THÈSE POUR OBTENIR LE GRADE DE DOCTEUR

DE L'UNIVERSITÉ DE MONTPELLIER

EN SCIENCE DE LA MER
PREPAREE AU SEIN DE L'ÉCOLE DOCTORALE GAIA DOCTORALE
ET DE L'UNITE DE RECHERCHE UMR MARBEC
EN PARTENARIAT INTERNATIONAL AVEC THE **FEDERAL RURAL UNIVERSITY OF PERNAMBUCO** (BRÉSIL)

# Diving into diversity: taxonomic and functional diversity of demersal and mesopelagic fishes from the Southwestern Tropical Atlantic

Présentée par
**Kátia Cristina APARECIDO**
Le 26 août 2024

Sous la direction de
**Bastien MÉRIGOT** (Directeur de thèse)
**Thierry FRÉDOU** (Directeur de thèse) et
**Leandro EDUARDO** (Co-encadrant)

**Devant le jury composé de**

| | |
|---|---|
| Victoria **NAHUM**, Professeure, Université Fédérale du Pará, Brésil | [Rapportrice] |
| José **MUELBERT**, Professeur, Université Fédérale du Rio Grande du Sul, Brésil | [Rapporteur] |
| Frida **LASRAM,** Professeure, Université du Littoral Côte d'Opale, France | [Examinatrice] |
| Beatrice **FERREIRA,** Professeure, Université Fédérale du Pernambuco, Brésil | [Présidente du jury] |
| Bastien **MÉRIGOT,** Maître de Conférences HDR, University of Montpellier, France | [Directeur de thèse] |
| Thierry **FRÉDOU**, Maître de Conférences, Université Fédérale Rurale du Pernambuco, Brésil | [Directeur de thèse] |
| Leandro **EDUARDO**, Chargé de recherche, IRD, France | [Co-encadrant] |

UNIVERSITÉ
DE MONTPELLIER

Thesis cover for the Federal Rural University of Pernambuco

Thesis to obtain the degree of doctor issued by the University of Montpellier and the Federal Rural University of Pernambuco

**FEDERAL RURAL UNIVERSITY OF PERNAMBUCO**
**PRO-RECTORATE OF RESEARCH AND GRADUATE STUDIES GRADUATE PROGRAM IN FISHERIES RESOURCES AND AQUACULTURE**

# Diving into diversity: taxonomic and functional diversity of demersal and mesopelagic fishes from the Southwestern Tropical Atlantic

**Kátia Cristina Aparecido**

Thesis presented to the Doctoral School GAIA of the University of Montpellier and to the Post-Graduation Program in Fishing Resources and Aquaculture of the Federal Rural University of Pernambuco as a requirement to obtain the title of Doctor.

**Thierry Frédou (Supervisor)**

**Bastien Mérigot (Supervisor)**

**Leandro Eduardo (Co-supervisor)**

Recife, 2024

Thesis cover for the Federal Rural University of Pernambuco

Thesis to obtain the degree of doctor issued by the University of Montpellier and the Federal Rural University of Pernambuco

# Diving into diversity: taxonomic and functional diversity of demersal and mesopelagic fishes from the Southwestern Tropical Atlantic

KÁTIA CRISTINA APARECIDO

## SUPERVISORS

Dr. Thierry Frédou — Federal Rural University of Pernambuco, Recife, Brazil

Dr. Bastien Mérigot — University of Montpellier, Sète, France

Dr. Leandro Eduardo – IRD, Sète, France

## JURIES

| | |
|---|---|
| Dr. Victoria **NAHUM**, Full professor, Federal of University of Pará, Brazil | [Reviewer] |
| Dr. José **MUELBERT**, Full professor, Federal University of Rio Grande, Brazil | [Reviewer] |
| Dr. Frida **LASRAM,** Full professor, University of Littoral Côte d'Opale, France | [Examiner] |
| Dr. Beatrice **FERREIRA,** Full professor, Federal University of Pernambuco, Brazil | [President of the jury] |
| Dr. Bastien **MÉRIGOT,** Associate Professor, University of Montpellier, France | [Supervisor] |
| Dr. Thierry **FRÉDOU**, Associate Professor, Federal Rural University of Pernambuco, Brazil | [Supervisor] |
| Dr. Leandro **EDUARDO**, Researcher, IRD, France | [Co-supervisor] |

Dados Internacionais de Catalogação na Publicação
Sistema Integrado de Bibliotecas da UFRPE
Bibliotecário(a): Auxiliadora Cunha – CRB-41134

A639< Aparecido, Kátia Cristina.
*Diving into diversity: taxonomic and functional diversity of demersal and mesopelagic fishes from the Southwestern Tropical Atlantic* / Kátia Cristina Aparecido. – Recife, 2024.

151 f.; il.

Orientador(a): Thierry Frédou.
Co-orientador(a): Bastien Mérigot.
Co-orientador(a): Leandro Eduardo.

Tese (Doutorado) – Universidade Federal Rural de Pernambuco, Programa de Pós-Graduação em Recursos Pesqueiros e Aquicultura, Recife, BR-PE, 2024.

Inclui referências.

1. *Peixes - Classificação*. 2. *Peixes - Distribuição geográfica*. 3. *Nicho (Ecologia)*. 4. *Ecossistema* 5. Comunidades de peixes. I. Frédou, Thierry, orient.

II. Mérigot, Bastien, coorient. III. Eduardo, Leandro, coorient. IV. Título

CDD 639.3

## ACKNOWLEDGEMENTS

And so, I conclude this chapter, which had its fair share of obstacles, but was beautiful and joyous. I would like to express my deep gratitude to the coordinators of Bioimpact, Flávia Lucena-Frédou and Thierry Frédou (also my supervisor), for all the great opportunities you provided me. I have learned very much from you over these years, through your invaluable lessons.

My sincere thanks to my supervisors Bastien Mérigot and Leandro Eduardo. Thank you so much for all the teachings, patience, and dedication you have shown me. I wish to show my gratitude for the feedback and efforts of all co-authors, committee members, and jurors who assisted during the conception and implementation of this project.

Throughout this entire journey, I had the opportunity to meet incredible laboratories and professionals. I appreciate the collaboration and support from all the students and staff at Bioimpact-UFRPE, Marbec-UM, and Nupem-UFRJ. To Arnaud Bertrand, many thanks for all the advice and words of encouragement during times of crisis.

I consider myself fortunate to have found my mentor, Ana Rodrigues, on this journey. Thank you for accompanying me this far and for showing me this entire process from another perspective.

Aos grandes amigos que trilharam comigo nesta caminhada — Jennifer, Léo, Rayssa, Andrey, Ítala, Alex, Júlio e Jonas — muito obrigada por todas as longas horas de conversas regadas a cafés e cervejas. Eu não teria chegado aqui sem vocês. Não posso deixar de expressar minha gratidão por todo o carinho e apoio que recebi da minha família francesa: Claudine, Valentin, Pierre, Julie, Madame Barthalinni e François. Un grand merci pour tout.

Um agradecimento especial à minha família e aos amigos de longa data pelo amor e carinho. Gostaria de ressaltar minha mãe, Luciene, e minha melhor amiga, Maju. Obrigada por sempre estarem disponíveis para me ouvir, me incentivar e por estarem ao meu lado em qualquer decisão que eu tome.

“Dias inteiros de calmaria, noites de ardentia,
dedos no leme e olhos no horizonte,
descobri a alegria de transformar
distâncias em tempo.

Um tempo em que aprendi
a entender as coisas do mar,
a conversar com as grandes ondas
e não discutir com o mau tempo.
A transformar o medo em respeito,
o respeito em confiança.

Descobri como é bom chegar quando se tem paciência.
E para se chegar onde quer que seja,
aprendi que não é preciso dominar a força,
mas a razão.
É preciso antes de mais nada querer.”

Amyr Klink

# TABLE OF CONTENTS

**ABSTRACT** ..... **8**

**RÉSUMÉ** ..... **10**

**RESUMO** ..... **12**

**SYNTHÈSE DES TRAVAUX EN FRANÇAIS** ..... **14**

**1. GENERAL INTRODUCTION** ..... **23**

1.1. BIODIVERSITY ..... 23
1.2. FUNCTIONAL DIVERSITY ..... 24
1.3. MARINE FISH COMMUNITIES' THREATS ..... 25
1.4. BETA DIVERSITY ..... 27
1.5. STUDY AREA ..... 29
1.6. OBJECTIVES AND MOTIVATIONS ..... 33

**2. CHAPTER 1. FUNCTIONAL TRAITS OF MESOPELAGIC FISHES: A DATABASE WITH A NOVEL PROPOSAL OF CLASSIFICATION** ..... **35**

2.1. ABSTRACT ..... 36
2.2. BACKGROUND & SUMMARY ..... 37
2.3. METHODS ..... 38
2.4. TECHNICAL VALIDATION ..... 51
2.5. USAGE NOTES ..... 52

**3. CHAPTER 2 – DISTRIBUTION OF FUNCTIONAL DIVERSITY OF MESOPELAGIC FISH COMMUNITY ACROSS DIURNAL CYCLE AND ENVIRONMENTAL GRADIENTS** ..... **53**

3.1. ABSTRACT ..... 54
3.2. INTRODUCTION ..... 55
3.3. MATERIALS AND METHODS ..... 57
3.4. RESULTS ..... 66
3.5. DISCUSSION ..... 77

**4. CHAPTER 3 – ASSESSING ECOLOGICAL PROCESSES ON DEMERSAL FISH COMMUNITY FROM TAXONOMIC AND FUNCTIONAL TRAIT Β-DIVERSITY** ..... **96**

4.1. ABSTRACT ..... 97
4.2. INTRODUCTION ..... 98
4.3. MATERIAL AND METHODS ..... 100
4.4. RESULTS ..... 105
4.5. DISCUSSION ..... 111

**ACKNOWLEDGEMENTS** ..... **116**

**5. GENERAL DISCUSSION** ..... **117**

5.1. IMPROVEMENT OF THE KNOWLEDGE ON MESOPELAGIC FISH FUNCTIONAL TRAITS AND THE IMPORTANCE OF OPEN SCIENCE. ..... 118
5.2. DYNAMICS OF FUNCTIONAL SPACE IN THE MESOPELAGIC ENVIRONMENT ..... 119
5.3. STRUCTURING PROCESSES OF DEMERSAL COMMUNITIES ..... 121
5.4. PERSPECTIVES OF CONSERVATION ..... 123

**6. GENERAL CONCLUSION** ..... **124**

**REFERENCES** ..... **126**

# ABSTRACT

Marine ecosystems face increasing anthropogenic threats. There is a growing interest in marine usage and exploitation, which in many cases can negatively impact fish communities, such as mineral exploitation, fishing, pollution, habitat destruction, and tourism. These anthropogenic activities can affect and endanger important ecosystem functioning and services, particularly those associated to demersal and mesopelagic fish communities, due to the unique functions and services they provide. Demersal fish, in particular, are highly relevant for food security, while mesopelagic fish, though still poorly studied, directly contribute to the carbon pump, meaning they help mitigate the impacts of climate change. However, conservation efforts for these communities remain ineffective due to a lack of information about their biology, diversity and distribution. To understand the functional and dynamic aspects of demersal and mesopelagic communities, this thesis is structured around three main complementary research axes to fill these gaps. The first axis investigated different functional traits related to locomotion, feeding, and survival of mesopelagic fish. Based on observations of sampled data and literature reviews, it is proposed to categorize traits, such as skin color and teeth, to standardize these characteristics and to assist in future ecological work. This allowed the development of a robust database of features for a unique community, that poses several challenges for its collection and storage. The second axis examined the distribution of traits within the mesopelagic fish community in the north-western Atlantic of Brazil, and their variation between diurnal and nocturnal periods, thus highlighting the community's dynamics and changes in functional space. This axis also investigated the environmental factors determining the distribution of these characteristics. Finally, the third axis investigated the distribution and partition of beta diversity in two facets of demersal communities: taxonomic and functional diversities.  Different environmental and spatial aspects of the region were incorporated into the analyses of demersal fish, aiming to identify the influences of these predictors on beta diversity. A predominance of turnover in the taxonomic facet was highlighted, with influences mainly from depth, as well as particle dispersion, and substrate type. The functional facet exhibited high diversity, and turnover and nestedness processes showed moderate values. This demonstrates significant functional variation in the region, with community structuring processes contributing equally. Overall, these results provide a robust basis for marine spatial management and planning, contributing to the conservation of important demersal and mesopelagic fish communities.

**Keywords:** Beta diversity, functional diversity, mesopelagic fish, demersal fish, conservation, species distribution, niche partition, ecological processes.

# RÉSUMÉ

Les écosystèmes marins sont confrontés à des menaces anthropiques croissantes. L'intérêt pour l'utilisation et l'exploitation marines est en augmentation, ce qui peut souvent avoir un impact négatif sur les communautés de poissons, comme l'exploitation minière, la pêche, la pollution, la destruction de l'habitat et le tourisme. Ces activités anthropiques peuvent affecter et mettre en danger le fonctionnement et les services importants des écosystèmes, en particulier ceux associés aux communautés de poissons démersaux et mésopélagiques, en raison des fonctions et services uniques qu'ils fournissent. Les poissons démersaux, en particulier, sont très pertinents pour la sécurité alimentaire, tandis que les poissons mésopélagiques, bien que peu étudiés, contribuent directement à la pompe à carbone, ce qui signifie qu'ils aident à atténuer les impacts du changement climatique. Cependant, les efforts de conservation pour ces communautés restent inefficaces en raison d'un manque d'informations sur leur biologie, leur diversité et leur distribution. Pour comprendre les aspects fonctionnels et dynamiques des communautés démersales et mésopélagiques, cette thèse est structurée autour de trois axes de recherche complémentaires pour combler ces lacunes. Le premier axe a étudié différents traits fonctionnels liés à la locomotion, à l'alimentation et à la survie des poissons mésopélagiques. Sur la base des observations des données échantillonnées et des revues de littérature, il est proposé de catégoriser des traits, tels que la couleur de la peau et les dents, pour standardiser ces caractéristiques et aider aux travaux écologiques futurs. Cela a permis le développement d'une base de données robuste de caractéristiques pour une communauté unique et qui pose plusieurs défis pour sa collecte et son stockage. Le deuxième axe a examiné la distribution des traits au sein de la communauté de poissons mésopélagiques dans l'Atlantique nord-ouest du Brésil, et leur variation entre les périodes diurnes et nocturnes, mettant ainsi en évidence la dynamique de la communauté et les changements dans l'espace fonctionnel. Cet axe a également étudié les facteurs environnementaux déterminant la distribution de ces caractéristiques. Enfin, le troisième axe a étudié la distribution et la partition de la beta diversité dans deux facettes des communautés démersales : les diversités taxonomique et fonctionnelle. Différents aspects environnementaux et spatiaux de la région ont été incorporés dans les analyses des poissons démersaux, visant à identifier les influences de ces prédicteurs sur la beta diversité. Une prédominance de renouvellement dans la facette taxonomique a été mise en évidence, avec des influences principalement de la profondeur, ainsi que de la dispersion des particules et du type de substrat. La facette fonctionnelle a présenté une grande diversité, tandis que les processus de renouvellement et de nidification ont montré des valeurs modérées. Cela démontre une variation fonctionnelle significative dans la région, avec une contribution équivalente des processus de structuration communautaire. Globalement, ces résultats fournissent une base robuste pour la gestion et la planification spatiales marines, contribuant à la conservation des communautés de poissons démersaux et mésopélagiques importantes.

**Mots-clés :** Diversité bêta, diversité fonctionnelle, poissons mésopélagiques, poissons démersaux, conservation, répartition des espèces, partition de niche, processus écologiques.

## RESUMO

Os ecossistemas marinhos enfrentam ameaças antropogênicas crescentes. Há um interesse crescente no uso e na exploração marinha, o que, em muitos casos, pode impactar negativamente as comunidades de peixes, como a exploração mineral, a pesca, a poluição, a destruição de habitats e o turismo. Essas atividades antropogênicas podem afetar e colocar em perigo o funcionamento e os serviços importantes do ecossistema, especialmente aqueles associados às comunidades de peixes demersais e mesopelágicos, devido às funções e serviços únicos que eles fornecem. Os peixes demersais, em particular, são altamente relevantes para a segurança alimentar, enquanto os peixes mesopelágicos, embora ainda pouco estudados, contribuem diretamente para a bomba de carbono, o que significa que ajudam a mitigar os impactos das mudanças climáticas. No entanto, os esforços de conservação dessas comunidades permanecem ineficazes devido à falta de informações sobre sua biologia, diversidade e distribuição. Para entender os aspectos funcionais e dinâmicos das comunidades demersais e mesopelágicas, esta tese está estruturada em torno de três principais eixos de pesquisa complementares para preencher essas lacunas. O primeiro eixo investigou diferentes traços funcionais relacionados à locomoção, alimentação e sobrevivência dos peixes mesopelágicos. Com base em observações de dados amostrados e revisões da literatura, propõe-se categorizar traços, como cor da pele e dentes, para padronizar essas características e auxiliar em futuros trabalhos ecológicos. Isso permitiu o desenvolvimento de um banco de dados robusto de características para uma comunidade única, que presenta vários desafios para sua coleta e armazenamento. O segundo eixo examinou a distribuição de traços dentro da comunidade de peixes mesopelágicos no Atlântico noroeste do Brasil, e sua variação entre os períodos diurnos e noturnos, destacando assim a dinâmica da comunidade e as mudanças no espaço funcional. Esse eixo também investigou os fatores ambientais que determinam a distribuição dessas características. Finalmente, o terceiro eixo investigou a distribuição e a partição da diversidade beta em duas facetas das comunidades demersais: diversidades taxonômica e funcional. Diferentes aspectos ambientais e espaciais da região foram incorporados nas análises dos peixes demersais, visando identificar as influências desses preditores na diversidade beta. Foi destacada uma predominância de turnover na faceta taxonômica, com influências principalmente da profundidade, bem como dispersão de partículas e tipo de substrato. A faceta funcional apresentou alta diversidade, enquanto os processos de substituição e aninhamento mostraram valores moderados. Isso demonstra uma variação funcional significativa na região, com os processos de estruturação da comunidade contribuindo igualmente. No geral, esses resultados fornecem uma base robusta para o gerenciamento e planejamento espacial marinho, contribuindo para a conservação de importantes comunidades de peixes demersais e mesopelágicos.

**Palavras-chave:** Diversidade beta, diversidade funcional, peixes mesopelágicos, peixes demersais, conservação, distribuição de espécies, partição de nicho, processos ecológicos.

## SYNTHÈSE DES TRAVAUX EN FRANÇAIS

La biodiversité marine est soumise à des impacts provenant de diverses sources, notamment le changement climatique, la surpêche et la pollution. Ces facteurs contribuent à des altérations de la composition et de l'abondance des espèces, ainsi qu'à des perturbations des cycles biologiques, entraînant une perte de biodiversité et une diminution de la productivité halieutique (Hughes et al., 2005; Harley et al., 2006; Paiva and Araújo, 2010; Ma et al., 2013). Les activités de pêche exercent des effets directs et indirects qui rivalisent avec ceux du changement climatique, affectant de plus en plus la fonctionnalité des communautés et des écosystèmes marins, et potentiellement les cycles biogéochimiques (Halpern et al., 2008). Comprendre et gérer durablement les écosystèmes marins nécessite des évaluations précises de leur fonctionnalité et de leur vulnérabilité (Levin and Lubchenco, 2008).

La perte de biodiversité représente une menace significative pour les structures et les fonctions des écosystèmes (Cardinale et al., 2012). Surveiller les multiples impacts de l'activité humaine directe et des changements environnementaux mondiaux implique d'évaluer divers aspects de la biodiversité des communautés, notamment le nombre d'espèces, l'équitabilité, la diversité taxonomique et/ou fonctionnelle. Les rôles fonctionnels des espèces sont évalués par leurs traits, qui influent indirectement sur la fitness à travers leurs effets sur la croissance, la reproduction et la survie (McGill et al., 2006; Violle et al., 2007). Cette approche, basée sur les rôles variés que les espèces établissent au sein des communautés, peut également permettre d’établir un lien entre diversité, fonctionnement et services écosystémiques. En intégrant la diversité fonctionnelle, il est possible d'évaluer les changements dans le fonctionnement des communautés et des écosystèmes en réponse aux perturbations externes, se révélant parfois encore plus sensible à la pression humaine que la richesse spécifique (Tilman et al., 1997; Hooper and Dukes, 2004; Gagic et al., 2015). Cette information peut être donc vitale pour la détermination des zones de gestion et/ou de protection.

La diversité fonctionnelle permet d'évaluer la complémentarité/redondance des espèces au sein et entre les communautés, et d'éclairer les processus d'assemblage d’espèces à partir de la décomposition de la diversité totale (gamma) en diversité intra (alpha) et inter (bêta) communautés (Whittaker, 1972; Jost, 2007; Baselga, 2010). La diversité fonctionnelle, plutôt que la richesse spécifique, est plus directement liée aux fonctions de l'écosystème telles que la productivité, et améliore la résilience aux perturbations et aux invasions, ainsi que les flux de matière (McGill et al., 2006; Worm et al., 2006; Tittensor et al., 2007; Halpern et al., 2008; Fraser, 2013). De plus, elle mesure la redondance fonctionnelle dans les écosystèmes, suggérant dans certains cas que la richesse spécifique élevée ne garantit pas nécessairement la préservation des fonctions. Cela est dû à la non prise en compte dans la richesse de la redondance fonctionnelle entre plusieurs espèces et au risque que certaines fonctions puissent dépendre d'une ou de quelques espèces singulières (espèces clés). Selon le degré de redondance fonctionnelle, la diversité fonctionnelle de la communauté est plus ou moins vulnérable à la perte d'espèces (Guillemot et al., 2011; Bender et al., 2013). En résumé, la diversité fonctionnelle offre une vision complémentaire des communautés, et est cruciale pour comprendre et préserver leur fonctionnement, ainsi que celui des écosystèmes, face aux pressions anthropiques et aux changements globaux.

Cette thèse vise à approfondir notre compréhension de la biodiversité (taxonomique et fonctionnelle) et de l'écologie des poissons mésopélagiques et démersaux, composantes essentielles des écosystèmes marins relativement peu étudiées dans les écosystèmes marins brésiliens en raison des défis inhérents à l'échantillonnage dans leurs habitats (Figure 1). Cette recherche adopte une approche intégrée combinant la taxonomie, la diversité fonctionnelle et l’écologie des communautés. La principale question de recherche posée par cette thèse est quelle est la distribution de la diversité taxonomique et fonctionnelle des communautés de poissons démersaux et mésopélagiques le long de la zone nord-est du Brésil, et quels en sont les principaux processus sous-jacents à ces distributions ? Pour répondre à cette question, les objectifs spécifiques de cette recherche sont les suivants :

- Définir les traits fonctionnels des poissons mésopélagiques et proposer une nouvelle classification de certains traits fonctionnels (chapitre 1). Ce chapitre est consacré à la définition et à la quantification des traits fonctionnels des poissons mésopélagiques. Il propose également une classification des traits mésopélagiques (article 1, Aparecido et al., en préparation) qui peut être appliquée dans les études écologiques et évolutives futures. La nouvelle proposition de classification vise à fournir un outil affiné pour analyser les communautés de poissons mésopélagiques, et potentiellement leur résilience et leurs liens avec les fonctions de l'écosystème face aux pressions anthropiques et aux changements globaux.

- Analyser la distribution de la diversité fonctionnelle des poissons mésopélagiques au cours des périodes diurnes et nocturnes, et comment les facteurs environnementaux l’influence (chapitre 2) : le chapitre est consacré à quantifier la diversité fonctionnelle des poissons mésopélagiques et comprendre sa distribution dans le nord-est du Brésil. Cette partie vise à combler d'importantes lacunes dans notre connaissance de la biodiversité des organismes habitant les profondeurs mésopélagiques (article 2, Aparecido et al. 2023), en examinant les traits fonctionnels et les rôles écologiques des poissons mésopélagiques. Il est exploré les relations complexes entre les facteurs environnementaux, les traits des espèces et les dynamiques des communautés. De plus, le rôle du filtrage environnemental dans la formation des assemblages d’espèces est étudié grâce à modèles basés sur les traits dans les communautés de poissons mésopélagiques.
- Examiner la distribution de la diversité bêta taxonomique et fonctionnelle des poissons démersaux, et analyser l'implication de facteurs environnementaux et spatiaux dans les processus agissants de la diversité bêta (chapitre 3). L'objectif est de discerner les schémas de distribution de ces poissons à travers des gradients environnementaux variés, identifiant ainsi les facteurs écologiques influençant leur distribution (Article 3, Aparecido et al., en préparation). Cette étude est destinée à élucider les mécanismes sous-jacents structurants les communautés demersales dans la zone étudiée, offrant des informations précieuses pour la conservation marine et la gestion des habitats essentiels.

## Caractéristiques de la zone d'étude

### *Zone 1 - Plateau Continental*

Le plateau continental est situé dans la partie orientale de la région de la plateforme de l'Amérique du Sud jusqu'à Rio Grande do Norte (5-9°S). La plateforme mesure 40 km de large et est presque entièrement recouverte de sédiments carbonatés biogéniques, avec des profondeurs variant de 40 à 80 mètres (Vital et al., 2010). Sur la côte nord-est, l'eau chaude prédomine et une thermocline permanente existe. Cette condition empêche la circulation verticale des masses d'eau, limitant ainsi l'apport de nutriments des couches plus profondes. Malgré la région oligotrophe et la rupture abrupte du plateau, il y a une grande diversité d'espèces (CBD, 2014). Les observations suggèrent la présence de points chauds de biodiversité pour les poissons démersaux (Eduardo et al., 2018 ; Nóbrega et al., 2009). La zone concentre diverses ressources halieutiques dans une région relativement étroite, soutenant des pêches multi-spécifiques importantes. La rupture du plateau sert également de point de convergence pour les événements de frai de diverses espèces de poissons d'importance commerciale (Frédou and Ferreira, 2005; Heyman and Kjerfve, 2008; Paxton et al., 2021).

### *Zone 2 - Chaîne sous-marine volcanique Fernando de Noronha*

L'archipel de Fernando de Noronha fait partie de la chaîne volcanique Fernando de Noronha, qui s'étend le long d'une zone de fracture océanique E-W. Comprenant l'archipel de Fernando de Noronha, l'atoll des Rocas et plusieurs monts sous-marins (Almeida, 2006), il se trouve à 345 km de la côte nord-est du Brésil (Fig. 4). Il est protégé par deux aires marines protégées (AMP). Une AMP est désignée pour l'utilisation durable des espèces marines et côtières, tandis que l'autre sert de réserve intégrale (ICMBio, 2024). Depuis 2001, les îles atlantiques brésiliennes de Fernando de Noronha et l'atoll des Rocas sont inscrites au Patrimoine Mondial Naturel (UNESCO, 2024).

La chaîne Fernando de Noronha est réputée pour sa haute productivité biologique et ses habitats critiques, qui servent de nurseries, de sites d'alimentation, de reproduction et de refuge pour diverses espèces résidentes et hautement migratrices. Désignés comme parc marin national et réserve biologique, Fernando de Noronha et l'atoll des Rocas incarnent des points chauds de biodiversité et une richesse endémique de la région. La protection étendue de l'archipel, tant sur terre qu'en mer, en fait un cadre idéal pour la recherche marine. Cependant, son éloignement de la côte présente des défis logistiques, la population locale dépendant fortement de la pêche artisanale pour sa subsistance et ses revenus (Dominguez et al., 2014). De plus, le tourisme constitue une activité économique importante, exerçant une pression démographique et des externalités associées tout en stimulant la demande de poisson et en augmentant les activités liées à la mer telles que la pêche récréative et la plongée (Lopes et al., 2017). En conséquence, ces activités intensifient la pression sur les stocks de poissons et posent des menaces à la biodiversité marine.

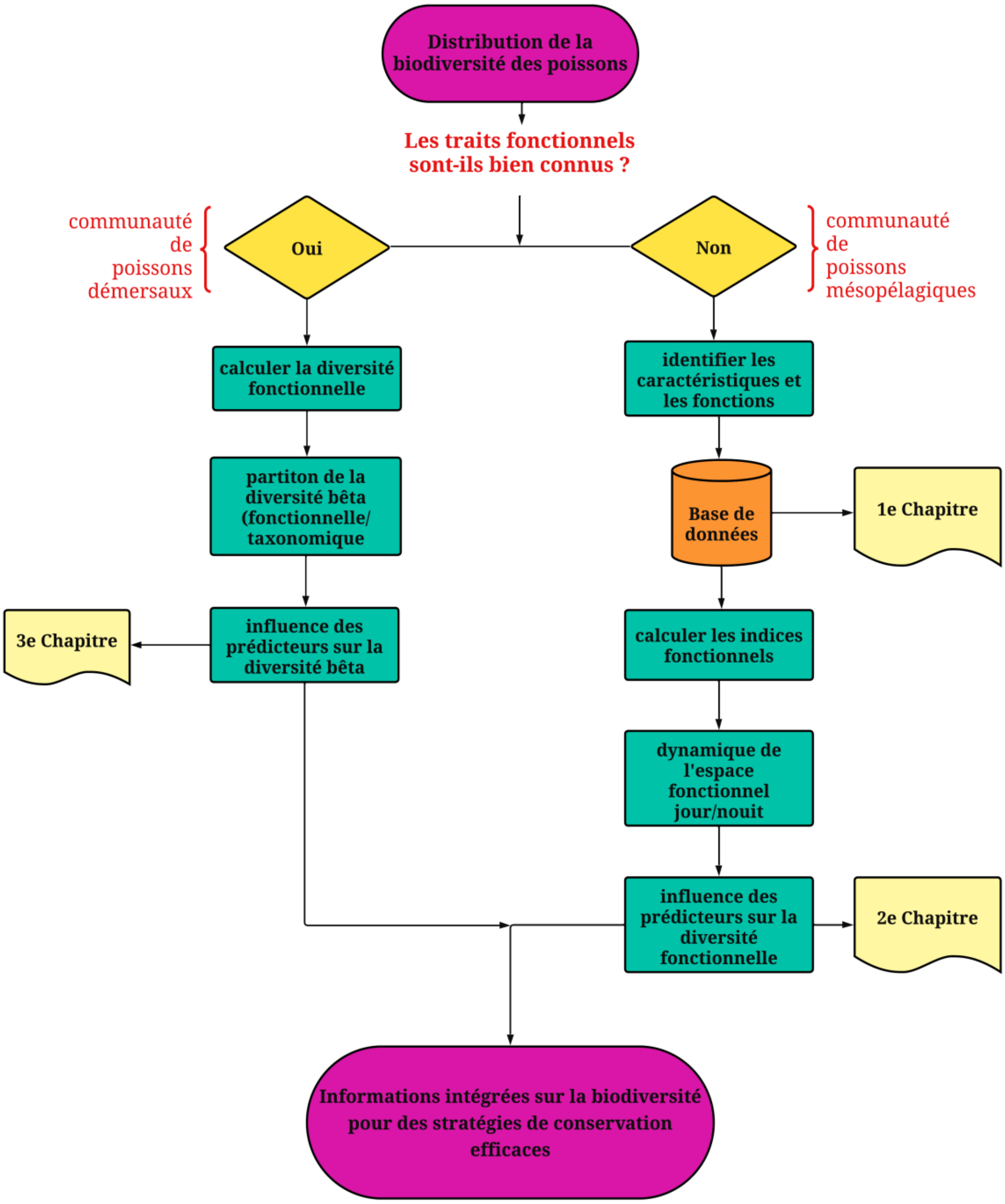


**Figure 1.** Organigramme présentant une vue d'ensemble du travail de thèse et de ses produits.

## Diversité fonctionnelle des poissons mésopélagiques

Nous avons exploré la diversité fonctionnelle des poissons mésopélagiques (vivant à des profondeurs de 200 à 1000 mètres) dans l'Atlantique tropical occidental dans la région de Pernambuco. Ces zones se caractérisent par de faibles niveaux de lumière, des eaux froides et souvent limitées en oxygène, formant un habitat stable mais néanmoins contraignant (Fock et al., 2004; Bertrand et al., 2010; Proud et al., 2017; Boswell et al., 2020). Pour surmonter ces contraintes, les poissons mésopélagiques ont développé diverses adaptations leur permettent de participer à des processus écologiques cruciaux, tels que le cycle des nutriments, le transport du carbone et la fourniture de stocks de poissons exploitables (Gjøsæter and Kawaguchi, 1980; Sutton, 2013; Priede, 2017).

Cependant, notre compréhension de la diversité fonctionnelle de ces poissons reste limitée, alors que l'augmentation des menaces humaines et les changements environnementaux possibles dans les écosystèmes profonds sont préoccupants. Dans ce contexte, la diversité fonctionnelle émerge comme un outil pertinent pouvant aider à évaluer les règles d'assemblage de la communauté, y compris la complémentarité et la redondance fonctionnelle des espèces.

Dans les deux premiers chapitres, nous avons focalisé sur l'analyse de la diversité fonctionnelle des poissons mésopélagiques. Les informations sur ce groupe sont limitées en raison des difficultés de collecte, de stockage et des coûts élevés des expéditions dans l'environnement mésopélagique. Pour pallier cela, nous avons initialement élaboré une base de données contenant des caractéristiques fonctionnelles liées à la locomotion, à l'alimentation et à la survie des poissons mésopélagiques. Pour certaines caractéristiques telles que la nageoire caudale et la forme du corps, des normes ont été établies, et de nouvelles classifications ont également été proposées, comme pour les dents et la couleur de la peau. La catégorisation des traits est fondamentale pour identifier la structure de l'espace fonctionnel et la façon dont cette structure se modifie en fonction de différents prédicteurs spatiaux et environnementaux. Cette base de données sera mise à disposition dans un référentiel ouvert afin de favoriser l'accès libre aux informations pour l'ensemble de la communauté scientifique, dans l'intention de rendre cette base de données collaborative, stimulant ainsi de nouvelles études sur la diversité fonctionnelle des poissons mésopélagiques.

Le deuxième chapitre a abouti à la publication de l'article Aparecido et al. (2023). Nous avons identifié 200 espèces de poissons à partir de plus de 7 000 spécimens pour déterminer la diversité fonctionnelle des assemblages de poissons mésopélagiques à différentes profondeurs et périodes du jour et de la nuit. Nous avons élaboré un ensemble de données comprenant 17 caractéristiques fonctionnelles qualitatives liées aux fonctions d'alimentation, de survie et de locomotion. Sur la base de ces informations, des espaces fonctionnels et des indices de diversité ont été calculés, et des groupes fonctionnels ont été établis.

Nos résultats ont montré que les poissons mésopélagiques présentent une diversité fonctionnelle élevée et peuvent être regroupés en 10 groupes fonctionnels principaux. De plus, 107 espèces ont présenté une composition unique de valeurs de traits fonctionnels, révélant une vaste complémentarité des fonctions au sein des communautés de poissonsmésopélagiques. La diversité fonctionnelle dans les écosystèmes mésopélagiques n'est ni statique au cours d’une journée ni homogène dans l’espace, avec des valeurs plus élevées dans les couches les plus profondes et variant entre le jour et la nuit. En outre, les variations de la diversité fonctionnelle des poissons sont en partie liées à des variables environnementales. Par conséquent, si les processus océanographiques et la période de l'année entraînent une augmentation ou une diminution de l'étendue de l'environnement mésopélagique, les espèces aux traits uniques pourraient être exposées à une interaction anthropique accrue, entraînant des changements potentiels dans la communauté de poissons mésopélagiques.

Bien que le filtrage environnemental puisse aussi contribuer à la structuration des communautés de poissons étudiées, nos résultats ont soutenu une prédominance de l'hypothèse de similarité limitante. Conjointement, la théorie de la compétition (Schoener, 1974; Abrams, 1992) pourrait également être un processus évolutif, où des chaînes trophiques plus courtes, avec moins de ressources alternatives disponibles, peuvent réduire le chevauchement alimentaire interspécifique, conduisant à une plus grande adaptation et spécialisation dans les environnements profonds. Dans ces zones, où la disponibilité de nourriture photosynthétique est moindre, l'adaptation et la spécialisation des espèces pourraient minimiser la compétition et la similarité fonctionnelle. Une telle spécialisation peut donc augmenter la diversité fonctionnelle, comme démontré pour certains poissons de récif corallien (Bender and Luiz, 2019).

### Diversité fonctionnelle des poissons dérmesaux

Dans l’étude de la diversité bêta des poissons démersaux sur le plateau continental du nord-est du Brésil à l'échelle régionale, sont évalués l'impact des principaux prédicteurs environnementaux et spatiaux. Nos résultats ont révélé des tendances congruentes entre la diversité bêta taxonomique et fonctionnelle par rapport à l'environnement, avec une influence minimale des prédicteurs spatiaux. Les processus écologiques prédominants affectant la diversité bêta différaient entre les facettes taxonomiques et fonctionnelles. Le turnover des espèces influençait principalement la facette taxonomique, tandis que nous avons trouvé de manière inattendue un effet de partitionnement similar sur la facette fonctionnelle. Nos résultats soutiennent l'idée que les composantes de la diversité bêta présentent une variabilité spatiale et peuvent être influencées par des prédicteurs distincts.

La partition de la diversité bêta fournit des informations précieuses au-delà des estimations locales et totales de la richesse spécifique. Malgré son potentiel, cet outil puissant est souvent sous-utilisé, en particulier dans les écosystèmes marins. Même dans les communautés bien étudiées, telles que la macrofaune benthique, il existe un manque d'études comparatives pour établir des mesures pour les valeurs élevées et faibles de la diversité bêta. De plus, les valeurs de la diversité bêta dépendent des échelles spatiales utilisées pour définir la diversité locale et régionale, un choix qui peut être quelque peu arbitraire. Par conséquent, tenter de comparer la diversité bêta avec des études antérieures semble peu pratique et peut conduire à des erreurs d'interprétation.

L'analyse complète de la diversité bêta fonctionnelle dans les ensembles de données taxonomiques révèle une hétérogénéité modérée dans la composition spécifique à travers différentes échelles spatiales et temporelles au sein des communautés de poissons. Les assemblages distincts observés entre les stations impliquent un degré significatif de différenciation spéficifique. Les processus de turnover et de nestedness contribuent tous deux à la diversité bêta fonctionnelle basée sur les données de présence-absence, exerçant des influences comparables. Cependant, l'analyse des données d'abondance révèle que malgré une variation significative de la présence d'espèces, comme indiqué par la diversité bêta taxonomique et fonctionnelle, les abondances relatives des espèces montrent moins de fluctuations. Cela pourrait indiquer que sur certains sites, il peut y avoir une dominance de quelques espèces fonctionnelles-clés (Ricotta et al., 2012), tandis que dans d'autres, la diversité fonctionnelle peut être plus équilibrée. Ces résultats suggèrent un degré élevé de différenciation dans la composition spécifique de la communauté démersale et une résilience dans la protection de ses fonctions écosystémiques testées, en d'autres termes, une faible capacité à préserver son intégrité fonctionnelle.

## Considérations finales

Cette thèse a établi une compréhension intégrée de la biodiversité, de l'écologie fonctionnelle et des schémas de distribution des poissons démersaux et mésopélagiques, contribuant ainsi à des perspectives de conservation marine et de gestion durable des ressources océaniques.

Les études sur les communautés écologiques sont particulièrement importantes, surtout dans les pays en développement, où il n'y a pas beaucoup d'incitations à la recherche, à la gestion et à la surveillance de l'utilisation de l'environnement marin. Spécifiquement pour le Brésil, les discussions sur la préservation de l'environnement sont encore initiales tant du côté du gouvernement que de la population en général. Par exemple, le pays n'élabore pas de rapports sur les statistiques de la pêche officielle depuis 2011. Cela rend les démarches de gestion irréalistes sans données brutes officielles. Ainsi, les communautés de poissons démersaux, qui sont la cible de la pêche commerciale, restent hautement vulnérables. En conséquence, cela peut affecter directement la communauté de poissons mésopélagiques, via la chaîne trophique et sa relation avec l'environnement épipélagique.

# 1. GENERAL INTRODUCTION

## 1.1. Biodiversity

The marine environment is subject to various sources of impact, including climate change, overfishing, and pollution. These factors contribute to alterations in species composition and abundance and disruptions in biological cycles, leading to biodiversity loss and decreased fishing productivity (Hughes et al., 2005; Harley et al., 2006; Paiva and Araújo, 2010; Ma et al., 2013). According to Halpern et al. (2008), fishing activities exert both direct and indirect effects that rival those from climate change, increasingly affecting the functionality of marine communities and ecosystems (Essington et al., 2006; Worm et al., 2006; Tittensor et al., 2007), and potentially impacting biogeochemical cycles (Darimont et al., 2009; Katz et al., 2009; Fraser, 2013).

Understanding and sustainably managing marine ecosystems need accurate assessments of their functionality and vulnerability (Levin and Lubchenco, 2008). Ecosystem vulnerability to environmental disturbances hinges on adaptability, defined as the capacity to maintain functionality under changing conditions (Houghton, 1990; Walker et al., 1999). Ecosystem adaptability is bolstered by biodiversity, as ecosystem functionality and resilience increase with species richness through functional redundancy (Loreau et al., 2001; Levin and Lubchenco, 2008). Thus, biodiversity studies are pivotal for understanding and preserving natural resources. They enable organisms to adapt to environmental shifts, and provide ecosystem goods and services essential for human well-being (Díaz et al., 2006). Biodiversity loss significantly threatens ecosystem structures and functions (Cardinale et al., 2012). Monitoring the impacts of direct human activity and global environmental changes involves assessing various biodiversity facets, including species number, evenness, taxonomic and/or functional diversity.

Recent proposals for measuring community diversity have aimed to incorporate these biological differences between species into complementary diversity indices (Schleuter et al., 2010; Stuart-Smith et al., 2013). Functional diversity can complement the assessment of changes in community and ecosystem functioning in response to external disturbances, proving even more sensitive to human pressure than species richness (D’agata et al., 2014). This information is thus vital for determining management and/or protection areas (Mouillot et al., 2011).

## 1.2. Functional diversity

Species' functional roles are gauged by their traits, defined as morpho-physio, or phenological characteristics (Violle et al., 2007). These traits indirectly influence fitness through their effects on growth, reproduction, and survival - the triad of individual performance (McGill et al., 2006; Violle et al., 2007). This approach can allow establishing a connection with the varied roles species fulfil within communities, as well as between biodiversity, ecosystem functioning and services (McGill et al., 2006). Functional diversity allows the assessment of species complementary/redundancy within and between communities (Lawton, 1999; Simberloff, 2004) and illuminates assembly processes from the decomposition of total diversity (gamma) into intra-diversity (alpha) and inter-diversity (beta) (Whittaker, 1972; Jost, 2007; Baselga, 2010). Research indicates that functional diversity, rather than species richness, amplifies ecosystem functions such as productivity (Tilman et al., 1997; Hooper and Dukes, 2004; Gagic et al., 2015), enhances resilience to disturbances and invasions (Dukes, 2001; Bellwood et al., 2004) and modulates material fluxes (Waldbusser et al., 2004). Furthermore, functional diversity measures redundancy in functions within ecosystems, suggesting in some cases that high species richness does not necessarily ensure the preservation of functions. This is due to the uncertainty of functional redundancy across multiple species and the risk that certain functions may rely on a, or few, singular species (key species), rendering functional diversity critically susceptible to species loss (Guillemot et al., 2011; Bender et al., 2013).

Despite the evident importance of the traits-based approach, its applications encounter obstacles and gaps that impede a comprehensive understanding of ecological systems. A significant challenge lies in standardizing trait measurement and quantification methods. Inconsistencies across studies in trait measurement hinder comparability and limit the robustness of trait-based analyses. In this study, we adopted the approach proposed by Villéger et al., 2010 (Fig. 1), which assesses traits based on fish characteristics, emphasizing feeding and locomotion functions to demersal and mesopelagic communities and, survival function for mesopelagic community. However, accurately measuring certain traits, particularly those related to behaviour or physiological processes, can be challenging. Additionally, trade-offs between traits and redundancy of functional traits within communities, such as in mesopelagic fish communities, pose further challenges. Understanding these trade-offs and their implications for ecosystem functioning necessitates comprehensive trait datasets and modelling approaches, which are often lacking. Spatial and temporal scales also present challenges to the traits-based approach. Traits can vary spatially due to dispersal limitations and habitat heterogeneity, while temporal dynamics, such as seasonal fluctuations, can influence trait expression and community composition. Integrating trait-based findings with broader community and ecosystem ecology frameworks remains a challenge, requiring interdisciplinary collaboration and the development of theoretical frameworks bridging multiple ecological scales.

Addressing these challenges and gaps in the traits-based approach will necessitate concerted efforts from the scientific community. Methodological advancements, interdisciplinary collaboration, long-term monitoring efforts, and the development of trait databases are crucial steps toward overcoming these obstacles and advancing our understanding of ecological systems through traits-based ecology.

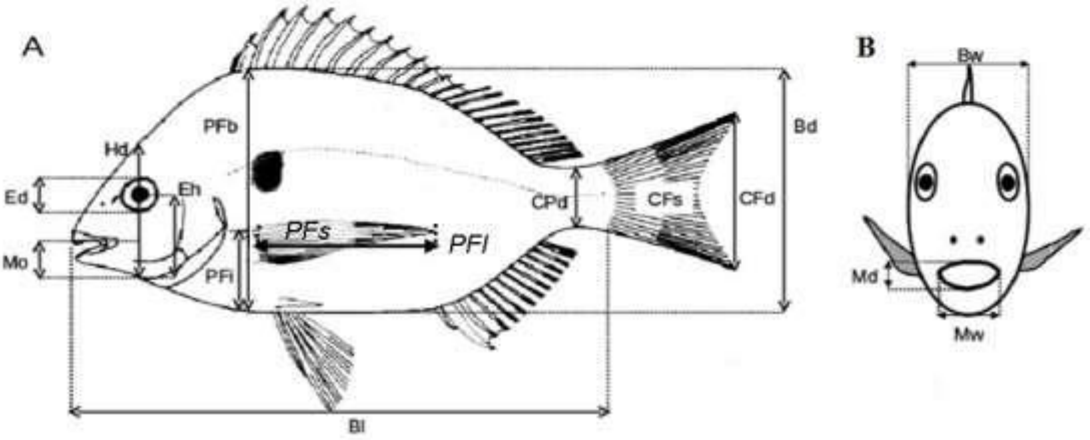


**Figure 1** – Morphological measures proposed by Villéger et al. (2010). *Figure adapted

## 1.3. Marine fish communities' threats

Marine fish communities confront a spectrum of threats attributable to environmental changes and anthropogenic endeavours. Demersal fish, situated on or adjacent to the seabed, alongside mesopelagic fish, dwelling in the ocean's twilight zone, are integral to their ecosystems. These communities underpin the marine food web, enriching biodiversity and oceanic functionality.

Nevertheless, demersal fishes are directly imperilled by overexploitation, climatic shifts, pollution, habitat loss, anthropogenic disturbances, and diminished functional diversity. Specifically, overfishing and destructive practices like bottom trawling devastate seabed habitats, impacting biodiversity and altering ecosystem dynamics (Bianchi et al., 2000). Climate change further compounds these impacts through modifications in sea temperatures, ocean acidification, and currents, which in turn affect migratory patterns and food accessibility for these species (Punzón et al., 2016; Whitehouse et al., 2017; Queirós et al., 2018; Petrik et al., 2020). Pollution from heavy metals, plastics, and other contaminants adversely impacts demersal fish's health and reproductive efficacy (Rummel et al., 2016; Galvao et al., 2021). Additionally, shipping and construction disrupt their natural behaviours and migration patterns (Peng et al., 2015; Siebeck et al., 2015). These threats highlight the critical need for sustainable management and conservation initiatives to safeguard demersal fish communities and bolster their resilience.

Likewise, mesopelagic fishes encounter challenges from ocean warming, deepwater spills, habitat loss, climate change, and the lack of overarching global protection policies (Eduardo et al., 2020; Lin et al., 2023). Elevated ocean temperatures may shift their distribution and ecological functions (Eduardo et al., 2020c; Lin et al., 2023). While deepwater oil spills introduce deleterious polycyclic aromatic hydrocarbons into their habitat (Pulster et al., 2020; Morzaria-Luna et al., 2022). Habitat destruction, driven by human activities such as deep-sea mining and trawling, imperils their existence by compromising crucial feeding, migration, and spawning zones (St. John et al., 2016; Eduardo et al., 2020c). The absence of dedicated global policies for mesopelagic zones renders these communities susceptible to exploitation and degradation (Schadeberg et al., 2023).

Demersal fish communities serve as a prime example of how overexploitation can lead to disturbing and overexploitation exhausting resources. Understanding the different facets of diversity in both demersal and mesopelagic communities enable us to forecast and suggest effective mitigating. This is particularly relevant for highly impacted communities and those where economic interests are just starting to surface.

Along the northeastern coast of Brazil, demersal and mesopelagic species may face additional localized threats. For instance, overfishing, habitat degradation, climate change, oil spills, invasive species, and a lack of comprehensive data are significant challenges (Viana et al., 2022; Alves et al., 2023; Rosa et al., 2023). In addition, the growing interest in building several wind farms offshore and the offshore oil and gas (O&G) industry (Carrascal et al., 2021) are capable of generating impacts that are not yet quantifiable. The region's complex oceanography, including the continental shelf-slope gradient, plays a vital role in the distribution of ichthyoplankton, highlighting the need for targeted conservation efforts (Santana et al., 2020). The presence of reef-building coral species and diverse fish assemblages in mesophotic ecosystems suggests potential refugia for threatened fish communities (de Oliveira Soares et al., 2018). However, overexploitation and environmental degradation pose continuous risks to these ecosystems, emphasizing the urgent need for conservation measures and sustainable practices (Amaral and Jablonski, 2005; Santana et al., 2020; Eduardo et al., 2022).

Despite the widespread use of beta diversity partitioning in ecological studies, it has been relatively neglected in the context of marine demersal fish communities in Northeastern Brazil. However, recent interest has emerged within the scientific community (Anderson et al., 2013; Cuesta Núñez et al., 2023; Pennino et al., 2024; Rbiai et al., 2024). To our knowledge, no studies have applied this approach to marine demersal fish communities in this region. In contrast, the mesopelagic fish in this area are constantly being studied, with new species described and new records made (Eduardo et al., 2018b, 2019; Mincarone et al., 2022; Villarins et al., 2023b, 2023a, 2024).

## 1.4. Beta diversity

Beta diversity is a key facet of biodiversity, distinct but linked to other aspects like alpha and gamma diversity. Beta diversity refers to the variation in species composition between assemblages and/or along environmental gradients (Baselga, 2010, 2013) or assemblage comparisons (temporal and/or spatial). It's not limited to species-level diversity but can also include functional, phylogenetic, and/or taxonomic diversity, providing a multi-dimensional view of biodiversity (Perez Rocha et al., 2018). Each offers complementary insights into community assembly and is influenced by both spatial and environmental factors (Li et al., 2021)

The importance of beta diversity lies in its ability to capture the influence of environmental and/or anthropogenic variables at multiple spatial scales in shaping biodiversity patterns. This includes how geography, climate, and habitat parameters drive taxonomic, functional, and phylogenetic diversities at different scales (Mugnai et al., 2022). Besides, based on species presence-absence data, beta-diversity can be split into turnover, which represents the replacement of species, and nestedness, referring to the gain or loss of species (Fig 2). These components provide comprehensive ecological information. Since it shows significant temporal variability and is essential for understanding how species or functional traits change over time, particularly in the context of global warming and potential shifts in species distribution depth ranges (Nunes et al., 2020). The variability of species composition across different sampling units within a region, shaped by environmental variability and dispersal mechanisms, constitutes a key facet of beta diversity. This concept is fundamental in deciphering the structure of communities across various scales in ecosystems, such as water systems (Heino et al., 2015). Additionally, it serves as a vital connector between local and regional ecological scales. A decline in beta diversity leads to an increased similarity among local sites, a phenomenon referred to as biotic homogenization. Understanding this dynamic is crucial for assessing the impacts of environmental changes and/or anthropogenic stressors on biodiversity (Le Tortorec et al., 2023).

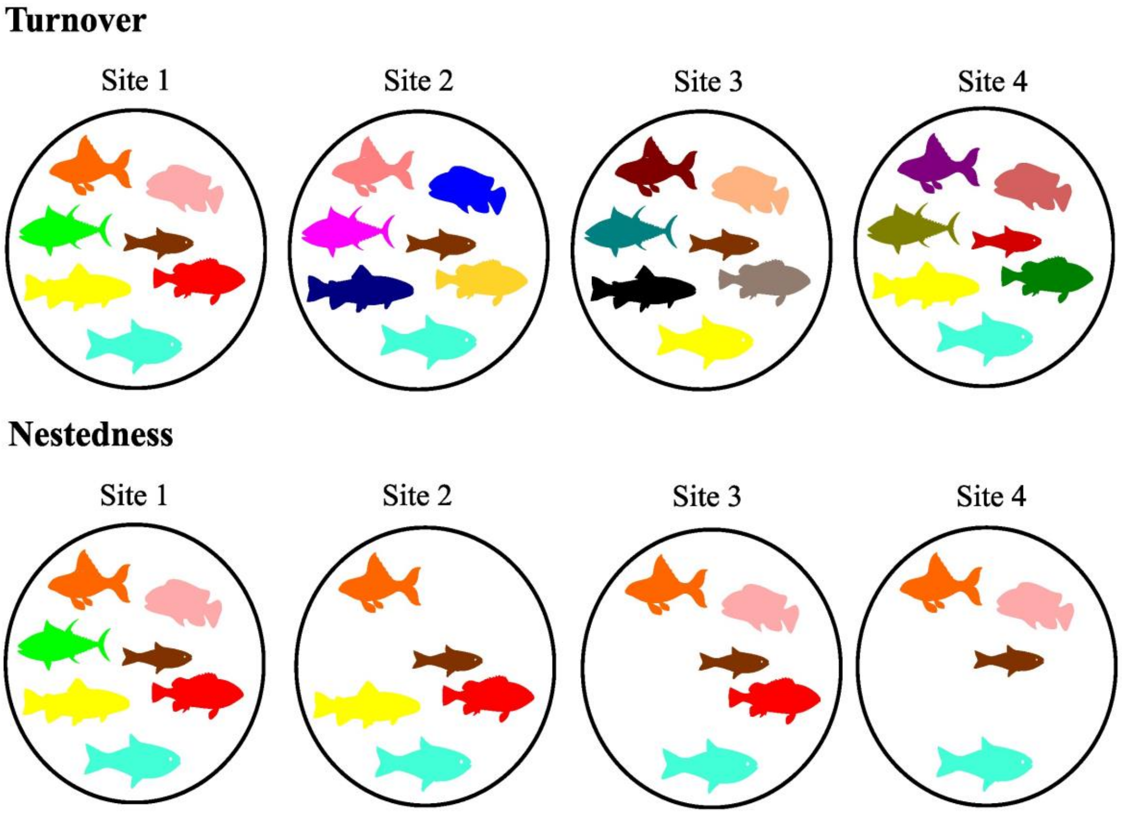


**Figure 2** – Schematic representation of the beta diversity partitioning. Each color denotes a distinct species. In examining species turnover, we observe an alteration in species composition characterized by the emergence of species absent from preceding sites. Regarding nestedness, the species compositions at various sites are subsets of those

encountered at previous sites. It is crucial to acknowledge that turnover and nestedness can manifest at varying degrees, quantitatively assessed on a scale ranging from 0 to 1.

## 1.5. Study area

### *Southwestern Tropical Atlantic (SWTA)*

The Southwestern Tropical Atlantic (SWTA) is a marine region renowned for its distinct biodiversity (CBD, 2014) and is classified as an oligotrophic area. It encompasses break shelves, oceanic islands, seamounts, and underwater canyons, which interact with local currents to enhance marine productivity (Travassos et al., 1999; Tchamabi et al., 2017). Moreover, the SWTA serves as near-surface northward pathway for the Atlantic Meridional Overturning Circulation, impacting the three-dimensional transport of heat, salt, and regional distributions of water mass boundaries, leading to shifts in biodiversity and ecosystems (Assunção et al., 2020; Dossa et al., 2021). Both study areas are classified as EBSAs (Ecological or Biological Significant Marine Areas), special areas in the ocean of fundamental importance for biodiversity and life cycles of marine species (CBD, 2014).

SWTA coast is influenced by low latitude marine, specifically between latitudes 10°S and 5°S; a significant oceanographic feature is the North Brazilian Under Current (NBUC). This current is distinctive for transporting a South Atlantic water mass rich in oxygen and elevated salinity levels (Arhan et al., 1998; Schott et al., 1998). Around the latitude of 5°S, the NBUC receives augmentation from the Central South Equatorial Current (cSEC), which merges into the western boundary current system, enhancing the southward movement of water. Consequently, the NBUC transitions into the North Brazil Current (NBC), influencing this region's ocean's surface layer. Western boundary currents (WBCs) play a crucial role in the global climate by transporting heat from the equatorial areas towards the poles (Todd et al., 2019). While WBCs typically exhibit lower biological productivity, geostrophic and eddy-driven upwelling can enhance nutrient availability, thereby boosting primary productivity along coastal regions (Pelegrí and Csanady, 1991). In areas with narrow continental shelves adjacent to intense WBCs, such as the northeastern coast of Brazil, these shelves experience a direct influence from deep-ocean currents, resulting in substantial material exchanges at the edge of the continental shelf (Todd et al., 2019).

The topography along continental margins plays a pivotal role in flux variation near the coastline, particularly due to advective processes generated by western boundary currents. Submarine canyons, typically perpendicular to the continental shelf break, enhance advective transport via currents flowing parallel to the coastline (She and Klinck, 2000; Iacono et al., 2014). The topographical configuration of submarine canyons facilitates the advection-induced pumping of colder, saltier waters, with each process being contingent upon the canyon’s morphology and dimensions (Lopez, 2001; Rennie et al., 2009; Jordá et al., 2013; Tubau et al., 2015).

In this region, the continental shelf and slope exhibit seabed topography, highlighted by channels and submarine canyons (Vital et al., 2010; Gomes et al., 2014; Bastos et al., 2015). Besides, in the south of the study area is the Pernambuco Plateau (Fig 3), which accounts for significant oceanographic and morphological variations in the northeastern coastline (Camargo et al., 2015; Buarque et al., 2016), especially near the shelf break, which connects shallower to deeper regions via canyons submarine located on the Pernambuco Plateau. Silva et al. (2021) observed an anti-cyclonic eddy with the tendency of vorticity control over that might favouring downwelling, into this process the surface water moves vertically downwards into deeper layers of the ocean.

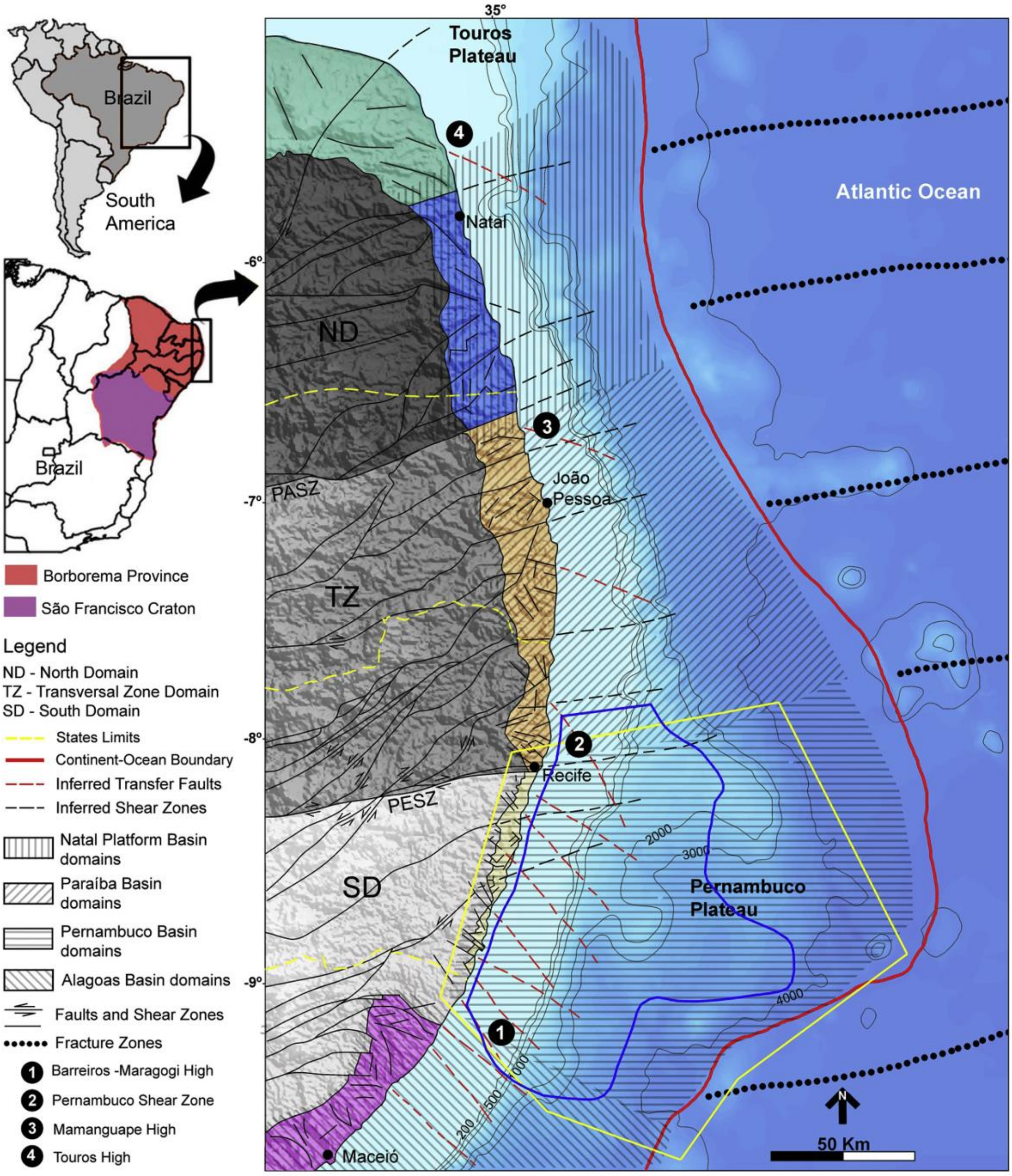


**Figure 3.** Map showing the Pernambuco Plateau and their limits from Buarque et al., 2016.

*Continental Shelf*

The continental shelf is located in the eastern part of the South American Platform region to Rio Grande do Norte (5-9oS) of the continental shelf. The platform measures 40 km wide and is almost entirely covered by biogenic carbonate sediments, with depths ranging from 40 to 80 metres (Vital et al., 2010). On the northeast coast, warm water predominates, and a permanent thermocline exists. This condition hinders the vertical circulation of water masses, thereby limiting the nutrient supply from deeper layers. Despite the oligotrophic region and the abrupt rupture of the shelf, there is a high diversity of species (Ekau and Knoppers, 1999; CBD, 2014). Observations suggest the presence of biodiversity hotspots for demersal fish (Lessa et al., 2009; Eduardo et al., 2018a). The area concentrates diverse fishing resources within a relatively narrow region, supporting important multi-specific fisheries. The shelf-break also serves as a convergence point for spawning events of various commercially important fish species (Frédou and Ferreira, 2005; Heyman and Kjerfve, 2008; Paxton et al., 2021).

### *Fernando de Noronha Ridge*

The Fernando de Noronha archipelago forms part of the eponymous volcanic ridge, the Fernando de Noronha Ridge, which extends along an E-W oceanic fracture zone. Comprising the Fernando de Noronha archipelago, Rocas Atoll, and several seamounts (Almeida, 2006), this oceanic archipelago lies 345 km from the Northeastern Brazilian coast (Fig. 4). It is safeguarded by two Marine Protected Areas (MPAs). One MPA is designated for sustainable marine and coastal species use, while the other serves as a no-take reserve (ICMBio, 2024). Since 2001, the Brazilian Atlantic islands of Fernando de Noronha and Rocas Atoll have been named World Natural Heritage Sites (UNESCO, 2024).

The Fernando de Noronha Chain is renowned for its high biological productivity and critical habitats, which serve as nurseries, feeding, breeding, and sheltering sites for various resident and highly migratory species. Designated as a national marine park and biological reserve, Fernando de Noronha and Rocas Atoll epitomize biodiversity hotspots and endemic richness in the region.

The archipelago's extensive protection, both on land and at sea, renders it an ideal setting for marine research. However, its remote location from the coast presents logistical challenges, with the local population heavily reliant on artisanal fisheries for sustenance and income (Domingues et al., 2017). Furthermore, tourism constitutes a significant economic activity, exerting demographic pressure and associated externalities while fuelling demand for fish and enhancing marine-related pursuits such as recreational fishing and diving (Lopes et al., 2017). Consequently, these activities intensify pressure on fish stocks and pose threats to marine biodiversity.

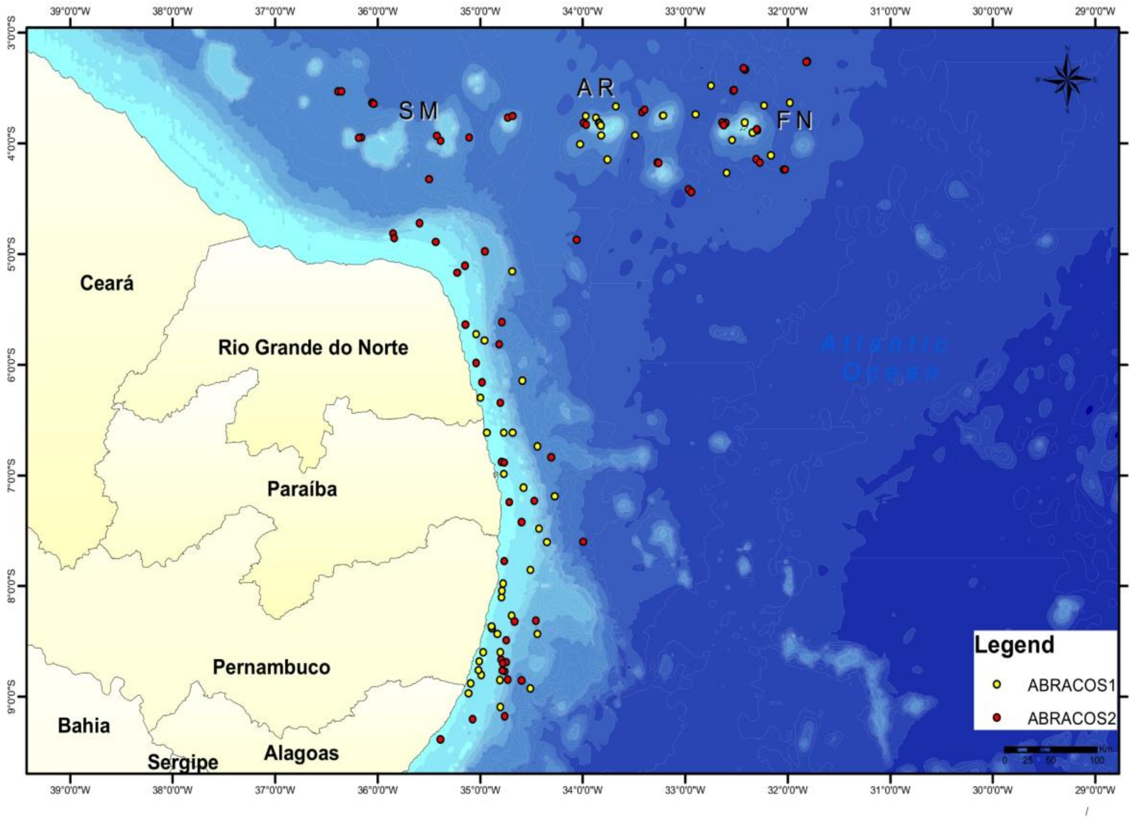


**Figure 4.** Sampled sites investigated in this study along the North-Eastern coast of Brazil and the oceanic islands.

## 1.6. Objectives and motivations

The thesis endeavours to enhance our understanding of the biodiversity (taxonomic and functional) and ecology of mesopelagic and demersal fishes, vital components of marine ecosystems that have been relatively understudied in Brazilian marine ecosystems due to the inherent challenges of sampling in their habitats. Through an integrated approach combining taxonomic, functional ecology, and biogeography, the specific aims of this research are articulated as follows:

**1º Chapter – Functional traits of mesopelagic fishes and a novel proposal for the classification of certain functional traits:** the first chapter focuses on identifying and measuring the functional traits of mesopelagic fish. It introduces a new classification system for these traits (article 1, Aparecido et al., *in preparation*) designed for use in future ecological and evolutionary research. The novel classification scheme aims to enhance the analysis of offer a refined tool for analyzing mesopelagic fish communities examining their resilience and connections to ecosystem functions in response to anthropogenic pressures and global changes.

**2º Chapter - Study of mesopelagic fish diversity and characterization of their traits:** the second chapter focuses on elucidating the functional diversity of mesopelagic fishes within the western tropical Atlantic. This section aims to fill significant gaps in our knowledge regarding the biodiversity of organisms inhabiting mesopelagic depths (Article 2, Aparecido et al. 2023). By investigating the functional traits and ecological roles of mesopelagic fishes, this chapter explores the intricate relationships between environmental factors, species traits, and community dynamics. It will also examine the role of environmental filtering in shaping community assembly and trait-based patterns in mesopelagic marine ecosystems.

**3º Chapter - Distribution of beta taxonomic and functional diversity of demersal fishes: t**he third chapter focuses on analyzing beta diversity, both taxonomic and functional, of demersal fishes. The goal is to uncover the distribution patterns of these fishes across different environmental gradients and identify the ecological factors driving these patterns (Article 3, Aparecido et al. *in preparation*). This study aims to reveal the underlying mechanisms of marine biodiversity across broad spatial scales, providing valuable insights for marine conservation and the management of essential habitats.

Overall, this thesis aims to develop a comprehensive understanding of the biodiversity, functional ecology, and distribution patterns of demersal and mesopelagic fishes in the North-Western Atlantic of Brazil, thereby contributing to marine conservation and sustainable management of ocean resources.

# 2. CHAPTER 1. Functional traits of mesopelagic fishes: a database with a novel proposal of classification

Functional traits are observable and measurable features of organisms that can reflect their adaptive strategies in response to various factors, like environmental pressures, as well as species' roles in the community. Studying trait patterns thus provides insights into species' responses and adaptation strategies to changing environments. It can predict responses to environmental changes, inform about community assembly rules, and species distribution, as well as make the link with ecosystem functioning. Therefore, functional traits are crucial tools in different fields of ecology, biodiversity, and ecosystem functioning. Nevertheless, this approach faces several significant challenges:

- Standardizing trait measurements and, considering the variability in traits within and between species.
- Data gaps, mainly for non-model species, with an urgent need to expand trait databases to include a broader spectrum of organisms.
- Scaling up these approaches from small to large-scale ecological processes
- Trait identification: one of the core challenges of functional diversity is the identification of traits that can accurately be linked to species roles and ecological processes.
- Data collection and sharing improving the accessibility and interoperability of trait databases and analytical tools are paramount to enhance the usability of functional trait data.

This chapter provides a refined tool that can be helpful in analyzing communities, examining resilience, and exploring ecosystem functions in response to global changes. We present new classification systems for certain mesopelagic traits, thereby providing a resource and standard for future research.

The standardization of mesopelagic fish traits is intended to enable a comprehensive analysis of their communities, thereby, shedding light on their ecological functions and resilience. This is particularly important in the deep-sea zone, where extreme depths, high pressures, and minimal light penetration present significant research challenges. Specialized equipment and innovative sampling techniques are required to study these delicate organisms effectively. By sharing data on this zone, we aim to collaborate more efficiently, reducing data deficiency and enhancing the overall understanding of the mesopelagic zone. The main role of data papers on these traits, particularly in the context of mesopelagic fish, lies in their capacity to enhance our understanding of the ecological and evolutionary dynamics of this group still understudied.

This section will be submitted during the second semester of 2024, probably to the *Scientific Data* journal.

## MESOFISHTRAITS: a functional traits database of mesopelagic fish community

Kátia C. Aparecido, Thierry Frédou, Bastien Mérigot, Michael M. Mincarone, Gerson D. Machado-Filho, Rayssa S. Lima, Arnaud Bertrand, Leandro N. Eduardo (*in prep.*)

### 2.1. Abstract

Meso-pelagic fish communities play pivotal roles in oceanic ecosystems, yet persistent gaps in understanding their functions, as well as hinder effective conservation and management strategies. Here, we provide a comprehensive dataset of traits for mesopelagic fish sampled in the western tropical Atlantic and the Amazon mouth, utilizing data from scientific expeditions. Through direct observation and literature review, we documented 16 traits related to feeding, locomotion, and survival. Our dataset illuminates patterns in the functional traits of mesopelagic fish and can contribute valuable insights into their roles within ecosystems. Nonetheless, challenges persist, including limited sampling accessibility, taxonomic ambiguity, and the need for standardized trait definitions. Addressing these gaps is paramount for predicting mesopelagic responses to environmental changes and implementing effective conservation measures. Our study underscores the importance of collaborative efforts and data sharing in advancing mesopelagic research and safeguarding these vital yet vulnerable ecosystems.

**Keywords:** Functional traits, functional diversity, morphometric, behaviour, dataset.

## 2.2. Background & Summary

Mesopelagic fish inhabit the first deep-sea layer of the ocean, also known as mesopelagic, midwater, or twilight zone (200-1000 m depth). This zone lies between the photic epipelagic and the aphotic bathypelagic zones and, is defined by light availability, beginning at the depth where only 1% of incident light penetrates and extending to the point where no light is present (del Giorgio and Duarte, 2002). While distributed at mesopelagic depths during the daytime (200 to 1000 m), some of these fish ascend to feed in the upper layers at night, with some even reaching the surface (Klevjer et al., 2016). This migration creates a highly dynamic environment with daily community cycles (Sutton, 2013; Proud et al., 2017; Aparecido et al., 2023).

Mesopelagic fish are integral to ecosystem functioning, being a key component of various ecological services. They contribute to the biological pump, which facilitates carbon transfer from the surface to the deep ocean (Cavan et al., 2019; Aksnes et al., 2023). Adapted to low-light environments, mesopelagic fish act as a direct link between plankton and higher-level predators, many of which are commercially fished (Iglesias et al., 2023). To successfully colonize this environment marked by environmental constraints, mesopelagic communities have evolved in diverse ways. Some exhibit ultra-black coloration, while others are transparent; some have large eyes and bioluminescent appendages, while others possess atrophied eyes (Warrant and Locket, 2004; Widder, 2010; Davis et al., 2020b; Aparecido et al., 2023). This morphological variety is a complicating factor in ecological studies that aim to identify community patterns, making studies of single species/family of greater interest to the scientific community.

Gaps in understanding the integration of mesopelagic communities hinder efforts to determine conservation actions and mitigation strategies. Impacts such as habitat destruction, mining, environmental destabilization, overfishing, and pollution, among others, may alter their distribution and ecological roles (Eduardo et al., 2020a; Lin et al., 2023). Without sufficient knowledge to develop specific global policies for mesopelagic zones, these communities remain vulnerable (Schadeberg et al., 2023). Understanding interspecies interactions, their functions, and how these communities are distributed is crucial for predicting and protecting them from expected ecological changes.

Under these urgent circumstances, trait-based approaches emerge as valuable tools, focusing on the mechanistic drivers of ecological interactions to predict variations in species distributions, community structures, and population dynamics in the face of global change (Laigle et al., 2018; Green et al., 2022). Furthermore, the identification of recurring traits across unrelated prey taxa can enhance our ability to anticipate predator-prey interactions within changing ecosystems (McGill et al., 2006). When combined, these traits can be used to describe the functional roles of species within an ecosystem (Hardy et al., 2024). Ultimately trait approaches seek to help scientists better predict interactions within ecological communities, especially in the scope of global change.

Exploration of the deep-sea zone presents a series of challenges. The extreme depth of this zone requires specialized equipment capable of withstanding the high-pressure conditions prevalent at these depths. Limited visibility due to minimal light penetration complicates visual observations and sampling efforts. Delicate organisms in the mesopelagic zone are particularly vulnerable to damage during collection and transportation to the surface, requiring careful handling techniques. Traditional sampling methods may not be sufficient to capture the diverse array of organisms found in this zone, necessitating the development of innovative sampling techniques. Additionally, the high cost associated with conducting research and sampling including the need for specialized vessels (Webb et al., 2010; Della Penna and Gaube, 2020; Govindarajan et al., 2021; Howell et al., 2021; Eduardo et al., 2022), further adds to the complexity of studying this enigmatic ecosystem. Therefore, sharing the data on this ecosystem helps to join endeavours and reduce uncertainty ranges to quantify and qualify the mesopelagic zone.

This study provides valuable insights into the functional traits present in the most species, or those we can reasonably deduce from our observations and photographic records. It's important to acknowledge that certain significant functional traits may remain elusive, as they are only documented for a limited set of species, such as reproductive aspects. However, we believe it is an important way to analyse the complexity of this ecological structure globally and discuss community relations and not just isolate certain groups. Although we know how delicate it is to make generalizations about this community. The following sections present the chosen traits, their respective categories, and the rationale behind their selection.

## 2.3. Methods

**Species list.** The Mesopelagic fish community functional traits database includes species sampled in the western tropical Atlantic during the ABRACOS scientific expeditions carried out between September-October/2015 and April/May/2017 (Bertrand, 2015, 2017) and, the mouth of the Amazon during AMAZOMIX scientific expeditions carried out August/2021 and September/2021. Mesopelagic fishes were sampled day and night at trawl stations using mesopelagic and micronekton nets. The targeted depth for each layer was defined according to the presence of scattered acoustic layers or patches of organisms. However, to improve the representativeness of biodiversity, we also conducted trawling in areas where no organism aggregations were observed and even beyond the range of the echosounder.

The samples were sorted to the lowest taxonomic level possible using published guides and personal/institutional reference collections (for further information on sampling procedures, see Eduardo et al., 2022). All specimens collected were deposited at the fish collection of the Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro (NPM; Macaé, Brazil).

### *2.3.1. Trait data collection*

For each species, we collected information on 16 traits related to feeding, locomotion and survival (Table. 1). We used the direct observation information under our samples, and when was not possible we used primary literature through bibliographic databases (Google Scholar [www.scholar.google.com], Web of Science [www.webofscience.com]) for species-level information and images. The research was based on adult traits and when the species presented sexual dimorphism, we used the female as a representative of the species.

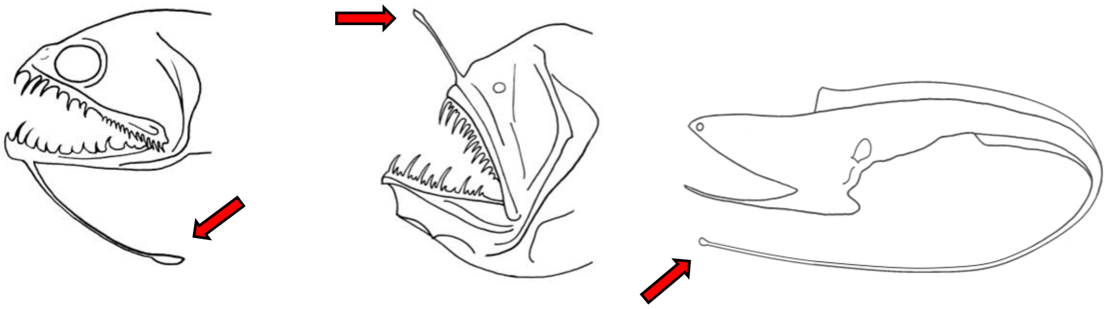
**Table 1.** Overview of key traits included in the Mesopelagic Species Trait Database. Binary values are present or absent, categorical values are listed in the description.

| Trait | Trait description | Categories/units |
|---|---|---|
| Lure apparatus | Structure used to glow and attract | Binary |
| Prey illumination | Structure used to illuminate or induce fluorescence in prey | Binary |
| Trophic guild | Group of species of explore the same class of resources similar | Zooplanctivores, micronektivores, generalists and, piscivores |

| | | |
|---|---|---|
| Eyes structure | Eye shape | Tubular/spherical |
| Eye position | Eye position relative to the head | Top/mid |
| Eye size | Ratio of size to head depth | Small, moderate and large |
| Vertical migration | Movement down-up in the water column | Binary |
| Caudal fin shape | Lateral shape of caudal fin | Forked, round, truncated, lunate, pointed, heterocercal, emarginate and, fan |
| Teeth type | Basic pattern of marginal teeth | 0- absent; 1- long, slender, sharp; 2- numerous small, needlelike, villiform; 3- falt-bladed; pointed, triangular; 4- recurved, conical, caniniform; 5- cardiform |
| Bioluminescence | Organ produces light | Binary |
| Oral position | Orientation of the mouth | Elongaed, inferior, superior, tubular and, ventral |
| Body shape | Lateral body shape and cross-section | Anguiliform, compreesiform, elongated, filiform, globiform, sagittiform and, taeniform |
| Body size | Maximum total length recorded | Numerical in cm |
| Skin color | Predominant skin color | Dark-bicolor; light-bicolor; black; silver; red and other color |
| Counterillumination | Camouflage that involves the use of ventral photophores to match the dim light coming from the surface | Binary |

## Lure appendages

The lures are specialized structures that produce light mimicking the bioluminescence of their prey’s typical food sources or peers, thereby attracting the prey and facilitating capture (Widder, 2010). In certain species, such as anglerfishes, these bioluminescent abilities are facilitated by symbiotic bacteria housed within the lure itself. These bioluminescent structures can manifest in various forms and may be located on different parts of the body, such as the dorsal-fin spine, the “fishing rod” appendage on the head, barbels near the mouth, or the caudal fin (Pietsch, 2009; Priede, 2017). Examples: *Astronesthes niger*, *Melanocetus johnsonii.*



**Prey illumination**

Structures that emit light or induce fluorescence in prey enhance their visibility for predators. These mechanisms aid in the identification and capture of prey by making them more conspicuous in their naturally dark environments.

**Counterillumination**

Some species have the behavior to modify and mask their body silhouettes through counterillumination (Young et al., 1980; Haddock et al., 2010; Widder, 2010). A form of camouflage that employs ventral (lower) photophores to mimic the faint light emanating from the surface, effectively obliterating any potential shadows. They might fit the intensity light of the photophores as the ambient light intensity noted by the eyes (Young et al., 1980; Priede, 2017).

**Trophic Guilds**

An ecological community of species that share common resource utilization patterns within a particular resource class. This classification was adapted based on Priede (2017) and Drazen and Sutton (2017).

Zooplaktivores: primarily feed on copepod eggs, nauplii and other varieties of zooplankton.

Micronektonivores: primarily feeding on micronekton organisms such as fish, small crustaceans, and squid, that inhabit the mesopelagic and bathypelagic zones.

Generalists: may make use of a variety of different resources such as zooplankton and micronekton organisms.

Piscivores: Feeding fish as the main prey item.

**Vertical migration**

Here we consider vertical migration as the vertical movement of juvenile and adult organisms to the surface or upper layers at night and returning to deeper waters during the day.

**Caudal fin shape**

Rounded

*Xenophthalmichthys danae*, *Zu cristatus*

Emarginate

Examples: *Winteria telescopa*, *Cetostoma regani*

Truncated

Examples:  *Paracaristius nudarcus*, *Antigona capros*

Forket

*Dolicholagus longirostris*, *Taractichthys longipinnis*

Lunated

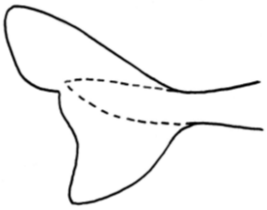
*Brama caribbea*, *Taractichthys longipinnis*

Pointed

*Avocettina infans*, *Serrivomer lanceolatoides*

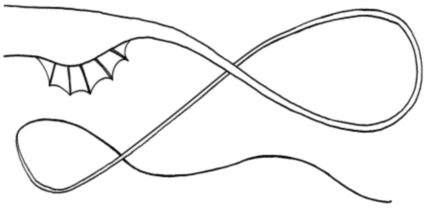
Heterocercal

Example: *Isistius basiliensis*, *Gigantura chuni*



Fan

Example: *Stylephorus 44rometheu*



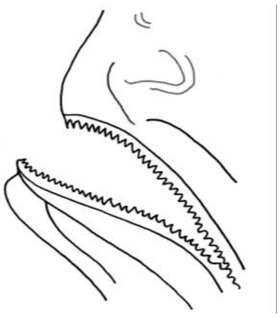
**Teeth type/morphology**

Mesopelagic fishes presented a high diversity of teeth, even in the same when observed species of the same family. This variety might represent different adaptations linked to prey size and types (Martin and Davis, 2020). Although some predators exhibit a mixture of dentition types, we classify them by predominant morphotype which reflects food characteristics. This classification was based on Helfman et al., (2009), except for Type 0.

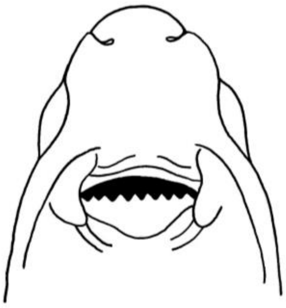
Type 0: absence of the teeth

Type 1: Typically, the long and slender teeth serve the purpose of grasping fish. In certain species, this extended dental structure is replicated on the palatine or vomerine bones. These central teeth are oriented rearward and could be hinged at their base with ligamentous attachments. This arrangement enables them to retract as the prey is transported towards the throat while inhibiting any escape through the anterior jaws. Examples: *Chauliodus sloani*, *Astronesthes gemmifer* and *Thysanactis dentex*.

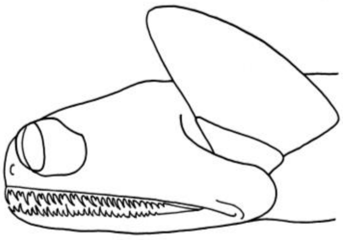
Type 2: Numerous small, needlelike, villiform teeth. Examplos: *Diretmus argenteus, Taaningichthys bathyphilus* and *Stemonidium hypomelas.*



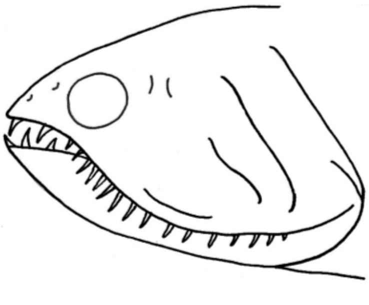
Type 3: Flat-bladed, pointed, triangular dentition is usually used for cutting off prey. Examples: *Anotopterus 45rometh* and *Isistius brasiliensis*.



Type 4: Recurved, conical, caniniform teeth with sharp points. Sharp, conical dentition serves to grasp and hold. Examples: *Gigantura chuni*, *Scopelarchus analis* and *Nesiarchus nasutus*.



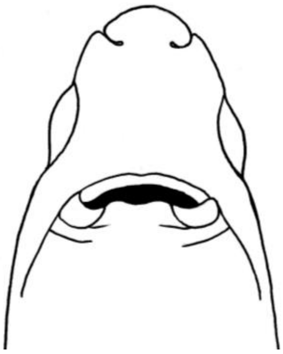
Type 5: having limited marginal cardiform dentition. They have a rough, sandpaper-like texture and consist of numerous, short, fine, pointed teeth. Examples: *Diplophos taenia, Gonostoma atlanticum* and *Argyropelecus aculeatus*.



**Oral position:** the orientation of the mouth.

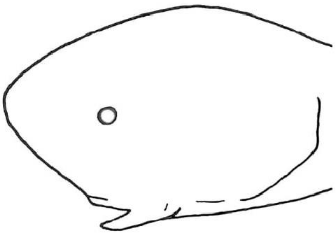
Ventral

Example: *Isistus brasiliensis*



Inferior

Examples: Aldrovandia, *Macrouides inflaticeps*



Terminal

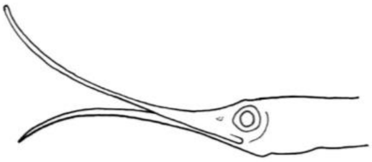
Examples: *Bathophilus nigerrimus*, *Grammatostomias dentatus*, *Benthalbella infans*

Superior

Examples: *Melanocetus johnsonii*, *Eurypharynx pelecanoides, Diretmoides pauciradiatus*

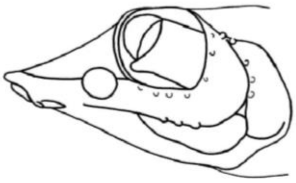
Elongated

Examples: *Avocettina infans, Nemichthys scolopaceus* and *Serrivomer lanceolatoides*



Tubular

Example: *Winteria 47rometheu*



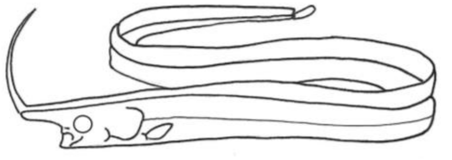
Protrusible

Example: *Bathysphyraenops simplex*

**Body shape:** Lateral body shape.

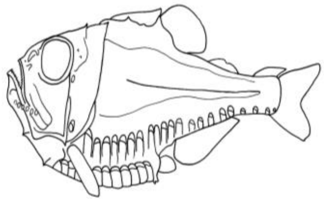
Anguilliform

Examples: *Eumecichthys fiski* and *Stylephorus chordates*.



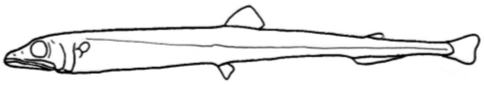
Compressiform

Examples: *Argyropelectus gigas* and *Sternoptyx diaphana*.



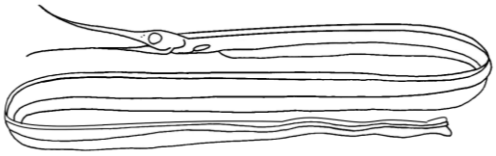
Elongated

Examples: *Ahliesaurus berryi* and *Promethichthys 48rometheus*.



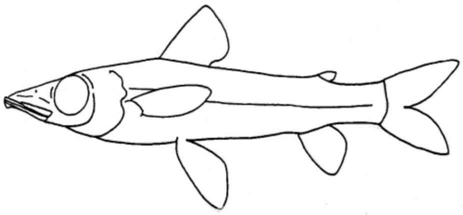
Fillifom

Examples: *Nemichthys scolopaceus* and *Labichthys carinatus*



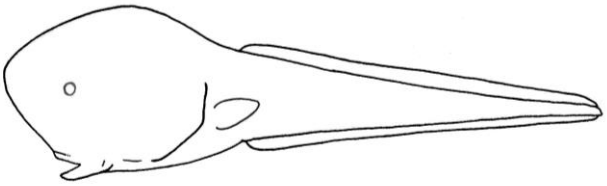
Fusiform

*Rhynchohyalus natalenses* and *Parasudis truculenta.*



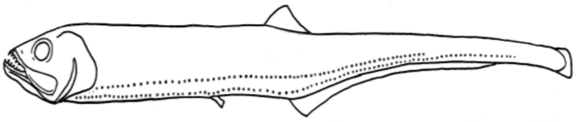
Globiform

Examples: *Macrouroides inflaticeps* and *Chaenophryne draco.*



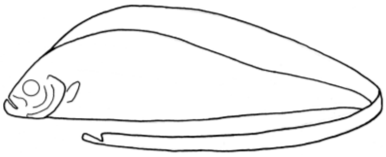
Sagittiform

Examples*: Diplophos taenia* and *Manducus maderensis.*



Taeniform

Examples: *Desmodema polystictum* and *Zu cristatus.*



**Skin color**

Bicolor dark

It is defined in animals with two colors, which can be in a gradient or not. In bicolor dark, the dark color predominates on the animal's body, which can be in shades of brown, greenish, black, and other variations of dark colors. Example: *Winteria telescope.*

Bicolor light

It is defined in animals with two colorations, which can be in a gradient or not. In bicolor light, the light color predominates on the animal's body, which can be in shades of white, light gray, yellowish, and other variations of light colors. Example: *Benthalbella infans.*

Black

Animals with entirely black skin color. Example: *Malacosteus niger*.

Silvery

Animals with entirely silvery skin color. Example: *Serrivomer beanie.*

Red

Animals with entirely red skin color. Example: *Ectreposebastes imus.*

Other

Animals with various color variations. Examples: *Paroncheilus affinis* and *Aulotrachichthys argyrophanus.*

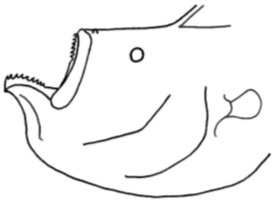
**Structure eyes**

Spherical: Spherical eyes in fish are ocular structures that have a rounded or spherical shape, similar to the majority of eyes fish.

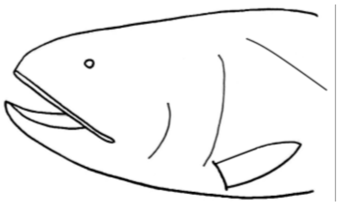
Tubular: tubular eyes are highly specialized eyes that are located dorsally on the head of some species of deep-sea teleosts. They are approximately cylindrical, with the base of the cylinder composed of a thick main retina subtending the dorsal visual field, and the medial wall composed of an accessory retina subtending the lateral visual field (Collin et al., 1997).

**Eye position**

Top of the head –Top position was considered when the species did not have space between the top of the head and the eye margin. Examples: *Odontostomops normalops* and *Ceratias uranoscopus.*



Mid of the head –Mid position was considered when the species has space between the top of the head and the eye margin. Examples: *Ditropichthys storeri* and *Melamphaes eulepis*.



**Eye size**

Degenerated/Small: Small eyes that do not have irises or absent eyes.

Moderate: Eyes size occupies less than 50% of the head length and has irises.

Large: Eye sizes occupy 50% or more of the head.

### *2.3.2. Data Records*

The dataset, which can be found in a repository (either Pangea or Zenodo), contains specific source information and notes on data collection presented in .csv tables. References are incorporated as a Zotero '.ris' file. The dataset primarily consists of two components: 1) an overview, and 2) trait data. The overview files comprise a README pdf, a Zotero reference file, and summary tables featuring key trait variables (Table 1). Additionally, they include a species list with comprehensive references, expanded versions of variables (whether categorical, binary, or ordinal), and notes on data collection. To facilitate future collaborations aimed at expanding this dataset to encompass other species, the data collection information also includes pdf files of protocols and raw data collection tables. The table presents species and their associated taxonomic classifications (e.g., Class, Order, Family, Genus) as rows, with their corresponding traits represented as columns. Any missing information is labelled with 'NA' to highlight gaps in the dataset.

## 2.4. Technical Validation

During the creation of the dataset, we employed tiered steps across the data collection, processing, and sharing phases to validate data and ensure its accuracy. Initially, all individuals involved in data collection underwent comprehensive training and were closely supervised throughout the dataset creation process. The data collection team manually curated trait variables, performing accuracy checks through cross-referencing between data collectors and multiple sources, with all references included in the dataset.

This collaborative effort also entailed comparing interpretations of data values, with the results discussed during a workshop with experts in the taxonomic and ecological aspects of mesopelagic fishes. Ambiguous information was systematically labelled as 'NA'. The entire process was managed under version control using collaborative tools such as OneDrive. The dataset files, including training materials like protocols and tables for trait data collection, were compiled and subjected to rigorous review by all data collectors and supervisors. Looking ahead, we plan to incorporate updated versions of the dataset to reflect new findings and improvements in methodology.

## 2.5. Usage Notes

We invite researchers to contact the authors to contribute data representing all regions and fish taxa to create a net collaborative of the traits of the mesopelagic fishes.

### *2.5.1. Code availability*

No specific code was developed in this work. The parameters and tools used for data processing were described in the Methods section.

# 3. CHAPTER 2 – Distribution of functional diversity of mesopelagic fish community across diurnal cycle and environmental gradients

Functional diversity in the marine environment is crucial for understanding the stability and resilience of marine ecosystems, which support a range of ecosystem functioning and services (Camara et al., 2023). In the marine environment, functional diversity can be influenced by environmental drivers, primarily related to habitat availability and complexity (Zhao et al., 2022). Understanding the distribution of functional diversity in the marine environment is vital for conservation efforts and sustainable fisheries management, as it provides valuable insights into ecosystem dynamics and aids in implementing climate-adaptive measures (Camara et al., 2023). Thus, studying functional diversity distribution in the marine environment is essential for maintaining ocean health and productivity.

Notably, the marine environment imposes a series of challenges for data collection, especially with deep-sea organism communities. This results in certain groups being under-studied, such as mesopelagic fish community. Mesopelagic fish play critical roles in ecosystems. They serve as prey for large predators like tunas and their vertical migration behavior contributes to the carbon cycle between lower and upper trophic levels, and between the surface and deep ocean. Consequently, they are responsible for a significant portion of the carbon fluxes in the oceans, influencing climate change factors. Despite the community's importance, few studies focus on it as a whole, concentrating instead on single species or families like Myctophidae. This is due to the difficulty in classifying and detecting patterns within the community, which exhibits a wide variety of shapes and behaviors. Additionally, their collection, storage, and transportation are costly and complex, creating obstacles and gaps that impede a comprehensive understanding of ecological systems.

The work presented in this chapter is the first to investigate the functional diversity of mesopelagic species, considering a broad taxonomic spectrum of fish and environmental variables.

**This section has been published in the journal Frontiers in Marine Science in 2023.**
https://doi.org/10.3389/fmars.2023.1117806

# Exploring the depths: the high functional diversity of mesopelagic fishes

Kátia Cristina Aparecido, Thierry Frédou, Leandro Nolé Eduardo, Michael Maia Mincarone, Rayssa Siqueira Lima, Maria Fernanda da Silva Morais, Bastien Mérigot

## 3.1. Abstract

Mesopelagic zones (200–1,000-m depth) are characterized by relatively low light levels, cold waters, and often limited oxygen, forming a stable yet challenging habitat for their inhabitants. To overcome these constraints, mesopelagic fishes have developed several adaptations that enable them to participate in crucial ecosystem processes such as nutrient cycling, carbon transport, and provisioning of harvestable fish stocks. However, our understanding of the functional diversity of mesopelagic fishes remains limited, while it is of particular importance considering the increase in human threats and possible environmental changes in the deep ecosystems. In this context, functional diversity emerges as a powerful tool and can help assess community assembly rules, including species complementary and redundancy. Here, we take advantage of scientific surveys that collected 200 species taxa identified from over 7,000 specimens to determine the functional diversity of mesopelagic fish assemblages across depths and the day–night period. We created a data set of 17 qualitative functional traits related to feeding, survival, and locomotion functions. Based on this information, functional spaces and diversity indices were calculated, and functional groups were established. Furthermore, the influence on the functional diversity of environmental variables and the day–night period was assessed by generalized additive models (GAMs). The hypothesis of functional complementary was tested. Overall, mesopelagic fishes displayed a high functional diversity and could be grouped into 10 major functional groups. Moreover, 107 species exhibited a unique composition of functional trait values, revealing a vast complementarity of functions within the deep-sea ecosystem. We also showed that functional diversity in mesopelagic ecosystems is neither static nor homogeneous, exhibiting higher values in the deepest layers and varying between day and night. We finally discuss processes that may structure mesopelagic fish assemblages and the implications of our findings for the conservation mesopelagic fishes.

**Keywords:** biodiversity, trait-based approach, functional indices, functional niche, conservation, deep sea, tropical Atlantic

### 3.2. Introduction

Functional diversity (FD) plays a crucial role in understanding the relationship between biodiversity and ecosystem processes (Naeem, 2006), complementing taxonomic and phylogenetic diversity analyses. FD takes into account the functional traits of species, which are essential for assessing the impact of environmental changes and human pressures on ecosystems (McGill et al., 2006; Villéger et al., 2010). Moreover, FD contributes to informing conservation and management strategies by identifying areas that require protection (Mouillot et al., 2011). One significant advantage of FD over taxonomic diversity is that it captures the ecological roles and functions that species perform within an ecosystem. This approach allows for identifying species with unique functional traits that may affect ecosystem processes disproportionately (Mouillot et al., 2013b). Taking a functional traits perspective, rather than focusing solely on species, can enhance predictions because ultimately these traits determine the nature and strength of animal impacts on ecosystems (Schmitz et al., 2023). Recent advances in FD research have led to indices that quantify complementary features of the functional space occupied by species, considering both their positions and abundance or biomass (Villéger et al., 2008; Mouillot et al., 2013a). The FD concept involves several components, mainly as follows: functional richness, evenness, divergence, dispersion, originality, specialization, and redundancy. Different indices were developed to quantify these components. They have improved our understanding of community responses to environmental variations and predictions of ecosystem feedback (Gagic et al., 2015; Lefcheck and Duffy, 2015; Dee et al., 2016). However, FD analysis requires detailed information on species distribution and trait data, often limited to poorly known ecological groups, such as those inhabiting the mesopelagic zones.

Mesopelagic zones (200–1,000-m depth) are characterized, for example, by relatively low light levels, cold waters, and often limited oxygen, which create a stable yet challenging habitat for their inhabitants (Fock et al., 2004; Bertrand et al., 2010; Proud et al., 2017; Boswell et al., 2020). To overcome these constraints, mesopelagic fishes developed adaptations such as bioluminescence, complex visual systems, and different patterns of vertical migration that may reach shallow waters (Gjøsæter and Kawaguchi, 1980; Sutton, 2013; Priede, 2017). These adaptations enable their contribution to several ecological processes that underpin oceanic ecosystems and offer numerous benefit to society. Notably, mesopelagic species are essential to nutrient cycling and carbon transportation across depth layers. They also provide food for larger predators in marine ecosystems. Nonetheless, despite their ecological significance, our understanding of mesopelagic species remains limited, while it is of critical importance considering the increase in threats such as climate change, plastic pollution, and exploitation of deep-sea resources (Levin et al., 2001; Davison and Asch, 2011; Hidalgo and Browman, 2019; Drazen et al., 2020; Ferreira et al., 2022; Justino et al., 2022a). For instance, there is a significant knowledge gap about the basic biology of many species, including their life history and crucial functional traits. Information such as maximum age, age of first maturity, spawning seasons, distribution of sex ratios across different layers, and variations in feeding based on sex or maturity stage are lacking. This deficit hinders our ability to investigate ecological patterns and community assembly rules in the context of unprecedented global changes.

More specifically, in mesopelagic research, a pivotal question revolves around how a zone with such environmental constraints can support important species diversity and biomass (Gjøsæter and Kawaguchi, 1980; Eduardo et al., 2022), challenging the initial supposition of reduced biodiversity in deep-sea ecosystems (Priede, 2017). The remarkable diversity found in these ecosystems may stem from the ecological specialization of species, considering their niche and functional roles (Devictor et al., 2010). In addition, community assembly rules, including stochastic and deterministic processes, aim to explain species coexistence. Two main deterministic processes have been defined: limiting similarity (MacArthur, 1958; Abrams, 1983) and environmental filtering (Van Der Valk, 1981; Weiher et al., 1998; Kraft et al., 2015). Limiting similarity suggests that species with different traits are more likely to coexist. This hypothesis is a corollary of the competitive exclusion principle (Gause, 1932), which states that two species competing for the same resources cannot stably coexist. Thus, the competitive exclusion will result in a pattern where functionally similar species cannot co-occur. Conversely, it leads to the co-occurrence of species that are complementary in resource use and, thus, in niche occupied. In contrast, the environmental filtering hypothesis favors species with traits better adapted to environment requirements and leads to more similar traits among species. In the mesopelagic zone, where photosynthetic primary production is scarce, species may have evolved specific traits and feeding habits to exploit different resources and/or depths and avoid direct competition (Gloeckler et al., 2018; Eduardo et al., 2023). Although their evolutionary processes have not yet been extensively studied, it is plausible to assume that these environmental pressures have influenced their evolution in distinct ways. As a result, mesopelagic fishes may have undergone specific adaptations and developed unique characteristics that contribute to their survival in this challenging habitat. Given the specialized nature of mesopelagic habitat and the unique adaptations of mesopelagic fishes, it is reasonable to assume that functional redundancy among these species may be low.

The main objective of this study is to investigate whether the mesopelagic fish community exhibits high functional diversity due to the presence of species with unique and complementary functions and to investigate functional diversity patterns according to environmental variables. We notably tested the hypothesis of functional complementarity among species. This means that the species perform distinct functions, and there is a relatively low degree of functional redundancy among them. This research contributes to filling knowledge gaps in understanding the functional diversity of the mesopelagic fishes. It provides valuable information to initiate a discussion on the conservation of this understudied community.

## 3.3. Materials and methods

### *Study area*

The study area is located Fernando de Noronha Ridge, northeastern Brazil (from Rio Grande do Norte to Pernambuco) (Figure 1). This area is classified as an Ecologically or Biologically Significant Marine Area (EBSA) that, by definition, is a unique place of fundamental importance for biodiversity and life cycles of marine species (CBD, 2014).

Several authors recently described the main oceanographic physicochemical features of this region (Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021). Overall, southwestern tropical Atlantic is considered to be oligotrophic. However, banks and oceanic islands act as barriers, enriching sub-surface waters and improving mass and energy fluxes in the food web (Travassos et al., 1999; Tchamabi et al., 2017).

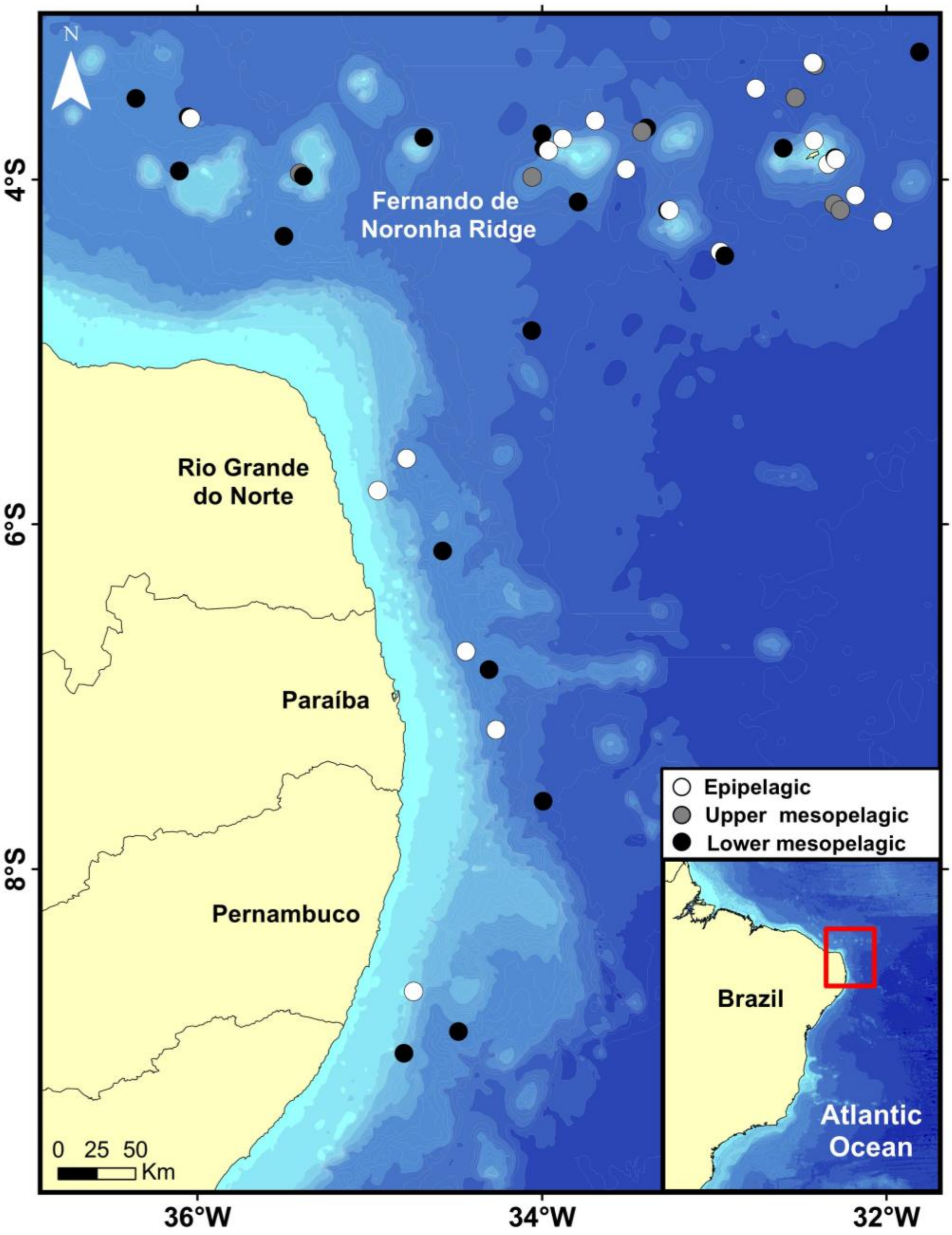


**Figure 1.** Sampling stations of Northeast Brazil are indicated by dots, and the color scheme defines the depth layers.

*Sampling*

Data were collected by the RV Antea during the ABRACOS scientific expeditions, carried out between September 29 and October 21, 2015 (AB 1; Bertrand, (2015)), and between April 9 and May 10, 2017 (AB 2; Bertrand, (2017)). Environmental profiles were collected using a CTDO SeaBird911+ with temperatures ranging from 4.36°C to 28.82°C, salinity from 34.40 to 37.34, and dissolved oxygen from 3.3 ml/L to 4.7 ml/L.

Mesopelagic fishes were sampled day and night at 62 trawl stations by using mesopelagic (AB1; body mesh 30 mm, cod-end mesh 4 mm, net mouth 16.6 × 8.4 m) and micronekton (AB2; body mesh 40 mm, cod-end mesh 10 mm, net mouth 24 × 24 m) nets. The targeted depth for each layer was defined according to the presence of scattered acoustic layers or patches of organisms. However, in an effort to improve the representativeness of biodiversity, we also conducted trawling in areas where no organism aggregations were observed and even beyond the range of the echosounder. Each trawl lasted approximately 30 minutes. Except for the layers 200–300 and 700–800 at night, where no aggregation of organisms was observed through acoustics, all depth strata were sampled at least once (for further information on sampling procedures, see Eduardo et al., 2022). A total of 7,190 fish specimens were collected, representing 200 distinct species (SI Table S1). All specimens collected were deposited at the fish collection of the Instituto de Biodiversidade e Sustentabilidade Universidade Federal do Rio de Janeiro (NPM; Macaé, Brazil).

Sampling data were organized as a matrix with the 200 species as variables (i.e., columns of the matrix) and 62 surveyed stations as statistical objects (i.e., lines). This matrix was used to compute the diversity indices in Section 2.4. All methods were approved and conducted following the regulations of the Brazilian Ministry of Environment (SISBIO authorization number: 47270-5). Operations of the RV Antea were approved by the Brazilian Navy Authority ("Estado-Maior da Armada") under Ordinances 178 (August 9, 2015) and 4 (January 24, 2017).

### *Trait selection*

Seventeen qualitative traits were selected to investigate the functions of feeding, locomotion, and survival (i.e., traits used as survival strategy) (Table 1) for 184 species among the 200 species (see Eduardo et al., 2022). Traits values were obtained from bibliographic references and the NPM museum specimens. When possible, missing data were inferred from observation and knowledge of experts in the field.

Regarding the skin color trait, fish skin colors were categorized into six modalities (Table 1). Notably, for fishes presenting two skin colors, we coded a predominant dark color as dark-bicolor, and a predominant lighted color as light-bicolor. More specifically, regarding certain anglefish species (Lophiiformes: Ceratioidei) with notable sexual dimorphism (Pietsch, 1976), we opted to focus on females as representatives of the species due to their higher capture frequency and easier identification when compared to males. Furthermore, anglerfishes have a unique reproductive strategy in which smaller males rely on females for survival. They merge with the female's skin as permanent parasitic appendages through a process known as "sexual parasitism". Consequently, after the reproductive engagement, the female assumes responsibility for feeding, locomotion, and survival functions considered in this study.

**Table 1.** Selected functional traits of feeding locomotion, and survival and their respective modalities.

| Function | Trait | Trait description | Trait categories |
|---|---|---|---|
| **Feeding** | Lure apparatus | Structure used to glow light and attract prey | Presence/absence |
| | Prey illumination | Structure used to illuminate or induce fluorescence in prey | Presence/absence |
| | Trophic guild | Group of species to explore the same class of resources similar | Zooplanctivores, micronektivores, generalists, and piscivores |
| | Eye structure | Eyes shape | Tubular/spherical |
| | Eye position | Eye position relative to the head | Top/mid |
| | Eye size | Ratio of eye size to head depth | Small (< 35%), moderate (35%–65%), and large (> 65%) |
| | Vertical migration | Movement of fish between mesopelagic and epipelagic waters over a period of the day | Presence/absence |
| | Caudal fin shape | Lateral shape of caudal fin | Forked, round, truncated, lunate, pointed, heterocercal, emarginate, and fan |
| | Teeth type | Basic patterns of marginal teeth | 0, without teeth; 1, long, slender, sharp; 2, numerous |

| | | | |
|---|---|---|---|
| | | | small, needlelike, villiform; 3, flat-bladed, pointed, triangular; 4, recurved, conical, caniniform; 5, cardiform dentition |
| | Bioluminescence | Organ producing light | Presence/absence |
| | Oral position | Orientation of the mouth | Presence/absence |
| **Locomotion** | Body shape | Lateral body shape and cross-section | Anguilliform, compressiform, elongated, filliform, globiform, sagittiform, and taeniform |
| | Caudal fin shape | Lateral shape of caudal fin | Forked, round, truncated, lunate, pointed, heterocercal, emarginate, and fan |
| | Aggregation | Pair/school formation | Presence/absence |
| | Body size | Maximum total length recorded in cm | Class (10 cm) |
| **Survival** | Skin color | Predominant skin color | Dark-bicolor, light-bicolor, black, silver, red, and other Colors |
| | Counter-illumination | Camouflage that involves the use of ventral photophores to match the dim light coming from the surface | Presence/absence |

From the information provided in Table 1, a functional trait matrix was created, with traits as variables (columns) and species as statistical objects (lines). This matrix was used to compute the functional diversity indices, including the functional space, and the fourth-corner analysis to study the relationship among functional traits and explanatory variables (see below).

### *Diversity indices*

Taxonomic species richness and the functional space occupied by species, based on the 17 traits associated with three primary functions (feeding, locomotion, and survival, Table 1), were first calculated for each depth layer (gamma diversity) to offer a comprehensive evaluation of the studied zones. Second, species richness and six additional functional diversity indices (Table 2) for each of the 62 sampled stations (alpha diversity) were also determined, and their mean values for each depth layer and day–night period were then computed to compare them (qualitative variables). Third, the alpha diversity values calculated for each station were further utilized to assess the effects of environmental conditions (quantitative variables, see *Data analyses* section).

The functional diversity indices are presented, with related references, in Table 2. In short, functional richness (FRic) quantifies how much niche space species occupy (i.e., convex hull volume). Higher index values indicate a larger volume occupied within trait space (Cornwell et al., 2006). Functional evenness (FEve) indicates how the species and their proportion (here based on abundance) are evenly distributed within the functional volume. Higher index values suggest that species and their proportions are more evenly distributed within the functional volume (Villéger et al., 2008). Functional divergence (FDiv) measures how far relatively highly abundant species with extreme traits are from the center of the functional trait space. It can be related to the levels of resource differentiation and competition among species (Mason et al., 2005). Functional dispersion (FDis) is the mean distance of individual species to the centroid of all species in the functional trait space. A high dispersion value infers a high species spread in the functional niche. Functional originality (FOri) computes the weighted mean distance between each species and the species closest to it in the functional space. Higher values might be interpreted as low functional redundancy (Mouillot et al., 2013b). Functional specialization (FSpe) is the mean distance among each species to the center of the functional space. It indicates the tendency of species to have extreme trait values (Lechêne et al., 2018). Therefore, it is possible to assess how generalist or specialist species are (Villéger et al., 2010; Mouillot et al., 2013b) with higher values indicating a predominance of specialist species.

**Table 2.** Functional diversity indices computed on species data and 17 functional traits (adapted from Brandl et al., 2016).

| Indices | Acronym | Definition |
|---|---|---|
| Functional richness (Cornwell et al., 2006; Villéger et al., 2008) | FRic | The proportional volume of the synthetic niche space is encompassed by the outermost vertices species of the community. |
| Functional evenness (Villéger et al., 2008) | FEve | The abundance-weighted regularity of species in functional niche space along a minimum spanning tree. |
| Functional divergence (Villéger et al., 2008) | FDiv | The proportion of abundance at the periphery of the synthetic niche space represents species with extreme trait combinations, based on the average distance from the center of the niche space. |
| Function dispersion (Laliberté and Legendre, 2010) | FDis | The abundance-weighted mean distance from the center of the synthetic niche space. |
| Functional originality (Mouillot et al., 2013b) | FOri | The abundance- weighted mean distance to the nearest species from the species community. It is thus the mean isolation of a species in the functional space of a given community. |
| Functional specialization (Villéger et al., 2010) | FSpe | The abundance- weighted mean distance among each species to the center of the functional space of a community |
| Functional entities (Elton, 1927) | FE | Species from the overall pool that share the same trait values. |
| Functional redundancy (Mouillot et al., 2014) | FRed | The ratio between species richness and functional entity richness (FEr). It represents the average number of species in FE present in a given assemblage. |

| | | |
|---|---|---|
| Functional over-redundancy (Mouillot et al., 2014) | FOr | The ratio of the species in the FE with more species than average redundancy. |

*Data analyses*

We calculated total species richness (gamma) and mean species richness of stations (alpha) by depth layer (epipelagic 0–200m, upper mesopelagic 200–500 m, and lower mesopelagic 500–1,000 m) and period stocks (day and night). We included all 200 taxa to compute taxonomic species richness since functional traits are not necessary for its calculation. We removed 16 species from the analyses because they had too many missing trait data (Johnson et al., 2021). Sampling stations (n = 15) with only two species were also removed, as calculating functional space is not feasible in such cases (e.g., fewer species than functional dimensions).

We computed pairwise functional species distances with the Gower distance metric between species based on functional trait values (considered as the variables). This metric can consider qualitative traits. As the distance between some species was 0 (i.e., functional redundancy), we also calculated FD based on functional entities (FEs). In this scenario, we grouped species into Fes according to their shared trait values (Mouillot et al., 2014). In addition, we computed functional redundancy FRed and over-redundancy FOr indices (Table 2) (Mouillot et al., 2014). To identify and visualize functional groups, we used the Gower trait-based distances among species in the average linkage clustering algorithm (unweighted pair group method with arithmetic mean (UPGMA)). It is a hierarchical method providing a dendrogram representation. Then, we employed the gap statistic method to determine the optimal number of functional groups (clusters) on the dendrogram (Tibshirani et al., 2001).

We tested the quality of the multidimensional space, representing the functional space built from a principal coordinates analysis (PCoA) considering two to 10 dimensions, using the R package mFD (Magneville et al., 2022) (SI Figure S1). To assess the quality of the representation, we used the lowest deviation between the original Gower trait-based distances among species and their Euclidean distances in the functional spaces from the PCoA (Maire et al., 2015). This index ranges between 0 and 1, with 0 being the lowest deviation. mSD values were very low for every number of dimensions considered (<0.13, Figure S1), and therefore, we kept only two dimensions to create and represent the functional space.

We calculated the six complementary indices of FD (Table 2), using the mFD package, for alpha diversity (i.e., computed for each sampled station, see values in Table S2). The values of the indices were scaled between 0 and 1 by dividing each value by the maximum value computed for a given index, except for FEve and FDiv, for which the values were already set between 0 and 1. Finally, the empirical pairwise relationships (i.e., complementary/redundancy) among alpha FD indices were investigated using a draftsman plot representing both i) x–y plot fitted by a nonparametric local regression (locally reweighted scatter plot smoothing (LOWESS)) and ii) correlation coefficient (Figure S2). Then, given the non-linear trends among each FD index and some explanatory variables (Figure S2), generalized additive models (GAMs) were used to assess the relationship among each complementary alpha FD index (i.e., non-linearly related and noncorrelated) and the environmental variables (oxygen, temperature, and depth), day and nighttime, and interactions among these explanatory variables. GAM analysis assesses the effect of multiple predictors in additive models and has the advantage of not requiring an a priori linear relationship. The models were chosen based on analyses of the multiple variable combinations, which were compared using the Akaike information criterion corrected for finite sample sizes (AICc). The best-fitted models were those with the lowest AICc. All GAM analyses were conducted using the R package “mgcv” (Wood, 2001).

### *Traits-environment relationship*

We performed a fourth-corner analysis (FCA) (Legendre et al., 1997; Dray and Legendre, 2008; ter Braak et al., 2012) on the three following tables: environmental variables (R), species abundance (L), and functional traits (Q). The fourth corner correlation allows us to quantify the overall amplitude of the association among traits and environmental variables. The square of this correlation is a score test statistic for trait–environment association in a Poisson log-linear model (Braak et al., 2017).

The analysis was performed among functional traits and environmental variables (depth and oxygen, but not temperature and salinity being negatively correlated to depth; see Figure S2) separated by period (day/night) to account for the daily movement of species in the water column. For the day period, 33 stations and 143 species were included in the analysis, and for the night period, 29 stations and 145 species were considered. To address multiple comparisons, the conservative Holm method was employed (Holm, 1979), which adjusts the p-values of each test using a threshold. Global hypothesis test model 6 was conducted, which consists of the simultaneous testing of model 2 (permutation of abundances among stations) and model 4 (permutation of abundances among species). Two permutation tests (n = 9,999) considering model 2 and model 4 were computed. Model 2 tests H0, assuming that environmental conditions do not influence species distribution with fixed traits. Model 4 tests H0, assuming that species traits do not influence the species composition of samples with fixed environmental conditions. The FCA used the “ade4” (Kleyer et al., 2012) R package (R Core Team, 2022).

### 3.4. Results

A total of 7,190 individuals were collected from 62 sampling stations using trawling techniques during both day and night. These individuals represented 200 different species, belonging to 131 genera and 57 families (Table S1). Detailed results related to gamma diversity according to sampling depth layers and periods (day/night) are included in Table 3. Accumulation curves of species richness (gamma diversity) are provided in Figure S3. These latter highlighted that both observed (when rarefied to a common sampling effort) and estimated total species richness are higher in the lower mesopelagic layer (Figure S3).

**Table 3.** Fish community features collected within each oceanographic layer and time period (day, night, and total (day+ night)).

| Layer | Period and stations (n) | Species richness (S) | Individuals (j) |
|---|---|---|---|
| Epipelagic | Day (12) | 17 | 80 |
| | Night (19) | 65 | 1.396 |
| | Total (31) | 71 | 1.476 |
| Upper mesopelagic | Day (8) | 46 | 714 |
| | Night (2) | 63 | 329 |
| | Total (10) | 82 | 1.043 |
| Lower mesopelagic | Day (13) | 142 | 2.271 |
| | Night (8) | 124 | 2.400 |
| | Total (21) | 180 | 4.671 |

Functional diversity was calculated for 184 out of the 200 species, as trait values were lacking for 16 of them (see *Data Analyses* section). Species were distributed across 47 stations (see above *Data Analyses* section), including 19 in the epipelagic layer, 7 in the upper mesopelagic layer, and 21 in the lower mesopelagic layer. The FEs were arranged into 134 groups. The largest group, FE1, was composed of seven species (*Benthosema suborbitale*, *Ceratoscopelus warmingii*, *Diogenichthys atlanticus*, *Hygophum hygomii*, *Hygophum macrochir*, *Hygophum reinhardtii*, and *Hygophum taaningi*). Additionally, two FEs comprised five species, one FE with four species, 10 FEs with three species, and 13 EFs with two species, totaling 77 species distributed in the FEs. No trait values were shared among 107 species (79.85%), thus having no functional redundancy with another species. The family Stomiidae exhibited the highest number of species with unique combinations of traits (n = 15). Likewise, the Myctophidae and Stomiidae encompassed a great number of FE with 10 and eight FEs, respectively.

As previously mentioned, we have identified 134 FEs based on precise combinations of trait values, among which 107 FEs had each only one species, and only 27 FEs had more than two species. Furthermore, the functional over-redundancy FOr index showed low values; each layer had mean values of 0.1, 0.074, and 0.09 for the epipelagic, upper mesopelagic, and lower mesopelagic zones, respectively. In addition, we found low mean values of functional redundancy FRed index of 1.23, 1.1, and, 1.26, for these three zones, respectively. To complement this analysis and provide a broader assessment of species' functional roles, we also conducted a hierarchical clustering analysis of functional traits. This analysis identified 10 major functional groups of species (Figure 2), which allowed us to better understand the interplay between species and their functional roles within their ecosystem. This dual approach provides a more comprehensive understanding of species complementarity and redundancy.

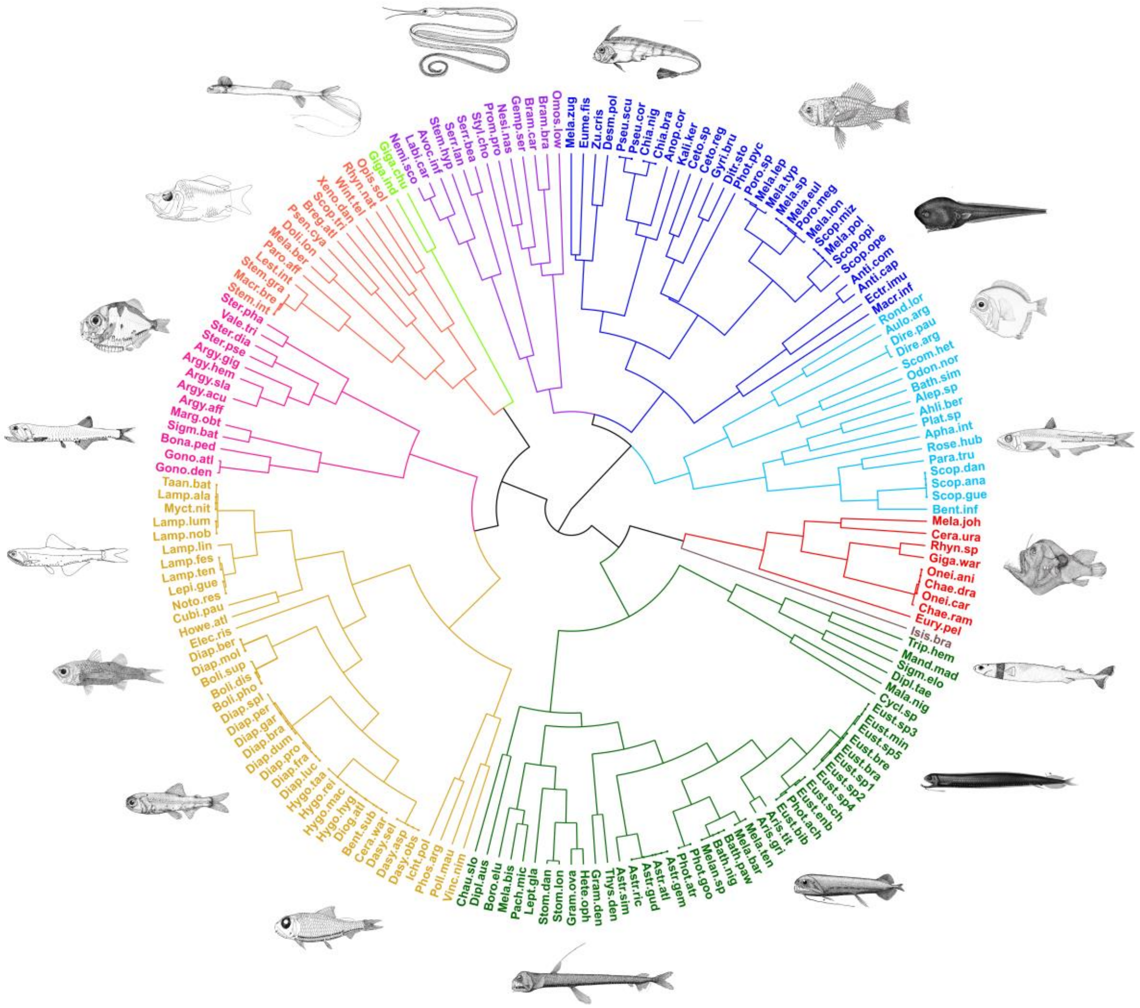


**Figure 2.** Hierarchial clustering of species defined based on their pairwise functional distances and groups identified according to the Gap stat criterion for optimal group partitioning (fish images adapted from Sutton et al., 2020).

These 10 major groups are the following:

Group 1 (green)

The largest group encompassed a total of 45 species, primarily composed of species belonging to the Stomiidae (86.36%). Key traits displayed by these species include a sagittiform body shape, black or dark-bicolor coloration, light emission, counter-illumination, lure apparatus, spherical eyes, and micronektonivorous feeding habits. Group 1 notably contains the highest number of species exhibiting unique trait combinations (21 species) and eight FEs.

Group 2 (yellow)

The second largest group, comprising 40 species, predominantly consisted of species of the Myctophidae (34 species), also including similar species of the Phosichthyidae (4), Nomeidae (1), and Howellidae (1). Species in this group exhibited characteristics such as relatively small overall size, vertical migration, zooplanktivorous feeding habits, large spherical eyes, counter-illumination, prey illumination, and dark-bicolor coloration. Group 2 had the highest number of FEs (10).

Group 3 (dark blue)

The third largest group, encompassing 30 species, primarily included members from the Melamphaidae (11), Chiasmodontidae (5), and Cetomimidae (4) families. These species were mainly characterized by moderate to small spherical eyes and the lack of bioluminescence (except for Pseudoscopelus). This group accounted for five FEs.

Group 4 (light blue)

This group comprised 17 species, encompassing all members of the Scopelarchidae (five species) as well as 11 species of other families. Species in this group were primarily characterized by bicolored light or silvery coloration, large eyes, and piscivorous habits. Interestingly, this group was composed of just one FE, which includes *Scopelarchus analis*, *Scopelarchus guentheri*, and *Scopelarchoides danae*.

Group 5 (pink)

This group consisted of 14 species and one FE. It encompassed all nine species of the Sternoptychidae found in our samples, along with five species of the Gonostomatidae. Species in this group displayed counter-illumination, zooplanktivorous feeding habits, and relatively short total body lengths. Most of the Sternoptychidae species exhibited a silvery color and a compressed body shape.

Group 6 (orange)

This group also consisted of 14 species and one FE. Group 6 predominantly featured species from families of the order Argentiniformes: Opisthoproctidae (three species), Bathylagidae (two species), and Microstomatidae (one species). Moreover, six additional families were part of this group. Most species in Group 6 exhibited relatively short body lengths, lack of bioluminescence, forked caudal fins, and zooplanktivorous feeding habits.

Group 7 (purple)

This group consisted of 13 species distributed across six families. Six species in this group belong to the order Anguilliformes (three Serrivomeridae and three Nemichthyidae). Most species in Group 7 displayed a filiform body shape, pointed caudal fins, spherical eyes, lack of bioluminescence, silvery coloration, and vertical migration patterns. No FE was identified in this group.

Group 8 (Red)

This group consisted of nine species from five families. Except for *Eurypharynx pelecanoides* (Anguiliformes), all species in this group were Lophiiformes. They were characterized by the presence of lure appendages, black coloration, globiform or sagittiform body shapes, and micronektonivorous habits. This group accounted for one FE.

Group 9 (light green) and Group 10 (brown)

Composed of only two and one species, respectively. Group 9 included two species of the Giganturidae (*Gigantura chuni* and *Gigantura indica*), characterized by sagittiform body shape, tubular eyes, and generalist feeding habits. Group 10 consisted of *Isistius brasiliensis*, the single elasmobranch species collected in our samples, characterized by a sagittiform body shape, spherical eyes, and piscivorous feeding habits. No FEs were identified in both groups.

In terms of functional space, overlaps were observed among depth layers and time periods (gamma-diversity, Figure 3). Nonetheless, the volume of the convex hull occupied by species was substantially greater in the lower mesopelagic layer (alpha mean FRic= 0.58 ± 0.28) compared to the epipelagic layer (alpha mean FRic = 0.19 ± 0.15) and the upper mesopelagic layer (alpha mean FRic = 0.38 ± 0.32, Figure 4). This indicates a broader mean functional range for mesopelagic fish species in assemblages of deeper waters.

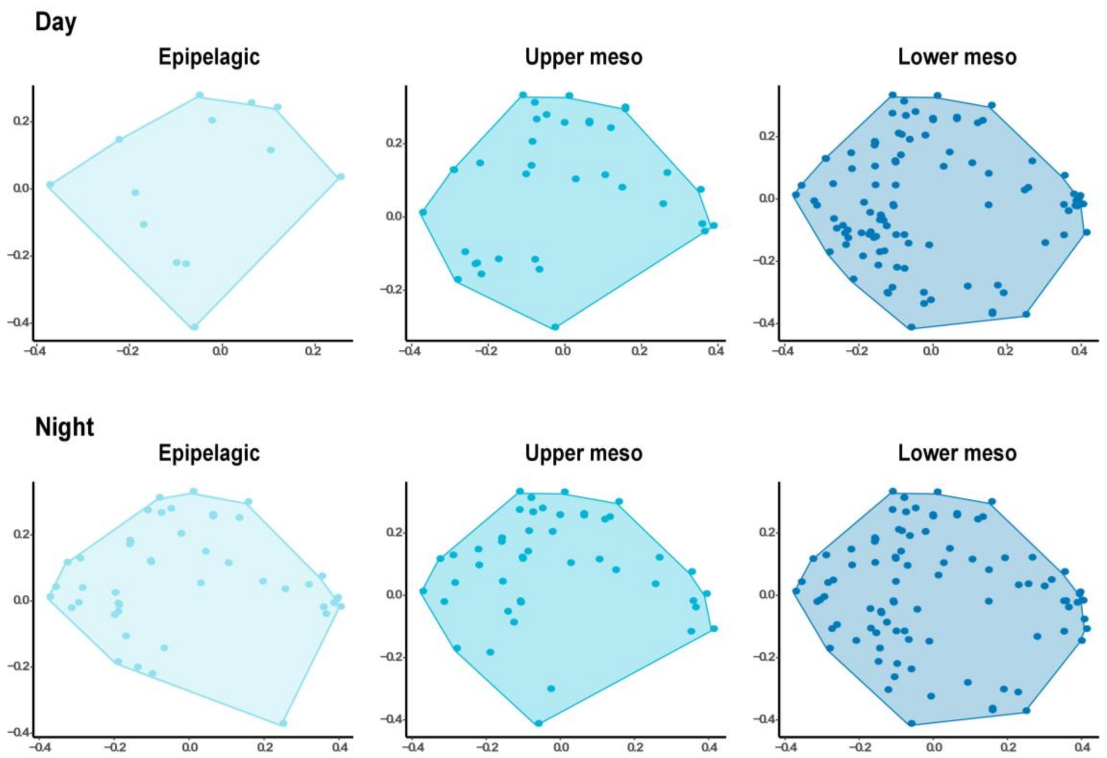


**Figure 3.** Comparison of functional space in 2-D from each oceanographic layer. The gray dashed line represents the global functional space (i.e., all layers combined). PCoA Principal Coordinates Analysis) was computed on functional trait values (number of species = 184). Barplots present the mean values with standard deviations (values provided in Table 4) of each functional diversity index (see definitions in Table 2) for each oceanographic layer).

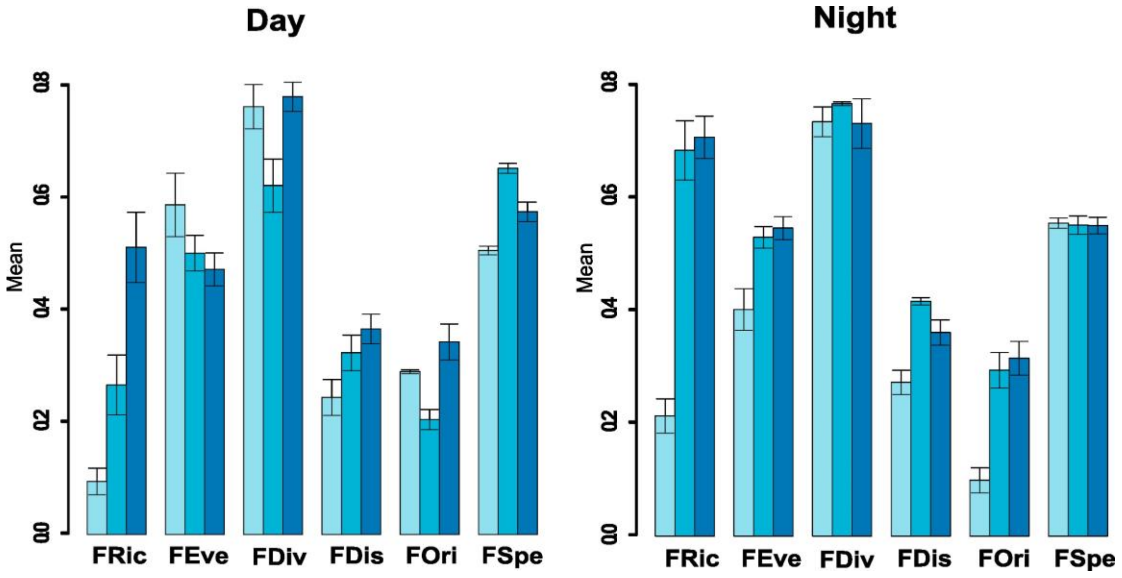


**Figure 4.** Barplots present the mean values with standard deviations (values provided in

Table 4) of each functional diversity index (see definitions in Table 2) for each oceanographic layer. PCoA, Principal Coordinates Analysis.

**Table 4.** Mean and standard deviation values of the complementary functional indices (see Table 2) by oceanographic layer.

| | **Fric** | **Feve** | **Fdiv** | **Fdis** | **Fori** | **Fspe** |
|---|---|---|---|---|---|---|
| Epipelagic | 0.19 ± 0.15 | 0.44 ± 0.16 | 0.74 ± 0.14 | 0.27 ± 0.12 | 0.14 ± 0.13 | 0.54 ± 0.05 |
| Upper meso. | 0.38 ± 0.32 | 0.50 ± 0.14 | 0.66 ± 0.21 | 0.35 ± 0.14 | 0.23 ± 0.10 | 0.62 ± 0.07 |
| Lower meso. | 0.58 ± 0.29 | 0.50 ± 0.14 | 0.76 ± 0.17 | 0.36 ± 0.12 | 0.33 ± 0.16 | 0.56 ± 0.08 |
| Total | 0.39 ± 0.13 | 0.48 ± 0.17 | 0.74 ± 0.17 | 0.32 ± 0.13 | 0.24 ± 0.16 | 0.56 ± 0.07 |

Fric, functional richness; Feve, functional evenness; Fdiv, functional divergence; Fdis, functional dispersion; Fori, functional originality; Fspe, functional specialization.

In both periods, Fric values were higher in the lower mesopelagic layer, although there was little difference in functional space in the upper mesopelagic layer during the night, with an average of 0.68 ± 0.05 in this layer and 0.70 ± 0.03 in the lower mesopelagic layer (Figure 4; Table S3). In Feve (Figure S4), the epipelagic layer obtained the highest uniformity, with an average of 0.58 ± 0.06 during the day, but this value decreased to 0.40 ± 0.03 during the night (Figure 4; Table S3).

Fdiv (Figure S5) reached 417, the highest means value in both periods (Figure 4; Table S3), with a peak in the upper mesopelagic layer at night with 0.76 ± 0.00. However, this layer had the lowest mean value during the day at 0.61 ± 0.04. Fdis (Figure S6) showed the highest mean value at the upper mesopelagic layer during the night, with 0.41 ± 0.00 (Figure 4; Table S3). During the day, the lower mesopelagic layer had the highest mean value among the other layers (Figure 4; Table S3).

Likewise, all layers presented relatively low values of Fori; however, during the night period, the mean values between the upper meso- and lower mesopelagic layers approached each other, with values of 0.29 ± 0.03 and 0.31 ± 0.02 (Figure 4; Table S3, Figure S7), respectively. The seven species contributed the most to this index (contribution > 6% obtained with the mFD package from individual species contribution to the overall index value) were *Malacosteus niger* (8.8%), *Melanonus zugmayeri* (8.5%), *E. pelecanoides* (7.9%), *Eumecichthys fiski* (7.1%), Platytroctidae sp. (7.0%), *Chauliodus sloani* (6.9%), and *Melanocetus johnsonii* (6.5%).

Regarding Fspe, the mean values were equal between the layers during the night period, at approximately 0.55 ± 0.01 for all layers, highlighting a moderate average distance of a species to the other species within the functional space (Figure S8). The analysis of the contribution of individual species to the Fspe index revealed that *M. johnsonii* (45%) contributed the most to this index. Additionally, important contributions (≥40%) were made by three species of the Stomiiformes (*Heterophotus ophistoma*, 42%; *Melanostomias biseriatus*, 42%; *Grammatostomias ovatus*, 41%, one species of adiformes (*M. zugmayeri*, 42%), and three species of Lophiiformes (*Oneirodes carlsbergi*, 40%; *Oneirodes anisacanthus*, 40%; *Chaenophryne draco*, 40%). These results indicate that species of Lophiiformes, including *M. johnsonii*, which stood out in both indices, played a crucial role in functional specialization and originality.

GAMs, fitting the variation of each index (alpha diversity values) in the function of explanatory variables and their interactions (see raw relationships in Figure S2), revealed that the influence of these variables explained between 40.4% and 83.1% of the deviance, depending on the indices (Table 5). Generally, depth proved to be a crucial variable for functional diversity indices, being I variables having a significant effect, as well as Figure S9 for all graphs of each variable included in the GAMs).

Fric exhibited the largest number of significant relationships (Table 5), with notable inverse relationships with depth according to day and night periods. Indeed, during the day, Fric increased with depth, while at night, there was a peak between 400 and 600 m and then a decrease (Figure 5A). In terms of the relationship with oxygen, Fric decreased with depth during the day, but at night, there was a peak at 4.5 dissolved oxygen, followed by a slight decrease (Figure 5A).

Concerning Feve, only a significant relationship with oxygen during the day was observed (Figure 5B; Table 5), with a sharp decrease at 4.5 dissolved oxygen before a rapid increase. Regarding Fdiv, depth and the interaction between oxygen and depth were significant (Table 5). Fdiv decreased with depth and had different mean values according to depth and the level of dissolved oxygen (Figure 5C). It notably reached an intermediate value of 0.4 at approximately 750–900-m depth and 3.4–3.7 of dissolved oxygen (red line at the bottom right of the interaction plot; Figure 5C).

Fdis exhibited opposite trends with dissolved oxygen, depending on the period considered, with a peak at 4.5 dissolved oxygen during the day, while a slight increase occurred at night (Figure 5D; Table 5). Regarding Fori, the interaction between depth and night was significant (Table 5), increasing with depth (Figure 5E; Table 5). Finally, for Fspe, the interaction between depth and day was significant (Table 5), with an increase of Fspe up to 500 m and then a slight decrease (Figure 5F).

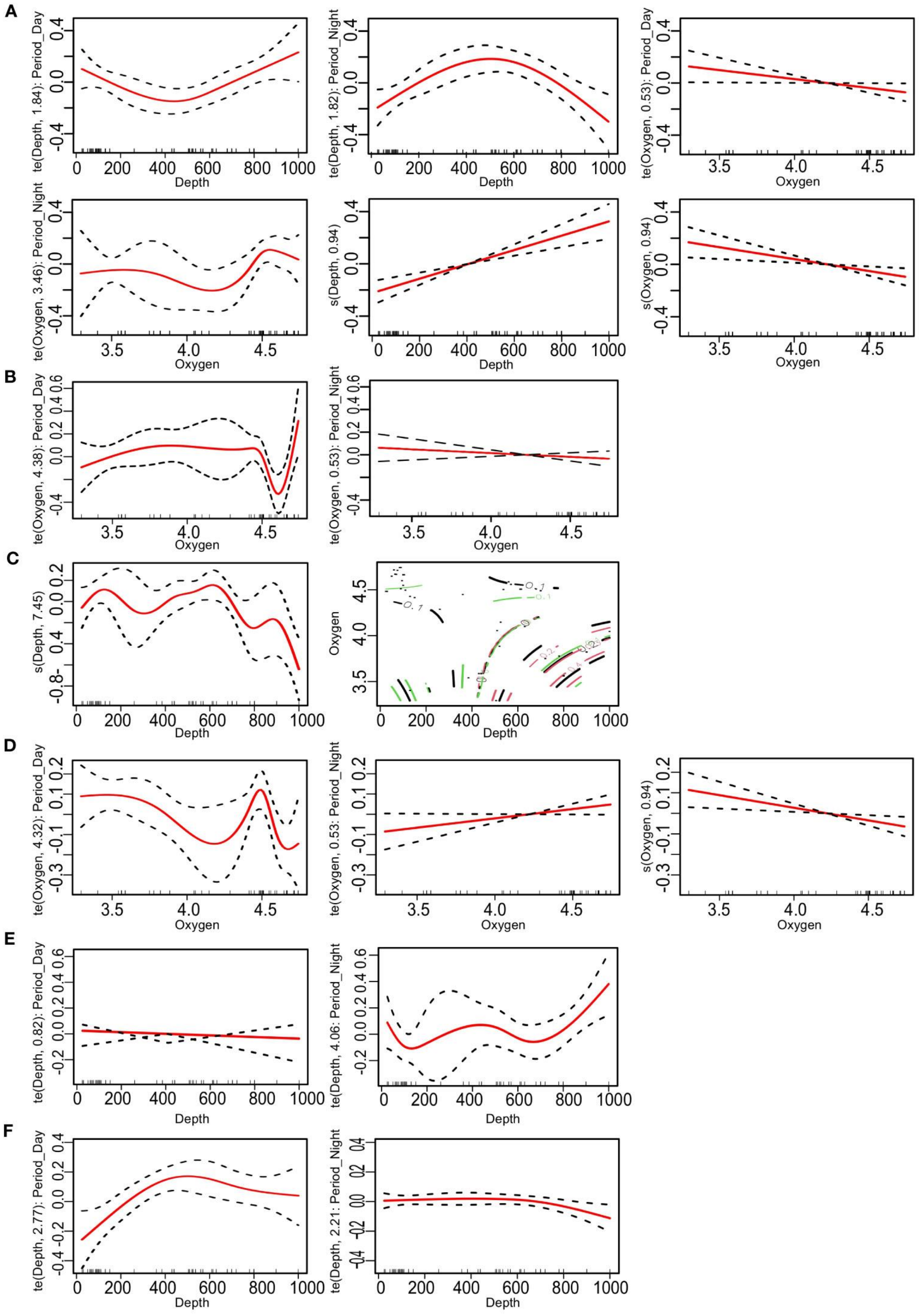


**Figure 5.** Generalized additive model (GAM) plots showing associations among functional diversity index (Table 2) and environmental variables (depth, oxygen, depth, time period, and oceanographic layer) with 95% confidence

intervals. (A) Fric. (B) Feve. (C) Fdis. (D) Fdiv. (E) Fspe. (F) Fori. Fric, functional richness; Feve, functional evenness; Fdis, functional dispersion; Fdiv, functional divergence; Fspe, functional specialization; Fori, functional originality.

**Table 5**. Generalized additive models (GAMs) with Gaussian function on the relationships among functional diversity indices (Table 2) and explanatory variables.

| Index Explan. Var. | Explan. Var. | Sum Sq. | Mean Sq. | F | p-Value | AIC | Dev_expl |
|---|---|---|---|---|---|---|---|
| FRic | s(depth) | 1.89987 | 1.89987 | 53.0519 | 2.34E−08*** | −9.7268 | 72.28% |
| | s(oxygen) | 0.31073 | 0.31073 | 8.6769 | 0.00587** | | |
| | Period | 0.49342 | 0.49342 | 13.7783 | 0.00076*** | | |
| | Layer | 0.09 | 0.045 | 1.2566 | 0.29788 | | |
| | Residuals | 1.18179 | 0.03581 | | | | |
| FEve | s(depth) | 0.02344 | 0.02344 | 0.8388 | 0.36602 | −22.608 | 28.65% |
| | s(oxygen) | 0.10101 | 0.10101 | 3.6137 | 0.06556 | | |
| | Period | 0.04791 | 0.04791 | 1.714 | 0.199 | | |
| | Residuals | 0.9783 | 0.02795 | | | | |
| FDis | s(depth) | 0.121 | 0.12101 | 9.0065 | 0.00509** | −55.805 | 42.73% |
| | s(oxygen) | 0.04643 | 0.04643 | 3.4558 | 0.07197· | | |
| | Period | 0.0228 | 0.0228 | 1.6972 | 0.20167 | | |
| | Layer | 0.15335 | 0.07667 | 5.7069 | 0.00744 ** | | |
| | Residuals | 0.44337 | 0.01344 | | | | |
| FDiv | s(depth) | 0.00005 | 0.00005 | 0.003 | 0.9569 | −40.751 | 51.50% |
| | s(oxygen) | 0.09616 | 0.09616 | 5.1957 | 0.02924 * | | |
| | Period | 0.15654 | 0.15654 | 8.4579 | 0.00646 ** | | |
| | Layer | 1.16457 | 0.58229 | 31.462 | 2.26E−08 *** | | |
| | Residuals | 0.61076 | 0.01851 | | | | |
| FSpe | s(depth) | 1.8E−05 | 1.8E−05 | 0.0042 | 0.94849· | −110.45 | 41.99% |
| | s(oxygen) | 0.00289 | 0.00289 | 0.6877 | 0.4129 | | |
| | Period | 0.00212 | 0.00212 | 0.5042 | 0.48264 | | |
| | Layer | 0.036 | 0.018 | 4.2846 | 0.02217 * | | |
| | Residuals | 0.13862 | 0.0042 | | | | |
| FOri | s(depth) | 0.40993 | 0.40993 | 21.479 | 5.39E−05 *** | | |
| | s(oxygen) | 0.02587 | 0.02587 | 1.3553 | 0.2527 | | |
| | Period | 0.09932 | 0.09932 | 5.2041 | 0.02912 * | | |
| | Layer | 0.02613 | 0.01307 | 0.6846 | 0.51133 | | |
| | Residuals | 0.62982 | 0.01909 | | | | |

No interactions among variables were found (i.e., $p > 0.05$) and are thus not presented.
AIC, Akaike information criterion; FRic, functional richness; FEve, functional evenness; FDis, functional dispersion; FDiv, functional divergence; FSpe, functional specialization; FOri, functional originality.
Significance codes: '***' 0.001 '**' 0.01 '*' 0.05.

The FCA showed positive correlations among some traits and depth according to the period (day and night) considered (Figure S10). The data collected during the day revealed that depth positively correlated with lure apparatus structure, non-migratory behavior, teeth type 01 (long, slender, sharp), and skin color black (Figure S10). During the night, no significant correlations were found between functional traits and environmental variables (Figure S10).

## 3.5. Discussion

Our study presents the first assessment of the FD of the mesopelagic fish community across contrasted environmental conditions. Examining the vertical gradient from the surface to 1,000-m depth, we discovered differences in niche occupancy across depth and period (day/night) and high functional diversity of fish in the deepest assemblages. We also observed low sharing of functional traits among species, indicating a wide range of unique trait combinations among major functional entities and groups. Likewise, assemblages of the different depth layers displayed low functional redundancy and over-redundancy among species. Overall, these results indicate that species play complementary functional roles. Our findings suggest that for mesopelagic fish communities, relatively high taxonomic species richness is not a proxy of functional redundancy and related insurance to buffer functions in case of species loss. Finally, we also offer insights into the relationships between traits and environmental factors. Here, we discuss these main results and the implications of our findings in the studied area.

### *Vertical variability in functional diversity of mesopelagic fishes*

The functional diversity analysis showed high functional diversity, with at least 10 major functional groups identified. Generally, the primary groups exhibit low functional redundancy, indicating that species perform a wide array of functions and ecological roles within the ecosystem. Furthermore, 107 species exhibited a unique composition of functional traits, emphasizing a significant potential for providing distinct contributions to ecosystem functioning. In addition, the functional diversity indices, computed at the station level (alpha diversity), were relatively high for the deepest assemblages, suggesting a higher degree of specialization among the species considered, and a wider range of functions performed by mesopelagic fishes. Furthermore, our analyses took into account the day and nighttime periods and thus the migration, partial, or non-migration behaviors of species, which can explain some patterns discussed below.

Indeed, regarding more specifically the indices analyzed, the alpha mean values of most indices were slightly to highly superior in the upper and lower mesopelagic layers than in the epipelagic layer, except for FEve (day) and FSpe (night). Lower mean alpha values of FEve were observed in the epipelagic layer compared to other layers, indicating potentially more efficient resource use by species with particular traits (Schleuter et al., 2010) during nighttime for species making vertical migration. Moreover, there was an increase in the mean alpha value of FEve during the day, where a regular distribution of species in the niche space and complementary resource use by species is observed that should be associated with the migration behavior of species. The high mean alpha values of FDiv in all analyzed situations (depth strata and time periods) suggest a high degree of niche partitioning (Mason et al., 2005). Furthermore, in all situations, FOri was higher in the lower mesopelagic layer, indicating that species in this depth strata, for those that did not migrate until this layer, are more isolated from each other from a functional point of view. It may indicate lower competition among species with a similar set of trait values in this layer (Brandl et al., 2016). However, we observed an increase in this index in the upper mesopelagic layer during the night period, for which the mean value of FOri became near one of the lower mesopelagic layers. Compared to the three layers, the epipelagic layer exhibits higher functional redundancy, except during the day period, which could potentially lead to higher community resilience (Rice et al., 2013), where only a few species were found, such as Bramma spp., *Gempylus serpens*, and *Zu cristatus*. This could be due to the higher migration of species with similar functional features during nighttime at the epipelagic layer. Finally, the mean alpha values of functional specialization (FSpe) found in the mesopelagic community, in particular during the day, may indicate greater ecological stability of the overall assemblages during that time a period, but also greater species vulnerability to environmental changes.

When comparing different depths, the mean alpha functional richness index (FRic) was found to be higher in the lower depths (Figure 4), along with a higher number of species (Figure S3). Eduardo et al. (2022) also observed higher species richness in the lower mesopelagic waters, while Martinez et al. (2021) noted an increase in morphological disparity of deep-sea fish, suggesting the deep sea as a potential hotspot for fish evolution. Tuset et al. (2014) also highlighted a depth effect on the morphospace established from morphological features of mesopelagic fishes. Gluchowska et al. (2017) similarly noted that depth-related variables are crucial in structuring the functional diversity of zooplankton assemblages, with mesopelagic assemblages being more diverse and uniformly distributed than epipelagic ones. Likewise, Mindel et al. (2016) found that for abyssal fishes (1,000–4,000 m), while abundance decreases with depth, there is an increase in functional diversity, with more distinct traits found in deeper layers, probably also because resources are scarcer. Overall, it highlights that the relationship between depth and functional diversity may depend on the type and features of the ecosystem studied.

*Relationships among traits, environment, and time period*

This study found a significant correlation among depth (salinity and temperature being correlated with depth), teeth type 1 (long, slender, and sharp), the presence of a lure apparatus structure, non-migration, behavior, and black skin color, but only during the day period (Figure S10). Interestingly, the family Stomiidae predominantly has these traits, especially for teeth type 1 (77.5% of species), the presence of a luring apparatus (70% of species), and black skin (41.1% of species).

Teeth type 1 enables these fish to easily hold and pierce prey, which, when combined with a wide jaw opening of some species (e.g., *M. niger* and *E. pelecanoides*), increases the likelihood of capturing prey. The black color, in contrast, provides effective camouflage, allowing these species to blend into their dark environment and evade predators or sneak up on prey. It also minimizes bioluminescent reflections, reducing detection by organisms using bioluminescence for communication or hunting. For example, some species found in the lower mesopelagic layer exhibit a coloration recently defined as ultra-black (e.g., Eustomias spp. and Melamphaes spp.), which absorbs most light and make them formidable hunters (Davis et al., 2020b), knowing also that some species have many photophores and silver body.

The presence of lure apparatus and non-migratory behavior related to depth are also notable examples of characteristics associated with species inhabiting deeper waters (other species of Stomiiformes with lure apparatus in the inferior mouth occurred in the upper layer). The non-migratory behavior may be related to preventing species in deeper strata from expending energy to move. While this might limit feeding opportunities, this appears to be counterbalanced by ambush-feeding strategies employed by certain species, such as anglerfishes, which utilize bioluminescent lures to attract their prey. These lure apparatuses imitate the bioluminescence of their prey’s food sources or conspecifics, enticing unsuspecting prey toward them and facilitating easier capture (Widder, 2010).

In addition to the traits that exhibit a significant correlation with depth, mesopelagic fishes present other important adaptations that allow them to explore and use deep environments that are important to be mentioned. For example, in some bristlemouths (Gonostomatidae), the eyes are small, yet the relative pupil diameter and aphakic gap are large. This adaptation substantially improves retinal illumination for peripheral targets in low-light environments, such as the mesopelagic zone (Davis et al., 2020a). Moreover, certain species possess multiple rhodopsin genes, which encode the protein crucial for vision in low-light conditions. For instance, *Diretmus argenteus* has 38 copies of the rhodopsin gene and two other distinct opsins (Turner et al., 2009). This enables the detection of bioluminescence wavelengths, suggesting an advantage in food capture and predator evasion tactics. However, such traits were not correlated with any specific layer, likely due to the movement of species between various layers.

### *Hypotheses on processes structuring mesopelagic fish community*

The first underlying hypothesis suggested by the observed patterns is that deeper and more stable environments led to more species specialization and thus encompass more different and functional complementary species as we quantified (Table S3; Figures 3, 4, S4–8). Indeed, environmental gradients play an important role in morphological evolution, impacting the nature and pattern of trait variation in organisms (Conover and Schultz, 1995; Goldberg and Lande, 2006; Mullen and Hoekstra, 2008; Juarez et al., 2019). Notably, depth-related factors like light, temperature, and oxygen can act as a barrier for some mesopelagic fishes, for which displacement represents a higher energetic expenditure (Robison, 2004). Some other species can inhabit areas with reduced oxygen levels (Olivar et al., 2017; Assunção et al., 2023). They may use these less oxygenated layers as protection from predators or as an energy-saving strategy during the day, leaving this zone at night. It is also known that environmental heterogeneity generates diversifying selection, so if there are no constraints on the ecological niche evolution, the breadth of adaptation should evolve to match the amount of environmental variation (Via and Lande, 1985). Therefore, ecological specialists should occur more in environments that are relatively homogeneous in space and time, such as in deep zones, whereas ecological generalists should occur more in environments that are heterogeneous in either dimension (Kassen, 2002).

In stable environments where photosynthetic primary production is absent, species specialization can also be an evolutionary advantage (Kassen, 2002). For instance, specialization is one of the primary mechanisms allowing sympatric species to coexist through the division of resources. Lanternfishes (Myctophidae) and hatchet fishes (Sternoptychidae), the two most abundant mesopelagic fish families in our samples, differ in their prey composition, space occupation, and morphology, displaying high specialization and multidimensional niche partitioning (Tuset et al., 2018; Eduardo et al., 2020b, 2021).

A second and linked underlying hypothesis suggested by the observed diversity patterns is a "limiting similarity" among species (MacArthur and Levins, 1967), presented in the Introduction section. While environmental filtering may contribute to structuring the fish communities studied (Figure 5; Table 5), our results supported a predominance of the limiting similarity hypothesis. Concurrently, competition theory (Schoener, 1974; Abrams, 1992) could also be an evolutionary process, where shorter trophic chains and fewer alternative resources available may reduce interspecific dietary overlap, leading to greater adaptation and specialization in deep environments. In these areas, where photosynthetic food availability is lower, adaptation and species specialization could minimize competition and functional similarity. Such specialization may, therefore, increase functional diversity, as demonstrated for some coral reef fish (Bender and Luiz, 2019).

Furthermore, environmental stability for mesopelagic fishes can vary across the bathymetric layers. On the one hand, environmental conditions in the epipelagic zone are affected by factors such as solar radiation, wind, and nutrient availability, which can vary on a daily or seasonal basis, leading to fluctuations in temperature, salinity, and nutrient concentrations. On the other hand, the mesopelagic zone is more stable in terms of temperature and salinity, as it is less influenced by surface-related factors (Priede, 2017).

The relationship between environmental variables and functional diversity indices provides insights into possible changes that may occur in functional space due to environmental variations. Our results showed that the variations in the functional diversity of fishes are partly related to environmental variables (Figures 5, S9; Table 5). Therefore, if oceanographic processes and the period of year cause the mesopelagic environment to move closer to the surface, species with unique traits could be exposed to increased anthropogenic interaction, resulting in potential changes to the mesopelagic fish community.

The preservation and management of the deep environment are of particular concern, as human interest in this zone is increasing in different areas worldwide, with potential impacts from fisheries(Hidalgo and Browman, 2019), deep-sea mining, plastic pollution (Drazen et al., 2020; Ferreira et al., 2022; Justino et al., 2022a), and climate change (warming, deoxygenation, and acidification, Ramirez-Llodra et al., 2011; Barry et al., 2013). Notably, while the study area is a well-oxygenated zone when compared to other mesopelagic areas in the world (Priede, 2017), the expansion of oxygen minimum zones (Gilly et al., 2013) could be of particular concern. If mesopelagic species are adapted to the stability of deep-sea waters, disturbances may threaten mesopelagic communities. Regarding the mesopelagic fish communities off north-western Brazil, we have highlighted a relatively low sharing of functional trait values among species, with more than half of them having unique trait combinations. It emphasizes a considerable potential for providing distinct species contributions to ecosystem functioning. However, it also underlines the relative functional uniqueness of species and thus the potential vulnerability of fish communities facing threats in cases where some species decrease in abundance or even disappear. Overall, this calls for particular attention to dedicated and accurate management measures for mesopelagic fish communities in the studied area.

## Supplementary material

**Table S1.** Species list (n=200 species).

| Order | Family | Species |
|---|---|---|
| ALEPOCEPHALIFORMES | Alepocephalidae | Alepocephalidae sp. |
| ALEPOCEPHALIFORMES | Alepocephalidae | *Photostylus pycnopterus* Beebe, 1933 |
| ALEPOCEPHALIFORMES | Platytroctidae | Platytroctidae sp. |
| ANGUILLIFORMES | Eurypharyngidae | *Eurypharynx pelecanoides* Vaillant, 1882 |
| ANGUILLIFORMES | Nemichthyidae | *Avocettina infans* (Günther, 1878) |
| ANGUILLIFORMES | Nemichthyidae | *Labichthys carinatus* Gill & Ryder, 1883 |
| ANGUILLIFORMES | Nemichthyidae | *Nemichthys scolopaceus* Richardson, 1848 |
| ANGUILLIFORMES | Serrivomeridae | *Serrivomer beanii* Gill & Ryder, 1883 |
| ANGUILLIFORMES | Serrivomeridae | *Serrivomer lanceolatoides* (Schmidt, 1916) |
| ANGUILLIFORMES | Serrivomeridae | *Stemonidium hypomelas* Gilbert, 1905 |
| ARGENTINIFORMES | Bathylagidae | *Dolicholagus longirostris* (Maul, 1948) |
| ARGENTINIFORMES | Bathylagidae | *Melanolagus bericoides* (Borodin, 1929) |
| ARGENTINIFORMES | Microstomatidae | *Xenophthalmichthys danae* Regan, 1925 |
| ARGENTINIFORMES | Opisthoproctidae | *Opisthoproctus soleatus* Vaillant, 1888 |
| ARGENTINIFORMES | Opisthoproctidae | *Rhynchohyalus natalensis* (Gilchrist & von Bonde, 1924) |
| ARGENTINIFORMES | Opisthoproctidae | *Winteria telescopa* Brauer, 1901 |
| ATELEOPODIFORMES | Ateleopodidae | Ateleopodidae sp. |
| AULOPIFORMES | Anotopteridae | *Anotopterus pharao* Zugmayer, 1911 |

| | | |
|---|---|---|
| AULOPIFORMES | Alepisauridae | *Omosudis lowii* Günther, 1887 |
| AULOPIFORMES | Evermannellidae | *Odontostomops normalops* (Parr, 1928) |
| AULOPIFORMES | Giganturidae | *Gigantura chuni* Brauer, 1901 |
| AULOPIFORMES | Giganturidae | *Gigantura indica* Brauer, 1901 |
| AULOPIFORMES | Chlorophthalmidae | *Parasudis truculenta* (Goode & Bean, 1896) |
| AULOPIFORMES | Notosudidae | *Ahliesaurus berryi* Bertelsen, Krefft & Marshall, 1976 |
| AULOPIFORMES | Paralepididae | *Lestrolepis intermedia* (Poey, 1868) |
| AULOPIFORMES | Paralepididae | *Macroparalepis brevis* Ege, 1933 |
| AULOPIFORMES | Paralepididae | *Stemonosudis gracilis* (Ege, 1933) |
| AULOPIFORMES | Paralepididae | *Stemonosudis intermedia* (Ege, 1933) |
| AULOPIFORMES | Scopelarchidae | *Benthalbella infans* Zugmayer, 1911 |
| AULOPIFORMES | Scopelarchidae | *Rosenblattichthys hubbsi* Johnson, 1974 |
| AULOPIFORMES | Scopelarchidae | *Scopelarchoides danae* Johnson, 1974 |
| AULOPIFORMES | Scopelarchidae | *Scopelarchus analis* (Brauer, 1902) |
| AULOPIFORMES | Scopelarchidae | *Scopelarchus guentheri* Alcock, 1896 |
| BERYCIFORMES | Cetomimidae | *Cetomimus* sp. |
| BERYCIFORMES | Cetomimidae | *Cetostoma regani* Zugmayer, 1914 |
| BERYCIFORMES | Cetomimidae | *Ditropichthys storeri* Goode & Bean, 1895 |
| BERYCIFORMES | Cetomimidae | *Gyrinomimus bruuni* Rofen, 1959 |
| BERYCIFORMES | Melamphaidae | *Melamphaes eulepis* Ebeling, 1962 |
| BERYCIFORMES | Melamphaidae | *Melamphaes leprus* Ebeling, 1962 |
| BERYCIFORMES | Melamphaidae | *Melamphaes longivelis* Parr, 1933 |
| BERYCIFORMES | Melamphaidae | *Melamphaes polylepis* Ebeling, 1962 |
| BERYCIFORMES | Melamphaidae | *Melamphaes typhlops* (Lowe, 1843) |
| BERYCIFORMES | Melamphaidae | *Melamphaes* sp. |
| BERYCIFORMES | Melamphaidae | *Poromitra megalops* (Lütken, 1878) |
| BERYCIFORMES | Melamphaidae | *Poromitra* sp. |
| BERYCIFORMES | Melamphaidae | *Scopeloberyx opercularis* Zugmayer, 1911 |
| BERYCIFORMES | Melamphaidae | *Scopeloberyx opisthopterus* (Parr, 1933) |
| BERYCIFORMES | Melamphaidae | *Scopelogadus mizolepis* (Günther, 1878) |
| BERYCIFORMES | Rondeletiidae | *Rondeletia loricata* Abe & Hotta, 1963 |
| CAPROIFORMES | Caproidae | *Antigonia capros* Lowe, 1843 |
| CAPROIFORMES | Caproidae | *Antigonia combatia* Berry & Rathjen, 1959 |
| GADIFORMES | Bregmacerotidae | *Bregmaceros* cf. *atlanticus* Goode & Bean, 1886 |
| GADIFORMES | Macrouridae | *Bathygadus* sp. |
| GADIFORMES | Macrouridae | *Macrouroides inflaticeps* Smith & Radcliffe, 1912 |
| GADIFORMES | Melanonidae | *Melanonus zugmayeri* Norman, 1930 |
| KUTIFORMES | Apogonidae | *Paroncheilus affinis* (Poey, 1875) |
| LAMPRIFORMES | Lophotidae | *Eumecichthys fiski* (Günther, 1890) |
| LAMPRIFORMES | Trachipteridae | *Desmodema polystictum* (Ogilby, 1898) |
| LAMPRIFORMES | Trachipteridae | *Trachipterus* sp. |
| LAMPRIFORMES | Trachipteridae | *Zu cristatus* (Bonelli, 1819) |
| LOPHIIFORMES | Caulophrynidae | *Caulophryne* sp. |
| LOPHIIFORMES | Ceratiidae | *Ceratias uranoscopus* Murray, 1877 |
| LOPHIIFORMES | Gigantactinidae | *Gigantactis watermani* Bertelsen, Pietsch & Lavenberg, 1981 |

| | | |
|---|---|---|
| LOPHIIFORMES | Gigantactinidae | *Rhynchactis* sp. |
| LOPHIIFORMES | Melanocetidae | *Melanocetus johnsonii* Günther, 1864 |
| LOPHIIFORMES | Himantolophidae | *Himantolophus sp.* |
| LOPHIIFORMES | Oneirodidae | *Chaenophryne draco* Beebe, 1932 |
| LOPHIIFORMES | Oneirodidae | *Chaenophryne ramifera* Regan & Trewavas, 1932 |
| LOPHIIFORMES | Oneirodidae | *Dolopichthys* sp. |
| LOPHIIFORMES | Oneirodidae | *Oneirodes anisacanthus* (Regan, 1925) |
| LOPHIIFORMES | Oneirodidae | *Oneirodes carlsbergi* (Regan & Trewavas, 1932) |
| LOPHIIFORMES | Thaumatichthyidae | *Thaumatichthys* sp. |
| MYCTOPHIFORMES | Myctophidae | *Benthosema suborbitale* (Gilbert, 1913) |
| MYCTOPHIFORMES | Myctophidae | *Bolinichthys distofax* Johnson, 1975 |
| MYCTOPHIFORMES | Myctophidae | *Bolinichthys photothorax* (Parr, 1928) |
| MYCTOPHIFORMES | Myctophidae | *Bolinichthys supralateralis* (Parr, 1928) |
| MYCTOPHIFORMES | Myctophidae | *Ceratoscopelus warmingii* (Lütken, 1892) |
| MYCTOPHIFORMES | Myctophidae | *Dasyscopelus asper* (Richardson 1845) |
| MYCTOPHIFORMES | Myctophidae | *Dasyscopelus obtusirostre* (Tåning, 1928) |
| MYCTOPHIFORMES | Myctophidae | *Dasyscopelus selenops* (Tåning, 1928) |
| MYCTOPHIFORMES | Myctophidae | *Diaphus bertelseni* Nafpaktitis, 1966 |
| MYCTOPHIFORMES | Myctophidae | *Diaphus brachycephalus* Tåning, 1928 |
| MYCTOPHIFORMES | Myctophidae | *Diaphus dumerilii* (Bleeker, 1856) |
| MYCTOPHIFORMES | Myctophidae | *Diaphus fragilis* Tåning, 1928 |
| MYCTOPHIFORMES | Myctophidae | *Diaphus garmani* Gilbert, 1906 |
| MYCTOPHIFORMES | Myctophidae | *Diaphus lucidus* (Goode & Bean, 1896) |
| MYCTOPHIFORMES | Myctophidae | *Diaphus mollis* (Tåning, 1928) |
| MYCTOPHIFORMES | Myctophidae | *Diaphus perspicillatus* (Ogilby, 1898) |
| MYCTOPHIFORMES | Myctophidae | *Diaphus problematicus* Parr, 1928 |
| MYCTOPHIFORMES | Myctophidae | *Diaphus splendidus* (Brauer, 1904) |
| MYCTOPHIFORMES | Myctophidae | *Diogenichthys atlanticus* (Tåning, 1928) |
| MYCTOPHIFORMES | Myctophidae | *Electrona risso* (Cocco, 1829) |
| MYCTOPHIFORMES | Myctophidae | *Hygophum hygomii* (Lütken, 1892) |
| MYCTOPHIFORMES | Myctophidae | *Hygophum macrochir* (Günther, 1864) |
| MYCTOPHIFORMES | Myctophidae | *Hygophum reinhardtii* (Lütken, 1892) |
| MYCTOPHIFORMES | Myctophidae | *Hygophum taaningi* Becker, 1965 |
| MYCTOPHIFORMES | Myctophidae | *Lampadena luminosa* (Garman, 1899) |
| MYCTOPHIFORMES | Myctophidae | *Lampanyctus alatus* Goode & Bean, 1896 |
| MYCTOPHIFORMES | Myctophidae | *Lampanyctus lineatus* Tåning, 1928 |
| MYCTOPHIFORMES | Myctophidae | *Lampanyctus festivus* Tåning, 1928 |
| MYCTOPHIFORMES | Myctophidae | *Lampanyctus nobilis* Tåning, 1928 |
| MYCTOPHIFORMES | Myctophidae | *Lampanyctus tenuiformis* (Brauer, 1906) |
| MYCTOPHIFORMES | Myctophidae | *Lepidophanes guentheri* (Goode & Bean, 1896) |
| MYCTOPHIFORMES | Myctophidae | *Myctophum nitidulum* Garman, 1899 |
| MYCTOPHIFORMES | Myctophidae | *Notoscopelus resplendens* (Richardson, 1845) |
| MYCTOPHIFORMES | Myctophidae | *Taaningichthys bathyphilus* (Tåning, 1928) |
| MYCTOPHIFORMES | Neoscopelidae | *Scopelengys tristis* Alcock, 1890 |
| NOTACANTHIFORMES | Halosauridae | *Aldrovandia* sp. |
| OPHIDIIFORMES | Bythitidae | *Bythitidae* sp. |

| | | |
|---|---|---|
| PERCIFORMES | Bramidae | *Brama brama* (Bonaterre, 1788) |
| PERCIFORMES | Bramidae | *Brama caribbea* Mead, 1972 |
| PERCIFORMES | Bramidae | *Taractichthys longipinnis* (Lowe, 1843) |
| PERCIFORMES | Caristiidae | *Paracaristius nudarcus* Stevenson & Kenaley, 2011 |
| PERCIFORMES | Caristiidae | *Platyberyx andriashevi* (Kukuev, Parin & Trunov, 2012) |
| PERCIFORMES | Caristiidae | *Platyberyx paucus* Stevenson & Kenaley, 2013 |
| PERCIFORMES | Caristiidae | *Platyberyx pietschi* Stevenson & Kenaley, 2013 |
| PERCIFORMES | Howellidae | *Bathysphyraenops simplex* Parr, 1933 |
| PERCIFORMES | Howellidae | *Howella atlantica* Post & Quéro, 1991 |
| SCOMBRIFORMES | Gempylidae | *Gempylus serpens* Cuvier, 1829 |
| SCOMBRIFORMES | Gempylidae | *Lepidocybium flavobrunneum* (Smith, 1843) |
| SCOMBRIFORMES | Gempylidae | *Nesiarchus nasutus* Johnson, 1862 |
| SCOMBRIFORMES | Gempylidae | *Promethichthys prometheus* (Cuvier, 1832) |
| SCOMBRIFORMES | Nomeidae | *Cubiceps pauciradiatus* Günther, 1872 |
| SCOMBRIFORMES | Nomeidae | *Psenes cyanophrys* Valenciennes, 1833 |
| SCOMBRIFORMES | Trichiuridae | *Aphanopus intermedius* Parin, 1983 |
| SCOMBROLABRACIFORMES | Scombrolabracidae | *Scombrolabrax heterolepis* Roule, 1921 |
| SCORPAENIFORMES | Setarchidae | *Ectreposebastes imus* Garman, 1899 |
| SQUALIFORMES | Dalatiidae | *Isistius brasiliensis* (Quoy & Gaimard, 1824) |
| STOMIIFORMES | Diplophidae | *Diplophos australis* Ozawa, Oda & Ida, 1990 |
| STOMIIFORMES | Diplophidae | *Diplophos taenia* Günther, 1873 |
| STOMIIFORMES | Diplophidae | *Manducus maderensis* (Johnson, 1890) |
| STOMIIFORMES | Diplophidae | *Triplophos hemingi* (McArdle, 1901) |
| STOMIIFORMES | Gonostomatidae | *Bonapartia pedaliota* (Goode & Bean, 1896) |
| STOMIIFORMES | Gonostomatidae | *Cyclothone* spp. |
| STOMIIFORMES | Gonostomatidae | *Gonostoma atlanticum* Norman, 1930 |
| STOMIIFORMES | Gonostomatidae | *Gonostoma denudatum* Rafinesque, 1810 |
| STOMIIFORMES | Gonostomatidae | *Margrethia obtusirostra* Jespersen & Tåning, 1919 |
| STOMIIFORMES | Gonostomatidae | *Sigmops bathyphilus* Vaillant, 1884 |
| STOMIIFORMES | Gonostomatidae | *Sigmops elongatus* (Günther, 1878) |
| STOMIIFORMES | Phosichthyidae | *Ichthyococcus polli* Blache, 1964 |
| STOMIIFORMES | Phosichthyidae | *Phosichthys argenteus* Hutton, 1872 |
| STOMIIFORMES | Phosichthyidae | *Pollichthys mauli* (Poll, 1953) |
| STOMIIFORMES | Phosichthyidae | *Vinciguerria nimbaria* (Jordan & Williams, 1895) |
| STOMIIFORMES | Sternoptychidae | *Argyropelecus aculeatus* Valenciennes, 1850 |
| STOMIIFORMES | Sternoptychidae | *Argyropelecus affinis* Garman, 1899 |
| STOMIIFORMES | Sternoptychidae | *Argyropelecus gigas* Norman, 1930 |
| STOMIIFORMES | Sternoptychidae | *Argyropelecus hemigymnus* Cocco, 1829 |
| STOMIIFORMES | Sternoptychidae | *Argyropelecus sladeni* Regan, 1908 |
| STOMIIFORMES | Sternoptychidae | *Sternoptyx diaphana* Hermann, 1781 |
| STOMIIFORMES | Sternoptychidae | *Sternoptyx pseudobscura* Baird, 1971 |
| STOMIIFORMES | Sternoptychidae | *Sternoptyx pseudodiaphana* Borodulina, 1977 |
| STOMIIFORMES | Sternoptychidae | *Valenciennellus tripunctulatus* (Esmark, 1871) |
| STOMIIFORMES | Stomiidae | *Aristostomias grimaldii* Zugmayer, 1913 |
| STOMIIFORMES | Stomiidae | *Aristostomias tittmanni* Welsh, 1923 |

| | | |
|---|---|---|
| STOMIIFORMES | Stomiidae | *Astronesthes atlanticus* Parin & Borodulina, 1996 |
| STOMIIFORMES | Stomiidae | *Astronesthes gemmifer* Goode & Bean, 1896 |
| STOMIIFORMES | Stomiidae | *Astronesthes gudrunae* Parin & Borodulina, 2002 |
| STOMIIFORMES | Stomiidae | *Astronesthes richardsoni* (Poey, 1852) |
| STOMIIFORMES | Stomiidae | *Astronesthes similus* Parr, 1927 |
| STOMIIFORMES | Stomiidae | *Bathophilus nigerrimus* Giglioli, 1882 |
| STOMIIFORMES | Stomiidae | *Bathophilus pawneei* Parr, 1927 |
| STOMIIFORMES | Stomiidae | *Borostomias elucens* (Brauer, 1906) |
| STOMIIFORMES | Stomiidae | *Chauliodus sloani* Bloch & Schneider, 1801 |
| STOMIIFORMES | Stomiidae | *Eustomias bibulbosus* Parr, 1927 |
| STOMIIFORMES | Stomiidae | *Eustomias braueri* Zugmayer, 1911 |
| STOMIIFORMES | Stomiidae | *Eustomias brevibarbatus* Parr, 1927 |
| STOMIIFORMES | Stomiidae | *Eustomias enbarbatus* Welsh, 1923 |
| STOMIIFORMES | Stomiidae | *Eustomias minimus* Clarke, 1999 |
| STOMIIFORMES | Stomiidae | *Eustomias schmidti* Regan & Trewavas, 1930 |
| STOMIIFORMES | Stomiidae | *Eustomias* sp. 1 |
| STOMIIFORMES | Stomiidae | *Eustomias* sp. 2 |
| STOMIIFORMES | Stomiidae | *Eustomias* sp. 3 |
| STOMIIFORMES | Stomiidae | *Eustomias* sp. 4 |
| STOMIIFORMES | Stomiidae | *Eustomias* sp. 5 |
| STOMIIFORMES | Stomiidae | *Grammatostomias dentatus* Goode & Bean, 1896 |
| STOMIIFORMES | Stomiidae | *Grammatostomias ovatus* Prokofiev, 2014 |
| STOMIIFORMES | Stomiidae | *Heterophotus ophistoma* Regan & Trewavas, 1929 |
| STOMIIFORMES | Stomiidae | *Leptostomias gladiator* (Zugmayer, 1911) |
| STOMIIFORMES | Stomiidae | *Malacosteus niger Ayres, 1848* |
| STOMIIFORMES | Stomiidae | *Melanostomias biseriatus* Regan & Trewavas, 1930 |
| STOMIIFORMES | Stomiidae | *Melanostomias bartonbeanis* Parr, 1927 |
| STOMIIFORMES | Stomiidae | *Melanostomias dio* Villarins, Fischer, Prokofiev, Mincarone, 2023 |
| STOMIIFORMES | Stomiidae | *Melanostomias tentaculatus* (Regan & Trewavas, 1930) |
| STOMIIFORMES | Stomiidae | *Pachystomias microdon* (Günther, 1878) |
| STOMIIFORMES | Stomiidae | *Photonectes achirus* Regan & Trewavas, 1930 |
| STOMIIFORMES | Stomiidae | *Photostomias atrox* (Alcock, 1890) |
| STOMIIFORMES | Stomiidae | *Photostomias goodyeari* Kenaley & Hartel, 2005 |
| STOMIIFORMES | Stomiidae | *Stomias danae* Ege, 1933 |
| STOMIIFORMES | Stomiidae | *Stomias longibarbatus* (Brauer, 1902) |
| STOMIIFORMES | Stomiidae | *Thysanactis dentex* Regan & Trewavas, 1930 |
| STYLEPHORIFORMES | Stylephoridae | *Stylephorus chordatus* Shaw, 1791 |
| TRACHICHTHYIFORMES | Anoplogastridae | *Anoplogaster cornuta* (Valenciennes, 1833) |
| TRACHICHTHYIFORMES | Diretmidae | *Diretmoides pauciradiatus* (Woods, 1973) |
| TRACHICHTHYIFORMES | Diretmidae | *Diretmus argenteus* Johnson, 1864 |
| TRACHICHTHYIFORMES | Trachichthyidae | *Aulotrachichthys argyrophanus* (Woods, 1961) |
| TRACHINIFORMES | Chiasmodontidae | *Chiasmodon braueri* Weber, 1913 |
| TRACHINIFORMES | Chiasmodontidae | *Chiasmodon niger* Johnson, 1864 |
| TRACHINIFORMES | Chiasmodontidae | *Kali kerberti* (Weber, 1913) |
| TRACHINIFORMES | Chiasmodontidae | *Pseudoscopelus cordilluminatus* Melo, 2010 |

| | | |
|---|---|---|
| TRACHINIFORMES | Chiasmodontidae | *Pseudoscopelus scutatus* Krefft, 1971 |

**Table S2.** Functional diversity index value in each station (alpha diversity) of *epipelagic, *upper mesopelagic and,*lower mesopelagic layers.

| **Station** | **Richness** | **Fdis** | **Feve** | **Fric** | **Fdiv** | **Fori** | **Fspe** |
|---|---|---|---|---|---|---|---|
| 1_1* | 11 | 0.31 | 0.29 | 0.15 | 0.93 | 0.05 | 0.57 |
| 1_12* | 12 | 0.27 | 0.55 | 0.32 | 0.55 | 0.07 | 0.57 |
| 1_14* | 21 | 0.39 | 0.60 | 0.49 | 0.78 | 0.41 | 0.49 |
| 1_15* | 7 | 0.27 | 0.54 | 0.07 | 0.72 | 0.25 | 0.62 |
| 1_20* | 3 | 0.30 | 0.14 | 0.02 | 0.66 | 0.11 | 0.61 |
| 1_21* | 3 | 0.17 | 0.32 | 0.01 | 0.76 | 0.31 | 0.53 |
| 1_22* | 25 | 0.50 | 0.74 | 0.70 | 0.70 | 0.22 | 0.55 |
| 1_25* | 4 | 0.26 | 0.58 | 0.06 | 0.78 | 0.11 | 0.44 |
| 1_26* | 4 | 0.15 | 0.21 | 0.06 | 0.69 | 0.39 | 0.72 |
| 1_31* | 4 | 0.20 | 0.39 | 0.04 | 0.70 | 0.37 | 0.56 |
| 1_34* | 9 | 0.52 | 0.69 | 0.30 | 0.84 | 0.08 | 0.51 |
| 1_4* | 3 | 0.17 | 0.88 | 0.01 | 0.90 | 0.27 | 0.45 |
| 1_5* | 9 | 0.26 | 0.45 | 0.21 | 0.95 | 0.02 | 0.59 |
| 1_51* | 9 | 0.19 | 0.57 | 0.31 | 0.23 | 0.61 | 0.40 |
| 1_52* | 3 | 0.12 | 0.12 | 0.17 | 0.98 | 0.72 | 0.39 |
| 1_9* | 13 | 0.22 | 0.48 | 0.49 | 0.62 | 0.03 | 0.56 |
| 2_16* | 36 | 0.37 | 0.40 | 0.82 | 0.64 | 0.28 | 0.52 |
| 2_21* | 32 | 0.35 | 0.51 | 0.58 | 0.58 | 0.33 | 0.51 |
| 2_28* | 23 | 0.28 | 0.34 | 0.35 | 0.57 | 0.02 | 0.50 |
| 2_35* | 25 | 0.22 | 0.58 | 0.55 | 0.94 | 0.07 | 0.67 |
| 2_39* | 59 | 0.32 | 0.45 | 0.84 | 0.85 | 0.32 | 0.57 |
| 2_40A* | 29 | 0.50 | 0.47 | 0.53 | 0.74 | 0.18 | 0.61 |
| 2_41A* | 53 | 0.44 | 0.46 | 0.87 | 0.75 | 0.18 | 0.61 |
| 2_41B* | 8 | 0.43 | 0.66 | 0.19 | 0.54 | 0.33 | 0.53 |
| 2_42A* | 55 | 0.43 | 0.52 | 0.90 | 0.65 | 0.45 | 0.52 |
| 2_44A* | 63 | 0.49 | 0.54 | 0.93 | 0.69 | 0.43 | 0.51 |
| 2_44B* | 5 | 0.49 | 0.79 | 0.27 | 0.90 | 0.29 | 0.53 |
| 2_45B* | 13 | 0.26 | 0.26 | 0.14 | 0.81 | 0.02 | 0.54 |
| 2_46A* | 3 | 0.27 | 0.28 | 0.05 | 0.79 | 0.35 | 0.71 |
| 2_46B* | 5 | 0.45 | 0.71 | 0.10 | 0.75 | 0.13 | 0.68 |
| 2_48A* | 10 | 0.53 | 0.38 | 0.58 | 0.93 | 0.22 | 0.68 |
| 2_48B* | 4 | 0.14 | 0.36 | 0.09 | 0.48 | 0.29 | 0.51 |
| 2_49A* | 40 | 0.47 | 0.60 | 0.69 | 0.82 | 0.30 | 0.54 |
| 2_49B* | 28 | 0.26 | 0.49 | 0.49 | 0.73 | 0.02 | 0.55 |
| 2_50A* | 22 | 0.51 | 0.65 | 0.53 | 0.86 | 0.43 | 0.61 |
| 2_52A* | 54 | 0.47 | 0.58 | 0.90 | 0.65 | 0.29 | 0.49 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 2_52B* | 23 | 0.31 | 0.44 | 0.59 | 0.62 | 0.14 | 0.62 |
| 2_53A* | 47 | 0.45 | 0.51 | 0.87 | 0.84 | 0.35 | 0.58 |
| 2_53B* | 10 | 0.30 | 0.41 | 0.21 | 0.65 | 0.06 | 0.61 |
| 2_54B* | 49 | 0.40 | 0.53 | 0.84 | 0.93 | 0.24 | 0.56 |
| 2_56B* | 4 | 0.09 | 0.60 | 0.05 | 0.20 | 0.22 | 0.62 |
| 2_56C* | 14 | 0.28 | 0.46 | 0.40 | 0.70 | 0.03 | 0.59 |
| 2_58A* | 13 | 0.30 | 0.54 | 0.21 | 0.82 | 0.25 | 0.61 |
| 2_59A* | 33 | 0.35 | 0.49 | 0.85 | 0.82 | 0.37 | 0.56 |
| 2_59B* | 14 | 0.18 | 0.29 | 0.20 | 0.87 | 0.20 | 0.61 |
| 2_60B* | 17 | 0.47 | 0.54 | 0.47 | 0.91 | 0.42 | 0.63 |
| 2_9* | 6 | 0.02 | 0.01 | 0.00 | 0.76 | 0.00 | 0.57 |

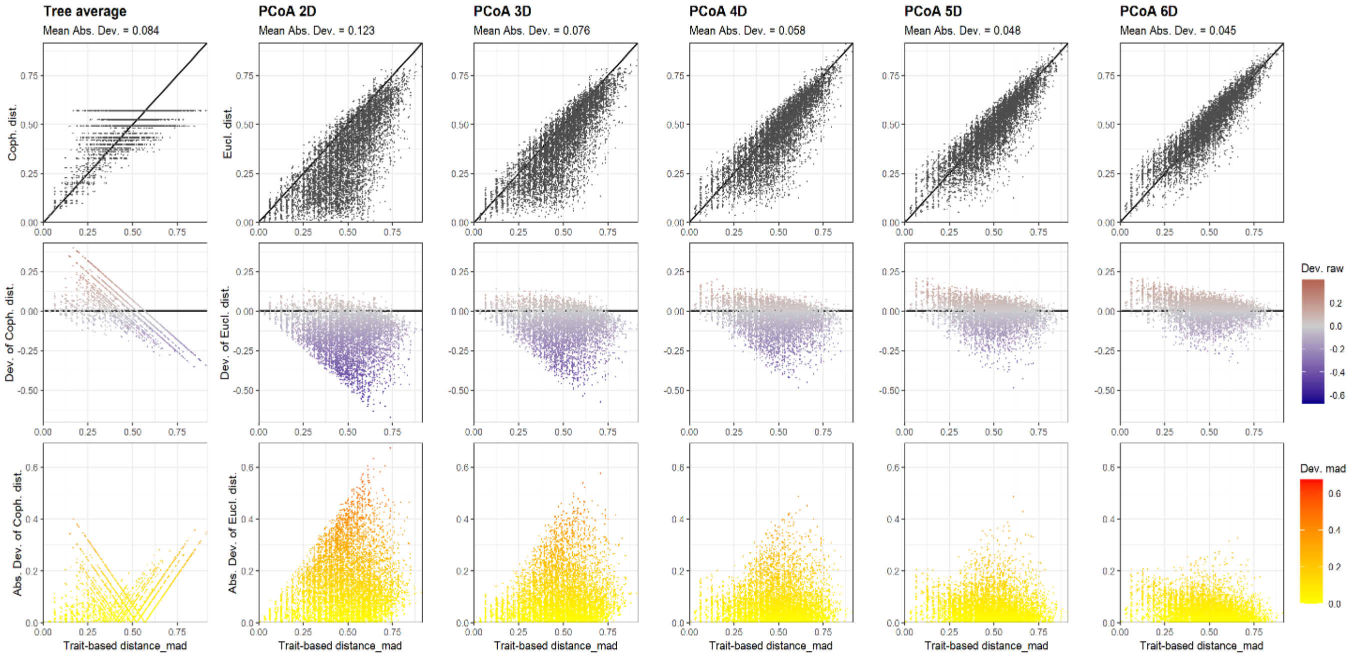


**Figure S1** Quality of functional space computed from the initial species trait-based matrix by (i) a clustering analyses (UPGMA dendrogram "tree average"), and (ii) a Principal Coordinated Analysis (PCoA) considering 2 to 5 dimensions (D). It shows the relation among the initial species trait-based distance matrix and species distance matrix from each multivariate analysis. Deviation among those distance matrices accesses if the matrix from the multi-variate analysis is faithful to the initial trait-based matrix (deviation metric ranges between 0 and 1). The higher the value of the deviation metric, the higher the deviations among the initial trait-based and space-based distances among species, hence the lower the quality of the functional space is.

**Table S3** Mean and standard deviation values of the complementary functional indices by oceanographic layer and period.

| | FRic | FEve | FDiv | FDis | FOri | FSpe |
|---|---|---|---|---|---|---|
| **Day** | | | | | | |
| Epipelagic | 0.094 ± 0.02 | 0.585 ± 0.06 | 0.759 ± 0.04 | 0.243 ± 0.03 | 0.289 ± 0.00 | 0.504 ± 0.01 |
| Upper meso | 0.265 ± 0.05 | 0.499 ± 0.03 | 0.619 ± 0.04 | 0.322 ± 0.03 | 0.204 ± 0.01 | 0.650 ± 0.01 |
| Lower meso | 0.509 ± 0.06 | 0.470 ± 0.03 | 0.777 ± 0.02 | 0.365 ± 0.03 | 0.341 ± 0.03 | 0.573 ± 0.02 |
| **Night** | | | | | | |
| Epipelagic | 0.212 ± 0.03 | 0.400 ± 0.03 | 0.732 ± 0.02 | 0.271 ± 0.02 | 0.289 ± 0.00 | 0.552 ± 0.00 |
| Upper meso | 0.681 ± 0.05 | 0.527 ± 0.01 | 0.764 ± 0.00 | 0.414 ± 0.00 | 0.204 ± 0.01 | 0.549 ± 0.01 |
| Lower meso | 0.704 ± 0.03 | 0.544 ± 0.02 | 0.728 ± 0.04 | 0.359 ± 0.02 | 0.314 ± 0.02 | 0.548 ± 0.01 |

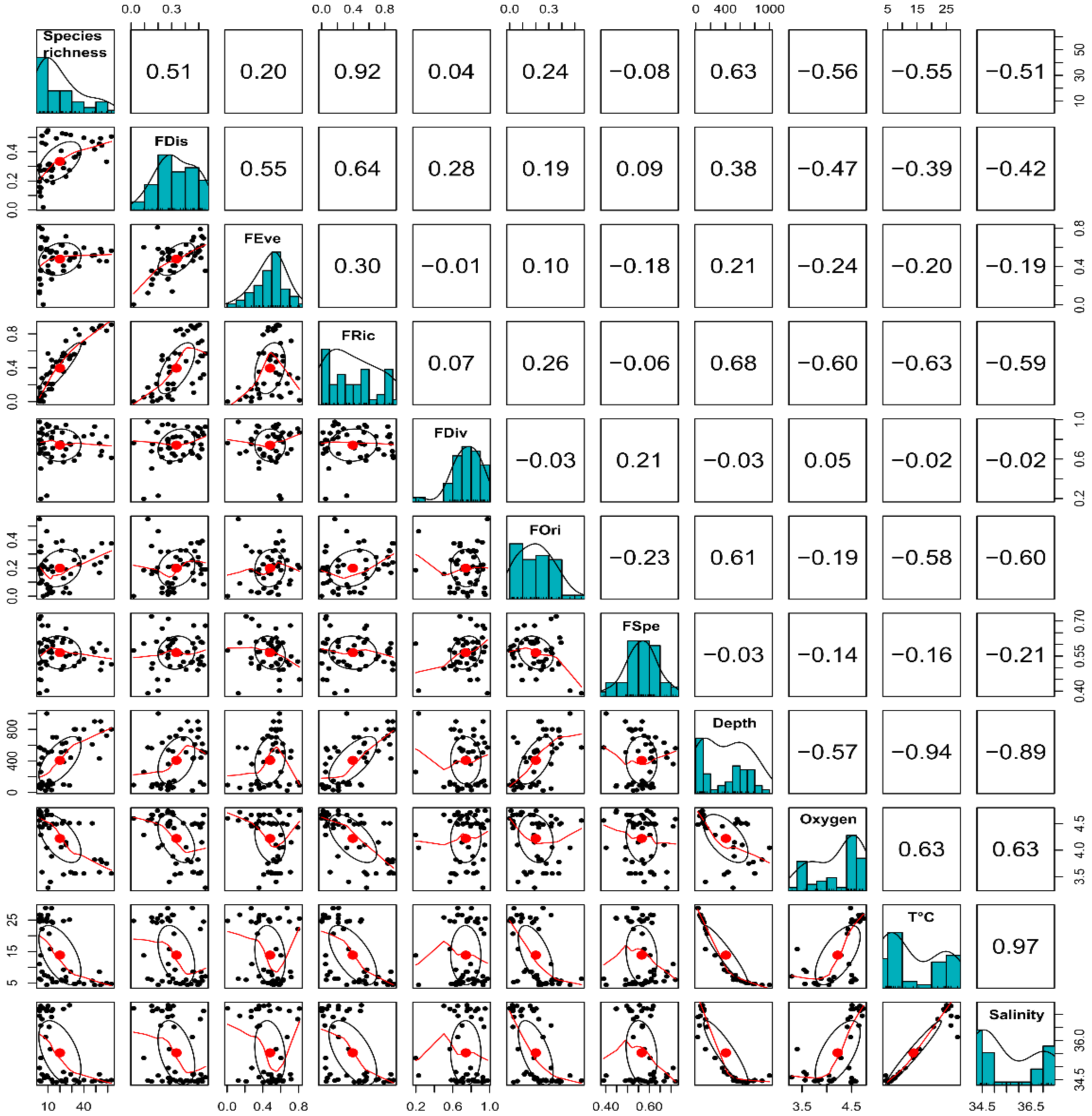


**Figure S2** Draftsman plot showing pairwise relationship among diversity indices (species richness and functional diversity indices, described in Table 1) and, environmental variables (depth, dissolved oxygen, temperature, salinity). Upper panel provides Pearson and Spearman correlation coefficients (chosen because linear relationships observed). Diagonal panel shows histograms of index values and density curves. Lower panel provides x-y plots for pairwise indices, with cloud of points fitted by a non-parametric local regression (LOcally WEighted Scatter plot Smoothing, LOWESS).

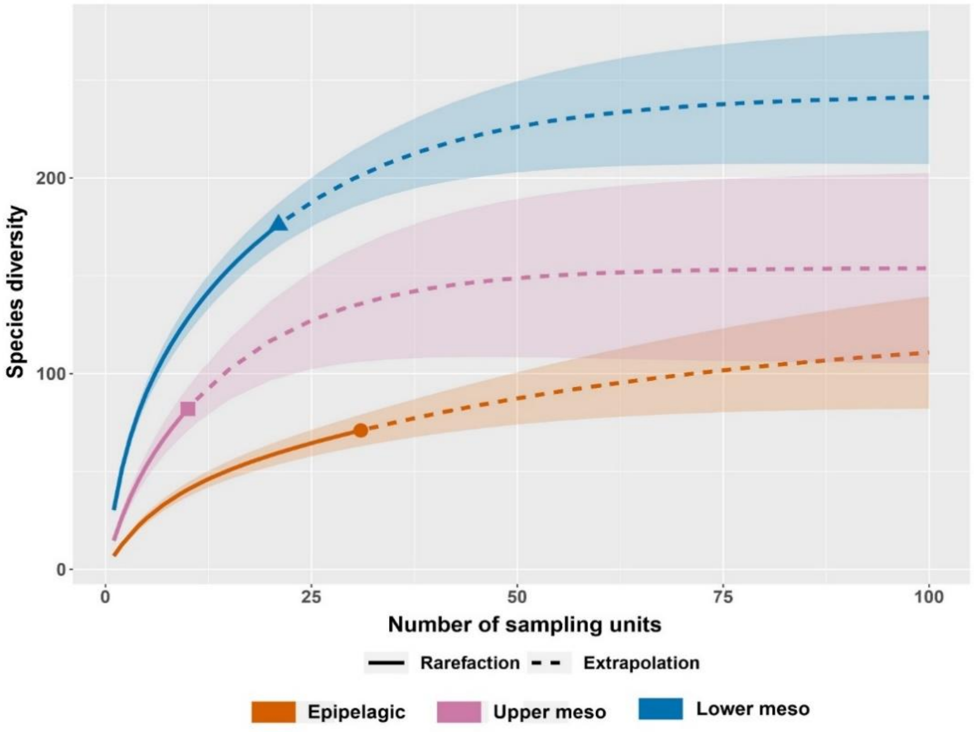


**Figure S3** - Sample-size-based accumulation curves of observed (solid line segment) and extrapolated (dotted line segments) species richness (gamma diversity) according to number of samples (here stations). Extrapolation is computed until 100 stations. Confidence intervals of 95% are drawn around curves (shaded areas).

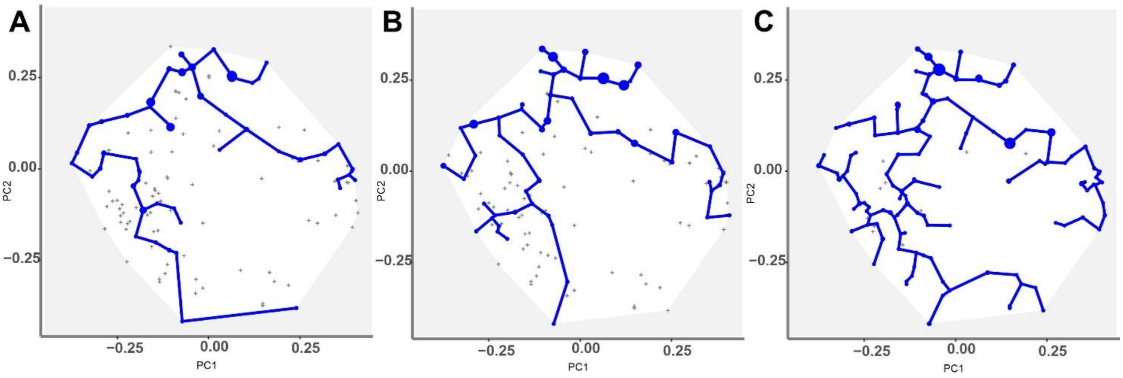


**Figure S4** Functional evenness index (FEve) - Minimum Spanning Tree linking species of each layer (A: epipelagic, B: upper meso and C: lower meso, respectively). Each species has a different size (blue round) given its relative weight in the layer.

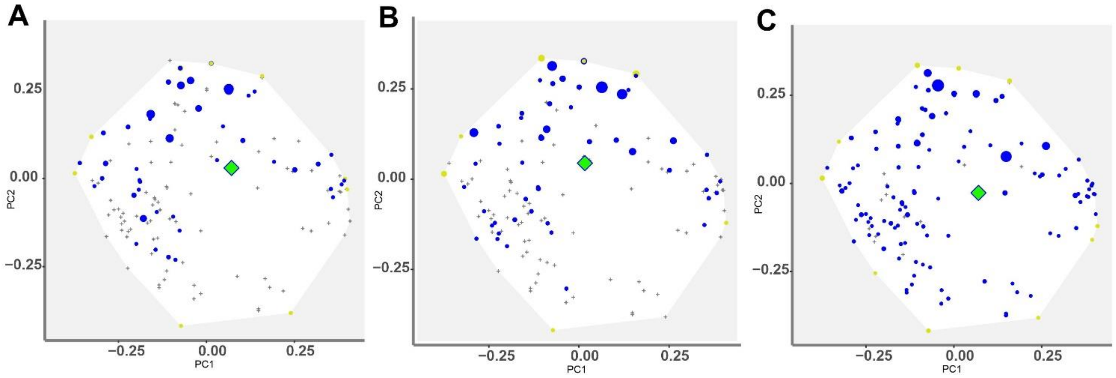


**Figure S5** Functional divergence index (FDiv) - The gravity center of vertices of each layer are plotted as a green square. Each species has a different size given its relative weight into the layer (A: epipelagic, B: upper meso and C: lower meso, respectively).

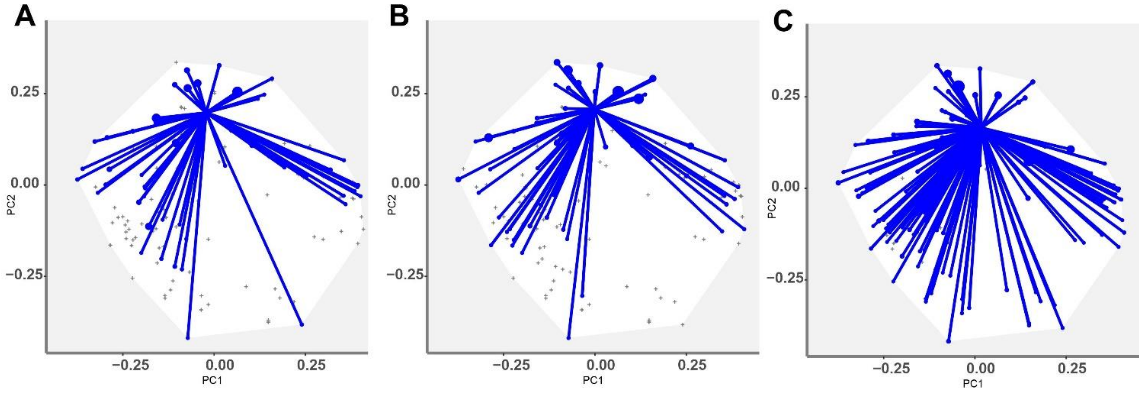


**Figure S6** Functional dispersion index (FDis) - The traits represent distances of each species to the center of gravity of species (defined by FIde values). The center of gravity of each layer is plotted using a square and a triangle. Each species has a different size given its relative weight into the layer (A: epipelagic, B: upper mesopelagic and C: lower mesopelagic, respectively).

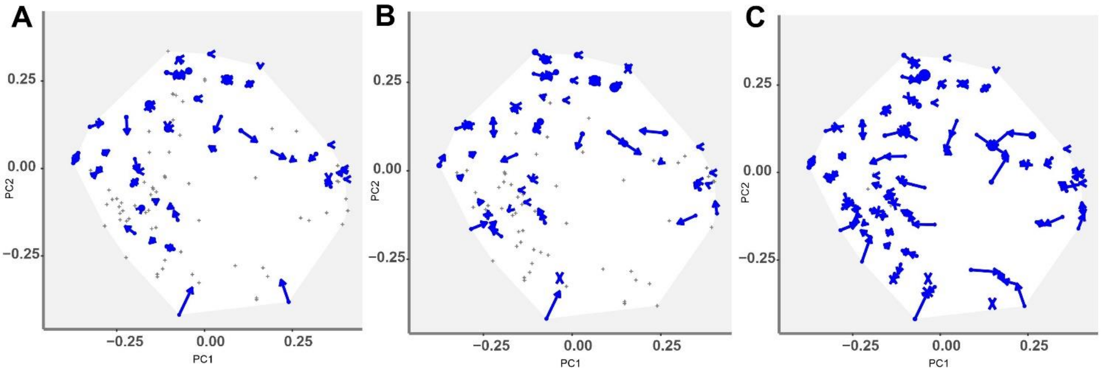


**Figure S7** Functional originality index (FOri) - The arrows represent the distances of each species to the nearest species in the global species pool, for each layer. Each specie has a different size given its relative weight into the layer (A: epipelagic, B: upper meso and C: lower meso, respectively).

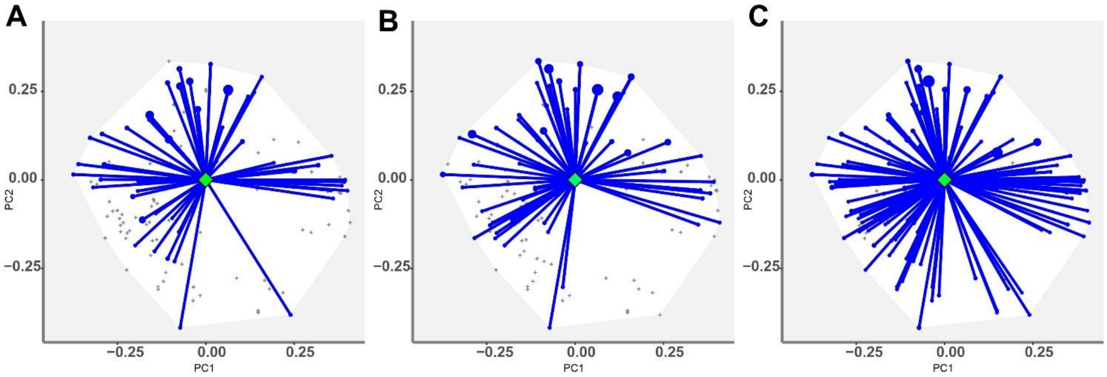


**Figure S8** Functional specialization index (FSpe) - The traits represent distances of each species to the center of gravity of the global pool. The center of gravity is plotted with a green diamond. Each species has a different size given its relative weight into the layer (A: epipelagic, B: upper meso and C: lower meso, respectively).

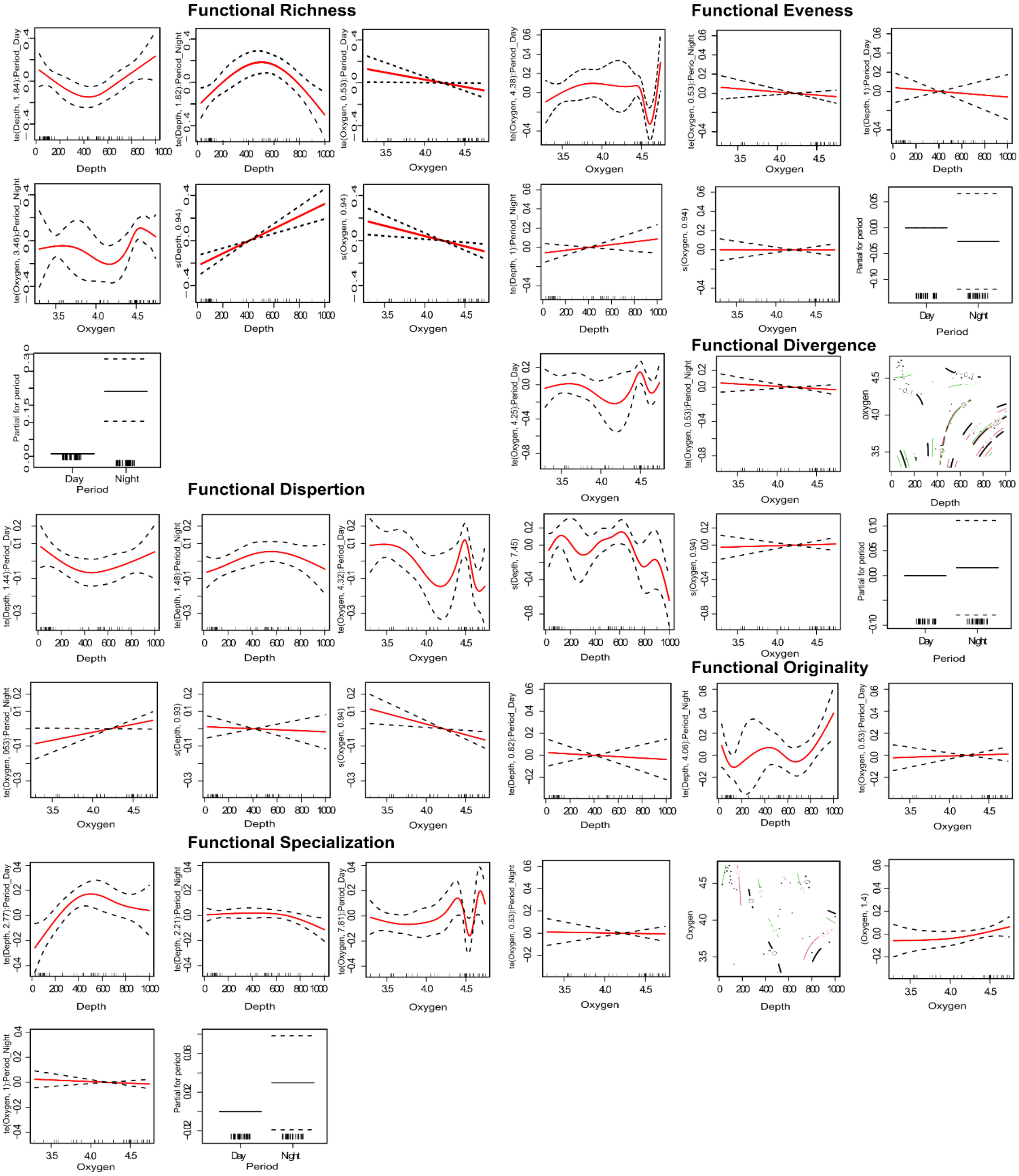
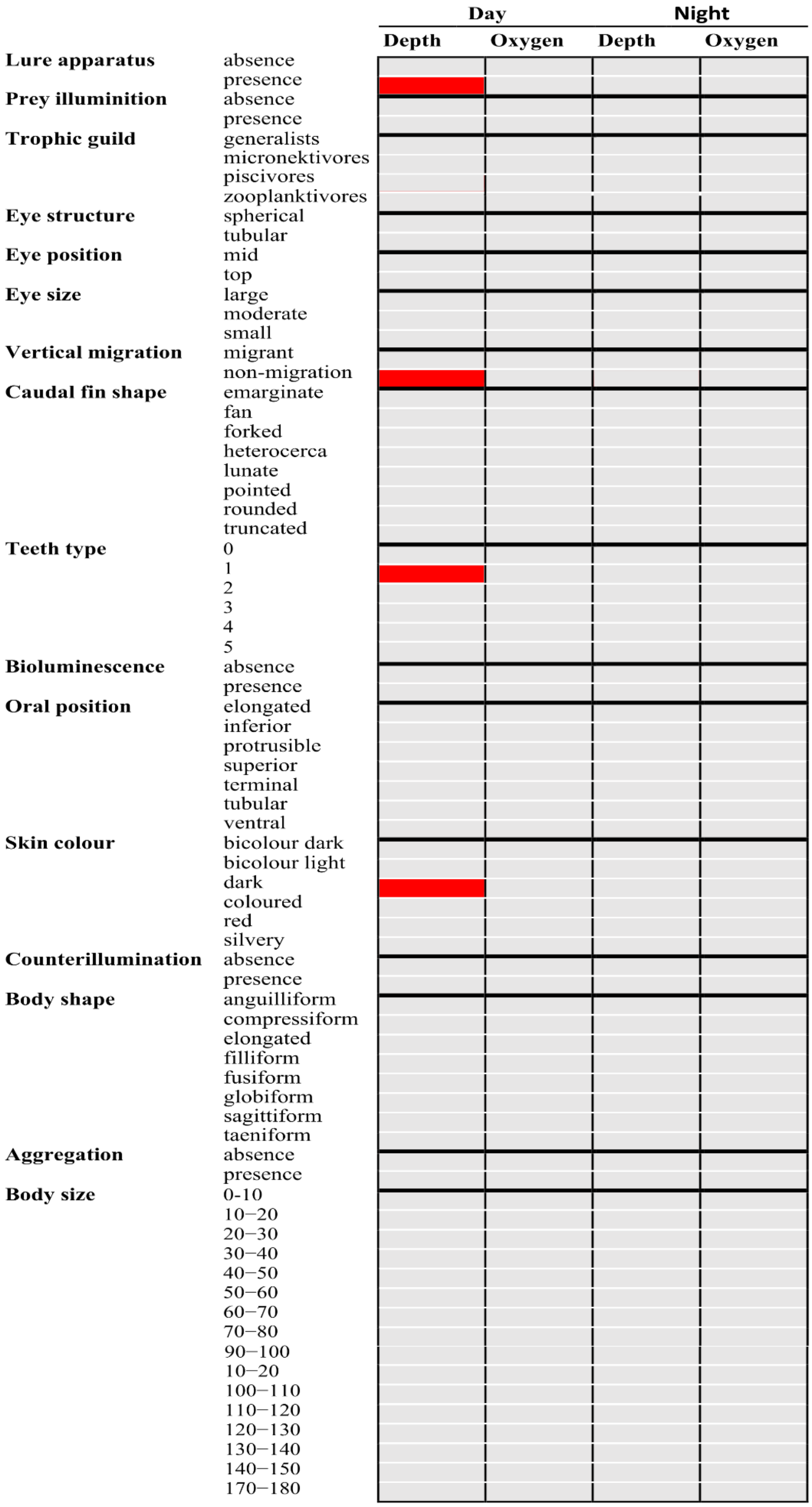


**Figure S9** Generalised additive models (GAM), plots showing associations among functional diversity index and environmental variables (depth, oxygen), and time period (day/night) with 95% confidence intervals. – FRic; FEve; FDiv; FDis; FOri and FSpe.



| | | Day | | Night | |
|---|---|---|---|---|---|
| | | Depth | Oxygen | Depth | Oxygen |
| **Lure apparatus** | absence | | | | |
| | presence | 🟥 | | | |
| **Prey illuminition** | absence | | | | |
| | presence | | | | |
| **Trophic guild** | generalists | | | | |
| | micronektivores | | | | |
| | piscivores | | | | |
| | zooplanktivores | | | | |
| **Eye structure** | spherical | | | | |
| | tubular | | | | |
| **Eye position** | mid | | | | |
| | top | | | | |
| **Eye size** | large | | | | |
| | moderate | | | | |
| | small | | | | |
| **Vertical migration** | migrant | | | | |
| | non-migration | 🟥 | | | |
| **Caudal fin shape** | emarginate | | | | |
| | fan | | | | |
| | forked | | | | |
| | heterocerca | | | | |
| | lunate | | | | |
| | pointed | | | | |
| | rounded | | | | |
| | truncated | | | | |
| **Teeth type** | 0 | | | | |
| | 1 | 🟥 | | | |
| | 2 | | | | |
| | 3 | | | | |
| | 4 | | | | |
| | 5 | | | | |
| **Bioluminescence** | absence | | | | |
| | presence | | | | |
| **Oral position** | elongated | | | | |
| | inferior | | | | |
| | protrusible | | | | |
| | superior | | | | |
| | terminal | | | | |
| | tubular | | | | |
| | ventral | | | | |
| **Skin colour** | bicolour dark | | | | |
| | bicolour light | | | | |
| | dark | 🟥 | | | |
| | coloured | | | | |
| | red | | | | |
| | silvery | | | | |
| **Counterillumination** | absence | | | | |
| | presence | | | | |
| **Body shape** | anguilliform | | | | |
| | compressiform | | | | |
| | elongated | | | | |
| | filliform | | | | |
| | fusiform | | | | |
| | globiform | | | | |
| | sagittiform | | | | |
| | taeniform | | | | |
| **Aggregation** | absence | | | | |
| | presence | | | | |
| **Body size** | 0-10 | | | | |
| | 10−20 | | | | |
| | 20−30 | | | | |
| | 30−40 | | | | |
| | 40−50 | | | | |
| | 50−60 | | | | |
| | 60−70 | | | | |
| | 70−80 | | | | |
| | 90−100 | | | | |
| | 10−20 | | | | |
| | 100−110 | | | | |
| | 110−120 | | | | |
| | 120−130 | | | | |
| | 130−140 | | | | |
| | 140−150 | | | | |
| | 170−180 | | | | |

**Figure S10** Fourth-corner analysis (FCA) with 9.999 permutations investigating pairwise correlations between traits and environmental variables (depth and oxygen) for day and night periods. Cells in red indicate positive correlations and cells in grey non-significant correlations. No negative correlations were observed.

# 4. CHAPTER 3 – Assessing ecological processes on demersal fish community from taxonomic and functional trait β-diversity

Mesopelagic and demersal species from coastal areas inhabit distinctly different environments and play unique yet complementary ecological roles. Mesopelagic species, residing at depths of 200 to 1000 meters, are adapted to dark, cold environments devoid of primary photosynthetic energy production. Many of these species undertake long vertical migrations to access nutrient-rich waters at the surface, participating in what is known as the largest migration on Earth. In contrast, demersal species thrive in well-lit coastal regions, closely interacting with benthic ecosystems and directly benefiting from photosynthetic processes. Despite their differing habitats, both groups are integral to marine ecosystem functioning. Mesopelagic species contribute to carbon transport through their diel vertical migrations, while demersal species influence nutrient cycling and energy flow within benthic communities. Both groups serve as essential trophic links in marine food webs and are critical for sustaining fisheries resources, directly through their harvest and indirectly by supporting higher trophic levels. However, both of them are still poorly known in the northeast of Brazil and are facing varying levels of anthropogenic impacts. Studying both communities is necessary for a more comprehensive understanding of ecological responses to environmental changes. Variations in ocean conditions, such as water temperature and nutrient availability, can affect both demersal and mesopelagic communities. An integrated analysis of different communities can provide more robust insights into these effects (Levin et al., 2001). However making such joint analysis requires first to assess demersal communities, notably by complementing current knowledge of the Northeastern Brazil region (Eduardo et al., 2018a; Cardoso de Melo et al., 2020; Soares et al., 2020).

In this chapter, we aim to address a significant gap in the study of demersal fish diversity in northeastern Brazil. Demersal fish face direct anthropogenic activities, such as fishing, pollution, and tourism. Although the study area includes five nearby environmental protection areas, they have the least restrictive level of exploitation. Additionally, the area is a well-known tourist destination. Therefore, understanding the structuring processes of the community, as well as its functional diversity distribution and species redundancy, becomes urgent for marine spatial planning and conservation strategies.

*This section will be submitted during the second semester of 2024.*

# Main drivers of taxonomic and functional beta diversity of demersal fish community in the Southwestern Tropical Atlantic, Brazil

Kátia C. Aparecido, Bastien Mérigot, Leandro N. Eduardo, Arnaud Bertrand, Everton G. Tosetto, Vincent Vantrepotte, Reis-Júnior, Paulo J. Duarte-Neto, Thierry Frédou (*in prep.*)

## 4.1. Abstract

Assessing the effects of environmental and spatial variables on community diversity is critical for understanding the processes that structure species assemblages, as well as for informing their management and conservation. While efforts have been made to understand changes in fish distribution in relation to environmental and spatial variables, the influence of these variables on fish beta-diversity (both taxonomic and functional) remains poorly understood on the Brazilian continental shelf. In this study, we computed the taxonomic and functional beta diversity partitioning of demersal fish assemblages on the continental shelf and assessed the relative influences of spatial and environmental drivers. We hypothesized that the taxonomic and functional beta diversity of marine demersal fishes in the studied region is influenced by environmental variations, with species replacement being the main component of beta diversity, reflecting species adaptation to local conditions. Partitioning of Jaccard (species presence-absence data) and Bray-Curtis (abundance data) dissimilarities revealed that turnover and balanced variation in abundance largely contributed to taxonomic beta-diversity (0.741 ± 0.121 and 0.722 ± 0.144, respectively). For functional beta diversity, overall functional β-diversity was high (0.718 ± 0.199), with turnover and nestedness contributing equally. However, for functional beta diversity based on abundance data, overall beta diversity was low (0.152 ± 0.460), suggesting that functional composition is different between stations, the relative abundance of these species is similar between stations. The dbRDA analyses indicated that substratum complexity, depth, and particle dispersion gradients significantly influence beta-diversity. Our results also support the fact that beta diversity components exhibit spatial variability and can be influenced by distinct predictors. This study serves as a baseline for future research on the impacts of global change on demersal fish communities.

**Keywords:** functional traits, beta partitioning, species compositio, fish community structure, conservation.

## 4.2. Introduction

Biodiversity is the foundation of ecosystem functioning and processes that underpin its health, as well as ecosystem services (Barbier, 2017). In seas and oceans, the distribution of marine community diversity can be influenced by several abiotic variables such as temperature, ocean currents, seabed habitat, nutrient availability, and/or anthropogenic activities (Nagelkerken and Munday, 2016; Borland et al., 2017, 2021). For instance, oceanic processes in which currents bring deep and nutrient-rich water to the surface or sub-surface of the ocean (i.e., vortices) can strongly shape local biodiversity hotspots as well as fishing grounds (Kidé et al., 2021). In oligotrophic regions, the augmentation of productivity and the amplification of fish biomass are notable even through localized upwelling and uplifting processes (Hazin, 2009).

Despite their significance, the intricate interplay between biodiversity and environmental factors, including these oceanic processes, and their relative impact compared to variables such as substratum and depth, remains incompletely elucidated, particularly for demersal fishes from southwestern tropical Atlantic. Johnson (2013), proposes a concentrated examination at smaller spatial scales in habitat studies, underscoring the need for a nuanced understanding. Moreover, Jacob (1998) and Moore et al. (2010) underscore the pivotal role of depth, temperature, and benthic habitat structure in shaping demersal fish assemblages. Notably, the factors responsible for generating patches of heightened local diversity (i.e., alpha diversity) within demersal fish communities remain elusive in certain regional oceanic areas, exemplified by the Brazilian continental shelf (Eduardo et al., 2018a, 2020a). This knowledge gap impedes our capacity to forecast the repercussions of environmental changes and formulate effective management strategies.

Furthermore, to better assess and understand spatial distribution of community diversity, it is important to consider the beta-diversity of community (inter-location differences). Indeed, analyzing only alpha diversity (intra-location) can lead to misinterpretations about influences of explanatory variables on community diversity (Edge et al., 2017). Beta-diversity measures variation among locations in species composition (i.e., compositional differences), coupled with species quantities (e.g., abundance), as well as species features (e.g. traits) when available (Whittaker, 1960; Tuomisto, 2010). Investing beta-diversity is a central concept in ecology, allowing the linking of spatial structures to ecological processes (Socolar et al., 2016). The underlying reasoning is that each kind of ecological or coexistence process should lead to particular beta-diversity patterns (Guerin et al., 2013). To assess more precisely beta-diversity and underlying processes, overall beta-diversity can be decomposed/partitioned into two components. First, on species presence-absence data, these components are (i) turnover sensu stricto, i.e., the dissimilarity related to the replacement of some species by others among locations, and (ii) nestedness-resultant dissimilarity, i.e., dissimilarity related to species loss in which a community in a location is a strict subset of another (Baselga et al., 2007).

Given the variety of underlying mechanisms that can produce turnover and /or nestedness patterns, it is crucial to disentangle the relative contribution of the two components to the overall beta-diversity (Baselga, 2010). Second, abundance-based beta-diversity can also be decomposed into two components, following the partitioning of Bray–Curtis dissimilarity (Baselga, 2013): (i) balanced variation in abundance (whereby the individuals of some species at one location are replaced by the same number of individuals of different species at another location), and (ii) abundance gradients (whereby some individuals are lost from one location to the other) (Baselga, 2013). In addition, the partitioning of the measure of the difference in functional diversity, using species functional traits, into independent alpha and beta components has also been proposed to complement the understanding of the underlying mechanisms driving changes in community composition and ecosystem functioning (Violle et al., 2014). Understanding how species composition and their abundances vary according to environmental variables is critically important to better understand species community changes, as well as to guide their management and conservation actions (Baselga, 2012; Sommer et al., 2014). Differences among the environmental factors analyzed in this study can reveal the mechanisms that lie behind ecological patterns and ultimately help define conservation planning as well as fishing management.

Such an understanding is particularly pertinent to regions like the tropical Brazilian continental shelf (TBCS), which is characterized by a rich assemblage of marine species, including both endemic and vulnerable ones. The region's unique ecological characteristics make it an ideal site for studying fish beta diversity. It holds a relatively high number of species, including both endemic and vulnerable ones, and is considered an Ecologically or Biologically Significant Area (EBSA, CBD, 2014). Additionally, it encompasses complex habitats crucial for marine life and coastal marine fisheries of Brazil (Demestre et al., 2000; Eduardo et al., 2018a, 2020a). In recent years, numerous studies have focused on the demersal community of the region from an alpha diversity perspective, highlighting, for instance, the areas richest and most diverse considering taxonomic diversity (Eduardo et al., 2018a; Cardoso de Melo et al., 2020; Soares et al., 2020). However, none of these studies directly address beta diversity, leading to a significant gap in information essential for understanding the ecosystem and supporting its management. However, investigating the influence of potentially important structuring environmental and spatial factors on fish beta diversity (species composition and abundances, as well as functional traits) remains poorly known. The objective of this study is to identify the distribution patterns of demersal fishes across varied environmental gradients, thus identifying the ecological factors that influence their distribution. We aim to elucidate the underlying mechanisms across spatial scales, offering valuable information for marine conservation and management of essential habitats. Here we hypothesize that the taxonomic and functional beta diversity of marine demersal fishes in the studied region is influenced by variations in environmental conditions, with species replacement being the main component of beta diversity, reflecting a specific adaptation of species to local conditions in an area, as found in reef fish community (Maxwell et al., 2022).

## 4.3. Material and methods

### *4.3.1. Study area*

The study area is located off the continental shelf of northeastern Brazil (5° – 9° S). The shelf averages 40 km in width and includes patches of different substratum (Fig. 1), with depth ranging from 40 to 80 m (Vital et al., 2010). Like many tropical waters, the area has mainly relatively low primary production and low abundance of species (Assunção et al., 2021). However, in a few locations, shelf valleys and blind canyons cause instability on the mixed layer depth, uplifting of isotherms, and disruption of the surface mixed layer, processes that enhance locally marine productivity (Silva et al., 2022), and fish biomass (Hazin, 2009). Consequently, some locations in the study area present a relatively high species richness (i.e., alpha-diversity) along the continental shelf of northeastern Brazil, mainly at locations between 30-60 m depth (Eduardo et al., 2018).

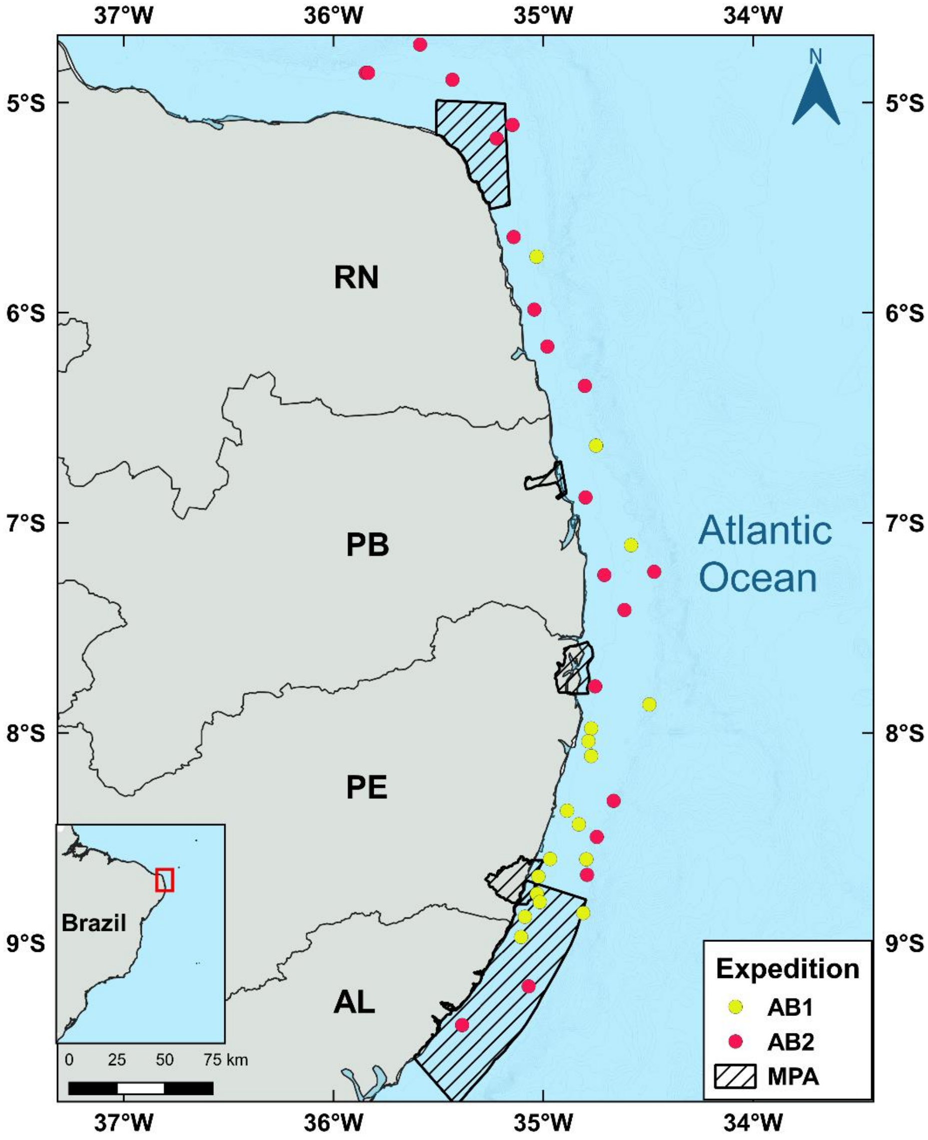


**Figure 1.** Study area with 2 expeditions, AB1 in 2015 and AB2 in 2017. Marine Protected Area’s highlights.

### *4.3.2. Sampling*

The sampling was conducted during two oceanographic expeditions, part of the 'Acoustics along the BRAzilian COaSt' (ABRACOS) project. This encompassed 36 stations situated at depths ranging from 15 to 60 meters along the northeast Brazilian continental shelf, stretching from Rio Grande do Norte to Alagoas (5° – 9° S). The expedition was carried out aboard the Research Vessel (R/V) ANTEA during 30 August to 20 September 2015 (Bertrand, 2015), and 9 April to 9 May 2017 (Bertrand, 2017). Trawling operations were conducted for approximately five minutes at a speed of 3.2 knots, utilizing a bottom trawl net designed with a body mesh of 40 mm, cod-end mesh of 25 mm, and entrance dimensions of 28 x 10 meters. Hauls were performed for about 5 minutes at 3.2 kt, using a bottom trawl net (body mesh: 40 mm, cod-end mesh: 25 mm, entrance dimensions: 28 x 10 m). A total of 7.394 individual fishes were sampled and identified at species level, representing 127 species collected.

### *4.3.3. Data analyses*

#### *Functional diversity measures*

The specimens' images were obtained with a digital camera. For the calculation of functional traits, the morphological traits of locomotion and acquisition of food will be measured by the free software Image J (Schneider et al., 2012), with an accuracy of 0.1 mm. The measurements of each individual will be calculated by ratio (Mason et al., 2007; Villéger et al., 2010; Mouillot et al., 2011), assuming that variations within species are lower variations among species (Dumay et al., 2004; Villéger et al., 2010) (SI,table S1). Functional traits were standardized so that the mean was equal to 0 and the standard deviation 1.

#### *Beta-diversity measures*

Beta diversity was computed across stations pairwise. Abundance data was first transformed using the Hellinger distance, as recommended by Legendre and Legendre (2012), to standardize variation among species and improve the comparability of our results. Following the methodology proposed by Ricotta et al. (2021), we assessed the beta diversity across all samples pairwise. within our study area. This approach relies on calculating pairwise functional dissimilarities, represented within a symmetric matrix. These dissimilarities vary between 0 and 1, thus offering a detailed view of their functional organization within samples. This measure optimally matches species abundances between samples to minimize the overall functional dissimilarity. The dissimilarity index is thus derived by matching individuals across samples to achieve a minimum sum of functional dissimilarities, thereby reflecting the minimum cost per individual required to transition character states between the species of two samples. This method, inherently a linear optimization problem, provides a robust framework for assessing the functional beta diversity by calculating the mean value for all possible sample pairs.

Presence-absence data were used to assess the respective influences of species turnover and nestedness on both taxonomic and functional beta diversity applying an additive partitioning approach based on pairwise Jaccard's dissimilarity index (Baselga, 2010, 2012; Villéger et al., 2013). Likewise, the overall beta-diversity based on abundance data was partitioned into balanced variation in abundance, characterized by the exchange of individuals of different species at equal quantities between sites and abundance gradients, depicting the loss of individuals from one site to another, in alignment, using the Bray-Curtis dissimilarity index (Baselga, 2013). Both indices, for overall beta diversity and each component, were computed for all stations pairwise, and then their mean value and standard deviation were calculated to provide an overview of the scale of the study area. For these analyses, we employed the betapart (Baselga and Orme, 2012) R packages.

### *Influence of the environmental and spatial factors on beta diversity*

The environmental explanatory variables and a set of spatial explanatory variables were considered in the models. Here, each of the eight variables is initially considered to be presented in Table 1. Empirical pairwise relationship among variables was indeed investigated using a draftsman plot representing both i) x-y plot fitted by non-parametric local regression (locally reweighted scatter plot smoothing (LOWESS) and ii) correlation coefficient (S1).

**Table 1**. Environmental variable description.

| Variable | Acro. | Ecological relevance | Reference |
|---|---|---|---|
| Particle distribution rate | Dermfish_ratio | Driven to species dispersion | (Giachini Tosetto et al., 2023) |
| Primary production | PP | Influence on food supply, fish size and biomass and ecosystem health | (Jennings and Collingridge, 2015; Marshak and Link, 2021; Tagliabue et al., 2021) |

| | | | |
|---|---|---|---|
| Distance of shore | Dist_Shore | Delimited areas serve as essential fish habitats and their complexity. Influences on temperature, salinity and depth | (Pittman and Brown, 2011; Pickens et al., 2021; Benadon et al., 2023) |
| Depth | Dep | Differentiate alfa fishes community | (Eduardo et al., 2018a) |
| Substratum | Substratum | Differentiate alfa fishes community | (Eduardo et al., 2018a) |
| Latitude | Lat | Influence on environmental factors and species distributions | (Dallas and Kramer, 2022) |
| Longitude | Long | Influence on environmental factors and species distributions | (Dallas and Kramer, 2022) |

To elucidate spatial patterns within ecological data, we employed the Principal Coordinates of Neighbor Matrices (PCNM) approach (Borcard and Legendre, 2002; Dray et al., 2006). This method facilitates an enhanced comprehension of how geographical proximity among locations shapes community composition. By detecting spatial structures that may elude conventional multivariate analyses. PCNM is instrumental in mitigating the impact of spatial autocorrelation in the dataset. Essentially, generates principal coordinates based on a matrix of neighbours, representing discernible spatial patterns. This approach creates spatial predictors that can be easily incorporated into regression or canonical analysis models based on a principal coordinate analysis (PCoA) of a truncated pairwise geographic distance matrix between sampling sites. It produces eigenvectors associated with the positive eigenvalues corresponding to the Euclidean representation of the truncated distance matrix.

The relative contributions of the environmental descriptors and spatial variables to the taxonomic and functional beta diversity patterns were evaluated using variation partitioning (Peres-Neto et al., 2006). Such analysis partitions the variance in community composition resulting from (i) each explanatory variable (E = environment and S = spatial), (ii) the unique contribution of each explanatory variable (E/S = environment—only environmental variables–or S/E = spatial–only spatial variables) and (iii) the total variance explained by the environmental and spatial variables together (spatially structured environmental variables). The variance explained by each fraction was based on the adjusted $R^2$ (Peres-Neto et al., 2006). We conducted separate significance tests to discern the true importance of these predictors in beta diversity. The significance of each fraction was tested by the anova.cca function from the Vegan package (Oksanen et al., 2022).

We applied distance-based redundancy analysis (db-RDA) to explore the relationships between beta diversity and environmental variables, for each beta diversity matrix. Db-RDA is particularly suited for ecological datasets, accommodating dissimilarity or distance matrices that reflect community similarity measures. Its capability to handle non-Euclidean distances, prevalent in ecological data, renders it a flexible and apt tool for our analysis. This method facilitates a direct examination of how environmental gradients and spatial configurations influence community composition variance. Through permutation tests, db-RDA assesses the significance of environmental variables in elucidating observed community patterns, offering a comprehensive framework for understanding the ecological drivers of beta diversity in varied landscapes (Legendre and Anderson, 1999; Legendre and Legendre, 2012). We selected only significant environmental predictors of variation in taxonomic and functional beta diversity, which then were used for the environmental model and spatial model (Blanchet et al., 2008). Our analyses were conducted using the Vegan package in R (Oksanen et al., 2022), leveraging its robust functionalities for ecological data analysis.

## 4.4. Results

### *4.4.1. Community composition: Taxonomic beta diversity*

Overall, taxonomic β-diversity was high for both Jaccard and Bray-Curtis, each with a mean value greater than 0.7 (theoretical maximum being 1) (Table 2, Figure 2), indicating a high degree of species variation between the sampled stations.

When partitioning the overall beta-diversities, it was evident that they were predominantly driven by turnover βTur (0.741 ± 0.121) and βBal (0.722 ± 0.144). This implies a notable replacement of species or functional groups between stations rather than simple gains or losses, indicating a dynamic and diverse community. Conversely, the contributions of nestedness βNes (0.067 ± 0.065 for taxonomic and βGra (0.028 ± 0.029) to the overall β-diversities were comparatively very low. The high overall β-diversity score of 0.81 reinforces the idea that the assemblages are changing and undergo high species composition variation change across space.

The total functional β-diversity based to the Jaccard index was high (0.718±0.199), indicating significant functional variation between stations. When partitioning the diversity components, both FβTur and FβNes contributed equally (0.374±0.281 and 0.344±0.272, respectively). FβTur indicates that species replacement plays an important role in the observed functional variation, while FβNes suggests that, in some stations, the functions performed by species are subsets of the functions found in other stations. However, for the FβTab abundance-based approach, the average was 0.152±0.460. This low value, combined with the high standard deviation, indicates that abundance-based functional beta diversity is highly variable between seasons. In some locations, there may be a dominance of a few key functional species, while in others, functional diversity may be more balanced.

**Table 2**. Beta-diversity partitioning of demersal fishes on the continental shelf of north-eastern Brazil. Mean and standard deviation (SD) values from indices computed among stations pairwise are given for Jaccard partitioning computed on species presence-absence data, and Bray-Curtis partitioning computed on species abundance. *Filled light grey – abundance data analysis.

| | **Components of beta-diversity** | **Mean/SD** |
|---|---|---|
| **Taxonomic diversity** | Turnover of β-diversity (**βTur**) | 0.741 ± 0.121 |
| | Nestedness of β-diversity (**βNes**) | 0.067 ± 0.065 |
| | Overall β-diversity (**βT**) | 0.808 ± 0.096 |
| | Balanced variation (**βBal**) | 0.722 ± 0.144 |
| | Abundance gradient (**βGra**) | 0.028 ± 0.029 |
| | Overall β-diversity (abundance, **βTabu**) | 0.750 ± 0.131 |
| **Functional diversity** | Overall functional β-diversity (**FβT**) | 0.718 ± 0.199 |
| | Turnover of functional β-diversity (**FβTur**) | 0.374 ± 0.281 |
| | Nestedness of functional β-diversity (**FβNes**) | 0.344 ± 0.272 |
| | Overall functional β-diversity (abundance, **FβTab**) | 0.152 ± 0.460 |

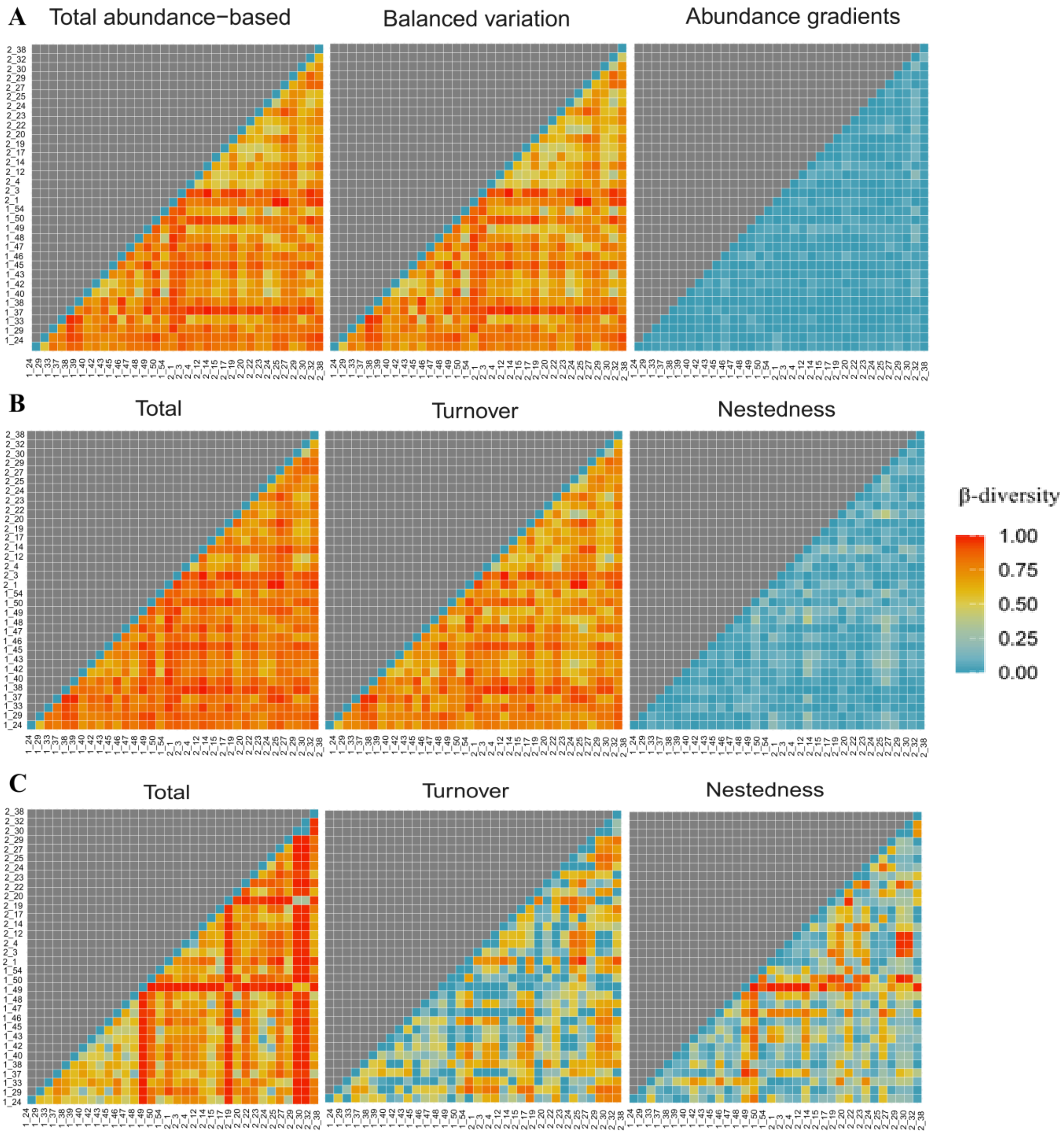


**Figure 2.** Heatmap of beta diversity partitioning between each station pairwise. A) Jaccard index's approach for taxonomic beta diversity. B) Bray Curtis index approach for taxonomic beta diversity. C) Jaccard index approach for functional beta diversity.

Distance from the coast and temperature were removed from the analysis due to their correlation with depth (Fig. S1). Regarding beta diversity, the complementary environmental predictors were particle dispersion (demfish_ratio), primary productivity (PP), substratum, depth (Dep), and spatial factors (Table 3). Overall, substratum, depth, and particle dispersion were the primary determinants of beta diversity (Table 3). In βTur, the adjusted R$^2$ indicated that a very low variability,7%, of the response variable was explained by the model. Depth appears as the stronger predictor (F = 2.8135, p = 0.002), and particle dispersion had a weak contribution (F = 1.4622, p = 0.041). Then, in βBal, the adjusted R$^2$ explains 9% of the variability in the response variable. Here, substratum composition was the stronger predictor (F = 2.7505, p = 0.009), with particle dispersion once again displaying marginal influence (F = 1.8161, p = 0.043). Meanwhile, FβT showed the adjusted R$^2$ value representing 25% of variability 0.25, indicating a higher explanatory power compared to the previous models. Depth was the stronger predictor (F = 2.4565, p = 0.026). Finally, regarding FβTab, the adjusted R$^2$ value underlined 20% of the variability explained by the model 0.20, with depth demonstrating the stronger effect (F = 2.7505, p = 0.009), reinforcing its consistent influence across models.

**Table 3.** dbRDA – Analyses for taxonomic and functional components on partitioning beta diversity. Full models and terms tests of significance for single environmental and spatial predictors (i.e, separate significance test for each predictor in a model when both predictors are in the model). And total variation (SS) from Variance Partitioning.

| **Taxonomic β diversity** | | | | | |
|---|---|---|---|---|---|
| **βTur** | | | **βBal** | | |
| Overall test R$^2$ajust: 0.07, SS: 9.308 | | | Overall test R$^2$ajust: 0.09, SS: 8.947 | | |
| Predictor Variable | *F* | *p* | Predictor Variable | *F* | *p* |
| Demfish_ratio | 1.7622 | 0.041* | Demfish_ratio | 1.8161 | 0.043* |
| PP | 0.8495 | 0.658 | PP | 0.8118 | 0.648 |
| Substratum | 0.8254 | 0.754 | Substratum | 2.0050 | 0.009** |
| Dep | 2.8135 | 0.002** | Dep | 1.1944 | 0.268 |
| Spatial | 1.0194 | 0.454 | Spatial | 1.0177 | 0.436 |
| **Functional β diversity** | | | | | |
| **FβT** | | | **FβTab** | | |
| Overall test R$^2$ajust:, 0.25, SS: 9.18 | | | Overall test R$^2$ajust: 0.20, SS: 0.418 | | |
| Predictor Variable | *F* | *p* | Predictor Variable | *F* | *p* |
| Demfish_ratio | 1.1260 | 0.362 | Demfish_ratio | 1.5147 | 0.158 |
| PP | 1.2613 | 0.280 | PP | 0.7991 | 0.566 |
| Substratum | 1.2573 | 0.237 | Substratum | 1.5585 | 0.098 |
| Dep | 2.4565 | 0.026* | Dep | 2.7505 | 0.009** |
| Spatial | 1.3837 | 0.077 | Spatial | 1.2309 | 0.176 |

About βBal (Fig. 3), calcareous algae played a major role, providing means to large and widespread abundance. Algae had a moderate influence, while sand was least influential, with low and scattered abundance. Regarding βTur (Fig. 3), calcareous algae again dominated, with substantial abundance and dispersion. Algae had a moderate effect, and sand showed more impact compared to the abundance data. About FβTab (Fig. 3), calcareous algae had a notable role, with a large and widespread abundance. Algae had a moderate influence, and sand was the least influential, with small, scattered circles. Regarding FβT (Fig. 3), calcareous algae remained dominant, with a large, dispersed abundance. Algae had a moderate influence, and sand had a more pronounced effect compared to the abundance-based analysis. Overview, calcareous algae and sand appeared to be associated with the most distinct taxonomic communities based on their distance.

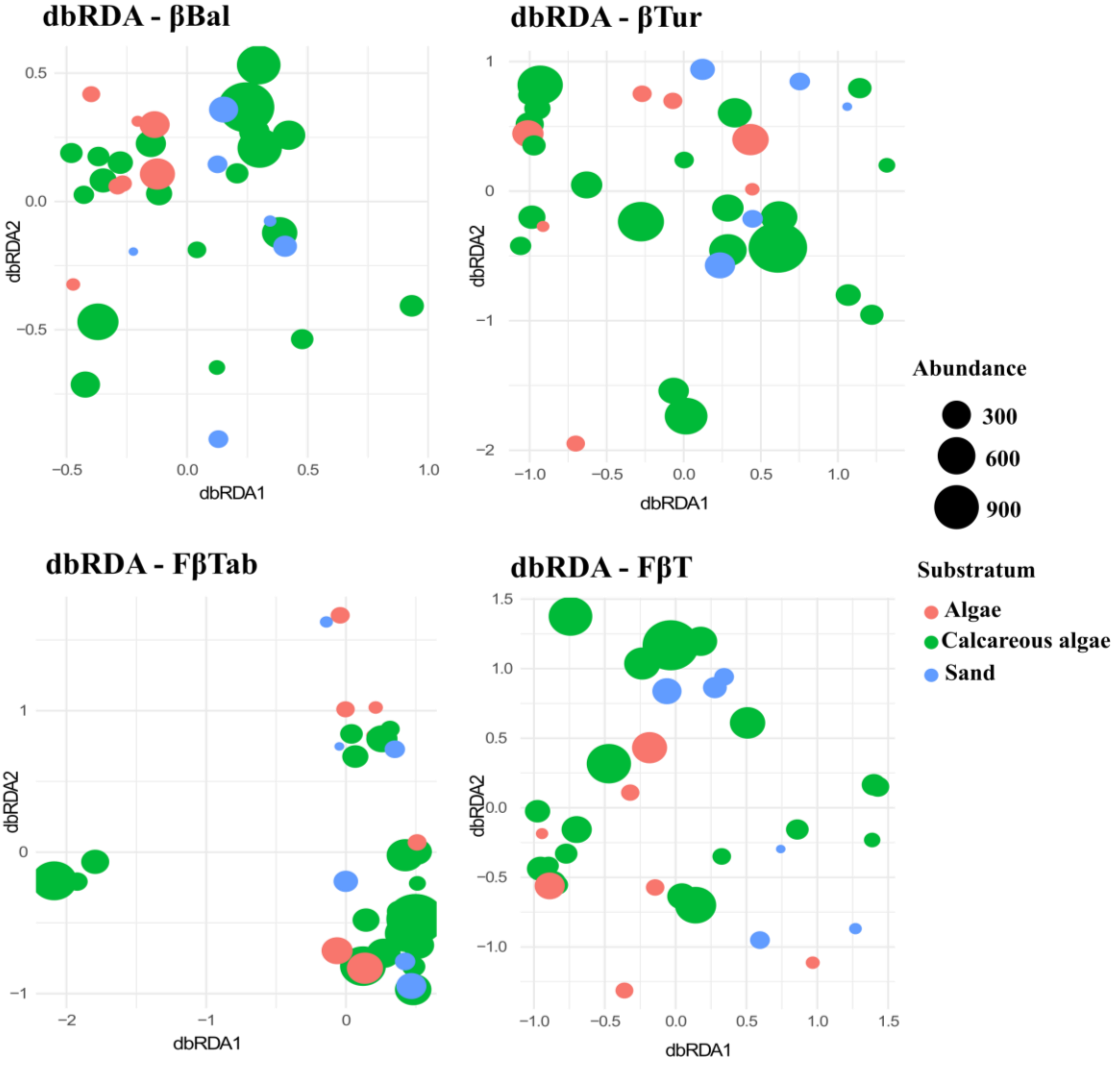


**Figure 3.** Distance-based Redundance Analysis (dbRDA). Relationship between substratum types and taxonomic and functional beta diversity distribution and their abundance.

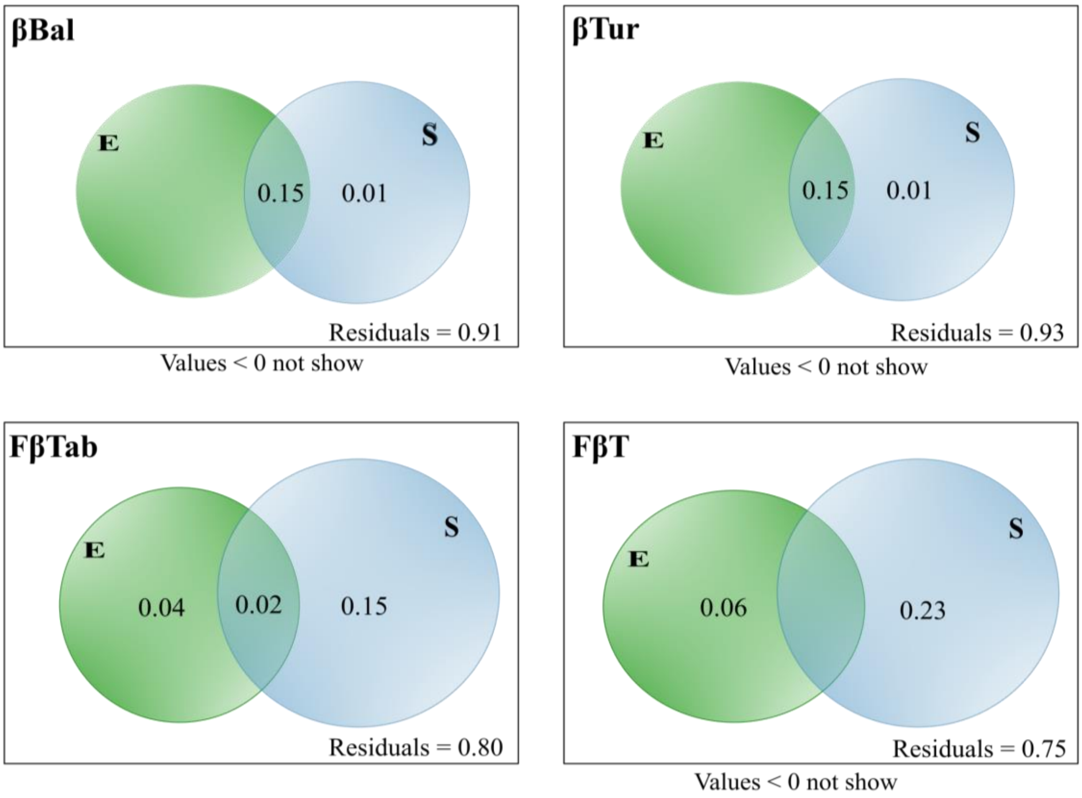


**Figure 4.** Venn diagrams of the Variation Partitioning. Representation of the explained unique and shared contributions of two sets of explanatory variables (E = environmental variables and S = spatial variables). Value <0 not show in the plot. The diagram is calibrated to display the actual contributions of the factors, incorporating overlaps and redundancies. Consequently, this may yield negative or minimal values. Therefore, the sum of the adjusted fractions and the residual variance may deviate from 100% due to adjustments addressing multicollinearity and data complexity.

Relative influence of variables on βBal (Fig. 4) illustrates that 15% of its variability was explained by environmental conditions spatially structured. The same relation was observed about βTur. Similar observations were made regarding βTur. However, a residual value of 0.91 and 0.93, respectively, implies a substantial amount of unexplained variation, suggesting the possible influence of unmeasured predictors on βTur (Fig. 3).

About FβTab (Fig. 4), the overlap contribution (2%) is less than in the taxonomic analyses. The environmental conditions contributed to 4% while the spatial predictor 15%, and both shared 2% of the effect on FβTab. No shared effect on FβT was observed. On the other hand, the spatial predictor contributed to 23% of the variability and the environment predictor 6%. Unexplained variation is notably lower (residuals = 75%) compared to other models.

## 4.5. Discussion

We employed a variation partitioning approach to elucidate the influence of key environmental and spatial predictors on fish beta diversity across the continental shelf of northeastern Brazil at a regional scale. Our findings revealed congruent trends between taxonomic and functional beta diversity in relation to the environment, with minimal influence from spatial predictors. However, the predominant ecological processes affecting beta diversity differed between the taxonomic and functional facets. Turnover predominantly influenced the taxonomic facet, while we unexpectedly found a distinct partitioning effect on the functional facet. The nestedness and turnover processes contributed equally to the observed patterns. Our results support the notion that beta diversity components exhibit spatial variability and can be influenced by distinct predictors (Leibold et al., 2004; Dobrovolski et al., 2012).

### *4.5.1. Beta diversity partitioning*

Beta diversity indices go beyond local and total species richness estimates, providing valuable insights into the variation in species composition across different sites (Baselga, 2010). Despite its potential, this powerful tool has often been underutilized in the functional facet, especially in marine ecosystems (Harborne et al., 2006; Marion et al., 2017). Even in well-studied communities, such as benthic macrofauna, there is a dearth of comparative studies to establish gauges for high and low beta diversity values. Additionally, beta diversity values are contingent upon the spatial scales used to define local and regional diversity (Loreau, 2000), a choice that can be somewhat arbitrary (Harrison et al., 1992). Hence, endeavoring to compare beta diversity with prior studies seems impractical and may lead to misinterpretation (Gaertner et al., 2007).

The study area presents relatively high change in the composition and abundance of species. The high overall taxonomic beta-diversity values (both for presence-absence and abundance, based indices) reinforce the idea that the assemblages are distinct and undergo almost complete species change composition and balanced variation component across space. These patterns are indicative of the varying environmental conditions across the continental shelf break. Turnover process appears to be a common factor in the structuring of fish assemblages, being described as predominant in several studies (Soininen et al., 2018; Medeiros et al., 2021; Barrilli et al., 2024).

The comprehensive analysis of the functional beta diversity based on the presence-absence datasets reveals a moderate heterogeneity in species composition across different spatial and period scales within fish communities. Distinct assemblages observed across stations imply a significant degree of ecological differentiation. Both turnover and nestedness processes contribute equally to functional beta diversity (Table 2).

Despite significant variation in species presence, the relative abundances of species demonstrated less fluctuation. This suggests that while species can vary significantly in between stations, might indicates that some sites, there may be a dominance of a few key functional species (Ricotta et al., 2012), while in others, functional diversity may be more balanced. Therefore, less abundant species, which may be absent or present in some stations, likely contribute more to the high functional diversity observed in the presence/absence analysis. These species may have unique functional traits that increase functional beta diversity when their presence or absence is considered. In this case, the most abundant species present a relative functional redundancy, safeguarding ecosystem functioning and services in the event of local population decline of specific species (Violle et al., 2007; Naeem et al., 2009; Mouillot et al., 2013b, 2014).

### *4.5.2. Spatial and environmental patterns*

The low to moderate influence of environmental variables on turnover species may be related to little variation in environmental variables in this study, which has already been reported in other studies (Eduardo et al., 2018a; Assunção et al., 2020; Dossa et al., 2021) showing the same pattern thermohaline on the continental shelf break (Assunção et al., 2020). Other contributing factors may influence diversity patterns, such as biotic interactions or some environmental factors, which we could not consider because data not available. The value of the interaction between environmental variables and spatial factor,

i. e. environmental factors spatially structured, with a contribution of around 15% for taxonomic beta-diversity, reflects the combined importance of these factors on the influence of the beta diversity. Thus, their overlapping influence suggests that neither can be considered in this model to better capture the influence on communities.

The depth, substratum and particle dispersion influenced the taxonomic facet. The existence of microhabitats formed by the substrate and the dispersion of particles favoured the presence of certain species. Their abundance is influenced by the type of substrate. Some species may be more abundant in one substrate due to favorable environmental conditions, while in another substrate, the same species may be less abundant. Barrilli et al (2024) also pointed the relevance of microhabitats linked to sediments was also recognized as influencing beta diversity in the continental shelf southern, where environmental conditions are different from those found in the northeast. Our results show that substrates with high heterogeneity (calcareous algae) harbor a greater abundance of species. Other authors indicate that for benthic fauna, heterogeneous microhabitats provide more essential resources for the feeding and shelter processes of most species (Mayor et al., 2012; Pusceddu et al., 2014; Barrilli et al., 2021).

Varied habitats also may impact intra- and interspecific competition within demersal fish communities, particularly in habitats with more complex substrates, which may intensify interspecific competition for certain species (Pelage et al., 2022). Additionally, substrate type can facilitate fish evasion from fishing nets and predators (De Barros et al., 2021), potentially contributing to the observed distribution patterns in beta diversity (Table 3, Fig. 3). Besides, influences ecological patterns and process, and can affect species distribution as well as composition and diversity (Huston, 1994; Ellingsen and Gray, 2002; Zajac et al., 2003). We noticed that, when testing the influence on beta diversity highlighted by the habitat (Fig. 3), there's a general trend where 'algae' and 'calcareous_algae' habitats tend to be more similar to each other in species composition and function than to 'sand', with 'sand' often appearing as the most distinct habitat in terms of species composition and functional attributes. The presence-absence data seems to flatten the distinctions between habitats, potentially indicating that many species are widespread but differ in abundance across habitats. These patterns might reflect that calcareous algae are more complex than sand or gravel habitats, which thus facilitate the cohabitation of a higher number and more diverse species, providing essential habitats and resources for demersal species within and in the vicinity of this habitat (Bertelli and

Unsworth, 2014; Darling et al., 2017). Consequently, it acts on environmental gradients or biological processes such as competition, predation, or habitat specialization.

The depth showed high influence on beta diversity. It is important to highlight that sites where depth is the primary determinant for turnover can be concerned, because it may indicate an unlikely reversal by immigrants in the event of local extinction (Medeiros et al., 2021). This makes few sites acting as refuge and refugium since this migration could occur for some species but not for the whole community (De O. Soares et al., 2020). In this way, our results corroborated with to Leibold et al., (2004) where greater contribution of turnover in explaining beta-diversity patterns at any depth suggests that the community is mainly structured by species sorting.

Overall, our work indicates that effective management of the demersal fish community, in relation to the relatively high turnover component, would require conservation of a larger number of different locations, not necessarily the richest ones as it should have been the case if nestedness component had mainly contributing to the overall beta-diversity (Baselga, 2010; Guareschi et al., 2015). Although these analyses contribute to a better understanding of demersal fish diversity, complementary assessments based on interactions of species can supplement our results. They may indeed provide further insights into the processes shaping community diversity and its link with ecosystem functioning.

## Supplementary material

**Table S1.** Functional traits of fishes. (See codes of morphometric measurements in Figure 1, General introduction chapter). Morphological measures (A): Bl body standard length, Bd body depth, CPd caudal peduncle minimal depth, CFd caudal fin depth, CFs caudal fin surface, PFi distance between the insertion of the pectoral fin to the bottom of the body, PFb body depth at the level of the pectoral fin insertion, PFl pectoral fin length, PFs pectoral fin surface, Hd head depth along the vertical axis of the eye, Ed eye diameter, Eh distance between the center of the eye to the bottom of the head, Mo distance from the top of the mouth to the bottom of the head along the head depth axis; and with an electronic caliper (B): Bw body width, Md mouth depth, Mw mouth width (See. Villéger et al. (2010)).

| Functional traits | | Formula |
|---|---|---|
| **Food acquisition** | Oral gape surface | $\frac{Mw\ x\ Md}{Bw\ x\ Bd}$ |
| | Oral gape shape | $\frac{Md}{Mw}$ |
| | Oral gape position | $\frac{Mo}{Hd}$ |
| | Eye size | $\frac{Ed}{Hd}$ |
| **Locomotion** | Eye position | $\frac{Ed}{Hd}$ |
| | Body transversal shape | $\frac{Bd}{Bw}$ |
| | Pectoral fin position | $\frac{PFi}{PFb}$ |
| | Aspect ratio of the pectoral fin | $\frac{PFl^2}{PFs}$ |
| | Caudal peduncle throttling | $\frac{CFd}{CPd}$ |
| | Aspect ratio of caudal fin | $\frac{CFd^2}{CFs}$ |
| | Fin surface ratio | $\frac{2\ x\ PFs}{CFs}$ |
| | Fin surface to body size ratio | $\frac{(2\ x\ PFs) + CFs}{\pi/4\ x\ (Bw\ x\ Bd)}$ |

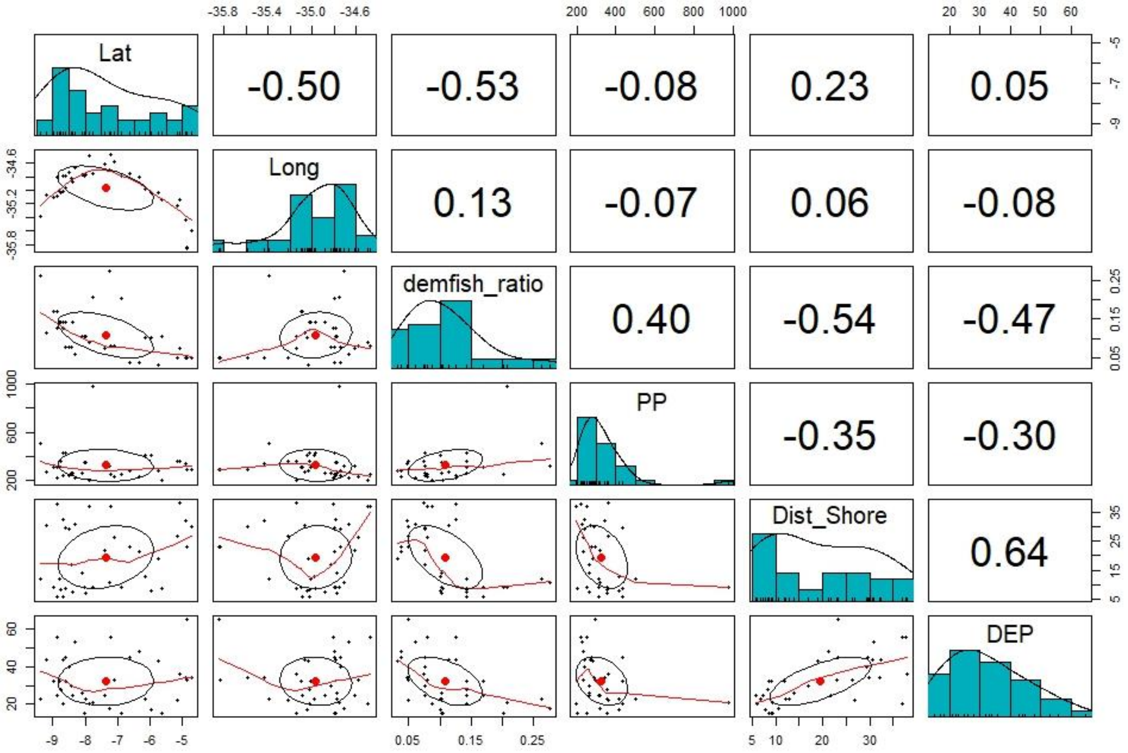


**Figure S1** Draftsman plot showing pairwise relationship among environmental variables (latitude, longitude, particle dispersion, primary production, distance of shore and, depth). Upper panel provides Pearson and Spearman correlation coefficients (chosen because linear relationships observed). Diagonal panel shows histograms of index values and density curves. Lower panel provides x-y plots for pairwise indices, with cloud of points fitted by a non-parametric local regression (LOcally WEighted Scatter plot Smoothing, LOWESS).

## ACKNOWLEDGEMENTS

We acknowledge the French oceanographic fleet for funding the at sea survey ABRAÇOS 1 and 2 (http://dx.doi.org/10.17600/15005600 /http://dx.doi.org/10.17600/17004100) and AMAZOMIX Project, the officers, crew and, researchers of the R/V Antea for their contribution to the success of the operations. This work is a contribution to the Tropical Atlantic Interdisciplinary laboratory on physical, biogeochemical, ecological and human dynamics International Laboratory (LMI TAPIOCA), supported by IRD, and EU H2020 TRIATLAS project (grant agreement 817578). Kátia Cristina Aparecido was funded by CAPES (Coordination for the Improvement of Higher Education Personnel) and by the CAPES/COFECUB (88881.142689/2017-01)

# 5. GENERAL DISCUSSION

This thesis aimed to elucidate the taxonomic and functional diversity of two distinct tropical fish communities associated with the continental shelf and oceanic islands of the Southwestern Atlantic, off the northeast region, Brazil. Divided into three chapters, it investigates the processes shaping marine fish demersal and mesopelagic communities and advances our knowledge to inform effective management strategies. Additionally, this research seeks to establish a robust database of functional traits to support future studies.

The first two chapters focused on the mesopelagic fish community, employing a traits-based approach integrating a novel functional traits data. Chapter one delineates and quantifies the functional traits characterizing mesopelagic fishes, proposing a refined classification system providing a comprehensive database for several species. This classification aims to enhance analytical frameworks for future ecological and evolutionary investigations, potentially shedding light on the resilience and ecosystem functioning considering mesopelagic fish communities amidst global environmental shifts.

Chapter two explores the diurnal and nocturnal distribution patterns of functional diversity among mesopelagic fishes, as well as examining the influence of environmental factors on these patterns. This investigation addresses significant gaps in understanding the biodiversity of mesopelagic organisms, elucidating species traits, ecological roles, and the intricate interplay between environmental conditions, species characteristics, and diversity patterns. Additionally, trait-based models were applied to explore the role of environmental filtering in shaping mesopelagic fish assemblages.

The third chapter focuses on analysing the taxonomic and functional beta diversity of demersal fishes, investigating the impacts of environmental and spatial factors on these processes. This study aimed to uncover distribution patterns of demersal fish across diverse environmental gradients, thereby identifying ecological drivers shaping community structure. The findings of this research endeavour hold implications for marine conservation efforts and the effective management of critical habitats in the study area.

## 5.1. Improvement of the knowledge on mesopelagic fish functional traits and the importance of open science.

Functional diversity, encompassing the variety of biological traits present within communities, is crucial for understanding ecosystem function and resilience. Unlike classical taxonomic approaches that focuses on species count and individuals' distribution, functional diversity emphasizes the species roles play within communities. The study of functional diversity, however, requires detailed information on traits, which are defined as "morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance" (Violle et al., 2007). While these traits are often readily available for many animals, mesopelagic regions present unique challenges.

First, collecting mesopelagic fish is expensive, time-consuming, and technologically demanding, often beyond the reach of many researches (Webb et al., 2010; Della Penna and Gaube, 2020; Govindarajan et al., 2021; Howell et al., 2021). This leads to unexplored traits for species and regions. Second, the fragility of most mesopelagic fish means they are aften damaged when collected, complicating trait analysis. Third, mesopelagic fish exhibit distinctive adaptations like forms of bioluminescence, extensible jaws and stomachs, or unique reproductive mechanisms, making initial trait studies both innovative and challenging (Turner et al., 2009; Priede, 2017). In this context, shifting the view of mesopelagic fish biodiversity from a taxonomic to a functional perspective requires a significant effort to define key traits, and extensively collect this information. Therefore, we sought to establish our data to support a broader range of ecological studies. This decision arose from recognizing the challenges in accessing this community and aligning with Porter (2018), who critiques the traditional model of ecological research. Often, the collected data is stored and not reused, under the assumption that its value is exhausted in the initial publications (Porter, 2018). Such practices lead to inefficiencies due to redundant data collection efforts (Magnuson, 1990; Cook et al., 2017; Porter, 2018), hindering the study of complex ecosystem processes that require multidisciplinary data integration. Additionally, ecological data holds vale over decades, with centuries-old data proving invaluable for detecting long-term changes (Magnuson, 1990; Cook et al., 2017).

Despite the challenges of organization and standardization inherent in building an accessible scientific database due to its heterogeneous nature, our illustrated study, featuring detailed illustrations of collected specimens, will facilitate the identification and categorization of traits. Using free repositories will enhance data sharing, use and exchange, in lines with the FAIR principles (Findable, Accessible, Interoperable, Reusable). This approach faces several challenges, such as organization and standardization, in making a scientific database available due to its heterogeneous nature. However, the illustrated guide we provided, with drawings based on the collected individuals, will facilitate the identification and categorization of traits. Free accessible storage allows the integration of information from different sources in an automated way, including dedicated checks, providing opportunities to model complex biological processes and extract intrinsic knowledge (Krochmal et al., 2018). Consequently, databases are indispensable for current and future scientific research. As Campbell (2009) noted, "Research cannot flourish if data are not preserved and made accessible." Our work strives to overcome these challenges, contributing to a robust, accessible foundation for ongoing and future ecological studies on mesopelagic fishes.

## 5.2. Dynamics of functional space in the mesopelagic environment

Chapter two investigates the diurnal and nocturnal distribution patterns of functional diversity among mesopelagic fish, with a focus on how environmental factors influence these patterns. This study aims to bridge significant knowledge gaps in mesopelagic diversity, detailing species characteristics, ecological roles, and the complex interaction between environmental conditions, species traits, and community patterns. Additionally, trait-based models were employed to explore the role of environmental filtering in shaping mesopelagic fish assemblages. In this chapter, we utilized data from scientific expeditions which sampled 200 taxa from over 7,000 specimens to assess the functional diversity of mesopelagic fish assemblages at various depths and times of day. Using the functional traits database introduced in chapter one, functional spaces and diversity indices were calculated, and functional groups were established. Furthermore, generalized additive models (GAMs) were used to evaluate the impact of environmental variables and diurnal-nocturnal cycles on functional diversity.

Our findings support the limiting similarity hypothesis (i.e. functional complementarity among species), as well as that functional diversity in mesopelagic ecosystems is both dynamic and heterogeneous. Notably, functional diversity peaks in deeper layers and exhibits significant diurnal variations. This complexity sets mesopelagic ecosystems apart from many other marine environments, such as coastal systems, adding a nuanced layer of information crucial for effective management and conservation efforts.

A similar dynamic had been previously documented by Eduardo (2020c, 2021), based on taxonomic data, highlighting high richness and diversity in lower mesopelagic layer (500-1000 m) during the day, with an increase in diversity in the epipelagic environment. Our study mirrors and complements these findings: functional richness is highest in the lower layer and the lowest in the epipelagic layer. Although the lower layer continues to show the highest functional richness, there is a significant increase of 125.53% in functional richness in the epipelagic layer at night (Fig. 5). This highlights the dynamic movement of changes in functional space. This substantial shift in functional space is related to the vertical migration of species that exhibit extreme functional traits, representing the most distinct set of functional traits in the community.

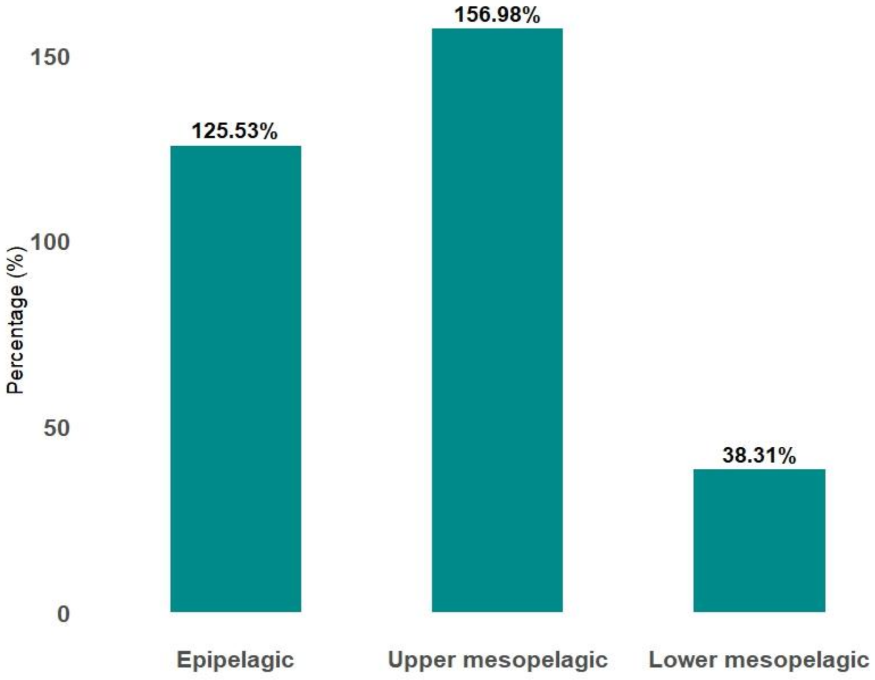


**Figure 5.** Percentage increase in functional space at night.

This dynamic nature of functional structure of mesopelagic fish may indicate the critical role in important function, like of carbon transfer to the deep sea. It has been shown that the carbon injection ranges from 1 to 30 mgC m−2 day−1, corresponding to

14-18% of the local passive sedimentation flux (Hilmi et al., 2023). Without this transport, atmospheric carbon levels would be approximately 200 ppm higher (Maier-Reimer et al., 1996). Hoagland et al. (2019) estimate the social cost of this function at approximately 300,000 to 900,000 million USD annually.

Our research also highlights the unique composition of functional traits in themesopelagic fish community, comprising 107 species, which demonstrates vast functional complementarity within this ecosystem. This underscores the uniqueness of this community. High values for unique compositions of functional traits serve as a conservation alert, indicating that if there is a population decline or extinction processes, the functions performed by these fish will be lost (Leitão et al., 2016). In other words, no other fish will be able to perform a functional role in the same manner within the ecosystem. Therefore, we can infer that the functions performed by mesopelagic fish in the study area present high vulnerability.

The environment's high daily dynamics and low functional redundancy raise concerns, especially given the increasing interest in deep-sea exploitation. Luxury seafood products (Olsen et al., 2020; Dowd et al., 2022) and the estimated biomass ranging between 1 and 16 GT (St. John et al., 2016; Proud et al., 2019; Martin et al., 2020) have prompted countries like Norway and Pakistan, among others, to issue new fishing licenses for deep-sea regions (The Economist, 2017; Brooks et al., 2022). While this trend is not yet observed in Brazil, it serves as a warning. The mesopelagic environment remains poorly understood, with recent discoveries of new species and occurrences recorded in the study area (Eduardo et al., 2018b, 2019; Mincarone et al., 2022; Villarins et al., 2023b, 2023a, 2024).

## 5.3. Structuring processes of demersal communities

Demersal fish communities play critical roles in ecosystem functioning, such as nutrient cycling and energy flow in benthic communities. Although collecting these communities is less challenging than sampling mesopelagic communities, the dynamics of demersal fish communities in northeastern Brazil remain poorly understood. Recent studies have focused on understanding diversity using traditional approaches, such as taxonomic alpha diversity (Eduardo et al., 2018a; Cardoso de Melo et al., 2020; Soares et al., 2020), but these approaches fall short in making possible links for safeguarding resilience and ecosystem services against environmental disturbances (Guillemot et al., 2011; Williams et al., 2014), as they focus on a part of the spatial variability in species distribution and abundance (Williams et al., 2014). Beta diversity alone is also insufficient for assessing community diversity and ensuring ecosystem functioning. Instead, integrated and complementary approaches are needed. By examining the structuring components of communities (turnover and nestedness), research can better address specific issues such as the need for expanded marine protected areas (MPAs) that encompass different communities and ecological corridors (Pendoley et al., 2014; Mouillot et al., 2016; Albouy et al., 2017). This is particularly relevant for the Brazilian coastal shelf, part of a faunal corridor linking cold habitats in southern Brazil with the Caribbean (Olavo et al., 2011).

In chapter 3, we aimed to understand community structuring through beta diversity. However, our analysis extends beyond species level, incorporating functional beta diversity to provide a multidimensional view of biodiversity.

Our study revealed that the predominant ecological processes affecting beta diversity differ between taxonomic and functional facets. Species turnover primarily influenced the taxonomic facet, while the functional facet was influenced equally by its components. This demonstrates that beta diversity components exhibit spatial variability and can be influenced by different predictors. Soininen et al. (2018) observed that species turnover is consistently the largest component of total beta diversity, suggesting that differences in species richness often play a minor role in generating beta diversity patterns (Viana et al., 2016; Hill et al., 2017). Thus, understanding regional diversity requires addressing various facets of diversity.

Ecosystems composed of a mosaic of different substrates, such as the continental shelf of Northeast Brazil, may promote variation in species diversity (Araújo et al., 2019). These differences in habitats within ecosystems can facilitate each other through structural complementarity and through exchange of material and energy across habitats (Alsterberg et al., 2017). The habitat heterogeneity and complexity likely influence both the functional and taxonomic distinction of the demersal fish community in this region.

Pelage et al. (2022) found significant differences in intra- and interspecific competition related to different substrate types in the demersal fish community of the study area. More complex substrates can intensify interspecific competition, limiting coexistence and selecting less related, functionally dissimilar species to co-occur in local communities (Gerhold et al., 2015). Although we did not test for competitive interaction factors, these relationships may influence the high taxonomic and functional beta diversity observed on the continental shelf.

Depth was identified as the strongest predictor of both taxonomic and functional beta diversity, underscoring the role of environmental filtering in structuring demersal fish communities. Eduardo et al. (2018a) had previously recognized depth as a key predictor of alpha diversity. This highlights the critical role of depth in marine fish communities, as it is a well-established factor in determining fish distribution and niche partitioning (Fitzpatrick et al., 2012; Zintzen et al., 2012; Willems et al., 2015; Medeiros et al., 2021; Galaiduk et al., 2022).

As an ecotone, a transitional area between distinct ecosystems—in this case, the continental shelf and the slope—this characteristic may impact community structuring, contributing to the high values of taxonomic and functional beta diversity. Impacts in this area can lead to the loss of beta diversity, biological homogenization, and even a reduction in ecosystem functions (Socolar et al., 2016). In extreme cases, such impacts could lead to desertification processes (Loreau et al., 2003; Wang et al., 2021).

### 5.4. Perspectives of conservation

This thesis offers an integrated understanding of the biodiversity, functional ecology and distribution patterns of demersal and mesopelagic fishes, thereby enhancing prospects for marine conservation and sustainable management of ocean resources.

Studies of ecological communities are especially crucial in developing countries, where there are not many incentives for research, management and monitoring of the use of the marine environment (Howell et al., 2021; Santos et al., 2023). In Brazil, discussions on environmental preservation need to be continued within the government and among the general population in general. For example, Brazil has not reported on official fishing statistics since 2011 (Santos et al., 2023). This lack of data makes management approaches challenging, leaving demersal fish communities—key targets of commercial fishing—highly vulnerable. Such vulnerabilities may also impact mesopelagic fish communities through the food chain and their relationship with the epipelagic environment.

Challenges facing these communities extend beyond overfishing to include habitat degradation, pollution, and climate change (Amaral and Jablonski, 2005; Bellas et al., 2016; Isaac and Ferrari, 2017; Justino et al., 2022b) more directly to demersal fish. These threats can lead to changes shifts in species composition, diversity, and size, as well as the loss of important critical habitats for fish at various life stages (Laidig et al., 2009). These threats are particularly concerning given the high diversity of demersal fishes in the region. Given the high diversity of demersal fishes in the region, which hold significant socio-economic value (Amaral and Jablonski, 2005), these threats are particularly concerning.

Mesopelagic fish, too, face increasing threats with unprecedented consequences. Climatic change can alter ocean stratification and environmental conditions (Levin et al., 2019; Brito-Morales et al., 2020), potentially compromising the conditions necessary for their basic functions, such as feeding and reproduction. Our study area has shown that mesopelagic fish exhibit extensive vertical migration, as highlighted by Eduardo et al. (2020b, 2021). This thesis showed the dynamic nature of this environment, with functional groups shifting throughout the day, creating a functionally distinct community.

The study area on the continental shelf, encompasses five Marine Protected Areas (MPAs) in the vicinity of the collection stations: MPA dos Corais, MPA Santa Cruz, MPA Recife Serrambi, MPA Guadalupe, and MPA Costa dos Corais (ICMBio, 2024). These areas are recognized as zones of vital importance for nature preservation. However, their regulations are heterogeneous with highly different regulations, which adds even more flexibility (Floeter et al., 2006; Pereira et al., 2021). This region is known to present biodiversity hotspots (Eduardo et al., 2018a). Our research could inform zoning discussions and support the expansion of MPAs, especially in areas with high taxonomic and functional turnover, indicating the most sensitive points for conservation, through the identification of the combination of key traits for the maintenance of ecosystem functions.

## 6. GENERAL CONCLUSION

This thesis represents a pioneering endeavor aimed at delineating the functional diversity within the mesopelagic fish community. It also constitutes one of the initial attempts to compare the functional and taxonomic beta diversity of demersal communities in Northeast Brazil. We provide a comprehensive examination of functional diversity across both mesopelagic and demersal fish communities.

Previous research on demersal fish communities has predominantly focused on functional alpha diversity within coastal or estuarine environments (Passos et al., 2016;

da Silva et al., 2019) or solely on taxonomic beta diversity (Medeiros et al., 2021). In mesopelagic communities, research has often been confined to individual species or dominant families, with functional trait consideration limited due to the complexities in defining trait patterns (Tuset et al., 2014, 2018; Mindel et al., 2016).

The novelty of this study lies in its detailed insights into the distribution patterns of both mesopelagic and demersal fish communities. The central research question of this thesis was: How the taxonomic and functional diversity of demersal and mesopelagic fish communities are distributed throughout the Northeast region of Brazil, and what are the main processes underlying these distributions? Chapter two showed that mesopelagic fish exhibit significant diurnal and nocturnal shifts in functional diversity, influenced by environmental factors such as light availability and prey distribution. Chapter three demonstrated that demersal fish communities are structured predominantly by depth gradients and substrate types, highlighting areas of high species turnover, alongside an analysis of environmental influences as elucidated in chapters two and three. Additionally, this thesis introduces an original dataset in Chapter one, proposing a comprehensive framework for the assessment of functional traits, which includes measurements of feeding behaviour, survival strategies, and morphological adaptations. These specific findings underscore the complexity of marine ecosystems and the necessity of multifaceted conservation approaches.

Our investigations have unveiled the intricacies of oceanic ecosystems and the interconnectedness between different components of fish communities. Through our analysis of functional and taxonomic diversity, we identified the turnover process as predominant in this region, in addition to identifying areas with greater variation, both at the species and function levels. This provides a comprehensive understanding of species distribution in the environment, emphasizing the importance of considering not only taxonomic diversity but also species functions and replacement patterns.

We have demonstrated that functional diversity indices, both alpha and beta, offer complementary insights for identifying critical areas necessitating preservation compared to traditional taxonomic indices. By capturing the roles played by species within communities, these functional metrics reveal nuanced biodiversity patterns essential for effective conservation planning. This approach enables a more precise identification of ecological hotspots and vulnerable habitats, guiding targeted preservation efforts.

The insights gained from this research will inform future conservation actions, ensuring that management practices are grounded in a robust understanding of both taxonomic and functional diversity. This comprehensive approach is essential for the sustainable management of marine resources, fostering resilience in marine ecosystems amidst ongoing environmental changes. Beyond the region considered in this work, these findings have broader implications for marine conservation efforts. By providing a model for integrating functional diversity into conservation planning, this research may give support for preserving marine biodiversity in other vulnerable regions. Data sharing and collaboration among scientists are crucial to advance our understanding and ensure the protection of these invaluable marine ecosystems for future generations.

While our studies have significantly advanced our understanding of fish diversity distribution, several processes remain unclear, such as the reproductive periods of key species, which can significantly alter community dynamics. Future research should focus on spatial studies that track reproductive cycles and their impacts on both mesopelagic and demersal fish communities. Additionally, investigating the effects of climate change on these reproductive periods and how they interact with other environmental stressors could provide critical insights into the resilience of these communities and ecosystems.

## REFERENCES

Abrams, P. (1983). The theory of limiting similarity. *Annual review of ecology and systematics* 14, 359–376.

Abrams, P. A. (1992). Why don’t predators have positive effects on prey populations? *Evol Ecol* 6, 449–457. doi: 10.1007/BF02270691

Aksnes, D. L., Løtvedt, A. S., Lindemann, C., Calleja, M. L., Morán, X. A. G., Kaarvedt, S., et al. (2023). Effects of migrating mesopelagic fishes on the biological carbon pump. *Marine Ecology Progress Series* 717, 107–126. doi: 10.3354/meps14373

Albouy, C., Delattre, V. L., Mérigot, B., Meynard, C. N., and Leprieur, F. (2017). Multifaceted biodiversity hotspots of marine mammals for conservation priorities. *Diversity and Distributions* 23, 615–626. doi: 10.1111/ddi.12556

Almeida, F. F. M. de (2006). Ilhas oceânicas brasileiras e suas relações com a tectônica atlântica. *Terrae Didatica* 2, 3–18. doi: 10.20396/td.v2i1.8637462

Alsterberg, C., Roger, F., Sundbäck, K., Juhanson, J., Hulth, S., Hallin, S., et al. (2017). Habitat diversity and ecosystem multifunctionality—The importance of direct and indirect effects. *Sci. Adv.* 3, e1601475. doi: 10.1126/sciadv.1601475

Alves, R. R. N., Pinto, M. F., Borges, A. K. M., and Oliveira, T. P. R. (2023). “Fisheries and Uses of Coastal Aquatic Fauna in the Northernmost Brazilian Atlantic Forest,” in *Animal Biodiversity and Conservation in Brazil’s Northern Atlantic Forest*, eds. G. A. Pereira Filho, F. G. R. França, R. R. N. Alves, and A. Vasconcellos (Cham: Springer International Publishing), 229–255. doi: 10.1007/978-3-031-21287-1_14

Amaral, A. C. Z., and Jablonski, S. (2005). Conservation of Marine and Coastal Biodiversity in Brazil. *Conservation Biology* 19, 625–631. doi: 10.1111/j.1523-1739.2005.00692.x

Anderson, M. J., Tolimieri, N., and Millar, R. B. (2013). Beta Diversity of Demersal Fish Assemblages in the North-Eastern Pacific: Interactions of Latitude and Depth. *PLOS ONE* 8, e57918. doi: 10.1371/journal.pone.0057918

Aparecido, K. C., Fredou, T., Eduardo, L. N., Mincarone, M. M., Lima, R. S., Morais, M. F. da S., et al. (2023). Living in darkness: functional diversity of mesopelagic fishes in the western tropical Atlantic. *Frontiers in Marine Science* 10, 1117806.

Araújo, F. G., de Azevedo, M. C. C., de Sousa Gomes-Gonçalves, R., and Guedes, A. P. P. (2019). Taxonomic and functional β-diversity patterns reveal random assembly rules in nearshore fish assemblages. *Marine Ecology Progress Series* 627, 109–123. doi: 10.3354/meps13081

Arhan, M., Mercier, H., Bourlès, B., and Gouriou, Y. (1998). Hydrographic sections across the Atlantic at 7°30N and 4°30S. *Deep Sea Research Part I: Oceanographic Research Papers* 45, 829–872. doi: 10.1016/S0967-0637(98)00001-6

Assunção, R., Lebourges-Dhaussy, A., Da Silva, A. C., Roudaut, G., Ariza, A., Eduardo, L. N., et al. (2023). Fine-scale vertical relationships between environmental conditions and sound scattering layers in the Southwestern Tropical Atlantic. *Plos one* 18, e0284953. doi: 10.1371/journal.pone.0284953

Assunção, R. V., Lebourges-Dhaussy, A., da Silva, A. C., Bourlès, B., Vargas, G., Roudaut, G., et al. (2021). On the use of acoustic data to characterise the thermohaline stratification in a tropical ocean. *Ocean Science Discussions*, 1–20. doi: 10.5194/os-2021-101

Assunção, R. V., Silva, A. C., Roy, A., Bourlès, B., Silva, C. H. S., Ternon, J.-F., et al. (2020). 3D characterisation of the thermohaline structure in the southwestern tropical Atlantic derived from functional data analysis of in situ profiles. *Progress in Oceanography* 187, 102399. doi: 10.1016/j.pocean.2020.102399

Barbier, E. B. (2017). Marine ecosystem services. *Current Biology* 27, R507–R510. doi: 10.1016/j.cub.2017.03.020

Barrilli, G. H. C., do Vale, J. G., Chahad-Ehlers, S., Verani, J. R., and Branco, J. O. (2024). Spatial patterns of beta diversity in marine benthic assemblages from coastal areas of southern Brazil and their implications for conservation. *Estuarine, Coastal and Shelf Science* 297, 108603. doi: 10.1016/j.ecss.2023.108603

Barrilli, G. H. C., Filho, J. L. R., do Vale, J. G., Port, D., Verani, J. R., and Branco, J. O. (2021). Role of the habitat condition in shaping of epifaunal macroinvertebrate bycatch associated with small-scale shrimp fisheries on the Southern Brazilian Coast. *Regional Studies in Marine Science* 43, 101695. doi: 10.1016/j.rsma.2021.101695

Barry, J., Mol, A. P. J., and Zito, A. R. (2013). Climate change ethics, rights, and policies: an introduction. *Environmental Politics* 22, 361–376. doi: 10.1080/09644016.2013.788861

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19, 134–143. doi: 10.1111/j.1466-8238.2009.00490.x

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* 21, 1223–1232. doi: 10.1111/j.1466-8238.2011.00756.x

Baselga, A. (2013). Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution* 4, 552–557. doi: 10.1111/2041-210X.12029

Baselga, A., Jiménez-Valverde, A., and Niccolini, G. (2007). A multiple-site similarity measure independent of richness. *Biology Letters* 3, 642–645. doi: 10.1098/rsbl.2007.0449

Baselga, A., and Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. *Methods Ecol Evol* 3, 808–812. doi: 10.1111/j.2041-210X.2012.00224.x

Bastos, A. C., Quaresma, V. S., Marangoni, M. B., D'Agostini, D. P., Bourguignon, S. N., Cetto, P. H., et al. (2015). Shelf morphology as an indicator of sedimentary regimes: A synthesis from a mixed siliciclastic–carbonate shelf on the eastern Brazilian margin. *Journal of South American Earth Sciences* 63, 125–136. doi: 10.1016/j.jsames.2015.07.003

Bellas, J., Martínez-Armental, J., Martínez-Cámara, A., Besada, V., and Martínez-Gómez, C. (2016). Ingestion of microplastics by demersal fish from the Spanish Atlantic and Mediterranean coasts. *Marine pollution bulletin* 109, 55–60. doi: 10.1016/j.marpolbul.2016.06.026

Bellwood, D. R., Hughes, T. P., Folke, C., and Nyström, M. (2004). Confronting the coral reef crisis. *Nature* 429, 827–833. doi: doi:10.1038/nature02691

Benadon, C., Zabin, C. J., Haram, L., Carlton, J. T., Maximenko, N., Nelson, P., et al. (2023). Marine debris facilitates the long-distance dispersal of fish species. *Mar Biol* 171, 43. doi: 10.1007/s00227-023-04365-3

Bender, M. G., Floeter, S. R., Mayer, F. P., Vila-Nova, D. A., Longo, G. O., Hanazaki, N., et al. (2013). Biological attributes and major threats as predictors of the vulnerability of species: a case study with Brazilian reef fishes. *Oryx* 47, 259–265. doi: 10.1017/S003060531100144X

Bender, M. G., and Luiz, O. J. (2019). Specialization boosts reef fish functional diversity. *Nat Ecol Evol* 3, 153–154. doi: 10.1038/s41559-018-0760-7

Bertelli, C. M., and Unsworth, R. K. (2014). Protecting the hand that feeds us: Seagrass (Zostera marina) serves as commercial juvenile fish habitat. *Marine pollution bulletin* 83, 425–429.

Bertrand, A. (2015). ABRACOS cruise,Antea R/V. doi: 10.17600/15005600

Bertrand, A. (2017). ABRACOS 2 cruise,Antea R/V. doi: 10.17600/17004100

Bertrand, A., Ballón, M., and Chaigneau, A. (2010). Acoustic Observation of Living Organisms Reveals the Upper Limit of the Oxygen Minimum Zone. *PLOS ONE* 5, e10330. doi: 10.1371/journal.pone.0010330

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., et al. (2000). Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science* 57, 558–571. doi: 10.1006/jmsc.2000.0727

Blanchet, F. G., Legendre, P., and Borcard, D. (2008). Forward Selection of Explanatory Variables. *Ecology* 89, 2623–2632. doi: 10.1890/07-0986.1

Borcard, D., and Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling* 153, 51–68. doi: 10.1016/S0304-3800(01)00501-4

Borland, H. P., Gilby, B. L., Henderson, C. J., Leon, J. X., Schlacher, T. A., Connolly, R. M., et al. (2021). The influence of seafloor terrain on fish and fisheries: A global synthesis. *Fish and Fisheries* 22, 707–734. doi: 10.1111/faf.12546

Borland, H. P., Schlacher, T. A., Gilby, B. L., Connolly, R. M., Yabsley, N. A., and Olds, A. D. (2017). Habitat type and beach exposure shape fish assemblages in the surf zones of ocean beaches. *Marine Ecology Progress Series* 570, 203–211. doi: 10.3354/meps12115

Boswell, K. M., D’Elia, M., Johnston, M. W., Mohan, J. A., Warren, J. D., Wells, R. J. D., et al. (2020). Oceanographic Structure and Light Levels Drive Patterns of Sound Scattering Layers in a Low-Latitude Oceanic System. *Frontiers in Marine Science* 7. doi: 10.3389/fmars.2020.00051

Braak, C. J. F. ter, Peres-Neto, P., and Dray, S. (2017). A critical issue in model-based inference for studying trait-based community assembly and a solution. *PeerJ* 5, e2885. doi: 10.7717/peerj.2885

Brandl, S. J., Emslie, M. J., Ceccarelli, D. M., and T. Richards, Z. (2016). Habitat degradation increases functional originality in highly diverse coral reef fish assemblages. *Ecosphere* 7, e01557. doi: 10.1002/ecs2.1557

Brito-Morales, I., Schoeman, D. S., Molinos, J. G., Burrows, M. T., Klein, C. J., Arafeh-Dalmau, N., et al. (2020). Climate velocity reveals increasing exposure of deep-ocean biodiversity to future warming. *Nature Climate Change* 10, 576–581. doi: 10.1038/s41558-020-0773-5

Brooks, C. M., Ainley, D. G., Jacquet, J., Chown, S. L., Pertierra, L. R., Francis, E., et al. (2022). Protect global values of the Southern Ocean ecosystem. *Science* 378, 477–479. doi: 10.1126/science.add9480

Buarque, B. V., Barbosa, J. A., Magalhães, J. R., Oliveira, J. T. C., and Correia Filho, O. J. (2016). Post-rift volcanic structures of the Pernambuco Plateau, northeastern Brazil. *Journal of South American Earth Sciences* 70, 251–267. doi: 10.1016/j.jsames.2016.05.014

Camara, E. M., de Andrade-Tubino, M. F., Franco, T. P., Neves, L. M., dos Santos, L. N., dos Santos, A. F. G. N., et al. (2023). Temporal dimensions of taxonomic and functional fish beta diversity: scaling environmental drivers in tropical transitional ecosystems. *Hydrobiologia* 850, 1911–1940. doi: 10.1007/s10750-023-05202-w

Camargo, J. M. R., Araújo, T. C. M., Ferreira, B. P., and Maida, M. (2015). Topographic features related to recent sea level history in a sediment-starved tropical shelf: linking the past, present and future. *Regional Studies in Marine Science* 2, 203–211. doi: 10.1016/j.rsma.2015.10.009

Campbell, P. (2009). Data's shameful neglect. *Nature* 461, 145.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., et al. (2012). Biodiversity loss and its impact on humanity. *Nature* 486, 59–67. doi: doi:10.1038/nature11148

Cardoso de Melo, C., Soares, A. P. C., Pelage, L., Eduardo, L. N., Frédou, T., Lira, A. S., et al. (2020). Haemulidae distribution patterns along the Northeastern Brazilian continental shelf and size at first maturity of the most abundant species. *Regional Studies in Marine Science* 35, 101226. doi: 10.1016/j.rsma.2020.101226

Carrascal, M. H., Shadman, M., Amiri, M. M., Silva, C., Estefen, S. F., and La Rovere, E. (2021). Environmental impacts of offshore wind installation, operation and maintenance, and decommissioning activities: A case study of Brazil. *Renewable and Sustainable Energy Reviews* 144, 110994. doi: 10.1016/j.rser.2021.110994

Cavan, E. L., Laurenceau-Cornec, E. C., Bressac, M., and Boyd, P. W. (2019). Exploring the ecology of the mesopelagic biological pump. *Progress in Oceanography* 176, 102125. doi: 10.1016/j.pocean.2019.102125

CBD (2014). *Ecologically or Biologically Significant Marine Areas (EBSAs).*, 2nd Edn. Secretariat of the Convention on Biological Diversity.

Collin, S. P., Hoskins, R. V., and Partridge, J. C. (1997). Tubular eyes of deep-sea fishes: a comparative study of retinal topography (Part 2 of 2). *Brain, behavior and evolution* 50, 347–357. doi: 10.1159/000316300

Conover, D. O., and Schultz, E. T. (1995). Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology & Evolution* 10, 248–252. doi: 10.1016/S0169-5347(00)89081-3

Cook, R. B., Wei, Y., Hook, L. A., Vannan, S. K. S., and McNelis, J. J. (2017). Preserve: protecting data for long-term use, Chapter 6. *Ecological informatics. Data management and knowledge discovery. Springer, Heidelberg*.

Cornwell, W. K., Schwilk, D. W., and Ackerly, D. D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology* 87, 1465–1471. doi: 10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2

Cuesta Núñez, J., Romero, M. A., Ocampo Reinaldo, M., González, R., Magurran, A., and Svendsen, G. M. (2023). Species turnover drives functional turnover with balanced functional nestedness in a Patagonian demersal assemblage. *Journal of Sea Research* 196, 102452. doi: 10.1016/j.seares.2023.102452

da Silva, V. E. L., Silva-Firmiano, L. P. S., Teresa, F. B., Batista, V. S., Ladle, R. J., and Fabré, N. N. (2019). Functional Traits of Fish Species: Adjusting Resolution to Accurately Express Resource Partitioning. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00303

D'agata, S., Mouillot, D., Kulbicki, M., Andréfouët, S., Bellwood, D. R., Cinner, J. E., et al. (2014). Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Current Biology* 24, 555–560. doi: 10.1016/j.cub.2014.01.049

Dallas, T. A., and Kramer, A. (2022). A latitudinal signal in the relationship between species geographic range size and climatic niche area. *Ecography* 2022, e06349. doi: 10.1111/ecog.06349

Darimont, C. T., Carlson, S. M., Kinnison, M. T., Paquet, P. C., Reimchen, T. E., and Wilmers, C. C. (2009). Human predators outpace other agents of trait change in the wild. *Proc. Natl. Acad. Sci. U.S.A.* 106, 952–954. doi: 10.1073/pnas.0809235106

Darling, E. S., Graham, N. A., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., and Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs* 36, 561–575.

Davis, A. L., Sutton, T. T., Kier, W. M., and Johnsen, S. (2020a). Evidence that eye-facing photophores serve as a reference for counterillumination in an order of deep-sea fishes. *Proceedings of the Royal Society B: Biological Sciences* 287, 20192918. doi: 10.1098/rspb.2019.2918

Davis, A. L., Thomas, K. N., Goetz, F. E., Robison, B. H., Johnsen, S., and Osborn, K. J. (2020b). Ultra-black Camouflage in Deep-Sea Fishes. *Current Biology* 30, 3470-3476.e3. doi: 10.1016/j.cub.2020.06.044

Davison, P., and Asch, R. G. (2011). Plastic ingestion by mesopelagic fishes in the North Pacific Subtropical Gyre. *Marine Ecology Progress Series* 432, 173–180. doi: 10.3354/meps09142

De Barros, M. J. G., Eduardo, L. N., Bertrand, A., Lucena-Fredou, F., Fredou, T., Lira, A. S., et al. (2021). Bottom trawling on a carbonate shelf: Do we get what we see? *Continental Shelf Research* 213, 104314. doi: 10.1016/j.csr.2020.104314

De O. Soares, M., Cruz, I. C. S., Santos, B. A., Tavares, T. C. L., Garcia, T. M., Menezes, N., et al. (2020). "Marginal Reefs in the Anthropocene: They Are Not Noah's Ark," in *Perspectives on the Marine Animal Forests of the World*, eds. S. Rossi and L. Bramanti (Cham: Springer International Publishing), 87–128. doi: 10.1007/978-3-030-57054-5_4

de Oliveira Soares, M., Davis, M., de Paiva, C. C., and de Macêdo Carneiro, P. B. (2018). Mesophotic ecosystems: coral and fish assemblages in a tropical marginal reef (northeastern Brazil). *Mar Biodiv* 48, 1631–1636. doi: 10.1007/s12526-016-0615-x

Dee, L. E., Miller, S. J., Peavey, L. E., Bradley, D., Gentry, R. R., Startz, R., et al. (2016). Functional diversity of catch mitigates negative effects of temperature variability on fisheries yields. *Proceedings of the Royal Society B: Biological Sciences* 283, 20161435. doi: 10.1098/rspb.2016.1435

del Giorgio, P. A., and Duarte, C. M. (2002). Respiration in the open ocean. *Nature* 420, 379–384. doi: 10.1038/nature01165

Della Penna, A., and Gaube, P. (2020). Mesoscale Eddies Structure Mesopelagic Communities. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00454

Demestre, M., Sanchez, P., and Abello, P. (2000). Demersal fish assemblages and habitat characteristics on the continental shelf and upper slope of the north-western Mediterranean. *Journal of the Marine Biological Association of the United Kingdom* 80, 981–988. doi: 10.1017/S0025315400003040

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., et al. (2010). Defining and measuring ecological specialization. *Journal of Applied Ecology* 47, 15–25. doi: 10.1111/j.1365-2664.2009.01744.x

Díaz, S., Fargione, J., Chapin III, F. S., and Tilman, D. (2006). Biodiversity loss threatens human well-being. *PLoS biology* 4, e277. doi: 10.1371/journal.pbio.0040277

Dobrovolski, R., Melo, A. S., Cassemiro, F. A. S., and Diniz-Filho, J. A. F. (2012). Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 21, 191–197. doi: 10.1111/j.1466-8238.2011.00671.x

Domingues, E. de C., Schettini, C. A. F., Truccolo, E. C., and Oliveira, J. C. de (2017). Hydrography and currents on the Pernambuco Continental Shelf. *RBRH* 22. doi: 10.1590/2318-0331.0217170027

Dossa, A. N., Silva, A. C., Chaigneau, A., Eldin, G., Araujo, M., and Bertrand, A. (2021). Near-surface western boundary circulation off Northeast Brazil. *Progress in Oceanography* 190, 102475. doi: doi.org/10.1016/j.pocean.2020.102475

Dowd, S., Chapman, M., Koehn, L. E., and Hoagland, P. (2022). The economic tradeoffs and ecological impacts associated with a potential mesopelagic fishery in the CALIFORNIA CURRENT. *Ecological Applications* 32, e2578. doi: 10.1002/eap.2578

Dray, S., and Legendre, P. (2008). Testing the Species Traits–Environment Relationships: The Fourth-Corner Problem Revisited. *Ecology* 89, 3400–3412. doi: 10.1890/08-0349.1

Dray, S., Legendre, P., and Peres-Neto, P. R. (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196, 483–493. doi: 10.1016/j.ecolmodel.2006.02.015

Drazen, J. C., Smith, C. R., Gjerde, K. M., Haddock, S. H., Carter, G. S., Choy, C. A., et al. (2020). Midwater ecosystems must be considered when evaluating environmental risks of deep-sea mining. *Proceedings of the National Academy of Sciences* 117, 17455–17460. doi: 10.1073/pnas.2011914117

Drazen, J. C., and Sutton, T. T. (2017). Dining in the deep: the feeding ecology of deep-sea fishes. *Annu. Rev. Mar. Sci* 9, 337–366.

Dukes, J. S. (2001). Productivity and complementarity in grassland microcosms of varying diversity. *Oikos* 94, 468–480. doi: 10.1034/j.1600-0706.2001.940309.x

Dumay, O., Costa, J., Desjobert, J.-M., and Pergent, G. (2004). Variations in the concentration of phenolic compounds in the seagrass Posidonia oceanica under conditions of competition. *Phytochemistry* 65, 3211–3220. doi: 10.1016/j.phytochem.2004.09.003

Edge, C. B., Fortin, M.-J., Jackson, D. A., Lawrie, D., Stanfield, L., and Shrestha, N. (2017). Habitat alteration and habitat fragmentation differentially affect beta diversity of stream fish communities. *Landscape Ecology* 32, 647–662. doi: 10.1007/s10980-016-0472-9

Eduardo, L. N., Bertrand, A., Frédou, T., Lira, A. S., Lima, R. S., Ferreira, B. P., et al. (2020a). Biodiversity, ecology, fisheries, and use and trade of Tetraodontiformes fishes reveal their socio-ecological significance along the tropical Brazilian continental shelf. *Aquatic Conservation: Marine and Freshwater Ecosystems* 30, 761–774. doi: 10.1002/aqc.3278

Eduardo, L. N., Bertrand, A., Lucena-Frédou, F., Villarins, B. T., Martins, J. R., Afonso, G. V. F., et al. (2022). Rich and underreported: First integrated assessment of the diversity of mesopelagic fishes in the Southwestern Tropical Atlantic. *Frontiers in Marine Science* 9. doi: 10.3389/fmars.2022.937154

Eduardo, L. N., Bertrand, A., Mincarone, M. M., Martins, J. R., Frédou, T., Assunção, R. V., et al. (2021). Distribution, vertical migration, and trophic ecology of lanternfishes (Myctophidae) in the Southwestern Tropical Atlantic. *Progress in Oceanography* 199, 102695. doi: 10.1016/j.pocean.2021.102695

Eduardo, L. N., Bertrand, A., Mincarone, M. M., Santos, L. V., Frédou, T., Assunção, R. V., et al. (2020b). Hatchetfishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic. *Progress in Oceanography* 187, 102389. doi: 10.1016/j.pocean.2020.102389

Eduardo, L. N., Frédou, T., Lira, A. S., Ferreira, B. P., Bertrand, A., Ménard, F., et al. (2018a). Identifying key habitat and spatial patterns of fish biodiversity in the tropical Brazilian continental shelf. *Continental Shelf Research* 166, 108–118. doi: 10.1016/j.csr.2018.07.002

Eduardo, L. N., Lucena-Frédou, F., Lanco Bertrand, S., Lira, A. S., Mincarone, M. M., Nunes, G. T., et al. (2023). From the light blue sky to the dark deep sea: Trophic and resource partitioning between epipelagic and mesopelagic layers in a tropical oceanic ecosystem. *Science of The Total Environment* 878, 163098. doi: 10.1016/j.scitotenv.2023.163098

Eduardo, L. N., Lucena-Frédou, F., Mincarone, M. M., Soares, A., Le Loc'h, F., Frédou, T., et al. (2020c). Trophic ecology, habitat, and migratory behaviour of the viperfish Chauliodus sloani reveal a key mesopelagic player. *Scientific reports* 10, 20996. doi: 10.1038/s41598-020-77222-8

Eduardo, L. N., Villarins, B. T., Lucena-Frédou, F., Frédou, T., Lira, A. S., Bertrand, A., et al. (2018b). First record of the intermediate scabbardfish Aphanopus intermedius (Scombriformes: Trichiuridae) in the western South Atlantic Ocean. *Journal of Fish Biology* 93, 992–995. doi: 10.1111/jfb.13796

Eduardo, L. N., Villarins, B. T., Martins, J. R., Lucena-Frédou, F., Frédou, T., Lira, A. S., et al. (2019). Deep-sea oceanic basslets (Perciformes, Howellidae) from Brazil: new records and range extensions. *Check List* 15, 965–971. doi: 10.15560/15.6.965

Ekau, W., and Knoppers, B. (1999). An introduction to the pelagic system of the North-East and East Brazilian shelf. *Archive of Fishery and Marine Research* 47, 113–132. Available at: https://www.researchgate.net/profile/Werner-Ekau/publication/279695392_An_introduction_to_the_pelagic_system_of_the_North-East_and_East_Brazilian_shelf/links/573470d608aea45ee83ab8d5/An-introduction-to-the-pelagic-system-of-the-North-East-and-East-Brazilian-shelf.pdf (Accessed June 2, 2024).

Ellingsen, Karie., and Gray, J. s. (2002). Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf? *Journal of Animal Ecology* 71, 373–389. doi: 10.1046/j.1365-2656.2002.00606.x

Elton, C. S. (1927). *Animal Ecology*. London: Sidgwick & Jackson.

Essington, T. E., Beaudreau, A. H., and Wiedenmann, J. (2006). Fishing through marine food webs. *Proc. Natl. Acad. Sci. U.S.A.* 103, 3171–3175. doi: 10.1073/pnas.0510964103

Ferreira, G. V. B., Justino, A. K. S., Eduardo, L. N., Lenoble, V., Fauvelle, V., Schmidt, N., et al. (2022). Plastic in the inferno: Microplastic contamination in deep-sea cephalopods (Vampyroteuthis infernalis and Abralia veranyi) from the southwestern Atlantic. *Marine Pollution Bulletin* 174, 113309. doi: 10.1016/j.marpolbul.2021.113309

Fitzpatrick, B. M., Harvey, E. S., Heyward, A. J., Twiggs, E. J., and Colquhoun, J. (2012). Habitat Specialization in Tropical Continental Shelf Demersal Fish Assemblages. *PLOS ONE* 7, e39634. doi: 10.1371/journal.pone.0039634

Floeter, S. R., Halpern, B. S., and Ferreira, C. E. (2006). Effects of fishing and protection on Brazilian reef fishes. *Biological Conservation* 128, 391–402. doi: 10.1016/j.biocon.2005.10.005

Fock, H. O., Pusch, C., and Ehrich, S. (2004). Structure of deep-sea pelagic fish assemblages in relation to the Mid-Atlantic Ridge (45°–50°N). *Deep Sea Research Part I: Oceanographic Research Papers* 51, 953–978. doi: 10.1016/j.dsr.2004.03.004

Fraser, D. J. (2013). The emerging synthesis of evolution with ecology in fisheries science. *Can. J. Fish. Aquat. Sci.* 70, 1417–1428. doi: 10.1139/cjfas-2013-0171

Frédou, T., and Ferreira, B. P. (2005). Bathymetric trends of northeastern Brazilian snappers (Pisces, Lutjanidae): implications for the reef fishery dynamic. *Braz. arch. biol. technol.* 48, 787–800. doi: 10.1590/S1516-89132005000600015

Gaertner, J.-C., Bertrand, J. A., Relini, G., Papaconstantinou, C., Mazouni, N., De Sola, L. G., et al. (2007). Spatial pattern in species richness of demersal fish assemblages on the continental shelf of the northern Mediterranean Sea: a multiscale analysis. *Marine Ecology Progress Series* 341, 191–203. doi: 10.3354/meps341191

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., et al. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences* 282, 20142620. doi: 10.1098/rspb.2014.2620

Galaiduk, R., Radford, B., Case, M., Bond, T., Taylor, M., Cooper, T., et al. (2022). Regional patterns in demersal fish assemblages among subsea pipelines and natural habitats across north-west Australia. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.979987

Galvao, P., Sus, B., Lailson-Brito, J., Azevedo, A., Malm, O., and Bisi, T. (2021). An upwelling area as a hot spot for mercury biomonitoring in a climate change scenario: A case study with large demersal fishes from Southeast Atlantic (SE-Brazil). *Chemosphere* 269, 128718. doi: 10.1016/j.chemosphere.2020.128718

Gause, G. F. (1932). Experimental studies on the struggle for existence: I. Mixed population of two species of yeast. *Journal of experimental biology* 9, 389–402. doi: 10.1242/jeb.9.4.389

Gerhold, P., Cahill Jr, J. F., Winter, M., Bartish, I. V., and Prinzing, A. (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology* 29, 600–614. doi: 10.1111/1365-2435.12425

Giachini Tosetto, E., Lett, C., Koch-Larrouy, A., Costa da Silva, A., Neumann-Leitão, S., Nogueira Junior, M., et al. (2023). Identifying community assembling zones and connectivity pathways in the Tropical Southwestern Atlantic Ocean. *Ecography*, e07110. doi: 10.1111/ecog.07110

Gilly, W. F., Beman, J. M., Litvin, S. Y., and Robison, B. H. (2013). Oceanographic and Biological Effects of Shoaling of the Oxygen Minimum Zone. *Annu. Rev. Mar. Sci.* 5, 393–420. doi: 10.1146/annurev-marine-120710-100849

Gjøsæter, J., and Kawaguchi, K. (1980). *A review of the world resources of mesopelagic fish*. Rome: FAO Fisheries Techinical Paper.

Gloeckler, K., Choy, C. A., Hannides, C. C. S., Close, H. G., Goetze, E., Popp, B. N., et al. (2018). Stable isotope analysis of micronekton around Hawaii reveals suspended particles are an important nutritional source in the lower mesopelagic and upper bathypelagic zones. *Limnology and Oceanography* 63, 1168–1180. doi: 10.1002/lno.10762

Gluchowska, M., Trudnowska, E., Goszczko, I., Kubiszyn, A. M., Blachowiak-Samolyk, K., Walczowski, W., et al. (2017). Variations in the structural and functional diversity of zooplankton over vertical and horizontal environmental gradients en route to the Arctic Ocean through the Fram Strait. *PLOS ONE* 12, e0171715. doi: 10.1371/journal.pone.0171715

Goldberg, EmmaE., and Lande, R. (2006). Ecological and Reproductive Character Displacement of an Environmental Gradient. *Evolution* 60, 1344–1357. doi: 10.1111/j.0014-3820.2006.tb01214.x

Gomes, M. P., Vital, H., Bezerra, F. H., de Castro, D. L., and Macedo, J. W. de P. (2014). The interplay between structural inheritance and morphology in the Equatorial Continental Shelf of Brazil. *Marine Geology* 355, 150–161. doi: 10.1016/j.margeo.2014.06.002

Govindarajan, A. F., Francolini, R. D., Jech, J. M., Lavery, A. C., Llopiz, J. K., Wiebe, P. H., et al. (2021). Exploring the Use of Environmental DNA (eDNA) to Detect Animal Taxa in the Mesopelagic Zone. *Front. Ecol. Evol.* 9. doi: 10.3389/fevo.2021.574877

Green, S. J., Brookson, C. B., Hardy, N. A., and Crowder, L. B. (2022). Trait-based approaches to global change ecology: moving from description to prediction. *Proc. R. Soc. B.* 289, 20220071. doi: 10.1098/rspb.2022.0071

Guareschi, S., Bilton, D. T., Velasco, J., Millán, A., and Abellán, P. (2015). How well do protected area networks support taxonomic and functional diversity in non-target taxa? The case of Iberian freshwaters. *Biological Conservation* 187, 134–144.

Guerin, G. R., Biffin, E., and Lowe, A. J. (2013). Spatial modelling of species turnover identifies climate ecotones, climate change tipping points and vulnerable taxonomic groups. *Ecography* 36, 1086–1096. doi: 10.1111/j.1600-0587.2013.00215.x

Guillemot, N., Kulbicki, M., Chabanet, P., and Vigliola, L. (2011). Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. *PloS one* 6, e26735. doi: 10.1371/journal.pone.0026735

Haddock, S. H. D., Moline, M. A., and Case, J. F. (2010). Bioluminescence in the Sea. *Annu. Rev. Mar. Sci.* 2, 443–493. doi: 10.1146/annurev-marine-120308-081028

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., et al. (2008). A Global Map of Human Impact on Marine Ecosystems. *Science* 319, 948–952. doi: 10.1126/science.1149345

Harborne, A. R., Mumby, P. J., ZŻychaluk, K., Hedley, J. D., and Blackwell, P. G. (2006). Modeling the Beta Diversity of Coral Reefs. *Ecology* 87, 2871–2881. doi: 10.1890/0012-9658(2006)87[2871:MTBDOC]2.0.CO;2

Hardy, N. A., Matuch, C., Roote, Z., George, I., Muhling, B. A., Jacox, M. G., et al. (2024). Trait-based analyses reveal global patterns in diverse diets of albacore tuna (Thunnus alalunga). *Fish and Fisheries* 25, 268–282. doi: 10.1111/faf.12807

Harley, C. D. G., Randall Hughes, A., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., et al. (2006). The impacts of climate change in coastal marine systems. *Ecology Letters* 9, 228–241. doi: 10.1111/j.1461-0248.2005.00871.x

Harrison, S., Ross, S. J., and Lawton, J. H. (1992). Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology*, 151–158. doi: 10.2307/5518

Hazin, F., H. V. (2009). *Coleção Programa revizee score nordeste.* Fortaleza: Martins & Cordeiro.

Heino, J., Melo, A. S., and Bini, L. M. (2015). Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. *Freshwater Biology* 60, 223–235. doi: 10.1111/fwb.12502

Helfman, G. S., Bruce B. Collette, Douglas E. Facey, and Brien W. Bowen (2009). *The Diversity of Fishes: Biology, Evolution, and Ecology*., 2nd Edn. Wiley-Blackwell.

Heyman, W. D., and Kjerfve, B. (2008). Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bulletin of marine science* 83, 531–551.

Hidalgo, M., and Browman, H. I. (2019). Developing the knowledge base needed to sustainably manage mesopelagic resources. *ICES Journal of Marine Science* 76, 609–615. doi: 10.1093/icesjms/fsz067

Hill, M. J., Heino, J., Thornhill, I., Ryves, D. B., and Wood, P. J. (2017). Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. *Oikos* 126, 1575–1585. doi: 10.1111/oik.04266

Hilmi, N., Sutherland, M., Farahmand, S., Haraldsson, G., van Doorn, E., Ernst, E., et al. (2023). Deep sea nature-based solutions to climate change. *Front. Clim.* 5. doi: 10.3389/fclim.2023.1169665

Hoagland, P., Jin, D., Holland, M., Kostel, K., Taylor, E., Renier, N., et al. (2019). Ecosystem services of the mesopelagic. *Woods Hole Oceanographic Inst* 35.

Holm, S. (1979). A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian Journal of Statistics* 6, 65–70.

Hooper, D. U., and Dukes, J. S. (2004). Overyielding among plant functional groups in a long-term experiment. *Ecology Letters* 7, 95–105. doi: 10.1046/j.1461-0248.2003.00555.x

Houghton, J. T. (1990). IPCC Scientific Assessment. *Climate change* 365. Available at: https://cir.nii.ac.jp/crid/1571417124422507008

Howell, K. L., Hilário, A., Allcock, A. L., Bailey, D., Baker, M., Clark, M. R., et al. (2021). A decade to study deep-sea life. *Nat Ecol Evol* 5, 265–267. doi: 10.1038/s41559-020-01352-5

Hughes, T. P., Bellwood, D. R., Folke, C., Steneck, R. S., and Wilson, J. (2005). New paradigms for supporting the resilience of marine ecosystems. *Trends in ecology & evolution* 20, 380–386. doi: doi.org/10.1016/j.tree.2005.03.022

Huston, M. A. (1994). *Biological diversity: the coexistence of species on changing landscapes*. Cambrigde: Cambridge University Press.

Iacono, C. L., Sulli, A., and Agate, M. (2014). Submarine canyons of north-western Sicily (Southern Tyrrhenian Sea): Variability in morphology, sedimentary processes and evolution on a tectonically active margin. *Deep Sea Research Part II: Topical Studies in Oceanography* 104, 93–105. doi: 10.1016/j.dsr2.2013.06.018

ICMBio (2024). ICMBio - Área de Proteção Ambiental. Available at: https://www.icmbio.gov.br/apacostadoscorais/guia-do-visitante.html (Accessed June 4, 2024).

Iglesias, I. S., Santora, J. A., Fiechter, J., and Field, J. C. (2023). Mesopelagic fishes are important prey for a diversity of predators. *Front. Mar. Sci.* 10, 1220088. doi: 10.3389/fmars.2023.1220088

Isaac, V. J., and Ferrari, S. F. (2017). Assessment and management of the North Brazil Shelf Large Marine Ecosystem. *Environmental Development* 22, 97–110. doi: 10.1016/j.envdev.2016.11.004

Jacob, W., McClatchie, S., Probert, P. K., and Hurst, R. J. (1998). Demersal fish assemblages off southern New Zealand in relation to depth and temperature. *Deep Sea Research Part I: Oceanographic Research Papers* 45, 2119–2155. doi: 10.1016/S0967-0637(98)00051-X

Jennings, S., and Collingridge, K. (2015). Predicting Consumer Biomass, Size-Structure, Production, Catch Potential, Responses to Fishing and Associated Uncertainties in the World's Marine Ecosystems. *PLOS ONE* 10, e0133794. doi: 10.1371/journal.pone.0133794

Johnson, A. F., Jenkins, S. R., Hiddink, J. G., and Hinz, H. (2013). Linking temperate demersal fish species to habitat: scales, patterns and future directions. *Fish and Fisheries* 14, 256–280. doi: 10.1111/j.1467-2979.2012.00466.x

Johnson, T. F., Isaac, N. J. B., Paviolo, A., and González-Suárez, M. (2021). Handling missing values in trait data. *Global Ecology and Biogeography* 30, 51–62. doi: 10.1111/geb.13185

Jordá, G., Flexas, M. del M., Espino, M., and Calafat, A. (2013). Deep flow variability in a deeply incised Mediterranean submarine valley (Blanes canyon). *Progress in Oceanography* 118, 47–60. doi: 10.1016/j.pocean.2013.07.024

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology* 88, 2427–2439. doi: 10.1890/06-1736.1

Juarez, B. H., Speiser, D. I., and Oakley, T. H. (2019). Context-dependent evolution of ostracod morphology along the ecogeographical gradient of ocean depth. *Evolution* 73, 1213–1225. doi: 10.1111/evo.13748

Justino, A. K. S., Ferreira, G. V. B., Schmidt, N., Eduardo, L. N., Fauvelle, V., Lenoble, V., et al. (2022a). The role of mesopelagic fishes as microplastics vectors across the deep-sea layers from the Southwestern Tropical Atlantic. *Environmental Pollution* 300, 118988. doi: 10.1016/j.envpol.2022.118988

Justino, A. K. S., Ferreira, G. V. B., Schmidt, N., Eduardo, L. N., Fauvelle, V., Lenoble, V., et al. (2022b). The role of mesopelagic fishes as microplastics vectors across the deep-sea layers from the Southwestern Tropical Atlantic. *Environmental Pollution* 300, 118988. doi: 10.1016/j.envpol.2022.118988

Kassen, R. (2002). The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology* 15, 173–190. doi: 10.1046/j.1420-9101.2002.00377.x

Katz, T., Yahel, G., Yahel, R., Tunnicliffe, V., Herut, B., Snelgrove, P., et al. (2009). Groundfish overfishing, diatom decline, and the marine silica cycle: Lessons from Saanich Inlet, Canada, and the Baltic Sea cod crash. *Global Biogeochemical Cycles* 23, 2008GB003416. doi: 10.1029/2008GB003416

Kidé, S. O., Manté, C., Demarcq, H., and Mérigot, B. (2021). Groundfish assemblages diversity in upwelling ecosystems: insights from the Mauritanian Exclusive Economic Zone. *Biodivers Conserv* 30, 2279–2304. doi: 10.1007/s10531-021-02189-5

Klevjer, T. A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios, V. M., and Kaartvedt., S. (2016). Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. *Sci Rep* 6, 19873. doi: 10.1038/srep19873

Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R. J., Strauss, B., et al. (2012). Assessing species and community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science* 23, 805–821. doi: 10.1111/j.1654-1103.2012.01402.x

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., and Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29, 592–599. doi: 10.1111/1365-2435.12345

Krochmal, M., Cisek, K., and Husi, H. (2018). "Database Creation and Utility," in *Integration of Omics Approaches and Systems Biology for Clinical Applications*, eds. A. Vlahou, H. Mischak, J. Zoidakis, and F. Magni (Wiley), 286–300. doi: 10.1002/9781119183952.ch17

Laidig, T. E., Watters, D. L., and Yoklavich, M. M. (2009). Demersal fish and habitat associations from visual surveys on the central California shelf. *Estuarine, coastal and shelf science* 83, 629–637. doi: 10.1016/j.ecss.2009.05.008

Laigle, I., Aubin, I., Digel, C., Brose, U., Boulangeat, I., and Gravel, D. (2018). Species traits as drivers of food web structure. *Oikos* 127, 316–326. doi: 10.1111/oik.04712

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

Lawton, J. H. (1999). Are there general laws in ecology? *Oikos*, 177–192.

Le Tortorec, E., Häkkilä, M., Zlonis, E., Niemi, G., and Mönkkönen, M. (2023). Increasing human environmental footprint does not lead to biotic homogenization of forest bird communities in northern USA. *Ecology and Evolution* 13, e10015. doi: 10.1002/ece3.10015

Lechêne, A., Lobry, J., Boët, P., and Laffaille, P. (2018). Change in fish functional diversity and assembly rules in the course of tidal marsh restoration. *PLoS ONE* 13, e0209025. doi: 10.1371/journal.pone.0209025

Lefcheck, J. S., and Duffy, J. E. (2015). Multitrophic functional diversity predicts ecosystem functioning in experimental assemblages of estuarine consumers. *Ecology* 96, 2973–2983. doi: 10.1890/14-1977.1

Legendre, P., and Anderson, M. J. (1999). Distance-Based Redundancy Analysis: Testing Multispecies Responses in Multifactorial Ecological Experiments. *Ecological Monographs* 69, 1–24. doi: 10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2

Legendre, P., Galzin, R., and Harmelin-Vivien, M. L. (1997). Relating Behavior to Habitat: Solutions to Thefourth-Corner Problem. *Ecology* 78, 547–562. doi: 10.1890/0012-9658(1997)078[0547:RBTHST]2.0.CO;2

Legendre, P., and Legendre, L. (2012). *Numerical ecology.*, 3rd Edn. Oxford: Elsevier.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7, 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Leitão, R. P., Zuanon, J., Villéger, S., Williams, S. E., Baraloto, C., Fortunel, C., et al. (2016). Rare species contribute disproportionately to the functional structure of species assemblages. *Proceedings of the Royal Society B: Biological Sciences* 283, 20160084. doi: 10.1098/rspb.2016.0084

Lessa, R., Nóbrega, M., and Santana, F. M. (2009). Peixes Marinhos da Região Nordeste do Brasil. *Programa REVIZEE-Score Nordeste*, 208. Available at: https://www.researchgate.net/publication/326753222 (Accessed June 12, 2024).

Levin, L. A., Baker, M., and Thompson, A. (2019). *Deep-ocean climate change impacts on habitats, fish and fisheries*. Food and Agriculture Organisation (FAO) of the United Nations Rome. Available at: https://openknowledge.fao.org/handle/20.500.14283/ca2528en

Levin, L. A., Boesch, D. F., Covich, A., Dahm, C., Erséus, C., Ewel, K. C., et al. (2001). The Function of Marine Critical Transition Zones and the Importance of Sediment Biodiversity. *Ecosystems* 4, 430–451. doi: 10.1007/s10021-001-0021-4

Levin, S. A., and Lubchenco, J. (2008). Resilience, robustness, and marine ecosystem-based management. *Bioscience* 58, 27–32. doi: 10.1641/B580107

Li, Z., Heino, J., Liu, Z., Meng, X., Chen, X., Ge, Y., et al. (2021). The drivers of multiple dimensions of stream macroinvertebrate beta diversity across a large montane landscape. *Limnology and Oceanography* 66, 226–236. doi: 10.1002/lno.11599

Lin, C.-H., Wei, C.-L., Ho, S. L., and Lo, L. (2023). Ocean temperature drove changes in the mesopelagic fish community at the edge of the Pacific Warm Pool over the past 460,000 years. *Science Advances* 9, eadf0656. doi: 10.1126/sciadv.adf0656

Lopes, P. F. M., Mendes, L., Fonseca, V., and Villasante, S. (2017). Tourism as a driver of conflicts and changes in fisheries value chains in Marine Protected Areas. *Journal of Environmental Management* 200, 123–134. doi: 10.1016/j.jenvman.2017.05.080

Lopez, M. (2001). Architecture and depositional pattern of the Quaternary deep-sea fan of the Amazon. *Marine and Petroleum Geology* 18, 479–486. doi: 10.1016/S0264-8172(00)00071-4

Loreau, M. (2000). Are communities saturated? On the relationship between α, β and γ diversity. *Ecology Letters* 3, 73–76. doi: 10.1046/j.1461-0248.2000.00127.x

Loreau, M., Mouquet, N., and Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci. U.S.A.* 100, 12765–12770. doi: 10.1073/pnas.2235465100

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., et al. (2001). Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science* 294, 804–808. doi: 10.1126/science.1064088

Ma, C., Zhang, X., Chen, W., Zhang, G., Duan, H., Ju, M., et al. (2013). China's special marine protected area policy: trade-off between economic development and marine conservation. *Ocean & coastal management* 76, 1–11. doi: 10.1016/j.ocecoaman.2013.02.007

MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39, 599–619. doi: 10.2307/1931600

MacArthur, R., and Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *The American Naturalist* 101. doi: https://doi.org/10.1086/282505

Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., et al. (2022). mFD: an R package to compute and illustrate the multiple facets of functional diversity. *Ecography* 2022. doi: 10.1111/ecog.05904

Magnuson, J. J. (1990). Long-term ecological research and the invisible present. *BioScience* 40, 495–501. Available at: https://www.jstor.org/stable/1311317 (Accessed June 6, 2024).

Maier-Reimer, E., Mikolajewicz, U., and Winguth, A. (1996). Future ocean uptake of CO2: interaction between ocean circulation and biology. *Climate Dynamics* 12, 711–722. doi: 10.1007/s003820050138

Maire, E., Grenouillet, G., Brosse, S., and Villéger, S. (2015). How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Global Ecology and Biogeography* 24, 728–740. doi: 10.1111/geb.12299

Marion, Z. H., Fordyce, J. A., and Fitzpatrick, B. M. (2017). Pairwise beta diversity resolves an underappreciated source of confusion in calculating species turnover. *Ecology* 98, 933–939. doi: 10.1002/ecy.1753

Marshak, A. R., and Link, J. S. (2021). Primary production ultimately limits fisheries economic performance. *Sci Rep* 11, 12154. doi: 10.1038/s41598-021-91599-0

Martin, A., Boyd, P., Buesseler, K., Cetinic, I., Claustre, H., Giering, S., et al. (2020). The oceans' twilight zone must be studied now, before it is too late. *Nature* 580, 26–28. doi: 10.1038/d41586-020-00915-7

Martin, R. P., and Davis, M. P. (2020). The evolution of specialized dentition in the deep-sea lanternfishes (Myctophiformes). *Journal of Morphology* 281, 536–555. doi: 10.1002/jmor.21120

Martinez, C. M., Friedman, S. T., Corn, K. A., Larouche, O., Price, S. A., and Wainwright, P. C. (2021). The deep sea is a hot spot of fish body shape evolution. *Ecology Letters* 24, 1788–1799. doi: 10.1111/ele.13785

Mason, N. W. H., Lanoiselée, C., Mouillot, D., Irz, P., and Argillier, C. (2007). Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. *Oecologia* 153, 441–452. doi: 10.1007/s00442-007-0727-x

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

Maxwell, M. F., Leprieur, F., Quimbayo, J. P., Floeter, S. R., and Bender, M. G. (2022). Global patterns and drivers of beta diversity facets of reef fish faunas. *Journal of Biogeography* 49, 954–967. doi: 10.1111/jbi.14349

Mayor, D. J., Thornton, B., Hay, S., Zuur, A. F., Nicol, G. W., McWilliam, J. M., et al. (2012). Resource quality affects carbon cycling in deep-sea sediments. *The ISME Journal* 6, 1740–1748. doi: 10.1038/ismej.2012.14

McGill, B. J., Enquist, B. J., Weiher, E., and Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in ecology & evolution* 21, 178–185. doi: doi.org/10.1016/j.tree.2006.02.002

Medeiros, A. P. M., Ferreira, B. P., Alvarado, F., Betancur-R, R., Soares, M. O., and Santos, B. A. (2021). Deep reefs are not refugium for shallow-water fish communities in the southwestern Atlantic. *Ecology and Evolution* 11, 4413–4427. doi: 10.1002/ece3.7336

Mincarone, M. M., Eduardo, L. N., Di Dario, F., Frédou, T., Bertrand, A., and Lucena-Frédou, F. (2022). New records of rare deep-sea fishes (Teleostei) collected from off north-eastern Brazil, including seamounts and islands of the Fernando de Noronha Ridge. *Journal of Fish Biology* 101, 945–959. doi: 10.1111/jfb.15155

Mindel, B. L., Neat, F. C., Trueman, C. N., Webb, T. J., and Blanchard, J. L. (2016). Functional, size and taxonomic diversity of fish along a depth gradient in the deep sea. *PeerJ* 4, e2387. doi: 10.7717/peerj.2387

Moore, C. H., Harvey, E. S., and Van Niel, K. (2010). The application of predicted habitat models to investigate the spatial ecology of demersal fish assemblages. *Mar Biol* 157, 2717–2729. doi: 10.1007/s00227-010-1531-4

Morzaria-Luna, H. N., Ainsworth, C. H., and Scott, R. L. (2022). Impacts of deep-water spills on mesopelagic communities and implications for the wider pelagic food web. *Marine Ecology Progress Series* 681, 37–51. doi: 10.3354/meps13900

Mouillot, D., Albouy, C., Guilhaumon, F., Lasram, F. B. R., Coll, M., Devictor, V., et al. (2011). Protected and threatened components of fish biodiversity in the Mediterranean Sea. *Current Biology* 21, 1044–1050. doi: 10.1016/j.cub.2011.05.005

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., et al. (2013a). Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. *PLoS Biol* 11, e1001569. doi: 10.1371/journal.pbio.1001569

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., and Bellwood, D. R. (2013b). A functional approach reveals community responses to disturbances. doi: 10.1016/j.tree.2012.10.004

Mouillot, D., Parravicini, V., Bellwood, D. R., Leprieur, F., Huang, D., Cowman, P. F., et al. (2016). Global marine protected areas do not secure the evolutionary history of tropical corals and fishes. *Nature communications* 7, 10359. doi: 10.1038/ncomms10359

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J. E., Bender, M., et al. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proc. Natl. Acad. Sci. U.S.A.* 111, 13757–13762. doi: 10.1073/pnas.1317625111

Mugnai, M., Trindade, D. P. F., Thierry, M., Kaushik, K., Hrček, J., and Götzenberger, L. (2022). Environment and space drive the community assembly of Atlantic European grasslands: Insights from multiple facets. *Journal of Biogeography* 49, 699–711. doi: 10.1111/jbi.14331

Mullen, L. M., and Hoekstra, H. E. (2008). Natural selection along an environmental gradient: A classic cline in mouse pigmentation. *Evolution* 62, 1555–1570. doi: https://doi.org/10.1111/j.1558-5646.2008.00425.x

Naeem, S. (2006). "Biodiversity and ecosystem functioning in restored ecosystems: extracting principles for a synthetic perspective," in *Foundations of restoration ecology*, (Donald A. Falk, Margarett A. Palmer, and Joy B. Zedler), 210–237.

Naeem, S., Bunker, D. E., Hector, A., Loreau, M., and Perrings, C. (2009). *Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective*. Oxford, UK: OUP Oxford.

Nagelkerken, I., and Munday, P. L. (2016). Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. *Global Change Biology* 22, 974–989. doi: 10.1111/gcb.13167

Nunes, C. A., Castro, F. S., Brant, H. S. C., Powell, S., Solar, R., Fernandes, G. W., et al. (2020). High Temporal Beta Diversity in an Ant Metacommunity, With Increasing Temporal Functional Replacement Along the Elevational Gradient. *Front. Ecol. Evol.* 8. doi: 10.3389/fevo.2020.571439

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., et al. (2022). Vegan: Community Ecology Package.

Olavo, G., Costa, P. A. S., Martins, A. S., and Ferreira, B. P. (2011). Shelf-edge reefs as priority areas for conservation of reef fish diversity in the tropical Atlantic. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21, 199–209. doi: 10.1002/aqc.1174

Olivar, M. P., Hulley, P. A., Castellón, A., Emelianov, M., López, C., Tuset, V. M., et al. (2017). Mesopelagic fishes across the tropical and equatorial Atlantic:

Biogeographical and vertical patterns. *Progress in Oceanography* 151, 116–137. doi: 10.1016/j.pocean.2016.12.001

Olsen, R. E., Strand, E., Melle, W., Nørstebø, J. T., Lall, S. P., Ringø, E., et al. (2020). Can mesopelagic mixed layers be used as feed sources for salmon aquaculture? *Deep Sea Research Part II: Topical Studies in Oceanography* 180, 104722. doi: 10.1016/j.dsr2.2019.104722

Paiva, A. de, and Araújo, M. de (2010). Environmental characterization and spatial distribution of fish fauna in estuaries in the State of Pernambuco, Brazil. *Tropical Oceanography* 38, 1–46. doi: 10.5914/tropocean.v38i1.5159

Passos, C. V. B., Fabré, N. N., Malhado, A. C. M., Batista, V. S., and Ladle, R. J. (2016). Estuarization increases functional diversity of demersal fish assemblages in tropical coastal ecosystems. *Journal of Fish Biology* 89, 847–862. doi: 10.1111/jfb.13029

Paxton, A. B., Harter, S. L., Ross, S. W., Schobernd, C. M., Runde, B. J., Rudershausen, P. J., et al. (2021). Four decades of reef observations illuminate deep-water grouper hotspots. *Fish and Fisheries* 22, 749–761. doi: 10.1111/faf.12548

Pelage, L., Lucena-Frédou, F., Eduardo, L. N., Le Loc'h, F., Bertrand, A., Lira, A. S., et al. (2022). Competing with each other: Fish isotopic niche in two resource availability contexts. *Frontiers in Marine Science* 9, 975091. doi: 10.3389/fmars.2022.975091

Pelegrí, J. L., and Csanady, G. T. (1991). Nutrient transport and mixing in the Gulf Stream. *Journal of Geophysical Research: Oceans* 96, 2577–2583. doi: 10.1029/90JC02535

Pendoley, K. L., Schofield, G., Whittock, P. A., Ierodiaconou, D., and Hays, G. C. (2014). Protected species use of a coastal marine migratory corridor connecting marine protected areas. *Marine biology* 161, 1455–1466. doi: 10.1007/s00227-014-2433-7

Peng, C., Zhao, X., and Liu, G. (2015). Noise in the Sea and Its Impacts on Marine Organisms. *International Journal of Environmental Research and Public Health* 12, 12304–12323. doi: 10.3390/ijerph121012304

Pennino, M. G., Zurano, J. P., Hidalgo, M., Esteban, A., Veloy, C., Bellido, J. M., et al. (2024). Spatial patterns of β-diversity under cumulative pressures in the Western Mediterranean Sea. *Marine Environmental Research* 195, 106347. doi: 10.1016/j.marenvres.2024.106347

Pereira, P. H., Côrtes, L. G., Lima, G. V., Gomes, E., Pontes, A. V., Mattos, F., et al. (2021). Reef fishes biodiversity and conservation at the largest Brazilian coastal Marine Protected Area (MPA Costa dos Corais). *Neotropical Ichthyology* 19, e210071. Available at: https://doi.org/10.1590/1982-0224-2021-0071 (Accessed June 7, 2024).

Peres-Neto, P. R., Legendre, P., Dray, S., and Borcard, D. (2006). Variation Partitioning of Species Data Matrices: Estimation and Comparison of Fractions. *Ecology* 87, 2614–2625. doi: 10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

Perez Rocha, M., Bini, L. M., Domisch, S., Tolonen, K. T., Jyrkänkallio-Mikkola, J., Soininen, J., et al. (2018). Local environment and space drive multiple facets of stream macroinvertebrate beta diversity. *Journal of Biogeography* 45, 2744–2754. doi: 10.1111/jbi.13457

Petrik, C. M., Stock, C. A., Andersen, K. H., van Denderen, P. D., and Watson, J. R. (2020). Large Pelagic Fish Are Most Sensitive to Climate Change Despite Pelagification of Ocean Food Webs. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.588482

Pickens, B. A., Carroll, R., Schirripa, M. J., Forrestal, F., Friedland, K. D., and Taylor, J. C. (2021). A systematic review of spatial habitat associations and modeling of marine fish distribution: A guide to predictors, methods, and knowledge gaps. *PLOS ONE* 16, e0251818. doi: 10.1371/journal.pone.0251818

Pietsch, T. W. (1976). Dimorphism, Parasitism and Sex: Reproductive Strategies among Deepsea Ceratioid Anglerfishes. *Copeia* 1976, 781–793. doi: 10.2307/1443462

Pietsch, T. W. (2009). *Oceanic anglerfishes: extraordinary diversity in the deep sea*. Univ of California Press. Available at: https://doi.org/10.1525/9780520942554

Pittman, S. J., and Brown, K. A. (2011). Multi-Scale Approach for Predicting Fish Species Distributions across Coral Reef Seascapes. *PLOS ONE* 6, e20583. doi: 10.1371/journal.pone.0020583

Porter, J. H. (2018). "Scientific Databases for Environmental Research," in *Ecological Informatics: Data Management and Knowledge Discovery*, eds. F. Recknagel and W. K. Michener (Cham: Springer International Publishing), 27–53. doi: 10.1007/978-3-319-59928-1_3

Priede, I. G. (2017). *Deep-sea fishes: biology, diversity, ecology and fisheries*. Cambridge, UK: Cambridge University Press.

Proud, R., Cox, M. J., and Brierley, A. S. (2017). Biogeography of the Global Ocean's Mesopelagic Zone. *Current Biology* 27, 113–119. doi: 10.1016/j.cub.2016.11.003

Proud, R., Handegard, N. O., Kloser, R. J., Cox, M. J., and Brierley, A. S. (2019). From siphonophores to deep scattering layers: uncertainty ranges for the estimation of global mesopelagic fish biomass. *ICES Journal of Marine Science* 76, 718–733.

Pulster, E. L., Gracia, A., Armenteros, M., Toro-Farmer, G., Snyder, S. M., Carr, B. E., et al. (2020). A first comprehensive baseline of hydrocarbon pollution in Gulf of Mexico fishes. *Scientific Reports* 10, 6437. doi: 10.1038/s41598-020-62944-6

Punzón, A., Serrano, A., Sánchez, F., Velasco, F., Preciado, I., González-Irusta, J. M., et al. (2016). Response of a temperate demersal fish community to global warming. *Journal of Marine Systems* 161, 1–10. doi: 10.1016/j.jmarsys.2016.05.001

Pusceddu, A., Bianchelli, S., Martín, J., Puig, P., Palanques, A., Masqué, P., et al. (2014). Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. *Proceedings of the National Academy of Sciences* 111, 8861–8866. doi: 10.1073/pnas.1405454111

Queirós, A. M., Fernandes, J., Genevier, L., and Lynam, C. P. (2018). Climate change alters fish community size-structure, requiring adaptive policy targets. *Fish and Fisheries* 19, 613–621. doi: 10.1111/faf.12278

R Core Team (2022). A language and environment for statistical computing. *http://www.R-project. org*.

Ramirez-Llodra, E., Tyler, P. A., Baker, M. C., Bergstad, O. A., Clark, M. R., Escobar, E., et al. (2011). Man and the Last Great Wilderness: Human Impact on the Deep Sea. *PLOS ONE* 6, e22588. doi: https://doi.org/10.1371/journal.pone.0022588

Rbiai, O., Badaoui, B., and Chlaida, M. (2024). Temporal β-diversity decomposition: Insights into fish biodiversity dynamics in the Moroccan South Atlantic. *Marine Environmental Research* 198, 106504. doi: 10.1016/j.marenvres.2024.106504

Rennie, S. J., Pattiaratchi, C. B., and McCauley, R. D. (2009). Numerical simulation of the circulation within the Perth Submarine Canyon, Western Australia. *Continental Shelf Research* 29, 2020–2036. doi: 10.1016/j.csr.2009.04.010

Rice, J., Daan, N., Gislason, H., and Pope, J. (2013). Does functional redundancy stabilize fish communities? *ICES Journal of Marine Science* 70, 734–742. doi: 10.1093/icesjms/fst071

Ricotta, C., Kosman, E., Caccianiga, M., Cerabolini, B. E. L., and Pavoine, S. (2021). On two dissimilarity-based measures of functional beta diversity. *Ecological Informatics* 66, 101458. doi: 10.1016/j.ecoinf.2021.101458

Ricotta, C., Pavoine, S., Bacaro, G., and Acosta, A. T. (2012). Functional rarefaction for species abundance data. *Methods in Ecology and Evolution* 3, 519–525. doi: 10.1111/j.2041-210X.2011.00178.x

Robison, B. H. (2004). Deep pelagic biology. *Journal of Experimental Marine Biology and Ecology* 300, 253–272. doi: 10.1016/j.jembe.2004.01.012

Rosa, R. S., Medeiros, A. P. M., Felinto, A., Brito, C., Santana, E. F. C., Albuquerque, F. V., et al. (2023). Marine teleost fishes of the northeastern Brazilian coast: 166 years of compiled data. *Systematics and Biodiversity* 21, 2228314. doi: 10.1080/14772000.2023.2228314

Rummel, C. D., Löder, M. G. J., Fricke, N. F., Lang, T., Griebeler, E.-M., Janke, M., et al. (2016). Plastic ingestion by pelagic and demersal fish from the North Sea and Baltic Sea. *Marine Pollution Bulletin* 102, 134–141. doi: 10.1016/j.marpolbul.2015.11.043

Santana, J. R., Costa, A. E. S. F. D., Veleda, D., Schwamborn, S. H. L., Mafalda Júnior, P. O., and Schwamborn, R. (2020). Ichthyoplankton community structure on the shelf break off northeastern Brazil. *An. Acad. Bras. Ciênc.* 92, e20180851. doi: 10.1590/0001-3765202020180851

Santos, J. P., Guimarães, E. C., Garciov-Filho, E. B., Brito, P. S. de, Corrêa Lopes, D. F., Andrade, M. C., et al. (2023). Fisheries monitoring in Brazil: How can the 2030 agenda be met without fisheries statistics? *Biota Neotrop.* 23, e20221439. doi: 10.1590/1676-0611-BN-2022-1439

Schadeberg, A., Kraan, M., Groeneveld, R., Trilling, D., and Bush, S. (2023). Science governs the future of the mesopelagic zone. *npj Ocean Sustain* 2, 1–9. doi: 10.1038/s44183-023-00008-8

Schleuter, D., Daufresne, M., Massol, F., and Argillier, C. (2010). A user's guide to functional diversity indices. *Ecological Monographs* 80, 469–484. doi: 10.1890/08-2225.1

Schmitz, O. J., Sylvén, M., Atwood, T. B., Bakker, E. S., Berzaghi, F., Brodie, J. F., et al. (2023). Trophic rewilding can expand natural climate solutions. *Nat. Clim. Chang.* 13, 324–333. doi: 10.1038/s41558-023-01631-6

Schneider, C. A., Rasband, W. S., and Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature methods* 9, 671–675. doi: 10.1038/nmeth.2089

Schoener, T. W. (1974). Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science* 185, 27–39. doi: 10.1126/science.185.4145.27

Schott, F. A., Fischer, J., and Stramma, L. (1998). Transports and pathways of the upper-layer circulation in the western tropical Atlantic. *Journal of Physical Oceanography* 28, 1904–1928. doi: https://doi.org/10.1175/1520-0485(1998)028<1904:TAPOTU>2.0.CO;2

She, J., and Klinck, J. M. (2000). Flow near submarine canyons driven by constant winds. *J. Geophys. Res.* 105, 28671–28694. doi: 10.1029/2000JC900126

Siebeck, U. E., O'connor, J., Braun, C., and Leis, J. M. (2015). Do human activities influence survival and orientation abilities of larval fishes in the ocean? *Integrative Zoology* 10, 65–82. doi: 10.1111/1749-4877.12096

Silva, A., Chaigneau, A., Dossa, A., Eldin, G., Araujo, M., and Bertrand, A. (2021). Surface circulation and vertical structure of upper ocean variability around Fernando de Noronha Archipelago and Rocas Atoll during spring 2015 and fall 2017. *Frontiers in Marine Science* 8, 598101. doi: 10.3389/fmars.2021.598101

Silva, M. V., Ferreira, B., Maida, M., Queiroz, S., Silva, M., Varona, H. L., et al. (2022). Flow-topography interactions in the western tropical Atlantic boundary off Northeast Brazil. *Journal of Marine Systems* 227, 103690. doi: 10.1016/j.jmarsys.2021.103690

Simberloff, D. (2004). Community Ecology: Is It Time to Move On? (An American Society of Naturalists Presidential Address). *The American Naturalist* 163, 787–799. doi: doi.org/10.1086/420777

Soares, A., Lira, A. S., Gonzalez, J. G., Eduardo, L. N., Lucena-Frédou, F., Le Loc'h, F., et al. (2020). Feeding habits and population aspects of the spotted goatfish, Pseudupeneus maculatus (Perciformes: Mullidae), on the continental shelf of northeast Brazil. *Scientia Marina* 84, 119–131. doi: 10.3989/scimar.04958.24A

Socolar, J. B., Gilroy, J. J., Kunin, W. E., and Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? *Trends in ecology & evolution* 31, 67–80. doi: 10.1016/j.tree.2015.11.005

Soininen, J., Heino, J., and Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecol Biogeogr* 27, 96–109. doi: 10.1111/geb.12660

Sommer, B., Harrison, P. L., Beger, M., and Pandolfi, J. M. (2014). Trait-mediated environmental filtering drives assembly at biogeographic transition zones. *Ecology* 95, 1000–1009. doi: 10.1890/13-1445.1

St. John, M. A., Borja, A., Chust, G., Heath, M., Grigorov, I., Mariani, P., et al. (2016). A Dark Hole in Our Understanding of Marine Ecosystems and Their Services: Perspectives from the Mesopelagic Community. *Front. Mar. Sci.* 3. doi: 10.3389/fmars.2016.00031

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., et al. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501, 539–542. doi: 10.1038/nature12529

Sutton, T. T. (2013). Vertical ecology of the pelagic ocean: classical patterns and new perspectives. *Journal of fish biology* 83, 1508–1527. doi: 10.1111/jfb.12263

Tagliabue, A., Kwiatkowski, L., Bopp, L., Butenschön, M., Cheung, W., Lengaigne, M., et al. (2021). Persistent Uncertainties in Ocean Net Primary Production Climate Change Projections at Regional Scales Raise Challenges for Assessing Impacts on Ecosystem Services. *Frontiers in Climate* 3. doi: 10.3389/fclim.2021.738224

Tchamabi, C. C., Araujo, M., Silva, M., and Bourlès, B. (2017). A study of the Brazilian Fernando de Noronha island and Rocas atoll wakes in the tropical Atlantic. *Ocean Modelling* 111, 9–18. doi: 10.1016/j.ocemod.2016.12.009

ter Braak, C. J. F., Cormont, A., and Dray, S. (2012). Improved testing of species traits–environment relationships in the fourth-corner problem. *Ecology* 93, 1525–1526. doi: 10.1890/12-0126.1

The Economist (2017). The mesopelagic: Cinderella of the oceans. *The Economist*. Available at: https://www.economist.com/science-and-technology/2017/04/15/the-mesopelagic-cinderella-of-the-oceans

Tibshirani, R., Walther, G., and Hastie, T. (2001). Estimating the number of clusters in a data set via the gap statistic. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 63, 411–423. doi: 10.1111/1467-9868.00293

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E. (1997). The Influence of Functional Diversity and Composition on Ecosystem Processes. *Science* 277, 1300–1302. doi: 10.1126/science.277.5330.1300

Tittensor, D. P., Micheli, F., Nyström, M., and Worm, B. (2007). Human impacts on the species–area relationship in reef fish assemblages. *Ecology Letters* 10, 760–772. doi: 10.1111/j.1461-0248.2007.01076.x

Todd, R. E., Chavez, F. P., Clayton, S., Cravatte, S., Goes, M., Graco, M., et al. (2019). Global Perspectives on Observing Ocean Boundary Current Systems. *Front. Mar. Sci.* 6. doi: 10.3389/fmars.2019.00423

Travassos, P., Hazin, F. H. V., Zagaglia, J. R., Advíncula, R., and Schober, J. (1999). Thermohaline structure around seamounts and islands off North-Eastern Brazil. *Archive of Fishery and Marine Research* 47, 211–222.

Tubau, X., Paull, C. K., Lastras, G., Caress, D. W., Canals, M., Lundsten, E., et al. (2015). Submarine canyons of Santa Monica Bay, Southern California: variability in morphology and sedimentary processes. *Marine Geology* 365, 61–79. doi: 10.1016/j.margeo.2015.04.004

Tuomisto, H. (2010). A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33, 2–22. doi: 10.1111/j.1600-0587.2009.05880.x

Turner, J. R., White, E. M., Collins, M. A., Partridge, J. C., and Douglas, R. H. (2009). Vision in lanternfish (Myctophidae): Adaptations for viewing bioluminescence in the deep-sea. *Deep Sea Research Part I: Oceanographic Research Papers* 56, 1003–1017. doi: 10.1016/j.dsr.2009.01.007

Tuset, V. M., Farré, M., Lombarte, A., Bordes, F., Wienerroither, R., and Olivar, P. (2014). A comparative study of morphospace occupation of mesopelagic fish assemblages from the Canary Islands (North-eastern Atlantic). *Ichthyol Res* 61, 152–158. doi: 10.1007/s10228-014-0390-2

Tuset, V. M., Olivar, M. P., Otero-Ferrer, J. L., López-Pérez, C., Hulley, P. A., and Lombarte, A. (2018). Morpho-functional diversity in Diaphus spp. (Pisces: Myctophidae) from the central Atlantic Ocean: Ecological and evolutionary implications. *Deep Sea Research Part I: Oceanographic Research Papers* 138, 46–59. doi: 10.1016/j.dsr.2018.07.005

Van Der Valk, A. G. (1981). Succession in wetlands: a gleasonian appraoch. *Ecology* 62, 688–696. doi: 10.2307/1937737

Via, S., and Lande, R. (1985). Genotype-Environment Interaction and the Evolution of Phenotypic Plasticity. *Evolution* 39, 505–522. doi: 10.1111/j.1558-5646.1985.tb00391.x

Viana, D. S., Figuerola, J., Schwenk, K., Manca, M., Hobæk, A., Mjelde, M., et al. (2016). Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales. *Ecography* 39, 281–288. doi: 10.1111/ecog.01231

Viana, M. G., Lima, M. S. P., Martinez, A. S., Barboza, A. R. P., Melo, C., Calado, J. F., et al. (2022). Marine fish and benthic biota before the 2019 oil spill: A baseline dataset for monitoring programs and impact assessments at Rio Grande Norte state, Northeastern Brazil. *An. Acad. Bras. Ciênc.* 94, e20210536. doi: 10.1590/0001-3765202120210536

Villarins, B. T., Fischer, L. G., Martins, J. R., and Mincarone, M. M. (2024). First Record of Margrethia valentinae (Gonostomatidae) in the Western South Atlantic, with Remarks on the Taxonomy and Distribution of the Genus Margrethia. *J. Ichthyol.* doi: 10.1134/S0032945224700073

Villarins, B. T., Fischer, L. G., Prokofiev, A. M., and Mincarone, M. M. (2023a). A New Species of the Dragonfish Genus Melanostomias (Stomiidae: Melanostomiinae) from the Western Tropical Atlantic. *cope.1* 111, 254–263. doi: 10.1643/i2022082

Villarins, B. T., Fischer, L. G., Prokofiev, A. M., and Mincarone, M. M. (2023b). Four new species of dragonfish genus Eustomias (Stomiiformes: Stomiidae: Melanostomiinae) from the western tropical Atlantic, with remarks on Eustomias minimus Clarke, 1999. *Zoological Journal of the Linnean Society*, zlad163. doi: 10.1093/zoolinnean/zlad163

Villéger, S., Grenouillet, G., and Brosse, S. (2013). Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography* 22, 671–681. doi: 10.1111/geb.12021

Villéger, S., Mason, N. W. H., and Mouillot, D. (2008). New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. *Ecology* 89, 2290–2301. doi: 10.1890/07-1206.1

Villéger, S., Miranda, J. R., Hernández, D. F., and Mouillot, D. (2010). Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications* 20, 1512–1522. doi: 10.1890/09-1310.1

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

Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J., and Kattge, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences* 111, 13690–13696. doi: 10.1073/pnas.1415442111

Vital, H., Gomes, M. P., Tabosa, W. F., Frazão, E. P., Santos, C. L. A., and Plácido Júnior, J. S. (2010). Characterization of the Brazilian continental shelf adjacent to Rio

Grande do Norte state, NE Brazil. *Braz. j. oceanogr.* 58, 43–54. doi: 10.1590/S1679-87592010000500005

Waldbusser, G. G., Marinelli, R. L., Whitlatch, R. B., and Visscher, P. T. (2004). The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. *Limnology & Oceanography* 49, 1482–1492. doi: 10.4319/lo.2004.49.5.1482

Walker, B., Kinzig, A., and Langridge, J. (1999). Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2, 95–113. doi: 10.1007/s100219900062

Wang, S., Loreau, M., De Mazancourt, C., Isbell, F., Beierkuhnlein, C., Connolly, J., et al. (2021). Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. *Ecology* 102, e03332. doi: 10.1002/ecy.3332

Warrant, E. J., and Locket, N. A. (2004). Vision in the deep sea. *Biological Reviews* 79, 671–712. doi: 10.1017/S1464793103006420

Webb, T. J., Vanden Berghe, E., and O'Dor, R. (2010). Biodiversity's big wet secret: the global distribution of marine biological records reveals chronic under-exploration of the deep pelagic ocean. *PloS one* 5, e10223. Available at: https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0010223 (Accessed April 11, 2024).

Weiher, E., Clarke, G. D. P., and Keddy, P. A. (1998). Community Assembly Rules, Morphological Dispersion, and the Coexistence of Plant Species. *Oikos* 81, 309–322. doi: 10.2307/3547051

Whitehouse, G. A., Buckley, T. W., and Danielson, S. L. (2017). Diet compositions and trophic guild structure of the eastern Chukchi Sea demersal fish community. *Deep Sea Research Part II: Topical Studies in Oceanography* 135, 95–110. doi: 10.1016/j.dsr2.2016.03.010

Whittaker, R. H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. *Ecological monographs* 30, 279–338.

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *TAXON* 21, 213–251. doi: 10.2307/1218190

Widder, E. A. (2010). Bioluminescence in the Ocean: Origins of Biological, Chemical, and Ecological Diversity. *Science* 328, 704–708. doi: 10.1126/science.1174269

Willems, T., De Backer, A., Mol, J. H., Vincx, M., and Hostens, K. (2015). Distribution patterns of the demersal fish fauna on the inner continental shelf of Suriname. *Regional Studies in Marine Science* 2, 177–188. doi: 10.1016/j.rsma.2015.10.008

Williams, R., Grand, J., Hooker, S. K., Buckland, S. T., Reeves, R. R., Rojas-Bracho, L., et al. (2014). Prioritizing global marine mammal habitats using density maps in place of range maps. *Ecography* 37, 212–220. doi: 10.1111/j.1600-0587.2013.00479.x

Wood, S. N. (2001). mgcv: GAMs and Generalized Ridge Regression for R. 1.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., et al. (2006). Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science* 314, 787–790. doi: 10.1126/science.1132294

Young, R. E., Kampa, E. M., Maynard, S. D., Mencher, F. M., and Roper, C. F. (1980). Counterillumination and the upper depth limits of midwater animals. *Deep Sea Research Part A. Oceanographic Research Papers* 27, 671–691. doi: 10.1016/0198-0149(80)90022-9

Zajac, R. N., Lewis, R. S., Poppe, L. J., Twichell, D. C., Vozarik, J., and DiGiacomo-Cohen, M. L. (2003). Responses of infaunal populations to benthoscape structure and the potential importance of transition zones. *Limnology and Oceanography* 48, 829–842.

Zhao, K., He, Y., Su, G., Xu, C., Xu, X., Zhang, M., et al. (2022). Implications for functional diversity conservation of China's marine fisheries. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.970218

Zintzen, V., Anderson, M. J., Roberts, C. D., Harvey, E. S., Stewart, A. L., and Struthers, C. D. (2012). Diversity and Composition of Demersal Fishes along a Depth Gradient Assessed by Baited Remote Underwater Stereo-Video. *PLOS ONE* 7, e48522. doi: 10.1371/journal.pone.0048522