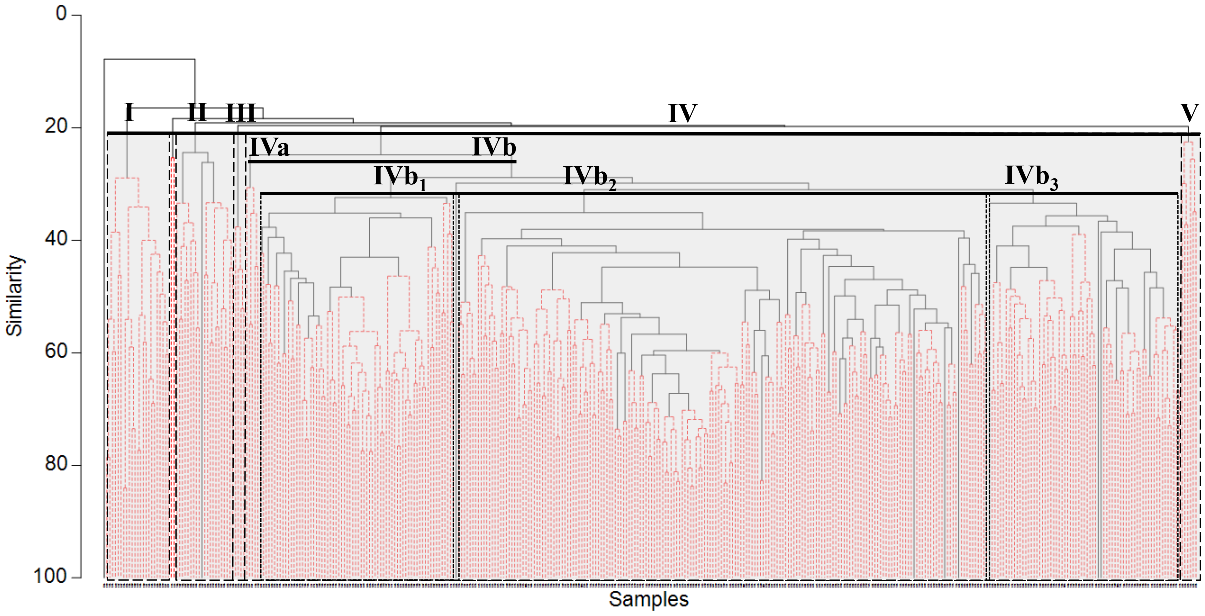


**Figure 22:** Hierarchical Cluster Analysis of macrofaunal composition led to five assemblages and several sub-assemblages based on $\log_{10}(x+1)$ transformed species abundances using Bray-Curtis similarity index and result of the SIMPROF test in red.

**Tableau 8:** Characteristics of the assemblages and sub-assemblages identified with the Hierarchical Cluster Analysis with the number of station-periods, mean species density, mean species richness (S), mean Shannon-Weaver index (H') and mean Pielou's evenness (J') ± SE (Standard Error) with a total of 388 station-periods spread across the assemblages.

| **Assemblage** | **Number of stations** | **Mean density (ind.0.5m$^{-2}$)** | **±SE** | **S** | **±SE** | **H'** | **±SE** | **J'** | **±SE** |
|---|---|---|---|---|---|---|---|---|---|
| I | 23 | 22.3 | 3.1 | 5.43 | 0.42 | 1.78 | 0.14 | 0.76 | 0.04 |
| II | 21 | 110.6 | 38.2 | 15.29 | 1.39 | 2.73 | 0.19 | 0.72 | 0.04 |
| III | 4 | 216.3 | 35.3 | 20.50 | 2.40 | 0.71 | 0.11 | 0.16 | 0.02 |
| IVa | 5 | 128.2 | 22.4 | 14.20 | 1.07 | 0.48 | 0.07 | 0.12 | 0.02 |
| IVb$_1$ | 70 | 383.1 | 43.3 | 18.40 | 0.91 | 2.44 | 0.07 | 0.60 | 0.02 |
| IVb$_2$ | 190 | 717.0 | 49.9 | 28.43 | 0.69 | 2.90 | 0.06 | 0.60 | 0.01 |
| IVb$_3$ | 69 | 194.5 | 18.8 | 27.19 | 1.11 | 0.69 | 0.04 | 0.14 | 0.01 |
| V | 6 | 38.3 | 5.6 | 13.67 | 1.31 | 3.26 | 0.12 | 0.87 | 0.02 |

Assemblage I was characterized by the lowest mean density (22.3 ind.0.5m$^{-2}$) and the lowest mean species richness (5.4 taxa; Tableau 8). Species which contributed the most to the similarity within each station-period of this assemblage were the polychaete *Nephtys hombergii* and in a lesser extent the bivalve *Abra alba* and the polychaete *Lagis koreni*

(Tableau 9). Each year, between one and six stations located in close proximity to the Seine estuary belonged to this assemblage (Figure 23).

**Tableau 9:** Results of the SIMPER analysis with the percentage of similarity within each assemblage identified by Hierarchical Cluster Analysis, species contribution to the similarity between stations within the same assemblage and mean species density.

| **Assemblage** | **Similarity (%)** | **Species** | **Contribution (%)** | **Mean density (ind.0.5m$^{-2}$)** |
|---|---|---|---|---|
| I | 36.6 | *Nephtys hombergii* | 51.9 | 6.6 |
| | | *Abra alba* | 17.0 | 3.5 |
| | | *Lagis koreni* | 11.3 | 2. |
| II | 30.5 | *Nephtys cirrosa* | 21.1 | 6.6 |
| | | *Magelona johnstoni* | 16.3 | 53.0 |
| | | *Nephtys hombergii* | 10.3 | 4.4 |
| | | Nemertea | 8.6 | 2. |
| | | *Glycinde nordmanni* | 7.0 | 2.0 |
| | | *Magelona filiformis* | 5.6 | 4.2 |
| | | *Echinocardium cordatum* | 5.2 | 9.5 |
| III | 42.6 | *Donax spp.* | 20.3 | 99.5 |
| | | *Lanice conchilega* | 16.1 | 11.3 |
| | | *Owenia fusiformis* | 9.4 | 7.8 |
| | | *Nephtys cirrosa* | 8.8 | 24.2 |
| | | *Fabulina fabula* | 7.7 | 3.0 |
| | | *Lagis koreni* | 6.2 | 4.0 |
| | | *Tritia reticulatus* | 5.0 | 5.3 |
| IVa | 36.3 | *Acrocnida brachiata* | 48.5 | 57.6 |
| | | *Echinocardium cordatum* | 11.1 | 7.0 |
| | | Nemertea | 7.4 | 1.8 |
| | | *Owenia fusiformis* | 6.5 | 13.6 |
| IVb$_1$ | 39.7 | *Owenia fusiformis* | 23.5 | 119.3 |
| | | *Nephtys hombergii* | 17.9 | 19.1 |
| | | *Lagis koreni* | 12.2 | 48.5 |
| | | *Fabulina fabula* | 7.3 | 16.7 |
| | | *Abra alba* | 6.0 | 16.9 |
| | | *Kurtiella bidentata* | 5.5 | 50.1 |
| IVb$_2$ | 41.7 | *Owenia fusiformis* | 13.3 | 264.0 |
| | | *Acrocnida brachiata* | 9.5 | 52.8 |
| | | *Nephtys hombergii* | 8.3 | 16.2 |
| | | *Phaxas pellucidus* | 7.0 | 38.5 |
| | | *Ampharete baltica* | 5.9 | 18.8 |
| | | *Lagis koreni* | 5.7 | 22.1 |
| | | *Kurtiella bidentata* | 5.2 | 120.7 |
| | | *Abra alba* | 4.8 | 30.4 |
| | | Nemertea | 4.4 | 9.1 |
| | | *Ophiura ophiura* | 4.2 | 6.5 |
| | | *Echinocardium cordatum* | 2.9 | 4.9 |

| Assemblage | Similarity (%) | Species | Contribution (%) | Mean density (ind.0.5m$^{-2}$) |
|---|---|---|---|---|
| IVb$_3$ | 39.6 | *Nephtys hombergii* | 8.6 | 6.9 |
| | | *Phaxas pellucidus* | 8.3 | 10.7 |
| | | *Glycinde nordmanni* | 8.0 | 6.7 |
| | | *Echinocardium cordatum* | 7.8 | 6.2 |
| | | *Chaetozone gibber* | 6.3 | 16.6 |
| | | *Euspira nitida* | 5.7 | 3.0 |
| | | Nemertea | 5.6 | 21.7 |
| | | *Magelona mirabilis* | 5.1 | 12.2 |
| | | *Acrocnida brachiata* | 5.0 | 16.1 |
| | | *Sigalion mathildae* | 4.3 | 3.1 |
| | | *Caulleriella alata* | 3.7 | 6.1 |
| | | *Owenia fusiformis* | 3.2 | 22.6 |
| V | 25.7 | *Nephtys hombergii* | 19.1 | 4.0 |
| | | *Hilbigneris gracilis* | 18.4 | 4.0 |
| | | *Phaxas pellucidus* | 16.3 | 4.2 |
| | | Nemertea | 13.2 | 1.3 |
| | | *Ampharete baltica* | 9.7 | 3.2 |

Assemblage II showed moderate values of N (110.6 ind.0.5m$^{-2}$), S (15.3 taxa) and H' (2.7). Characteristic species of this assemblage were mainly those inhabiting clean fine and medium sand like the polychaetes *Nephtys cirrosa* and *Magelona johnstoni* and the echinoderm *Echinocardium cordatum* (Tableau 9). This assemblage was mainly observed off the Seine estuary, but in 2011, it was also reported at two stations off Deauville (Figure 23).

Assemblage III was only observed at four stations in 2016 off Deauville (Figure 23). It was characterized by the local presence of the bivalve *Donax* spp. in fine sand whose average densities reached 100 ind.0.5m$^{-2}$. As a result of dominance by a single species, the Shannon index and Pielou's evenness of this sub-assemblage were low (Tableau 8).

Assemblage IV was the core assemblage of the muddy fine sand benthic community of the eastern Bay of Seine. It was subdivided into a small sub-assemblage (sub-assemblage IVa) and a major sub-assemblage (sub-assemblage IVb) at a 25% similarity level (Figure 22). Sub-assemblage IVa was a small assemblage observed only at five station-periods in 1988, 2011 and 2016 (Figure 23). It was mainly dominated by one species, the brittle star *Acrocnida brachiata,* such that the Shannon index and Pielou's evenness were low (Tableau 8). Sub-assemblage IVb, which extended from Antifer harbour to Ouistreham, was divided further into three sub-assemblages which differed in terms of mean densities, mean species richness and the relative density of dominant species (Tableau 8 and Tableau 9).

Sub-assemblage $IVb_2$, which was the most important in terms of the number of station-periods, showed the highest mean density (717 ind.0.5m$^{-2}$) and the highest mean species richness (28.4 taxa; Tableau 8). It was characterized by dominance of the polychaete *Owenia fusiformis* and high densities of "typical" species of the community like the brittle star *Acrocnida brachiata*, the polychaetes *Nephtys hombergii* and *Lagis koreni*, and the bivalves *Phaxas pellucidus*, *Kurtiella bidentata* and *Abra alba* (Tableau 9). The polychaete *Ampharete baltica* which has had an increasing influence, being ranked amongst the ten most dominant species in all surveys since 2006 made a large contribution to the assemblage. Sub-assemblage $IVb_1$ differed from the previous one by a lower mean density (383.1 ind.0.5m$^{-2}$) and a lower mean species richness (18.4 taxa; Tableau 8). Whilst *Owenia fusiformis* remained the most abundant species in this sub-assemblage, its mean density was about half that within sub-assemblage $IVb_2$. Only *Lagis koreni* was more abundant in this sub-assemblage than in the previous. According to SIMPER results, this sub-assemblage was characterised by five of the seven "typical" species of the community except *Acrocnida brachiata* and *Phaxas pellucidus* (Tableau 9). Finally, sub-assemblage $IVb_3$ showed a high mean species richness (27.2 taxa) but a lower mean density than sub-assemblages $IVb_1$ and $IVb_2$ (Tableau 8). The species contributing most to the similarity among station-periods of this sub-assemblage were species which were commonly observed in sandier environments such as *Phaxas pellucidus*, *Glycinde nordmanni*, *Echinocardium cordatum*, *Chaetozone gibber* and *Euspira nitida* (Tableau 9). These three sub-assemblages should be defined as three different facies of the community: (1) a *Lagis koreni* facies for the sub-assemblage $IVb_1$, (2) an *Owenia fusiformis* - *Acrocnida brachiata* facies for the sub-assemblage $IVb_2$ and (3) an impoverished *Phaxas pellucidus* facies for the sub-assemblage $IVb_3$.

The relative importance and the distribution of these three sub-assemblages changed with time (Figure 23). The sub-assemblage $IVb_1$ was reported each year off the Seine estuary and off Deauville and was slightly more extended in 2006. The sub-assemblage $IVb_2$ was observed from Antifer harbour to Ouistreham each year whereas the sub-assemblage $IVb_3$ was distributed at the western periphery of the sampling area, mostly from Cap de la Hève to Ouistreham, and disappeared from 2011 onwards. After this date, there was a tendency for homogenisation of the community with an extension of the sub-assemblage $IVb_2$.

Assemblage V was only found at coastal stations between the Cap de la Hève and Antifer harbour in 1991, 1996, 2011 and 2016 (Figure 23). Its species richness and mean densities were low. However, due to the lack of dominant species, Shannon index (H') and Pielou's evenness (J') of this assemblage were high, with the most characteristic species being the polychaetes *Nephtys hombergii* and *Hilbigneris gracilis,* and the bivalve *Phaxas pellucidus,* which were sampled at relatively low densities (Tableau 9).

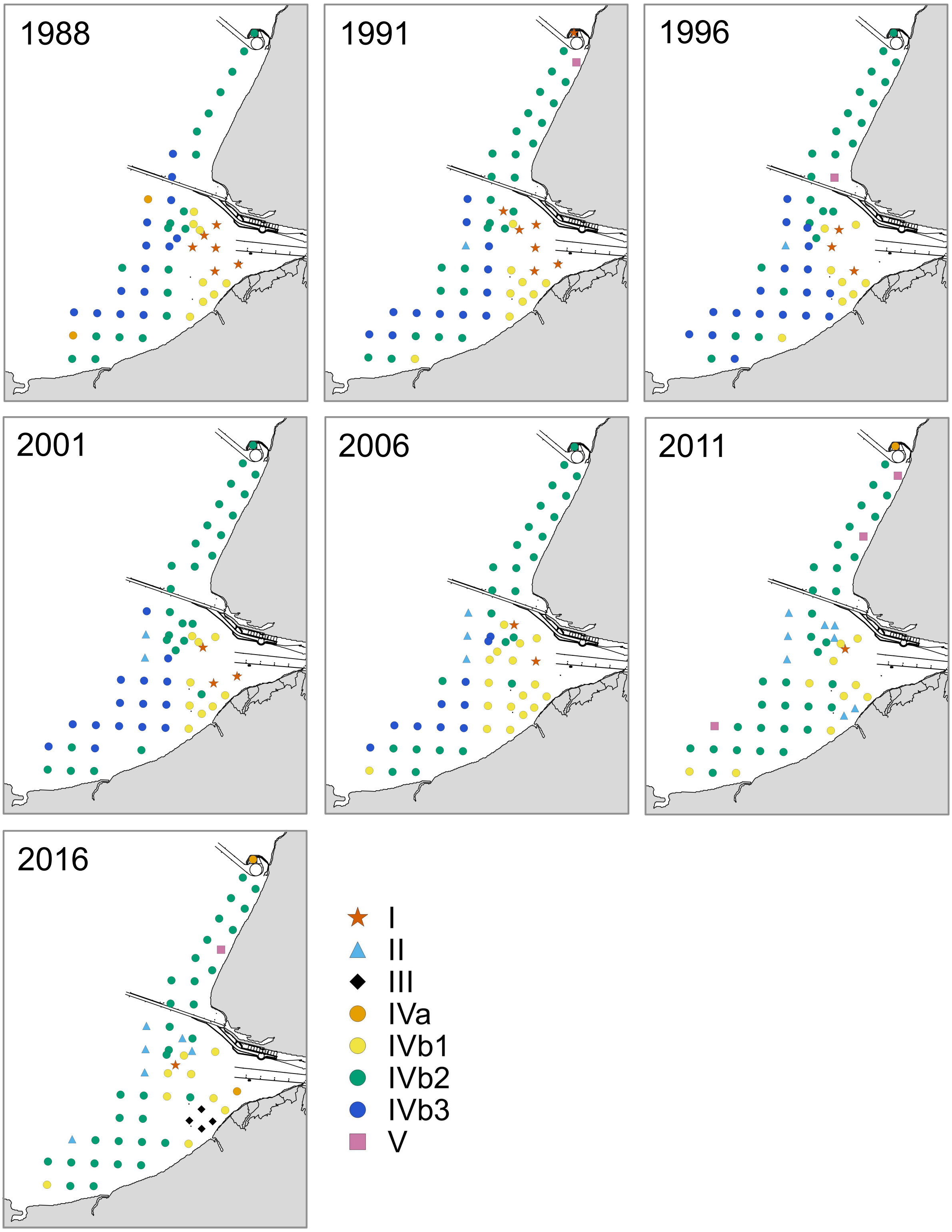


**Figure 23:** Spatial distribution of assemblages and sub-assemblages identified with Hierarchical Cluster Analysis in the eastern Bay of Seine for each survey. The number of stations for each survey was 50 in 1988, 57 in 1991, 55 in 1996, 56 in 2001, 58 in 2006, 56 in 2011 and 56 in 2016.

To assess the extent of change in the community structure over time at local scale, the mean value of the Bray-Curtis similarity coefficient was calculated at each station between all pairs of sampling surveys (Figure 24). The less variable stations (i.e. Bray-Curtis similarity coefficient > 50 %) were located in the Northeast of the Bay of Seine, along the Pays de Caux between Antifer harbour and Le Havre, and to a lesser extent at some stations between Ouistreham and Deauville. These stations belonged mostly to the sub-assemblage $IVb_2$ each year (Figure 23). Conversely, the year-to-year changes were more marked at stations located in front of the estuary and at some stations between Deauville and Ouistreham. These patterns of relative stability/variability of community structure at the local scale remained consistent when quantifying only compositional change by using the Jaccard similarity coefficient (Figure 24). The relationship between average values of the Bray-Curtis and Jaccard similarity coefficients was positive and highly significant ($R^2$= 0.894; N= 43; $p < 0.001$) (Figure 25).

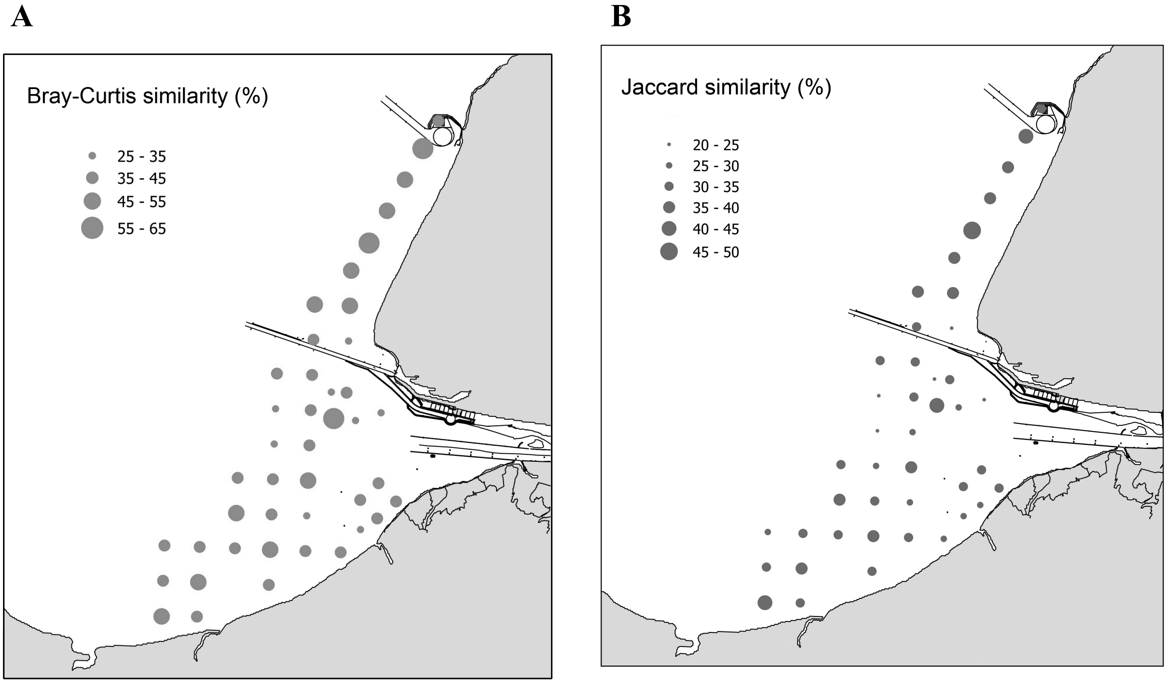


**Figure 24:** Spatial distribution of the mean values of (A) Bray-Curtis and (B) Jaccard similarity coefficients (temporal beta diversity) at each of the 43 common stations sampled on every survey in the eastern Bay of Seine.

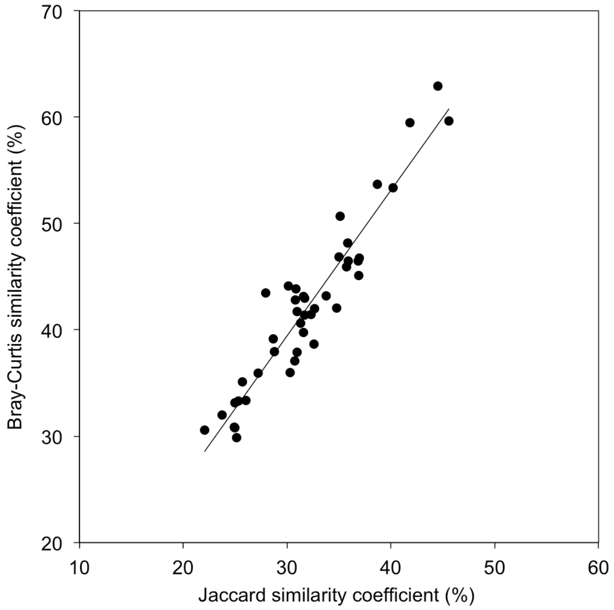


**Figure 25:** Linear regression between mean values of Bray-Curtis and Jaccard similarity coefficients at each station ($R^2 = 0.894$; N= 43; $p < 0.001$).

The DistLM showed that the sediment type had a highly significant effect on the spatio-temporal changes in the community structure ($p < 0.001$) but explained only 4.6% in the variation of the community structure.

## II.4. Discussion

### II.4.1. Stability *vs.* variability at different scales

This study investigated the spatio-temporal changes in the composition and structure of the muddy fine sand benthic community of the eastern Bay of Seine between 1988 and 2016 to understand how the macrobenthic community varies according to the scale of observation (i.e. the "study area" scale, the "assemblage" scale and the "local station" scale) and the different measures of stability (e.g. variability of densities based on CV, β-diversity). Whilst the eastern Bay of Seine is exposed to multiple anthropogenic stressors that have persisted over time, the main changes during the study period have been the evolution of sediment dynamics, resulting in repercussions at different scales: widespread increased siltation in the eastern Bay of Seine since 2006 as evidenced by our results and Lesourd et al. (2016) at the regional scale, and large volumes of dredged and dumped sediments at the local scale [4.5 million $m^3.y^{-1}$ at the Kannik dumping site (Marmin et al., 2016) and 2-2.5 million $m^3.y^{-1}$ at the Octeville dumping site (Baux et al., 2019)].

#### II.4.1.1. Variability at the study area scale

At the “study area” scale, only 10% of the total number of identified taxa (21 out of 221) was ever among the first ten most abundant taxa. A pool of only seven typical species were ranked among the most abundant taxa at least five times out of the seven surveys and drove the temporal evolution of the community composition: *Owenia fusiformis*, *Acrocnida brachiata*, *Lagis koreni, Nephtys hombergii*, *Kurtiella bidentata*, *Abra alba* and *Phaxas pellucidus*. However, the first observation of *Melinna palmata* in 2002 (Dauvin et al., 2007b), its ranking within the ten dominant species since 2011 and the increase in density of the polychaete *Ampharete baltica*, which are both associated with mud and muddy sand habitats (Oyenekan, 1988; Zettler et al., 2013), reflect major effects of the recent siltation of the eastern part of the Bay of Seine. The siltation resulted from both alteration of the morpho-sedimentary dynamics of the Seine estuary *via* river flows and flood intensity, and the increase of dredged sediment deposit following the extension of Le Havre harbour along the Cap de la Hève-Antifer area (Lesourd et al., 2001; Méar et al., 2018; Baux et al., 2019).

At the scale of the whole study area, the total species richness as well as mean values of local diversity (i.e. local taxonomic richness, Shannon’s index and Pielou’s eveness) displayed no general trend of increasing alpha and gamma diversity although significant differences between years were observed, in particular alpha diversity was lowest at the beginning of the study in 1988 and in 1996. Such year-to-year differences could be partly explained by large variations in dominance patterns of some abundant species like *Owenia fusiformis* for which mean densities varied from 214.8 ind.0.5m$^{-2}$ in 1991 to 90.3 ind.0.5m$^{-2}$ in 1996. Dauvin and Gillet (1991) already reported large year-to-year variations in *Owenia fusiformis* densities which were related to large year-to-year variations in the recruitment. They proposed several hypotheses to explain these variations: a failure in the reproduction, an export of most larvae outside the bay, and a low survivorship of young recruits. The lowest local species richness in 1988 and 1996 was to be compared with lowest gamma diversity in the same years which was partly related to the proportion of rare species.

The five years sampling frequency precluded assessment of the effects of climatic oscillations on species densities or local diversity at decadal or sub-decadal scales as observed in the German Bight (North Sea) in response to the North Atlantic Oscillation (Kröncke et al., 1998; Shojaei et al., 2016) or in the Bay of Banyuls (Mediterranean Sea) in response to the Western Mediterranean Oscillation (Bonifácio et al., 2019). However, analysis of temporal changes in the benthic community at one station off the Seine estuary sampled yearly between

1983 and 1992 showed that greatest change occurs at seasonal time scales (Fromentin et al., 1997). Year-to-year changes in community structure, in response to the alternation of cold and mild winters, were of low amplitude.

### II.4.1.2. Variations at the assemblage scale

At the "assemblage" scale, the overall community structure persisted over time with three dominant assemblages which differed in terms of taxonomic richness and relative densities of the dominant species: the *Lagis koreni* facies off the Seine estuary and off Deauville, the *Owenia fusiformis* - *Acrocnida brachiata* facies from Antifer harbour to Ouistreham and the impoverished *Phaxas pellucidus* facies at the periphery of the study area. These assemblages, which represent 84% of the sampling station-periods from 1988 to 2016, were very similar in terms of distribution and characteristic species with those already described by Thiébaut et al. (1997) from observations carried out through four winter surveys between 1986 and 1991. The remaining assemblages included only a small number of station-periods, between 1 and 8 %, and were characterized by low internal similarity. They were interspersed within the other assemblages with no specific spatial identity and seemed to correspond to very local assemblage composition and structure.

The relative importance and the distribution of the three main assemblages changed little with time but the *Owenia fusiformis* - *Acrocnida brachiata* facies extended in 2016 to cover 58% of sampled stations. This extension led to a decrease in the spatial beta diversity and consequently a biotic homogenization of the community structure which is now recognized to be a major broad-scale consequence of anthropogenic stressors in both terrestrial and marine ecosystems (Thrush et al., 2006; Socolar et al., 2016). In soft sediments, biotic homogenization can be the result of various stressors including physical disturbance such as increased sediment inputs and deposition, the selective removal of habitat-forming species and the proliferation of engineer or non-indigenous species (Thrush et al., 2004; Rigolet et al., 2014). The recent spread of fine particles over the entire eastern Bay of Seine, corresponding to a decrease in the total muddy area and relative increases in sandy mud and muddy sand, is likely an important contributor to the observed biotic homogenization (Lesourd et al., 2016).

### II.4.1.3. Variability at the local station scale

At a smaller scale, i.e. the "local station" scale, variability of species densities and community structure were more complex. Several patterns were observed regarding the spatio-temporal variations of species densities. For some species, temporal variation of densities varied little in space (i.e. between stations), whether these were low variations as for *Nephtys hombergii* or high variations as for *Melinna palmata*. Conversely, for other species like *Owenia fusiformis*, temporal variation in density varied greatly in space, with some stations showing low temporal variation whilst others showed considerably higher levels of variation. Beyond temporal variation in density at the bay scale that could be attributed to inter-annual variation in recruitment intensity depending on the species biological traits, such spatial variability in temporal variations suggest that some stations are more stable than others. This population level observation was also observed at the community level, with high variability in temporal variation in community composition and community structure amongst stations. The least variable stations were reported along the Pays de Caux and between Ouistreham and Deauville within the *Owenia fusiformis - Acrocnida brachiata* facies, whilst those displaying highest variability were located in front of the Seine estuary and off Deauville. Higher temporal variability in these shallow parts of the bay could be related to their exposure to greater instability in morpho-sedimentary dynamics in response to several human and natural stressors. In particular, high seasonal variations in the sedimentary regime were reported with soft mud deposits in winter greatly reworked by waves and tidal currents, leading to alternations of deposition and erosion periods corresponding with the seasons and meteorological events (Lesourd et al., 2001; Garnaud et al., 2002). On the contrary, the high densities of the tubicolous worm *Owenia fusiformis* which dominated the assemblage reported along the Pays de Caux and off Ouistreham are expected to have sediment stabilizing effects with positive effects on the persistence of the community despite the presence of the Octeville dumping site off Cap de la Hève (Volkenborn et al., 2009).

## II.4.2. Mechanisms involved in the long-term persistence of the community

At the regional scale, the composition and the structure of the macrobenthic community did not show any major changes over the 30 years of the study despite the presence of continuous anthropogenic pressures since the beginning of the monitoring program, in particular the redevelopment of Le Havre harbour with the "Port 2000" project.

Contrary to what would be expected for a system exposed to multiple stressors including climate change which are known to have important non-linear effects on coastal benthic communities (Hewitt et al., 2016), a relative stability of the community is highlighted. For example in the North Sea, changes in the distribution of various species were reported at a large regional scale between 1986 and 2000, in response to environmental factors such as increased sea surface temperature and primary production (Kröncke et al., 2011). At shorter time scales, decadal changes in a local community structure have also been observed in different parts of the North Sea in response to climate change and eutrophication (Frid et al., 2009; Shojaei et al., 2016). At the scale of the Gulf of Lions (Mediterranean Sea), Bonifácio et al. (2018) showed important changes in macrofauna composition in a littoral fine sand community at a 12-year interval due to climatic events which control changes in the density of the dominant polychaete, *Ditrupa arietina*. These communities, although still present at the end of the studies, have undergone such changes that they could not be considered as "persistent" compared to the *Abra alba* - *Lagis koreni* community in the eastern Bay of Seine. However, the situation of a "persistent" community *sensu* Grimm & Wissel (1997), i.e. a stability property which considers a dynamic equilibrium within boundaries, is not unique. In Swansea Bay, a coastal area considered as a "heavily modified water body" exposed to diffuse and point pollution, strong similarities in the spatial distribution and species composition of benthic communities occurred between 1984 and 2014 with a group of five common species particularly persistent over 30 years (Callaway, 2016).

Different mechanisms might explain the observed persistence of the macrobenthic community in the eastern Bay of Seine over 30 years. Whilst areas more heavily impacted by human activities are assumed to have a lower biodiversity than areas less impacted by the same activities (Johnston & Roberts, 2009), these observations from small-scale studies may not occur at a larger scale. Firstly, it has been shown that communities in modified estuaries exposed to high level of toxic contaminants can be comparable in diversity to those in unmodified estuaries for epibiota or infaunal polychaetes (Dafforn et al., 2013; Clark et al., 2015). The negative impacts of contaminants on species diversity observed at small scales in laboratory experiments are not necessarily observed within field experiments performed at larger spatial scales where they could be compensated by positive effects of organic enrichment and increases in productivity. Such a compensation mechanism could occur in the highly productive eastern Bay of the Seine where maximal primary production can exceed 20 $mgC.m^{-2}.d^{-1}$ during spring (Napoléon et al., 2014).

Secondly, as pointed out by Dauvin et al. (2017), the persistence of the community could be partly due to the bentho-pelagic life cycle of dominant species, with dispersal at larval and post-larval stages influencing the capacity of species to recover from local disturbances. In particular, post-settlement dispersal which has been reported for most dominant species (Olivier et al., 1996) and is frequent over long time periods could allow species to track environmental variations by escaping adverse conditions and colonizing quickly undisturbed areas, a mechanism which can be important for the persistence of benthic communities (Pilditch et al., 2015). Bi-monthly monitoring of the sediment dynamics in the northern part of the Seine estuary showed rapid restructuring of benthic communities by juvenile drifters in response to intense episodes of sediment transport (Desroy et al., 2007). Each station evolves independently of the others, so one station can be affected by localized environmental change without others being affected, creating a small-scale mosaic. Such observations suggest that the turnover of individuals can be very high at local scale but contribute to the long-term persistence of the community at the regional scale.

Thirdly, we observed the integration of new species into the community, either in response to changes in the sedimentary environment like the polychaete *Melinna palmata* or as non-indigenous species like the North American bivalve *Ensis leei*. This assimilation occurred without any drastic changes in the community structure although the long-term risks of assimilating non-indigenous species are their influence on the recovery and the resilience of the community (Thrush et al., 2008). Introduced to the North Sea in the 1970's by the transport of its larvae in ballast water from North American Atlantic coasts and now present from Spain to Norway (Gollasch et al., 2015), the jack-knife clam *Ensis leei* was first reported in 1998 in the eastern Bay of Seine (Dauvin et al., 2007b) and has become increasingly abundant with a maximum of 78 ind.m$^{-2}$ in 2001 and 200 ind.m$^{-2}$ in 2016. The consequences of *Ensis leei* introduction appeared highly variable among regions. In the Bay of Seine, its installation did not drastically disrupt the community, and its population remains at low to moderate densities, contrary to what has been observed in the southern part of the North Sea where *Ensis leei* changed dramatically the abundance and biomass of the fine sand community in this area (Ghertsos et al., 2000). In the *Abra alba* fine sand community along the Belgian coasts, *Ensis leei* has become the most common species causing a decline in the densities of other bivalves (Van Hoey et al., 2004). In the eastern German Bight, it could facilitate the settlement of some deposit feeders by forming dense mats that stabilize the sediment and trap organic matter. Thus in this latter area, it seems to act positively by diversifying the community and not as a nuisance for other species (Dannheim & Rumohr, 2012).

Similar to *Ensis leei*, the tubicolous polychaete *Melinna palmata* was first recorded in 2002 in the eastern Bay of Seine (Dauvin et al., 2007b) and reached maximum densities of 298 ind.m$^{-2}$ in 2011 in response to the siltation of the bay. Ranked amongst the 10 most abundant taxa since 2011, *Melinna palmata* has not significantly altered the community structure nor its spatial organization over the last three decades even if, in a recent description of benthic habitats in the Bay of Seine, Baffreau et al. (2017) have described a "*Melinna palmata* sandy mud community" defined as a very muddy facies of the *Abra alba* muddy fine sand community. Indeed, although the sediment type and consequently the silt content had a significant effect on the structure of the community, its role was minor over the last three decades. This result is consistent with the relative stability of the community. We hypothesized that the increase in silt content had modified the relative abundances of some secondary species inhabiting either muddy habitat (e.g. *Melinna palmata*) or sandy habitats (e.g. *Echinocardium cordatum*) but that the dominant typical species which structured the community occupied a relatively large sediment range that remained within the sediment range observed in the present study.

### II.4.3. Sampling strategy and spatial scales

Historical data are very valuable to highlight the long-term persistence of the composition and structure of benthic communities (Callaway, 2016). The two main strategies developed to assess long-term changes in macrobenthic communities have advantages and disadvantages. The long-term monitoring of one or few stations on a regular frequency has the advantage of describing the dynamics of macrobenthic communities in relation to changes in climatic and environmental variables, which is not possible from a comparison at long time intervals of a network of stations. Such an approach is also favoured in monitoring programs dedicated to the assessment of the ecological status of French coastal water bodies for the EU Water Framework Directive (WFD). However, it raises the questions of the representativeness of the sampling station and of the spatial heterogeneity in the long-term variability of a macrobenthic community observed at a local scale. In the case study of the eastern Bay of Seine, the magnitude of temporal variations in the density of dominant species and in the community composition or structure varied greatly in space, suggesting that the perception of stability/variability of a community can vary according to the sampling station. In a heavily modified area exposed to multiple stressors acting at different spatial and temporal scales, we recommend a management strategy based on a nested sampling design that considers a variety of both spatial and temporal scales and is economically sustainable. In the case of the eastern Bay of Seine, this hierarchical strategy could be implemented as follows: (1) a network of 60 stations sampled every five years to assess the long-term changes in the beta diversity (i.e. assemblages distribution) which is now recognized as a major issue in marine ecosystems management (Thrush et al., 2006, 2008) and is essential to determine how changes in alpha diversity scale-up at larger scales (e.g. spreading of non-indigenous species); (2) a small number of four or five stations sampled at least once a year to analyse the heterogeneity in the responses of local community to multiple stressors (e.g climate change, changes in the river flow) (Hewitt et al., 2016). These stations should be representative of the main macrofaunal assemblages in the region and of areas exhibiting different levels of temporal variability.

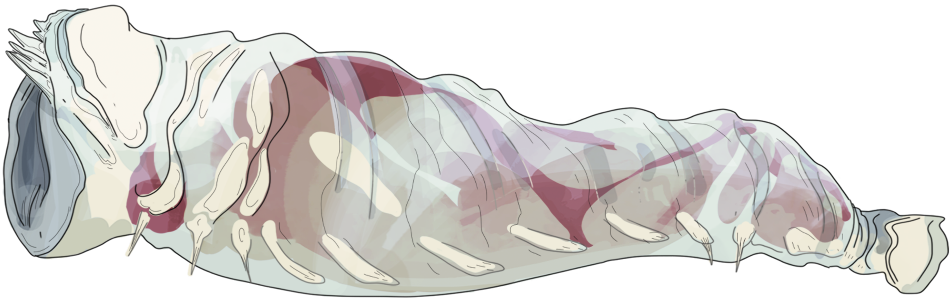
## II.5. Conclusion

Like most European estuaries and coastal embayments, the eastern Bay of Seine has been exposed to strong human impacts since the 19th century in relation to the development of industrial activities and the continued need to ensure and improve maritime traffic. Therefore the oldest data collected in 1988 are unlikely to represent a pristine state of the community, nevertheless major morpho-sedimentary changes have occurred during the last 30 years in response to variations in the Seine river flow and the development of Le Havre harbour (Lesourd et al., 2016), and the introduction of new species has been reported (Dauvin et al., 2007b). Despite its exposure to multiple stressors including climate change, the *Abra alba* - *Lagis koreni* muddy fine sand community of the eastern Bay of Seine and its facies have been persistent in terms of species composition, relative densities of the dominant species and spatial organization over the last 30 years of the study. The community is dominated by highly resilient species capable of quickly rebuilding their populations. This persistence of the benthic community was dependent on scales of space (i.e. local *vs*. regional scale), time (i.e. sampling frequency) and biological organization (i.e. population *vs*. assemblage) emphasizing the need to implement sampling strategies combining different scales. The regional persistence of the community observed in the eastern Bay of Seine differed from findings in other coastal areas where climate change drives major shifts in benthic communities at different biological levels of organisation. These results suggest that the sensitivity of benthic communities to climate change is not consistent across regions and might be reduced in heavily modified ecosystems exposed to multiple stressors. The macrobenthic community in the eastern Bay of Seine appears to be a very resilient system at a 30-year time scale, and it is likely that more time will be required to observe the consequences of climate change on the subtidal benthos in this area.

## Acknowledgments

This study was successively supported by the “French National Program on the Determinism of the Recruitment” (PNDR), the “French National Program on Coastal Environment” (PNEC) and the “Seine-Aval” program coordinated by the GIP Seine-Aval. It forms part of the doctoral research work of Lise Bacouillard partly funded by the Brittany region. We thank the crew of the research vessels “Pluteus II”, “Côtes d’Aquitaine” and “Côtes de la Manche” for their valuable assistance during the different field surveys. We also gratefully acknowledge all students, technicians and colleagues who contribute to the sampling and laboratory works since 1988, and Louis Cabioch and Christian Retière who initiated this long-term program in the eastern part of the Bay of Seine in the 1980’s. We would like to express our gratitude to Céline Houbin for her help in map production and to Lydia White for English proof reading. We thank three anonymous referees for their valuable comments on a first version of this manuscript.

# Addendum Chapter II : Long-term changes in the species and functional diversity of the muddy fine sand benthic community of the Bay of Seine



# II.6. Prerequisite

## II.6.1. Context

This study investigated the spatio-temporal changes in the composition and structure of the muddy fine sand benthic community of the eastern Bay of Seine between 1988 and 2016. Contrary to results obtained in many coastal areas, our results showed a long-term persistence of the *Abra alba* - *Lagis koreni* muddy fine sand community of the eastern Bay of Seine in terms of species composition and structure although a general shift towards muddy sediment has resulted in an increased colonisation by species associated with muddy habitats and a decrease in spatial beta diversity. This community appeared to be dominated by highly resilient species able of quickly rebuilding their populations and to be characterized by a strong spatial organization in different assemblages spread across the eastern Bay of Seine.

However, the species diversity approach used in this study was focused only on the structural properties of the community's biodiversity. Therefore the conclusions made from these results referred to only one aspect of the community diversity. According to Lausch et al. (2016) and Cochrane et al. (2016) as mentioned previously, this single aspect is not sufficient to properly assess the response of this community to the various pressures to which it is exposed. To obtain a more complete picture of the organisation and evolution of the community it could be interesting to use a complementary approach more directly related to the functioning of the ecosystem, the functional diversity based on the use of functional traits. This approach can be used as a proxy for ecosystem functioning, which is then the result of key ecological functions and community resistance/resilience after disturbance. We could use this approach to study whether the strong spatial structuration observed in terms of species would also be observed in terms of traits. Indeed, Bremner et al. (2003) found different spatial organizational patterns for the megafauna in the eastern English Channel and southern North Sea depending of the approach used, suggesting that the factors that explain the distribution of species are not the same as those that explain the distribution of traits. These authors found more small-scale heterogeneity with the functional diversity approach than with the species diversity approach. The strength and the shape of the relationship between species and functional diversity corresponds to the ecological redundancy, i.e. the number of distinct species with the same ecological functions (Micheli & Halpern, 2005). The joint use of these two approaches is then necessary because the ecological redundancy gives information on the sensitivity to disturbances.

The objectives of this complementary study were (1) to investigate the link between species and functional diversity at different spatial scales and (2) to assess how the relative long-term stability of the community structure and species composition was reflected in the ecosystem functioning.

### II.6.2. Materials and methods

The functional diversity approach was implemented in this study through a Biological Traits Analysis (BTA) based on the number, the type and the distribution of species functional traits linked to dominant ecological functions of soft-bottom benthic communities (nutrient cycling, secondary production, resistance/resilience). For this purpose, eight functional traits were used (i.e. maximum body size, life span, feeding mode, reproductive mode, development type, movement type, sediment reworking type, tolerance to disturbance) subdivided in 36 modalities. The Tableau 5 in Chapter I details the different traits and their relationship to ecosystem processes. Even if they were not exactly the same species found in the Bay of Seine and the Bay of Morlaix, trait data have been gathered in exactly the same way as for the species of the fine sand *Abra alba* community of the Bay of Morlaix (see I.2.3.3). We coded the belonging of species to the different modalities of traits with a fuzzy coding procedure on a 0 to 3 scale to include intra-specific variability and then we transformed the result for a given species and a given trait in percentage (Chevenet et al., 1994). The 'species by traits' matrix thus obtained was combined with the 'species by station-periods' matrix to obtain a 'traits by station-periods' matrix.

For the measurement of local diversity (alpha diversity), we used five different functional diversity indices which reflect complementary aspects of functional diversity (see Tableau 2 in the Introduction): functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis) and Rao's quadratic entropy (RaoQ). The different indices were computed using the dbFD function of the FD package with R (Laliberté et al., 2014). All these indices were calculated at each of the 403 station-periods from the 'traits by station-periods' matrix. The Simpson diversity index not presented in the previous study as a measure of species diversity was also calculated. Some indices were complementary between species and functional diversity: the species richness (SpRic) and functional richness (FRic); the Pielou's evenness (SpEve) and functional evenness (FEve); the Simpson diversity index and Rao's quadratic entropy (RaoQ) which is highly correlated with functional dispersion (FDis). To assess the year-to-year variations in univariate indices among surveys, a Kruskal-Wallis non-parametric test was computed and for those indices presenting a significant difference among surveys, a Dunn multiple comparison test was applied to identify which surveys are significantly different from the others (i.e. $p < 0.05$). A Principal Component Analysis (PCA) was performed on the values of the species and functional diversity indices calculated at all 403 station-periods to study their relationships. These analysis were computed with R language (R Core Team, 2014).

For the measurement of regional diversity (beta diversity), we performed a Hierarchical Cluster Analysis (HCA) using the group average linkage method and the Bray-Curtis similarity index on the $\log_{10}(x+1)$ transformed relative abundance of modalities at each station-period ('traits by stations' matrix). For this analysis, 11 station-periods out of the 403 sampling station-periods were identified as outliers and were excluded, leaving a total of 392 station-periods The resulting sub-clusters were tested using a type 1 "similarity profile" permutation test (i.e. SIMPROF test) to determine if they could be interpreted as distinct assemblages. The assemblages were characterized with a Similarity Percentage analysis (SIMPER; Clarke, 1993) to determine which modalities of traits contribute the most to the similarity between station-period combinations of a given assemblage. These analysis were performed using PRIMER 7® (Clarke et al., 2014).

## II.7. Results

### II.7.1. Study area scale

Functional diversity indices measured at each of the 403 sampling station-periods showed significant differences between years except for FEve (Kruskal-Wallis test; FRic: $p < 0.01$; FEve: $p > 0.05$; FDiv: $p < 0.001$; FDis: $p < 0.01$; RaoQ: $p < 0.01$) (Figure 26). For all indices we observed inter-annual variability with no obvious temporal trend. FRic varied between 0.02 and 7.90 and was significantly lower during the years 1996-2001 than the years 2006-2011-2016. The Fric of the years 1988-1991 was not significantly different from the other years. FEve varied between 0.19 and 0.97 with large variations among stations within a year but no significant difference between years. FDiv varied between 0.19 and 0.98 and showed erratic variations with time. FDis varied between 0 and 2.12 and RaoQ between 0 and 4.52. Both of these indices were significantly lower during the year 1988. For complementary indices of richness and evenness, Dunn tests on functional diversity indices showed less difference between successive years than Dunn tests on species diversity indices.

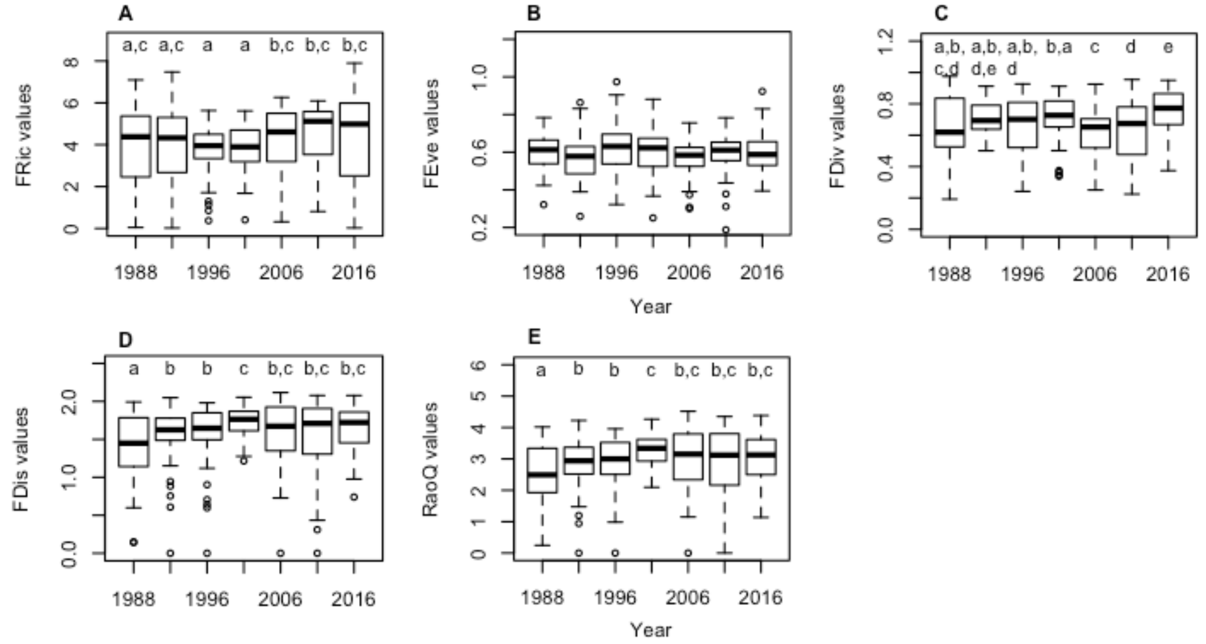


**Figure 26:** Boxplot representation of the functional diversity indices calculated for each survey at each station: (A) Functional richness (FRic); (B) Functional evenness (FEve); (C) Functional divergence (FDiv); (D) Functional dispersion (FDis); (E) Rao's quadratic entropy (RaoQ). For each plot, similar letters (a, b, c, d and e) above each bar indicate no statistical differences among years following the Dunn tests ($p < 0.05$).

The first two axes of the PCA performed on the different species and functional diversity indices explained 74% of the variance among stations with 46.94% explained by the first axis and 21.66% explained by the second axis (Figure 27). The contribution of indices to the first two axes of the PCA was relatively high for all species and functional diversity indices. The first axis was mainly explained by Simpson index, FDis and RaoQ and to a lesser extent by Pielou's evenness. The second axis was mainly described by the number of individuals, FEve and FDiv and to a lesser extent by species richness and Fric. On the PCA, the complementary indices (SpRic-FRic; SpEve-FEve; Simpson-RaoQ/FDis) were strongly correlated with a lower correlation for the evenness, suggesting that their spatio-temporal variations were consistent. FDiv and SpEve were also partially correlated.

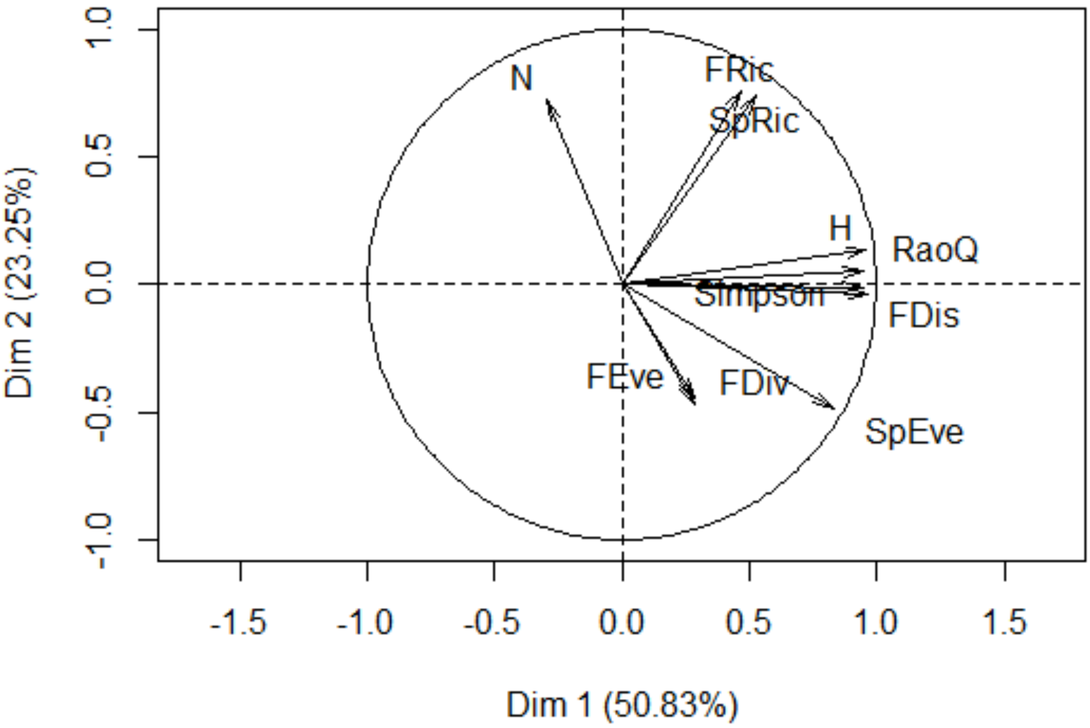


**Figure 27:** Principal Component Analysis (PCA) performed on the values of the species and functional diversity indices for the 403 station-periods sampled in the eastern Bay of Seine.

The correlations between diversity indices identified on the PCA (richness, evenness, Simpson index and Rao's quadratic entropy) were also reported on Figure 28. All correlations were positive but with different magnitude of correlation, from a $R^2$ of 0.17 for the evenness ($p < 0.001$) to a $R^2$ of 0.80 for Simpson index and RaoQ ($p < 0.001$). The regression coefficient $R^2$ was equal to 0.70 between the species and functional richness ($p < 0.001$) (Figure 28).

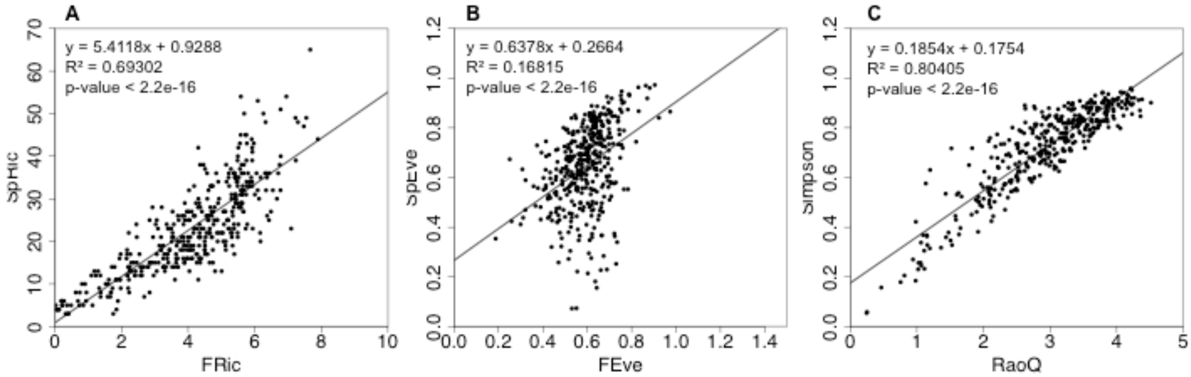


**Figure 28:** Scatter plot representation between complementary indices: (A) Richness; (B) Evenness; (C) Simpson's index and Rao's quadratic entropy.

### II.7.2. Regional scale

With a compromise between the results of the SIMPROF test and the need to identify a limited number of assemblages on the 392 station-periods, four assemblages in terms of traits composition were identified from the HCA (Figure 29): the largest assemblage IV including 349 station-periods was divided in the sub-assemblages IVa with 35 station-periods, IVb1 with 207 station-periods and IVb2 with 72 station-periods; the assemblage II comprised 54 station-periods, the assemblage I 13 station-periods and the assemblage III 7 station-periods. Four stations-periods were not grouped within these assemblages leaving a total of 388 station-periods spread across the assemblages and sub-assemblages. The results of the SIMPER analysis are provided in Tableau 10 and their spatial distribution was represented in Figure 30.

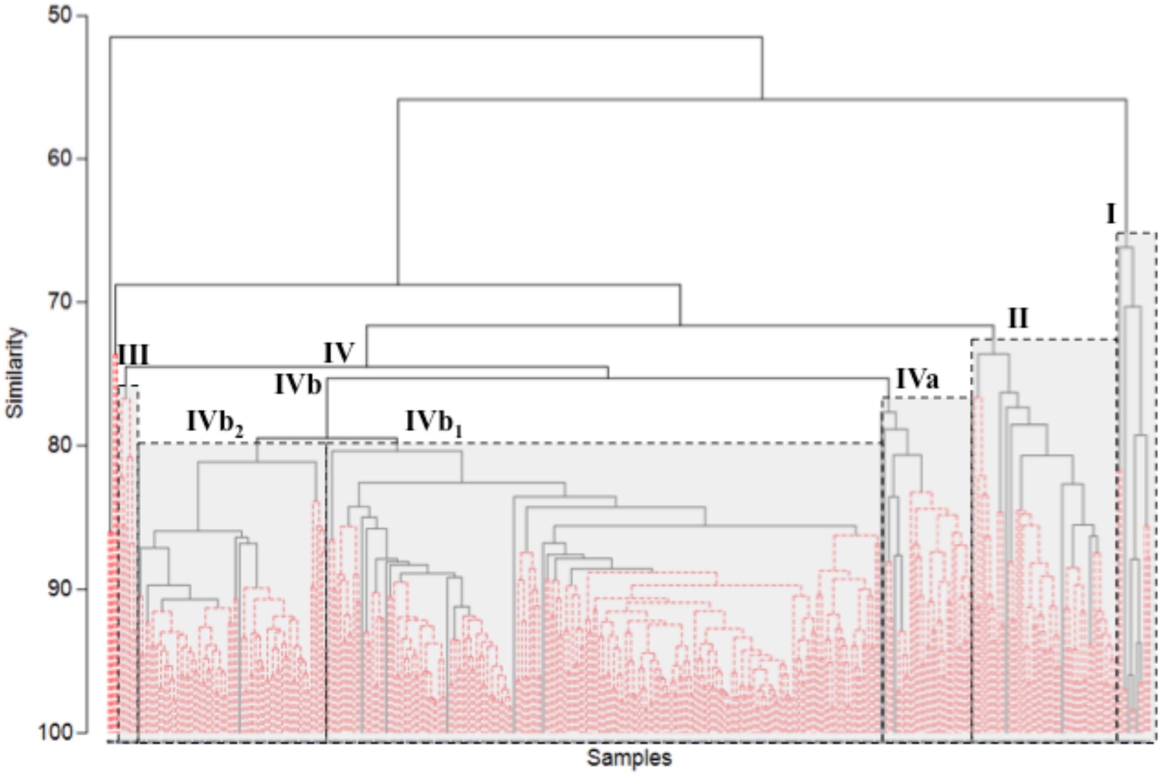


**Figure 29:** Functional Hierarchical Cluster Analysis (HCA) led to four assemblages and several sub-assemblages based on the $\log_{10}(x+1)$ transformed relative abundance of modalities using Bray-Curtis similarity index and result of the SIMPROF test in red.

**Tableau 10:** Results of the SIMPER analysis with the percentage of similarity within each assemblage identified by Hierarchical Cluster Analysis, modalities contribution to the similarity between stations within the same assemblage.

| **Assemblage** | **Similarity** | **Traits modalities** | **Contribution (%)** |
|---|---|---|---|
| I | 76.29 | Burrower | 14.51 |
| | | Crawler | 13.87 |
| | | Swimmer | 13.62 |
| | | Medium | 12.27 |
| | | Long | 11.82 |
| | | Surface deposit-feeder | 8.98 |
| II | 79.79 | Sexual | 9.01 |
| | | Surface deposit-feeder | 8.52 |
| | | Burrower | 8.32 |
| | | Filter-feeder | 8.32 |
| | | Medium | 8.12 |
| | | Long | 8.08 |
| | | Crawler | 8.02 |
| | | Swimmer | 7.69 |
| | | Asexual | 7.56 |
| III | 79.98 | Medium | 7.41 |
| | | Long | 7.21 |
| | | Lecithotrophic larva | 6.96 |
| | | Filter-feeder | 6.9 |
| | | Crawler | 6.87 |
| | | Direct development | 6.66 |
| | | Sub-surface deposit-feeder | 6.58 |
| | | Swimmer | 6.56 |
| | | Burrower | 5.63 |
| | | Surface deposit-feeder | 5.49 |
| | | Predator - Scavenger | 5.36 |
| IVa | 83.18 | Sexual | 8.1 |
| | | Planktotrophic larva | 8.07 |
| | | Medium | 7.82 |
| | | Burrower | 7.8 |
| | | Crawler | 7.46 |
| | | Long | 7.45 |
| | | Short | 7.17 |
| | | Asexual | 6.86 |
| | | Direct development | 6.71 |
| | | Surface deposit-feeder | 6.31 |
| $IVb_1$ | 85.56 | Sexual | 5.84 |
| | | Medium | 5.67 |
| | | Burrower | 5.52 |
| | | Long | 5.5 |
| | | Filter-feeder | 5.48 |
| | | Surface deposit-feeder | 5.46 |
| | | Crawler | 5.25 |
| | | Asexual | 5.1 |
| | | Short | 5.06 |
| | | Swimmer | 4.9 |
| | | Planktotrophic larva | 4.74 |
| | | Direct development | 4.59 |
| | | Sub-surface deposit-feeder | 4.34 |
| | | Upward conveyors | 4.02 |

| Assemblage | Similarity | Traits modalities | Contribution (%) |
|---|---|---|---|
| $IVb_2$ | 87.07 | Medium | 4.85 |
| | | Sexual | 4.81 |
| | | Filter-feeder | 4.8 |
| | | Burrower | 4.77 |
| | | Surficial modifiers | 4.76 |
| | | Biodiffusors | 4.69 |
| | | Long | 4.6 |
| | | Surface deposit-feeder | 4.55 |
| | | Short | 4.46 |
| | | Crawler | 4.45 |
| | | Upward conveyors | 4.23 |
| | | Asexual | 4.2 |
| | | Predator - Scavenger | 4.02 |
| | | Sub-surface deposit-feeder | 4.01 |
| | | Downward conveyors | 3.98 |
| | | Epifauna | 3.83 |

The assemblage I located in close proximity to the Seine estuary is composed each year, of one in 2001 and 2006 to three stations in 1991. Modalities which contributed the most to the similarity between each station-period of this assemblage were the movement types ‘burrower’, ‘crawler’ and ‘swimmer’ and the medium and long life span. The assemblage II was observed each year, mainly at stations off the Seine estuary and in front of Deauville but also along the Pays de Caux and off Cabourg only in 1996. It was mainly characterized by the sexual reproductive mode, the feeding modes ‘surface deposit-feeder’ and ‘filter-feeder’, the movement type ‘burrower’ and the medium and long life span. The assemblage III was reported in 1988 at one station near the Octeville dumping site, in 1996 at three stations off the Seine Estuary and one off Ouistreham and in 2016 at two stations off the Seine estuary and off Cabourg. This assemblage was characterized by the modalities medium and long life span, a development type with a lecitotrophic larva, the feeding mode ‘filter-feeder’ and the movement type ‘crawler’. The assemblage IVa was present each year and contained between one and eight stations in 2006 and 2011 respectively. This assemblage included stations located throughout the study area, from the Pays de Caux to Ouistreham. Characteristic modalities of this assemblage were mainly the sexual reproductive mode, a development type with a planktotrophic larva, the medium life span and the movement types ‘burrower’ and ‘crawler’. The assemblage $IVb_{1,}$ which was the most important in terms of the number of station-periods, was reported each year from Antifer harbour to Ouistreham and was more extended in 1988 and 2011. This assemblage was mainly characterized by the modalities sexual reproductive mode, medium and long life span, burrower, filter-feeder and surface deposit feeder. The assemblage IVb2 was also observed each year at stations from the Pays de Caux to Ouistreham and was more extended in 1991 and 2006 with many stations between Deauville and Cabourg. It was characterized by the modalities medium life span, sexual reproductive mode, filter-feeder, burrower, surficial modifier and biodiffusor.

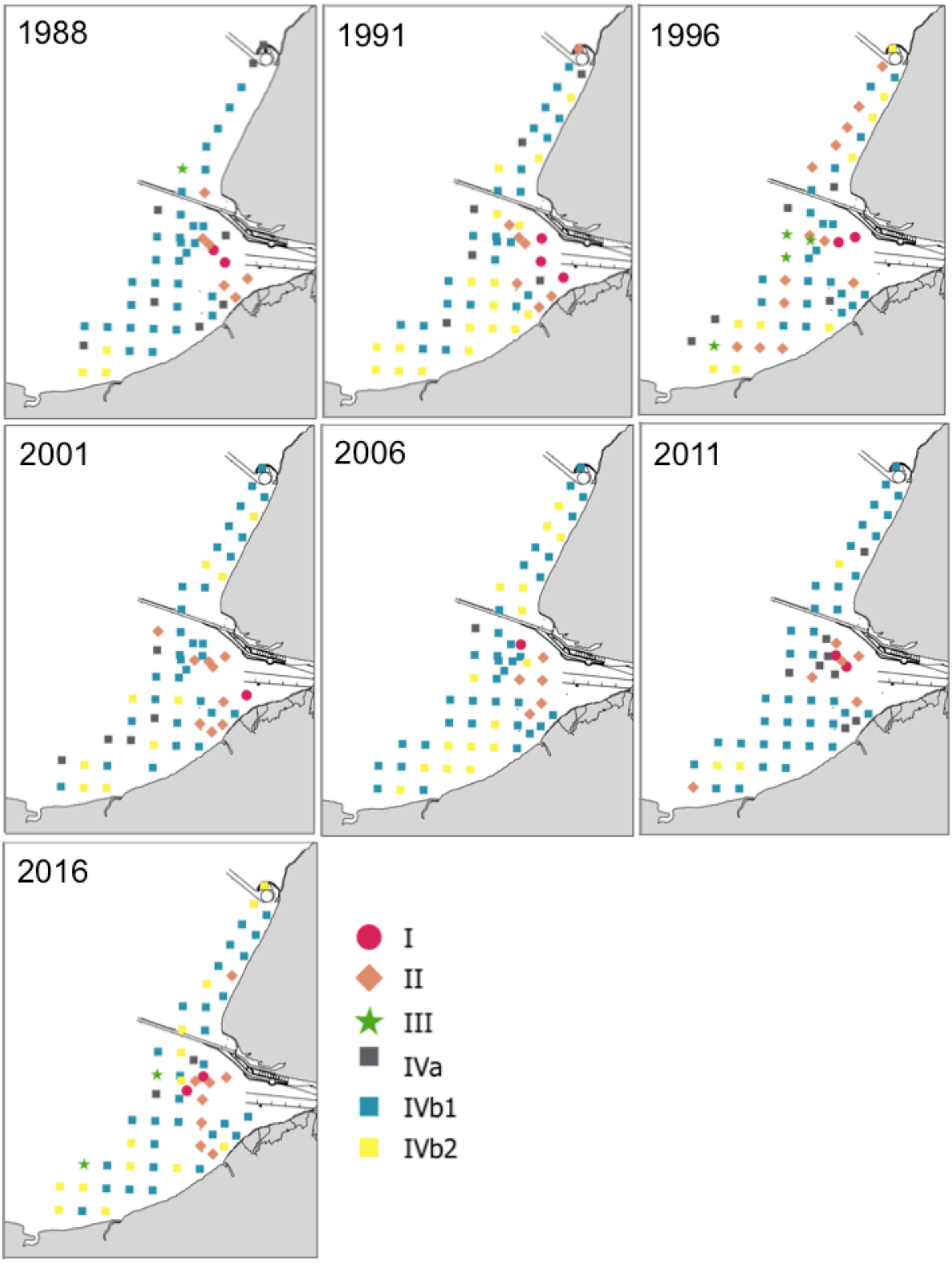


**Figure 30:** Spatial distribution of assemblages and sub-assemblages identified with the functional Hierarchical Cluster Analysis in the eastern Bay of Seine for each survey. The number of stations for each survey was 50 in 1988, 57 in 1991, 54 in 1996, 55 in 2001, 58 in 2006, 57 in 2011 and 57 in 2016.

## II.8. Discussion

This additional study investigated the link between species and functional diversity of benthic macrofauna in the muddy fine sand habitat of the eastern Bay of Seine between 1988 and 2016 at different scales of observation. It allowed assessing how the relative long-term stability of the community structure and species composition was reflected in the ecosystem functioning.

At the scale of the whole study area, the temporal evolution of the functional and specific diversity indices showed mostly erratic variations and low differences between years. These year-to-year differences partly explained by large variations in densities of some abundant species like *Owenia fusiformis*, could be also explained by variations in the functions presented by the species. Functional diversity indices showed even less differences between successive years than species diversity indices. Large inter-annual changes in species densities therefore did not have a dramatic effect on functional diversity suggesting that compensation by functionally redundant species can compensate for population fluctuations (Clare et al., 2015).

We observed highly significant correlations between species and functional diversity indices suggesting that both approaches could be redundant. This result confirms the observations already made in the Bay of Morlaix where the modalities of the traits of the most dominant species governed the temporal changes of functional diversity. Although some functional diversity indices could be also significantly correlated (e.g. Functional Dispersion and Rao's quadratic entropy, Functional Eveness and Functional Divergence), no single functional diversity index is enough to explain the spatio-temporal dynamics of local functional diversity in the bay of Seine. This result confirm the assumptions made previously by Villéger et al. (2008) and Mouchet et al. (2010) to use indices that investigate the three main components of functional diversity: richness, evenness and divergence, the two later indices being rather independent of species richness. A significant correlation between FEve and FDiv was also obtained by Mouchet et al. (2010) on artificial data sets miming various community structure.

At the scale of the eastern Bay of Seine, we did not observe exactly the same spatial organization of the benthic community by using either species or traits although there are a number of similarities. In both cases, one can distinguish assemblages which were present in front of the Seine estuary and one large assemblage subdivided in different sub-assemblages at the periphery of the community from Antifer harbour to Ouistreham. However, the decrease in the spatial beta diversity and consequently the biotic homogenization of the community structure reported on species data were not observed with the trait data (Bacouillard et al., 2020).

The traits that contributed the most to the similarity of the assemblages were life span, feeding mode, movement type, reproductive mode and development mode. The functional assemblage I seemed to correspond to a part of the species assemblage I as the stations belonging to these assemblages were located in close proximity to the Seine estuary, but the species assemblage had more station-periods. The species assemblage I was characterized by the species *Nephtys hombergii* which presents the trait modalities that characterize the functional assemblage I, i.e. burrower, crawler, swimmer and medium/long life span. Functional assemblages IVb1 and IVb2 were the most widely distributed and were characterized by the traits modalities medium life span, filter-feeder, surface deposit feeder and sexual reproduction. These trait modalities were presented by the polychaete *Owenia fusiformis* and the ophiurid *Acrocnida brachiata* which characterized the dominant specific assemblage IVb2. A parallel can thus be drawn with the sub-assemblages IVb2 and IVb3 on species data. The functional assemblage II was mostly distributed in front of the estuary, where species presenting the trait modalities surface deposit feeder, burrower, crawler and swimmer were found. It could be very partially compared to the sub-assemblage IVb1 on species data.

In detail, the overall spatial organization was more heterogeneous with the trait data than the species data and it is less easy to identify sub-assemblages which were spatially consistent. The year 1996 was very representative of this. For instance, along the Pays de Caux, the different stations belonged to 4 assemblages with trait data against only one assemblage with species data (Bacouillard et al., 2020). A similar difference was also observed for the same year off Cabourg. If this difference may in part result from the cutoff levels used on the dendrogram to identify the different assemblages and sub-assemblages, it could also reflect differences in the processes controlling the species and trait distribution as reported for benthic megafauna in the eastern Channel and south North Sea (Bremner et al., 2003). While the structure identified on species data highlight a geographical gradient from the Seine estuary that could be explained by environmental parameters like sediment grain size, organic matter content or salinity (Thiébaut et al., 1997), biological traits analysis highlighted more small-scale heterogeneity than the relative species composition analysis, with more stations in general differing from their nearest neighbour.

While the use of data on biological traits thus provided a slightly different picture of the spatio-temporal variability of the benthic community of the eastern Bay of Seine, it did not call into question the relative stability demonstrated with the species data. However, it highlighted that trait composition and consequently ecosystem functioning could vary at small spatial scales and could be driven mainly by processes acting at small scales.

# Chapter III : Density *vs.* biomass: effects of the traits weighting on the measure of functional diversity

Article en préparation.

Lise Bacouillard[1], Noémie Baux[2, 3, 4], Jean-Claude Dauvin[2], Nicolas Desroy[5], Katja Juliana Geiger[1], Franck Gentil[1], Céline Houbin[6], Éric Thiébaut[1]

[1] Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR7144, Adaptation et Diversité en Milieu Marin, Place Georges Teissier, F-29680 Roscoff, France

[2] Normandie Université, UNICAEN, UMR6143, Laboratoire Morphodynamique Continentale et Côtière, 24 rue de Tilleuls, F-14000 Caen, France

[3] Normandie Université, UNICAEN, Laboratoire des Sciences Appliquées de Cherbourg, EA 4253, 50100 Cherbourg, France

[4] Conservatoire National des Arts et Métiers, INTECHMER, 50100 Cherbourg, France

[5] IFREMER, Station de Dinard, LER Bretagne Nord, 38 rue du Port Blanc, 35800 Dinard, France

[6] Sorbonne Université, CNRS, Station Biologique de Roscoff, FR2424, Place Georges Teissier, F-29680 Roscoff, France

## ABSTRACT

While coastal ecosystems experience increasing pressures due to human activities and climate change, measurement of functional diversity indices based on biological traits is increasingly used as a tool to assess ecosystem functioning and its responses to disturbance. A review of 94 papers published since 2003 highlights large differences in the methodology used in the weighting of species abundance (density vs. biomass) to measure functional diversity in benthic systems. Using two different datasets on benthic macrofauna in the English Channel (i.e. a time-series of samples collected yearly from 1977 to 2016, and a spatial survey of 72 stations sampled once in 2016), we analysed how the weighting modify our ability to depict the spatial variability or temporal dynamics of functional diversity measured using five different indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis) and Rao's quadratic entropy (RaoQ). Except for FRic calculated on presence-absence data, the relationships among indices computed on either density or biomass data were highly variables and not consistent among communities. They depended on the differences in the distribution of species density and biomass within communities. The weighting of the relative abundance of species within a community will depend on the questions but could be also influenced by the sampling protocol (sampling date, number of replicates).

## Keywords

Functional diversity indices; Traits weighting; Methodology; Benthic community; English Channel

## III.1. Introduction

In a global aim of preservation of the functioning of coastal ecosystems, there is a growing need of operational tools to assess functional responses of ecosystems to environmental changes and anthropogenic disturbances. Traditional methods are based on the species diversity but are incomplete because they address indirectly the role of organisms in the ecosystem. Recently, the use of functional traits, morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival (Violle et al., 2007) tends to be democratized in many disciplines as well as in marine biology (Bremner, 2008; Törnroos & Bonsdorff, 2012; Villéger et al., 2012; Banas & Campbell, 2016; Givan et al., 2017). The analysis of functional diversity is becoming increasingly popular for understanding biodiversity issues (Degen et al., 2018; Morelli et al., 2018). Nevertheless, the use of this method remains limited in benthic ecology and raises a number of methodological questions such as the traits to be used and according to which selection criteria, the number of traits and modalities of traits to be retained, the traits weighting in relation to the density or biomass of the species, or the integration of intraspecific differences. Recent bibliographical reviews made it possible to clarify some methodological aspects and to define a framework but the issue of trait weighting is relatively little studied (Beauchard et al., 2017; Degen et al., 2018).

In a bibliographic review of 94 studies measuring functional diversity of benthic macrofauna and megafauna, from 2003 to 2019, we identified large disparities in the methodological choices done to measure functional diversity, in particular in the number of traits, the identity of the traits and the nature of raw data used - density or biomass (List of the studies in supplementary material). This review highlighted that for benthic macrofauna, densities rather than biomasses were used in most cases but with no explanation on this particular choice (Figure 31). An emblematic example concerns two studies carried out on the functional diversity of benthic macrofauna in the Mondego estuary (Portugal) by the same authors. In a first study, 5 stations located in the northern and southern arms of the estuary were sampled in summer 2009 and winter 2010, and functional diversity indices were computed on traits x stations matrix calculated from density data (van der Linden et al., 2012). In a second study published a couple of years later, 6 stations in the estuary were samples from 2004 to 2008, and functional diversity indices were computed on traits x stations matrix calculated from biomass data (van der Linden et al., 2016). A hypothesis we propose for the use of densities rather than biomasses for macrofauna is that the measure of density data is quicker and easier to acquire, assuming that the measure of biomass requires additional lab work. For megafauna, we did not observe any differences in the use of densities and biomasses, the two variables being used in equivalent proportions. This could be related to habits such as measuring directly on board the wet weight of the megafauna traditionally sampled by a beam-trawl. It is important to notice that with the use of functional indices, species will be distributed in a functional space according to their functional traits and their relative abundance in terms of number of individuals or biomass will weight those traits in the space.

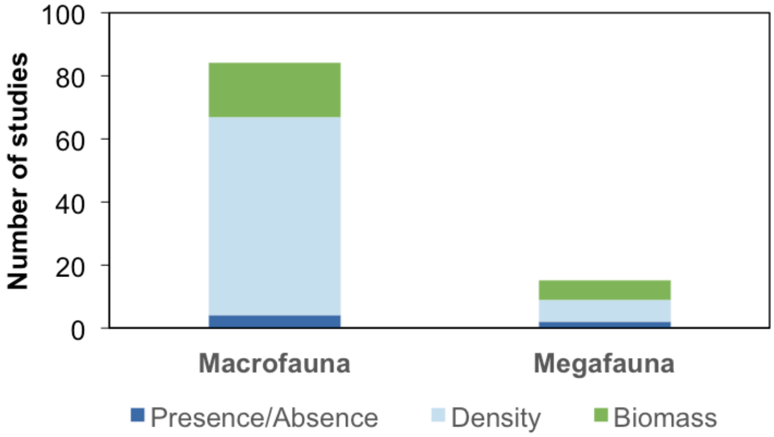


**Figure 31:** Number of studies dealing with the use of traits in benthic ecology on macrofauna or megafauna in relation to the nature of the data used (i.e. presence/absence, density, biomass).

Density data are therefore generally used without justification and biomass data are used more out of habit on megafauna. As the species density distribution will differ from species biomass distribution, the use of density or biomass data will affect the weighting of traits and possible ecological interpretations of functional diversity indices. In particular, in polluted environment, benthic communities are numerically dominated by smaller species with a short life span but are dominated in terms of biomass by larger species (Pearson and Rosenberg, 1978; Warwick, 1984; Warwick et al., 1986). The objective of this study was therefore to analyse how one methodological choice, the selection of biomass data rather than the more commonly used density data, affected the measures of functional diversity, its spatial or temporal changes, by using two different datasets on benthic macrofauna in the English Channel.

# III.2. Materials and methods

## III.2.1. Datasets

Two datasets on fine sand benthic communities in the English Channel were used in this study. The first one, located in the eastern Bay of Seine, was used to study the spatial aspect in the traits weighting. The Bay of Seine is largely open to the central English Channel and characterized by the presence of the Seine estuary, the largest macrotidal estuary in the English Channel (Figure 32 A). This study site is subject to multiple anthropogenic disturbances such as maritime traffic, civil engineering works, fisheries, sediment dredging and dumping, and pollution (Dauvin, 2006). The dataset used corresponded to the 2016 PECTOW sampling survey being part of the original long-term monitoring program of the *Abra alba - Lagis koreni* muddy fine sand community. The community is characterized by a strong spatial structuration in different assemblages spread across the eastern Bay of Seine (Bacouillard et al., 2020). In winter time (February/March 2016), 190 species were sampled at 71 stations. For this purpose, five samples were taken at each station using a 0.1 $m^2$ Hamon grab. Macrofauna was collected by sieving samples through a 2 mm circular mesh sieve on board and preserved in a 10% buffered formalin solution. In the laboratory, macrofaunal organisms were sorted and stored in 70% ethanol before being identified to the lowest possible taxa, generally the species level, and counted for each station. Species or taxa names were checked with the World Register of Marine Species (WORMS, http://www.marinespecies.org) on February 2020. Densities of the different taxa are expressed as number of individuals per 0.5 $m^2$. The biomass per taxa was estimated in ash-free dry weight (AFDW, g) and was measured by pooling individuals of the same taxa at each station.

The second one, located in the Bay of Morlaix, was used to study the temporal aspect in the traits weighting. The sampling site Pierre Noire (PN) consisting of fine sand sediment, is located in the Bay of Morlaix along the French coasts of the Western English Channel at a depth of 17 m (Figure 32 B). The fine sand *Abra alba* community of the Bay of Morlaix at PN has been monitored since 1977 (Dauvin, 1998) and was characterized by very dense populations of amphipods *Ampelisca* (Dauvin, 1987; Poggiale & Dauvin, 2001). This study site was subject to the one-off pressure of the Amoco Cadiz oil spill in March 1978 and an abrupt shift of the community in 2004-2005 (Thiébaut et al., in prep; see chapter I). The dataset used corresponds to a time series from 1977 to 2016 sampled at the PN sampling site with a total of 250 species. In spring time (March/April), ten samples were taken using a

Smith McIntyre grab. Macrofauna was collected by sieving samples through a 1 mm circular mesh sieve on board and preserved in a 10 % buffered formalin solution. In the laboratory, macrofaunal organisms were sorted, identified at the lowest taxonomic level, generally the species level, and counted. Species or taxa names were checked with the World Register of Marine Species (WORMS, http://www.marinespecies.org) on July 2020. Densities of the different taxa are expressed as number of individuals per m$^2$. The biomass per taxon was estimated in dry weight (DW, g). It was first measured for each taxon from 1977 to 1982 and for common taxa from 1977 to 1999. These data were used to build abacuses providing the mean individual biomass of each taxon in March-April and to estimate the total biomass of each taxon each year.

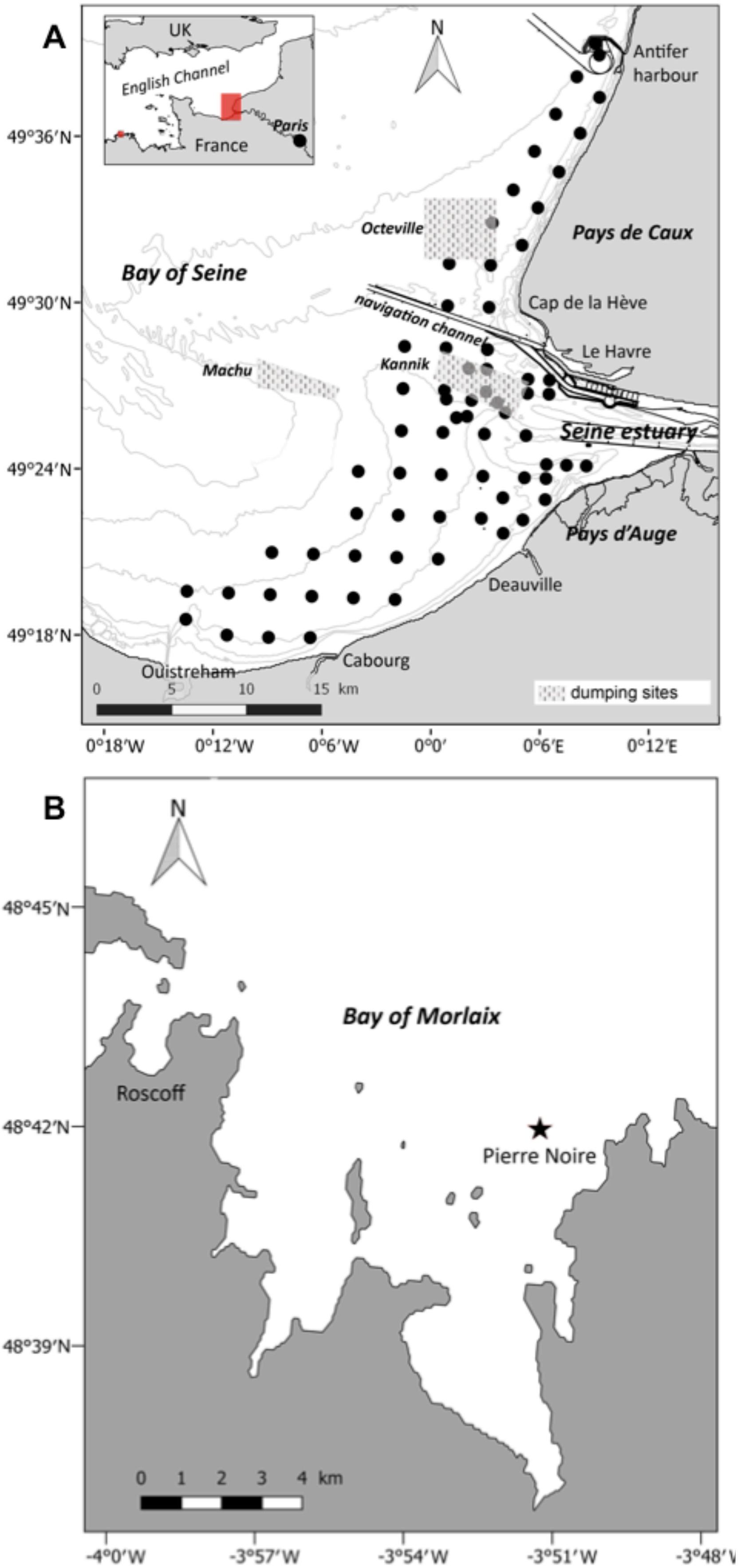


**Figure 32:** Location of the two datasets used in this study: (A) Eastern Bay of Seine and the 2016 Pectow survey; (B) Bay of Morlaix and the sampling site Pierre Noire (PN).

## III.2.2. Functional traits

To measure the functional diversity, eight functional traits subdivided in 36 modalities were used in relation to three major ecosystem functions of soft bottom benthic communities (secondary production, nutrient cycling, resilience/resistance): maximum body size, life span, feeding mode, reproductive mode, development type, movement type, sediment reworking type and tolerance to disturbance (AMBI). The functional traits and their modalities are described in the Tableau 11. Trait data were gathered from a variety of sources including publicly available databases such as the Biological Traits Information Catalogue (BIOTIC) developed by the Marine Life Information Network (http://www.marlin.ac.uk/biotc), Polytraits (http://polytraits.lifewatchgreece.eu) and the list of the AZTI Marine Biotic Index (AMBI) (http://ambi.azti.es), species identification guides, reviews on some traits, primary literature on species and expert knowledge. When data at the species level was missing, information was collected at the lowest taxonomic level, generally the genus or the family level. We coded the belonging of taxa to the different trait modalities with a fuzzy coding procedure on a 0 to 3 scale to include intra-specific variability (Chevenet et al., 1994). For a given trait, the sum of the scores of all modalities should be equal to 3 and then we transformed the result for a given taxa and a given trait in percentage. The ‘species by traits’ matrix thus obtained was combined with the ‘species by stations’ matrix for the dataset in the Bay of Seine to obtain a ‘traits by stations’ matrix and with the ‘species by dates’ matrix for the dataset in the Bay of Morlaix to obtain a ‘traits by dates’ matrix. ‘Species by stations’ and ‘species by dates’ matrices were built using either density or biomass data.

**Tableau 11:** Functional traits and their modalities used in this study.

| Functional trait | Trait modalities |
|---|---|
| Maximum body size | Very small (< 1 cm)<br>Small (1-2cm)<br>Small-Medium (3-10 cm)<br>Medium (11-20 cm)<br>Medium-Large (> 20 cm) |
| Life span | Short (< 2 years)<br>Medium (2-5 years)<br>Long (> 5 years) |
| Feeding mode | Filter-feeder<br>Surface deposit-feeder<br>Sub-surface deposit-feeder<br>Predator - Scavenger<br>Omnivore<br>Grazer |
| Reproductive mode | Sexual<br>Asexual |
| Development type | Direct development<br>Planktotrophic larva<br>Lecithotrophic larva |
| Movement type | Burrower<br>Crawler<br>Swimmer<br>Walker<br>Sessile<br>Tube dweller |
| Sediment reworking type | Epifauna/None<br>Surficial modifiers<br>Biodiffusors<br>Upward conveyors<br>Downward conveyors<br>Regenerators |
| Tolerance to disturbance (AMBI) | Sensitive<br>Indifferent<br>Tolerant<br>Second-order opportunistic<br>First-order opportunistic |

## III.2.3. Functional diversity indices

Five functional diversity indices were used to measure different components of the functional diversity as proposed by Villéger et al. (2008) and Mouchet et al. (2010): functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis) and Rao's quadratic entropy (RaoQ). Their definitions are given in Tableau 12. The different indices were computed using the dbFD function of the FD package with R (Laliberté et al., 2014). This function allowed from the 'traits by stations' and 'traits by dates' matrices to compute a species-species distance matrix from which a Principal Coordinates Analysis (PCoA) was performed. The resulting PCoA axes were used as the new 'traits' to compute the three indices FRic, FEve and FDiv. All indices are supposed to decrease after a disturbance (van der Linden et al., 2016). All the indices were calculated at each station for the dataset in the Bay of Seine and for each year for the dataset in the Bay of Morlaix with both density and biomass data.

Regressions between functional indices calculated either with density or biomass data were calculated for both datasets. For the spatial dataset in the Bay of Seine, the distribution of two representative functional diversity indices, FEve and FDiv, calculated with density and biomass data was mapped. These two indices were chosen as their regression coefficients $R^2$ were the highest and the lowest for FDiv and FEve respectively. For the temporal dataset in the Bay of Morlaix, temporal changes of all functional diversity indices calculated with density and biomass data were plotted. The Principal Coordinates Analyses (PCoA) performed on the trait matrices with density or biomass data on the temporal dataset in 1998 and 2006 were used to show the species distribution in the 2D-functional space according to their trait modalities and density or biomass. These two years were chosen as the inconsistencies between indices calculated on density and biomass data were highly different. In 1998, the values of the different indices computed on density and biomass data were highly different for all indices while they were rather similar in 2006.

**Tableau 12:** Functional diversity indices used in this study and their definition.

| Functional diversity indices | Definition |
|---|---|
| Functional richness (FRic) | Trait space filled by species |
| Functional evenness (FEve) | Regularity in the distribution of species abundance in the trait space |
| Functional divergence (FDiv) | Dispersion in the distribution of species abundances in the trait space |
| Functional dispersion (FDis) | Mean distance of individual species to the centre of the trait space |
| Rao's quadratic entropy (RaoQ) | Amount of trait dissimilarity between two random entities in the community |

# III.3. Results

## III.3.1. Relationships among indices

The regressions between functional diversity indices calculated with density and biomass data for both datasets are presented in Figure 33. Obviously, FRic is independent of the relative abundance of species so the relation perfectly fitted for both datasets. For the spatial dataset in the Bay of Seine, significant positive regressions between indices calculated with density and biomass data were reported for all indices but the magnitude of the regression varied among the indices with values of the $R^2$ varying from 0.06 for FEve to 0.46 for FDiv (Figure 33A). FDis presented a $R^2$ equal to 0.28 and RaoQ a $R^2$ equal to 0.33. For the temporal dataset in the Bay of Morlaix, significant regressions between indices calculated with density and biomass data were also reported but the sign of the correlation could vary according to the functional diversity indices. For FEve and FDiv, the correlations were positive and the regression coefficients $R^2$ varied from 0.15 to 0.49 respectively (Figure 33B). FDis and RaoQ had negative correlations with regression coefficients $R^2$ of 0.19 and 0.21 respectively. So for a given index, the magnitude of the regressions between the indices calculated on density or biomass as well as the sign of the regression may vary between the two datasets.

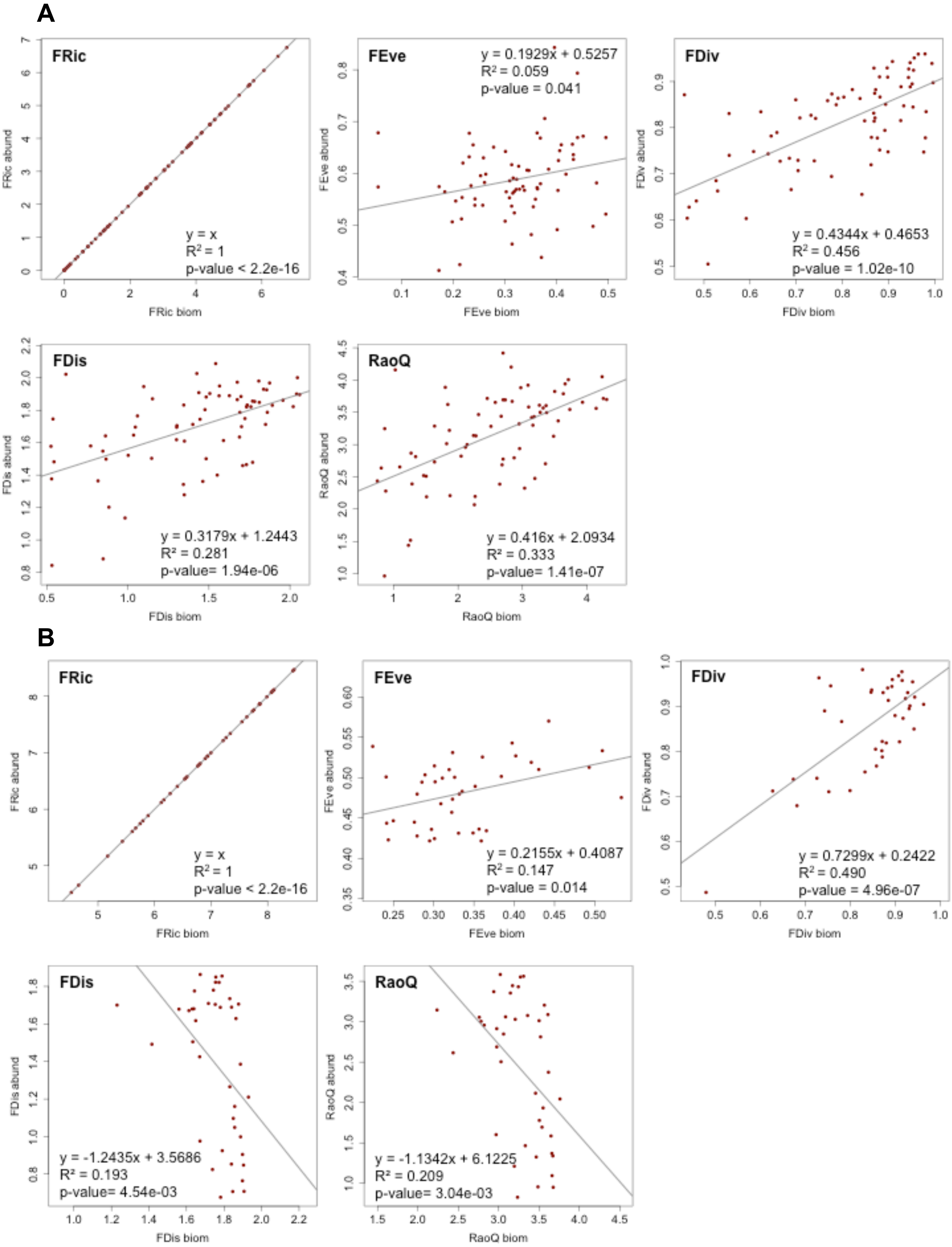


**Figure 33:** Regression plots between functional indices calculated with density and biomass data for (A) the spatial dataset in the Bay of Seine and (B) the temporal dataset in the Bay of Morlaix.

### III.3.2. Spatial distribution

The FEve and FDiv index values calculated from the density and biomass data for the spatial dataset in Bay of Seine were represented at each station on the Figure 34. Although some minor differences were observed in the spatial distribution of the two indices calculated with density or biomass data, higher values were mainly reported in front of the Seine estuary, off Deauville and in a lesser extent along the coasts of Pays de Caux for both indices. Some stations could present very different values depending on the data used. Finally, the values of the two indices appeared to be more patchily with the density data.

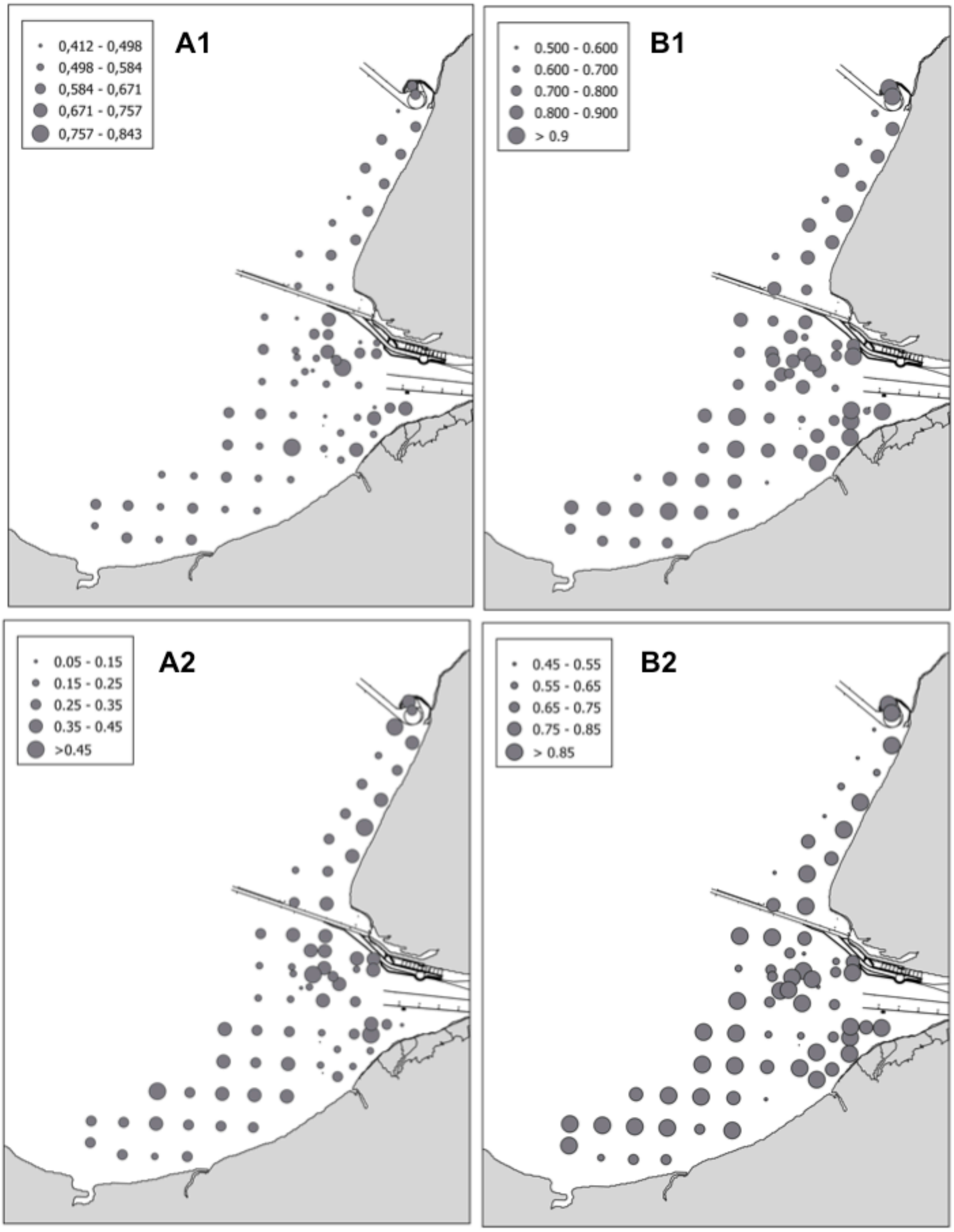


**Figure 34:** Spatial distribution in the Bay of Seine of the values of two indices (A) FEve and (B) FDiv calculated with (1) density or (2) biomass data.

### III.3.3. Temporal evolution

The indices calculated with density or biomass data showed different temporal changes (Figure 35). The range of values for FEve was different by using density or biomass data suggesting that species biomasses were more patchily distributed in the functional space (Figure 35A). FEve showed globally a similar temporal evolution with density or biomass data with some peaks in 1978, 1982, 1989 or 1995 but in 2004, the value of FEve calculated with the biomass data showed the lowest value, while it was among the highest value with the density data. On the other hand, FEve computed on biomass data exhibited higher year-o-year variations. FDiv showed a very similar temporal evolution except in 1977. Thus, a strong decrease in FDiv after the Amoco Cadiz oil spill was observed when FDiv was computed with densities. Conversely, no effect of the Amoco Cadiz oil spill was detected with FDiv when this index is calculated with biomass (Figure 35B). The high densities of the Amphipods *Ampelisca* with low biomass observed in 1977 could explain this pattern. After 1980, FDiv increased during a few years whatever the weighting of traits and remained quite high from 1983 to early 2000s before decreasing at the end of the time-series. The indices for which the results were the most different were FDis and RaoQ (Figure 35C, D). In 1977, before the Amoco Cadiz oil spill, the values of these two indices calculated with densities were much lower than the values of the indices calculated with biomasses. The effect of the Amoco Cadiz oil spill was noticeable in 1978 with the increase of the value of indices calculated with densities but not with the biomass data. From 1987 to 1994, during the recovery period, there was a decrease in the values of these two indices calculated with the density data but not with the biomass data. A second major increase in both indices on density data was also observed during the second regime shift in the Bay of Morlaix. While major changes in the RaoQ and FDis calculated with the density data were highlighted after the two major disturbances in the Bay of Morlaix but in a direction opposite to the expectations, these indices calculated on biomass data were rather stable.

Although all indices were supposed to decrease after a perturbation, the changes of the indices with density or biomass were not always the same and showed sometimes responses contrary to expectations.

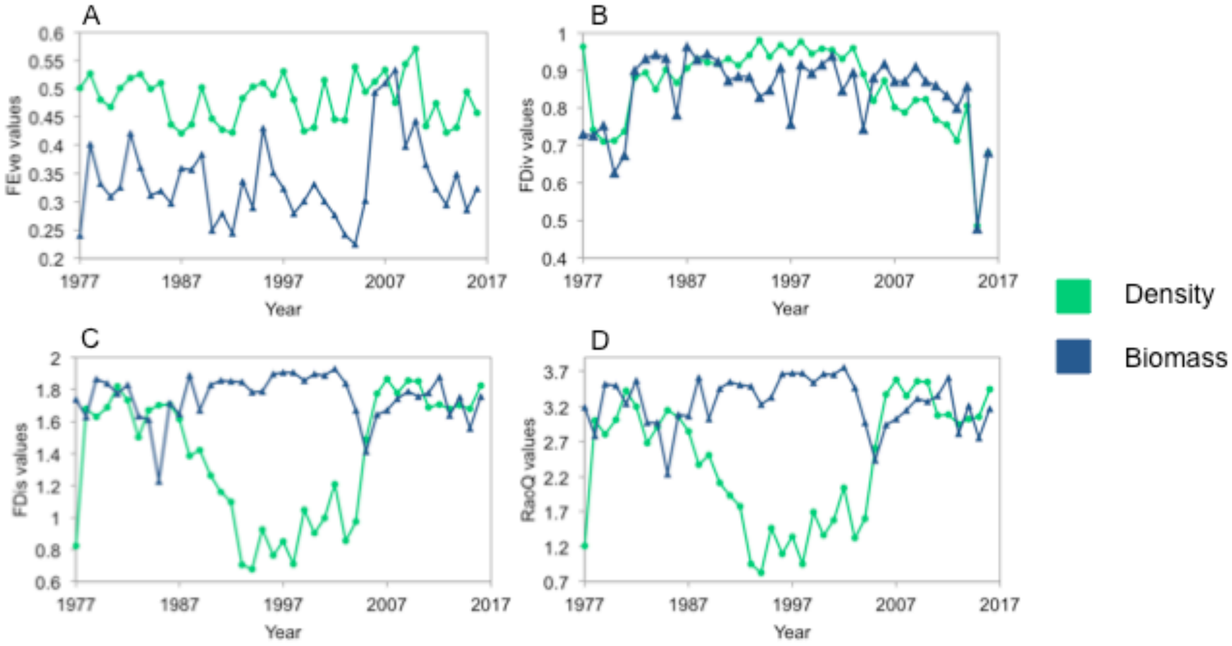


**Figure 35:** Temporal evolution of functional diversity indices for the temporal dataset in the Bay of Morlaix (A) FEve; (B) FDiv; (C) FDis; (D) RaoQ.

Depending on the type of data used, the species that impacted the analysis in the PCoA and therefore in the calculation of functional diversity indices were different (Figure 36). In 1998, the species with the highest densities were *Ampelisca tenuicornis*, *A. sarsi* and *A. armoricana* while those with the highest biomass data were *Nephtys spp*., *Tritia reticulata* and *A. armoricana*. The species with highest densities are rather similar in terms of trait modalities. Conversely, species with the highest biomass were more evenly distributed in the functional space. In 2006, the species with highest densities were *A. sarsi*, *Scoloplos armiger* and *A. armoricana* while for biomass data the most important species were *Tritia reticulata*, *Nephtys spp*. and *Acanthocardia echinata*. In 2006, species with highest densities are more evenly distributed than in 1998 that could explain the higher value of FEve in 2006. The large year-to-year variations in FEve when biomass data were used can be explained by the fact the largest biomass can be due to some rare overdispersed species like the bivalve *Acanthocardia echinata* for which the biomass could be poorly estimated.

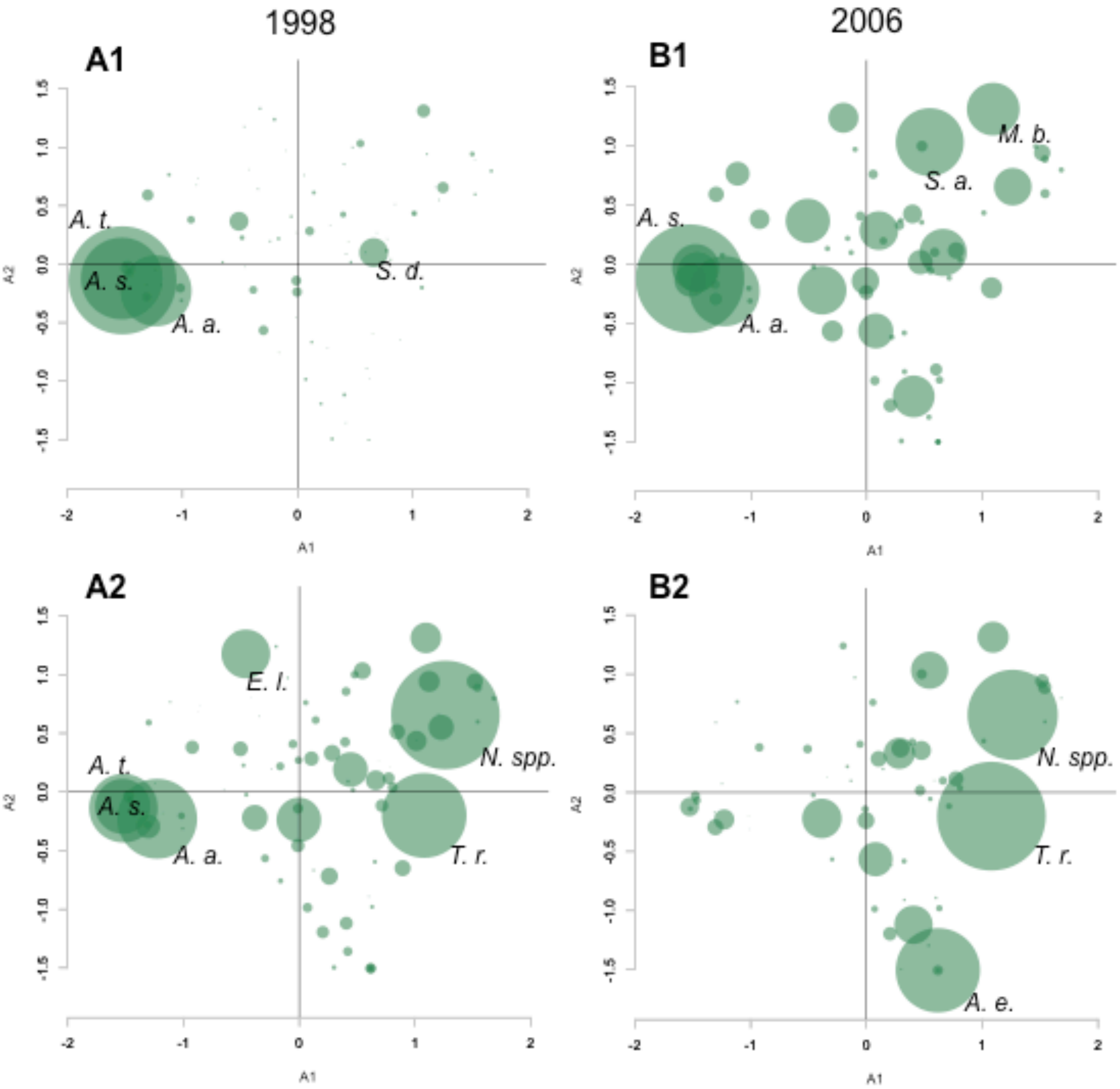


**Figure 36:** Results of the PCoA performed on the Pierre Noire temporal dataset for the year 1998 and the (A1) density or (A2) biomass data and for the year 2006 and the (B1) density or (B2) biomass data. The size of the circles is proportional to the relative abundance of the species (density or biomass). *A. t.: Ampelisca tenuicornis; A. s.: Ampelisca sarsi; A. a.: Ampelisca armoricana; S. a.: Scoloplos armiger; M. b.: Marphysa bellii; N. spp.: Nephtys spp.; T. r.: Tritia reticulata; E. l.: Eunereis longissima; A. e.: Achantocardia echinata.*

## III.4. Discussion

The increasing use of Biological Traits Analysis (BTA) in marine biology goes hand in hand with the need to define a standardized methodological framework for this method. Although several specific methodological decisions need to be considered prior to the calculation of functional diversity including the number of traits, their identity and the way to quantify the relative abundance of species in a community (density or biomass), the issue of the weighting procedure has received relatively little attention (but see Leps et al., 2006 for plant communities). Our bibliographic review showed that a minority of studies on macrofauna use biomass data and that there is a lack of biological justification for this choice. The values of all the functional diversity indices chosen in this study depended on the relative abundance of the species, so the choice of the nature of the data is a major factor in the interpretation of the indices values (Botta-Dukát, 2005; Villéger et al., 2008; Laliberté and Legendre, 2010). Indeed, species are distributed according to their relative abundance in the multidimensional functional space. Bolam & Eggleton (2014) found that descriptions of community trait composition vary greatly depending on whether abundance or biomass is used.

We showed that for a given dataset, the magnitude of the regression between indices calculated using density and biomass data varied among indices therefore the different indices have different sensitivity to the nature of data in a same dataset. For both datasets, FDiv is the index for which the values seemed the least different between density and biomass data. For a given index, the magnitude of the regression was different between the two datasets therefore the indices can react differently to the distribution of density or biomass in different benthic communities. For FEve, the regressions between indices calculated with either density or biomass data were significant but low as distribution of density and biomass are generally highly different in most marine communities. For FDis and RaoQ, the relationships between indices calculated with either density or biomass data did not even have the same sign for the two datasets. For the Bay of Seine, these indices showed a positive correlation between density and biomass data, whereas in the Bay of Morlaix it was negative. This means that in the Bay of Morlaix a low FDis or RaoQ value calculated with the density data for a particular year would correspond to an opposite value if these indices would be calculated with the biomass data. In these cases, the weighting procedure could lead to opposite interpretation of the results. These results can be seen in the temporal evolution of the FDis and RaoQ indices in the Bay of Morlaix. Their year-to-year changes with the indices calculated with density data mirrored the changes reported for the Shannon index (Thiébaut et al., in prep) but not the indices calculated with biomass data, their temporal evolution being almost opposite to that of the density data. These contradictory results are caused by the properties of these two indices which are sensitive to the trait dissimilarity between individuals of dominant species in a community. For communities largely dominated by a few species, variations in FDis and RaoQ should be interpreted with caution (van der Linden et al., 2016).

The FDis and RaoQ indices calculated with the densities will be then influenced by the most abundant species, the polychaete *Owenia fusiformis* in the Bay of Seine and the amphipods *Ampelisca* spp. in the Bay of Morlaix. In the Bay of Morlaix, variations in the

FDis and RaoQ indices calculated with density data were due to fluctuations in the density of *Ampelisca* which represented more than 80% of the individuals at some dates. The traits modalities of the *Ampelisca* draw then all the analysis in their direction. We did not find the same variations for the indices calculated with the biomass data because the *Ampelisca* species have a very low biomass (Dauvin, 1998), so their fluctuations in density have very little impact on the total biomass. The more even distribution of biomass at Pierre Noire limited the bias due to important dominance patterns. Likewise, in the Bay of Seine, even *Owenia fusiformis* was not so dominant, and the variations in FEve and RaoQ calculated on abundance or biomass data were moving in the same direction.

The interpretation of the changes of the functional diversity of the community could be then different by using density or biomass data. After a perturbation, the structure of communities is expected to change, leading to different responses according to the level of pollution in terms of density or biomass according to the Pearson & Rosenberg model for organic enrichment and pollution on benthic communities (Pearson & Rosenberg, 1978). Faunal succession following disturbance involves the massive arrival of small sized opportunistic species with low biomass in polluted area and the disappearance of large species. This profound upheaval in the distribution patterns of densties and biomasses after a disturbance could thus have a significant impact on the values of some indices of functional diversity independently of changes in the identity of species or of the modalities of traits they possess. In the Bay of Morlaix, the responses of benthic communities did not followed the scheme proposed by Pearson & Rosenberg (1978) as the unpolluted community was largely dominated in terms of densities by small non polychaetes species and showed a dominance pattern with a low evenness which is characteristic of a moderately to highly polluted environment.

In this bay, the role of *Ampelisca* was dominant in analyses using densities, whereas the species that stand out in analyses using biomass were the polychaetes *Nephthys spp.* and the gastropod *Tritia reticulata*. According to this, *Ampelisca* will therefore be the drivers for functional analyses carried out with density data and large polychaetes or bivalves will be the drivers for analyses carried out with biomass data (Gusmao et al., 2016). Thus biomass-based analyses seem more relevant in cases where the information is too much driven by small very abundant species. On the other hand, rare species do not have the same dominance patterns as other species and can influence the calculation of functional indices based on biomass. Rare species may induce a bias in these analyses because it is difficult to sample over-dispersed large species for example, suggesting that the number of replicates could be important to properly assess functional diversity with biomass data. Finally, the sampling date could have also a large impact on the computation of functional diversity indices. In late spring or summer, the unpredictable presence of large numbers of a few species with small biomass in response to a large influx of juveniles could then give a false impression of a change in functional diversity.

As observed by Bolam & Eggleton (2014) or Breine et al. (2018), the differences observed between density or biomass analyses also appear to be trait dependent and related to the ‘morphology’ or ‘life span’ traits, as larger species tend to live longer. A dominant trait weighted by density data will not necessarily have the same functional role in the ecosystem as a dominant trait weighted by biomass data (Bolam and Eggleton, 2014). Since the analysis of changes in trait composition can be used to detect changes in ecosystem functioning, it may be more logical to do biomass based analysis because biomass of organisms is a better descriptor of the distribution of resources in an ecosystem and better reflect ecological processes than density (Cesar and Frid, 2009). Theoretically, density-based analyses seem better suited to describe demographic processes and biotic interactions like competition and biomass-based analyses to describe ecosystem processes such as nutrient cycling and productivity (Leps et al., 2006). However, the availability of data and in particular the time needed to acquire biomass data may be a barrier to use adequate data. It is therefore necessary within the framework of a functional approach to justify the weighting procedure in order to be able to interpret the results obtained and compare studies. This justification should be governed by the question one would like to address rather than by the availability of data. The weighting could be then partly linked with the choice of traits and their relevance for the ecosystem functions one would like to study. Beyond benthic communities, the question of the weighting of species in the calculation of functional diversity indices can also be important for planktonic communities for which the development of imaging techniques can provide abundance or biovolume data (Martini et al., in press).

## Acknowledgments

The study in the Bay of Seine was supported by the "Seine-Aval" program coordinated by the GIP Seine-Aval and the study and the long-term monitoring program in the Bay of Morlaix was successively supported by different contracts from the 'Réseau National d'Observation' coordinated by Ifremer and the REBENT programme funded by the 'Agence de l'Eau Loire Bretagne', the 'Région Bretagne' and the 'DREAL Bretagne'. Both studies form part of the doctoral research work of Lise Bacouillard partly funded by the 'Région Bretagne'. The authors are grateful to the captains and the crews of the RV 'Côtes de la Manche', Mysis' and 'Neomysis' and all students, technicians and colleagues who contribute to the sampling and laboratory works.

## Supplementary materials

List of the 91 articles (94 studies) of the bibliographic review carried out on the subject of functional diversity in benthic ecology (macrofauna and megafauna).

| **Authors** | **Year** | **Title** | **Journal** |
|---|---|---|---|
| Aarnio et al. | 2011 | Zoobenthos as an environment quality element: the ecological significance of sampling design and functional traits | Marine Ecology - an Evolutionary Perspective, 32, 58-71 |
| Astudillo et al. | 2009 | Detached aquaculture buoys in the SE Pacific: potential dispersal vehicles for associated organisms | Aquatic Biology, 5, 219-231 |
| Atalah et al. | 2012 | Diversity of demersal and megafaunal assemblages inhabiting sandbanks of the Irish Sea | Marine Biodiversity, 43(2), 121-132 |
| Barrio Frojan et al. | 2011 | Assessing the recovery of functional diversity after sustained sediment screening at an aggregate dredging site in the North Sea | Estuarine, Coastal and Shelf Science, 92(3), 358-366 |
| Belley & Snelgrove | 2017 | The role of infaunal functional and species diversity in short-term response of contrasting benthic communities to an experimental food pulse | Journal of Experimental Marine Biology and Ecology, 491, 38-50 |
| Berthelsen et al. | 2015 | Biological traits and taxonomic composition of invertebrate assemblages associated with coralline turf along an environmental gradient | Marine Ecology Progress Series, 530, 15-27 |
| Bolam | 2014 | Macrofaunal recovery following the intertidal recharge of dredged material: A comparison of structural and functional approaches | Marine Environmental Research, 97, 15-29 |
| Bolam & Eggleton | 2014 | Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf | Journal of Sea Research, 88, 47-58 |
| Bolam et al. | 2014 | Sensitivity of macrobenthic secondary production to trawling in the English sector of the Great North Sea: A biological trait approach | Journal of Sea Research, 85, 162-177 |
| Bolam et al. | 2016 | Application of biological traits to further our understanding of the impacts of dredged material disposal on benthic assemblages | Marine Pollution Bulletin, 105(1), 180-192 |
| Bolam et al. | 2017 | Differences in biological traits composition of benthic assemblages between unimpacted habitats | Marine Environmental Research, 126, 1-13 |
| Bostrom et al. | 2010 | Invertebrate dispersal and habitat heterogeneity: Expression of biological traits in a seagrass landscape | Journal of Experimental Marine Biology and Ecology, 390(2), 106-117 |
| Breine et al. | 2018 | Structural and functional diversity of soft-bottom macrobenthic communities in the Southern North Sea | Estuarine, Coastal and Shelf Science, 214, 173-184 |

| | | | |
|---|---|---|---|
| Bremner et al. | 2005 | Biological traits of the North Sea benthos: Does fishing affect benthic ecosystem function? | American Fisheries Society Symposium |
| Bremner et al. | 2003a | Assessing marine ecosystem health: The long-term effects of fishing on functional diversity in North Sea benthos | Aquatic Ecosystem Health & Management, 6(2), 131-137 |
| Bremner et al. | 2003b | Assessing functional diversity in marine benthic ecosystems: a comparison of approaches | Marine Ecology Progress Series, 254, 11-25 |
| Bremner et al. | 2006b | Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA) | Ecological Indicators, 6(3), 609-622 |
| Bremner et al. | 2006a | Matching biological traits to environmental conditions in marine benthic ecosystems | Journal of Marine Systems, 60(3-4), 302-316 |
| Brooks et al. | 2015 | Biological effects of long term fine limestone tailings discharge in a fjord ecosystem | Marine Pollution Bulletin, 96(1-2), 321-336 |
| Clare et al. | 2015 | Community variability and ecological functioning: 40 years of change in the North Sea benthos | Marine Environmental Research, 107, 24-34 |
| Cochrane et al. | 2012 | Benthic fauna and functional traits along a Polar Front transect in the Barents Sea - Advancing tools for ecosystem-scale assessments | Journal of Marine Systems, 94, 204-217 |
| Cooper et al. | 2008 | Assessment of ecosystem function following marine aggregate dredging | Journal of Experimental Marine Biology and Ecology, 366(1-2), 82-91 |
| Culhane et al. | 2014 | Structural and functional indices show similar performance in marine ecosystem quality assessment | Ecological Indicators, 43, 271-280 |
| Darr et al. | 2014 | Functional changes in benthic communities along a salinity gradient - a western Baltic case study | Journal of Sea Research, 85, 315-324 |
| de Juan & Demestre | 2012 | A trawl disturbance indicator to quantify large scale fishing impact on benthic ecosystems | Ecological Indicators, 18, 183-190 |
| de Juan et al. | 2007 | Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea) | Marine Ecology Progress Series, 334, 117-129 |
| de Juan et al. | 2015 | Standardising the assessment of Functional Integrity in benthic ecosystems | Journal of Sea Research, 98, 33-41 |
| Dimitriadis et al. | 2012 | Functional diversity and redundancy of soft bottom communities in brackish waters areas: Local vs regional effects | Journal of Experimental Marine Biology and Ecology, 426-427, 53-59 |
| Dolbeth et al. | 2013 | Drivers of estuarine benthic species distribution patterns following a restoration of a seagrass bed: A functional trait analyses | Marine Pollution Bulletin, 72(1), 47-54 |

| | | | |
|---|---|---|---|
| Ellingsen et al. | 2007 | Rare species, habitat diversity and functional redundancy in marine benthos | Journal of Sea Research, 58(4), 291-301 |
| Ellis et al. | 2017 | Multiple stressor effects on marine infauna: responses of estuarine taxa and functional traits to sedimentation, nutrient and metal loading | Scientifc Reports, 7(1), 1-16 |
| Faulwetter et al. | 2015 | Resistance of polychaete species and trait patterns to simulated species loss in coastal lagoons | Journal of Sea Research, 98, 73-82 |
| Fleddum et al, | 2013 | Changes in biological traits of macro-benthic communities subjected to different intensities of demersal trawling along the west coast of southern Africa | Journal of the Marine Biological Association of the United Kingdom, 93(08), 2027-2038 |
| Frid et al. | 2008 | Incorporating ecological functioning into the designation and management of marine protected areas | Hydrobiologia, 606(1), 69-79 |
| Frid | 2011 | Temporal variability in the benthos: Does the sea floor function differently over time? | Journal of Experimental Marine Biology and Ecology, 400(1-2), 99-107 |
| Frid & Caswell | 2015 | Is long-term ecological functioning stable: The case of the marine benthos? | Journal of Sea Research, 98, 15-23 |
| Gambi et al. | 2016 | Distribution and functional traits of polychaetes in a CO2 vent system: winners and losers among closely related species | Marine Ecology Progress Series, 550, 121-134 |
| Garaffo et al. | 2018 | Assessing functional diversity of macrobenthic assemblages in sewage-affected intertidal shores | International Aquatic Research, 10(4), 333-347 |
| Gogina et al. | 2014 | Approach to assess consequences of hypoxia disturbance events for benthic ecosystem functioning | Journal of Marine Systems, 129, 203-213 |
| Greenfield et al. | 2016 | Mapping functional groups can provide insight into ecosystem functioning and potential resilience of intertidal sandflats | Marine Ecology Progress Series, 548, 1-10 |
| Gusmao et al. | 2016 | Functional diversity of macrobenthic assemblages decreases in response to sewage discharges | Ecological Indicators, 66, 65-75 |
| Henseler et al. | 2019 | Coastal habitats and their importance for the diversity of benthic communities: A species- and trait-based approach | Estuarine, Coastal and Shelf Science, 226, 106272 |
| Hewitt et al. | 2008 | Habitat variation, species diversity and ecological functioning in a marine system | Journal of Experimental Marine, Biology and Ecology, 366(1-2), 116-122 |
| Hewitt et al. | 2016 | Species and functional trait turnover in response to broad-scale change and an invasive species | Ecosphere, 7(3), e01289 |
| Hu et al. | 2019 | Macrobenthos functional trait responses to heavy metal pollution gradients in a temperate lagoon | Environmental Pollution, 253, 1107-1116 |

| | | | |
|---|---|---|---|
| Jimenez et al. | 2016 | Harvesting effects on functional structure and composition of tropical invertebrates assemblages | ICES Journal of Marine Science, 73(2), 420-428 |
| Jones & Frid | 2009 | Altering intertidal sediment topography: effects on biodiversity and ecosystem functioning | Marine Ecology, 30(Suppl, 1), 83-96 |
| Kenchington et al. | 2007 | Multi-decadal changes in the megabenthos of the Bay of Fundy: The effects of fishing | Journal of Sea Research, 58(3), 220-240 |
| Krumhansl et al. | 2016 | Using species traits to assess human impacts on near shore benthic ecosystems in the Canadian Arctic | Ecological Indicators, 60, 495-502 |
| Marchini et al. | 2008 | Functions and ecological status of eight Italian lagoons examined using biological traits analysis (BTA) | Marine Pollution Bulletin, 56(6), 1076-1085 |
| Munari | 2013 | Benthic community and biological trait composition in respect to artificial coastal defence structures: A study case in the northern Adriatic Sea | Marine Environmental Research, 90, 47-54 |
| Muntadas et al. | 2015 | Integrating the provision of ecosystem services and trawl fisheries for the management of the marine environment | Science of the Total Environment, 506-507, 594-603 |
| Muntadas et al. | 2016 | Assessing functional redundancy in chronically trawled benthic communities | Ecological Indicators, 61, 882-892 |
| Neumann et al. | 2016 | Functional composition of epifauna in the south-eastern North Sea in relation to habitat characteristics and fishing effort | Estuarine, Coastal and Shelf Science, 169, 182-194 |
| Neumann & Kroncke | 2011 | The effect of temperature variability on ecological functioning of epifauna in the German Bight | Marine Ecology, 32, 49-57 |
| Nordstrom et al. | 2015 | Nestedness of trophic links and biological traits in a marine food web | Ecosphere, 6(9), 161 |
| Otegui et al. | 2016 | Matching ecological functioning with polychaete morphology: Consistency patterns along sedimentary habitats | Journal of Sea Research, 114, 13-21 |
| Oug et al. | 2012 | Biological traits analyses in the study of pollution gradients and ecological functioning of marine soft bottom species assemblages in a fjord ecosystem | Journal of Experimental Marine Biology and Ecology, 432-433, 94-105 |
| Pacheco et al. | 2011 | Functional diversity of marine macrobenthic communities from sublittoral soft-sediment habitats off northern Chile | Helgoland Marine Research, 65(3), 413-424 |
| Pacheco et al. | 2013 | Dispersal of post-larval macrobentos in subtidal sedimentary habitats: Roles of vertical diel migration, water column, bedload transport and biological traits' expression | Journal of Sea Research, 77, 79-92 |
| Paganelli et al. | 2012 | Functional structure of marine benthic assemblages using Biological Traits Analysis (BTA): A study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea) | Estuarine, Coastal and Shelf Science, 96, 245-256 |

| | | | |
|---|---|---|---|
| Pecuchet et al. | 2019 | Spatio-temporal dynamics of multi-trophic communities reveal ecosystem-wide functional reorganization | Ecography, 42, 1-12 |
| Pommer et al. | 2016 | Impact and distribution of bottom trawl fishing on mud-bottom communities in the Kattegat | Marine Ecology Progress Series, 548, 47-60 |
| Pranovi et al. | 2008 | Historical changes in the structure and functioning of the benthic community in the lagoon of Venice | Estuarine, Coastal and Shelf Science, 76(4), 753-764 |
| Rigolet et al. | 2014 | Benthic control freaks: Effects of the tubicolous amphipod *Haploops nirae* on the specific diversity and functional structure of benthic communities | Journal of Sea Research, 85, 413-427 |
| Rijnsdorp et al. | 2016 | Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem | ICES Journal of Marine Science, 73(Suppl. 1), 27-38 |
| Rodil et al. | 2013 | Tracking environmental stress gradients using three biotic integrity indices: Advantages of locally-developed traits-based approach | Ecological Indicators, 34, 560-570 |
| Sigala et al. | 2012 | Functional diversity in three Mediterranean transitional water ecosystems | Estuarine, Coastal and Shelf Science, 110, 202-209 |
| Smale | 2008 | Ecological traits of benthic assemblages in shallow Antarctic waters: does ice scour disturbance select for small, mobile, secondary consumers with high dispersal potential? | Polar Biology, 31(10), 1225-1231 |
| Szostek et al. | 2016 | Natural vs. fishing disturbance: drivers of community composition on traditional king scallop, *Pecten maximus*, fishing grounds | ICES Journal of Marine Science, 73(Suppl. 1), 70-83, |
| Thrush et al. | 2011 | Habitat-diversity relationships in rocky shore algal turf infaunal communities | Marine Ecology Progress Series, 424, 119-132 |
| Tillin et al. | 2006 | Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale | Marine Ecology Progress Series, 318, 31-45 |
| Törnroos & Bonsdorff | 2012 | Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species | Ecological Applications, 22(8), 2221-2236 |
| Törnroos et al. | 2013 | Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities | PlosOne, 8(10), e78910 |
| Törnroos et al. | 2015 | Marine benthic ecological functioning over decreasing taxonomic richness | Journal of Sea Research, 98, 49-56 |
| Törnroos et al. | 2018 | Four decades of functional community change reveals gradual trends and low interlinkage across trophic groups in a large marine ecosystem | Global Change Biology, 25(4), 1235-1246 |
| Tyler-Walters et al. | 2009 | A method to assess the sensitivity of sedimentary communities to fishing activities | Aquatic Conservation: Marine and Freshwater Ecosystems, 19(3), 285-300 |

| | | | |
|---|---|---|---|
| Van Denderen et al. | 2015 | Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats | Marine Ecology Progress Series, 541, 31-43 |
| Van der Linden et al. | 2012 | A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem | Ecological Indicators, 20, 121-133 |
| Van der Linden et al. | 2015 | The performance of trait-based indices in an estuarine environment | Ecological Indicators, 61, 378-389 |
| van der Wal et al. | 2017 | Hydrodynamic conditioning of diversity and functional traits in subtidal estuarine macrozoobenthic communities | Estuarine, Coastal and Shelf Science, 197, 80-92 |
| Verissimo et al. | 2012 | Assessment of the subtidal macrobenthic community functioning of a temperate estuary following environmental restoration | Ecological Indicators, 23, 312-322 |
| Villnas et al. | 2011 | Structural and functional shifts in zoobenthos induced by organic enrichment - Implications for community recovery potential | Journal of Sea Research, 65(1), 8-18 |
| Villnas et al. | 2018 | Template for using biological trait groupings when exploring large-scale variation in seafloor multifunctionality | Ecological Applications, 28(1), 78-94 |
| Villnas et al. | 2019 | Changes in macrofaunal biological traits across estuarine gradients: implications for the coastal nutrient filter | Marine Ecology Progress Series, 622, 31-48 |
| Vinagre et al. | 2017 | Do structural and functional attributes show concordant responses to disturbance? Evidence from rocky shore macroinvertebrate communities | Ecological Indicators, 75, 57-72 |
| Wahl et al. | 2013 | Natural variability in hard-bottom communities and possible drivers assessed by a time-series study in the SW Baltic Sea: know the noise to detect the change | Biogeoscience, 10, 5227-5242 |
| Wan Hussin et al. | 2012 | Impacts of physical disturbance on the recovery of a macrofaunal community: A comparative analysis using traditional and novel approaches | Ecological Indicators, 12(1), 37-45 |
| Webb et al. | 2009 | Life history mediates large-scale population ecology in marine benthic taxa | Marine Ecology Progress Series, 396, 293-306 |
| Weigel et al. | 2016 | Maintained functional diversity in benthic communities in spite of diverging functional identities | Oikos, 125(10), 1421–1433 |
| Wong & Dowd | 2015 | Patterns in taxonomic and functional diversity of macrobenthic invertebrates across seagrass habitats: a case study in Atlantic Canada | Estuaries & Coasts, 38(6), 2323-2336 |

# Chapter IV : Year-to-year changes in trophic diversity of the fine sand benthic community in the Bay of Morlaix (western English Channel).

# Chapter IV

Article en préparation.

Lise Bacouillard[1], Raphaël Dupont[1], Céline Houbin[2], François Gaudin[1], Cédric Leroux[2], Pascal Riera[1], Éric Thiébaut[1]

[1] Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR7144, Adaptation et Diversité en Milieu Marin, Place Georges Teissier, F-29680 Roscoff, France

[2] Sorbonne Université, CNRS, Station Biologique de Roscoff, FR2424, Place Georges Teissier, F-29680 Roscoff, France

# ABSTRACT

The fine sand community of the Bay of Morlaix at the Pierre Noire site (northern Brittany) has been monitored since 1977 in late winter (March) and late summer (October). In 2010, this macrofaunal monitoring was supplemented by an isotopic monitoring to study the trophic network of the community and add a functional dimension to it. The aim of this study is to investigate in parallel the year-to-year changes in the structure of the community and its trophic network over the period 2013 to 2018 using different methods of analysis and to evaluate the relevance of isotopic indices to assess the ecosystem health in the context of the Marine Strategy Framework Directive (MSFD). In addition to an analysis of the structure of the community using a n-MDS and a PCoA, a pool of 13 isotopic indices were used to characterise the food web. The results highlighted a food web characterised (1) by a high diversity of diets between the different species, resulting from a relative trophic specialisation within the Sedimented Organic Matter (SOM) and Particulate Organic Matter (POM) pools and (2) by a trophic plasticity of the species according to the seasons. A continuum of isotopic values was observed from the base of the network to its summit, reflecting a high level of omnivory and the absence of distinct trophic niches. There was a relative seasonality in the structure of the community, which is not reflected in the isotopic indices. The isotopic indices allowed us to highlight a relative temporal stability of the food web between 2013 and 2018 regardless of the changes in the biomass of dominant species. Nevertheless, it is still necessary to consider the relevance and limits of isotopic indices before their possible implementation in the Marine Strategy Framework Directive (MSFD).

## Keywords

Trophic ecology; Stable isotopes; Functional ecology; Coastal zone; Macrofauna; Bay of Morlaix

## IV.1. Introduction

Global environmental change, which results in particular in the destruction and/or artificialization of environments, overexploitation of resources, increased pollution and changes in climatic conditions, is a major concern for the management of marine ecosystems (Halpern et al., 2008, 2015). In this context of increasing pressures on marine environments, the Marine Strategy Framework Directive (MSFD), established by the European Union in 2008, aims to build a legal framework which imposes member states to take the necessary measures to maintain or restore the good ecological status of marine waters under national jurisdiction by 2020 (Borja et al., 2013). The MSFD promotes an ecosystem approach to assess the state of ecosystem health based on 11 state or pressure descriptors, including descriptor 1 dedicated to biological diversity and descriptor 4 dedicated to the integrity of food webs. Its implementation is based on repeated 6-year cycles that include the definition of the initial state of marine habitats, establishment of a monitoring programme and a programme of measures. The aim of the monitoring programme is to monitor the response of marine communities to changes in pressures, natural environmental conditions and management measures.

Within the framework of the MSFD, descriptor 4 aims to assess the good ecological status of marine environments regarding the structure of the food web according to the following postulate: "All the elements building the marine food web, insofar as they are known, are present in normal abundance and diversity and at levels that can guarantee the long-term abundance of species and the total maintenance of their reproductive capacities". The aim is thus to bring an integrative and functional approach to the marine ecosystems, in particular through the rates of energy and matter transfer and the productivity of the different trophic levels. Three indicators have been selected in France for this descriptor:

- Indicator 4.1.1. "Performance of key predatory species using their production per unit biomass (productivity)";
- Indicator 4.2.1. "Large fish (by weight)";
- Indicator 4.3.1. "Abundance trends of functionally important selected groups/species".

Whereas the first two indicators focus exclusively on the upper trophic levels, the third indicator takes into account all the biological compartments of an ecosystem but ignores the trophic links between these compartments.

The analysis of trophic networks is based on "ecological tracers". These tracers are (bio)chemical, isotopic or lipidic parameters measured in the tissues of organisms and are relatively reliable indicators (Chouvelon et al., 2011). Thus, the analysis of trophic networks can rely on the use of stable isotopes and is based on the commonly accepted principle "you are what you eat". The trophic network is organised in different complex levels, starting with primary producers who produce organic matter from inorganic matter, and then different groups of consumers building the network (Riera, 2006). The isotopic signature of the consumer is an integrating value over time that reflects its assimilation of food over a given period of time, generally ranging from weeks to months, depending on the species, tissue type and specimen size (Kaufman et al., 2008). In the case of marine invertebrates, this integration time can be estimated at about 3 months (Riera, comm. pers.). For fish at higher trophic levels, this time may be three months or more depending on their size when considering the animal as a whole (Riera, comm. pers.); the isotope turnover time increases with the size. Monitoring the isotopic composition of the species in a community makes it possible to highlight the evolution of their functional roles and interactions within the food web over the short and long term. Thus, we can link changes in signatures to environmental changes in the ecosystem (Cucherousset et al., 2012).

Trophic networks have more or less complex organisations that are structured differently depending on the environment, the season and the communities of organisms that compose them (Riera, 2006). Beyond the use of isotopic data to identify the diet of species and their trophic interactions, the use of isotopic indices based on the distribution of the signatures of the species of a community in the isotopic space $\delta^{13}C$ - $\delta^{15}N$ makes it possible to quantitatively measure the variations in the structure of networks and their complexity over time or in space (Layman et al., 2007; Cucherousset et al., 2012). They make it possible to highlight changes in the diversity of sources at the base of the trophic network, the number of trophic levels, trophic diversity or trophic redundancy.

Following the creation of the first isotopic indices by Layman et al. (2007), many indices have been developed to integrate the relative abundances or biomasses of species in communities, most often based on the model of functional diversity indices (Jackson et al., 2011; Clark et al., 2012; Cucherousset and Villéger, 2015; Rigolet et al., 2015). These different indices can be classified into several categories according to the information they provide on the properties of the food web. The general indices of the type " $\delta^{13}C$ range" and "$\delta^{15}N$ range" describe the amplitude of the network (Layman et al., 2007). Measures of functional trophic richness describe the isotopic diversity of the community and the accessible resources space. Measures of trophic dispersion and divergence reflect the degree of resource use and the degree of trophic specialisation of species. Measurements of trophic evenness provide information on trophic redundancy, the distribution of trophic niches in the network and the degree of competition between species. Overlap measurements are indices that make it possible to compare the level of trophic overlap between two communities, two functional groups or a given community at two different dates (Cucherousset & Villéger, 2015).

In order to better understand the interannual variability of food webs and the relevance of isotopic indices to inform the MSFD descriptor 4, we were interested in this study in the fine sand community of the Bay of Morlaix at the Pierre Noire long-term monitoring site (western English Channel). The macrofauna at the Pierre Noire site has been monitored since 1977 in order to describe the interannual variability of the structure of the macrobenthic community (Ibanez et al., 1993; Dauvin, 1998). This community was particularly impacted by the Amoco Cadiz oil spill in 1978. Following preliminary observations in 2010, a programme dedicated to the study of the community-associated trophic network has supplemented this monitoring since 2013. This monitoring programme is based on measurements of the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic signatures of the organisms present at two seasons corresponding to the minimum and the maximum biomass: late winter and late summer (Saulnier et al., 2019). The main aim of this complementary programme is to provide a functional dimension to the traditional long-term monitoring in order to gain a better understanding of the functional consequences of changes in community structure in terms of the food web and the flow of matter and energy, and ultimately ecosystem management and conservation (Thompson et al., 2012). Central issues concern for instance the resilience of trophic food webs, the variability in interaction networks and their complex interactions with biodiversity changes (McCann & Rooney, 2009; Poisot et al., 2015; Ushio et al., 2018). Such long-term programme considering multiple trophic levels and species interactions at the same time is highly valuable to address these questions (Barnes et al., 2018), especially in benthic coastal environments for which there is little multi-year monitoring of food webs ( but see Olivier et al., 2019 for a long-term series of 18 years in the German Bight, North Sea).

Focusing on the period between winter 2013 and winter 2018, the objectives of the present study were to:

(1) Describe the structure of the macrobenthic community and identify the existence of seasonal and interannual variations in the community over time.

(2) Characterise the food web and its evolution at both seasons and over the different years using the various isotopic indices developed in recent years.

(3) Finally identify the similarities in the seasonal and interannual patterns of variation in the structure of the community and the associated food web characterised by the isotopic indices. We hypothesized that food web structure fluctuated over time due to changes in community composition.

## IV.2. Materials and methods

### IV.2.1. Study area

The Bay of Morlaix forms a semi-enclosed coastal embayment of about 105 km$^2$ located along the coast of North Brittany (Western English Channel) with a wide opening to the north (Figure 37). The bay received low freshwater inputs from three main rivers, the “Rivière de Morlaix” (mean annual discharge of 4 m$^3$ s$^{-1}$), the “Penzé” (mean annual discharge of 3 m$^3$ s$^{-1}$) and the ”Dourduff” (mean annual discharge of 1 m$^3$ s$^{-1}$). The salinity within the bay varies between 34.4 in winter and 35.6 at the beginning of autumn except in the inner part of the bay where it can be below 25 during the river floods. In parallel, bottom seawater temperature fluctuates between 8.0°C in winter and 16.9°C in summer. Strong tidal currents which characterized the English Channel produce a homogeneous water column throughout the year and result in the formation of bio-sedimentary sequence from offshore waters to the inner part of the bay, from coarse sands to mudflats (Cabioch et al., 1980). The sampling site Pierre Noire (PN) (48°42'30"N; 3°51'58"W) is located in the northeastern part of the bay of Morlaix at a depth of 17m. It is representative of a well-defined area of about 20 km$^2$ where lower current velocity promotes an accumulation of sedimentary particles. The sediment is fine sand with a median particle size between 150 and 190 µm and a low proportion of silt (below 6 %). The benthic community is mainly composed by the amphipods *Ampelisca sarsi* and *A. armoricana*, the bivalve *Abra alba*, and the polychaetes *Spio decoratus*, *Paradoneis armata*, *Euclymene oerstedii* and *Hyalinoecia bilineata*.

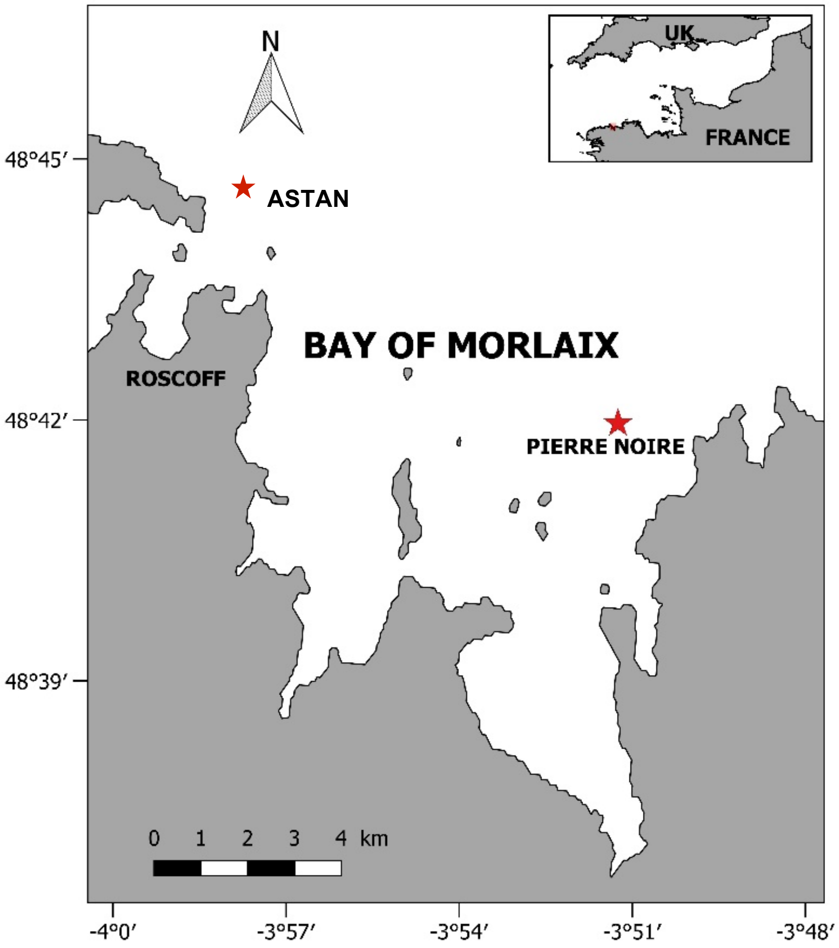


**Figure 37:** Location of the study area in the Bay of Morlaix and the sampling station Pierre Noire.

### IV.2.2. Sample collection

The samples were collected during two annual campaigns carried out each year in February/March and September/October from 2013 to 2018, corresponding respectively to the minimum biomass at the end of winter and to the maximum biomass at the end of summer (Saulnier et al., 2018). Three samplers were used: a 3-m wide beam trawl with a 10 mm mesh in the cod-end and tickler chains for demersal ichthyofauna and benthic megafauna, a 0.1 m$^2$ Smith Mclntyre grab for benthic macrofauna, and a Rallier du Baty dredge to increase the harvesting of over-dispersed macrofaunal and megafaunal species. For the trawl sampling, five counter-current hauls of about 15 minutes each were made at a constant speed of about two knots (i.e., hauls about 1 km long). The mean sampling surface covered an area of about 3000 m$^2$ per haul. All individuals collected in the net were identified at the species level, counted, measured and weighed on board before being frozen at -20°C. For the grab sampling, fifteen replicates were collected at each date and sieved through a 1 mm mesh sieve with seawater. The first ten replicates were fixed in a 4% buffered formaldehyde solution before further processing in the laboratory where the macrofauna was sorted, determined at the lowest taxonomic level and counted to estimate their densities and biomass (see chapter 3). Four replicates were dedicated to macrofauna isotopic measurements while the last replicate was used for sediment characterization including isotopic measurements of the Sedimented Organic Matter (SOM). Macrofauna samples for isotopic analyses were sorted on fresh material in the laboratory, identified at the lowest taxonomic level and frozen at -20°C until the samples were processed.

## IV.2.3. Isotopic sample processing

### IV.2.3.1. Preparation

In the preparation for isotopic analyses, consumers were prepared at the individual level when possible. In rare instances, several individuals were pooled to obtain enough material required for accurate stable isotope analyses. The isotopic analyses of large invertebrates and fishes were performed on the muscle tissues to minimize isotopic variability. Due to the relatively low metabolic turnover, the isotopic composition of muscular tissues revealed the integrative assimilation of sources by the consumer (DeNiro & Epstein, 1978; Tieszen et al., 1983; Pinnegar & Polunin, 1999; Yokoyama et al., 2005). The foot muscle was separated from their shell for large mollusks and muscle was taken off from their periopods for Brachyura, Caridea and Anomoura. The muscle tissue of each fish individual was extracted by dissection from the dorsal part of the fish. For smaller invertebrates, the entire individuals were considered. The samples were briefly acidified when necessary (HCl 1 N) to remove any possible residual carbonates, rinsed with distilled water and dried (60 °C, 48 h). Then, all samples were ground to a fine powder using a mortar and an agate pestle.

For the measurements of stable isotope ratios of the Sedimented Organic Matter (SOM), SOM samples were obtained by sediment resuspension in a filtered seawater (0.7 µm) column. The suspended SOM was left to settle for one hour, after which the supernatant was removed. This manipulation was repeated three times to remove most of the sedimentary organic particles and to separate sand grains from most of the SOM because sand grains cannot be included in isotopic analyses (Riera, 2010). Then, the SOM fraction was acidified (HCl 1 N), rinsed several times with distilled water, dried (60 °C) and ground to powder. Finally, all these samples were placed in tin capsules in quantities of 1.5–3 mg according to their C and N content and analysed for their isotopic composition.

Stable isotope values for marine suspended Particulate Organic Matter (POM) were obtained from the SOMLIT network (Astan sampling point, Roscoff, France, data available at http://somlit-db.epoc.u-bordeaux1.fr/bdd.php). These values are based on data recorded on the surface every two weeks by the SOMLIT coastal observation service at Astan site off Batz Island (48°74'90"N; 3°96'27"W) Figure 37. The Astan site is the closest site to our study site and has similar open sea characteristics. These values were averaged over the three months preceding macrofauna sampling to obtain a time-integrated measurement of the isotopic signature of this food source assume to be the major food source for macrofauna.

### IV.2.3.2. Stable isotope measurements

Carbon and nitrogen isotope ratios were determined using a Flash EA CN analyzer coupled with a Finnigan Delta Plus mass spectrometer, *via* a Finnigan Con-Flo III interface. Data were expressed using the standard δ unit as follows:

$$\delta\mathrm{X}\ (‰) = \left[\left(\frac{\mathrm{Rsample}}{\mathrm{Rreference}}\right) - 1\right] \times 10^3$$

with R = $^{13}C/^{12}C$ for carbon and $^{15}N/^{14}N$ for nitrogen

These ratios were calculated relative to the certified reference materials Vienna Pee Dee Belemnite-limestone (V-PDB) and atmospheric dinitrogen (at-air) for C and N respectively. The V-PDB and at-air scaling was carried out using in-house protein standards that have been calibrated against NBS-19 and IAEA N3 reference materials. The standard deviation of repeated measurements of $\delta^{13}C$ and $\delta^{15}N$ values of the laboratory standard was 0.10‰ versus V-PDB and 0.05‰ versus at-air, respectively.

## IV.2.4. Data analysis

### IV.2.4.1. Analysis of the structure of the macrobenthic community

To quantify the temporal variability of the community structure, species diversity indices were calculated at each sampling date from the ‘species-dates’ matrix with abundances. These indices include species richness (S), Shannon-Weaver index (H’) using $\log_2$ in its formulation, and Pielou’s evenness (J’). The number of individuals per $m^2$ (N) at each sampling date was also calculated. Year-to-year changes among samples were visualized from a non-metric multidimensional scaling (n-MDS) plot and a Principal Coordinate

Analysis (PCoA) based on a Bray-Curtis similarity matrix calculated from log-transformed abundances to decrease the contribution of the most abundant species.

### IV.2.4.2. Biomass calculation

Species biomass data were calculated from abacus providing the average individual weight of each species at each season (February/March and September/October) and the mean species densities expressed in ind. m$^{-2}$ from the 10 grab samples. These abacuses were established from the decalcified dry weights (DW) of each species measured from samples collected between 1977 and 1996. For demersal fish species whose fresh weight has been directly measured on board, dry weight (DW) was estimated assuming a dry weight/fresh weight ratio (DW/FW) equal to 20% for all species. This ratio is an average of the conversion values given by Cresson et al. (2017) for different fish species in the English Channel which could vary between and within species depending on their ontogenetic developmental status, sexual maturity or condition index. Fish biomass in dry weight per m$^2$ was calculated as follows:

$$Biomass_{Fish} = \frac{(FW_i \times 0.2)}{(BTW \times HD)}$$

where $FW_i$ is the fresh weight of the species $i$ in g, $BTW$ is beam trawl width in m, and $HD$ is the haul distance cumulated for the 5 hauls in m.

Sampling gears such as a 3-m beam trawl can be considered to be semi-quantitative and the catching efficiency of the trawl used in the present study is unknown. Previous studies on the catch efficiency of beam-trawls showed that it varies according to the gear characteristics (e.g. addition of tickler chains) and the target species (Kuipers, 1975; Creutzberg et al., 1987; Rogers & Lockwood, 1989; Reiss et al., 2006). For juvenile plaice in the Wadden Sea, Kuipers (1975) reported a catch efficiency of 20 % decreasing with the length of the fish for a 2-m beam trawl. For a standard 2-m beam trawl with tickler chains, Rogers & Lockwood (1989) estimated a catch efficiency for flatfish varying from 20.4 % for the sole to 51.7 % for the plaice. Reiss et al. (2006) proposed values between 27 % for *Buglossidum luteum* and 35 % for *Arnoglossus laterna*. For ground fish like bib and whiting, Hamerlynck & Hostens (1993) assumed a catch efficiency of 20 %. In view of this variability among studies, a value of 20% was retained in our study for all species.

Invertebrate and fish biomass were expressed in g m$^{-2}$.

### IV.2.4.3. Trophic level

To compare the trophic groups of each species based on the stable isotopes with postulated trophic groups, each species was classified into 5 trophic groups following a literature review completed by expert knowledge (Tableau 13): suspension feeders (S), suspension feeders and surface deposit-feeders (S/SD), surface deposit-feeders (SD), subsurface deposit-feeders (SSD) and predators/scavengers (P/S). Although, the nitrogen is commonly used to assess the trophic level of marine organisms, the definition of the $\delta^{15}N$ baseline is a central issue to determine the trophic level of primary consumers (Vander Zanden & Rasmussen, 2001). These authors showed that the error variance in consumer trophic position is 3 times higher when this position is calculated from primary producers rather than primary consumers as baseline. Furthermore, the suspended particulate organic matter is a heterogeneous source composed of a mixture of organic, living and detrital particulate matter, whose isotope values are sometimes higher than the isotope signatures of the primary consumers. Even when the POM is largely dominated by phytoplankton, its $\delta^{15}N$ signature is largely influence by local biogeochemistry and shows short-term temporal variations that are incompatible with the establishment of a trophic baseline. For these reasons, two approaches have been recently proposed to establish the trophic baseline: (1) the use of a species-specific baseline to estimate the relative differences in trophic position among species and (2) the use of long-lived consumers like large bivalves as baseline to estimate the absolute trophic position (Layman et al., 2012). In this context, the bivalves *Timoclea ovata* or *Corbula gibba* which are assumed to be strict primary consumers (i.e. trophic level II) were used as the trophic baseline to calculate the theoretical trophic levels of other consumers assuming a $^{15}N$ trophic-enrichment factor of 3.4 ‰ according to Minagawa & Wada (1984).

**Tableau 13:** Definition of the trophic groups used for the study of the Pierre Noire food web.

| Trophic groups | Definition |
|---|---|
| Suspension feeders (S) | Benthic species that feed by active or passive filtration of particulate organic matter present in the water column. |
| Suspension feeders and surface deposit-feeders (S/SD) | Species that can feed both by filtering particulate organic matter and by collecting detrital material at the water-sediment interface. |
| Surface deposit-feeders (SD) | Sedentary or semi-sedentary species that feed at the water-sediment interface by collecting organic particles. |
| Subsurface deposit-feeders (SSD) | Species that feed by ingesting sediment and digesting the associated organic matter. |
| Predators/scavengers (P/S). | Mainly mobile species that feed on prey on the sediment surface and/or dead organisms. |

### IV.2.4.4. Indices

To characterize the food web, different isotopic diversity indices have been calculated (Tableau 14). Layman's indices were used to characterize the dimensions of the food web which can be explained by the diversity of sources, $\delta^{13}$C Range (CR), or the number of trophic levels, $\delta^{15}$N Range (NR) (Layman et al., 2007). Other indices have been used to measure different aspects of diversity. The Total Area (TA) measured by the convex hull area, the corrected standard ellipse area (SEAc) and the $\text{Hull}_{\text{biom}}$ were used to characterize the isotopic richness of the network (Layman et al., 2007; Jackson et al., 2011; Rigolet et al., 2015). The divergence and dispersion of species relative to the barycentre or to their nearest neighbour were measured by the distance to the centroid (CD), the isotopic divergence (IDiv) and the isotopic dispersion (IDis) indices respectively (Layman et al., 2007; Cucherousset & Villéger, 2015; Rigolet et al., 2015). The regularity of the distribution of species or trophic groups within the isotopic space was measured with the mean nearest neighbour distance (MNND), the standard deviation of the nearest neighbour distance (SDNDD) and the isotopic evenness (IEve) (Layman et al., 2007; Cucherousset & Villéger, 2015; Rigolet et al., 2015). Unweighted and biomass-weighted indices were considered because the trophic importance of a species is not always linked with the biomass and these indices are complementary. The overlap among consumers at different dates was measured using two indices: the isotopic similarity (ISim) and the isotopic nestedness (INess) (Cucherousset & Villéger, 2015).

Detailed descriptions of these different indices were available in Layman et al. (2007), Cucherousset & Villéger (2015) and Rigolet et al. (2015). The isotopic indices values and graphs were obtained with R language (R Core Team, 2014). We used as a basis the work done by Cucherousset & Villéger (2015) and Rigolet et al (2015), and adapted their scripts to our study. The main packages used in these scripts are SIAR and SIBER.

**Tableau 14:** Description of the unweighted and biomass-weighted trophic diversity indices used in this study. Biomass-weighted indices are indicated in italics

| Indices | Description | References |
|---|---|---|
| CR | $\delta^{13}C$ Range | (Layman et al., 2007) |
| NR | $\delta^{15}N$ Range | (Layman et al., 2007) |
| TA | Convex hull area (minimum area encompassed by species in the isotopic space) | (Layman et al., 2007) |
| SEAc | A measure of the mean core niche area of the community isotopic niche | (Jackson et al., 2011) |
| *$Hull_{biom}$* | *Convex hull area weighted by species biomasses* | (Rigolet et al., 2015) |
| CD | Mean species distance to the centroid | (Layman et al., 2007) |
| *IDiv* | *Species deviance from the mean distance to the centre of gravity weighted by relative biomass* | (Cucherousset & Villéger, 2015; Rigolet et al., 2015) |
| *IDis* | *Weighted mean distance of species to the community weighted centre of gravity of all species* | (Cucherousset & Villéger, 2015; Rigolet et al., 2015) |
| MNND | Mean distance of each species to its nearest neighbour in the $\delta^{13}C$ - $\delta^{15}N$ bi-plot space | (Layman et al., 2007) |
| SDNND | Standard deviation of distance of each species to its nearest neighbour in the $\delta^{13}C$ - $\delta^{15}N$ bi-plot space | (Layman et al., 2007) |
| *IEve* | *Evenness of biomasses distribution in the minimum spanning tree* | (Cucherousset & Villéger, 2015; Rigolet et al., 2015) |
| ISim | Ratio between the convex hull volume of the intersection and the convex hull volume of the union of the organisms at different dates | (Cucherousset & Villéger, 2015) |
| INess | Ratio between the convex hull volume of the intersection and the minimal convex hull volume filled by organisms at different dates | (Cucherousset & Villéger, 2015) |

## IV.3. Results

### IV.3.1. Variability of the community structure

The results of the analysis of the structure community are presented in Figure 38. Number of individuals fluctuated between 2,658 and 8,601 ind.m$^{-2}$ with a mean of 4,670 ind.m$^{-2}$ (Figure 38A). They tended to be highest in October (summer) and lowest in March (winter), with strong interannual fluctuations. Two summer seasons were noteworthy with a peak of 7,384 ind.m$^{-2}$ in 2013 and a peak of 8,601 ind.m$^{-2}$ in 2017. The lowest abundances were recorded for the winters 2013, 2016 and 2018 with values of 3,373, 2,658 and 2,985 ind.m$^{-2}$ respectively. The species richness of the benthic community varied between 85 and 109 species with a mean value of 98 species (Figure 38B). There was a pronounced seasonal variation in species richness with a maximum in late summer and a minimum in late winter. The Shannon diversity index (H') varied between 3.85 and 4.90 with a mean value of 4.45 (Figure 38C). With the notable exception of March 2015, which was characterized by a low value of 3.91, it increased steadily from March 2013 to October 2016 when it reached its maximum value, before dropping to a value of 3.85 in October 2017. The Pielou's evenness (J') varied between 0.57 and 0.72 with a mean value of 0.67 (Figure 38D). It showed variations very similar to those described for the Shannon index with minima in March 2015 and October 2017. These two low values of H' and J' imply a decrease in diversity and a decrease in equitability between species at both dates.

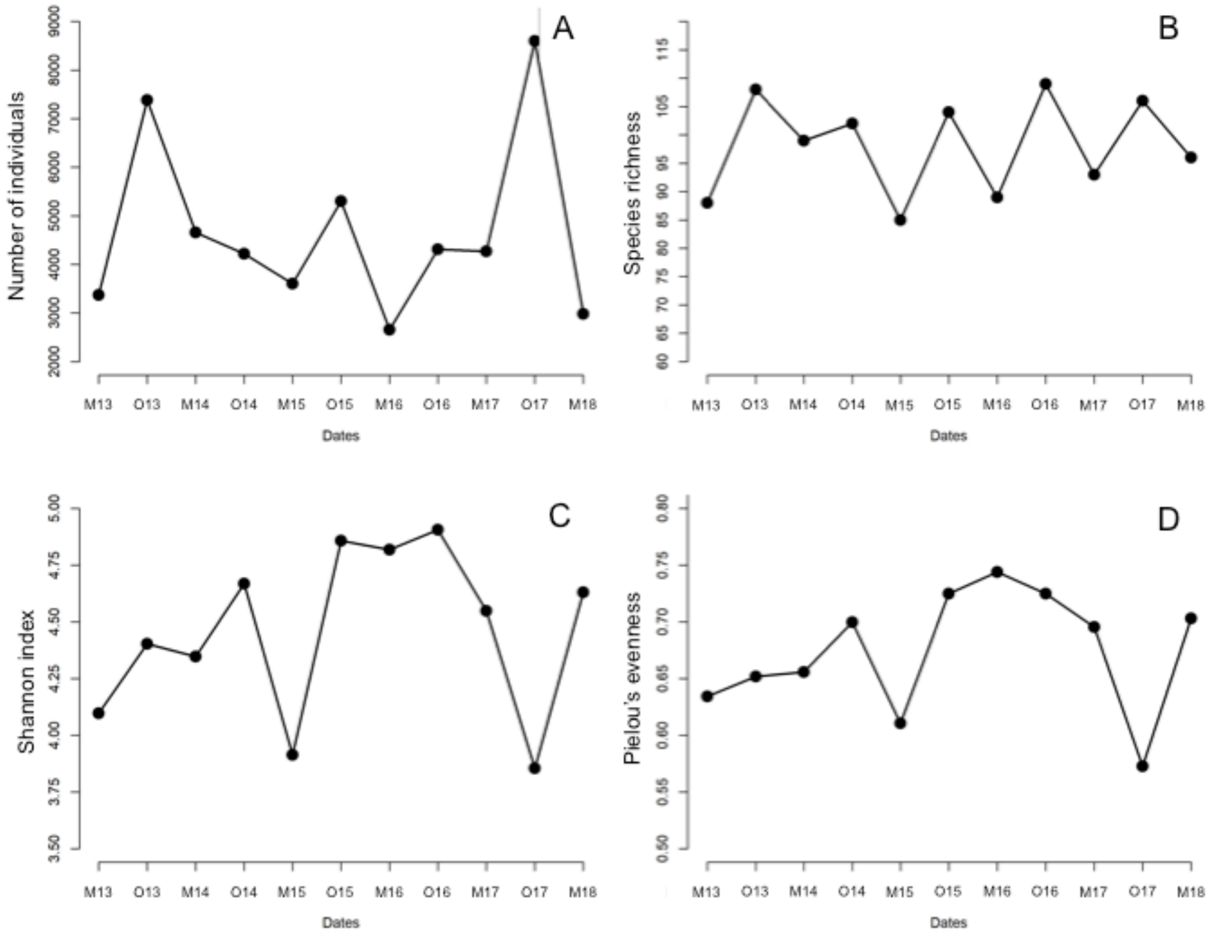


**Figure 38:** Temporal evolution of diversity indices from March 2013 to March 2018. (A) Number of individuals (ind.m$^{-2}$); (B) Species richness; (C) Shannon index (H'); (D) Pielou's evenness (J').

Multivariate analyses (i.e., n-MDS and PCoA) confirmed seasonal variability in community structure with samples divided into two separate groups according to season (Figure 39 and Figure 40). On the PCoA whose first two axes explain 43.7% of the variability, two groups were distinctly separated along axis 1 related to the seasons (Figure 40). In addition, there was an interannual variability in the structure of the communities along axis 2. For example, winters 2015, 2016, 2017 and 2018 were marked by higher abundances of the Ophiuroidea *Amphiura filiformis*.

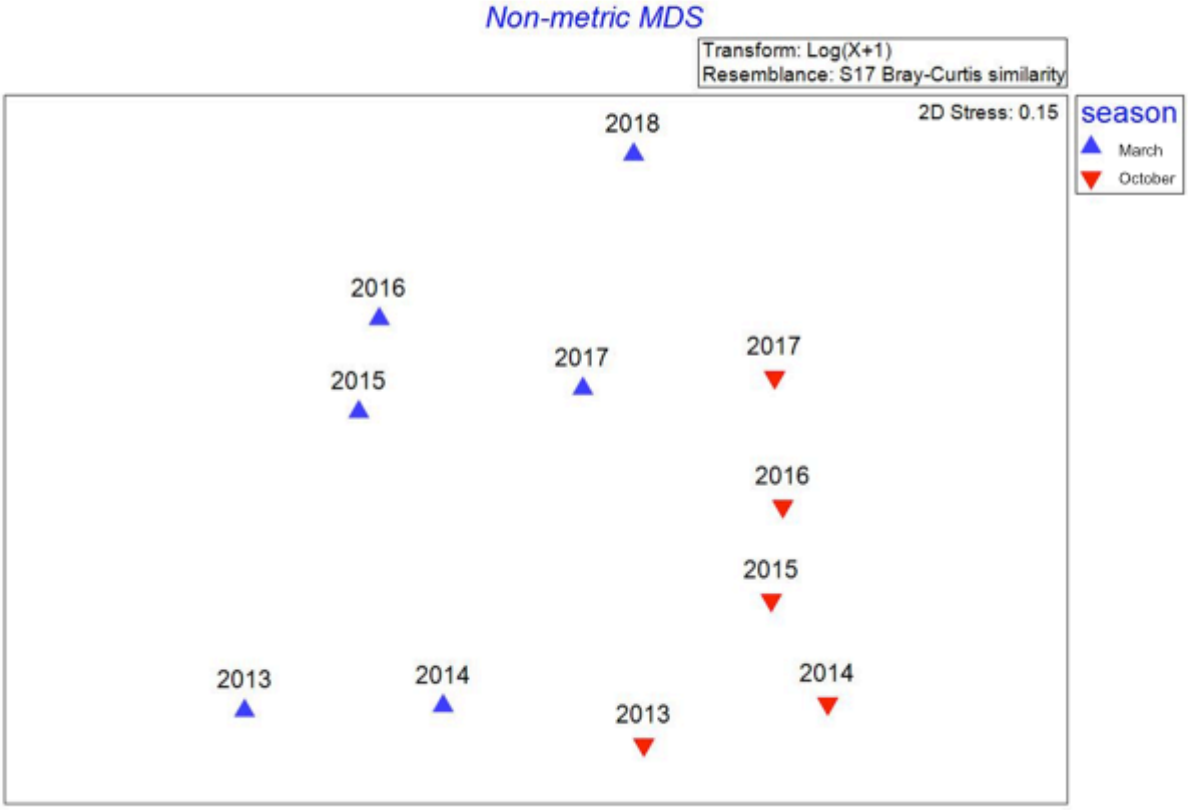


**Figure 39:** Non-metric multidimensional scaling (n-MDS) ordination plot of macrofaunal community from March 2013 to March 2018 showing seasonal and the year-to-year changes in the community. The n-MDS plot is based on Bray-Curtis similarities after a log-transformation of species abundances.

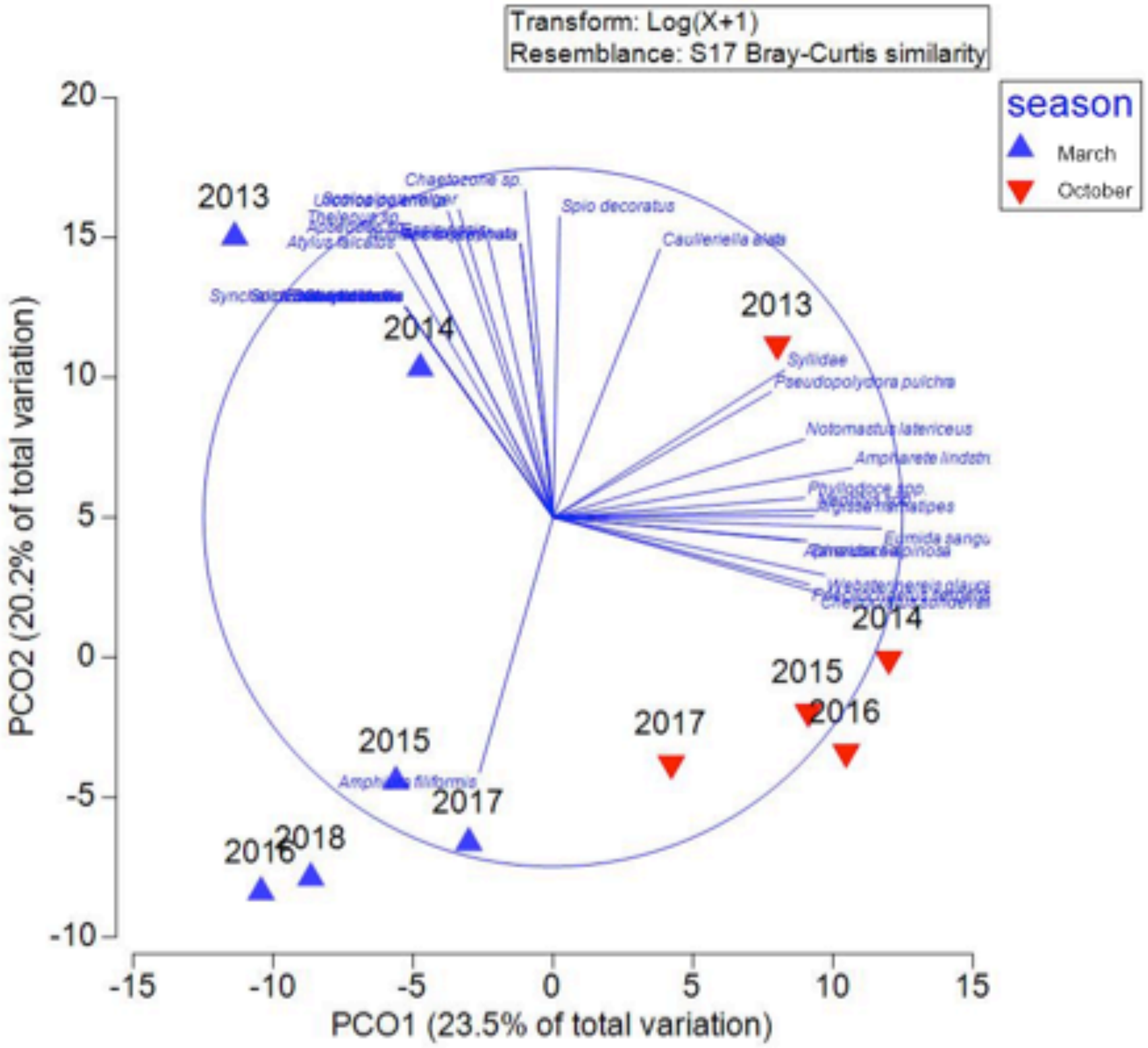


**Figure 40:** Principal Coordinate Analysis (PCoA) based on Bray-Curtis similarities after a log-transformation of species abundance from March 2013 to March 2018. Species with a Pearson correlation coefficient greater than 0.75 with the first two axes of the analysis are shown.

### IV.3.2. Trophic structure

The isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of consumers sampled in late winter and late summer over the period 2013 to 2018 are shown in Figure 41. They represent the main structural characteristics of the food web. The list of species with their assigned numbers used on these graphs is given in supplementary material (Supplementary material 1).

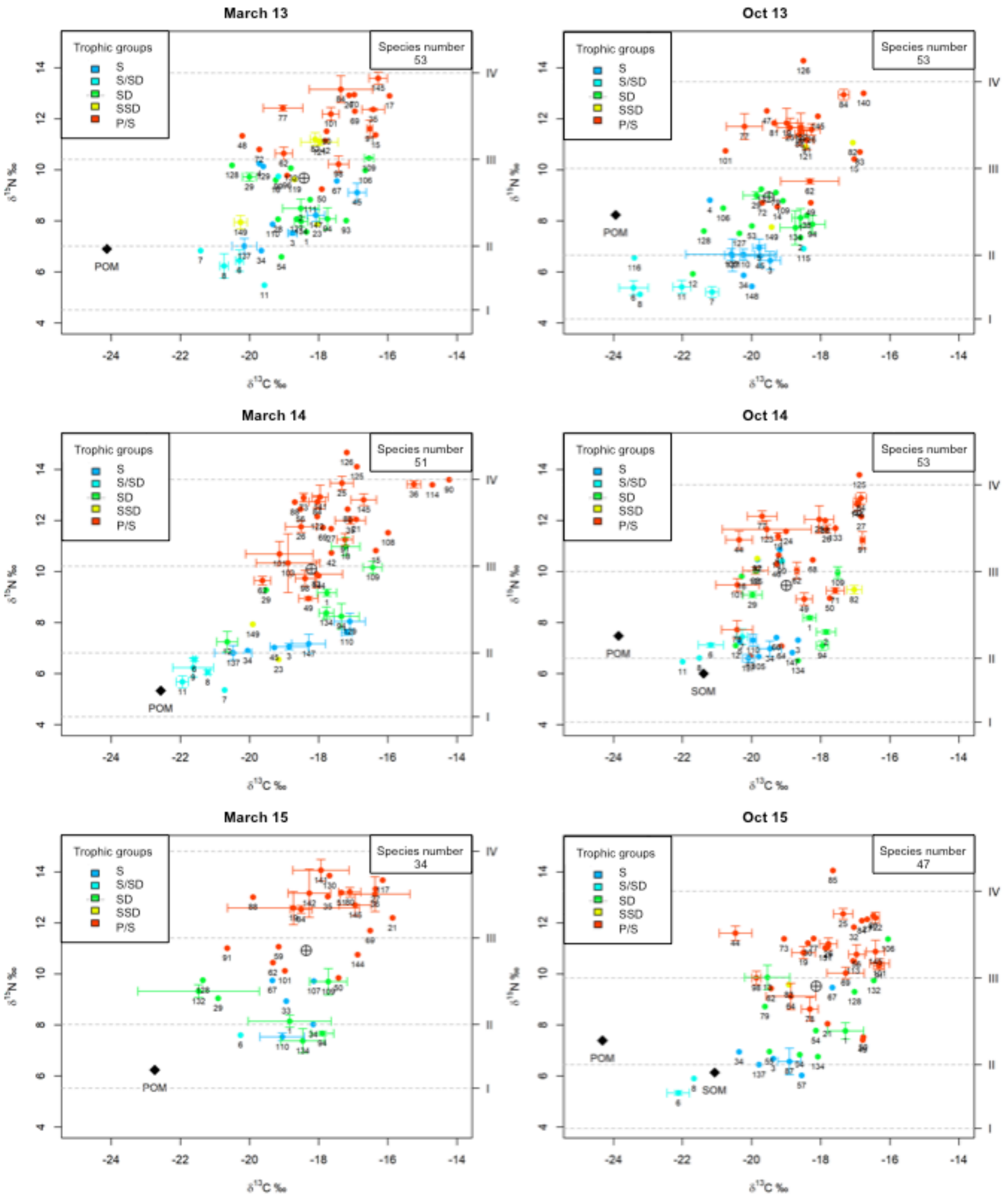
The range of $\delta^{13}C$ mean values for the entire food web of consumers was, for the majority of dates, between -22 and -16 ‰, regardless of the season. These values are consistent with the $\delta^{13}C$ ranges commonly observed in temperate coastal areas. The maximum value of $\delta^{13}C$ (-14 ‰) was observed in March 2014 for the taxa *Crangon crangon*, Nemertea and *Pleuronectes platessa*. The minimum value of $\delta^{13}C$ (-24 ‰) was observed for the *Ampelisca armoricana* in October 2013. The mean $\delta^{13}C$ of the POM varied only slightly, between -24 and -22 ‰ over the study period. The $\delta^{13}C$ values of the SOM were only measured at the end of the summer and varied only slightly too, between -21 and -20 ‰. The $\delta^{13}C$ values of the barycentre of the isotopic data set of the two-dimensional space $\delta^{13}C$ *vs* $\delta^{15}N$ varied slightly between -19 and -18 ‰, which highlighted the global stability of the food web.

The range of $\delta^{15}N$ mean values for the entire food web was between 5 and 14 ‰, regardless of the season. $\delta^{15}N$ of POM varied between 5 and 8 ‰ while $\delta^{15}N$ of SOM in summer varied between 6 and 7 ‰. On the $\delta^{15}N$ axis, the values of the barycentre varied little, between 9 and 11 ‰.

At the level of the different trophic groups, the base of the network represented by suspension feeders had isotopic signatures between -24 and -18 ‰ on the $\delta^{13}C$ axis and between 5 and 8 ‰ on the $\delta^{15}N$ axis. Predators and scavengers logically represented the summit of the food web with the highest $\delta^{15}N$ between 10 and 14 ‰ and $\delta^{13}C$ between -21 and -14 ‰.

The estimation of the different trophic levels indicated that the trophic network of the community was composed of four levels. Level II included mainly suspension feeders and some surface deposit feeders. Level III included mainly surface and sub-surface deposit feeders. Level IV consisted almost exclusively of predators and scavengers. There was thus an overall coherence in the distribution of trophic groups with regard to the isotopic signatures of the species. Primary consumers had low isotope values in $\delta^{15}N$ (i.e. from 5 to 8 ‰) while their predators and the scavengers had high isotope values in $\delta^{15}N$ (i.e. from 10 to 14 ‰). Despite this overall consistency, there was variability in isotopic signatures between species within each trophic group but also variability for a given taxa. This can be described in more detail using the example of suspension feeders. If we consider the case of *Ampelisca brevicornis* and *Timoclea ovata*, their relative isotopic positions in the isotopic space varied over the seasons. These species tended to be close to each other in certain seasons (e.g. summer 2017) with nearby values of $\delta^{13}C$ (-20.95 ‰ and -21.44 ‰) and $\delta^{15}N$ (6.44 ‰ and 7.14 ‰) for *T. ovata* and *A. brevicornis* respectively or, on the contrary, to be more distant in other seasons (e.g. winter 2016) with values of $\delta^{13}C$ (-19.25 ‰) and $\delta^{15}N$ (7.25 ‰) for *T. ovata* and $\delta^{13}C$ (-22.23 ‰) and $\delta^{15}N$ (6.38 ‰) for *A. brevicornis*. These isotopic variations of some species in relation to each other reflect trophic plasticity within the global network.

Finally, some species had an isotopic signature that did not conform to the trophic group to which we had assigned them. For example, during the summer 2014, the predators *Inachus spp.* (64), *Hyas spp.* (63) and *Macropodia spp.* (78) had lower $\delta^{15}N$ isotopic values than expected for predators, while the suspension feeders *Dosinia lupinus* (41) and *Owenia fusiformis* (99) had higher isotopic values than expected for primary consumers. Similar results were observed in summer 2017 for the predator *Corystes cassivelaunus* (35), the suspension feeder *Lanice conchilega* (67) or the surface feeder *Paraonidae* (106). These results reflected a lack of knowledge of the diets of many marine invertebrates, a high degree of omnivory in species commonly classified as predatory, and consequently a continuity in the values of $\delta^{15}$N between trophic groups.



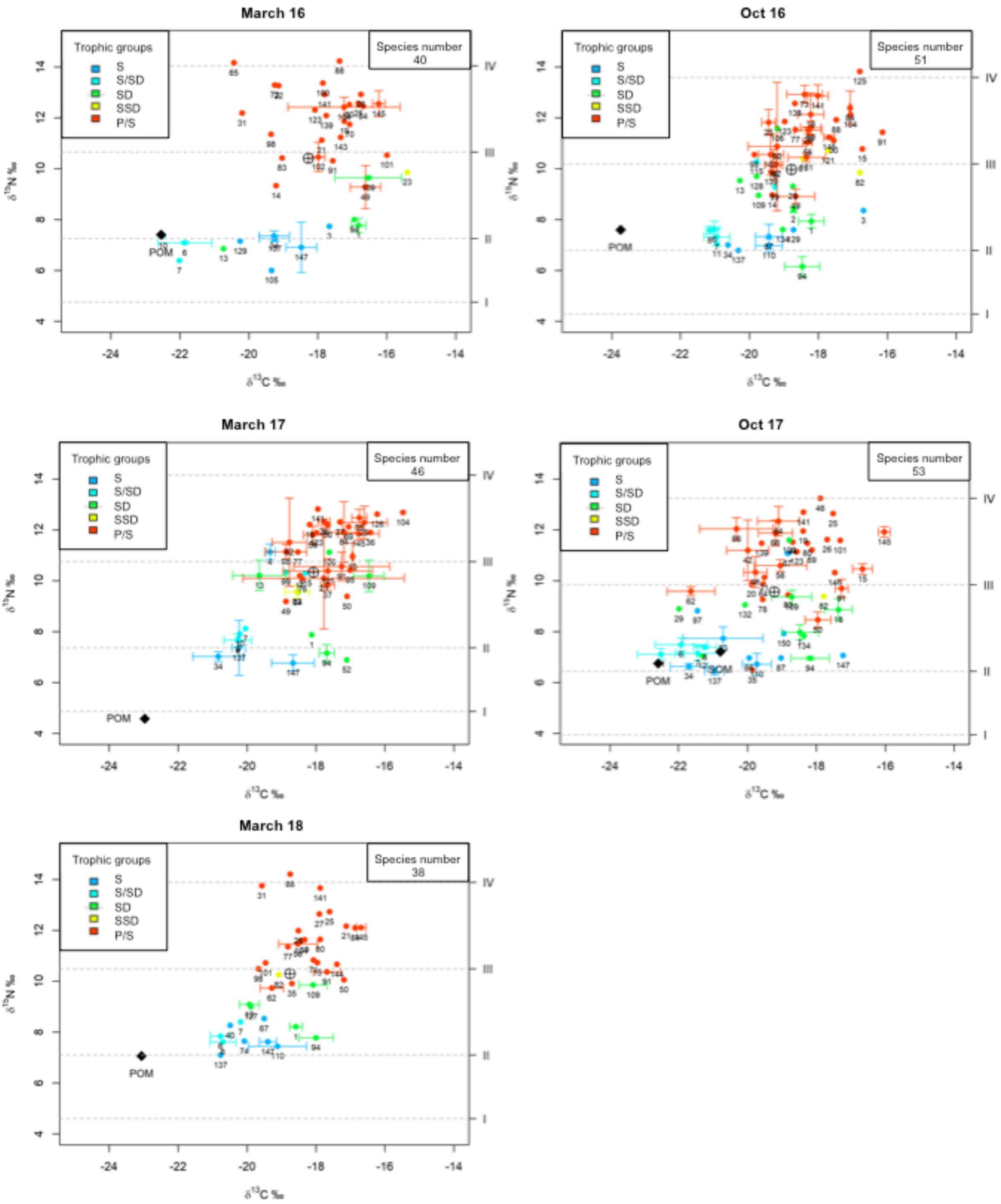
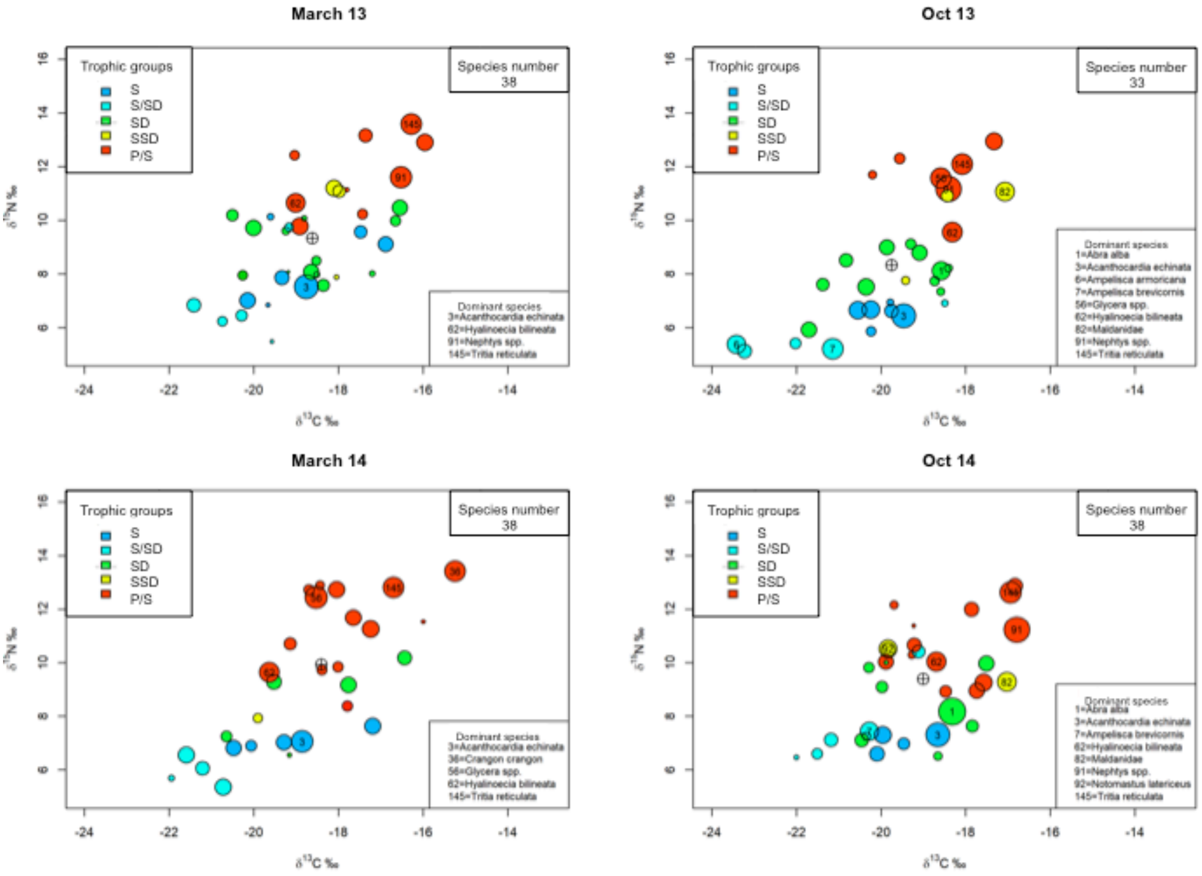


**Figure 41:** Two-dimensional scatterplot ($\delta^{13}C$ vs. $\delta^{15}N$) of the food web at the Pierre Noire site at different dates. The trophic groups are the suspension feeders (S), the suspension and surface deposit feeders (S/SD), surface deposit feeders (SD), sub-surface deposit feeders (SSD) and predators/scavengers (P/S) Each point corresponds to the mean value of the isotopic signatures; standard deviations are represented for $n \geq 3$. Theoretical trophic levels are added on the basis of the theoretical trophic level II established from the isotopic values of *Timoclea ovata* or *Corbula gibba*. A cross within a circle represents the barycentre of the isotopic space. The sources (POM and SOM) are represented by black diamonds.

In order to highlight the species that mobilise the most organic matter in the food web and probably play a more important role, the previous figures have been repeated by including the species biomass (Figure 42). For better readability, a log transformation was applied to the biomass data. The number of species taken into account varied between 21 and 40, whereas it was 34 to 53 for the previous graphs. This difference resulted from a bias in the sampling protocol. Some benthic invertebrates were only sampled with the 3-m beam trawl or the anchor dredge. For these species isotopic signatures were available while their biomass could not be estimated from the 10 grab samples used to calculate the species densities. In winter, the dominant species in terms of biomass present each year was *Tritia reticulata*, followed by *Nephtys spp.* and *Glycera spp.*. In summer, the species present each year and dominant in terms of biomass was also *Tritia reticulata*, followed by *Glycera spp.* These are carnivorous and/or scavenging species. We also note that *Abra alba* and *Acanthocardia echinata*, two primary consumers at the base of the food web, had high biomasses. These results highlight a feature that is rarely found in marine food webs: high biomasses associated with species at high trophic levels, i.e. predators and scavengers. As these species feed at lower trophic levels, these results show the importance of trophic groups such as suspension feeders and surface deposit-feeders in the structure and stability of this trophic network for which a significant part of the biomass is mobilised by carnivores.



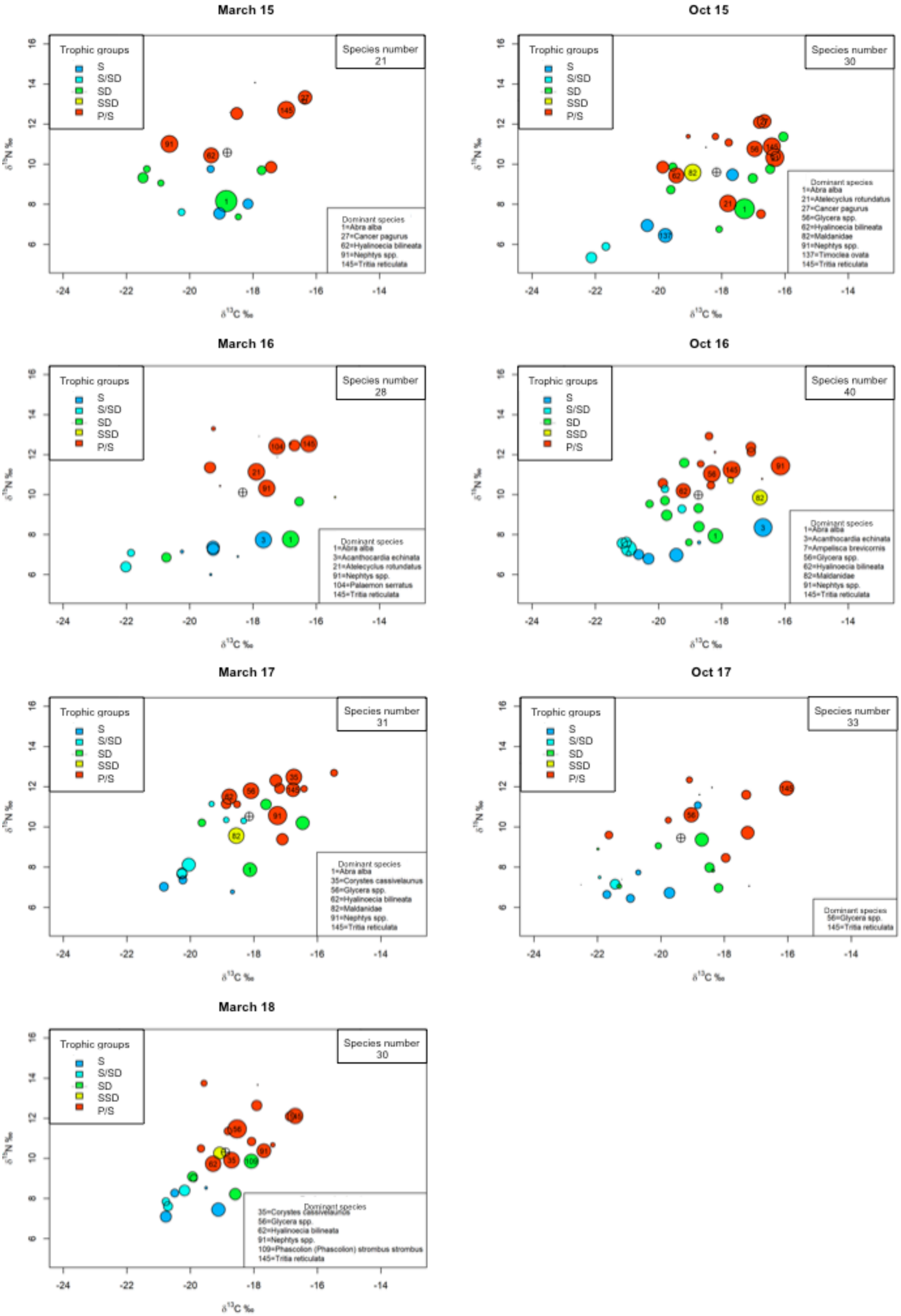


**Figure 42:** Graphical representation of the trophic network weighted by the biomass of each species. The species biomasses are log transformed and are proportional to the size of the circles. Species for which log values are greater than 2.5 are indicated as dominant species. The trophic groups are the same as those shown in **Figure 41**.

### IV.3.3. Temporal evolution of the isotopic indices

Based on the 21 to 40 different species for which biomass was available (Figure 42), the 13 isotopic indices were calculated in order to describe their temporal evolution (Figure 43).

The $\delta^{13}C$ range (CR) varied between 6.06 and 9.32 with a mean of 7.45. It tended to decrease over time and showed maximum values during March 2014 and March 2016. The $\delta^{15}N$ range (NR) fluctuated from 4.08 to 7.23 with a mean of 5.81 and showed higher values in March 2014 and March 2016 in parallel with fluctuations in CR. A third maximum in NR values was observed in October 2017.

The isotopic richness described from the TA or SEAc indices showed a strong temporal variability with values between 0.49 and 1 (mean 0.73) for TA and between 0.46 and 1 (mean 0.69) for SEAc respectively. Similarly, $\text{Hull}_{\text{biom}}$ showed a strong temporal variability with higher values exceeding 0.4 between October 2014 and October 2016, while values between 0.1 and 0.2 were observed in March 2013 and October 2017.

Isotopic divergence and dispersion measurements presented relatively high values. The CD, with high values ranging from 0.71 to 1 (mean = 0.82), indicated a strong functional divergence between species. However, the CD fluctuated quite sharply from one date to the next, with peaks observed in March 2014 and March 2016. The IDiv index was relatively stable around its mean value of 0.73 (range = 0.69 to 0.79) but this high value suggests a strong trophic specialisation and therefore a greater differentiation of specific isotope niches within the community. The IDis index, whose values fluctuated between 0.37 and 0.67 (mean = 0.49), showed pronounced temporal variations with two peaks observed in March 2015 and October 2017.

With the exception of MNND, the different indices of isotopic regularity were relatively constant over time but with very different absolute values. The IEve varied between 0.74 and 0.81 (mean = 0.78), reflecting a regular distribution of species in the isotopic space and therefore a good use of resources thanks to complementarity between species. For the SDNND, the observed low values varied between 0.24 and 0.37 (mean = 0.32). The MNDD had intermediate values to those recorded for the IEve and SDNND, which fluctuate between 0.44 and 0.74 (mean = 0.55). MNNDD presented a temporal variation that was not perfectly synchronous with the one described above for the CD and IDis indices, and was characterised by two maxima in March 2015 and March 2016.

The generally high values of the ISim and INess overlap indices between seasons, most often above 0.5 for ISim and 0.7 for INess, indicate that the food web had an organisation of the isotopic space quite similar for the two seasons. The differences between the seasons measured by these overlap indices, are independent of a seasonal change of the isotopic space measured by TA, which measures the isotopic space occupied by the food web in each season. Only the year 2015 differed conspicuously from other years by low values of the overlap indices (Figure 44).

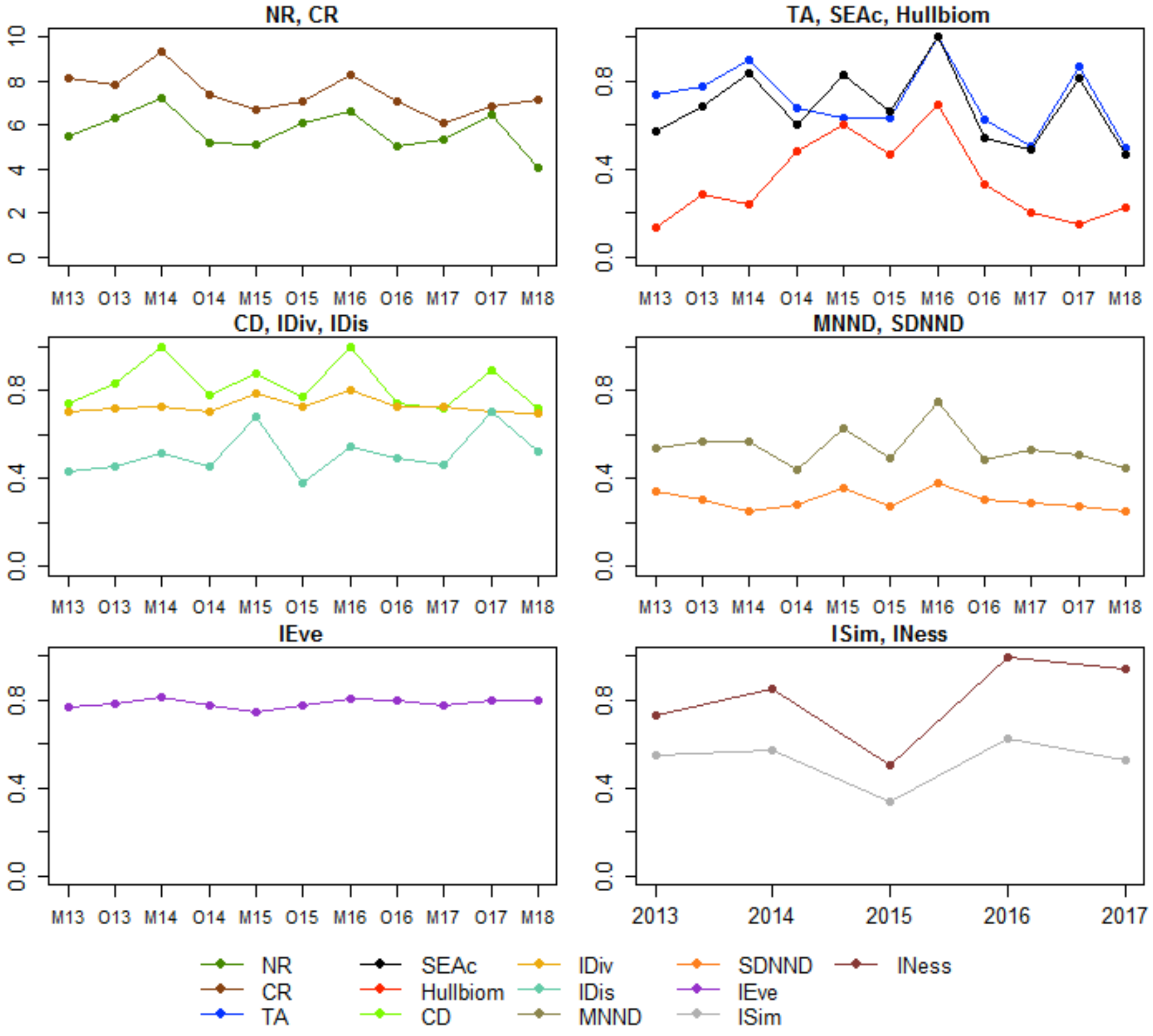


**Figure 43:** Temporal evolution of the different isotopic indices.

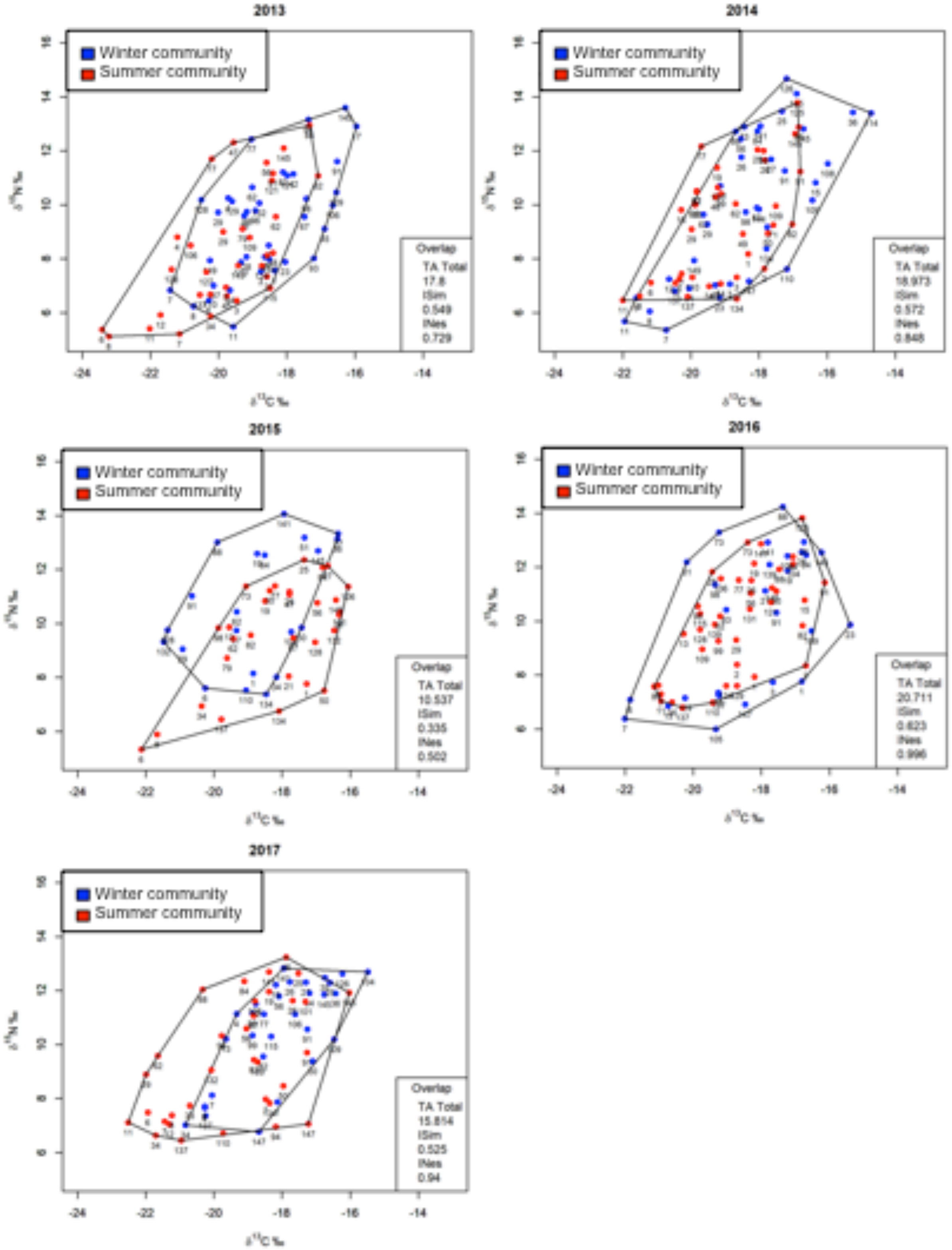


**Figure 44**: Graphical representation of the overlap between seasons (winter and summer) for all years. Values for March months (winter) are indicated in blue and values for October months (summer) in red.

# IV.4. Discussion

## IV.4.1. Temporal variability of the community structure

The results on the temporal variability of the structure of the Pierre Noire fine sand community indicated a strong seasonality of the number of individuals and species richness. This seasonality was characterised by a species richness which increased in summer and decreased in winter. This pattern was also found in the fluctuations of the number of individuals and was explained by the massive recruitment of juveniles during the summer and their decline during autumn and winter by natural mortality and/or trophic competition within the community (Thouzeau, 1991). Richness and number of individuals values in winter correspond to the baseline of the community (Dauvin, 1988). Such seasonal variations in benthic communities are common in temperate zones and the importance of this signal has already been mentioned many times for the Pierre Noire community (Dauvin, 1984; Fromentin et al., 1997; Saulnier et al., 2019; Thiébaut et al., in prep). In addition to this seasonal variability, there are interannual variations in species composition, diversity and relative abundances of dominant species. During the period studied, between 2013 and 2018, these variations remain small compared with what was previously described for the period 1977-2016 (Dauvin, 1984, 2000; Thiébaut et al., in prep). For example, following the Amoco-Cadiz oil spill in March 1978, abundances dropped from over 45,000 ind.m$^{-2}$ at the end of summer 1977 to about 3,000 ind.m$^{-2}$ at the end of summer 1978, while species richness decreased from 97 to 69 species. This pollution also led to a profound change in the composition of the community with the almost disappearance of some species such as *Ampelisca spp.* and the development of opportunistic species. Although the community had regained characteristics similar to those of 1977 in the mid-1990s, it was again profoundly modified from 2005 with a further decline in abundances, which was now low and around a few thousand individuals per m$^2$ during the last years (Thiébaut et al., in prep).

With this analysis of the benthic community based on species diversity, abundance and biomass, it was interesting to examine whether the seasonality observed during these six years and the low interannual variations are also reflected in the isotopic data and thus in the temporal evolution of the local food web.

## IV.4.2. Temporal variability of the food web structure

### IV.4.2.1. General structure of the food web

Particulate Organic Matter (POM) suspended in the water column and Sedimented Organic Matter (SOM) within and on the sediment are heterogeneous mixtures of dead and living plankton (only for POM), microorganisms and detrital organic matter such as faecal balls and organic debris (Liénart et al., 2018). The $\delta^{13}C$ POM values (-24 to -22 ‰) observed at the Astan site during this study were higher than the values of $\delta^{13}C$ (-22 to -19 ‰) previously reported by Gaudin (2012) on samples taken at the Pierre Noire site in 2011 and 2012. On the other hand, the $\delta^{15}N$ POM values (5 to 8 ‰) were very close to those measured at the Pierre Noire site (6 to 7 ‰) for samples acquired during 2011 and 2012 (Gaudin, 2012). Thus, it is likely that the Astan site presented isotopic values, and therefore a POM composition, slightly different from those of the Pierre Noire site, which would have a more coastal signature. This difference in values could be explained by the hydrodynamics of the English Channel and a greater pelagos-benthos coupling at the Pierre Noire site (Dauvin, 1987). Conversely, the advantage of using Astan data in the present study was to integrate the values of the isotopic signatures of POM during the weeks preceding the sampling of benthic organisms. A better understanding of the spatial variability of the POM isotopic signature within the bay could be very useful in the future.

The Pierre Noire site with a sandy bottom was characterised by a limited diversity of trophic sources typical of open sea environments (Grall et al., 2006; Le Loc'h et al., 2008) and was clearly distinguishable from many coastal systems for which the nutrient sources were more varied and included macroalgae in rocky areas with *Ascophyllum nodosum* or *Laminaria spp.* (Schaal et al., 2010; Golléty et al., 2010), or seagrass beds of marine phanerogams (Carlier et al., 2007; Ouisse et al., 2012) and microphytobenthos (Rigolet et al., 2014) in sedimentary areas. Despite this lack of diversity of potential food sources, consumers had a wide $\delta^{13}C$ range reflecting the ability of species to select their diet from the heterogeneous pools of POM and SOM.

The isotopic signatures of SOM and POM at the Pierre Noire site were very close to those of some suspension feeders and suspension/surface deposit-feeders species such as *Ampelisca sarsi* and *Ampelisca armoricana*. At some dates, the signatures of SOM and POM could even be higher than these two species, such as summers 2015 and 2017. Several hypotheses have already been proposed to explain this phenomenon (Gaudin, 2012). Some primary consumers would preferentially feed on a single source of organic matter according to their trophic modes, or some suspension feeders would preferentially feed on fractions more or less enriched in $^{13}C$ within the heterogeneous mixture of SOM and POM. The suspension feeders could select these more or less enriched fractions during filtration, ingestion or absorption. Thus, for some suspension feeders that preferentially feed on POM such as the oyster *Crassostrea gigas*, the mussel *Mytilus edulis* or the slipper limpet *Crepidula fornicata*, differences in isotopic signatures have been reported, for example in the Bay of Mont-Saint-Michel (Riera, 2007). These differences may come from selectivity mechanisms (i) between living organic material and decomposing material, or (ii) between different size classes of POM (Wainright & Fry, 1994; Rolff, 2000). A relative diversity in the composition of the sources (SOM and POM) and in the diets of consumers would partly explain the species diversity encountered at the Pierre Noire site.

With the observation of particular isotopic signatures for some species such as *Corystes cassivelaunus* or *Hyas spp.* classified in the predatory trophic group, we could see that this selectivity was also present in other trophic groups (McClintock & Lawrence, 1985; Moens, et al., 2006). These unexpected differences in isotopic signatures demonstrated a complexity of the network that made it impossible to only rely on theoretical trophic levels to determine levels in the food web. The Pierre Noire food web thus presented continuous trophic levels that reflected a trophic continuum and a high degree of omnivory for many species. This continuum showed the capacity of species to share the resources according to the seasons and to adapt their diets according to the resources available in the environment, defined as trophic plasticity (Carlier et al., 2007; Dubois et al., 2007; Chouvelon et al., 2011). For instance, Dubois et al. (2007) reported interspecific food partitioning among co-occurring suspension-feeders (ascidians, polychaetes, bivalves and barnacles) colonising oyster culture structures and suggested that plastic diets contributed to reduce inter-specific competition.

Differences in the isotopic values of the species were also reported between winter and summer seasons but the sign of the differences varied among years and species (Supplementary material 2). These differences could be explained by both the seasonal variations in the isotopic signatures of the sources, and the temporal variation in the supply to consumers. These isotopic differences reflected the plasticity of the diet of some consumers who could use different sources and preys or consume them in different proportions. In addition to trophic plasticity, different processes may contribute to temporal variations in the isotopic signatures of the sources. For example, a decrease in the value of $\delta^{13}C$ during the winter period can be linked to a greater contribution of terrigenous inputs and a lower contribution of marine inputs to the POM (Briant et al., 2018). On the other hand, temperature variations can also cause variations in the isotopic signature of carbon, an increase in temperature resulting in an increase in $\delta^{13}C$ of phytoplankton. Finally, seasonal changes in the composition of phytoplankton communities influence the isotopic signature of carbon: small phytoplankton cells have a lower value of $\delta^{13}C$ than large phytoplankton cells of the diatom type (Popp et al., 1998).

Another specificity of the Pierre Noire trophic network was the importance of the biomass of trophic group IV composed by predators and scavengers. It suggested an important link between this group and other macrofaunal and meiofaunal groups (Chardy & Dauvin, 1992) although no data was available in the present study on meiofauna. The high trophic plasticity of these predators and their ability to modify their diets according to the season and available resources may help to explain this observation.

### IV.4.2.2. Food web analysis with the isotopic indices

The results obtained using isotopic indices confirmed or complemented some of the results described above from the analysis of the 2-D isotopic space. The wide range of $\delta^{13}C$ indicated the diversity of diets within this trophic network, which can be explained by the heterogeneous nature of the composition of the POM and SOM and the diversification of dietary behaviour; it thus reflected the diversity of trophic niches within this network (Layman et al., 2007). The wide range of $\delta^{15}N$ was to be linked to the existence of four trophic levels. The limits indicated by these two ranges gave us an idea of the maximum size of the network for each season (Layman et al., 2012).

The measure of functional richness provided by TA and SEAc showed that the various trophic resources available were used, suggesting optimal productivity of the system which could be related to the trophic plasticity of the species (Layman et al., 2007; Jackson et al., 2011; Rigolet et al., 2015). These indices were highly correlated with indices measuring the ranges of $\delta^{13}C$ and $\delta^{15}N$. The use of the $Hull_{biom}$ index, which is a biomass-weighted index of functional richness, provided a different perspective from the two previous indices, as already highlighted by Rigolet et al. (2015) in a comparison of different coastal macrobenthic communities of soft substrates. While the first two indices indicated a small temporal variation, $Hull_{biom}$ varied over time suggesting an inter-annual variation in productivity and use of available resources. Furthermore, $Hull_{biom}$ has an additional quality; it is a less sensitive index to sample size than TA and SEAc, whose value may be strongly influenced by the presence or absence of rare species (Brind'Amour & Dubois, 2013; Rigolet et al., 2015).

The different measurements of isotopic dispersion and divergence (CR, IDiv and IDis) indicated a relatively high dispersion and thus a high differentiation of isotopic niches within the community, with dominant species located mostly at the extremities of the food web relative to its barycentre. In contrast to isotopic richness measurements, the weighting of the indices by the biomass does not lead to greater temporal variability in the values of the indices. Thus, CR and IDis fluctuated over time while IDiv remained relatively constant.

Measurements of isotopic regularity showed an average proportion of species that were characterised by relatively close trophic niches but a distribution of trophic niches of the species that tended to be rather uniform. IEve reflected a better use of resources thanks to complementarity between species.

The results on isotopic indices highlighted the importance of biomass-weighted indices, which can lead to different conclusions compared to unweighted indices. This importance was explained by the fact that most macrobenthic communities were dominated in terms of biomass by a small number of species, as was demonstrated for the Pierre Noire community (Dauvin, 2000). Given that the biomass weighting procedure made indices less sensitive to the number of species needed to properly describe the structural characteristics of food webs (Rigolet et al., 2015), only taking into account the dominant species in terms of biomass could be enough. Nevertheless, the results obtained were likely to be strongly influenced by the presence or absence in the samples of large, over-dispersed and most often poorly sampled species. This was the case, for example, at the Pierre Noire site of the bivalve *Acanthocardia echinata*.

Similar to the results obtained on rocky shoreline dominated by *Fucus spp.* (Bordeyne et al., 2017), the Pierre Noire trophic network did not show marked seasonality in its general organisation. This lack of seasonality was marked by the absence of major changes from one season to the next in the general architecture of the food web as described on the species distribution in the isotopic space or in the values of the different indices. Finally, the overlap indices showed strong similarity in both seasons with at least half of the isotopic space being shared. This lack of seasonality contrasted with seasonal variations in abundance, species richness and structure of the macrobenthic community (Thiébaut et al., in prep). This shows that Pierre Noire's “trophic network” system was maintained in terms of trophic niche diversity despite seasonal variations in the community. On the other hand, occasional seasonal variations in the trophic status (diet and trophic levels) of a given species could exist.

The inter-annual variability of the trophic structure of the Pierre Noire community was generally low even if some indices showed greater variations than others. This stability was to be linked with the small changes in the structure of the community observed between 2013 and 2018 in comparison with the variations described between 1977 and 2016.

## IV.5. Conclusion

The evolution of the benthic community at Pierre Noire site and the associated food web has been characterised for the period from 2013 to 2018 at two seasons. The analysis of the structure of the community showed seasonality in the number of individuals and species richness. SOM and POM represented the main sources of the food web. Nevertheless, this low diversity of sources did not translate into a low range of $\delta^{13}C$ or low isotopic richness due to consumer selectivity processes within the heterogeneous pools of SOM and POM. This indicated trophic specialisation. Variations in the isotopic signatures of some species at some seasons indicated a relative trophic plasticity of the species according to the available resources. Within the range of variation in the community structure observed between 2013 and 2018, the general properties of the food web appeared relatively stable. Seasonal variability of the community structure was not observed in the isotopic indices and their little interannual variability suggested a high resilience of the trophic network. Only the continuation of this monitoring will enable a better understanding of the sensitivity of the isotopic indices in the event of more significant changes in the macrobenthic community.

An alternative would be to compare the food web architecture of different fine sand macrobenthic communities distinguished by their organisational complexity and their degree of exposure to different anthropogenic disturbances. Although isotopic indices could be powerful tools for characterising the properties of a food web, their use requires certain limits to be taken into account depending on the structure of the food web (Jabot et al., 2017). It has been shown that these indices are reliable for a minimum number of species representative of a community and this number differs from one index to another, around 20 for CD and SEAc, 30 for MNND and more than 50 for TA (Brind'Amour & Dubois, 2013). In the future, it will be important to check the extent to which the variability in the number of species taken into account at different dates will influence the results obtained and to ensure that the sampling protocol does not cause any species important in terms of biomass to be excluded from the analyses. On the other hand, isotopic indices, in particular isotopic functional diversity indices, are sensitive to changes in the isotopic baselines (Belle & Cabana, 2020) and a standardization of the isotopic signatures according to the signature of the POM could be useful.

## Acknowledgments

This study was supported by the REBENT programme funded by the ‘Agence de l’Eau Loire Bretagne’, the ‘Région Bretagne’ and the ‘DREAL Bretagne’, and by the ‘Agence Française pour la Biodiversité”. It forms part of the research doctoral research work of Lise Bacouillard partly funded by the Brittany region. We thank the crew of the research vessel “Neomysis” for their valuable assistance during the field surveys.

## Supplementary materials

**Supplementary material 1**: List of species included in the present study with their identifier. The different trophic group of each species is provided: suspension feeder (S), suspension feeder and surface deposit-feeder (S/SD), surface deposit-feeder (SD), subsurface deposit-feeder (SSD) and predators/scavengers (P/S).

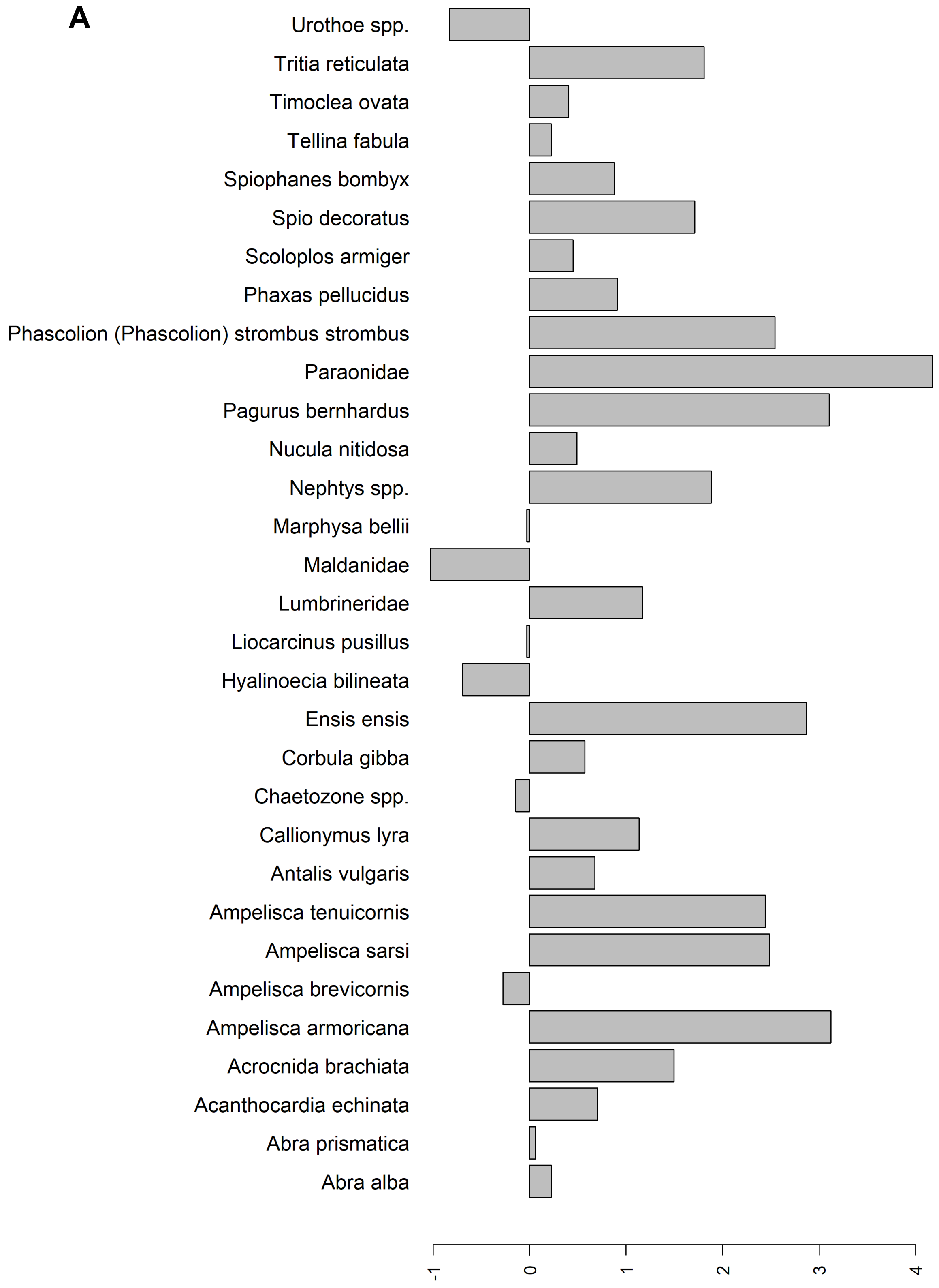
| **Species** | **Identifier** | **Trophic group** |
|---|---|---|
| *Abra alba* | 1 | SD |
| *Abra prismatica* | 2 | SD |
| *Acanthocardia echinata* | 3 | S |
| *Acrocnida brachiata* | 4 | S |
| *Aequipecten opercularis* | 5 | S |
| *Ampelisca armoricana* | 6 | S/SD |
| *Ampelisca brevicornis* | 7 | S/SD |
| *Ampelisca sarsi* | 8 | S/SD |
| *Ampelisca spinimana* | 9 | S/SD |
| *Ampelisca spinipes* | 10 | S/SD |
| *Ampelisca tenuicornis* | 11 | S/SD |
| *Ampharete lindstroemi* | 12 | SD |
| *Amphiura filiformis* | 13 | SD |
| *Anapagurus hyndmanni* | 14 | P/S |
| *Antalis vulgaris* | 15 | P/S |
| *Aphelochaeta spp.* | 16 | SD |
| *Aphrodita aculeata* | 17 | P/S |
| *Aporrhais pespelecani* | 18 | SD |
| *Arnoglossus laterna* | 19 | P/S |
| *Astropecten jonstoni* | 20 | P/S |
| *Atelecyclus rotundatus* | 21 | P/S |
| *Atherina presbyter* | 22 | P/S |
| *Bathyporeia spp.* | 23 | SSD |
| *Bittium reticulatum* | 24 | SD |
| *Buglossidium luteum* | 25 | P/S |
| *Callionymus lyra* | 26 | P/S |
| *Cancer pagurus* | 27 | P/S |
| *Caulleriella spp.* | 28 | SD |
| *Chaetozone spp.* | 29 | SD |
| *Chelidonichthys lucerna* | 30 | P/S |
| *Ciliata mustela* | 31 | P/S |
| *Claparedepelogenia inclusa* | 32 | P/S |
| *Clausinella fasciata* | 33 | S |
| *Corbula gibba* | 34 | S |
| *Corystes cassivelaunus* | 35 | P/S |
| *Crangon crangon* | 36 | P/S |
| *Mangelia costata* | 37 | P/S |
| *Diplocirrus glaucus* | 38 | SD |
| *Lucinella divaricata* | 39 | SD |

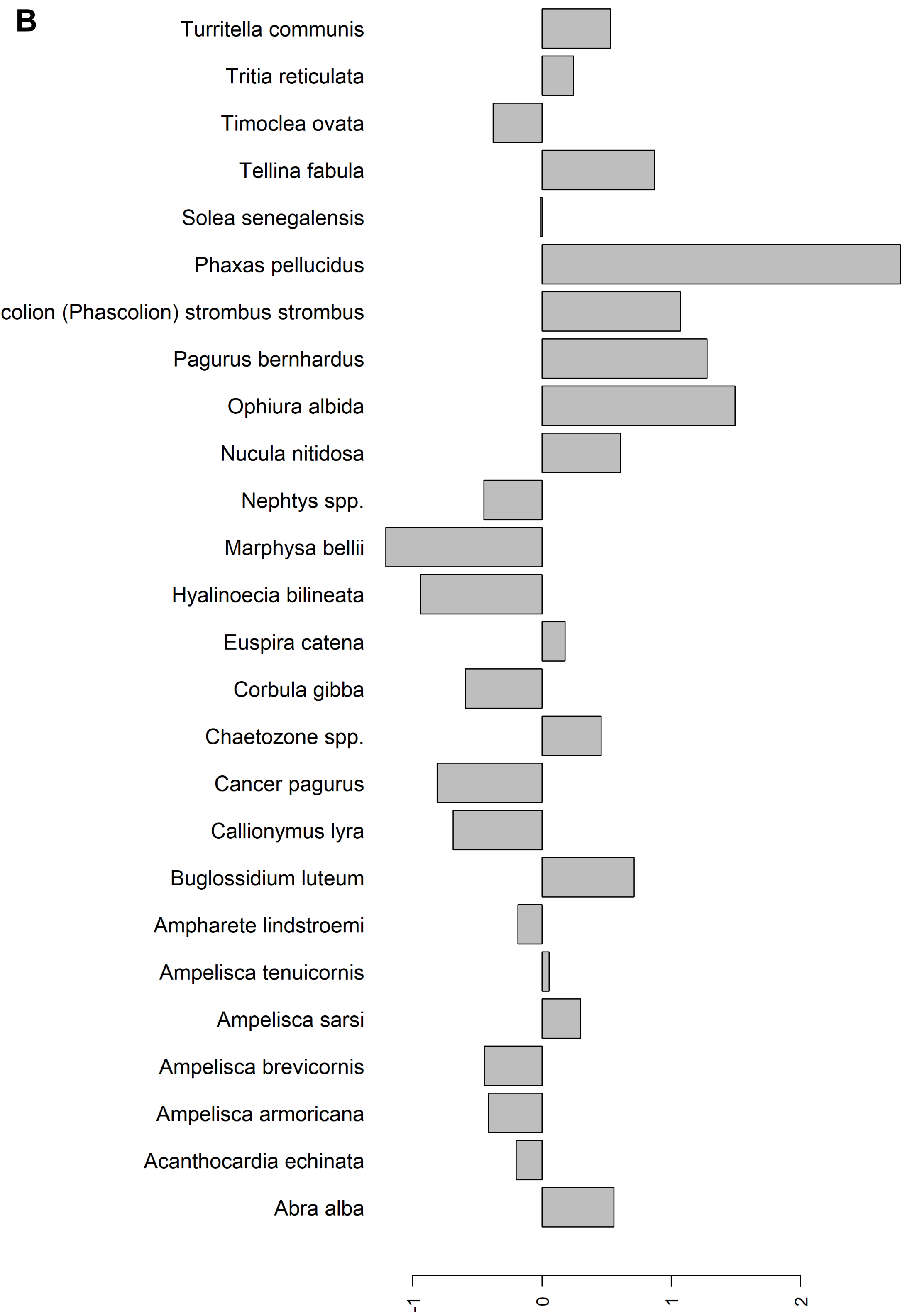
| **Species** | **Identifier** | **Trophic group** |
|---|---|---|
| *Dosinia exoleta* | 40 | S |
| *Dosinia lupinus* | 41 | S |
| *Ebalia spp.* | 42 | P/S |
| *Echiichthys vipera* | 43 | P/S |
| *Echinaster (Echinaster) sepositus* | 44 | P/S |
| *Ensis ensis* | 45 | S |
| *Eteone spp.* | 46 | P/S |
| *Eumida sanguinea* | 47 | P/S |
| *Eurydice pulchra* | 48 | P/S |
| *Euspira catena* | 49 | P/S |
| *Euspira nitida* | 50 | P/S |
| *Eutrigla gurnardus* | 51 | P/S |
| *Fabulina fabula* | 52 | SD |
| *Galathea spp.* | 53 | SD |
| *Gari fervensis* | 54 | SD |
| *Gari tellinella* | 55 | SD |
| *Glycera spp.* | 56 | P/S |
| *Glycymeris glycymeris* | 57 | S |
| *Goniada maculata* | 58 | P/S |
| *Gymnammodytes semisquamatus* | 59 | P/S |
| *Harmothoe spp.* | 60 | P/S |
| *Laetmonice hystrix* | 61 | SSD |
| *Aponuphis bilineata* | 62 | P/S |
| *Hyas spp.* | 63 | P/S |
| *Inachus spp.* | 64 | P/S |
| *Labrus bergylta* | 65 | P/S |
| *Laevicardium crassum* | 66 | S |
| *Lanice conchilega* | 67 | S |
| *Lepadogaster spp.* | 68 | P/S |
| *Liocarcinus depurator* | 69 | P/S |
| *Liocarcinus holsatus* | 70 | P/S |
| *Liocarcinus marmoreus* | 71 | P/S |
| *Liocarcinus pusillus* | 72 | P/S |
| *Loligo spp.* | 73 | P/S |
| *Loripes orbiculatus* | 74 | S |
| *Lucinoma borealis* | 75 | S |
| *Luidia atlantidea* | 76 | P/S |
| *Lumbrineridae* | 77 | P/S |
| *Macropodia spp.* | 78 | P/S |
| *Magelona spp.* | 79 | SD |
| *Maja squinado* | 80 | P/S |
| *Malacoceros spp.* | 81 | P/S |
| *Maldanidae* | 82 | SSD |
| *Bela nebula* | 83 | P/S |
| *Paucibranchia bellii* | 84 | P/S |
| *Marthasterias glacialis* | 85 | P/S |
| *Merlangius merlangus* | 86 | P/S |

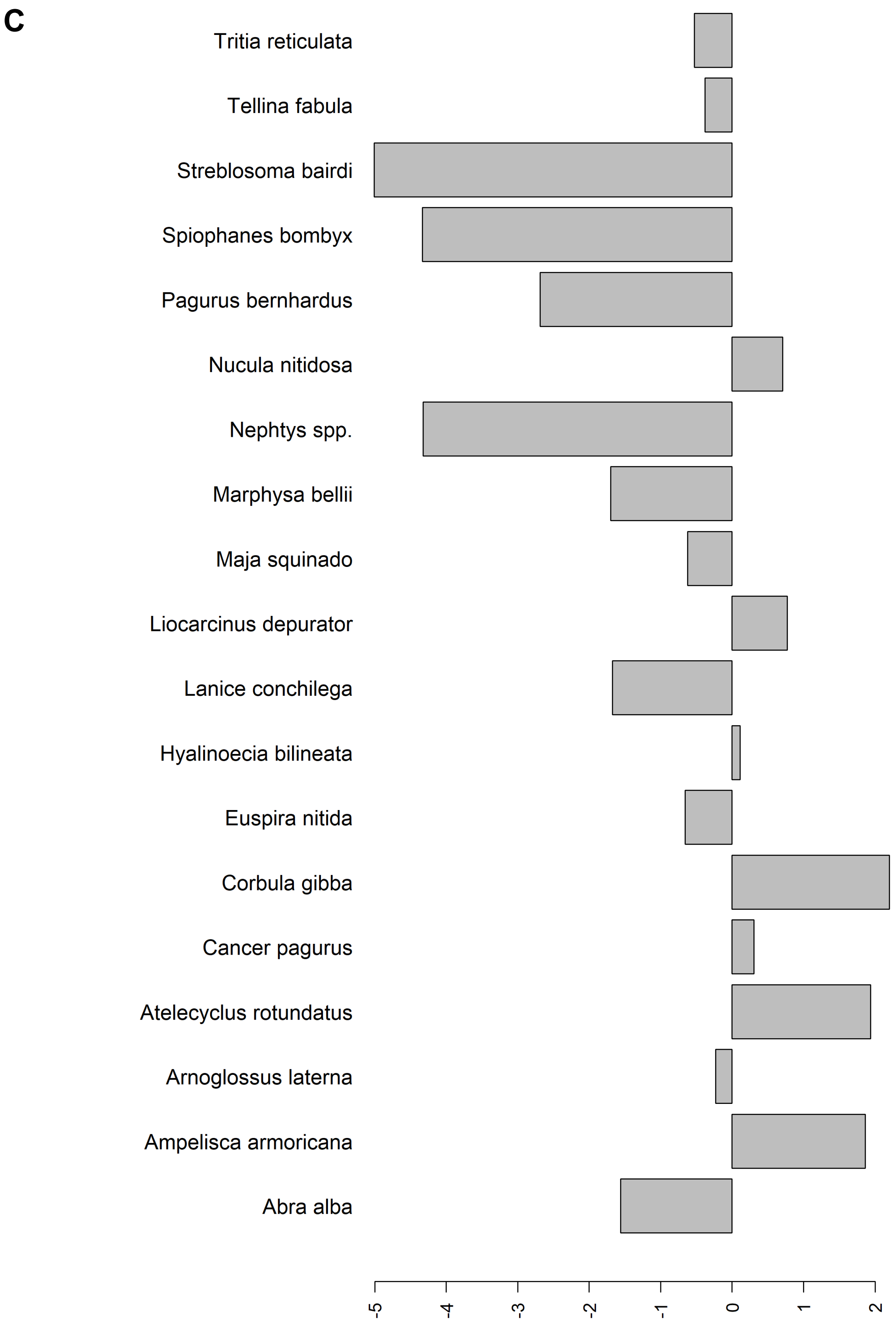
| **Species** | **Identifier** | **Trophic group** |
|---|---|---|
| *Mimachlamys varia* | 87 | S |
| *Mullus surmuletus* | 88 | P/S |
| *Lysidice unicornis* | 89 | P/S |
| *Nemertea* | 90 | P/S |
| *Nephtys spp.* | 91 | P/S |
| *Notomastus latericeus* | 92 | SSD |
| *Nucula pusilla* | 93 | SD |
| *Nucula nitidosa* | 94 | SD |
| *Ocenebra spp.* | 95 | P/S |
| *Odontosyllis gibba* | 96 | P/S |
| *Ophiothrix fragilis* | 97 | S |
| *Ophiura albida* | 98 | P/S |
| *Owenia fusiformis* | 99 | S/SD |
| *Pagellus acarne* | 100 | P/S |
| *Pagurus bernhardus* | 101 | P/S |
| *Pagurus cuanensis* | 102 | P/S |
| *Pagurus prideaux* | 103 | P/S |
| *Palaemon serratus* | 104 | P/S |
| *Pandora inaequivalvis* | 105 | S |
| *Paraonidae* | 106 | SD |
| *Pecten maximus* | 107 | S |
| *Pegusa lascaris* | 108 | P/S |
| *Phascolion strombus* | 109 | SD |
| *Phaxas pellucidus* | 110 | S |
| *Pherusa plumosa* | 111 | SD |
| *Platyhelminthes* | 112 | P/S |
| *Platynereis dumerilii* | 113 | P/S |
| *Pleuronectes platessa* | 114 | P/S |
| *Poecilochaetus serpens* | 115 | S/SD |
| *Polydora spp.* | 116 | S/SD |
| *Pomatoschistus minutus* | 117 | P/S |
| *Processa canaliculata* | 118 | SD |
| *Ptychodera spp.* | 119 | SSD |
| *Scaphander lignarius* | 120 | P/S |
| *Scoloplos armiger* | 121 | SSD |
| *Sepia officinalis* | 122 | P/S |
| *Sepiola spp.* | 123 | P/S |
| *Sigalion mathildae* | 124 | P/S |
| *Solea senegalensis* | 125 | P/S |
| *Solea solea* | 126 | P/S |
| *Spio decorata* | 127 | SD |
| *Spiophanes bombyx* | 128 | SD |
| *Spisula elliptica* | 129 | S |
| *Spondyliosoma cantharus* | 130 | P/S |
| *Sthenelais limicola* | 131 | P/S |
| *Streblosoma bairdi* | 132 | SD |
| *Syllidae* | 133 | P/S |

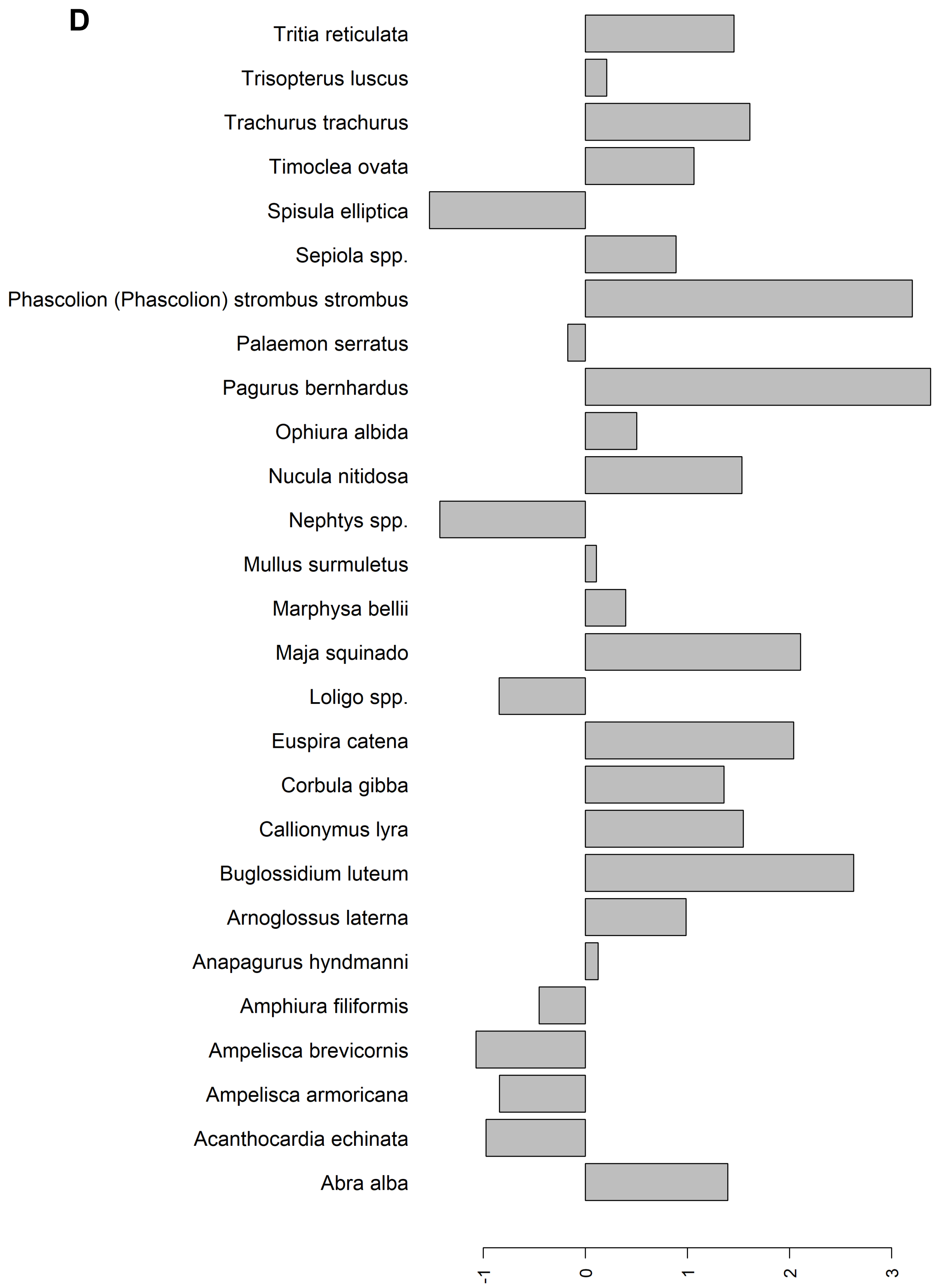
| **Species** | **Identifier** | **Trophic group** |
|---|---|---|
| *Fabulina fabula* | 134 | SD |
| *Terebellidae* | 135 | SD |
| *Thyasira flexuosa* | 136 | S/SD |
| *Timoclea ovata* | 137 | S |
| *Trachinus draco* | 138 | P/S |
| *Trachurus trachurus* | 139 | P/S |
| *Chelidonichthys lastoviza* | 140 | P/S |
| *Trisopterus luscus* | 141 | P/S |
| *Trisopterus minutus* | 142 | P/S |
| *Tritia incrassata* | 143 | P/S |
| *Tritia pygmaea* | 144 | P/S |
| *Tritia reticulata* | 145 | P/S |
| *Pyrgiscus crenatus* | 146 | P/S |
| *Turritella communis* | 147 | S |
| *Upogebia spp.* | 148 | S |
| *Urothoe spp.* | 149 | SSD |
| *Venus casina* | 150 | S |
| *Zeus faber* | 151 | P/S |

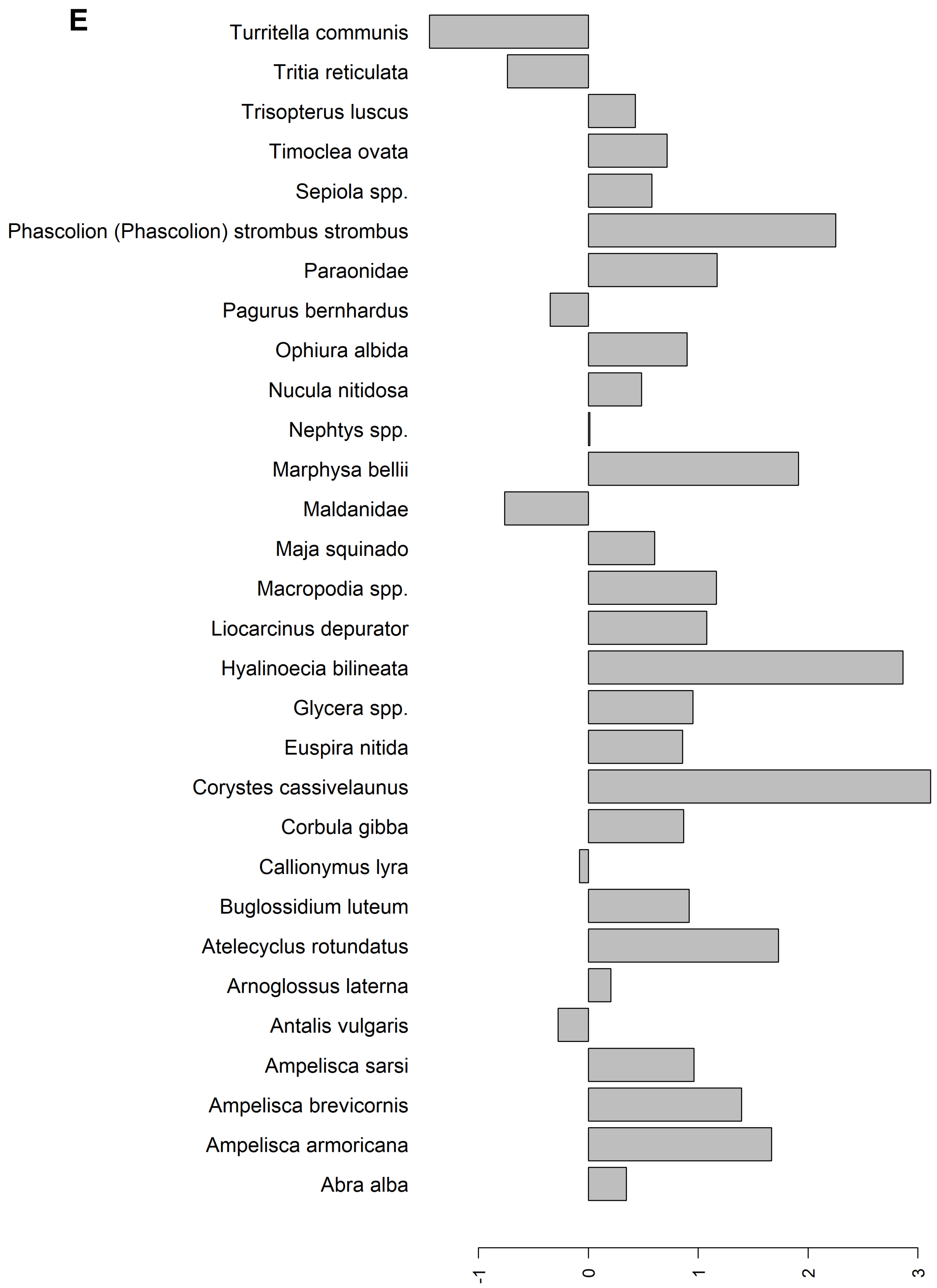
**Supplementary material 2:** Difference in the isotopic values for common species between winter and summer seasons for each year: (winter isotopic signature) - (summer isotopic signature) (A) 2013; (B) 2014; (C) 2015; (D) 2016; (E) 2017; (F) 2018.

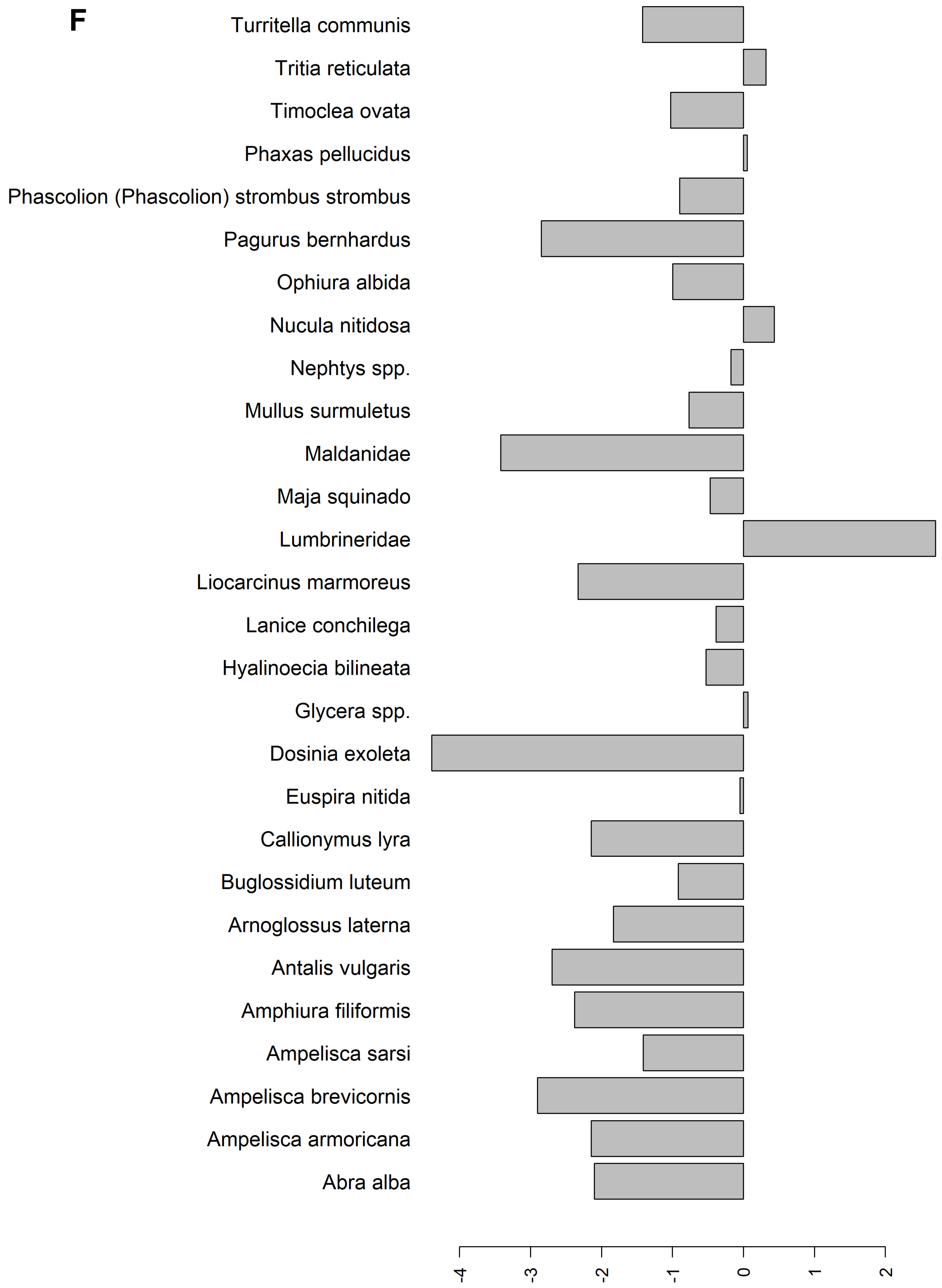



B
Turritella communis
Tritia reticulata
Timoclea ovata
Tellina fabula
Solea senegalensis
Phaxas pellucidus
Phascolion (Phascolion) strombus strombus
Pagurus bernhardus
Ophiura albida
Nucula nitidosa
Nephtys spp.
Marphysa bellii
Hyalinoecia bilineata
Euspira catena
Corbula gibba
Chaetozone spp.
Cancer pagurus
Callionymus lyra
Buglossidium luteum
Ampharete lindstroemi
Ampelisca tenuicornis
Ampelisca sarsi
Ampelisca brevicornis
Ampelisca armoricana
Acanthocardia echinata
Abra alba
-1
0
1
2

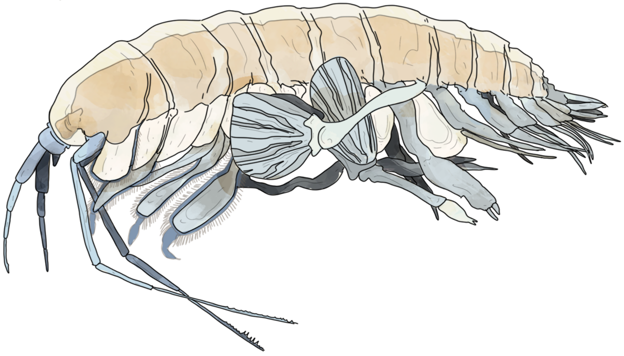

C
Tritia reticulata
Tellina fabula
Streblosoma bairdi
Spiophanes bombyx
Pagurus bernhardus
Nucula nitidosa
Nephtys spp.
Marphysa bellii
Maja squinado
Liocarcinus depurator
Lanice conchilega
Hyalinoecia bilineata
Euspira nitida
Corbula gibba
Cancer pagurus
Atelecyclus rotundatus
Arnoglossus laterna
Ampelisca armoricana
Abra alba
-5
-4
-3
-2
-1
0
1
2

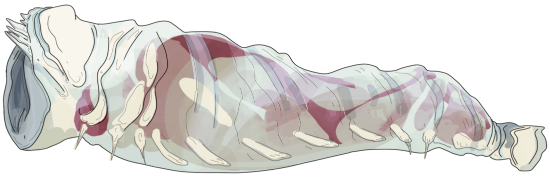

D
Tritia reticulata
Trisopterus luscus
Trachurus trachurus
Timoclea ovata
Spisula elliptica
Sepiola spp.
Phascolion (Phascolion) strombus strombus
Palaemon serratus
Pagurus bernhardus
Ophiura albida
Nucula nitidosa
Nephtys spp.
Mullus surmuletus
Marphysa bellii
Maja squinado
Loligo spp.
Euspira catena
Corbula gibba
Callionymus lyra
Buglossidium luteum
Arnoglossus laterna
Anapagurus hyndmanni
Amphiura filiformis
Ampelisca brevicornis
Ampelisca armoricana
Acanthocardia echinata
Abra alba
-1
0
1
2
3

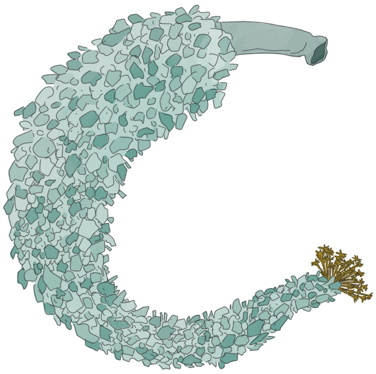

E
Turritella communis
Tritia reticulata
Trisopterus luscus
Timoclea ovata
Sepiola spp.
Phascolion (Phascolion) strombus strombus
Paraonidae
Pagurus bernhardus
Ophiura albida
Nucula nitidosa
Nephtys spp.
Marphysa bellii
Maldanidae
Maja squinado
Macropodia spp.
Liocarcinus depurator
Hyalinoecia bilineata
Glycera spp.
Euspira nitida
Corystes cassivelaunus
Corbula gibba
Callionymus lyra
Buglossidium luteum
Atelecyclus rotundatus
Arnoglossus laterna
Antalis vulgaris
Ampelisca sarsi
Ampelisca brevicornis
Ampelisca armoricana
Abra alba
-1
0
1
2
3

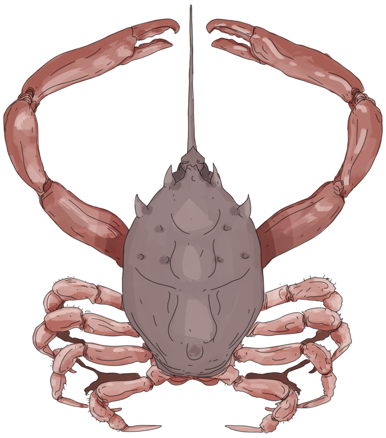

F
Turritella communis
Tritia reticulata
Timoclea ovata
Phaxas pellucidus
Phascolion (Phascolion) strombus strombus
Pagurus bernhardus
Ophiura albida
Nucula nitidosa
Nephtys spp.
Mullus surmuletus
Maldanidae
Maja squinado
Lumbrineridae
Liocarcinus marmoreus
Lanice conchilega
Hyalinoecia bilineata
Glycera spp.
Dosinia exoleta
Euspira nitida
Callionymus lyra
Buglossidium luteum
Arnoglossus laterna
Antalis vulgaris
Amphiura filiformis
Ampelisca sarsi
Ampelisca brevicornis
Ampelisca armoricana
Abra alba
-4
-3
-2
-1
0
1
2

# Conclusion générale et perspectives









Les pressions anthropiques croissantes vont se traduire par des modifications de la structure des communautés (richesse spécifique, composition en espèces, densité des espèces dominantes) caractéristiques des écosystèmes côtiers qui se répercutent sur leur fonctionnement et donc sur les différents services écosystémiques qu'ils peuvent fournir (Cardinale et al., 2012; Gamfeldt et al., 2015). La préservation de ces services écosystémiques essentiels passe obligatoirement par la compréhension du fonctionnement des écosystèmes afin de mettre en place des indicateurs fonctionnels opérationnels de surveillance dans une logique d'aide à la gestion des espaces côtiers (indicateurs du bon état écologique, indicateurs de la capacité des habitats à fournir certains services écosystémiques). L'étude de la réponse des communautés marines à une perturbation permet de détecter les processus qui contrôlent la structure et le fonctionnement des écosystèmes marins. À cet égard, les séries temporelles à long terme sont des outils précieux qui peuvent être utilisées d'une part pour décrire et comprendre la dynamique à long terme de la diversité des communautés face aux variations des conditions environnementales, et d'autre part pour développer des indicateurs écologiques d'évaluation de l'état de santé des écosystèmes. Selon Cochrane et al. (2016), trois facettes de la diversité biologique sont à prendre en considération pour traiter de la réponse des écosystèmes marins aux pressions environnementales et anthropiques: la structure taxonomique, l'écosystème fonctionnel et le réseau trophique.

Ce mémoire présente une démarche intégrée de l'évaluation de la réponse fonctionnelle des écosystèmes benthiques aux pressions naturelles et anthropiques grâce à l'utilisation conjointe de trois approches complémentaires. La diversité spécifique basée sur les propriétés structurelles se concentre sur la composition taxonomique des communautés. La diversité fonctionnelle basée sur les traits biologiques des espèces représente la résultante des principales fonctions écologiques et de la résistance/résilience des communautés après une perturbation. Enfin, la diversité isotopique basée sur les signatures isotopiques des espèces représente la niche trophique réalisée d'une communauté. L'analyse de la variabilité spatio-temporelle des différentes facettes de la diversité biologique et l'étude de leur complémentarité a permis de décrire de manière plus exhaustive l'évolution à long terme des communautés benthiques côtières en réponse à différentes pressions anthropiques. Cette démarche intégrée a nécessité l'exploitation de deux jeux de données contrastés de suivis à long terme de communautés benthiques de sables fins en Manche (Baie de Seine orientale et Baie de Morlaix).

## Évolution temporelle

L'étude de l'évolution temporelle de ces deux communautés montre des dynamiques temporelles très contrastées qui peuvent s'avérer complexes et qui sont très variables d'une région côtière à une autre, d'où l'intérêt des séries à long terme. D'un côté l'évolution de la structure de la communauté en Baie de Morlaix à Pierre Noire présente une forte variabilité temporelle marquée par deux changements de régime majeurs d'intensité comparable mais de nature différente, associés d'une part à la marée noire causée par les hydrocarbures de l'Amoco Cadiz en 1978, et d'autre part à une modification brutale de la communauté en réponse à des changements progressifs des conditions environnementales (Chapitre I). Ces résultats soulèvent la question de la définition de l'état de référence d'une communauté. Dans ce cas précis, l'évolution de la structure de la communauté avant la perturbation liée au naufrage de l'Amoco Cadiz n'a pas été étudiée donc on ne peut pas affirmer que la communauté revienne à cet état de référence après la perturbation.

D'un autre côté, différentes métriques décrivant la stabilité/variabilité de la communauté en Baie de Seine orientale à différentes échelles montrent une stabilité relative remarquable de la structure de la communauté malgré l'existence de nombreuses pressions anthropiques et une tendance à l'envasement mise en évidence (Chapitre II). Dans une logique d'aide à la gestion de cette communauté, il serait intéressant de compléter la stratégie d'échantillonnage mise en place pour l'acquisition de cette série temporelle en prenant en considération l'hétérogénéité spatiale des réponses de la communauté et en combinant les différentes échelles spatiales et temporelles. Cette nouvelle stratégie d'échantillonnage consisterait en un réseau de 60 stations réparties dans la Baie de Seine orientale et échantillonnées tous les 5 ans pour suivre l'évolution dans la distribution des assemblages et un petit nombre de stations représentatives de différents assemblages d'espèces échantillonné tous les ans pour analyser l'hétérogénéité des réponses de la communauté locale à des facteurs de stress multiples.

Concernant l'utilisation complémentaire de la diversité spécifique et fonctionnelle afin d'étudier l'évolution des communautés en Baie de Morlaix et en Baie de Seine, des résultats très similaires sont observés entre les deux approches. Ces résultats diffèrent de ce qui a pu être observé en Mer du Nord par exemple où la composition des traits n'a pas varié de manière significative entre des périodes qui ont connu des changements importants dans la composition taxonomique (Clare et al., 2015). Donc le changement observé dans les traits de ces deux communautés est lié à des changements dans les abondances relatives des espèces dominantes, il n’y aurait pas de forte compensation par des espèces fonctionnellement similaires. Les fortes corrélations observées entre indices de diversité spécifique et indices de diversité fonctionnelle confirment ces résultats. Toutefois, la composition des traits, et par conséquent le fonctionnement de l'écosystème, est susceptible de varier à de petites échelles spatiales et d’être principalement déterminés par des processus agissant à petite échelle. L’intérêt de l’approche fonctionnelle est qu’elle permet d’expliciter en terme de fonctionnement les changements observés grâce à la diversité spécifique.

## Considérations méthodologiques

Nos travaux menés en Baie de Morlaix et en Baie de Seine orientale montrent un fort niveau de concordance entre les résultats obtenus sur les mesures de la diversité spécifique et ceux obtenus sur les mesures de la diversité fonctionnelle, soulevant des interrogations sur la plus-value de cette approche au regard du caractère très chronophage de l’obtention des traits propres à chaque espèce. Cette approche décrit explicitement les conséquences des changements de structure sur le fonctionnement global de l’écosystème mais elle est sensible aux propriétés des indices. En effet, en Baie de Morlaix les indices d’Entropie quadratique de Rao (RaoQ) et de Dispersion Fonctionnelle (FDis) présentent des résultats contraires à ceux attendus à la suite d’une perturbation. Ces indices sont sensibles aux patrons de dominance des espèces qui sont très variables d’une communauté à une autre donc il est primordial de comprendre les dynamiques complexes avant de les utiliser. Le manque de recul sur l’utilisation de ces indices ne nous permet pas de les inclure dans une routine de calcul d’indices afin de détecter des changements de l’écosystème par exemple, ils sont donc à utiliser avec parcimonie.

En considérant les densités des espèces, ces indices donne un poids différentiel aux traits des espèces les plus abondantes ce qui peut biaiser l’image du fonctionnement de l’écosystème. Dans des communautés dominées par un petit nombre d’espèces comme en Baie de Morlaix, la forte concordance entre diversité fonctionnelle et diversité spécifique est à mettre en relation avec l’utilisation des densités pour pondérer le poids relatif des espèces. En effet, dans ce cas les modalités des traits des espèces les plus dominantes régissent les changements temporels de la diversité fonctionnelle. De même, il faut être attentif à la période de l’échantillonnage car des évènements de nature différente peuvent modifier les patrons de dominances des espèces. Un échantillonnage en été en période de recrutement avec les fortes densités de juvéniles de faible biomasse pourrait donner une fausse impression de changement dans la diversité fonctionnelle. Également, après une perturbation la structure des communautés change, entraînant des réponses différentes selon le niveau de pollution en termes de densité ou de biomasse selon le modèle de Pearson & Rosenberg (Pearson & Rosenberg, 1978). Ce profond bouleversement des schémas de distribution des densités et des biomasses après un événement pourrait ainsi avoir un impact significatif sur les valeurs de certains indices de diversité fonctionnelle indépendamment des changements d'identité des espèces ou des modalités des traits qu'elles possèdent. Il apparaît donc plus logique de ne pas échantillonner après le recrutement pour mettre en évidence des bouleversements dans le fonctionnement de l'écosystème car cela pourrait biaiser l'interprétation.

Dans la majorité des études traitant de l'approche par les traits biologiques en écologie benthique, il n'y a aucune justification concernant le choix de la pondération des traits des espèces dans l'espace fonctionnel par les densités ou des biomasses (Chapitre III). Les données de densités sont le plus souvent utilisées pour caractériser l'abondance relative de la macrofaune. Or cela a des conséquences directes sur les valeurs des indices de diversité fonctionnelle et donc sur l'interprétation du fonctionnement des écosystèmes car les indices ont des sensibilités différentes à la nature des données. L'acquisition des données de biomasses pour la campagne d'échantillonnage 2016 en Baie de Seine a nécessité de longues heures de préparation et de pesée. Les données de biomasses sont donc plus difficiles à acquérir ce qui peut expliquer le faible nombre d'études utilisant ce type de données. Or théoriquement, les analyses basées sur la biomasse semblent mieux adaptées pour décrire les processus des écosystèmes comme le cycle des nutriments et la productivité (Leps et al., 2006). Il est donc nécessaire de justifier le choix de la méthode de pondération des traits en fonction des caractéristiques de la communauté, des traits choisis ou encore des fonctions de l'écosystème étudiées.

## Perspectives

En terme de perspectives, il pourrait être intéressant d'utiliser des données environnementales afin de mieux comprendre la dynamique de la communauté de Pierre Noire et de pouvoir expliquer le second changement récent. Les paramètres physico-chimiques mesurés en Baie de Morlaix depuis 1997 et issus du Service d'Observation en Milieu Littoral (SOMLIT) pourraient être mobilisés dans cet objectif.

L'approche de la diversité fonctionnelle en écologie marine reste une approche exploratoire donc il pourrait être utile pour la communauté scientifique marine d'améliorer le cadre méthodologique autour de l'utilisation de cette approche. Pour rendre cela plus accessible, la bancarisation des bases de données des traits fonctionnels représenterait un bon avancement. Cela pourrait permettre à terme la mise en place d'outils de diversité fonctionnelle opérationnels et utilisables dans le cadre de programme de gestion.

L'étude de l'évolution du réseau trophique de la communauté en Baie de Morlaix montre l'existence d'une grande diversité de régimes alimentaires entre les différentes espèces, résultant d'une spécialisation trophique relative au sein des pools de Matière Organique Sédimentée et de Matière Organique Particulaire, et d'une plasticité trophique des espèces en fonction des saisons (Chapitre IV). Un continuum de valeurs isotopiques est observé depuis la base du réseau jusqu'à son sommet, reflétant un niveau élevé d'omnivorie et l'absence de niches trophiques distinctes. Les indices de diversité trophique mettent en évidence une relative stabilité du réseau trophique. La variabilité saisonnière de la structure de la communauté n'est pas observée dans les indices de diversité isotopiques et leur faible variabilité interannuelle suggère une forte résilience du réseau trophique. Afin d'observer la réponse des réseaux trophiques à des changements plus importants, il pourrait être intéressant d'étudier l'évolution de leurs caractéristiques le long d'un gradient spatial de perturbations. En effet, dans cette thèse l'accent a été mis sur l'aspect temporel du fonctionnement des écosystèmes et les séries temporelles en Baie de Morlaix et en Baie de Seine mises à disposition nous ont permis de détecter des changements suite à des perturbations plus ou moins brutales. Il est cependant difficile d'acquérir de telles séries temporelles, car elles nécessitent du temps et sont coûteuses. De plus ces séries sont soumises à des perturbations occasionnelles que l'on ne maîtrise pas. Par exemple en Baie de Morlaix, la communauté de sables fins n'a pas subi de profonds bouleversements depuis la pollution de l'Amoco Cadiz en 1978 donc la mise en évidence de mécanismes de réponses fonctionnelles de la communauté n'est pas aisée. De plus, la mise en place de suivis à long terme pour quantifier les perturbations et ainsi obtenir des données environnementales peut s'avérer compliqué. Une alternative à ces contraintes pratiques pourrait être de comparer l'architecture de réseaux trophiques de différentes communautés macrobenthiques de sables fins qui se distinguent par leur complexité organisationnelle et leur degré d'exposition à différentes perturbations anthropiques, le long d'un gradient estuarien par exemple dans des baies distinctes. De manière similaire, Rigolet et al. (2015) ont comparé le réseau trophique de deux communautés benthiques largement présentes dans les eaux côtières peu profondes: la communauté sablo-vaseuse *Haploops nirae* et la communauté vaso-sableuse *Amphiura filiformis*. Ils ont montré que la richesse fonctionnelle isotopique était plus élevée dans la communauté à *Haploops nirae* et que la biomasse était concentrée aux extrémités du réseau trophique.

Pour compléter notre démarche intégrée de l'évaluation de la réponse fonctionnelle des écosystèmes benthiques aux pressions naturelles et anthropiques grâce à l'utilisation conjointe de trois approches complémentaires, il serait cohérent de poursuivre le travail et, comme nous l'avons fait pour la diversité spécifique et la diversité fonctionnelle, de comparer des mesures de diversité fonctionnelle et des mesures de diversité isotopique. En effet, il est possible de comparer la niche trophique réalisée des espèces d'un réseau trophique et la niche potentielle de ces espèces. La niche théorique est définie par les traits biologiques et peut alors être construite grâce à des traits en rapport avec le mode alimentaire (taille maximale, mode d'alimentation et méthode de capture des ressources) et la niche réalisée est définie par les signatures isotopiques des espèces (Rigolet et al., 2015 ; Jones, 2017). Les indices de diversité fonctionnelle sont calculés sur ces traits et les indices de diversité isotopique sur les signatures isotopiques. Ce type d'analyses permettrait donc de prendre en considération les trois facettes de la diversité biologique nécessaires pour traiter de la réponse des écosystèmes marins aux pressions environnementales et anthropiques.

# Bibliographie

Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanogr. Mar. Biol. Ann. Rev. 45, 345–405. https://doi.org/10.1201/9781420050943.ch7

Alizier, S., 2011. Echelles spatio-temporelles d'observation des relations macrobenthos–sédiments: organisation et changements à long terme (1988-2009) des communautés benthiques subtidales de la partie orientale de la Baie de Seine (PhD thesis). Université de Lille 1, France.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist: Roadmap for beta diversity. Ecol. Lett. 14, 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E Ltd, Plymouth, UK.

Auber, A., Travers-Trolet, M., Villanueva, M.C., Ernande, B., 2015. Regime Shift in an Exploited Fish Community Related to Natural Climate Oscillations. PLoS ONE 10, e0129883. https://doi.org/10.1371/journal.pone.0129883

Bachelet, G., Boucher, G., Hily, C., 1997. Principales caractéristiques des substrats meubles, in: Dauvin, J.-C. (Ed.), Les biocénoses marines et littorales françaises des côtes Atlantique, Manche et Mer du Nord. Synthèse, menaces et perspectives. Patrimoines Naturels, Paris, pp. 79–82.

Bacouillard, L., Baux, N., Dauvin, J.-C., Desroy, N., Geiger, K.J., Gentil, F., Thiébaut, É., 2020. Long-term spatio-temporal changes of the muddy fine sand benthic community of the Bay of Seine (eastern English Channel). Mar. Environ. Res. 161, 105062. https://doi.org/10.1016/j.marenvres.2020.105062

Baffreau, A., Pezy, J.-P., Dancie, C., Chouquet, B., Hacquebart, P., Poisson, E., Foveau, A., Joncourt, Y., Duhamel, S., Navon, M., Marmin, S., Dauvin, J.-C., 2017. Mapping benthic communities: An indispensable tool for the preservation and management of the eco-socio-system in the Bay of Seine. Reg. Stud. Mar. Sci. 9, 162–173. https://doi.org/10.1016/j.rsma.2016.12.005

Baldrighi, E., Grall, J., Quillien, N., Carriço, R., Verdon, V., Zeppilli, D., 2019. Meiofauna communities' response to an anthropogenic pressure: The case study of green macroalgal bloom on sandy beach in Brittany. Estuar. Coast. Shelf Sci. 227, 106326. https://doi.org/10.1016/j.ecss.2019.106326

Banas, N., Campbell, R., 2016. Traits controlling body size in copepods: separating general constraints from species-specific strategies. Mar. Ecol. Prog. Ser. 558, 21–33. https://doi.org/10.3354/meps11873

Barnes, A.D., Jochum, M., Lefcheck, J.S., Eisenhauer, N., Scherber, C., O'Connor, M.I., de Ruiter, P., Brose, U., 2018. Energy flux: the link between multitrophic biodiversity and ecosystem functioning. Trends Ecol. Evol. 33, 186–197. https://doi.org/10.1016/j.tree.2017.12.007

Barrio Froján, C.R.S., Cooper, K.M., Bremner, J., Defew, E.C., Wan Hussin, W.M.R., Paterson, D.M., 2011. Assessing the recovery of functional diversity after sustained sediment screening at an aggregate dredging site in the North Sea. Estuar. Coast. Shelf Sci. 92, 358–366. https://doi.org/10.1016/j.ecss.2011.01.006

Baux, N., Murat, A., Faivre, Q., Lesourd, S., Poizot, E., Méar, Y., Brasselet, S., Dauvin, J.-C., 2019. Sediment dynamic equilibrium, a key for assessing a coastal anthropogenic disturbance using geochemical tracers: application to the eastern part of the Bay of Seine. Cont. Shelf Res. 175, 87–98. https://doi.org/10.1016/j.csr.2019.02.002

Beauchard, O., Veríssimo, H., Queirós, A.M., Herman, P.M.J., 2017. The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. Ecol. Indic. 76, 81–96. https://doi.org/10.1016/j.ecolind.2017.01.011

Beaugrand, G., 2015. Theoretical basis for predicting climate-induced abrupt shifts in the oceans. Phil. Trans. R. Soc. B 370, 20130264. https://doi.org/10.1098/rstb.2013.0264

Belle, S., Cabana, G., 2020. Effects of changes in isotopic baselines on the evaluation of food web structure using isotopic functional indices. PeerJ 8, e9999. https://doi.org/10.7717/peerj.9999

Bolam, S.G., 2014. Macrofaunal recovery following the intertidal recharge of dredged material: A comparison of structural and functional approaches. Mar. Environ. Res. 97, 15–29. https://doi.org/10.1016/j.marenvres.2014.01.008

Bolam, S.G., Coggan, R.C., 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. https://doi.org/10.1016/j.seares.2013.05.003

Bolam, S.G., Eggleton, J.D., 2014. Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. J. Sea Res. 88, 47–58. https://doi.org/10.1016/j.seares.2014.01.001

Bonada, N., Dolédec, S., Statzner, B., 2007. Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. Glob. Change Biol. 13, 1658–1671. https://doi.org/10.1111/j.1365-2486.2007.01375.x

Bonifácio, P., Grémare, A., Amouroux, J.-M., Labrune, C., 2019. Climate-driven changes in macrobenthic communities in the Mediterranean Sea: A 10-year study in the Bay of Banyuls-sur-Mer. Ecol. Evol. 9, 10483–10498. https://doi.org/10.1002/ece3.5569

Bonifácio, P., Grémare, A., Gauthier, O., Romero-Ramirez, A., Bichon, S., Amouroux, J.-M., Labrune, C., 2018. Long-term (1998 vs. 2010) large-scale comparison of soft-bottom benthic macrofauna composition in the Gulf of Lions, NW Mediterranean Sea. J. Sea Res. 131, 32–45. https://doi.org/10.1016/j.seares.2017.08.013

Bordeyne, F., Davoult, D., Migné, A., Bertaud du Chazaud, E., Leroux, C., Riera, P., 2017. Trophic structure of two intertidal *Fucus spp.* communities along a vertical gradient: Similarity and seasonal stability evidenced with δ13C and δ15N. J. Sea Res. 120, 50–59. https://doi.org/10.1016/j.seares.2016.12.004

Borja, A., Elliott, M., Andersen, J.H., Cardoso, A.C., Carstensen, J., Ferreira, J.G., Heiskanen, A.-S., Marques, J.C., Neto, J.M., Teixeira, H., Uusitalo, L., Uyarra, M.C., Zampoukas, N., 2013. Good Environmental Status of marine ecosystems: What is it and how do we know when we have attained it? Mar. Poll. Bull. 76, 16–27. https://doi.org/10.1016/j.marpolbul.2013.08.042

Borja, Á., Elliott, M., Carstensen, J., Heiskanen, A.-S., van de Bund, W., 2010. Marine management – Towards an integrated implementation of the European Marine Strategy Framework and the Water Framework Directives. Mar. Poll. Bull. 60, 2175–2186. https://doi.org/10.1016/j.marpolbul.2010.09.026

Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J. Veg. Sci. 16, 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x

Breine, N.T., De Backer, A., Van Colen, C., Moens, T., Hostens, K., Van Hoey, G., 2018. Structural and functional diversity of soft-bottom macrobenthic communities in the

Southern North Sea. Estuar. Coast. Shelf Sci. 214, 173–184. https://doi.org/10.1016/j.ecss.2018.09.012

Bremner, J., 2008. Species' traits and ecological functioning in marine conservation and management. J. Exp. Mar. Biol. Ecol. 366, 37–47. https://doi.org/10.1016/j.jembe.2008.07.007

Bremner, J., Rogers, S.I., Frid, C.L.J., 2006a. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol. Indic. 6, 609–622. https://doi.org/10.1016/j.ecolind.2005.08.026

Bremner, J., Rogers, S.I., Frid, C.L.J., 2006b. Matching biological traits to environmental conditions in marine benthic ecosystems. J. Mar. Syst. 60, 302–316. https://doi.org/10.1016/j.jmarsys.2006.02.004

Bremner, J., Rogers, S.I., Frid, C.L.J., 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Mar. Ecol. Prog. Ser. 254, 11–25. https://doi.org/10.3354/meps254011

Briant, N., Savoye, N., Chouvelon, T., David, V., Rodriguez, S., Charlier, K., Sonke, J.E., Chiffoleau, J.F., Brach-Papa, C., Knoery, J., 2018. Carbon and nitrogen elemental and isotopic ratios of filter-feeding bivalves along the French coasts: An assessment of specific, geographic, seasonal and multi-decadal variations. Sci. Total Environ. 613–614, 196–207. https://doi.org/10.1016/j.scitotenv.2017.08.281

Brind'Amour, A., Dubois, S.F., 2013. Isotopic diversity indices: how sensitive to food web structure? PLoS ONE 8, e84198. https://doi.org/10.1371/journal.pone.0084198

Cabioch, L., 1968. Contribution à la connaissance des peuplements benthiques de la Manche occidentale. Cah. Biol. Mar. 9, 493–720.

Cabioch, L., Dauvin, J.-C., Gentil, F., 1978. Preliminary observations on pollution of the sea bed and disturbance of sub-littoral communities in northern Brittany by oil from the Amoco Cadiz. Mar. Poll. Bull. 9, 303–307. https://doi.org/10.1016/0025-326X(78)90255-2

Cabioch, L., Dauvin, J.-C., Mora Bermudez, J., Rodriguez Babio, C., 1980. Effets de la marée noire de l'"Amoco Cadiz" sur le benthos sublittoral du nord de la Bretagne. Helgolander Meeresuntersuchungen 33, 192–208. https://doi.org/10.1007/BF02414746

Cabioch, L., Gentil, F., 1975. Distribution des peuplements benthiques dans la partie orientale de la Baie de Seine. C. R. Acad. Sci. Paris 280, 571–574.

Cadotte, M.W., Cavender-Bares, J., Tilman, D., Oakley, T.H., 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. PLoS ONE 4, e5695. https://doi.org/10.1371/journal.pone.0005695

Callaway, R., 2016. Historical data reveal 30-year persistence of benthic fauna associations in heavily modified waterbody. Front. Mar. Sci. 3, 1–13. https://doi.org/10.3389/fmars.2016.00141

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148

Carlier, A., Riera, P., Amouroux, J.-M., Bodiou, J.-Y., Grémare, A., 2007. Benthic trophic network in the Bay of Banyuls-sur-Mer (northwest Mediterranean, France): An assessment based on stable carbon and nitrogen isotopes analysis. Estuar. Coast. Shelf Sci. 72, 1–15. https://doi.org/10.1016/j.ecss.2006.10.001

Carney, R.S., 2007. Use of diversity estimations in the study of sedimentary benthic communities. Oceanogr. Mar. Biol. Ann. Rev. 45, 139–172.

Cesar, C.P., Frid, C.L.J., 2009. Effects of experimental small-scale cockle ( *Cerastoderma edule* L.) fishing on ecosystem function. Mar. Ecol. 30, 123–137. https://doi.org/10.1111/j.1439-0485.2009.00305.x

Chardy, P., Dauvin, J.-C., 1992. Carbon flows in a subtidal fine sand community from the western English Channel: a simulation analysis. Mar. Ecol. Prog. Ser. 81, 147–161.

Chevenet, F., Dolédec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshw. Biol. 31, 295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x

Chouvelon, T., Spitz, J., Cherel, Y., Caurant, F., Sirmel, R., Mèndez-Fernandez, P., Bustamante, P., 2011. Inter-specific and ontogenic differences in δ13C and δ15N values and Hg and Cd concentrations in cephalopods. Mar. Ecol. Prog. Ser. 433, 107–120. https://doi.org/10.3354/meps09159

Clare, D.S., Robinson, L.A., Frid, C.L.J., 2015. Community variability and ecological functioning: 40 years of change in the North Sea benthos. Mar. Environ. Res. 107, 24–34. https://doi.org/10.1016/j.marenvres.2015.03.012

Clare, D.S., Spencer, M., Robinson, L.A., Frid, C.L.J., 2017. Explaining ecological shifts: the roles of temperature and primary production in the long-term dynamics of benthic faunal composition. Oikos 126, 1123–1133. https://doi.org/10.1111/oik.03661

Clark, C.M., Flynn, D.F.B., Butterfield, B.J., Reich, P.B., 2012. Testing the link between functional diversity and ecosystem functioning in a Minnesota grassland experiment. PLoS ONE 7, e52821. https://doi.org/10.1371/journal.pone.0052821

Clark, G.F., Kelaher, B.P., Dafforn, K.A., Coleman, M.A., Knott, N.A., Marzinelli, E.M., Johnston, E.L., 2015. What does impacted look like? High diversity and abundance of epibiota in modified estuaries. Environ. Pollut. 196, 12–20. https://doi.org/10.1016/j.envpol.2014.09.017

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Austral Ecol. 18, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke, K.R., Gorley, R.N., Somerfield, P.J., Warwick, R.M., 2014. Change in marine communities: an approach to statistical analysis and interpretation, 3rd edition. ed. PRIMER-E Ltd, Plymouth, UK.

Cochrane, S.K.J., Andersen, J.H., Berg, T., Blanchet, H., Borja, A., Carstensen, J., Elliott, M., Hummel, H., Niquil, N., Renaud, P.E., 2016. What Is marine biodiversity? towards common concepts and their implications for assessing biodiversity status. Front. Mar. Sci. 3, 14. https://doi.org/10.3389/fmars.2016.00248

Conversi, A., Dakos, V., Gårdmark, A., Ling, S., Folke, C., Mumby, P.J., Greene, C., Edwards, M., Blenckner, T., Casini, M., Pershing, A., Möllmann, C., 2015. A holistic view of marine regime shifts. Phil. Trans. R. Soc. B 370, 20130279. https://doi.org/10.1098/rstb.2013.0279

Cresson, P., Travers-Trolet, M., Rouquette, M., Timmerman, C.-A., Giraldo, C., Lefebvre, S., Ernande, B., 2017. Underestimation of chemical contamination in marine fish muscle tissue can be reduced by considering variable wet:dry weight ratios. Mar. Poll. Bull. 123, 279–285. https://doi.org/10.1016/j.marpolbul.2017.08.046

Creutzberg, F., Duineveld, G.C.A., van Noort, G.J., 1987. The effect of different numbers of tickler chains on beam-trawl catches. ICES Journal of Marine Science 43, 159–168. https://doi.org/10.1093/icesjms/43.2.159

Cucherousset, J., Bouletreau, S., Martino, A., Roussel, J. -M., Santoul, F., 2012. Using stable isotope analyses to determine the ecological effects of non-native fishes. Fish. Manag. Ecol. 19, 111–119. https://doi.org/10.1111/j.1365-2400.2011.00824.x

Cucherousset, J., Villéger, S., 2015. Quantifying the multiple facets of isotopic diversity: New metrics for stable isotope ecology. Ecol. Indic. 56, 152–160. https://doi.org/10.1016/j.ecolind.2015.03.032

Dafforn, K.A., Kelaher, B.P., Simpson, S.L., Coleman, M.A., Hutchings, P.A., Clark, G.F., Knott, N.A., Doblin, M.A., Johnston, E.L., 2013. Polychaete richness and abundance enhanced in anthropogenically modified estuaries despite high concentrations of toxic contaminants. PLoS ONE 8, e77018. https://doi.org/10.1371/journal.pone.0077018

Dakos, V., Carpenter, S.R., van Nes, E.H., Scheffer, M., 2015. Resilience indicators: prospects and limitations for early warnings of regime shifts. Phil. Trans. R. Soc. B 370, 20130263. https://doi.org/10.1098/rstb.2013.0263

Dannheim, J., Rumohr, H., 2012. The fate of an immigrant: *Ensis directus* in the eastern German Bight. Helgol. Mar. Res. 66, 307–317. https://doi.org/10.1007/s10152-011-0271-2

Dauvin, J.-C., 2015. History of benthic research in the English Channel: From general patterns of communities to habitat mosaic description. J. Sea Res. 100, 32–45. https://doi.org/10.1016/j.seares.2014.11.005

Dauvin, J.-C., 2012. Are the eastern and western basins of the English Channel two separate ecosystems? Mar. Poll. Bull. 64, 463–471. https://doi.org/10.1016/j.marpolbul.2011.12.010

Dauvin, Jean-Claude, 2008. The main characteristics, problems, and prospects for Western European coastal seas. Mar. Poll. Bull. 57, 22–40. https://doi.org/10.1016/j.marpolbul.2007.10.016

Dauvin, J.-C., 2008. Effects of heavy metal contamination on the macrobenthic fauna in estuaries: The case of the Seine estuary. Mar. Poll. Bull. 57, 160–169. https://doi.org/10.1016/j.marpolbul.2007.10.012

Dauvin, J.-C., 2006. The Seine estuary, a highly developed area. Seine-Aval Special Issue, September 2006. North Atlantic Estuaries, Problems and Perspectives 27–32.

Dauvin, J.-C., 2000. The muddy fine sand *Abra alba–Melinna palmata* community of the Bay of Morlaix twenty years after the Amoco Cadiz oil spill. Mar. Poll. Bull. 40, 528–536. https://doi.org/10.1016/S0025-326X(99)00242-8

Dauvin, J.-C., 1998. The fine sand *Abra alba* community of the bay of morlaix twenty years after the Amoco Cadiz oil spill. Mar. Poll. Bull. 36, 669–676. https://doi.org/10.1016/S0025-326X(98)00058-7

Dauvin, J.-C., 1988. Life cycle, dynamics, and productivity of Crustacea-Amphipoda from the western English Channel. 4. *Ampelisca armoricana* Bellan-Santini et Dauvin. J. Exp. Mar. Biol. Ecol. 123, 235–252. https://doi.org/10.1016/0022-0981(88)90045-7

Dauvin, J.-C., 1987. Évolution à long terme (1978-1986) des populations d'amphipodes des sables fins de la Pierre Noire (Baie de Morlaix, Manche occidentale) après la catastrophe de l'Amoco Cadiz. Mar. Environ. Res. 21, 247–273. https://doi.org/10.1016/0141-1136(87)90049-3

Dauvin, J.-C., 1984. Dynamique d'écosystèmes macrobenthiques des fonds sédimentaires de la baie de Morlaix et leur perturbations par les hydrocarbures de l'Amoco Cadiz (PhD thesis). Université Pierre & Marie Curie, France.

Dauvin, J.-C., Dewarumez, J.-M., Elkaim, B., Bernardo, D., Fromentin, J.-M., Ibanez, F., 1993. Cinétique de *Abra alba* (Mollusque bivalve) de 1977 à 1991 en Manche-Mer du Nord, relation avec les facteurs climatiques. Oceanol. Acta 16, 413–422.

Dauvin, J.-C., Gillet, P., 1991. Spatio-temporal variability in population structure of *Owenia fusiformis* Delle Chiaje (Annelida: Polychaeta) from the Bay of Seine (eastern English Channel). J. Exp. Mar. Biol. Ecol. 152, 105–122. https://doi.org/10.1016/0022-0981(91)90138-M

Dauvin, J.-C., Ibanez, F., 1986. Variations à long-terme (1977–1985) du peuplement des sables fins de la Pierre Noire (baie de Morlaix, Manche occidentale): analyse statistique de l'évolution structurale. Hydrobiologia 142, 171–186. https://doi.org/10.1007/978-94-009-4049-9_16

Dauvin, J.-C., Lucas, S., Navon, M., Lesourd, S., Méar, 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. https://doi.org/10.1016/j.ecss.2017.03.014

Dauvin, J.-C., Ruellet, T., Desroy, N., Janson, A.-L., 2007a. The ecological quality status of the Bay of Seine and the Seine estuary: Use of biotic indices. Mar. Poll. Bull. 55, 241–257. https://doi.org/10.1016/j.marpolbul.2006.04.010

Dauvin, J.-C., Ruellet, T., Thiébaut, E., Gentil, F., Desroy, N., Janson, A.-L., Duhamel, S., Jourde, J., Simon, S., 2007b. The presence of *Melinna palmata* (Annelida: Polychaeta) and *Ensis directus* (Mollusca: Bivalvia) related to sedimentary changes in the Bay of Seine (English Channel, France). Cah. Biol. Mar. 48, 391–401.

de Arruda Almeida, B., Green, A.J., Sebastián-González, E., dos Anjos, L., 2018. Comparing species richness, functional diversity and functional composition of waterbird communities along environmental gradients in the neotropics. PLoS ONE 13, 1–18. https://doi.org/10.1371/journal.pone.0200959 de Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J., Janeček, Š., Lepš, J., 2011. Quantifying the relevance of intraspecific trait variability for functional diversity: Intraspecific variability in functional diversity. Methods in Ecology and Evolution 2, 163–174. https://doi.org/10.1111/j.2041-210X.2010.00071.x

Degen, R., Aune, M., Bluhm, B.A., Cassidy, C., Kędra, M., Kraan, C., Vandepitte, L., Włodarska-Kowalczuk, M., Zhulay, I., Albano, P.G., Bremner, J., Grebmeier, J.M., Link, H., Morata, N., Nordström, M.C., Shojaei, M.G., Sutton, L., Zuschin, M., 2018. Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans. Ecol. Indic. 91, 722–736. https://doi.org/10.1016/j.ecolind.2018.04.050

de-la-Ossa-Carretero, J.A., Del-Pilar-Ruso, Y., Giménez-Casalduero, F., Sánchez-Lizaso, J.L., Dauvin, J.-C., 2012. Sensitivity of amphipods to sewage pollution. Estuar. Coast. Shelf Sci. 96, 129–138. https://doi.org/10.1016/j.ecss.2011.10.020

DeNiro, M.J., Epstein, S., 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta 45, 341–351. https://doi.org/10.1016/0016-7037(81)90244-1

DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta 42, 495–506. https://doi.org/10.1016/0016-7037(78)90199-0

Desroy, N., Janson, A.-L., Denis, L., Charrier, G., Lesourd, S., Dauvin, J.-C., 2007. The intra-annual variability of soft-bottom macrobenthos abundance patterns in the North Channel of the Seine estuary. Hydrobiologia 588, 173–188. https://doi.org/10.1007/s10750-007-0661-2

deYoung, B., Barange, M., Beaugrand, G., Harris, R., Perry, R.I., Scheffer, M., Werner, F., 2008. Regime shifts in marine ecosystems: detection, prediction and management. Trends Ecol. Evol. 23, 402–409. https://doi.org/10.1016/j.tree.2008.03.008

deYoung, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N., Shannon, L., 2004. Detecting regime shifts in the ocean: Data considerations. Prog. Oceanogr. 60, 143–164. https://doi.org/10.1016/j.pocean.2004.02.017

Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655.

Díaz, S., Lavorel, S., Chapin, F.S., Tecco, P.A., Gurvich, D.E., Grigulis, K., 2007. Functional Diversity — at the Crossroads between Ecosystem Functioning and Environmental Filters, in: Canadell, J.G., Pataki, D.E., Pitelka, L.F. (Eds.), Terrestrial Ecosystems in a Changing World. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 81–91. https://doi.org/10.1007/978-3-540-32730-1_7

Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K., Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proc Natl Acad Sci USA 104, 20684–20689. https://doi.org/10.1073/pnas.0704716104

Dippner, J.W., Möller, C., Kröncke, I., 2014. Loss of persistence of the North Atlantic Oscillation and its biological implication. Front. Ecol. Evol. 2, 8. https://doi.org/10.3389/fevo.2014.00057

Dolbeth, M., Cardoso, P., Grilo, T., Raffaelli, D., Pardal, M.Â., 2013. Drivers of estuarine benthic species distribution patterns following a restoration of a seagrass bed: A functional trait analyses. Mar. Poll. Bull. 72, 47–54. https://doi.org/10.1016/j.marpolbul.2013.05.001

Dolbeth, M., Teixeira, H., Marques, J.C., Pardal, M.Â., 2009. Feeding guild composition of a macrobenthic subtidal community along a depth gradient. Sci. Mar. 73, 225–237. https://doi.org/10.3989/scimar.2009.73n2225

Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., Healy, K., Jackson, A.L., Lurgi, M., McClean, D., O'Connor, N.E., O'Gorman, E.J., Yang, Q., 2016. Navigating the complexity of ecological stability. Ecol. Lett. 19, 1172–1185. https://doi.org/10.1111/ele.12648

Donohue, I., Petchey, O.L., Montoya, J.M., Jackson, A.L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N.E., Emmerson, M.C., 2013. On the dimensionality of ecological stability. Ecol. Lett. 16, 421–429. https://doi.org/10.1111/ele.12086

Dubois, S., Orvain, F., Marin-Léal, J., Ropert, M., Lefebvre, S., 2007. Small-scale spatial variability of food partitioning between cultivated oysters and associated suspension-feeding species, as revealed by stable isotopes. Mar. Ecol. Prog. Ser. 336, 151–160. https://doi.org/10.3354/meps336151

Duffy, J.E., Amaral-Zettler, L.A., Fautin, D.G., Paulay, G., Rynearson, T.A., Sosik, H.M., Stachowicz, J.J., 2013. Envisioning a marine biodiversity observation network. BioScience 63, 350–361. https://doi.org/10.1525/bio.2013.63.5.8

Dutkiewicz, S., Morris, J.J., Follows, M.J., Scott, J., Levitan, O., Dyhrman, S.T., Berman-Frank, I., 2015. Impact of ocean acidification on the structure of future phytoplankton communities. Nature Clim. Change. 5, 1002–1006. https://doi.org/10.1038/nclimate2722

Eleftheriou, A., Moore, D.C., 2008. Macrofauna Techniques, in: Eleftheriou, A., McIntyre, A. (Eds.), Methods for the Study of Marine Benthos. Wiley - Blackwell, p. 160.

Field, J., Clarke, K., Warwick, R., 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8, 37–52. https://doi.org/10.3354/meps008037

Fisson, C., 2014. Qualité des eaux de l'estuaire de la Seine. Fascicule Seine-Aval, Rouen, France 3.2, 1–52.

Foveau, A., Desroy, N., Dewarumez, J.-M., Dauvin, J.-C., Cabioch, L., 2008. Long-term changes in the sessile epifauna of the Dover Strait pebble community. J. Oceanogr. Res. Data 1, 1–11.

Fraschetti, S., Pipitone, C., Mazaris, A.D., Rilov, G., Badalamenti, F., Bevilacqua, S., Claudet, J., Carić, H., Dahl, K., D'Anna, G., Daunys, D., Frost, M., Gissi, E., Göke, C., Goriup, P., Guarnieri, G., Holcer, D., Lazar, B., Mackelworth, P., Manzo, S., Martin, G., Palialexis, A., Panayotova, M., Petza, D., Rumes, B., Todorova, V., Katsanevakis, S., 2018. Light and shade in marine conservation across european and contiguous seas. Front. Mar. Sci. 5, 420. https://doi.org/10.3389/fmars.2018.00420

Frid, C.L.J., Garwood, P.R., Robinson, L.A., 2009. Observing change in a North Sea benthic system: A 33 year time series. J. Mar. Syst. 77, 227–236. https://doi.org/10.1016/j.jmarsys.2008.01.011

Fromentin, J.-M., Dauvin, J.-C., Ibanez, F., Dewarumez, J.-M., Elkaïm, B., 1996. Long-term variations of four macrobenthic community structures. Oceanologica Acta 20, 43–53.

Fromentin, J.-M., Ibanez, F., Dauvin, J.-C., Dewarumez, J.-M., Elkaim, B., 1997. Long-term changes of four macrobenthic assemblages from 1978 to 1992. J. Mar. Biol. Ass. U.K. 77, 287–310. https://doi.org/10.1017/S002531540007168X

Gamfeldt, L., Lefcheck, J.S., Byrnes, J.E.K., Cardinale, B.J., Duffy, J.E., Griffin, J.N., 2015. Marine biodiversity and ecosystem functioning: what's known and what's next? Oikos 124, 252–265. https://doi.org/10.1111/oik.01549

Garnaud, S., Lesueur, P., Lesourd, S., Poupinet, N., Brun-Cottan, J.-C., 2002. Caractérisation des variations lithologiques saisonnières des sédiments de la baie de Seine orientale ; impact des crues de la Seine (France). C. R. Geosci. 334, 323–330. https://doi.org/10.1016/S1631-0713(02)01759-5

Gaudin, F., 2012. Architecture globale du réseau trophique du peuplement macrobenthique du site de suivi à long terme Pierre Noire (baie de Morlaix) et statut trophique des différentes espèces d'Ampelisca. Université Pierre et Marie Curie, Station Biologique de Roscoff.

Gentil, F., Cabioch, L., 1997. Carte des peuplements benthiques de la Baie de Seine et Manche centrale sud.

Ghertsos, K., Luczak, C., Dewarumez, J.-M., Dauvin, J.-C., 2000. Influence of spatial scales of observation on temporal change in diversity and trophic structure of fine-sand communities from the English Channel and the southern North Sea. ICES J. Mar. Sci. 57, 1481–1487. https://doi.org/10.1006/jmsc.2000.0916

Giron-Nava, A., James, C., Johnson, A., Dannecker, D., Kolody, B., Lee, A., Nagarkar, M., Pao, G., Ye, H., Johns, D., Sugihara, G., 2017. Quantitative argument for long-term ecological monitoring. Mar. Ecol. Prog. Ser. 572, 269–274. https://doi.org/10.3354/meps12149

Givan, O., Parravicini, V., Kulbicki, M., Belmaker, J., 2017. Trait structure reveals the processes underlying fish establishment in the Mediterranean: Non-indigenous fish trait structure. Global Ecol. Biogeogr. 26, 142–153. https://doi.org/10.1111/geb.12523

Goberville, E., Beaugrand, G., Sautour, B., Tréguer, P., Somlit, T., 2010. Climate-driven changes in coastal marine systems of western Europe. Mar. Ecol. Prog. Ser. 408, 129–147. https://doi.org/10.3354/meps08564

Gollasch, S., Kerckhof, F., Craeymeersch, J.A., Goulletquer, P., Jensen, K., Jelmert, A., Minchin, D., 2015. Alien species alert: *Ensis directus*. Current status of invasion by the marine bivalve *Ensis directus*. (No. 323). International Council for the Exploration of the Sea.

Golléty, C., Riera, P., Davoult, D., 2010. Complexity of the food web structure of the *Ascophyllum nodosum* zone evidenced by a δ13C and δ15N study. Journal of Sea Research 64, 304–312. https://doi.org/10.1016/j.seares.2010.04.003

Grall, J., Le Loc'h, F., Guyonnet, B., Riera, P., 2006. Community structure and food web based on stable isotopes (δ15N and δ13C) analysis of a North Eastern Atlantic maerl bed. J. Exp. Mar. Biol. Ecol. 338, 1–15. https://doi.org/10.1016/j.jembe.2006.06.013

Gray, J.S., 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. J. Exp. Mar. Biol. Ecol. 250, 23–49. https://doi.org/10.1016/S0022-0981(00)00178-7

Gray, J.S., Clarke, K.R., Warwick, R.M., Hobbs, G., 1990. Detection of initial effects of pollution on marine benthos: an example from the Ekofisk and Eldfisk oilfields, North Sea. Mar. Ecol. Prog. Ser. 66, 285–299. https://doi.org/10.3354/meps066285

Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109, 323–334. https://doi.org/10.1007/s004420050090

Gusmao, J.B., Brauko, K.M., Eriksson, B.K., Lana, P.C., 2016. Functional diversity of macrobenthic assemblages decreases in response to sewage discharges. Ecol. Indic. 66, 65–75. https://doi.org/10.1016/j.ecolind.2016.01.003

Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., Lowndes, J.S., Rockwood, R.C., Selig, E.R., Selkoe, K.A., Walbridge, S., 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. Nat. Commun. 6, 7615. https://doi.org/10.1038/ncomms8615

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952. https://doi.org/10.1126/science.1149345

Hamerlynck, O., Hostens, K., 1993. Growth, feeding, production, and consumption in 0-group bib (*Trisopterus luscus L.*) and whiting (*Merlangius merlangus L.*) in a shallow coastal area of the south-west Netherlands. ICES J. Mar. Sci. 50, 81–91. https://doi.org/10.1006/jmsc.1993.1009

Hayward, Peter.J., Ryland, John.S. (Eds.), 2017. Handbook of the Marine Fauna of North-West Europe, Second edition. ed. Oxford University Press, Oxford, UK.

Hewitt, J.E., Ellis, J.I., Thrush, S.F., 2016. Multiple stressors, nonlinear effects and the implications of climate change impacts on marine coastal ecosystems. Glob. Change Biol. 22, 2665–2675. https://doi.org/10.1111/gcb.13176

Hewitt, J.E., Thrush, S.F., Dayton, P.D., 2008. Habitat variation, species diversity and ecological functioning in a marine system. J. Exp. Mar. Biol. Ecol. 366, 116–122. https://doi.org/10.1016/j.jembe.2008.07.016

Hinz, H., Capasso, E., Lilley, M., Frost, M., Jenkins, S., 2011. Temporal differences across a bio-geographical boundary reveal slow response of sub-littoral benthos to climate change. Mar. Ecol. Prog. Ser. 423, 69–82. https://doi.org/10.3354/meps08963

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning:

a consensus of current knowledge. Ecol. Monogr. 75, 3–35. https://doi.org/10.1890/04-0922

Ibanez, F., Dauvin, J.-C., Etienne, M., 1993. Comparaison des évolutions à long terme (1977-1990) de deux peuplements macrobenthiques de la baie de Morlaix (Manche occidentale): relations avec les facteurs hydroclimatiques. J. Exp. Mar. Biol. Ecol. 169, 181–214. https://doi.org/10.1016/0022-0981(93)90193-R

Ilarri, M.I., Amorim, L., Souza, A.T., Sousa, R., 2018. Physical legacy of freshwater bivalves: Effects of habitat complexity on the taxonomical and functional diversity of invertebrates. Sci. Total Environ. 634, 1398–1405. https://doi.org/10.1016/j.scitotenv.2018.04.070

Jabot, F., Giraldo, C., Lefebvre, S., Dubois, S., 2017. Are food web structures well represented in isotopic spaces? Funct. Ecol. 31, 1975–1984. https://doi.org/10.1111/1365-2435.12895

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson, D.A., 1993. Multivariate analysis of benthic invertebrate communities: the implication of choosing particular data standardizations, measures of association, and ordination methods. Hydrobiologia 268, 9–26. https://doi.org/10.1007/BF00005737

Johnston, E.L., Roberts, D.A., 2009. Contaminants reduce the richness and evenness of marine communities: A review and meta-analysis. Environ. Pollut. 157, 1745–1752. https://doi.org/10.1016/j.envpol.2009.02.017

Jones, A., 2017. Effect of an engineer species on the diversity and functioning of benthic communities: The *Sabellaria alveolata* reef habitat (PhD thesis). Université de Bretagne Occidentale, Université de Bretagne Loire, France.

Jourde, J., Alizier, S., Dancie, C., Dauvin, J.-C., Desroy, N., Dubut, S., Gentil, F., Grall, J., Hanin, C., Lanshere, J., Thiébaut, E., 2012. First and repeated records of the tropical-temperate crab *Asthenognathus atlanticus* Monod, 1932 (Decapoda: Brachyura) in the eastern part of the Bay of Seine (eastern English Channel, France). Cah. Biol. Mar. 53, 525–532.

Jumars, P.A., Dorgan, K.M., Lindsay, S.M., 2015. Diet of worms emended: an update of polychaete feeding guilds. Annu. Rev. Mar. Sci. 7, 497–520. https://doi.org/10.1146/annurev-marine-010814-020007

Kaufman, M.R., Gradinger, R.R., Bluhm, B.A., O'Brien, D.M., 2008. Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod Onisimus litoralis. Oecologia 158, 11–22. https://doi.org/10.1007/s00442-008-1122-y

Kelly, R.P., Erickson, A.L., Mease, L.A., Battista, W., Kittinger, J.N., Fujita, R., 2015. Embracing thresholds for better environmental management. Phil. Trans. R. Soc. B 370, 20130276. https://doi.org/10.1098/rstb.2013.0276

Kröncke, I., Dippner, J., Heyen, H., Zeiss, B., 1998. Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. Mar. Ecol. Prog. Ser. 167, 25–36. https://doi.org/10.3354/meps167025

Kröncke, I., Neumann, H., Dippner, J.W., Holbrook, S., Lamy, T., Miller, R., Padedda, B.M., Pulina, S., Reed, D.C., Reinikainen, M., Satta, C.T., Sechi, N., Soltwedel, T., Suikkanen, S., Lugliè, A., 2019. Comparison of biological and ecological long-term trends related to northern hemisphere climate in different marine ecosystems. Nat. Cons. 34, 311–341. https://doi.org/10.3897/natureconservation.34.30209

Kröncke, I., Reiss, H., Eggleton, J.D., Aldridge, J., Bergman, M.J.N., Cochrane, S., Craeymeersch, J.A., Degraer, S., Desroy, N., Dewarumez, J.-M., Duineveld, G.C.A., Essink, K., Hillewaert, H., Lavaleye, M.S.S., Moll, A., Nehring, S., Newell, R., Oug, E., Pohlmann, T., Rachor, E., Robertson, M., Rumohr, H., Schratzberger, M., Smith, R., Berghe, E.V., van Dalfsen, J., van Hoey, G., Vincx, M., Willems, W., Rees, H.L., 2011. Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. Estuar. Coast. Shelf Sci. 94, 1–15. https://doi.org/10.1016/j.ecss.2011.04.008

Kuipers, B., 1975. On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes Platessa*). Neth. J. Sea Res. 9, 69–85. https://doi.org/10.1016/0077-7579(75)90023-X

Labat, J.-P., Mayzaud, P., Sabini, S., 2005. Population dynamics of Themisto gaudichaudii in Kerguelen Islands waters, Southern Indian Ocean. Polar Biol. 28, 776–783. https://doi.org/10.1007/s00300-005-0003-7

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. https://cran.r-project.org/web/packages/FD/index.html.

Larsonneur, C., Bouysse, P., Auffret, J.-P., 1982. The superficial sediments of the English Channel and its Western Approaches. Sedimentology 29, 851–864. https://doi.org/10.1111/j.1365-3091.1982.tb00088.x

Lausch, A., Bannehr, L., Beckmann, M., Boehm, C., Feilhauer, H., Hacker, J.M., Heurich, M., Jung, A., Klenke, R., Neumann, C., Pause, M., Rocchini, D., Schaepman, M.E., Schmidtlein, S., Schulz, K., Selsam, P., Settele, J., Skidmore, A.K., Cord, A.F., 2016. Linking Earth Observation and taxonomic, structural and functional biodiversity: Local to ecosystem perspectives. Ecol. Indic. 70, 317–339. https://doi.org/10.1016/j.ecolind.2016.06.022

Lavorel, S., Garnier, E., 2002a. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R.J., Díaz, S., Harrington, R., 2013. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. J. Veg. Sci. 24, 942–948. https://doi.org/10.1111/jvs.12083

Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., Bearhop, S., 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biol. Rev. 87, 545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x

Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope ratios provide for community-wide measures of trophic structure ? Ecology 88, 42–48. https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Le Hir, P., Ficht, A., Jacinto, R.S., Lesueur, P., Dupont, J.-P., Lafite, R., Brenon, I., Thouvenin, B., Cugier, P., 2001. Fine sediment transport and accumulations at the mouth of the Seine estuary (France). Estuaries 24, 950–963. https://doi.org/10.2307/1353009

Le Loc'h, F., Hily, C., Grall, J., 2008. Benthic community and food web structure on the continental shelf of the Bay of Biscay (North Eastern Atlantic) revealed by stable isotopes analysis. J. Mar. Syst. 72, 17–34. https://doi.org/10.1016/j.jmarsys.2007.05.011

Leps, J., de Bello, F., Lavorel, S., Berman, S., 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. Preslia 78, 481–501.

Lesourd, S., Lesueur, P., Brun-Cottan, J.-C., Auffret, J.-P., Poupinet, N., Laignel, B., 2001. Morphosedimentary evolution of the macrotidal Seine estuary subjected to human impact. Estuaries 24, 940–949. https://doi.org/10.2307/1353008

Lesourd, S., Lesueur, P., Fisson, C., Dauvin, J.-C., 2016. Sediment evolution in the mouth of the Seine estuary (France): A long-term monitoring during the last 150 years. C. R. Geosci. 348, 442–450. https://doi.org/10.1016/j.crte.2015.08.001

Levin, P.S., Möllmann, C., 2015. Marine ecosystem regime shifts: challenges and opportunities for ecosystem-based management. Phil. Trans. R. Soc. B 370, 20130275. https://doi.org/10.1098/rstb.2013.0275

Liénart, C., Savoye, N., David, V., Ramond, P., Rodriguez Tress, P., Hanquiez, V., Marieu, V., Aubert, F., Aubin, S., Bichon, S., Boinet, C., Bourasseau, L., Bozec, Y., Bréret, M., Breton, E., Caparros, J., Cariou, T., Claquin, P., Conan, P., Corre, A.-M., Costes, L., Crouvoisier, M., Del Amo, Y., Derriennic, H., Dindinaud, F., Duran, R., Durozier, M., Devesa, J., Ferreira, S., Feunteun, E., Garcia, N., Geslin, S., Grossteffan, E., Gueux, A., Guillaudeau, J., Guillou, G., Jolly, O., Lachaussée, N., Lafont, M., Lagadec, V., Lamoureux, J., Lauga, B., Lebreton, B., Lecuyer, E., Lehodey, J.-P., Leroux, C., L'Helguen, S., Macé, E., Maria, E., Mousseau, L., Nowaczyk, A., Pineau, P., Petit, F., Pujo-Pay, M., Raimbault, P., Rimmelin-Maury, P., Rouaud, V., Sauriau, P.-G., Sultan, E., Susperregui, N., 2018. Dynamics of particulate organic matter composition in coastal systems: Forcing of spatio-temporal variability at multi-systems scale. Prog. Oceanogr. 162, 271–289. https://doi.org/10.1016/j.pocean.2018.02.026

Litchman, E., Klausmeier, C.A., 2008. Trait-Based Community Ecology of Phytoplankton. Annu. Rev. Ecol. Evol. Syst. 39, 615–639. https://doi.org/10.1146/annurev.ecolsys.39.110707.173549

Litchman, E., Ohman, M.D., Kiørboe, T., 2013. Trait-based approaches to zooplankton communities. J. Plankton Res. 35, 473–484. https://doi.org/10.1093/plankt/fbt019

Loreau, M., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808. https://doi.org/10.1126/science.1064088

Lyashevska, O., Farnsworth, K.D., 2012. How many dimensions of biodiversity do we need? Ecol. Indic. 18, 485–492. https://doi.org/10.1016/j.ecolind.2011.12.016

MacArthur, R., 1955. Fluctuations of animal populations and a measure of community stability. Ecology 36, 533–536. https://doi.org/10.2307/1929601

Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.McP., Elston, D.A., Scott, E.M., Smith, R.I., Somerfield, P.J., Watt, A.D., 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends Ecol. Evol. 25, 574–582. https://doi.org/10.1016/j.tree.2010.06.016

Maire, E., Grenouillet, G., Brosse, S., Villéger, S., 2015. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces: Assessing functional space quality. Global Ecol. Biogeogr. 24, 728–740. https://doi.org/10.1111/geb.12299

Marmin, S., Lesueur, P., Dauvin, J.-C., Samson, S., Tournier, P., Gallicher Lavanne, A., Dubrulle-Brunaud, C., Thouroude, C., 2016. An experimental study on dredge spoil of estuarine sediments in the Bay of Seine (France): A morphosedimentary assessment. Cont. Shelf Res. 116, 89–102. https://doi.org/10.1016/j.csr.2016.01.010

Martini, S., Larras, F., Boyé, A., Faure, É., Aberle, N., Archambault, P., Bacouillard, L., Beisner, B.E., Bittner, L., Castella, E., Danger, M., Gauthier, O., Karp-Boss, L., Lombard, F., Maps, F., Stemmann, L., Thiébaut, É., Usseglio-Polatera, P., Vogt, M., Laviale, M., Ayata, S.-D., in press. Functional trait-based approaches as a common framework for aquatic ecologists. Limnol. Oceanogr.

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118. https://doi.org/10.1111/j.0030-1299.2005.13886.x

McCann, K.S., Rooney, N., 2009. The more food webs change, the more they stay the same. Phil. Trans. R. Soc. B 364, 1789–1801. https://doi.org/10.1098/rstb.2008.0273

McClintock, J.B., Lawrence, J.M., 1985. Characteristics of foraging in the soft-bottom benthic starfish *Luidia clathrata* (Echinodermata: Asteroidea): prey selectivity, switching behavior, functional responses and movement patterns. Oecologia 66, 291–298.

McGill, B., Enquist, B., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Méar, Y., Poizot, E., Murat, A., Beryouni, K., Baux, N., Dauvin, J.-C., 2018. Improving the monitoring of a dumping site in a dynamic environment. Example of the Octeville site (Bay of Seine, English Channel). Mar. Poll. Bull. 129, 425–437. https://doi.org/10.1016/j.marpolbul.2017.10.011

Metcalfe, K., Delavenne, J., Garcia, C., Foveau, A., Dauvin, J.-C., Coggan, R., Vaz, S., Harrop, S.R., Smith, R.J., 2013. Impacts of data quality on the setting of conservation planning targets using the species–area relationship. Divers. Distrib. 19, 1–13. https://doi.org/10.1111/j.1472-4642.2012.00921.x

Meyer, J., Kröncke, I., 2019. Shifts in trait-based and taxonomic macrofauna community structure along a 27-year time-series in the south-eastern North Sea. PLoS ONE 14, e0226410. https://doi.org/10.1371/journal.pone.0226410

Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. Ecol. Lett. 8, 391–400. https://doi.org/10.1111/j.1461-0248.2005.00731.x

Minagawa, M., Wada, E., 1984. Stepwise enrichment of 15N along food chains: Further evidence and the relation between δ15N and animal age. Geochim. Cosmochim. Acta 48, 1135–1140. https://doi.org/10.1016/0016-7037(84)90204-7

Moens, T., Traunspurger, W., Bergtold, M., 2006. Feeding ecology of free-living Benthic Nematodes, in: Abebe, E., Andrássy, I., Traunspurger, W. (Eds.), Freshwater Nematodes: Ecology and Taxonomy. Cabi publishing, pp. 105–113.

Möllmann, C., Folke, C., Edwards, M., Conversi, A., 2015. Marine regime shifts around the globe: theory, drivers and impacts. Phil. Trans. R. Soc. B 370, 20130260. https://doi.org/10.1098/rstb.2013.0260

Morelli, F., Benedetti, Y., Perna, P., Santolini, R., 2018. Associations among taxonomic diversity, functional diversity and evolutionary distinctiveness vary among environments. Ecol. Indic. 88, 8–16. https://doi.org/10.1016/j.ecolind.2018.01.022

Moretti, M., de Bello, F., Roberts, S.P.M., Potts, S.G., 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. J. Anim. Ecol. 78, 98–108. https://doi.org/10.1111/j.1365-2656.2008.01462.x

Mouchet, M.A., Burns, M.D.M., Garcia, A.M., Vieira, J.P., Mouillot, D., 2012. Invariant scaling relationship between functional dissimilarity and co-occurrence in fish assemblages of the Patos Lagoon estuary (Brazil): environmental filtering consistently overshadows competitive exclusion. Oikos 122, 247–257. https://doi.org/10.1111/j.1600-0706.2012.20411.x

Mouchet, M.A., Villéger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules: Functional diversity measures. Funct. Ecol. 24, 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Mouillot, D., Dumay, O., Tomasini, J.A., 2007. Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. Estuar. Coast. Shelf Sci. 71, 443–456. https://doi.org/10.1016/j.ecss.2006.08.022

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28, 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Mouillot, D., Spatharis, S., Reizopoulou, S., Laugier, T., Sabetta, L., Basset, A., Do Chi, T., 2006. Alternatives to taxonomic-based approaches to assess changes in transitional water communities. Aquatic Conserv: Mar. Freshw. Ecosyst. 16, 469–482. https://doi.org/10.1002/aqc.769

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., Woodfin, R.M., 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368, 734–737. https://doi.org/10.1038/368734a0

Naeem, S., Wright, J.P., 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecol. Lett. 6, 567–579. https://doi.org/10.1046/j.1461-0248.2003.00471.x

Napoléon, C., Fiant, L., Raimbault, V., Riou, P., Claquin, P., 2014. Dynamics of phytoplankton diversity structure and primary productivity in the English Channel. Mar. Ecol. Prog. Ser. 505, 49–64. https://doi.org/10.3354/meps10772

Navarro-Barranco, C., McNeill, C.L., Widdicombe, C.E., Guerra-García, J.M., Widdicombe, S., 2017. Long-term dynamics in a soft-bottom amphipod community and the influence of the pelagic environment. Mar. Environ. Res. 129, 133–146. https://doi.org/10.1016/j.marenvres.2017.04.013

Neumann, H., Diekmann, R., Kröncke, I., 2016. Functional composition of epifauna in the south-eastern North Sea in relation to habitat characteristics and fishing effort. Estuar. Coast. Shelf Sci. 169, 182–194. https://doi.org/10.1016/j.ecss.2015.12.011

Neumann, H., Kröncke, I., 2011. The effect of temperature variability on ecological functioning of epifauna in the German Bight. Mar. Ecol. 32, 49–57. https://doi.org/10.1111/j.1439-0485.2010.00420.x

Olivier, F., Vallet, C., Dauvin, J.-C., Retière, C., 1996. Drifting in post-larvae and juveniles in an *Abra alba* (Wood) community of the eastern part of the Bay of Seine (English Channel). J. Exp. Mar. Biol. Ecol. 199, 89–109. https://doi.org/10.1016/0022-0981(95)00187-5

Olivier, P., Frelat, R., Bonsdorff, E., Kortsch, S., Kröncke, I., Möllmann, C., Neumann, H., Sell, A.F., Nordström, M.C., 2019. Exploring the temporal variability of a food web using long-term biomonitoring data. Ecography 42, 1–15. https://doi.org/10.1111/ecog.04461

Ouisse, V., Riera, P., Migné, A., Leroux, C., Davoult, D., 2012. Food web analysis in intertidal *Zostera marina* and *Zostera noltii* communities in winter and summer. Mar. Biol. 159, 165–175. https://doi.org/10.1007/s00227-011-1796-2

Oyenekan, J.A., 1988. Population dynamics and secondary production in *Melinna palmata* (Polychaeta: Ampharetidae). Mar. Biol. 98, 247–251. https://doi.org/10.1007/BF00391202

Paganelli, D., Marchini, A., Occhipinti-Ambrogi, A., 2012. Functional structure of marine benthic assemblages using Biological Traits Analysis (BTA): A study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea). Estuar. Coast. Shelf Sci. 96, 245–256. https://doi.org/10.1016/j.ecss.2011.11.014

Paillex, A., Dolédec, S., Castella, E., Mérigoux, S., Aldridge, D.C., 2013. Functional diversity in a large river floodplain: anticipating the response of native and alien macroinvertebrates to the restoration of hydrological connectivity. J. Appl. Ecol. 50, 97–106. https://doi.org/10.1111/1365-2664.12018

Paterson, D.M., Defew, E.C., Jabour, J., 2012. Ecosystem function and co-evolution of terminology in marine science and management, in: Solan, M., Aspden, R.J., Paterson, D.M. (Eds.), Marine Biodiversity and Ecosystem Functioning. Oxford University Press, pp. 24–33. https://doi.org/10.1093/acprof:oso/9780199642250.003.0003

Pavoine, S., Dolédec, S., 2005. The apportionment of quadratic entropy: a useful alternative for partitioning diversity in ecological data. Environ. Ecol. Stat. 12, 125–138. https://doi.org/10.1007/s10651-005-1037-2

Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev. 16, 229–311.

Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., Bruford, M.W., Brummitt, N., Butchart, S.H.M., Cardoso, A.C., Coops, N.C., Dulloo, E., Faith, D.P., Freyhof, J., Gregory, R.D., Heip, C., Hoft, R., Hurtt, G., Jetz, W., Karp, D.S., McGeoch, M.A., Obura, D., Onoda, Y., Pettorelli, N., Reyers, B., Sayre, R., Scharlemann, J.P.W., Stuart, S.N., Turak, E., Walpole, M., Wegmann, M., 2013.

Essential Biodiversity Variables. Science 339, 277–278. https://doi.org/10.1126/science.1229931

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Evol. Syst. 18, 293–320. https://doi.org/10.1146/annurev.es.18.110187.001453

Pilditch, C., Leduc, D., Nodder, S., Probert, P., Bowden, D., 2015. Spatial patterns and environmental drivers of benthic infaunal community structure and ecosystem function on the New Zealand continental margin. New Zeal. J. Mar. Fresh. 49, 224–246. https://doi.org/10.1080/00288330.2014.995678

Pinnegar, J.K., Polunin, N.V.C., 1999. Differential fractionation δ13C and δ15N among fish tissues: implications for the study of trophic interactions. Funct. Ecol. 13, 225–231. https://doi.org/10.1046/j.1365-2435.1999.00301.x

Poggiale, J., Dauvin, J., 2001. Long-term dynamics of three benthic Ampelisca (Crustacea-Amphipoda) populations from the Bay of Morlaix (western English Channel) related to their disappearance after the “Amoco Cadiz” oil spill. Mar. Ecol. Prog. Ser. 214, 201–209. https://doi.org/10.3354/meps214201

Poisot, T., Stouffer, D.B., Gravel, D., 2015. Beyond species: why ecological interaction networks vary through space and time. Oikos 124, 243–251. https://doi.org/10.1111/oik.01719

Pomerleau, C., Sastri, A.R., Beisner, B.E., 2015. Evaluation of functional trait diversity for marine zooplankton communities in the Northeast subarctic Pacific Ocean. J. Plankton Res. 37, 712–726. https://doi.org/10.1093/plankt/fbv045

Popp, B.N., Laws, E.A., Bidigare, R.R., Dore, J.E., Hanson, K.L., Wakeham, S.G., 1998. Effect of phytoplankton cell geometry on carbon isotopic fractionation. Geochim. et Cosmochim. Acta 62, 69–77. https://doi.org/10.1016/S0016-7037(97)00333-5

Post, D.M., 2002. Using stable isotopes to estimate trophic position: Models, methods and assumptions. Ecology 83, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Queirós, A.M., Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P.J., Van Colen, C., Van Hoey, G., Widdicombe, S., 2013. A bioturbation classification of European marine infaunal invertebrates. Ecol. Evol. 3, 3958–3985. https://doi.org/10.1002/ece3.769

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffaelli, D., Solan, M., Webb, T.J., 2005. Do marine and terrestrial ecologists do it differently? Mar. Ecol. Prog. Ser. 304, 283–289. https://doi.org/10.2307/24869863

Reise, K., 2002. Sediment mediated species interactions in coastal waters. J. Sea Res. 48, 127–141. https://doi.org/10.1016/S1385-1101(02)00150-8

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. https://doi.org/10.1016/j.icesjms.2006.06.001

Reiss, J., Bridle, J.R., Montoya, J.M., Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends Ecol. Evol. 24, 505–514. https://doi.org/10.1016/j.tree.2009.03.018

Riera, P., 2010. Trophic plasticity of the gastropod Hydrobia ulvae within an intertidal bay (Roscoff, France): A stable isotope evidence. J. Sea Res. 63, 78–83. https://doi.org/10.1016/j.seares.2009.10.001

Riera, P., 2007. Trophic subsidies of *Crassostrea gigas*, *Mytilus edulis* and *Crepidula fornicata* in the Bay of Mont Saint Michel (France): A δ13C and δ15N investigation. Estuar. Coast. Shelf Sci. 72, 33–41. https://doi.org/10.1016/j.ecss.2006.10.002

Riera, P., 2006. Les isotopes stables en écologie littorale et côtière : principe, exemples de résultats et perspectives. Océanis 32, 163–183.

Rigolet, C., Dubois, S.F., Thiébaut, E., 2014. Benthic control freaks: Effects of the tubiculous amphipod *Haploops nirae* on the specific diversity and functional structure of benthic communities. J. Sea Res. 85, 413–427. https://doi.org/10.1016/j.seares.2013.07.013

Rigolet, C., Thiébaut, E., Brind'Amour, A., Dubois, S.F., 2015. Investigating isotopic functional indices to reveal changes in the structure and functioning of benthic communities. Funct. Ecol. 29, 1350–1360. https://doi.org/10.1111/1365-2435.12444

Rogers, S.I., Lockwood, S.J., 1989. Observations on the capture efficiency of a two-metre beam trawl for juvenile flatfish. Neth. J. Sea Res. 23, 347–352. https://doi.org/10.1016/0077-7579(89)90054-9

Rolff, C., 2000. Seasonal variation in δ13C and δ15N of size-fractionated plankton at a coastal station in the northern Baltic proper. Mar. Ecol. Prog. Ser. 203, 47–65. https://doi.org/10.3354/meps203047

Rosenberg, R., 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. Neth. J. Sea Res. 34, 303–317. https://doi.org/10.1016/0077-7579(95)90040-3

Rouse, G.W., Pleijel, F., 2006. Reproductive biology and phylogeny of Annelida, Science Publishers. ed. Enfield, NH, USA.

Salomon, J.-C., Breton, M., 1991. Courants résiduels de marée dans la Manche. Oceanol. Acta 11, 47–53.

Saulnier, E., Brind'Amour, A., Tableau, A., Rufino, M.M., Dauvin, J., Luczak, C., Le Bris, H., 2019. Seasonality in coastal macrobenthic biomass and its implications for estimating secondary production using empirical models. Limnol. Oceanogr. 64, 935–949. https://doi.org/10.1002/lno.11086

Schaal, G., Riera, P., Leroux, C., 2010. Trophic ecology in a Northern Brittany (Batz Island, France) kelp (*Laminaria digitata*) forest, as investigated through stable isotopes and chemical assays. J. Sea Res. 63, 24–35. https://doi.org/10.1016/j.seares.2009.09.002

Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol. Evol. 18, 648–656. https://doi.org/10.1016/j.tree.2003.09.002

Schleuter, D., Daufresne, M., Massol, F., Argillier, C., 2010. A user's guide to functional diversity indices. Ecol. Monogr. 80, 469–484. https://doi.org/10.1890/08-2225.1

Schmera, D., Podani, J., Heino, J., Erős, T., Poff, N.L., 2015. A proposed unified terminology of species traits in stream ecology. Freshw. Sci. 34, 823–830. https://doi.org/10.1086/681623

Shantz, A.A., Ladd, M.C., Burkepile, D.E., 2020. Overfishing and the ecological impacts of extirpating large parrotfish from Caribbean coral reefs. Ecol. Monogr. 90. https://doi.org/10.1002/ecm.1403

Sherr, E.B., Fry, B., 1984. δ13C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib. Mar. Sci. 27, 13–47.

Shojaei, M., Gutow, L., Dannheim, J., Rachor, E., Schröder, A., Brey, T., 2016. Common trends in German Bight benthic macrofaunal communities: Assessing temporal variability and the relative importance of environmental variables. J. Sea Res. 107, 25–33. https://doi.org/10.1016/j.seares.2015.11.002

Silberberger, M.J., Renaud, P.E., Kröncke, I., Reiss, H., 2018. Food-web structure in four locations along the european shelf indicates spatial differences in ecosystem functioning. Front. Mar. Sci. 5, 119. https://doi.org/10.3389/fmars.2018.00119

Snelgrove, P.V.R., Thrush, S.F., Wall, D.H., Norkko, A., 2014. Real world biodiversity–ecosystem functioning: a seafloor perspective. Trends Ecol. Evol. 29, 398–405. https://doi.org/10.1016/j.tree.2014.05.002

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How should beta-diversity inform biodiversity conservation? Trends Ecol. Evol. 31, 67–80. https://doi.org/10.1016/j.tree.2015.11.005

Solan, M., Scott, F., Dulvy, N.K., Godbold, J.A., Parker, R., 2012. Incorporating extinction risk and realistic biodiversity futures: implementation of trait-based extinction scenarios, in: Solan, M., Aspden, R.J., Paterson, D.M. (Eds.), Marine Biodiversity and Ecosystem Functioning. Oxford University Press, pp. 127–148. https://doi.org/10.1093/acprof:oso/9780199642250.003.0010

Solan, M., Wigham, B., Hudson, I., Kennedy, R., Coulon, C., Norling, K., Nilsson, H., Rosenberg, R., 2004. In situ quantification of bioturbation using time-lapse fluorescent sediment profile imaging (f-SPI), luminophore tracers and model simulation. Mar. Ecol. Prog. Ser. 271, 1–12. https://doi.org/10.3354/meps271001

Somerfield, P.J., Clarke, K.R., 2013. Inverse analysis in non-parametric multivariate analyses: distinguishing groups of associated species which covary coherently across samples. J. Exp. Mar. Biol. Ecol. 449, 261–273. https://doi.org/10.1016/j.jembe.2013.10.002

Stachowicz, J.J., Bruno, J.F., Duffy, J.E., 2007. Understanding the effects of marine biodiversity on communities and ecosystems. Annu. Rev. Ecol. Evol. Syst. 38, 739–766. https://doi.org/10.1146/annurev.ecolsys.38.091206.095659

Tecchio, S., Chaalali, A., Raoux, A., Tous Rius, A., Lequesne, J., Girardin, V., Lassalle, G., Cachera, M., Riou, P., Lobry, J., Dauvin, J.-C., Niquil, N., 2016. Evaluating ecosystem-level anthropogenic impacts in a stressed transitional environment: The case of the Seine estuary. Ecol. Indic. 61, 833–845. https://doi.org/10.1016/j.ecolind.2015.10.036

Thiébaut, E., Bacouillard, L., Dauvin, J.-C., Gentil, F., Houbin, C., Broudin, C., Somerfield, P.J., in prep. Long-term changes in the biodiversity and community structure of the macrobenthos in the Bay of Morlaix (western English Channel): 40 years of sampling.

Thiébaut, E., Cabioch, L., Dauvin, J.-C., Retière, C., Gentil, F., 1997. Spatio-temporal persistence of the *Abra alba-Pectinaria koreni* muddy-fine sand community of the eastern Bay of Seine. J. Mar. Biol. Ass. U.K. 77, 1165–1185. https://doi.org/10.1017/S0025315400038698

Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., Kitching, R.L., Martinez, N.D., Rantala, H., Romanuk, T.N., Stouffer, D.B., Tylianakis, J.M., 2012. Food webs: reconciling the structure and function of biodiversity. Trends Ecol. Evol. 27, 689–697. https://doi.org/10.1016/j.tree.2012.08.005

Thouzeau, G., 1991. Déterminisme du pré-recrutement de *Pecten maximus* (L.) en baie de Saint-Brieuc: processus régulateurs de l'abondance, de la survie et de la croissance des post-larves et juvéniles. Aquat. Liv. Res. 4, 77–99. https://doi.org/10.1051/alr:1991008

Thrush, S., Hewitt, J., Cummings, V., Ellis, J., Hatton, C., Lohrer, A., Norkko, A., 2004. Muddy waters: elevating sediment input to 299 coastal and estuarine habitats. Front. Ecol. Environ. 2, 299–306. https://doi.org/10.2307/3868405

Thrush, S.F., Gray, J.S., Hewitt, J.E., Ugland, K.I., 2006. Predicting the effects of habitat homogenization on marine biodiversity. Ecol. Appl. 16, 1636–1642. https://doi.org/10.1890/1051-0761(2006)016[1636:PTEOHH]2.0.CO;2

Thrush, S.F., Halliday, J., Hewitt, J.E., Lohrer, A.M., 2008. The effects of habitat loss, fragmentation, and community homogenization on resilience in estuaries. Ecol. Appl. 18, 12–21. https://doi.org/10.1890/07-0436.1

Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., Slade, N.A., 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for δ 13 C analysis of diet. Oecologia 57, 32–37. https://doi.org/10.1007/BF00379558

Tillin, H., Hiddink, J., Jennings, S., Kaiser, M., 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Mar. Ecol. Prog. Ser. 318, 31–45. https://doi.org/10.3354/meps318031

Tilman, D., 2001. Functional diversity, in: Encyclopedia of Biodiversity. Elsevier Inc., pp. 587–596.

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.

Tréguer, P., Goberville, E., Barrier, N., L'Helguen, S., Morin, P., Bozec, Y., Rimmelin-Maury, P., Czamanski, M., Grossteffan, E., Cariou, T., Répécaud, M., Quéméner, L., 2014. Large and local-scale influences on physical and chemical characteristics of coastal waters of Western Europe during winter. J. Mar. Syst. 139, 79–90. https://doi.org/10.1016/j.jmarsys.2014.05.019

Tyler, E.H.M., Somerfield, P.J., Berghe, E.V., Bremner, J., Jackson, E., Langmead, O., Palomares, M.L.D., Webb, T.J., 2012. Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. Global Ecol. Biogeogr. 21, 922–934. https://doi.org/10.1111/j.1466-8238.2011.00726.x

Urbina, M.A., 2016. Temporal variation on environmental variables and pollution indicators in marine sediments under sea Salmon farming cages in protected and exposed zones in the Chilean inland Southern Sea. Science of The Total Environment 573, 841–853. https://doi.org/10.1016/j.scitotenv.2016.08.166

Ushio, M., Hsieh, C., Masuda, R., Deyle, E.R., Ye, H., Chang, C.-W., Sugihara, G., Kondoh, M., 2018. Fluctuating interaction network and time-varying stability of a natural fish community. Nature 554, 360–363. https://doi.org/10.1038/nature25504

Usseglio-Polatera, P., Bournaud, M., Richoux, P., Tachet, H., 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. Freshw. Biol. 43, 175–205. https://doi.org/10.1046/j.1365-2427.2000.00535.x

van der Linden, P., Marchini, A., Dolbeth, M., Patrício, J., Veríssimo, H., Marques, J.C., 2016. The performance of trait-based indices in an estuarine environment. Ecol. Indic. 61, 378–389. https://doi.org/10.1016/j.ecolind.2015.09.039

van der Linden, P., Patrício, J., Marchini, A., Cid, N., Neto, J.M., Marques, J.C., 2012. A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem. Ecol. Indic. 20, 121–133. https://doi.org/10.1016/j.ecolind.2012.02.004

Van Hoey, G., Degraer, S., Vincx, M., 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. Estuar. Coast. Shelf Sci. 59, 599–613. https://doi.org/10.1016/j.ecss.2003.11.005

Van Hoey, G., Vincx, M., Degraer, S., 2007. Temporal variability in the Abra alba community determined by global and local events. J. Sea Res. 58, 144–155. https://doi.org/10.1016/j.seares.2007.02.007

Vander Zanden, M.J., Rasmussen, J.B., 2001. Variation in δ15N and δ13C trophic fractionation: Implications for aquatic food web studies. Limnol. Oceanogr. 46, 2061–2066. https://doi.org/10.4319/lo.2001.46.8.2061

Veríssimo, H., Bremner, J., Garcia, C., Patrício, J., van der Linden, P., Marques, J.C., 2012. Assessment of the subtidal macrobenthic community functioning of a temperate estuary following environmental restoration. Ecol. Indic. 23, 312–322. https://doi.org/10.1016/j.ecolind.2012.04.020

Vieira, R., Martin, A., Engelen, A.H., Thomsen, M.S., Arenas, F., 2020. Interactive effects of co-occurring anthropogenic stressors on the seagrass, *Zostera noltei*. Ecol. Indic. 109, 105780. https://doi.org/10.1016/j.ecolind.2019.105780

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1

Villéger, S., Miranda, J.R., Hernandez, D.F., Mouillot, D., 2012. Low Functional β-Diversity Despite High Taxonomic β-Diversity among Tropical Estuarine Fish Communities. PLoS ONE 7, 10. https://doi.org/10.1371/journal.pone.0040679

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Volkenborn, N., Robertson, D.M., Reise, K., 2009. Sediment destabilizing and stabilizing bio-engineers on tidal flats: cascading effects of experimental exclusion. Helgol. Mar. Res. 63, 27–35. https://doi.org/10.1007/s10152-008-0140-9

Wainright, S.C., Fry, B., 1994. Seasonal variation of the stable isotopic compositions of coastal marine plankton from Woods Hole, Massachusetts and Georges Bank. Estuaries 17, 552–560. https://doi.org/10.2307/1352403

Warwick, R., Ashman, C., Brown, A., Clarke, K., Dowell, B., Hart, B., Lewis Re Shillabeer, N., Somerfield, P., Tapp, J., 2002. Inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional environmental events. Mar. Ecol. Prog. Ser. 234, 1–13. https://doi.org/10.3354/meps234001

Warwick, R.M., 1984. Species size distributions in marine benthic communities. Oecologia 61, 32–41. https://doi.org/10.1007/BF00379085

Warwick, R.M., Collins, N.R., Gee, J.M., George, C.L., 1986. Species size distributions of benthic and pelagic Metazoa: evidence for interaction? Mar. Ecol. Prog. Ser. 34, 63–68.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251. https://doi.org/10.2307/1218190

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 279–338. https://doi.org/10.2307/1943563

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314, 787–790. https://doi.org/10.1126/science.1132294

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403

Yates, M.L., Andrew, N.R., Binns, M., Gibb, H., 2014. Morphological traits: predictable responses to macrohabitats across a 300 km scale. PeerJ 2, e271. https://doi.org/10.7717/peerj.271

Yokoyama, H., Tamaki, A., Harada, K., Shimoda, K., Koyama, K., Ishihi, Y., 2005. Variability of diet-tissue isotopic fractionation in estuarine macrobenthos. Mar. Ecol. Prog. Ser. 296, 115–128. https://doi.org/10.3354/meps296115

Zar, H.J., 1999. Biostatistical analysis, Fourth Edition. ed. Prentice-Hall, New Jersey.

Zettler, M.L., Proffitt, C.E., Darr, A., Degraer, S., Devriese, L., Greathead, C., Kotta, J., Magni, P., Martin, G., Reiss, H., Speybroeck, J., Tagliapietra, D., Van Hoey, G., Ysebaert, T., 2013. On the myths of indicator species: Issues and further consideration in the use of static concepts for ecological applications. PLoS ONE 8, e78219. https://doi.org/10.1371/journal.pone.0078219

# Annexe

# Functional trait-based approaches as a common framework for aquatic ecologists

Séverine Martini[1,2§], Floriane Larras*[3], Aurélien Boyé*[4], Emile Faure*[1,5], Nicole Aberle[6], Philippe Archambault[7], Lise Bacouillard[8], Beatrix E Beisner[9], Lucie Bittner[5], Emmanuel Castella[8], Michael Danger[11,12], Olivier Gauthier[4], Lee Karp-Boss[13], Fabien Lombard[1,12], Frédéric Maps[7], Lars Stemmann[1], Eric Thiébaut[8], Philippe Usseglio-Polatera[11], Meike Vogt[14], Martin Laviale[#11], Sakina-Dorothée Ayata[#§1,5]

*Published in Limnology and Oceanography December 10, 2020*

§ Corresponding authors: severine.martini@mio.osupytheas.fr

* These authors contributed equally to this work

# These authors contributed equally to this work

[1] Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche, LOV, 06230 Villefranche-sur-mer, France

[2] Aix Marseille Univ., Université de Toulon, CNRS, IRD, MIO UM 110, 13288 Marseille, France

[3] Helmholtz Center for Environmental Research, Leipzig, Germany

[4] Laboratoire des Sciences de l'Environnement Marin (LEMAR) UMR 6539 CNRS UBO IRD IFREMER, Institut Universitaire Européen de la Mer, Université de Bretagne Occidentale, 29280 Plouzané, France

[5] Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, CP 50, 57 rue Cuvier, 75005 Paris, France

[6] Norwegian University of Science and Technology (NTNU), Trondhjem Biological Station, Trondheim, Norway

[7] Québec-Océan and Unité Mixte Internationale Takuvik Ulaval-CNRS, Département de Biologie, Université Laval, Québec, Canada

[8] Sorbonne Université, CNRS, Station Biologique de Roscoff, Laboratoire Adaptation et Diversité en Milieu Marin, Place Georges Teissier, 29680 Roscoff, France

[9] Department of Biological Sciences, University of Québec at Montréal, Montréal, Québec, Canada

[10] Department F.-A. Forel for Environmental and Aquatic Sciences, Earth and Environmental Science Section and Institute for Environmental Sciences, University of Geneva, Geneva, Switzerland

[11] Université de Lorraine, CNRS, LIEC, F-57000 Metz, France

[12] Institut Universitaire de France Paris, Île-de-France, France

[13] School of Marine Sciences, University of Maine, Orono, ME USA

[14] Environmental Physics, Institute of Biogeochemistry and Pollutant Dynamics, ETH Zürich, Switzerland

## ABSTRACT

Aquatic ecologists face challenges in identifying the general rules of the functioning of ecosystems. A common framework, including freshwater, marine, benthic, and pelagic ecologists is needed to bridge communication gaps and foster knowledge sharing. This framework should transcend local specificities and taxonomy in order to provide a common ground and shareable tools to address common scientific challenges. Here, we advocate the use of functional trait-based approaches (FTBAs) for aquatic ecologists, and propose concrete paths to go forward. Firstly, we propose to unify existing definitions in FTBAs to adopt a common language. Secondly, we list the numerous databases referencing functional traits for aquatic organisms. Thirdly, we present a synthesis on traditional as well as recent promising methods for the study of aquatic functional traits, including imaging and genomics. Finally, we conclude with a highlight on scientific challenges and promising venues for which FTBAs should foster opportunities for future research. By offering practical tools, our framework provides a clear path forward to the adoption of trait-based approaches in aquatic ecology.

## Keywords

Functional trait; Marine; Freshwater; Trait-based approaches; Databases: Imaging; Omics; Aquatic ecology; Limnology; Oceanography

# 1. Introduction

The aquatic realm encompasses very diverse environments from freshwater ponds, lakes, and rivers to estuaries, salt marshes, mangroves, coasts, continental shelves, deep-seas, marginal seas, and open ocean areas. It plays a major role in the Earth's climate system and supplies important ecosystem services for human populations (Grizzetti et al. 2016). Yet, different aquatic ecosystems are still studied by distinct scientific communities that have limited interactions with each other, as illustrated by the tendency to train graduate students independently, to publish in different journals and to attend distinct conferences (with a few exceptions, such as the Association for the Sciences of Limnology and Oceanography (ASLO) and its conferences and journals, including Limnology and Oceanography). Freshwater and marine ecosystems even belong to different Sustainable Development Goals for the United Nations, with one dedicated to the marine environment (#14: Life below water), and another to terrestrial systems including freshwater (#15: Life on land) (United Nations 2015).

Ecology seeks to understand interactions between organisms and the environment, as well as to identify general rules that elucidate the functioning of ecosystems, to ultimately improve our ability to predict ecosystem changes (Loreau 2010). In both freshwater and marine environments, and for both pelagic and benthic habitats, the crucial questions remain the same (Heino et al. 2015): (1) What are the processes that control the structure and functioning of aquatic ecosystems? (2) What ecological patterns emerge at various spatio-temporal scales, and what are their key drivers? (3) How will aquatic organisms respond to increasing anthropogenic pressures? Some efforts have been made to integrate aquatic ecology for planktonic (Margalef 1978; Hecky and Kilham 1988; Leibold and Norberg 2004; Litchman and Klausmeier 2008) and benthic (Mermillod-Blondin and Rosenberg 2006) studies. Despite recent efforts to bring the communities together (e.g. the AQUASHIFT and DynaTrait projects priority programmes of the German Research Foundation, or such as the bi-annual Trait workshop https://www.traitspace.com/ including limnologists, benthic ecologists, terrestrial ecologists), a unified framework for addressing ecological questions in pelagic and benthic habitats of both environments has been slow to develop. A recent review highlights the potential of trait-based ecology for studying aquatic ecosystems and the need for collaborative approaches among aquatic ecologists was emphasized (Kremer et al. 2017). In addition to bridging the gap between freshwater and marine studies, there is a crucial need to integrate planktonic and benthic studies, especially because of the strong coupling between these two habitats (Griffiths et al. 2017). The present synthesis proposes a practical framework to address these needs.

Indeed, trait-based approaches, defined in ecological research as any method that focuses on individual properties of organisms (so-called traits) rather than species, could provide this common framework (McGill et al. 2006; Kremer et al. 2017). These approaches emerged from terrestrial ecology when attributes at the individual level, initially used to describe ecosystem function based on elements common to multiple species, were considered to gather individuals into functional groups (i.e., “plant functional types”) based on their physical, phylogenetic and phenological characteristics, rather than on their taxonomy (e.g. species). Trait-based models of aquatic ecosystems can be traced back to the pioneering work of Riley in the 1940’s (Riley 1946), who modelled the phytoplankton bloom dynamics in the North Atlantic focusing on the main physiological and biological characteristics of phytoplankton as a group. Since earlier attempts to classify phytoplankton by “life-forms” (Sournia 1982; Reynolds 1988), a similar approach was applied to identify functional groups for freshwater benthic macrofauna (Usseglio-Polatera et al. 2000, 2001), marine benthos (Rigolet et al. 2014), benthic algae (Tapolczai et al. 2016), submerged plants (Willby et al. 2000; Lukács et al. 2019), or marine zooplankton (Benedetti et al. 2016). The underlying assumption is that functional grouping would make it easier to link community ecology to biogeochemical processes and biodiversity to ecosystem functioning (Naeem and Wright 2003). Through the study of functional diversity and functional traits, these approaches allow for the quantitative assessment of community or ecosystem resistance or resilience to changes through functional redundancy (Lavorel and Garnier 2002; McGill et al. 2006) which could potentially enhance generality and predictability in future projections of ecosystem function and service provision than the species-centred or taxonomic approaches (Levine 2016).

In aquatic ecology alone, more than 2,476 articles were published between 1991 and 2018 using the terms “functional trait” or “trait-based” (see Supplementary Information). The percentage of those publications relative to the total ones published in freshwater and marine ecology (using those terms as keywords in Web of Science) has increased over time. This emergent and still increasing area of research in aquatic ecology has been the topic of several recent reviews, which summarize the state of the knowledge with regard to specific taxonomic or trophic groups, or traits (Litchman and Klausmeier 2008; Litchman et al. 2013;

Nock et al. 2016; Meunier et al. 2017; Hébert et al. 2017; Kremer et al. 2017; Beauchard et al. 2017; Degen et al. 2018; Kiørboe et al. 2018). Previous studies focused either on one species (Pardo and Johnson 2005), on one taxonomic group of organisms (e.g. crustaceans in Hébert et al. 2016, 2017), on one compartment of the ecosystem (e.g. pelagic primary producers in Litchman and Klausmeier (2008); benthic primary producers in Tapolczai et al. (2016); zooplankton in Litchman et al. (2013) and Hébert et al. (2017); stream fish in Frimpong and Angermeier (2010)), on a particular ecosystem (e.g. oceans in Barton et al. (2013) and Kiørboe et al. (2018) marine benthos in Degen et al. (2018); running water benthos in Statzner and Bêche (2010)) or even on a single type of trait (e.g. size in Andersen et al. (2016) or stoichiometric traits in Meunier et al. (2017)). A network analysis of key words associated with the aquatic trait-based literature highlights differences between studies, both in the terminology used to characterize traits and in the application of trait-based approaches in studies of freshwater and marine systems (Figure S1).

The goal of this review is to facilitate exchanges of FTBAs and their products across different aquatic fields. To do so, we propose: 1) A table compiling the main definitions of traits that are commonly used in trait-based studies, in addition to recommendations for using a common and unambiguous vocabulary, 2) A unified typology of 40 aquatic functional traits that could be used in multicompartment studies (including several biological compartments, or different habitats e.g. sediment and water), 3) A summary of existing databases that contain information on functional traits, 4) A review of traditional and emerging methods for estimating and using traits of aquatic organisms, and 5) The main challenges that aquatic ecologists can now address using FTBAs and that should inspire future studies.

## 2. Trait definition and aquatic trait description

The term "trait" depicts specific attributes of an individual that are both inherent and characteristic to its nature. However, as highlighted by our literature survey (Supplementary Figure S1 and S2, see also Supplementary Information), this term is used in multiple contexts to describe a diverse set of attributes such as: "physiological traits", "functional traits", "life history traits", "biological traits", "ecological traits", "response traits", "effect traits", "behavioral traits", etc (see Table 1). To avoid misunderstandings, clear definitions of these concepts are needed (Violle et al. 2007).

## 2.1. Adopting common definitions for aquatic FTBAs

Trait definitions vary between scientific communities, from the individual organism (e.g. life- history traits) to the population (e.g. demographic traits), community (e.g. response traits) and the ecosystem scale (e.g. effect traits; Hébert et al. 2017). Traits can also be directly measured *in situ* (e.g. realized traits) or inferred from the literature (e.g. potential traits). Realized traits are ultimately one of the sources for potential traits found in databases (see section 3.1). To establish a unified framework and avoid subjectivity in these definitions, we recommend the use of the definitions that focus on the individual level only. These are the ones proposed by Violle et al. (2007), by Litchman and Klausmeier (2008) and by Reu et al. (2011) are summarized in Table 1.

**Table 1: Main definitions related to traits in aquatic trait-based studies**. Examples are given in grey. For clarity and consistency in trait-based aquatic ecology, this table presents only recommended definitions, while a full table including all the definitions currently used is available as Suppl. Table. 1.

| **Term** | **Recommended definitions** | **References** | **Examples** |
|---|---|---|---|
| Trait | Any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization. | (Violle et al., 2007b) | |
| Functional trait | Any trait that impacts fitness indirectly via its effects on growth, reproduction and survival. | (Violle et al., 2007b) | |
| Realized trait | Trait actually measured *in situ* or in the laboratory | (Reu et al., 2011) | |
| Potential trait | Trait described from the literature, usually at the species level, and ideally covering a large variety of environmental conditions. | (Reu et al., 2011) | |
| Life history traits | Traits referring to life history | (Litchman and Klausmeier, 2008b) | Type of reproduction (sexual versus asexual) or the ability to form resting stages. |
| | Traits that are relevant at the individual level | (Hébert et al., 2017) | Fitness-related traits. |
| Morphological trait | Traits related to the morphology of organisms | (Litchman and Klausmeier, 2008b) | Cell size, cell shape. |
| Physiological trait | Traits related to the physiology of organisms | (Litchman and Klausmeier, 2008b) | Nutrient acquisition, response to light. |
| Behavioral trait | Traits related to the behavior of organisms | (Litchman and Klausmeier, 2008b) | Motility. |

Since it is the diversity of organismal functions that structures communities and eventually ecosystems, trait-based approaches should rather refer to "functional traits" (sensu Violle et al. 2007: Any trait that impacts fitness indirectly via its effects on growth, reproduction and survival) than to "traits" and should in fact be called functional trait-based approaches. Functional traits have been further divided into four types: life history traits, morphological traits, physiological traits, and behavioral/mobility traits (Litchman and Klausmeier 2008; Litchman et al. 2013, 2015; Desrosiers et al. 2019). The term "ecological traits" has also been used in the context of "functional traits" to describe the environmental preference of the organisms, especially for benthic ones (e.g. Desrosiers et al. 2019). Where "ecological traits" refer to ecological or environmental preferences of organisms, they should rather be called physiological traits (e.g. salinity preference/tolerance) or behavioral traits (e.g. relationship with the substrate). In contrast, ecological traits referring to taxonomic information, sampling location or habitat features (e.g. depth, substratum type) should neither be considered as functional traits nor as traits.

### 2.2. Functional traits as a common framework beyond taxonomy to transcend ecosystems

Functional traits provide a "*common currency across biological organizational levels and taxonomic groups*" (Violle et al. 2014), beyond taxonomic variation and geographic or ecosystemic peculiarities. Firstly, functional trait-based ecology describes emergent properties related to ecosystem functioning, without necessarily having to explicitly identify the organisms at a given taxonomic level. Secondly, FTBAs in aquatic ecology can account for a continuous degree of plasticity in the trait expressed (Chevenet et al. 1994), thus allowing for a better quantification of intra-specific variability (see also 4.1.3). Moreover, phenotypic plasticity can result in substantial intra-specific variation (Des Roches et al. 2018), with clonal differences in plasticity. For instance, many aquatic species can exhibit a high degree of morphological plasticity in response to different environmental cues. Zooplankters such as *Daphnia* can form elongated carapaces (e.g. longer tailspines or helmets) in response to strong predation (O'Brien et al. 1979; Lüning 1992; Swaffar and O'Brien 1996) while the freshwater phytoplankters *Desmodesmus* can increase the size of their colonies to avoid mortality from numerous grazers (Lürling 2003). These are examples among a vast amount of abilities for phenotypic plasticity that can in and of themselves be seen as functional trait of the organisms that possess this flexibility (Barnett et al. 2007; Weithoff and Beisner 2019). Intra-specific variability can be substantial in aquatic organisms (e.g. Sanford and Kelly

2011), and can impact community and ecosystem dynamics similarly to inter-specific trait variability (Des Roches et al. 2018; Raffard et al. 2019). Within the climate context, understanding the drivers and link between intra- and inter-specific trait variability is another argument for the use of FTBAs instead of species-centered approaches (Violle et al. 2012).

To go further towards a unified framework, we propose a common typology of functional traits for aquatic organisms (Figure 1). It not only follows what was previously proposed for phytoplankton (Litchman and Klausmeier 2008) and zooplankton (Litchman et al. 2013; Brun et al. 2016) but now incorporates new elements proposed for marine benthic ecosystems (Degen et al. 2018). Moreover, in the typologies proposed by Litchman and colleagues, functional traits are classified in one of four types (morphological, physiological, behavioral and life-history) and associated to three main ecological functions (resource acquisition, reproduction and predator avoidance for phytoplankton; feeding, growth/reproduction, and survival for zooplankton). Here we propose to separate growth and reproduction into two distinct columns (Figure 1). Compared to earlier typologies, ours identifies key functional traits that can be used for multicompartmental studies because they transcend the taxonomic specificities of the different aquatic ecosystems (Salguero-Gómez et al. 2018). For instance it includes some traits that have been disregarded so far in studies focusing on only one compartment. These traits are: water content, color, breeding type, life-cycle, life span, diapause, reproduction strategy, salinity preference/tolerance, chemical compounds for mating or detecting congeners, diet/food preference, allochemical compounds, dissemination potential, substrate relation (plankton/benthos, including substrate specific relation for benthos), ecosystem engineering, including bioturbation/irrigation for benthos, and finally perception/production of sounds. Most of the 40 functional traits presented in this typology can be estimated quantitatively (Costello et al. 2015), making them good candidates for comparative studies. In addition, a dynamic representation of this typology is proposed as an online mental map (http://doi.org/10.5281/zenodo.3635898) which links to associated research articles. This mental map is not only a different way to represent the functional traits proposed in Figure 1, but it also provides a dynamic visual representation. It can serve as a pedagogical tool for teaching purposes and as a basis to identify trade-offs between related traits. Further work could initiate a globally shared ontology for aquatic traits, for instance as part of Open Biological and Biomedical Ontology (OBO) Foundry (http://obofoundry.org/).

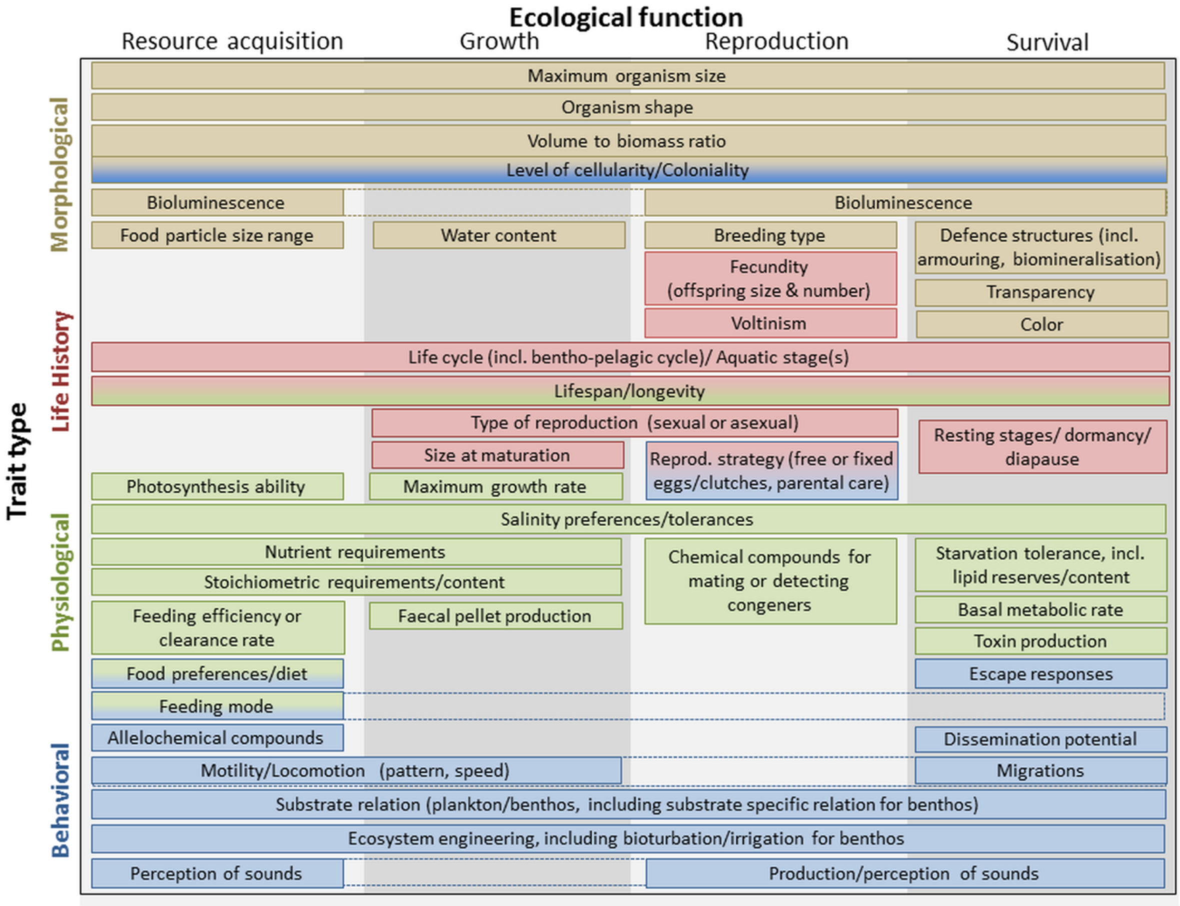


**Figure 1: Unified typology of aquatic functional traits that could be used in multicompartmental studies**. This typology focuses on the key functional traits that transcend taxonomic peculiarities of the different aquatic ecosystems. Traits are classified by type and ecological function (as in Litchman and Klausmeier 2008) and most of them are quantitative. The dashed lines are a representation for similar traits crossing multiple ecological functions that are not close. A mental map providing a network visualisation of this figure is available online, with each trait node linking towards associated research articles (http://doi.org/10.5281/zenodo.3635898).

## 2.3. Estimating functional diversity from functional traits

Traits are useful tools to quantify not only the functional biogeography of a system or organism, but also the diversity of a system, its functional redundancy, and/or its likely resilience to perturbations. Those traits that have been measured at the individual level, or estimated for each species of a given community, can be used to estimate trait-based Shannon diversity (Usseglio-Polatera et al. 2000) or Rao's quadratic entropy indices (Rao 1982). Functional diversity (FD) and its various dimensions, such as functional richness, functional divergence, or functional evenness (Mason et al. 2005; Ricotta 2005) can further be quantified, either using dendrogram-based metrics (e.g. Petchey and Gaston 2007; Mouchet et al. 2008), or from the definition of a functional space (e.g. Villéger et al. 2008; Laliberté and Legendre 2010) Several indices taking explicitly into account intraspecific trait variability were also proposed (e.g. Bello et al. 2011; Carmona et al. 2016). Functional beta diversity can be estimated too, including through the more classical Biological Trait Analysis (BTA) (e.g. Bremner et al. 2006; Beauchard et al. 2017). To aid ecologists in finding their way among the many functional diversity metrics, several guides were published about their definition and use (Schleuter et al. 2010; Mason et al. 2013; Mouillot et al. 2013; Carmona et al. 2016; Schmera et al. 2017; Legras et al. 2018). Many of these indices are sensitive to the number and the type of traits that are considered (e.g. Legras et al. 2019), as well as to the species richness of the communities, meaning that the comparison of sites with different richness levels would require using comparable indices that are unbiased by species richness and trait selection.

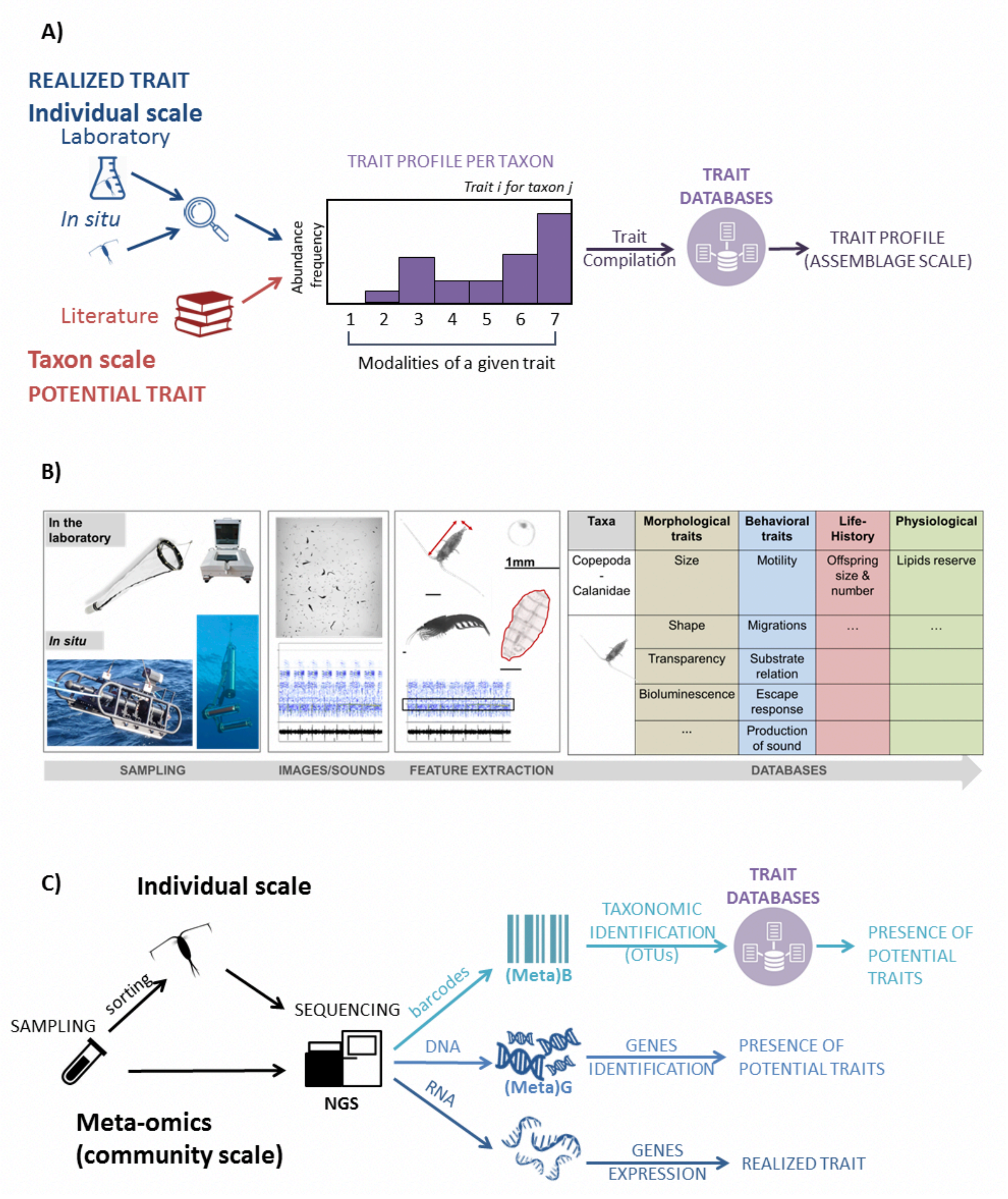
## 3. Estimating and using traits: tools and limits for studying functional traits

Several observational methods, both used *in situ* as well as *in vitro,* allow for the quantification or identification of functional traits; but they are predominantly used in either oceanographical or limnological applications, not both. Currently available methods to measure or estimate traits include classical trait measurements (laboratory and field), imaging and acoustic techniques, as well as molecular sequencing (-omics). These methods will be described in the following sections and opportunities for sharing between scientific communities will be outlined.

### 3.1. Empirical studies of traits as a source for trait databases

The investigation of functional traits has been largely based on empirical studies. Such studies rely on three complementary approaches that can be described by: 1) measurements of traits *in situ*, 2) measurements of traits under controlled laboratory conditions, and 3) metadata analyses of databases and literature (Figure 2A). The metadata approach has been undoubtedly the most developed across aquatic ecosystems (Degen et al. 2018; Kiørboe et al. 2018) and the literature has been the basis of a number of reviews describing functional traits. For example, in freshwater ecology, Kolkwitz and Marsson (1909) pioneered a compilation of types of organisms in relation to the presence of various pollution levels. In marine ecosystems, metadata compilations allowed mapping of key traits of marine copepods at a global scale and evaluation of their relationships with environmental conditions (Brun et al. 2016b; Benedetti et al. 2018). One effective way to merge functional traits with taxa, based on a variety of sources and literature, is the fuzzy coding procedure (e.g. Chevenet et al.

1994). In functional trait-based approaches, the fuzzy coding uses positive scores to describe the affinity of a species for the different categories of a given trait, *e.g.* using “0”, “1”, “2” and “3” for species exhibiting respectively “no”, “weak”, “moderate” and “strong” link with a given trait category (Chevenet et al. 1994; Usseglio-Polatera et al. 2000). When a trait applies to a subset of the different stages of the species life cycle (egg, larva, pupa, and adult), the relative duration of each stage is considered in assigning appropriate scores to the different categories of this trait. To standardize the description of species attributes, trait category scores are converted into a relative abundance distribution so that the sum of the trait category scores for an individual trait and a given taxon equals one. This technique of coding is robust enough to compensate for different types and levels of information available for different taxa.



| Taxa | Morphological traits | Behavioral traits | Life-History | Physiological |
|---|---|---|---|---|
| Copepoda<br>-<br>Calanidae | Size | Motility | Offspring size & number | Lipids reserve |
| | Shape | Migrations | … | … |
| | Transparency | Substrate relation | | |
| | Bioluminescence | Escape response | | |
| | … | Production of sound | | |

**Figure 2: Main methods to study traits. A:** Use of empirical studies to measure realized traits (in laboratory or *in situ*) or to estimate potential traits from the literature. The abundance frequency the modalities a given trait can be used to code trait profile by taxon using fuzzy coding and thereby inform trait databases. **B:** Use of imaging and acoustic techniques to identify or measure functional traits of aquatic organisms from sampling, images/sound recording, features extraction to databases (ZooVis picture has been kindly provided by H. Bi). **C:** Use of sequencing techniques to identify or measure functional traits. Sequencing can be done at the community scale (meta-omics) or at the individual scale after manual or automatic sorting. (Meta)B: (Meta)Barcoding, (Meta)G: (Meta)Genomics, (Meta)T: (Meta)Transcriptomic.

In recent years, numerous open access databases recording functional traits have been developed to document traits included in existing databases (Table 2). This diversity of databases gathers trait information not only for widely studied traits (e.g. body size or feeding strategy), but also for less common traits or for those that are more difficult to measure (e.g. age at first reproduction, migration mode, or nutrient affinities). Some large trait databases were published online and open access (e.g. Herring 1987; Barnett et al. 2007; Benedetti 2015; Hébert et al. 2016; Degen and Faulwetter 2019), thus allowing for follow-up studies that compare and merge trait data across taxa, species and environments. In some instances (e.g. freshwater invertebrates) published databases rapidly became foundational for environmental assessment procedures (e.g. Mondy et al. 2012; Mondy and Usseglio-Polatera 2013; Larras et al. 2017). The main caveat of these FTBAs is that only a limited number of species and/or traits have been reported so far, thus not yet allowing for a generalisation of findings across taxa, the definition of fitness landscapes, and/or the characterisation of ecological niches or responses to environmental change. Indeed, these databases often focus on the dominant and most easily sampled or cultivable species. Moreover, metadata associated with trait measurement methods are usually lacking. Until now, shortfalls in the knowledge of many aquatic taxa (Troudet et al. 2017) restrict the application of trait databases at the community scale and remain a limiting factor for the integration of FTBAs into macroecology (Tyler et al. 2012; Borgy et al. 2017). However, the main limit so far to provide and share trait data remains the lack of an ecological standard for data (Schneider et al. 2018). Attempts to increase unification are currently emerging on various fronts such as the terminology of traits (e.g. Schmera et al. 2015 for stream ecology), the cross-taxa compatibility of functional traits (e.g. Weiss and Ray 2019 for plants and animals) or the actual measurements of such traits (e.g. Moretti et al. 2017 for terrestrial invertebrates). Large efforts are still needed to combine and integrate all these various trait databases (Degen et al. 2018), but applying Open Science principles should accelerate trait-based science (see for example the Open Traits Network initiative, Gallagher et al. 2019). Such databases are already numerous, large-sized and of increasing complexity. Therefore, their manipulation requires strong computational abilities (Durden et al. 2017). As a result, aquatic research is evolving into a more biostatistical- and bioinformatical-based field, enabling the extraction of large-scale information on traits and putting to full use taxonomic surveys recorded over time. Despite this, naturalist taxonomic knowledge per se remains critical and future challenges in ecology will undoubtedly benefit from a combination of modern functional trait-based approaches and a modern integrative taxonomic knowledge.

The traits documented by these databases originate from direct measurements of realized traits in the laboratory or *in situ* (Figure 2A). Laboratory experiments allow for the quantification of functional traits of model species within a large range of controlled environmental conditions. They provide a well-constrained system, both in physical variables and species content, to measure functional traits at the individual level. However, they are often limited to a few cultured species that do not necessarily reflect the actual functional diversity and complexity of whole ecosystems, as should FTBAs do. One of the few examples of lab-measured traits tested the existence of trade-offs across many phytoplankton species between maximum growth rate, competitive ability for phosphorus acquisition, and ability to store phosphorus (Edwards et al. 2013a).

**Table 2: Online databases documenting functional traits of aquatic organisms.** Databases without a primary focus on traits, but that also provide trait information, are included. This list is available at https://github.com/severine13/FonctionalTrait_databases.

| **Name of the database** | **Taxonomic groups of interest and habitats** | **Reference** | **Brief description** | **Web link** |
|---|---|---|---|---|
| **Traitbank - Encyclopedia of Life** | All taxa across the tree of life, including marine and freshwater organisms | (Parr et al., 2014) | Provides traits, measurements, interactions and other facts. Actively growing resource covering all ecosystems (not restricted to aquatic ecosystems). | http://eol.org/info/516 |
| **Bromeliad invertebrate traits** | Aquatic invertebrates in bromeliads from South America | (Céréghino et al., 2018) | 12 functional traits of 852 taxa | https://knb.ecoinformatics.org/#view/doi:10.5063/F1VD6WMF |
| **South-East Australian freshwater macroinvertebrate traits** | Freshwater macroinvertebrates from South-East Australia | (Schäfer et al., 2011 | 9 traits, described at the family level for 172 taxa | Supplementary information to the article |
| **EPA Freshwater Biological Traits Database** | Freshwater macroinvertebrates from North America rivers and streams | (U.S. EPA., 2012) | Includes functional traits (e.g. life history, mobility, morphology traits) but also ecological and habitat information for 3,857 North American taxa. | https://www.epa.gov/risk/freshwater-biological-traits-database-traits |

| Name of the database | Taxonomic groups of interest and habitats | Reference | Brief description | Web link |
|---|---|---|---|---|
| **Biological Traits Information Catalogue (BIOTIC)** | Benthic marine macrofauna and macroalgae | (MARLIN, 2006) | Includes 40 biological trait categories. | http://www.marlin.ac.uk/biotic |
| **EMODnet Biology database** | European seaweeds | (Robuchon et al., 2015) | Functional traits (morphology, life history, ecophysiology) and ecological information (incl. biogeography) for the 1800 seaweed species listed in Europe. | Ongoing work |
| **Functional traits of marine macrophytes** | European marine macrophytes, including seaweeds | (Jänes et al., 2017) | Functional traits (morphology, ecophysiology) and ecological information for 68 species. | https://www.datadryad.org/resource/doi:10.5061/dryad.964pf/1 |
| **POLYTRAITS** | Marine polychaetes | (Faulwetter et al., 2014) | 47 traits describing morphological, behavioral, physiological, life-history characteristics, as well as the environmental preferences, for a total of 27198 trait records for 952 species. | http://polytraits.lifewatchgreece.eu/ |
| **The Arctic Traits Database** | Marine organisms from the Arctic | (Degen and Faulwetter, 2019) | Traits for 478 species-level taxa. | https://www.univie.ac.at/arctictraits/team |
| **WoRMS Marine Species Traits portal** | Marine species | (WoRMS Editorial Board, 2019) | Provides 10 traits that have been prioritized within EMODnet Biology, as part of the World Register of Marine Species (WoRMS). | http://www.marinespecies.org/traits/index.php |
| **Functional traits of marine protists** | Marine protists, including fungi. | (Ramond et al., 2018) | Provides 30 functional traits for 2,007 taxonomic references associated to V4 18S rDNA sequences. | https://doi.org/10.17882/51662 |
| **COPEPEDIA/COPEPOD** | Marine plankton | (O'Brien, 2014) | Database of plankton taxa distribution maps, photographs, biometric traits, and genetic markers. | https://www.st.nmfs.noaa.gov/copepod/documentation/contact-us.html |
| **Trait database for marine copepods** | Marine pelagic copepods | (Brun et al., 2017) | Trait databases providing 9,306 records for 14 functional traits of about 2,600 species. | https://doi.pangaea.de/10.1594/PANGAEA.862968 |
| **Mediterranean copepods' functional traits** | Marine copepods present in the Mediterranean Sea | (Benedetti, 2015; Benedetti et al., 2016) | Seven functional traits for 191 species. | https://doi.org/10.1594/PANGAEA.854331 |

| Name of the database | Taxonomic groups of interest and habitats | Reference | Brief description | Web link |
|---|---|---|---|---|
| **Freshwater Ecology** | European freshwater organisms belonging to fishes, macro-invertebrates, macrophytes, diatoms and phytoplankton | (Schmidt-Kloiber and Hering, 2015) | Covers environmental preferences, distribution patterns, and functional traits for 20,000 taxa. | https://www.freshwaterecology.info/ |
| **Freshwater benthic diatoms** | European rivers | (Rimet and Bouchez, 2012) | life-forms, cell-sizes and ecological guilds for c.a. 1,200 taxa | https://data.inra.fr/dataset.xhtml?persistentId=doi:10.15454/XLQ40G |
| | Fresh and weakly brackish waters in The Netherlands | (Van Dam et al., 1994) | First comprehensive checklist of ecological traits (pH, saprobity…) for 948 diatom taxa | https://doi.org/10.1007/BF02334251 |
| **Phytoplankton of temperate lakes** | Phytoplankton of temperate lakes | (Rimet and Druart, 2018) | Database of morphological and physiological traits of more than 1,200 taxa. | https://zenodo.org/record/1164834#.XRNrPXvgrOR |
| **Freshwater benthic micro-meiofauna** | River benthic micro-meiofauna | (Neury-Ormanni et al., 2019) | First integrative database of 23 morphological traits linked to resource acquisition for 35 taxa | https://doi.org/10.1007/s10750-019-04120-0 |
| **FishBase** | Fishes | (Beukhof et al., 2019; Froese and Pauly, 2019) | Provides information on 34,100 species, including traits related to trophic ecology and life history. | www.fishbase.org<br>https://doi.org/10.1594/PANGAEA.900866. |
| **The Coral Trait Database** | Coral species from the global oceans | (Madin et al., 2016) | Includes 68,494 coral observations with 106,462 trait entries of 158 traits for 1,548 coral species. | https://coraltraits.org/ |
| **FishTraits** | Freshwater fishes of the United States. | (Frimpong and Angermeier, 2010) | More than 100 traits are informed for 809 fish species of the USA, including 731 native and 78 exotic species. | http://www.fishtraits.info/ |
| **ECOTAXA** | Marine planktonic eukaryotes and prokaryotes (Viruses in prep.) | (Picheral et al., 2017) | 50 morphological features including size, shape or opacity. | http://ecotaxa.obs-vlfr.fr/<br>http://ecotaxa.sb-roscoff.fr |
| **Protist Ribosomal Reference database (PR2)** | Protists | (Guillou et al., 2013) | Sequence database for which the inclusion of functional traits is under development. | https://github.com/pr2database/pr2database |
| **Eukaryotic Reference Database (EukRef)** | A wide range of eukaryotic organisms across the tree of life | (del Campo et al., 2018) | Collaborative annotation initiative for referencing 18S rRNA sequences, for which the inclusion of functional traits is under development. | https://eukref.org |

| Name of the database | Taxonomic groups of interest and habitats | Reference | Brief description | Web link |
|---|---|---|---|---|
| **The Kyoto Encyclopedia of Genes and Genomes (KEGG)** | A wide range of organisms across the tree of life | (Kanehisa and Goto, 2000) | Collection of databases on genomes and biological pathways that provides molecular-level information on gene functions, which could inform on potential functional traits. | https://www.genome.jp/kegg/ |
| **sFDvent: A global trait database for deep-sea hydrothermal vent fauna** | Deep-sea hydrothermal-vent fauna with species-level identification present or in progress | (Chapman et al., 2019) | Six hundred and forty-six vent species names, associated location information, and scores for 13 traits | https://doi.org/10.5061/dryad.cn2rv96 |

In recent years, innovative instruments and tools have become available to measure *in situ* new functional traits. They include imaging and genomics tools that have the potential to provide a comprehensive picture of aquatic ecosystem composition, structure and function. Their implementation should greatly help advance the use of functional traits in aquatic studies.

### 3.2. Imaging and acoustic techniques

Imaging systems are best suited for the quantification of morphological traits, such as size, transparency, bioluminescence or shape (Forest et al. 2012; Barton et al. 2013; Fontana et al. 2014; Andersen et al. 2016), but also for the estimation of some behavioral (e.g. motility or substrate relationships), life-history or physiological traits (Table 1; Figure 2B,Schmid et al. 2018; Ohman 2019). Imagery has been used as a tool in marine science since the 1950's and a variety of imaging systems have been successfully developed to record individual characteristics (see imaging and acoustic instruments listed in Table 3; e.g. Lombard et al. 2019). Over the last 15 years, novel imaging techniques have allowed for rapid and less-intrusive visual observation of organisms' traits from pico- to macro-scales (e.g. (Culverhouse et al. 2006; Stemmann et al. 2008; Sieracki et al. 2010; Biard et al. 2016). To date, imaging tools have mostly been used by marine ecologists (Table 3), in both benthic and pelagic ecosystems, with only a few implementations in freshwater environments (e.g. (Althaus et al. 2015; González-Rivero et al. 2016). This is mainly due to the large amount of particles, the higher turbidity and the relatively smaller size of the crustacean zooplankton in freshwater ecosystems. Benthic imaging tools include baited, unbaited, towed, autonomous- and diveroperated systems (Matabos et al. 2014; de Juan et al. 2015; Mérillet et al. 2018), while pelagic ones are mainly *in situ* or bench-top systems. Since the turbidity and obstacles in benthic, coastal or river ecosystems strongly modify optical characteristics, systems with external light are more commonly used to efficiently capture morphological traits of aquatic organisms.

**Table 3:** Examples of instruments for imaging and acoustic assessment, used for trait description and quantification in aquatic ecosystems.

| Taxonomic groups | Instrument | References | Applications |
|---|---|---|---|
| **Protists** | FlowCam | (Sieracki et al., 1998) | Marine microplankton, abundance, size |
| | Imaging FlowCytobot (IFCB) | (Olson and Sosik, 2007) | Marine coastal, nano- and microplankton, quantification, particle profile (morphology) |
| | Cytobuoy | (Dubelaar et al., 1999; Dubelaar and Gerritzen, 2000) | Freshwater and marine coastal, phytoplankton biomass, particle profile (morphology) |
| **Large protists and meso-plancton** | Zooscan | (Gorsky et al., 2010) | Marine, shelf, coastal, pelagic plankton, morphological features |
| | Zooglider | (Ohman et al., 2019) | Imaging and acoustics, marine, shelf, coastal, pelagic plankton, morphological features |
| **Macro-organisms and fish** | Laser Optical Plankton Counter (LOPC) | (Finlay et al., 2007) | Freshwater and marine, zooplankton size, biomass, abundance |
| | ZOOplankton Visualization and Imaging System (ZOOVIS) | (Bi et al., 2012) | Marine pelagic, zooplankton, size |
| | Underwater Video Profiler (UVP) | (Picheral et al., 2010) | Marine, shelf, coastal, pelagic plankton, morphological features |
| | Lightframe On-sight Keyspecies Investigation (LOKI) | (Schmid et al., 2016; Schulz et al., 2010) | Marine zooplankton, species, stages, morphological features |
| | In situ Ichthyoplankton Imaging System (ISIIS) | (Cowen and Guigand, 2008) | Marine, ichtyoplankton, meso-zooplankton, abundances, species |
| | Hydrophone | (Coquereau et al. 2016; Desjonquères 2016) | Marine, freshwater, benthic |

A major advantage of imaging systems is their variable degree of invasiveness during observation. Imaging systems can analyse discrete measurement of water samples (living or fixed samples), but they can also acquire *in situ* continuous records on living organisms. For instance, imaging techniques applied to marine plankton revealed that the abundance of the most fragile organisms (such as gelatinous zooplankton, Rhizaria, etc.) has been underestimated for a long time using traditional observation techniques (e.g. Biard et al. 2016), as they tend to break when collected using plankton nets (Stemmann et al. 2008). The use of *in situ* imaging systems also provides information on poorly studied traits, such as transparency and water content of gelatinous organisms. For benthic systems, imaging techniques provide non-intrusive and non-destructive methods that can be valuable to assess endangered habitats and/or marine protected areas and to collect information on the distribution of large over-dispersed epifaunal species inadequately sampled by traditional gears like grabs (e.g. Althaus et al. 2015).

In addition to classical imaging, acoustic methods (passive and active) are also tools of increasing importance to quantify particular functional traits. Acoustic Doppler current profilers (ADCPs) have been successfully used in lakes to capture diel migration behavior in larger planktonic species such as the insect larval predators of zooplankton (e.g. *Chaoborus*; Lorke et al. 2004). Hydrophone recordings can be used to record sound emissions by the organisms themselves. The sounds produced by freshwater organisms represent a highly overlooked trait and such trait recordings might provide relevant non-invasive tools to monitor the complexity and changes in aquatic communities. In a literature survey, Desjonquères (2016) showed that at least 271 freshwater species amongst French aquatic fauna (89% insects, but also fish and crustaceans) produce sounds. Using continuous underwater recordings with hydrophones, it was shown that the acoustic diversity of ponds and floodplain water bodies reflects the taxonomic diversity of aquatic communities (Desjonquères et al. 2018). Similarly, sound production by benthic invertebrates in the bay of Brest (France) was used to describe the soundscape and assess the ecological status of maerl beds (Coquereau et al. 2016).

One of the main caveats of imaging methods for FTBAs is that imaging tools have a low resolution below a certain size (most of these tools are of limited accuracy below a size limit of 200 µm for zooplankton, and 30-40 µm for phytoplankton, see Table 3), and may not allow for a reliable analysis of smaller size fractions, often associated with detrital matter or particles with a lack of discernible morphological differences. This limit is especially true for organisms without hard structures such as naked dinoflagellates or aloricate ciliates. However, imaging and acoustic methods generate high frequency and automated datasets at large spatial scales, with some of them recorded by inter-calibrated instruments, which allow for their comparison and combination in space and time (e.g. UVP for marine plankton; Table 3). These data are also suitable for the validation of trait-based marine ecosystem models (Kiørboe et al. 2018) and new ecological questions have been addressed by combining both recent imaging techniques and FTBAs (Schmid et al. 2018). New opportunities using imaging and acoustics include the evaluation of feeding behaviors and network associations (Choy et al. 2017), filtration rates and carbon fluxes (Katija et al. 2017) and migration patterns of zooplankton (Benoit-Bird and Lawson 2016).

Because the number of images stored on acoustic and imaging systems is limited, and even short deployment times lead to considerable data volumes, the development of artificial intelligence (AI) techniques such as machine learning, deep learning recognition and classification has been a crucial tipping point in the extraction of traits from these large datasets (Villon et al. 2016; Maps et al. 2019). Bigger storage capacity, standardized learning sets for machine learning combined with the automatized pre-processing of data directly in autonomous sampling instruments are already under development and will be an asset for the future of functional traits quantification by imaging.

## 3.3. -Omics techniques for FTBAs

Another opportunity for automatic measurements of functional traits has emerged from the recent rise of high-throughput sequencing techniques (HTS, also called NGS, for Next Generation Sequencing, or "-omics" in the broader sense). These techniques provide fast and relatively cheap nucleic acid sequencing and have opened new perspectives for investigating the structure and functioning of aquatic communities, both in marine (Raes et al. 2011; Sunagawa et al. 2015; Mock et al. 2016) and freshwater systems (Chonova et al. 2019). Methods based on DNA or RNA sequencing can be used for large-scale studies of environmental samples, investigating water samples in which any nucleic acid that is present can theoretically be retrieved.

For FTBAs, the identification of targeted DNA sequences (or metabarcoding; Bucklin et al. 2011; Valentini et al. 2016) can be used as a first step for fast and automatic taxon recognition, prior to the attribution of traits to the respective taxa using trait databases (Figure 2C; Table 2). This was recently done to describe the biogeography of mixotrophic traits of marine protists at global scale (Faure et al. 2019), or to estimate the functional diversity of coastal protist communities (Ramond et al. 2019). In freshwater systems, metabarcoding of benthic diatoms was used to assess the water quality status of rivers (Vasselon et al. 2017) and metabarcoding was combined with text-mining or phylogenetic inference of ecological profiles and traits for biomonitoring (Keck et al. 2018; Compson et al. 2018). Yet, metabarcoding is inherently biased in multiple ways, such as its lack of quantitative link between the number of copies of barcodes (targeted DNA sequences) and the biomass or abundance distribution of organisms, the risk of gene amplification from dead material (not currently influencing ecosystem function), or the use of universal barcodes that may not be adapted to distinguish taxa for all lineages (e.g. Deiner et al. 2017). However, the main obstacle to using metabarcoding data for FTBAs is the low number of taxa for which barcodes have been documented (in addition to the low number of taxa for which trait information is available). This limitation precludes a full assessment of ecosystem structure from metabarcoding (e.g. de Vargas et al. 2015; Le Bescot et al. 2016). Thus, a strong effort remains to be made to supplement existing genomic databases with more taxonomically-referenced sequences and trait information to allow the metabarcoding-based monitoring of aquatic functional traits (e.g. Ramond et al. 2018; PR2: Guillou et al. 2013; EukRef: del Campo et al. 2018; Diat.barcode: Rimet et al. 2019).

Beyond metabarcoding, -omics approaches are of particular interest to identify or measure functional traits linked to metabolic pathways (e.g. photosynthesis, nitrification, diazotrophy, calcification, etc.), using either (meta-)genomic or (meta-)transcriptomic approaches (Figure 2C). When combined with databases like KEGG (Kanehisa and Goto 2000), which includes the genes (for genomics/transcriptomics), proteins (for proteomics) and metabolites (for metabolomics) implied in a specific pathway, -omics approaches open up the possibility of monitoring functional traits (defined at the individual level) across different levels of biological organisation (from organisms to communities). For example, approaches that report the expression level of genes, proteins and metabolites are increasingly used in ecotoxicology to assess functional traits (e.g. photosynthesis, chemical degradation) in response to stressor(s) *via* targeted approaches (e.g. q-PCR on pre-identified candidate genes, Pesce et al. 2013; Moisset et al. 2015). Although it is still very challenging to relate -omics data to functional traits (Stec et al. 2017), the identification of certain genes coding for particular metabolic or physiological traits (e.g. iron uptake, nitrogen fixation) may help to directly link ecosystem structure to ecosystem functions (Mock et al. 2016), while taking into account the majority of organisms that in fact cannot be classified based on their morphological characteristics (e.g. picophytoplankton), and/or cannot be captured by imaging methods due to their small size or behavior. For instance, using metagenomic data, Farrell et al. (2018) created a machine-learning algorithm that can predict values of 65 phenotypic traits with more than 90% accuracy, thus allowing the investigation of the functional profiles of 660 uncultured marine prokaryotes based only on their metagenomically-assembled genomes or MAGs (i.e. genomes putatively reconstructed from metagenomics data). This very promising method cannot yet be applied to eukaryotes, as relating genes to potential traits in eukaryotes remains much more challenging than for prokaryotes (Sunagawa et al. 2015; Salazar et al. 2019). However, transcriptomics techniques were successfully used to estimate putative traits for marine protists using sequence similarity network-based approaches (i.e. toxicity and symbiosis for dinoflagellates; Meng et al. 2018). For pluricellular organisms, many challenges remain for the application of such methods in FTBAs, especially because of the large size of their genomes and because reference genomes are lacking (hence, the function of their DNA or RNA remains unknown). Yet, the use of transcriptomics approaches seem promising for these organisms (e.g. Lenz et al. 2014; Blanco-Bercial and Maas 2018).

Substantial progress remains to be made before aquatic ecologists can fully exploit -omics information using a FTBA. This includes the design of new methods to estimate the quantitative aspects of -omics information, but also to decipher the large quantity of sequences that cannot be assigned to any taxon in an environmental sample, and to circumvent the low proportion of genomic functional annotation (especially for eukaryotes). However, ongoing and future -omics studies may allow skipping taxonomic assignation and even the identification of gene functions as an intermediary between ecosystem composition and function. Such studies would fully contribute to FTBAs of aquatic ecosystems by targeting the -omics signature of relevant functional traits (Mock et al. 2016; Stec et al. 2017).

Another application would be the use of -omics data to develop a new generation of trait- based models (Mock et al. 2016; Stec et al. 2017; Coles et al. 2017). Metatranscriptomic data could be used to identify physiological traits of phytoplankton, combined with a mechanistic model of the phytoplankton cell, and used to construct a trait-based global marine ecosystem model (Mock et al. 2016). Emergent communities of marine microbes (from bacteria to phytoplankton) have already been predicted by directly simulating their metagenomes and metatranscriptomes (Coles et al. 2017). In summary, the idea of improving ecosystem models using -omics is not new (Hood et al. 2006), but FTBAs could constitute the common framework needed for next-generation ecosystem modellers, observers, molecular biologists, and ecologists working in limnology and oceanography. This would advance our ecological understanding of aquatic ecosystems and the links between ecosystem structure, function and ecosystem services or bioindicators relevant for ecosystem monitoring and management.

Using either empirical studies, imaging/acoustics, or -omics, both quantitative and qualitative traits can be estimated. One advantage of qualitative traits is that they do not have to be measured using the same instruments, and can be more easily described across compartments and realms. For quantitative traits, metrics and indices, one challenge is to be able to compare trait-based functional diversity among studies. In the next section we will focus on such traits that can be shared between ecological compartments and we will describe new opportunities in aquatic ecology to highlight spatio-temporal patterns, study anthropogenic impacts and better describe trophic interactions between plankton species (Figure 3).

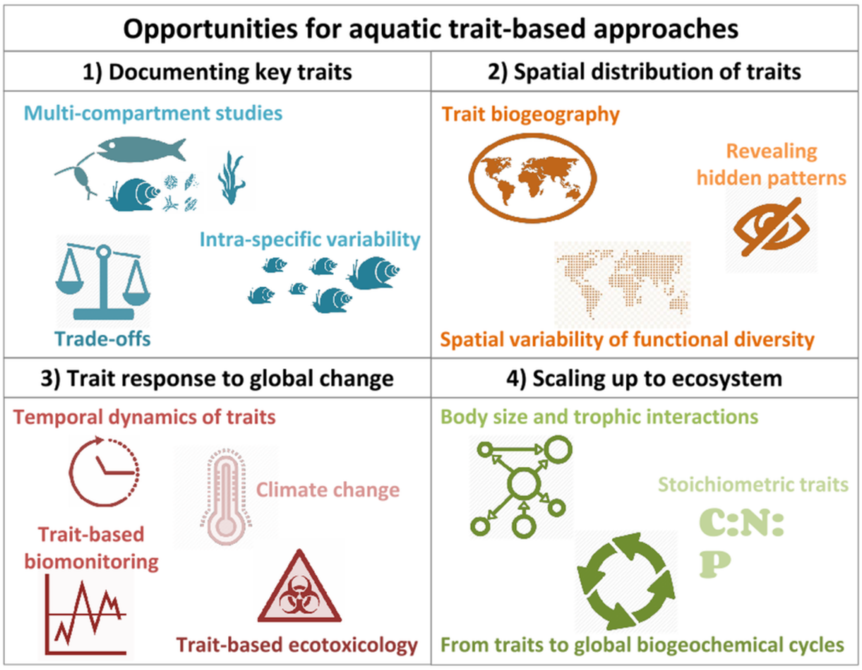


**Figure 3: Main opportunities for trait-based approaches in aquatic ecology.** These four opportunities are described in section 4.

# 4. Future opportunities for aquatic FTBAs

## 4.1. Going further towards a trait-based aquatic ecology by identifying key traits

### 4.1.1. Documenting key traits in multi-compartment studies

Given that the main power of FTBAs is to transcend both taxonomy and realms, trait-based ecological studies could result in a common set of ecological rules and theoretical principles that could be applied to multiple systems (e.g. benthos and pelagos, including plankton and fish). Following our framework, aquatic functional traits could be described at various spatio- temporal scales for both benthic and planktonic organisms, for instance taking benthic- pelagic coupling into account. To do so, we recommend a closer collaboration among aquatic ecologists, including process-oriented projects and comparative studies of freshwater and marine systems, focusing on the aquatic functional traits that we have identified and on their links to ecosystem functions (Figure 1). In addition to morphological traits that are relatively easy to identify and to measure (such as size, shape, cellularity, defences and colour), priority traits to be investigated should also include: 1) life history traits such as voltinism (number of generation or breeding per year), life cycle, life span, type of reproduction, and reproduction strategy, 2) physiological traits such as photosynthesis ability, diet, feeding mode, salinity preference, and trophic regime, and 3) behavioral traits like motility, dispersal potential, and substrate relation. Indeed, among all the traits identified in Figure 1, these traits are the most easily identified for any aquatic organisms, including both uni- and pluricellular organisms, and cover all ecological functions and all types of traits (Figure 3.1).

One recent example, that could lead future novelty in trait-based studies, is the use of morphological traits estimated from multiple images. Statistically-defined multidimensional morphological space can be synthesized from many individual images to generate a suite of interpretable continuous traits. Looking at the spatial distribution across the Arctic ecosystem of key traits, including body size, opacity, or appendage visibility, revealed meaningful information of copepods distribution and ecology in relation to ice-coverage (Vilgrain et al. under review). Such statistical approaches using these continuous traits can easily be applied to multi-compartment studies, (for example using transparency to describe gelatinous ecological patterns).

### 4.1.2. Documenting the trade-offs between key traits

Multi-compartmental studies that aggregate effects across species and trophic levels, hence taking into account the network structure of a community or the food-web structure of an ecosystem, would also enable a better understanding and quantification of the trade-offs occurring between two or multiple traits. Trade-offs, which result from the inherent metabolic, energetic or behavioral costs associated with each expressed trait, provide the fundamental basis to understand species coexistence and the trait composition of communities (Ehrlich et al. 2017). In particular, the competition-colonization trade-off is a major mechanism for biodiversity maintenance (Tilman 1994; Muthukrishnan et al. 2020; Ehrlich et al. 2020). Strong competitors able to exclude other species in any given habitat are often slow dispersers. In contrast, poor competitors are often strong colonizers, able to easily disperse and find unoccupied niches. A trade-off between resource acquisition and survival (or predation vulnerability) was reported for zooplankton: organisms that feed using feeding currents, increase their risk of being detected by predators that are sensitive to flow disturbances (Kiørboe and Hirst 2014). Unexpected trade-offs can often explain the relative mismatch between expected and observed individual traits in aquatic communities along gradients of anthropogenic pressure, complexifying the trait-based diagnostic of water bodies (Resh et al. 1994; Mondy and Usseglio-Polatera 2014; Desrosiers et al. 2019). Indeed, the success of a species in adverse conditions might be due to a particularly effective adaptation without the need for further adaptive traits. Moreover, investing in a given adaptation can leave fewer resources available for the investment in another adaptation. Species of various lineages (e.g. different phyla in invertebrate assemblages) may also solve the same ecological constraint with different adaptations.

Trade-offs have been globally recognised as a central component of trait-based approaches in aquatic ecology (Resh et al. 1994; Kremer et al. 2017) especially in plankton ecology (Litchman et al. 2007, 2013, 2015; Litchman and Klausmeier 2008; Hébert et al. 2017; Kiørboe et al. 2018; Ehrlich et al. 2020). In benthic studies, there has been a clear lack of work that considers simultaneously several traits relative to what has been done in studies on marine plankton (e.g. Litchman et al. 2013) and in freshwater ecology (Verberk et al. 2008). As a case in point, the term trade-off is not mentioned in the recent review on benthic traits by Degen et al. (2018). More studies are needed to explore trade-offs among traits across compartments and realms in order to identify the rules governing the links between traits, trade-offs, community structure and function. To accomplish this, researchers will have to put effort on measuring multiple traits, focusing on those related to resource acquisition, growth, storage and predation avoidance (i.e. directly related to fitness) on a variety of taxa within the same habitat. Comparison of how such relationships that trade-off (i.e. negatively related) change under different abiotic or biotic conditions will allow determination of how flexible such trade-offs are as ecological conditions change. Recently, the shape of the trade-off curve, representing the boundary of the set of feasible trait combinations, has been described as explaining traits of co-existing species and changes in trait values along environmental gradients (Ehrlich et al. 2017, 2020). Convex trade-offs would facilitate the coexistence of specialized species with extreme trait values while concave trade-offs would promote species with intermediate trait values.

To further explore trait relationships, aquatic ecologists may be inspired by what has been done in terrestrial plant ecology: the identification of so-called trait syndromes. Trait syndromes are relationships between traits that are defined by fundamental trade-offs amongst taxa that determine their ecological roles in ecosystems. The classic example in plant ecology is the "leaf economics spectrum" that characterizes taxa according to the speed at which they are able to take up nutrients and invest in leaf biomass (Wright et al. 2004). In this vein, some work was done with aquatic organisms by considering trade-offs amongst lotic insects (e.g. Poff et al. 2006), fishes (e.g. Winemiller et al. 2015) and phytoplankton (e.g. Edwards et al. 2013a). By considering trait syndromes, FTBAs are likely to better predict competitive outcomes as well as distributions of traits across environmental gradients. We thus encourage the aquatic ecology community to engage with the vast array of accessible trait databases provided in Table 2 and to take the next steps to characterize trait syndromes across the different groups of aquatic organisms.

### 4.1.3. Documenting the variability of key traits

Finally, more attention should be given to document the variability of all key traits at all organisational levels, i.e. at the community scale, between individuals in a given population (i.e. intra-specific variability; Raffard et al. 2019), but also for one individual throughout its lifespan (i.e. ontogenic variability; e.g. Zhao et al. 2014). Indeed, with the exception of a few studies (e.g. Maps et al. 2014b; Banas and Campbell 2016), intra-specific variability of traits is rarely taken into account, mainly because of a lack of empirical information on this variability. For example, the ability to engage fully in autotrophy or to add in heterotrophic feeding is a characteristic of mixotrophic phytoplankton taxa. By characterizing the conditions under which one or the other condition is utilized by a taxon, we can begin to characterize intra-specific variability. Therefore, the question of the scale of variation of functional traits, both at community and population scales, and its impact on ecosystem structure and functioning should be further explored, especially with the use of new methodological development to measure traits (see section 3). Trait-based models could also be used (see review on trait-based modeling in Kiørboe et al. 2018) to quantify the impact of environmental changes on the intra- and inter-specific variability of functional traits (e.g. lipid content and size of copepods, Renaud et al. 2018), and to assess the variation of peculiar traits along environmental gradients (Edwards et al. 2012).

Identifying key traits common in limnology and oceanography and their trade-offs, syndromes, and variability, will allow aquatic ecologists to better address central ecological questions, including understanding: 1) the spatial patterns of functional diversity and its drivers, 2) the effects of environmental and anthropogenic pressures on ecosystem structure and functioning, and 3) the interactions among organisms and associated food web organisation and dynamics. For each of these main opportunities, we will briefly describe what has been done to date and then identify potential ways to advance the field of aquatic ecology using FTBAs.

## 4.2. New opportunities emerging from the study of the spatial distribution of aquatic traits

### 4.2.1. The description of aquatic trait biogeography

To date, trait biogeography has been studied for a few compartments in marine ecosystems, such as marine plankton (Barton et al. 2013) including: bacterioplankton (Brown et al. 2014), zooplankton (Prowe et al. 2019), copepods (Brun et al. 2016b; Record et al. 2018), pelagic diatoms (Fragoso et al. 2018), estuarine fish (Henriques et al. 2017) and reef fish (e.g. Stuart- Smith et al. 2013). Large-scale studies of the trait biogeography of freshwater organisms are more rare (e.g. for amphibians see Trakimas et al. 2016). Aquatic trait biogeography studies covering multi-compartments, including plankton, fish and benthos, remain scarce and usually focus on one realm (e.g. marine organisms in Pecuchet et al. 2018). Similarly, aquatic trait biogeography studies covering different environments (marine and freshwater) are few and usually target only one compartment (e.g. phytoplankton in Thomas et al. 2016).

Based on the biogeography of some key traits (e.g. size, feeding strategy), aquatic ecologists can now relate functional traits to environmental conditions and identify general rules governing trait diversity distribution. For instance, the description of key traits of marine copepods (body size, offspring size and myelination) has highlighted latitudinal global patterns in trait biogeography. These patterns are in agreement with the temperature-size rule and have unveiled relationships between these traits and environmental conditions, such as water column transparency, but also biotic conditions, such as chlorophyll seasonality or phytoplankton size (Brun et al. 2016a). More recently, the study of taxonomic and functional diversity of fish communities between two different regions (Caribbean and Great Barrier Reef) and among three habitats (coral reef, seagrass, and mangrove) revealed that traits and functional groups varied among habitats, whereas taxonomic composition varied between regions (Hemingson and Bellwood 2018). Similar relationships should now be tested across ecosystems, geographical regions and trophic levels to verify whether these findings can be generalized to other aquatic organisms/ecosystems (Figure 3.2). The trait databases now available for many groups of aquatic organisms (see Table 2) should provide relevant information to explore this direction.

### 4.2.2. Using traits for revealing hidden community assembly rules at various spatial scales

Based on the spatial description of functional traits, hypotheses underlying community assembly rules can also be tested and community composition can be predicted (Cadotte et al. 2015). For example, the description of physiological and behavioral traits of dragonfly larvae in various lakes recently suggested that traits can drive species distribution and community assembly, through the direct impact of physiological and behavioral traits (activity rate and burst swimming speed) on foraging and predator avoidance behavior (Start et al. 2018). The traits considered in this study were driven by two biomolecules, the expression of which could predict more than 80% of the variation in dragonfly community structure across lakes, and which were involved in the interactions between the dragonfly larvae and their fish predators. Measurements made by new observational methods such as metabolomics, transcriptomics (see section 3.3) or *in situ* imaging (see section 3.2) would nicely complement presence-absence data by providing indication of the physiological state (e.g. healthy or stressed) of the individuals and hence help teasing apart the ideal and realized niche of organisms.

#### 4.2.3. From trait biogeography to spatial variation in functional diversity

Traits that are shared among compartments could also be used to describe the spatial variability of functional diversity (Petchey and Gaston 2006). Among the metrics that were proposed to measure functional diversity and its different dimensions (see section 2.4), aquatic ecologists have to adopt common metrics for comparative studies. Based on these common metrics, the spatial variation of the functional diversity of aquatic communities could be estimated across environments and in multi-compartment studies. For example, the functional diversity of macrophytes was described along a water depth gradient in a freshwater lake (Fu et al. 2014): future studies could cover similar environmental gradients in both freshwater and marine environments (e.g. rivers, estuaries, coasts, islands, etc.) and also include other organisms and higher trophic levels, both benthic and pelagic, to test whether the resulting spatial patterns of functional diversity can be generalized. The spatial distribution of traits and functional diversity could also be used to identify functional diversity hotspots and propose protected areas for a trait-based conservation. The diversity of functional traits is indeed correlated to both taxonomic diversity (e.g. Petchey and Gaston 2006) and the provision of ecosystem services. Conservation programs usually aim to protect both. Trait-based conservation could then rely on the rarity of species traits (or functional rarity) to identify conservation priorities (e.g. for coral reef fish in Grenié et al. 2018).

In addition to studying spatial patterns, traits can be used to study the temporal variation of functional diversity and how aquatic organisms respond to increasing global changes from anthropogenic pressures in the context of biomonitoring.

### 4.3. Trait response to global changes

#### 4.3.1. Temporal dynamics of traits and their response to climate change

FTBAs can be used to estimate the temporal response of aquatic organisms and ecosystems to environmental forcing (Figure 3.3). For example, functional traits have been shown to explain community structure and seasonal dynamics of marine phytoplankton

(Edwards et al. 2013b). It is also possible to combine classical data sets, and especially time-series of species abundance, with trait databases described at the species level (see section 3.1) to apply a FTBA to *in situ* observations and/or monitoring datasets previously collected. In such reanalyses, key traits could be targeted (see section 4.1) to compare their temporal changes, identify tipping points, and reveal trade-offs among traits. Hence, FTBAs offer novel perspectives for *a posteriori* (re)analysis of historical or long term monitoring data for the study of climate change and its impact on communities and ecosystem functioning (Pomerleau et al. 2015; Abonyi et al. 2018; Floury et al. 2018).

Marine ecologists have long since used FTBAs to study the impact of climate change on aquatic ecosystems (c.f. purple cluster in Supplementary Figure S1). For example, numerous marine studies explored the response of individual size to climate change (e.g. Schmidt et al. 2006; Genner et al. 2010; Finkel et al. 2010), showing that ocean warming is likely to cause a shift towards a larger contribution of smaller organisms to total biomass. Freshwater ecology could benefit from this experience, but currently, two main challenges can be pointed out for both freshwater and marine systems: the identification of links between functional traits and climate-change related variables (e.g. acidification and temperature increase in oceans, rivers and lakes; increase of freshwater shortage/scarcity in small streams) but also the deconvolution of the effects of multiple stressors on marine ecosystems (Mouillot et al. 2013). The joint pressure of multiple simultaneous stressors makes the identification of relationships between stressors and functional traits even more complicated, since interactions (e.g. synergism, antagonism, additivity, or inhibition) need to be taken into account. Under such conditions, monitoring functional traits of various types (Figure 1) may prove useful to disentangle these complex interactions.

### 4.3.2. Impact of climate change on functional diversity

The study of functional diversity may also reveal functional redundancies at the community scale, which may have implications for ecosystem responses to climate change. As a consequence, because functional groups gather together individuals belonging to different species, the loss of a given species with a particular function does not necessarily mean that such function will be lost at higher ecological scale. Indeed, some ecosystems were shown to be insensitive to species loss because multiple species share similar functional roles (mixotrophy, nutrient uptake or requirements), or some species only make a small contribution to the ecosystem processes (Hooper et al. 2005). Recently, it was suggested that climate change may have minor impacts on marine zooplankton functional diversity, due to strong functional redundancy (Benedetti et al. 2019). Conversely, climate change may have contrasting impacts on stream fishes (Buisson and Grenouillet 2009) or decrease their functional diversity (Buisson et al. 2013). By combining climate change scenario modeling with species distribution modeling and functional trait databases, the impact of climate change on the functional diversity of aquatic ecosystems can be assessed at broader scales and across biological compartments and ecosystem boundaries. For aquatic insects, such a combined modeling-FTBA study revealed the spatial patterns of vulnerability to climate change, which also opens opportunities for biomonitoring (Conti et al. 2014). However, limitations remain in the use of trait-based approaches for the assessment of the effects of multiple stressors in the context of climate change, as emphasized recently by (Hamilton et al. 2019) for freshwater invertebrates. These authors pointed out the need to better account for trait redundancy, to better define the appropriate spatial scales for trait applicability and to progress towards the quantification of categorical traits.

### 4.3.3. Trait-based biomonitoring

Traditionally, the ecological health or "good environmental status" of aquatic ecosystems has been assessed in terms of species composition or relative abundance/biomass of specific indicators, initially within the context of the European Water Framework Directive (WFD- 2000/60/CE). However, trait-based approaches offer new opportunities for the monitoring of aquatic ecosystems (Culp et al. 2011), since they can provide new tools that transcend taxonomical denomination, directly related to ecological functions, and exploit the traits available in open databases (Usseglio-Polatera et al. 2000; Baird et al. 2011, see also Table 2). To date, trait-based biomonitoring has been mainly applied to freshwater ecosystems (cf. the corresponding cluster in Supplementary Figure S1). Indeed, the links between traits of organisms and natural environmental variables (e.g. pH, flow velocity) or even anthropogenic pressures (e.g. nutrient or organic matter contamination) have been explored for decades by freshwater ecologists. More specifically, biomonitoring studies put a strong emphasis on the definition and the attribution of traits to taxa such as freshwater benthic macroinvertebrates (Usseglio-Polatera et al. 2000; Menezes et al. 2010), benthic diatoms (Van Dam et al. 1994; Passy 2007) and phytoplankton (Reynolds et al. 2002). As a consequence, the last versions of several biological indices for stream monitoring are mainly based on functional traits (e.g. I2M2 in Mondy et al. 2012, BDI in Coste et al. 2009). Within the context of lake monitoring, FTBAs mainly investigated the abundance and the seasonal variability of phytoplanktonic functional groups, as they are known to respond to nutrient concentrations (St-Gelais et al. 2017; Huang et al. 2018). Furthermore, the traits of macroinvertebrates (e.g. reproduction mode, size) and diatoms (e.g. auto-ecological guilds, life form) are now used in ecotoxicological and ecological models to identify the probability that chemical and/or land use related pressures impair natural communities (Mondy and Usseglio-Polatera 2013; Larras et al. 2017) even in multiple stressor scenarios. Combined with statistical modeling, traits also allow deriving stressor-specific models to assess environmental quality (e.g. focusing on invertebrates inhabiting large rivers, Desrosiers et al. 2019).

In comparison to routine monitoring activities in freshwater systems, the use of trait-based monitoring of marine ecosystem is still in its infancy, yet under active development for coastal environments, especially through the implementation of the European Marine Strategy Framework Directive (MSFD-2008/56/EC). FTBAs were proposed to monitor the effects of human activities on benthic communities (e.g. Xu et al. 2018), such as bottom trawling and dredging (Tillin et al. 2006), aggregate dredging (Bolam et al. 2016) or pollution (Oug et al. 2012). These approaches can also be used to estimate the success of management strategies, and to predict the effects of future disturbances (including climate change) for marine benthos, by defining critical limits beyond which ecosystem functioning is altered (Bremner 2008). However, functional traits are not yet included in biological indicators and institutional monitoring programs of marine ecosystems, in contrast to what is included in freshwater monitoring efforts. Assessments of functional diversity could inform different MSFD indicators (such as ‘biological diversity’, ‘habitat condition’, and ‘ecosystem structure’). To our knowledge, trait-based monitoring on marine pelagic ecosystems does not exist. Similar efforts should be extended to open ocean monitoring, for example by incorporating trait data in the reanalysis of long term observations such as the Continuous Plankton Recorder (CPR) time-series in the North Atlantic existing since the 1930s (Richardson et al. 2006).

Both the European Water Framework Directive and the European Marine Strategy Framework Directive require the estimation of the biological status of aquatic ecosystems from the evaluation of each compartment (benthic diatoms, macrophytes and macroalgae, benthic macroinvertebrates, phytoplankton, zooplankton, and fish) independently (e.g. Birk et al. 2012). Universal and standardized trait-based indices for biomonitoring should now cover all compartments (Borja et al. 2010). To this end, freshwater ecologists, who have a greater experience in multi-compartment monitoring (Lainé et al. 2014), could inspire marine ecologists, who are more used to focus on one compartment only (e.g. benthos, plankton, or fish).

### 4.3.4. Trait-based ecotoxicology

Besides the policy frameworks, FTBAs can also be used in ecotoxicology to highlight the impact of various stressors (e.g. organic synthetics products) on aquatic ecosystems (Baird and Van den Brink 2007). In fact, trait-based ecological risk assessments have been proposed as the new frontier in ecotoxicology (Baird et al. 2008; Rubach et al. 2011). In freshwater systems, diatom traits such as life form (e.g. colonial, solitary) or affinities to water quality have already been linked to pesticides contamination (Roubeix et al. 2011). The deformation of their silicified exoskeleton (teratology) has also been considered as a morphological trait that can inform on organisms exposure to heavy metals or pesticides (Lavoie et al. 2017). Similar studies have reported the response of freshwater benthic macroinvertebrate traits to environmental stressors (e.g. Statzner and Bêche 2010). For example, Peter et al. (2018) demonstrated that functional traits such as the feeding mode of zooplankton can be used as indicators for the level of metal pollution in freshwater invertebrates at the community level. For marine ecosystems, trait-based ecological risk assessments remain scarce (e.g. Neuparth et al. 2002 for marine amphipods). More recently, -omics techniques offer new ways for estimating physiological traits related to pollutant catabolism, for example, by detecting the activity of particular genes (e.g. mercury methylating genes in the ocean, Villar et al. 2019). The recent development of appropriate statistical tools will help to integrate omics data within the framework for ecological risk assessment (Larras et al. 2018). Similarly, imaging could allow to automatically identify changes in morphological traits as a response to environmental stressors (e.g. Maps et al. 2019). Altogether, the high-throughput acquisition of -omics data and images could allow the detection of new environmental stressors (e.g. Bowler et al. 2009; Reid and Whitehead 2016). Such state-of-the-art tools can contribute to the development of universal multi-compartment indices, that could provide estimates automatically and in almost real time. Ultimately, this could expand biomonitoring approaches beyond traditional taxonomically based assessments.

## 4.4. Scaling up from functional traits to community structure and ecosystem functions

Finally, FTBAs could be used to explore trophic interactions and food webs (Reiss et al. 2009). Indeed, several traits directly reflect trophic interactions (e.g. diet, size, stoichiometric traits) and can be used to better understand food web structure and dynamics (Figure 3.4). However, scaling-up from individual traits to populations, communities, and ecosystems requires taking trait variation at multiple intermediate organisation scales into account (e.g. population, meta-population, and community scales; Gibert et al. 2015). Rather than considering a collection of traits independently, one approach is to analyse how these traits influence or reveal the biotic interactions and trophic structure of aquatic communities. To do so, the numerous traits that are directly related to the way consumers interact with their prey (e.g. diet, feeding modes, motility, and perception of sounds) or the way prey interact with their predators (e.g. toxin production, bioluminescence, migration) are emphasized in the following subparts.

### 4.4.1. Body size as a major functional trait driving trophic interactions

The functional trait of body/cell size plays a particularly important role and is often referred to as “a master trait”. Size influences most of the ecological, physiological and behavioral functions of organisms due to metabolic laws, underpinning trophic position and interactions that are especially influenced by relative prey and predator sizes (Weitz and Levin 2006; Conley et al. 2018). Size or morphological characteristics can potentially be measured directly using imaging methods (see section 3.2), and could be used to infer trophic relationships. Predator traits (i.e., body/cell size and motility type) may also be responsible for the body-size architecture of natural food webs in freshwater, marine and terrestrial ecosystems (Brose et al. 2019). At large spatial scales, body size and prey selection were shown to be modified by climate change and therefore to strongly impact food webs and ecosystem functions in return (Hoegh-Guldberg and Bruno 2010; Sheridan and Bickford 2011). For example, ocean warming was associated with a reduction in copepod body size, which may impact upper trophic levels and ultimately fisheries (Beaugrand et al. 2010, but see also Renaud et al. 2018). More general laws between size, trophic interactions and environmental variables could be tested in future trait-based studies, especially by taking advantage of automatic morphological measurements (including but not restricted to size) through imaging. More specifically, direct observations of predator-prey interactions and associated traits could be performed by combining imaging (Choy et al. 2017; Ohman 2019) with gut content and/or faeces analysis based on taxonomic and/or -omics description, such tools being complementary and sometimes even more informative than the stable isotope methods that have been traditionally used so far (e.g. Majdi et al. 2018).

### 4.4.2. Including stoichiometric traits to study trophic interactions

In addition to body size, stoichiometric traits are highly promising for integrating FTBAs into food web models and to bridge the gap between community structure and ecosystem functioning (Meunier et al. 2017). Because all organisms are composed of the same major elements (e.g. C, N, and P), their balance not only reflects nutrient cycling in the ecosystem but also food web topologies. Quantifying stoichiometric traits across taxonomic and trophic groups allows the depiction of trophic interactions. In food web approaches, trophic position is associated with significant changes in C:N:P ratios, as well as altered isotope ratios due to selective uptake. As an example, heterotrophs are generally relatively less rich in carbon than autotrophs (Hessen et al. 2004; Persson et al. 2010). However, while stoichiometric composition and variation have been quantified for some species in different taxonomic groups (e.g. some plants, marine bacteria or plankton), there is still a lack of knowledge of the C:N:P ratios and their variations for numerous taxa, including higher-level consumers (e.g. Frost et al. 2002, 2006). Stoichiometric gradients may also inform on some specific traits such as growth rate, food preferences, nutrient acquisition and on some life history traits type such as fecundity, or even genome and cell size (see review in Carnicer et al. 2015). Indeed, stoichiometric ratios have the advantage of being directly related to organismal growth rates, which are central life history traits. The “growth rate hypothesis” demonstrates that rapidly growing organisms commonly have low biomass C:P and N:P ratios. This observation is explained by a high demand for P-rich ribosomal RNA, but also by the shorter lifespan of faster growing organisms, which prevents large investments into reserve structures (Elser et al. 1996, 2003). Consumers stoichiometry, in addition to metabolic characteristics, also gives important information on consumers driven nutrient recycling (Allen and Gillooly 2009). Better documenting the stoichiometric ratios of aquatic organisms in existing trait databases would help to identify their drivers and thus improve our understanding of the impact of stoichiometric traits on food web dynamics and ecosystem functioning.

### 4.4.3. From aquatic functional traits to global biogeochemical cycles

Finally, studying aquatic food webs following a FTBA should improve predictions of nutrient and carbon fluxes at the ecosystem scale (Vanni and McIntyre 2016). For example, trait- based models of food webs could be constructed to infer trophic interactions influencing ecosystem stocks and fluxes (Woodward et al. 2005). In addition to size and stoichiometry, several other functional traits could be taken into account in these models, such as predator foraging and prey vulnerability traits (Boukal 2014). To do so, one promising pathway is to increase the exploitation of trait databases. For example, global datasets of marine plankton abundances and biomass were recently coupled with a trait-based model used to predict dominant feeding strategies in pelagic ambush predators and to estimate the effects of these feeding traits on energy and biomass transfer efficiency (Prowe et al. 2019). For fish, diets and trophic strategies can be predicted from their functional traits (Albouy et al. 2011). This approach could be extended to other aquatic organisms. Scaling-up from individual traits to food web dynamics should ultimately contribute to better understand the response of aquatic ecosystems to environmental changes in terms of biogeochemical cycling, ultimately improving long-term prediction of ecosystem dynamics and feedback mechanisms to climate.

## 5. Conclusions

The main goal of FTBAs is to improve our understanding of the links between community structure, ecosystem function and ecosystem service provision. The main advantages of such approaches come from the definition of traits at the individual level. Indeed, this allows for the direct measurement of the functional traits of any organism without an additional step of taxonomic assignment that may be time-consuming. This can also provide access to universal ecological rules (transcending trophic levels and ecosystems). On the contrary, FTBAs would not be adapted to study population dynamics that require taxonomic description at the species level, nor to directly estimate bulk properties of the communities (which would require summing of individual-level information). For these reasons, the description and quantification of functional traits provide a common basis across diverse ecological fields, from ecophysiology to community and ecosystem ecology, via population and evolutionary biology. Yet, distinct questions and methods are often specific to each identified habitat (i.e. benthic and pelagic) or even to each biological compartment (i.e. invertebrates and diatoms for the freshwater benthic habitat). Here, we proposed functional trait-based pathways across multiple ecological components. As a first step, we: i) homogenized the terminology used in FTBAs and provided a common typology for aquatic functional traits that can be used across various aquatic systems and for multi-compartment studies, ii) listed the currently available databases dedicated to (aquatic) functional traits, iii) described classical and emerging methods for estimating traits of marine and freshwater organisms, and iv) highlighted some key traits that could be used for multi-compartment and trans-ecosystem studies. Establishing such a common ground among aquatic ecologists is required to further encourage and stimulate collaborative research across disciplines. The next step would be to create a common ontology dedicated to FTBAs, such as the Open Traits Network initiative (Gallagher et al. 2019), in order to improve the sharing of trait information in databases.

The recent methodologies we described offer new opportunities to study traits at various scales, from -omic sequences to whole-ecosystem approaches and biogeochemical cycles. Imaging, -omics and modeling tools are amongst the most promising emerging approaches to work with traits across the tree of life. We propose extending discussions within aquatic ecologists, including freshwater, marine, benthic and pelagic fields, to better share expertise in these tools, thereby improving our knowledge on potential and realized functional traits. With these methodologies, FTBAs provide promising foundations for the development of integrated frameworks that combine ecological theories with empirical knowledge across scales.

## References

Abonyi, A., Z. Horváth, and R. Ptacnik. 2018. Functional richness outperforms taxonomic richness in predicting ecosystem functioning in natural phytoplankton communities. Freshw. Biol. 63: 178–186. doi:10.1111/fwb.13051

Albouy, C., F. Guilhaumon, S. Villéger, and others. 2011. Predicting trophic guild and diet overlap from functional traits: statistics, opportunities and limitations for marine ecology. Mar. Ecol. Prog. Ser. 436: 17–28. doi:10.3354/meps09240

Allen, A. P., and J. F. Gillooly. 2009. Towards an integration of ecological stoichiometry and the metabolic theory of ecology to better understand nutrient cycling. Ecol. Lett. 12: 369–384. doi:10.1111/j.1461-0248.2009.01302.x

Althaus, F., N. Hill, R. Ferrari, and others. 2015. A Standardised Vocabulary for Identifying Benthic Biota and Substrata from Underwater Imagery: The CATAMI Classification Scheme J. Hewitt [ed.]. PLOS ONE 10: e0141039. doi:10.1371/journal.pone.0141039

Andersen, K. H., N. S. Jacobsen, and K. D. Farnsworth. 2016. The theoretical foundations for size spectrum models of fish communities J. Baum [ed.]. Can. J. Fish. Aquat. Sci. 73: 575–588. doi:10.1139/cjfas-2015-0230

Baird, D. J., C. J. O. Baker, R. B. Brua, M. Hajibabaei, K. McNicol, T. J. Pascoe, and D. de Zwart. 2011. Toward a knowledge infrastructure for traits-based ecological risk assessment. Integr. Environ. Assess. Manag. 7: 209–215. doi:10.1002/ieam.129

Baird, D. J., M. N. Rubach, and P. J. V. den Brinkt. 2008. Trait-based ecological risk assessment (TERA): The new frontier? Integr. Environ. Assess. Manag. 4: 2–3. doi:10.1897/IEAM_2007-063.1

Baird, D. J., and P. J. Van den Brink. 2007. Using biological traits to predict species sensitivity to toxic substances. Ecotoxicol. Environ. Saf. 67: 296–301. doi:10.1016/j.ecoenv.2006.07.001

Banas, N. S., and R. G. Campbell. 2016. Traits controlling body size in copepods: separating general constraints from species-specific strategies. Mar. Ecol. Prog. Ser. 558: 21– 33. doi:10.3354/meps11873

Barnett, A. J., K. Finlay, and B. E. Beisner. 2007. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. Freshw. Biol. 52: 796–813. doi:10.1111/j.1365-2427.2007.01733.x

Barton, A. D., A. J. Pershing, E. Litchman, N. R. Record, K. F. Edwards, Z. V. Finkel, T. Kiørboe, and B. A. Ward. 2013. The biogeography of marine plankton traits. Ecol. Lett. 16: 522–534. doi:10.1111/ele.12063

Beauchard, O., H. Veríssimo, A. M. Queirós, and P. M. J. Herman. 2017. The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. Ecol. Indic. 76: 81–96. doi:10.1016/j.ecolind.2017.01.011

Beaugrand, G., M. Edwards, and L. Legendre. 2010. Marine biodiversity, ecosystem functioning, and carbon cycles. Proc. Natl. Acad. Sci. 107: 10120–10124. doi:10.1073/pnas.0913855107

Bello, F. de, S. Lavorel, C. H. Albert, W. Thuiller, K. Grigulis, J. Dolezal, Š. Janeček, and J. Lepš. 2011. Quantifying the relevance of intraspecific trait variability for functional diversity. Methods Ecol. Evol. 2: 163–174. doi:10.1111/j.2041-210X.2010.00071.x

Benedetti, F. 2015. Mediterranean copepods' functional traits. PANGAEA. doi:https://doi.org/10.1594/PANGAEA.854331

Benedetti, F., S. Gasparini, and S.-D. Ayata. 2016. Identifying copepod functional groups from species functional traits. J. Plankton Res. 38: 159–166. doi:10.1093/plankt/fbv096

Benedetti, F., L. Jalabert, M. Sourisseau, and others. 2019. The Seasonal and Inter-Annual Fluctuations of Plankton Abundance and Community Structure in a North Atlantic Marine Protected Area. Front. Mar. Sci. 6. doi:10.3389/fmars.2019.00214

Benedetti, F., M. Vogt, D. Righetti, F. Guilhaumon, and S.-D. Ayata. 2018. Do functional groups of planktonic copepods differ in their ecological niches? J. Biogeogr. 45: 604–616. doi:10.1111/jbi.13166

Benoit-Bird, K. J., and G. L. Lawson. 2016. Ecological Insights from Pelagic Habitats Acquired Using Active Acoustic Techniques. Annu. Rev. Mar. Sci. 8: 463–490. doi:10.1146/annurev-marine-122414-034001

Beukhof, E., T. S. Dencker, M. L. D. Palomares, and A. Maureaud. 2019. A trait collection of marine fish species from North Atlantic and Northeast Pacific continental shelf seas.doi:https://doi.org/10.1594/PANGAEA.900866

Bi, H., S. Cook, H. Yu, M. C. Benfield, and E. D. Houde. 2012. Deployment of an imaging system to investigate fine-scale spatial distribution of early life stages of the ctenophore *Mnemiopsis leidyi* in Chesapeake Bay. J. Plankton Res. 35: 270–280.

Biard, T., L. Stemmann, M. Picheral, and others. 2016. In situ imaging reveals the biomass of giant protists in the global ocean. Nature 532: 504–507. doi:10.1038/nature17652

Birk, S., W. Bonne, A. Borja, and others. 2012. Three hundred ways to assess Europe's surface waters: An almost complete overview of biological methods to implement the Water Framework Directive. Ecol. Indic. 18: 31–41. doi:10.1016/j.ecolind.2011.10.009

Blanco-Bercial, L., and A. E. Maas. 2018. A transcriptomic resource for the northern krill *Meganyctiphanes norvegica* based on a short-term temperature exposure experiment. Mar. Genomics 38: 25–32. doi:10.1016/j.margen.2017.05.013

Bolam, S. G., P. S. O. McIlwaine, and C. Garcia. 2016. Application of biological traits to further our understanding of the impacts of dredged material disposal on benthic assemblages. Mar. Pollut. Bull. 105: 180–192. doi:10.1016/j.marpolbul.2016.02.031

Borgy, B., C. Violle, P. Choler, and others. 2017. Sensitivity of community-level trait–environment relationships to data representativeness: A test for functional biogeography. Glob. Ecol. Biogeogr. 26: 729–739. doi:10.1111/geb.12573

Borja, Á., M. Elliott, J. Carstensen, A.-S. Heiskanen, and W. van de Bund. 2010. Marine management – Towards an integrated implementation of the European Marine Strategy Framework and the Water Framework Directives. Mar. Pollut. Bull. 60: 2175–2186. doi:10.1016/j.marpolbul.2010.09.026

Boukal, D. S. 2014. Trait- and size-based descriptions of trophic links in freshwater food webs: current status and perspectives. J. Limnol. doi:10.4081/jlimnol.2014.826

Bowler, C., D. M. Karl, and R. R. Colwell. 2009. Microbial oceanography in a sea of opportunity. Nature 459: 180–184. doi:10.1038/nature08056

Bremner, J. 2008. Species' traits and ecological functioning in marine conservation and management. J. Exp. Mar. Biol. Ecol. 366: 37–47. doi:10.1016/j.jembe.2008.07.007

Bremner, J., S. I. Rogers, and C. L. J. Frid. 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol. Indic. 6: 609–622. doi:10.1016/j.ecolind.2005.08.026

Brose, U., P. Archambault, A. D. Barnes, and others. 2019. Predator traits determine food-web architecture across ecosystems. Nat. Ecol. Evol. 3: 919–927. doi:10.1038/s41559-019-0899-x

Brown, M. V., M. Ostrowski, J. J. Grzymski, and F. M. Lauro. 2014. A trait based perspective on the biogeography of common and abundant marine bacterioplankton clades. Mar. Genomics 15: 17–28. doi:10.1016/j.margen.2014.03.002

Brun, P., T. Kiørboe, P. Licandro, and M. R. Payne. 2016a. The predictive skill of species distribution models for plankton in a changing climate. Glob. Change Biol. 22: 3170–3181. doi:10.1111/gcb.13274

Brun, P., M. R. Payne, and T. Kiørboe. 2016b. Trait biogeography of marine copepods – an analysis across scales. Ecol. Lett. 19: 1403–1413. doi:10.1111/ele.12688

Brun, P., M. R. Payne, and T. Kiørboe. 2017. A trait database for marine copepods. Earth Syst. Sci. Data Discuss. 9: 99–113. doi:10.5194/essd-9-99-2017

Bucklin, A., D. Steinke, and L. Blanco-Bercial. 2011. DNA Barcoding of Marine Metazoa. Annu. Rev. Mar. Sci. 3: 471–508. doi:10.1146/annurev-marine-120308-080950

Buisson, L., and G. Grenouillet. 2009. Contrasted impacts of climate change on stream fish assemblages along an environmental gradient. Divers. Distrib. 15: 613–626. doi:10.1111/j.1472-4642.2009.00565.x

Buisson, L., G. Grenouillet, S. Villéger, J. Canal, and P. Laffaille. 2013. Toward a loss of functional diversity in stream fish assemblages under climate change. Glob. Change Biol. 19: 387–400. doi:10.1111/gcb.12056

Cadotte, M. W., C. A. Arnillas, S. W. Livingstone, and S.-L. E. Yasui. 2015. Predicting communities from functional traits. Trends Ecol. Evol. 30: 510–511. doi:10.1016/j.tree.2015.07.001

del Campo, J., M. Kolisko, V. Boscaro, and others. 2018. EukRef: Phylogenetic curation of ribosomal RNA to enhance understanding of eukaryotic diversity and distribution. PLOS Biol. 16: e2005849. doi:10.1371/journal.pbio.2005849

Carmona, C. P., F. de Bello, N. W. H. Mason, and J. Lepš. 2016. Traits Without Borders: Integrating Functional Diversity Across Scales. Trends Ecol. Evol. 31: 382–394. doi:10.1016/j.tree.2016.02.003

Carnicer, J., J. Sardans, C. Stefanescu, A. Ubach, M. Bartrons, D. Asensio, and J. Peñuelas. 2015. Global biodiversity, stoichiometry and ecosystem function responses to human-induced C–N–P imbalances. J. Plant Physiol. 172: 82–91. doi:10.1016/j.jplph.2014.07.022

Céréghino, R., V. D. Pillar, D. S. Srivastava, and others. 2018. Constraints on the functional trait space of aquatic invertebrates in bromeliads. Funct. Ecol. 32: 2435–2447. doi:10.1111/1365-2435.13141

Chapman, A. S. A., S. E. Beaulieu, A. Colaço, and others. 2019. sFDvent: A global trait database for deep-sea hydrothermal-vent fauna. Glob. Ecol. Biogeogr. 28: 1538–1551. doi:10.1111/geb.12975

Chevenet, Fran., S. Doleadec, and D. Chessel. 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshw. Biol. 31: 295–309. doi:10.1111/j.1365-2427.1994.tb01742.x

Chonova, T., R. Kurmayer, F. Rimet, J. Labanowski, V. Vasselon, F. Keck, P. Illmer, and A. Bouchez. 2019. Benthic Diatom Communities in an Alpine River Impacted by Waste Water Treatment Effluents as Revealed Using DNA Metabarcoding. Front. Microbiol. 10. doi:10.3389/fmicb.2019.00653

Choy, C. A., Haddock, S. H. D., and B. H. Robison. 2017. Deep pelagic food web structure as revealed by in situ feeding observations. Proc. R. Soc. B Biol. Sci. 284: 20172116. doi:10.1098/rspb.2017.2116

Coles, V. J., M. R. Stukel, M. T. Brooks, and others. 2017. Ocean biogeochemistry modeled with emergent trait-based genomics. Science 358: 1149–1154. doi:10.1126/science.aan5712

Compson, Z. G., W. A. Monk, C. J. Curry, and others. 2018. Chapter Two - Linking DNA Metabarcoding and Text Mining to Create Network-Based Biomonitoring Tools: A Case Study on Boreal Wetland Macroinvertebrate Communities, p. 33–74. *In* D.A. Bohan, A.J. Dumbrell, G. Woodward, and M. Jackson [eds.], Advances in Ecological Research. Academic Press.

Conley, K. R., F. Lombard, and K. R. Sutherland. 2018. Mammoth grazers on the ocean's minuteness: a review of selective feeding using mucous meshes. Proc. Biol. Sci. 285. doi:10.1098/rspb.2018.0056

Conti, L., A. Schmidt-Kloiber, G. Grenouillet, and W. Graf. 2014. A trait-based approach to assess the vulnerability of European aquatic insects to climate change. Hydrobiologia 721: 297–315. doi:10.1007/s10750-013-1690-7

Coquereau, L., J. Grall, L. Chauvaud, C. Gervaise, J. Clavier, A. Jolivet, and L. Di Iorio. 2016. Sound production and associated behaviours of benthic invertebrates from a coastal habitat in the north-east Atlantic. Mar. Biol. 163: 127. doi:10.1007/s00227-016-2902-2

Coste, M., S. Boutry, J. Tison-Rosebery, and F. Delmas. 2009. Improvements of the Biological Diatom Index (BDI): Description and efficiency of the new version (BDI-2006). Ecol. Indic. 9: 621–650. doi:10.1016/j.ecolind.2008.06.003

Costello, M. J., S. Claus, S. Dekeyzer, L. Vandepitte, É. Ó. Tuama, D. Lear, and H. Tyler-Walters. 2015. Biological and ecological traits of marine species. PeerJ 3: e1201. doi:10.7717/peerj.1201

Cowen, R. K., and C. M. Guigand. 2008. In situ ichthyoplankton imaging system (ISIIS): system design and preliminary results. Limnol. Oceanogr. Methods 6: 126–132. doi:10.4319/lom.2008.6.126

Culp, J. M., D. G. Armanini, M. J. Dunbar, J. M. Orlofske, N. L. Poff, A. I. Pollard, A. G. Yates, and G. C. Hose. 2011. Incorporating traits in aquatic biomonitoring to enhance causal diagnosis and prediction. Integr. Environ. Assess. Manag. 7: 187–197. doi:10.1002/ieam.128

Culverhouse, P. F., R. Williams, M. Benfield, P. R. Flood, A. F. Sell, M. G. Mazzocchi, I. Buttino, and M. Sieracki. 2006. Automatic image analysis of plankton: future perspectives. Mar. Ecol. Prog. Ser. 312: 297–309. doi:10.3354/meps312297

Degen, R., M. Aune, B. A. Bluhm, and others. 2018. Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans. Ecol. Indic. 91: 722–736. doi:https://doi.org/10.1016/j.ecolind.2018.04.050> , hdl:10013/epic.17e23bd4-199d-4ab9-8235-bc1818a1aec6

Degen, R., and S. Faulwetter. 2019. The Arctic Traits Database – a repository of Arctic benthic invertebrate traits. Earth Syst. Sci. Data 11: 301–322. doi:https://doi.org/10.5194/essd-11-301-2019

Deiner, K., H. M. Bik, E. Mächler, and others. 2017. Environmental DNA metabarcoding: Transforming how we survey animal and plant communities. Mol. Ecol. 26: 5872–5895. doi:10.1111/mec.14350

Des Roches, S., D. M. Post, N. E. Turley, J. K. Bailey, A. P. Hendry, M. T. Kinnison, J. A. Schweitzer, and E. P. Palkovacs. 2018. The ecological importance of intraspecific variation. Nat. Ecol. Evol. 2: 57–64. doi:10.1038/s41559-017-0402-5

Desjonquères, C. 2016. Ecologie et diversité acoustique des milieux aquatiques : exploration en milieux tempérés. thesis. Paris, Muséum national d'histoire naturelle.

Desjonquères, C., F. Rybak, E. Castella, D. Llusia, and J. Sueur. 2018. Acoustic communities reflects lateral hydrological connectivity in riverine floodplain similarly to macroinvertebrate communities. Sci. Rep. 8: 14387. doi:10.1038/s41598-018-31798-4

Desrosiers, M., P. Usseglio-Polatera, V. Archaimbault, F. Larras, G. Méthot, and B. Pinel-Alloul. 2019. Assessing anthropogenic pressure in the St. Lawrence River using traits of benthic macroinvertebrates. Sci. Total Environ. 649: 233–246. doi:10.1016/j.scitotenv.2018.08.267

Dubelaar, G. B. J., and P. L. Gerritzen. 2000. CytoBuoy: a step forward towards using flow cytometry in operational oceanography. Sci. Mar. 64: 255–265. doi:10.3989/scimar.2000.64n2255

Dubelaar, G. B. J., P. L. Gerritzen, A. E. R. Beeker, R. R. Jonker, and K. Tangen. 1999. Design and first results of CytoBuoy: A wireless flow cytometer for in situ analysis of marine and fresh waters. Cytometry 37: 247–254. doi:10.1002/(SICI)1097-0320(19991201)37:4<247::AID-CYTO1>3.0.CO;2-9

Durden, J. M., J. Y. Luo, H. Alexander, A. M. Flanagan, and L. Grossmann. 2017. Integrating "Big Data" into Aquatic Ecology: Challenges and Opportunities. Limnol. Oceanogr. Bull. 26: 101–108. doi:10.1002/lob.10213

Edwards, K. F., C. A. Klausmeier, and E. Litchman. 2013a. A Three-Way Trade-Off Maintains Functional Diversity under Variable Resource Supply. Am. Nat. 182: 786–800. doi:10.1086/673532

Edwards, K. F., E. Litchman, and C. A. Klausmeier. 2013b. Functional traits explain phytoplankton community structure and seasonal dynamics in a marine ecosystem. Ecol. Lett. 16: 56–63. doi:10.1111/ele.12012

Edwards, K. F., M. K. Thomas, C. A. Klausmeier, and E. Litchman. 2012. Allometric scaling and taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton. Limnol. Oceanogr. 57: 554–566. doi:10.4319/lo.2012.57.2.0554

Ehrlich, E., L. Becks, and U. Gaedke. 2017. Trait–fitness relationships determine how trade-off shapes affect species coexistence. Ecology 98: 3188–3198. doi:10.1002/ecy.2047

Ehrlich, E., N. J. Kath, and U. Gaedke. 2020. The shape of a defense-growth trade-off governs seasonal trait dynamics in natural phytoplankton. ISME J. 14: 1451–1462. doi:10.1038/s41396-020-0619-1

Elser, J. J., K. Acharya, M. Kyle, and others. 2003. Growth rate–stoichiometry couplings in diverse biota. Ecol. Lett. 6: 936–943. doi:10.1046/j.1461-0248.2003.00518.x

Elser, J. J., D. R. Dobberfuhl, N. A. MacKay, and J. H. Schampel. 1996. Organism Size, Life History, and N:P Stoichiometry. BioScience 46: 674–684. doi:10.2307/1312897

Farrell, F., O. S. Soyer, and C. Quince. 2018. Machine learning based prediction of functional capabilities in metagenomically assembled microbial genomes. bioRxiv 307157. doi:10.1101/307157

Faulwetter, S., V. Markantonatou, C. Pavloudi, and others. 2014. Polytraits: A database on biological traits of marine polychaetes. Biodivers. Data J. e1024. doi:10.3897/BDJ.2.e1024

Faure, E., F. Not, A.-S. Benoiston, K. Labadie, L. Bittner, and S.-D. Ayata. 2019. Mixotrophic protists display contrasted biogeographies in the global ocean. ISME J. 13: 1072. doi:10.1038/s41396-018-0340-5

Finkel, Z. V., J. Beardall, K. J. Flynn, A. Quigg, T. A. V. Rees, and J. A. Raven. 2010. Phytoplankton in a changing world: cell size and elemental stoichiometry. J. Plankton Res. 32: 119–137. doi:10.1093/plankt/fbp098

Finlay, K., B. E. Beisner, and A. J. D. Barnett. 2007. The use of the Laser Optical Plankton Counter to measure zooplankton size, abundance, and biomass in small freshwater lakes. Limnol. Oceanogr. Methods 5: 41–49. doi:10.4319/lom.2007.5.41

Floury, M., Y. Souchon, and K. V. Looy. 2018. Climatic and trophic processes drive long-term changes in functional diversity of freshwater invertebrate communities. Ecography 41: 209–218. doi:10.1111/ecog.02701

Fontana, S., J. Jokela, and F. Pomati. 2014. Opportunities and challenges in deriving phytoplankton diversity measures from individual trait-based data obtained by scanning flow-cytometry. Front. Microbiol. 5. doi:10.3389/fmicb.2014.00324

Forest, A., L. Stemmann, M. Picheral, L. Burdorf, D. Robert, L. Fortier, and M. Babin. 2012. Size distribution of particles and zooplankton across the shelf-basin system in southeast Beaufort Sea: combined results from an Underwater Vision Profiler and vertical net tows. Biogeosciences 9: 1301–1320. doi:10.5194/bg-9-1301-2012

Fragoso, G. M., A. J. Poulton, I. M. Yashayaev, E. J. H. Head, G. Johnsen, and D. A. Purdie. 2018. Diatom Biogeography From the Labrador Sea Revealed Through a Trait- Based Approach. Front. Mar. Sci. 5.

Frimpong, E., and P. Angermeier. 2010. Trait-based approaches in the analysis of stream fish communities. 73: 109–136.

Froese, R., and D. Pauly. 2019. FishBase. World Wide Web electronic publication. Frost, P. C., J. P. Benstead, W. F. Cross, H. Hillebrand, J. H. Larson, M. A. Xenopoulos, and

T. Yoshida. 2006. Threshold elemental ratios of carbon and phosphorus in aquatic consumers. Ecol. Lett. 9: 774–779. doi:10.1111/j.1461-0248.2006.00919.x

Frost, P. C., R. S. Stelzer, G. A. Lamberti, and J. Elser. 2002. Ecological stoichiometry of trophic interactions in the benthos: Understanding the role of C:N:P ratios in lentic and lotic habitats. J. North Am. Benthol. Soc. 21: 515–528.

Fu, H., J. Zhong, G. Yuan, L. Ni, P. Xie, and T. Cao. 2014. Functional traits composition predict macrophytes community productivity along a water depth gradient in a freshwater lake. Ecol. Evol. 4: 1516–1523. doi:10.1002/ece3.1022

Gallagher, R., D. S. Falster, B. Maitner, and others. 2019. The Open Traits Network: Using Open Science principles to accelerate trait-based science across the Tree of Life. preprint EcoEvoRxiv.

Genner, M. J., D. W. Sims, A. J. Southward, and others. 2010. Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. Glob. Change Biol. 16: 517–527. doi:10.1111/j.1365-2486.2009.02027.x

Gibert, J. P., A. I. Dell, J. P. DeLong, and S. Pawar. 2015. Chapter One - Scaling-up Trait Variation from Individuals to Ecosystems, p. 1–17. *In* S. Pawar, G. Woodward, and A.I. Dell [eds.], Advances in Ecological Research. Academic Press.

González-Rivero, M., O. Beijbom, A. Rodriguez-Ramirez, and others. 2016. Scaling up Ecological Measurements of Coral Reefs Using Semi-Automated Field Image Collection and Analysis. Remote Sens. 8: 30. doi:10.3390/rs8010030

Gorsky, G., M. D. Ohman, M. Picheral, and others. 2010. Digital zooplankton image analysis using the ZooScan integrated system. J. Plankton Res. 32: 285–303. doi:10.1093/plankt/fbp124

Grenié, M., D. Mouillot, S. Villéger, P. Denelle, C. M. Tucker, F. Munoz, and C. Violle. 2018. Functional rarity of coral reef fishes at the global scale: Hotspots and challenges for conservation. Biol. Conserv. 226: 288–299. doi:10.1016/j.biocon.2018.08.011

Griffiths, J. R., M. Kadin, F. J. A. Nascimento, and others. 2017. The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world. Glob. Change Biol. 23: 2179–2196. doi:10.1111/gcb.13642

Grizzetti, B., D. Lanzanova, C. Liquete, A. Reynaud, and A. C. Cardoso. 2016. Assessing water ecosystem services for water resource management. Environ. Sci. Policy 61: 194–203. doi:10.1016/j.envsci.2016.04.008

Guillou, L., D. Bachar, S. Audic, and others. 2013. The Protist Ribosomal Reference database (PR2): a catalog of unicellular eukaryote Small Sub-Unit rRNA sequences with curated taxonomy. Nucleic Acids Res. 41: D597–D604. doi:10.1093/nar/gks1160

Hamilton, A. T., R. B. Schäfer, M. I. Pyne, and others. 2019. Limitations of trait-based approaches for stressor assessment: The case of freshwater invertebrates and climate drivers. Glob. Change Biol. doi:10.1111/gcb.14846

Hébert, M.-P., B. E. Beisner, and R. Maranger. 2016. A meta-analysis of zooplankton functional traits influencing ecosystem function. Ecology 97: 1069–1080. doi:10.1890/15-1084.1

Hébert, M.-P., B. E. Beisner, and R. Maranger. 2017. Linking zooplankton communities to ecosystem functioning: toward an effect-trait framework. J. Plankton Res. 39: 3–12. doi:10.1093/plankt/fbw068

Hecky, R. E., and P. Kilham. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. Limnol. Oceanogr. 33: 796–822. doi:10.4319/lo.1988.33.4part2.0796

Heino, J., J. Soininen, J. Alahuhta, J. Lappalainen, and R. Virtanen. 2015. A comparative analysis of metacommunity types in the freshwater realm. Ecol. Evol. 5: 1525–1537. doi:10.1002/ece3.1460

Hemingson, C. R., and D. R. Bellwood. 2018. Biogeographic patterns in major marine realms: function not taxonomy unites fish assemblages in reef, seagrass and mangrove systems. Ecography 41: 174–182. doi:10.1111/ecog.03010

Henriques, S., F. Guilhaumon, S. Villéger, S. Amoroso, S. França, S. Pasquaud, H. N. Cabral, and R. P. Vasconcelos. 2017. Biogeographical region and environmental conditions drive functional traits of estuarine fish assemblages worldwide. Fish Fish. 18: 752–771. doi:10.1111/faf.12203

Herring, P. J. 1987. Systematic distribution of bioluminescence in living organisms. J. Biolumin. Chemilumin. 1: 147–163. doi:10.1002/bio.1170010303

Hessen, D. O., G. I. Ågren, T. R. Anderson, J. J. Elser, and P. C. de Ruiter. 2004. Carbon Sequestration in Ecosystems: The Role of Stoichiometry. Ecology 85: 1179–1192. doi:10.1890/02-0251

Hoegh-Guldberg, O., and J. F. Bruno. 2010. The Impact of Climate Change on the World's Marine Ecosystems. Science 328: 1523–1528. doi:10.1126/science.1189930

Hood, R. R., E. A. Laws, R. A. Armstrong, and others. 2006. Pelagic functional group modeling: Progress, challenges and prospects. Deep Sea Res. Part II Top. Stud. Oceanogr. 53: 459–512. doi:10.1016/j.dsr2.2006.01.025

Hooper, D. U., F. S. Chapin, J. J. Ewel, and others. 2016. Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. Ecol. Monogr. 3–35. doi:10.1890/04-0922@10.1002/(ISSN)1557-7015(CAT)VirtualIssue(VI)ECM

Huang, G., X. Wang, Y. Chen, L. Xu, and D. Xu. 2018. Seasonal succession of phytoplankton functional groups in a reservoir in central China.doi:info:doi/10.1127/fal/2018/1083

Jänes, H., J. Kotta, M. Pärnoja, T. P. Crowe, F. Rindi, and H. Orav-Kotta. 2017. Functional traits of marine macrophytes predict primary production E. Carrington [ed.]. Funct. Ecol. 31: 975–986. doi:10.1111/1365-2435.12798

de Juan, S., J. Hewitt, S. Thrush, and D. Freeman. 2015. Standardising the assessment of Functional Integrity in benthic ecosystems. J. Sea Res. 98: 33–41. doi:10.1016/j.seares.2014.06.001

Kanehisa, M., and S. Goto. 2000. KEGG: Kyoto Encyclopedia of Genes and Genomes. Nucleic Acids Res. 28: 27–30. doi:10.1093/nar/28.1.27

Katija, K., C. A. Choy, R. E. Sherlock, A. D. Sherman, and B. H. Robison. 2017. From the surface to the seafloor: How giant larvaceans transport microplastics into the deep sea. Sci. Adv. 3: e1700715. doi:10.1126/sciadv.1700715

Keck, F., V. Vasselon, F. Rimet, A. Bouchez, and M. Kahlert. 2018. Boosting DNA metabarcoding for biomonitoring with phylogenetic estimation of operational taxonomic units' ecological profiles. Mol. Ecol. Resour. 18: 1299–1309. doi:10.1111/1755-0998.12919

Kiørboe, T., and A. G. Hirst. 2014. Shifts in Mass Scaling of Respiration, Feeding, and Growth Rates across Life-Form Transitions in Marine Pelagic Organisms. Am. Nat. 183: E118–E130. doi:10.1086/675241

Kiørboe, T., A. Visser, and K. H. Andersen. 2018. A trait-based approach to ocean ecology. ICES J. Mar. Sci. 75: 1849–1863. doi:10.1093/icesjms/fsy090

Kolkwitz, R., and M. Marsson. 1909. Ökologie der tierischen Saprobien. Beiträge zur Lehre von der biologischen Gewässerbeurteilung. Int. Rev. Gesamten Hydrobiol. Hydrogr. 2: 126–152. doi:10.1002/iroh.19090020108

Kremer, C. T., A. K. Williams, M. Finiguerra, A. A. Fong, A. Kellerman, S. F. Paver, B. B. Tolar, and B. J. Toscano. 2017. Realizing the potential of trait-based aquatic ecology: New tools and collaborative approaches: Challenges of trait-based aquatic ecology. Limnol. Oceanogr. 62: 253–271. doi:10.1002/lno.10392

Lainé, M., S. Morin, and J. Tison-Rosebery. 2014. A Multicompartment Approach - Diatoms, Macrophytes, Benthic Macroinvertebrates and Fish - To Assess the Impact of Toxic Industrial Releases on a Small French River. PLoS ONE 9. doi:10.1371/journal.pone.0102358

Laliberté, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91: 299–305. doi:10.1890/08-2244.1

Larras, F., E. Billoir, V. Baillard, and others. 2018. DRomics: A Turnkey Tool to Support the Use of the Dose–Response Framework for Omics Data in Ecological Risk Assessment. Environ. Sci. Technol. 52: 14461–14468. doi:10.1021/acs.est.8b04752

Larras, F., R. Coulaud, E. Gautreau, E. Billoir, J. Rosebery, and P. Usseglio-Polatera. 2017. Assessing anthropogenic pressures on streams: A random forest approach based on benthic diatom communities. Sci. Total Environ. 586: 1101–1112. doi:10.1016/j.scitotenv.2017.02.096

Lavoie, I., P. B. Hamilton, S. Morin, and others. 2017. Diatom teratologies as biomarkers of contamination: Are all deformities ecologically meaningful? Ecol. Indic. 82: 539–550. doi:10.1016/j.ecolind.2017.06.048

Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16: 545–556. doi:10.1046/j.1365-2435.2002.00664.x

Le Bescot, N., F. Mahé, S. Audic, and others. 2016. Global patterns of pelagic dinoflagellate diversity across protist size classes unveiled by metabarcoding. Environ. Microbiol. 18: 609–626. doi:10.1111/1462-2920.13039

Legras, G., N. Loiseau, and J.-C. Gaertner. 2018. Functional richness: Overview of indices and underlying concepts. Acta Oecologica 87: 34–44. doi:10.1016/j.actao.2018.02.007

Legras, G., N. Loiseau, J.-C. Gaertner, J.-C. Poggiale, and N. Gaertner-Mazouni. 2019. Assessing functional diversity: the influence of the number of the functional traits. Theor. Ecol. doi:10.1007/s12080-019-00433-x

Leibold, M. A., and J. Norberg. 2004. Biodiversity in metacommunities: Plankton as complex adaptive systems? Limnol. Oceanogr. 49: 1278–1289. doi:10.4319/lo.2004.49.4_part_2.1278

Lenz, P. H., V. Roncalli, R. P. Hassett, L.-S. Wu, M. C. Cieslak, D. K. Hartline, and A. E. Christie. 2014. *De Novo* Assembly of a Transcriptome for *Calanus finmarchicus* (Crustacea, Copepoda) – The Dominant Zooplankter of the North Atlantic Ocean. PLOS ONE 9: e88589. doi:10.1371/journal.pone.0088589

Levine, J. M. 2016. A trail map for trait-based studies. Nature 529: 163–164. doi:10.1038/nature16862

Litchman, E., and C. A. Klausmeier. 2008. Trait-Based Community Ecology of Phytoplankton. Annu. Rev. Ecol. Evol. Syst. 39: 615–639. doi:10.1146/annurev.ecolsys.39.110707.173549

Litchman, E., C. A. Klausmeier, O. M. Schofield, and P. G. Falkowski. 2007. The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level. Ecol. Lett. 10: 1170–1181. doi:10.1111/j.1461-0248.2007.01117.x

Litchman, E., M. D. Ohman, and T. Kiørboe. 2013. Trait-based approaches to zooplankton communities. J. Plankton Res. 35: 473–484. doi:10.1093/plankt/fbt019

Litchman, E., P. de T. Pinto, K. F. Edwards, C. A. Klausmeier, C. T. Kremer, and M. K. Thomas. 2015. Global biogeochemical impacts of phytoplankton: a trait-based perspective. J. Ecol. 103: 1384–1396. doi:10.1111/1365-2745.12438

Lombard, F., E. Boss, A. M. Waite, and others. 2019. Globally Consistent Quantitative Observations of Planktonic Ecosystems. Front. Mar. Sci. 6. doi:10.3389/fmars.2019.00196

Loreau. 2010. Linking biodiversity and ecosystems: towards a unifying ecological theory. Philos. Trans. R. Soc. B Biol. Sci. 365: 49–60. doi:10.1098/rstb.2009.0155

Lorke, A., D. F. McGinnis, P. Spaak, and A. Wüest. 2004. Acoustic observations of zooplankton in lakes using a Doppler current profiler. Freshw. Biol. 49: 1280–1292. doi:10.1111/j.1365-2427.2004.01267.x

Lukács, B. A., A. E-Vojtkó, T. Erős, A. M. V, S. Szabó, and L. Götzenberger. 2019. Carbon forms, nutrients and water velocity filter hydrophyte and riverbank species differently: A trait-based study. J. Veg. Sci. 30: 471–484. doi:10.1111/jvs.12738

Lüning, J. 1992. Phenotypic plasticity of Daphnia pulex in the presence of invertebrate predators: morphological and life history responses. Oecologia 92: 383–390. doi:10.1007/BF00317464

Lürling, M. 2003. Phenotypic plasticity in the green algae *Desmodesmus* and *Scenedesmus* with special reference to the induction of defensive morphology. Ann. Limnol. - Int. J. Limnol. 39: 85–101. doi:10.1051/limn/2003014

Madin, J. S., K. D. Anderson, M. H. Andreasen, and others. 2016. The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Sci. Data 3: 160017. doi:10.1038/sdata.2016.17

Majdi, N., N. Hette-Tronquart, E. Auclair, and others. 2018. There's no harm in having too much: A comprehensive toolbox of methods in trophic ecology. Food Webs 17: e00100. doi:10.1016/j.fooweb.2018.e00100

Maps, F., J.-O. Irisson, and S.-D. Ayata. 2019. Book of abstract of the ARTIFACTZ Workshop. Proceedings of the ARTIFACTZ Workshop artificial intelligence for characterizing plankton traits from images. 12pp.

Maps, F., N. R. Record, and A. J. Pershing. 2014. A metabolic approach to dormancy in pelagic copepods helps explaining inter- and intra-specific variability in life-history strategies. J. Plankton Res. 36: 18–30. doi:10.1093/plankt/fbt100

Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanol. Acta I 493–509.

MARLIN. 2006. BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network.

Mason, N. W. H., F. de Bello, D. Mouillot, S. Pavoine, and S. Dray. 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. J. Veg. Sci. 24: 794–806. doi:10.1111/jvs.12013

Mason, N. W. H., D. Mouillot, W. G. Lee, and J. B. Wilson. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111: 112–118. doi:10.1111/j.0030-1299.2005.13886.x

Matabos, M., A. O. V. Bui, S. Mihály, J. Aguzzi, S. K. Juniper, and R. S. Ajayamohan. 2014. High-frequency study of epibenthic megafaunal community dynamics in Barkley Canyon: A multi-disciplinary approach using the NEPTUNE Canada network. J. Mar. Syst. 130: 56–68. doi:10.1016/j.jmarsys.2013.05.002

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21: 178–185. doi:10.1016/j.tree.2006.02.002

Menezes, S., D. J. Baird, and A. M. V. M. Soares. 2010. Beyond taxonomy: a review of macroinvertebrate trait-based community descriptors as tools for freshwater biomonitoring. J. Appl. Ecol. 47: 711–719. doi:10.1111/j.1365-2664.2010.01819.x

Meng, A., E. Corre, I. Probert, and others. 2018. Analysis of the genomic basis of functional diversity in dinoflagellates using a transcriptome-based sequence similarity network. Mol. Ecol. 27: 2365–2380. doi:10.1111/mec.14579

Mérillet, L., M. Mouchet, M. Robert, M. Salaün, L. Schuck, S. Vaz, and D. Kopp. 2018. Using underwater video to assess megabenthic community vulnerability to trawling in the Grande Vasière (Bay of Biscay). Environ. Conserv. 45: 163–172. doi:10.1017/S0376892917000480

Mermillod-Blondin, F., and R. Rosenberg. 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. Aquat. Sci. 68: 434–442. doi:10.1007/s00027-006-0858-x

Meunier, C. L., M. Boersma, R. El-Sabaawi, H. M. Halvorson, E. M. Herstoff, D. B. Van de Waal, R. J. Vogt, and E. Litchman. 2017. From Elements to Function: Toward Unifying Ecological Stoichiometry and Trait-Based Ecology. Front. Environ. Sci. 5. doi:10.3389/fenvs.2017.00018

Mock, T., S. J. Daines, R. Geider, S. Collins, M. Metodiev, A. J. Millar, V. Moulton, and T. M. Lenton. 2016. Bridging the gap between omics and earth system science to better understand how environmental change impacts marine microbes. Glob. Change Biol. 22: 61–75. doi:10.1111/gcb.12983

Moisset, S., S. K. Tiam, A. Feurtet-Mazel, S. Morin, F. Delmas, N. Mazzella, and P. Gonzalez. 2015. Genetic and physiological responses of three freshwater diatoms to realistic diuron exposures. Environ. Sci. Pollut. Res. 22: 4046–4055. doi:10.1007/s11356-014-3523-2

Mondy, C. P., and P. Usseglio-Polatera. 2013. Using conditional tree forests and life history traits to assess specific risks of stream degradation under multiple pressure scenario. Sci. Total Environ. 461–462: 750–760. doi:10.1016/j.scitotenv.2013.05.072

Mondy, C. P., and P. Usseglio-Polatera. 2014. Using fuzzy-coded traits to elucidate the non-random role of anthropogenic stress in the functional homogenisation of invertebrate assemblages. Freshw. Biol. 59: 584–600. doi:10.1111/fwb.12289

Mondy, C. P., B. Villeneuve, V. Archaimbault, and P. Usseglio-Polatera. 2012. A new macroinvertebrate-based multimetric index (I2M2) to evaluate ecological quality of French wadeable streams fulfilling the WFD demands: A taxonomical and trait approach. Ecol. Indic. 18: 452–467. doi:10.1016/j.ecolind.2011.12.013

Moretti, M., A. T. C. Dias, F. de Bello, and others. 2017. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Funct. Ecol. 31: 558–567. doi:10.1111/1365-2435.12776

Mouchet, M., F. Guilhaumon, S. Villéger, N. W. H. Mason, J.-A. Tomasini, and D. Mouillot. 2008. Towards a consensus for calculating dendrogram-based functional diversity indices. Oikos 117: 794–800. doi:10.1111/j.0030-1299.2008.16594.x

Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2013. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28: 167–177. doi:10.1016/j.tree.2012.10.004

Muthukrishnan, R., L. L. Sullivan, A. K. Shaw, and J. D. Forester. 2020. Trait plasticity alters the range of possible coexistence conditions in a competition–colonisation trade-off. Ecol. Lett. 23: 791–799. doi:10.1111/ele.13477

Naeem, S., and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecol. Lett. 6: 567–579. doi:10.1046/j.1461-0248.2003.00471.x

Neuparth, T., F. O. Costa, and M. H. Costa. 2002. Effects of Temperature and Salinity on Life History of the Marine Amphipod *Gammarus locusta*. Implications for Ecotoxicological Testing. Ecotoxicology 11: 61–73. doi:10.1023/A:1013797130740

Neury-Ormanni, J., J. Vedrenne, M. Wagner, G. Jan, and S. Morin. 2019. Micro-meiofauna morphofunctional traits linked to trophic activity. Hydrobiologia. doi:10.1007/s10750-019-04120-0

Nock, C. A., R. J. Vogt, and B. E. Beisner. 2016. Functional Traits, p. 1–8. *In* eLS. American Cancer Society.

O'Brien, T. D. 2014. COPEPOD: The Global Plankton Database. An overview of the 2014 database contents, processing methods, and access interface. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS-F/ST-37,.

O'Brien, W. J., D. Kettle, and H. Riessen. 1979. Helmets and Invisible Armor: Structures Reducing Predation from Tactile and Visual Planktivores. Ecology 60: 287–294. doi:10.2307/1937657

Ohman, M. D. 2019. A sea of tentacles: optically discernible traits resolved from planktonic organisms in situ. ICES J. Mar. Sci. 76: 1959–1972. doi:10.1093/icesjms/fsz184

Ohman, M. D., R. E. Davis, J. T. Sherman, K. R. Grindley, B. M. Whitmore, C. F. Nickels, and J. S. Ellen. 2019. Zooglider: An autonomous vehicle for optical and acoustic sensing of zooplankton. Limnol. Oceanogr. Methods 17: 69–86. doi:10.1002/lom3.10301

Olson, R. J., and H. M. Sosik. 2007. A submersible imaging-in-flow instrument to analyze nano-and microplankton: Imaging FlowCytobot. Limnol. Oceanogr. Methods 5: 195–203. doi:10.4319/lom.2007.5.195

Oug, E., A. Fleddum, B. Rygg, and F. Olsgard. 2012. Biological traits analyses in the study of pollution gradients and ecological functioning of marine soft bottom species assemblages in a fjord ecosystem. J. Exp. Mar. Biol. Ecol. 432–433: 94–105. doi:10.1016/j.jembe.2012.07.019

Pardo, L. M., and L. E. Johnson. 2005. Explaining variation in life-history traits: growth rate, size, and fecundity in a marine snail across an environmental gradient lacking predators. Mar. Ecol. Prog. Ser. 296: 229–239. doi:10.3354/meps296229

Parr, C. S., N. Wilson, P. Leary, and others. 2014. The Encyclopedia of Life v2: Providing Global Access to Knowledge About Life on Earth. Biodivers. Data J. 2: e1079. doi:10.3897/BDJ.2.e1079

Passy, S. I. 2007. Diatom ecological guilds display distinct and predictable behavior along nutrient and disturbance gradients in running waters. Aquat. Bot. 86: 171–178. doi:10.1016/j.aquabot.2006.09.018

Pecuchet, L., G. Reygondeau, W. W. L. Cheung, P. Licandro, P. D. van Denderen, M. R. Payne, and M. Lindegren. 2018. Spatial distribution of life-history traits and their response to environmental gradients across multiple marine taxa. Ecosphere 9: e02460. doi:10.1002/ecs2.2460

Persson, J., P. Fink, A. Goto, J. M. Hood, J. Jonas, and S. Kato. 2010. To be or not to be what you eat: regulation of stoichiometric homeostasis among autotrophs and heterotrophs. Oikos 119: 741–751. doi:10.1111/j.1600-0706.2009.18545.x

Pesce, S., J. Beguet, N. Rouard, M. Devers-Lamrani, and F. Martin-Laurent. 2013. Response of a diuron-degrading community to diuron exposure assessed by real- time quantitative PCR monitoring of phenylurea hydrolase A and B encoding genes. Appl. Microbiol. Biotechnol. 97: 1661–1668. doi:10.1007/s00253-012-4318-3

Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9: 741–758. doi:10.1111/j.1461-0248.2006.00924.x

Petchey, O. L., and K. J. Gaston. 2007. Dendrograms and measuring functional diversity. Oikos 116: 1422–1426. doi:10.1111/j.0030-1299.2007.15894.x

Peter, D. H., S. Sardy, J. Diaz Rodriguez, E. Castella, and V. I. Slaveykova. 2018. Modeling whole body trace metal concentrations in aquatic invertebrate communities: A trait-based approach. Environ. Pollut. 233: 419–428. doi:10.1016/j.envpol.2017.10.044

Picheral, M., S. Colin, and J. O. Irisson. 2017. EcoTaxa, a tool for the taxonomic classification of images.

Picheral, M., L. Guidi, L. Stemmann, D. M. Karl, G. Iddaoud, and G. Gorsky. 2010. The Underwater Vision Profiler 5: An advanced instrument for high spatial resolution studies of particle size spectra and zooplankton. Limnol. Oceanogr. Methods 8: 462–473. doi:10.4319/lom.2010.8.462

Poff, N. L., J. D. Olden, N. K. M. Vieira, D. S. Finn, M. P. Simmons, and B. C. Kondratieff. 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. J. North Am. Benthol. Soc. 25: 730–755. doi:10.1899/0887-3593(2006)025[0730:FTNONA]2.0.CO;2

Pomerleau, C., A. R. Sastri, and B. E. Beisner. 2015. Evaluation of functional trait diversity for marine zooplankton communities in the Northeast subarctic Pacific Ocean. J. Plankton Res. 37: 712–726. doi:10.1093/plankt/fbv045

Prowe, A. E. F., A. W. Visser, K. H. Andersen, S. Chiba, and T. Kiørboe. 2019. Biogeography of zooplankton feeding strategy. Limnol. Oceanogr. 64: 661–678. doi:10.1002/lno.11067

Raes, J., I. Letunic, T. Yamada, L. J. Jensen, and P. Bork. 2011. Toward molecular trait-based ecology through integration of biogeochemical, geographical and metagenomic data. Mol. Syst. Biol. 7: 473. doi:10.1038/msb.2011.6

Raffard, A., F. Santoul, J. Cucherousset, and S. Blanchet. 2019. The community and ecosystem consequences of intraspecific diversity: a meta-analysis. Biol. Rev. 94: 648–661. doi:10.1111/brv.12472

Ramond, P., R. Siano, and M. Sourisseau. 2018. Functional traits of marine protists.doi:10.17882/51662

Ramond, P., M. Sourisseau, N. Simon, and others. 2019. Coupling between taxonomic and functional diversity in protistan coastal communities: Functional diversity of marine protists. Environ. Microbiol. 21: 730–749. doi:10.1111/1462-2920.14537

Rao, C. R. 1982. Diversity and dissimilarity coefficients: A unified approach. Theor. Popul. Biol. 21: 24–43. doi:10.1016/0040-5809(82)90004-1

Record, N. R., R. Ji, F. Maps, Ø. Varpe, J. A. Runge, C. M. Petrik, and D. Johns. 2018. Copepod diapause and the biogeography of the marine lipidscape. J. Biogeogr. 45: 2238–2251. doi:10.1111/jbi.13414

Reid, N. M., and A. Whitehead. 2016. Functional genomics to assess biological responses to marine pollution at physiological and evolutionary timescales: toward a vision of predictive ecotoxicology. Brief. Funct. Genomics 15: 358–364. doi:10.1093/bfgp/elv060

Reiss, J., J. R. Bridle, J. M. Montoya, and G. Woodward. 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends Ecol. Evol. 24: 505–514. doi:10.1016/j.tree.2009.03.018

Renaud, P. E., M. Daase, N. S. Banas, and others. 2018. Pelagic food-webs in a changing Arctic: a trait-based perspective suggests a mode of resilience. ICES J. Mar. Sci. 75: 1871–1881. doi:10.1093/icesjms/fsy063

Resh, V. H., A. G. Hildrew, B. Statzner, and C. R. Townsend. 1994. Theoretical habitat templets, species traits, and species richness: a synthesis of long-term ecological research on the Upper Rhône River in the context of concurrently developed ecological theory. Freshw. Biol. 31: 539–554. doi:10.1111/j.1365-2427.1994.tb01756.x

Reu, B., R. Proulx, K. Bohn, J. G. Dyke, A. Kleidon, R. Pavlick, and S. Schmidtlein. 2011. The role of climate and plant functional trade-offs in shaping global biome and biodiversity patterns. Glob. Ecol. Biogeogr. 20: 570–581. doi:10.1111/j.1466-8238.2010.00621.x

Reynolds, C. S. 1988. Functional morphology and the adaptive strategies of freshwater phytoplankton. Growth Reprod. Strateg. Freshw. Phytoplankton 388–433.

Reynolds, C. S., V. Huszar, C. Kruk, L. Naselli-Flores, and S. Melo. 2002. Towards a functional classification of the freshwater phytoplankton. J. Plankton Res. 24: 417–428. doi:10.1093/plankt/24.5.417

Richardson, A. J., A. W. Walne, A. W. G. John, T. D. Jonas, J. A. Lindley, D. W. Sims, D. Stevens, and M. Witt. 2006. Using continuous plankton recorder data. Prog. Oceanogr. 68: 27–74. doi:10.1016/j.pocean.2005.09.011

Ricotta, C. 2005. A note on functional diversity measures. Basic Appl. Ecol. 6: 479–486. doi:10.1016/j.baae.2005.02.008

Rigolet, C., S. F. Dubois, and E. Thiébaut. 2014. Benthic control freaks: Effects of the tubiculous amphipod *Haploops nirae* on the specific diversity and functional structure of benthic communities. J. Sea Res. 85: 413–427. doi:10.1016/j.seares.2013.07.013

Riley, G. A. 1946. Factors controlling phytoplankton population on George’s Bank. J Mar Res 6: 54–73.

Rimet, F., and A. Bouchez. 2012. Life-forms, cell-sizes and ecological guilds of diatoms in European rivers. Knowl. Manag. Aquat. Ecosyst. 01. doi:10.1051/kmae/2012018

Rimet, F., and J.-C. Druart. 2018. A trait database for Phytoplankton of temperate lakes. Ann. Limnol. - Int. J. Limnol. 54: 18. doi:10.1051/limn/2018009

Rimet, F., E. Gusev, M. Kahlert, and others. 2019. Diat.barcode, an open-access barcode library for diatoms.doi:10.15454/TOMBYZ

Robuchon, M., S. Vranken, L. Vandepitte, S. Dekeyzer, R. Julliard, L. Le Gall, and O. De Clerck. 2015. Towards a seaweed trait database for European species. Proceedings of the 6th European Phycological Congress.

Roubeix, V., N. Mazzella, L. Schouler, V. Fauvelle, S. Morin, M. Coste, F. Delmas, and C. Margoum. 2011. Variations of periphytic diatom sensitivity to the herbicide diuron and relation to species distribution in a contamination gradient: implications for biomonitoring. J. Environ. Monit. 13: 1768–1774. doi:10.1039/C0EM00783H

Rubach, M. N., R. Ashauer, D. B. Buchwalter, H. D. Lange, M. Hamer, T. G. Preuss, K. Töpke, and S. J. Maund. 2011. Framework for traits-based assessment in ecotoxicology. Integr. Environ. Assess. Manag. 7: 172–186. doi:10.1002/ieam.105

Salazar, G., L. Paoli, A. Alberti, and others. 2019. Gene Expression Changes and Community Turnover Differentially Shape the Global Ocean Metatranscriptome. Cell 179: 1068-1083.e21. doi:10.1016/j.cell.2019.10.014

Salguero-Gómez, R., C. Violle, O. Gimenez, and D. Childs. 2018. Delivering the promises of trait-based approaches to the needs of demographic approaches, and vice versa. Funct. Ecol. 32: 1424–1435. doi:10.1111/1365-2435.13148

Sanford, E., and M. W. Kelly. 2011. Local Adaptation in Marine Invertebrates. Annu. Rev. Mar. Sci. 3: 509–535. doi:10.1146/annurev-marine-120709-142756

Schäfer, R. B., B. J. Kefford, L. Metzeling, and others. 2011. A trait database of stream invertebrates for the ecological risk assessment of single and combined effects of salinity and pesticides in South-East Australia. Sci. Total Environ. 409: 2055–2063. doi:10.1016/j.scitotenv.2011.01.053

Schleuter, D., M. Daufresne, F. Massol, and C. Argillier. 2010. A user's guide to functional diversity indices. Ecol. Monogr. 80: 469–484. doi:10.1890/08-2225.1

Schmera, D., J. Heino, J. Podani, T. Erős, and S. Dolédec. 2017. Functional diversity: a review of methodology and current knowledge in freshwater macroinvertebrate research. Hydrobiologia 787: 27–44. doi:10.1007/s10750-016-2974-5

Schmera, D., J. Podani, J. Heino, T. Erős, and N. L. Poff. 2015. A proposed unified terminology of species traits in stream ecology. Freshw. Sci. 34: 823–830. doi:10.1086/681623

Schmid, M. S., C. Aubry, J. Grigor, and L. Fortier. 2016. The LOKI underwater imaging system and an automatic identification model for the detection of zooplankton taxa in the Arctic Ocean. Methods Oceanogr. 15–16: 129–160. doi:10.1016/j.mio.2016.03.003

Schmid, M. S., F. Maps, and L. Fortier. 2018. Lipid load triggers migration to diapause in Arctic *Calanus* copepods—insights from underwater imaging. J. Plankton Res. 40: 311–325. doi:10.1093/plankt/fby012

Schmidt, D. N., D. Lazarus, J. R. Young, and M. Kucera. 2006. Biogeography and evolution of body size in marine plankton. Earth-Sci. Rev. 78: 239–266. doi:10.1016/j.earscirev.2006.05.004

Schmidt-Kloiber, A., and D. Hering. 2015. www.freshwaterecology.info – An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. Ecol. Indic. 53: 271–282. doi:10.1016/j.ecolind.2015.02.007

Schneider, F. D., M. Jochum, G. Le Provost, and others. 2018. Towards an Ecological Trait-data Standard. bioRxiv. doi:info:doi:10.1101/328302

Schulz, J., K. Barz, P. Ayon, A. Lüdtke, O. Zielinski, D. Mengedoht, and H.-J. Hirche. 2010. Imaging of plankton specimens with the lightframe on-sight keyspecies investigation (LOKI) system. J. Eur. Opt. Soc. - Rapid Publ. 5. doi:10.2971/jeos.2010.10017s

Sheridan, J. A., and D. Bickford. 2011. Shrinking body size as an ecological response to climate change. Nat. Clim. Change 1: 401–406. doi:10.1038/nclimate1259

Sieracki, C. K., M. E. Sieracki, and C. S. Yentsch. 1998. An imaging-in-flow system for automated analysis of marine microplankton. Mar. Ecol. Prog. Ser. 168: 285–296. doi:10.3354/meps168285

Sieracki, M. E., M. E. Sieracki, M. E. Sieracki, and others. 2010. Optical Plankton Imaging and Analysis Systems for Ocean Observation. *Proceedings of OceanObs'09: Sustained Ocean Observations and Information for Society*. Proceedings of the OceanObs'09: Sustained Ocean Observations and Information for Society. European Space Agency. 878–885.

Sournia, A. 1982. Form and Function in Marine Phytoplankton. Biol. Rev. 57: 347–394. doi:10.1111/j.1469-185X.1982.tb00702.x

Start, D., S. McCauley, and B. Gilbert. 2018. Physiology underlies the assembly of ecological communities. Proc. Natl. Acad. Sci. 115: 6016–6021. doi:10.1073/pnas.1802091115

Statzner, B., and L. A. Bêche. 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? Freshw. Biol. 55: 80–119. doi:10.1111/j.1365-2427.2009.02369.x

Stec, K. F., L. Caputi, P. L. Buttigieg, and others. 2017. Modelling plankton ecosystems in the meta-omics era. Are we ready? Mar. Genomics 32: 1–17. doi:10.1016/j.margen.2017.02.006

Stemmann, L., M. Youngbluth, K. Robert, and others. 2008. Global zoogeography of fragile macrozooplankton in the upper 100–1000 m inferred from the underwater video profiler. ICES J. Mar. Sci. 65: 433–442. doi:10.1093/icesjms/fsn010

St-Gelais, N. F., A. Jokela, and B. E. Beisner. 2017. Limited functional responses of plankton food webs in northern lakes following diamond mining. Can. J. Fish. Aquat. Sci. 75: 26–35. doi:10.1139/cjfas-2016-0418

Stuart-Smith, R. D., A. E. Bates, J. S. Lefcheck, and others. 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature 501: 539– 542. doi:10.1038/nature12529

Sunagawa, S., L. P. Coelho, S. Chaffron, and others. 2015. Structure and function of the global ocean microbiome. Science 348: 1261359. doi:10.1126/science.1261359

Swaffar, S. M., and W. J. O'Brien. 1996. Spines of Daphnia lumholtzi create feeding difficulties for juvenile bluegill sunfish (Lepomis macrochirus). J. Plankton Res. 18: 1055–1061. doi:10.1093/plankt/18.6.1055

Tapolczai, K., A. Bouchez, C. Stenger-Kovács, J. Padisák, and F. Rimet. 2016. Trait-based ecological classifications for benthic algae: review and perspectives. Hydrobiologia 776: 1–17. doi:10.1007/s10750-016-2736-4

Thomas, M. K., C. T. Kremer, and E. Litchman. 2016. Environment and evolutionary history determine the global biogeography of phytoplankton temperature traits. Glob. Ecol. Biogeogr. 25: 75–86. doi:10.1111/geb.12387

Tillin, H. M., J. G. Hiddink, S. Jennings, and M. J. Kaiser. 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Mar. Ecol. Prog. Ser. 318: 31–45. doi:10.3354/meps318031

Tilman, D. 1994. Competition and Biodiversity in Spatially Structured Habitats. Ecology 75: 2–16. doi:10.2307/1939377

Trakimas, G., R. J. Whittaker, and M. K. Borregaard. 2016. Do biological traits drive geographical patterns in European amphibians?: Traits of European amphibians. Glob. Ecol. Biogeogr. 25: 1228–1238. doi:10.1111/geb.12479

Troudet, J., P. Grandcolas, A. Blin, R. Vignes-Lebbe, and F. Legendre. 2017. Taxonomic bias in biodiversity data and societal preferences. Sci. Rep. 7: 9132. doi:10.1038/s41598-017-09084-6

Tyler, E. H. M., P. J. Somerfield, E. V. Berghe, J. Bremner, E. Jackson, O. Langmead, M. L. D. Palomares, and T. J. Webb. 2012. Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology: Biological knowledge of UK marine fauna. Glob. Ecol. Biogeogr. 21: 922–934. doi:10.1111/j.1466-8238.2011.00726.x

United Nations. 2015. Transforming our world: the 2030 Agenda for Sustainable Development. U.S. EPA. 2012. Freshwater Biological Traits Database (Final Report).

Usseglio-Polatera, P., M. Bournaud, P. Richoux, and H. Tachet. 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. Freshw. Biol. 43: 175–205. doi:10.1046/j.1365-2427.2000.00535.x

Usseglio-Polatera, P., M. Bournaud, P. Richoux, and H. Tachet. 2000. Biomonitoring through biological traits of benthic macroinvertebrates: how to use species trait databases? Hydrobiologia 422: 153–162. doi:10.1023/A:1017042921298

Usseglio-Polatera, P., Richoux, P., Bournaud, M., and Tachet, H. 2001. A functional classification of benthic macroinvertebrates based on biological and ecological traits: Application to river condition assessment and stream management. Arch. Für Hydrobiol. Suppl. Monogr. Beitr. 139: 53–83.

Valentini, A., P. Taberlet, C. Miaud, and others. 2016. Next-generation monitoring of aquatic biodiversity using environmental DNA metabarcoding. Mol. Ecol. 25: 929–942. doi:10.1111/mec.13428

Van Dam, H., A. Mertens, and J. Sinkeldam. 1994. A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. Netherland J. Aquat. Ecol. 28: 117–133. doi:10.1007/BF02334251

Vanni, M. J., and P. B. McIntyre. 2016. Predicting nutrient excretion of aquatic animals with metabolic ecology and ecological stoichiometry: a global synthesis. Ecology 97: 3460–3471. doi:10.1002/ecy.1582

de Vargas, C., S. Audic, N. Henry, and others. 2015. Eukaryotic plankton diversity in the sunlit ocean. Science 348: 1261605. doi:10.1126/science.1261605

Vasselon, V., F. Rimet, K. Tapolczai, and A. Bouchez. 2017. Assessing ecological status with diatoms DNA metabarcoding: Scaling-up on a WFD monitoring network (Mayotte island, France). Ecol. Indic. 82: 1–12. doi:10.1016/j.ecolind.2017.06.024

Verberk, W. C. E. P., H. Siepel, and H. Esselink. 2008. Applying life-history strategies for freshwater macroinvertebrates to lentic waters. Freshw. Biol. 53: 1739–1753. doi:10.1111/j.1365-2427.2008.02036.x

Vilgrain, L., F. Maps, M. Picheral, M. Babin, J.-O. Irisson, and S.-D. Ayata. under review. Trait-based approach on zooplankton in situ images reveals contrasted ecological patterns along ice melt dynamics. Limnol. Oceanogr. LO-20-0190.

Villar, E., L. Cabrol, and L.-E. Heimbürger-Boavida. 2019. Widespread microbial mercury methylation genes in the global ocean. bioRxiv 648329. doi:10.1101/648329

Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. Ecology 89: 2290–2301. doi:10.1890/07-1206.1

Villon, S., M. Chaumont, G. Subsol, S. Villéger, T. Claverie, and D. Mouillot. 2016. Coral Reef Fish Detection and Recognition in Underwater Videos by Supervised Machine

Learning: Comparison Between Deep Learning and HOG+SVM Methods. *Advanced Concepts for Intelligent Vision Systems*. Springer International Publishing. 160–171.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: intraspecific variability in community ecology. Trends Ecol. Evol. 27: 244–252. doi:10.1016/j.tree.2011.11.014

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos 116: 882–892. doi:10.1111/j.0030-1299.2007.15559.x

Violle, C., P. B. Reich, S. W. Pacala, B. J. Enquist, and J. Kattge. 2014. The emergence and promise of functional biogeography. Proc. Natl. Acad. Sci. 111: 13690–13696. doi:10.1073/pnas.1415442111

Weiss, K. C. B., and C. A. Ray. 2019. Unifying functional trait approaches to understand the assemblage of ecological communities: synthesizing taxonomic divides. Ecography 42: 2012–2020. doi:10.1111/ecog.04387

Weithoff, G., and B. E. Beisner. 2019. Measures and Approaches in Trait-Based Phytoplankton Community Ecology – From Freshwater to Marine Ecosystems. Front. Mar. Sci. 6. doi:10.3389/fmars.2019.00040

Weitz, J. S., and S. A. Levin. 2006. Size and scaling of predator–prey dynamics. Ecol. Lett. 9: 548–557. doi:10.1111/j.1461-0248.2006.00900.x

Willby, N. J., V. J. Abernethy, and B. O. L. Demars. 2000. Attribute-based classification of European hydrophytes and its relationship to habitat utilization. Freshw. Biol. 43: 43–74. doi:10.1046/j.1365-2427.2000.00523.x

Winemiller, K. O., D. B. Fitzgerald, L. M. Bower, and E. R. Pianka. 2015. Functional traits, convergent evolution, and periodic tables of niches. Ecol. Lett. 18: 737–751. doi:10.1111/ele.12462

Woodward, G., D. C. Speirs, and A. G. Hildrew. 2005. Quantification and Resolution of a Complex, Size-Structured Food Web, p. 85–135. *In* Advances in Ecological Research. Elsevier.

WoRMS Editorial Board. 2019. World Register of Marine Species. WoRMS Editor. Board 2019 World Regist. Mar. Species Available Httpwwwmarinespeciesorg VLIZ Accessed 2019-07-12 Doi1014284170.

Wright, I. J., P. B. Reich, M. Westoby, and others. 2004. The worldwide leaf economics spectrum. Nature 428: 821–827. doi:10.1038/nature02403

Xu, Y., T. Stoeck, D. Forster, Z. Ma, L. Zhang, and X. Fan. 2018. Environmental statusassessment using biological traits analyses and functional diversity indices of benthic ciliate communities. Mar. Pollut. Bull. 131: 646–654. doi:10.1016/j.marpolbul.2018.04.064

Zhao, T., S. Villéger, S. Lek, and J. Cucherousset. 2014. High intraspecific variability in the functional niche of a predator is associated with ontogenetic shift and individual specialization. Ecol. Evol. 4: 4649–4657. doi:10.1002/ece3.1260

## Acknowledgements

This paper emerged from informal discussions about trait-based ecology between aquatic ecologists, especially through visit of SDA at TAKUVIK, ISYEB and LIEC during her sabbatical periods. SM was funded by a postdoctoral grant from Sorbonne Université while SDA sabbaticals were funded by Sorbonne Université and CNRS. The authors declare no conflict of interests.

## Authors contribution statement

SM, SDA and ML proposed the initial idea and wrote the original draft. FL, AB and EF contributed to writing some subsections of the original draft. EF performed the mental map. All authors contributed to and reviewed the different portions and versions of the manuscript according to their respective scientific expertise.

## Supplemental information

Code and resource for the bibliographic network (Supplementary Figure S1) is available at: https://github.com/severine13/Biblio-Functional- traits. The mental map presenting the functional trait typology is available online at http://doi.org/10.5281/zenodo.3635898.

# Variations à long terme de la diversité fonctionnelle des communautés benthiques en Manche

## Résumé

Face au changement global, le maintien de la biodiversité et du bon fonctionnement des écosystèmes nécessite la mise en place d'outils de surveillance et de gestion adaptés. L'objectif de ce travail de thèse est d'analyser la variabilité spatio-temporelle des différentes facettes de la biodiversité (diversité spécifique, diversité fonctionnelle et diversité isotopique) et d'étudier leur complémentarité afin de décrire de manière la plus exhaustive l'évolution à long terme des communautés benthiques côtières en réponse à différentes pressions anthropiques. Pour cela, deux jeux de données de suivis à long terme de communautés benthiques de sables fins de la Manche ont été exploités: en Baie de Seine orientale et en Baie de Morlaix. L'étude de l'évolution temporelle de ces communautés a montré des dynamiques temporelles très contrastées. A la relative stabilité de la communauté de la Baie de Seine orientale s'oppose la forte variabilité de la communauté de la Baie de Morlaix marquée par deux changements abrupts. Des résultats partiellement congruents ont été observés entre les mesures de diversité spécifique et de diversité fonctionnelle ; si l'approche par les traits décrit explicitement les conséquences des changements de structure sur le fonctionnement global de l'écosystème, elle est sensible aux propriétés des indices. Par ailleurs, leur variabilité est sensible à la pondération des espèces par leurs densités ou leurs biomasses et donc à leur distribution au sein des communautés. L'utilisation d'indices de diversité isotopique a été testée afin d'offrir une autre approche de la variabilité fonctionnelle des communautés benthiques centrée sur les réseaux trophiques.

**Mots clés** : Macrofaune benthique ; Séries à long terme ; Diversité spécifique ; Diversité fonctionnelle ; Traits biologiques ; Diversité isotopique ; Manche

# Long-term variations in the functional diversity of benthic communities in the English Channel

## Abstract

Faced with global change, maintaining biodiversity and the proper functioning of ecosystems requires the implementation of appropriate monitoring and management tools. The aim of this thesis work is to analyse the spatio-temporal variability of the different facets of biodiversity (species diversity, functional diversity and isotopic diversity) and to study their complementarity in order to describe more exhaustively the long-term evolution of coastal benthic communities in response to different anthropogenic pressures. To this end, two datasets of long-term monitoring programs on fine sands benthic communities in the English Channel were used: one in the eastern Bay of Seine and one in the Bay of Morlaix. The study of the temporal changes of these communities showed very contrasted temporal dynamics. A relative stability of the community in the eastern Bay of Seine opposes the high variability of the community of the Bay of Morlaix marked by two abrupt changes. Partially congruent results between species diversity and functional diversity were reported; if the trait approach describes explicitly the consequences of structural changes on the global functioning of the ecosystem, it is sensitive to the properties of the indices. Furthermore, their values vary according to whether the species are weighted by densities or biomass, and then to their distribution within communities. The use of isotopic diversity indices has been tested to offer another approach to assess the functional variability on benthic communities centred on food webs.

**Keywords** : Benthic macrofauna ; Long-term series ; Species diversity ; Functional diversity ; Biological traits ; Isotopic diversity ; English Channel