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**Mise en lumière des profondeurs nocturnes :
Distribution, fonctionnement trophique et diversité
fonctionnelle de la communauté de poissons épi- à
bathypélagiques dans les canyons du golfe de Gascogne**

Liz Loutrage

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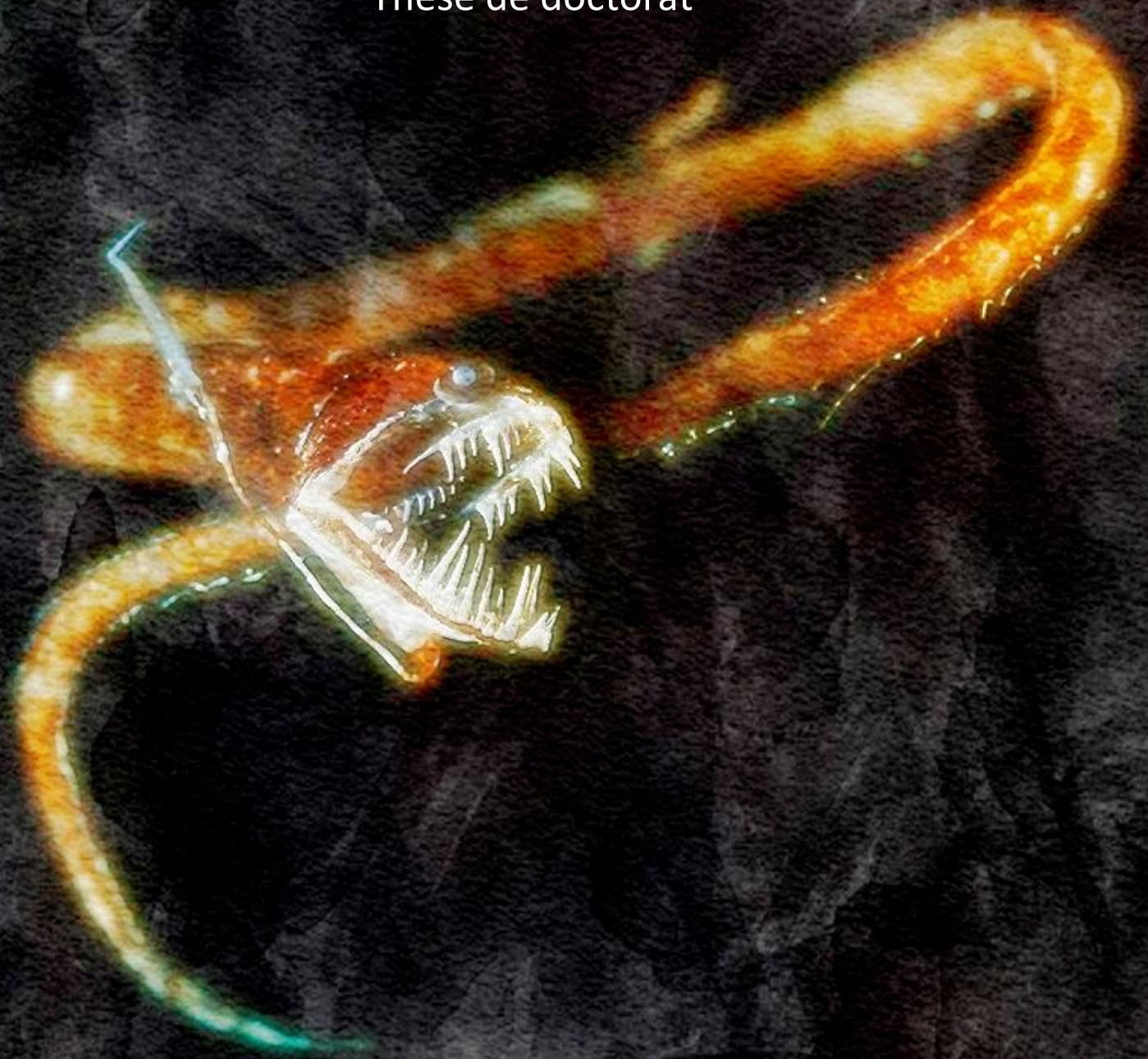
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Mise en lumière des profondeurs nocturnes :
Distribution, fonctionnement trophique et diversité fonctionnelle
de la communauté de poissons épi- à bathypélagiques dans les
canyons du golfe de Gascogne

Liz Loutrage
Thèse de doctorat



Sous la supervision de Jérôme Spitz et Anik Brind'Amour
La Rochelle Université - 2024

THÈSE

présentée par :

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Discipline : Biologie de l'environnement, des populations, écologie

Mise en lumière des profondeurs nocturnes : Distribution, fonctionnement trophique et diversité fonctionnelle de la communauté de poissons épi- à bathypélagiques dans les canyons du golfe de Gascogne

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Jeux de données

Spitz, J., **Loutrage, L.**, Iglesias, S., Chauvelon, T., Quero, J.-C., Bellail, R., Duhamel, E., Garren, F., Laffargue, P., Leaute, J.-P., Mahe, J.-C., Pawlowski, L., Poulard, J.-C., Salaun, M., Brind'Amour, A., 2023. Diversity and abundance of deep-pelagic fish on the Bay of Biscay slope (North-East Atlantic) from 56 trawls hauls between 2002 and 2019. <https://doi.org/10.1594/PANGAEA.959551>

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Rapports (projet SUMMER)

Spitz, J., Pérez-Jorge, S., Lebon, M., Gilbert, L., **Loutrage, L.**, Jonasdottir, J., Olivar, P., Chauvelon, T., Silva, M., Report on analysis of interactions among the mesopelagic community and with predators.

Olivar, P., Silva, M., Spitz, J., Jónasdóttir, S., Bernal, A., López-Pérez, C., Pérez-Jorge, S., Chauvelon, T., **Loutrage, L.** Database of new and existing diet/trophic level data of key mesopelagic species and predators and of nutritional quality of mesopelagic organisms.

Conférences

Présentation orale

Loutrage, L., Brind'Amour, A., Chauvelon, T., Spitz, J., Nocturnal distribution and trophic structure of meso to bathypelagic fish along depth gradients in the Bay of Biscay slope area. European Marine Biology Symposium, 2023. Reykjavik, Islande.

Présentations de poster

Loutrage, L., Spitz, J., Brind'Amour, A. Biodiversity of mesopelagic fish community on the slope of the Bay of Biscay. 16th DSBS Deep-Sea Biology Symposium, 2021. Brest, France.

Loutrage, L., Chauvelon, T., Brind'Amour, A., Spitz, J. La ségrégation trophique limite la compétition interspécifique au sein de la communauté de poissons pélagiques profonds du golfe de Gascogne. 15^{ème} colloque de l'Association Française d'Halieutique, 2022. Brest, France.

Formations et ateliers

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Avant-Propos

Ces travaux de thèse ont été entièrement financés par le projet de recherche H2020 SUMMER (*“Sustainable Management of Mesopelagic Resources”* ; convention de subvention ID : 817806). Ce projet européen, s'étendant sur une période de quatre ans (2020-2024), avait pour objectif principal d'établir un protocole pour estimer la biomasse des poissons mésopélagiques, quantifier les services écosystémiques fournis par la communauté mésopélagique (nourriture, régulation du climat et potentiel pour les composés bioactifs) et développer un outil d'aide à la décision pour mesurer les compromis entre les différents services. Parmi les différentes sections de ce projet cette thèse a contribué en partie à deux d'entre elles. Une partie des travaux de cette thèse s'inscrit dans la section n°2 « Biodiversité et Biomasse » qui avait les objectifs spécifiques suivants :

- Estimer la biomasse de la communauté mésopélagique (comprenant des poissons, des crustacés, des céphalopodes et des organismes gélatineux).
- Quantifier la biodiversité taxonomique et fonctionnelle de la communauté mésopélagique,
- Estimer la part des poissons dans la biomasse globale de la communauté mésopélagique,
- Fournir une estimation de la biomasse des organismes qui migrent et contribuent ainsi au transport descendant du carbone,
- Fournir une procédure opérationnelle standard de meilleure pratique pour l'estimation de la biomasse des poissons mésopélagiques.

La deuxième section à laquelle cette thèse s'inscrit est la n°3 « Structure du réseau trophique et résilience ». Les objectifs spécifiques étaient les suivants :

- Quantifier les interactions trophiques et compétitives entre les proies les organismes mésopélagiques et les prédateurs,
- Identifier les espèces/groupes fonctionnels clés et les interactions contrôlant le flux d'énergie et de biomasse au sein de l'écosystème pélagique verticalement intégré,
- Quantifier la réponse des réseaux trophiques pélagiques à l'exploitation mésopélagique et évaluer leur sensibilité,
- Prévoir les impacts de l'exploitation sur la résilience et les services des écosystèmes pélagiques.

Les résultats de cette thèse ont pu être intégrés à différents rapports produits lors du projet.

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Introduction

1. Quelles sont les règles d'assemblage qui façonnent la structure d'une communauté ?

Pourquoi observe-t-on une certaine diversité d'espèces au sein d'une communauté ? Pourquoi certaines espèces sont présentes dans une communauté et pas dans une autre ? Ces questions sur la compréhension des règles d'assemblage des espèces ont depuis longtemps été centrales dans les recherches en écologie (Diamond, 1975). Ces règles d'assemblage peuvent être définies comme toute contrainte limitant le nombre, l'abondance ou l'identité des espèces observées au sein d'un assemblage (De Bello et al., 2021). Ces règles peuvent influencer la composition des communautés via des facteurs stochastiques ou déterministes (Figure 0-1). Les facteurs stochastiques comprennent les perturbations imprévisibles, la dispersion et les événements aléatoires de naissance ou de mort (Chase and Myers, 2011). Les facteurs déterministes influençant l'assemblage des communautés comprennent la sélection imposée par l'environnement et les interactions entre les espèces (par exemple la compétition ou encore la facilitation) (Gause, 1932; Bruno et al., 2003). Ces différents processus s'appliquent à différentes échelles spatiales : globale (spéciation, extinction et migration), régionale (dispersion) et locale (conditions environnementales et interactions biotiques) (Götzenberger et al., 2012; Vellend, 2016).

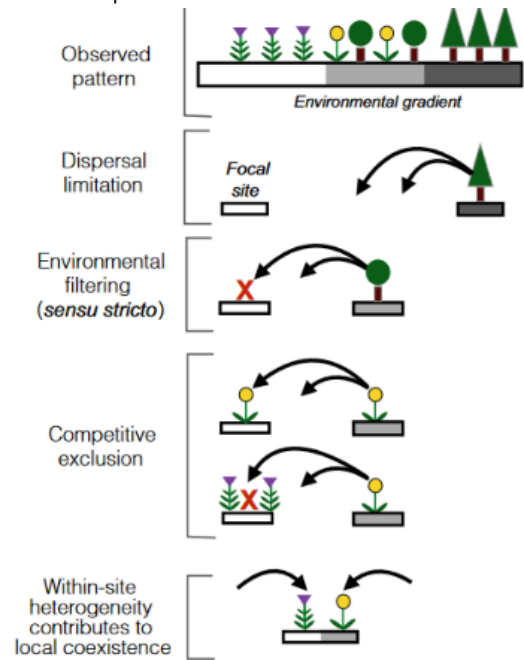


Figure 0-1. Le filtrage environnemental en relation avec d'autres processus d'assemblage de la communauté dans le contexte des changements d'abondance des espèces à travers un gradient environnemental. Extrait de Kraft et al., 2015.

En effet, si une espèce a la capacité de se disperser dans un site donné, sa persistance au sein de ce site va être dictée par sa capacité à s'adapter aux conditions environnementales locales. Certaines espèces non adaptées ne vont pas être présentes au sein de ce site, c'est le filtrage

environnemental (Kraft et al., 2015). Ce concept est à mettre en lien avec celui de la niche écologique d'une espèce, qui définit l'optimum où les conditions abiotiques vont lui permettre de survivre, grandir et se reproduire suivant un gradient environnemental. Des différences peuvent apparaître entre les espèces généralistes présentant une niche écologique relativement large et les espèces spécialistes présentant des niches écologiques plus restreintes. Différents types de gradients environnementaux peuvent être définis : les gradients en lien avec les ressources, les gradients directs qui ont un impact sur la physiologie des organismes (par exemple, la température) et enfin les gradients indirects tels que la profondeur ou l'altitude qui sont des approximations d'un ou plusieurs gradients directs ou de ressources (Kraft et al., 2015). De par l'importance que peuvent avoir ces gradients environnementaux dans les écosystèmes verticalement stratifiés tel que l'écosystème pélagique océanique, il est essentiel de les prendre en compte pour tenter d'appréhender la complexité de la niche écologique en trois dimensions des espèces dans ces milieux (Gámez and Harris, 2022).

Cependant, les conditions abiotiques expliquent souvent seulement une partie de la répartition des espèces au sein d'un assemblage donné. Les interactions biotiques, telles que la compétition, la facilitation ou le mutualisme, façonnent également la distribution des espèces (Gause, 1932; Chesson, 2000; Bruno et al., 2003; Bimler et al., 2018). Parmi ces interactions biotiques, la compétition a tout particulièrement retenu l'attention des écologues. L'effet de la compétition sur la composition en espèces a principalement été décrit par le principe de compétition exclusive. Premièrement développé par le modèle Lotka-Volterra, ce principe stipule que deux espèces entrant en compétition pour la même ressource ne peuvent pas se maintenir dans un système donné si la compétition interspécifique est plus forte que la compétition intraspécifique, engendrant l'exclusion de l'une des deux espèces (Lotka, 1925; Volterra, 1926; Gause, 1932). La quantification de la différence entre ces deux types de compétition est rendue possible par la comparaison de la compétitivité et de l'utilisation des ressources entre les espèces (Figure 0-2). Ainsi pour coexister dans un même

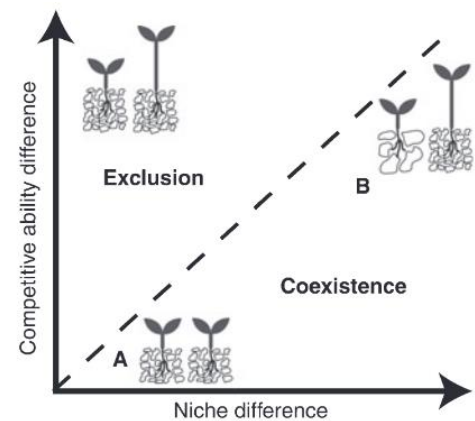


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environnement les espèces doivent soit avoir une capacité de compétitivité égale ou alors avoir une utilisation des ressources différente (Chesson, 2000; Mayfield and Levine, 2010). Cet aspect de limitation de la similarité des niches des espèces pour l'utilisation des ressources pointe l'importance de l'aspect trophique dans le façonnage de la composition des communautés (Hutchinson, 1959; Abrams, 1980).

Bien que les écologues aient essentiellement traité ces questions avec des espèces comme étant des unités statiques dans le temps et dans l'espace d'importants changements intraspécifiques peuvent ajouter de la complexité à la niche écologique réalisée des espèces. Ces déplacements de niche au niveau intraspécifique jouent un rôle important dans les interactions compétitives et la répartition des niches au sein des communautés (Woodward and Hildrew, 2002; Woodward et al., 2005). Ces changements, qui peuvent être notamment en lien avec l'ontogénie, peuvent induire des modifications dans l'utilisation des ressources et de l'habitat des espèces (Sánchez-Hernández et al., 2019). Ces différences marquées reflètent l'importance de la prise en compte de cette variabilité au niveau intraspécifique dans les règles d'assemblage des communautés.

L'applicabilité de ces concepts en écologie fondamentale représente désormais un enjeu crucial pour anticiper et prédire les effets sur les communautés des multiples pressions liées aux changements globaux et à l'augmentation des activités anthropiques. Ceci est essentiel pour élaborer des mesures de conservation pertinentes.

2. Les divisions du domaine pélagique océanique

2.1. Gradients verticaux

Le domaine pélagique océanique, c'est-à-dire la zone marine s'étendant au-delà du talus continental et au-dessus des plaines abyssales, constitue le plus grand biome de la planète. Ces écosystèmes océaniques sont caractérisés par des gradients environnementaux importants notamment verticaux. Ainsi, la division du domaine pélagique a premièrement été réalisée en lien avec la profondeur (gradient indirect) et ses covariables (gradients directs, Figure 0-3). Plus spécifiquement, les propriétés de pénétration de la lumière vont définir la division en différentes strates d'eaux (Angel, 2003; Robison, 2004; Sutton, 2013). La première zone, la zone épipélagique ou zone photique, est définie par la présence de lumière qui va permettre la production primaire phytoplanctonique. La frontière

inférieure de cette première couche se situe environ à 200 m de profondeur même si des variations spatio-temporelles peuvent la faire varier. Cette zone présente la plus grande variabilité environnementale en comparaison avec les couches plus profondes du fait des schémas de circulation de surface et de l'influence directe des changements de température, notamment saisonniers (Longhurst, 1995).

Plus en profondeur, lorsque moins de 1% de l'intensité lumineuse de surface est restante, la production primaire phytoplanctonique n'est plus possible et la zone mésopélagique, ou « zone crépusculaire », commence. La zone mésopélagique constitue le point de départ de l'océan profond. Il a été couramment admis que cette zone s'étend jusqu'à 1000 m de profondeur, traduisant principalement la profondeur où les espèces peuvent encore différencier les cycles jour-nuit. La zone mésopélagique est donc quatre fois plus large que la couche épipélagique. Cette zone est caractérisée par une forte thermocline et bien que les variabilités spatio-temporelles soient réduites, cette couche n'est pas homogène d'un point de vue environnemental en particulier à l'interface avec la couche épipélagique (Robinson et al., 2010; Sutton, 2013).

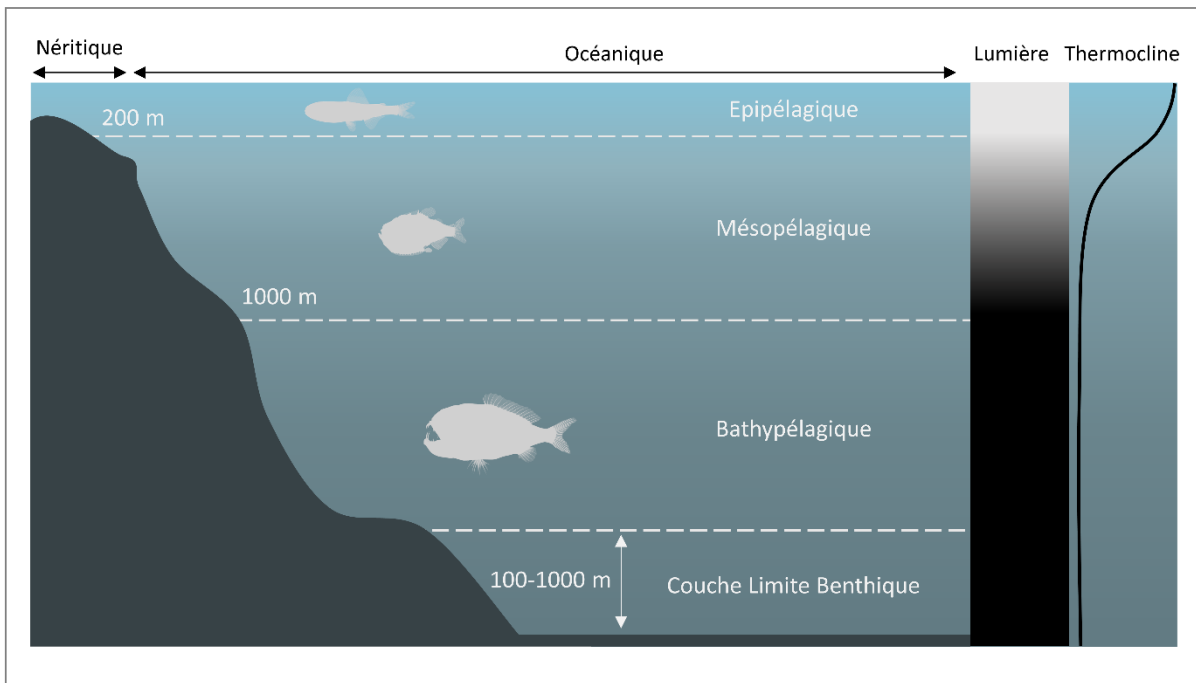


Figure 0-3. Division verticale de l'océan pélagique en plusieurs couches d'eau fonctionnelles. Adapté de Herring 2002.

La zone bathypélagique ou « zone de minuit », s'étend au-delà de 1000 m de profondeur et est principalement définie par l'absence totale de lumière, une pression hydrostatique élevée, et une

faible concentration en ressources alimentaires (Haedrich, 1996; Angel, 1997). Bien qu'il soit raisonnable de penser que les variabilités environnementales s'atténuent davantage dans cette zone, le manque de données à échelle globale ne permet pas de le confirmer pour tous les écosystèmes (par exemple, canyons du golfe de Gascogne, J. Spitz pers. comm. ; Sutton, 2013). La subdivision des couches plus profondes en couches abyssopélagique et hadopélagique n'est pas universellement admise et acceptée et elles sont souvent incluses dans la couche bathypélagique (Sutton, 2013).

Une dernière zone est définie cette fois par sa distance au fond, c'est la couche limite benthique. Au sein de cette couche les interactions physiques et biologiques avec le fond modifient la nature de la couche d'eau. D'un point de vue physique, la couche limite benthique est relativement homogène et s'étend entre 100 et 1000 m de distance avec le fond en fonction de la présence de mélanges turbulents (Weatherly and Kelley, 1985).

2.2. Gradients horizontaux et différences entre systèmes topographiques

A échelle spatiale équivalente, les gradients horizontaux en zone pélagique sont moins marqués que les verticaux (Herring, 2002; Angel, 2003; Sutton et al., 2008). A plus large échelle, des différences peuvent apparaître, mais elles s'estompent avec la profondeur (Vecchione et al., 2015). D'un point de vue de la productivité, des différences entre zones oligotrophes situées principalement dans les gyres et les zones à forte productivité sous influence terrestre comme les pentes continentales apparaissent. La modification des régimes de courant dans les zones à topographies abruptes telles que les monts-sous-marins, les pentes continentales et les rides médio-océaniques peuvent également induire des changements dans la répartition des ressources alimentaires et donc des espèces (Sutton, 2013). Ces zones peuvent devenir de réelles oasis de vie en comparaison avec les zones de pleine mer au-dessus des plaines abyssales (Ramirez-Llodra et al., 2010) (Figure 0-4). Par exemple, les canyons sous-marins qui incisent les pentes continentales, sont des structures topographiques particulièrement complexes qui modifient les régimes de courants et ont un rôle primordial dans le transport du carbone organique particulière du plateau vers les profondeurs (Borja et al., 2019; Lavin et al., 2004).

Il est important de noter que de par sa variabilité spatio-temporelle, ces divisions de l'écosystème pélagique profond doivent être appréhendées comme des limites dynamiques et des zones de transition et non comme des frontières fixes (Ramirez-Llodra et al., 2010; Vecchione et al., 2015; Sutton et al., 2017).

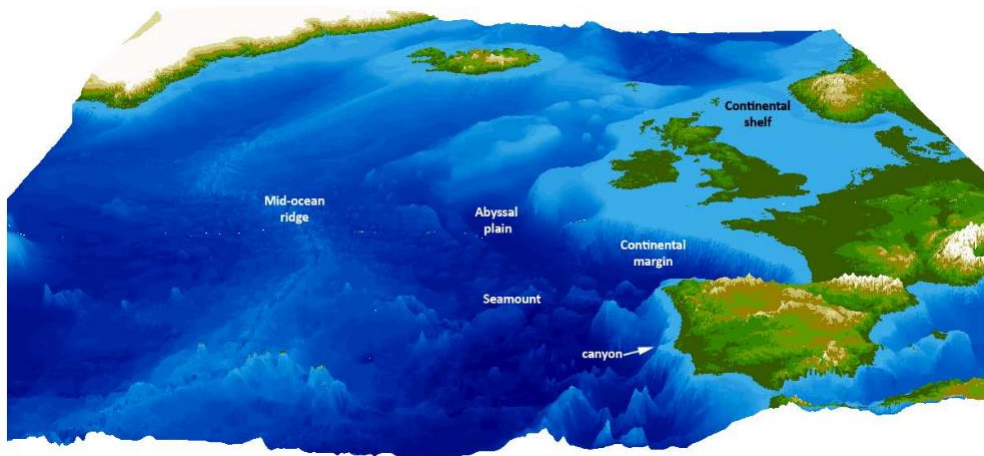


Figure 0-4. Le fond marin de l'Atlantique Nord-Est montrant certains des écosystèmes distincts des grands fonds : les marges continentales, les plaines abyssales, les monts sous-marins et la dorsale médio-océanique, extrait de Ramirez-Llodra et al., 2010. ©Age Høines, MAR-ECO.

3. S'alimenter dans les profondeurs : réseau trophique et cas unique des poissons pélagiques

3.1. Du producteur primaire au prédateur supérieur

Dans le domaine pélagique océanique, les réseaux trophiques, c'est-à-dire les réseaux d'interactions alimentaires qui incluent l'ensemble des flux énergétiques entre les ressources et les consommateurs, sont soutenus par la production primaire phytoplanctonique générée dans les eaux de surface éclairées par le soleil. Cette matière organique nouvellement produite en zone épipélagique peut être ensuite directement utilisée soit par les communautés microbiennes soit par les consommateurs primaires que sont le zooplancton ou les filtreurs gélatineux tels que les salpes. La totalité de cette production primaire n'étant pas consommée, elle peut soutenir le réseau trophique profond d'abord par le biais de la migration verticale des organismes tels que le zooplancton ou le micronecton (Buesseler et al., 2008) (Figure 0-5). Le micronecton, est constitué essentiellement de crustacés, d'organismes gélatineux et de poissons pouvant nager contre les courants et mesurant entre 2 et 20 cm de longueur. Le micronecton sera ensuite la proie des carnivores supérieurs, tels que les mammifères marins, les thons ainsi que des espèces profondes de niveau trophique supérieur tels que les poissons dragon (famille des Stomiidae) ou les grands calmars (Sutton and Hopkins, 1996; Pauly et al., 1998; Pusineri et al., 2005; Cherel et al., 2009; Battaglia et al., 2013). Dans les zones de pente les

poissons démersaux profonds s'alimentent aussi en partie sur ces organismes micronectoniques (Trueman et al., 2014).

Il existe également une autre voie d'entrée énergétique au réseau trophique océanique profond, dérivée directement ou indirectement du phytoplancton, et elle est nommée « neige marine ». Cette dernière se présente sous la forme de microparticules et d'agrégats détritiques de plus grande taille qui coulent vers les profondeurs (Allredge and Silver, 1988). Cette neige marine peut être dégradée par les bactéries ou directement être filtrée par des organismes méso et bathypélagiques tels que les salpes ou encore broutée par le zooplancton et certains crustacés comme les isopodes (Steinberg et al., 2008). Les agrégats de taille plus importante, peuvent également être consommés par des céphalopodes ou certains poissons qui seront eux ensuite au menu de différentes espèces de niveau trophique supérieur tels que les cétacés (Clarke, 1996; Villanueva et al., 2017).

Les réseaux trophiques pélagiques profonds sont ainsi caractérisés par l'absence de production autotrophe. La dépendance à la matière organique produite en surface résulte en une diminution de l'ensemble des concentrations en ressources alimentaires avec la profondeur pour laquelle les espèces ont dû s'adapter (Herring, 2002; Buesseler et al., 2008; Ramirez-Llodra et al., 2010).

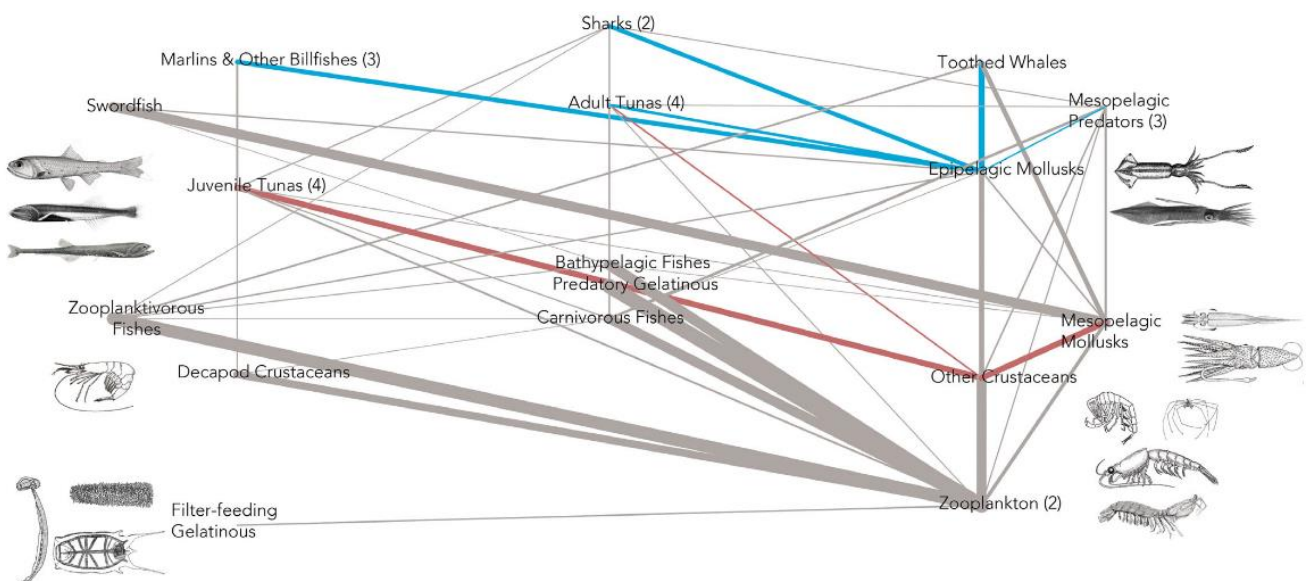


Figure 0-5. Exemple de diagramme simplifié du réseau trophique montrant le flux d'énergie à travers les groupes fonctionnels clés du micronecton et des prédateurs supérieurs dans le centre nord du Pacifique, extrait de Choy et al., 2016.

3.2. Les poissons pélagiques profonds : adaptations et stratégies d'alimentation

Au sein de ce réseau trophique, les poissons pélagiques profonds représentent une composante très diversifiée, aussi bien en terme de nombre d'espèces que de morphologies (poissons-lanternes, poissons hache d'argent, poissons-dragons ou poissons anguilliformes) (Gjørseter and Kawaguchi, 1980; St. John et al., 2016). L'étude de l'écologie trophique de ces espèces a récemment progressée apportant de nouvelles informations sur leur alimentation ou leur spécialisation morphologiques (Drazen and Sutton, 2017). Cependant, de nombreuses zones d'ombres subsistent. Les mécanismes par lesquels les interactions trophiques entre ces espèces façonnent l'assemblage des communautés restent encore peu compris.

Un des particularités des poissons pélagiques profonds est qu'ils ont dû s'adapter à la diminution de la concentration en ressources alimentaires et en lumière avec la profondeur. Les différentes espèces ont dû trouver des compromis énergétiques entre les gains apportés par leur nourriture et les pertes d'énergie allouées à sa recherche dans cet espace vaste et sombre. De manière générale, trois grandes guildes trophiques ont été décrites pour les poissons pélagiques profonds: les zooplanctivores, les micronectivores et les généralistes (Gartner Jr et al., 1997; Drazen and Sutton, 2017). L'herbivorie et l'alimentation par filtration étant rendues quasiment impossibles dans les profondeurs, la diversité des guildes trophiques serait plus faible en comparaison avec les communautés du domaine néritique ou benthique profond (Drazen and Sutton, 2017). Les zooplanctivores représentent la majorité des espèces mésopélagiques. Une partie de ces espèces zooplanctivores migrent dans la couche épipélagique pour profiter de la plus grande quantité de ressources alimentaires tout en réduisant leur risque de prédation visuelle en l'effectuant la nuit (Roe and Badcock, 1984; Hopkins et al., 1996; Hammerschlag et al., 2017). Les Myctophidae, ou poissons lanternes, sont un des groupes de poissons mésopélagiques migrants comprenant la plus grande diversité d'espèces. Une autre partie en revanche ne réalise pas de migration et s'alimente de jour comme de nuit dans les profondeurs (Bernal et al., 2015; Romero-Romero et al., 2019). Ces organismes mésopélagiques non migrants comprennent des espèces appartenant à la famille des Sternoptychidae, ou haches d'argent, ou encore à celle des Gonostomatidae. Ces espèces qui occupent la zone mésopélagique de jour sont nombreuses à posséder des côtés réfléchissants et des photophores ventraux qui leur permettent de se camoufler des prédateurs en se confondant avec la lumière du jour

descendante (Clarke, 1963; Denton et al., 1985). Plus en profondeur, à partir de la couche mésopélagique inférieure, la migration nyctémérale se fait plus rare (Sutton, 2013). Les micronectivores vont donc ensuite s'alimenter sur ces espèces. La grande majorité des poissons micronectivores serait piscivores et peu s'alimentent uniquement de crustacés ou de céphalopodes même si des biais d'échantillonnage ou de technique analytique peuvent fausser en partie cette vision (Sutton and Hopkins, 1996; Drazen and Sutton, 2017). Enfin, le régime alimentaire des espèces bathypélagique reste à ce jour très peu connu et quantifié. Les concentrations en ressources alimentaires diminuant encore plus dans la couche bathypélagique le régime généraliste y est potentiellement plus répandu (Drazen and Sutton, 2017). La prédation visuelle n'est plus la norme et les espèces présentent souvent une ouverture de bouche importante, une dentition bien développée et une musculature réduite (Marshall, 1980). *Anoplogaster cornuta*, ou poisson ogre, en est un bon exemple car il se nourrit de manière opportuniste grâce à des récepteurs chimiques et des crocs proéminents qui servent de piège et lui permettent de se nourrir de proies plus grandes que lui (Hopkins et al., 1996). Côté camouflage, contrairement aux photophores ventraux des espèces de la zone mésopélagique, les espèces bathypélagiques possèdent des couleurs plus foncées, même parfois qualifiées d'ultra-noires pouvant absorber plus de 99% de la lumière (Davis et al., 2020).

3.3. Une communauté méconnue, mais déjà sous pression ?

De par ces adaptations uniques, les poissons profonds fournissent des services écosystémiques importants. Ces services rendus sont d'autant plus significatifs de par l'immense biomasse que pourrait représenter les poissons mésopélagiques. Malgré une large incertitude, elle pourrait s'élever jusqu'à 19 gigatonnes (Irigoiien et al., 2014). Cette communauté joue un rôle fonctionnel clé dans les réseaux trophiques en s'alimentant des consommateurs primaires et en étant une source de proies importante pour des espèces de niveau trophique supérieur et notamment des espèces avec un intérêt commercial fort tel que les thons (Pusineri et al., 2005; Battaglia et al., 2013) ou des espèces patrimoniales et protégées comme les mammifères et les oiseaux marins (Connan et al., 2007; Pusineri et al., 2007). Les poissons pélagiques profonds vont aussi jouer un rôle primordial dans le stockage du carbone à long terme via différents processus (Figure 0-6). Premièrement, dans les zones de pente via les interactions trophiques avec les poissons démersaux profonds (Trueman et al., 2014). Leur migration quotidienne pour aller s'alimenter dans les eaux de surface, reconnue comme la plus grande

migration de la planète, représente aussi une voie majeure de stockage du carbone (Passow and Carlson, 2012). La possibilité de consommer directement ces espèces, leur utilisation pour la farine de poisson, mais également la recherche de produits nutraceutiques et pharmaceutiques potentiels augmente également l'intérêt de l'homme pour ces espèces (Hidalgo and Browman, 2019; Lauritano et al., 2020). Cependant beaucoup d'aspect biologiques ou écologiques restent encore mal compris ou inconnus, incluant des informations basiques tels que leur nombre, leur diversité ou leur fonction (Webb et al., 2010). Il est donc essentiel d'apporter ces informations pour mieux évaluer les conséquences que pourraient avoir les trois grandes pressions qui pèsent sur ces communautés : le changement climatique, l'exploitation de ces ressources pour l'alimentation et l'exploitation minière des grands fonds (Drazen et al., 2019; Hidalgo and Browman, 2019; Seibel and Wishner, 2019; Martin et al., 2020).

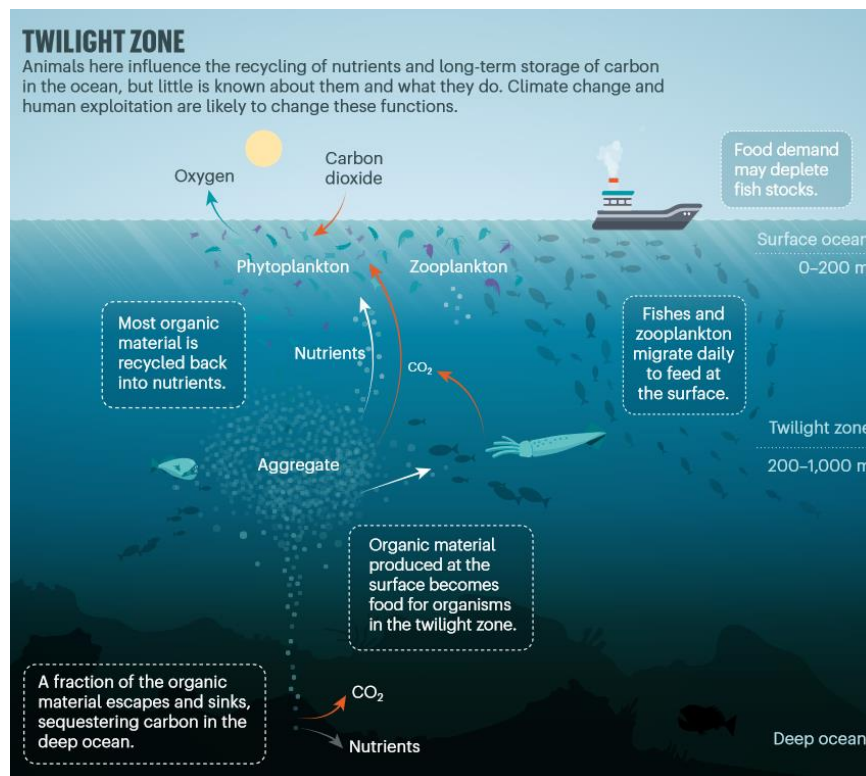


Figure 0-6. Influence des organismes mésopélagiques sur le recyclage des nutriments et le stockage à long terme du carbone, extrait de Martin et al., 2020. © 2020 Springer Nature.

4. Zoom géographique, questions de recherche et hypothèses

4.1. Le golfe de Gascogne : un système méconnu au-delà du plateau ?

La zone océanique du golfe de Gascogne est un cas d'étude particulièrement intéressant et pertinent pour étudier la communauté de poissons pélagiques profonds. D'un point de vue topographique, la pente du golfe de Gascogne est incisée par de nombreux canyons avec des morphologies différentes et complexes permettant d'en apprendre plus sur la structure de cette communauté au sein de ces systèmes particuliers (Borja et al., 2019). Le golfe de Gascogne a subi une importante exploitation de ses ressources biologiques sur le plateau et en haut de talus, conduisant à l'effondrement des stocks de certaines populations de poissons (Borja et al., 2019). Les campagnes scientifiques halieutiques réalisées depuis plusieurs dizaines d'années en zone néritique, aussi bien en milieu pélagique que démersal (notamment PELGAS et EVHOE ; <https://doi.org/10.18142/18> et <https://doi.org/10.18142/8>), ont permis une meilleure connaissance des communautés du plateau continental et la mise en place de quotas de pêche pour tenter de gérer les différents stocks d'intérêt halieutique. Malgré une recherche scientifique intensive menée sur le plateau par la flotte océanographique française, l'échantillonnage du système océanique reste en comparaison marginal avec un total de 66 traits de chaluts réalisés entre 2002 et 2022, comparé aux 1965 traits de chaluts pélagiques réalisés sur le plateau entre 2000 et 2019 (campagnes PELGAS). Les menaces qui pèsent sur ces communautés ne cessent de s'intensifier, et une nouvelle exploitation future, bien que potentiellement peu rentable d'un point de vue économique pour le moment, n'est pas à exclure au vu de l'augmentation des besoins mondiaux en ressources alimentaires (Ramirez-Llodra et al., 2011).

4.2. Questions de recherche, hypothèses et jeux de données

L'objectif général de cette thèse était de déterminer comment l'environnement et les interactions trophiques influent sur la structure de cette communauté pendant la nuit, en se concentrant spécifiquement sur la zone de pente du golfe de Gascogne (Figure 0-7). La nuit est un moment clé de l'alimentation de ces espèces, conduisant à des interactions trophiques et une structure de communauté plus complexe (Hammerschlag et al., 2017).

Le premier objectif était d’apporter de premières informations sur la distribution verticale nocturne de la communauté de poissons pélagiques profonds dans cette zone de pente (Chapitre 1) (Loutrage et al., 2023b). Plus spécifiquement, nous avons exploré les questions suivantes :

- Quelles sont les variables environnementales (dynamique, topographique, bathymétrique) qui influencent majoritairement la distribution de cette communauté la nuit dans cette zone de pente ?
- Quelle est la distribution verticale nocturne des espèces composant cette communauté et correspond-elle aux patrons de distribution déjà décrits pour ces espèces ?

Les gradients environnementaux verticaux étant très marqués pour le milieu pélagique océanique, l’hypothèse était que la profondeur, reflétant plusieurs gradients environnementaux, jouerait un rôle primordial dans la structure observée de cette communauté. Deuxièmement, la majorité des espèces mésopélagiques étant migratrices nyctémérales, l’hypothèse émise était que le maximum de biomasse de la communauté serait retrouvé dans cette couche, ainsi que l’essentiel de la diversité spécifique.

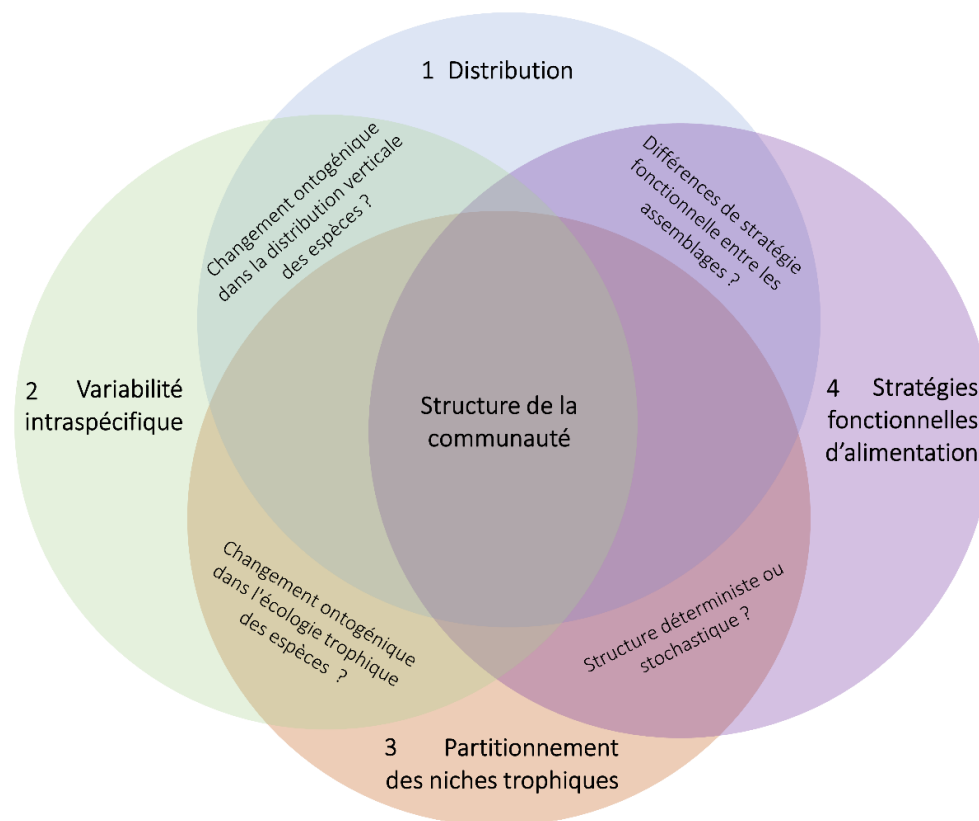


Figure 0-7. Schéma conceptuel des grandes parties de la thèse et des chevauchements entre les différents chapitres. Les numéros correspondent aux numéros des chapitres et à l’ordre dans lequel ils apparaissent dans le manuscrit.

Pour répondre à ces questions et tester ces différentes hypothèses, j'ai pu utiliser les données de chalutage pélagique réalisés dans la zone océanique du golfe de Gascogne, et notamment dans les différents canyons qui incisent la pente continentale (<https://doi.pangaea.de/10.1594/PANGAEA.959551>; Spitz et al., 2023). Ces échantillonnages ont été réalisés depuis 2002 à bord des campagnes halieutiques EVHOE qui ont pour objectif premier d'évaluer les stocks de poissons démersaux sur le plateau ; j'ai pu participer à deux campagnes pour l'acquisition de ces données. Les chaluts pélagiques profonds ont historiquement été ajoutés dans le programme de ces campagnes par le biais de la recherche d'une meilleure connaissance des proies disponibles pour l'alimentation des petits cétacés et des grands poissons océaniques qui s'alimentent en partie sur ces communautés de poissons pélagiques profonds et ont ainsi permis l'étude de la communauté de poissons pélagiques profonds (Pusineri et al., 2007; Spitz et al., 2010).

Le deuxième objectif était de déterminer si les espèces subissaient des changements ontogéniques à la fois dans leur distribution verticale (c'est-à-dire changements dans la taille moyenne des individus avec la profondeur) et dans leur écologie trophique (inférée par des changements de valeurs en $\delta^{15}\text{N}$ avec la taille des individus ; chapitre 2) (Loutrage et al., 2023a). Différentes questions importantes sont apparues à l'échelle de la communauté et à l'échelle intraspécifique :

- Est-ce que les changements ontogéniques dans la distribution verticale des espèces mésopélagiques engendre une augmentation de la taille moyenne des espèces avec la profondeur niveau de la communauté ?
- Au niveau de la communauté, est-ce qu'une augmentation des signatures en $\delta^{15}\text{N}$ avec la taille des individus est observée ?
- Au niveau intraspécifique, existe-t-il des changements ontogéniques de la distribution verticale ou de l'écologie trophique des espèces ?

L'hypothèse était ici qu'une augmentation de la taille moyenne des individus au niveau de la communauté serait observée avec la profondeur. Concernant les changements ontogéniques dans l'écologie trophique, l'hypothèse était que les plus grandes espèces de la communauté s'alimentent sur de plus grosses proies que les petites espèces induisant une augmentation des valeurs de $\delta^{15}\text{N}$ avec la taille des individus au niveau de la communauté. De même au niveau intraspécifique, les espèces de poissons d'autres systèmes opérant souvent un changement ontogénique dans leur

alimentation, l'hypothèse était que ces changements seraient aussi retrouvés dans la plupart des espèces pélagiques profondes (Sánchez-Hernández et al., 2019).

Pour apporter des réponses à ces questions, deux jeux de données ont été utilisés et 12 espèces étudiées. Le jeu de données de distribution des tailles des individus en fonction de la profondeur a été extrait du jeu de données historique d'EVHOE (*Length and depth distributions of twelve deep-pelagic fish of the Bay of Biscay slope, Northeast Atlantic, between 2011 and 2021*, en cours de soumission). Le jeu de données utilisé pour l'analyse de la variabilité dans l'écologie trophique des espèces provient de 500 échantillons de muscles que j'ai pu échantillonner lors de la campagne EVHOE de 2021 ainsi que de données déjà disponibles récoltées lors des précédentes campagnes (n = 175 échantillons) (*Individual carbon and nitrogen stable isotope compositions with length, weight, and trawling depth for twelve deep pelagic fish species from the Bay of Biscay, Northeast Atlantic, between 2007 and 2021*, en cours de soumission).

L'étude de la répartition des niches isotopiques des espèces dans les différents assemblages le long de la colonne d'eau a constitué l'objectif principal du chapitre 3. Plusieurs questions précises ont constitué les sous-parties de ce chapitre :

- A l'échelle de la communauté, est-ce qu'il y a un chevauchement important des niches isotopiques des espèces ?
- Est-ce que la profondeur est un axe de ségrégation utilisé par les espèces pour réduire la compétition interspécifique ?
- A l'échelle des assemblages (c'est-à-dire des couches de profondeur), est-ce que ce sont des processus déterministes (par exemple, la compétition) ou stochastiques (c'est-à-dire une distribution qui ne diffère pas de celle due au hasard) qui façonnent la répartition des niches isotopiques des espèces ?
- En lien avec la détermination de ces processus d'assemblage, observe-t-on ainsi des assemblages d'espèces spécialistes avec des niches isotopiques réduites et de faibles chevauchements entre les niches des différentes espèces ou, à l'inverse, des espèces avec de larges niches isotopiques et de forts chevauchements interspécifiques ? et retrouve-t-on la même structure au sein de tous les assemblages ?

J'avais, ici, fait l'hypothèse que les espèces de l'assemblage de la couche épipélagique, profitant d'une importante concentration en ressources alimentaires, n'auraient pas besoin de limiter leur compétition et présenteraient donc un niveau de ségrégation faible. Plus en profondeur en revanche, les espèces présenteraient un fort niveau de ségrégation de leur niche isotopique afin de réduire la compétition interspécifique. Pour répondre à ces questions, 7 stations dans les différentes couches de profondeur définies dans le chapitre 1 ont été échantillonnées. Les résultats des précédents chapitres soulignant l'importance du fond pour certaines de ces espèces, une station a été réalisée près du fond (moyenne de 100 m au-dessus du fond par 1000 m de profondeur). Dans chaque couche de profondeur, j'ai donc échantillonné les espèces représentant une majorité de la biomasse de l'assemblage. Au total 16 espèces de poissons et une espèce de krill constituent ce jeu données (n = 640 échantillons) qui en partie a aussi été utilisé pour le chapitre 2.

L'ensemble des résultats acquis au cours des trois chapitres précédents, a mis en lumière l'importance d'approfondir notre compréhension des interactions entre les organismes et leur environnement en mettant l'accent sur les rôles spécifiques des traits biologiques dans les écosystèmes. L'application d'une approche fonctionnelle portant sur l'étude des traits morphologiques impliqués dans l'acquisition de nourriture avait donc pour objectif d'améliorer notre évaluation de la diversité des espèces entre les différentes couches de profondeurs et d'explorer de manière complémentaire les résultats du chapitre 3 sur l'importance de la compétition dans le façonnage de la structure de la communauté. Spécifiquement les questions de ce chapitre étaient les suivantes :

- Quels sont les traits fonctionnels clés impliqués dans les stratégies de recherche de nourriture de ces espèces ?
- La diversité fonctionnelle et la structure de cette communauté varient-elles en fonction des couches de profondeur ?
- La structure de la communauté résulte-t-elle principalement de la limitation de la concurrence par la dissimilitude (lorsque des espèces cooccurrentes présentent des traits différents) ou du filtrage environnemental (lorsque les espèces s'adaptent de la même manière et présentent des traits comparables) ?
- Certaines espèces sont-elles particulièrement rares en termes de diversité fonctionnelle ?

En lien avec les résultats et observations réalisées lors des précédentes études, l'hypothèse principale était que la communauté présenterait une diversité de stratégies fonctionnelles élevée, en lien avec une limitation de la similarité pour éviter une compétition exclusive (Chapitre 3). Au vu de la diversité de morphologies observée au sein de la couche bathypélagique, j'ai supposé que plusieurs espèces au sein de cette couche supporteraient une combinaison de traits uniques, impliquant des fonctions uniques au sein de la communauté.

Pour cela, plusieurs traits morphologiques en lien avec l'acquisition de la nourriture ont été sélectionnés. Des données morphologiques étaient déjà disponibles sur un total de 11 espèces (n= 365 individus mesurés). Pour appréhender une plus grande diversité d'espèces et de stratégies j'ai pu mesurer et ajouter un total 31 espèces (n= 358 individus mesurés) à ce jeu de données. Une partie de la récolte et des mesures ont été réalisées lors de la deuxième campagne EVHOE à laquelle j'ai participé en 2022 et le reste a été complété au laboratoire sur des individus conservés des campagnes des années précédentes.

La discussion des principaux résultats de ces recherches et leurs limitations fait l'objet de la dernière grande partie de cette thèse. Plusieurs perspectives de recherche sur ces communautés peu connues sont également proposées.

Chapitre 1 - The nocturnal distribution of deep-pelagic fish on the continental slope of the Bay of Biscay



1. Introduction

The deep-pelagic realm is the largest biome on the planet. This habitat is separated into different strata based on sunlight penetration and the associated biota (Sutton, 2013). The mesopelagic zone begins at approximately 200m depth, where sunlight can no longer support photosynthesis, and ends where there is not enough solar illumination for fauna to differentiate day-night cycles (Sutton, 2013). In this zone, the main thermocline is present, hydrostatic pressure increases with depth and the food supply is episodic (Robinson et al., 2010). Below 1000m, the bathypelagic zone begins. Its lower boundary is generally admitted to be 100m above the seafloor (Sutton, 2013). There is a logarithmic decline in available food energy availability in this zone (Haedrich, 1996; Angel, 1997). Finally, the Benthic Boundary Layer (BBL) is defined based on the distance from the seafloor. This zone can be found between 100m to 1000m to the seafloor depending on the presence of turbulent mixing (Weatherly and Kelley, 1985). A nepheloid layer of suspended particulate matter can be observed and bottom currents are accelerated over abrupt topography (Sutton, 2013).

In the deep-pelagic realm fishes are a dominant component in terms of biomass. The initially underestimated mesopelagic fish biomass could represent up to 90% of the total fish biomass on the planet (Irigoien et al., 2014). Below 1000m, pioneering investigations found a decline in fish biomass with depth (Angel and de C. Baker, 1982; Angel, 1989). However, more recent studies have reported noticeably higher biomass values than previously reported (Sutton et al., 2008; Cook et al., 2013). In particular at the benthic boundary layer where a peak of biomass has been described in slope areas and seamount (Marshall, 1977; Reid et al., 1991; Boehlert et al., 1994). This abundant deep-pelagic biomass represents a huge potential for exploitation (Hidalgo and Browman, 2019; Drazen et al., 2020). Deep-pelagic fish play multiple key ecological roles in open-ocean ecosystems. The daily vertical migration of mesopelagic organisms, recognized as the largest migration on earth, allows the transfer of energy and matter between the different depth layers of the ocean (Irigoien et al., 2014; Young et al., 2015). Trophic interactions between deep-pelagic and deep-demersal fishes in slope areas have also been shown to play an important role in the ocean carbon cycle, bypassing the detrital particle flux and transferring carbon to deep long-term storage (Trueman et al., 2014). Mesopelagic fish is also a key intermediate link in the trophic food web by feeding on primary consumers (Drazen and Sutton,

2017) and by being an important source of prey for higher trophic levels such as tuna (Pusineri et al., 2005; Battaglia et al., 2013), marine mammals (Pauly et al., 1998), and seabirds (Connan et al., 2007). In addition, they are an unexplored bio-resource, and, recently anticancer and antimicrobial activities in one mesopelagic species have been discovered (Lauritano et al., 2020). Consequently, the knowledge of their ecology and function is needed to be able to plan efficient sustainable management and conservation measures (Martin et al., 2020) in the context of global warming (L. A. Levin et al., 2019) and exploitation of deep-sea resources (Hidalgo and Browman, 2019; Drazen et al., 2020).

The nocturnal spatial distribution of this deep-pelagic fish biomass and the environmental factors that control it remains a major gap in understanding the structure of this community. Because the vertical spatial scale variability of the deep-pelagic habitat is much finer than the horizontal, differences in ichthyofaunal composition along the water column have been observed (Sutton et al., 2008, 2010). In fact, in several studies, immersion depth explained most of the variability, with characteristic species in limited water depths and others occurring over a wide depth range (Angel, 2003; Sutton et al., 2008, 2010; Cook et al., 2013; Kenchington et al., 2020; García-Seoane et al., 2021). A high proportion of mesopelagic fish species migrate to the surface at night to feed. Migration behavior exposes fish to a wide range of environmental conditions throughout a single day. In deeper layers, migration becomes less common and species appear to have a stronger relationship with topography especially in slope areas and seamounts (Marshall, 1977; Reid et al., 1991). Differences in the nocturnal distribution patterns of deep-pelagic fishes also appear between the open ocean and areas where this distribution interacts with steep topography (i.e. seamounts, mid-ocean ridges, and continental slopes). In contrast to the paradigm of decreasing biomass with depth in the open ocean, the deep-pelagic fish community has shown an increase in biomass in association with the Mid-Atlantic Ridge, with a vertical extension of the range at depth for many species (Sutton et al., 2008). In slope areas, a mesopelagic boundary community has been defined with a composition different from the adjacent open ocean with some species associated with the slope (Reid et al., 1991). In these areas, an active nocturnal horizontal migration towards the slope has also been reported (Benoit-Bird et al., 2001).

The Bay of Biscay (Northeast-Atlantic) presents a variety of geographic features with the continental slope intersected by different types of canyons (i.e. different morphologies). The

oceanographic circulation is composed of an inter-gyre zone and large spring algal blooms occur with a peak of productivity in the southwestern part of the Bay (Pollard et al., 1996; Sutton et al., 2017; Borja et al., 2019). This region is historically subject to the impact of anthropogenic activities including fisheries (Lorance et al., 2009). The slope has also been identified as a productive key area with high densities of marine top predators feeding on mesopelagic resources (Pusineri et al., 2005, 2007; Pettex et al., 2017; Laran et al., 2017). The functional importance of this area for marine predators led to the creation of a large Special Area of Conservation (SAC) designated under the Natura 2000 network. However, the nocturnal distribution of mesopelagic fish species and the factors influencing it remains unknown in this specific slope area.

The objectives of this study are (1) to describe the nocturnal vertical distribution of the main species present in the first 2000m of on the continental slope and (2) to investigate the relationship between the distribution of these deep-sea pelagic fish assemblages and their environment on the slope of the Bay of Biscay by including a range of variables at different spatial and temporal scales (physico-chemical, topographic, bathymetric).

2. Materials and Methods

2.1. Study area

The Bay of Biscay is located in the North-East Atlantic Ocean, between North-West France and NE Spain (Figure 1-1). The continental slope is very pronounced, with a slope of the order of 10%–12% of inclination. Numerous canyons intersect this slope. Canyons generally present narrow channels, with steep, linear, and sinuous sides. The deep valleys allow the transport of continental sediments from the main rivers to the adjacent abyssal basin (Lavin et al., 2004; Borja et al., 2019).

Horizontal circulation in the bay depends on multiple factors: bathymetry, tides, density-driven currents, and wind (Borja et al., 2019). The oceanic circulation is characterized by a weak and variable anticyclonic circulation in the central zone. This circulation becomes cyclonic when the water reaches the slope of the continental shelf. Instabilities created by this cyclonic circulation at the slope contact tend to create cyclonic and anticyclonic eddies (Pingree, 1993; Koutsikopoulos and Cann, 1996). Regarding dynamic variables, phytoplankton blooms induce two annual peaks in zooplankton abundance

and biomass in spring and fall (Valdés et al., 2007) and temperature exhibits an annual cycle with maximum and minimum values in August and January respectively (Borja et al., 2019).

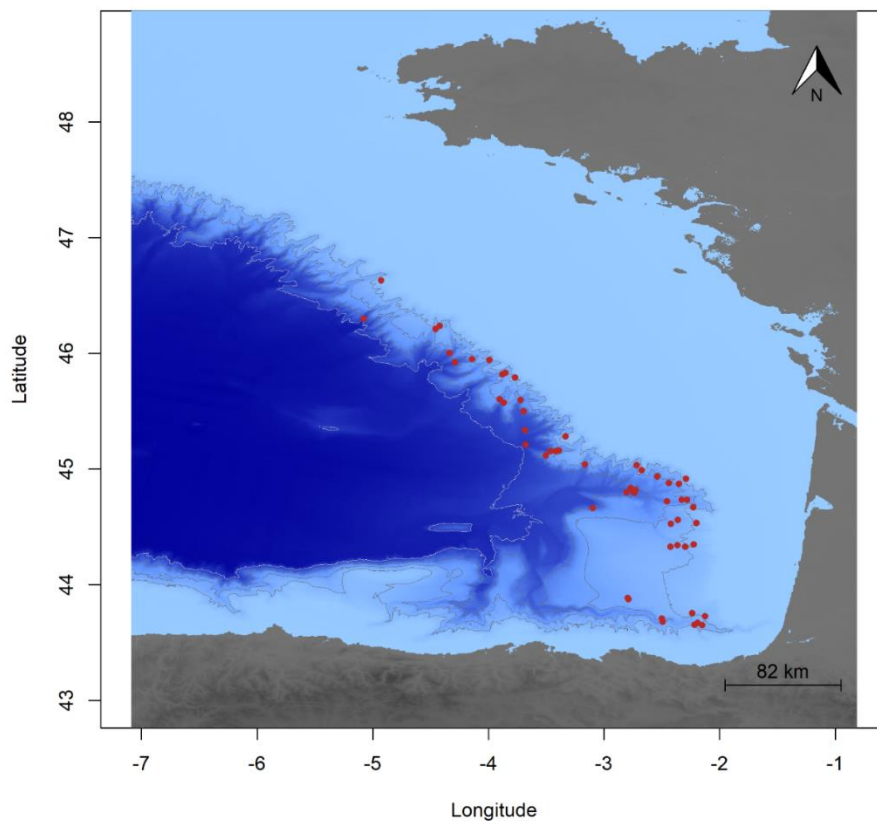


Figure 1-1. Trawl hauls’ average spatial position in the Bay of Biscay. The background blue colours represent the seabed depth (where lighter colours are shallower). The lines represent 1000, 2000, 3000, and 4000m isobaths. The scale represents the number of kilometres for one degree of longitude ($\approx 82\text{km}$).

2.2. Sample collection

The data were collected at 56 stations by night pelagic trawling in the canyons of the Bay of Biscay slope (North-East Atlantic) in the fall between 2002 and 2019 during the scientific campaigns EVHOE (“*Evalutation Halieutique de L’Ouest de l’Europe*”, <https://doi.org/10.18142/8>) conducted by the “*Institut Français de Recherche pour l’Exploitation de la Mer*” (Ifremer) on R/V Thalassa. The same pelagic trawl net dedicated to the monitoring of small pelagic fish (Doray et al., 2018) has been consistently used since 2002. The trawl net was 192m long with a headline of 76m and a foot rope of 70m. The average vertical mean mouth opening was about 24m and the horizontal opening of about 58m. The mesh size gradually decreases from very large 8m (stretched mesh) at the mouth to 20mm

(stretched mesh) in the cod-end. To allow the capture of very small specimens, the trawl is also equipped with a 7.5m long sock with a 12mm mesh size. The complete raw biological data and metadata are available on the PANGAEA platform <https://doi.pangaea.de/10.1594/PANGAEA.959551> (Spitz et al., 2023).

Midwater hauls were conducted at night from 20 to 2000m immersion depth. Each haul was made at a specific chosen immersion depth (i.e., sampling depth, figure 1-2). Once the trawl reached the pre-set depth it was towed horizontally (i.e., constant immersion depth) for 1 hour at 4 kn. A higher trawl speed on deployment and a low speed on retrieval were implemented to reduce bycatch at shallower depths than the target depth (Kashkin and Parin, 1983; Sinclair et al., 1999; Eduardo et al., 2020a). The main disadvantage of a pelagic trawl of this size is the absence of an opening or closing mechanism generating potential contamination of the sample. In our results, this could result in an overestimation of the presence of species in a deeper layer than their actual vertical distribution. Indeed, during the trawl run, some individuals may be caught and assigned to a higher target depth. In an attempt to reduce this bias, a filter was applied at the trawl level. To do this, within each trawl, species representing less than 1% of the relative biomass were removed. This reduces the inclusion of species that are potentially caught on the run and thus represent a small percentage of the biomass sampled in the trawl.

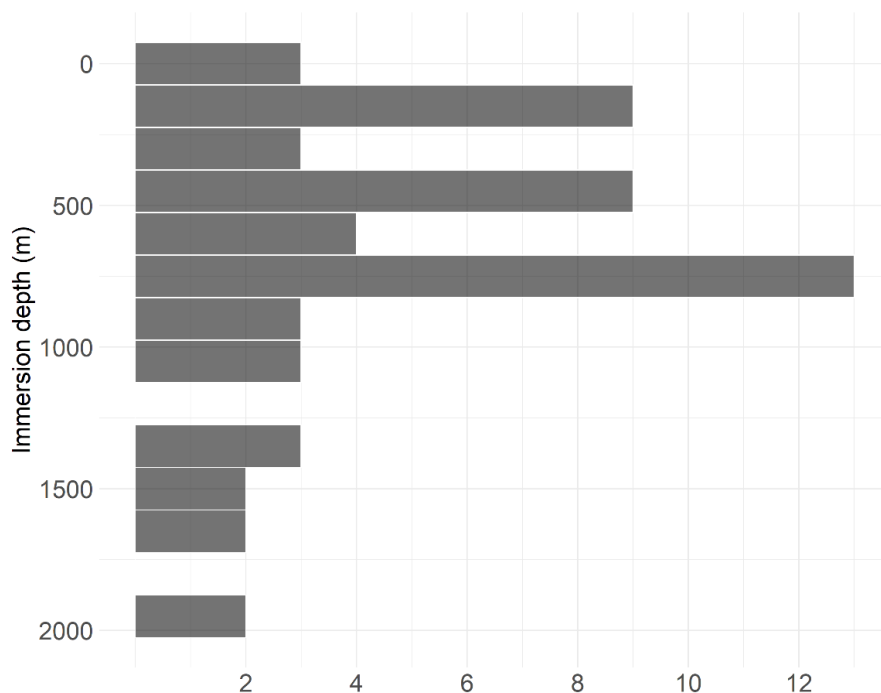


Figure 1-2. Number of hauls per immersion depth.

Individuals were identified at the species level whenever possible, otherwise, they were identified at the genus or family level, notably when individuals were too small or damaged. Species or taxa were counted and most often weighed. When weighing was not possible, an estimate of the average individual weight over the entire time series was calculated and the total weight by species was estimated. The term biomass refers here to the relative Catch-Per-Unit-Effort (CPUE). For this purpose, the biomass of each species within each trawl was divided by the volume filtered by the trawl during the fishing phase (vertical opening x horizontal opening x distance trawled). Thus, a comparison of the distribution along the water column can be made at the intraspecific level but comparisons of absolute biomass between species are not possible due to the difference in catchability between species which is not well known. The final biological dataset is thus translated into a species (biomass g.m^{-3})-sites matrix.

2.3. Environmental variables

For each trawl made, the start and end coordinates of the fishing were used to trace the trajectory of the trawl. Then, for each environmental variable, the values of the cells crossed by the trawl were extracted (<https://resources.marine.copernicus.eu/>) (Table 1-1). This was done specifically for each year sampled and on different time scales with the mean and standard deviation of the values extracted at one, three, six, and twelve months before the sampling date. The objective was to see if any longer or shorter-term processes influenced the distribution of deep-sea pelagic fish (the different time scales) and if it was the mean of the values or the variations of these values (mean or standard deviation) that influenced it most. Then, two strategies were used depending on the variables studied: for chlorophyll and zooplankton concentration, values were extracted at the surface to provide information on the productivity of the area, while for the other variables (temperature, salinity, current velocity), values were extracted at trawl depth (i.e. the average of the depth between the beginning and end of the fishing phase). Three depth-related parameters were used and defined as follows: immersion depth is the fishing depth, bottom depth is the bathymetry, and proximity to the bottom is defined as the difference between bottom depth and fishing depth.

Bathymetry of the Bay of Biscay was taken from the General Bathymetric Chart of the Oceans (GEBCO, <https://www.gebco.net/>). From this data, different terrain parameters were calculated using

the R package *raster* (Hijmans, 2023). These parameters were: average bottom depth, proximity to the bottom, slope inclination in degrees, the terrain roughness defined as the ratio of the surface to the planar surface across the neighbourhood of the central pixel, the bathymetric Position Index (BPI) which indicates whether the pixel is part of a positive (ridge) or negative (trough) characteristic of the surrounding terrain and the terrain Ruggedness Index (TRI) which is calculated by comparing a central pixel with its neighbours, taking the absolute values of the differences, and averaging the result. To capture strong terrain variations, we chose to use the 75% quantile value for each terrain parameter (i.e. slope inclination, terrain roughness, BPI, and TRI). The R package *marmap* was used to estimate the smallest distance between the sampling station and the 200m-isobath representing the ocean shelf (Pante and Simon-Bouhet, 2013).

Some hauls being conducted above canyons and others out of canyons, the influence of this parameter on the distribution of the fish was verified. For this, a set of geo-referenced canyon characteristics was extracted (area, length, width and mean depth) and a typology of canyons was defined using an ascending hierarchical classification (AHC) (Harris et al., 2014). AHC was performed using the kmeans method for several k groups between 2 and 10. The optimal number of groups was estimated using the percentage of explained inertia.

All these environmental variables (and the different time scales) for each station were compiled into a data matrix (Table 1-1) to study the relationship between these variables and the distribution of deep-pelagic fish biomass in the Bay of Biscay. However, before analysing the data, the collinearity between explanatory variables was checked. Only variables with a correlation of less than 0.7 were retained (Dormann et al., 2013), except the variable of proximity to the bottom and the bottom depth, which had a correlation of 0.87. The high correlation between these two variables is probably due to the maximum sampling depth of our trawl. Given that the two variables can be explained by different relationships with the species, we decided to keep them in the models despite their correlation.

Table 1-1. Summary of environmental variables with unit, source, and resolutions.

Environmental variables	Unit	Source (dataset name)	Spatial resolution	Temporal resolution
Immersion depth	m	Cruise data	-	-
Latitude	°	Cruise data	-	-
Temperature	°C	Copernicus (Atlantic-Iberian Biscay Irish- Ocean Physics Reanalysis)	0.083° arc	1, 3, 6, 12 - months average

Salinity	-	Copernicus (Atlantic-Iberian Biscay Irish- Ocean Physics Reanalysis)	0.083° arc	1, 3, 6, 12 - months average
Current velocity	m.s ⁻¹	Copernicus (Atlantic-Iberian Biscay Irish- Ocean Physics Reanalysis)	0.083° arc	1, 3, 6, 12 - months average
Surface chlorophyll concentration	mg.m ⁻³	Copernicus (Atlantic-Iberian Biscay Irish- Ocean BioGeoChemistry)	0.083° arc	1, 3, 6, 12 - months average
Surface zooplankton concentration	g.m ⁻²	Copernicus (Global ocean low and mid trophic levels biomass content hindcast)	0.083° arc	1, 3, 6, 12 - months average
Mixed layer depth	m	Copernicus (Atlantic-Iberian Biscay Irish- Ocean Physics Reanalysis)	0.083° arc	1, 3, 6, 12 - months average
Moon phase	new-moon, quarter-moon, full-moon	https://tidesandcurrents.noaa.gov/	-	Day
Bottom depth	m	GEBCO	15 arc- seconds	-
Proximity to the bottom	m	GEBCO + cruise data	-	-
Distance to 200m-isobath	km	GEBCO	15 arc- seconds	-
Slope	°	GEBCO	15 arc- seconds	-
Roughness	m	GEBCO	15 arc- seconds	-
Bathymetric Position Index (BPI)	m	GEBCO	15 arc- seconds	-
Terrain Ruggedness Index (TRI)	m	GEBCO	15 arc- seconds	-
Canyon area	km ²	Blue habitats	30 arc- seconds	-
Canyon length	km	Blue habitats	30 arc- seconds	-
Canyon width	km	Blue habitats	30 arc- seconds	-
Canyon mean depth	m	Blue habitats	30 arc- seconds	-

2.4. Data analyses

2.4.1. Definition of assemblages and indicator species

Groups of co-occurring species forming assemblages were identified by accounting for the influence of environmental variables using a Multivariate Regression Tree (MRT) (De'ath, 2002). MRT allows the modelling of linear and non-linear complex relationships between response and environmental

variables. The MRT defines groups by minimizing the difference in species composition between them. Thus, the MRT identifies where the most significant change in community composition occurs along an environmental gradient. Environmental ruptures are represented by nodes and each most probable community composition by a leaf (De'ath, 2002). Before constructing the tree, a Hellinger transformation was applied to the species data to account for the double zero problems (Borcard et al., 2011). The number of nodes was selected using a cross-validation procedure with 100 iterations. The number of nodes minimizing the relative cross-error validation (CVRE) was therefore selected (De'ath, 2002). The R package *mvpart* was used for this analysis (De'ath, 2014).

In this study, we built the MRT using standardized biomass (biomass per-unit-effort, i.e. g.m⁻³) data on which a square root transformation has been applied. Biomass is not evenly distributed among deep-sea pelagic species, with small species often being very abundant (e.g. *Benthoosema glaciale*, *Ceratoscopelus maderensis*). However, ecological issues associated with ecosystem functioning and energy flows are more related to biomass than to abundance, which explains our choice to use this measure. To maximize the detection of dominant community-environment relationships only species with a percent occurrence $\geq 10\%$ (=37 species) were retained (Poos and Jackson, 2012).

The Dufrêne-Legendre Index (DLI) was used to help identify indicator species for each MRT assemblage. Indicator species are defined by Dufrêne and Legendre as organisms whose presence, absence, or abundance (or biomass) reflects specific environmental conditions (Dufrêne and Legendre, 1997). This index is the product of the average abundance (or biomass) in the assemblage divided by the sum of the average abundance (or biomass) in all other groups, multiplied by the proportion of sites in the group where the species occurs, multiplied by 100. Thus, DLI ranges from 0, with no occurrences of a species in an assemblage, to 100, if a species is present in all sites in the assemblage (fidelity) and in no other assemblage (specificity) (Dufrêne and Legendre, 1997). Thus, in our case study, a species will have a high index if it is caught in every trawl carried out within an assemblage (fidelity) and if it is found less or not at all in trawls carried out under other environmental conditions, thus in the other assemblages defined by the MRT (specificity).

Immersion depth distributions of indicator and most important species in terms of biomass were evaluated graphically using a density plot. The plot was performed on the square-root transformed total biomass data using the R package *ggplot2* and the median of the distribution was added for each

species (Wickham et al., 2016).

2.4.2. Model selection

Once the assemblages and indicator species had been determined by the MRT, General Additive Models (GAM) were used to explore the influence of environmental variables (excluding depth) on the distribution of their biomass. For this purpose, the entire depth distribution of biomass of each species was used (i.e. not only that within the depth layer to which it belongs). GAMs can capture complex relationships by fitting smooth non-linear functions to the data (Guisan et al., 2002). GAMs for all the different depth assemblages (y) can be described as follows:

$$y = \beta_0 + f_1(x_1) + f_2(x_2) + \dots + f_n(x_n) + \varepsilon$$

where y is either the sum of the biomass of all species within a depth assemblage or the biomass of individual species, β_0 is the model intercept, f is a smooth function of the n explanatory variables, and ε is the stochastic error term. The REstricted Maximum Likelihood (REML) approach was chosen to define the smoothing parameter. Before performing the analyses, we excluded immersion depth as an explanatory variable to avoid redundancy as it had been incorporated into the different depth assemblages with the MRT. A total of 14 variables (after the removal of highly correlated variables) were used to build the models. These variables correspond to the variables described in Table 1-1. The selection of the variables was done by dividing the variables into subgroups of 6 variables and keeping only those that were significant at the 0.05 threshold. Different groups were tested to consolidate and stabilise the selection of candidate variables in the final model. For our model selection, we added shrinkage to the smoothers in our model so that they could be penalised out of the model if they were not significant (Marra and Wood, 2011). Biomass data were square-root transformed. The R package *mgcv* was used for this analysis (Wood, 2017). All statistical analyses were performed in the R environment version 4.2.3. (R Core Team, 2023).

3. Results

3.1. Temporal effect

Since the data set spans over 17 years, the influence of time may affect our results. However, it is difficult to properly test this because some depths were preferentially sampled in certain years. To test the temporal effect, a linear model was run between a subsample of species biomass (per CPUE) between 500 and 800m (depths with the most data) and time. No significant decrease or increase in biomass was found for the species studied and we therefore chose to treat the entire data set as belonging to the same set.

3.2. Faunal composition

A total number of 30 270 individuals were captured at 56 stations during the night. The fish community included 95 different species belonging to 30 families, with *Myctophidae* being the most diverse family with 23 different species recorded. In terms of density, 95% of the specimens caught belonged to only 15 different species. The dominant species in number of individuals were some myctophids (*Benthosema glaciale*, *Ceratoscopelus maderensis*, *Notoscopelus kroyeri*, and *Myctophum punctatum*), an alepocephalid (*Xenodermichthys copei*) and a paralepidid (*Arctozenus risso*). Five species represented more than half of the total biomass caught (55%): *Notoscopelus kroyeri*, *Serrivomer beanii*, *Stomias boa*, *Xenodermichthys copei*, and *Lampanyctus crocodilus*.

3.3. Environmental variables

The variability of environmental variables extracted from Copernicus (see methodology) was investigated (Figure 1-3). Variabilities in temperature and current velocity with depth were estimated to account for differences in water mass characteristics along the water column. Similarly, variabilities in zooplankton and chlorophyll concentrations were estimated as a function of latitude to account for variability in the productivity of the sampled area. Temperature decreased with depth with values of about 16°C at the surface and 4°C near 2000m depth. Current velocity showed little variability with

values ranging from 0.001 to 0.079 $\text{m}\cdot\text{s}^{-1}$ and a maximum around 800m depth. The chlorophyll concentration also showed weak variability with values between 0.09 and 0.32 $\text{g}\cdot\text{m}^{-2}$ with the highest concentrations around 46° latitude, while the maximum concentration of zooplankton was rather located around 45° latitude.

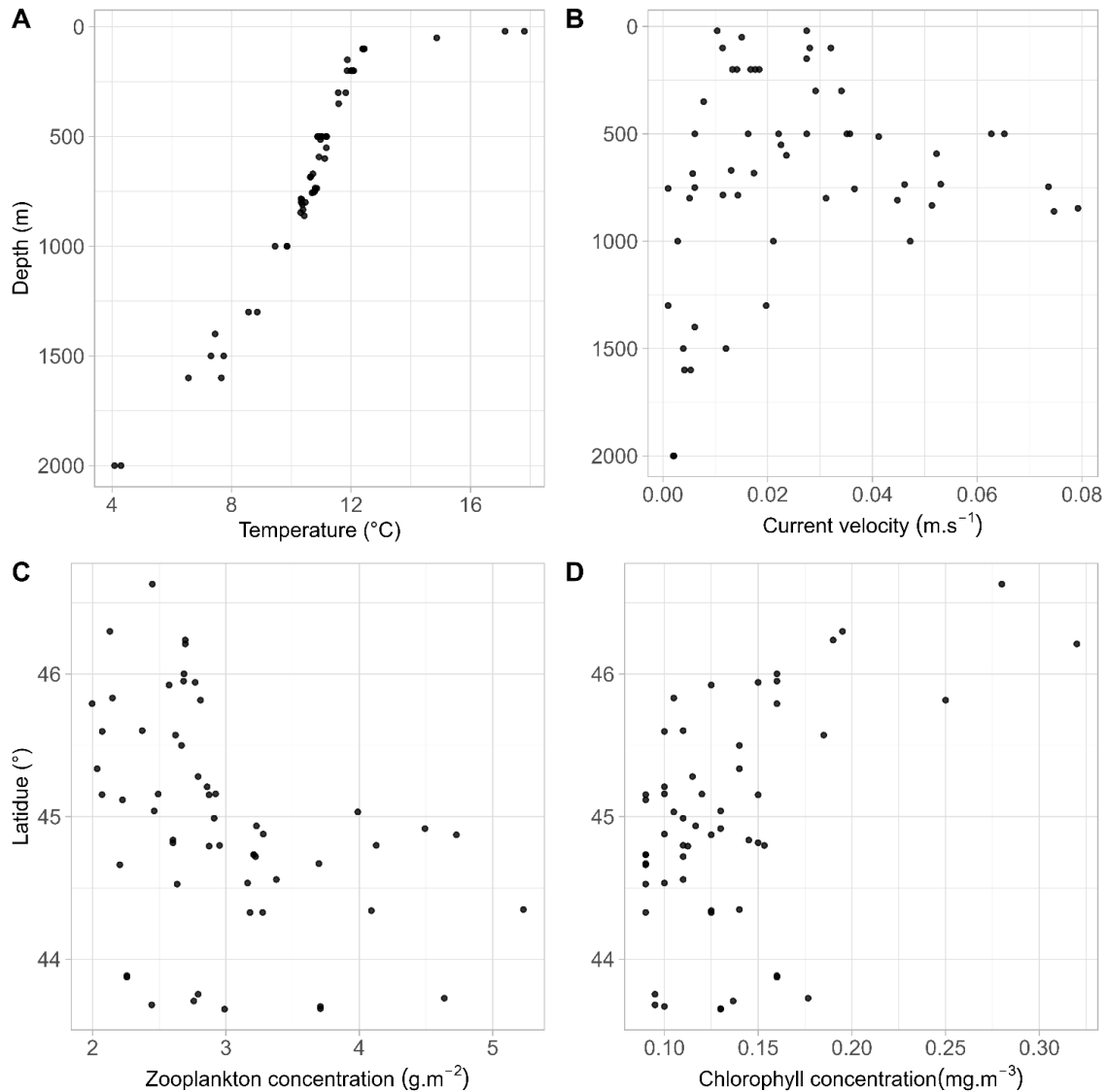


Figure 1-3. Variability of temperature (A) and current velocity (B) as a function of depth and variability of zooplankton concentration (C) and chlorophyll concentration (D) as a function of latitude. The results presented here are values averaged over the month before the sampling date.

3.4. Definition of assemblage and indicator species

The most parsimonious tree presented three nodes (environmental ruptures) with four leaves (assemblage composition) with an explained variation in fish biomass distribution of 33% (Figure 1-4).

Immersion depth was the variable accountable for the formation of all the nodes. Thus, the greatest change in faunal composition at night occurred along the water column. The first node separated the epipelagic layer (20-175 m) from the deeper layers. The second and third nodes consecutively separated the upper mesopelagic (175-700 m), lower mesopelagic (700-1000 m), and bathypelagic (1000-2000 m) zones.

A total of 15 indicator species were identified (Figure 1-4). A decrease in the number of indicator species with depth was also observed. The epipelagic assemblage contained only one indicator species, *Ceratoscopelus maderensis* (DLI = 60). The upper mesopelagic assemblage also contained one indicator species: *Xenodermichthys copei* (DLI = 39). The lower mesopelagic was composed of five indicator species with *Cyclothone spp.* and *Searsia koefoedi* having the highest DLI values (62 and 47 respectively). Finally, the bathypelagic contained the higher number of indicator species with a total of 8 species, *Normichthys operosus* and *Serrivomer beanii* having the highest DLI values (83 and 44).

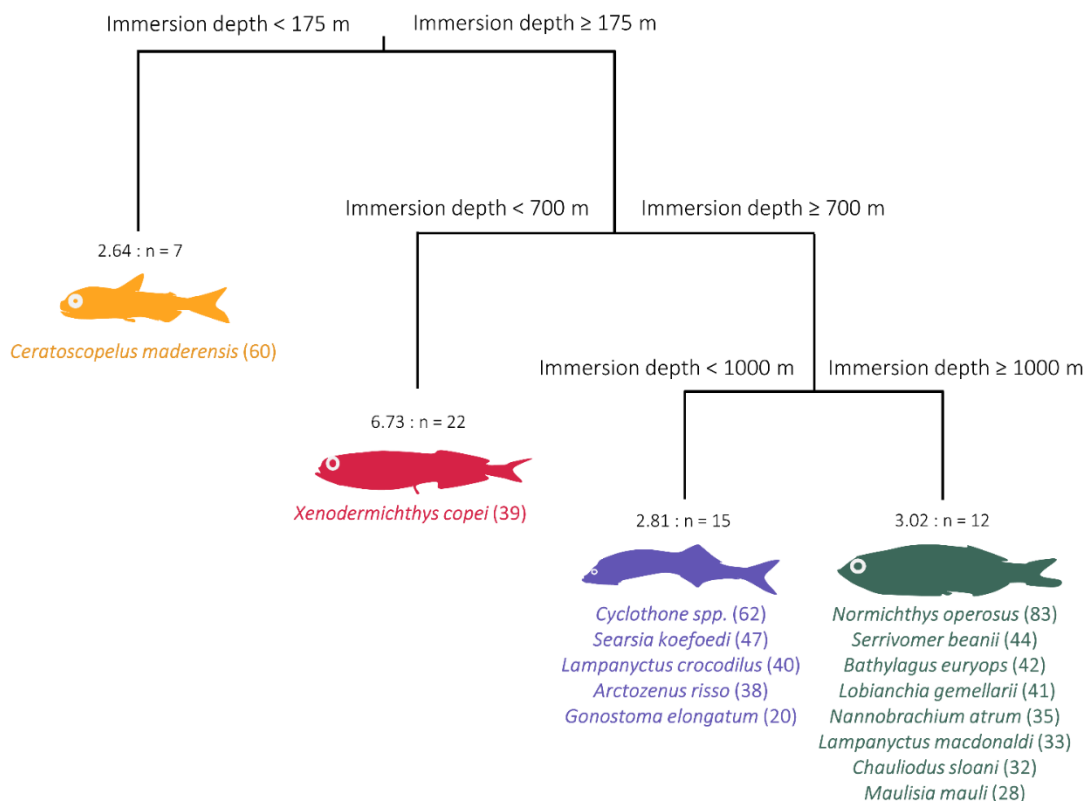


Figure 1-4. Multivariate Regression Tree constrained by 16 environmental variables (Error: 0.674; CV Error: 0.885; SE: 0.074). For each leaf, the number of stations (n) and the group's relative error are indicated. For each terminal leaf, the indicator species with their Dufrêne-Legendre index is indicated in the bracket.

Given the computation of the DLI, indicator species may not account for the higher percentage of biomass in each depth range defined by the MRT (Table 1-2). In the epipelagic layer, *Myctophum punctatum* (22%), *Benthosema glaciale* (15%), and *Stomias boa* (13%) accounted for half of the total percentage of biomass captured between 20 and 175m immersion depth. In the upper mesopelagic assemblage, between 175m and 700m deep, *Xenodermichthys copei* (36%), *Lampanyctus crocodilus* (12%), and *Argyrolepecus olfersii* (11%) accounted for the majority of the sampled biomass. In the lower mesopelagic zone, three species represented 57% of the total biomass in this depth range: *Lampanyctus crocodilus* (27%), *Xenodermichthys copei* (23%), and *Stomias boa* (7%). Finally, the deepest division (> 1000m), showed a high proportion of biomass of *Lampanyctus crocodilus* (19%), *Normichthys operosus* (13%), and *Serrivomer beanii* (11%).

Table 1-2. Percentage of species caught most frequently at night in terms of biomass within each depth layer defined by the MRT. Indicator species are shown in bold.

Assemblage	Species	Relative biomass of species (%)
Epipelagic (20-175m)	<i>Myctophum punctatum</i>	22
	<i>Benthosema glaciale</i>	15
	<i>Stomias boa</i>	13
	<i>Lampanyctus crocodilus</i>	12
	<i>Ceratoscopelus maderensis</i>	10
Upper mesopelagic (175-700m)	<i>Xenodermichthys copei</i>	36
	<i>Lampanyctus crocodilus</i>	12
	<i>Argyrolepecus olfersii</i>	11
	<i>Notoscopelus kroyeri</i>	11
	<i>Arctozenus risso</i>	8
Lower mesopelagic (700-1000m)	<i>Lampanyctus crocodilus</i>	27
	<i>Xenodermichthys copei</i>	23
	<i>Stomias boa</i>	7
	<i>Arctozenus risso</i>	7
	<i>Maurolicus muelleri</i>	7
Bathypelagic (1000-2000m)	<i>Lampanyctus crocodilus</i>	19
	<i>Normichthys operosus</i>	13
	<i>Serrivomer beanii</i>	11
	<i>Benthosema glaciale</i>	9
	<i>Stomias boa</i>	7

Differences appeared between the indicator species of the shallow assemblages and those of the deeper assemblages in terms of biomass repartition along the water column at the intraspecific level (Table 1-3). *Ceratoscopelus maderensis* presented only 11% of its biomass in the epipelagic layer (20-175m) where it is the indicator species, whereas the species in the deepest assemblages (i.e. lower mesopelagic and bathypelagic) presented higher percentages (i.e. never less than 46%). Thus, although

Ceratoscopelus maderensis presented only 11% of its biomass in the epipelagic layer, it has a relatively high Dufrêne Legendre index (DLI = 60), which means that it was caught repeatedly (fidelity) in trawls conducted at a depth of less than 175 m. Three species of the bathypelagic assemblage (i.e. *Normichthys operosus*, *Bathylagus euryops*, and *Lampanyctus macdonaldi*) presented 100% of their biomass within this assemblage, meaning that they were never caught at depths less than 1000m. Thus, the lower DLI of *Bathylagus euryops* and *Lampanyctus macdonaldi* (DLI = 42 and 33 respectively) means that, although they were not caught in assemblages other than those to which they belong (specificity), they were not caught in all the trawls made below 1000m (fidelity).

Table 1-3. Percentage of biomass of each indicator species within the depth layer to which it belongs and its DLI.

Assemblage	Indicator species	Biomass of the species in the depth layer (%)	DLI
Epipelagic (20-175m)	<i>Ceratoscopelus maderensis</i>	11	60
Upper mesopelagic (175-700m)	<i>Xenodermichthys copei</i>	42	39
	<i>Cyclothone spp.</i>	88	62
Lower mesopelagic (700-1000m)	<i>Searsia koefoedi</i>	82	47
	<i>Lampanyctus crocodilus</i>	49	40
	<i>Arctozenus risso</i>	46	38
	<i>Gonostoma elongatum</i>	83	20
	<i>Normichthys operosus</i>	100	83
	<i>Serrivomer beanii</i>	65	44
Bathypelagic (1000-2000m)	<i>Bathylagus euryops</i>	100	42
	<i>Lobianchia gemellarii</i>	72	41
	<i>Nannobranchium atrum</i>	70	35
	<i>Lampanyctus macdonaldi</i>	100	33
	<i>Chauliodus sloani</i>	83	32
	<i>Maulisia maui</i>	96	28

3.5. Species' nocturnal water depth range distribution

Different water depth distribution patterns were observed during the night based on their biomass per unit effort, with species such as *Gonostoma elongatum* or *Lampanyctus macdonaldi* having a restricted distribution and others like *Arctozenus risso* or *Ceratoscopelus maderensis* found along the entire water column (Figure 1-5). However, species sampled over a wide range of depths still showed a peak in biomass at a certain depth. For example, *Lampanyctus crocodilus* was found between 100 and 2000m but the peak of its biomass was found around 800m.

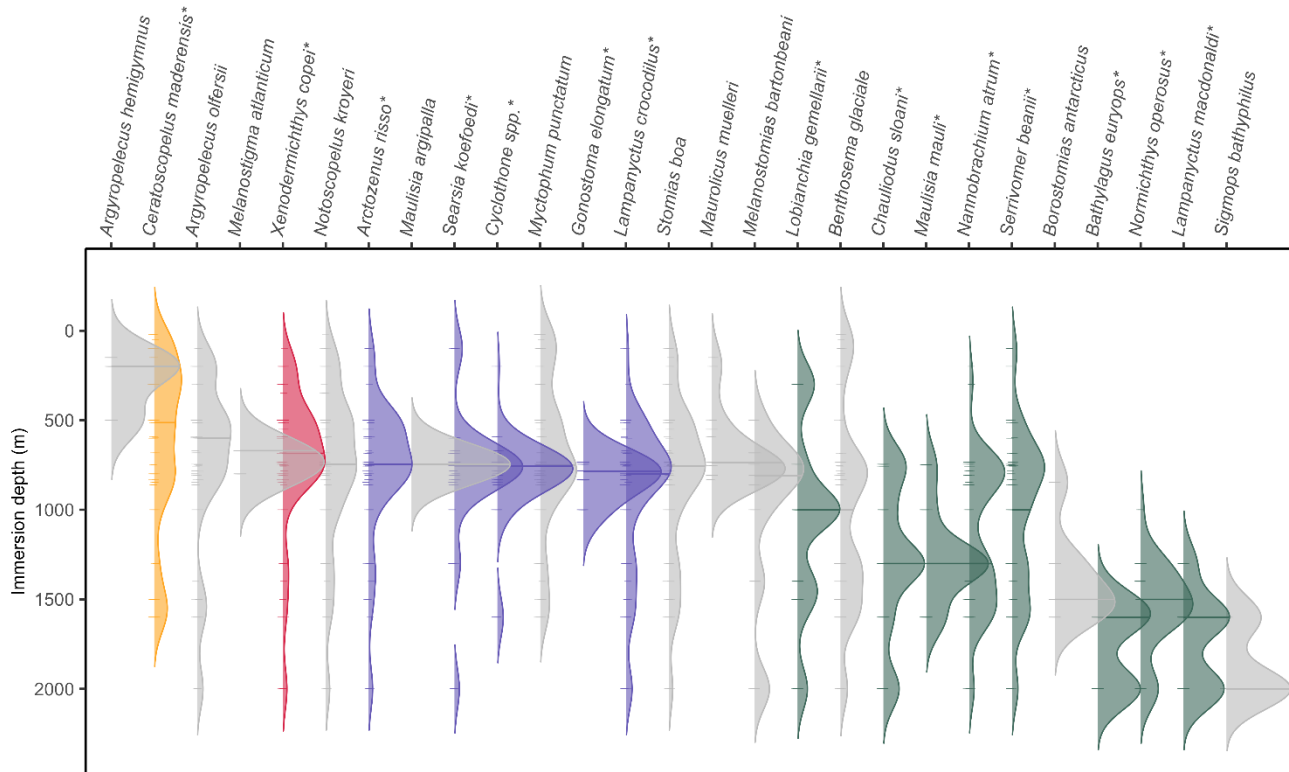


Figure 1-5. Vertical nocturnal distribution of the most important species of the community in terms of biomass per unit effort. Colours represent the assemblages defined by the MRT: the epipelagic assemblage in yellow, the upper mesopelagic assemblage in red, the lower mesopelagic assemblage in purple, and the bathypelagic assemblage in green. Species in grey are those with significant biomass but are not indicative of any assemblages. The asterisk indicates the indicator species. Vertical lines denote the median of the respective distribution of each species. The dashes show where each species was found and permit to visualize the depths not sampled.

3.6. Relations between indicator species and their Environment

Globally, two to five environmental variables significantly explained the biomass distribution of indicator species in each of the four assemblages (Figure 1-6 and Table 1-4). The epipelagic assemblage showed two significant relationships with a total explained variance of 22%. The most significant variable was the bottom proximity (p-value =0.009) with the highest biomass values at 2500m from the seafloor and the second was the zooplankton surface concentration (p-value =0.017) with an increase of fish biomass with zooplankton concentration.

Table 1-4. Explained variance of global GAM models and the significance of each environmental variable at night.

Assemblage	% of explained variance	Environmental variables	p-values
Epipelagic (20-175m)	22	Proximity to the bottom	0.009
		Surface zooplankton concentration (1-month average)	0.017
Upper mesopelagic (175-700m)	67	Proximity to the bottom	5.18×10^{-6}
		Surface zooplankton concentration (1-month average)	4.84×10^{-5}
		Roughness	8.12×10^{-5}
		Current velocity (1-month average)	0.015
Lower mesopelagic (700-1000m)	54	Bottom depth	2.04×10^{-5}
		Proximity to the bottom	7.36×10^{-5}
		Surface chlorophyll concentration (6-month average)	0.002
		Current velocity (1-month average)	0.003
		Roughness	0.006
Bathypelagic (1000-2000m)	76	Bottom depth	2×10^{-16}
		Proximity to the bottom	2×10^{-16}
		Surface chlorophyll concentration (6-month average)	1×10^{-41}
		Current velocity (3-month average)	4×10^{-4}

Four significant variables explained the biomass distribution of the upper mesopelagic assemblage: proximity to the bottom (p-value = 5.10^{-6}), roughness (p-value = 8.10^{-5}), surface zooplankton concentration (p-value = 5.10^{-5}) and current velocity (p-value = 0.015) for a total deviance explained of 67%. Overall, the biomass increased with increasing proximity to the bottom, roughness, and current velocity. Five variables accounted for 54% of the variance explained for the lower mesopelagic assemblage: proximity to the bottom (p-value = 7.10^{-5}), bottom depth (p-value = 2.10^{-5}), surface chlorophyll concentration (p-value = 0.002), current velocity (p-value = 0.003), and roughness (p-value = 0.006). The biomass of the lower mesopelagic assemblage increased as bottom depth and terrain roughness increased. Higher biomass values were found near the seafloor. Finally, the bathypelagic assemblage model had a total explained variance of 76 % with bottom depth (p-value = 2.10^{-16}), proximity to the bottom (p-value = 2.10^{-16}), surface chlorophyll concentration (p-value = 1.10^{-4}) and current velocity (p-value = 4.10^{-4}) being the four environmental variables that best explained the assemblage biomass distribution. The biomass of the bathypelagic assemblage increased with increasing proximity to the bottom and the bottom depth. Moreover, bathypelagic assemblage biomass decreased with decreasing values of surface chlorophyll concentration and current velocity values.

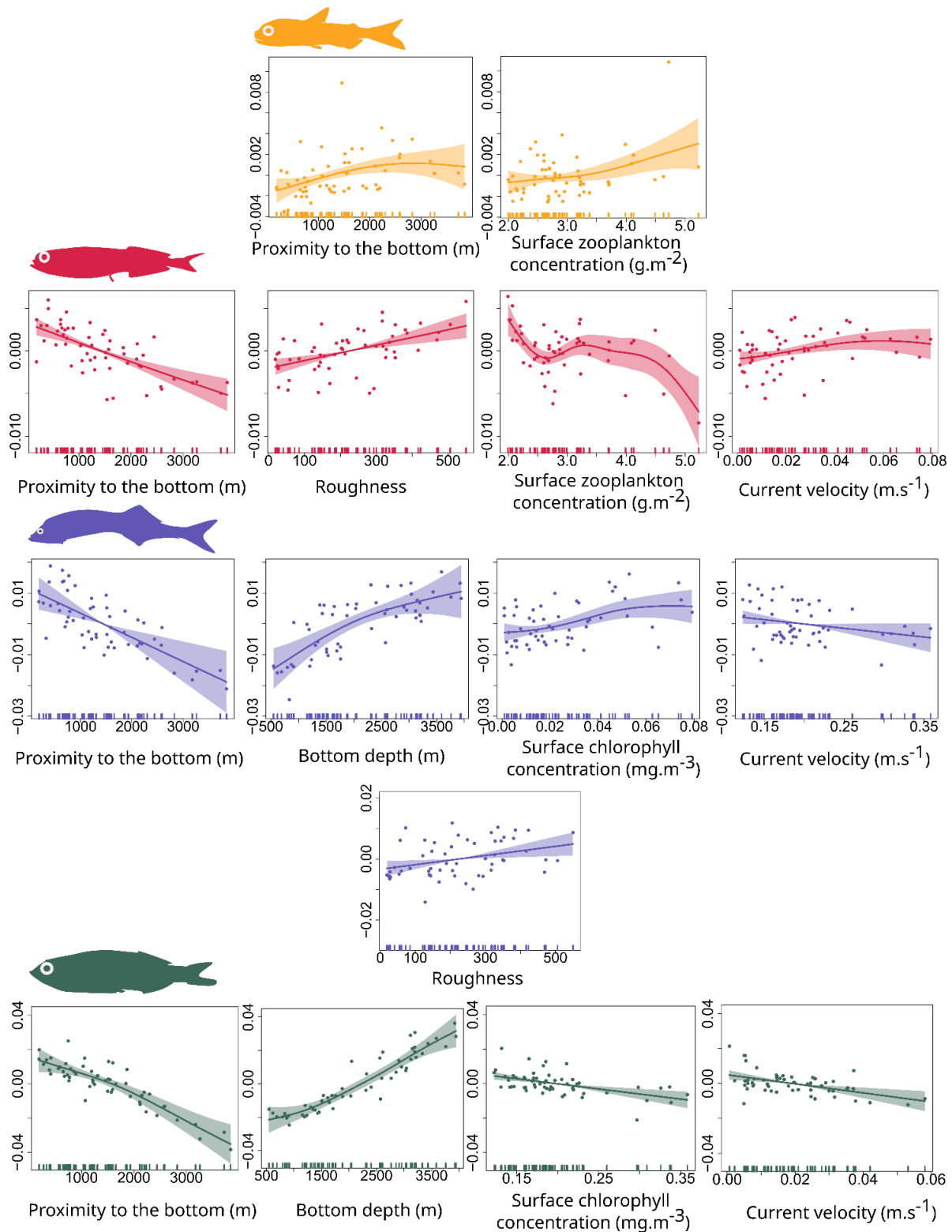
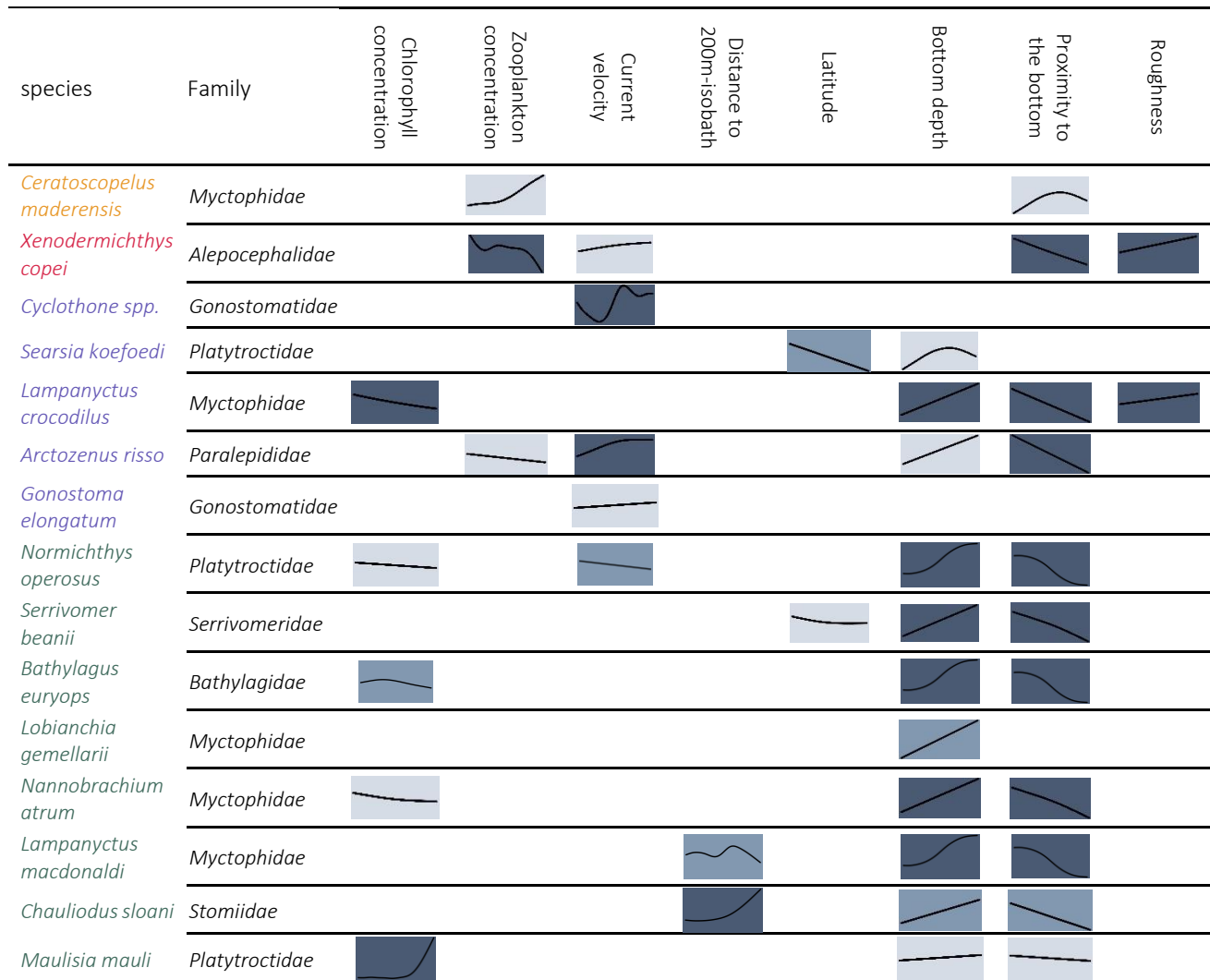


Figure 1-6. Significant effect of environmental variables on each MRT-defined assemblage at night including all indicator species. The colours represent the assemblages defined by the MRT: the epipelagic assemblage in yellow, the upper mesopelagic assemblage in red, the lower mesopelagic assemblage in purple, and the bathypelagic assemblage in green. Variables are ranked according to their relative importance in explaining the deviance.

In each assemblage, species presented different relationships with the environment (Table 1-5).

Table 1-5. Individual GAM models performed on each indicator species. Colours represent the significance of the relationship with the darker being the more significant. The shape of the relation is also represented.



In the lower mesopelagic assemblage, current velocity emerged as a significant explanatory variable for more than 60% of the species composing this group (*Cyclothone spp.*, *Arctozenus risso*, and *Gonostoma elongatum*). In addition, 60% of the species in this assemblage showed at least one significant relationship with a bathymetric variable (i.e. depth of the bottom, proximity to the bottom, or terrain roughness).

In the bathypelagic assemblage, all the species showed a significant relationship between biomass distribution and bottom depth, and only *Lobianchia gemellarii* showed no significant relationship with proximity to the bottom. The surface chlorophyll concentration, on the other hand, had a significant influence on the biomass distribution of only half the species in this assemblage.

4. Discussion

Immersion depth was the most structuring variable for the deep-pelagic fish community at night on the continental slope of the Bay of Biscay. This finding was already observed at a larger scale for deep-pelagic fish communities (Angel, 2003; Collins et al., 2008; Sutton et al., 2008, 2010; Ross et al., 2010; Cook et al., 2013; Kenchington et al., 2020; García-Seoane et al., 2021). Three environmental ruptures (i.e. major changes in community composition associated with an environmental factor) were identified along the water column defining four assemblages: the epipelagic assemblage (0-175m), the upper mesopelagic assemblage (175m-700m), the lower mesopelagic assemblage (700-1000m), and the bathypelagic assemblage (>1000m). Furthermore, in contrast to the open ocean paradigm where the biomass of meso- to bathypelagic fishes decreases with depth, here almost 70% of the species showed an increase in biomass with proximity to the bottom. The echograms also showed a low density of individuals at the surface at night, which differs from open ocean models where nocturnal migration results in a high density of mesopelagic organisms in the epipelagic layer.

Differences in environmental factors influencing the nocturnal distribution of indicator species were observed along the water column. Species composing the shallowest layers of the water column were primarily influenced by dynamic variables (i.e. surface zooplankton concentration and current velocity). High zooplankton biomass near the surface of the Bay of Biscay results in vertical movement of migratory mesopelagic fish at night to feed in these shallow layers (Robison, 2003; Zarauz et al., 2007). In our results, *Ceratoscopelus maderensis* was defined as the indicator species of the epipelagic zone, which means that it was repeatedly caught in trawls carried out above a depth of 175 m during the night. Furthermore, *C. maderensis* showed a decrease in biomass with proximity to the bottom, so this species is preferentially distributed near the surface at night in the Bay of Biscay suggesting that it migrates to the surface at night to feed. This pattern has already been demonstrated in the western Mediterranean where *C. maderensis* was one of the most abundant species near the surface at night (Olivar et al., 2012). However, *C. maderensis* has also been reported to form aggregations near the bottom on the slopes of North Carolina and Virginia, which probably implies a site-dependent distribution for this species (Gartner et al., 2008).

The species with deeper distribution (>200m) showed more significant relationships with topographic and bathymetric variables. Three of the four defined assemblages showed a significant

increase in their biomass with proximity to the bottom. Aggregation of meso and bathypelagic fish near the bottom has been previously observed in areas of interaction between their distribution and steep topography (Parin and Golovan, 1976; Golovan, 1978; Merrett, 1986; Hulley, 1989; Mauchline and Gordon, 1991; Reid et al., 1991; Koslow, 1996; Porteiro and Sutton, 2007; Sutton et al., 2008). Changes in species composition have already been described with increasing proximity to continental slopes, defining a mesopelagic boundary layer community (Reid et al., 1991; Wilson and Boehlert, 2004; Benoit-Bird and Au, 2006). The sources of this phenomenon may be multiple: concentration of food resources in the BBL, ontogenetic changes in the vertical distribution of some species, importance of the bottom for reproduction, concentration of individuals in areas of high relief, and active horizontal migration.

At a distance of 100 to 1000m from the seafloor, a benthopelagic layer can be observed. This is a homogenous stratum where a nepheloid layer of suspended particle matter is present and enhances the biomass of zooplankton (Weatherly and Kelley, 1985; Sutton et al., 2008). As a result, some species accumulate in this layer for feeding, particularly in slope areas, mid-oceanic ridges, and seamounts (Reid et al., 1991; Porteiro and Sutton, 2007; Sutton et al., 2008). In particular, large numbers of planktonic predators such as lanternfish have been observed, which in turn attract higher trophic level feeders, including species such as *Stomias boa* and *Chauliodus sloani* (Gartner et al., 2008).

The increase of biomass at the proximity of the seafloor can be also explained by the ontogenetic shift in the vertical distribution of some species, with juveniles occurring at shallower depths than larger adult individuals (Badcock and Merrett, 1976; Willis and Percy, 1980; Auster et al., 1992; Vinnichenko, 1997). This is the case for *Serrivomer beanii*, an indicator species in the bathypelagic assemblage, which in the Mid-Atlantic Ridge region, had its largest individuals in its population near the bottom, suggesting an affinity of adults for the benthopelagic layer (Sutton et al., 2008). In the Gulf of Mexico, *C. sloani* also showed this relationship with larger individuals found at greater depths (Eduardo et al., 2020b) even forming aggregations on the bottom along the continental slope of the south-eastern U.S (Gartner et al., 2008). These two species, therefore, showed the same patterns in the Bay of Biscay slope with a significant increase of their biomass near the bottom at night. Indeed, large adults of some species stop migrating and adopt a benthopelagic life strategy (Stefanescu

and Cartes, 1992). This is well-established for *Lampanyctus crocodilus* which also showed a positive relationship with bottom proximity in our results. In fact, in the Mediterranean Sea adults adopt a benthopelagic behaviour and feed on epibenthic prey at the BBL (Stefanescu and Cartes, 1992; Valls et al., 2014b). This could be a consequence of a reduced or atrophied swim bladder, thus influencing feeding behaviour (Butler and Pearcy, 1972; Gartner Jr et al., 1997). In the north-eastern Atlantic, *Normichthys operosus*, *Bathylagus euryops*, *Melanostigma atlanticum*, and *Xenodermichthys copei* have been sampled in both pelagic and demersal trawls (Markle and Wenner, 1979; Mauchline and Gordon, 1983, 1984). In addition, all individuals of *X. copei* in pelagic trawls were juveniles and the largest fish were caught at the deeper stations in the Rockall Trough (Mauchline and Gordon, 1983). Similarly, the largest individuals of *B. euryops* have been reported in demersal trawls, suggesting a benthopelagic affinity of this species (Mauchline and Gordon, 1983). As all these species have shown a significant increase in biomass with proximity to the bottom in our models, these same phenomena certainly also occur in the continental slope zone of the Bay of Biscay.

Demersal spawning behavior has already been observed for oceanic pelagic fish species such as *X. copei* and *M. atlanticum* (Markle and Wenner, 1979). In particular, adults of *M. atlanticum* adopt a benthic behavior during the spawning period, and egg fertilization takes place in burrows located below the seafloor surface (Silverberg et al., 1987; Silverberg and Bossé, 1994; Dallarés et al., 2021). A concentration of individuals close to the bottom may favour reproduction for some species (Sutton et al., 2008). As the surveys took place during the *X. copei* spawning period (October-November), we observed a large number of spawning individuals, which may partly explain the relationship between this species and the proximity to the bottom found in our results. An alternative theory of increased near-bottom biomass in relation to demersal spawning behavior has been described for the Mid-Atlantic Ridge population. This theory states that the concentration of larger males with larger (and more fecund) females near the bottom increases the relative percentage of offspring from the best of the gene pool (Sutton et al., 2008). This theory attempts to explain the balance between the energetic benefit associated with BBL feeding behavior and the mortality cost caused by demersal predation over a longer period.

X. copei, *M. atlanticum*, and *L. crocodilus* also presented significant positive relationships with the increasing terrain roughness. These zones may provide important refuges from predation, feeding

areas, and spawning zones for these species with a strong relationship to the seafloor (Møller and Jørgensen, 2000; Bouchet et al., 2017; Farmer et al., 2017; Pirtle et al., 2019; Borland et al., 2021). Several species of Platyroctidae (*Normichthys operosus* and *Maulisa mauli*) and one species of Bathylagidae (*B. euryops*), which exhibited a relationship with proximity to the bottom, have also been reported to be associated with steep topographies (Kukuev, 1982, 2002). On the continental slopes of the northwest Atlantic, *B. euryops* and *S. Beanii* presented a greater number of catches in areas of high sponge abundance (Kenchington et al., 2013). Aggregations of sponges have also been reported in the Bay of Biscay, which could partly explain the distribution of these species on the slope (Howell et al., 2016). Several myctophid species caught at high densities in our study were also associated with the shelf edge of the Mid-Atlantic Ridge: *L. crocodilus*, *Lobianchia gemellarii*, and *Benthoosema glaciale* (Fock et al., 2004). *Arctozenus risso* (Paralepididae) and *Maurolicus muelleri* (Sternoptychidae) are also known to be particularly common species on continental slopes (Gartner et al., 2008; Chouinard and Dutil, 2011; Feagans-Bartow and Sutton, 2014; Ross et al., 2015; Bañon et al., 2016). Thus, all these relationships show that the Bay of Biscay is no exception in the patterns of the specific distribution of meso to bathypelagic fish species near continental slopes.

Active horizontal migrations during nocturnal ascent near the slope have been reported for this community (Benoit-Bird et al., 2001). This may partly explain the almost universal increase in species biomass with proximity to the bottom in our results. Indeed, as the sampling was carried out at night, some species may have migrated horizontally near the slope. Near continental slopes, land-based nutrient inputs can enhance the available food supply for the deep-pelagic fish communities. These horizontal aggregations have been shown to be correlated with bathymetric slopes and current patterns (Roden, 1987; Brodeur and Yamamura, 2005). In particular, large micronekton aggregations have been observed in submarine canyon areas (Genin, 2004).

All these slope-specific behaviours may explain the particular nocturnal distribution of the species observed in our results. Indeed, in the open ocean, many mesopelagic species enter the epipelagic layer to feed at night (Robinson et al., 2010; Sutton, 2013). Although our sampling was conducted at night, few species were found in the epipelagic layer, with only one species defined as an indicator species for this layer (i.e. *C. maderensis*). This means that the vast majority of species do not regularly migrate to the epipelagic zone to feed at night in our study area. This was also suggested

in the night-time acoustic backscatter echograms taken during sampling, with low acoustic detection observed in the epipelagic zone, contrasting with the aggregation observed near the bottom (Figure 1-7). This observation thus contrasts with echograms from the open ocean, which show a higher abundance in the epipelagic layer (Klevjer et al., 2016).

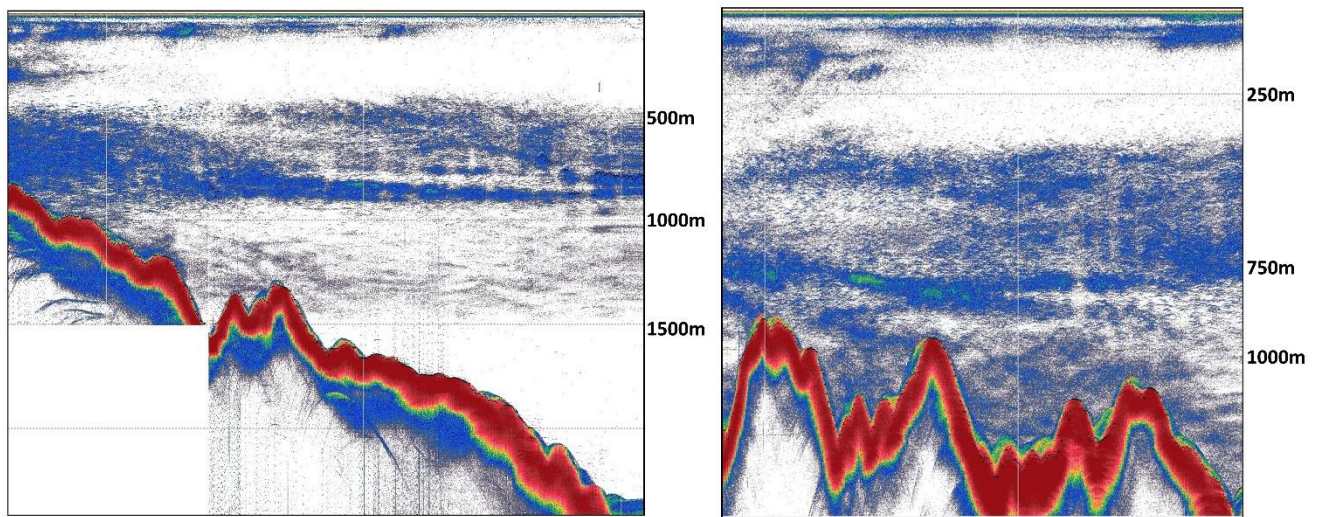


Figure 1-7. Examples of echograms of acoustic backscatter showing pelagic-benthic interactions during night-time trawling in the Bay of Biscay at 38kHz (Simrad EK80). The acoustic backscatter strength is measured in Sv (dB) during the fishing operation. The x-axis is in local time, so each facet represents approximately a distance of 5 nautical miles covered in 2 hours.

Differences in vertical distribution between steep topography and the open ocean have already been observed (Sutton et al., 2008; Eduardo et al., 2020b; Duncan et al., 2022). In the Atlantic, in association with the ridge, several meso and bathypelagic species have shown a deeper vertical distribution than previously reported (Sutton et al., 2008). In contrast, in a large submarine canyon off the coast of Nova Scotia, several deep-pelagic fishes showed an elevation or truncation of their vertical distribution in association with the canyon head (Kenchington, 2018). Although the data from our study could not identify a downward extension of the vertical distribution of the majority of species (the deepest trawl was at 2000 m), specific nocturnal distributions were observed for certain species in relation to the specific slope and canyon topography of the Bay of Biscay. Firstly, some species showed an elevation in their nocturnal vertical distribution compared with the open sea areas. For example, *S. beanii*, which is usually caught between 800 and 2500m (Mauchline and Gordon, 1984; Maul, 1990), was caught up to the epipelagic layer in our study area. Interaction with topography has probably elevated the distribution of this species, as previously observed in a submarine canyon for the largest

individuals of this species (Kenchington, 2018). The same phenomenon was observed for the *Cyclothone* genus, which was captured at depths of less than 200m. This elevation has also been reported in a submarine canyon in Nova Scotia (Kenchington, 2018). Generally found between 500 and 3000m in the North Atlantic, *B. euryops*, on the other hand, was found at greater depths with the shallowest sampling at 1000m (Mauchline and Gordon, 1983; Cohen, 1984). Another example of an upper truncation of the vertical distribution of species is that of *C. sloani* which, in our study area, was defined as an indicator species of the bathypelagic assemblage and whose shallowest occurrence was around 500 m depth with a biomass peak below 1000 m depth. This pattern contrasts with that found for this species in open ocean areas where individuals have been recorded in epipelagic waters (Eduardo et al., 2020b). Tropical areas are an exception: the species has only been observed there from 400m depth and Eduardo et al. attributed this pattern to the higher water temperature; here, we have shown that topography, probably linked to trophic aspects also modify the nocturnal vertical distribution of this species (Gartner et al., 2008). All these observations support the hypothesis that the nocturnal distribution of meso and bathypelagic fish species is modulated by the specific characteristics of the continental slope. In terms of species diversity, comparisons between studies are difficult due to differences in the fishing gear used. However, it seems that our results show a slightly lower number of species than the Atlantic studies in the open sea area (García-Seoane et al., 2021).

Some limitations that could affect the interpretation of the results must be considered. In fact, in this study, we used data obtained in the fall over 17 years. Although the effect of time cannot be excluded, having a long data set allowed us to obtain a longitudinal picture of the composition of this community. Since the data for this study were only obtained at night, the definition of deep-pelagic fish community structure presented here cannot be extrapolated to daytime. Another limitation is the non-proportional sampling of the water column. The selectivity of a fishing gear varies with its characteristics and likely influences the diversity and size of the individuals collected. The size of the pelagic trawl used in this study (192m long, 24 x 58m open mouth pelagic trawl) associated with a high fishing speed (4kn) allowed for efficient sampling of a large range of midwater species, including large *S. beanii* or even *Aphanopus carbo*. The small mesh (20mm) in the cod-end, combined with the presence of a long sock at the end of the trawl (12 mm mesh) allowed also the sampling of small individuals, including fish belonging to the *Cyclothone* genus for instance. In this study, 95 different

species were thus caught with individuals ranging in total length from 2 to over 70 cm. The principal drawback of a pelagic trawl of this size at the depths which we explored is the absence of an opening or closing mechanism generating potential sampling contamination. However, the decrease in vessel velocity during the descent and ascent of the trawl combined with the acceleration during the fishing period optimized catches at the target depth and reduced the contamination of species at shallower depths. In addition, the study of the vertical distribution showed that each species had only one mode of distribution at depth. Indeed, if significant contamination from the upper layers had occurred, one or more species would have one mode of distribution at depth (due to contamination of individuals caught during the descent or ascent of the trawl but counted at a higher target depth) and one mode of distribution in the upper layers (corresponding to their actual distribution), which was not observed here. We cannot therefore exclude some cases of contamination implying that we may be overestimating the presence of shallow species in the deeper water layers, but the general vertical distribution patterns observed for the species presented here are unlikely affected. Furthermore, the general vertical distribution of species described here is largely congruent with data available in the literature. Beyond these limitations, this is the first study including data from 56 trawls over a fishing depth range of 2000 m, which allows us to clarify the general vertical distribution patterns of the deep-sea pelagic fish community in the Bay of Biscay.

Proper sampling covering night-day cycles and including other sampling approaches (*e.g.* acoustics) would likely help confirm the potential mechanisms explaining the water depth distribution of mesopelagic fish in our study. Multiple environmental factors influence migratory behavior: light which controls the extent of vertical migration (Balino and Aksnes, 1993; Staby and Aksnes, 2011), the lunar cycle (Linkowski, 1996; Benoit-Bird et al., 2009) and food availability (Gjørseter and Kawaguchi, 1980). Satiation status also appears to have an impact at the intraspecific level (Carmo et al., 2015; Bos et al., 2021). The Hunger-Satiation hypothesis states that not all individuals in a population migrate at night; individuals, with high stomach fullness indices, do not migrate (Pearre, 2003; Carmo et al., 2015). That phenomenon, in addition to the ontogenetic shift in vertical distribution, might explain why some species were sampled throughout the water column. The study of the trophic ecology of these species linked with the migration behavior would therefore also help shed light on the mechanism involved in the water depth distribution of deep-pelagic species.

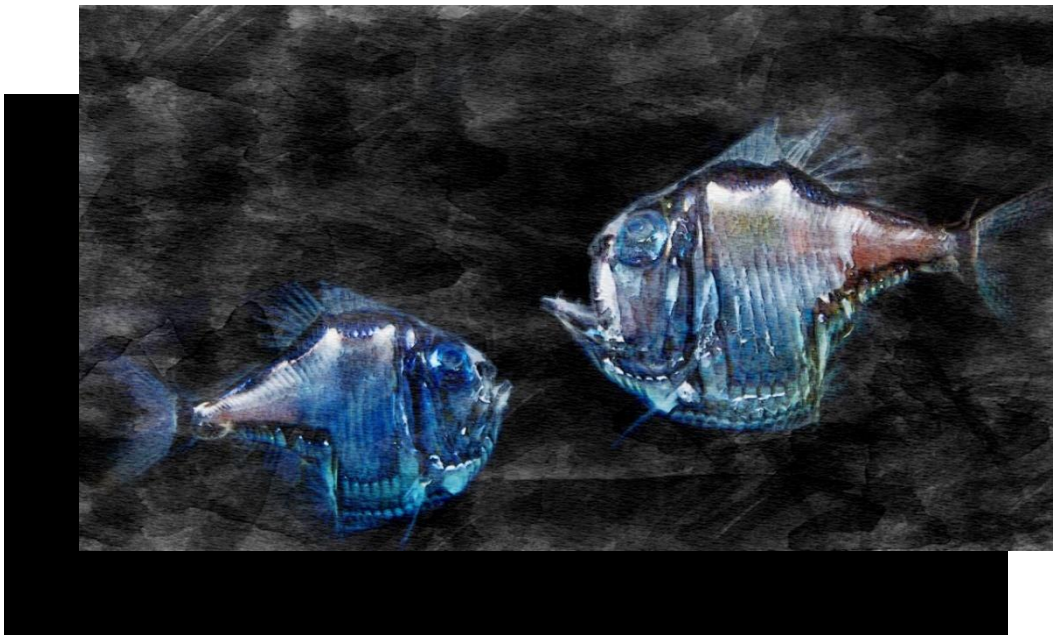
Although the deep pelagic realm is the least understood ecosystem on the planet, it is already threatened in several ways (by fishing, seabed mining, and climate change), hence the importance of rapidly increasing our knowledge of these communities (Martin et al., 2020). Our results show an increase in the biomass of the deep pelagic fish community near the bottom and an atypical nocturnal vertical distribution on the slope. These results could influence the transition of carbon and energy flows in marine ecosystems (Company et al., 2008). In particular, deep-pelagic fish communities in slope waters may be believed to be highly productive, reflecting the generally high productivity in these areas of interface of coastal and oceanic habitats (Brodeur and Yamamura, 2005). In particular the Bay of Biscay slope, this community serves as an important source of prey in this key area where marine top predators are abundant (Pusineri et al., 2005, 2007; Laran et al., 2017; Pettex et al., 2017). A better knowledge of the factors that determine the nocturnal vertical distribution of this deep-pelagic community is therefore essential for understanding the functioning of the food web in this large Special Area of Conservation (SAC). Future conservation measures must therefore consider all three dimensions of marine habitats to be effective in protecting the ecosystem as a whole (Venegas-Li et al., 2018; Gámez and Harris, 2022).

Data Availability

The raw data supporting the conclusions of this chapter are publicly available through the PANGAEA platform: <https://doi.pangaea.de/10.1594/PANGAEA.959551>

Chapitre 2 - Ontogenetic shift or not?

Different foraging trade-offs within the meso-
to bathypelagic fish community



1. Introduction

Ontogenetic shifts in marine predators are major drivers in the mechanisms underlying ecosystem structure and functioning (Rudolf and Rasmussen, 2013; Nakazawa, 2015). They are also considered a determinant of food web diversity and stability, community resilience, and responses to disturbance (de Roos and Persson, 2013; Nakazawa, 2015; Nilsson et al., 2018). Although the importance of these ubiquitous changes in ecosystems is well established, community ecology has traditionally been based on species, thereby erasing intraspecific differences. During ontogeny, individuals must make trade-offs between their dietary needs, conditions necessary for reproduction, and predator avoidance (Sutherland, 1996; Kimirei et al., 2013; Sánchez-Hernández et al., 2019). All of these needs and trade-offs change over the lifetime of species, requiring them to find habitats that meet their needs (Werner and Gilliam, 1984; McNamara and Houston, 1986; Werner and Hall, 1988; Ludwig and Rowe, 1990). Thus, shifts in diet and habitat use during ontogeny can lead to segregation in the niches occupied by individuals of a species and thus reduce intraspecific competition within a population (Sánchez-Hernández and Cobo, 2012; Wollrab et al., 2013). At the interspecific level, these shifts also play an important role in competitive interactions and niche partitioning (Woodward and Hildrew, 2002; Woodward et al., 2005; de Roos and Persson, 2013).

Fish species often show a close relationship between body size, which is generally related to the size of the mouth opening, and the size of the prey they consume (Dunic and Baum, 2017). Therefore, ontogenetic shifts in resource use are very common in fish (Werner and Gilliam, 1984). In general, early-stage fish feed on phytoplankton, zooplankton, or small invertebrates (Nunn et al., 2012). As their vision and swimming performance improve, fish begin to feed on macroinvertebrates and fish (Huss et al., 2013). These shifts in food types are often associated with or caused by a shift in habitat use (Sánchez-Hernández et al., 2019; Werner and Gilliam, 1984). For instance, a change in diet may be the consequence of a change in habitat to cope with new predation risks during ontogeny, or it may be caused by the search for more nutritious and/or more abundant prey (Sánchez-Hernández et al., 2019). An example of the consequences of a change in diet dictated by a change in habitat use is that of small individuals of the Gobiidae species *Pterogobius elapoides*, feeding on abundant pelagic copepods in the water column where predation is high. As the individuals grow larger, they limit the

risk of predation by feeding only on prey found in the sediments of the sandy bottom (Choi and Suk, 2012).

Meso- and bathypelagic fish communities (i.e., inhabiting the mesopelagic zone between 200-1000 m, and the bathypelagic zone below 1000 m depth) are believed to dominate the fish biomass worldwide (Irigoien et al., 2014). The deep pelagic food web is supported solely by phytoplankton primary production, resulting in the segregation of deep pelagic fish trophic niches essentially along a continuum of trophic levels (Stowasser et al., 2012; Valls et al., 2014b; Chouvelon et al., 2022; Richards et al., 2023). Three main food guilds are generally described for midwater fishes: zooplanktivores (e.g., Myctophidae), micronektivores (e.g., Stomiidae), and generalists (e.g., Eurypharyngidae, in which a wide variety of prey even benthic, is found) (Gartner Jr et al., 1997; Drazen and Sutton, 2017). In addition to these guilds, two main foraging strategies are employed by deep pelagic fishes. Part of the community performs diurnal vertical migrations (DVM) at night from the mesopelagic to the epipelagic zone to feed (Clarke, 1963; Badcock and Merrett, 1976; Watanabe et al., 1999). This migratory behaviour is very energy-consuming but is compensated by the high prey density in the epipelagic zone and the reduction of visual predation at night. The non-migratory part of the community remains at depth. The non-migratory species thus live in an environment of low prey density but have lower energy requirements and a low risk of predation (Marshall, 1980; Herring, 2002).

Most deep pelagic species, particularly Myctophidae, spend their larval stage in the productive epipelagic zone (Ahlstrom, 1959; Loeb, 1979; Moser and Smith, 1993; Sassa et al., 2002, 2004; Bowlin, 2016). Within species, individual size generally increases with depth, indicating ontogenetic vertical migrations (Loeb, 1979; Kawaguchi and Mauchline, 1982; Badcock and Araujo, 1988; Sassa and Kawaguchi, 2006). This ontogenetic shift along the vertical habitat is related to shifts in morphology and pigmentation (i.e., individuals becoming darker, having photophores, and well-developed musculature) (Moser, 1996). Similarly, the adults of several species have a different depth distribution according to size, with larger individuals at deeper depths (Badcock and Merrett, 1976; Loeb, 1979; Willis and Percy, 1980; Auster et al., 1992; Stefanescu and Cartes, 1992; Sassa et al., 2007; Fanelli et al., 2014). These ontogenetic shifts in habitat use may be related to shifts in diet, as in the case of *Lampanyctus crocodilus*, where senescent adults stop migrating and adopt benthopelagic behavior by feeding on epibenthic prey (Stefanescu and Cartes, 1992; Fanelli et al., 2014).

Intraspecific trophic changes can be monitored from stable isotope signatures (Hammerschlag-Peyer et al., 2011; Layman et al., 2012). For decades, stable isotope ratios of nitrogen ($\delta^{15}\text{N}$ values) have been widely used as an indicator of species' trophic level (Peterson and Fry, 1987; Zanden and Rasmussen, 2001; Drazen and Sutton, 2017). This is because nitrogen isotopes undergo a significant and relatively predictable level of fractionation during trophic transfer between a predator and its prey, leading to a difference in $\delta^{15}\text{N}$ values ($\sim 3\text{-}5\%$) between two theoretical trophic levels and allowing the relative trophic level of species to be inferred from their $\delta^{15}\text{N}$ values (Peterson and Fry, 1987; Post, 2002; Hussey et al., 2014). Since the pelagic ecosystem has a wide depth gradient, microbial degradation of organic matter in suspended particles also influences $\delta^{15}\text{N}$ values, with increasing values with depth (Saino and Hattori, 1980; Casciotti et al., 2008). An enrichment in ^{15}N is thus found in zooplankton at greater depths (Koppelman et al., 2009; Hannides et al., 2013) and in deep benthic communities (Bergmann et al., 2009; Trueman et al., 2014).

Only a few studies examined the effect of species size and depth on $\delta^{15}\text{N}$ values of deep pelagic fish, such as in the Iberian Peninsula (North-East Atlantic) and the Gulf of Mexico (North-West, Atlantic) (Romero-Romero et al., 2019; Richards et al., 2023), but never at the intraspecific scale. Here, we aimed to quantify the intraspecific influence of body size on nocturnal habitat use and trophic ecology for 12 deep pelagic fish belonging to nine genera, including both migratory and non-migratory species from the Bay of Biscay, NE Atlantic. Differences in nocturnal body size distribution within each species were deduced from trawling data, while trophic shifts were studied using stable isotopes of nitrogen measured in fish muscle tissues. The first objective was to investigate if a shift in body size with depth (i.e., relationships between individual size and sampling depth) is observed at both the intraspecific and community level. The second objective was to explore if a shift in the trophic ecology is also observed in relation to body size (from the measurement of $\delta^{15}\text{N}$ values). To this end, the influence of individual size and/or sampling depth on $\delta^{15}\text{N}$ values was quantified for each species.

2. Materials and methods

2.1. Sampling

Organisms were collected by epi- to bathypelagic trawling in canyons of the Bay of Biscay continental

slope (North-East Atlantic) during EVHOE scientific cruises (“*Evaluation Halieutique de l’Ouest de l’Europe*”; <https://doi.org/10.18142/8>) that took place in autumn between 2002 and 2021. Trawls were conducted at night between 25 m to 2000 m depth at 25 stations (Figure 2-1). The trawl net was 192 m long with a headline of 76 m and a foot rope of 70 m. The average vertical mean mouth opening was about 24 m and the horizontal opening of about 58 m. The mesh size gradually decreased from a very large 8 m (stretched mesh) at the mouth to 20 mm (stretched mesh) in the cod-end. To allow the capture of very small specimens, the trawl was also equipped with a 7.5 m long sock with a 12 mm mesh size. Each trawl was performed at a specifically chosen immersion depth, meaning that only one depth was sampled at each station. The choice of trawl depth was determined by the depth of the scattering layer, with the additional goal of encompassing a broad depth range across the dataset. Consequently, some trawls were conducted significantly above or below the deep scattering layer. Once the trawl reached the selected depth it was towed horizontally (i.e., constant immersion depth) for 1 hour at 4 kn. In addition, trawling was always carried out in complete darkness. The aim was to check whether the size distribution of a species remains consistent throughout the water column, particularly during the night feeding period when most species are active feeders (Eduardo et al., 2021; Kinzer and Schulz, 1985). Night sampling therefore presented optimal conditions for examining ontogenic movements.

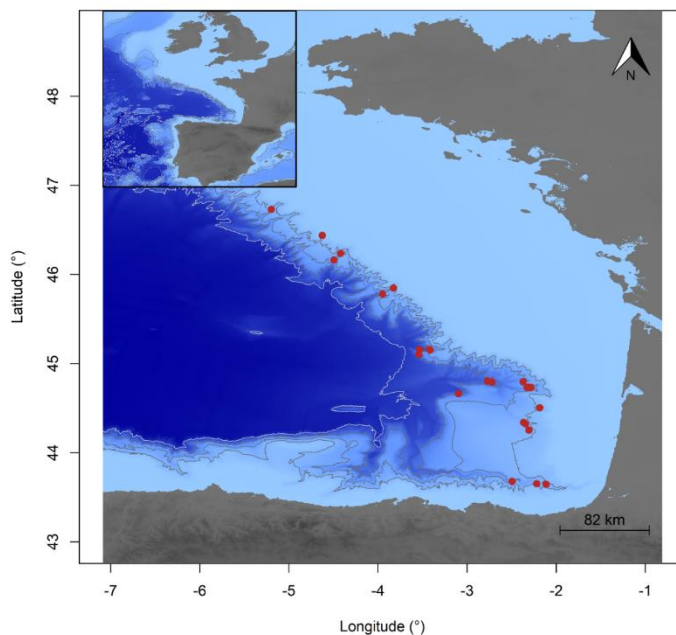


Figure 2-1. Trawl hauls’ spatial position in the Bay of Biscay. The background blue colours represent the seabed depth (where lighter colours are shallower). The lines represent 1000, 2000, 3000, and 4000 m isobaths. The scale represents the number of kilometres for one degree of longitude (= 82km).

2.2. Datasets

Two different datasets were used to study ontogenetic changes in deep-sea pelagic fish species from the Bay of Biscay. The trawling (first) dataset included all data collected by trawls (i.e. number of individuals per species per sampling depth and total body length of each individual; $n = 4165$). To study the trophic aspects of ontogeny (see methodology below), muscle sampling was performed on 12 species of the trawling dataset to access the $\delta^{15}\text{N}$ values of individuals ($n = 682$). This constituted the isotopic (second) dataset. The size measured for the individuals sampled for the isotopic dataset was the standard length. As a result, size measurements differed between the two datasets. Total length was used for all catches made on board, as this is the usual measurement on fishing campaigns. However, the measurement used for individuals processed in the laboratory for analysis of $\delta^{15}\text{N}$ values was standard length, as mesopelagic fish often have damaged tails. Based on repeated measurements of the species studied in the laboratory, we were able to compare the two measurements between our datasets. The conversions are available in the R code supplied. The size distribution of the individuals composing the species included in the isotopic dataset was representative of the size distribution observed in the trawling dataset (see appendix 1).

2.3. Nitrogen stable isotope analysis

A total of 682 muscle samples belonging to 12 of the most abundant species (seven migratory and five non-migratory) were collected. For each individual, the standard length (cm) was measured on board and a small piece of muscle was collected and frozen at -20°C . To have sufficient material for stable nitrogen isotope analysis, the muscles of the smallest individuals were pooled. Within each of these pools, the individuals were of equivalent size and were sampled at the same depths. At the laboratory, muscle samples were freeze-dried (72h). To reduce the samples to a fine powder, samples containing a single individual were manually homogenised, while samples containing a pool of individuals were homogenised using a ball mill (MM400 Retsch®) with zirconium oxide-coated bowls and balls. A fraction of this powder ($0.50 \pm 0.05\text{mg}$ dry mass) was weighed in tin cups. Analyses were then performed with an isotope ratio mass spectrometer (Delta V Advantage with a Conflo IV interface, Thermo Scientific) coupled to an elemental analyser (Flash EA, 2000; Thermo Scientific). Results are

presented in the usual δ notation relative to the deviation from an international standard (atmospheric nitrogen, for $\delta^{15}\text{N}$ values), in parts per thousand (‰). Based on repeated measurements of USGS-61 and USGS-62 used as laboratory internal standards, the experimental analytical precision was $<0.15\%$.

The isotopic dataset included individuals sampled from different years (i.e. between 2007 and 2021), which could have affected our data. However, more than 90% of the muscle samples were collected between 2019 and 2021 and nearly 75% in 2021, which reduces the potential inter-annual effect. An analysis was also performed using only the years 2019 and 2021 to test the temporal variability and no effect changing our conclusions has been detected we have therefore used all the data (from 2007 to 2021) for all the analyses. In addition, as sampling was always carried out during the same season (in autumn, at the end of October), potential seasonal variability bias was also limited. We hypothesize that changes in size and depth have a much greater influence on the $\delta^{15}\text{N}$ values than does the temporal aspect. Details on the sampling by year for each species are presented in the appendix 2. In addition, our sampling covered stations located at different latitudes within the bay, and this variability in the isotopic baseline could potentially affect our results. It is indeed difficult to disentangle the effects of depth, latitude, and individual size on $\delta^{15}\text{N}$ values. However, it is worth noting that all our sampling stations were situated in canyons at relatively consistent distances from the plateau, ranging from 9 to 32 km from the 200 m isobath, and the latitudinal range is limited ($\sim 3^\circ$). This geographical consistency minimizes the potential variations in the baseline. Moreover, in the Bay of Biscay, differences in $\delta^{15}\text{N}$ values were observed between the northern and southern regions for coastal species, primarily driven by variations in river discharge, but not for oceanic species (Chouvelon et al., 2012). To test this factor in our dataset, we analyzed the variance of $\delta^{15}\text{N}$ values in relation to depth and latitude across all data. However, we did not observe any significant effect.

2.4. Relationships between size distribution and depth

The different depth layers were defined as follows: the epipelagic zone between 25 and 175m, the upper mesopelagic zone between 175 and 700m, the lower mesopelagic zone between 700 and 1000m, and the bathypelagic zone below 1000m. This division corresponds to the one used in the literature (Sutton, 2013) and is congruent with the depth structuration observed in the canyons of the Bay of Biscay (Loutrage et al., 2023b). To study the changes in size distribution with depth, the trawling

dataset was used. At both community and specific levels, a linear model was performed, the sampling depth corresponding to a continuous explanatory variable. Results were considered significant when the *p-value* was ≤ 0.05 .

2.5. Relationships between $\delta^{15}\text{N}$ values and size

The relationship between $\delta^{15}\text{N}$ values and individual size was explored with the isotopic dataset at both community and species levels. In the case of pooled samples for nitrogen isotope analysis, the size data is the mean size of all pooled individuals. Linear models were employed for both species-level and community-level analyses, ensuring that the models adhered to the underlying assumptions of linear regression. Coefficients of variation were also calculated to assess the dispersion of values.

2.6. Variance partitioning

Variance partitioning was used to calculate the variance explained by the different variables included in a model (Borcard et al., 1992; Legendre and Legendre, 2012). This is done by developing a set of partial models (in a multivariate or univariate framework) created using a subset of predictor variables. Here, the objective was to test to what extent the individual size and the sampling depth influence the $\delta^{15}\text{N}$ values at the specific level. Due to the restricted depth range at which *Aphanopus carbo* and *Stomias boa* were captured ($\leq 100\text{m}$), the variance partitioning was not performed on these two species. The model results are composed of the proportion of $\delta^{15}\text{N}$ values influenced by size and depth separately, and a third fraction representing the shared fraction of variation explained when both variables are included in the model. An ANOVA-type permutation test was performed for each model to test the significance of the influence of each variable (depth and size) on $\delta^{15}\text{N}$ values. Since the third fraction is deduced from the sum of variances, it cannot be tested statistically. The R package *vegan* was used to perform the tests (Oksanen et al., 2022). All the graphics were performed with the *ggplot2* R package and all statistical analyses were performed in the R environment version 4.3 (R Core Team, 2023; Wickham et al., 2016).

3. Results

3.1. Relationships between size distribution and depth

We observed a significant increase (p -value <0.001) in fish size (total length) with depth at the community level (Table 2-1). The median individual size increased consecutively between the epipelagic, upper mesopelagic, and lower mesopelagic depth layers (median individual size equal to 7.0, 9.0, and 10.6 cm respectively; Figure 2-2). Median individual size then decreased slightly between the lower mesopelagic and bathypelagic layers, with a median individual size of 10 cm in the bathypelagic layer.

Table 2-1. Results of the linear models at both community and species levels between size distribution and depth. Significant relationships are shown in bold.

Family	Species	N	Slope	R ²	p -value
Alepocephalidae	<i>Xenodermichthys copei</i> (Bluntnout smooth-head)	1070	1×10^{-3}	0.01	<0.001
Myctophidae	<i>Lampanyctus crocodilus</i> (Jewel lanternfish)	1200	2×10^{-3}	0.05	<0.001
	<i>Lampanyctus macdonaldi</i> (Rakery beaconlamp)	72	2×10^{-4}	<0.001	0.605
	<i>Myctophum punctatum</i> (Spotted lanternfish)	397	3×10^{-4}	0.01	0.040
	<i>Notoscopelus kroyeri</i> (Lancet fish)	585	3×10^{-5}	<0.01	0.912
Paralepididae	<i>Arctozenus risso</i> (Spotted barracudina)	246	7×10^{-4}	<0.01	0.226
Platytroctidae	<i>Searsia koefoedi</i> (Koefoed's searsid)	68	2×10^{-4}	<0.01	0.863
Serrivomeridae	<i>Serrivomer beanii</i> (Stout sawpalate)	63	6×10^{-4}	<0.01	0.866
Sternophidae	<i>Argyropelecus olfersii</i> (Olfer's Hatchetfish)	205	1×10^{-4}	<0.01	0.706
Stomiidae	<i>Stomias boa</i> (Boa dragonfish)	63	2×10^{-4}	<0.01	0.939
Trichiuridae	<i>Aphanopus carbo</i> (Black scabbardfish)	39	1×10^{-2}	0.06	0.136
Zoarcidae	<i>Melanostigma atlanticum</i> (Atlantic soft pout)	157	5×10^{-3}	0.15	<0.001
Community	-	4165	3×10^{-3}	0.01	<0.001

Furthermore, while the first three depth layers had an unimodal distribution, the bathypelagic layer presented a bimodal distribution with a peak of around 8 cm and another around 13 cm.

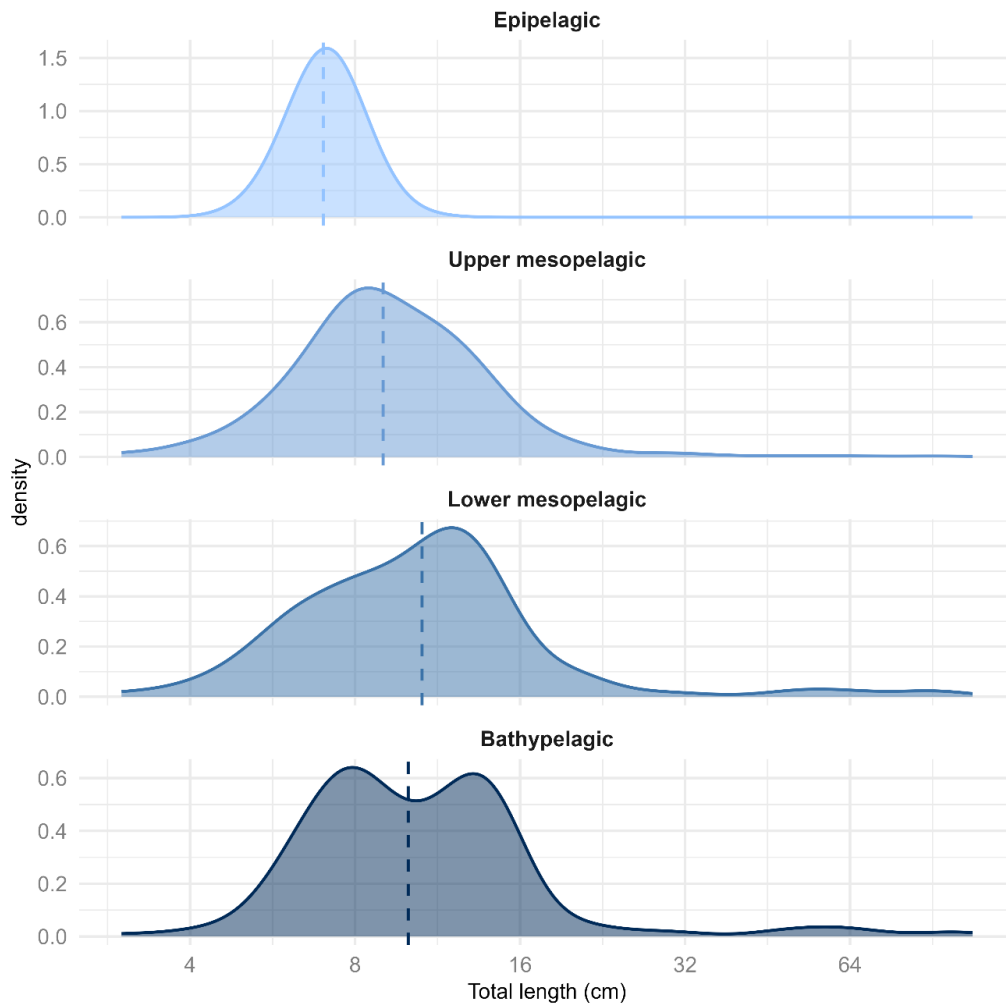


Figure 2-2. Size distribution (total length in cm) of individuals of the deep pelagic fish community according to the different depth layers (epipelagic: 25-175m, upper-mesopelagic: 175-700m, lower-mesopelagic: 700-1000m, and bathypelagic: ≥ 1000 m). The x-axis is in log2 for clarity. The median size is indicated for each depth layer by a dashed line.

The relationship between size distribution and depth was also analysed at the species level (Table 2-1). Among the 12 species examined, only four exhibited a statistically significant linear relationship in the models. *Melanostigma atlanticum*, *Lampanyctus crocodilus*, and *Xenodermichthys copei* showed a significant increase in individual size with depth. *Myctophum punctatum* was the only species showing a significant decrease in the individual size with depth. *Lampanyctus crocodilus* showed an increase in individual size between the upper and lower mesopelagic layers, from a median size (total length) of 10.0 cm to 12.0 cm (Figure 2-3). This was followed by a stabilisation between the lower mesopelagic and bathypelagic layers with the same median size of 12.0 cm. *Melanostigma atlanticum* showed a continuous increase in the size of individuals with depth, with median individual sizes of 6.0,

7.45, and 9 cm respectively. *Xenodermichthys copei* showed a maximum median size in the lower mesopelagic layer (= 10.2cm total length). Although *Myctophum punctatum* showed a significant decrease in the size of its individuals with increasing depth (p-value = 0.040), there appeared to be little variation between depth layers, with a median size of between 6.6 and 7.0 cm. Relationships for other species are available in Appendix 3.

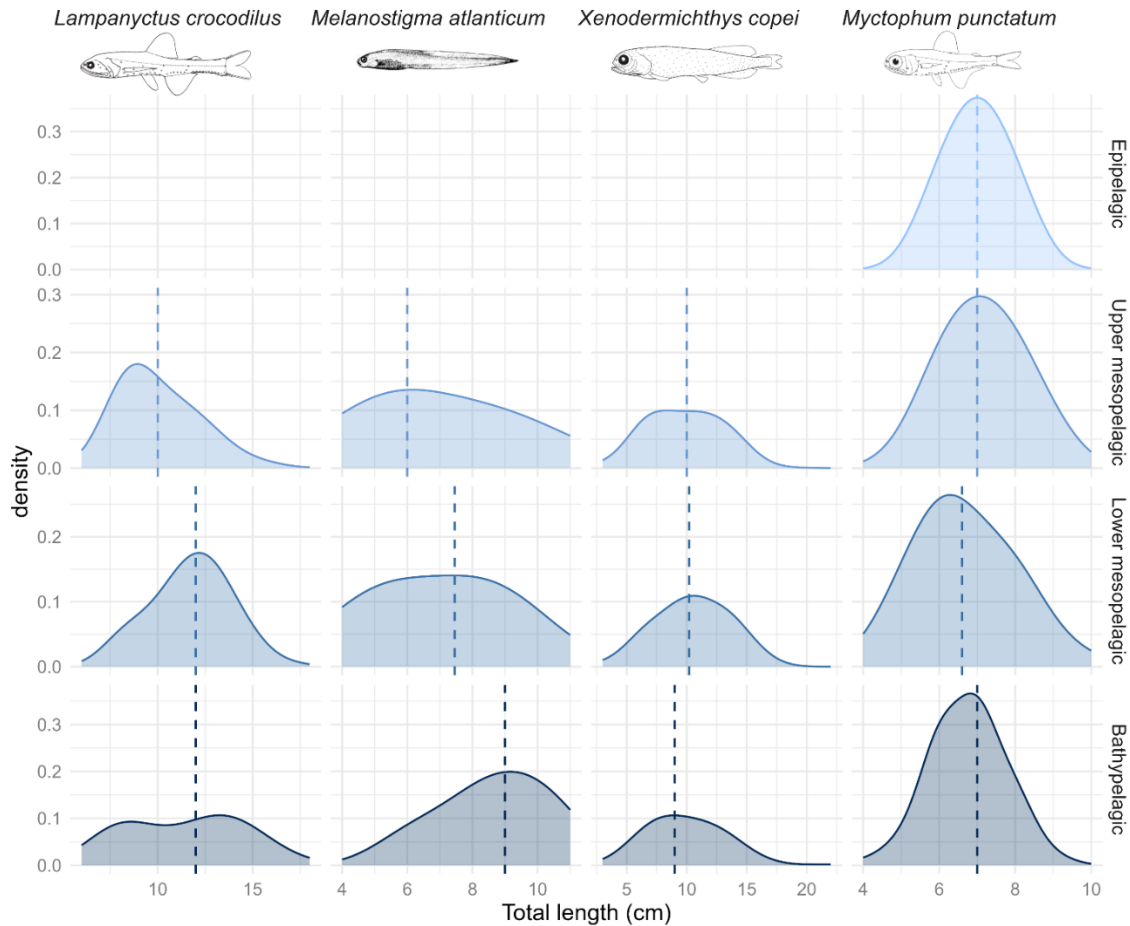











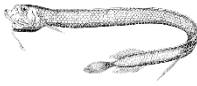


Figure 2-3. Size distribution (total length in cm) as a function of depth layer for the four species that showed significant relationships. The x-axis is in log2 for clarity. The median size is indicated for each depth layer by a dashed line.

3.2. Relationships between $\delta^{15}\text{N}$ values and size

$\delta^{15}\text{N}$ values were determined for seven migratory and five non-migratory or short migratory species, for a total of 682 individuals (= isotopic dataset). Mean $\delta^{15}\text{N}$ values ranged from $9.49 \pm 0.57\text{‰}$ for *Serrivomer beanii* to $12.36 \pm 0.33\text{‰}$ for *Aphanopus carbo* (Table 2-2). For this dataset, mean values of standard length ranged from 6.3 ± 1.7 cm for *Argyropelecus olfersii* to 77.3 ± 10.8 cm for *Aphanopus*

carbo, with *Serrivomer beanii* having the widest size range (45.0 cm between the minimum and the maximum length) and *Lampanyctus macdonaldi* the narrowest (3.3 cm).

Table 2-2. Number of samples for stable isotope analysis (N) and the total number of individuals (n) when some pools were made for the species, the minimum and maximum standard length of individuals (size, cm), sampling depth range (m), and mean \pm standard deviation of $\delta^{15}\text{N}$ values for each species. Migratory patterns are from www.fishbase.org, Lusher et al. (2016), and references therein. DVM = Diel Vertical Migration.

Family	Species		N samples (n individuals)	Migratory pattern	Sampling depth (m)	Size range (cm)	Max size FishBase (cm)	$\delta^{15}\text{N}$ (‰)
Alepocephalidae	<i>Xenodermichthys copei</i> (Bluntnout smooth-head)		114 (126)	DVM	370- 1335	5.6- 9.5	31.0	9.83 \pm 0.64
	<i>Lampanyctus crocodilus</i> (Jewel lanternfish)		142 (154)	DVM	370- 1600	6.5- 14.8	30.0	10.46 \pm 0.66
Myctophidae	<i>Lampanyctus macdonaldi</i> (Rakery beaconlamp)		23	Probably no DVM*	1335- 2000	11.5- 14.8	16.0	11.54 \pm 0.31
	<i>Myctophum punctatum</i> (Spotted lanternfish)		80 (95)	DVM	25-1335	5.0- 9.0	11.0	9.99 \pm 0.51
	<i>Notoscopelus kroyeri</i> (Lancet fish)		75 (181)	DVM	25-780	3.6- 11.0	14.3	11.18 \pm 0.24
Paralepididae	<i>Arctozenus risso</i> (Spotted barracudina)		78 (89)	No DVM	370-780	11.0- 20.5	30.0	10.53 \pm 0.36
Platyroctidae	<i>Searsia koefoedi</i> (Koefoed's searsid)		20 (22)	Probably no DVM*	750- 1000	8.5- 14.5	15.0	11.80 \pm 0.57
Serrivomeridae	<i>Serrivomer beanii</i> (Stout sawpalate)		31 (37)	DVM	715- 1335	26.5- 75.5	78.0	9.49 \pm 0.54
Sternophidae	<i>Argyropelecus olfersii</i> (Olfer's Hatchetfish)		64 (70)	Short DVM	370- 1335	3.3- 10.0	9.0	10.18 \pm 0.47
Stomiidae	<i>Stomias boa</i>		20 (30)	DVM	680-780	11.8- 33.6	32.2	11.61 \pm 0.71
Trichiuridae	<i>Aphanopus carbo</i>		9	DVM	750-780	59.0- 102.0	151.0	12.36 \pm 0.33
Zoarcidae	<i>Melanostigma atlanticum</i> (Atlantic pout) soft		26 (34)	No DVM	730- 1010	7.0- 11.0	15.0	11.21 \pm 0.50

The relationship between $\delta^{15}\text{N}$ values and individual size was first investigated at the community level (Figure 2-4). The linear model results showed a significant increase in $\delta^{15}\text{N}$ values with individual size. However, the R^2 was very low ($= 0.01$), indicating high variability in the values.

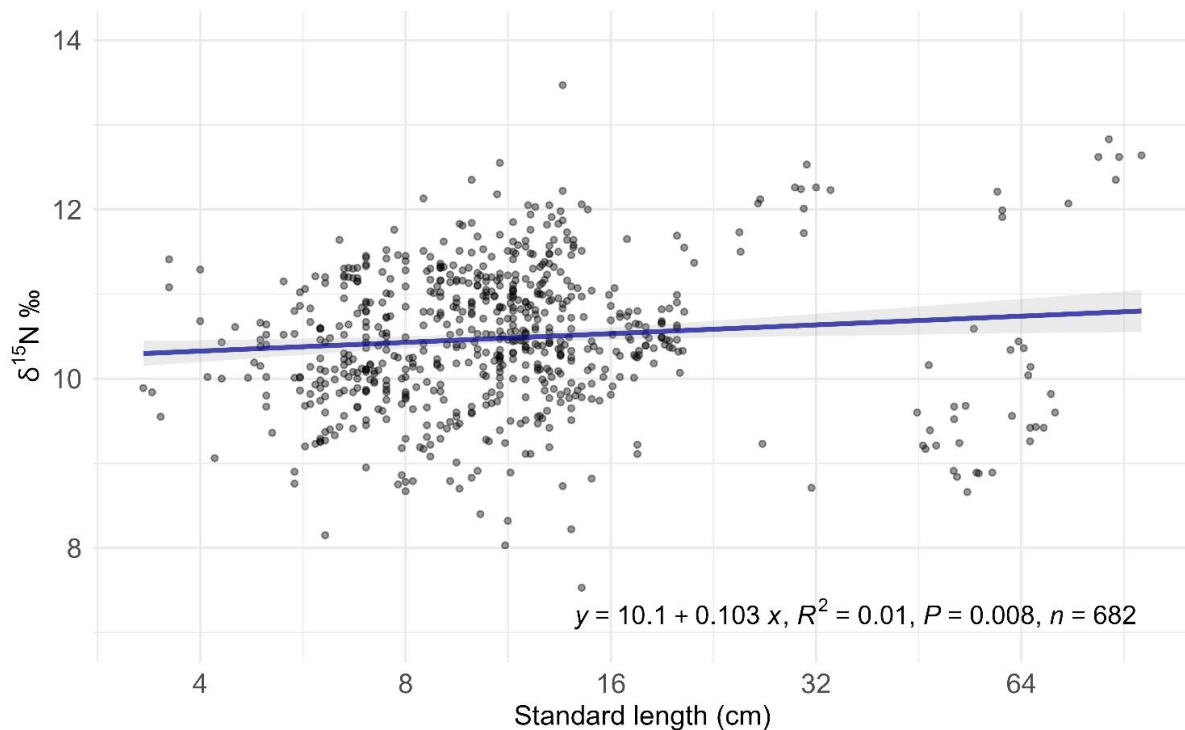


Figure 2-4. $\delta^{15}\text{N}$ as a function of individual size (standard length, in cm) at the community level. The colour shades of the points correspond to their superposition. The x-axis is in \log_2 for clarity.

The relationship between $\delta^{15}\text{N}$ values and size was then investigated at the species level (Figure 2-5A). The results of the individual linear models showed that six species had a significant increase of $\delta^{15}\text{N}$ values with increasing individual size: *Myctophum punctatum*, *Melanostigma atlanticum*, *Lampanyctus crocodilus*, *Stomias boa*, *Serrivomer beanii*, and *Aphanopus carbo*. Only *Arctozenus risso* had a significant decrease of $\delta^{15}\text{N}$ values with increasing size. In addition, differences in R^2 values were observed among species. In fact, despite the statistical significance of certain relationships, the low R^2 values may indicate that, from an ecological point of view, size explains little of the variation in isotopic values. *Stomias boa* had an R^2 of 0.72, indicating that the relationship between $\delta^{15}\text{N}$ and size was accurately predicted by linear regression. In contrast, *Arctozenus risso* had a lower R^2 of 0.09, revealing that linear regression less accurately predicted the change in $\delta^{15}\text{N}$ values of individuals with increasing body size for this species. The other five species had no significant relationship between the two variables (Figure 2-5B). The $\delta^{15}\text{N}$ values were stable regardless of the size increase. However, the

coefficient of variations allowed to distinguish species with low interindividual variability (e.g., *N. kroyeri*) from species with high interindividual variability (*X. copei*).

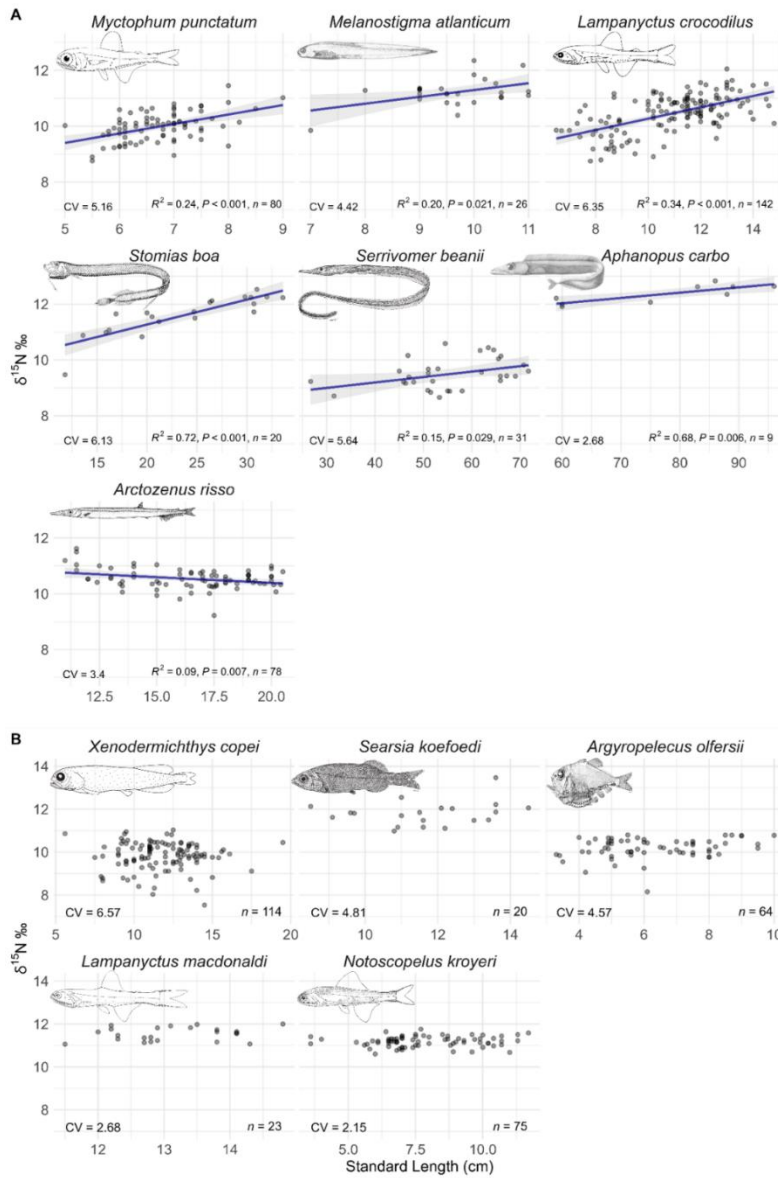


Figure 2-5. Relationships between $\delta^{15}\text{N}$ values and individual size (standard length, in cm). A: significant relationships and B: non-significant relationships. For the non-significant relationships, the coefficient of variation (CV) is shown. The colour shades of the points correspond to their superposition.

3.3. Variance partitioning

Results of the variation partitioning analyses showed that five species (the same as above) had their $\delta^{15}\text{N}$ values significantly influenced by individual size (Figure 2-6 and Table 2-3, NB: *S. boa* and *A. carbo* not considered in these analyses due to small depth range). *L. crocodilus* had the highest proportion

of variation in $\delta^{15}\text{N}$ values explained by size (25.7%), followed by *M. punctatum* (24.7%), *M. atlanticum* (10.1%), *S. beanii* (13.2%) and *A. risso* (5.8%). Alternatively, in *A. olfersii* and *X. copei*, variations in $\delta^{15}\text{N}$ were significantly explained by depth, at a proportion of 5.7% and 5.5% respectively.

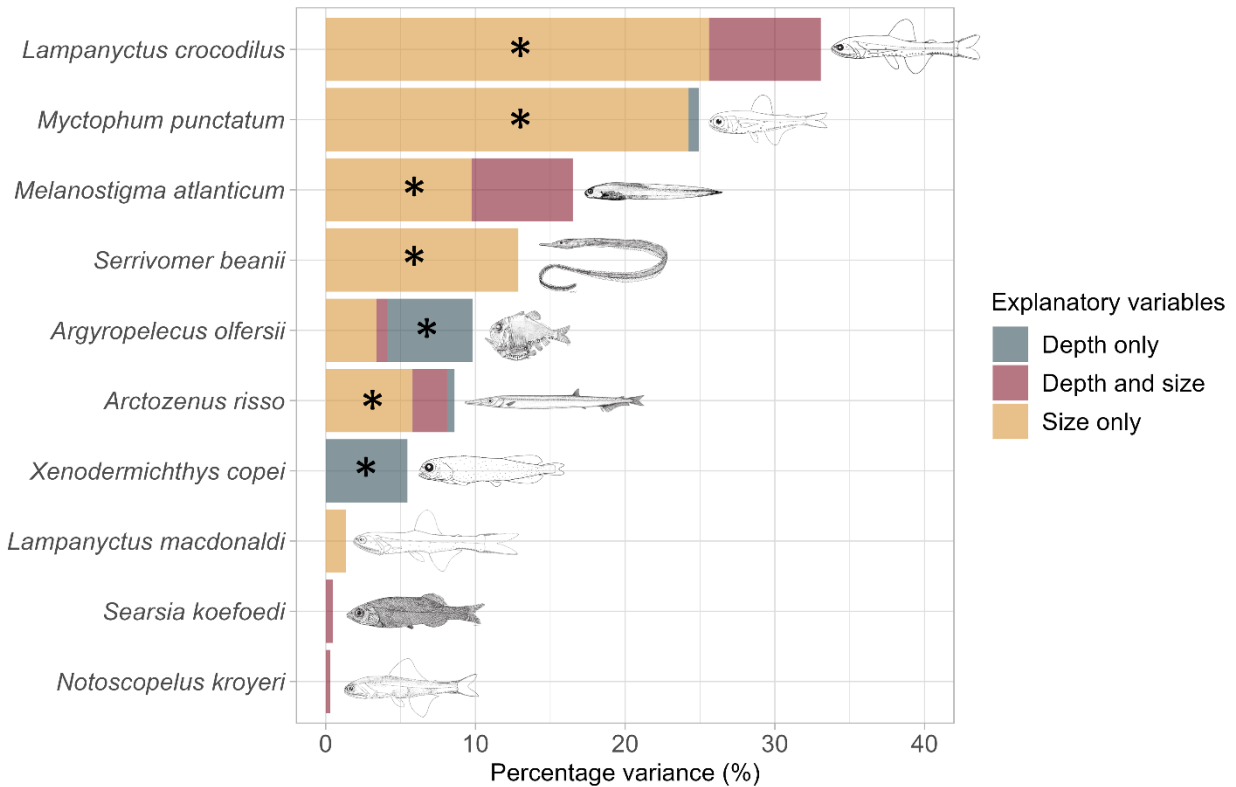


Figure 2-6. Proportions of variance in $\delta^{15}\text{N}$ values explained by size and depth alone and by size and depth together. Asterisks indicate a significant influence of one or other of the variables tested. The unexplained variance has been omitted for graphical clarity and corresponds to the difference between one and the sum of the explained variance.

Table 2-3. Results of the variance partitioning analysis (ANOVA) for each species.


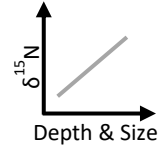

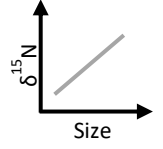
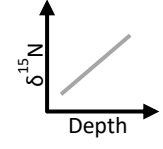
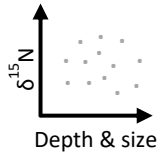

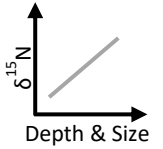
Species	Variable	Variance	F value	p-value
<i>Xenodermichthys copei</i> (Bluntnout smooth-head)	Size	<0.001	0.058	0.824
	Depth	0.026	7.48	0.009
<i>Lampanyctus crocodilus</i> (Jewel lanternfish)	Size	0.115	54.5	0.001
	Depth	<0.001	0.081	0.771
<i>Lampanyctus macdonaldi</i> (Rakery beaconlamp)	Size	0.006	1.30	0.252
	Depth	0.003	0.578	0.477
<i>Myctophum punctatum</i> (Spotted lanternfish)	Size	0.067	26.2	0.001
	Depth	0.004	1.75	0.202
<i>Notoscopelus kroyeri</i> (Lancet fish)	Size	<0.001	0.320	0.578
	Depth	<0.001	0.480	0.500
<i>Arctozenus risso</i> (Spotted barracudina)	Size	0.009	5.78	0.019
	Depth	0.002	1.43	0.219
<i>Searsia koefoedi</i>	Size	0.016	0.880	0.380

(Koefoed's searsid)	Depth	0.006	0.350	0.578
<i>Serrivomer beanii</i> (Stout sawpalate)	Size	0.045	5.28	0.032
	Depth	0.003	0.409	0.510
<i>Argyropelecus olfersii</i> (Olfer's Hatchetfish)	Size	0.010	3.34	0.072
	Depth	0.015	4.92	0.026
<i>Melanostigma atlanticum</i> (Atlantic soft pout)	Size	0.032	3.81	0.044
	Depth	<0.001	<0.001	0.994

3.4. Summary of relationships at specific and community levels

Based on the distinct relationships between size-depth and $\delta^{15}\text{N}$ -size, various species patterns are described (Table 2-4). Specifically, two species (*L. crocodilus* and *M. atlanticum*) showed body size change in both their vertical distribution and their $\delta^{15}\text{N}$ values. Larger individuals of these species were caught at greater depth and their $\delta^{15}\text{N}$ values increased with individual size. Meanwhile, four other species showed a change in their $\delta^{15}\text{N}$ values with body size but showed no variation in their vertical distribution (from trawling data): *A. risso*, *S. beanii*, *S. boa*, and *A. carbo*. Among the species that did not show any significant change in their trophic ecology (as indicated by $\delta^{15}\text{N}$ values) with increasing size, variations in the dispersion of $\delta^{15}\text{N}$ values were observed. Some species such as *N. kroyeri* and *L. macdonaldi* had a restricted range of $\delta^{15}\text{N}$ values whatever the size of individuals (i.e. variation coefficients = 2.15 and 2.68, respectively) whereas some species such as *X. copei* showed a high dispersion of $\delta^{15}\text{N}$ values (CV = 6.57). Finally, three species showed no relationships among the variables tested: *N. kroyeri*, *L. macdonaldi*, and *S. koefoedi*. However, for *L. macdonaldi*, a particularly low size range was sampled for isotopic analysis (= 3 cm between the minimum and the maximum individual size). At the community level, an increase in individual size with depth was observed, as well as an increase in $\delta^{15}\text{N}$ values with increasing size (Table 2-4).

Table 2-4. Summary of the relationships investigated for each species and the community considered as a whole. CV = Coefficient of Variation.

Species	Family	Mechanism driving ontogenetic shift	Relationships	Description
<i>L. crocodilus</i>	Myctophidae	<u>Trophic & and habitat shifts with body size</u> 		Species showing shifts in both their vertical distribution (largest individuals at greater depth) and their trophic ecology (increase of δ¹⁵N values with the size of the individuals) with body size.
<i>M. atlanticum</i>	Zoarcidae			
<i>M. punctatum</i>	Myctophidae	<u>Trophic shift with body size</u> 		Species showing only a shift in their trophic ecology with body size (influence of individual size on δ¹⁵N values, but no effect of depth whenever it could be tested).
<i>A. risso</i>	Paralepididae			
<i>S. beanii</i>	Serrivomeridae			
<i>S. boa*</i>	Stomiidae			
<i>A. carbo*</i>	Trichiuridae			
<i>A. olfersii</i>	Sternoptychidae	<u>Depth-driven increase in δ¹⁵N values</u>		Species showing an increase of their δ¹⁵N values with depth (but no effect of size). <i>X. copei</i> also showed a shift in the vertical distribution of individuals (the smallest individuals were not found in the deepest stations).
<i>X. copei</i>	Alepocephalidae			
<i>N. kroyeri</i>	Myctophidae	<u>No shift</u>		Species with no observed shifts in relation with body size (no effect of depth on δ¹⁵N values). Moreover, <i>N. kroyeri</i> and <i>L. macdonaldi</i> had a low CV of their δ¹⁵N values (CV <3) while <i>S. koefoedi</i> had a wider dispersion of δ¹⁵N values (CV = 4.81).
<i>L. macdonaldi</i>	Myctophidae			
<i>S. koefoedi</i>	Platyroctidae			
Community	-	<u>Trophic & and habitat shifts with body size</u> 		The whole community showed an increase in individual sizes with depth. A weak but significant relationship was also found between δ¹⁵N values and individual size.

* Only the δ¹⁵N-size relationship was tested for *A. carbo* and *S. boa* due to too low depth ranges sampled for these two species (test with linear models only, not through variance partitioning analyses).

4. Discussion

The present study confirms, for the Bay of Biscay, the global trend towards observing larger fish at greater depth for deep pelagic fish communities, as described in other systems (Badcock and Merrett, 1976; Willis and Percy, 1980; Auster et al., 1992; Stefanescu and Cartes, 1992; Gartner Jr et al., 1997). The presence or not of ontogenetic shifts and their associated main drivers (trophic and/or habitat) were described: i) species undergoing both body size shifts in vertical habitat use (as inferred from trawling data) and in their trophic ecology (as inferred by $\delta^{15}\text{N}$ values): *L. crocodilus* and *M. atlanticum*; ii) species showing only a body size shift in their trophic ecology (i.e. the significant influence of size on $\delta^{15}\text{N}$ values): *M. punctatum*, *A. risso*, *S. beanii*, *S. boa*, and *A. carbo*; iii) species for which only depth influences their $\delta^{15}\text{N}$ values (*X. copei* and *A. olfersii*), although *X. copei* also presented an ontogenetic shift in habitat use from trawling data (with the smallest individuals not found in the deepest stations); and iv) species showing no ontogenetic shift: *L. macdonaldi*, *S. koefoedi*, and *N. kroyeri*.

When investigating ontogenetic shifts in habitat use and trophic ecology within deep pelagic fish communities, several key aspects must be considered. One primary limitation is the restricted depth or size range covered by the isotopic dataset for certain species. In fact, not all the individuals in the trawl dataset could be sampled for the analysis of stable isotopes of nitrogen. In particular, species like *A. carbo* and *S. boa*, which had depth ranges of 685 and 1630 m respectively in the trawl dataset, had their sampled individuals collected in a depth range of less than 100 m. Alternatively, *L. macdonaldi* was sampled over a small size range (≈ 3 cm), which may potentially explain the lack of significant relationships found with individual size for this species. Given that the isotopic sampling spanned 14 years, potential temporal bias in $\delta^{15}\text{N}$ values cannot be excluded. However, analyses performed exclusively on data from 2019 and 2021 yielded similar results for the $\delta^{15}\text{N}$ -size relationship at the community and specific levels, indicating that the temporal variability of $\delta^{15}\text{N}$ values remains relatively low in our dataset. Additionally, it is important to note that all samples were collected during the autumn season. In addition, the influence of organism physiology on $\delta^{15}\text{N}$ values cannot be discounted, especially for fast-growing species (Vander Zanden et al., 2015). While this parameter was not tested, the lack of significant size changes among several species with varying $\delta^{15}\text{N}$ values suggests that growth

does not affect these values. We assumed that the size and depth parameters have a greater impact on these values.

4.1. Community level

A significant increase in the size of individuals with depth was observed at the community level. This pattern has already been observed for migratory species, with older stages generally found at greater depths than younger ones, as individuals that may have reduced their migratory range or stopped migrating with age (Badcock and Merrett, 1976; Clarke and Wagner, 1976; Nafpaktitis, 1977; Willis and Percy, 1980; Lancraft et al., 1988; Auster et al., 1992; Stefanescu and Cartes, 1992; Gartner Jr et al., 1997). This general trend in the deep pelagic realm may be a consequence of the trade-off between foraging and predation. To satisfy their energetic needs, juveniles and adults of some species migrate to the epipelagic layer to feed at night. Alternatively, at the senescent stage, some species undergo a reduction in swim bladder size as they age (e.g., *L. crocodilus*), so that the energetic cost of migration may be greater than the benefit provided. Some of these species, therefore, adopt a benthopelagic behaviour, which allows them to reduce the energy expended on foraging by taking advantage of the higher concentrations of zooplankton in the benthopelagic zone (Angel and de C. Baker, 1982; Vinogradov, 2005).

At the community level, a slight but significant increase in $\delta^{15}\text{N}$ values with individual size was also found. However, this relationship was very weak ($R^2 = 0.01$). Indeed, it has previously been shown that within fish communities, the increase in $\delta^{15}\text{N}$ values as a function of individual size was more strongly linked to ontogenetic changes than to the fact that the largest species in the community fed on higher trophic-level prey (Jennings et al., 2002; Stowasser et al., 2012). There are several possible causes: omnivory, large predators feeding on smaller prey, large pelagic suspension feeders feeding on small suspended particulate organic matter, and morphological adaptations of small predators to feed on larger prey (Bode et al., 2007; Jacob, 2005; Jennings, 2005). In particular, in our study, *S. beanii* was the second largest species sampled (= 55 cm) but had the lowest mean $\delta^{15}\text{N}$ values (= 9.5‰). This could be partly explained by their serpentine morphology, with a large individual size that is not proportionally reflected in the size of the mouth opening, limiting their ability to capture large prey

compared to other species with similar individual sizes. Indeed, our study includes a wide variety of morphology, including lanternfish, hatchetfish, dragonfish, and eelfish. This diversity in shape is bound to lead to large differences in feeding strategies. Consequently, body size may not be the best measure to infer the trophic ecology of these species, although it is often correlated with several other measures. The analysis was conducted using individual body mass, and the correlation exhibited identical patterns ($R^2 = 0.04$, $P > 0.001$). For example, size, or shape of the mouth opening may be more relevant to study this relationship at the community level (Villéger et al., 2017).

4.2. Trophic-driven ontogenetic shift

Intraspecific shift in fish trophic ecology with body size (as inferred from $\delta^{15}\text{N}$ values variation with size) is generally a consequence of the ability of fish to catch larger prey. This ability is proportional to mouth size, which in turn is proportional to body size, allowing species to feed on larger prey (Dunic and Baum, 2017). Such a pattern has already been observed in mesopelagic fish species (Gartner Jr et al., 1997). In the present study, half of the studied species showed a significant change in their $\delta^{15}\text{N}$ values with the increasing size of individuals. Of these species, four had their $\delta^{15}\text{N}$ values influenced solely by the size of individuals: *M. punctatum*, *S. beanii*, *S. boa*, and *A. carbo*. However, in the case of *A. carbo* and *S. boa*, the depth range sampled for these species was too small to test the other relationships. *M. punctatum* was previously described as a generalist feeder in the Mediterranean Sea with a mixed diet during all stages of its development, except small individuals that seem to feed exclusively on copepods (Scotto di Carlo et al., 1982). As they grow, individuals become more efficient predators and begin to select larger, more nutritious prey (Bernal et al., 2015). In another study in the Northern Atlantic, *A. carbo* also showed an increase in $\delta^{15}\text{N}$ values with individual size, confirming the probable ontogenetic diet or trophic level shift for this species (Farias et al., 2014). Its diet would shift from pelagic zooplankton to bathypelagic prey, reflecting an improvement in its predatory ability (Farias et al., 2014). To our knowledge, this is the first time that a shift in trophic ecology with body size is reported for *S. beanii* and *S. boa*. The diet of *S. beanii* is generally described as being composed of crustaceans and small fish, whereas that of *S. boa* is composed of crustaceans and mesopelagic fish, so our results suggest that the proportions may vary with individual size (Whitehead et al., 1984).

Finally, among the studied species, only *A. risso* has undergone a significant but weak decrease in $\delta^{15}\text{N}$ values with individual size. This trend has already been found for two species of the southern Kerguelen mesopelagic community belonging to the families Platytroctidae and Myctophidae (Woods et al., 2019). A significant decrease in $\delta^{15}\text{N}$ values was also found in a small pelagic neritic fish species, the European sardine (*Sardina pilchardus*). This reduction was attributed to the greater efficiency of large sardines in capturing phytoplankton, which is less enriched in ^{15}N than zooplankton prey (Bode et al., 2006, 2004, 2003). In addition, several species belonging to the Paralepididae family (which includes *A. risso*) have shown tooth loss in adult specimens and a recent study in the western Atlantic also found this pattern for *A. risso* (Devine and Van Guelpen, 2021; Ho and Duhamel, 2019). This tooth loss may lead to dietary changes in this species, partially explaining the negative relationship between $\delta^{15}\text{N}$ values and size found in our results.

4.3. Trophic and habitat-driven ontogenetic shifts

L. crocodilus and *M. atlanticum* showed, in addition to an increase in $\delta^{15}\text{N}$ values with individual size, an increase in individual size with depth. In the Mediterranean Sea, *L. crocodilus* has already been shown to make a change in its diet in relation to its changes in migratory activity (Fanelli et al., 2014; Stefanescu and Cartes, 1992). *L. crocodilus* has a diet dominated by epipelagic crustaceans in its pelagic phase and its migratory activity decreases or even stops when it reaches the senescent stage. It then adopts a benthopelagic behaviour and feeds on fish at greater depth (Stefanescu and Cartes, 1992; Valls et al., 2014b; Bernal et al., 2023). Our present results, therefore, suggest that this behaviour may also occur in the Bay of Biscay. As for *M. atlanticum*, it has a particular mode of reproduction. This species adopts a benthic behaviour during the spawning period and the fertilization of its eggs takes place in burrows located under the surface of the sea bed (Silverberg et al., 1987; Dallarés et al., 2021). This specific reproductive behaviour may explain our results that the largest, and thus reproductive individuals are found at greater depth. From a trophic perspective, it has been shown in the Mediterranean Sea that the diet of *M. atlanticum* consists almost exclusively of pelagic prey (Dallarés et al., 2021). Larger individuals may have the ability to capture larger prey, which can also explain the relationship between $\delta^{15}\text{N}$ values and individual size found for this species. These two species (*L. crocodilus* and *M. atlanticum*), in addition to having these two significant relationships (larger

individuals are found deeper and have higher $\delta^{15}\text{N}$ values), presented the highest percentages of the variance in $\delta^{15}\text{N}$ values explained by both size and depth (i.e., the red portion, >7%) in the partition models. This part reflects the proportion of the model that cannot distinguish the effect of depth and size on $\delta^{15}\text{N}$ values. The benthopelagic behaviour of these species in the adult stage may also partly explain this influence, as $\delta^{15}\text{N}$ values (including those of POM at the base of food webs) are higher at greater depth and particularly in the benthic domain (Bergmann et al., 2009; Richards et al., 2020; Trueman et al., 2014).

4.4. Depth-driven increase in $\delta^{15}\text{N}$ values

Two species, *X. copei*, and *A. olfersii* had their $\delta^{15}\text{N}$ values significantly influenced only by depth (and not by individual size). In addition, in the case of *X. copei* the smallest individuals were not found at greater depth. Like *M. atlanticum*, *X. copei* was previously reported to spawn demersally in the North Atlantic, with individuals in pelagic trawls that were juveniles and larger fish that were caught in the deeper stations near the bottom (Mauchline and Gordon, 1983). As the sampling in our study was carried out during the spawning season of this species (October-November), many spawning individuals were observed. The capture of large spawning individuals of *X. copei* at depth suggests that spawning of this species also occur on the slope area at that period in the Bay of Biscay. Although *X. copei* did not show a significant relationship with size, it stood out for its wide dispersion of values $\delta^{15}\text{N}$ values (CV = 6.57). In the North Atlantic, pelagic individuals of this species have a diet limited mainly to copepods and ostracods, while benthic individuals show a wider variety of food, maybe explaining in part this high variability in $\delta^{15}\text{N}$ values (Mauchline and Gordon, 1983). In addition, it has been observed that both immature and larger individuals may graze on inactive prey or debris such as small copepods, potentially decoupling the relationship between size and $\delta^{15}\text{N}$ values (Roe et al., 1984). In addition, the $\delta^{15}\text{N}$ values of *X. copei* were significantly influenced by depth. This may be a consequence of the reproductive individuals residing at depth for this period and therefore integrating the enrichment of the $\delta^{15}\text{N}$ values at depth (Choy et al., 2015; Gloeckler et al., 2018; Richards et al., 2020; Romero-Romero et al., 2019). As for *A. olfersii*, it is a short-migratory species described to feed on crustaceans and small fish (Muus et al., 1999). It has already been shown that non-migratory species such as *A. olfersii* integrate changes in zooplankton $\delta^{15}\text{N}$ with depth (Koppelman et al., 2009;

Hannides et al., 2013). Indeed, individuals located deeper are more dependent on the food web based on bacterially degraded organic particles and thus enriched in $\delta^{15}\text{N}$ than individuals located less deep (Choy et al., 2015; Gloeckler et al., 2018; Richards et al., 2020; Romero-Romero et al., 2019). This result was already observed for two non-migratory species near the island of Hawaii: *Cyclothone pallida* and *Melanocetus johnsonii* (Romero-Romero et al., 2019). Among the non-migratory species in our study, *A. olfersii* was the species with the largest range of depth sampled ($\approx 1000\text{m}$) which may explain the significant influence of depth on $\delta^{15}\text{N}$ values for this species. For the other non-migratory species (i.e. *L. macdonaldi*, *A. risso*, *S. koefoedi*), the depth range sampled was maybe too small to detect any influence of depth on the $\delta^{15}\text{N}$ values.

4.5. No ontogenetic change and no influence of depth on $\delta^{15}\text{N}$ values cases

Finally, five species showed no trophic-driven change with body size: *X. copei*, *S. koefoedi*, *A. olfersii*, *L. macdonaldi*, and *N. kroyeri*. Among these species, some showed high variability in $\delta^{15}\text{N}$ values (*X. copei*, *S. koefoedi*, *A. olfersii*) while others had relatively constant values across their size range (*L. macdonaldi* and *N. kroyeri*). This result could potentially reflect differences in feeding strategies between species. Species with a high dispersion of $\delta^{15}\text{N}$ values may have higher dietary plasticity, allowing them to feed on a wide variety of prey. Such a pattern has already been found for several small pelagic neritic species such as *Scomber scombrus* in the Iberian Peninsula (Bode et al., 2006). However, information on the diet of the Platytroctidae family is very scarce in the literature. *S. koefoedi* has been reported to have a diet composed largely of copepods, but also ostracods, chaetognaths, and polychaetes, which could partly explain the large variability in $\delta^{15}\text{N}$ values found during its ontogeny (Hopkins et al., 1996; Novotny, 2018). In contrast, species with low variability in $\delta^{15}\text{N}$ values could have implemented an alternative strategy to the one classically observed, based on an increase in the size of the prey associated with an increase in mouth size. In this case, meeting energy requirements would be based on an increase in the quantity of resources ingested, made possible by the increase in mouth size, while maintaining the same type (size) of food resources rather than a higher energy content per larger prey ingested. The two Myctophidae species of this group, *N. kroyeri*, and *L. macdonaldi* showed weak variability in $\delta^{15}\text{N}$ values with increasing body size. These two species have been reported to have a

diet mainly composed of crustaceans (Coad and Reist, 2004; Gjørseter, 1981). However, for the *L. macdonaldi* case, the restricted size range sampled can explain part of this absence of relation (= 3 cm). In addition, the smaller individuals sampled had a standard length of 11.5 cm, which is important considering the maximum size of 16 cm reported for this species. In the case of *N. kroyeri*, individuals' diets may not be size-restricted like in the case of filter feeders, with a strategy of increasing the quantity of ingested food with size.

4.6. The Myctophidae case study

An important observation from our results is that the Myctophidae species studied here appeared to have significant differences in their feeding strategies during ontogeny. They were found in three of the four groups of species formed from the different relationships. First, *L. crocodilus* differs from the other species in that it undergoes changes in both its diet and depth distribution with increasing body size. As large adults have a reduced swim bladder, the energy gain associated with nocturnal migration to feed in productive surface waters may outweigh the costs, making feeding in the benthic boundary layer more cost-effective (Fanelli et al., 2014). While both *M. punctatum* and *N. kroyeri* are known to migrate vertically at night in the epipelagic layer, they appeared to have adopted opposite feeding strategies, with *M. punctatum* appearing to change its diet (i.e. increasing $\delta^{15}\text{N}$ values with size), whereas not only was this change not seen in *N. kroyeri*, but its $\delta^{15}\text{N}$ values remained very stable across the species size gradient. Thus, by not shifting its diet towards larger or more energetic prey with increasing body size, *N. kroyeri* appears to have opted for an increase in food quantity rather than a change in quality. Finally, *L. macdonaldi* had the deepest distribution (i.e. median depth = 2000 m), which probably explains in part the lack of profitability for this species to move into the epipelagic layer to feed at night. *L. macdonaldi* also appeared not to have undergone any dietary changes during ontogeny, although this remains to be confirmed with a wider sampling across the size range of the species. All these differences in the ontogenetic foraging strategies of these phylogenetically related species may be partially explained by differences in morphological traits. Indeed, differences in morphological traits can lead to differences in swimming ability, prey capture, detection ability visual

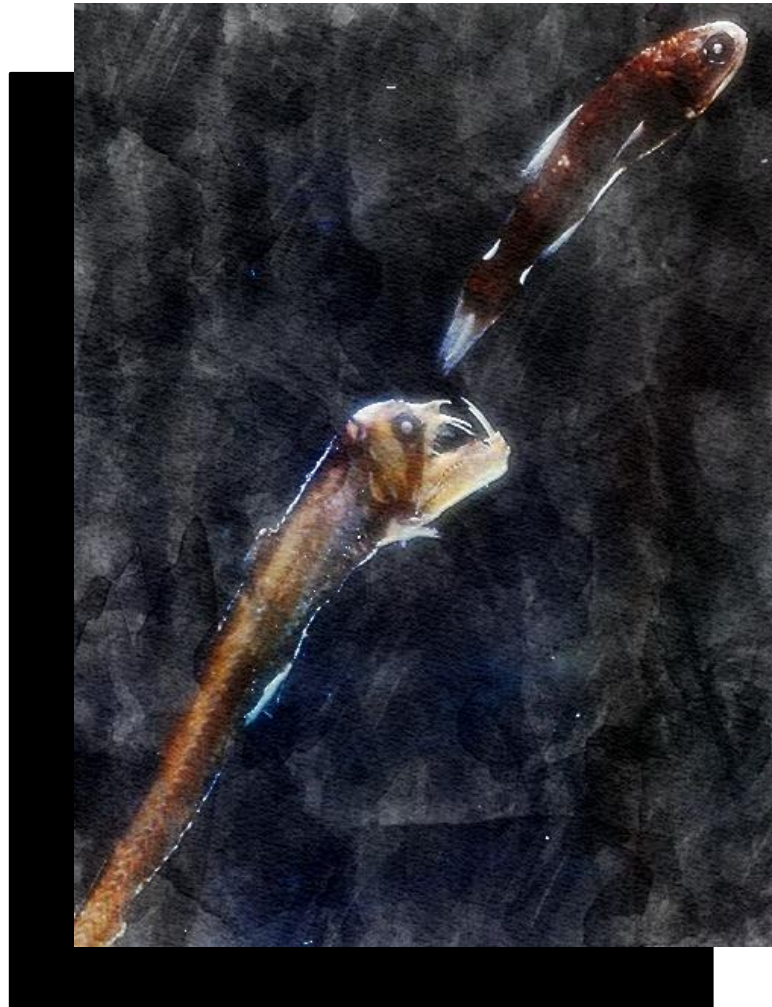
acuity, etc. (Villéger et al., 2017). Differences in feeding strategies and depth distribution in relation to body size suggest divergence within this highly diverse family to avoid competition.

Overall, we identified significant variations in foraging trade-offs related to ontogenetic changes in the community. These variations could influence the functional roles played by the species within the ecosystem, highlighting the need for further incorporation into future research (Nakazawa, 2015). Network-based approaches have demonstrated that the role of fish is stage-specific in terms of their functionality, with significant impacts on energy pathways, food web structure, and dynamics (Miller and Rudolf, 2011; Nakazawa, 2015; Ramos-Jiliberto et al., 2011; Woodward et al., 2005). Therefore, characterizing these changes for the twelve relatively unknown species examined in this study constitutes a crucial initial step towards a more profound comprehension of the trophodynamic functioning of deep pelagic food webs.

Data Availability Statement

The isotopic (*Individual carbon and nitrogen stable isotope compositions with length, weight, and trawling depth for twelve deep pelagic fish species from the Bay of Biscay, Northeast Atlantic, between 2007 and 2021*) and trawling datasets (*Length and depth distributions of twelve deep-pelagic fish of the Bay of Biscay slope, Northeast Atlantic, between 2011 and 2021.*) will be available from an open-access data repository. The code will be made available on Github.

Chapitre 3 - Competition shapes the trophic structure of epi- to bathypelagic fish community in the Bay of Biscay



1. Introduction

Significant vertical environmental gradients (e.g., resources gradient) characterize the pelagic ecosystem in oceanic waters (Sutton, 2013). In the epipelagic layer, phytoplankton, through the conversion of solar energy into organic matter via photosynthesis, serves as a key driver of primary production, fostering high productivity. This primary production is rapidly consumed by zooplankton, which can be consumed by vertically migrating mesopelagic fish (Koppelman and Frost, 2008). The remainder of the primary production that is not consumed is transported to deeper depths by a vertical flow of particles on which non-migratory organisms depend (Choy et al., 2015; Gloeckler et al., 2018). Remineralization of these particles by microbial communities leads to a decrease in organic carbon concentration with increasing depth (Buesseler et al., 2007). Near the bottom, suspended particles aggregate, increasing productivity and potentially leading to the aggregation of deep pelagic fish in areas with steep topography (i.e., the continental slope, seamounts, and mid-ocean ridges) (Reid et al., 1991; Gartner et al., 2008; Porteiro and Sutton, 2007; Sutton et al., 2008).

These conditions of the evolution of productivity with depth, leads to a reduction in food resources as depth increases. The basic assumption about the diet of deep-pelagic organisms has been "eat everything you see in a food-poor environment," leading to the conclusion that most of them should have a generalist diet at depth (Drzen and Sutton, 2017). On the contrary, various studies examining the trophic ecology of mesopelagic to bathypelagic species, especially fish, found a considerable degree of niche partitioning between certain species that have specialized along different axes of their ecological niche (i.e., time, space, diet) (Hopkins and Gartner, 1992; Eduardo et al., 2020a, 2021). These two hypotheses reflect the two main mechanisms driving species co-existence: stochasticity or determinism. From a stochastic point of view, functionally similar species can exist within the same system through ecological equivalence (Chesson, 2000; Hubbell, 2005; Rosindell et al., 2011). According to this theory, species display broad trophic niches with little specialization (i.e., opportunistic feeding behavior) and a high degree of overlap. In contrast, a community regulated by deterministic mechanisms exhibits a species composition shaped by ecological processes such as competition or predation rather than relying on randomness (Gause, 1932). Within such communities, species will possess smaller and more distinct trophic niches, reducing overlap.

Understanding the trophic dynamics of mesopelagic communities across different depths has become imperative, particularly in light of the current challenges posed by global changes and the possibility of exploiting mesopelagic resources in the future (Hidalgo and Browman, 2019; Levin et al., 2019; Drazen et al., 2020; Walters et al., 2021). Trophic interactions regulate populations, determine energy pathways, and influence the resilience of communities to perturbations (Winemiller and Polis, 1996; Chipps and Garvey, 2007). The consequences of these perturbations, such as the addition of species (i.e., species shifting their habitat northward) or the removal of species (i.e., extinction or overharvesting) to the food web, will differ depending on the associated functioning hypothesis (i.e., between deterministic and stochastic mechanisms; Alp and Cucherousset, 2022). A community with low trophic redundancy will be less resilient and stable in the face of disturbance than a community composed of several species with similar trophic ecologies (Raffaelli, 2006; Rigolet et al., 2015). Optimal resource use through species complementarity results in higher community productivity, stability, and resilience (Hooper et al., 2005). All this information is made all the more important by the key ecological and functional roles deep-pelagic fishes play within ecosystems. Daily feeding migration activities of most of these fishes in the epipelagic layer impact the oceanic carbon cycle, enabling energy and matter transfer between the deep ocean layers (Cook et al., 2013; Drazen and Sutton, 2017). Moreover, the trophic relationships between pelagic and demersal fish in slope regions redirect detrital particle flow and facilitate carbon transfer for long-term storage at depth (Trueman et al., 2014).

Carbon and nitrogen stable isotope analysis (SIA), which reflects integrated information over time on the matter assimilated by organisms, and the resulting metrics are valuable tools for monitoring pelagic food webs' trophic functioning (Peterson and Fry, 1987; Zanden and Rasmussen, 2001; Alp and Cucherousset, 2022). Stable isotopes of carbon can be used to infer energy sources as it undergoes little fractionation during trophic transfer, whereas stable isotopes of nitrogen, which show a higher level of fractionation, rather provide information on the trophic level of organisms (Post, 2002; Fry, 2006). Combining these two measures provides access to the isotopic niche of a species in a two-dimensional space (Newsome et al., 2007). Comparison of isotopic niches within a community enables the determination of the relative positioning of species within the isotopic space and the potential overlap between them (Jackson et al., 2011). When comparing species niches, it is crucial to

consider each species' biomass. Biomass distribution across species within a community is rarely uniform, leading to the development of specific isotopic measures designed to accommodate this variability (Cucherousset and Villéger, 2015). Species with higher biomass are indeed anticipated to exert a more substantial influence on ecosystem functioning, especially within the food web context (Rigolet et al., 2015; Graham et al., 2017). Lastly, in vertically stratified environments such as deep pelagic ecosystems, considering the vertical distribution of species becomes critical. These environments offer significant opportunities for species segregation due to their distinct layers and the varied ecological niches they offer to species (Gámez and Harris, 2022).

The application of null models facilitates the comparison of expected outcomes without ecological pressures (i.e., predation, competition). It allows for a meaningful assessment by contrasting these values with those observed within the assemblages studied. In our study, we used the methodology proposed by Suchomel and Belk (2022) to determine whether resampling the isotopic values of species would yield distinct niche sizes or overlap values compared to a random distribution. This approach enables us to discern whether stochastic or deterministic processes govern the species assemblages.

Here, we estimated different isotopic metrics to assess the ecological functioning of a deep pelagic fish community in the Bay of Biscay (Northeast Atlantic). Anthropogenic activities, including fishing, have historically impacted this region (Borja et al., 2019). The arrival of species from southern areas has led to a tropicalization of the shelf's marine communities in recent decades, and this phenomenon is expected to intensify in the future (Le Marchand et al., 2020). As these various phenomena are already affecting species on the continental shelf, it is important to understand better the trophic functioning of the deep pelagic fish community to detect and predict possible changes and, where appropriate, anticipate management measures to mitigate any negative impacts.

The first specific objective of this study was to investigate whether, at the community level, the main species (based on biomass) of meso- to bathypelagic fish on the slope of the Bay of Biscay exhibit segregation along two key axes: 1) diet (or trophic) segregation among the main fish species using carbon and nitrogen stable isotope data to define the isotopic niche of these species, and treating it as a distinct subset within their broader trophic niche; 2) spatial segregation, by investigating vertical

habitat use along the water column for each species, using nocturnal trawling data, thereby offering insights into the distribution and habitat preferences of the studied fish species at night.

The second objective of this study aimed to understand the mechanisms facilitating the coexistence of deep-pelagic species in diverse habitats. The competitive exclusion principle was examined by assessing whether the distribution of the isotopic niches among different species was influenced by stochastic (non-driven) processes or deterministic processes (competition/predation). This involved a comparison of observed values of niche size and overlap with those derived from a null model. Additionally, various trophic diversity indices weighted by species biomass were used for a more comprehensive understanding of trophic functioning and species distribution in isotopic space.

2. Materials and Methods

2.1. Sampling

Organisms were collected by epi- to bathypelagic trawling in canyons of the Bay of Biscay continental slope (Northeast Atlantic) during the EVHOE ("*Evaluation Halieutique de l'Ouest de l'Europe*"; <https://doi.org/10.18142/8>) scientific cruise in autumn 2021. The trawl net was 192 m long with a headline of 76 m and a foot rope of 70 m. The average vertical opening was about 24 m, and the horizontal opening was 58 m. The mesh size gradually decreased from 8 m (stretched mesh) at the mouth to 20 mm (stretched mesh) at the cod-end. To allow the capture of very small specimens, the trawl was also equipped with a 7.5 m long sock with a 12 mm mesh size. Each haul was conducted at a specifically chosen immersion depth, meaning only one depth was sampled at each station. Once the trawl reached the selected depth, it was towed horizontally (i.e., constant immersion depth) for 1 hour at 4 kn. Trawls were conducted at night at seven trawling depths: 25, 370, 555, 715, 1000, 1010, and 1335 m. The station at 1010 m was conducted close to the bottom, with an average distance to the bottom of approximately 100 m, while the other stations had a distance to the bottom between 1120 and 3500 m. The different depth layers were then defined as follows: the epipelagic zone above 175 m, the upper mesopelagic zone between 175 and 700 m, the lower mesopelagic zone between 700 and 1000 m, the bathypelagic zone below 1000 m, and finally, the near-bottom zone corresponding to the station made 100 m from the bottom. This division corresponds to that used in the literature (Sutton, 2013) and is congruent with the structuring of depths observed in the canyons of the Bay of Biscay (Loutrage et al., 2023b).

2.2. Stable Isotopes Analysis

To investigate the isotopic niches of the main species in the community, stable isotope analyses of nitrogen ($\delta^{15}\text{N}$ values) and carbon ($\delta^{13}\text{C}$ values) were carried out on the muscles of 16 different fish species ($n = 604$ samples). Additionally, one species of krill *Meganyctiphanes norvegica* ($n = 35$ samples) was analyzed to obtain the isotopic signature of a primary consumer. Muscle samples were prepared on board and cleaned with distilled water. Muscle samples from the smallest fish and krill species were pooled (between 2 and 4 individuals per fish sample and five individuals per krill sample, respectively) to have sufficient material for stable isotope analysis. Individuals constituting a pool were of equivalent size and sampled at the same station. In the laboratory, muscle samples were freeze-dried for 72 hours. To reduce the samples into a fine powder, samples containing a single individual were manually homogenized, while samples containing a pool of individuals were homogenized using a ball mill (MM400 Retsch®). A fraction of this powder (0.50 ± 0.05 mg dry mass) was then weighed in tin cups. Analyses were conducted using an isotope ratio mass spectrometer (Delta V Advantage with Conflo IV interface, Thermo Scientific) coupled to an elemental analyzer (Flash EA, 2000; Thermo Scientific). Results are presented in the usual δ notation relating to deviation from international standards (Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ values, atmospheric nitrogen for $\delta^{15}\text{N}$ values) in parts per thousand (‰). Based on repeated measurements of USGS-61 and USGS-62 samples used as internal laboratory standards, the experimental analytical precision was $< 0.15\text{‰}$ for $\delta^{15}\text{N}$ and $< 0.10\text{‰}$ for $\delta^{13}\text{C}$. This first set of analyses allowed the C:N ratio of each species to be determined, providing information on the lipid content of the muscle samples (Post et al., 2007; Hoffman et al., 2015). As lipids are highly depleted in ^{13}C , variations in $\delta^{13}\text{C}$ values can occur between species with very different lipid contents while their food may be similar, biasing the interpretation of $\delta^{13}\text{C}$ values. To avoid this bias, three different strategies were used depending on the bulk (untreated) C:N ratio of each species (and the same strategy was applied to all individuals composing a species):

- i) Species whose individuals had a low lipid content (i.e., C:N < 3.5) were not treated nor corrected mathematically for their lipid content (if some individuals had a C:N slightly > 3.5 they were corrected mathematically);
- ii) species for which the majority of individuals had a C:N ratio between 3.5 and 5 had their $\delta^{13}\text{C}$ values mathematically standardized using the equation for aquatic animals (Post et al., 2007):

$$\delta^{13}\text{C}_{\text{corrected}} = \delta^{13}\text{C}_{\text{untreated sample}} - 3.32 + 0.99 \times \text{C:N}_{\text{untreated sample}};$$

- iii) species whose most individuals were high in lipids (i.e. C:N > 5) were treated to remove lipids. To remove lipids, between 20 and 40 mg of ground samples were placed in glass tubes, and 2 ml of cyclohexane was added. The tubes were placed in an ultrasonic bath for 1 minute and then in a rotary shaker for 1 hour. All tubes were centrifuged at 2500g for 10 minutes, and the lipids supernatant was carefully removed. All these steps were performed twice. The pellet from each tube was then rinsed with 1 ml of cyclohexane and returned to the centrifuge (same settings as the first time), and the supernatant was removed before the samples were dried in a drying bath for at least 2 hours. The lipid-free powder was then placed in tin cups and subjected to the same procedure described above for the first set of measurements (before lipid removal). The $\delta^{15}\text{N}$ values used in the analyses are all those obtained on untreated samples (before lipid extraction, if any).

2.3. Isotopic niches

Species isotopic niches were measured using standard ellipses with a threshold of 0.40, meaning that each ellipse contains approximately 40% of the individuals of the species (Jackson et al., 2011). Then, the measurement of isotopic niches overlaps among species at 40% was performed. Overlap is defined as the size of the overlapping region between niche A and niche B divided by the total niche size of B (and vice versa). All results were presented in a matrix where overlap values ranged from 1, meaning that the niche of species A at the bottom of the matrix was entirely covered by the niche of species B on the left of the matrix, to 0, meaning that there was no overlap. These analysis were performed with the R package *rKIN* (Eckrich et al., 2020; Albeke, 2023).

2.4. Depth-driven segregation

Sampling was carried out exclusively at night, so the same sampling during the day might have resulted in different depth distributions of species. However, most mesopelagic fish species are known to feed preferentially at night, which allowed us to study the trophic segregation among species (through isotope data) concomitantly with their nocturnal depth distribution (through trawling data) (Hopkins et al., 1996; Hammerschlag et al., 2017). The first step in determining whether depth is a dimension that can explain some of the segregation of isotopic niches among species was to group them into

trophic guilds. To do this, the previously calculated asymmetric isotopic overlap matrix was used to perform the clustering with the k-means algorithm. The optimal number of clusters was determined using the Gap statistic method, with the number of Monte-Carlo samples fixed at 100. The Gap statistic method compares the dispersion within a group with its expectation under an appropriate null reference distribution (Tibshirani et al., 2001). The clusters were visualized with a dendrogram using the R package *dendextend* (Galili, 2015). The second step was to compare the depth distribution of species within each trophic guild to determine whether the species with the closest isotopic niches also had the same depth distribution or were separated along the water column. To do this, the distribution of biomass density at depth for each species was plotted using the R package *ggplot2* (Wickham et al., 2016). To approach a more accurate representation of the biomass distribution of species, this analysis incorporates the complete depth distribution for each species.

2.5. Trophic structure at each depth

Within each depth layer, we aimed to determine whether the coexistence of species based on their isotopic niche was likely governed by deterministic (i.e., competition and/or predation) or stochastic processes (i.e., due to chance via ecological equivalence). For this, we used a method of resampling isotopic values within the convex hull following the approach developed by Suchomel and Belk (2022). The latter is assumed to represent the spectrum of resources available within the depth layer. A total of 10,000 bivariate random samples were applied with a replacement of $n = 10$ within the convex hull. Two metrics were then calculated within each assemblage using the randomly generated data and the observed data with the rKIN package: the size of the ellipses containing 40% of the individuals and the sum of the overlaps within each assemblage standardized by the number of species. The distribution of the values of these two metrics obtained from the random data (i.e., null model) was compared with those obtained from the observed data. If the observed data lie outside the distribution of values obtained from the random data, this means that deterministic processes govern the assemblage. Conversely, if they do not differ from the null model, this means that the assembly of isotopic niches within the assemblage is governed by stochastic processes. While not presented, we assessed the impact of varying the threshold (i.e., the percentage of individuals within the ellipse) to determine if differences emerged. Through a sensitivity analysis employing thresholds of 0.40, 0.60, and 0.80, we

found that our results remained consistent, and our conclusions remained unchanged. The results obtained using a threshold of 0.40 are thus presented here.

Then, the characterization of the trophic structure at each depth layer was performed using biomass-weighted isotopic metrics defined by Cucherousset and Villéger (2015) (Table 3-1). These metrics (i.e., isotopic divergence, dispersion, evenness, and uniqueness) were adapted from metrics initially developed in functional ecology (Villéger et al., 2008). They complement the previously described isotope metrics (niche size and overlap) and offer the advantage of being mathematically independent of the number of individuals while accounting for species biomass (Layman et al., 2007; Cucherousset and Villéger, 2015). Before calculating the isotopic metrics, each axis (i.e., $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) was scaled between 0 and 1 to avoid misinterpretation, as the range of values can vary considerably between isotopes (Fry, 2006; Cucherousset and Villéger, 2015).

Table 3-1. The isotopic diversity indices used, their definition, and the associated ecological interpretation employed in this study. Low value= tends to 0; high value= tends to 1.

Indices	abbreviation	Definition	Ecological interpretation
Isotopic Divergence	IDiv	Measures species distribution in the convex hull area	Low value: Biomass dominant species are generalists.
			High value: Biomass dominant species are trophically specialized. Indicates a high degree of niche differentiation within the assemblage.
Isotopic Dispersion	IDis	Measures the distance between the species with the highest biomass and the centroid	Low value: biomass dominant species have similar isotopic values, resulting in low trophic diversity.
			High value: biomass dominant species are far from the center of gravity of all species, resulting in high trophic diversity.
Isotopic Evenness	IEve	Quantifies the regularity of the distribution of species biomass along the shortest tree linking all the species	Low value: biomass dominant species are isotopically similar, implying trophic redundancy and food competition.
			High value: biomass dominant species are evenly distributed in the isotopic space, implying optimal resource use through niche partitioning.
Isotopic Uniqueness	IUni	Measures the average proximity of species in isotopic space	Low value: biomass dominant species are packed in the isotopic space, implying high trophic redundancy.
			High value: biomass dominant species are isolated in the isotopic space, implying low trophic redundancy.

All the metrics were calculated using the R script *sj_div* provided by Cucherousset and Villéger

(2015). In each depth layer, not all species underwent isotopic sampling. Nevertheless, within each depth layer, the sampled species accounted for at least 60% of the total biomass, and in three out of five layers, this percentage exceeded 70%. The unsampled species, species characterized by minimal biomass and, in some cases, represented by only a few individuals, suggest that our focus has been on species with potential functional importance. Importantly, the biomass-weighted indices remain minimally affected by these unsampled species.

The R environment, version 4.3.2, was used for all statistical analyses (R Core Team, 2023).

3. Results

3.1. Isotopic niches

The meso- to bathypelagic fish community showed a significant gradient of $\delta^{15}\text{N}$ values of nearly 6‰ for the extreme values (Figure 3-1). The two Platytrichtidae species, *Searsia koefoedi*, and *Maulisia argipalla* showed the highest mean $\delta^{15}\text{N}$ values (i.e. 11.85 ± 0.64 and 12.01 ± 0.38 ‰ respectively) while the Serrivomeridae, *Serrivomer beanii*, showed the lowest mean $\delta^{15}\text{N}$ value (i.e. 9.47 ± 0.55 ‰; Table 3-2). $\delta^{13}\text{C}$ values showed less variability at the community level, with a variation equal to

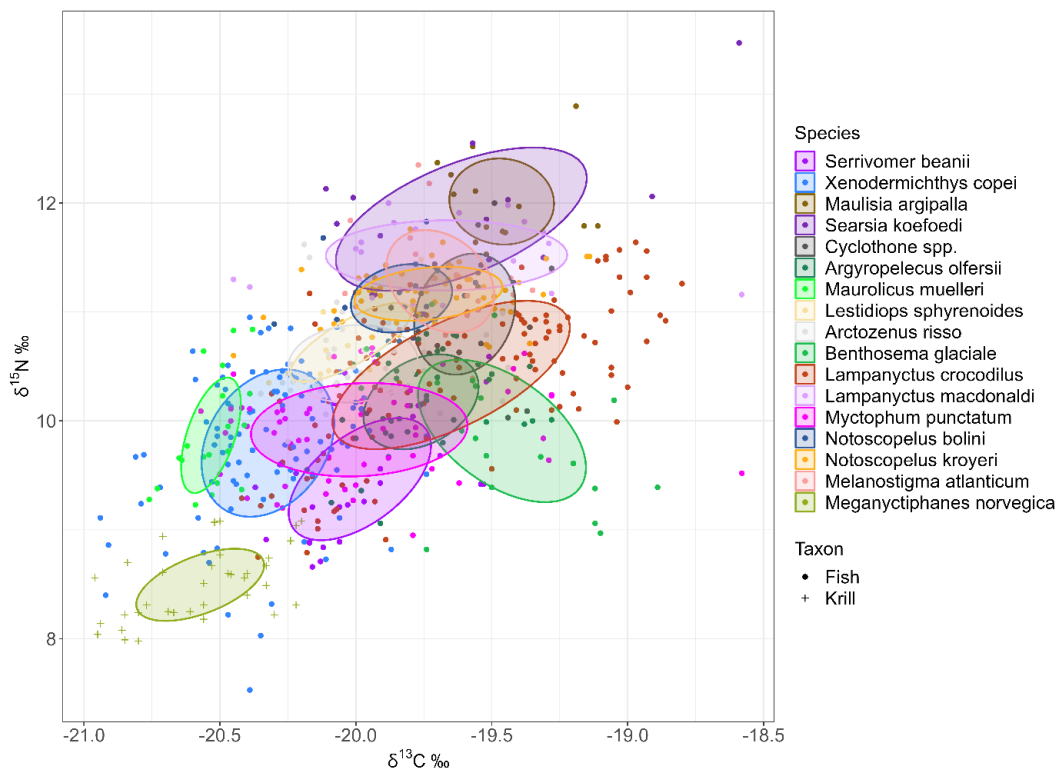


Figure 3-1. Standard ellipses at 40% of the 16 fish species (dots) and the krill *Meganyctiphanes norvegica* (crosses) with all sampling depths considered for each species.

2.36‰ between the lowest value measured and the highest one. The most ^{13}C -depleted species were *Maurolicus muelleri* and *Xenodermichthys copei* (mean $\delta^{13}\text{C}$ values = -20.53 ± 0.11 and -20.32 ± 0.24 ‰) and the most enriched *Benthoosema glaciale* and *Maulisia argipalla* (i.e. mean $\delta^{13}\text{C}$ values = -19.46 ± 0.30 and -19.46 ± 0.19 ‰).

Maurolicus muelleri had the lowest standard ellipse area (0.14 ‰ 2 ; Table 3-2) and *Searsia koefoedi* had the highest (0.71 ‰ 2).

Table 3-2. Number of samples for stable isotope analysis (N), number of individuals pooled for the species, mean \pm standard deviation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for each species and its niche area (SEA_B).

Taxon	order	Family	Species (initial)	Standard length (cm)	N samples (n by sample)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Isotopic niche area, SEA_B (‰ 2)
Fish	Anguilliformes	Serrivomeridae	<i>Serrivomer beanii</i> (Sb)	54.4 ± 10.6	26 (1)	-19.99 ± 0.26	9.47 ± 0.55	0.38
	Osmeriformes	Alepocephalidae	<i>Xenodermichthys copei</i> (Xc)	11.8 ± 2.2	97 (1)	-20.32 ± 0.24	9.80 ± 0.67	0.50
		Platyroctidae	<i>Maulisia argipalla</i> (Ma)	9.0 ± 1.5	14 (1)	-19.46 ± 0.19	12.01 ± 0.38	0.23
	<i>Searsia koefoedi</i> (Sk)		11.7 ± 1.6	14 (1)	-19.61 ± 0.45	11.85 ± 0.64	0.75	
	Stomiiformes	Gonostomatidae	<i>Cyclothone spp.</i> (C spp.)	5.45 ± 1.3	20 (2)	-19.60 ± 0.18	10.98 ± 0.54	0.31
		Sternoptychidae	<i>Argyropelecus olfersii</i> (Ao)	5.6 ± 1.4	41 (1)	-19.76 ± 0.21	10.18 ± 0.43	0.27
	<i>Maurolicus muelleri</i> (Mm)		3.0 ± 1.1	20 (4)	-20.53 ± 0.11	9.87 ± 0.52	0.15	
	Aulopiformes	Lestidiidae	<i>Lestidipos sphyrenoides</i> (Ls)	13.4 ± 0.9	12 (1)	-20.02 ± 0.22	10.72 ± 0.35	0.15
		Paralepididae	<i>Arctozenus risso</i> (Ar)	17.0 ± 2.8	43 (1)	-20.01 ± 0.23	10.52 ± 0.35	0.26
	Myctophiformes	Myctophidae	<i>Benthoosema glaciale</i> (Bg)	4.3 ± 0.5	20 (3)	-19.46 ± 0.30	9.91 ± 0.64	0.53
			<i>Lampanyctus crocodilus</i> (Lc)	10.9 ± 2.0	120 (1)	-19.65 ± 0.43	10.42 ± 0.67	0.72
			<i>Lampanyctus macdonaldi</i> (Lm)	13.2 ± 0.9	20 (1)	-19.67 ± 0.43	11.52 ± 0.32	0.44
			<i>Myctophum punctatum</i> (Mp)	6.7 ± 0.6	57 (1)	-19.99 ± 0.39	9.92 ± 0.42	0.53
			<i>Notoscopelus bolini</i> (Nb)	8.0 ± 0.2	20 (1)	-19.83 ± 0.18	11.13 ± 0.31	0.18
<i>Notoscopelus kroyeri</i> (Nk)			7.9 ± 1.5	20 (1)	-19.73 ± 0.27	11.17 ± 0.25	0.20	
Perciformes	Zoarcidae	<i>Melanostigma atlanticum</i> (Ma)	10.0 ± 0.7	20 (1)	-19.69 ± 0.19	11.28 ± 0.46	0.28	
krill	Euphausiacea	Euphausiidae	<i>Meganyctiphanes norvegica</i>	-	35 (5)	-20.57 ± 0.23	8.50 ± 0.33	0.20

Despite the strong gradient in $\delta^{15}\text{N}$ values, considerable overlap between species remains (Figure 3-2). For example, high overlaps were found between *Argyropelecus olfersii* and the two Myctophidae *Lampanyctus crocodilus* and *Myctophum punctatum* (overlap values ≥ 0.61). High overlaps were also identified between phylogenetically closely related species. For instance, the isotopic niche of *Maulisia argipalla* exhibited nearly complete coverage by the isotopic niche of *Searsia koefoedi*, resulting in an overlap value of 0.94 between these two Platytroctidae species. Similar substantial overlaps, with values exceeding 0.65, were observed between the two species of the genus *Notoscopelus*, *bolini* and *kroyeri*.

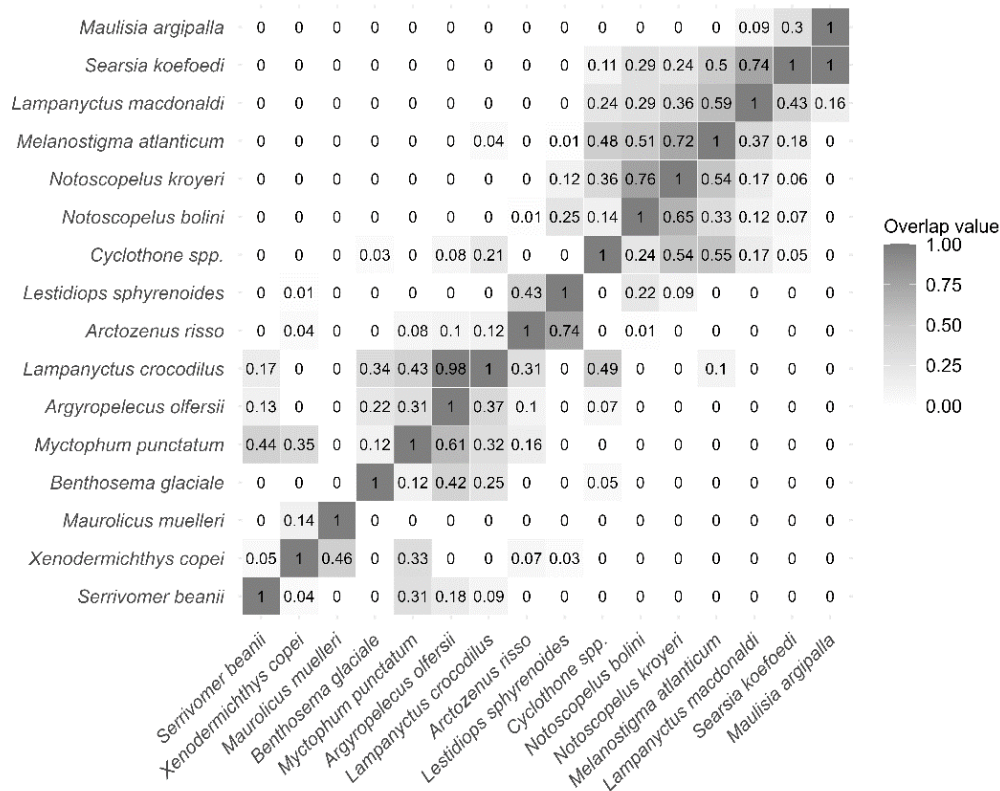


Figure 3-2. Matrix of isotopic niche overlap between the different species sampled at all sampling depths considered for each species. The isotopic niche was estimated using a 40% ellipse. The overlap values are between 1 (i.e. the niche of species 1 at the bottom of the matrix is completely covered by the niche of species 2 on the left of the matrix) and 0 (i.e., the niches of the two species are completely separate).

3.2. Depth-driven segregation

Five trophic guilds were defined based on the isotopic niche overlap matrix (Figure 3-3A). Within each cluster, the species with the greatest overlap were grouped. Each group comprised species from different taxonomic families. The first trophic guild (light green), composed of five species, presented more ^{13}C -enriched values. The second and third (yellow and dark green) trophic guilds comprised

species exhibiting the highest $\delta^{15}\text{N}$ values. The fourth guild (light blue) contained two species, the two barracudina species, *Arctozenus risso* and *Lestidiops sphyrenoides*. The last trophic guild included two species, *Xenodermichthys copei* and *Maurolicus muelleri*, which had the most ^{13}C -depleted isotopic niches and relatively low $\delta^{15}\text{N}$ values.

In each trophic guild, not all species have the same nocturnal depth distribution, which illustrates another segregation pathway (Figure 3-3B). For example, the two barracudina species, *Arctozenus risso* and *Lestidiops sphyrenoides*, formed a cluster based on their isotopic values but had different depth distributions, with *L. sphyrenoides* having its nocturnal median depth of occurrence at 25 m and *A. risso* at 555 m. The same type of segregation occurred between *Maurolicus muelleri* (median depth = 25 m) and *Xenodermichthys copei* (median depth = 555 m). Within other trophic guilds, a noticeable overlap in the depth distributions of species was observed, as exemplified by the strong overlap between the two species of Platytroctidae, *Maulisia argipalla*, and *Searsia koefoedi*. See appendix 4 for a representation of isotopic niche of each cluster pooled.

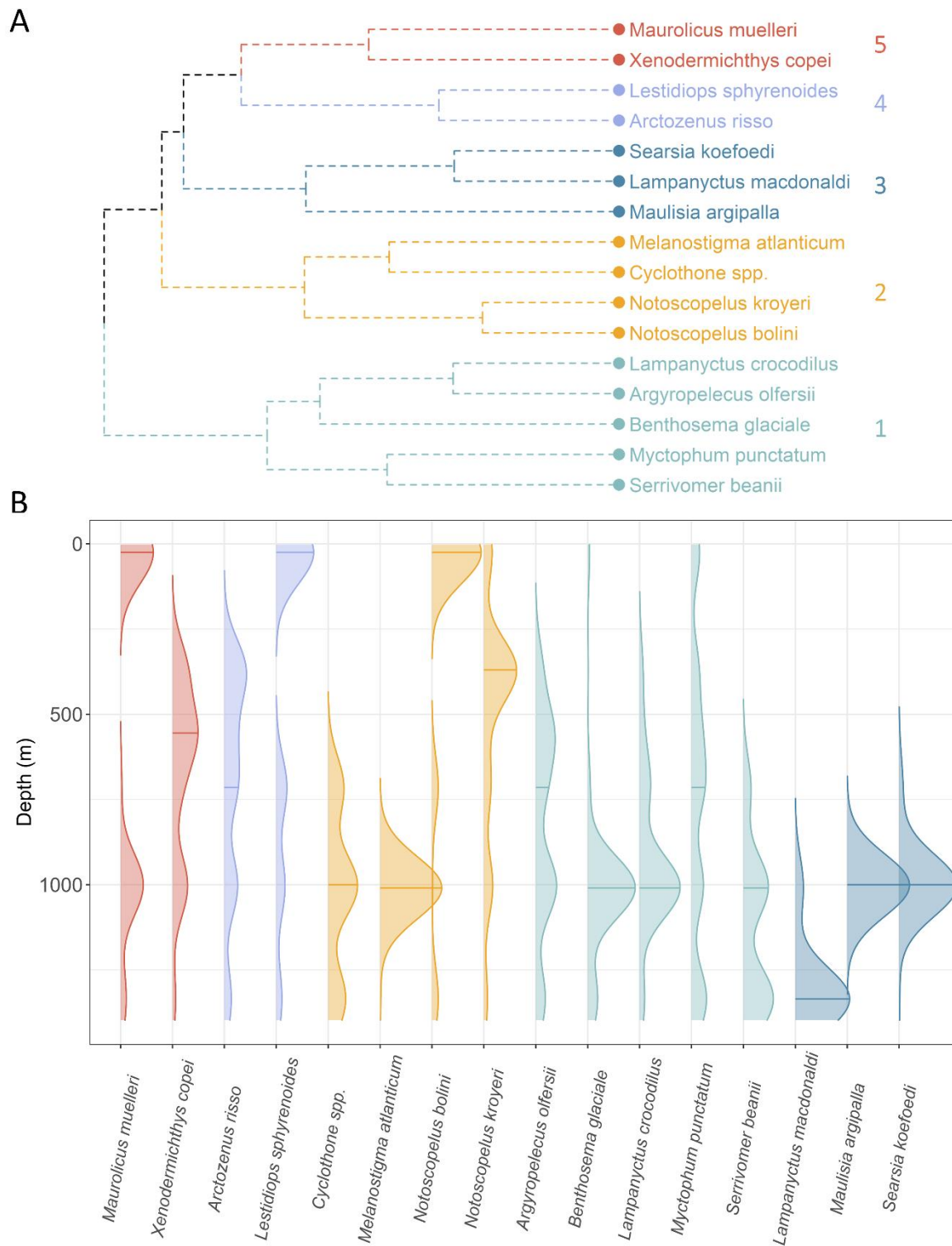


Figure 3-3. A: Clusters of fish isotopic niche overlap obtained using the Gap statistic method. B: Vertical nocturnal distribution of the 16 species sampled in terms of biomass with the total trawling data realized in 2021. Colors represent the cluster defined by the gap statistic method. Vertical lines denote the median of the respective distribution of each species.

3.3. Trophic structure at each depth

The trophic niche sizes observed in deep-pelagic species differed from the null model for almost all species across various depths. The null model effectively predicted the mean isotopic niche size for species in the near-bottom assemblage only. In the other depth layers, all species showed values below those predicted by the null model (Figure 3-4).

Isotopic niche overlaps estimated at each depth layer showed significantly lower observed values than those predicted by the null model (Figure 3-5). However, the differences between the mean values of the null model and the observed values varied between depth layers, with the highest difference for the lower mesopelagic layer (difference = 4.49) and the smallest difference for the epipelagic layer and the near-bottom layer (differences of 2.34 and 1.92 respectively).

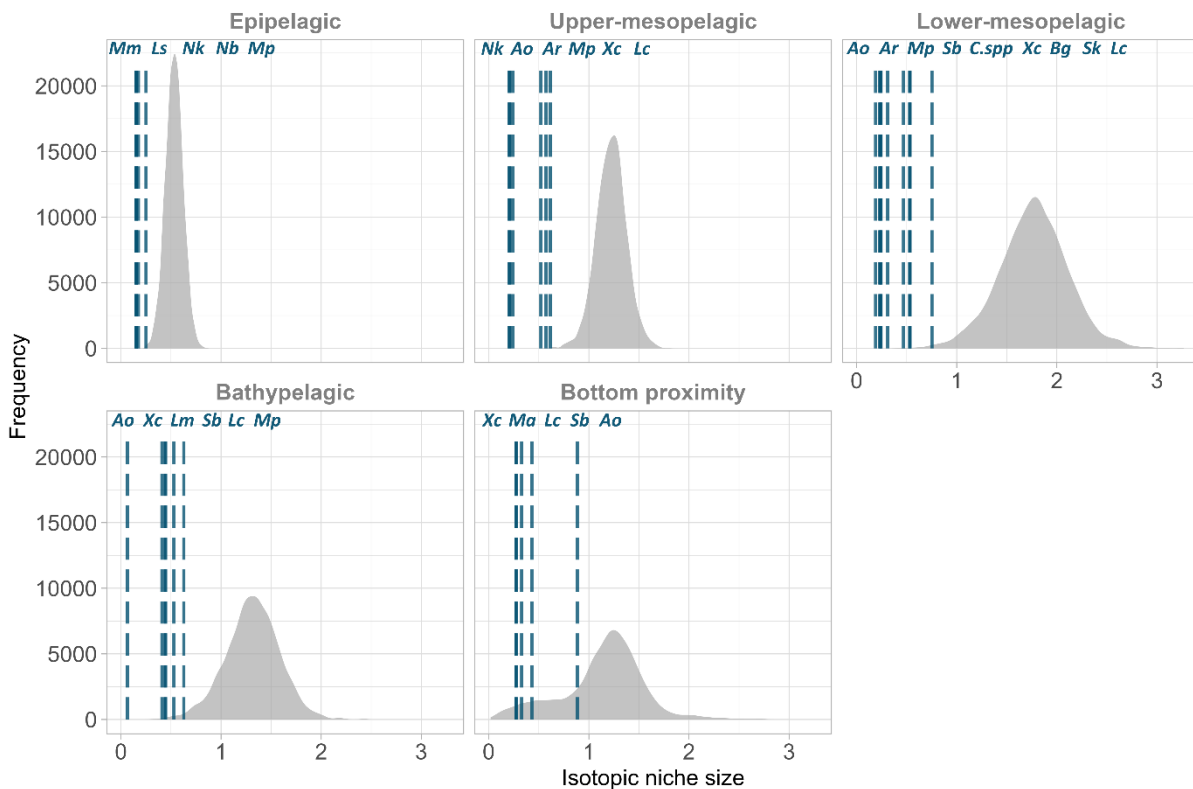


Figure 3-4. Comparison of the isotopic niche area of each species in the different depth layers. Density plots represented the distributions of the estimated isotopic niche area based on the resampling of isotopic values (i.e., null model). The dotted vertical line represents the actual niche of each species, and the initials correspond to the name of each species (the genus name in capitals and the species name in lower case) in ascending order of niche size.

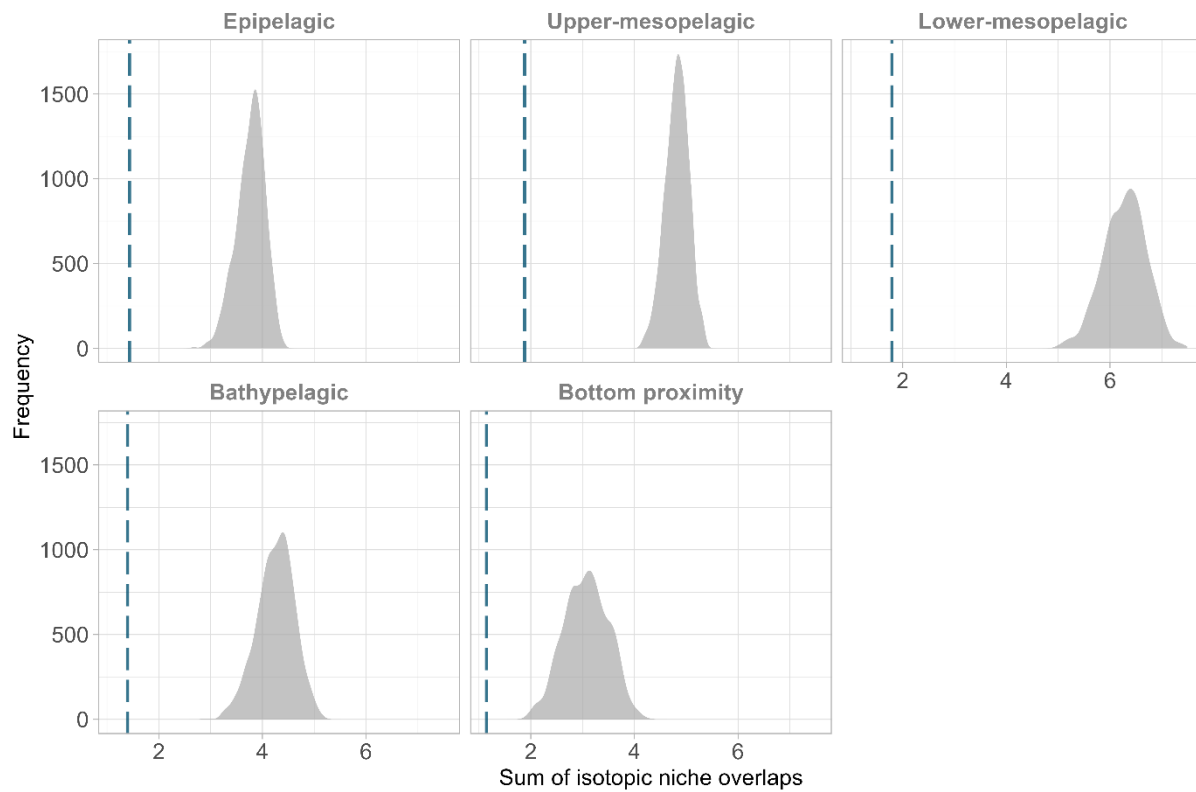


Figure 3-5. Comparison of cumulative isotopic niche overlap standardized by the number of species in each depth layer. The distributions represent the cumulative overlap of isotopic niches based on the resampling of isotopic values (i.e., null model). The dashed lines represent the cumulative isotopic niche overlap observed in each depth layer.

Four depth layers presented high divergence values (i.e., $IDiv \geq 0.862$; Figure 3-6). This means that within most assemblages, the species with extreme isotopic values dominate the food web regarding biomass. In terms of isotopic dispersion ($IDis$), the two shallowest layers (i.e., epipelagic and upper-mesopelagic layers) had the highest dispersion values ($IDis = 0.898$ and 0.823 respectively), suggesting that the species with the highest biomass had contrasting isotopic values in these two layers. In the epipelagic layer, *Maurollicus muelleri* (38.7% of the biomass) was located at the lower left of the isotopic space (low $\delta^{15}N$ and $\delta^{13}C$ values). In comparison, the two species of the genus *Notoscoepus* (sum of biomass = 45.9%) were located at the opposite end, at the upper right of the isotopic space (high $\delta^{15}N$ and $\delta^{13}C$ values). A similar structure was found at the upper-mesopelagic layer with *Xenodermichthys copei* (34% of the biomass) located at the lower left of the isotopic space and *Notoscoepus kroyeri* (35% of the biomass) located at the opposite end. The bathypelagic layer also presented a high dispersion value ($iDis = 0.755$). Still, the species with the highest biomass values were more separated along the $\delta^{15}N$ gradient: *Lampanyctus macdonaldi* (18.8% of the biomass) had a mean

$\delta^{15}\text{N}$ value of $11.52 \pm 0.32\text{‰}$, *Lampanyctus crocodilus* (13.9% of the biomass) $10.48 \pm 0.59\text{‰}$ and *Serrivomer beanii* (15.8% of the biomass) $9.56 \pm 0.56\text{‰}$. The epipelagic layer presented the lowest evenness and uniqueness indices (IEve = 0.448 and IUUni = 0.564). Thus, at the surface, resources were less optimally used, and the species with the highest biomass values were more isotopically redundant (high overlap between the two species of *Notoscopelus*). On the contrary, the upper mesopelagic layer had no index value below 0.800, meaning that the species with the highest biomass values had extreme isotopic values and were isolated and evenly distributed in isotopic space. See Appendix 5 for a representation of all indices.

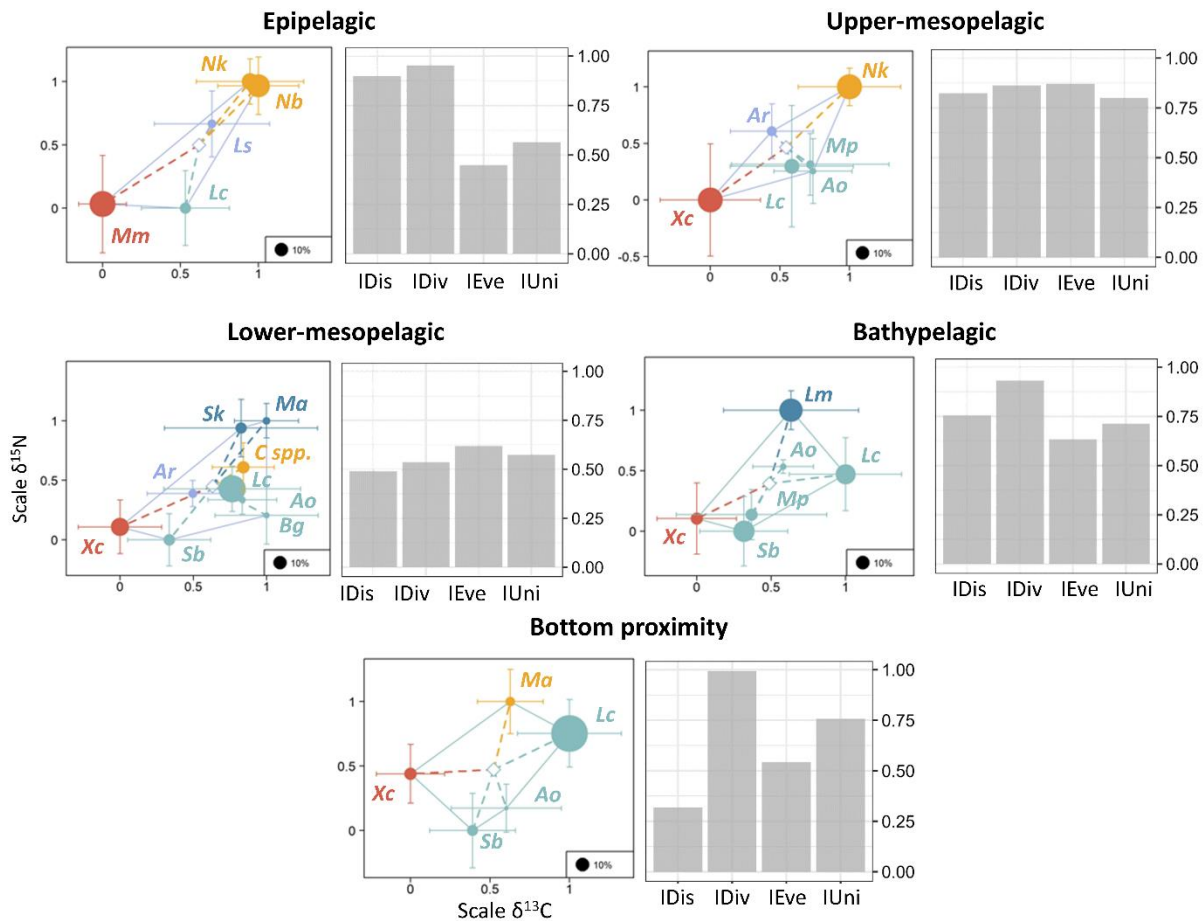


Figure 3-6. Stable isotope values of fish species at each depth layer with the convex hull display. Each point represents a species, and the size of the point is weighted by the species relative biomass (in %) in the depth layer. The colors represent the trophic guild to which each species belongs. The greater the distance between two points, the greater the isotopic divergence between these species. The initials correspond to the name of each species (the genus name in capitals and the species name in lower case). Barplots represented the isotopic diversity index values for each depth layer. IDiv = Isotopic Divergence, IDis = Isotopic Dispersion, IEve = Isotopic Evenness, and IUUni = isotopic Uniqueness.

Comparison of isotopic diversity index values between depth layers showed that the bathypelagic and near-bottom layers had similar patterns, with low trophic redundancy and relatively high specialization (Figure 3-7). The epipelagic layer stood out for its high rate of species specialization and low trophic redundancy. Conversely, the lower mesopelagic layer showed higher trophic redundancy and a lower rate of specialization.

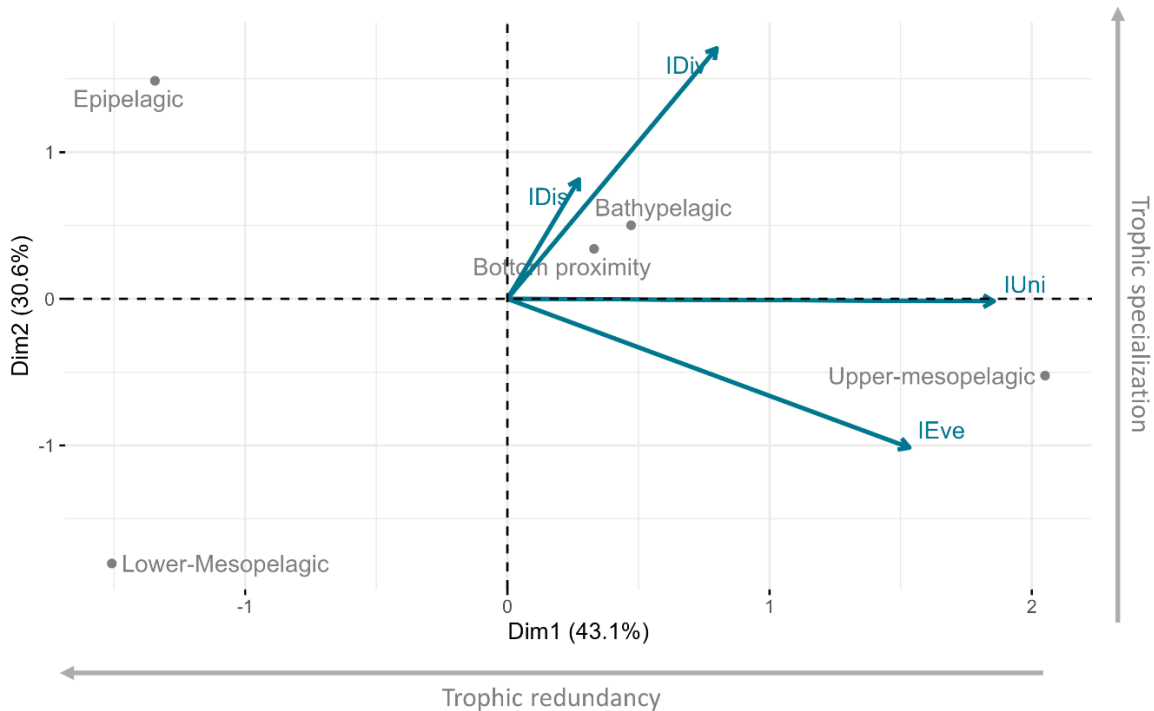


Figure 3-7. Biplot of principal component analysis (PCA). Results of the four functional diversity indices for the different layers.

4. Discussion

Competition shapes the assemblages of this community at night by reducing the similarity of species niches and inducing a segregation of species with similar niches along the depth axis. At each depth layer, the community showed strong partitioning of isotopic niches and significant species specialization. This trophic functioning may make this community highly sensitive to global change and exploitation.

4.1. Limits to consider

Several aspects need to be considered when interpreting our findings. Primarily, stable isotope ratios

can be influenced by several factors. In the case of deep pelagic fish, the $\delta^{15}\text{N}$ values are not solely impacted by dietary variations but also by the degradation of organic particles facilitated by bacteria. This process increases the $\delta^{15}\text{N}$ values in the muscle tissues of fish as the depth increases (Choy et al., 2015; Gloeckler et al., 2018; Richards et al., 2020; Romero-Romero et al., 2019). Variations in the isotopic baseline can also occur on large spatial scales. However, our sampling was carried out in canyons along the continental slope, thus reducing near/offshore gradient (i.e., sampling made between 9 and 30 km to the 200 m-isobath). Regarding the north-south gradient in the bay, a previous study had shown that oceanic species (some of which were common to our study) were not significantly affected by this gradient (Chouvelon et al., 2012). Finally, while we made efforts to minimize the size range sampled for each species, it's important to acknowledge that intraspecific variance could still have played a role in influencing the $\delta^{15}\text{N}$ values, particularly in species undergoing ontogenetic shift (Loutrage et al., 2023a). Although not considered in our study, it is possible that certain taxa such as cephalopods or crustaceans use similar niches, leading to competition with these fish species. Finally, stable isotope analysis can be used to interpret differences, but conversely, similar isotopic niches may result from different trophic ecologies.

4.2. Species use the depth dimension to segregate

The results showed that when species shared similar isotopic niches, they generally used their nocturnal depth distribution as a mechanism for segregation. For example, the two species in the first trophic guild, which showed the lowest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, *Xenodermichthys copei* and *Maurolicus muelleri* had a nocturnal distribution that peaked at different depths (555 and 25 m respectively). Similarly, for the second guild, the isotopic niche of *Lestidiops sphyrenoides* was 64% covered by the niche of *Arctozenus risso*, indicating significant potential competition. These species (both belonging to the order Aulopiformes) showed different depth distributions, with individuals of the species *A. risso* appearing to be more widely distributed in the meso- to bathypelagic layers, whereas the *L. sphyrenoides* population was more restricted to the epipelagic layer. This result of depth as a means of segregation for deep-pelagic species has already been found in other areas, notably for Myctophids and Hatchetfishes (Hopkins et al., 1996; Hopkins and Sutton, 1998; Cherel et al., 2010; Eduardo et al., 2020a, 2021).

The broad range of $\delta^{15}\text{N}$ values ($\Delta \delta^{15}\text{N} \approx 6\text{‰}$) may imply variations in trophic sources and species-feeding strategies (Stowasser et al., 2012; Valls et al., 2014a; Chouvelon et al., 2022; Richards et al., 2023). Individuals located at greater depths have a greater dependence on the food chain based on bacterial degradation of organic particles, leading to enrichment in $\delta^{15}\text{N}$ measures compared to individuals located shallower (Choy et al., 2015; Gloeckler et al., 2018; Romero-Romero et al., 2019; Richards et al., 2020). Migration leads to a decoupling of this relationship, as migratory species are more dependent on surface phytoplankton and are, therefore, more depleted in ^{15}N than non-migratory species. This could partly explain the relatively high mean $\delta^{15}\text{N}$ values of *Cyclothone* spp., a non-migratory species with a deep distribution (i.e., median depth = 715m), in contrast to its small size, since it ranks as the third species with the smallest body size in our study (mean size = 5.5 cm). *Melanostigma atlanticum*, another species in the same trophic guild, exhibited mean $\delta^{15}\text{N}$ values of $11.28 \pm 0.46\text{‰}$. The species is described as non-migratory and its highest biomass was found in the near-bottom layer. *Melanostigma* genus feed on pelagic crustaceans, but due to their poor locomotion, it has been hypothesized that these species may have been scavengers (Gartner Jr et al., 1997). Part of these explanations for relatively high $\delta^{15}\text{N}$ values of *Cyclothone* spp. and *Melanostigma atlanticum* due to depth are reinforced by the distribution pattern of the three species in the last trophic guild (i.e., *Lampanyctus macdonaldi*, *Searsia koefoedi* and *Maulisia argipalla*), which are all non-migratory and dispersed between the lower mesopelagic and bathypelagic layers (with a median depth between 1000 and 1335 m) and had the highest $\delta^{15}\text{N}$ values, ranging from 11.52 to 12.01‰. In addition to this increase in $\delta^{15}\text{N}$ values with increasing immersion depth, the benthopelagic habits of certain species may also play a role. As an example, *Lampanyctus crocodilus* is known to adopt a benthopelagic behavior at the senescent age and to feed then on epibenthic prey at the benthic boundary layer (Stefanescu and Cartes, 1992; Valls et al., 2014b). In our study, this species presented the highest mean $\delta^{15}\text{N}$ values in the near-bottom layer ($10.82 \pm 0.48\text{‰}$). Information on Platytroctidae, even as basic as vertical distribution, is very scarce in the literature. *S. koefoedi* has been reported to have a diet composed largely of copepods but also ostracods, chaetognaths, and polychaetes, which could partly explain its large isotopic niche (Novotny, 2018). Several species in this family have been found to have increasing biomass with decreasing distance from the bottom of the Bay of Biscay

(Loutrage et al., 2023b). Consequently, the higher $\delta^{15}\text{N}$ values of these two species may also be partly explained by benthopelagic habits.

4.3. Trophic functioning along the depth gradient

Our study highlights a fundamental outcome: deterministic processes play a crucial role in shaping the deep pelagic fish community in the Bay of Biscay. More precisely, values of niche size and overlap in epi- to bathypelagic layers were significantly lower than null model values, indicating that competition is a driving force shaping the trophic structure of the community. This implies that each species in a depth layer has a comparatively smaller isotopic niche size – due to interspecific competition – than if stochastic processes dominated (i.e., null model) and that each niche is slightly distinct to alleviate competition with the other species present (i.e., niche partitioning) (Chesson, 2000). Limiting similarities to avoid strong competition seems to be the primary strategy adopted by species in the deep sea. Contrary to the first hypothesis on the trophic ecology of deep-sea fishes, "eat everything you see in a poor environment," numerous studies have found multiple axes of segregation used by species to avoid strong competition in deep environments (Mauchline, 1986; Hopkins and Gartner, 1992; Hopkins and Sutton, 1998; Eduardo et al., 2020a, 2021, 2023). The geological age of the deep pelagic ecosystem and its environmental stability are likely two important factors that have permitted the shape of interspecific relationships over time to limit competition (Klomp maker and Finnegan, 2018). The limited food supply in the deep sea may encourage trophic specialization to optimize resource utilization and minimize competition (Schoener, 1974; Abrams, 1983). In line with this last hypothesis, we might have expected the epipelagic layer, which is the most productive, to show a different pattern, with species that do not necessarily need to segregate to limit competition. The opposite was found, with species presenting values of niche and overlap sizes smaller than those of a distribution governed by stochastic processes. A possible explanation for this result could be the greater diversity of resources used by the species in the epipelagic zone. This was reflected by high isotopic diversity in the biomass of the dominant species (highest dispersion indices, $\text{IDis} = 0.898$). *Maurolicus muelleri* had low $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, indicating a dependence on phytoplankton sources. In contrast, both *Notoscopelus* species had high $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, indicating that they may also feed at greater depth.

In the near-bottom layer, the isotopic niches of the species were identical in size to those of the null model, suggesting that the species from this depth layer have a more generalist feeding behavior. This is further confirmed by the lowest value of isotopic dispersion found in this layer (IDis = 0.318), indicating that the species with the highest biomass (*Lampanyctus crocodilus* = 56% of the relative biomass) is generalist. This result may be due to a rise in the availability and variety of food resources in this depth layer (Gartner et al., 2008). The benthic boundary layer creates a two-dimensional concentration of resources, making them more accessible to species, in contrast to the water column, where resources are scattered in three dimensions (Gartner et al., 2008). Furthermore, the presence of pelagic and benthic resources in this layer facilitates a broader diet for species belonging to this layer. The sum of isotopic niche overlaps was less than that of the null model. Under conditions of high resource diversity, species niches will expand and diverge to reduce interspecific competition (Costa-Pereira et al., 2019). Although the sum of the observed overlaps within each depth layer was significantly different from the null model, the two layers with potentially more resources (epipelagic and near-bottom layers) showed the smallest differences between the observed data and those of the null model. This result may indicate that productivity plays a role in shaping, at least in part, the trophic structure of these communities across the depth gradient.

Suchomel et al. (2022) described that assemblages resulting from a stochastic model are characterized by niches that share similar positions in isotopic space, exhibit a relatively large size compared to the available niche space, and present a high degree of overlap. However, the near-bottom layer in our study did not fulfil all of these criteria, as the sum of overlaps within this layer was significantly smaller than the null model. This depth layer also presented high dispersion and uniqueness indices, suggesting that the dominant species (*Lampanyctus crocodilus*, constituting 56% of the relative biomass) was isolated in the isotopic space, leading to low trophic redundancy within the assemblage. Contrary to a binary perspective on niche arrangement models, our findings suggest that the two models could represent the two extremes of a continuum (Gravel et al., 2006).

4.4. Implication for fish community stability

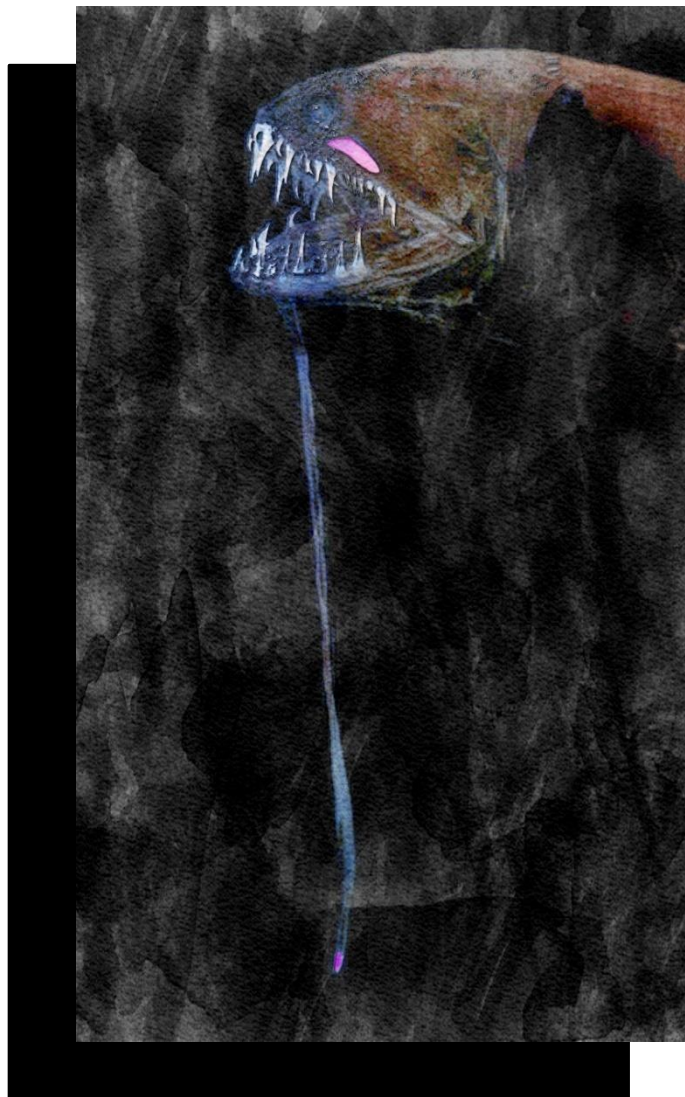
The significant level of isotopic specialization within this community, as indicated by high divergence indices and low isotopic niche area in comparison to the null model, may have significant implications in the present context of global changes and the future exploitation of mesopelagic resources. The

community's high isotopic diversity, combined with low trophic redundancy across the depth gradient, renders it important from an ecological perspective but may also be more sensitive to disturbances. Communities presenting these characteristics may have improved ecosystem functions by optimizing their food resources, leading to heightened productivity (Rigolet et al., 2015). This finding is significant for epi- to mesopelagic fish communities, given the species' vertical migration, which facilitates the exchange of matter and energy between ocean depth layers (Sutton, 2013). Aggregation of mesopelagic species near the bottom in slope areas enables long-term carbon storage through the predation of these species by demersal communities (Gartner et al., 2008; Trueman et al., 2014). At night, the migration of these species towards the surface also makes them accessible to epipelagic top predators such as cetaceans, pinnipeds, birds and large fish (Pauly et al., 1998; Pusineri et al., 2005, 2007; Connan et al., 2007; Battaglia et al., 2013). The community's low trophic redundancy along the depth gradient may suggest a decreased capacity to buffer against disturbances. Specialist species may be more vulnerable to global changes than generalist ones (Clavel et al., 2011). This could result in reduced resilience, particularly in situations of diversity loss, as isotopically similar species may not moderate the effects of species loss (Raffaelli, 2006; Rigolet et al., 2015). Species and communities will not respond to disturbance in the same way. For this reason, it has been hypothesized that a community composed of many specialized species, which therefore has a high degree of possible response complementarity directly related to niche partitioning, should show greater resistance and resilience than a community composed mainly of generalists (Clavel et al., 2011). Our ability to make clear predictions about how different types of communities will react to a new disturbance is, therefore, still limited.

In conclusion, competition appears to be the main factor determining the trophic structure of the epi- to bathypelagic fish community in the Bay of Biscay. As a result, species have adapted over time to reduce competition by occupying slightly different niches. The environmental stability of deep pelagic ecosystems and the dependence on primary production subsidies from the upper layers are probably at the origin of the taxonomic, morphological, and trophic diversity observed in these ecosystems. The functioning of these ecosystems is currently threatened by human activities (Levin et al., 2019). Characterizing the trophic structure and its control mechanisms at the community level is a crucial first step. It will be essential to anticipate the extent to which changes due to human activities

will modify this trophic structure by also integrating other taxa, such as cephalopods and decapod crustaceans, in order to assess the resilience of the deep-pelagic ocean, depending on the functioning hypotheses (i.e. generalist vs specialist communities) (Clavel et al., 2011).

Chapitre 4 - Unlocking the Depths: Exploring diverse nocturnal foraging strategies in epi- to bathypelagic fish



1. Introduction

The assessment of biodiversity has recently undergone a paradigm shift from measuring species diversity to measuring functional diversity (Cernansky, 2017). The species' characteristics and role within ecosystems would thus be better understood by studying species' traits, which are translated into functions (Violle et al., 2007; Mouillot et al., 2013a). Grouping species according to their functional traits appears to be a more relevant approach to understanding the interactions between species, assessing the effect of anthropogenic pressures, and, more broadly, the functioning of ecosystems. This growing interest in trait-based ecology responds to the increasingly urgent need to understand the consequences of global change in biodiversity and the feedback of traits into ecosystem functions (Mcgill et al., 2006; Cadotte et al., 2011). The functional approach provides solutions for quantifying the role of species in a community by providing an integrated approach. It enables the quantification of the vulnerability of specific communities to functional loss and allows for the identification of distinct functional traits that influence communities in relation to the environment (Brind'Amour et al., 2011; Mouillot et al., 2013a). Additionally, it contributes to an enhanced understanding of the evolutionary strategies that enable species to survive (Adler et al., 2014).

The study of functional diversity can also inform assembly rules within communities. Two concepts arise from focusing on the deterministic processes of community assembly, leading to divergent patterns in observed functional diversity. On the one hand, the principle of environmental filtering dictates that the species within a community are adapted to local conditions, resulting in a selection of traits that maximise their survival. This process should reduce functional diversity within the community as species with similar traits are favored (Van Der Valk, 1981; Weiher et al., 1998; Kraft et al., 2015). Conversely, the principle of competitive exclusion suggests that species within a community limit their similarity to avoid excessive competition for resources (Gause, 1932; Macarthur and Levins, 1967; Abrams, 1983). This mechanism should increase functional diversity within the community, as species specialize in the use of different resources, leading to more efficient resource partitioning and reduced competition (Hector et al., 1999). Assessing functional diversity provides insight into the assembly mechanisms that shape community diversity and structure. Answering these specific questions can improve our ability to predict species ecology, trophic interactions, community responses to species invasions or changes in distribution that may lead to new competition.

Another aspect of functional diversity refers to the uniqueness or scarcity of certain functional traits within a community. While functional diversity looks at the overall range and distribution of functional traits, functional rarity focuses on those traits that are rare or uncommon among the species present. The rarity of a species can be addressed in terms of abundance or geographical range, or in terms of functional rarity (Violle et al., 2017). Rare species may provide irreplaceable ecosystem functions by possessing a unique combination of traits (Mouillot et al., 2013a; Jain et al., 2014). The disappearance of these species could lead to a reduction in the diversity of ecological niches within the community, disrupting established trophic interactions, eliminating highly specialized forms of resource use, and compromising the integrity of essential ecological processes (Leitão et al., 2016).

In aquatic ecosystems, fishes are an essential component. There are around 28,000 identified living species, just over half the number of known tetrapods. They are widely distributed horizontally and vertically (the deepest observations have been made at over 8300 m) and have significant biomass at the scale of marine ecosystems (Jamieson et al., 2023). They also exhibit diverse behavior, size, and feeding habits, giving them essential functional roles within ecosystems (Nelson et al., 2016; Villéger et al., 2017). The functional approach applied to fish communities has made it possible to estimate the sensitivity of species to environmental disturbance (McLean et al., 2019), the arrival of invasive species (Su et al., 2023), and fishing (Martins et al., 2012). Our knowledge of the functional diversity of fish communities is still almost exclusively limited to communities in the coastal and neritic zones. Deep-sea fishes are currently the least known of fish communities despite their potentially enormous biomass and the ecosystem services they provide (Webb et al., 2010; Irigoien et al., 2014). They play an essential role in nutrient recycling and carbon transport between depth layers and provide an important source of prey for species of high commercial interest (Pusineri et al., 2005; Irigoien et al., 2014; Young et al., 2015). At the same time, deep pelagic fish are subject to increasing anthropogenic pressures such as climate change, pollution, and exploitation (Hidalgo and Browman, 2019; Levin et al., 2019; Drazen et al., 2020).

The environmental characteristics of the deep-sea environment have given rise to specific adaptations to survive in a cold environment, with little or no light, reduced oxygen levels, and fewer food resources, relying solely on productivity at the surface (Fock et al., 2004; Proud et al., 2017). These constraints have led species to adopt strategies to find food while limiting predation risk. Therefore,

unique and diverse morphologies and adaptations have emerged, such as bioluminescence, nychthemeral migration, or complex visual system (Figure 4-1) (Sutton, 2013; Aparecido et al., 2023; Eduardo et al., 2023).

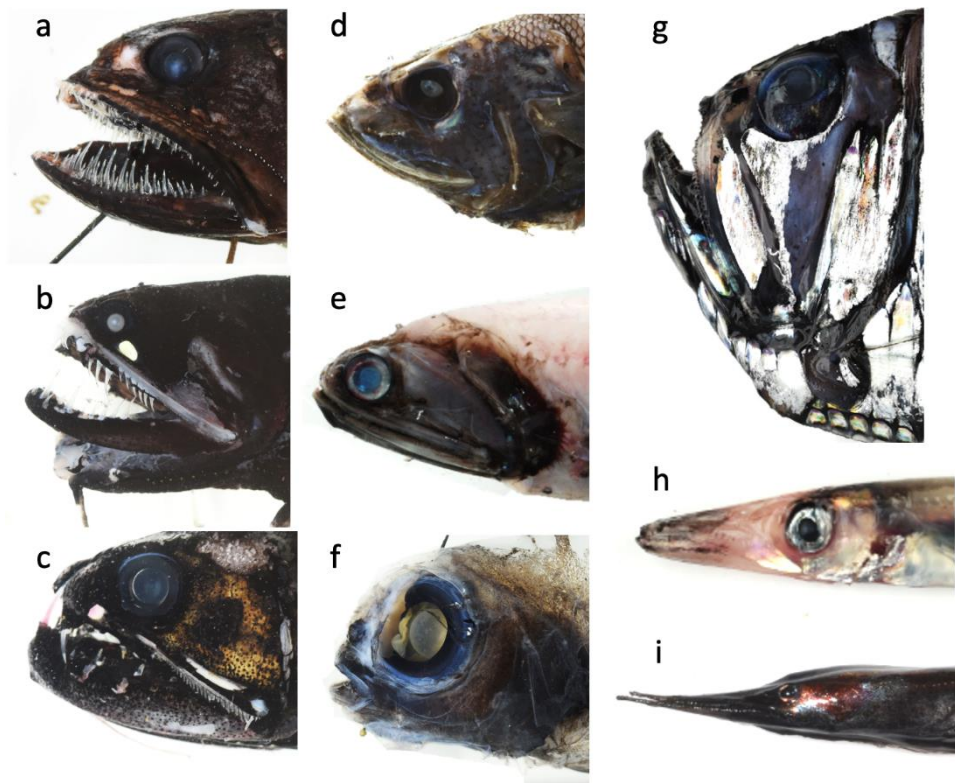


Figure 4-1. Lateral-view photographs of the heads of various deep pelagic species (© Samuel P. Iglesias, MNHN). a- *Pseudoscopelus altipinnis*, b- *Melanostomias bartonbeani*, c- *Astronesthes niger*, d- *Maulisia maui*, e- *Lampanyctus crocodilus*, f- *Bathylagus euryops*, g- *Argyropelecus olfersii*, h- *Lestidiops sphyrenoides*, i- *Serrivomer beanii*.

Although trait-based approaches can greatly enlighten our knowledge of the trophic ecology of these species, functional ecology of deep-pelagic fish species has still been little studied due to the lack of morphology data available on an individual scale for these species, which are difficult to access. In this context, beyond to provide a first comprehensive dataset on morphological measurements for a broad diversity of deep-pelagic fish species, we aimed to answer these questions:

- What are the key functional traits that are involved in the foraging strategies of these species?
- What is the functional diversity and structure of this community at each depth layer?
- Which assembly rules, environmental filtering (where species adapt similarly and exhibit comparable traits) or competitive exclusion (where co-occurring species will exhibit different traits), are more likely to explain the community structure of deep pelagic fish?

- Are some species particularly rare in terms of functional diversity?

2. Materials and methods

2.1. Sampling

Species sampling was carried out between 2001 and 2022 using the methodology described in the previous chapters. All sampling was realized at night on the continental slope and covered a range of depths from 20 m to 2000 m. A division into four depth layers was made to compare differences in diversity and structure along the depth gradient. This division into epipelagic, upper mesopelagic, lower mesopelagic, and bathypelagic layers followed the nocturnal vertical stratification observed for this community in the same area (Table 4-1) (Loutrage et al., 2023b). Since we only sampled at night, the results cannot be extrapolated to daytime.

Table 4-1. Depth range of each layer and the number of trawl hauls made within each layer. The number of species measured for this study and the sum of their biomass in each depth layer are also shown.

Depth layer	Depth range (m)	n trawl hauls	Species richness	Total biomass (g.m ³)
Epipelagic	20-175	8	24	5.47 x 10 ⁻⁴
Upper mesopelagic	175-700	26	28	4.55 x 10 ⁻³
Lower mesopelagic	700-1000	16	32	4.77 x 10 ⁻³
Bathypelagic	1000-2000	16	41	7.49 x 10 ⁻³

2.2. Missing data and trait selection

The species trait dataset encompasses information for a total of 42 species (722 individuals). The measurements were acquired either on board during the EVHOE 2022 campaign or in the laboratory, where individuals were frozen before being included in the dataset. Species with fewer than three individuals were not considered. A total of 27 traits were selected for their potential importance in resource acquisition for the 42 species (Table 4-2). See appendices 6, 7, 8, 9 and 10 for a representation of the traits measured.

Out of 2 660 measurements, less than 1% were missing. As the missing data were not randomly distributed between species, an imputation algorithm was used to fill in the missing data. Removing these data could have affected our interpretation, as rare species or species from certain clades could be underrepresented (Penone et al., 2014). The approach of multivariate imputation by chained equations was therefore used with a number of imputations of five and fifty iterations. The R package mice was used to realize the imputation (Van Buuren and Groothuis-Oudshoorn, 2011). Only one species, *Eurypharynx pelecanooides*, was removed from the dataset as it presented seven missing traits.

Table 4-2. Description and formulas of the traits computed from morphological measurements. (Webb, 1984; Winemiller, 1991; Sibbing and Nagelkerke, 2000; Dumay et al., 2004; Diderich, 2006; Boyle and Horn, 2006; Ibañez et al., 2007; Albouy et al., 2011; Habib et al., 2019; Aneesh Kumar et al., 2017). The abbreviations used in the formulae are provided by the raw measurements and are detailed in the appendices. P/A = Presence or Absence of the trait.

Trait	Description	Formula
Oral gape axis	Feeding position and depth in the water column	Superior, supra-terminal, terminal, sub-terminal, inferior
Eye size	Detection of prey and visual acuity for predators	Ed/hd
Orbital length	Prey size and behavior (buried, camouflaged)	Ed/sl
Oral gape surface	Type and size of prey	Mw*md/bw/bd
Oral gape shape	Strategy to capture prey	Md/hd
Oral gape position	Feeding position in the water column	Mo/hd
Lower jaw length	Compromise between power and opening speed of the mouth	Ljl/sl
Gill raker type	Filtration capacities of fish	Absent or rudimentary, low-developed, well developed
Gill outflow	Suction capacities of fish	ow
Head length	Maximum prey size	Hl/sl
Gland head	Illumination of prey	P/A
Chin barbel	Strategy to attract prey (lure)	P/A
Small teeth	Ability to capture and handle different type and size of prey	P/A
Large teeth	Ability to capture and handle different type and size of prey	P/A
Fang teeth	Enables prey to be pierced and captured	P/A
Retractable teeth	Allow species to engulf and capture large prey	P/A
Internal teeth		P/A
Body depth	Swimming capacities of fish linked to their food prospection behavior	Bd/sl
Pectoral fin position	Maneuverability of fish	Pfi/pfb
Pectoral fin insertion	Maneuverability of fish	Ppl/sl
Transversal shape	Position in the water column and hydrodynamism	Bd/bw
Caudal throttle width	Swimming strategy (cruiser/sprinter) and endurance	Cpd
Dorsal fin insertion	Swimming type and behavior	Pdl/sl
Eye position	Position in the water column (pelagic/sedentary)	Eh/hd
Photophore position ventral	Camouflage, counter illumination	P/A
Operculum volume	Filtering capacity and oxygen caption	Pd/ow

2.3. Data analyses

2.3.1. Functional space and diversity metrics

To access the functional space of the community and calculate diversity indices, a dissimilarity matrix was first calculated using the Gower distance as it allows both numerical and categorical variables to

be included. Then, to generate a multidimensional space in which functional diversity indices can be calculated (Mouillot et al., 2013b), Principal Components Analyses (PCoA) were performed using trait-based distances. The quality of multidimensional spaces based on PCoAs was investigated as a function of the difference between trait-based distances and distances in the functional space. A compromise between the quality of the multidimensional space and the number of axes was found at $n = 4$ (Maire et al., 2015). Six functional diversity metrics were investigated: functional richness, dispersion, divergence, evenness, specialization, and identity (Table 4-3). As most indices allow weighting by species abundance, standardized biomass was used. This was done by dividing the biomass of each species in each trawl by the volume filtered by the trawl during the fishing phase (vertical opening \times horizontal opening \times distance trawled). As biomass is directly related to the amount of energy and resources assimilated within species, measuring biomass rather than abundance was deemed more relevant to our study (Villéger et al., 2008). Furthermore, biomass is not evenly distributed among deep-sea pelagic species, with small species often abundant. All these analyses were made with the R package mFD (Magneville et al., 2022).

Table 4-3. The functional diversity indices used, their definition, and the associated ecological interpretation employed in this study.

Functional metrics	Abbreviation	Definition	Ecological interpretation
Richness	FRic	Amount of functional space filled by a community.	High FRic indicates a community with a broad spectrum of functional trait values, suggesting diverse ecological strategies. This metric can inform ecosystem stability and resilience by tackling the community's ability to respond to environmental changes.
Evenness	FEve	Regularity of species spacing along a functional trait gradient and evenness of biomass distribution across species.	High FEve suggests that functional traits are evenly distributed among species, indicating a balanced utilization of resources and a potential for efficient resource use within the community. This can contribute to stable ecosystem functioning.
Divergence	FDiv	Refers to how biomass is distributed within the volume of functional trait space occupied by species.	High FDiv implies a greater range or divergence of functional traits among co-occurring species. This may indicate niche differentiation, where species specialize in different ecological roles, potentially reducing competition and promoting coexistence.
Dispersion	FDis	Biomass-weighted deviation of species trait values from the center of the functional space.	High FDis signifies that species in the community are dispersed widely across the functional trait space. This may indicate a community with various distinct ecological strategies, reducing competition and enhancing ecosystem stability.
Specialization	FSpe	Mean distance of a species from the rest of the species	High Fspe means that specialized species are efficient in exploiting specific resources. Functional

		pool in the functional space.	specialization refers to the degree to which a species is adapted to a specific ecological niche or performs a specific set of functions within a community.
Identity	Fide	Mean value of functional traits, weighted by biomass, across all species present in a community.	High Fide might indicate niche convergence, where species have evolved similar traits to exploit similar ecological niches. This convergence could be driven by environmental filters or interspecific interactions.

2.3.2. Community Weighted Mean (CWM)

To characterize the functional structure of the community, a calculation of the Community Weighted Mean (CWM) trait values was performed. For each trait, this index corresponds to the mean trait values in the community weighted by the species-relative biomass. For quantitative traits, this index represents the mean value that would be more likely to be found if an individual were randomly sampled from the community. For categorical traits, this index represents the percentage of a given category of the trait in the community.

2.3.3. Functional rarity

To access the different forms of rarity, we calculated several indices. First, the two indices related to species' presence (or biomass) were the scarcity, the relative biomass of the species, and the restrictedness, which is calculated as the ratio of the sites occupied by a species to the total number of sites. The two indices related to the functional originality of species are distinctiveness, which is the average dissimilarity of the focal species with all other species in the community, and functional uniqueness, which is the smallest dissimilarity between the focal species and all other species in the assemblage. In this study, the regional scale is defined as the whole community (all depth layers) and the local scale as a specific depth layer. All analyses were made with the R package *funrar* (Grenié et al., 2017).

3. Results

On the 42 species measured, the size range was equal to 51.5 cm (standard length). *Argyropelecus olfersii* was the smallest (3.1 cm) and *Serrivomer beanii* the largest (54.6 cm) (Table 4-4). Myctophidae and Platytroctidae were the two taxonomic families with the highest diversity of species measured (11 and 8 respectively).

Table 4-4. Order and taxonomic family, number of individuals and standard size (cm) \pm standard deviation of each species measured.

Order	Family	Species	N individuals	Standard length
Myctophiformes	Myctophidae	<i>Bolinichthys supralateralis</i>	11	9.6 \pm 0.6
		<i>Ceratoscopelus maderensis</i>	30	6.3 \pm 0.7
		<i>Diaphus metopoclampus</i>	4	6.1 \pm 1.7
		<i>Lampanyctus ater</i>	22	10.9 \pm 1.1
		<i>Lampanyctus crocodilus</i>	39	10.8 \pm 1.7
		<i>Lampanyctus macdonaldi</i>	21	12.9 \pm 0.6
		<i>Lobianchia gemellarii</i>	22	8.3 \pm 0.7
		<i>Myctophum punctatum</i>	25	6.5 \pm 0.8
		<i>Notoscopelus bolini</i>	20	7.6 \pm 0.4
		<i>Notoscopelus kroyeri</i>	36	7.6 \pm 1.6
		<i>Benthoosema glaciale</i>	20	4.3 \pm 0.2
Alepocephaliformes	Platyroctidae	<i>Holtbyrnia anomala</i>	3	6.6 \pm 0.7
		<i>Holtbyrnia macrops</i>	9	7.9 \pm 2.3
		<i>Maulisia argipalla</i>	5	9.5 \pm 1.9
		<i>Maulisia maui</i>	11	11.7 \pm 2.8
		<i>Maulisia microlepis</i>	4	23.1 \pm 2.2
		<i>Normichthys operosus</i>	38	10.5 \pm 1.8
		<i>Sagamichthys schnakenbecki</i>	9	9.2 \pm 2.1
		<i>Searsia koefoedi</i>	36	12.0 \pm 1.4
	Alepocephalidae	<i>Photostylus pycnopterus</i>	8	9.6 \pm 1.5
		<i>Xenodermichthys copei</i>	38	11.0 \pm 1.2
Stomiiformes	Stomiidae	<i>Borostomias antarcticus</i>	14	12.2 \pm 5.6
		<i>Chauliodus sloani</i>	12	22.9 \pm 5.9
		<i>Malacosteus niger</i>	5	15.7 \pm 4.1
		<i>Melanostomias bartonbeani</i>	9	23.3 \pm 2.5
		<i>Stomias boa</i>	26	23.9 \pm 4.5
	Gonostomatidae	<i>Cyclothone spp.</i>	12	5.3 \pm 0.6
		<i>Gonostoma elongatum</i>	3	23.6 \pm 1.4
		<i>Sigmops bathyphilus</i>	20	9.2 \pm 1.8
	Sternoptychidae	<i>Maurolicus muelleri</i>	11	3.2 \pm 0.2
		<i>Argyropelecus hemigymnus</i>	17	3.1 \pm 0.4
<i>Argyropelecus olfersii</i>		37	5.7 \pm 1.1	
Aulopiformes	Paralepididae	<i>Arctozenus risso</i>	30	15.8 \pm 1.5
		<i>Paralepis coregonoides</i>	19	7.3 \pm 1.5
		<i>Lestidiops sphyrenoides</i>	7	14.8 \pm 0.9
	Evermannellidae	<i>Evermannella balbo</i>	4	10.5 \pm 0.3
Anguilliformes	Derichthyidae	<i>Derichthys serpentinus</i>	7	22.6 \pm 3.3
	Serrivomeridae	<i>Serrivomer beanii</i>	30	54.6 \pm 12.1
Argentiniformes	Bathylagidae	<i>Bathylagus euryops</i>	19	12.3 \pm 3.6
Perciformes	Zoarcidae	<i>Melanostigma atlanticum</i>	20	8.4 \pm 1.1

Saccopharyngiformes	Eurypharyngidae	<i>Eurypharynx pelecanooides</i>	6	36.5 ± 6.5
Trachichthyiformes	Anoplogastridae	<i>Anoplogaster cornuta</i>	3	13.0 ± 1.7

3.1. Functional space and key traits

At the community level, the four-dimensional functional space contained 26 species vertices and 15 non-vertices (Table 4-4, Figures 4-2 and 4-3). The vertices species are those with the most extreme trait values and are, therefore, on the edge of the convex hull, defining its shape. At the community level, the first principal component (PC) explained 16% of the variation, and 14 traits were significantly correlated with this axis and considered as key traits for foraging, including two with an Eta^2 or R^2 value > 0.400 (Table 4-5). These two traits were related to the type of teeth and the presence or absence of large and fang teeth. The PC2 was mainly controlled by the length of the lower jaw, the gill outflow, and the surface of the oral gape. This axis explained 12.4% of the total variance. The last two PCs showed only one significant correlation with a trait having Eta^2 values > 0.400 : the presence or absence of internal teeth and the presence of photophores on the ventral position for PC3 and PC4, respectively. Together, these two axes explained 15.2% of the variance. Consequently, the four principal components explained a total of 43.6% of the variance. As the bathypelagic zone includes all species, these results at the community level are also valid for this layer. The other depth layers showed several traits significantly correlated with the PC1 in common: the head length, the orbital length, and the gill raker type. The second principal component was significantly correlated with two traits related to the mouth for these three depth layers: the oral gape surface and axis. For the PC3, the presence or absence of internal teeth was significantly correlated for each depth layer. Finally, the last PC was significantly influenced by operculum volume for the epipelagic and by the presence or absence of ventral photophores for the two mesopelagic layers.

Table 4-5. Percentage of variance explained by the four principal components and the traits significantly correlated with it. R^2 values are shown for numerical traits, and Eta^2 values for categorical traits. Only traits with R^2/Eta^2 values > 0.400 are shown.

Assemblage	PC axis (% variance explained)	Trait	Eta^2/r^2 value	p-value
Epipelagic	1 (24.0)	Head length	0.775	<0.001
		Orbital length	0.643	<0.001
		Gill raker types	0.491	0.004
		Pectoral fin insertion	0.443	0.001
		Body depth	0.410	0.002

	2 (21.0)	Eye size	0.602	<0.001
		Oral gape surface	0.600	<0.001
		Oral gape axis	0.525	0.003
		Photophores ventral position	0.458	0.002
		Gill outflow	0.448	<0.001
	3 (13.2)	Internal teeth	0.565	<0.001
	4 (6.6)	Operculum volume	0.539	<0.001
Upper Mesopelagic	1 (21.7)	Gill raker types	0.0496	<0.001
		Fang teeth	0.487	<0.001
		Head length	0.457	<0.001
		Orbital length	0.434	<0.001
		Small teeth	0.412	<0.001
	2 (14.4)	Lower jaw length	0.653	<0.001
		Oral gape axis	0.543	<0.001
		Oral gape surface	0.484	<0.001
		Gill outflow	0.418	<0.001
		Caudal throttle width	0.403	<0.001
	3 (10.0)	Internal teeth	0.646	<0.001
	4 (8.4)	Photophores ventral position	0.408	<0.001
Lower mesopelagic	1 (19.6)	Head length	0.712	<0.001
		Pectoral fin insertion	0.603	<0.001
		Orbital length	0.601	<0.001
		Gill raker types	0.558	<0.001
		Lower jaw length	0.416	<0.001
	2 (13.5)	Oral gape axis	0.542	<0.001
		Eye size	0.463	<0.001
		Oral gape surface	0.456	<0.001
		Large teeth	0.438	<0.001
	3 (10.1)	Internal teeth	0.667	<0.001
	4 (6.9)	Operculum volume	0.497	<0.001
Total/bathypelagic	1 (16.0)	Large teeth	0.467	<0.001
		Fang teeth	0.410	<0.001
	2 (12.4)	Lower jaw length	0.689	<0.001
		Gill outflow	0.505	<0.001
		Oral gape surface	0.489	<0.001
		Caudal throttle width	0.406	<0.001
		Pectoral fin insertion	0.405	<0.001
	3 (8.0)	Internal teeth	0.634	<0.001
	4 (7.2)	Photophores ventral position	0.597	<0.001

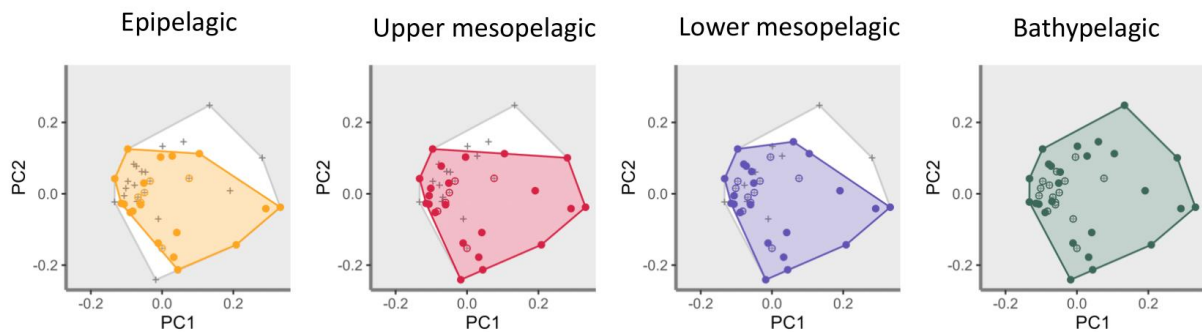
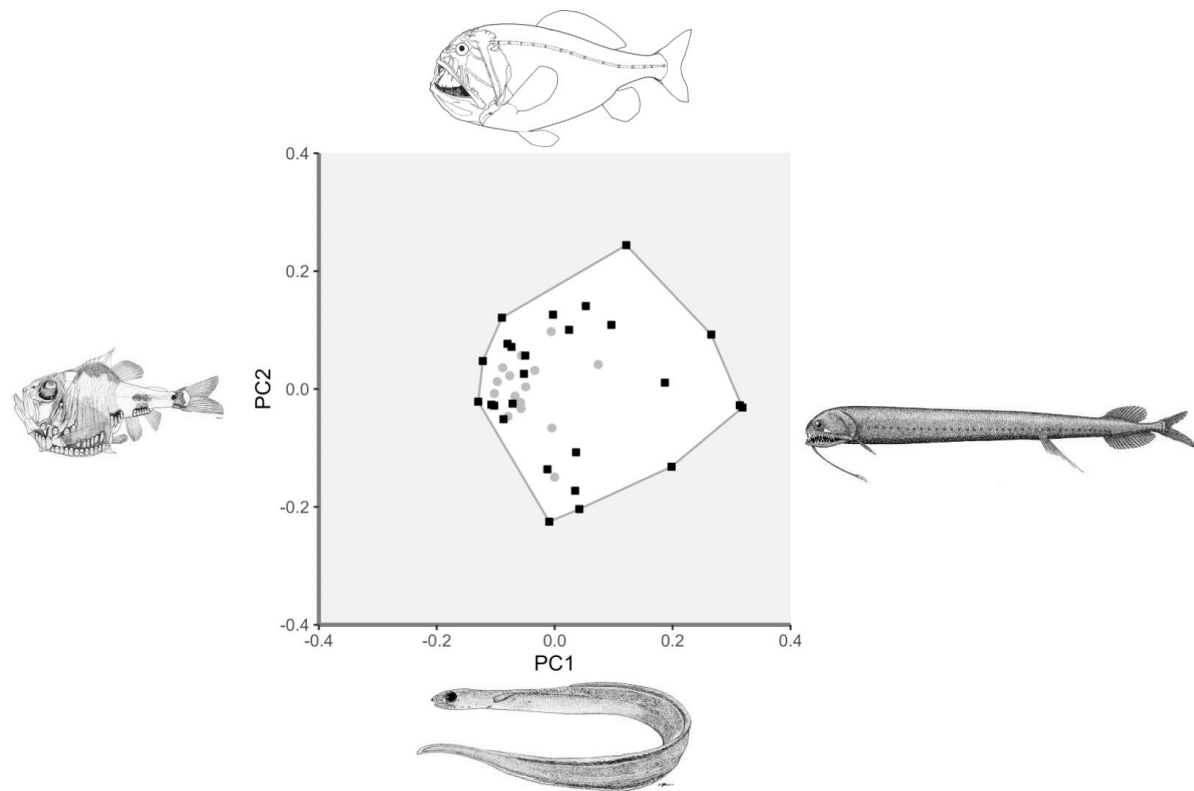


Figure 4-2. Representation of functional space on principal components 1 and 2 for the total community and the epipelagic, upper mesopelagic, lower mesopelagic, and bathypelagic layers. In each plot, the solid colored circles represent the vertex species, the colored circles represent the species present in the layer but not vertices, and the grey crosses the vertices species in the other depth layers. An image of the vertices species has been added to illustrate the morphological variation across the plot, from top to bottom: *Anoplogaster cornuta*, *Derichthys serpentinus*, from left to right: *Argyropelecus olfersii* and *Melanostomias bartonbeani* —images from (Sutton et al., 2020).

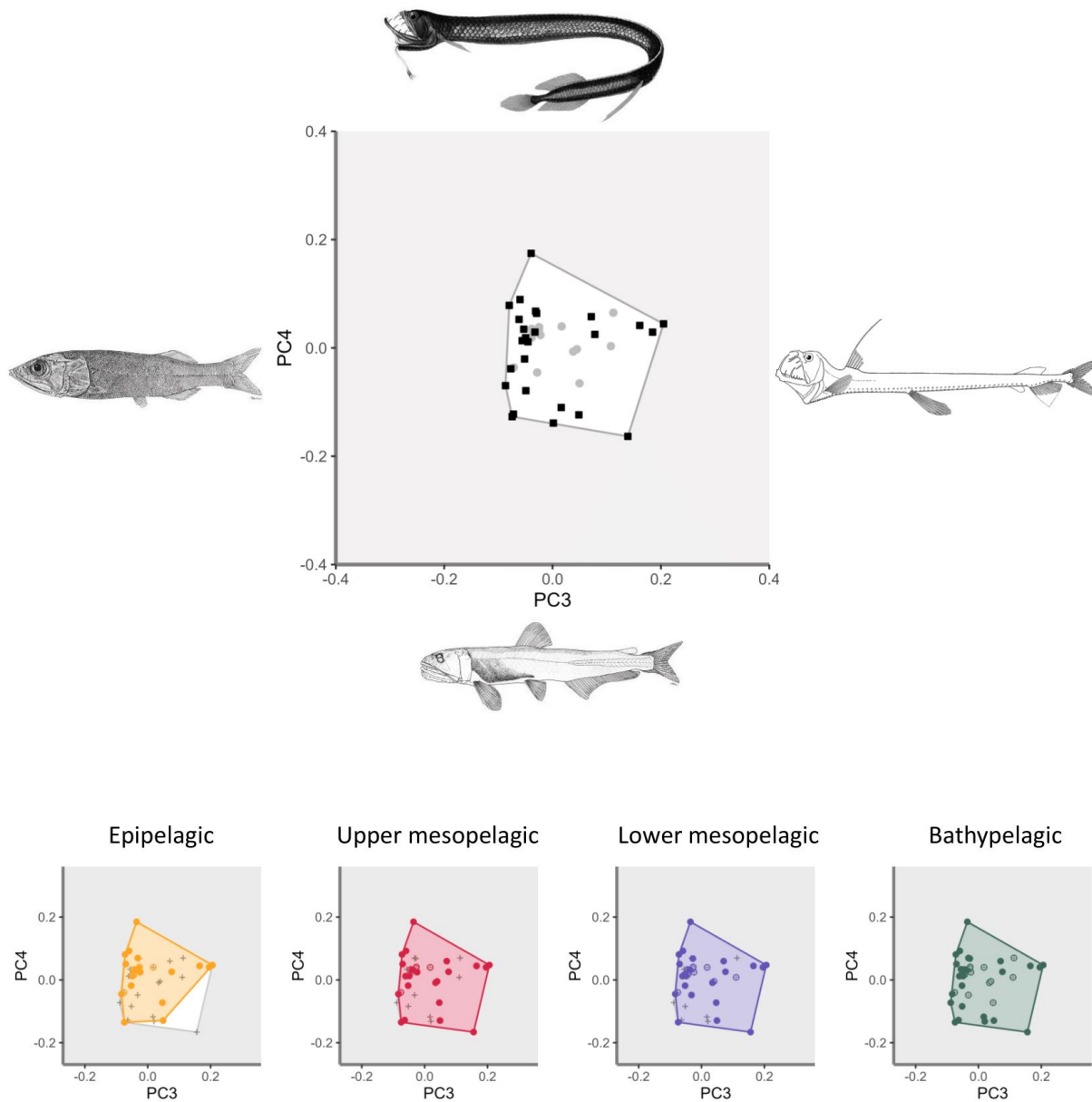


Figure 4-3. Representation of functional space on principal components 3 and 4 for the total community and the epipelagic, upper mesopelagic, lower mesopelagic, and bathypelagic layers. In each plot, the solid colored circles represent the vertex species, the colored circles represent the species present in the layer but not vertices, and the grey crosses the vertices species in the other depth layers. An image of the vertices species has been added to illustrate the morphological variation across the plot, from top to bottom: *Stomias boa*, *Evermannella balbo* and from left to right: *Maulisia microlepis* and *Chauliodus sloani* —images from (Sutton et al., 2020).

The CWM calculation revealed differences in value patterns along the depth gradient (Figure 4-4). The value of some traits increased linearly with depth, while others showed extreme values in the shallower layers. Firstly, three traits showed increased value with depth: caudal throttle width, oral gape surface, and the proportion of species weighted by biomass with large teeth. Three traits showed

marked differences between the epipelagic and upper mesopelagic layers and the deepest layers: eye size, orbital length, and the presence of small teeth, with the highest values in the shallower layers. The epipelagic layer differs from the other layers for several traits. This layer showed marked differences for gill outflow with lower values than in the other layers. Higher values were also found for operculum volume and the presence of photophores in the ventral position.

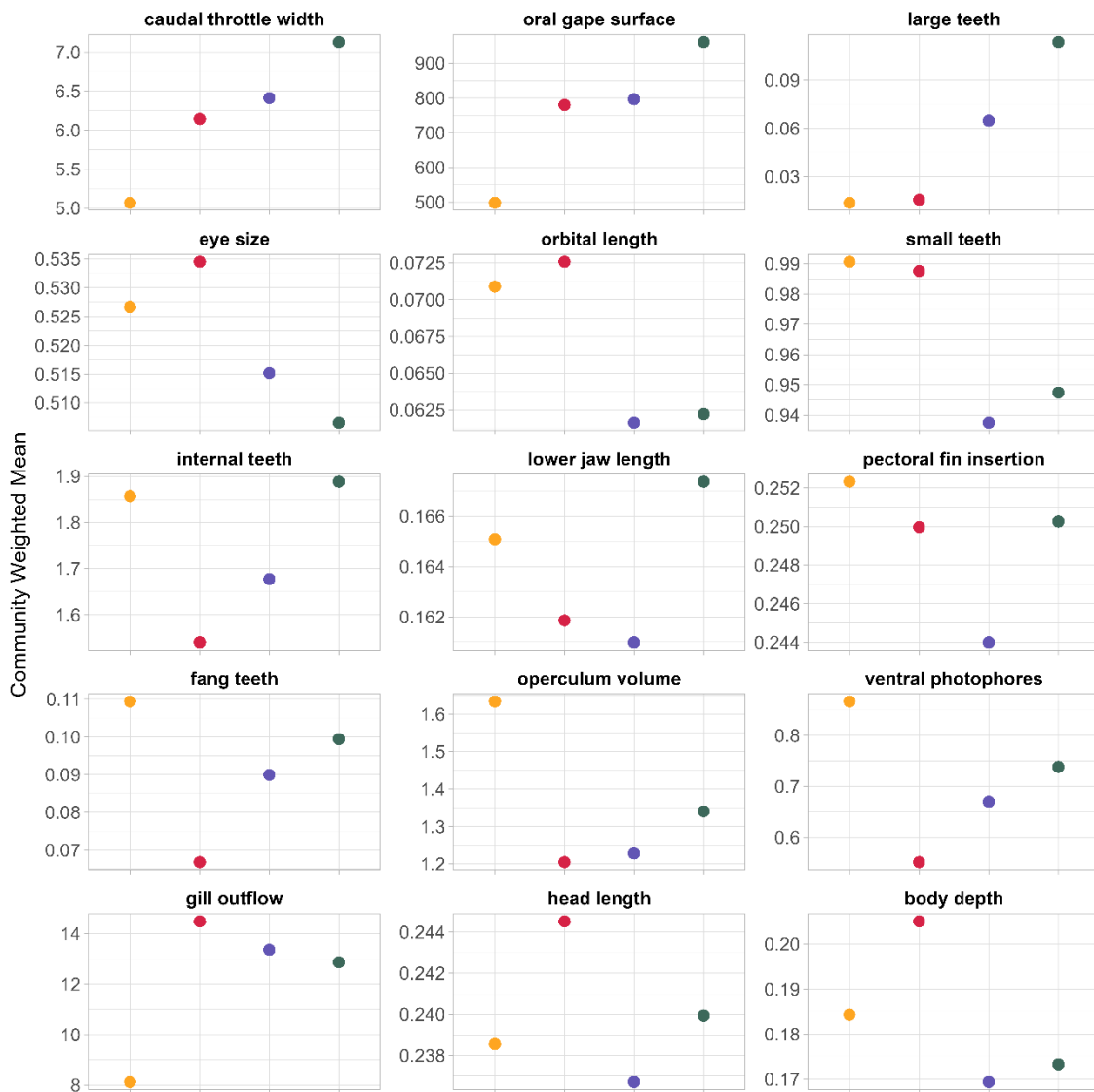


Figure 4-4. Community weighted mean (CWM) of each trait of Table 4-2 and for each depth layer. The weighting was realized with the standardized species biomass. The colors represent the different depth layers: the epipelagic layer in yellow, the upper mesopelagic layer in red, the lower mesopelagic layer in purple, and the bathypelagic layer in green.

The results of the calculation of functional identity on the four PCs showed that it was mainly the epipelagic layer that differed functionally from the rest of the community (Figure 4-5). A gradient between the shallowest and deepest layers was observed regarding functional identity on the PCs. Functional identity on PC2 also showed a marked difference between the epipelagic layer and the others. Another pattern emerged for the functional identity of PC3 (correlated with the presence of internal teeth) and PC4 (presence of photophores on ventral position), with the two assemblages located at the end of the water column (epipelagic and bathypelagic layers) showing the highest or lowest values.



Figure 4-5. Barplots of functional identity indices (definition in table 4-2) for each principal component and each depth layer. The colors represent the different depth layers : the epipelagic layer in yellow, the upper mesopelagic layer in red, the lower mesopelagic layer in purple and the bathypelagic layer in green.

3.2. Alpha diversity: functional indices

Except for the functional richness index, the community showed slight differences in the functional index between depth layers (Figure 4-6). In addition, all values for functional dispersion, evenness, and specialization were below 0.5. Therefore, species showed low specialization in all depth layers, and the dominant species in terms of biomass were not highly specialized and showed similar trait values. The

low FEve values also indicate that the biomass-dominant species were not evenly distributed in the functional space, suggesting functional redundancy. However, FDiv had values between 0.602 and 0.655, indicating that the vertices species had high biomass values. Finally, functional richness was the index with the greatest variability between depth layers, ranging from 0.356 for the epipelagic layer to 1 for the bathypelagic layer. Thus, all functional strategies of the community were contained in the bathypelagic layer. When comparing functional and taxonomic richness, differences were found, with taxonomic richness increasing linearly with depth, in contrast to functional richness, where the lower mesopelagic layer had a lower value than the upper mesopelagic layer (0.724 and 0.639, respectively). Furthermore, taxonomic richness was lower than functional richness in the epipelagic layer, suggesting functional redundancy.

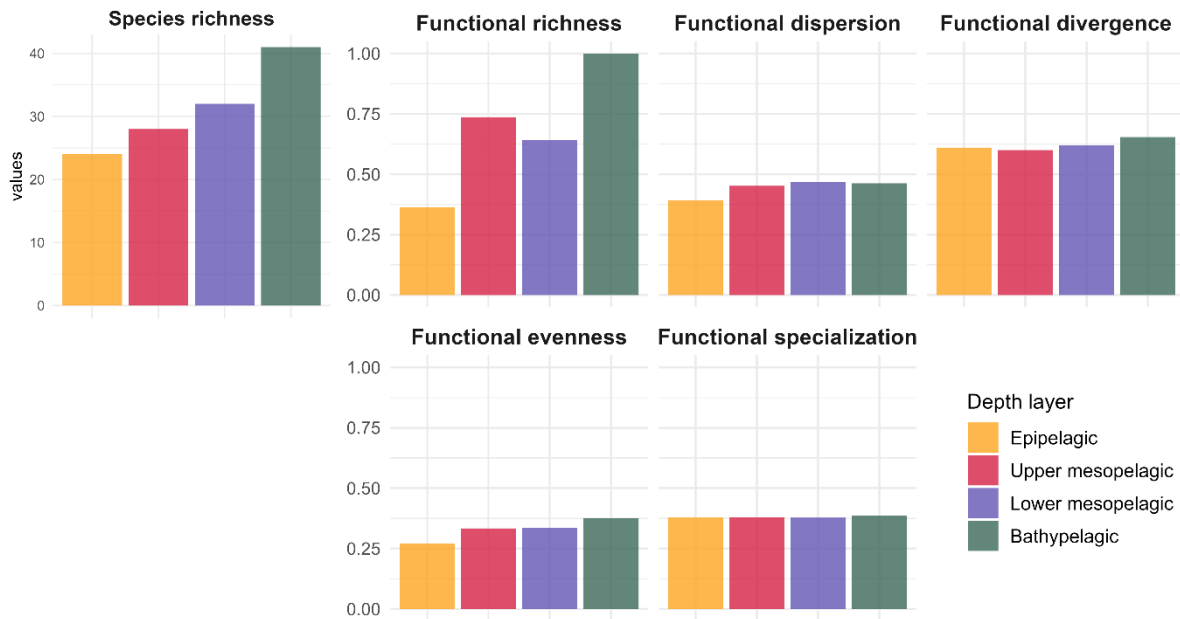


Figure 4-6. Barplots of functional diversity index (definition in Table 4-3) and species richness for each depth layer.

3.3. Comparison between depth layers

Comparison of the functional spaces between the depth layers revealed significant similarities with a high level of overlap between them (Figure 4-7). The functional spaces of the shallowest layers were nested within the bathypelagic layer (green), which contained all the community's functional strategies. Several species were located at the top of each functional space, thus defining its shape (i.e., vertices species): *Stomias boa*, *Argyropelecus hemigymnus*, *Serrivomer beanii*, *Melanostigma atlanticum* or *Chauliodus sloani*.

The increase in functional space between the epipelagic and the upper mesopelagic layers was mainly due to the addition of the species *Malacosteus niger* and *Derichthys serpentinus*. The functional space was significantly increased in the bathypelagic layer by the addition of the species *Anoplogaster cornuta*.

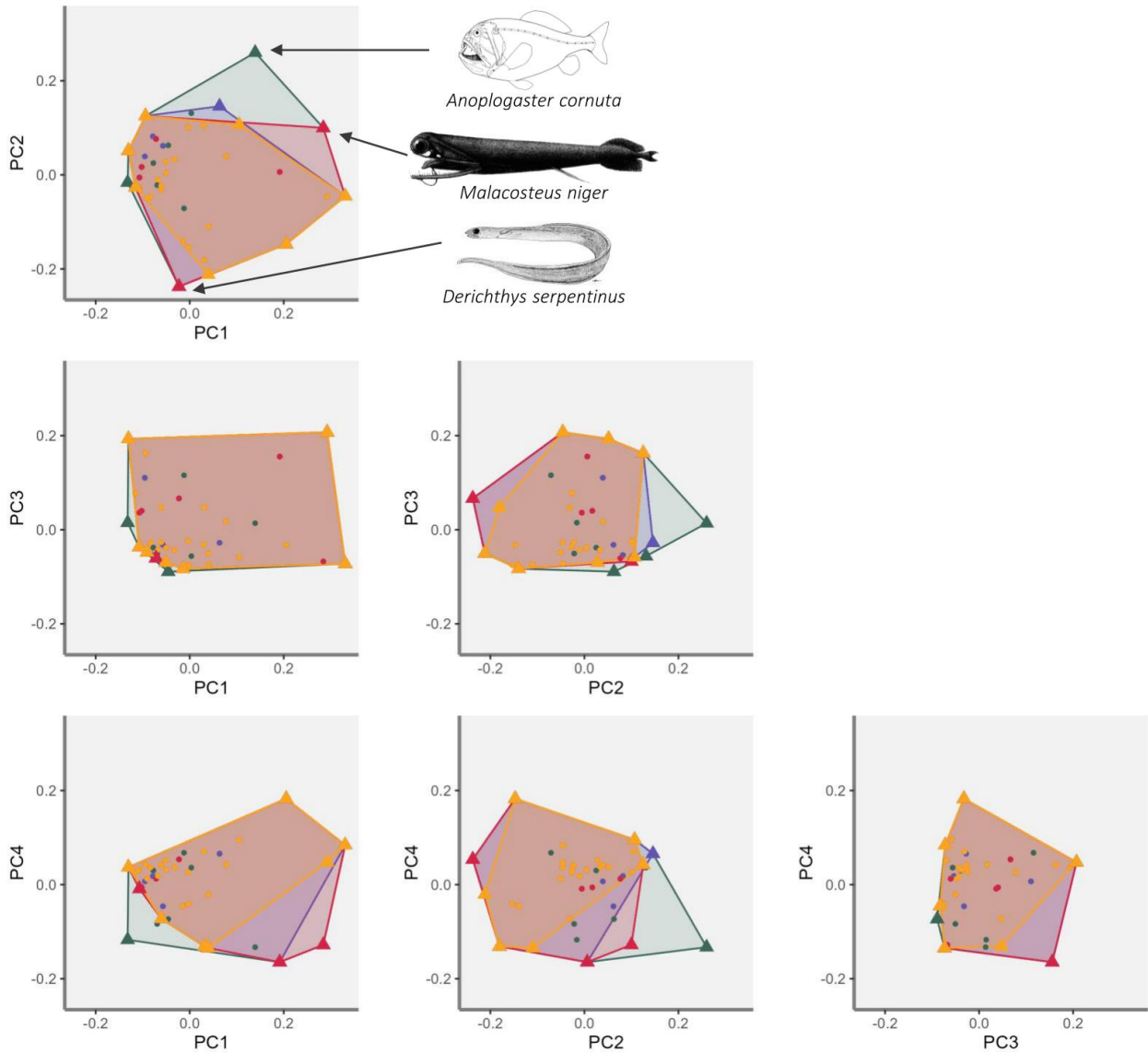


Figure 4-7. Representation of the functional space of each depth layer along the four dimensions. Triangles represent the vertices species and the dot the non-vertices species. The epipelagic layer is represented in yellow, the upper mesopelagic layer in red, the lower mesopelagic layer in purple, and the bathypelagic layer in green.

3.4. Focus on functional rarity

The functional uniqueness index calculation showed that the families containing the greatest number of species, namely the Myctophidae (n= 11 species) and the Platytroctidae (n= 8 species), had lower

uniqueness than the other families (Figure 4-8). On the other hand, the Stomiidae, the third largest family in the number of species with five species, had four species with a uniqueness value greater than 0.19 and ranked among the top six most unique species.

Uniqueness and distinctiveness values on a regional scale were highly correlated ($R^2 = 0.80$, p -value < 0.001). A comparison of distinctiveness values for each species between depth layers revealed little variability. Differences were only found for Myctophidae species, which showed a decrease in distinctiveness values in the epipelagic layer. Proportionally, more Myctophidae are found in this layer at night. This result can be explained both by the nocturnal feeding behavior of this family at the surface and by the low diversity of taxonomic families in this layer ($n=10$ in the epipelagic layer, $n=12$ in the mesopelagic layers and $n=14$ in the bathypelagic layer).

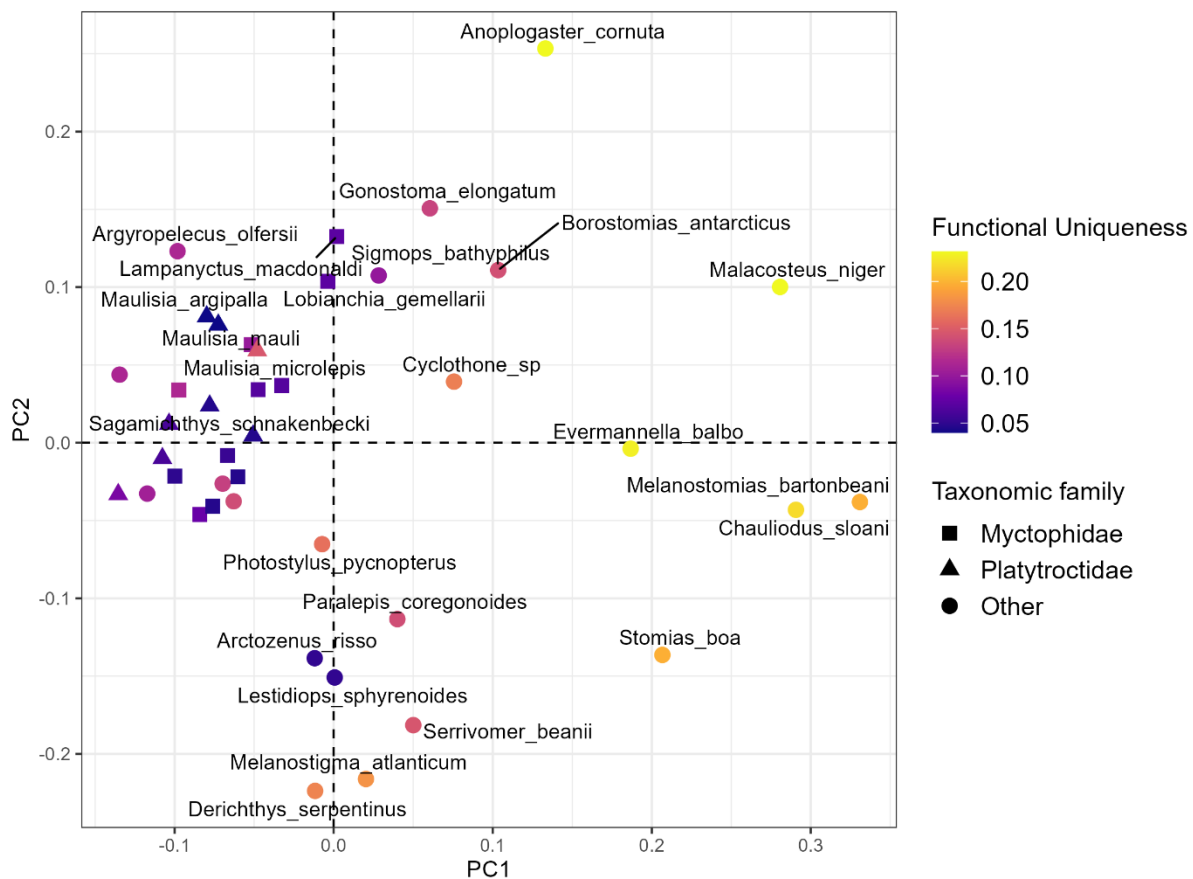


Figure 4-8. The first two components of the functional space at the community level have functional uniqueness values highlighted in color, with the most functional unique species in lighter color. The two taxonomic families with the largest number of species have been highlighted with differently shaped dots.

Three traits at the regional level exerted a notable influence on uniqueness values, with an R^2 or Eta^2 exceeding 0.300: fang teeth, with species possessing them being functionally more unique (p -value $<$

0.001), small teeth, with their absence also indicating more unique species (p -value < 0.001) and finally gill raker type, resulting in species with absent or rudimentary gill rakers being the most unique (p -value = 0.001).

Comparison of uniqueness values with species biomass showed that functionally unique species were generally those with low or moderate biomass, such as *Anoplogaster cornuta* and *Evermannella balbo* (Figure 4-9). Two exceptions were *Stomias boa* and *Serrivomer beanii*, which had relatively high biomasses within the community and were functionally unique.

Regarding the geographical distribution of these species (i.e., their depth range), the majority were distributed over a relatively narrow depth range. Species with high functional uniqueness values were restricted to a particular depth interval (Figure 4-10). Again, *S. boa* was an exception, with a similarly high functional uniqueness but a wide distribution.

Two patterns emerged among species with unique combinations of traits: functionally rare species with low biomass representativeness within the community and restricted distribution and *S. boa* with wide distribution and high biomass.

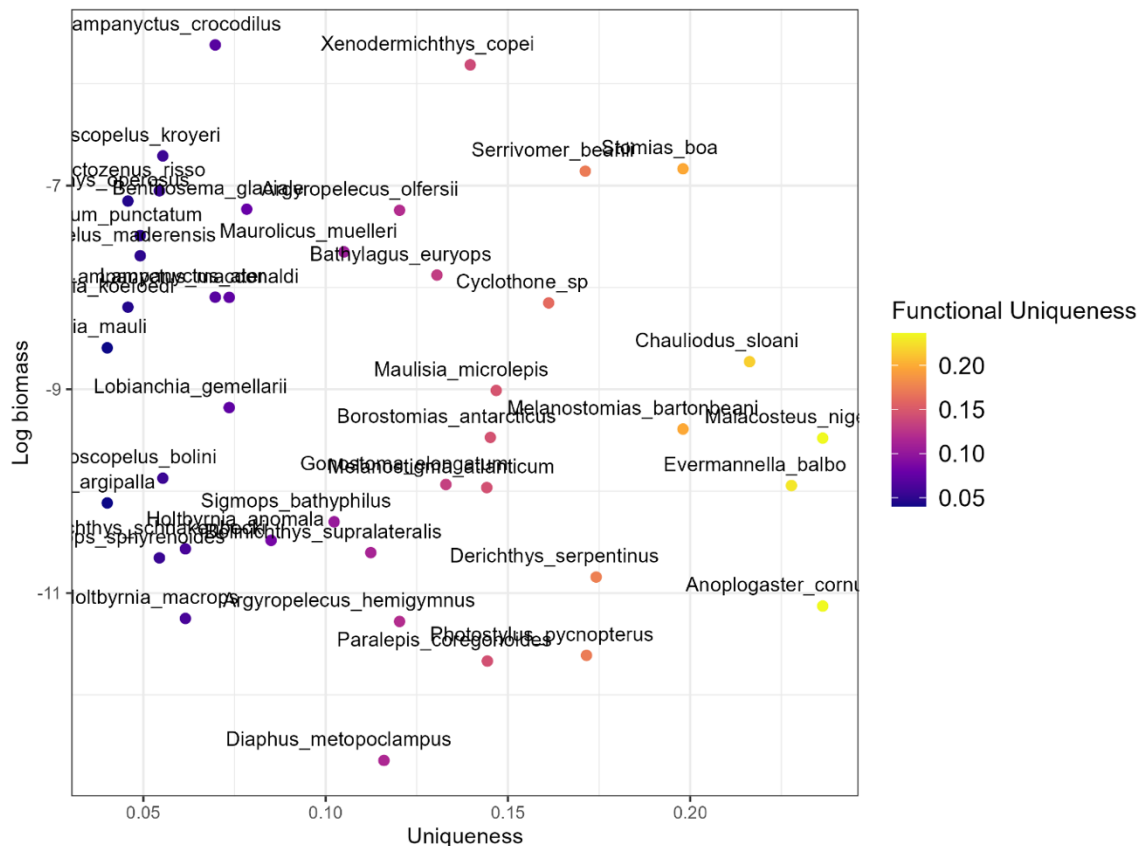


Figure 4-9. Functional uniqueness values as a function of species distribution along the water column. The median depth of each species is represented by the point's color, with the lighter colors representing the shallower depths.

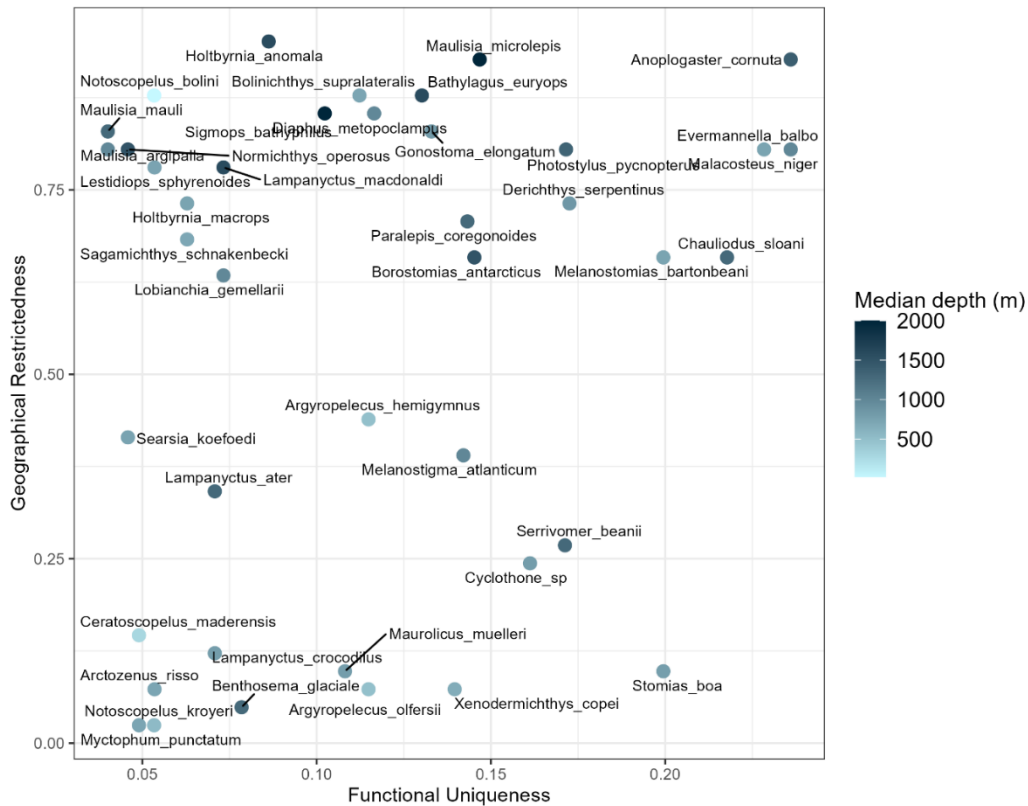


Figure 4-10. Functional uniqueness values as a function of the biomass that the species represent within the community. For graphical clarity, the biomass values have been log-transformed.

4. Discussion

This study provided new information on the functional diversity of deep pelagic fishes notably in identifying key traits related to food acquisition. The measurement of several morphological traits on 42 species has highlighted interspecific differences between depth layers, particularly between the epipelagic and the deeper layers. In terms of community structure, a maximum functional diversity was found in the bathypelagic layer, extending the result already found in studies of the mesopelagic layers (Tuset et al., 2014; Aparecido et al., 2023). Higher functional divergence indices allowed us to deduce a high level of niche partitioning, confirming the results already found for this community (Eduardo et al., 2020a, 2021, 2023). Several unique species were identified, combining low biomass representativeness in the community, reduced distribution along the water column, and a unique combination of functional traits.

4.1. Differences in functional strategies adopted by fish between depth layers

Differences in the functional food acquisition strategies employed by deep pelagic fish could be identified between depth layers. The evolution of these changes did not follow a uniform pattern as some traits showed a linear increase while others showed marked differences, mainly between the epipelagic layer and deeper layers. The traits that increased linearly with depth were oral gape surface, caudal throttle width and the proportion of species with large teeth. The large gape surface of the deepest species was initially interpreted as a sign that these species were opportunistic feeders and had a generalist feeding regime to cope with the reduced concentration of food resources at depth (Childress and Meek, 1973; Ebeling and Cailliet, 1974). The combination of this trait with other adaptations observed in deep pelagic fishes, such as luminescent appendages, the presence of large teeth, highly flexible jaws and neurocranial attachments, could also be interpreted as allowing higher catch rates per encounter. This is particularly relevant in these environments where resource density is low (Widder, 2010; Drazen and Sutton, 2017). Several species in our study combined a large gape surface, absent or rudimentary gill raker and large or fangs teeth: *Malacosteus niger*, *Melanostomias bartonbeani* and *Chauliodus sloani*, which although not among the species with the largest gape surface in our dataset, can detach its skull and open its jaw to 90 degrees to feed. The combination of these traits could reflect a strategy of “sit-and-wait ambush predator”. The reduced resistance to water with the reduction in gill raker and their large teeth allowing them to pierce, trap and capture their prey after detection (Gartner Jr et al., 1997). Two of these species, *Stomias boa* and *Chauliodus sloani*, have already shown asynchronous migrations, moving into the range of their migrating prey to feed on them (Sutton and Hopkins, 1996; Gartner Jr et al., 1997). A decrease in eye size compared with the standard size in the bathypelagic zone indicates that species in this layer make less use of vision to capture their prey (Robison, 2004). An example is the species *Anoplogaster cornuta*, whose observations showed that a chemosensory mechanism via touch triggered the feeding response rather than vision or the gustatory sense alone (Childress and Meek, 1973). Deeper species, for which food resources are scarcer, spend more time searching for prey than pursuing them (MacArthur and Pianka, 1966).

Species living in shallow waters live in a vision-dominated world, where encounters with predators

are primarily mediated by vision. This sensory system enables detection at a distance and facilitates behavior such as stalking and the pursuit of prey. This distinction probably accentuates the importance of a strong locomotor capacity for epipelagic fish, underlining the influence of light concentration on the species' locomotor capacity (Seibel and Drazen, 2007). The lower values of the width of the caudal throttle in the shallower layers of our results confirm this. This effectively translates into a better swimming capacity, which is necessary for nocturnal migration and their feeding strategy (Pauly, 1989; Sambilay Jr, 1990). The presence of well-developed gill rakers, which allow the retention of small prey, can induce feeding on small particles or prey in the manner of species from neritic zones such as the Clupeiformes (Gerking, 2014). This trait has been found in most epipelagic species, particularly Myctophidae (Gartner Jr et al., 1997). The presence of photophores in ventral positions was also supported by a high proportion of the biomass of species distributed in epipelagic and mesopelagic zones at night. The part of these species that are migratory are found in the mesopelagic zone during the day and can therefore limit the risk of predation from below by imitating the descending daylight (Lawry, 1974; Denton et al., 1985).

4.2. Functional structure of the community

The community presented low values of dispersion and evenness within each depth layer. This result may result from particularly unique trait combinations of some species that stretch the functional space and, therefore, increase the distance between species. High divergence indices across all depth layers may translate to a high degree of niche partitioning for this community, at least at night (Mason et al., 2005). This result confirms that competition primarily shapes the structure of species assemblages. In response to this competitive pressure, it underlines that species tend to limit their functional similarity as a strategy to mitigate intense competition (Gause, 1932; MacArthur and Levins, 1967; Abrams, 1983). This result aligns with previous findings observed for the most important species in terms of biomass in Chapter 3. The broad scope of species studied in this chapter adds robustness to the consistency of the result, particularly when viewed from a functional perspective.

Another important result of our study is that the highest functional richness was found in the bathypelagic layer. All of the community's functional strategies were thus found in this layer. Although this may be partly a result of sampling with a non-closing trawl, it seems to be a result that is consistent

with other studies on these communities (Tuset et al., 2014; Martinez et al., 2021; Aparecido et al., 2023). An important aspect to consider is the ontogenetic shift undergone by certain species of the community as adults, which modify their vertical distribution to be found at greater depths (Chapter 2) (Loutrage et al., 2023a). Certain species of Myctophidae, for example, can be found in the bathypelagic layer when they reach the senescent stage (i.e., *Lampanyctus crocodilus*), leading to the finding of functional strategies, which were first found in shallower layers, at depth. The deep sea has been described to be a hot spot for fish evolution (Martinez et al., 2021). The hypothesis to explain this result was considering the ecosystem's environmental stability that permits the species' specialization (Kassen, 2002; Klompmaker and Finnegan, 2018). The important environmental gradients in the ecosystem may promote the variation of species traits (Conover and Schultz, 1995; Goldberg and Lande, 2006; Mullen and Hoekstra, 2008; Juarez et al., 2019). Our result seems thus to promote the “limiting similarity” hypothesis. In these conditions of decrease of food resources with depth, species have to adapt and limit the competition by occupying a slightly different part of the functional space (Macarthur and Levins, 1967; Schoener, 1974; Abrams, 1983). Such specialization may increase functional diversity, as demonstrated by some coral reef fish (Bender and Luiz, 2018).

4.3. Functional rarity

Low functional evenness values were observed for the community (i.e., FEve \leq 0.38). In the functional space, Myctophidae and Platytroctidae families, which have the largest number of species, are grouped together in one area. Several species stand out at significant distances from the rest of the community (e.g., *Anoplogaster cornuta*, *Malacosteus niger*, *Chauliodus sloani* or *Melanostomias bartonbeani*). These functionally unique species therefore stretch the functional space, increasing the distance between species and reducing FEve. The traits that make these species functional unique were primarily the presence of fang teeth, the rudimentary or absence of gill raker and the absence of small teeth. These traits were characteristic of ambush predators adopting the “sit and wait” strategy (Gartner Jr et al., 1997). The similarly low values of the functional specialization index and the relationship between biomass and functional uniqueness values of these species indicate that they represent proportionally little biomass within the community. The combination of the most unique traits was therefore supported by the rarest species in term of biomass, a result already found in other communities (Mouillot et al., 2013a). The majority of these species presented also a relatively

restricted vertical depth distribution. By combining a low proportion of biomass, a restricted spatial distribution and a combination of unique functional traits, these species represent therefore the extreme end of the common-rare species continuum (Violle et al., 2017). These species are more sensitive to demographic, environmental, and genetic stochasticity due to their rarity (Simberloff, 1986; Nogueira et al., 2010). Despite their unique and often irreplaceable functions within ecosystems, they are likely to be the first to go extinct in the face of the crisis of biodiversity loss (Bracken and Low, 2012; Leitão et al., 2016). Communities' ability to respond in various ways is crucial for mitigating the consequences of global change (Loreau and Hector, 2001; Leitão et al., 2016). Species that support rare functions enhance ecosystem stability, making it essential to preserve the global pool of functions within a community.

4.4. Limits and perspectives to consider

By comparing the morphological adaptations exhibit by species at different depths, it became apparent that there could be significant differences in metabolisms between species. Nychthemeral migratory species are adapted to swim rapidly over proportionally long distances and therefore have muscles that are richer in lipids and should have high energy requirements (Childress et al., 1990). In contrast, non-migratory species that remain at depth potentially have much slower metabolisms, enabling them to feed at lower frequencies. This difference could reflect differences in feeding strategies between species, with some hunting visually and others not (Seibel and Drazen, 2007). This aspect highlights the fact that, more generally, the traits in the life cycle of these species are largely unknown. The lack of information on, for example, variations in feeding according to sex or stage of maturity hampers our ability to study the ecological patterns and assembly rules of these communities.

The difficulty of accessing these species is an aspect essential to consider when interpreting the functions linked here to the morphological traits of the species. Few *in situ* observations have been made on these species, so the strategies discussed here remain uncertain as relation between traits and functions have been developed for shallow-water fish species. An interesting case study is the species *Malacosteus niger* which, as described above, has morphological adaptations for capturing large prey (i.e., large gape surface, no gill raker, and large teeth). Investigations into the diet of this species in several oceanic basins showed that it was mainly a zooplanktivore, deviating from other

species in its clade (Sutton, 2005). Another example is the case of *Eurypharynx pelecanooides*, which was the species with the largest oral gape surface in our study (five times larger than the second species) but which has a diet composed of plankton, copepods, crustaceans, and even algae (Nielsen et al., 1989). To feed, this species may engulf its prey by swimming slowly over it with its mouth open (Gartner Jr et al., 1997). There is therefore a need for further research into the relationships between morphological traits and their associated functions for deep-sea pelagic species.

Discussion

1. La profondeur : force majeure structurant la communauté des poissons pélagiques profonds la nuit

1.1. Le reflet de plusieurs gradients environnementaux

L'objectif principal de ces travaux de thèse était la description de la communauté de poissons épi- à bathypélagiques des canyons du golfe de Gascogne et des mécanismes la structurant à la nuit tombée. Nos résultats du chapitre 1 ont pu montrer que la profondeur est le gradient environnemental le long duquel les plus grands changements dans la composition en espèces apparaissent (Loutrage et al., 2023b). Ce résultat a déjà été retrouvé pour cette communauté dans la zone Atlantique Nord-Est ou dans la zone de ride médio-Atlantique (Sutton et al., 2008, 2010; Sutton, 2013; Cook et al., 2013; Kenchington et al., 2020; García-Seoane et al., 2021). Plus précisément, quatre couches de profondeur ont pu être définies : la zone épipélagique (0-175 m), la zone mésopélagique supérieure (175-700 m), la zone mésopélagique inférieure (700-1000 m) et la zone bathypélagique (1000-2000 m). Ces divisions correspondent à celles déjà décrites précédemment pour le domaine pélagique océanique (Sutton, 2013). Cependant, plutôt que la profondeur en elle-même qui peut être considérée comme proxy, certaines covariables structurent de manière directe cette communauté. Ces gradients sont notamment ceux en lumière, température, pression mais aussi en ressources alimentaires. Un résultat inattendu réside dans l'identification d'une relation positive entre la proximité du fond et la biomasse pour trois des quatre assemblages définis. Cette situation dans les canyons du golfe de Gascogne contraste avec le paradigme général des zones océaniques où la biomasse des poissons méso- et bathypélagiques diminue avec la profondeur (Angel and de C. Baker, 1982; Angel, 1989). Ce résultat est d'autant plus important la nuit, moment où la majorité des espèces mésopélagiques migrent vers les couches plus en surface (Roe and Badcock, 1984; Hopkins et al., 1996; Robison, 2003; Hammerschlag et al., 2017). Au vu des observations réalisées par différentes méthodes (c'est-à-dire par acoustique, caméras, submersibles et traits de chaluts réalisés près du fond), il devient de plus en plus évident que les zones à topographies abruptes telles les pentes continentales, les monts sous-

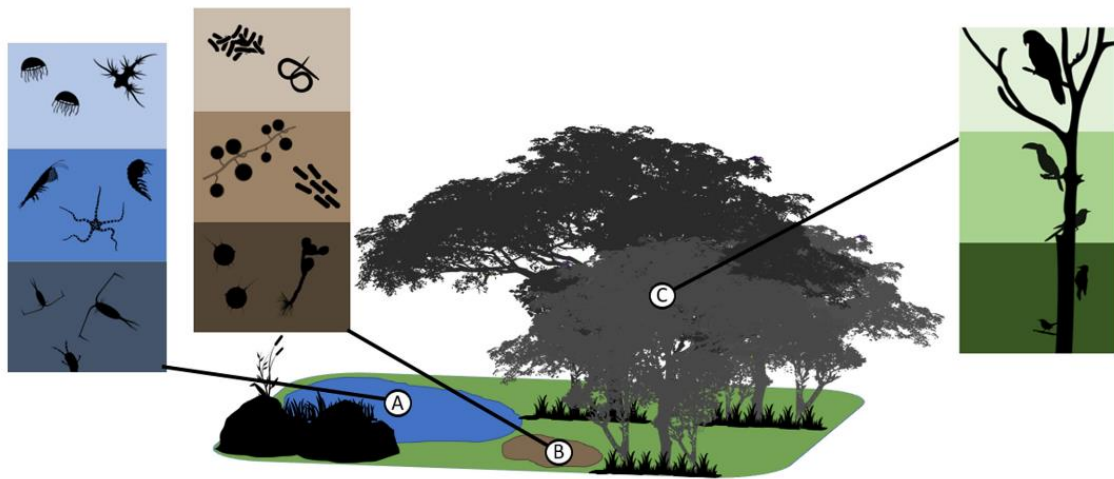
marins et les rides médio-océaniques sont le lieu d'agrégations importantes de biomasse de poissons pélagiques (Marshall, 1977; Fock et al., 2004; Genin, 2004; Pusch et al., 2004; Sutton et al., 2008; Cook et al., 2013; Kenchington et al., 2020).

A l'échelle spécifique, certaines espèces présentent des répartitions verticales relativement larges le long de la colonne d'eau quand d'autres apparaissent restreintes à une couche particulière. Ces observations traduisent des différences interspécifiques de plasticité environnementale et de capacité migratoire. Une importante variabilité dans les changements ontogéniques de distribution verticale entre les espèces a aussi été observée (Chapitre 2).

Par la suite, nous nous sommes concentrés de manière plus spécifique aux différences adaptatives des espèces entre les couches de profondeur à travers l'étude de traits morphologiques impliqués dans l'acquisition de la nourriture (chapitre 4). Les résultats de cette thèse ont mis en évidence des différences et des gradients morphologiques en fonction de la distribution verticale des espèces étudiées. La lumière et la concentration en ressources alimentaires semblent induire des stratégies adaptatives différentes chez les espèces en fonction de la profondeur. Alors que dans la couche épipélagique la prédation peut se faire de manière visuelle, dans les profondeurs la taille des yeux se réduit, l'ouverture de la bouche s'agrandit et la proportion d'espèces possédant des grandes dents augmente.

Dans le chapitre 3, nous avons observé que les espèces présentant une niche trophique proche pouvaient utiliser la profondeur comme axe de ségrégation. La prise en compte de cette dimension est donc essentielle pour une meilleure compréhension de la niche écologique des espèces dans le cas des environnements verticalement stratifiés comme l'océan pélagique (Figure 5-1). Cette dimension offre des opportunités de ségrégation et de spécialisation pour les espèces (Gámez and Harris, 2022). L'augmentation de l'espace vertical modifie la fréquence, l'intensité et l'issue de la compétition. Les interactions de compétition façonnent ensuite la structure des communautés, en partie par l'utilisation ou l'évitement dans l'espace des espèces (Tilman, 2004). Cela est visible en écologie terrestre, comme illustré par certaines espèces d'arbres dans les forêts tropicales. Bien qu'elles coexistent sur le plan horizontal, la concurrence interspécifique entraîne une ségrégation sur le plan vertical, entraînant des disparités significatives dans leur répartition spatiale (Zambrano et al., 2022).

Il apparaît ainsi crucial d'étudier la biodiversité et le fonctionnement des écosystèmes pélagiques océaniques le long du gradient de profondeur et non pas seulement intégrés à l'échelle de la colonne d'eau.



Trends in Ecology & Evolution

Figure 5-1 Stratification verticale de trois communautés distinctes. (A) Invertébrés aquatiques dans une colonne d'eau. (B) Microbes du sol à différentes profondeurs. (C) Oiseaux de la forêt tropicale divisant les zones verticales de la forêt. L'ombrage dans chaque écosystème correspond à la pénétration de la lumière. Extrait de Gámez et Harris, 2022.

1.2. Des couches de profondeur interconnectées

Bien que la division verticale de l'océan pélagique océanique aide à sa compréhension et son étude, des connections importantes existent entre ces différentes couches de profondeur (Sutton, 2013; Hopkins et al., 1996). Il est essentiel de souligner l'aspect dynamique de l'utilisation verticale de l'habitat et sa variabilité selon les espèces. Dans notre zone d'étude, à l'échelle de la journée, certaines espèces vont migrer dans la couche épipélagique pour s'alimenter (Roe and Badcock, 1984; Hopkins et al., 1996; Hammerschlag et al., 2017). La faune bathypélagique pourrait aussi pratiquer une migration nyctémérale vers la zone mésopélagique et même épipélagique (Sutton et al., 2008; Cook et al., 2013). Des différences importantes existent entre des espèces migrant sur plusieurs couches de profondeur et d'autres ne pratiquant que de faible migration. Des variations au niveau intra-populationnel peuvent potentiellement aussi exister. Par exemple, les espèces présentant une large distribution verticale pourrait présenter des différences avec la partie de la population plus en profondeur qui ne migre pas ou peu et celle plus proche de la couche épipélagique qui migre. La fréquence de migration des espèces reste aussi peu connue mais de larges variations interspécifiques

semblent être observées. Dans le Golfe du Mexique, 81% des migrateurs asynchrones (c'est-à-dire que ne migrent pas toutes les nuits) restent un jour en profondeur avant d'aller se réalimenter mais cette durée peut atteindre huit jours pour d'autres espèces (Sutton and Hopkins, 1996; Woodstock et al., 2022).

Sur une échelle temporelle plus étendue, comme nous l'avons observé dans le chapitre 2, les changements ontogéniques vont amener certaines espèces à modifier leur distribution verticale. Une partie des espèces mésopélagiques au stade larvaire et juvéniles réside dans la zone épipélagique pour profiter de la concentration élevée en ressources alimentaires. Les individus migrent ensuite vers les profondeurs pour afin de réduire le risque de prédation à mesure qu'ils grandissent. Parmi ces espèces, certaines adopteront un comportement benthopélagique à l'âge adulte et résideront dans la couche limite benthique (Badcock and Merrett, 1976; Willis and Percy, 1980; Auster et al., 1992; Vinnichenko, 1997). Par exemple, l'espèce de Myctophidae *Lampanyctus crocodilus*, espèce majeure de la communauté de poissons pélagiques profonds du golfe de Gascogne en termes de biomasse, opère un changement en lien avec la perte de sa vessie natatoire. La migration nycthémerale dans la couche épipélagique n'étant plus énergétiquement rentable *L. crocodilus* reste s'alimenter dans la couche limite benthique (Chapitre 2) (Stefanescu and Cartes, 1992; Fanelli et al., 2014). Il a été aussi proposé que les changements ontogénétiques de certaines espèces bathypélagiques les amenaient à résider plus en profondeur, pouvant ainsi fournir de la nourriture à de très grandes profondeurs (Vinogradov, 1953, 1970).

En plus des changements ontogéniques, la couche limite benthique a une importance écologique particulière pour plusieurs espèces. L'augmentation des concentrations en ressources alimentaires amènent certaines espèces à venir s'y alimenter (Weatherly and Kelley, 1985; Sutton et al., 2008). D'autres espèces, comme *Xenodermichthys copei* ou encore l'espèce de Zoarcidae *Melanostigma atlanticum*, s'y reproduisent (Markle and Wenner, 1979). Ces espèces peuvent ensuite être prédatés par des espèces démersales (Trueman et al., 2014)

Ces résultats soulignent l'importance de considérer l'ensemble de la colonne d'eau, de la surface au fond, afin de comprendre la structure de ces communautés et les liens qui existent entre les différentes couches (Sutton, 2013; Drazen and Sutton, 2017). Le paradigme qu'une espèce appartient spécifiquement à une couche de profondeur est vraisemblablement obsolète. La

considérable variabilité de l'utilisation de la colonne d'eau par ces espèces suggère que, de manière similaire aux temps de résidence définis horizontalement pour les mammifères marins, il pourrait être pertinent d'envisager des temps de résidence définis par couches de profondeur spécifiques à chaque espèce. Cette prise en compte permettrait une compréhension plus réaliste du fonctionnement de la communauté de poissons pélagiques profonds.

2. Une communauté façonnée par la compétition

2.1. Partitionnement des niches

Comme nous l'avons vu dans le chapitre 3, en plus de l'influence des gradients environnementaux, la compétition façonne aussi la structure de la communauté de poissons pélagiques profonds du golfe de Gascogne. J'ai pu mettre en évidence que les chevauchements des niches isotopiques entre les espèces majeures en termes de biomasse au sein des différentes couches étaient plus petits que ceux attendus avec les modèles nuls. Ce résultat indique que pour réduire la compétition, les espèces tendent à restreindre leur similarité. La divergence entre les espèces d'un point de vue isotopique mais aussi via les stratégies fonctionnelles était également relativement élevée (chapitre 3 et 4), indiquant une différenciation importante entre les espèces. Les tailles des niches isotopiques des espèces étaient aussi significativement plus petites que celles attendues avec les modèles nuls au sein des couches épi- à bathypélagique, indiquant une spécialisation des espèces. Les résultats obtenus à l'échelle de la communauté contredisent l'hypothèse historiquement admise que les poissons profonds, faisant face à la pauvreté en ressources alimentaires, devraient adopter un régime alimentaire généraliste (Ebeling and Cailliet, 1974; Marshall, 1980; Gartner Jr et al., 1997; Drazen and Sutton, 2017). Ce fonctionnement avec une forte ségrégation des niches écologiques des espèces a déjà été retrouvé notamment pour les communautés mésopélagiques (Mauchline, 1986; Hopkins and Gartner, 1992; Hopkins and Sutton, 1998; Eduardo et al., 2020a, 2021, 2023). Ainsi, en accord avec la théorie de la compétition, face à la concurrence dans un milieu pauvre en ressources, les espèces réduisent leur niche et se spécialisent pour éviter l'exclusion compétitive (Schoener, 1974; Abrams, 1983). Les adaptations morphologiques uniques de ces espèces (c'est-à-dire les appendices lumineux, les grandes dents ou encore une bouche extensible) permettraient un taux de capture par rencontre plus élevé plutôt qu'une traduction d'un régime purement généraliste (Drazen and Sutton, 2017).

Le haut niveau de ségrégation des niches observé en lien avec la diminution en ressources alimentaires, n'est pas la norme au sein de toutes les communautés. Inversement à nos résultats, la structure trophique d'une communauté de poissons benthiques et démersaux en mer Baltique entre deux zones à productivité différentes a présenté une redondance trophique plus importante dans la zone la plus productive (De La Vega et al., 2023). La variabilité des concentrations en ressources alimentaires n'est pas l'unique facteur modulant la niche écologique des espèces. La stabilité des environnements sur le plan spatio-temporel est également reconnue comme un facteur déterminant la spécialisation des espèces (Kassen, 2002). Les communautés benthiques marines fossiles et modernes ont aussi présenté une ségrégation faible avec des cas de compétition exclusive rares. La prédation et les perturbations importantes que subissent ces communautés empêchent les communautés locales d'atteindre leur capacité de charge théorique et de devenir écologiquement saturées, réduisant ainsi l'intensité de la compétition interspécifique (Klompaker and Finnegan, 2018). Plus en profondeur ces communautés ont cependant montré une augmentation de la ségrégation en lien avec la diminution des perturbations et de la prédation en profondeur (Harper and Peck, 2016). Contrairement aux communautés néritiques, les espèces océaniques profondes sont moins impactées par les perturbations environnementales et les pressions anthropiques comme la pêche. La communauté du golfe de Gascogne pourrait présenter une structure plus « primitive » ou la spécialisation a été rendue possible et non influencée par des décennies d'exploitation. La stabilité environnementale en profondeur comparée aux grandes variations spatio-temporelles environnementales dans les couches de surface a également pu participer à la spécialisation trophique des poissons pélagiques profonds mis en évidence dans ce travail de thèse.

2.2. Les zones d'ombre de l'écologie trophique des poissons pélagiques profonds

Les résultats de cette thèse apportent des informations nouvelles sur l'écologie trophique des poissons pélagiques profonds. Ils occupent un rôle majeur dans les transferts énergétiques au sein des réseaux trophiques en exerçant des forçages ascendants par la consommation importante de producteurs primaires et descendants en étant une source de proies importante pour les prédateurs supérieurs (Griffiths et al., 2013). Par exemple, dans la région du courant de Californie les poissons mésopélagiques consomment la même quantité de zooplancton que les sardines et les anchois

(Koslow et al., 2014). Néanmoins, de nombreuses zones d'ombre subsistent. Une des lacunes les plus importantes concernant le régime alimentaire des poissons pélagiques profonds réside dans la difficulté à quantifier la proportion du zooplancton gélatineux (Robison, 2004; Drazen and Sutton, 2017). Certaines espèces au comportement benthopélagique, telles que les espèces de la famille des Alepocephalidae ou encore des Platyroctidae, sont notamment suspectées d'être « gélativores » (Gartner Jr et al., 1997; Sutton et al., 1995). Des agrégations de salpes et méduses ont déjà été observées sur la pente et au sein des canyons, fournissant une ressource alimentaire pour ces espèces (Billett et al., 2006; Smith et al., 2014). Une part de l'énergie et de la biomasse transférée des poissons vers les niveaux trophiques supérieurs pourrait donc dépendre des gélatineux, ayant un impact majeur sur le fonctionnement du réseau trophique.

Une autre facette peu explorée et insuffisamment quantifiée de l'écologie trophique des poissons pélagiques profonds concerne leurs besoins métaboliques et leur fréquence d'alimentation. Ces estimations des rythmes d'alimentation sont essentielles pour quantifier les flux de biomasse et évaluer l'impact des prédateurs sur les populations de proies (Drazen and Sutton, 2017). Une des adaptations possibles à la diminution en ressources alimentaires avec la profondeur pourrait être la réduction du métabolisme. Plus en profondeur les espèces, notamment bathypélagiques, présentent une baisse du métabolisme par le biais de la réduction des capacités de locomotion (Childress and Somero, 1979). En lien avec cette diminution des capacités de locomotion, trois espèces de Myctophidae mésopélagiques ont présenté une relation directe entre le taux de consommation de nourriture et la capacité de migration verticale (Moku et al., 2000). Cependant, l'absence de lumière dans la couche bathypélagique pourrait aussi expliquer cette diminution de métabolisme. Les espèces bathypélagiques ne chassent plus de manière visuelle et n'ont pas non plus à échapper à des prédateurs chassant de manière visuelle expliquant la réduction des capacités de locomotion, et donc de métabolisme (Childress et al., 1990; Seibel and Drazen, 2007).

3. Filtres ayant façonnés notre vision

3.1. Le chalut

L'originalité de ces travaux de recherche tient en partie à la large gamme de profondeur échantillonnée, allant de la couche épi- à bathypélagique avec certains zooms près du fond. Cette

approche nous a permis dans un premier temps d'apporter de précieuses informations sur une des communautés les moins bien connues de la planète, la communauté bathypélagique (Webb et al., 2010). L'échantillonnage sur de large gamme de profondeur permet de mieux comprendre et appréhender les différences de structure entre les assemblages de cette communauté. La récolte de ces résultats a été rendue possible par l'utilisation d'un chalut de grande taille mesurant 192 m de long et présentant une ouverture moyenne verticale de 24 m et horizontale de 58 m. Les deux principaux avantages de ce type de chalut sont les grandes profondeurs qu'il peut atteindre et l'échantillonnage des grandes espèces qui semble être meilleur qu'avec d'autres types de chaluts. Les chaluts utilisés principalement pour les études des communautés épi- et mésopélagiques sont des chaluts rectangulaires qui sont de plus petite taille et peuvent être évités par les espèces de grandes tailles et celles avec des capacités d'évitement importantes, par exemple des espèces bathypélagiques tels que les *Platyroctidae*. Si ces dernières contribuent de manière significative à la biomasse totale, l'utilisation de ces chaluts rectangulaires pourrait mener à sous-estimer leurs contributions et à l'inverse surestimer la contribution des espèces de petites tailles (Sutton, 2013).

Un des désavantages du type de chalut que nous avons utilisé pour récolter les données présentées dans cette thèse est en revanche l'absence d'un système de fermeture. Malgré un protocole pour éviter au maximum les contaminations à la remontée et à la descente du chalut (voir méthodes chapitre 1), la présence de certaines espèces à grandes profondeurs peut être un artéfact du chalut. Il convient donc de toujours mettre en lumière les résultats apportés par les différentes études par le type de chalut utilisé puisque ce dernier détermine d'une manière ou d'une autre la vision de la communauté étudiée.

3.2. Aspect temporel

Plusieurs aspects à différentes échelles temporelles sont aussi à prendre en compte pour bien appréhender nos résultats. Premièrement, toutes nos observations sont à mettre en lien direct avec la période de la journée échantillonnée, c'est-à-dire la nuit. Divers processus écologiques régissant la structure de cette communauté ont été décrits comme étant plus complexes la nuit (Hammerschlag et al., 2017). La migration de certaines espèces à la nuit tombée entraîne de nouvelles interactions trophiques que ce soit dans la zone épipélagique ou dans des couches plus profondes, certaines espèces bathypélagiques migrant également la nuit (Cook et al., 2013; Hammerschlag et al., 2017).

A échelle temporelle plus longue, la variabilité saisonnière n'a pas pu être prise en compte, l'ensemble des échantillonnages ayant été réalisé en automne. De manière globale, l'influence de la variabilité saisonnière sur les communautés méso- à bathypélagiques reste encore très peu étudiée (Sutton et al., 2017). Pourtant des différences en fonction des pics de productivité, notamment lors des blooms phytoplanctoniques printaniers, ou de la stratification de la colonne d'eau pourraient avoir un impact sur la structure de ces communautés. Par exemple, en mer Méditerranée et dans le système d'upwelling du Benguela un changement saisonnier dans les signatures isotopiques en lien avec les changements de la composition des producteurs primaires a été observé (Valls et al., 2014a; Duncan et al., 2023).

Bien que la couverture temporelle de notre étude s'étende sur deux décennies, la variabilité temporelle à plus long terme n'a pas été investiguée de manière approfondie. Les tests statistiques réalisés dans les chapitres 1 et 2 ne permettent pas d'exclure totalement l'absence de différences. La principale limite rencontrée est qu'en fonction des années, l'effort d'échantillonnage varie avec la profondeur. La variabilité spatiale des échantillonnages rend également difficile de démêler les potentiels effets temporels des effets spatiaux. Il est important de noter que certaines différences, bien que non quantifiées ont pu être observées. L'espèce *Notoscopelus bolini* a notamment été retrouvée de manière systématique depuis 2021 alors que l'espèce n'avait jamais été échantillonnée depuis le début des campagnes, indiquant potentiellement une remontée vers le nord de cette espèce à affinité tropicale et subtropicale. Le maintien et la standardisation de ces échantillonnages sont donc essentiels pour permettre la mise en évidence de changements à l'échelle de la communauté sur le long-terme.

3.3. Aspect spatial

Aucunes différences spatiales liées à la latitude ou à des variations entre les canyons n'ont été identifiées au sein de la communauté dans le chapitre 1. De manière générale, la répartition horizontale des espèces semble correspondre aux limites des principales masses d'eaux océaniques (Nafpaktitis et al., 1977; Robison, 2004; Sutton et al., 2017; Milligan and Sutton, 2020). Les mécanismes influençant cette répartition agissent donc à une échelle spatiale plus large que celle de notre étude. Cependant, il est possible que certaines différences aient pu nous échapper. L'utilisation d'un chalut peut gommer en partie les variations à fine échelle dans la distribution horizontale des espèces,

occultant certains processus opérant à haute résolution. La dynamique des mouvements horizontaux des espèces mésopélagiques reste peu connue, que ce soit entre les canyons ou des canyons vers les zones plus océaniques. Au niveau intraspécifique, la reproduction de certaines espèces sur le fond près de la pente indique que des différences de répartition spatiale au cours du cycle de vie pourraient être observées (Markle and Wenner, 1979).

4. Perspectives

4.1. Elargissement de notre vision

Différents aspects abordés durant ces travaux de thèse pourraient être étendus. Premièrement, l'extension des échantillonnages pendant la période de jour permettrait la comparaison de la structuration de la communauté de poissons pélagiques profonds avec la nuit. Cela pourrait permettre d'identifier des espèces migratrices et d'ajouter une dynamique temporelle à la distribution verticale des espèces étudiées. Dans le golfe de Gascogne, la comparaison jour-nuit de la distribution verticale de plusieurs espèces via l'analyse de l'ADN environnemental a permis de décrire différents patrons de migration entre les espèces (Canals et al., 2021). Il serait également intéressant de voir si, inversement à notre vision de nuit, moment où la majorité des espèces s'alimente, les espèces avec des écologies similaires peuvent se retrouver aux mêmes profondeurs avec des niches isotopiques qui se chevauchent, n'ayant pas besoin d'utiliser l'axe de la profondeur pour se ségréger.

L'analyse de la structure trophique observée pourrait être étendue à d'autres taxons qui peuvent entrer en compétition avec les poissons comme les céphalopodes ou les crustacés. Cela permettrait d'identifier si des chevauchements trophiques existent ou si au contraire, un fort partitionnement des niches est aussi observé entre taxons dans le golfe de Gascogne. Dans le golfe du Mexique, un partitionnement des niches trophiques entre les espèces de poissons et de crustacés méso- et bathypélagiques a été observé (Hopkins and Sutton, 1998; Burghart et al., 2010).

4.2. Qui mange qui ? Et où ? Nouvelles perspectives analytiques.

Afin d'étudier l'écologie trophique des espèces nous avons utilisé la méthode des isotopes stables de l'azote et du carbone. Bien que cette méthode, relativement peu coûteuse, permet d'avoir une image intégrée sur le temps (de quelques semaines à mois) elle reste une méthode indirecte qui ne permet pas de connaître le régime alimentaire des espèces. L'étude des restes non-digérés dans les contenus

stomacaux pourrait permettre d'en apprendre davantage sur la diversité des proies consommées par ces espèces (Bernal et al., 2015). Cependant, cette méthode est très chronophage et requiert des spécialistes capables d'identifier les proies. Cette méthode est également sujette à plusieurs biais comme la régurgitation des espèces à la remontée du chalut, la courte représentativité temporelle du régime analysé et la digestion différentielle de certains taxons comme les organismes gélatineux.

Les traceurs écologiques restent donc un axe majeur à développer pour étudier le réseau trophique profond. Une de ces méthodes est l'analyse spécifique des composés des acides aminés. Une partie des acides aminés, les acides aminés « sources », ne fractionne pas et reflète ainsi la signature isotopique de base du réseau trophique. En revanche, les acides aminés dits « trophiques » fractionnent en moyenne de 7‰. La différence entre ces deux types d'acides aminés permet d'évaluer le niveau trophique des espèces sans le biais de la variation de la ligne de base isotopique (McClelland and Montoya, 2002; Chikaraishi et al., 2009). Cette approche sur les communautés de poissons mésopélagiques a pu mettre en évidence que les larges variations que certaines espèces présentaient dans leurs signatures en $\delta^{15}\text{N}$ étaient liées à des variations de la ligne isotopique de base et non à un changement dans leur position trophique (Choy et al., 2012). L'augmentation des valeurs des acides aminés sources des poissons mésopélagiques avec la profondeur implique une contribution des particules en suspension dans le réseau trophique profond (Choy et al., 2015). Cette approche pourrait, dans notre cas d'étude, apporter des informations sur la source du régime trophique de certaines espèces pour lesquelles nous avons fait l'hypothèse d'une alimentation benthopélagique (par exemple, les *Platyroctidae*).

Une autre approche qui pourrait permettre également de mieux appréhender l'écologie trophique de ces espèces est l'étude de l'isotope stable du mercure. Les concentrations en mercure augmentent avec la profondeur permettant le traçage des profondeurs d'alimentation (Choy et al., 2009). D'autres approches, encore moins largement développées, promettent aussi de belles avancées dans la compréhension de l'écologie trophique de ces espèces : les visualisations directes des interactions trophiques par le biais de caméras, l'identification des proies via leur ADN dans les contenus stomacaux des espèces ou encore l'utilisation de prédateurs supérieurs comme échantillonneurs biologiques via leurs contenus stomacaux (Figure 5-2) (Paquin et al., 2014; Choy et al., 2017; Portner et al., 2023). Les observations *in situ*, réalisées notamment par des véhicules sous-

marins téléopérés, pourraient apporter des informations précieuses sur le comportement d'alimentation des espèces pélagiques profondes. Ces informations pourraient être mise en lien avec l'étude des stratégies fonctionnelles d'acquisition de la nourriture via l'étude basée sur les traits morphologiques (Chapitre 4). Ces observations pourraient aussi révéler de nouvelles interactions trophiques non détectables avec d'autres méthodes (par exemples les isotopes stables).

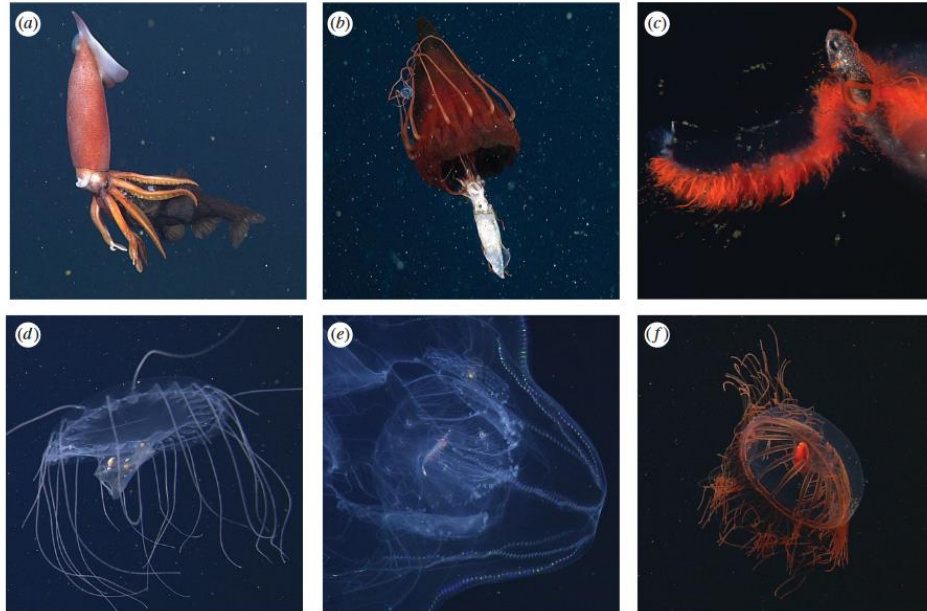


Figure 5-2. Série de six images ROV illustratives de prédateurs pélagiques et de leurs proies. Description complète des interactions dans Choy et al., 2022.

4.3. De la pente à l'océan ouvert

Au vu de l'ensemble de nos résultats, l'association avec la pente semble façonner la composition et une partie de la structure trophique de la communauté de poissons pélagiques profonds du golfe de Gascogne. Afin d'élargir cette vision, une étude le long de l'axe plateau-large pourrait nous permettre de mieux caractériser les différences entre ces deux écosystèmes et notamment de répondre à ces questions :

- Est-ce que des différences importantes dans la composition en espèces apparaissent le long de ce gradient ? Et en particulier certaines espèces sont-elles inféodées à la pente ? Et est-ce que suivant la couche de profondeur étudiée des différences plus ou moins importantes apparaissent ?

- Le fonctionnement trophique entre les différentes couches de profondeur est-il le même entre les deux systèmes ? Et plus spécifiquement, est-ce que la communauté plus au large présente aussi une ségrégation trophique importante ?
- Est-ce que ce sont les mêmes stratégies fonctionnelles qui sont retrouvées entre les deux systèmes ?

Les réponses à ces questions pourraient être apportées au niveau du golfe de Gascogne en réalisant le même type d'échantillonnage que ceux réalisés pendant ces travaux de thèse. Concernant l'étude de la structure trophique de la communauté, l'approche de Suchomel et al., (2022), pourrait être de nouveau appliquée pour déterminer si des processus déterministes tels que la compétition façonne aussi la répartition des niches isotopiques des espèces. Le calcul des indices de diversité trophique pourrait aussi mettre en évidence des différences de fonctionnement trophique entre les deux systèmes (Cucherousset and Villéger, 2015).

L'étude des stratégies fonctionnelles employées par les espèces entre les deux systèmes (c'est-à-dire entre celles près de la pente et celles plus au large) pourrait être réalisée par la mesure de traits morphologiques (chapitre 4). Cette approche, réalisée à l'échelle des différentes couches de profondeur, nous permettrait de mettre en évidence des différences de fonctionnement autant sur le plan vertical qu'horizontal entre ces deux communautés.

4.4. Plongée dans les profondeurs

La difficulté d'étudier ces espèces dans leur milieu limite la compréhension de leur écologie. Des informations détaillées sur le comportement et les migrations des poissons sont cependant nécessaires pour mieux comprendre, protéger et gérer ces communautés. L'élaboration de mesures de protection efficaces dépend de la connaissance du temps de résidence et des patrons de migration des poissons à différentes échelles temporelles. Ces informations peuvent être en parties obtenues par la pose de balises télémétriques. La limite principale à l'utilisation de ces instruments en milieu profond est la non-possibilité de remonter la plupart des espèces vivantes pour les équiper. Une des solutions serait de le réaliser sur les espèces migratrices qui remontent à la surface la nuit. Le développement de nouvelles technologies permet d'envisager des installations *in situ* sur une plus grande diversité d'espèces (Edwards et al., 2019). La pose d'un dispositif de marquage *in situ* a pu être réalisé sur une espèce de sébaste via un dispositif de marquage fixé à un chalut. Les poissons

entrent dans le chalut puis pénètrent dans une chambre de marquage pour y être maintenus, marqués, puis relâchés (Sigurdsson et al., 2006). Ces innovations étant principalement utilisées sur des espèces démersales, leur application aux espèces pélagiques profondes, souvent fragiles et de petite taille (< 20 cm), reste encore un défi à l'heure actuelle.

5. Conclusion

Ces travaux ont permis d'apporter de nouvelles informations sur différents mécanismes façonnant la structure de la communauté de poissons épi- à bathypélagiques la nuit dans une zone de pente. Mais de nombreuses questions et aspects de l'écologie de ces espèces restent à explorer (Martin et al., 2020). En particulier, la zone bathypélagique fait figure encore de boîte noire, des informations basiques telles que la biomasse des espèces, leur diversité et leurs fonctions restant manquantes (Webb et al., 2010). Le développement de technologies et techniques analytiques innovantes pour échantillonner ce milieu particulièrement vaste et difficile d'accès permettra sûrement de répondre en partie à ces questions. En lien avec les objectifs du projet de recherche H2020 SUMMER ("*Sustainable Management of Mesopelagic Resources*" ; convention de subvention ID : 817806) qui a financé ces travaux de thèse, il est essentiel d'en apprendre davantage sur le fonctionnement de ces communautés dans le but de ne pas reproduire les erreurs du passé sur la gestion des ressources halieutiques des zones néritiques. Ces informations pourront également permettre de mieux prédire les impacts à la fois d'une future exploitation mais aussi ceux à plus long terme des changements climatiques (Martin et al., 2020). Bien que des progrès aient été réalisés dans le domaine de la conservation de cet environnement, au vu de l'ampleur de cette tâche, il est probable que les avancées scientifiques ne soient pas assez rapides. On peut légitimement se questionner sur la pertinence de l'application d'un principe de précaution en faveur de ces communautés uniques tant d'un point de vue fonctionnel que dans le cadre de la conservation de notre patrimoine commun (Robison, 2009; Ryabinin et al., 2019).

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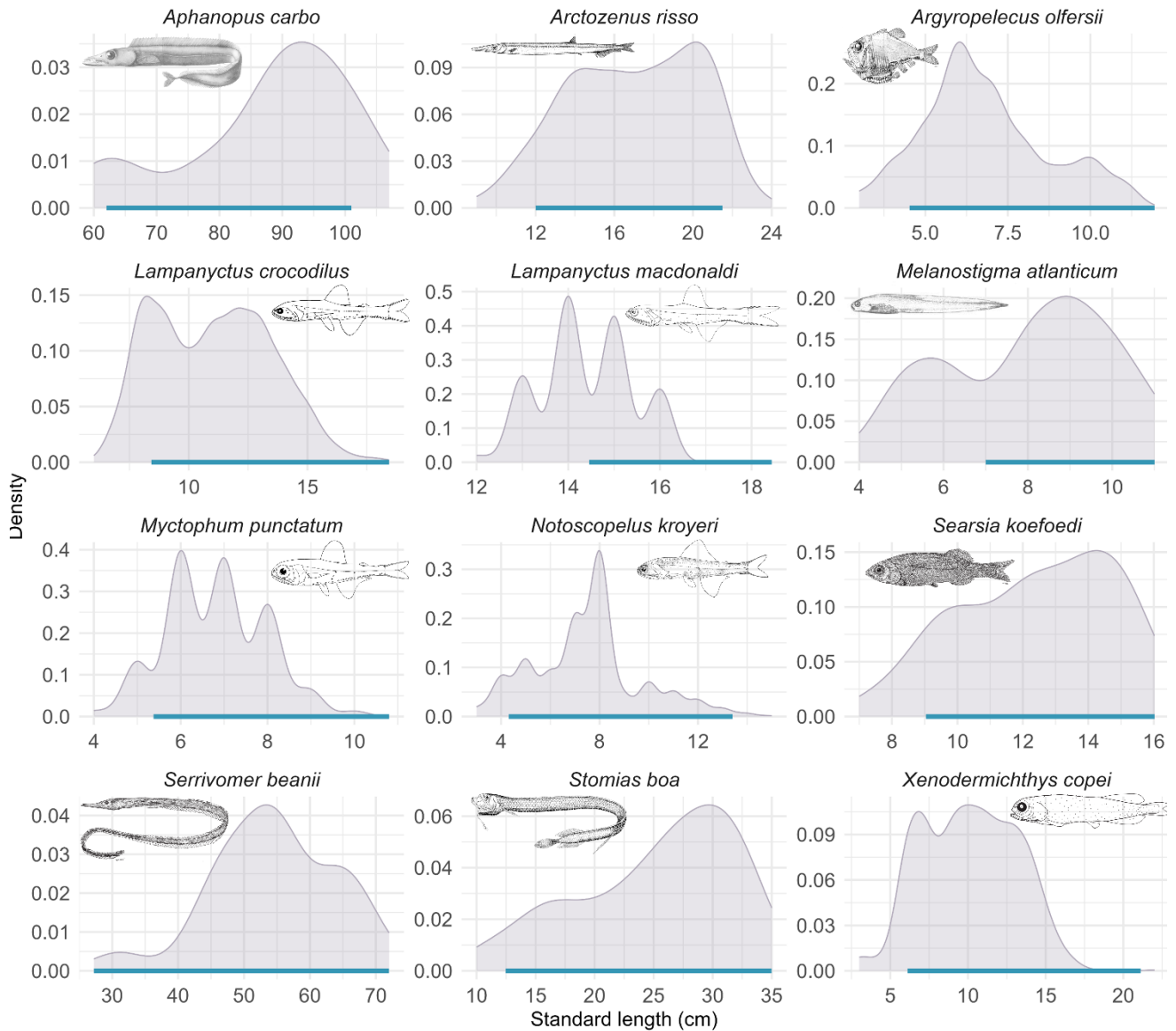
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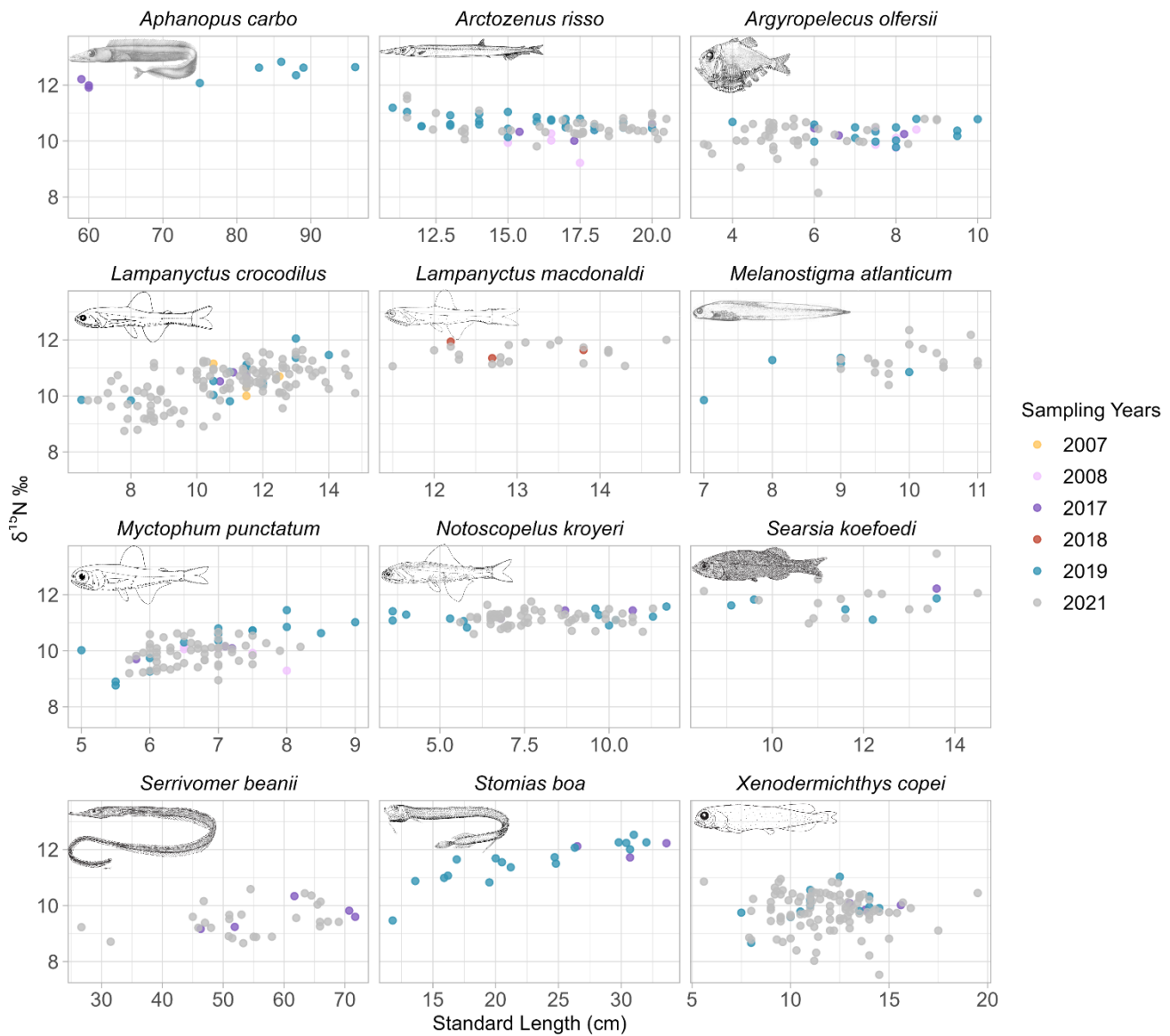
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Annexes

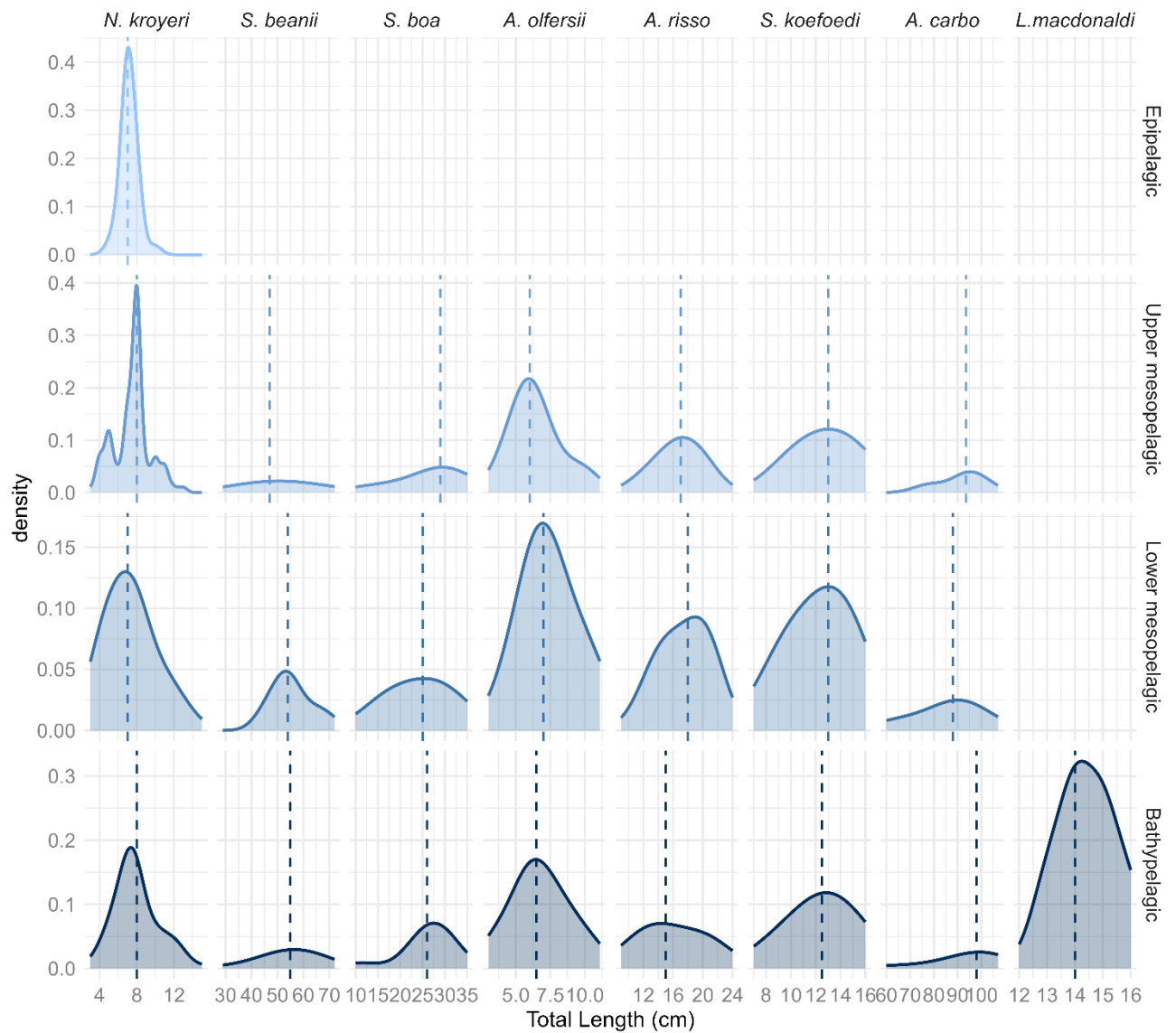
Chapitre 2



Appendix 1: Comparison of sampled size ranges in trawling (density plot in grey) and isotopic (segment in blue) data sets for each species.

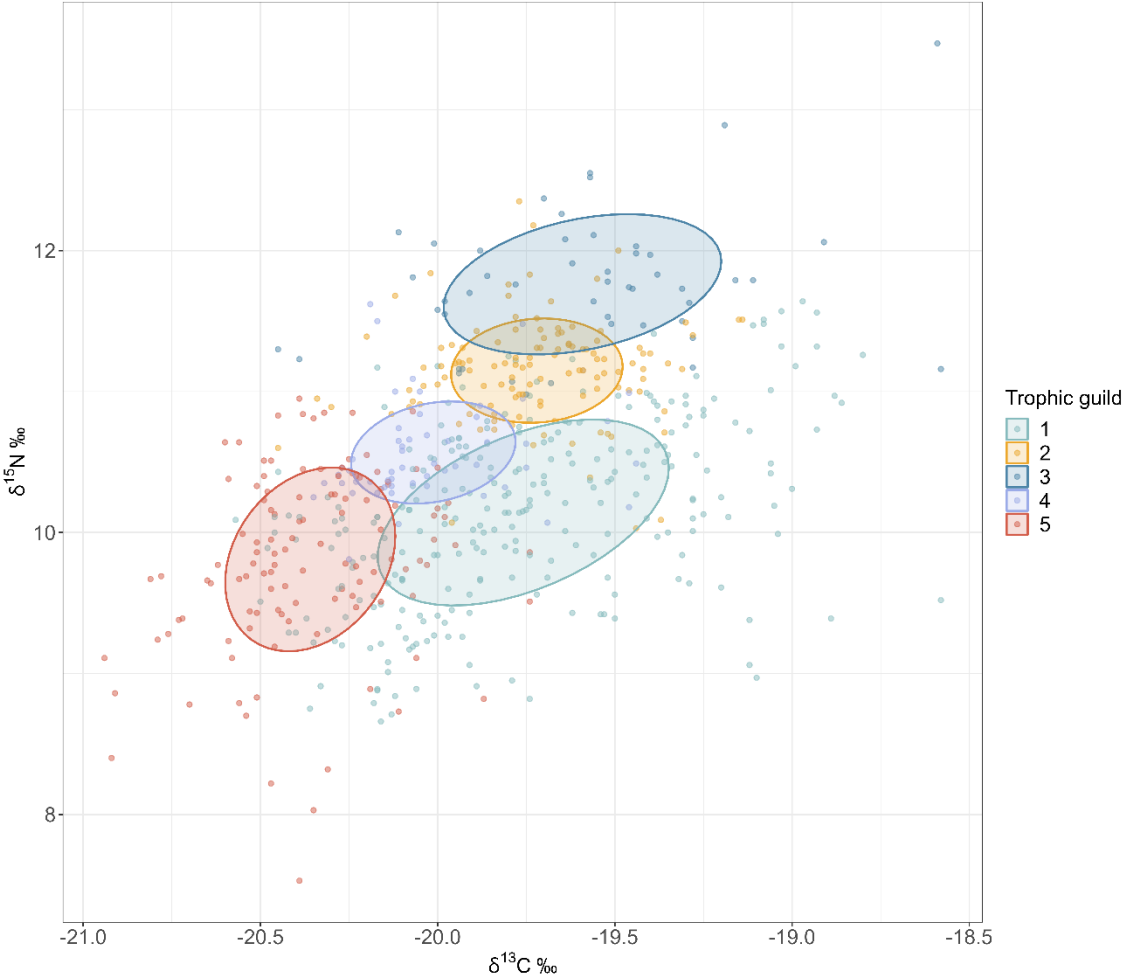


Appendix 2: Relationship between $\delta^{15}\text{N}$ values and body size (standard length) for each species, with the different sampling years shown in color.

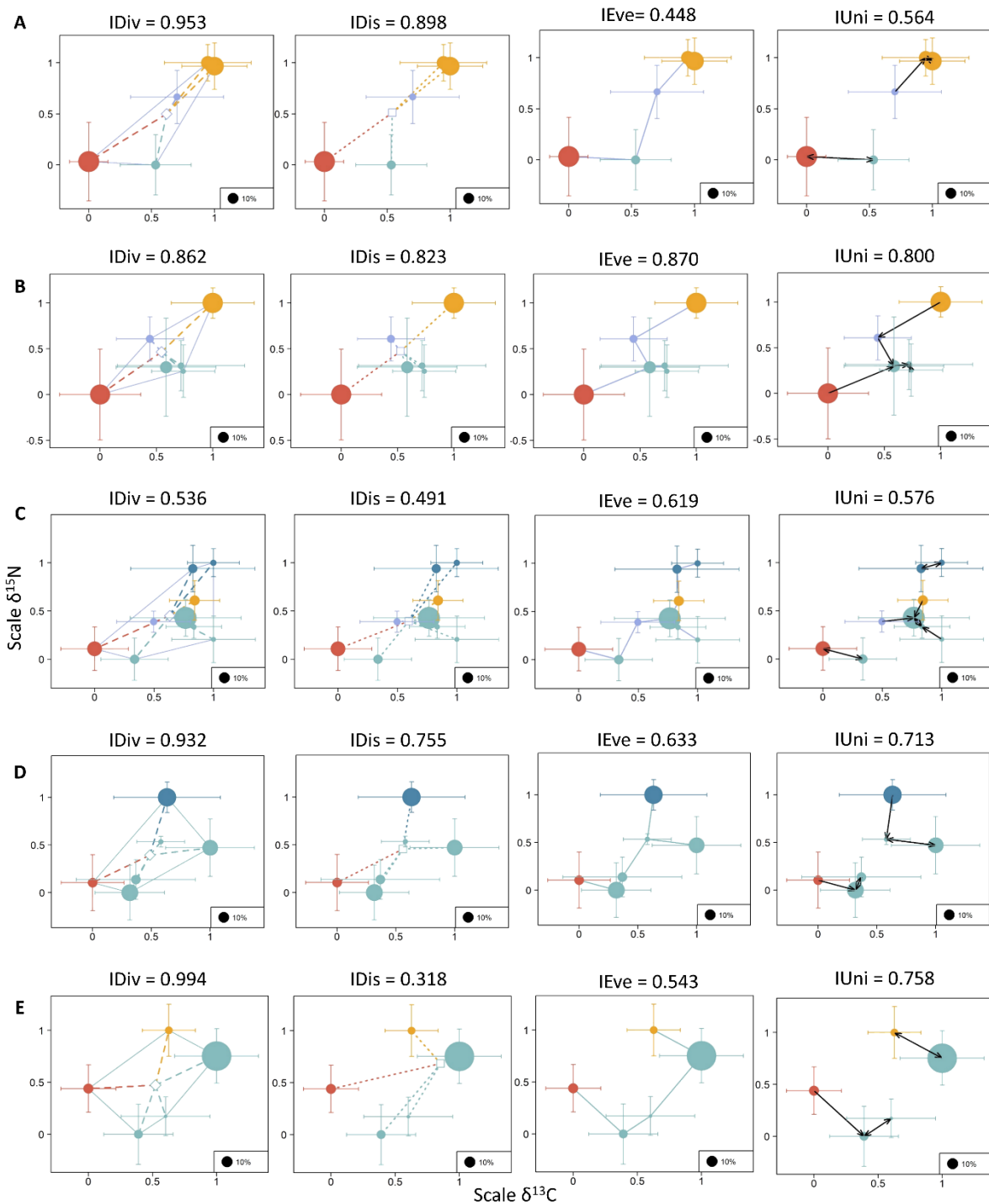


Appendix 3: Size distribution (total length in cm) as a function of depth for the species that showed non-significant relationships. The median size is indicated for each depth layer by a dashed line.

Chapitre 3

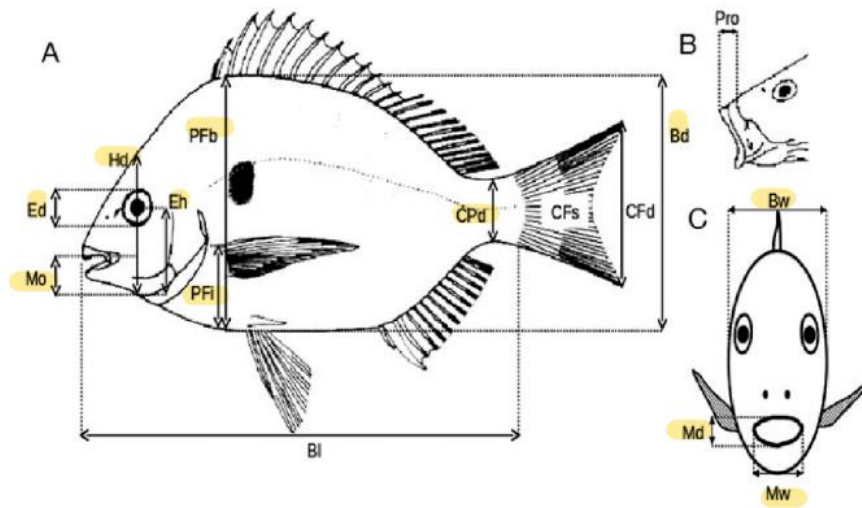


Appendix 4. Isotopic niches of each pooled trophic guilds.

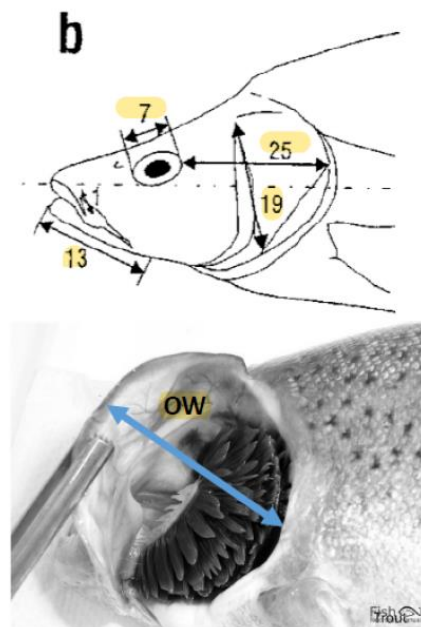


Appendix 5. Values of each of the four isotopic indices, weighted by the relative biomass of each species, at each depth layer (A= epipelagic, B= upper-mesopelagic, C= lower-mesopelagic, D= bathypelagic and E= bottom-proximity). IDiv = divergence, IDis = dispersion, IEve = evenness and IUni = uniqueness. The colors represent the trophic guild to which each species belongs.

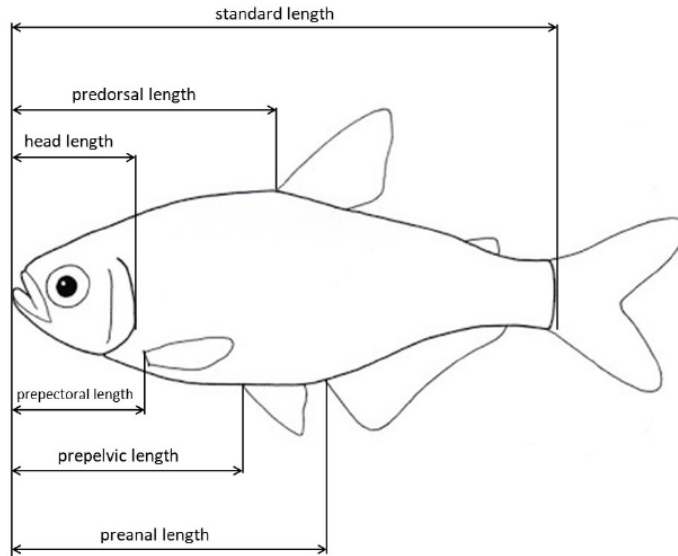
Chapitre 4



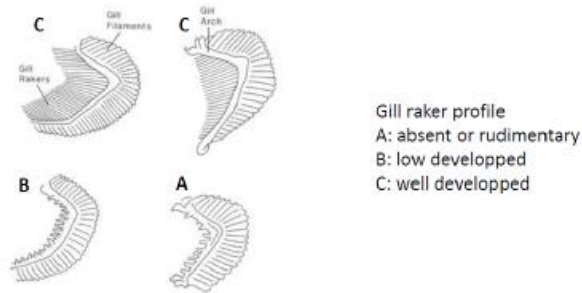
Appendix 6: Morphological measurements, from Albouy *et al.* (2011). bd, body depth bw, body width; cpd, caudal peduncle minimal depth ed, eye diameter; eh, distance between the bottom of the head and the eye center along the head depth axis; hd, head depth along the vertical axis of the eye; md, mouth depth; mo, distance between the tip of the upper jaw and bottom of the head; mw, mouth width; pfb, body depth at the level of the pectoral insertion; pfi, distance between the insertion of pectoral fin and the bottom of the body.



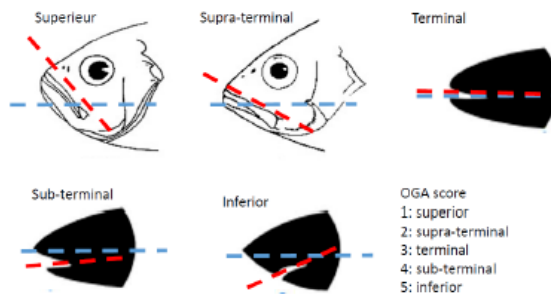
Appendices 7: Morphological head measurements, from Diderich (2006), following Sibbing & Nagelkerke (2000). 7 being ed, eye diameter; 13 lj, distance between the tip and the insertion point of lower jaw; 19 od, depth of the operculum from point of insertion to bottom; 25 pol, shortest distance between the eye and the end of the head; ow, operculum maximum width.



Appendices 8: Morphological measurements of the head and fins (Habib et al., 2019; Keat-Chuan et al., 2017). hl, head length, from the nose to the closest-to-caudal-fin point of the operculum; pal, distance between the tip of the nose and the insertion of anal fin; pdl, distance between the tip of the nose and the insertion of dorsal fin, ppl, distance between the tip of the nose and the insertion of pectoral fin; sl, standard length.



Appendices 9: Scores of gills rakers types git, based on their length.



Appendices 10: Scores of oral gape axis oga, based on the angle between mouth orientation (red) and a fictive mid-depth lateral line (blue).

Mise en lumière des profondeurs nocturnes : Distribution, fonctionnement trophique et diversité fonctionnelle de la communauté de poissons épi- à bathypélagiques dans les canyons du golfe de Gascogne

Résumé :

Les poissons pélagiques profonds occupent des rôles fonctionnels clés dans les écosystèmes marins, notamment au sein des réseaux trophiques. Cependant, de nombreuses connaissances restent manquantes telles que leur biomasse, leur diversité ou les fonctions qu'ils occupent au sein de l'écosystème, ce qui mine notre capacité à comprendre et prédire l'effet de changements. Ce travail visait à mieux comprendre les mécanismes qui façonnent l'assemblage de la communauté de poissons pélagiques profonds la nuit dans la zone de pente du golfe de Gascogne entre la surface et 2000 m de profondeur. Différentes approches ont été utilisées pour étudier l'influence des variables environnementales et de la compétition sur l'assemblage de la communauté le long du gradient de profondeur. La variabilité intraspécifique a également pu être quantifiée. Nous avons montré que la profondeur était le gradient environnemental influençant le plus la composition en espèce de cette communauté. Une augmentation de la diversité et de la biomasse près du fond a été constatée la nuit, un résultat inattendu pour cette communauté. Une variabilité interspécifique importante a été observée dans les changements ontogéniques opérés par différentes espèces. La complémentarité des approches, portant sur l'analyse des isotopes stables et la diversité fonctionnelle, a permis de démontrer l'influence significative de la compétition sur la structuration de cette communauté. Ainsi, les espèces tendent à réduire leur similarité et à se spécialiser afin de minimiser la compétition interspécifique. L'apport de ces nouvelles informations revêt une importance cruciale dans l'élaboration de mesures de gestion pertinentes.

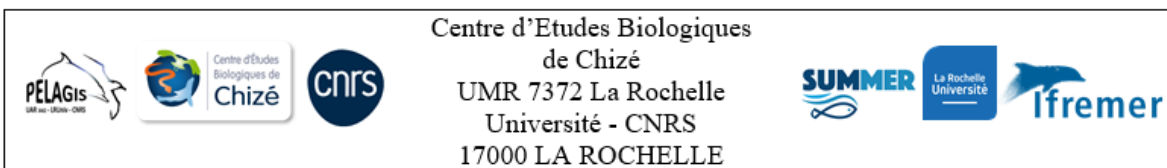
Mots clés : Poisson, Mésopélagique, Bathypélagique, Gradient environnemental, Couche limite benthique, Structure trophique, Diversité fonctionnelle, Ontogénie, Compétition

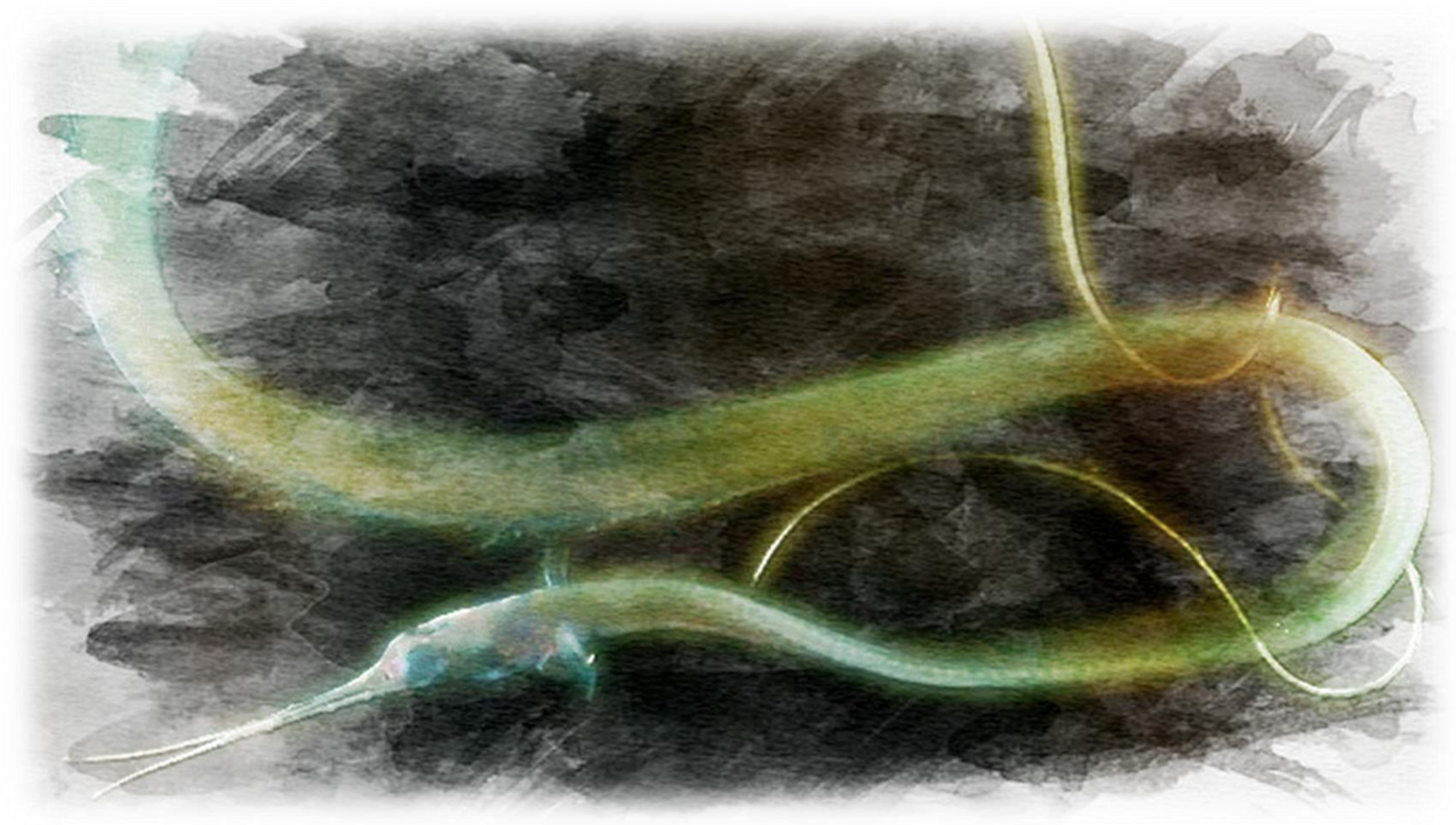
Shedding light on the nocturnal depths: Distribution, trophic functioning and functional diversity of the epi- to bathypelagic fish community in the canyons of the Bay of Biscay.

Summary:

Deep pelagic fishes play key functional roles in marine ecosystems, particularly within food webs. However, much remains unknown about their biomass, diversity, and functions within the ecosystem, which undermines our ability to understand and predict the impacts of change. This work aimed to gain a better understanding of the mechanisms that shape the assembly of the deep pelagic fish community at night in the Bay of Biscay slope zone between the surface and 2000 m depth. Different approaches were used to investigate the influence of environmental variables and competition on community assembly along the depth gradient. Intraspecific variability was also quantified. We showed that depth was the environmental gradient with the greatest influence on the species composition of this community. An increase in diversity and biomass near the bottom was observed at night, an unexpected result for this community. Significant interspecific variability was observed in the ontogenic changes undergone by different species. Complementary approaches, based on stable isotope analysis and functional diversity, have demonstrated the significant influence of competition on the structuring of this community. As a result, species tend to reduce their similarity and specialize to minimize interspecific competition. This new information is crucial for the development of appropriate management measures.

Keywords: Fish, Mesopelagic, Bathypelagic, Environmental gradient, Benthic boundary layer, Trophic structure, Functional diversity, Ontogeny, Competition





Les poissons pélagiques profonds occupent des rôles fonctionnels clés dans les écosystèmes marins, notamment au sein des réseaux trophiques. Cependant, de nombreuses connaissances restent manquantes telles que leur biomasse, leur diversité ou les fonctions qu'ils occupent au sein de l'écosystème, ce qui mine notre capacité à comprendre et prédire l'effet de changements. Ce travail visait à mieux comprendre les mécanismes qui façonnent l'assemblage de la communauté de poissons pélagiques profonds la nuit dans la zone de pente du golfe de Gascogne entre la surface et 2000 m de profondeur. Différentes approches ont été utilisées pour étudier l'influence des variables environnementales et de la compétition sur l'assemblage de la communauté le long du gradient de profondeur. La variabilité intraspécifique a également pu être quantifiée. Nous avons montré que la profondeur était le gradient environnemental influençant le plus la composition en espèce de cette communauté. Une augmentation de la diversité et de la biomasse près du fond a été constatée la nuit, un résultat inattendu pour cette communauté. Une variabilité interspécifique importante a été observée dans les changements ontogéniques opérés par différentes espèces. La complémentarité des approches, portant sur l'analyse des isotopes stables et la diversité fonctionnelle, a permis de démontrer l'influence significative de la compétition sur la structuration de cette communauté. Ainsi, les espèces tendent à réduire leur similarité et à se spécialiser afin de minimiser la compétition interspécifique. L'apport de ces nouvelles informations revêt une importance cruciale dans l'élaboration de mesures de gestion pertinentes.