Lighting up the dark side of the ocean : biodiversity and ecology of deep-sea fishes from the Southwestern Tropical Atlantic

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Lighting up the dark side of the ocean: biodiversity and ecology of deep-sea fishes from the Southwestern Tropical Atlantic

Présentée par

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Le 29 mars 2021

Sous la direction de
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Lighting up the dark side of the ocean: biodiversity and ecology of deep-sea fishes from the Southwestern Tropical Atlantic

Leandro Nolé Eduardo

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Leandro Nolé Eduardo

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ABSTRACT

Here we propose a comprehensive study on the biodiversity and ecology of mesopelagic fishes from the Southwestern Tropical Atlantic (SWTA). For that, we combined information on the diversity, abundance, distribution, trophic ecology, and physical and chemical habitat of thousands of mesopelagic specimens recently collected on the surveys of the project ABRACOS (Acoustics along the BRAzilian COaSt; 2015 and 2017).

This thesis is organized over a general introduction, two main chapters, and a conclusion. In the first chapter, organized over five articles, we addressed the biodiversity, distribution, and morphometrical aspects of mesopelagic fishes, providing the first baseline of mesopelagic fish biodiversity from the SWTA. In the first article, which included a synthesis of the mesopelagic fish fauna in the area, we showed that a relatively high number of taxa occurs in the study area, including at least 24 orders, 56 families, and 207 species. From those, nine species (4%) are potentially new and 61 (30%) represented new records for Brazilian waters. Five families were predominant and accounted for 52% of the diversity of taxa, 90% of the specimens collected, and 72% of the total biomass: Myctophidae, Stomiidae, Gonostomatidae, Melamphaidae, and Sternoptychidae. In two complementary articles (and more four additional articles in the appendix), we detailed the diversity, distribution, and morphometry of the following fish groups: Trichiuridae, Howelidae, Caristiidae, Argentiniformes, Stephanoberycoidei, and Ceratioidei. In these studies, we not only report the new occurrence of species in the SWTA, but also reviewed, re-identified, and discussed previously records of mesopelagic species along the SWTA. Finally, in two articles we provided novel length-weight relationships for twenty-three species.

In the second chapter, organized over three articles, we addressed the ecology of the most important (in terms of abundance and biomass) species identified in chapter one: Sternoptychidae (hatchetfishes), Myctophidae (lanternfishes), and the viperfish *Chauliodus sloani*. We pointed out which species in the SWTA vertically migrate to the surface to feed at night and actively transport the ingested carbon to deep waters during daylight. Moreover, we showed how it might be related to physical-chemical features. We demonstrated that several species occupy an important trophic position by consuming zooplankton and providing forage for numerous epipelagic and deep-sea predators.

Additionally, we showed high consumption of gelatinous organisms, a crucial trophic relationship that has been historically underestimated. By combining all the information, we demonstrated that mesopelagic fishes are segregated into functional groups with different diet preferences, isotopic composition, vertical abundance peaks, and responses to environmental constraints (temperature and oxygen). As an example, we defined five functional groups for hatchetfishes, whereas over three patterns of prey preference and four patterns of migratory behaviour for lanternfishes. These patterns reveal a high resource partitioning and several mechanisms to avoid competitive exclusion.

Finally, through the study case of the viperfish we explored how physical drivers affect the ecology of mesopelagic species and how these relationships are likely to change over large oceanic areas. We showed that the ecology and functional roles of the viperfish are expected to be modulated by the latitudinal change in temperature. For instance, in most tropical regions the viperfish stay full-time feeding, excreting, and serving as prey at deep layers. On the contrary, in temperate regions, the viperfish ascend to superficial waters where it trophically interacts with epipelagic predators and may release carbon where remineralization is the greatest. Information presented here significantly contributes to the overall understanding of the biodiversity and ecology of several deep-sea species. This data may be important for further studies addressing the functioning, conservation, and ecosystem processes of mesopelagic communities.

RÉSUMÉ

L’objectif de cette thèse est de proposer une étude intégrée de la biodiversité et l'écologie des poissons mésopélagiques de L'Atlantique tropical sud-ouest (ATSO). Pour cela, nous avons combiné des informations sur la diversité, l'abondance, la distribution, l'écologie trophique et l'habitat physique et chimique de milliers de spécimens mésopélagiques collectés en 2015 et 2017 dans le cadre du projet ABRACOS (Acoustics along the BRAzilian COaSt).

Dans le premier chapitre, organisé sous la forme de cinque articles, nous proposons une révision de la biodiversité, la distribution et la morphométrie des poissons mésopélagiques de l’ATSO. Les résultats du premier et principal article montrent que l’ATSO recèle un nombre élevé de taxons, dont au moins 24 ordres, 56 familles et 207 espèces. Parmi celles-ci, neuf espèces (4%) sont potentiellement nouvelles et 61 (30%) représentent de nouveaux records pour les eaux brésiliennes. Les cinq familles dominantes, Myctophidae, Stomiidae, Gonostomatidae, Melamphaidae et Sternoptychidae, représentaient 52 % de la diversité taxonomique, 90 % des spécimens collectés et 72 % de la biomasse totale. Dans deux articles complémentaires (et plus quatre articles supplémentaires en annexe), nous proposons des études détaillées de la diversité, la distribution et la morphométrie des groupes suivants: Trichiuridae, Howelidae, Caristiidae, Argentiniformes, Stephanoberycoidei et Ceratioidei. Enfin, dans deux articles, nous fournisons de nouvelles relations longueur-poids pour vingt-trois espèces.

Dans le deuxième chapitre, organisé sous la forme de trois articles, nous avons abordé l'écologie des espèces les plus importantes (en termes d’abondance et de biomasse) identifiées au premier chapitre. Nous identifions les espèces qui migrent verticalement vers la surface pour se nourrir la nuit et transporter activement le carbone ingéré vers les eaux profondes pendant la journée. De plus, nous avons montré comment ces patrons de distribution verticale peuvent être liés aux caractéristiques physico-chimiques. Nous avons démontré que plusieurs espèces occupent une position trophique pivot en consommant du zooplancton et en fournissant du fourrage à de nombreux prédateurs épipélagiques et d'eaux profondes. En outre, nous montrons que les organismes gélatineux sont des proies importantes des poissons mésopélagiques, illustrant ainsi une relation trophique cruciale qui a été historiquement sous-estimée. En combinant toutes ces informations, nous avons démontré que les poissons

mésopélagiques sont séparés en différents groupes fonctionnels en termes de préférence alimentaire, composition isotopique, pic d'abondance verticale et de réponse aux contraintes environnementales (température et oxygène). À titre d'exemple, nous avons défini cinq groupes fonctionnels pour les poissons hachette, et plus de trois modèles de préférence alimentaire et quatre modèles de comportement migratoire pour les poissons lanterne. Ces schémas révèlent une forte partition des ressources et plusieurs mécanismes pour éviter l'exclusion compétitive.

Enfin, à travers le cas d'étude de le poisson-vipère, nous avons exploré comment les facteurs physiques affectent l'écologie des espèces mésopélagiques et comment ces relations sont susceptibles de changer dans les grandes zones océaniques. Nous avons montré que l'écologie et les rôles fonctionnels de le poisson-vipère semblent être modulés par le changement latitudinal de température. Par exemple, dans la plupart des régions tropicales, ces poissons se nourrissent, excrétent et servent de proies en continu dans les couches profondes. Au contraire, dans les régions tempérées, les poissons-vipère remontent vers les eaux superficielles où ils interagissent avec les prédateurs épipélagiques libérant ainsi du carbone à une profondeur où la reminéralisation est la plus importante. Les informations présentées ici contribuent à la compréhension globale de la biodiversité et de l'écologie de plusieurs espèces d'eaux profondes. Ces données peuvent être utiles pour des études ultérieures portant sur le fonctionnement, la conservation et les processus écosystémiques des communautés mésopélagiques.

RESUMO

Neste trabalho propomos um estudo sobre a biodiversidade e ecologia dos peixes mesopelágicos (0–200 m de profundidade) do Atlântico Sudoeste Tropical (AST). Para isso, foram utilizados dados provenientes de dois cruzeiros oceanográficos, realizados em 2015 e 2017, no âmbito do Projeto ABRACOS. Com base nesse material, foram compiladas informações sobre o habitat, diversidade, abundância, distribuição, e ecologia trófica de milhares de espécimes mesopelágicos. Dessa forma, esta tese está organizada sobre uma introdução geral, dois capítulos principais e uma conclusão.

No primeiro capítulo, organizado em cinco artigos, abordamos a diversidade, distribuição e aspectos morfométricos de peixes mesopelágicos, fornecendo a primeira referência base sobre a biodiversidade dos peixes mesopelágicos do AST. No primeiro artigo, que inclui uma síntese da fauna de peixes mesopelágicos coletados, mostrámos que um número relativamente elevado de espécies ocorre na área de estudo, incluindo pelo menos 24 ordens, 56 famílias, e 207 espécies. Destas, nove espécies (4%) são potencialmente novas e 61 (30%) representaram novos registos para as águas brasileiras. Cinco famílias foram predominantes e representaram 52% da diversidade de espécies, 90% dos espécimes coletados, e 72% da biomassa total: Myctophidae, Stomiidae, Gonostomatidae, Melamphaidae e Sternoptychidae. Em dois artigos complementares (e mais 4 artigos em anexo), também foram detalhados a diversidade e distribuição dos seguintes grupos: Trichiuridae, Howelidae, Caristiidae, Argentiniformes, Stephanoberycoidei e Ceratioidei. Nestes estudos, não só relatamos a nova ocorrência de espécies para área de estudo, mas também revemos, identificamos e discutimos registros anteriores em águas brasileiras. Finalmente, em dois artigos, fornecemos informações morfométricas e relações de peso-comprimento inéditas para 23 espécies.

No segundo capítulo, organizado em três artigos, abordámos a ecologia das principais espécies (em termos de abundância e biomassa) identificadas no capítulo um: Sternoptychidae (peixes machadinha), Myctophidae (peixes lanterna), e o peixe víbora *Chauliodus sloani*. Destacamos, por exemplo, quais espécies ao longo da área de estudo migram verticalmente para regiões superficiais durante a noite, processo no qual o sequestro de carbono é fortemente potencializado. Além disso, mostramos como esse comportamento está relacionado com as características físico-químicas do ambiente (oxigênio e temperatura). Considerando a ecologia alimentar, demonstramos que várias espécies ocupam uma posição trófica importante, uma vez que consomem zooplâncton e servem como importante presas para inúmeros predadores de regiões superficiais e

profundas. Além disso, mostramos um alto consumo de organismos gelatinosos, uma importante ligação trófica que historicamente tem sido subestimada. Ao combinar todas as informações, demonstramos que algumas espécies de peixes mesopelágicos são segregados em grupos funcionais com diferentes preferências alimentares, composição isotópica, picos de abundância vertical e respostas às restrições ambientais. Como exemplo, definimos cinco grupos funcionais para os peixes machadinha, enquanto três padrões de preferência alimentar e quatro padrões de comportamento migratório foram identificados para os peixes lanterna. Estes padrões revelam não só uma alta variabilidade no uso recursos, mas também vários mecanismos adquiridos ao longo da evolução para evitar a exclusão competitiva.

Finalmente, através do estudo do caso do peixe víbora, exploramos como forçantes físicas podem afetar a ecologia das espécies mesopelágicas e como essas relações podem mudar em grandes áreas oceânicas. Mostramos que tanto ecologia como os papéis funcionais do peixe víbora são modulados pela mudança latitudinal na temperatura. Por exemplo, na maioria das regiões tropicais, o peixe víbora permanece em águas profundas por tempo integral, onde se alimenta, excreta e serve como presa em camadas profundas. Pelo contrário, em regiões temperadas, o peixe víbora migra para águas superficiais onde interage com predadores epipelágicos e pode liberar carbono onde a sua remineralizarão é potencialmente maior. As informações aqui apresentadas contribuem para o entendimento geral da biodiversidade e da ecologia de várias espécies do oceano profundo. Estes dados podem ser importantes para estudos futuros sobre o funcionamento, conservação e processos ecossistêmicos de comunidades mesopelágicas.

SYNTHÈSE DES TRAVAUX EN FRANÇAIS

Pendant plus de 200 millions d'années, les poissons mésopélagiques ont habité les océans de la Terre, où ils ont vécu, évolué et acquis plusieurs adaptations pour surmonter les défis imposés par les grandes profondeurs (Nelson et al., 2016 ; Pried, 2017). Au fil du temps, ces espèces sont devenues l'un des groupes de poissons les plus abondants et les plus diversifiés de l'océans mondial, contribuant à de nombreux processus écosystémiques (Pried, 2017). Par exemple, elles jouent un rôle important dans le piégeage du carbone, la régénération des nutriments, la production halieutique et l'absorption des déchets (Eduardo et al., 2020a, 2020b). Les espèces mésopélagiques sont de plus en plus menacées par les impacts anthropiques (ex. l'exploitation minière des fonds marins, la pollution par les plastiques, le réchauffement des océans et la désoxygénation) (John et al., 2016; Martin et al., 2020). Elles restent cependant pour la plupart largement sous-étudiées. Étant donné la difficulté de l'échantillonnage en haute mer, même les connaissances biologiques de base font défaut pour de nombreuses espèces, ce qui entrave la compréhension de leurs nombreuses fonctions dans l'écosystème (ex. le transport du carbone entre les couches océaniques) et leur gestion durable.

La biodiversité, l'écologie trophique ou les migrations verticales sont des exemples de connaissances qui font encore défaut pour de nombreuses espèces mésopélagiques (Eduardo et al., 2020a, 2020b). Sans ces informations, il est difficile de comprendre pleinement comment ces espèces évitent l'exclusion compétitive, comment les facteurs physiques (par exemple, la température et l'oxygène) structurent leurs communautés et comment ces relations sont susceptibles de changer dans l'espace et le temps. En outre, cela entrave l'évaluation réelle de l'importance des poissons mésopélagiques dans les écosystèmes marins, comme leur contribution aux flux d'énergie dans les réseaux trophiques. Clarifier et développer nos connaissances sur la biodiversité et l'écologie de ces espèces est également nécessaire pour comprendre comment ces espèces pourraient réagir aux changements globaux et quelles conséquences ces derniers pourraient avoir sur leur rôle fonctionnel et donc sur la santé des écosystèmes.

L'Atlantique tropical sud-ouest (ATSO), dont la zone mésopélagique est peu étudiée, abrite une biodiversité spécifique (CBD, 2014). Situé dans une zone oligotrophe, l'ATSO comprend des îles océaniques, des canyons sous-marins et des monts sous-marins qui interagissent avec les courants locaux et accroissent la productivité marine

(Travassos et al., 1999 ; Tchamabi et al., 2017 ; CBD, 2014). Par conséquent, cette zone comprend de nombreuses zones qui ont été qualifiées un "oasis de vie dans un désert océanique" et classées comme «EBSA-Ecological or Biological Significant Marine Areas », une zone spéciale dans l'océan d'une importance fondamentale pour la biodiversité et les cycles de vie des espèces marines.

En 2015 et 2017, deux expéditions ont été effectuées à bord du RV *Antea* dans le cadre du projet ABRACOS (Acoustics along the BRAzilian CoaSt). Pour la première fois, la zone mésopélagique de l'ATSO a fait l'objet d'une étude approfondie avec la collecte de données hydrologiques et de milliers d'invertébrés et de poissons entre la surface et plus de 1000 de profondeur. Ces données sont à la base de cette thèse dont l'objectif principal est l'étude de la biodiversité et l'écologie des poissons mésopélagiques de l'ATSO. Plus précisément, dans cette thèse, nous avons cherché à répondre aux questions suivantes : (i) quels sont les poissons mésopélagiques et les principaux groupes présents dans l'ATSO ?, (ii) comment se distribuent-ils ?, (iii) quelles sont les caractéristiques de leur migration verticale nycthémérale ?, (iv) quelles sont leurs principales proies et relations trophiques ?, (v) comment sont-ils liés aux conditions océanographiques physico-chimiques ?, et (vi) quels sont leurs rôles fonctionnels ? Enfin, en guise de synthèse, nous avons construit des modèles conceptuels pour décrire leur répartition en niches écologiques, leurs groupes fonctionnels et leurs rôles dans les écosystèmes océaniques. Cette thèse est organisée sous la forme d'une introduction générale, deux chapitres principaux et une conclusion.

Dans le premier chapitre, organisé sous la forme de cinque articles (plus quatre articles supplémentaires en annexe), nous proposons une révision de la biodiversité, la distribution et la morphométrie des poissons mésopélagiques de l'ATSO. Pour cela, nous fournissons une liste complète des espèces mésopélagiques collectées au cours des expéditions ABRACOS, en indiquant les principaux groupes (basés sur l'abondance, la biomasse et la diversité), les nouvelles occurrences pour la région et les nouvelles espèces potentielles. En outre, nous proposons des études détaillées de la diversité et la distribution des groupes suivants : Trichiuridae, Howelidae, Caristiidae, Argentiniformes, Stephanoberycoidei et Ceratioidei.

Les résultats du premier et principal article montrent que l'ATSO recèle un nombre élevé de taxons, dont au moins 24 ordres, 56 familles et 207 espèces. Parmi celles-ci, neuf espèces (4%) sont potentiellement nouvelles et 61 (30%) représentent de nouveaux records pour les eaux brésiliennes. En outre, nous avons mis à jour les connaissances biogéographiques de plusieurs espèces rares dans le monde. Cinq familles étaient prédominantes et représentaient 52 % de la diversité des taxons, 90 % des spécimens collectés et 72 % de la biomasse totale : Myctophidae (38 spp. ; 36% des spécimens ; 24% de la biomasse), Stomiidae (38 spp. ; 8% ; 21%), Gonostomatidae (11 spp. ; 16% ; 4%) Melamphaidae (11 spp. ; 2% ; 7%), et Sternoptychidae (10 spp. ; 24% ; 10%). La richesse et la diversité étaient plus élevées dans les eaux mésopélagiques inférieures (500-1000 m) pendant la journée. Ceci semble être dû à la présence d'espèces bathypélagiques, probablement associée à la présence de nombreux monts sous-marins dans la zone d'étude. La nuit, la migration verticale de nombreuses espèces (ex. myctophidae et sternophichtydae) entrainent une augmentation de la richesse dans les eaux épipélagiques ; certaines espèces pouvant supporter des variation nycthémérales de température atteignant 25°C. Dans des articles complémentaires, nous détaillons la diversité et la répartition des groupes de poissons suivants : Trichiuridae, Howelidae, Caristiidae, Argentiniformes, Stephanoberycoidei et Ceratioidei. Dans ces études, nous ne nous présentons de nouvelles occurrences d'espèces dans l'ATSO et nous examinons, ré-identifions et discutons les observations antérieures d'espèces mésopélagiques de la région. Enfin, nous fournissons de nouvelles informations morphométriques et des relations longueur-poids pour vingt-trois espèces. L'ensemble de ces travaux permet de fournir la première base de référence de la biodiversité des poissons mésopélagiques dans l'ATSO. En outre, nos résultats permettent d'améliorer les connaissances générales sur la diversité et la morphométrie de plusieurs espèces de poissons mésopélagiques rares et importantes.

Dans le chapitre deux, organisé sous la forme de trois articles, nous proposons une étude intégrée de l'écologie des principales espèces identifiées au chapitre un. Pour cela, nous avons utilisé des informations sur l'abondance, la distribution, la diversité, l'écologie trophique et l'habitat physique et chimique de ces espèces. Nous avons notamment combiné des analyses de contenu stomacal avec des données d'isotopes stables (carbone et azote) pour les poissons mésopélagiques mais également leurs principaux liens trophiques (zooplancton, crustacés, larves de poissons, et prédateurs épipélagiques et bathypélagiques potentiels).

Sur la base de leur comportement trophique et vertical, les résultats montrent que nombre de ces espèces contribuent à plusieurs processus écosystémiques d'importance locale et mondiale. À titre d'exemple, plusieurs espèces (par exemple, les poissons lanterne et les poissons hachette) migrent verticalement vers la surface pour se nourrir la nuit et transporter activement le carbone ingéré vers les eaux profondes pendant la journée, une voie qui renforce le stockage du carbone océanique. De plus, ils jouent un rôle important dans les échanges trophique en consommant du zooplancton et en fournissant du fourrage à de nombreux prédateurs épipélagiques et d'eaux profondes. Ces processus sont notamment cruciaux pour le maintien de stocks de poissons exploitables et le lien entre les écosystèmes superficiels et profonds. En outre, en se nourrissant d'organismes de la famille des thaliacea et des siphonophores, ces espèces convertissent de « l’énergie gélatineuse » en « énergie de poisson » utilisable par les niveaux trophiques supérieurs. Cette une voie trophique est probablement en augmentation dans l'Anthropocène en raison de la prolifération d’organismes gélatineux dans de nombreux écosystèmes impactés par les activités humaines. Par ailleurs, nous avons démontré que même les espèces qui restent à plein temps en eaux profondes peuvent jouer un rôle clé dans les échanges verticaux. Le cas du poisson vipère (*Chauliodus sloani*) est exemplaire à ce sujet. Nous avons pu explorer ses rôles fonctionnels, comment les facteurs physiques peuvent affecter son écologie et comment ces relations sont susceptibles de changer sur de grandes zones océaniques. Dans la zone d’étude le poisson vipère ne migrent jamais dans les eaux superficielles. Il se nourrit principalement d’espèces migratrices épipélagiques, en particulier les poissons lanternes, stockant ainsi le carbone en profondeur. Par ailleurs nous montrons que c’est la température qui limite sa distribution verticale. Par conséquent, son comportement migratoire sa trophodynamique, et ses rôles fonctionnels sont modulés par le changement latitudinal de la température. Dans la plupart des régions tropicales, le poisson vipère se nourrit, excrète et sert de proie (notamment pour les prédateurs bathypélagiques) à plein temps dans les couches profondes. Au contraire, dans les régions tempérées, le poisson vipère remonte vers les eaux superficielles la nuit où il interagit avec les prédateurs épipélagiques et peuvent libérer du carbone là où sa reminéralisation est la plus importante.

Nous avons également construits des modèles conceptuels décrivant les différentes niches écologiques des poissons mésopélagiques. En combinant les informations sur leur habitat et leur écologie, nous démontrons que ces espèces sont probablement séparées en de nombreux groupes fonctionnels ayant des préférences alimentaires, une composition isotopique, des pics d'abondance verticale et des réponses aux contraintes environnementales (température et oxygène) différentes. Comme cas d'étude, nous avons défini cinq groupes fonctionnels pour les poissons hachette. Dans le cas des poissons lanterne, nous avons défini trois modèles de préférence de proie et quatre modèles de comportement migratoire. Ces schémas révèlent une forte partition des ressources et plusieurs mécanismes pour éviter l'exclusion compétitive. Ici, nous nous sommes concentrés sur les deux familles les plus abondantes. Cependant, il est probable que ces caractéristiques soient présentes dans la plupart des communautés mésopélagiques. Par conséquent, nous réaffirmons que la clarification de la distribution, du comportement vertical et des relations trophiques des espèces mésopélagiques fournira probablement des connaissances clés sur le fonctionnement et l'importance des systèmes mésopélagiques.

Dans la conclusion générale, nous passons brièvement en revue les études antérieures et soulignons certaines des principales menaces pesant sur les espèces mésopélagiques. Tout d'abord, nous montrons que le changement climatique peut affecter directement plusieurs espèces par des changements rapides sur la stratification des océans, la température, l'acidification et les niveaux d'oxygène. Deuxièmement, nous montrons que les poissons mésopélagiques représentent l'une des dernières ressources marines inexplorées et que les incitations à leur exploitation commerciale sont de plus en plus nombreuses. Troisièmement, nous expliquons l'intérêt croissant pour l'exploitation des minéraux d'eau profonde et ses nombreux impacts potentiels sur les poissons mésopélagiques. Et, quatrièmement, nous discutons de l’impact des polluants dont les micro-plastiques dans l'environnement marin.

Finalement, nous montrons que les nombreuses nouvelles découvertes présentées ici reflètent non seulement les efforts d'une recherche multidisciplinaire et la grande diversité de le SOAT, mais aussi le manque d'informations scientifiques sur les eaux profondes. La feuille de route de la Décennie des Nations unies pour l'océanographie reconnaît que les eaux profondes sont une frontière de la science et de la découverte. La capacité à mener des recherches scientifiques est inégale d'un pays à l'autre, les économies en développement étant confrontées à des obstacles importants pour participer à la recherche en eaux profondes. Par conséquent, les parties les moins étudiées des grands fonds marins se trouvent dans les zones économiques exclusives des pays les moins développés économiquement. Alors que l'homme étend l'extraction des ressources et l'impact sur l'habitat dans les profondeurs océaniques, la compréhension des écosystèmes mésopélagiques, de leurs processus et de leurs fonctions est incontournable, en particulier lorsque l'on veut parvenir à la durabilité.

GENERAL INTRODUCTION

Mesopelagic fishes (200–1000 m depth) are numerically the most important vertebrate component of the world's oceans, usually presenting global distribution, high biodiversity, and several adaptations to overcome challenges imposed by the deep-sea (Gjøsaeter and Kawaguchi, 1980; Irigoien et al., 2014; Nelson et al., 2016). Low metabolic rates, high tolerance for environmental changes, and complex visual and bioluminescence systems are some of these adaptations (Priede, 2017). Many of these species forms high-density biological layers at around 500 m in search of predator refuge during daytime (Sutton, 2013), and ascend to epipelagic layers (0–100 m) at night for feeding, following the diel vertical migration of zooplankton (Merrett and Roe, 1974). This "largest daily migration of animals on earth" (Hays, 2003) represents a major pathway enhancing oceanic carbon storage and thus global carbon cycles. Moreover, they are an important food source for harvestable fish stocks, a key link between shallow and deep-sea ecosystems, and a potential source of unexplored bio-resources (e.g. Hopkins et al., 1996; Cherel et al., 2010; Lauritano et al., 2020). For instance, anticancer and antimicrobial activities in mesopelagic fishes have just been discovered (Lauritano et al., 2020).

It is worrying, then, that this notable fish group remains poorly known worldwide while it is increasingly at risk in several ways (St. John et al., 2016; Martin et al., 2020). Indeed, while mesopelagic ecosystems are placed amongst the largest and least understood environments on Earth, side effects of global warming (Levin et al., 2019), plastic pollution (Davison and Asch, 2011), and exploitation of deep-sea resources (Hidalgo and Browman, 2019; Watling et al., 2020) are accelerating. As threats increase, further investigations on these species are required. Research has already addressed important aspects of their taxonomy (e.g., Nafpaktitis et al., 1977; Gjøsæter et al., 1980; Sutton et al., 2020), distribution (e.g. Fock et al., 2004; Olivar et al., 2017; Sutton et al., 2017), morphometry (e.g. Tuset et al., 2018; López-Pérez et al., 2020), vertical migration (e.g. Watanabe et al., 1999; Olivar et al., 2012; Sutton, 2013) and trophic ecology (e.g. Bernal et al., 2015; Olivar et al., 2018; Czudaj et al., 2020). These studies demonstrated, among others, that mesopelagic fishes are a major component of marine ecosystem (abundance, biomass, and diversity) and extremely diverse in their behaviour and functional roles. As an example, four major guilds were identified for mesopelagic species (Zooplanktivores, Pelagic Micronektonivores, Pelagic Generalists, and

Gelativores; Gartner et al. 1997); while at least four patterns of vertical migration were recognized (Watanable et al., 1999).

Although studies on mesopelagic species have made considerable progress in recent years, knowledge on the biodiversity and ecology of many species remains deficient. In an ecological context, there are four Priority Research Areas (PRA) to improve the understating of the mesopelagic zone: (i) biodiversity census; (ii) links between oceanographic regimes and mesopelagic biomass and biodiversity; (iii) role of the mesopelagic community in the food web; and (iv) role of individual species and the community in ecosystem processes (St. John et al., 2016; Hidalgo and Browman, 2019; Martin et al., 2020).

The first PRA advocates for answering a primary question in studies addressing the ecology and conservation of marine systems, which is “who is down there (biodiversity)?”. The participating Nations at COP 21 noted the “importance of ensuring the integrity of all ecosystems, including oceans, and the protection of biodiversity¨. There is, however, a major lack of knowledge of the global composition and distribution of mesopelagic diversity, which is under-sampled and sparse in data (St. John et al, 2016). The roadmap for the United Nations Decade of Ocean Science recognizes the deep-sea as a frontier of science and discovery (Ryabinin et al., 2019). Yet, there is an unequal capacity to conduct science among nations, with developing economies facing substantial barriers to participating in deep-sea research (Howell et al., 2020). Consequently, the least-studied parts of the deep-sea are within the Exclusive Economic Zones of the least economically developed countries (Howell et al., 2020). Without a basic knowledge of biodiversity, it is difficult to plan and implementing sustainable management, as well as fully understand the functioning and the role of these species on the ecosystem (Glover et al., 2018).

The second PRA recommends a better assessment of the relationship between oceanographic variables and mesopelagic species. Indeed, variations on temperature, oxygen, and upper circulation processes may play an important role in the ecology and movement of deep-pelagic fishes (Fock et al., 2004; Bertrand et al., 2010; Proud et al., 2017; Boswell et al., 2020). However, the importance of these variables is highly dependent on community dynamics and only a few studies have focused on how oceanographic processes may influence their ecology and biodiversity (e.g., Olivar et al., 2017; Milligan and Sutton, 2020). It is therefore not clear how physical drivers (e.g., temperature, oxygen) structure their communities, and how these relationships are likely to change in space and time, especially under global climatic changes.

The third PRA proposes a better understanding of the trophic role of mesopelagic species in marine food-webs. In this topic, many important works have already been done (e.g., Hopkins and Baird, 1981; Sutton and Hopkins, 1996; Carmo et al., 2015). Yet, this information is still restricted to a few locations, and food web studies considering multiple approaches are still scarce. Indeed, only a few studies included epipelagic and deep-sea predators to evaluate the importance of mesopelagic species as prey, hampering the real assessment of the trophodynamics of these species. Additionally, previous studies were mostly based on gut content analyses (GCA) (e.g., Hopkins and Baird, 1981; Sutton and Hopkins, 1996; Carmo et al., 2015). Whilst GCA may provide high taxonomic resolution of the diet, the approach is restricted by its short temporal representation and includes biases due to prey misidentification (Hyslop, 1980). Furthermore, the importance of key prey groups that are quickly digested (e.g. gelatinous organisms) remains underestimated, hampering a more complete understanding of pelagic food webs (Hopkins and Baird, 1985; Hidalgo and Browman, 2019). Alternatively, stable isotope analysis (SIA) is a useful tool to study food web structure, as it provides time-integrated information on all the material assimilated by organisms, including prey that is usually not accounted on GCA (Cherel et al., 2008; Post, 2002). Hence, combining both GCA and SIA allows for a more comprehensive picture of the flows of biomass across trophic compartments.

The fourth PRA suggests a better comprehension of the contribution of mesopelagic species in ecosystem processes, as the Biological Carbon Pump (BCP). The BCP is the active and passive transport of particulate organic carbon produced on the ocean surface by photosynthesis to the deep ocean (Cavan et al., 2019; Davison et al., 2013). Given their behaviour, high biomass, and feeding ecology, mesopelagic fishes substantially contribute to the active part of this process (Davison et al., 2013; Kwong and Pakhomov, 2017). As carbon storage depends on the depth difference between the ingestion of carbon and its release (e.g., respiration, excretion, and mortality), the contribution of mesopelagic species to the BCP are directly linked with their diel vertical migration between their prey and predators. Therefore, clarification on these aspects will likely provide key knowledge to better inform biogeochemical models projecting carbon sequestration now and in the future.

Together, these four PRA may also work synergistically and provide new approaches and insights in mesopelagic ecosystems. As an example, characteristics in terms of trophic ecology, habitat, distribution, and migration patterns allow classifying species by functional groups, which is a powerful approach to investigate the effect of species on ecosystem functions, functional equivalence among species, and organisms adaptation to changing environmental conditions (McGill et al., 2006; Villéger et al., 2017). Additionally, it may help to understand how these species are scattered over different patterns of resource use (niche partitioning), and thereby avoiding competitive exclusion. Ultimately, it may contribute to clarifying the coexistence of sympatric species and how resources use shapes their contribution to ecological processes (i.e., fluxes of carbon and nutrients; Brandl et al., 2020).

The Southwestern Tropical Atlantic (SWTA; Fig. 1) is a marine area holding distinct biodiversity and an understudied mesopelagic zone (CBD, 2014). Located in an oligotrophic area, the SWTA encompasses oceanic islands, seamounts, and underwater canyons that interact with local currents and enhance marine productivity (Travassos et al., 1999; Tchamabi et al., 2017). As an example, this area encompasses the Fernando de Noronha Archipelago (FN) and the Rocas Atoll, which together form a unique biogeographical unite. Moreover, the SWTA acts as near-surface northward paths for the Atlantic Meridional Overturning Circulation. Its variability affects the 3D transport of heat, salt, and regional distributions of water mass boundaries, leading to shifts in the biodiversity and ecosystems (Bourlès et al., 1999a; Assunção et al., 2020; Dossa et al., 2021). Consequently, this location includes many zones that have been referred to as an "oasis of life in an oceanic desert" (Hazin, 1993) and 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). For instance, recent studies in FN are revealing many new species and new occurrences, placing this area amongst the most important in number of species whitin the South Atlantic Ocean (Pimentel et al., 2020).

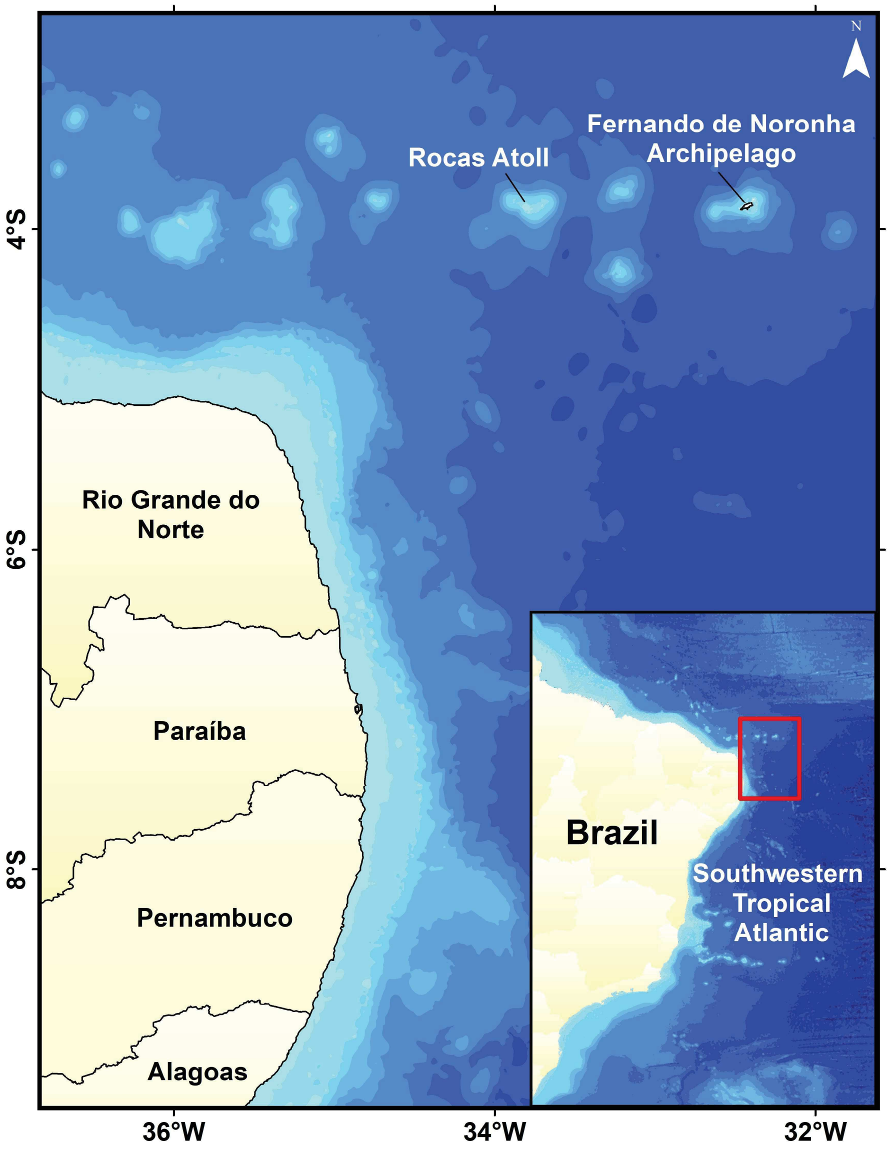

Figure 1- Southwestern Tropical Atlantic with study area highlighted.

The first collection of deep-sea fishes in the SWTA was carried out by the H.M.S. *Challenger* (1872–1876; Günther, 1887). Since then, these species have been sporadically explored by different vessels such as the RV *Walther Herwig* (1966–1971; many authors), the RV *Marion Dufresne* (1987; Séret & Andreata, 1992), the RV *Atlântico Sul* (1996–1999; Figueiredo et al., 2002; Bernardes et al., 2005), the RV *Thalassa* (1999–2000; Costa et al., 2007), the RV *Astro Garoupa* (2003; Costa & Mincarone, 2010), the RV *Gyre* (2008; Mincarone et al., 2017), and the RVs *Luke Thomas* and *Seward Johnson* (2009, 2011; Lins Oliveira et al., 2015). Although these expeditions substantially contributed to the understanding of fish communities, they were highly sparse and mostly focused on demersal communities. Consequently, mesopelagic fishes represent less than 20% of the species recorded on the SWTA (Melo et al., 2020). The overall knowledge of these species is thus still scarce, leaving many gaps in our understanding of marine ecosystems.

More recently, two expeditions were made onboard the RV *Antea*, as part of the project ABRACOS (Acoustics along the BRAzilian COaSt; Bertrand, 2015, 2017). For the first time, the mesopelagic zone of the SWTA was extensively surveyed, resulting in the collections of thousands of deep-sea invertebrates and fishes. Based on these collections, we constructed this thesis, to focus on the four PRA and develop a comprehensive study of the biodiversity and ecology of mesopelagic fishes. Specifically, we aimed at answering the following questions: (i) what are the mesopelagic fishes and main groups of the STWA, (ii) where are they distributed, (iii) what are the features of their diel vertical migration, (iv) what are their main prey and trophic relationships, (v) how are they related with physical-chemical oceanographic conditions, and (vi) what are their functional roles?

This thesis is organized over two main chapters. In chapter one, organized over nine papers, we propose an integrative study of the biodiversity of mesopelagic fishes from the SWTA. For that, we first provide a full list of mesopelagic species collected during the ABRACOS expeditions, pointing out main groups (based on abundance, biomass, and diversity), new records, and potentially new species. Also, we provided eight more specific papers focusing on the diversity, distribution, and morphometry of some relevant fish groups such as Argentiniformes, Stomiiformes, Ceratioidei, Stephanoberycoidei, Caristiidae, Howelidae, and Trichiuridae.

In chapter two, we propose a comprehensive study on the ecology of the major species (in terms of abundance and biomass) identified in chapter one: Sternoptychidae, Myctophidae, and the viperfish *Chauliodus sloani*. For that, we use information on their abundance, distribution, diversity, and physical and chemical habitat. Additionally, we also included information on their trophic ecology by combing gut content analyses with stable isotope data (carbon and nitrogen) carried out on the mesopelagic fishes and their main trophic links, including zooplankton, crustaceans, fish larvae, and epi- and bathypelagic potential predators. By doing that, we could define functional groups, multidimensional niches, and underestimated trophic links, which together provided a novel vision on the ecology of mesopelagic species.

Finally, we propose a general conclusion where we synthesize our main finds and explain how the works include in this thesis may contribute to the overall knowledge of mesopelagic ecosystems. Additionally, we highlighted and discussed the crescent threats on mesopelagic species in the coming years.

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CHAPTER 1 - BIODIVERSITY AND BIOLOGY

The biodiversity of species can be defined as the variability among living organisms from all sources. It is the foundation of ecosystem processes to which human well-being and all other species are intimately connected. For instance, biodiversity is directly linked with the provisioning of habitat, food, regulation of climate, medicinal resources, and energy. However, there is no feature of Earth experiencing more dramatic change at the hands of humans than the layer of living organisms that occupy its surfaces and its seas. As an example, while mesopelagic ecosystems are placed amongst the largest and least understood environments on Earth, side effects of global warming, plastic pollution, and exploitation of deep-sea resources are accelerating.

The participating Nations at COP 21 noted the "importance of ensuring the integrity of all ecosystems, including oceans, and the protection of biodiversity¨. There is, however, a major lack of knowledge of the global composition and distribution of mesopelagic diversity, which is under-sampled and sparse in data. Also, even basic biological knowledge is lacking for many species. As an example, several fishes are lacking knowledge on the length-weight relationships, which are widely applied in the management of populations, ecological modeling, and stock assessment analyses. Without this knowledge, it is difficult to plan and implementing sustainable management, as well as fully understand the functioning and the role of these species on the ecosystem.

In this chapter, we provide an integrative study on the biodiversity and morphometry of mesopelagic fishes from the SWTA, a poorly known area that encompass oceanic islands, seamounts, and unique biodiversity. For that, we first present a main article providing a full list of species collected during the ABRACOS expeditions, pointing out main groups (based on abundance, biomass, and diversity), new records, and potentially new species. Moreover, we addressed mesopelagic fishes biodiversity through several indexes, considering different depth strata and diel periods.

In addition, we provided two articles (and four additional articles in the appendix) focusing on the diversity and distribution of the following fish groups: Trichiuridae, Howelidae, Caristiidae, Argentiniformes, Stephanoberycoidei, Ceratioidei, and Stomiiformes. In these studies, we not only report the new occurrence of species in the SWTA, but also review, re-identify, and discuss previous records of mesopelagic species from this region. Finally, we include two articles providing length-weight relationships and morphometric information for twenty-three species.

List of articles included in this chapter:

Article 1: **Eduardo L.N.,** et al. Rich and unreported: the astonishing diversity of mesopelagic fishes in the southwestern Tropical Atlantic. *Deep-sea Research Part I* ***(submitted)***

Article 2: **Eduardo L.N.**, et al 2018. First record of the intermediate scabbardfish *Aphanopus intermedius* Parin 1983 (Scombriformes: Trichiuridae) in the western South Atlantic. *Journal of Fish Biology*. https://doi.org/10.1111/jfb.13796

Article 3: **Eduardo L.N.** et al. 2019. Deep-sea oceanic basslets (Perciformes, Howellidae) from Brazil: new records and range extensions. *Checklist.* https://doi.org/10.15560/15.6.965

Article 4: **Eduardo L.N.** et al. 2018. Length-weight relationships of eleven mesopelagic fishes from oceanic islands of the Southwestern Tropical Atlantic. *Journal of Applied Ichthyology*. https://doi.org/10.1111/jai.13840

Article 5: **Eduardo L.N.**, et al. 2020. Length-weight relationship of twelve mesopelagic fishes from the western Tropical Atlantic. *Journal of Applied Ichthyology*. https://doi.org/10.1111/jai.14084.

List of additional articles included in the appendix:

Additional Article 1: Mincarone M.M., Villarins B.T., **Eduardo L.N.**, et al. 2019. Deep-sea manefishes (Perciformes: Caristiidae) from oceanic islands and seamounts off northeastern Brazil, with comments on the caristiids previously reported in Brazilian waters. *Marine Biology Research*. https://doi.org/10.1080/17451000.2019.1636281

Additional Article 2: Mincarone M.M., Martins, J., Di Dario, F., **Eduardo L.N.**, et al. (2020) Deep-sea smelts, pencil smelts, and barreleyes (Teleostei: Argentiniformes) from oceanic islands and seamounts off northeastern Brazil. *Marine Biology Research.* https://doi.org/10.1080/17451000.2021.1891806

Additional Article 3: Mincarone M.M., Di Dario, F.; Gabriel, A.; **Eduardo L.N.**, et al. Deep-sea anglerfishes (Lophiiformes: Ceratioidei) from off northeastern Brazil, with remarks on the ceratioids reported from the Brazilian Exclusive Economic Zone. Neotropical Ichthyology. https://doi.org/10.1590/1982-0224-2020-0151

Additional Article 4: Gabriel, A., Di Dario, F., **Eduardo L.N.**, et al. (2021) Taxonomy and distribution of deep-sea bigscales and whalefishes (Teleostei: Stephanoberycoidei) collected off mortheastern Brazil, including seamounts and oceanic islands. *Ichthyology and Herpetology.* 109, No. 2.

Rich and underreported: the diversity of mesopelagic fishes in the southwestern Tropical Atlantic

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ABSTRACT

Mesopelagic fishes play critical ecological roles by sequestering carbon, recycling nutrients, and acting as a key trophic link between primary consumers and higher trophic levels. They are also an important food source for harvestable economically valuable fish stocks and a key link between shallow and deep-sea ecosystems. Despite their relevance, mesopelagic ecosystems are increasingly threatened by direct and indirect anthropomorphic activities while representing some of the largest and least understood environments on Earth. The composition, diversity, and other aspects of the most basic biological features of numerous mesopelagic fishes are still totally unknown. Here, we provide the first integrative study of the biodiversity of mesopelagic fishes of the southwestern Tropical Atlantic (STWA), based on two expeditions in northeastern Brazil in 2015 and 2017. A full list of mesopelagic fishes of the region is provided, including rare species and new records for the Brazilian Exclusive Economic Zone and the indication of potentially new species in groups such as the Stomiiformes and Stephanoberycoidei. Key aspects of the diversity of mesopelagic fishes of the region were also assessed, considering different depth strata and diel periods. At least 206 species in 55 families and 23 orders of the Teleostei and one shark (*Isistius brasiliensis*) were recorded, with potentially nine new species (4%) and 62 (30%) new records for Brazilian waters. Five families accounted for 52% of the diversity, 90% of specimens collected, and 72% of the total biomass: the Myctophidae (38 spp., 36% of specimens, 24% of the biomass), Stomiidae (38 spp., 8%, 21%), Gonostomatidae (11 spp., 16%, 4%), Melamphaidae (11 spp., 2%, 7%), and Sternoptychidae (10 spp., 24%, 10%). During the day, richness and diversity were higher at lower mesopelagic depths (500–1000 m), with contributions of typically bathypelagic species likely associated with seamounts and oceanic islands. At night, richness and diversity increased at epipelagic depths, indicating the diel ascension of several species (e.g., myctophids and sternoptychids) that can endure temperatures range up to 25°C. Information on the geographic distribution of several rare species worldwide is also provided.

Keywords: Deep-sea; Oceanic Islands; Seamounts; biodiversity; Brazil; Fernando de Noronha Ridge.

INTRODUCTION

Mesopelagic fishes (200–1,000 m depth) are among the most abundant vertebrates in the biosphere (Gjøsaeter and Kawaguchi, 1980; Irigoien et al., 2014; Nelson et al., 2016). They usually have a global distribution, vertical migratory behaviour, and several adaptations to overcome challenges imposed by the deep-sea environment (Gjøsaeter and Kawaguchi, 1980; Sutton, 2013; Priede, 2017). Low metabolic rates, high tolerance to environmental changes, and complex visual and bioluminescence systems are some of these adaptations (Priede, 2017). Consequently, the mesopelagic zone holds one of the most diverse fish communities of the world's ocean, contributing to several ecosystem processes (Gjøsaeter and Kawaguchi, 1980; John et al., 2016). For instance, mesopelagic fishes play critical roles by sequestering carbon, recycling nutrients, and acting as a key trophic link between primary consumers and higher trophic levels (e.g., larger fishes, mammals, and seabirds) (e.g., Ariza et al., 2015; Cavan et al., 2019; Eduardo et al., 2020a, 2020b). They are also an important food source for harvestable fish stocks and a key link between shallow and deep-sea ecosystems (e.g., Cherel et al., 2010; Eduardo et al., 2020b; Eduardo et al., 2021).

Despite their importance, mesopelagic communities are increasingly threatened by climate change (Levin et al., 2019), plastic pollution (Davison and Asch, 2011), and exploitation of deep-sea resources (Hidalgo and Browman, 2019; Drazen et al., 2020). Additionally, there is a major lack of knowledge of the biology, ecology, distribution, and diversity of mesopelagic species, which are under-sampled and sparse in data (Glover et al., 2018; Hidalgo and Browman, 2019; Martin et al., 2020).

The southwestern Tropical Atlantic (SWTA), which encompasses oceanic islands, underwater canyons, and several seamounts (Travassos et al., 1999; Tchamabi et al., 2017), holds distinct marine biodiversity and remains severely understudied (CBD, 2014). The region includes Marine Protected Areas and Ecologically or Biologically Significant Marine Areas (EBSAs) that, by definition, are special places of fundamental importance for biodiversity and life cycles of marine species (CBD, 2014). Moreover, the SWTA includes different biogeographic provinces with contrasting thermodynamic features, current systems, and water-mass properties, leading to shifts in biodiversity and ecosystems (Bourlès et al., 1999; Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021; Tosetto et al., 2021).

The first collection of deep-sea fishes in the SWTA was carried out by the HMS *Challenger* (1872–1876; Günther, 1887). Since then, mesopelagic fishes have been sporadically collected by different vessels, such as the RV *Walther Herwig* (1966–1971; many authors), RV *Marion Dufresne* (1987; Séret & Andreata, 1992), RV *Atlântico Sul* (1996–1999; Figueiredo et al., 2002; Bernardes et al., 2005), RV *Thalassa* (1999–2000; Costa et al., 2007), RV *Astro Garoupa* (2003; Costa & Mincarone, 2010), RV *Gyre* (2008; Mincarone et al., 2017), and the RV *Luke Thomas* and RV *Seward Johnson* (2009, 2011; Lins Oliveira et al., 2015). Although these expeditions substantially contributed to the understanding of the diversity and ecology of several groups, they were sparse and focused mostly on demersal species (Melo et al., 2020). Only a few studies focused on the mesopelagic communities of the SWTA in particular, with most of them being restricted to the composition and taxonomy of specific groups (e.g., Mincarone, 2008; Lima et al., 2011). Consequently, a more integrative overview of the mesopelagic fish community of the region is still lacking, leaving a “dark hole” in our understanding of their diversity, ecology, and function in marine ecosystems.

Two recent expeditions focused on mesopelagic species were made aboard the RV *Antea*, as part of the project ABRACOS (Acoustics along the BRAzilian COaSt; Bertrand, 2015, 2017). For the first time, the mesopelagic zone of the SWTA was extensively surveyed, resulting in collections of thousands of deep-sea invertebrates and fishes. Based on these collections, various studies have been published addressing the diversity and ecology of some fish groups, such as Argentiniformes (Mincarone et al., 2021), Stomiiformes (Eduardo et al., 2020a, 2020b; Villarins et al., 2021), Ceratioidei (Mincarone et al., 2021), Caristiidae (Mincarone et al., 2019), Howelidae (Eduardo et al., 2019a), and Trichiuridae (Eduardo et al., 2018). However, most of the results of these cruises remain unpublished. Here, we present an integrative study of the biodiversity of mesopelagic fishes from the SWTA. A full list of mesopelagic species collected during the ABRACOS expeditions, including new records and the indication of potentially new species, is provided. Key aspects of the mesopelagic fish diversity of the region were also addressed, considering different depth strata and diel periods.

Methodology

Study area

The study area comprised the northeast Brazilian coast, from Rio Grande do Norte to Alagoas states (5°–9°S), and the seamounts and oceanic islands of the Fernando de Noronha Ridge, including the Rocas Atoll (3°52′S, 33°49′W) and the Fernando de Noronha Archipelago (3°50′S, 32°25′W) (Fig. 1). The main oceanographic physico-chemical features of the region were recently described by Assunção et al. (2020), Dossa et al. (2021), and Silva et al. (2021). Overall, the southwestern Tropical Atlantic is considered oligotrophic. However, locally the banks and islands act as topographic obstacles to currents, driving subsurface enriched waters to the surface (Travassos et al., 1999; Tchamabi et al., 2017; Silva et al., 2021). This process increases primary production and enhances the mass and energy fluxes throughout the food web (Travassos et al., 1999; Tchamabi et al., 2017).

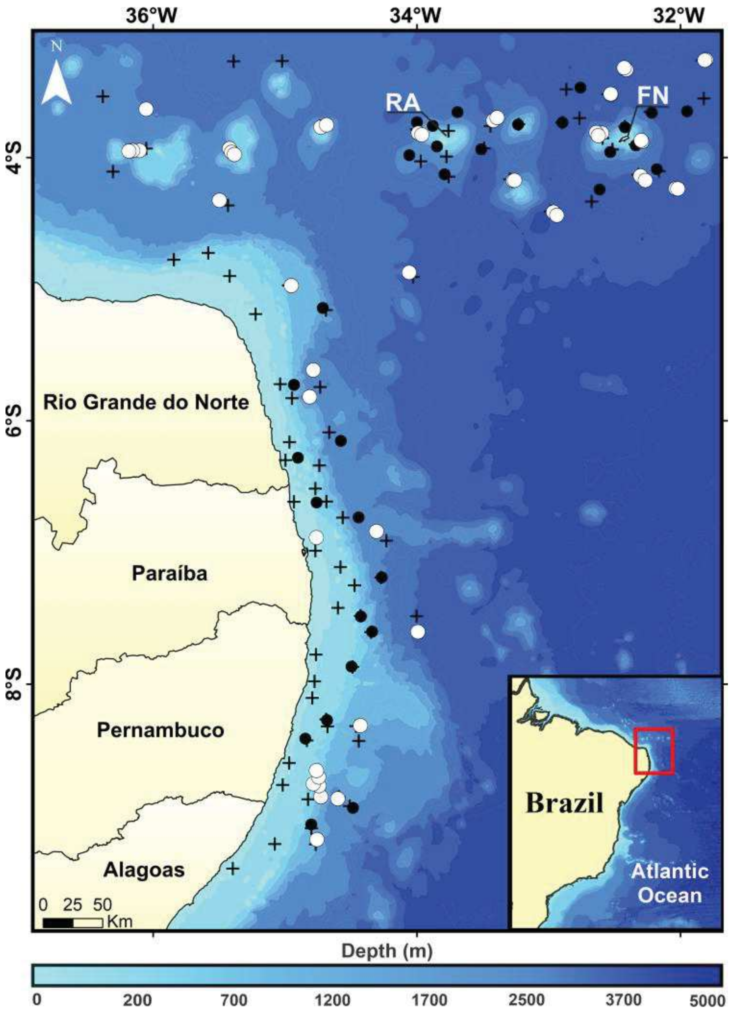

Figure 1. Study area with CTDO profile (cross) and trawl samples (dots). Black and white symbols for ABRACOS 1 and ABRACOS 2, respectively.

Data and specimen collection

Data were collected during the Acoustics along the BRAzilian COaSt (ABRACOS) surveys, carried out from 30 August to 20 September 2015 (AB1) and from 9 April to 9 May 2017 (AB2), aboard the French RV *Antea* (Bertrand, 2015, 2017). Temperature profiles were collected using a CTDO SeaBird911+. Mesopelagic fishes were collected during day and night at 80 trawl stations by using a mesopelagic (AB1; body mesh 30 mm, cod-end mesh 4 mm; Bertrand, 2015) and micronekton (AB2; body mesh 40 mm, cod-end mesh 10 mm; Bertrand, 2017) nets (Fig. 1; Supplementary Material S1). Targeted depth ranged from 10 to 1,113 m (Fig. 1) and was defined by the presence of acoustic scattered layer or patches detected by a Simrad EK60 (Kongsberg Simrad AS) split-beam scientific echosounder, operating at 38, 70, 120, and 200 kHz. The net geometry was monitored using SCANMAR sensors, to give headline height, depth, and distance of wings and doors to ensure the net was fishing correctly. As the trawl was not fitted with an opening and closing mechanism, the collection of specimens during the lowering or hoisting of the net was reduced as much as possible by decreasing ship velocity and increasing winch speed.

Specimens were sorted to the lowest taxonomic level and frozen or, in the case of rare species or of taxonomic uncertainty, fixed in 4% formalin and then preserved in a 70% alcohol solution (Eduardo et al., 2020a). In the laboratory, specimens were identified, measured (nearest 0.1 cm of standard length, SL), and weighed (nearest 0.01 g of total weight, TW). Excluding a few specimens of the Stomiidae, Sternoptychidae, and Myctophidae utilised for biological analyses (Eduardo, et al., 2020a; 2020b, 2021), all specimens were deposited in the NPM – Fish Collection of the "Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro" (NUPEM/UFRJ).

Richness estimators and Biodiversity indexes

We first computed a randomised species accumulation curve to assess whether the fish community was exhaustively sampled with the gears employed (Gotelli and Colwell, 2001). This enables the calculation of a mean number of species for a given number of samples within a 95% confidence interval. The Chao1 index, which extrapolates the total expected number of species in the area for a given sampling gear, was subsequently calculated (Magurran, 2004).

Other aspects of the biodiversity were assessed based on the sample-size-based rarefaction and extrapolation sampling curves, calculated for the species richness; Shannon diversity; and Simpson dominance, the three most widely used species diversity indexes (Magurran, 2004). For that, we used the Hill's numbers, which integrate species richness and species relative abundance to propose a more intuitive and statistically rigorous alternative to calculate diversity measures (Chao et al., 2014). Statistical significance was evaluated based on the confidence interval overlapping of the curves.

Additionally, sample-size-based rarefaction and extrapolation sampling curves (Hsieh et al., 2016) were constructed to test for differences in diversity indexes when considering depth strata (epipelagic 0–200 m; upper mesopelagic 200–500 m; lower mesopelagic 500–1000 m) and the diel period (day and night). As the sampling strategy employed in the AB2 expedition was much more efficient to collect mesopelagic fishes (see Discussion), diversity indexes were only calculated for this survey. Statistical analyses and the calculation of diversity indices were performed using the software R version 4.0.3 through the package "iNext" (Hsieh et al., 2016). Fish larvae and species traditionally classified as epipelagic were excluded from the list of species (Table 2), and they were not considered for the diversity assessments. Specimens identified at the genus level only (small-sized and/or damaged specimens), which might represent more than one species, were also excluded from the analyses (Supplementary Material S1).

Results

Biodiversity

Overall, 6,870 specimens of mesopelagic fishes, representing 206 species in 135 genera, 55 families, and 23 orders of the Teleostei and one shark (*Isistius brasiliensis*: Dalatiidae, Squaliformes), were collected and identified (Table 1). The species accumulation curve was steep, indicating that more species would be recorded with additional sampling using the same gears (Fig. 2). Indeed, richness estimators indicated that about 100 (48%) additional mesopelagic species of fishes are expected to occur in the area (Fig. 2). Additionally, 772 specimens representing about 40 fish taxa were sampled but could not be identified to species given their small size and/or poor condition. Hence, it was not possible to determine whether these specimens belong to species not listed in Table 1. To ensure a more robust assessment of species diversity, we placed these taxa in a separate list (Supplementary Material S2).

The range of standard length (SL) and wet weight for all species collected are provided in Table 1. In general, a wide size range was sampled, from 30 mm (an unidentified member of the Ceratiidae) to 1,880 mm SL (*Eumecichthys fiski*, Lophotidae). However, 90% of the specimens measured between 20 and 200 mm SL.

The five orders with the highest number of taxa were the Stomiiformes (at least 63 species, four families), Myctophiformes (39 spp., two families), Aulopiformes (17 spp., seven families), Beryciformes (16 spp., three families), and Lophiiformes (12 spp., seven families), accounting for 70% of the total number of species recorded. Thirteen orders included less than five species. Considering families, the most representative were the Myctophidae (38 spp.), Stomiidae (38 spp.), Gonostomatidae (11 spp.), Melamphaidae (11 spp.), and Sternoptychidae (10 spp.) (Fig. 3). Half of the families (28) were represented by a single species.

In terms of abundance, the most representative families were the Myctophidae (Myctophiformes; 36%); Sternoptychidae (Stomiiformes; 26%); Gonostomatidae (Stomiiformes; 16%); Stomiidae (Stomiiformes; 8%); and Melamphaidae (Beryciformes; 2%) (Fig. 3). These families together accounted for 88% of all fishes collected. The remaining families represented individually no more than 2% of the total number of specimens collected. At the alpha taxonomic level, the following taxa represented almost 50% of all specimens collected: *Sternoptyx diaphana* (14%), *Cyclothone* spp. (11%; see Discussion), *Diaphus brachycephalus* (6%), *Argyropelecus affinis* (6%), *Chauliodus sloani* (5%), *Lampanyctus nobilis* (4%), and *Diaphus perspicillatus* (4%). About 130 species were represented by five specimens or less, of which 64 were represented by a single specimen.

Considering biomass, the most representative families were the Myctophidae (24%), Stomiidae (21%), Setarchidae (Scorpaeniformes, 11%), Sternoptychidae (10%), and Melamphaidae (7%) (Fig. 3). These families together accounted for 73% of the biomass of all fishes collected. The remaining families individually accounted for less than 4% of the total weight. At the specific level, the following species represented 42% of the biomass: *Ectreposebastes imus* (11%), *Chauliodus sloani* (9%), *Borostomias* *elucens* (6%), *Eumecichthys fiski* (6%, a single specimen), *Sternoptyx diaphana* (4%), *Melamphaes polylepis* (3%), and *Argyropelecus affinis* (3%).

Distribution, vertical migration, biodiversity indexes, and size

Overall, 60 species (29%) were recorded in a wide longitudinal distribution (Table 1). In contrast, 133 species (64%) were collected only in a few localities, with 116 being restricted to oceanic islands and seamounts, which aggregates most samples (Table 1). Considering depth and period, the highest diversity, abundance, and biomass were found between 700–1000 m depth during the day (Fig.4). At night, the highest number of species was recorded at lower mesopelagic depths (500–1000 m). However, a much greater number of species, abundance, and biomass were detected in shallow waters (0–200m), indicating an ascent in the water column of several species at night. Indeed, at least 50 species seem to have a wide range of depth distribution and tolerance to variations in water temperature (up to 800 m and 25°C; e.g., Sternoptychidae and Myctophidae; Table 2). 66 species, nevertheless, seem to be restricted to deeper (> 600 m) and colder waters (< 6º C) (e.g., Lophiiformes and Beryciformes; Table 1).

Significant differences in biodiversity indexes were found when considering diel periods and depth. Higher values of richness and diversity were found in lower mesopelagic waters and during the daytime. Dominance values, however, were significantly higher at epipelagic waters, also at daytime (Fig. 4).

Table 1. Species recorded, survey (1: ABRACOS 1; 2: ABRACOS 2), number of specimens (N), frequency of occurrence to overall samples (FO%), standard length (mean and range), total wet weight (mean and range), collection locality (PE: Pernambuco; PB: Paraíba; RN: Rio Grande do Norte; FNR: Fernando de Noronha Ridge), depth range, temperature range (T°C), and new records in the Brazilian Exclusive Economic Zone (EEZ). Classification follows Nelson et al. (2016).

Species	**Survey**	**N**	**FO%**	**SL (mm)**	**TW (g)**	**Site**	**Depth (m)**	**T (°C)**	**New record Brazilian EEZ**
SQUALIFORMES									
Dalatiidae									
Isistius brasiliensis (Quoy & Gaimard, 1824)	1	1	1.2	172 (TL)	20.0	PB	100	24.4	
NOTACANTHIFORMES									
Halosauridae									
Aldrovandia sp.*	2	1	1.2	167	3.4	FNR	900	4.3	
ANGUILLIFORMES									
Eurypharyngidae									
Eurypharynx pelecanoides Vaillant, 1882	2	13	4.9	287(99–524)	6.5(1.0–33.9)	FNR	780–900	4.3–4.7	
Nemichthyidae									
Avocettina infans (Günther, 1878)	2	1	1.2	502	2.2	FNR	900	4.3	
Labichthys carinatus Gill & Ryder, 1883	2	2	2.4	397(227–568)	7.0(0.5–13.5)	FNR-PE	680–720	4.9–5.2	
Nemichthys scolopaceus Richardson, 1848	1	7	3.7	290(235–330)	2.9(2.0–4.7)	FNR	105–525	6.8–24.4	
Serrivomeridae									
Serrivomer beanii Gill & Ryder, 1883	2	49	13.4	422(60–592)	14.5(0.5–65.4)	FNR-PB-PE-RN	90–900	4.3–25.1	
Serrivomer lanceolatoides (Schmidt, 1916)	2	1	1.2	413	4.6	FNR	900	4.3	
Stemonidium hypomelas Gilbert, 1905	2	2	2.4	256	6.2(3.4–9.0)	FNR	800–900	4.3–4.7	
ALEPOCEPHALIFORMES									
Platytroctidae									
Platytroctidae sp.*	2	1	1.2	55	0.8	FNR	610	5.6	
Alepocephalidae									
Alepocephalidae sp.*	2	1	1.2	45	0.7	FNR	900	4.3	
Photostylus pycnopterus Beebe, 1933	2	2	2.4	85(75–95)	4.1(2.7–5.5)	FNR	800–900	4.3–4.7	Yes[9]
ARGENTINIFORMES									
Opisthoproctidae									
Opisthoproctus soleatus Vaillant, 1888	2	1	1.2	49	1.0	FNR	385	9.2	Yes[1]
Rhynchohyalus natalensis (Gilchrist & von Bonde, 1924)	2	1	1.2	109	12.3	FNR	800	4.7	Yes[1]
Winteria telescopa Brauer, 1901	2	31	9.8	95(51–118)	6.7(1.3–10.6)	FNR-RN	440–900	4.3–8.5	Yes[1]
Microstomatidae									
Xenophthalmichthys danae Regan, 1925	2	2	2.4	87(60–114)	3.2(2.1–4.3)	FNR	385–505	7.0–9.2	Yes[1]
Bathylagidae									
Dolicholagus longirostris (Maul, 1948)	2	8	7.3	79(41–100)	3.3(1.3–4.8)	FNR	430–900	4.3–8.5	

Melanolagus bericoides (Borodin, 1929)	2	9	3.7	148(128–167)	17.8(11.7–25.8)	FNR	430–900	4.3–8.54	
STOMIIFORMES									
Gonostomatidae									
Bonapartia pedaliota Goode & Bean, 1896	2	184	15.9	57(37–81)	1.2(0.5–4.7)	FNR-PB	130–900	4.3–22.1	Yes[2]
Cyclothone spp.*	1-2	874	28.0	33(12–45)	1.4(0.2–7.4)	FNR-PB-PE-RN	350–1000	4.3–27.6	
Diplophos australis Ozawa, Oda & Ida, 1990	2	3	2.4	81(71–99)	0.8(0.5–1.3)	FNR	780–800	4.6–4.7	
Diplophos taenia Günther, 1873	1-2	25	12.2	71(42–129)	1.9(0.6–4.3)	FNR-PB	25–800	4.7–28.8	
Gonostoma atlanticum Norman, 1930	1-2	67	18.3	51(19–68)	1.8(0.13–7.8)	FNR-PB-PE-RN	100–900	4.3–24.6	
Gonostoma denudatum Rafinesque, 1810	2	1	1.2	122	7.8	FNR	440	8.5	Yes[3]
Manducus maderensis (Johnson, 1890)	2	2	3.7	56(42–65)	1.3(0.7–1.4)	FNR	90–615	5.6–25.1	
Margrethia obtusirostra Jespersen & Tåning, 1919	1	1	1.2	27	3.2	FNR	525	6.8	
Sigmops bathyphilus (Vaillant, 1884)	2	1	1.2	155	17.3	FNR	800	4.7	
Sigmops elongatus (Günther, 1878)	1-2	41	14.6	145(45–250)	13.1(0.5–26.8)	FNR-PB-PE-RN	100–1000	4.3–24.6	
Triplophos hemingi (McArdle, 1901)	2	1	1.2	196	13.5	FNR	800	4.7	Yes[3]
Sternoptychidae									
Argyropelecus aculeatus Valenciennes, 1850	2	51	12.2	56(30–82)	6.1(0.8–20.9)	FNR-PB-PE-RN	100–900	4.3–24.6	
Argyropelecus affinis Garman, 1899	2	439	14.6	52(27–82)	2.7(0.5–6.9)	FNR-PB-RN	30–800	4.6–28.7	
Argyropelecus gigas Norman, 1930	2	9	2.4	86(78–91)	14.2(10.4–17.0)	FNR-RN	610–700	5.2–5.6	
Argyropelecus hemigymnus Cocco, 1829	1-2	80	22.0	24(8–36)	2.4(0.2–4.9)	FNR-PE-RN	260–900	4.3–13.7	
Argyropelecus sladeni Regan, 1908	2	27	11.0	57(32–94)	4.1(0.7–14.2)	FNR	30–800	4.6–28.7	
Maurolicus weitzmani Parin & Kobyliansky, 1993	1	1	1.2	25	1.5	FNR	510	6.0	
Sternoptyx diaphana Hermann, 1781	2	1091	20.7	24(11–43)	2.0(0.4–4.9)	FNR-PB-PE-RN	65–900	4.3–26.5	
Sternoptyx pseudobscura Baird, 1971	2	123	12.2	35(13–59)	2.9(0.5–9.9)	FNR-PB-PE	520–900	4.3–6.3	
Sternoptyx pseudodiaphana Borodulina, 1977	2	3	2.4	49(42–59)	6.9(5.2–9.9)	FNR	800–900	4.4–4.7	
Valenciennellus tripunctulatus (Esmark, 1871)	1-2	19	8.5	24(23–32)	1.6(1.0–2.3)	FNR-PE	360–1000	4.3–10.9	
Phosichthyidae									
Ichthyococcus polli Blache, 1964	1-2	14	9.8	52(41–72)	2.5(1.1–8.4)	FNR-PB	385–900	4.3–9.2	Yes[3]
Phosichthys argenteus Hutton, 1872	2	1	1.2	64	8.1	RN	630	5.6	
Pollichthys mauli (Poll, 1953)	1	1	1.2	38	1.5	RN	75	25.7	
Vinciguerria nimbaria (Jordan & Williams, 1895)	1-2	24	11.0	26(17–49)	2.0(0.4–6.5)	FNR-PB-PE-RN	50–780	4.6–26.6	
Stomiidae									
Aristostomias grimaldii Zugmayer, 1913	2	5	2.4	74(65–86)	3.1(1.8–5.0)	FNR	700–800	4.7–5.26	Yes[3]
Aristostomias tittmanni Welsh, 1923	2	3	3.7	43(32–76)	2.5(2.0–3.5)	FNR-PB	30–800	4.6–28.7	
Astronesthes atlanticus Parin & Boroduli , 1996	1-2	3	3.7	38(31–51)	1.2(0.62–2.0)	FNR-RA	90–525	6.8–25.1	
Astronesthes gudrunae Parin & Boroduli , 2002	2	1	1.2	111	11.1	FNR	610	5.6	Yes[3]
Astronesthes richardsoni (Poey, 1852)	2	7	6.1	71(22–132)	5.7(1.1–13.5)	FNR	25–780	4.6–28.8	
Astronesthes similus Parr, 1927	1-2	10	3.7	43(36–75)	2.9(0.5–4.9)	FNR-PB	100–800	4.7–24.4	
Astronesthes gemmifer Goode & Bean, 1896	2	1	1.2	146	21.6	FNR	430	8.5	
Bathophilus nigerrimus Giglioli, 1882	2	2	2.4	89(84–95)	6.1(5.1–7.2)	FNR	90–610	5.6–25.1	Yes[3]
Bathophilus pawneei Parr, 1927	2	4	3.7	66(30–124)	3.2(1.2–8.7)	FNR	65–440	8.5–26.5	
Borostomias elucens (Brauer, 1906)	2	55	8.5	168(46–299)	48.2(0.5–218.9)	FNR	610–900	4.3–5.6	Yes[3]
Chauliodus sloani Bloch & Schneider, 1801	1-2	348	22.0	162(55–270)	9.6(0.3–53.9)	FNR-PB-PE-RN	430–900	4.3–8.5	
Eustomias bibulbosus Parr, 1927	2	1	1.2	87	0.6	PE	680	5.2	Yes[3]

Eustomias braueri Zugmayer, 1911	2	2	1.2	69(56–82)	1.6(0.6–2.6)	PE	680	5.2	Yes[3]
Eustomias brevibarbatus Parr, 1927	2	6	7.3	97(85–128)	1.8(0.5–4.6)	FNR	90–900	4.3–25.1	
Eustomias enbarbatus Welsh, 1923	2	2	2.4	54(54–55)	2.1(2.1–2.1)	FNR-PE	680–780	4.6–5.2	
Eustomias schmidti Regan & Trewavas, 1930	2	1	1.2	68	4.9	FNR	780	4.6	Yes[3]
Eustomias sp. 1**	2	1	1.2	168	8.2	FNR	800	4.7	Yes[3]
Eustomias sp. 2**	2	1	1.2	120	2.3	FNR	430	8.5	Yes[3]
Eustomias sp. 3**	2	4	2.4	68(49–78)	2.4(1.6–2.8)	FNR	90–720	4.9–25.1	Yes[3]
Eustomias sp. 4**	2	1	1.2	122	2.1	FNR	800	4.7	Yes[3]
Eustomias sp. 5**	2	3	1.2	54(28–98)	0.5(0.4–0.6)	FNR	780	4.6	Yes[3]
Eustomias sp. 6**	2	1	1.2	69	3.2	FNR	780	4.6	Yes[3]
Grammatostomias circularis Morrow, 1959	1	1	1.2	67	1.5	PE	1000	4.3	Yes[3]
Grammatostomias dentatus Goode & Bean, 1896	1	1	1.2	114	3.5	PE	1000	4.3	Yes[3]
Heterophotus ophistoma Regan & Trewavas, 1929	2	8	6.1	205(96–253)	57.9(0.7–107.6)	FNR	430–900	4.3–8.5	
Leptostomias gladiator (Zugmayer, 1911)	2	1	1.2	83	0.9	FNR	780	4.6	Yes[3]
Malacosteus niger Ayres, 1848	2	46	9.8	107(633–181)	8.3(1.4–34.4)	FNR	610–900	4.3–5.6	
Melanostomias sp.**	2	1	1.2	180	11.4	FNR	440	8.5	
Melanostomias spilorhynchus Parr, 1927	1-2	2	2.4	117(50–185)	10.9(2.3–19.6)	FNR-PB	100–780	4.6–24.4	Yes[3]
Melanostomias tentaculatus (Regan & Trewavas, 1930)	1-2	5	4.9	162(48–201)	15.7(2.6–20.7)	FNR-PB-PE	430–1000	4.3–8.5	
Melanostomias biseriatus Regan & Trewavas, 1930	2	2	2.4	103 (29–177)	11.1(4.9–17.2)	FNR-PE	610–680	5.6	Yes[3]
Pachystomias microdon (Günther, 1878)	2	9	8.5	137(39–181)	23.2(2.3–42.5)	FNR	430–900	4.3–8.5	Yes[3]
Photonectes achirus Regan & Trewavas, 1930	2	3	2.4	56(33–79)	3.4(1.2–3.4)	PB-RN	100–800	4.7–24.6	Yes[3]
Photostomias atrox (Alcock, 1890)	2	1	1.2	118	1.0	PE	680	5.2	
Photostomias goodyeari Kenaley & Hartel, 2005	2	1	1.2	64	0.7	FNR	720	4.9	Yes[3]
Stomias danae Ege, 1933	2	1	1.2	95	1.8	PB	800	4.7	
Stomias longibarbatus (Brauer, 1902)	2	5	6.1	281(173–390)	9.7(1.4–25.7)	FNR	260–800	4.7–13.7	
Thysanactis dentex Regan & Trewavas, 1930	1-2	41	19.5	90(43–150)	3.1(0.5–10.6)	FNR-RN	90–900	4.3–25.1	Yes[2]
ATELEOPODIFORMES									
Ateleopodidae									
Ateleopodidae sp.*	2	1	1.2	122	0.6	FNR	800	4.7	
AULOPIFORMES									
Giganturidae									
Gigantura chuni Brauer, 1901	2	3	2.4	111(42–181)	19.4(4.9–33.9)	FNR	610–800	4.7–5.6	Yes[9]
Gigantura indica Brauer, 1901	1-2	31	22.0	102(16–190)	3.9(0.6–11.7)	FNR-PB-PE	50–900	4.3–27.6	
Chlorophthalmidae									
Parasudis truculenta (Goode & Bean, 1896)	1	2	1.2	31(30–33)	3.8(3.2–4.5)	FNR	105	24.4	
Notosudidae									
Ahliesaurus berryi Bertelsen, Krefft & Marshall, 1976	2	1	1.2	198	17.8	FNR	800	4.7	
Scopelarchidae									
Benthalbella infans Zugmayer, 1911	1	1	1.2	57	4.0	RN	560	5.9	Yes[9]
Rosenblattichthys hubbsi Johnson, 1974	2	4	1.2	79(40–100)	4.5(0.5–6.9)	PB	800–800	4.7–4.7	Yes[9]
Scopelarchoides danae Johnson, 1974	2	1	1.2	80	2.3	FNR	780	4.6	
Scopelarchus analis (Brauer, 1902)	1	2	2.4	103(91–115)	7.9(4.7–11.2)	FNR	510–525	6.0–6.8	
Scopelarchus guentheri Alcock, 1896	2	8	6.0	79(38–113)	4.9(0.5–12.2)	FNR-PB-RN	385–900	4.3–9.2	

Evermannellidae								
Odontostomops normalops (Parr, 1928)	2	4	3.7	134(121–166)	11.9(9.9–17.3)	FNR	610–900	4.3–5.6
Paralepididae								
Anotopterus pharao Zugmayer, 1911	1	1	1.2	27	1.0	RN	20	26.7
Lestidiops sp.*	2	2	2.4	80(58–102)	1.6(1.6–1.7)	FNR	110–430	8.5–24.1
Lestrolepis intermedia (Poey, 1868)	2	1	1.2	–	5.7	FNR	90	25.1
Macroparalepis brevis Ege, 1933	2	1	1.2	72	6.6	FNR	800	4,7
Stemonosudis gracilis (Ege, 1933)	2	1	1.2	217	3.9	FNR	100	24.6
Stemonosudis intermedia (Ege, 1933)	1-2	4	3.7	130(71–205)	1.1(0.5–2.26)	FNR-PB	50–900	4.3–27.6
Alepisauridae								
Omosudis lowii Günther, 1887	2	10	7.3	82(39–212)	7.2(0.5–38.6)	FNR	385–900	4.3–9.2
MYCTOPHIFORMES								
Neoscopelidae								
Scopelengys tristis Alcock, 1890	2	2	2.4	121(98–145)	12.5(5.34–19.71)	FNR	780–800	4.6–4.71
Myctophidae								
Benthosema suborbitale (Gilbert, 1913)	1-2	20	8.5	24(13–31)	1.7(0.21–3.3)	FNR-PB-RN	30–440	8.5–28.7
Bolinichthys distofax Johnson, 1975	2	85	11.0	62(32–91)	6.4(0.5–23.8)	FNR-PB-PE-RN	430–900	4.3–8.5
Bolinichthys photothorax (Parr, 1928)	1-2	55	13.4	53(22–67)	5.8(0.51–27.8)	FNR-PB	510–900	4.3–6.0
Bolinichthys supralateralis (Parr, 1928)	2	4	3.7	75(50–92)	10.2(6.6–16.3)	FNR	720–900	4.3–4.9
Ceratoscopelus warmingii (Lütken, 1892)	1-2	41	20.7	50(18–74)	2.6(0.5–6.2)	FNR-RN	30–900	4.3–28.7
Dasyscopelus asperum (Richardson 1845)	1-2	53	13.4	58(14–75)	3.8(0.9–7.1)	FNR-PE-RN	25–900	4.3–28.8
Dasyscopelus obtusirostre (Tåning, 1928)	1-2	17	9.8	66(25–84)	5.0(0.6–7.8)	FNR-PB-PE-RN	30–800	4.7–28.7
Dasyscopelus selenops (Tåning, 1928)	2	2	3.7	45(27–59)	2.5(2.2–2.8)	FNR-PE	430–900	4.3–8.5
Diaphus bertelseni Nafpaktitis, 1966	2	2	2.4	84(74–94)	8.0(6.8–9.3)	FNR-RN	100–385	9.2–24.7
Diaphus brachycephalus Tåning, 1928	1-2	470	29.3	38(09–58)	1.5(0.5–17)	FNR-PE-RN	30–1000	4.3–28.7
Diaphus dumerilii (Bleeker, 1856)	1-2	114	24.4	45(26–59)	2.4(0.5–11)	FNR-PB-PE-RN	65–900	4.3–26.5
Diaphus fragilis Tåning, 1928	1-2	147	24.4	49(14–86)	2.6(0.4–11.7)	FNR-PB-PE-RN	65–900	4.3–26.5
Diaphus garmani Gilbert, 1906	1-2	137	11.0	41(25–51)	2.6(0.5–9.9)	FNR-PE-RN	65–900	4.3–26.5
Diaphus holti Tåning, 1918	2	1	1.2	20	1.0	FNR	385	9.2
Diaphus lucidus (Goode & Bean, 1896)	2	43	11.0	76(31–96)	5.3(1.3–9.7)	FNR-PB-PE-RN	25–800	4.7–28.8
Diaphus mollis Tåning, 1928	1-2	52	20.7	48(15–59)	1.9(0.2–4.0)	FNR-RN	105–900	4.3–24.4
Diaphus perspicillatus (Ogilby, 1898)	1-2	279	20.7	49(18–69)	2.1(0.5–4.9)	FNR-PB-PE-RN	65–900	4.3–26.5
Diaphus problematicus Parr, 1928	1-2	4	3.7	69(52–77)	4.1(1.7–5.8)	FNR-RA	430–720	4.9–8.5
Diaphus splendidus (Brauer, 1904)	1-2	241	18.3	53(20–85)	2.3(0.5–6.6)	FNR-PB-PE-RN	100–900	4.3–24.6
Diogenichthys atlanticus (Tåning, 1928)	1	9	3.7	18(15–23)	0.5(0.2–1.0)	FNR	60–525	6.0–26.6
Electrona risso (Cocco, 1829)	2	76	17.1	66(50–81)	7.4(3.2–12.4)	FNR-PB-RN	385–900	4.3–9.2
Hygophum hygomii (Lütken, 1892)	2	2	1.2	53(52–54)	2.2(1.9–2.4)	FNR	800	4.7
Hygophum macrochir (Günther, 1864)	1-2	28	8.5	50(34–60)	1.9(0.5–8.0)	FNR-PB	30–800	4.6–28.7
Hygophum reinhardtii (Lütken, 1892)	1-2	5	3.7	51(24–76)	2.5(1.2–6.8)	FNR	30–150	20.0–28.7
Hygophum taaningi Becker, 1965	1-2	108	12.2	51(26–66)	1.9(0.9–3.1)	FNR-RN	90–900	4.3–25.1
Lampadena anomala Parr, 1928	1-2	4	2.4	72(35–176)	10.0(2.7–28.9)	FNR	525–610	5.6–6.8
Lampadena chavesi Collett, 1905	1	1	1.2	42	9.0	PE	1000	4.3
Lampadena luminosa (Garman, 1899)	1-2	29	4.9	28(19–51)	2.2(0.5–5.4)	FNR-PB-RN	100–900	4.3–24.6

Lampadena notialis Nafpaktitis & Paxton, 1968	2	1	1.2	20	0.7	FNR	65	26.5	
Lampanyctus alatus Goode & Bean, 1896	2	2	1.2	37(37–38)	3.5(2.9–4.2)	FNR	430	8.5	
Lampanyctus lineatus (Tåning, 1928)	1-2	5	4.9	137(26–178)	19.0(0.63–29.46)	FNR-PB	50–900	4.3–26.5	
Lampanyctus festivus Tåning, 1928	2	4	1.2	87(56–120)	6.8(1.3–13.7)	FNR	900	4.3	
Lampanyctus tenuiformis (Brauer, 1906)	2	26	9.8	111(44–149)	16.0(0.7–46.4)	FNR-PE-RN	25–900	4.3–28.8	
Lepidophanes guentheri (Goode & Bean, 1896)	1-2	219	29.3	48(22–62)	3.6(0.5–9.9)	FNR-PB-PE-RN	25–1000	4.3–28.8	
Myctophum nitidulum Garman, 1899	1-2	12	11.0	59(38–70)	3.6(1.8–5.1)	FNR-PB-RN	30–800	4.7–28.7	
Notolychnus valdiviae (Brauer, 1904)	1	28	4.9	20(17–24)	0.4(0.2–0.5)	FNR	130–537	6.0–15.7	
Notoscopelus resplendens (Richardson, 1845)	2	2	2.4	75(67–84)	3.1(2.7–3.5)	FNR	430–780	4.6–8.54	
Taaningichthys bathyphilus (Tåning, 1928)	2	10	4.9	62(54–71)	1.7(1.1–2.8)	FNR	720–900	4.3–4.98	
LAMPRIFORMES									
Lophotidae									
Eumecichthys fiski (Günther, 1890)	2	1	1.2	1880	2190.0	FNR	780	4.6	
Trachipteridae									
Desmodema polystictum (Ogilby, 1898)	2	1	1.2	74	1	FNR	800	4.7	
Trachipterus cf. *jacksonensis* (Ramsay, 1881)	2	5	6.1	36(18–55)	3.1(0.1–7.0)	FNR-PE-RN	100–510	6.0–24.4	
Zu cristatus (Bonelli, 1819)	1-2	9	11.0	57(10–89)	14.7(0.1–93.1)	FNR-RN	20–720	4.9–26.7	Yes[9]
STYLEPHORIFORMES									
Stylephoridae									
Stylephorus chordatus Shaw, 1791	1-2	64	18.3	176(59–279)	3.7(0.5–11.0)	FNR-PB-RN	25–900	4.3–28.8	Yes[9]
GADIFORMES									
Melanonidae									
Melanonus zugmayeri Norman, 1930	2	21	11.0	115(64–265)	11.6(1.0–11.9)	FNR	95–900	4.3–24.7	
Macrouridae									
Bathygadus sp.*	2	2	1.2	76(72–81)	–	FNR	900	4.3	
Macrouroides inflaticeps Smith & Radcliffe, 1912	2	2	2.4	197(179–215)	91.4(67.4–115.4)	FNR	800–900	4.3–4.7	
Bregmacerotidae									
Bregmaceros cf. *atlanticus* Goode & Bean, 1886	1-2	20	7.3	65(32–85)	1.9(0.5–4.4)	FNR-RN	90–800	4.7–25.1	
TRACHICHTHYIFORMES									
Anoplogastridae									
Anoplogaster cornuta (Valenciennes, 1833)	2	4	3.7	100(85–107)	31.2(18.3–43.4)	FNR-RN	610–800	4.7–5.6	
Diretmidae									
Diretmoides pauciradiatus (Woods, 1973)	1-2	23	8.5	26(4–62)	3.4(0.5–8.5)	FNR	85–900	4.3–25.4	
Diretmus argenteus Johnson, 1864	2	116	13.4	53(14–75)	8.1(0.6–67.4)	FNR	430–900	4.3–8.5	
Trachichthyidae									
Aulotrachichthys argyrophanus (Woods, 1961)	2	6	3.7	28(24–34)	1.2(0.7–1.5)	FNR	230–780	4.6–12.4	
BERYCIFORMES									
Rondeletiidae									
Rondeletia loricata Abe & Hotta, 1963	1-2	3	3.7	53(34–78)	4.8(1.2–10.4)	FNR	525–900	4.3–6.8	
Cetomimidae									
Cetomimus sp.*	2	2	2.4	70(69–72)	1.8(1.5–2.1)	FNR-PE	680–780	4.6–5.2	Yes[4]
Cetostoma regani Zugmayer, 1914	1-2	5	4.9	97(83–130)	5.8(1.6–18.4)	FNR	525–900	4.3–6.8	
Ditropichthys storeri (Goode & Bean, 1895)	2	1	1.2	49	1.5	FNR	610	5.6	Yes[4]

Gyrinomimus bruuni Rofen, 1959	2	2	1.2	62(59–66)	8.6(1.2–16.1)	FNR	900–900	4.3–4.3	Yes[4]
Melamphaidae									
Melamphaes eulepis Ebeling, 1962	2	10	4.9	43(35–47)	20.3(10.8–24.6)	FNR	430–900	4.3–8.5	Yes[4]
Melamphaes leprus Ebeling, 1962	2	1	1.2	88	14.0	FNR	430	8.5	Yes[4]
Melamphaes longivelis Parr, 1933	2	2	2.4	75(75–76)	46.8(8.0–85.7)	FNR	630–780	4.6–5.6	Yes[4]
Melamphaes polylepis Ebeling, 1962	2	37	9.8	61(36–69)	34.1(2.0–60.0)	FNR-PE	610–900	4.3–5.6	
Melamphaes sp.**	2	1	1.2	62	43.9	FNR	900	4.3	
Melamphaes typhlops (Lowe, 1843)	2	7	7.3	61(37–70)	31.6(1.0–60.8)	FNR-PE	430–900	4.3–8.5	Yes[4]
Poromitra megalops (Lütken, 1878)	1-2	27	9.8	46(25–59)	1.78(0.5–4.2)	FNR-RN	525–900	4.3–6.8	
Poromitra sp.**	1-2	28	11.0	80(49–124)	10.6(1.3–37.3)	FNR-PE-RN	430–1000	4.3–8.5	Yes[4]
Scopeloberyx opercularis Zugmayer, 1911	2	1	1.2	32	3.9	FNR	780	4.6	Yes[4]
Scopeloberyx opisthopterus (Parr, 1933)	2	4	3.7	29(25–32)	2.7(1.9–3.6)	FNR	720–800	4.7–4.9	
Scopelogadus mizolepis (Günther, 1878)	1-2	19	9.8	46(30–70)	9.8(0.8–39.1)	FNR	430–900	4.3–8.5	
OPHIDIIFORMES									
Bythitidae									
Bythitidae sp.*	2	2	2.4	87(86–89)	2.7(2.6–2.8)	FNR-PE	680–900	4.3–5.26	
KUTIFORMES									
Apogonidae									
Paroncheilus affinis (Poey, 1875)	1	1	1.2	28	4.2	RN	75	25,6	
PERCIFORMES									
Howellidae									
Bathysphyraenops simplex Parr, 1933	1	3	3.7	65(41–78)	7.5(5.0–9.0)	FNR	525–900	4.3–6.8	Yes[5]
Howella atlantica Post & Quéro, 1991	2	25	8.5	58(52–69)	4.0(2.6–6.5)	FNR-PE	680–900	4.3–5.2	
Bramidae									
Brama brama (Bonaterre, 1788)	2	1	1.2	28	1.0	FNR	900	4.3	
Brama caribbea Mead, 1972	1-2	64	15.9	25(12–55)	2.0(0.4–9.8)	FNR-PE-RN	58–900	4.3–26.6	
Taractichthys longipinnis (Lowe, 1843)	2	1	1.2	32	1.3	PE	240	14.8	
Caristiidae									
Paracaristius nudarcus Stevenson & Kenaley, 2011	2	1	1.2	175	181	FNR	430	8.5	Yes[6]
Platyberyx andriashevi (Kukuev, Parin & Trunov, 2012)	2	3	2.4	68(24–149)	31.2(1.1–87.8)	FNR	230–800	4.7–12.4	Yes[6]
Platyberyx paucus Stevenson & Kenaley, 2013	2	3	3.7	95(92–98)	33.4(31.1–36.7)	FNR-RN	630–800	4.7–5.6	Yes[6]
Platyberyx pietschi Stevenson & Kenaley, 2013	2	1	1.2	74	9.2	RN	630	5.6	Yes[6]
SCOMBROLABRACIFORMES									
Scombrolabracidae									
Scombrolabrax heterolepis Roule, 1921	2	1	1.2	76	6.1	FNR	900	4.3	
SCOMBRIFORMES									
Gempylidae									
Gempylus serpens Cuvier, 1829	1-2	3	3.7	68(44–112)	1.1(0.9–1.3)	FNR	70–900	4.3–25.8	
Lepidocybium flavobrunneum (Smith, 1843)	1	1	1.2	36	4.1	FNR	110	24.0	
Nesiarchus nasutus Johnson, 1862	2	4	3.7	107(85–145)	1.7(0.7–2.8)	FNR	90–800	4.7–25.1	
Promethichthys prometheus (Cuvier, 1832)	1	15	1.2	154(112–191)	20.2(15.0–34.0)	FNR	150	20.6	
Nomeidae									
Cubiceps pauciradiatus Günther, 1872	2	10	7.3	91(75–129)	13.2(6.7–30.3)	FNR	65–720	4.9–26.5	

Psenes cyanophrys Valenciennes, 1833	1-2	5	3.7	86(14–133)	38.9(8.9–70.2)	FNR	25–570	6.3–28.8	
Trichiuridae									
Aphanopus intermedius Parin, 1983	2	1	1.2	720	550	FNR	610	5.7	Yes[7]
TRACHINIFORMES									
Chiasmodontidae									
Kali kerberti (Weber, 1913)	2	1	1.2	156	16.2	FNR	800	4.7	
Chiasmodon braueri Weber, 1913	2	2	1.2	82(70–95)	2.9(2.2–3.7)	FNR	900	4.3	
Chiasmodon niger Johnson, 1864	2	1	1.2	90	7.9	FNR	800	4.7	Yes[9]
Kali kerberti (Weber, 1913)	2	5	4.9	127(69–170)	11.8(1.1–29.3)	FNR	720–800	4.6–4.9	
Pseudoscopelus cordilluminatus Melo, 2010	2	2	2.4	44(31–57)	3.3(2.2–4.3)	FNR-PE	240–800	4.7–14.8	Yes[9]
Pseudoscopelus scutatus Krefft, 1971	2	2	2.4	71(67–75)	2.3(2.0–2.7)	FNR	430–900	4.3–8.5	
SCORPAENIFORMES									
Setarchidae									
Ectreposebastes imus Garman, 1899	2	27	4.9	167(29–234)	144.0(0.8–290.3)	FNR	90–800	4.7–25.1	
CAPROIFORMES									
Caproidae									
Antigonia capros Lowe, 1843	2	1	1.2	29	1.9	FNR	440	8.5	
Antigonia combatia Berry & Rathjen, 1959	2	1	1.2	38	2.7	FNR	800	4.7	
LOPHIIFORMES									
Caulophrynidae									
Caulophryne sp.*	1	1	1.2	60	0.2	FNR	100	24.5	Yes[8]
Melanocetidae									
Melanocetus johnsonii Günther, 1864	1-2	5	4.9	16(14–19)	1.6(0.7–3.3)	FNR	58–900	4.3–26.6	
Himantolophidae									
Himantolophus sp.*	1-2	13	12.2	23(5–37)	1.6(0.5–5.3)	FNR-PE	85–800	4.6–25.4	
Oneirodidae									
Chaenophryne draco Beebe, 1932	2	2	2.4	72(55–90)	60.3(12.0–108.7)	FNR-PE	680–900	4.3–5.2	
Chaenophryne ramifera Regan & Trewavas, 1932	2	4	4.9	41(32–50)	3.6(2.5–6.2)	FNR	505–800	4.7–7.0	Yes[8]
Dolopichthys sp.*	2	1	1.2	35	0.7	FNR	900–900	4,3	Yes[8]
Oneirodes anisacanthus (Regan, 1925)	2	2	2.4	39(30–48)	3.0(1.1–4.9)	FNR	505–900	4.3–7.0	Yes[8]
Oneirodes carlsbergi (Regan & Trewavas, 1932)	2	2	2.4	59(21–98)	32.6(0.4–64.8)	FNR-PE	680–720	4.9–5.2	Yes[8]
Thaumatichthyidae									
Thaumatichthys sp.*	2	1	1.2	32	–	FNR	900	4.3	Yes[8]
Ceratiidae									
Ceratias uranoscopus Murray, 1877	2	1	1.2	76	8.1	FNR	800	4.7	
Gigantactinidae									
Gigantactis watermani Bertelsen, Pietsch & Lavenberg, 1981	2	1	1.2	17	45.1	FNR	800	4.7	Yes[8]
Rhynchactis sp.*	2	2	2.4	81(42–120)	6.7(4.0–9.4)	FNR-RN	720–780	4.6–4.9	Yes[8]

* Specimen(s) damaged. ** Potential new species. [1] Mincarone et al. (2021a), [2]Eduardo et al. (2018a), [3] Villarins et al. (2021), [4] Afonso et al. (2021), [5] Eduardo et al. (2019), [6]Mincarone et al. (2019), [7]Eduardo et al. (2018b), [8]Mincarone et al. (2021b).

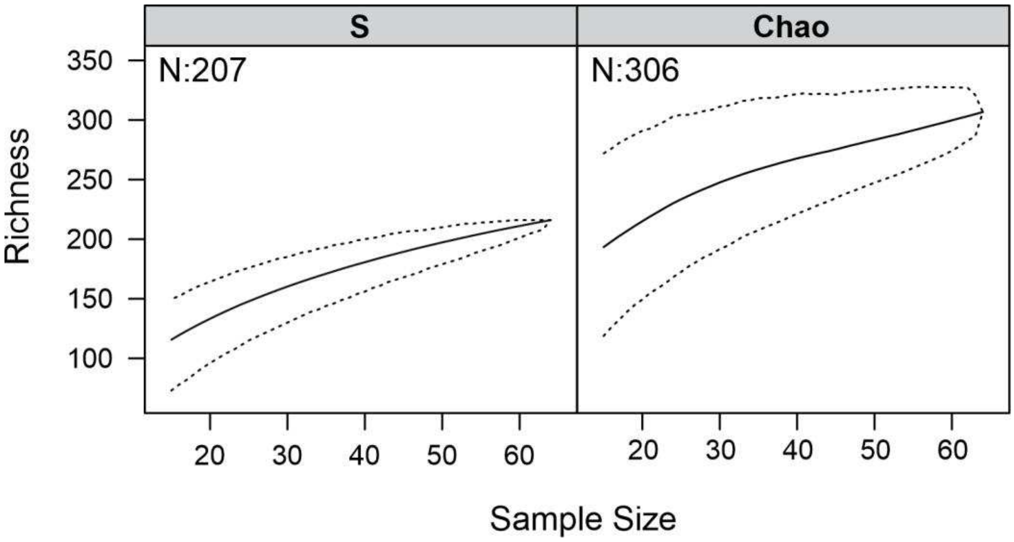

Figure 2. Species accumulation (S) and Chao1 estimator for ABRACOS 1 and 2 together. Dashed lines represent the confidence interval of 95%.

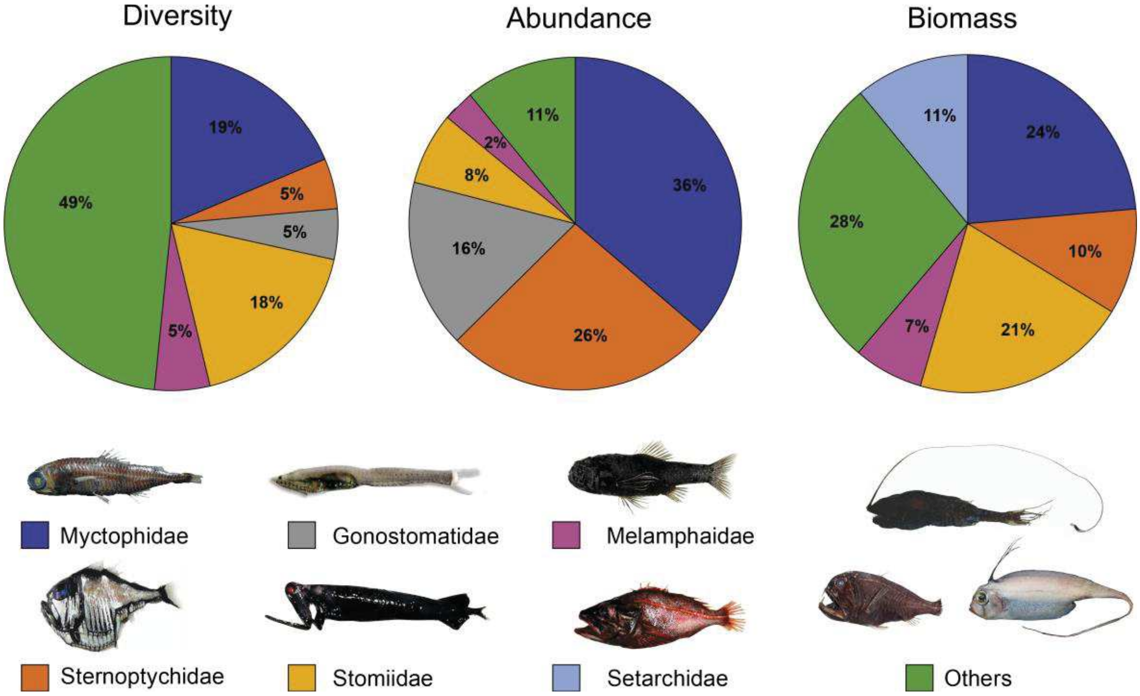

Figure 3. Main mesopelagic fish families when considering diversity, abundance, and biomass. Fish images represent only examples of species included in the group.

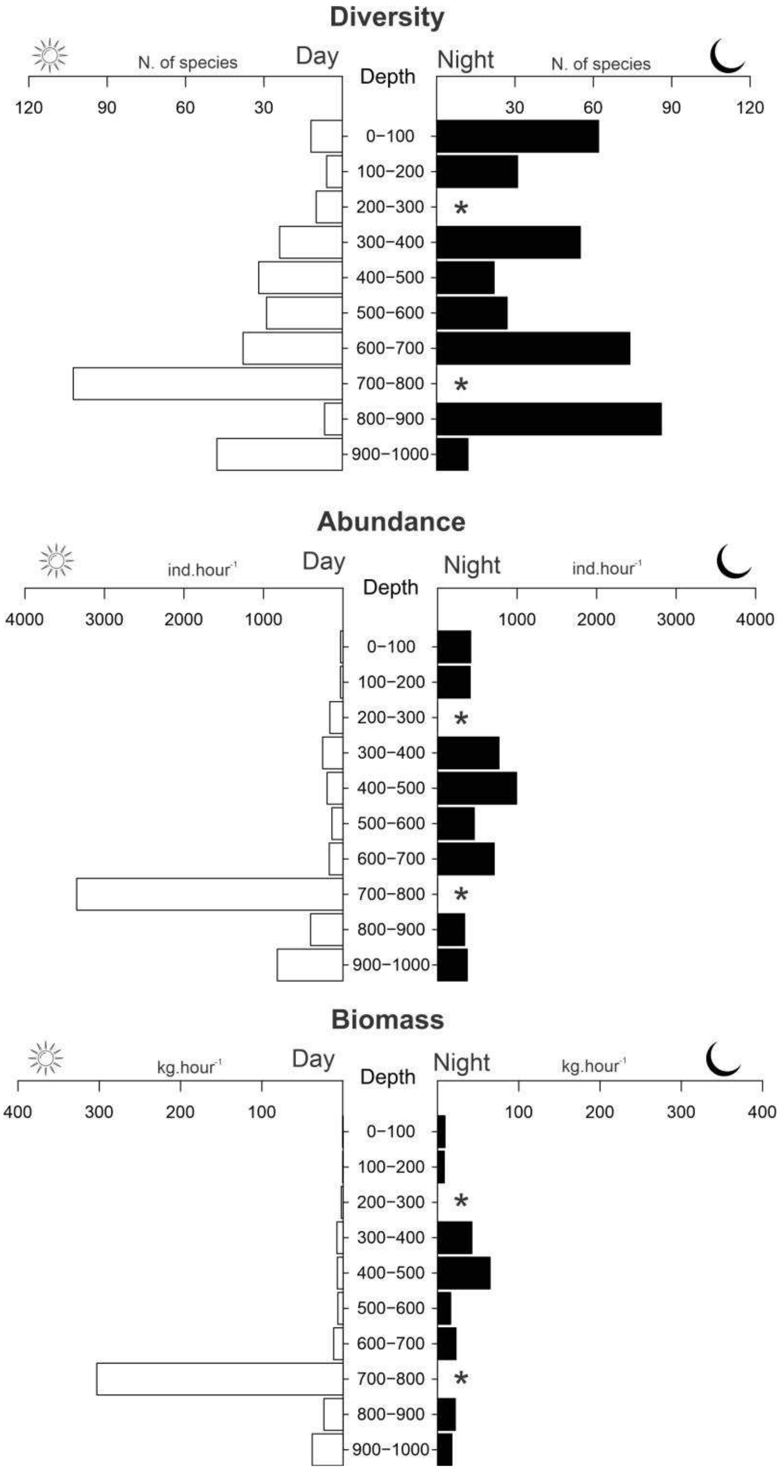

Figure 4. Number of species and average values of abudance (individuals.hour^{-1}) and biomass (individuals.hour^{-1}) of mesopelagic species of fishes collected on the survey ABRACOS 2. * Depth strata not sampled.

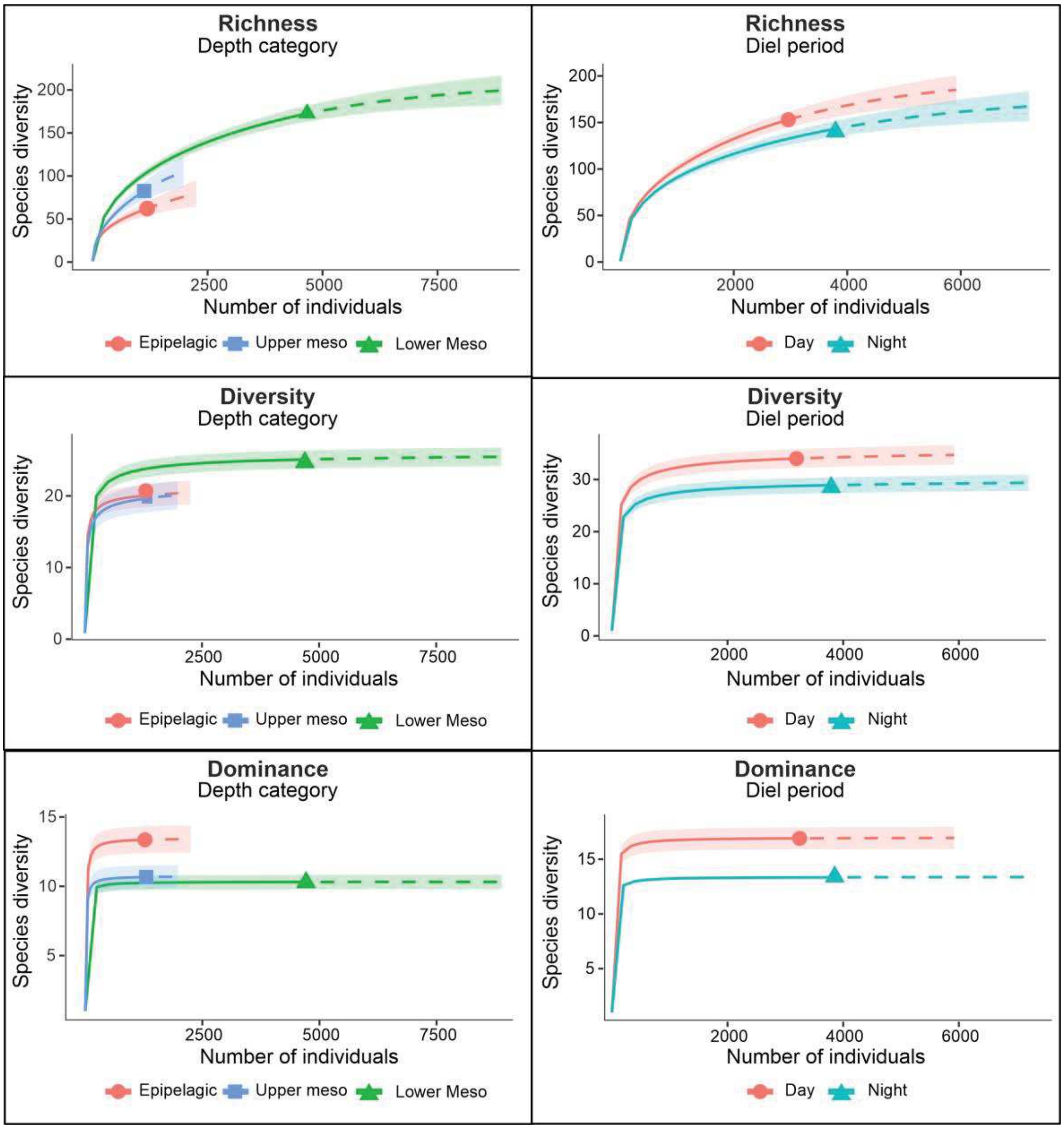

Figure 5. Sample-size-based rarefaction (solid line segment) and extrapolation (dotted line segments) sampling curves for species richness, diversity, and dominance of mesopelagic fish data at the different depth category and diel periods. Curves include the confidence intervals of 95% (shaded areas). For this analysis, only species recorded in the ABRACOS 2 survey were considered.

Discussion

Diversity and distribution

Our data indicate the occurrence of at least 207 mesopelagic species of fishes in the southwestern Tropical Atlantic (STWA), more specifically in the region considered in the study. Results also indicate that about 75 additional species could have been collected if sampling efforts were increased. The taxonomically diverse pool of mesopelagic species recorded in the region also reveals a vast array of diversity not only in terms of number of species but also in terms of size, anatomy, and behaviour. The Tropical and West Equatorial Atlantic, which is the larger area encompassing the STWA, was not highlighted by the high diversity of mesopelagic species, as it was the Gulf of Mexico in a recent global biogeographic classification of the mesopelagic zone (Sutton et al., 2017). However, the mesopelagic species richness revealed by our study is higher than those reported of other parts of the world, such as in the Mediterranean Sea (25 spp.; Olivar et al., 2012), central Equatorial Pacific (113 spp.; Barnett, 1984), southwestern Indian Ocean (121 spp.; Cherel et al., 2020), eastern Equatorial Atlantic (132 spp.; Olivar et al., 2017), and South China Sea (169 spp.; Wang et al., 2019). The species richness of mesopelagic fishes in the STWA is actually more similar to that reported for the North Pacific (228 spp.; Barnett, 1984) and the Gulf of Mexico (approximately 300 spp.; Sutton et al., 2020), which are considered as some of the most speciose deep-sea ichthyofaunas of the world (Sutton et al., 2017). Major factors driving deep-sea biodiversity, such as climate, seabed structure, and water masses, might indeed be responsible for the variation in species richness of different parts of the world, but an asymmetry in sampling effort is certainly affecting values recorded so far. In the Gulf of Mexico, for instance, a much higher sampling effort has been deployed to assess the deep-sea diversity when compared with most regions of the world, with several expeditions conducted since 2010 (Sutton et al., 2020). That situation is in striking contrast to the STWA, where only a handful of expeditions aimed at assessing the deep-sea diversity have been conducted in the last centuries.

The relatively high number of mesopelagic species of fishes recorded in the SWTA is likely related to the diversity of habitats and the high variability of oceanographic processes present in the region. Despite being located in an oligotrophic portion of the ocean, the SWTA is also characterised by the presence of underwater canyons, oceanic islands, and several seamounts that interact with local currents and enhance marine productivity (Travassos et al., 1999; Tchamabi et al., 2017; Silva et al., 2021). As an example, small upwelling processes have been reported along the shelf-break and oceanic islands of the region (Travassos et al., 1999; MMA, 2006; Tchamabi et al., 2017), a situation that has been directly associated with the occurrence of hotspots of fish biodiversity (Hazin, 1993; Eduardo et al., 2018, 2020a). Distinct biogeographic provinces, with different thermodynamic features, current systems and water mass properties, are also present in the SWTA (Bourlès et al., 1999; Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021; Tosetto et al., 2021). This results in a higher complexity of habitats and oceanographic conditions that likely contribute to higher levels of species diversity (Levin et al., 2001).

The highest levels of richness and diversity were found at lower mesopelagic depths (500–1000 m), with several species collected only at these depths (e.g., species of the Beryciformes and Lophiiformes). Interestingly, many of these species are considered bathypelagic and/or benthopelagic (Priede, 2017; Melo et al., 2020). The collection of those species in mesopelagic waters is likely related to the presence of seamounts and oceanic islands in the study area. In addition to being related with an increase in habitat complexity, seamounts may increase the occurrence of pelagic and benthic predators that actively seek these areas to hunt for prey trapped by flow-topographic processes (Cascão et al., 2019). For instance, in the Azorean seamounts plateau, the micronekton community is dominated by non- or weakly migratory benthopelagic fishes (Cascão et al., 2019). Summing up, our results also seem to indicate that seamounts play a significant role in the biodiversity structuring and ecology of mesopelagic fishes in the SWTA.

The two surveys conducted during this study (AB1 and Ab2) resulted in different patterns of species richness. For example, 17 species were exclusively documented in AB1 (mesopelagic trawl), whereas 136 species were solely recorded in AB2 (micronekton trawl). The two campaigns were conducted in different seasons, but the significant disparity in species richness between the two collections is clearly related to differences in sampling strategies. The use of multiple sampling gears is vital to maximising the representation of fish diversity (Magurran, 2004), especially in the deep-sea. However, in the context of this study, the sampling strategy used in AB2, which included the use of larger gear, with greater mesh sizes, deeper hauls, and broader sampling area, resulted in the collection of a higher number of specimens of different species in a broader size range (Supplementary Material S3).

In terms of taxonomic composition, five families of the Teleostei accounted for 52% of the species richness, 90% of the specimens collected, and 72% of the total biomass: the Myctophidae (38 spp.; 36% of the specimens, 24% of the biomass), Stomiidae (38 spp.; 8%, 21%), Gonostomatidae (11 spp.; 16%, 4%) Melamphaidae (11 spp.; 2%, 7%), and Sternoptychidae (10 spp.; 24%, 10%). These families, therefore, seem to be the most representative in the mesopelagic fish fauna of the SWTA. The dominance of these families in mesopelagic waters has also been noted in other parts of the world (e.g., Gjøsaeter and Kawaguchi, 1980b; Fock et al 2004; Olivar et al., 2017; Wang et al., 2019a; Cherel et al., 2020). A strong pattern of dominance was also observed within these families, with few species accounting for 50% of the total number of specimens: *Sternoptyx diaphana* (14%), *Cyclothone* spp. (11%), *Diaphus brachycephalus* (6%), *Argyropelecus affinis* (6%), *Chauliodus sloani* (5%), *Lampanyctus nobilis* (4%), and *Diaphus perspicillatus* (4%). The pattern of dominance at the species level detected in the SWTA was, however, distinct from those of other parts of the world. In the eastern Tropical Atlantic, for instance, the lanternfishes *B. suborbitale*, *C. warmingii*, and *H. macrochir* were dominant (Olivar et al., 2017), whereas these same species were considered rare in our study. The viperfish *C. sloani* is usually globally recorded in low abundances (e.g., Olivar et al., 2017; Wang et al., 2019a; Cherel et al., 2020); whereas, the species is among the most relevant mesopelagic species in the SWTA considering the abundance and total weight (Eduardo et al., 2020c). These differences in the pattern of dominance in different regions of the world at the species level are likely associated with differences in oceanographic and biogeographic features (e.g., seabed structure, water masses, and hydrographic fronts), which are major factors driving the structure and composition of mesopelagic assemblages (Hulley and Krefft, 1985; Olivar et al., 2017; Cascão et al., 2019). *Cyclotone* is another seemingly abundant genus of mesopelagic fish in the SWTA (Olivar, et al., 2017). Nine species of the genus were reported for the SWTA: *C. acclinidens*, *C. alba*, *C. braueri*, *C. microdon*, *C. obscura*, *C. pallida*, *C. pseudopallida*, *C. parapallida*, and *C. signata* (Villarins et al., 2021). The sampling gears employed in the study, however, seemed to be only partially adequate to collect representatives of the genus. In several trawls we observed onboard that a substantial number of specimens of *Cyclothone* escaped back into the sea during the hoisting of the net. Additionally, given their poor condition of preservation, specimens of the genus could not be identified to species. Therefore, the abundance of species of *Cyclothone* presented here is likely underestimated.

Notable records

Among the 207 species of mesopelagic fishes recorded during the ABRACOS expeditions, 62 (30%) represent new records for Brazilian waters, all of which have been dealt with in a series of recent papers (Table 1). Among these 62 new records, nine (six *Eustomias*, one *Melanostomias*, one *Melamphaes*, and one *Poromitra*) potentially represent new species that will be described in future studies. Several species recorded here are also rare worldwide, and their occurrence in the SWTA adds new information on their global distribution. For instance, three specimens of *Platyberyx paucus* and one of *Platyberyx pietschi* were collected during the AB2. Before these records, only four specimens of *P. paucus* were known, from the central North Pacific and western Central Atlantic. *Platyberyx pietschi*, in turn, was known based on just two specimens from the western Central Atlantic, one specimen from the central Pacific, and one from the western South Pacific (Stevenson & Kenaley, 2013; Mincarone et al., 2019). Other species considered rare worldwide that were collected in the ABRACOS expeditions are *Rhynchohyalus natalensis*, *Eumecichthys fiski*, *Macrouroides inflaticeps*, *Pseudoscopelus cordilluminatus*, *Melamphaes leprus*, and *Gigantactis watermani* (Afonso et al., 2021; Mincarone et al., 2021a; Mincarone et al., 2021b).

Conclusion

The relatively high level of species diversity of mesopelagic fishes detected in the ABRACOS expeditions reveal a variety of multiscale ecological niches, implying the existence of different mechanisms to avoid competition (Eduardo et al., 2020a; Eduardo et al., *under review*). Summing up with information provided here, new approaches on the diversity, ecology, and ecosystem processes of the deep-sea are possible.

The outstanding number of new records reflect not only the high diversity of the SWTA but also the lack of scientific information on deep-sea fishes in the region, as noted previously (e.g., Reis et al., 2016). The roadmap for the United Nations Decade of Ocean Science recognises the deep-sea as a frontier of science and discovery (Ryabinin et al., 2019). There is an unequal capacity to conduct science among nations, with developing economies facing substantial barriers to participating in deep-sea research. Consequently, when the Exclusive Economic Zones are considered, the least-studied parts of the deep-sea are located off the least economically developed countries (Howell et al., 2020). These biases are highlighted by the fact that the surveys described here were financed by a

French research institution, and that those expeditions are among the very few that have addressed the mesopelagic ichthyofauna of Brazil. To achieve sustainability, we need a well-known and predictable ocean. Only by thinking globally and strengthening international cooperation will we develop an ocean research that corrects asymmetry in funding and knowledge among countries, meeting the crucial need for a more encompassing deep-sea knowledge aimed at the conservation and sustainable use of its unique habitats.

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BRIEF COMMUNICATION

First record of the intermediate scabbardfish *Aphanopus intermedius* (Scombriformes: Trichiuridae) in the western South Atlantic Ocean

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This study reports on the first record of the intermediate scabbardfish *Aphanopus intermedius* in the western South Atlantic Ocean, based on a single specimen 725 mm standard length collected between 0 and 610 m depth around Rocas Atoll off north-eastern Brazil. Measurements and counts are provided and compared with those available in the literature.

KEYWORDS

Brazil, deep-sea fish, Rocas Atoll, scabbardfish, western South Atlantic Ocean

Fishes of the family Trichiuridae are mainly distributed in tropical and temperate seas from 50 to 1,500 m depth (rarely 2,300 m), with many species exhibiting diel vertical migrations (Nakamura & Parin, 1993). Species of this family are commonly known as cutlassfishes, hairtails, or scabbardfishes and make up a large fishery worldwide, with total landings of around 3.36 Mt in 2016 (FAO, 2018). Currently, there are *c.* 47 valid species of Trichiuridae (Eschmeyer *et al.*, 2018), of which at least six species have been reported in Brazilian waters (Costa *et al.*, 2007; Menezes, 2003).

Among trichiurids, representatives of the deep-sea genus *Aphanopus* Lowe 1839 have been caught by commercial fisheries in the north-east Atlantic Ocean for more than 200 years, probably representing the oldest deep longline commercial fishery in the world (Maul, 1950). Owing to the growing commercial importance of the fisheries of deep-water species, there is an increasing number of studies addressing the distribution, ecology and populational parameters of scabbardfish species (Delgado *et al.*, 2013). For a long time, the black scabbardfish *Aphanopus carbo* Lowe 1839 was the only recognized species in this genus. In 1983, the second valid species, the intermediate scabbardfish *Aphanopus intermedius* Parin 1983, was described and currently the genus comprises seven species distributed almost worldwide (Biscoito *et al.*, 2011; Parin, 1983, 1994). Among these species, *A. intermedius* and *A. carbo* are the most important for fisheries, contributing to total annual landings of 10,500 t in 2016 (FAO, 2018). Both species are benthopelagic, almost sympatric and difficult to distinguish, as separation using meristic and morphological characteristics is only possible through multivariate analysis and by counting the number of vertebrae and dorsal-fin elements (Biscoito *et al.*, 2011; Delgado *et al.*, 2013). Discrimination between these closely related species has also been tested using molecular techniques (Biscoito *et al.*, 2011; Stefanni *et al.*, 2009). The distribution of *A. intermedius* was thought to be wider in the past, with records in the Atlantic and Pacific Oceans (Nakamura & Parin, 1993). However, this view was changed after a taxonomic revision by Parin (1994) and currently the species is only known from the tropical and subtropical Atlantic Ocean, except off the coast of South America (Biscoito *et al.*, 2011; Parin, 1994; Parin & Nakamura, 2016). The purpose of this study is to report the first occurrence of *A. intermedius* in the western South Atlantic Ocean, based on the collection of a single specimen around Rocas Atoll (3.8668 °S, 33.8020 °W), off north-eastern Brazil. The material examined is part of a large collection of mesopelagic fishes and invertebrates sampled during the ABRACOS expeditions (Acoustics along the BRAzilian COaSt), conducted by the French R.V. *Antea* off north-eastern Brazil, including Rocas Atoll, Fernando de Noronha Archipelago and sea-mounts off Rio Grande do Norte, in September–October 2015 and April–May 2017.

The extensive survey of the area with 80 fishing stations from 0 to 1,113 m depth resulted in the collection of only one specimen of *A. intermedius* (725 mm standard length, L_S; Figure 1) caught around Rocas Atoll, from 3°48′ 58.7″ S, 33° 59′ 17.1″ W to 3° 50′ 05.8″ S, 33° 58′ 46.5″ W, between 0 and 610 m depth, on 2 May, 2017, between 22:08 and 22:40 hours. The sample was captured using a micronekton mid-water trawl net (body mesh: 40–80 mm; cod-end mesh: 10 mm; maximum horizontal and vertical openings: 24 m). Trawl depth was continuously recorded using a Scanmar depth sensor (www.scanmar.no) fitted on the upper part of the trawl mouth. After capture, the specimen of *A. intermedius* was preserved in a solution of 4% formalin in seawater and deposited in the Fish Collection of the Núcleo em Ecologia e Desenvolvimento Socioambiental de Macaé, Universidade Federal do Rio de Janeiro (NPM 4515). Radiographs were taken using a Faxitron LX-60 (www.faxitron.com) to aid fin-ray and vertebral counts. Measurements were made using calipers to the nearest 0.1 mm. Identification followed Parin (1994) and Biscoito *et al.* (2011); differentiation from *A. carbo* relied on the total number of vertebrae and dorsal-fin elements.

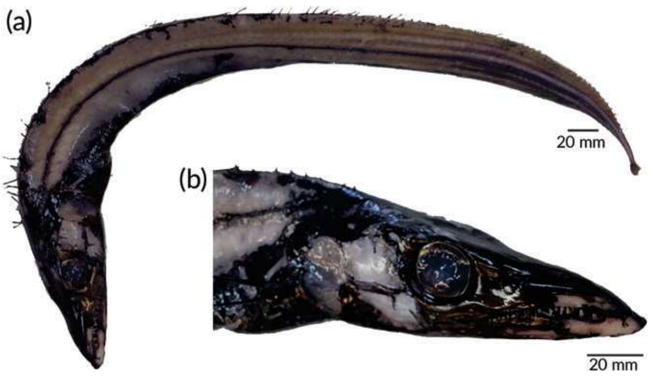

FIGURE 1 (a) Whole specimen and (b) head profile of *Aphanopus intermedius* (NPM 4515, 725 mm standard length) collected around Rocas Atoll, off north-eastern Brazil

Morphometric and meristic data for the specimen reported here were similar to those recorded by Parin (1994) and Biscoito *et al.* (2011), except for the pre-anal length, which was slightly shorter (±1% L_S) than those previously reported (Table 1). Nakamura and

TABLE 1 Proportions and counts for *Aphanopus intermedius* collected around Rocas Atoll, western South Atlantic Ocean, compared with those reported in other Atlantic areas

	This study; NPM 4515	Parin (1994); range (*n*)	Biscoito *et al.* (2011); range (*n*)
Standard length (L_S, mm)	725	515–1,010 (17)	622–1,345 (63)
Measurements in % of L_S			
Head length	18.8	18.5–21.0 (17)	17.9–22.5 (63)
Pre-anal length	60.7	–	57.0–63.8 (46)
Pre-first anal-spine length	56.1	56.1–58.0[a]	55.2–60.0 (46)
Pre-anal length	51.7	52.8–55.0[a]	52.7–64.0 (63)
Prepectoral length	18.6	–	18.6–20.8 (46)
Pre-dorsal length	16.6	16.2–17.8[a]	14.9–18.5 (46)
Pre-first dorsal soft ray length	54.8	54.8–56.9[a]	50.4–59.2 (40)
Maximum body depth	8.0	6.1–8.6 (17)	6.9–12.7 (46)
Depth of body at level of first anal fin spine	7.3	–	6.0–10.5 (63)
Least depth of caudal peduncle	0.4	0.3–0.4[a]	0.3–0.5 (46)
Caudal-peduncle length	2.6	–	2.0–4.2 (46)
Head length (L_H, mm)	136	95.3–212.1 (17)	123–270 (70)
Measurements in % of L_H			
Preopercular length	80.1	–	77.0–83.9 (46)
Snout length	42.6	40.4–43.2 (17)	36.7–50.4 (70)
Eye diameter	19.1	17.8–20.1 (17)	13.8–24.8 (70)
Interorbital width	16.2	12.3–15.6 (17)	11.6–21.7 (70)
Maxillary length	49.3	46.9–49.4 (17)	45.6–49.8 (45)
Head height	40.4	34.5–35.6[a]	31.4–42.1 (46)
Dorsal-fin spines	41	40–44 (55)	39–43 (41)
Dorsal-fin soft rays	59	54–59 (55)	52–60 (41)
Total dorsal-fin elements	100	96–101 (55)	92–102 (60)
Anal-fin rays	47	46–50 (55)	45–50 (59)
Precaudal vertebrae	46	44–47 (55)	43–47 (46)
Caudal vertebrae	61	57–61 (55)	56–61 (46)
Total vertebrae	107	102–107 (55)	101–105 (46)

[a] Data from holotype and three paratypes (from Parin, 1983).

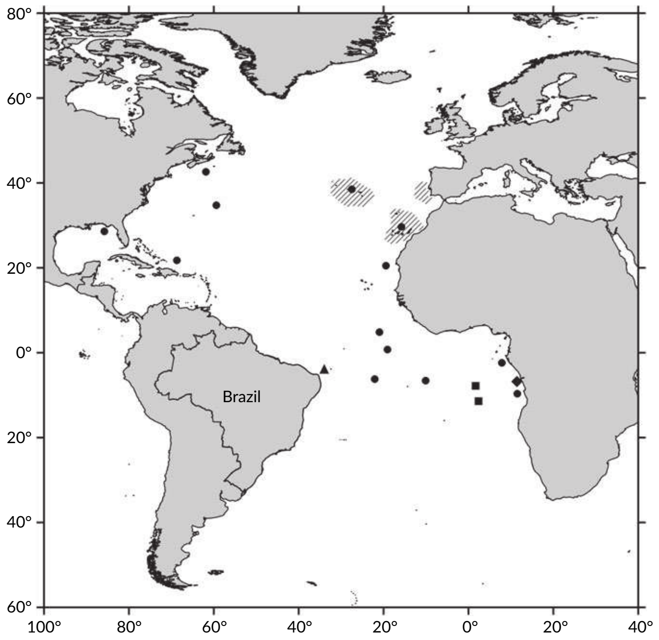

FIGURE 2 Distribution of *Aphanopus intermedius* based on literature, Biscoito *et al*. (2011; ▨), Parin (1994; ●), Vasil'eva *et al*. (2001; ◆), Pakhorukov *et al*. (2014; ■) and the present study (▲)

Parin (1993) erroneously expanded distribution of *A. intermedius* in the Pacific Ocean to include species not described at that time (*e.g*., *Aphanopus capricornis* Parin, 1994) or misidentified (Parin, 1994). However, the taxonomic review by Parin (1994) restricted the distribution of *A. intermedius* to the warm, tropical waters of the Atlantic Ocean. Among the South Atlantic records available in the literature, *A. intermedius* has been reported along the African coast (to about 15°S) and around Ascension Island (Pakhorukov *et al*., 2014; Parin, 1990, 1994; Parin & Nakamura, 2016; Vasil'eva *et al*., 2001; Wirtz *et al*., 2017). Thus, the specimen reported here considerably extends the known distribution of this species to the western South Atlantic Ocean (Figure 2).

Aphanopus intermedius is a fast swimming species that has a bathymetric distribution ranging from 200 to 2,300 m and is mostly caught through deep longlines around 1,000 m depth (Nakamura & Parin, 1993; Tuset *et al*., 2010). As initiatives aimed at searching for benthopelagic species caught by longlines, or any other type of fishing gear, in Brazilian waters are scarce, it seems at least plausible that the *A. intermedius* occurs throughout the benthopelagic zone of the Brazilian exclusive economic zone. Thus, we suggest more studies and research cruises to evaluate the distribution and ecology of *Aphanopus* spp. in the western South Atlantic Ocean, as well as the presence of other unknown deep-sea species in the area.

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PENSOFT

Deep-sea oceanic basslets (Perciformes, Howellidae) from Brazil: new records and range extensions

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Abstract

This study reports the occurrence of the oceanic basslet (Howellidae) in Brazilian waters. *Bathysphyraenops simplex* Parr, 1933, a rare species with a worldwide distribution, is recorded for the first time in Brazilian waters, based on three specimens collected off Rocas Atoll and Rio Grande do Norte. *Howella atlantica* Post & Quéro, 1991, known from the western and eastern Atlantic Ocean (64°N to 21°S), including waters around the Trindade Island, is reported off Rio Grande do Norte, Pernambuco, Rocas Atoll, and the Fernando de Noronha Archipelago. In addition, specimens previously reported in the literature as *Howella brodie* Ogilby, 1899 are reidentified as *H. atlantica*, extending the known distribution of this species to northeastern and southeastern Brazil. Measurements and counts for all specimens examined are provided.

Keywords

Mesopelagic fishes, tropical islands, western South Atlantic.

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Introduction

The representatives of the family Howellidae Ogilby, 1899, commonly known as oceanic basslets or alternatively as pricklefishes (Heemstra 2016), are poorly known mesopelagic to bathypelagic fishes inhabiting the tropical and temperate waters of all oceans (Fedoryako 1976; Post and Quéro 1991; Heemstra 2016). Reaching 120 mm in standard length (SL), these fishes occur in loose aggregations, present internal ventral luminescence, and usually exhibit diel vertical migrations (Post and Quéro 1991; Herring 1992).

Species currently classified as belonging to the Howellidae have been historically placed in other families, including Serranidae (Norman 1966), Cheilodipteridae (= Apogonidae) (Schultz 1940; Mead and De Falla 1965; Fedoryako 1976), and Percichthyidae (Fraser 1972; Post and Quéro 1991). However, Prokofiev (2007a, 2007b) demonstrated that howellids differ significantly from all other percoid groups and, as first described by Ogilby (1899), placed these species in a separate family. Prokofiev (2007b) provided a revised diagnosis of the Howellidae. Currently, the family comprises nine species in three genera: *Howella* Ogilby, 1899, *Bathysphyraenops* Parr, 1933, and *Pseudohowella* Fedoryako, 1976 (Prokofiev 2007a, 2007b; Fricke et al. 2019).

Although considered common in some locations, the diversity and distribution of howellids have been insufficiently studied, and only a few specimens have been recorded in the western South Atlantic. This study reports the occurrence of two poorly known species of Howellidae in Brazilian waters: *Bathysphyraenops simplex* Parr, 1933 and *Howella atlantica* Post & Quéro, 1991. The identity of howellids previously reported in Brazilian waters is further discussed.

Methods

The material examined was collected during the ABRACOS expeditions (Acoustics along the BRAzilian COaSt), carried out in October 2015 (Bertrand 2015) and April 2017 (Bertrand 2017) and conducted by the French RV *Antea* off northeastern Brazil, including Rocas Atoll, the Fernando de Noronha Archipelago, and the seamounts off Rio Grande do Norte. The extensive survey in 80 fishing stations from 0 to 1113 m depth resulted in the collection of about 9,000 specimens of meso- and bathypelagic fishes. Sampling was conducted using midwater (body mesh: 40 mm, cod-end mesh: 10 mm) and mesopelagic (body mesh: 30 mm, cod-end mesh: 4 mm) trawl nets. Trawl depth was continuously recorded using a Scanmar sensor fitted on the upper part of the trawl net. All specimens taken in ABRACOS expeditions are deposited in the Fish Collection of the Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro (NPM; Macaé, Brazil). Additional specimens examined from the eastern Brazilian coast are deposited in the Museu Nacional (MNRJ; Rio de Janeiro, Brazil). Morphometric and meristic data were taken according to Post and Quéro (1991) and compared with those previously reported in the literature (Table 1). Measurements were taken with calipers to the nearest 0.1 mm. Counts of vertebrae and unpaired fin elements were obtained through a Faxitron LX 60 Cabinet X-ray System. Identification followed Post and Quéro (1991) and Prokofiev (2007b).

Results

Bathysphyraenops simplex Parr, 1933

Figure 1a, Table 1

New records (northeastern Brazil). 3 specimens • NPM 3266, 1 spec. (36 mm SL), RV *Antea*, ABRACOS1, sta. 22, off Rocas Atoll, 04°07′43″S, 033°47′28″W to 04°07′00″S, 033°48′59″W, 0–525 m depth, mesopelagic trawl, 8 October 2015, 21:32–22:12h • NPM 4477, 1 spec. (77 mm SL), RV *Antea*, ABRACOS2, sta. 39, off Rio Grande do Norte, 04°52′27″S, 034°35′23″W to 04°50′53″S, 034°51′05″W, 0–800 m depth, midwater trawl, 24 April 2017, 21:49–22:37h • NPM 5052, 1 spec. (75 mm SL), RV *Antea*, ABRACOS2, sta. 54B, off Rio Grande do Norte, 03°45′17″S, 034°41′04″W to 03°44′39″S, 034°40′05″W, 0–1030 m depth, midwater trawl, 3 May 2017, 13:11–13:47h.

Identification. *Bathysphyraenops* can be distinguished from other howellid genera by the following combination of characters: upper angle of opercle with two simple spines (two simple or a cluster of spines in *Howella*), two well-separated spines of equal sizes on the subopercle (one long spine with 1–3 much shorter spines join downwards and upwards in *Howella*), and preopercle with spines along its lower margin (without spines in *Pseudohowella*). In addition, *Bathysphyraenops simplex* can be distinguished from its single congener, *B. declivifrons*, by having a compressed snout (vs rounded snout), and 15 or 16 pseudobranchs (vs 20 or 21) (Fedoryako 1976).

Distribution. *Bathysphyraenops simplex* has a worldwide distribution in tropical and subtropical seas (Fedoryako 1976; Carpenter 1999; Heemstra and Yamanoue 2003; Heemstra 2016). It was originally described from the Bahamas (Parr 1933; Moore and Boardman 1991) and subsequently reported in other localities of the Atlantic Ocean, including off western Africa, Cape Verde Islands (Backus et al. 1965), Puerto Rico, Ascencion Island (Fedoryako 1976), Cuba (Heemstra and Yamanoue 2003), off New England (Moore et al. 2003), southern Gulf of Mexico (McEachran and Fechhelm 2005), and Portugal (Carneiro et al. 2014). In the Pacific Ocean, the species was reported off eastern Philippines, Kiribati (Fedoryako 1976), South China Sea (Randall and Lim 2000), off Japan, Okinotorishima Islands (Uyeno and Kubota 1970; Masuda et al. 1984; Hatooka 2002), Hawaiian Islands (Mundy 2005), Ryukyu Islands (Shinohara et al. 2005), southern Taiwan (Shao et al. 2008), New Caledonia (Fricke et al. 2011), Ogasawara Islands (Tatsuta et al. 2014), and off southern California (Davison et al. 2015). In the Indian Ocean, it is known off the northeastern Seychelles (Mead and De Falla 1965). The species is reported here for the first time in Brazilian waters, based on three specimens collected around Rocas Atoll and off Rio Grande do Norte (Fig. 2).

Howella atlantica Post & Quéro, 1991

Figure 1b, Table 1

New records (northeastern Brazil). 25 specimens • NPM 4478, 10 spec. (52–67 mm SL), RV *Antea*, ABRACOS2, sta. 54B, off Rio Grande do Norte, 03°45′17″S, 034°41′04″W to 03°44′39″S, 034°40′05″W, 0–1030 m depth, midwater trawl, 3 May 2017, 13:11–13:47h • NPM 4479, 1 spec. (57 mm SL), RV *Antea*, ABRACOS2, sta. 39, off Rio Grande do Norte, 04°52′27″S, 034°35′23″W

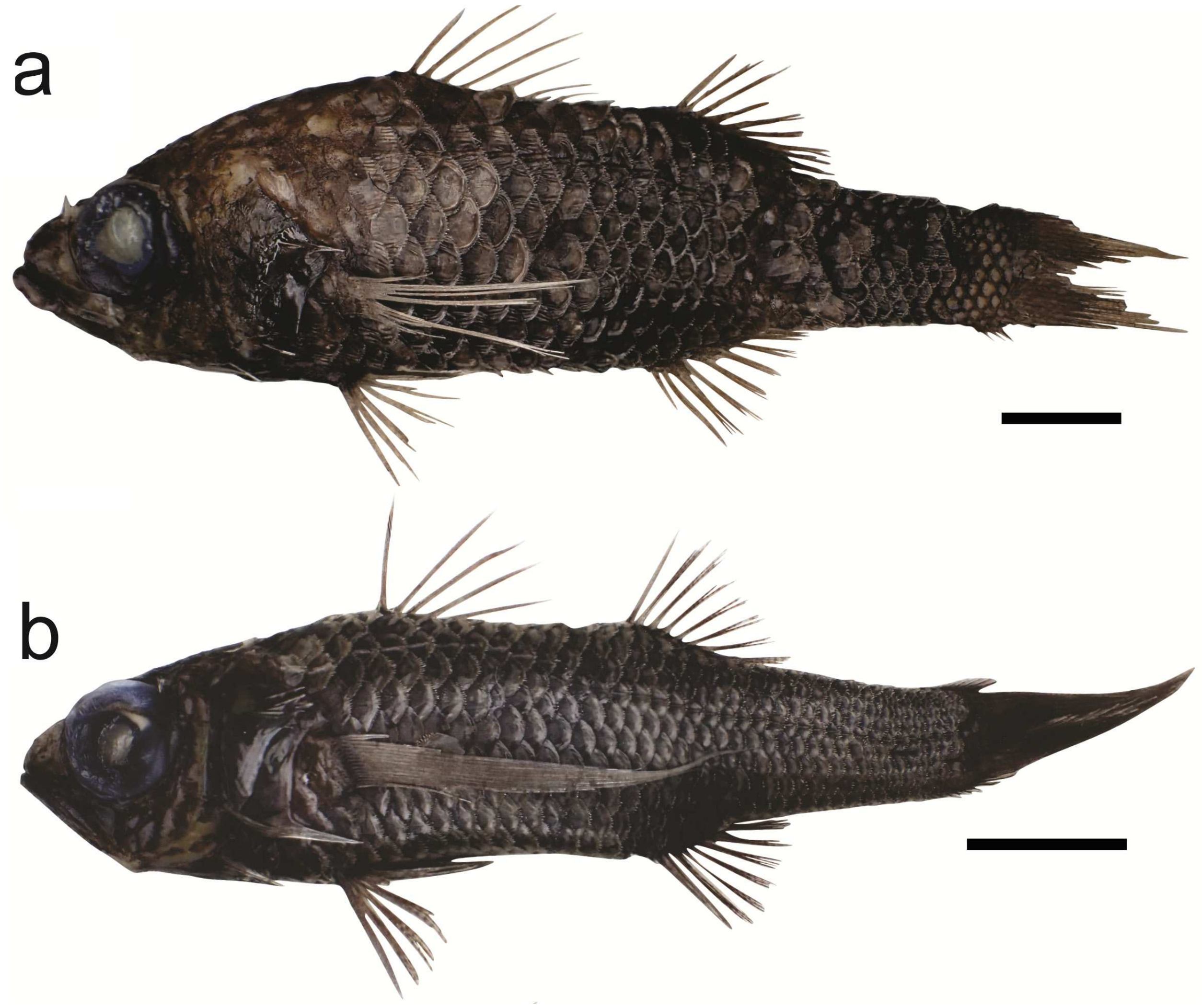

Figure 1. a. *Bathysphyraenops simplex* (NPM 4477, 77 mm SL). **b.** *Howella atlantica* (NPM 4483, 59 mm SL). Scale bars = 10 mm.

to 04°50′53″S, 034°51′05″W, 0–800 m depth, midwater trawl, 24 April 2017, 21:49–22:37h • NPM 4480, 1 spec. (60 mm SL), RV *Antea*, ABRACOS2, sta. 16, off Pernambuco, 07°36′15″S, 033°59′30″W to 07°36′49″S, 033°57′19″W, 0–680 m depth, midwater trawl, 14 April 2017, 21:53h • NPM 4481, 2 spec. (54–60 mm SL), RV *Antea*, ABRACOS2, sta. 42A, off Fernando de Noronha Archipelago, 03°15′28″S, 031°48′29″W, 03°15′28″S, 031°50′41″W, 0–780 m depth, midwater trawl, 27 April 2017, 12:23–12:26h • NPM 4482, 7 spec. (51–64 mm SL), RV *Antea*, ABRACOS2, sta. 44A, off Fernando de Noronha Archipelago, 03°52′53″S, 032°17′33″W to 03°52′13″S, 032°16′28″W, 0–850 m depth, midwater trawl, 28 April 2017, 12:44–13:17h • NPM 4483, 1 spec. (59 mm SL), RV *Antea*, ABRACOS2, sta. 52A, off Rocas Atoll, 03°43′16″S, 033°25′10″W to 03°42′14″S, 033°24′36″W, 0–984 m depth, midwater trawl, 2 May 2017, 11:47–12:18h • NPM 4484, 3 spec. (52–59 mm SL), RV *Antea*, ABRACOS2, sta. 49A, off Rocas Atoll, 04°10′38″S, 033°16′07″W to 04°10′58″S, 033°15′04″W, 0–1020 m depth, midwater trawl, 27 April, 21:17–21:52h.

Additional materials examined (eastern Brazil). 11 specimens • MNRJ 45291, 8 spec. (58–62 mm SL), RV *Thalassa*, sta. D-471, off Rio de Janeiro, 21°31′27.4″S, 039°47′30.8″W, 117.5 m depth, mid-water trawl, 23 June 1999, 19:56h • MNRJ 45457, 1 spec. (68 mm SL), RV *Thalassa*, sta. E-496, off Bahia, 13°17′34.8″S, 038°17′35.9″W to 13°12′01.8″S, 038°14′52.4″W, 1635.0–1863.6 m depth, bottom trawl, 7 June 2000, 9:27h • MNRJ 45458, 1 spec. (65 mm SL), RV *Thalassa*, sta. E-507, off Bahia, 15°08′35.7″S, 038°40′38.3″W to 15°07′09.5″S, 038°40′32.5″W, 1012.4–1049.0 m depth, bottom trawl, 11 June 2000, 10:28h • MNRJ 45478, 1 spec. (64 mm SL), RV *Thalassa*, sta. E-512, off Bahia, 15°50′31.9″S, 038°02′16.4″W to 15°50′35.9″S, 038°02′30.4″W, 1036.0–1050.8 m depth, bottom trawl, 13 June 2000, 12:06h.

Identification. *Howella* can be distinguished from other howellid genera by the following combination of characters: preopercle with spines along its lower margin (without spines in *Pseudohowella*), one long spine with 1–3 much shorter spines join downwards and upwards on the subopercle (two well-separated spines of equal sizes in *Bathysphyraenops*), and upper angle of opercle with two simple or a cluster of spines (two simple spines in *Bathysphyraenops*) (Fedoryako 1976). In addition, *H. atlantica* can be distinguished from its congeners

Table 1. Measurements and counts for specimens of *Bathysphyraenops simplex* (*n* = 3) and *Howella atlantica* (*n* = 36) from Brazil.

	Bathysphyraenops simplex			***Howella atlantica***		
	NPM 3266	**NPM 4477**	**NPM 5052**	**Range**	**Mean**	**SD**
Standard length (SL, mm)	36.0	77.0	74.6	51–68		
Measurements in % SL						
Head length	37.2	32.2	34.9	32.9–38.3	36.2	1.1
Body depth	23.3	29.2	29.0	24.1–29.7	27.7	1.2
Body width	9.7	15.6	12.1	12.5–17.6	15.2	1.2
First predorsal length	41.1	40.3	41.8	34.6–41.9	39.8	1.4
Second predorsal length	63.9	63.2	65.8	61.4–68.5	64.6	1.6
Preanal length	61.1	61.6	61.7	63.5–68.5	66.1	1.4
Prepelvic length	34.7	33.4	33.0	34.2–38.8	36.0	1.1
Prepectoral length	34.4	31.7	34.0	31.3–37.2	34.7	1.2
Pectoral fin length	19.4	28.6	24.1	31.9–48.9	42.1	3.5
Pelvic fin length	18.3	13.0	13.1	14.9–21.0	17.1	1.7
Caudal peduncle length	30.6	25.2	25.6	22.8–30.0	27.1	1.8
Caudal peduncle depth	10.0	12.5	11.8	9.1–13.4	11.9	0.9
First dorsal fin base	15.0	16.9	14.7	11.5–18.5	14.9	1.8
Second dorsal fin base	17.2	14.3	12.3	9.7–15.6	12.7	1.2
Anal fin base	12.8	13.0	10.6	9.3–15.2	11.5	1.4
Length between dorsal fins	9.4	12.1	11.5	9.6–16.3	12.2	1.7
Pelvic origin to anus	22.2	29.1	23.5	25.6–32.5	29.2	1.9
Maxilla length	12.2	13.5	13.1	13.4–16.5	14.9	0.6
Mandible length	9.7	11.2	9.4	10.4–14.1	12.1	0.9
Snout length	11.1	7.1	6.8	6.9–10.3	8.2	0.7
Eye diameter	11.7	10.9	11.1	11.2–16.0	12.8	1.1
Interorbital width	7.2	7.8	8.0	8.6–11.2	9.5	0.6
Counts						
First dorsal fin spines	8	8	8	8–8	8.0	0.0
Second dorsal fin spine	1	1	1	1–1	1.0	0.0
Second dorsal fin rays	9	9	9	8–9	8.9	0.2
Anal fin spines	3	3	3	3–3	3.0	0.0
Anal fin rays	7	7	7	6–8	7.0	0.3
Pectoral fin rays	14	14	14	14–14	14.1	0.4
Pelvic fin spine	1	1	1	1–1	1.0	0.0
Pelvic fin rays	5	5	5	5–5	5.0	0.0
Caudal fin procurrents (upper)	—	10	8	7–9	8.7	0.5
Caudal fin rays (upper)	10	9	10	9–10	9.2	0.4
Caudal fin rays (lower)	9	8	10	8–10	8.7	0.5
Caudal fin procurrents (lower)	—	10	7	6–9	7.9	0.7
Scales on lateral line (anterior)	—	—	—	2–3	2.1	0.3
Scales on lateral line (central)	—	—	—	6–9	7.8	0.6
Scales on lateral line (posterior)	—	—	—	19–27	23.7	1.9
Scales on transverse row	11	11	11	10–12	11.2	0.5
Scales on longitudinal row	34	34	—	30–37	34.7	1.7
Upper gill rakers (rudimentary)	3	3	4	3–5	3.6	0.6
Upper gill rakers	3	3	3	3–6	3.8	0.8
Upper gill rakers (total)	6	6	7	6–9	7.3	0.8
Lower gill rakers	13	13	13	11–18	13.9	1.7
Lower gill rakers (rudimentary)	6	5	5	4–8	6.0	1.1
Lower gill rakers (total)	19	18	18	18–22	19.5	1.1
Total gill rakers	25	24	25	24–30	27.1	1.5
Pseudobranchs	—	—	15	18–23	19.6	1.4
Precaudal vertebrae	10	10	10	10–10	10.0	0.0
Caudal vertebrae	16	16	16	16–17	16.1	0.3
Total vertebrae	26	26	26	26–27	26.1	0.3

by the following combination of characters: a cluster of 3–6 spines at rear end of opercle, lateral line interrupted below gap between dorsal fins, three rows of scales from lateral line to second dorsal-fin origin, and pectoral-fin rays 14–16 (Post and Quéro 1991).

Distribution. This species has been previously reported from the western and eastern Atlantic Ocean, from 64°N to 21°S (Post and Quéro 1991; Heemstra 2016). In the Brazilian EEZ, it has only been recorded around Trindade Island (Post and Quéro 1991). The current study

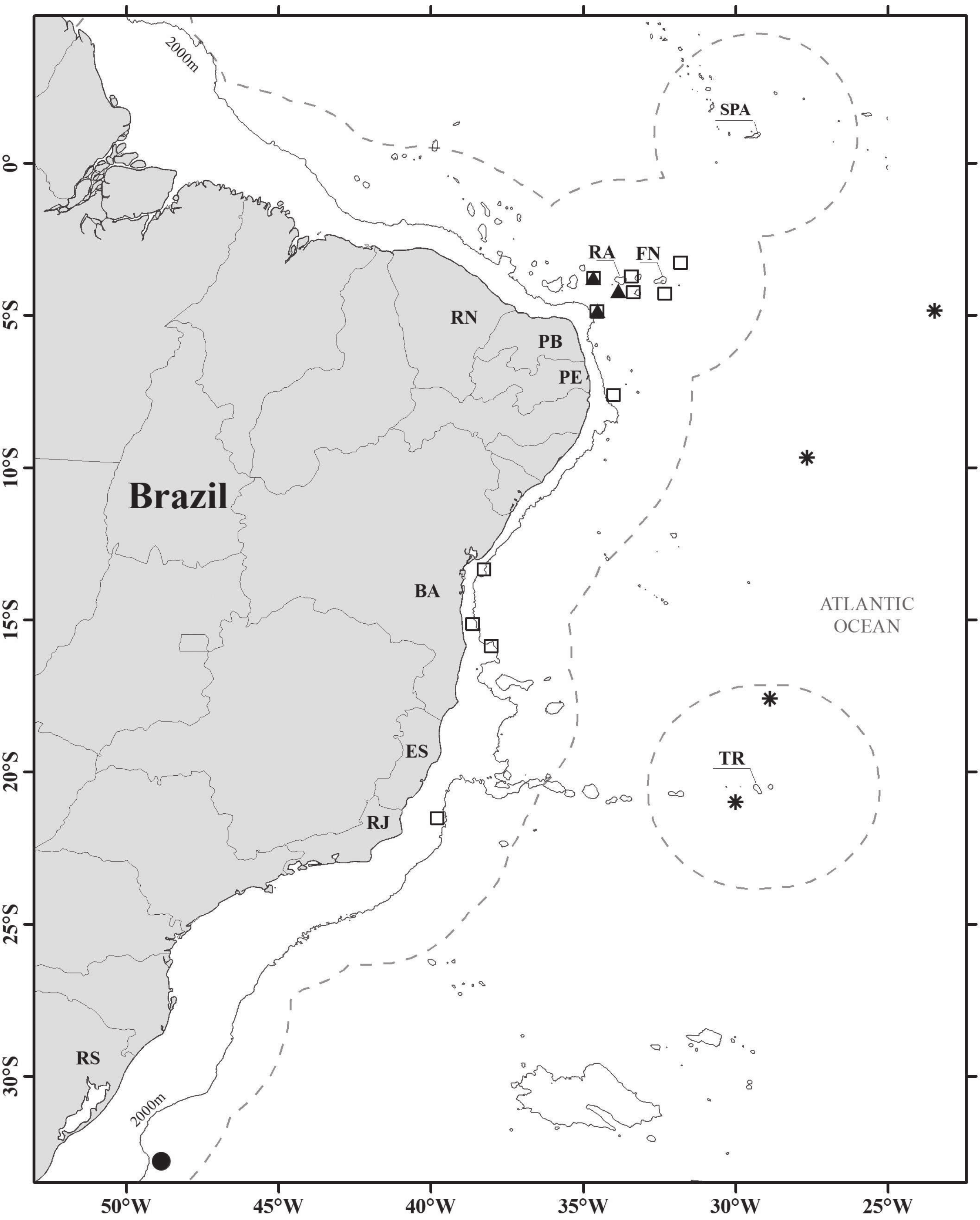

Figure 2. Distribution of *Bathysphyraenops simplex* (full triangle) and *Howella atlantica* (open square) examined in the present study. Previous records of *Howella atlantica* (asterisk) and *Howella sherborni* (full circle) along Brazilian waters (from Post and Quéro 1991). Limits of the Brazilian Exclusive Economic Zone in dash line. Oceanic islands: **SPA** – São Pedro e São Paulo Archipelago; **RA** – Rocas Atoll; **FN** – Fernando de Noronha Archipelago; **TR** – Trindade Island. Selected Brazilian states: **RN** – Rio Grande do Norte; **PB** – Paraíba; **PE** – Pernambuco; **BA** – Bahia; **ES** – Espírito Santo; **RJ** – Rio de Janeiro, **RS** – Rio Grande do Sul.

extends the known distribution of *H. atlantica* to other areas of Brazilian waters; 24 specimens were collected off Rio Grande do Norte, Pernambuco, Rocas Atoll, and the Fernando de Noronha Archipelago. Eleven specimens, previously identified as *Howella brodie* by Costa et al. (2007), were trawled off Bahia and Rio de Janeiro (Fig. 2).

Discussion

Among more than 9000 specimens of mesopelagic fishes caught during the two ABRACOS expeditions (October 2015 and April 2017), three specimens of *B. simplex* and 25 of *H. atlantica* were collected. Eleven specimens of *H. brodiei* Ogilby, 1899 reported off Bahia and Rio de

Janeiro by Costa et al. (2007) were here reidentified as *H. atlantica*. These re-identifications extend the known distribution of *H. atlantica* to northeastern and southeastern Brazil. Other howellids previously reported in Brazilian waters include: two specimens of *Howella sherborni* (Norman, 1930) (ISH 931/66: 80.7–87.8 mm SL) reported off Rio Grande do Sul (Post and Quéro 1991), and 18 specimens of *H. atlantica* (ISH 742/66 [3]: 59.1–62.7 mm SL and ISH 777/66 [15]: 61.1–71.2 mm SL) collected around Trindade Island (Post and Quéro 1991) (Fig. 2).

Knowledge regarding the diversity of deep-water fishes off Brazil is based on a few scientific expeditions and a scarcity of specimens deposited in zoological collections. Howellid species may thus be more frequent in Brazilian waters than currently thought. In addition, due to the lack of data on this group, important ecological information such as habitats niche, vertical migration, growth pattern, reproduction, and feeding behavior remain understudied. Additional studies focused on the diversity, distribution, and ecology of howellid species, as well as other poorly known deep-sea fishes in Brazilian waters are recommended.

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Authors’ Contributions

LNE, BTV, JRM, and MMM identified specimens, made measurements, and wrote the manuscript with contributions of AB, ASL, FLF, PET, and TF. AB and FLF conceived and coordinated the research project. All authors participated of the at-sea surveys and/or contributed substantially to the biological analyses.

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TECHNICAL CONTRIBUTION

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Length–weight relationships of eleven mesopelagic fishes from oceanic islands of the Southwestern Tropical Atlantic

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Summary

This study provides the length-weight relationship for eleven mesopelagic fishes from oceanic islands of the Southwestern Tropical Atlantic: *Bonapartia pedaliota*, *Sigmops elongatus* (Gonostomatidae), *Argyropelecus aculeatus*, *Argyropelecus affinis*, *Argyropelecus sladeni*, *Sternoptyx diaphana*, *Sternoptyx pseudobscura* (Sternoptychidae), *Malacosteus niger*, *Thysanactis dentex* (Stomiidae), *Melanonus zugmayeri* (Melanonidae), and *Ectreposebastes imus* (Setarchidae). Data were collected during a scientific survey (2017) around Rocas Atoll, Fernando de Noronha Archipelago and adjacent seamounts, using a micronekton trawl (side length of body mesh: 40 mm, side length of cod-end mesh: 10 mm) at 35 stations from 0 to 1,113 m depth. A new maximum standard length for *Bonapartia pedaliota* and *Ectreposebastes imus* are also provided.

1 | INTRODUCTION

In the western Tropical Atlantic, the Fernando de Noronha Archipelago, Rocas Atoll and adjacent seamounts host a remarkable biodiversity (Fiedler et al., 2016; Hazin, Zagaglia, Broadhurst, Travassos, & Bezerra, 1998). For this reason, the marine ichthyofauna of this large biogeographic unit categorized as Ecologically or Biologically Significant Marine Areas—EBSA (CBD, 2014) has been studied by many authors (Dominguez, Zeineddine, Rotundo, Barrella, & Ramires, 2016; Kikuchi & Schobbenhaus, 2002; Oliveira et al., 2011). However, most efforts focused on fishes living near to the surface (0–200 m) and few studies described the mesopelagic zone (200–1,000 m depth) of this region, which is considered as one of the most understudied of the world ocean (St. John, 2016).

The mesopelagic community is a key resource for higher trophic levels, maintaining part of the marine biodiversity and playing an important role in carbon sequestration and thus on the biological carbon pump (Proud, Cox, & Brierley, 2017; St. John et al., 2016). To better account for the role of this community in the ecosystem structure and function, a prerequisite is to have the necessary biological information. One of such key basic knowledge concerns the length-weight relationships (LWR) that are one of the requisites for fisheries management and conservation (Froese, 2006; Froese, Tsikliras, & Stergiou, 2011). Indeed, LWRs are used to estimate body weight by length measurements, assess the condition factor or well-being of species of interest, as well as for the calculation of production and biomass of a fish stock (Froese, 2006). Despite this, information on LWRs are still lacking for many deep-sea fishes. Here, we provide new LWRs for eleven mesopelagic fish species collected along the northeast Brazilian oceanic islands, in order to increase the biological data and general knowledge of these species.

2 | MATERIALS AND METHODS

The study area comprises the northeast Brazilian oceanic islands, including Rocas Atoll (3°52′S, 33°49′W), Fernando de Noronha Archipelago (3°50′S, 32°25′W) and adjacent seamounts. Data were collected during the scientific survey ABRACOS (Acoustics along the BRAzilian COaSt) conducted on board the RV *Antea*, from

9th April to 6th May 2017. Mesopelagic sampling was conducted using a micronekton trawl (side length of body mesh: 40 mm, side length of cod-end mesh: 10 mm) at 35 stations from 0 to 1,113 m depth. After capture, the material was fixed in a 4% formalin solution for one month and then preserved in a 70% alcohol solution for proximally six months before processing for length and weight. At the laboratory, species were identified, measured (nearest 0.1 cm of standard length, SL) and weighed (nearest 0.01 g of total weight, TW). All specimens were deposited in the Fish Collection of the Núcleo em Ecologia e Desenvolvimento Socioambiental de Macaé (NPM), Universidade Federal do Rio de Janeiro (NUPEM/UFRJ).

The parameters of the LWR were estimated through the equation: $TW = a \times SL^b$, where TW is the total weight (g), SL is the standard length (cm), a is a constant being the initial growth index and b is the slope of the regression. Prior to the calculation of LWRs, the relationship plots were executed for visual inspection and removal of outliers (Froese & Binohlan, 2000). The significance of the regression was tested by ANOVA and the degree of association between TW and SL was calculated by the determination coefficient (r^2). We only included LWRs for species with $n > 30$, except for three species for which a wide fish-length range was available.

3 | RESULTS

A total of 11 species belonging to five families and three orders were analysed (Table 1). All regressions were highly significant ($p < 0.01$), with the coefficient of determination (r^2) ranging from 0.9511 to 0.9868. The value of b varied between 2.66 for *Sternoptyx pseudobscura* and 3.22 for *Sigmops elongatus*, while the parameter a ranged between 0.0012 for *Thysanactis dentex* and 0.0754 for *S. pseudobscura*.

TABLE 1 Descriptive statistics and parameters of LWRs for 11 mesopelagic fishes caught using a micronekton trawl at the northeast Brazilian oceanic islands and seamounts, from 9th April to 6th May 2017

		SL (cm)		TW (g)		Regression parameters		
Taxa	*n*	Min	Max	Min	Max	*a* (95% CI)	*b* (95% CI)	r^2
Stomiiformes								
Gonostomatidae								
Bonapartia pedaliota Goode and Bean, 1896	85	3.7	7.5	0.4	2.7	0.0074 (0.0058–0.0094)	2.94 (2.80–3.08)	0.9571
Sigmops elongatus (Günther, 1878)	35	4.9	25	0.2	28	0.0015 (0.0009–0.0023)	3.229 (3.07–3.39)	0.9814
Sternoptychidae								
Argyropelecus aculeatus Valenciennes, 1850	49	3.0	8.2	0.8	20.9	0.0350 (0.0245–0.0496)	2.996 (2.77–3.21)	0.9529
Argyropelecus affinis Garman, 1899	260	2.8	7.8	0.31	6.09	0.0218 (0.0183–0.0258)	2.807 (2.70–3.91)	0.9511
Argyropelecus sladeni Regan, 1908	26	2.0	6.6	1.15	7.2	0.0425 (0.0257–0.0705)	2.703 (2.39– 3.01)	0.9618
Sternoptyx diaphana Hermann, 1781	600	1.2	4.3	0.1	4.3	0.0570 (0.0370–0.0770)	2.89 (2.79–2.99)	0.9675
Sternoptyx pseudobscura Baird, 1971	51	1.3	5.6	0.24	6.6	0.0754 (0.0582–0.0970)	2.663 (2.45–2.88)	0.9655
Stomiidae								
Malacosteus niger Ayres, 1848	33	6.3	18.1	1.5	34.4	0.0057 (0.0009–0.0030)	2.956 (2.74–3.17)	0.9635
Thysanactis dentex Regan and Trewavas, 1930	35	4.3	14.5	0.1	10.6	0.0012 (0.0009–0.0012)	3.197 (3.07–3.33)	0.9868
Gadiformes								
Melanonidae								
Melanonus zugmayeri Norman, 1930	20	6.4	19.1	1.06	32.31	0.0036 (0.0018–0.0071)	2.973 (2.68–3.26)	0.9623
Scorpaeniformes								
Setarchidae								
Ectreposebastes imus Garman, 1899	25	5.2	23.4	3.43	290.3	0.0250 (0.0138–0.0482)	3.025 (2.81–3.24)	0.9728

Note. CI: confidence interval; SL: standard length; TW: total weight; a: initial growth index; b: slope of the regression; r^2: determination coefficient.

4 | DISCUSSION

This work provides the first LWR for six species: *S. pseudobscura*, *B. pedaliota*, *S. elongatus*, *T. dentex*, *M. zugmayeri*, and *E. imus*. LWR information has been previously available for *A. aculeatus*, *A. affinis*, *A. sladeni*, *S. diaphana*, and *M. niger*, but it was based on a small length range, small sample size (<5) and/or without the descriptive statistics of the relationships (Alpoim et al., 2002; Davison, Lara-Lopez, & Koslow, 2015). All species presented here but *A. aculeatus* and *M. niger*, have no LWRs available in FishBase. In addition, the highest standard length values for *Bonapartia pedaliota* and *Ectreposebastes imus* are reported herein.

As established by Froese (2006), the allometric coefficients for all LWRs were within the expected range of 2.5–3.5. These values are reflection of intrinsic characteristics and process of adaptations of each species, as ontogenetic reproductive or environmental variations, mainly between sexes (Froese, 2006). In addition, fixation in alcohol and formaldehyde can affect length and weight measurements through the shrinking and dehydration of specimens. For that reason, we recommend consider the LWRs presented here as being tentative.

Overall, this study increases the knowledge on mesopelagic fishes, providing basic biological information useful for further studies in ecology, conservation, and fisheries assessment.

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TECHNICAL CONTRIBUTION

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Length-weight relationship of twelve mesopelagic fishes from the western Tropical Atlantic

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Abstract

Length-weight relationship parameters were calculated for twelve mesopelagic fish species from the western Tropical Atlantic: *Diretmus argenteus*, *Melamphaes polylepis*, *Bolinichthys distofax*, *Diaphus lucidus*, *Diaphus splendidus*, *Electrona risso*, *Hygophum taaningi*, *Taaningichthys bathyphilus*, *Melanolagus bericoides*, *Winteria telescopa*, *Diplophos taenia*, *Astronesthes similus*. Data was collected off northeastern Brazil from April 9th to May 6th, 2017. Hauls were conducted during day and night at 47 stations by using a micronekton trawl (body mesh: 40 mm, cod-end mesh: 10 mm) from 10 to 1,113 m depth. The material was fixed in a 4% formalin solution for 1 month and then preserved in a 70% alcohol solution for proximally 6 months before processing for length (nearest 0.1 cm of standard length) and weight (nearest 0.01 g of total weight). A new maximum standard length for *Winteria telescopa* is also provided.

KEYWORDS

Brazil, deep-sea, lanternfish, oceanic islands, seamounts

1 | INTRODUCTION

Mesopelagic fishes (0–1,000 m depth) are major components of the oceans usually presenting global distribution, vertical migratory behavior, and a diverse array of morphological adaptations (Priede, 2017). These species are crucial for several ecosystem processes, such as carbon sequestration, nutrient regeneration, fisheries production, and waste absorption (Mengerink et al., 2014; Cavan et al., 2019; Eduardo et al., 2020). However, despite their importance, mesopelagic species remain mostly understudied and increasingly threatened by anthropogenic impacts (e.g. seabed mining, plastic pollution, ocean warming, and deoxygenation) (Steinberg et al., 2012; Mengerink et al., 2014; Levin & Bris, 2015). Given the difficulty of sampling in the deep-sea, even basic biological knowledge is lacking for many species, hampering the sustainable management of mesopelagic species as well as the comprehension of their numerous functions in the ecosystem (e.g. transport of carbon between oceanic layers).

One of the key basic knowledge concerns the length-weight relationships (LWR), which is widely applied in the management of fish populations (Froese & Binohlan, 2000; Froese, 2006; Froese et al., 2011). For example, LWR is an effective approach for assessing fish biomass based on the conveniently obtained length data (Froese, 2006). Additionally, this parameter may be used for ecological modeling, infer body condition indices, and estimating fish growth patterns as a part of stock assessment and conservation strategies (Froese, 2006; Eduardo et al., 2018a). Nevertheless, available information on LWR of many mesopelagic species from the western Tropical Atlantic is still lacking (Catelani et al., 2017; Eduardo et al., 2018a, 2018b). In this study, we take advantage of a large-scale deep-sea expedition to provide new LWRs for twelve mesopelagic fish species. Data were acquired along the western Tropical Atlantic, a poorly studied area with a high biodiversity, where MPAs (Marine Protected Area) and EBSAs (Ecologically or Biologically Significant Marine Area) have been established (CBD, 2014; Eduardo et al., 2018c). Information provided herein aims to improve general knowledge and biological data on mesopelagic species.

2 | MATERIAL AND METHODS

Samples were collected off northeast Brazil, including Rocas Atoll (3°52′S, 33°49′W), Fernando de Noronha Archipelago (3°50′S, 32°25′W) and adjacent seamounts. Data were collected during the ABRACOS 2 (Acoustics along the BRAzilian COaSt) expedition, carried out from April 9th to May 6th, 2017, onboard the French RV *Antea* (Bertrand, 2017). Sampling of mesopelagic fishes was conducted during day and night at 47 stations by using a micronekton trawl (body mesh: 40 mm, cod-end mesh: 10 mm) from 10 to 1,113 m depth. After capture, the material was fixed in a 4% formalin solution for 1 month and then preserved in a 70% alcohol solution for proximally 6 months before processing for length and weight. At the laboratory, specimens were identified, measured (nearest 0.1 cm of standard length, SL) and weighed (nearest 0.01 g of total weight, TW). Voucher specimens were deposited in the NPM - Fish Collection of the Instituto de Biodiversidade e Sustentabilidadae, Universidade Federal do Rio de Janeiro (UFRJ).

The LWR values were estimated using the equation: $TW = a \times SL^b$, where TW is the total weight (g); SL is the standard length (cm); *a* is the intercept of the regression curve (intercept of TW when SL is zero or initial growth coefficient) and *b* is the regression slope (coefficient indicating isometric or allometric growth) (Froese, 2006; Froese et al., 2011). Prior to calculation of the LWR, outliers for each species were graphically identified using SL versus TW plots (Froese & Binohlan, 2000) and removed. The fit of the model to the data was measured by the coefficient of determination *r*-squared (r^2).

3 | RESULTS

The study presents LWRs for twelve species, representing seven families and four orders (Table 1). Myctophidae is represented by six species, while the remaining families are represented by just one species. All regressions were highly significant ($p < 0.01$), with the coefficient of determination (r^2) ranging from 0.952 to 0.991. The value of *b* varied between 2.55 and 3.12, while the parameter *a* ranged between 0.0038 and 0.0436. Summarized additional data including sample size (n), measurement range (SL and TW), regression parameters *a* and *b*, and associated statistics are presented in Table 1.

4 | DISCUSSION

The present study provides the highest standard length value for *Winteria telescopa* and novel LWRs information for twelve species. All estimated values of the parameter *b* fell within the expected range (2.5–3.5) predicted by Froese (2006). Thus, estimated values can be used within the referred length range. These equation parameters are the reflection of not only local environmental variations, but also intrinsic characteristics and adaptative processes of each species like ontogenetic reproductive and variations between sexes (Froese, 2006; Eduardo et al., 2018a). Since fixation in formaldehyde and preservation in alcohol can affect length and weight measurements through the shrinking and dehydration of specimens, LWRs presented here may be slightly different than those found for fresh specimens. For that reason, we thus recommend consider the parameters presented here as being tentative. Moreover, since shrinking in preservatives is timedependent, we indicated the storage time before measurement. This is important as later studies, measuring freshly caught fish and preserving them for remeasurement after certain time intervals would offer an opportunity to provide a correction factor. Hence, data from previous studies who identified the time window under preservation can be recalculated and incorporated in a time series analysis. We strongly recommend that all studies that need to preserve the samples before measurement register the time elapsed from preservation to measurement.

In conclusion, information provided here contributes to fill gaps in elementary biological knowledge and may, thus, give support to a sustainable management for the conservation of deep-sea species.

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TABLE 1 Descriptive statistics and parameters of LWRs for twelve mesopelagic fishes caught using a micronekton trawl (from 10 to 1,113 m depth) at the western Tropical Atlantic, from April 9th to May 6th, 2017

		SL (cm)		TW (g)		Regression parameters		
Taxa	*n*	Min	Max	Min	Max	*a* (95% CI)	*b* (95% CI)	r^2
Beryciformes								
Diretmidae								
Diretmus argenteus Johnson, 1864*	116	1.4	7.5	0.1	17.9	0.0436 (0.0370–0.0513)	3.01 (2.91–3.10)	0.971
Melamphaidae								
Melamphaes polylepis Ebeling, 1962	37	3.6	6.9	0.8	6.4	0.0163 (0.0103–0.0257)	3.06 (2.93–3.19)	0.958
Myctophiformes								
Myctophidae								
Bolinichthys distofax Johnson, 1975	85	3.2	9.1	0.3	10.1	0.0126 (0.0104–0.0153)	3.03 (2.92–3.14)	0.974
Diaphus lucidus (Goode & Bean, 1896)	40	3.1	9.6	0.3	9.5	0.0161 (0.0129–0.0200)	2.82 (2.71–2.93)	0.986
Diaphus splendidus (Brauer, 1904)	232	2.0	8.5	0.1	5.8	0.0079 (0.0073–0.0083)	3.10 (3.06–3.14)	0.991
Electrona risso (Cocco, 1829)*	67	5.0	8.0	3.4	12.2	0.0365 (0.0256–0.0519)	2.78 (2.60–2.97)	0.952
Hygophum taaningi Becker, 1965	78	2.6	6.6	0.2	3.5	0.0180 (0.0134–0.0242)	2.86 (2.68–3.05)	0.957
Taaningichthys bathyphilus (Tåning, 1928)	10	5.4	7.1	1.0	2.4	0.0113 (0.0059–0.0214)	2.73 (2.52–2.92)	0.976
Argentiniformes								
Bathylagidae								
Melanolagus bericoides (Borodin, 1929)*	9	12.8	16.7	12	26	0.0038 (0.0012–0.0063)	3.12 (2.77–3.47)	0.963
Opisthoproctidae								
Winteria telescopa Brauer, 1901*	26	5.1	11.8	1.0	10.4	0.0081 (0.0036–0.0178)	2.92 (2.58–3.28)	0.964
Stomiiformes								
Gonostomatidae								
Diplophos taenia Günther, 1873*	23	4.2	12.9	0.8	14.9	0.0161 (0.0090–0.0287)	2.80 (2.69–2.91)	0.952
Stomiidae								
Astronesthes similus Parr, 1927*	9	3.6	7.5	0.2	1.7	0.0107 (0.0058–0.0119)	2.55 (2.43–2.67)	0.976

Abbreviations: *a*, initial growth index; *b*, slope of the regression; r^2, determination coefficient; SL, Standard Length; TW, Total Weight.

*Estimative based on a limited size range and thus considered as tentative.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon request.

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CHAPTER 1 - OUTLOOK

In this chapter we aimed at the first PRA (biodiversity census) and on a primary question to develop the understating of mesopelagic zones: who is down there? For that, we provided an integrative study on the biodiversity and morphometry of mesopelagic fishes from the Southwestern Tropical Atlantic, a poorly known area that encompass oceanic islands, seamounts, and unique biodiversity. In the first article, we demonstrated that, in the SWTA, there is a relatively high number of mesopelagic fishes, including at least 24 orders, 56 families, and 207 species. From those, nine species (4%) are potentially new and 61 (30%) represented new records for Brazilian waters. Five families accounted for 52% of the diversity of taxa, 90% of the specimens collected, and 72% of the total biomass: Myctophidae (38 spp.; 36% of the specimens; 24% of the biomass), Stomiidae (38 spp.; 8%; 21%), Gonostomatidae (11 spp.; 16%; 4%) Melamphaidae (11 spp.; 2%; 7%), and Sternoptychidae (10 spp.; 24%; 10%). In addition, we provided additional articles focusing on the diversity, distribution, and morphometry of fish groups that are globally rare and further discussions were needed.

In the Article two, we discussed the first record of the intermediate scabbardfish *Aphanopus intermedius* in the SWTA. In addition, we provided detailed meristic counts and measurements, comparing them with those available in the literature. In the Article 3 and Additional article 1, we focused on the families Howellidae and Caristiidae, reporting on the first record of five species and providing anatomical data (meristic and morphometric). In these articles, we also reviewed, re-identified, and discussed previous records from the STWA. For instance, specimens previously reported in the literature as *Howella brodie* were reidentified as *H. atlantica*, extending the known distribution of this species. Additionally, specimens previously recorded as *Caristius* sp. and *C. macropus* were reidentified as *Platyberyx pietschi* and *Platyberyx andriashevi*, respectively.

In the additional articles two, three, and four, we provided new data on the taxonomic composition and distribution of rare deep-sea species of Argentiniformes, Stephanoberycoidei, and Ceratioidei. In these works, we presented new anatomical data and remarks on the distribution of several species. As an example, we reported on the new occurrence of three genera and 31 species in the SWTA. Also, we reviewed previous records of these fish groups and provided a list of species in the study area. Finally, in the articles four and five, we included novel length-weight relationships for twenty-three mesopelagic fishes and provided new maximum standard lengths for *Bonapartia pedaliota*, *Ectreposebastes imus*, and *Winteria telescopa*.

Overall, the information presented here increases knowledge on several deep-sea species and may be useful for further studies addressing the ecology, conservation, and fisheries assessment of deep-sea. However, this knowledge is still insufficient. Data presented here, for instance, was based on two relatively short deep-sea collecting campaigns, indicating that a substantial diversity of deep-sea fishes is still awaiting to be discovered and properly studied in the region. As presented in the first article, about 75 additional species could have been collected using the same gears. In this context, we reaffirm that to properly access the diversity of mesopelagic species more investments in deep-sea collections are needed, especially in historically neglected regions such as the South Atlantic.

Based on the information presented in this chapter, some species were selected for further studies addressing its ecology: the viperfish *Chauliodus sloani* and members of the families Sternoptychidae (hatchetfishes, 9 species), and Myctophidae (lanternfishes, 33 spp.) (see Chapter 2). This selection was made given their abundance, biomass, level of details in taxonomical identifications, and importance in a local and global context.

CHAPTER 2 - ECOLOGY

Mesopelagic fishes are major components of the oceans usually presenting global distribution, vertical migratory behavior, and important participation in several ecosystem processes (e.g., carbon sequestration, nutrient regeneration, and fisheries production). Yet this zone is poorly understood — physically, biogeochemically, and ecologically. Even the number of organisms that live there remains a mystery, letting alone their diversity and function.

In an ecological context, four Priority Research Areas (PRA) have been listed in which more knowledge is needed to improve the understating of the mesopelagic zone: (i) biodiversity census; (ii) links between oceanographic regimes and mesopelagic biomass and biodiversity; (iii) the role of the mesopelagic community in the food web; and (iv) the role of individual species and the community in ecosystem process. In the first chapter, we focused on answering the first PRA and showed the occurrence of 207 taxa, with the viperfish *Chauliodus sloani* and members of the families Sternoptychidae (hatchetfishes, 9 species) and Myctophidae (lanternfishes, 33 spp.) being amongst the most important in terms of abundance and biomass. In this second chapter, we focused on answering the three remaining PRA. For that, we organized this chapter over three articles and proposed a comprehensive study on the ecology of these highlighted species. We used information on their abundance, distribution, diversity, and physical and chemical habitat. Additionally, we also included information on their trophic ecology by combing gut content analyses with stable isotope data (carbon and nitrogen) carried out on the mesopelagic fishes and their main trophic links, including zooplankton, crustaceans, fish larvae, and epi- and bathypelagic potential predators. Finally, we constructed conceptual models to describe their niche partitioning, functional groups, and ecosystem roles across large oceanic areas.

List of articles included in this chapter:

Article 6: **Eduardo L.N.**, et al. 2020. Hatchetfishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic. *Progress in Oceanography*. https://doi.org/10.1016/j.pocean.2020.102389.

Article 7: **Eduardo L.N.**, et al. Distribution, vertical migration, and trophic ecology of lanternfishes (Myctophidae) in the western Tropical Atlantic. *Progress in Oceanography* (***under review***).

Article 8: **Eduardo L.N.**, et al. 2020. Trophic ecology, habitat, and migratory behaviour of the viperfish *Chauliodus sloani* reveal a key mesopelagic player. *Scientific Reports* https://doi.org/10.1038/s41598-020-77222-8

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Hatchetfishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic

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ABSTRACT

Species of the family Sternoptychidae (hatchetfishes) occur worldwide and play critical roles by sequestering carbon, recycling nutrients, and acting as a key trophic link between epipelagic primary consumers and higher trophic levels in marine ecosystems. Nevertheless, basic knowledge on their ecology is still lacking and their functional ecology remains understudied with respect to composition, organization, functions and environment interactions. Here we integrated comprehensive information collected in the western Tropical Atlantic on the diversity, abundance, distribution and trophic ecology of hatchetfishes, including physicochemical features of their habitats and extensive carbon and nitrogen stable isotope data on its main prey groups. On this basis we defined five functional groups of hatchetfishes with different diet preference, isotopic composition, and vertical abundance peaks and reveal a possible high resource partitioning. Additionally, these species might have a different feeding tie chronology. Hence, hatchetfishes segregate in different ecological groups responding differently to environmental constraints including oxygen concentration and presenting diverse functional roles. As deep-sea species that migrate to epipelagic waters, hatchetfishes may play a key role in the transfer of subsurface photoassimilated carbon to deeper waters, a pathway through which the effects of climate change at the surface are transferred to the deep ocean. Moreover, as consumers of gelatinous organisms, these species convert "gelatinous energy" into "fish energy" readily usable by higher trophic levels, including endangered and commercially important species. This is a crucial trophic relationship that has been historically underestimated due to methodology limitations (e.g., quickly digested gelatinous organisms were probably underestimated in previous studies, based solely on stomach contents). Considering in ecosystem models this trophic relationship, as well as the functional organization of hatchetfishes, is important to properly answer key ecological questions including resource use, carbon transportation, and influence of mesopelagic community in climate change process.

1. Introduction

Mesopelagic fishes, distributed from the surface to approximately 1000 m, are numerically the most important vertebrate component of all temperate and tropical oceanic waters (Gjøsaeter and Kawaguchi, 1980; Irigoien et al., 2014). Most part of these communities forms high-density biological layers at around 500 m in search of predator refuge during daytime (Sutton, 2013), and ascend to epipelagic layers (0–100 m) at night for feeding, following the diel vertical migration of zooplankton (Merrett and Roe, 1974). This "largest daily migration of animals on earth" (Hays, 2003) represents a major mechanism for transporting organic matter below the euphotic zone (St. John et al.,

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2016). Mesopelagic fishes play a critical role in marine ecosystems by sequestering carbon, recycling nutrients, and acting as a key trophic link between primary consumers and higher trophic levels (e.g. larger fish, mammals and sea-birds) (Hedd and Montevecchi, 2006; Cherel et al., 2010; Drazen and Sutton, 2017).

In terms of abundance and biomass, representatives of the family Sternoptychidae (hatchetfishes) are one of the most conspicuous components of the mesopelagic ichthyofauna (Gjøsaeter and Kawaguchi, 1980). In the eastern Tropical Atlantic, for example, hatchetfishes are amongst the most abundant and diverse mesopelagic fish group (Olivar et al., 2017, Olivar et al., 2018). This family, which occurs in all oceans, includes 73 valid species that usually present small body size (< 100 mm of standard length, SL), numerous photophores and a highly variable intergeneric body morphology (Nelson et al., 2016). Previous studies on hatchetfishes provided important knowledge on biodiversity, abundance, vertical migration and feeding habits (e.g. Hopkins and Baird, 1985; Olivar et al., 2012; Carmo et al., 2015). Hatchetfishes are classified as a complex midwater group presenting a variety of migration patterns and feeding behaviour (Hopkins and Baird, 1985; Carmo et al., 2015). For instance, while vertical migration patterns are observed in some species (Hopkins and Baird, 1985; Kinzer and Schulz, 1985), it seems to be absent in others (Olivar et al., 2017). Hence, this taxonomic group may be constituted by different functional groups with diverse spatiotemporal distribution, responding differently to environmental constraints, and having distinct ecological roles.

Characteristics in terms of trophic ecology, habitat, distribution and migration patterns allow classifying species by functional groups, which is a powerful approach to investigate effect of species on ecosystem functions, functional equivalence among species, and organisms adaptation to changing environmental conditions (McGill et al., 2006; Villéger et al., 2017). However, this approach requires integrated knowledge on biophysical and ecological aspects of the species that is often lacking in mesopelagic ecosystems. As an example, the ecology of hatchetfishes and how they interact with their environment remains poorly known worldwide and unexplored in many large oceanic areas, such as in the western Tropical Atlantic. Additionally, although knowledge on mesopelagic trophic ecology has progressively improved in the last decades, comprehensive food web studies considering multiple approaches are still scarce. Indeed, previous studies on the trophic ecology of hatchetfishes were mostly based on gut content analyses (GCA) (e.g. Hopkins and Baird, 1981; Sutton and Hopkins, 1996b; Carmo et al., 2015). Whilst GCA may provide high taxonomic resolution of the diet, the approach is restricted by its short temporal representation and includes biases due to prey misidentification (Hyslop, 1980). Furthermore, the importance of key prey groups that are quickly digested (e.g. gelatinous organisms) remains underestimated, hampering a more complete understanding of pelagic food webs (Hopkins and Baird, 1985; Hidalgo and Browman, 2019). Alternatively, stable isotope analysis (SIA) is a useful tool to study food web structure, as it provides time-integrated information on all the material assimilated by organisms, including prey that are usually not accounted on GCA (Cherel et al., 2008; Post, 2002). Hence, combining both GCA and SIA allows for a more comprehensive picture of the flows of biomass across trophic compartments.

Here, we propose a comprehensive study on hatchetfishes by taking advantage of a set of data combining information on their abundance, distribution, diversity, trophic ecology and physical and chemical habitat. We combined gut content analyses with stable isotope data carried out on particulate organic matter, hatchetfishes and on their most likely prey, including zooplankton, crustaceans, fish larvae, and gelatinous organisms. Data were acquired around oceanic islands and seamounts in the western Tropical Atlantic, a poorly studied area of high biodiversity where Marine Protected Areas and Ecologically or Biologically Significant Marine Areas have been established (EBSAs; CBD, 2014). Specifically, we aim at answering the following questions: (i) what are the main species and functional groups of hatchetfishes, (ii) where are they distributed, (iii) what are the features of their diel vertical migration, (iv) what are their main prey and trophic relationships, and (v) how are they related with physical–chemical oceanographic conditions? Finally, as a synthesis, we propose a conceptual model describing the use of the environmental and trophic habitat of functional groups of hatchetfishes.

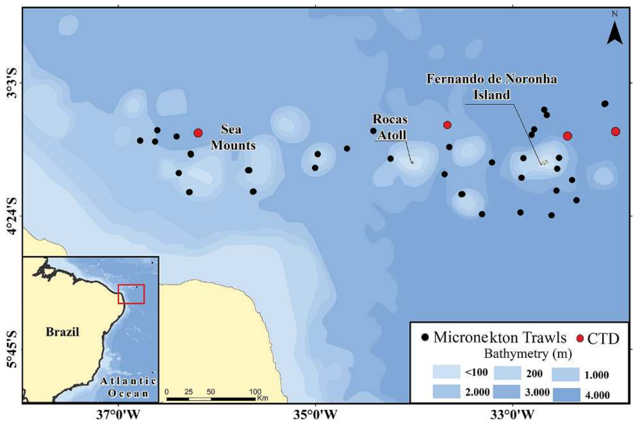

Fig. 1. Study area with the CTD and micronekton-trawl sampling stations.

2. Material and methods

2.1. Study area

The study area comprises the surroundings of Rocas Atoll (3°52′S, 33°49′W), Fernando de Noronha Archipelago (3°50′S, 32°25′W) and adjacent seamounts (Fig. 1). Located in the western Tropical Atlantic, an oligotrophic area, these islands cause eddies and turbulences that drive subsurface enriched waters to the surface, increasing primary production and therefore enhancing mass and energy fluxes throughout the food web (Travassos et al., 1999; Tchamabi et al., 2017). As a consequence, this large biogeographic unit has been referred to as an “oasis of life in an oceanic desert” (Hazin, 1993) and classified as ‘EBSA - Banks Chain of Northern Brazil and Fernando de Noronha’, a special area in the ocean of fundamental importance for biodiversity and life cycles of several marine species (CBD, 2014).

2.2. Data

Data were collected over 31 sampling stations (Fig. 1, Suppl. Material 1) during the scientific survey ABRACOS 2 (Acoustics along the BRAzilian COaSt 2), conducted onboard the R/V *Antea* from 9th April to 6th May 2017 (Bertrand, 2017). Conductivity, Temperature, Depth and Oxygen hydrographic profiles were collected using a CTDO SeaBird911 +. Particulate organic matter (POM) was sampled by filtering seawater from the maximum fluorescence depth through GF/F filters (47 mm), followed by a dry proceeding of 36 h (40 °C). Zooplankton samples were collected using a Bongo net (60 cm of mouth diameter and mesh size of 300 µm) that was obliquely towed from 200 m depth up to the surface.

Mesopelagic fishes, crustaceans and gelatinous organisms were collected during day and night with a micronekton trawl (body mesh: 40 mm, cod-end mesh: 10 mm) from 10 to 1113 m depth for about 30 min at 2–3 knots (Fig. 1). Targeted depth was defined for each tow according to the presence of acoustic scattered layers or patches, as observed using a Simrad EK60 (Kongsberg Simrad AS) split-beam scientific echosounder operating at 38, 70, 120 and 200 kHz. Except the layers 200–300 and 700–800 at night, where no aggregation of organism was observed through acoustics, all depth strata were sampled at least once (Suppl. Material 1). Tow duration was considered as the moment of the arrival of the net on the pre-set depth to the lift-off time, recorded by means of a SCANMAR system. The net geometry was monitored using SCANMAR sensors providing headline height, depth, and distance of wings and doors. As the trawl did not have any opening or closing mechanism, the collection of specimens during the lowering or hoisting of the net was reduced as much as possible by decreasing ship velocity and increasing winch speed.

Hatchetfishes and their potential food were sorted to the lowest taxonomic level and frozen or, in the case of rarity or taxonomic uncertainty, fixed in a 4% formalin solution for one month and then preserved in a 70% alcohol solution. At the laboratory, individuals were identified, measured (nearest 0.1 cm of standard length, SL) and weighed (nearest 0.01 g of total weight, TW). Voucher specimens were deposited in the Fish Collection of the “Instituto de Biodiversidade e Sustentabilidadae” (NUPEM), Universidade Federal do Rio de Janeiro (UFRJ).

2.3. Hatchetfishes catch composition, abundance and vertical migration

The relative index of fish abundance (Catch Per Unit of Effort–CPUE) was calculated considering the number of specimens per hour, standardized to a similar mouth area of 120 m^2 (estimated through SCANMAR sensors). These values were obtained for each species considering the period of the day (day/night), depth strata (10–1000 m, intervals of 100 m) and sample stations. Daytime was considered to the extend from one hour after sunrise to one hour before sunset, while the night was from one hour after sunset to one hour before sunrise. Dawn or dusk samples were discarded when studying day/night vertical distributions. Migration patterns were classified as synchronous migrant (entire population responds synchronously to daily light variation), asynchronous migrant (only part of the population responds synchronously to diel daily light variation), and non-migrant (no evidence of vertical migration) (Sutton and Hopkins, 1996a). Patterns of interaction among hatchetfishes and their environment were analysed by combining data on vertical distributions and mean profiles of temperature and oxygen.

2.4. Trophic ecology

Two approaches were implemented to assess the trophic ecology of hatchetfishes: Gut Content Analyses (GCA) and Stable Isotopes Analyses (SIA). The GCA was applied for four species with at least 15 non-empty stomachs, following the method developed by Sutton and Hopkins (1996b): *Argyropelecus aculeatus, A. affinis, Sternoptyx diaphana,* and *S. pseudobscura*. Each specimen was dissected for removal of the digestive apparatus and only stomachs were analysed, with contents being removed and sorted into major taxa under a stereoscope.

Wherever is possible, consumed prey size measurements to the nearest 0.1 mm were carried out with a binocular stereoscope using an ocular micrometric scale. We measured the standard length of fishes; back of eye socket to tip of telson (excluding terminal spines) of decapods; tip of rostrum to tip of telson (excluding terminal spines) of euphausiids; anterior end of eyes to tip of uropods or telson (depending which was longer) of amphipods; valve length of ostracods; prosome length of copepods; maximum shell length of pteropods (Carmo et al., 2015). For very small-sized prey, food items were fixed in a labelled glass slide and measured using a microscope to the nearest 0.1 mm.

The contribution of each prey taxon to the composition of the diet was assessed using three metrics computed by pooled stomachs: frequency of occurrence (%FO), numerical abundance (%N) and weight percentage (%W) (Hyslop, 1980). The vacuity index (VI, %) was calculated as follows: $VI = \frac{Nv}{Ne}x100$, where Nv is the number of empty stomachs and Ne the total number of examined stomachs. This index was calculated for each species considering day, night, and pooled periods. The feeding strategy was characterized through the modified Costello diagram (Amundsen et al., 1996), a graphic representation of prey items that allows the inference about the degree of the diet variability of a predator. Through this analysis, it is possible to plot the consumed prey specific importance of each consumed prey taxa against the frequency of occurrence in 2D diagram, with three axes representing the feeding strategy, prey importance, and niche width. For this analysis, the prey-specific abundance was calculated as follows: $P_i = (\sum S_i \sum S_{ti}) \times 100$, where P_i is the prey-specific abundance of prey i, S_i is the total abundance (in number) of prey i, and S_{ti} is the total stomach content in only those specimens with prey i in their stomachs. Niche breadth was estimated by Levin’s standardized index as follows (Levins, 1968): $B_J = \frac{1}{n-1}(\frac{1}{\sum p_{ij}^2} - 1)$, where B_j is the Levin's standardized index for predator j, whereas p_{ij}^2 is the proportion in weight of prey i in the diet of predator j and n is the number of prey categories. This index ranges between 0 and 1, indicating a generalist diet when a high value is obtained and a diet dominated by few prey items (specialist predator) when the index has a value close to zero.

The stable isotope analyses were conducted on five hatchetfishes species. Additionally, isotopic information on POM and on the following potential hatchetfishes prey were included: two fish larvae groups (Teleostei larvae 15–20 mm and Teleostei larvae 5–10 mm); five crustaceans; five gelatinous groups (divided into Siphonophorae and Thaliacea), and zooplankton (200–500 µm, mainly composed by copepods) (Table 1). Potential hatchetfishes prey were selected based on stomach contents analyses and literature (e.g. Hopkins and Baird, 1985; Carmo et al., 2015; Bernal et al., 2015). Despite not identified at species levels, fish larvae were grouped into size-classes, diminishing the isotopic variability within groups. The size of all prey groups was selected aiming to be size-adequate for hatchetfishes ingestion (based on prey size previously reported on literature). For isotopic analyses, the following soft tissues were extracted: white dorsal muscle for fishes, abdomen for crustaceans and body wall for larvae and gelatinous. After removal, soft tissues were cleaned with distilled water to remove exogenous material such as carapace, scales, and bones. Whole zooplankton samples have been stored in Eppendorf micro tubes. Samples were dried in an oven at 60 °C for 48 h and grounded into a fine powder with a mortar and pestle. In order to obtain unbiased values of $\delta^{13}C$, zooplankton and POM samples was separated to remove the carbonates. Zooplankton were acidified according to Cresson et al. (2012) by adding approximately 2 ml of 0.5 mol.l^{-1} hydrochloric acid (HCl). POM filters were exposed to hydrochloric acid (HCl) vapour. After 4 h, the filters and zooplankton were dried at 40 °C during 36 h. Untreated sub-samples of POM and zooplankton were used to measure $\delta^{15}N$ and acidified one for $\delta\ ^{13}C$. Each sample was analysed for carbon and nitrogen isotope ratios through a mass spectrometer (Thermo Delta V+) coupled to an element analyser (Thermo Flash 2000, interface Thermo ConFio IV) in the Platform Spectrometry Ocean (PSO, IUEM), France. Results of stable isotope analysis for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are derived from the relation of the isotopic value from the sample and

Table 1
List of hatchetfishes and potential prey groups analysed for stable carbon and nitrogen isotopic compositions.

Group	Category	Species	
Hatchetfishes	predator	*Argyropelecus aculeatus*	*Sternoptyx diaphana*
	predator	*Argyropelecus affinis*	*Sternoptyx pseudobscura*
	predator	*Argyropelecus hemigymnus*	–
Fish larvae	potential prey	Teleostei larvae 15–20 mm	Teleostei larvae 5–10 mm
Crustaceans	potential prey	*Euphausia gibboides*	Pasiphaeidae sp.
	potential prey	*Euphausia* sp.	*Phronima* sp.
Siphonophorae	potential prey	*Abylopsis tetragona*	Siphonophorae sp.
Thaliacea	potential prey	*Salpa* sp.	*Soestia zonaria*
	potential prey	*Pyrosoma atlanticum*	–
Zooplankton	potential prey	200–500 µm, mainly composed by copepods	

a known standard: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$; in which R corresponds to the ratio between ^{13}C:^{12}C or ^{15}N:^{14}N. As differential lipid contents can bias the interpretation of $\delta^{13}C$ values, here we explored the potential lipid bias by using % elemental by mass C:N ratios and the relationship between C:N (i.e., lipid content) and $\delta^{13}C$. As samples were not treated to remove lipids before analysis to prevent loss of material, the few prey groups that exhibited C:N dynamics consistent with high lipid content (C:N > 3.5) were normalized using the equation for aquatic animals provided by Post et al. (2007): $\Delta\delta^{13}C = -3.32 + 0.99 \times C{:}N$. $\Delta\delta^{13}C$ is the change in $\delta^{13}C$ caused by lipids and C:N is the carbon-to-nitrogen ratio (by mass) of the sample.

Fish trophic position (TP_{SIA}) based on nitrogen stable isotopes was assessed based on the following equation (Post, 2002):

$$TP_{SIA} = \lfloor(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/TDF\rfloor + TP_{baseline}$$

where $\delta^{15}Nc_{onsumer}$ and $\delta^{15}N_{baseline}$ are the $\delta^{15}N$ values of the target consumer and the baseline respectively; TDF is the trophic discrimination factor and $TP_{baseline}$ is the trophic position of the baseline. As POM may be influenced by the co-occurrence of detritus (Montoya et al., 2002) and microzooplankton in the water column (Post, 2002), primary consumers (TP2) are usually a better isotopic baseline to assess TP. Following the methodology of previous studies on the trophic position of mesopelagic fishes (Cherel et al., 2010; Ménard et al., 2014), the baseline utilized was the Salps, which are known to be filter-feeders primary consumers grazing on phytoplankton and other small food items. To account for uncertainty in TL estimation, a Bayesian model was incorporated in the calculation of TP_{SIA} using predict $\delta^{15}N$ values of hatchetfishes and a TDF of 3.15‰ ± 1.28‰ (McCutchan et al., 2003). For comparison, trophic positions were also estimated using stomach content data (TP_g) (Adams et al., 1983), applying the equation:

$$TP_{SCA} = \sum (W_i T_i) + 1$$

where, W_i and T_i are the relative weight and the trophic position of the *i*th prey item respectively (adapted from Winemiller, 1990). W_i is the weight of prey *i* divided by the total weight of prey items.

The Bayesian mixing model, MixSIAR (Stock and Semmens, 2013), provides the most accurate estimations of source or prey contributions when tissue and species-specific discrimination factors are used (Caut et al., 2008). We applied this analysis to estimate the relative contribution of specific prey of hatchetfishes to their diet. Potential dietary endpoints applicable to hatchetfishes included in SIAR analysis were derived from stomach contents analyses and published information (e.g. Bernal et al., 2015; Carmo et al., 2015; Hopkins and Baird, 1985). The following prey groups were included (Table 1): (i) Zooplankton; (ii) *Abylopsis tetragona* (Siphonophorae); (iii) *Euphausia gibboides* (Euphausiacea); (iv) *Phronima* sp. (Amphipoda); (v) *Salpa* sp. (Thaliacea); (vi) *Soestia zonaria* (Thaliacea); (vi) Teleostei larvae 15–20 mm (Teleostei), and (vii) Teleostei larvae 5–10 mm (Teleostei). As trophic discrimination factors for mesopelagic fishes are poorly known, according to previous studies (Richards et al., 2018; Valls et al., 2014) we run mixing models using discrimination factors of 3.15‰ ± 1.28‰ and 0.97‰ ± 1.08‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively (Sweeting et al., 2007; Cherel et al., 2010; Ménard et al., 2014).

All statistical analyses were performed with R version 3.4.4, using the packages *SIAR* (Stable Isotope Analysis in R; Parnell et al., 2010) and *SIBER* (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011) for the estimation of isotopic niche areas and overlaps and Mixing models respectively. The package *tRophicPosition* (Bayesian Trophic Position Calculation with Stable Isotopes; Quezada-Romegialli et al., 2017) was used for trophic positions calculations.

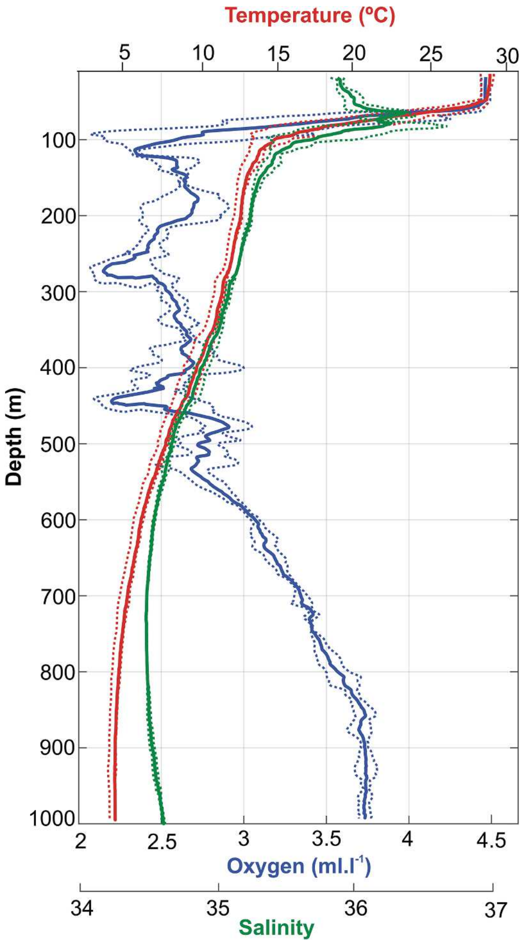

Fig. 2. Mean and standard deviation of vertical profiles of temperature (red), salinity (green) and dissolved oxygen (blue) off oceanic islands of the western Tropical Atlantic between April and May 2017.

3. Results

3.1. Oceanographic conditions

Throughout the study area, the surface layer was characterized by warm waters (28 °C) within a shallow (~50 m) and homogeneous mixed layer (Fig. 2). The temperature profile was characterized by a sharp thermocline extending from 86 m to 132 m, presenting a thermal difference of 12.3 °C from the upper to the lower limit of the thermocline. The vertical profile of salinity was quasi-homogeneous, with the highest gradient located between 80 and 120 m. The profile of dissolved oxygen concentration was homogeneous within the mixing layer, decreasing at the upper limit of the thermocline and usually presenting three minima, at depths of 110 m, 280 m, and 450 m. In contrast to the decreasing temperature and salinity, the dissolved oxygen slowly increased below 550 m. Within our study area, the vertical profiles of temperature, salinity and oxygen were very homogeneous.

3.2. Hatchetfishes catch composition, abundance and vertical migration

The thirty-one hauls conducted off the northeast Brazilian oceanic islands corresponded to an effort of 695 min and 76 km of trawled distance. A total of 1756 specimens of hatchetfishes were collected, comprising the following genera and species: *Argyropelecus* (*A. aculeatus, A. affinis, A. gigas, A. hemigymnus, A. sladeni*), *Sternoptyx* (*S. diaphana, S. pseudobscura*, and *S. pseudodiaphana*), and *Valenciennellus*

Table 2

Absolute number of specimens (*n*), frequency of occurrence in relation to overall samples (FO%), depth range, observed migration pattern (AM: asynchronous migrant; NM: non-migrant), standard length [mean ± standard deviation (range)], total weight [mean ± standard deviation (range)], temperature (T) and dissolved oxygen (DO) range of hatchetfishes occurrence from oceanic islands and seamounts of the western Tropical Atlantic. *Pattern derived from a very small number of specimens.

Species	*n*	FO%	Depth (m)	Migration pattern	Standard length (cm)	Total weight (g)	T (°C)	DO ($ml.l^{-1}$)
Argyropelecus aculeatus	53	26	200–1000	AM	5.2 ± 1.3(3.0–8.2)	6.0 ± 4.8(0.89–20.99)	4.5–12.0	1.9–3.6
Argyropelecus affinis	427	31	50–800	AM	5.2 ± 0.8(2.7–8.2)	2.6 ± 1.3(0.31–6.96)	5.0–29.0	1.9–4.5
Argyropelecus gigas	9	9	600–700	NM*	8.6 ± 0.4(7.8–9.1)	14.2 ± 2.4(10.49–17.00)	5.0–6.0	2.8–2.9
Argyropelecus hemigymnus	49	34	300–1000	NM	2.4 ± 0.4(1.4–3.6)	0.3 ± 0.1(0.10–0.66)	4.5–12.0	1.9–3.6
Argyropelecus sladeni	26	23	50–800	AM	5.1 ± 0.9(3.2–6.6)	3.7 ± 1.7(0.71–7.20)	5.0–29.0	1.9–4.5
Sternoptyx diaphana	1076	43	130–1000	AM	2.2 ± 0.4(1.1–4.3)	0.6 ± 0.4(0.05–4.30)	4.5–15.0	1.9–3.6
Sternoptyx pseudobscura	118	23	520–1000	NM	3.5 ± 1.1(1.3–5.9)	2.4 ± 1.7(0.24–7.60)	4.5–7.0	2.3–3.6
Sternoptyx pseudodiaphana	3	6	850–1000	NM*	4.9 ± 0.8(4.2–5.9)	6.9 ± 2.5(5.29–9.94)	4.5–5.0	2.3–3.6
Valenciennellus tripunctulatus	4	9	400–430	NM*	3.1 ± 0.1(3.1–3.2)	0.2 ± 0.0(0.19–0.22)	9.0–9.0	1.9–2.5

(*V. tripunctulatus*) (Table 2). The most abundant species were *S. diaphana* and *A. affinis*, representing together 85% of individuals by number. *Argyropelecus gigas, S. pseudodiaphana,* and *V. tripunctulatus* were relatively rare, representing together less than 1% of all specimens (Table 2). Overall, standard length of sampled specimens ranged from 2.2 cm (*S. diaphana*) to 8.6 cm (*A. gigas*) (Table 2, Suppl. Material 2).

Argyropelecus aculeatus abundance peaked from 500 to 600 m at daytime, with its distribution ranging from 300 to 1000 m (Fig. 3). At night, the vertical distribution of this species expanded to 100–1000 m depth and was polymodal, possibly indicating that only part of the population performed diel vertical migration. Water temperature range for this species varied from 4.5 to 12 °C, with no occurrence above the thermocline or within the zones of minimum oxygen concentrations (Table 2). *Argyropelecus affinis* and *A. sladeni*, presented very similar vertical distribution and migration patterns, with a peak in abundance at 400–500 m during daytime and at 0–100 m at night (Fig. 3). Both species presented a broad polymodal distribution (0–1000 m) and temperature range (5–29 °C), being, however, able to swim close/above the upper thermocline layer (50 m). In addition, at daytime, the peak of abundance for both species coincided with the layer of lowest oxygen concentration (1.9 $ml.l^{-1}$) (Table 2). *Argyropelecus hemigymnus* presented two peaks of abundance during daytime (300–400 m, 700–800 m), being found between 4.5 and 12 °C and in oxygen minimum layers (300–400 m) (Fig. 3).

Sternoptyx diaphana was the only species of the genus presenting vertical migration. It was mostly distributed in the range 700–900 m during both day and night, but a small portion of the population was observed migrating up to 100–200 m at night. This species was found between 4.5 and 15 °C and showed no clear relationship with oxygen minimum layers. *Sternoptyx pseudobscura* did not present diel vertical migration patterns, being more frequent at 800–1000 m (4.5–5 °C). Finally, only a short size range and few specimens of *Argyropelecus gigas*, *Valenciennellus tripunctulatus*, and *S. pseudodiaphana* were sampled, precluding inferences about the vertical distribution or migration of these species (Fig. 3).

Horizontally, *A. aculeatus* and *A. affinis* were collected along the entire latitudinal range, showing the highest values of abundance in the seamount areas (Fig. 4). *Argyropelecus hemigymnus, A. sladeni, Sternoptyx diaphana*, and *S. pseudobscura* were also found in a relatively broad latitudinal range, but highest values of abundance were located at the east side of Fernando de Noronha. *Sternoptyx pseudodiaphana* and *V. tripunctulatus* were only captured off Fernando de Noronha and Rocas Atoll. Finally, *Argyropelecus gigas* was sampled at two locations around the seamount areas and one close to Rocas Atoll.

3.3. Gut content analyses

Among the 361 individuals analysed, 305 (84%) had stomachs with content. Stomachs with content represented 90% and 57% of those sampled at night and at daytime, respectively (Table 3). For *Argyropelecus aculeatus,* 14 stomachs had content and few prey items were identified. All stomachs analysed for this species came from fish caught during the day. *Argyropelecus aculeatus* fed largely on juveniles of hatchetfishes (63%W) and *Euphausia* spp. (36% W), occasionally complementing its diet with amphipods (6% FO) (Fig. 5; Table 3). *Sternoptyx pseudobscura* presented the highest percentage of stomachs with content and high prey diversity. The vacuity index for this species was 2.8% and 0% during the day and at night, respectively. *Sternoptyx pseudobscura* fed predominantly on unidentified Teleostei (32% W), *Euphausia* spp. (24%W), and gelatinous organisms belonging to the class Thaliacea (12%W). Likewise, *S. diaphana* presented a high percentage of stomachs with content, high prey diversity, and relatively low vacuity index (17% day; 14% night). This species fed predominantly on *Euphausia* spp. (21% W), Teleostei larvae (17%W), and amphipods (15% W). Finally, *A. affinis* diet was essentially composed of unidentified Teleostei (32%W), Teleostei larvae (24%W), Gonostomatidae (13%W), and *Euphausia* spp. (9%W). For this species, the vacuity index was 100% and 9% during the day and at night, respectively (Fig. 5; Table 3).

The Costello diagrams of all species showed a high proportion of points positioned towards the lower and upper portion of the vertical y-axis of the graph, indicating a generalist habit with some prime prey groups (*Euphausia* spp., Teleostei and Thaliacea). This generalist behaviour, with main prey groups, is confirmed by the intermediary-high values of Levins standardized index for *A. affinis* (Bi = 0.88), *S. pseudobscura* (Bi = 0.69), and *S. diaphana* (Bi = 0.47), which indicate a moderate-broad trophic niche breadth. *Argyropelecus aculeatus,* however, presented a restricted niche breadth (Bi = 0.29).

3.4. Stable isotope analysis

Mean δ^{13}C values for hatchetfishes were similar among species, with a difference of only 1‰ separating the most depleted (*S. pseudobscura*: −19.08 ± 0.11‰) and the most enriched species (*A. aculeatus*: −17.98 ± 0.35‰) (Table 4; Fig. 6). However, a much higher range was found between δ^{15}N mean values, with 3.9‰ separating the most enriched (*A. affinis*: 11.85 ± 0.27‰) and the most depleted species (*A. aculeatus*: 7.95 ± 1.29‰) (Table 4; Fig. 6). Considering prey groups, crustaceans included the most δ^{13}C and δ^{15}N enriched taxa, with mean isotopic values raging from 7.31 ± 0.5‰ and −19.47 ± 0.51‰ (*Euphausia* sp.) to 5.88 ± 0.28‰ and −19.03 ± 0.18‰ (*Phronima* sp.) for δ^{15}N and δ^{13}C respectively. Gelatinous organisms (Siphonophorae and Thaliacea) showed a wide range of stable isotopic values, ranging from 2.99 ± 0.68‰ (*Pyrosoma atlanticum)* and −20.27 ± 0.25‰ (*Soestia zonaria*) to 9.10 ± 0.25‰ and −19.25 ± 0.04‰ (Siphonophorae sp.) for δ^{15}N and δ^{13}C respectively. The zooplankton presented mean isotopic values of 3.04 ± 0.60‰ for δ^{15}N and − 19.45 ± 0.31‰ for δ^{13}C. Lastly, the POM had the mean isotopic values of 2.82 ± 1.19‰ and − 22.41 ± 0.69‰. Based on the TEF assumed for δ^{15}N

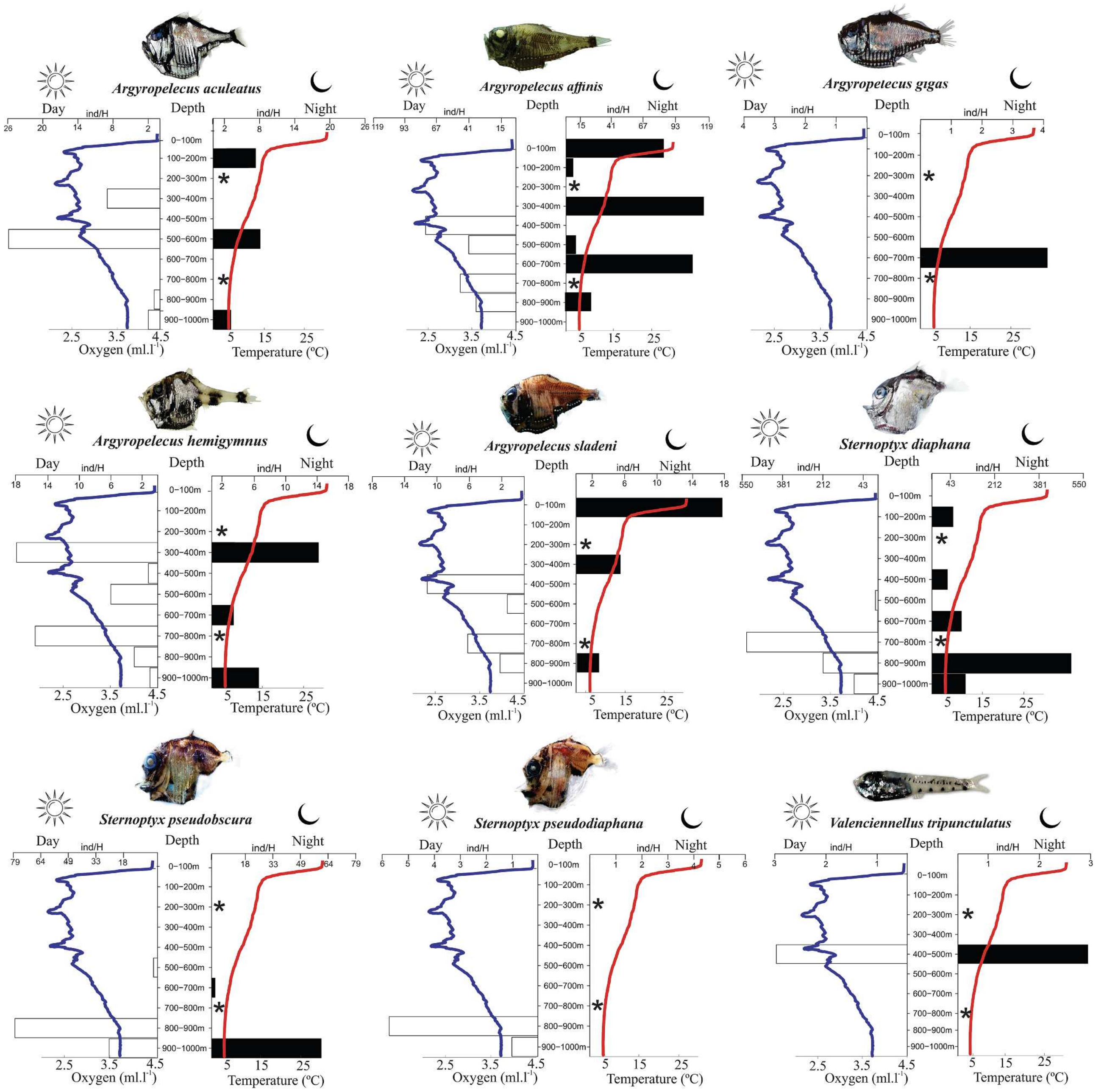

Fig. 3. Average relative abundance (individuals.hour^{-1}) per depth strata and day period of hatchetfishes species from oceanic islands and seamounts of the western Tropical Atlantic. Coloured lines represent the average vertical profile of temperature (red) and dissolved oxygen (blue). * Depth strata not sampled. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(3.15 ± 1.28‰), the zooplankton and Thaliacea species mostly represented primary consumers, while crustaceans, Siphonophorae and Teleostei larvae were secondary consumers. Hatchetfishes are thus a mixing of secondary and tertiary consumers.

The mean trophic levels calculated by isotopic analyses (TP_{sia}) ranged from 2.9 ± 0.3 (*A. aculeatus*) to 3.7 ± 0.2 (*A. affinis*) (Fig. 6). Compared with TP_{sia}, the gut content trophic levels (TP_g) were higher in all cases: *A. aculeatus* (3.8 *vs*. 2.9 ± 0.3), *S. pseudobscura* (3.7 *vs*. 3.1 ± 0.3), *A. affinis* (3.8 *vs*. 3.7 ± 0.2) and *S. diaphana* (3.6 *vs*. 3.4 ± 0.3).

The mixing model is in general agreement with the stomach content analyses (SCA) (Table 5). However, in comparison with SCA, the isotopic analyses showed a much higher contribution (up to 40%) of gelatinous prey (Thaliacea and Siphonophorae). Overall, *Abylopsis tetragona*, *Euphausia gibboides*, *Phronima* sp., and Teleostei larvae 15–20 mm were the most important prey for all species of the genus *Argyropelecus*. For *S. diaphana,* the most important prey was *Soestia zonaria*, *Phronima* sp. and Teleostei larvae 5–10 mm. Lastly, the major prey for *S. pseudobscura* were *Euphausia gibboides, Soestia zonaria*, and Teleostei larvae 5–10 mm.

4. Discussion

In the present study, we define functional groups based on the use of the vertical habitat and the trophic ecology to provide a novel vision of hatchetfishes ecology. Indeed, we reveal an important environmental and ecological niche partitioning among groups with further consequences in terms of ecological processes in pelagic ecosystems, including predator–prey relationships. Among other, we show that hatchetfishes forage more on gelatinous than previously considered,

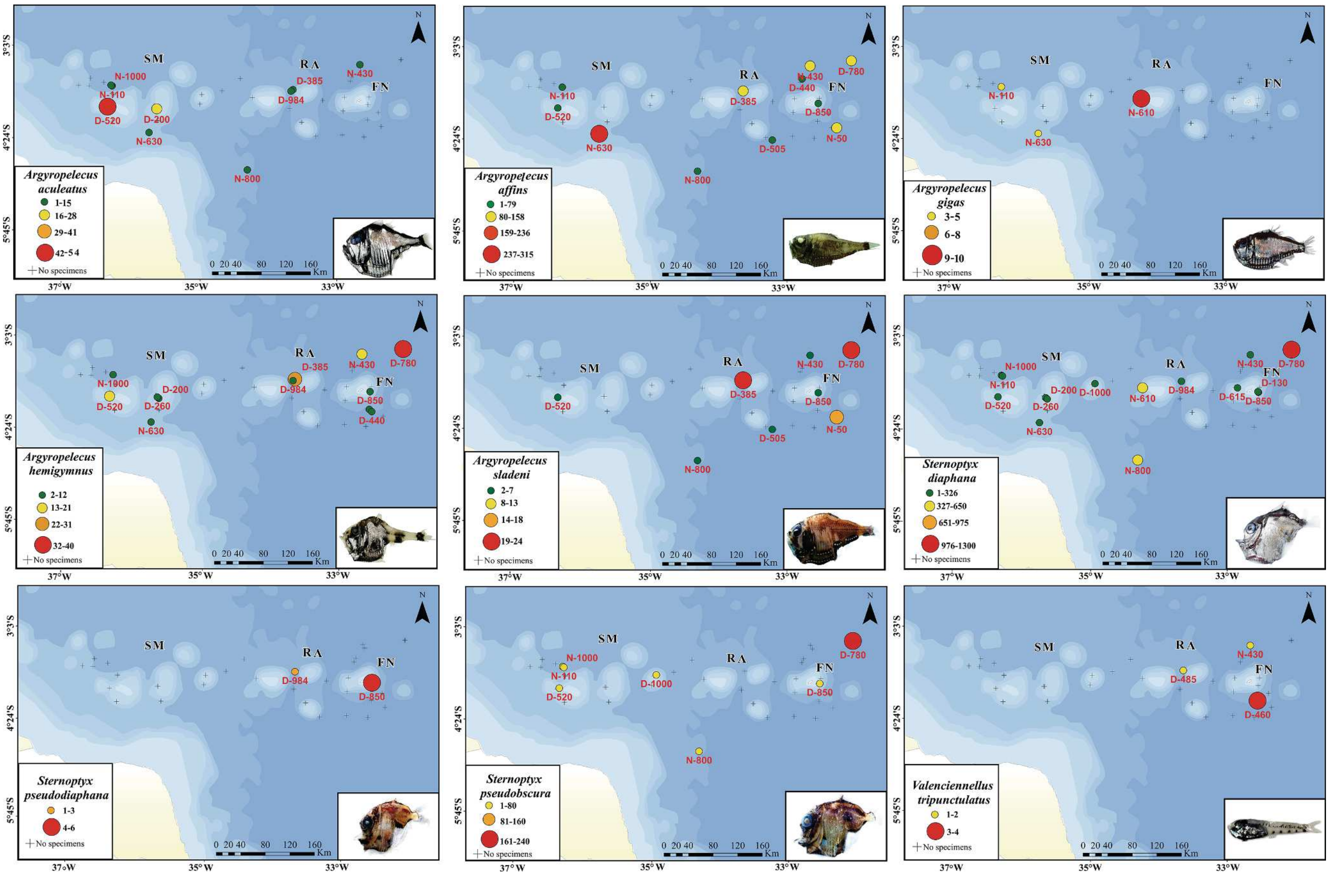

Fig. 4. Catch per unit of effort (CPUE; individuals/hour) of hatchetfishes from oceanic islands and seamounts of the western Tropical Atlantic. SM–seamounts; RA–Rocas Atoll; FN–Fernando de Noronha Archipelago; D–day; N–night; red numbers–depth.

with important consequences for the energetic transfer in the food web but also vertically in the water column. Additionally, for the first time we describe the habitat, vertical migration and, trophic ecology of hatchetfishes along the western Tropical Atlantic.

Before interpreting our data some considerations should be made regarding our methodology. First, mesopelagic fishes usually present efficient net avoidance behaviour (Kaartvedt et al., 2012) and, as in all studies based on trawls, the micronekton net we used might not be equally selective for all species. Thus, the diversity of hatchetfishes observed here may not be only a consequence of biogeographic patterns of this group, but also reflects the gear selectivity. Further, despite we took precautions to avoid collection of specimens during the lowering or hoisting (see methodology), our gear did not have an opening or closing mechanism. For that reason, we focused on the major patterns of vertical migration, avoiding a precise quantification of standing stocks in different depth strata. Finally, the trophic analyses might be influenced by sample number, fish size, season, depth, geographic location, taxonomic identification of prey, and species utilized to run mixing models. Due to the rarity and low sample number of some of the studied species (e.g. *A. gigas*, *S. pseudodiaphana*, and *V. tripunctulatus*), it was not possible to test all these variables in our study. The analyses were conducted by coupling stomachs and mixing several size classes (e.g. juveniles and adults), which may lead to loss of information on ontogenetic variation of both vertical behaviour and trophodynamics patterns (Olivar et al., 2017; Olivar et al., 2018; Silveira et al., 2020). Therefore, we do not aim at exhaustively describe the trophic ecology and vertical behaviour of all hatchetfishes but at providing new valuable information for an important understudied group worldwide.

We captured nine species of hatchetfishes along the oceanic islands of the Western Tropical Atlantic (WTA), being the second most important mesopelagic fish group in terms of biomass and abundance (30% of all specimens collected in micronekton trawls), after myctophids (L. N. Eduardo, unpublished data). Six additional species of Sternoptychidae have also been recorded in the western South Atlantic: *Argyripnus atlanticus*, *Maurolicus stehmanni*, *M. weitzmani*, *Polyipnus clarus*, *P. laternatus*, and *Sonoda megalophthalma* (Lima et al., 2011; Lins Oliveira et al., 2015). Hence, with a total of 15 valid species (our study and the literature), the richness of sternoptychids in the western South Atlantic is similar to those reported in the western (Harold, 2003) and eastern Central Atlantic (Harold, 2016) and higher than those observed in the Mediterranean Sea (2 species; Olivar et al., 2012), China (9 species; Wang et al., 2019a), California (7 species; Davison et al., 2015), and western Indian Ocean (5 species; Annasawmy et al., 2019). Controversially, the diversity of hatchetfishes along the WTA seems to be lower than that reported in the western Central Pacific (40 species; Harold, 1999), where a high diversification of the genus *Polyipnus* has been reported (22 species). However, in addition to the influence of intrinsic biogeographic differences among locations (e.g. oceanographic conditions and food availability), sampling strategy and effort were different among studies, which may also affect the observed picture of diversity (Eduardo et al., 2018).

At our spatial scale we did not observe clear pattern in the horizontal distribution of hatchetfishes, but the presence of horizontal patterns could be hampered by the relatively low number of specimens by station. This is also the case of physicochemical conditions since no differences in vertical profiles were observed. Indeed, the study area was recently characterised as homogeneous in terms of thermohaline structure (Assunção et al., 2020). On the other hand, clear differences were found in term of vertical space occupation and we could define five functional groups based on the foraging ecology, diel vertical migration, space occupation, and relationship with physico-chemical conditions.

Table 3

Diet composition of hatchetfishes based on gut content analyses and dietary indexes calculated for each prey item: Standard Length (SL), number of stomachs analysed (N), number of stomachs with content (NSC), abundance percentage (%N), weight percentage (%W), frequency of occurrence (%F), percentage index of relative abundance (%IRI), vacuity index total (%VI), vacuity index day (%VD), vacuity index Night (%VN), mean and range of prey size (PS, mm).

Prey		*Argyropelecus aculeatus* SL:7.6 ± 0.9 **N:19 NSC:14** VI:26 **VD:** 26 **VN:** –				*Argyropelecus affinis* SL:5.5 ± 0.6 **N:36 NSC:21** VI:41 VD:9 VN:100				*Sternoptyx diaphana* SL:2.3 ± 0.4 **N:216 NSC:181** VI:16 VD:17 VN:14				*Sternoptyx pseudobscura* SL:3.0 ± 0.9 **N:90 NSC:89** VI:1.1 **VD:2.8** VN:0			
Group/taxa		%N	%W	%Fo	PS	%N	%W	%Fo	PS	%N	%W	%Fo	PS	%N	%W	%Fo	PS
Fishes	Teleostei larvae	–	–	–	–	14.3	24.1	9.5	12.3	4.5	17.2	1.7	15.0	1.1	2.0	2.5	17.0(9.0–25.0)
	Teleostei	–	–	–	–	9.5	31.1	9.5	13.0	1.3	6.0	4.2	18.0(13.0–22.0)	12.6	32.1	6.2	20.5(19.0–22.0)
	Myctophidae larvae	–	–	–	–	–	–	–	–	0.4	1.8	1.7	–	–	–	–	–
	Gonostomatidae	–	–	–	–	4.8	13.1	4.8	19.0	–	–	–	–	–	–	–	–
	Sternoptychidae	1.1	63.4	5.6	12.6	–	–	–	–	–	–	–	–	–	–	–	–
Crustaceans	Amphipoda	1.1	0.7	5.6	8.2	4.8	6.9	4.8	1.2(0.3–2.2)	30.8	15.4	33.1	3.6(1.5–8.2)	8.2	7.2	11.1	4.0
	Ostracoda	–	–	–	–	19.0	2.8	14.3	4.2(3.3–4.5)	24.5	11.0	20.3	4.3(3.6–5.1)	6.6	2.6	3.7	4.0(3.0–5.0)
	Copepoda	–	–	–	–	–	–	–	–	11.4	2.1	5.1	2.4(1.2–3.0)	1.6	3.2	2.5	–
	Decapoda	–	–	–	–	9.5	7.0	9.5	–	8.2	11.2	9.3	25.0(20.0–28.9)	1.6	3.2	2.5	13.0(10.0–16.0)
	Euphausia spp.	97.7	36.0	38.9	9.2 (8.4–10.2)	9.5	9.0	9.5	9.7 (9.5–10.0)	14.2	20.7	7.7	21.0	34.1	23.7	9.9	10.5(9.0–12.0)
Mollusks	Gastropod	–	–	–	–	–	–	–	–	1.5	0.1	0.8	–	–	–	–	–
	Pteropoda	–	–	–	–	–	–	–	–	1.1	0.4	4.2	7.4	0.5	0.6	1.2	–
	Cephalopod	–	–	–	–	–	–	–	–	0.4	1.0	1.7	–	0.5	6.7	1.2	–
Gelatinous	Thaliacea	–	–	–	–	4.8	2.2	4.8	6.2	0.9	11.2	2.5	–	9.3	12.4	6.2	6.1
	Cnidaria	–	–	–	–	4.8	4.0	9.5	–	0.9	2.0	3.4	–	0.5	7.7	9.9	–

The first functional group (Group 1), composed by *A. affinis* and *A. sladeni*, presented the highest vertical range of distribution from > 800 m deep to the surface layer, which correspond to a 23 °C variation. During daytime these species were mostly distributed at 400–500 m in the layer presenting the minimum oxygen level. Oxygen concentration at this depth (1.9 ml.l^{-1}) may be classified as mild hypoxia, which is defined as low oxygen conditions where sensitive species show avoidance reactions (Hofmann et al., 2011). These species were previously reported inhabiting low oxygenated waters (classified as near to hypoxia) of the eastern Tropical Atlantic (Olivar et al., 2017). Therefore, during the day, species from Group 1 are likely in search for predator refuge and/or saving energy by resting in a water mass with low temperature and dissolved oxygen concentration (Bertrand et al., 2006; Sutton, 2013). At night, they ascended to epipelagic waters (0–100 m) presumably to feed, following the nightly ascension of zooplankton (Sutton, 2013). Indeed, all stomach of *A. affinis* collected at night had food content, while those sampled at daytime were mostly empty. Additionally, the major prey taxa recovered in the stomachs of this species were fish larvae (13 mm) and ostracods (3.3–4.5 mm), organisms typically found in higher densities in epipelagic waters (especially at night) (Parra et al., 2019; Stefanoudis et al., 2019). The nightly ascension of these species has also been reported in the western Indian Ocean and central equatorial Atlantic (Kinzer and Schulz, 1988; Annasawmy et al., 2019). However, this pattern was not observed along the eastern tropical Atlantic (Olivar et al., 2018). Additionally, this work is the first reporting *A. affinis* and *A. sladeni* in waters above 100 m. Differences on oceanographic features, food availability, species competition and/or sample methods may explain dissimilarities among locations.

The mixing model based on stable isotope data for species from the Group 1 revealed a relatively high contribution of *Abylopsis tetragona* (19%), a siphonophore that performs daily vertical migration and concentrate above 150 m depth at night (Andersen et al., 1992). *Argyropelecus affinis* also helds the highest trophic position. This could be an adaptation to overcome the high energetically demanding migrating diel behaviour. Finally, as reported for other hatchetfishes here and elsewhere (Kinzer and Schulz, 1985; Sutton and Hopkins, 1996a), this Group, as well as Groups 2 and 4, presented an asynchronous pattern of vertical migration, where the entire population apparently does not respond synchronously to diel variation in the light intensities. This pattern of migration seems to be regulated by feeding, with only the hungry portion of the population migrating a given day (Sutton and Hopkins, 1996a).

The second functional group (Group 2) was composed by *A. aculeatus*, peaking at 500–600 m during daytime and 100–200 m at night. Whatever the diel period, this species was not found at the layers with minimum oxygen concentration (Fig. 3) or above the thermocline. This restricted vertical pattern (8 °C of temperature range) seems to be reflected in the trophic ecology of *A. aculeatus,* since this species that cannot benefit from the epipelagic fish larvae, presented different prey preferences (euphausiids and sternoptychids) and a lower trophic level than the Group 1. *Argyropelecus aculeatus* also presented a relatively high isotopic contribution (20%) of the vertically migrating siphonophore *A. tetragona* (Andersen et al., 1992). A similar vertical distribution for this species was also observed along the eastern Gulf of Mexico and central equatorial Atlantic (Hopkins and Baird, 1985; Kinzer and Schulz, 1985).

The third functional group (Group 3), composed of *A. hemigymnus,* does not perform clear diel vertical migration. Whatever the time it presented a bimodal distribution with two peaks of abundance at 300–400 m and at 700–800 m. Interestingly, no exemplar was collected in shallow layers while studies performed in colder waters have registered a shallower distribution (150 m) (Merrett and Roe, 1974; Andersen et al., 1992). Hence, temperature might be an important factor regulating the upper distribution of this species. Although we did not analyse the stomach content of *A. hemigymnus*, our isotopic analyses

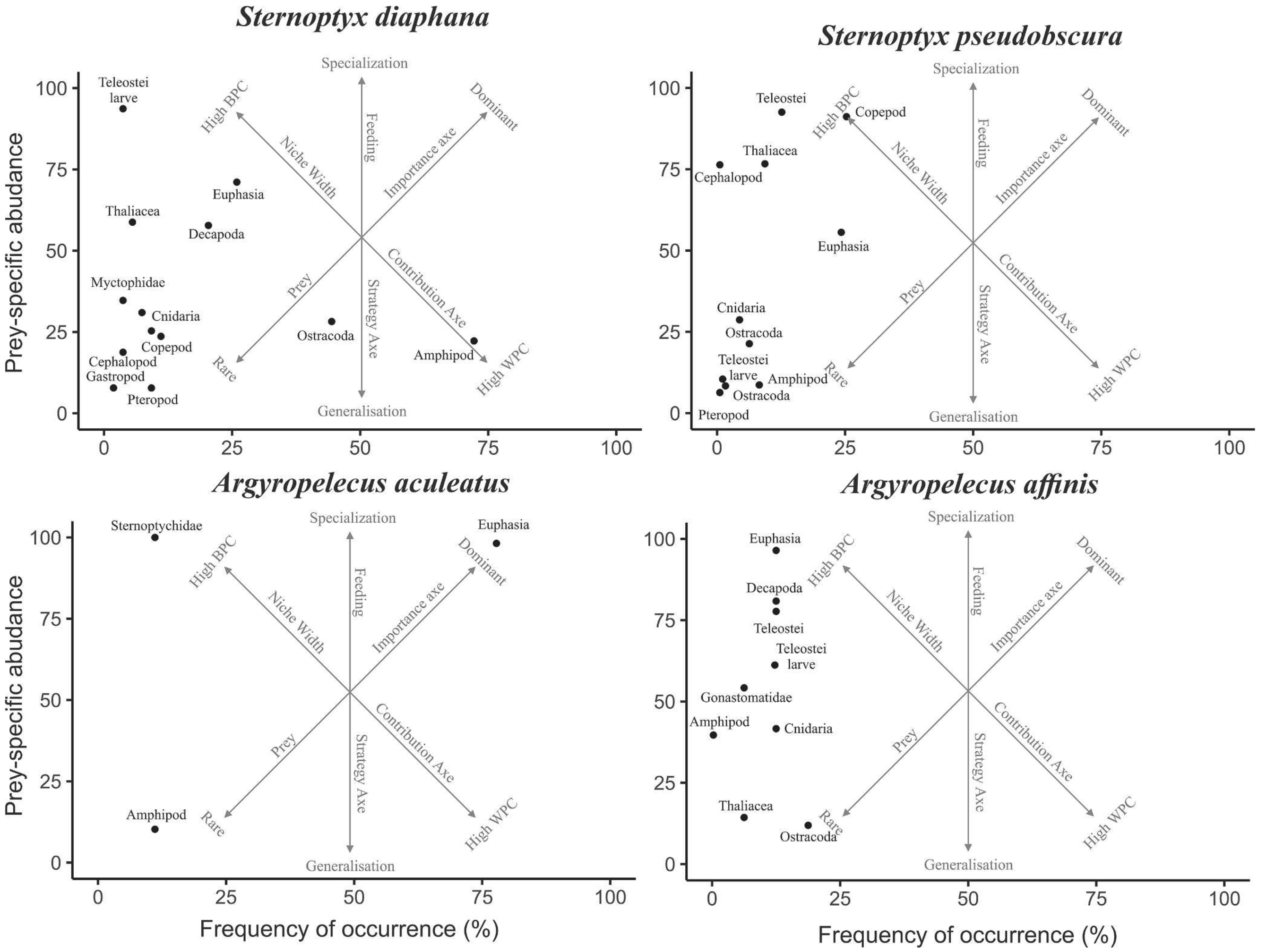

Fig. 5. Costello graph showing the relationships between prey-specific abundance and frequency of occurrence (%FO) of prey items in the diet of hatchetfishes. The explanatory Costello diagram and its interpretation of feeding strategy (BPC = between-phenotype component, WPC = within-phenotype component) are shown in the background of the graphs.

Table 4
Number of samples, standard length (cm) and stable isotope values of hatchetfishes (predator), potential prey and POM analysed for isotopic composition.*Lipid corrected species.

Group	Species	Category	*n*	Standard Length	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N
				mean ± SD	mean ± SD	mean ± SD	mean ± SD
Fishes	*Argyropelecus aculeatus*	predator	5	5.80 ± 0.63	−17.98 ± 0.35	7.95 ± 1.29	3.33 ± 0.05
	Argyropelecus affinis	predator	10	5.34 ± 0.25	−18.36 ± 0.13	11.85 ± 0.27	3.31 ± 0.04
	Argyropelecus hemigymnus	predator	10	2.98 ± 0.53	−18.83 ± 0.23	11.46 ± 0.53	3.40 ± 0.90
	Sternoptyx diaphana	predator	5	2.87 ± 0.22	−18.88 ± 0.12	10.94 ± 0.50	3.34 ± 0.05
	Sternoptyx pseudobscura	predator	5	4.08 ± 0.38	−19.08 ± 0.11	10.11 ± 0.20	3.58 ± 0.01
Fish larvae	Teleostei larvae 15–20 mm	potential prey	6	–	−18.51 ± 0.40	7.16 ± 0.66	3.23 ± 0.01
	Teleostei larvae 5–10 mm	potential prey	10	–	−19.69 ± 0.11	5.92 ± 0.20	3.24 ± 0.01
Crustaceans	*Euphausia gibboides*	potential prey	6	1.50 ± 0.11	−19.30 ± 1.01	6.93 ± 0.09	3.28 ± 0.04
	Euphausia sp.	potential prey	3	1.43 ± 0.13	−19.47 ± 0.51	7.31 ± 0.88	3.26 ± 0.09
	Pasiphaeidae sp.	potential prey	3	–	−19.11 ± 0.05	6.06 ± 0.09	3.14 ± 0.02
	Phronima sp.	potential prey	3	–	−19.03 ± 0.18	5.88 ± 0.28	3.60 ± 0.20
Siphonophorae	*Abylopsis tetragona*	potential prey	3	–	−17.84 ± 0.29	7.25 ± 1.00	3.31 ± 0.09
	Siphonophorae sp.	potential prey	3	–	−19.25 ± 0.04	9.10 ± 0.25	3.48 ± 0.11
Thaliacea	*Pyrosoma atlanticum**	potential prey	11	–	−18.50 ± 0.20	2.99 ± 0.68	5.34 ± 0.24
	Salpa sp.*	potential prey	6	–	−19.82 ± 0.53	5.47 ± 0.54	4.50 ± 0.77
	Soestia zonaria	potential prey	6	–	−20.27 ± 0.25	3.77 ± 0.58	3.35 ± 0.19
Zooplanckton		potential prey	19	–	−19.45 ± 0.31	3.04 ± 0.60	4.52 ± 0.51
POM		–	17	–	−22.41 ± 0.69	2.82 ± 1.19	–

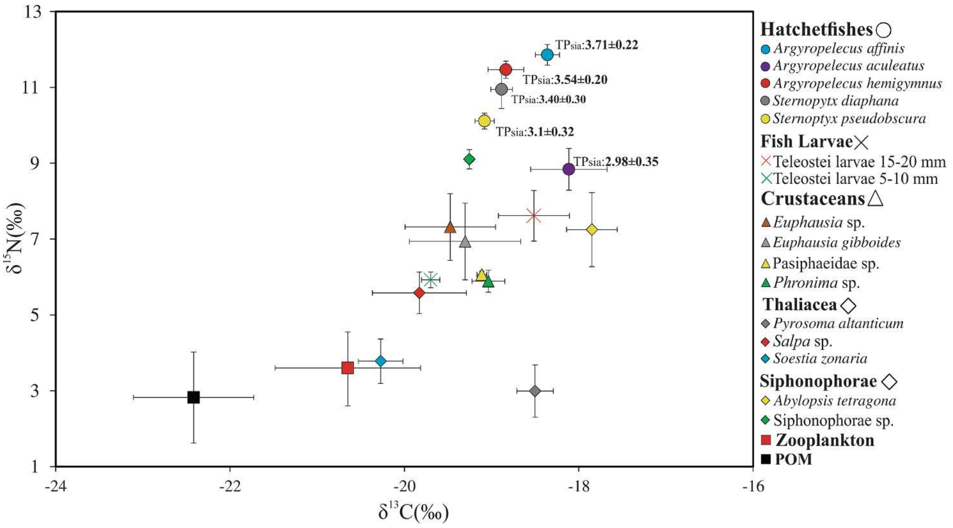

Fig. 6. Stable carbon and nitrogen isotope values of particulate organic matter (POM), zooplankton, gelatinous organisms, crustaceans and hatchetfishes. TPsia– Trophic position based on stable isotope analyses.

and previous studies on stomach contents indicate that this species has a relatively high trophic level (3.5) and forage on euphausiids, copepods, chaetognaths, fish and gelatinous (Hopkins and Baird, 1973; Ikeda et al., 1994).

The fourth functional group (Group 4), composed by *S. diaphana*, presented the peak of abundance at 700–800 (day) and 800–900 m (night), presenting no clear relationship with thermocline or minimum oxygen layers. In contrary to other functional groups, only a small part of *S. diaphana* seems to perform daily vertical migrations. Indeed, this species seem to forage both day and night (based on vacuity index). This pattern was found in previous studies, where this species was defined as a generalist predator with limited pursuit capability, whose feeding strategy consists of taking the nearest available prey within a very limited distance (Hopkins and Baird, 1973). In fact, the largest diversity of prey was found for this species. However, *S. diaphana* prey diversity seems vary according to the sampling locations (e.g. Hopkins and Baird, 1973; Sutton and Hopkins, 1996a; Carmo et al., 2015), probably following the variation of food availability in different sites. As an example, while *S. diaphana* primarily ingests copepods and euphausiids along the Pacific Ocean (Hopkins and Baird, 1973), in the current study, however, among its main prey taxa were amphipods and Teleostei larvae, despite euphausiids was also present.

The fifth functional group (Group 5) was composed by *S. pseudobscura*. This species presented no patterns of vertical migration or clear relationship with thermocline and minimum oxygen layers, being mostly found in the deeper waters (< 700 m). This same pattern was observed in the eastern Gulf of Mexico (Hopkins and Baird, 1985). The trophic level of this species was relatively low (3.1), which may be explained by the lower energy costs to feed and lower metabolism due to a colder water habitat. *Sternoptyx pseudobscura* presented a generalist behaviour with preferences on ostracods and euphausiids. As these prey groups usually perform daily vertical migration (Hays, 2003), it is likely that *S. pseudobscura* has daily feeding behaviour. According to our data, *A. gigas* and *S. pseudodiaphana* may have a similar migration and spatial pattern than *S. pseudobscura.* However, due to our low sample number ($n < 9$) and restricted sizes (e.g. only large size classes of *A. gigas* were caught) these species were not allocated to any functional group. Additional data and/or different sample methods may complement distribution patterns for these species. The last species, *V. tripunctulatus,* was also rare (6 specimens sampled), presented no pattern of vertical migration, and was only found at the layer of minimum oxygen values (400–500 m). Previous studies reported that, as other hatchetfishes, *V. tripunctulatus* usually feeds on copepods, ostracods, and euphausiids (Hopkins and Baird, 1981; Sutton and Hopkins, 1996a).

Finally, we observed two interesting patterns on mesopelagic trophodynamics. First, a high contribution of Teleostei (based on stomach content and isotopes) was noted for all hatchetfishes species included in trophic analyses. This pattern diverges from those find for hatchetfishes in the northern Mid-Atlantic Ridge, eastern Gulf of Mexico, and western Mediterranean Sea (Hopkins and Baird, 1973; Bernal et al., 2015; Carmo et al., 2015). This variability in fish larvae consumption is likely driven by variation in food availability. Indeed, many teleostei larvae were caught during our trawling operations and a recent study addressing zooplankton communities in the same location, highlights a high biovolume of fish larvae on sample size fraction higher than 2000 μm (Figueiredo et al., in press). This might be related with presence of islands and seamounts within the study area. As an example, Fernando de Noronha Island and Rocas Atoll include several coral reefs and have been referred to as an “oasis of life in an oceanic desert” (Hazin, 1993; CBD, 2014). Second, some of the potential prey included on isotopic analyses presented relatively high mean $\delta^{15}N$ values. For instance, mean $\delta^{15}N$ values for euphausiids (7.3) were higher than

Table 5

Isotopic mixing-model estimates of prey contribution (mean ± SD) for hatchetfishes species from oceanic islands and seamounts of the western Tropical Atlantic.

Species/prey		*Argyropelecus aculeatus*	*Argyropelecus affinis*	*Argyropelecus hemigymnus*	*Sternoptyx diaphana*	*Sternoptyx pseudobscura*
Crustaceans	Zooplanckton (Copepods)	0.25 ± 0.15%	8.56 ± 5.90%	9.98 ± 6.95%	6.36 ± 5.00%	9.65 ± 7.00%
	Euphausia gibboides	14.42 ± 8.17%	14.14 ± 7.00%	13.74 ± 7.86%	10.35 ± 7.00%	13.31 ± 7.23%
	Amphipoda (*Phronima* sp.)	17.07 ± 8.4%	13.24 ± 6.55%	13.68 ± 7.55%	19.68 ± 6.83%	11.99 ± 6.66%
Siphonophorae	*Abylopsis tetragona*	19.47 ± 7.98%	18.40 ± 6.21%	16.55 ± 7.51%	12.35 ± 7.00%	12.90 ± 6.83%
Thaliacea	*Salpa* sp.	13.48 ± 1.00%	8.81 ± 6.16%	10.25 ± 6.68%	12.56 ± 6.82%	11.45 ± 7.00%
	Soestia zonaria	11.95 ± 7.67%	9.83 ± 6.45%	11.14 ± 6.82%	15.79 ± 7.31%	14.47 ± 6.77%
Fishes	Teleostei larvae 15–20 mm	16.26 ± 7.35%	17.64 ± 7.30%	16.34 ± 8.15%	10.49 ± 7.23%	11.12 ± 7.19%
	Teleostei larvae 5–10 mm	7.00 ± 6.00%	9.38 ± 5.33%	8.32 ± 5.00%	13.74 ± 7.36%	15.21 ± 6.13%

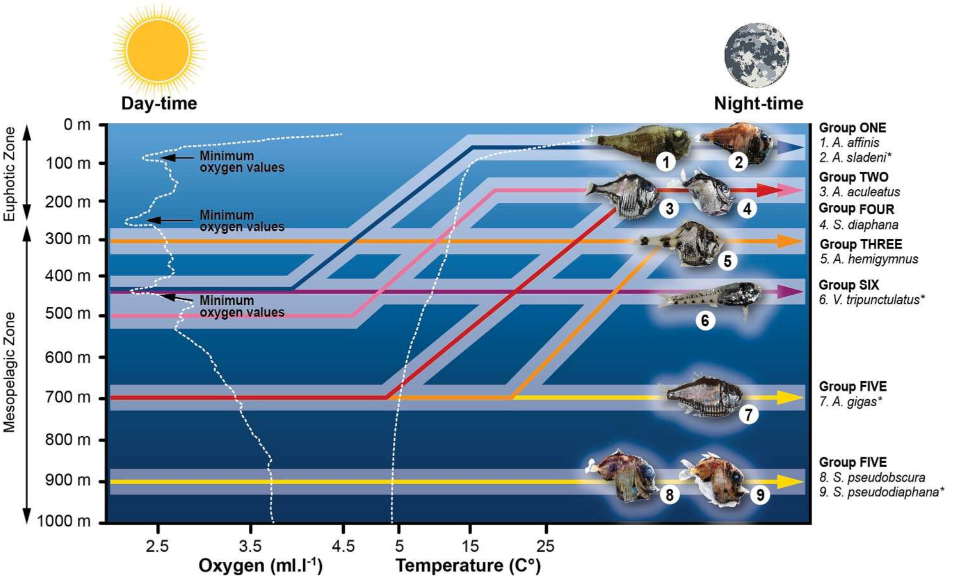

Fig. 7. Conceptual model exhibiting vertical niche partitioning of hatchetfishes from the western Tropical Atlantic. Coloured horizontal lines indicate the peak of abundance of each species at day and upper limit distribution at night. It does not necessarily mean that the species are totally partitioned, but rather that the centres of their distribution are different. The depth layers 200–300 m and 700–800 m were not sampled at night. White vertical lines indicate the mean vertical profile of temperature and dissolved oxygen along the study area. *Migration pattern based on very low-observed species ($n < 10$).

those reported on the western Mediterranean (2.8) (Valls et al., 2014). Moreover, Siphonophorae sp. δ^{15}N mean (9.1) was relatively high (e.g. greater than those found for *A. aculeatus*). This pattern of high nitrogen values may be associated with differences on species size, feeding behavior, and variations on oceanographic features (e.g. low oxygenated areas facilitates denitrification) and nutrients availability (Montoya, 2008).

4.1. Diversity of functional group reveals vertical niche partitioning and multiple ecosystem processes

The deep-sea is usually characterized by a relatively high environmental stability and a decrease of productivity and food availability with depth (Priede, 2017), which should promote the competition for limited resources (Kumar et al., 2017). Even so, mesopelagic ecosystems are one of the richest and diverse environments on earth (St. John et al., 2016). This implies that species are distributed unevenly throughout different multidimensional niches and thereby avoiding competitive exclusion (Drazen and Sutton, 2017; Kumar et al., 2017). Indeed, by defining five functional groups of hatchetfishes with different diet preference, isotopic composition, and vertical abundance peaks (Fig. 7), we reveal a possible high resource partitioning. Additionally, these species might have a different feeding tie chronology (Hopkins and Baird, 1985). Hence, hatchetfishes segregate in different ecological groups responding differently to environmental constraints and presenting diverse functional roles. Vertical segregation has also been described for euphausiids, copepods and gelatinous organisms (Siphonophorae and Thaliacea), main prey groups of hatchetfishes (Hu, 1978; Barange, 1990; Andersen et al., 1992; Stefanoudis et al., 2019), but without proposing a multidimentional description of their niche. Identifying, understanding, and considering the multidimensional functional groups structure of the mesopelagic environment is fundamental to answer important ecological questions such as resource use, carbon sequestration and associated role in climate regulation.

Groups 1, 2, and 4 are vertical migrants playing an important role in transporting organic matter between euphotic zone and deeper oceanic layers (Fig. 7). As epipelagic habitants at night, these groups may be more vulnerable to anthropogenic impacts including pollution, fisheries, sound and light pollution, and climate-related changes (e.g. alterations in temperature, pH, stratification and oxygenation) (Steinberg et al., 2012). On the other hand, Group 5 is composed by a non-migrant species (*S. pseudobscura*) that occur in deeper waters and might be less vulnerable to human impacts. This species (and likely *A. gigas* and *S. pseudodiaphana*) also contributes indirectly to active transport of carbon, once It feeds on zooplankton undertaking dial vertical migration (e.g. euphausiids and copepods). Thus, the actively vertically transported organic matter by zooplankton remains in the mesopelagic layer. This process will also sequester carbon and act as a sink in the global carbon cycle (Wang et al., 2019b). These non-migrant species also interact with higher trophic levels that migrate to feed at the lower mesopelagic zone (500–1000 m) (Drazen and Sutton, 2017). This relationship also accelerates carbon sequestration in the mesopelagic layer.

4.2. Gelatinous prey as an important underestimated trophic resource

Differences in digestibility may cause certain taxa to stand out more than others because their hard parts resist digestion (Robison, 2004; Carmo et al., 2015). For example, the exoskeletons of crustaceans usually resist digestion and conserve taxonomic characters. Gelatinous prey, on the other hand, are often unidentifiable in the stomachs, especially after chemical preservation (Henschke et al., 2016). As in previous studies on hatchetfishes, gelatinous prey was not significant in any diet index based on our gut content analyses. The mixing model, however, revealed that Thaliacea and Siphonophorae appeared to be important prey groups, as they may contribute up to 40% of the diet of some hatchetfishes. For example, *S. diaphana* and *S. pseudobscura* (mostly found in deeper waters) had a high diet contribution of *Soestia zonaria* ($> 20\%$), while *A. affinis*, *A. aculeatus* and *A. hemigymnus* (usually in shallower waters) showed a great contribution of *Abylopsis tetragona*. Indeed, gelatinous prey is a highly diverse group that may constitute up to 90% of the biomass of zooplankton community (Henschke et al., 2016), and zooplankton feeders likely take advantage of that. In the mixing model, we included three abundant gelatinous prey as study case. However, further isotopic information on gelatinous groups (e.g. larvaceans and other salps species) may provide more insightful information on the trophodynamics between hatchetfishes and gelatinous groups. These trophic relationships also reflect on trophic position, which may be overestimated when based solely on stomach contents. TPg were higher than TPsia in all cases. For instance, *A. aculeatus* that presented the highest contribution of gelatinous prey had the highest TPg but the lowest TPsia.

The high importance of gelatinous organisms for mesopelagic species has also been recently highlighted in other studies (McClain-Counts et al., 2017). In the same way, our results indicate that gelatinous organisms (mainly Thaliacea and Siphonophorae) are an important prey group for hatchetfishes. This feature has been historically underestimated due to methodological limitations, hampering the understanding of pelagic food webs, flows of biomass across compartments and, eventually, the influence of fishes in regulating climate in the coming decades (Hopkins and Baird, 1985; Hidalgo and Browman, 2019).

5. Conclusion: General patterns and ecological roles

Hatchetfishes comprise a diverse and abundant mesopelagic fish group acting as secondary and tertiary consumers. Based on their habitat and trophic ecology, five functional groups of hatchetfishes with different diet preference, isotopic composition, and vertical abundance peaks were defined. It revealed a possible high multidimensional resource partitioning (Fig. 7) linked with complex patterns of migration, feeding behaviour, and interactions with the environment. Hatchetfishes are species-specific in feeding habits and important predators on the zooplankton community, especially on amphipods, euphausiids, ostracods, copepods, fish larvae, and chaetognaths. Additionally, hatchetfishes species seems to be differently distributed in relation to minimum oxygen layers and the thermocline. As a result of climate changes, both oceanographic features may be changing in the next decades (Levin et al., 2019), affecting the distribution, feeding and ecological interactions of hatchetfishes.

As vertical migrators, hatchetfishes play a role by transferring material and energy from the subsurface waters to deeper layers, a pathway through which the effects of climate change are mitigated by a carbon transfer to the deep ocean. Moreover, as consumers of Thaliacea and Siphonophorae organisms, these species convert “gelatinous energy” into “fish energy” readably usable by higher trophic levels, including endangered and commercially important species (Ibáñez et al., 2004; Potier et al., 2007; Varghese and Somvanshi, 2016). This is a crucial trophic relationship that has been historically underestimated. As the density of gelatinous organisms might be highly increased upon intense anthropogenic impacts (e.g. eutrophication, overfishing, or climate change) (Henschke et al., 2016), it is likely that these organisms will have even higher importance for hatchetfishes in the Anthropocene. Despite the importance of hatchetfishes, challenges of sampling in the deep-sea hamper a complete assessment of the biodiversity, ecology and ecosystem roles of this group. As humans expand resource extraction and habitat impact in the deep ocean, the understanding of mesopelagic ecosystems, their processes, and functions is mandatory, especially when sustainability is intended to be achieved.

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2020.102389.

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Distribution, vertical migration, and trophic ecology of lanternfishes (Myctophidae) in the Southwestern Tropical Atlantic

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Abstract

Lanternfishes (Myctophidae) are amongst the most abundant, widespread, and diverse fish groups in the world's ocean. They account for a significant part of oceanic fish biomass and play crucial roles in a variety of ecosystem processes, including carbon sequestration and nutrient recycling. However, they remain poorly known while increasingly at risk in numerous ways (*e.g.,* global warming, plastic pollution, and exploitation of deep-sea resources). Here, we investigate the species composition, vertical migration, and trophic ecology of lanternfishes in the Southwestern Tropical Atlantic (SWTA), as well as the influence of physicochemical factors on their horizontal structuring. We show that lanternfishes are a highly diverse and abundant fish family of the SWTA, comprising at least 33 species and contributing 40% of all fish collected (in number). We reveal that some of these species may have different patterns of prey preference and migratory behaviour, leading to multidimensional niches, underestimated trophic links (*e.g.,* gelatinous organisms), and several mechanisms to avoid competitive exclusion. At least 72% of the lanternfish species reported here seem to migrate to the surface to feed at night. Additionally, they are a central food source for epipelagic and deep-sea predators, a pathway enhancing the connection between shallow and deep-sea ecosystems. Finally, we show that lanternfishes are ubiquitous to environmental conditions analyzed here (*e.g.,* thermohaline structure and current systems), leading to weak horizontal assemblage segregation.

Keywords: Mesopelagic; Seamounts; Oceanic Islands; Stable Isotopes; Deep-sea, Diel Vertical Migration, Niche Partitioning, Trophodynamics.

Introduction

Lanternfishes (Myctophidae) are amongst the most abundant, widespread, and diverse fish groups in the world's ocean (Gjøsaeter and Kawaguchi, 1980; Catul et al., 2011). This family includes 254 species that usually present small body size (mean maximum length of 90 mm), numerous photophores, and are dominant in pelagic environments (Poulsen et al., 2013; Priede, 2017; Fricke et al., 2020; Cherel et al., 2020). Most of myctophid species vertically migrate to the surface to feed at night and actively transport the ingested carbon to deep waters at day (Catul et al., 2011). Moreover, they play a significant role in energetic pathways by consuming zooplankton and providing forage for numerous epipelagic (*e.g.,* tuna, mammals, squids, and diving seabirds) and deep-sea (*e.g.,* viperfish, lancetfish, and bigeye opah) predators (Sutton and Hopkins, 1996; Cherel et al., 2010; Choy et al., 2013; Rosas-Luis et al., 2014; Eduardo et al., 2020b). These traits are crucial for connecting epipelagic and deep-sea ecosystems and oceanic carbon storage (Catul et al., 2011; Sutton, 2013; Cavan et al., 2019).

It is worrying that many species of this notable fish group remain poorly known worldwide while increasingly at risk in several ways (St. John et al., 2016; Martin et al., 2020). Indeed, while there is a lack of scientific information on the diversity and ecology of lanternfishes in most oceanic basins, side effects of global warming (Levin et al., 2019), plastic pollution (Davison and Asch, 2011), and exploitation of deep-sea resource (Hidalgo and Browman, 2019; Drazen et al., 2020) are accelerating. As threats increase, further investigations on the ecology and conservation of lanternfishes are required. Researches have already addressed important aspects of their taxonomy (*e.g.,* Wisner 1976; Nafpaktitis et al., 1977; Hulley, 1992; Martin et al., 2018), distribution (*e.g.,* Braga and Costa, 2014; Olivar et al., 2017; Cherel et al., 2020; Melo et al., 2020), morphometry (Tuset et al., 2018; Eduardo et al., 2020c; López-Pérez et al., 2020), vertical migration (Watanabe et al., 1999; Olivar et al., 2012, 2017; Annasawmy et al., 2018; Wang et al., 2019) and trophic ecology (*e.g.,* Hudson et al., 2014; Bernal et al., 2015; Olivar et al., 2018; Annasawmy et al., 2020; Czudaj et al., 2020; Contreras et al., 2020; Bode et al., 2021). These studies demonstrated, among others, that lanternfishes are dominant in mesopelagic fish fauna (biomass and richness) and present a high range of vertical and feeding behaviours (Hopkins and Gartner, 1992; Watanabe et al., 1999; Catul et al., 2011). However, how these species are scattered over different patterns of resource use (niche partitioning), thereby avoiding competitive exclusion, is much less explored.

Understanding lanternfishes niche partitioning is central to resolve the paradox between ecological theories demonstrating competitive exclusion and the fact that many lanternfishes species are morphologically and ecologically similar but do not drive one another extinct (Schoener, 1974; Hopkins and Gartner, 1992; Finke and Snyder, 2008). Additionally, understanding niche partitioning helps clarify the coexistence of sympatric species and how resources use shapes their contribution to ecological processes (i.e., fluxes of carbon and nutrients; Brandl et al., 2020). However, addressing the use of resources in the unified framework of niche segregation requires simultaneous information of biophysical and ecological aspects that are usually lacking. As an example, niche segregation typically occurs along three axes: diet (feeding ecology), space (habitat), and time (feeding chronology; Schoener, 1974). For lanternfishes, this information is sparse and restricted to a few locations (Hopkins et al., 1996; Hopkins and Gartner, 1992; Hopkins and Sutton, 1998; Catul et al., 2011). Additionally, most previous studies addressing the trophodynamics of these species did not include predators and were based solely on stomach contents, while further approaches (e*.g.,* stable isotopes, fatty acids, and genetics) are required to provide a comprehensive picture of resource uses. Additional data on the trophic ecology of lanternfishes should help to clarify their trophic links and thus niche differentiation.

Another key point in the study of lanternfishes is how physical drivers shape their diversity and community structure. Variations on temperature, oxygen, and upper circulation processes play an important role in the ecology and movement of deep-pelagic species (Bertrand et al., 2010; Proud et al., 2017; Boswell et al., 2020). However, the importance of these variables in the distribution and assemblage structuring of these organisms is highly dependent on community dynamics and local oceanographic features. For lanternfishes, only a few studies have focused on how oceanographic processes may influence their ecology and biodiversity (Olivar et al., 2017; Milligan and Sutton, 2020).

Oceanic islands and seamounts of the Southwestern Tropical Atlantic (SWTA), for instance, are interesting locations to study the influence of physical drivers on biological communities, as they hold distinctive biodiversity and Ecologically or Biologically Significant Marine Areas (EBSAs) that, by definition, are special places of fundamental importance for biodiversity and life cycles of marine species (CBD, 2014). Additionally, this region includes different biogeographic provinces with contrasting thermohaline features, current systems, and water-mass properties, leading to shifts in biodiversity and ecosystems (Bourlès et al., 1999; Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021; Tosetto et al., 2021).

On this basis, we take advantage of a comprehensive set of data collected along the SWTA to propose an integrative study on the ecology of lanternfishes. First, we assess their vertical migration and trophic ecology by coupling information on their abundance, vertical distribution, habitat (oxygen, temperature, and fluorescence), and trophodynamics. For that, we explore the main trophic links of lanternfishes through the analysis of stable isotopes (carbon and nitrogen) of zooplankton, gelatinous organisms, crustaceans, fish larvae, and epipelagic and deep-sea fish predators. Second, we assess the importance of oceanographic features on lanternfishes by comparing their species composition, spatial distribution, and assemblage structuring across two different physicochemical scenarios. Finally, we discuss the functional roles of lanternfishes.

Material and Methods

Study area

The study area is located off northeastern Brazil, including the Fernando de Noronha Archipelago (03°50′S, 32°25′W), the Rocas Atoll (03°52′S, 33°49′W), and the seamounts of the Fernando de Noronha Ridge (Fig. 1). This region is divided into two areas with significant differences in currents and thermohaline structures (Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021). The first region, named here Area 1, is mainly located along the brazilian continental slope and encompasses the seamounts off northern Rio Grande do Norte State (Fig. 1). This area is under the western boundary current system, characterized by the North Brazil Undercurrent (NBUC) and the North Brazil Current (NBC) (Dossa et al., 2021). The second region, named here Area 2, encompasses the Fernando de Noronha Archipelago, Rocas Atoll, and seamounts around and between these islands (Fig. 1). This area is mainly under the influence of the central branch of the South Equatorial Current (cSEC) in surface and South Equatorial Undercurrent (SEUC) in the subsurface (Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021).

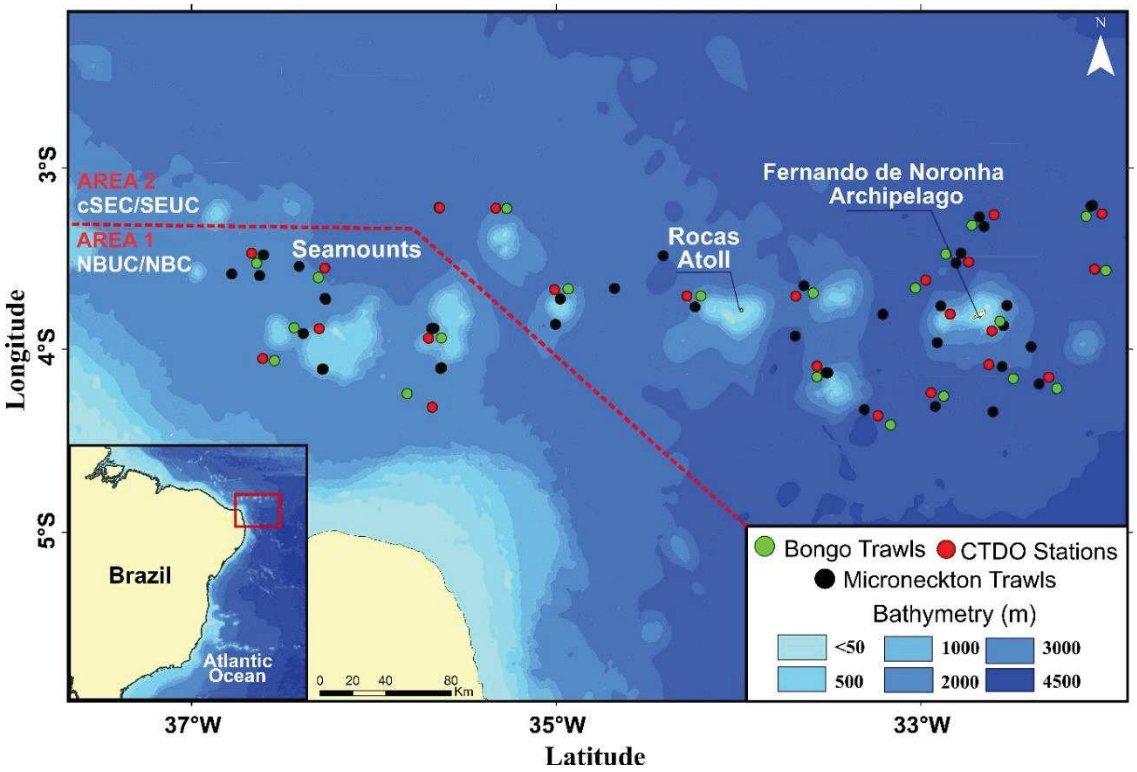

Figure 1. Study area (Fernando de Noronha Ridge) with CTD, bongo, and micronekton-trawl sampling stations. Red dashed line divides the study area according to current systems: cSEC– central branch of the South Equatorial Current; SEUC– South Equatorial Undercurrent; NBC– North Brazil Current; NBUC– North Brazil Undercurrent (Assunção et al., 2020; Dossa et al., 2021; Silva et al., 2021) .

Collection of specimens and data

Specimens and data were collected off northeastern Brazil during a research cruise (Acoustics along the BRAzilian COaSt 2; ABRACOS2) carried out from 9th April to 6th May 2017, aboard the French RV *Antea* (Bertrand, 2017). Sampling of mesopelagic fishes, crustaceans, and gelatinous organisms was conducted at day and night at 33 stations by using a micronekton trawl (body mesh: 40 mm, cod-end mesh: 10 mm, estimated opening area: 120 m^2) from 10 to 1,113 m depth (Fig. 1; Eduardo et al., 2020a). Targeted depth was defined for each tow according to the presence of acoustic scattered layers or patches as observed using a Simrad EK60 (Kongsberg Simrad AS) split-beam scientific echosounder, operating at 38, 70, 120, and 200 kHz. Each trawl was performed for about 30 min at 2–3 kt. Tow duration was considered from the moment of the arrival of the net on the pre-set depth to the lift-off time, recorded utilizing a SCANMAR system (Eduardo et al., 2020a). The net geometry was also monitored using SCANMAR sensors to give headline height, depth, and distance of wings and doors to ensure the net was fishing correctly. As the trawl was not fitted with an opening or closing mechanism, the collection of specimens during the lowering and hoisting of the net was reduced as much as possible by decreasing ship velocity and increasing winch speed; see Eduardo et al., (2020a,b) for more information on field procedures.

Captured organisms were sorted to the lowest taxonomic level and frozen (-20°C) or, in the case of rarity or taxonomic uncertainty, fixed in a 4% formalin solution for one month and then preserved in a 70% alcohol solution. At the laboratory, myctophids were identified according to Nafpaktitis et al., (1977), measured (nearest 0.1 cm of standard length, SL), and weighed (nearest 0.01 g of total weight, TW). Voucher specimens were deposited in the NPM – Fish Collection of the “Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro” (NUPEM/UFRJ).

For isotopic analyses, particulate organic matter (POM) was sampled at 22 stations by filtering seawater from the maximum fluorescence depth through pre-combusted GF/F filters (47 mm), followed by an oven-drying for 36 hours (40°C). Zooplankton samples were collected using bongo nets (four nets fitted with 64, 120, 300, and 500 µm mesh sizes) that were towed from 200 m depth up to the surface at 22 stations (Fig. 1). After collection, these samples were pooled and sieved into five size fractions, using a multi-mesh array (100 µm; 200 µm; 500 µm; 1000 µm; 2000 µm). Additional epipelagic samples, targeting potential epipelagic fish predators, were collected with hook-and-line around the Fernando de Noronha Archipelago using a sport-fishing boat.

Conductivity, temperature, depth, oxygen, and fluorescence hydrographic profiles were collected using a CTDO SeaBird911+ at 22 stations (Fig. 2). The thermohaline limits (e.g., upper and lower thermocline depths) were defined using the criteria from Assunção et al. (2020).

Catch composition and patterns of dominance for lanternfishes

The relative index of lanternfishes abundance (Catch Per Unit of Effort, CPUE) was calculated considering the number of specimens of a given species captured per hour for each trawl. Trawls were classified considering the period (day/night) and the depth strata (10–1,000 m, intervals of 100 m), and areas (Area 1 and Area 2). Except for the layers 200–300 m and 700–800 m at night, where no aggregation of organisms was observed through acoustics, all depth strata were sampled at least once (Table 1; Eduardo et al., 2020a). Day was considered to the extent from one hour after sunrise to one hour before sunset, while the night was from one hour after sunset to one hour before sunrise (Eduardo et al., 2020a). Dawn or dusk samples were discarded when studying day/night vertical distributions.

Table 1. Number of trawls per depth strata (m) and period of the day.

Depth Strata	Day	Night
10–100	3	3
100–200	3	1
200–300	3	–
300–400	1	1
400–500	3	1
500–600	1	1
600–700	1	1
700–800	2	–
800–900	1	1
900–1000	2	2

Patterns of dominance were obtained by calculating a relative importance index (RII; Garcia et al., 2006; Eduardo et al., 2018), based on the frequency of occurrence (%FO; the number of occurrences of a species divided by the total number of trawls) and CPUE in each pre-established area (Area 1, Area 2, and both areas combined). Species showing %FO > average %FO were considered frequent fishes, whereas those with %FO < average %FO were considered rare. A similar method was applied to %CPUE, resulting in highly abundant (%CPUE > average %CPUE) and scarce (%CPUE < average %CPUE) categories. Finally, based on these criteria, species were classified into four groups of relative importance: (1) highly abundant and frequent, (2) highly abundant and rare, (3) scarce and frequent, and (4) scarce and rare. Species were considered dominant when classified within the first category (Garcia et al., 2006).

Vertical behaviour

Vertical distribution patterns were investigated for the 18 species with a sample number higher than 30. Patterns of migration were categorized for each species based on their migration depth and peak of abundance at day and night. Despite the thermohaline structure and stratification at shallow layers (0–300 m) being significantly different between areas 1 and 2, the thermal gradients between surface and deeper layers were alike. Therefore, in vertical migration analyses, the samples of both areas were grouped. This allowed to increase the sample number and improve the robustness of analyses.

Trophic ecology

To investigate trophodynamics, stable isotope analyses of carbon and nitrogen were conducted on nine dominant lanternfishes (based on the IRI index) and their most probable groups of prey (17) and predators (10) (Table 2). While the stable isotopes of carbon undergo small levels of fractionation (0.5–1‰) during trophic transfer and can be used to define energy pathways from primary producers to consumers, the nitrogen stable isotopes undergo larger levels of fractionation (2–4‰) and can be used to make estimations of trophic position and food chain length (Post, 2002).

Potential prey and predators of myctophids were selected based on literature and locally abundant species (Kinzer and Schulz, 1988; Bernal et al., 2015; Battaglia et al., 2016; McClain-Counts et al., 2017; ABRACOS unpubl. data). Samples of Particulate Organic Matter (POM) were also included. All isotopic information was obtained from individuals collected in Area 2, where a greater number of species was available. For each fish and crustacean, white muscular tissue was extracted and cleaned with distilled water to remove exogenous material such as carapaces, scales, and bones. The entire body of gelatinous organisms was used. Zooplankton was divided into six size fractions (see table 2). Each sample was analyzed for carbon and nitrogen isotope ratios through a mass spectrometer (Thermo Delta V+) coupled to an element analyzer (Thermo Flash 2000, interface Thermo ConFio IV) in the Platform Spectrometry Ocean (PSO, IUEM), France. Results of stable isotope analysis for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are derived from the relation of the isotopic value from the sample and a known standard: $\delta^{13}C$ or $\delta^{15}N = [(Rsample/Rstandard) - 1] \times 10^3$; in which R corresponds to the ratio between ^{13}C:^{12}C or ^{15}N:^{14}N.

As differential lipid contents can bias the interpretation of $\delta^{13}C$ values, here we explored the potential lipid bias by using % elemental by mass C:N ratios and the relationship between C:N (i.e., lipid content) and $\delta^{13}C$. As samples were not treated to remove lipids before analysis to prevent loss of material, the few prey groups that exhibited C:N dynamics consistent with high lipid content (C:N > 3.5) were normalized using the equation for aquatic animals provided by Post et al., (2007): $\Delta\delta^{13}C = -3.32 + 0.99 \times C{:}N$. $\Delta\delta^{13}C$ is the change in $\delta^{13}C$ caused by lipids and C:N is the carbon-to-nitrogen ratio (by mass) of the sample. Further information on isotopic sample treatments is provided in Eduardo et al., (2020a).

Table 2. Lanternfishes and their potential prey and predator groups considered in carbon and nitrogen stable isotopes analyses.

Group	Category	Species		
Myctophidae	–	*Diaphus brachycephalus*	*Diaphus dumerilii*	*Diaphus fragilis*
	–	*Diaphus mollis*	*Diaphus perspicillatus*	*Electrona risso*
	–	*Hygophum taaningi*	*Lampanyctus nobilis*	*Lepidophanes guentheri*
Stomiidae	Deep-sea predator	*Borostomias elucens*	*Chauliodus sloani*	*Malacosteus niger*
Scorpaenidae	Deep-sea predator	*Ectreposebastes imus*	–	–
Sphyraenidae	Epipelagic predator	*Sphyraena barracuda*	–	–
Coryphaenidae	Epipelagic predator	*Coryphaena hippurus*	–	–
Carangidae	Epipelagic predator	*Elagatis bipinnulata*	–	–
Scombridae	Epipelagic predator	*Acanthocybium solandri*	*Katsuwonus pelamis*	*Thunnus albacares*
Fish larvae	Prey	Teleostei larvae 5–10 mm	Teleostei larvae 15–20 mm	–
Crustacea	Prey	*Euphausia gibboides*	*Euphausia* sp.	*Phronima* sp.
		Pasiphaeidae sp.	–	–
Siphonophorae	Prey	*Abylopsis tetragona*	Siphonophorae sp.	–
Thaliacea	Prey	*Pyrosoma altanticum*	*Salpa* sp.	*Soestia zonaria*
Zooplankton	Prey	Zoo A (<100 μm)	Zoo B (100–200 μm)	Zoo C (200–500 μm)
		Zoo D (500–1000 μm)	Zoo E (1000–2000 μm)	Zoo F (>2000 μm)

The relationship between lanternfishes and potential prey and predators was analyzed through a bi-dimensional plot of carbon and nitrogen. Additionally, for each group corrected standard ellipse areas (SEAc), which allow inferences of isotopic niches (Jackson et al., 2011), were included. The relative contribution of each potential prey to lanternfishes diet was estimated through the Bayesian mixing model MixSIAR (Stock and Semmens, 2013). This analysis provides estimations of source or prey contributions when tissue and species-specific discrimination factors are used (Caut et al., 2008). As diet determination from MixSIAR is closely related to sources utilized in this analysis, the potential dietary endpoints applicable to lanternfishes were chosen based on a literature review and picking the most abundant local species (Kinzer and Schulz, 1988; Bernal et al., 2015; Battaglia et al., 2016; McClain-Counts et al., 2017; ABRACOS, unpubl. data). The following prey groups were included: i) Zooplankton (200–500 μm); ii) *Abylopsis tetragona* (Siphonophorae); iii) *Euphausia gibboides* (Euphausiacea); iv) *Phronima* sp. (Amphipoda); v) *Salpa* sp. (Thaliacea); vi) *Soestia zonaria* (Thaliacea); vii) Teleostei larvae 5−10 mm, and viii) Teleostei larvae 15−20 mm. Trophic discrimination factors for mesopelagic fishes are poorly known. However, based on previous studies (Valls et al., 2014; Richards et al., 2019), we run mixing models using discrimination factors of 3.15‰ ± 1.28‰ and 0.97‰ ± 1.08‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively (Cherel et al., 2008; Ménard et al., 2014; Eduardo et al., 2020a).

All statistical analyses were performed with R version 4.0.3, using the packages SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011) and SIAR (Stable Isotope Analysis in R; Parnell et al., 2010) for the estimation of isotopic SEAc and Mixing models, respectively.

Horizontal distribution and assemblage structure

Fish assemblage structure and horizontal distribution were analyzed through a complete linkage agglomerative clustering by calculating a Bray-Curtis similarity resemblance matrix based on log-transformed (log (x+1)) fish relative abundance. The non-parametric permutation procedure ANOSIM (Analysis of Similarity; Clarke and Warwick, 2001) was applied to test for differences between physicochemical scenarios (Area 1 vs. Area 2), period (day vs. night), and depth (epipelagic 0–200 m; upper mesopelagic 200–500 m; lower mesopelagic 500–1000 m). The similarity percentage routine (SIMPER) was applied to determine the species contribution to the similarity within a group of sampled sites and the dissimilarity between groups. The species that cumulatively contributed to over 70% of dissimilarity between groups were classified as discriminating species (Eduardo et al., 2018). All statistical analyses were performed with R version 4.0.3, using the package Vegan (Oksanen et al., 2019).

Results

Oceanographic data

The thermal difference between the surface (29°C) and 1,000 m depth (4°C) was 25°C in both areas. Area 1 was characterized by a weak thermal stratification, a deep thermocline (lower limit at 166 m), and a fluorescence maximum peaking at 100 m (Fig. 2). In this area, the water column was evenly oxygenated (Fig. 2), and subsurface salinity was high (>36.5). On the opposite, Area 2 was characterized by a strong thermal stratification with a well-marked and shallow thermocline (60–120 m). This area encompassed a shallow fluorescence peak (60 m) and a layer with low oxygen concentration (minimum ~2.5 $ml.l^{-1}$) ranging between the base of the thermocline down to ~600 m depth.

In both Areas, the mixed layer was formed by the warm Tropical Surface Water (Fig. 3; TSW; $\sigma\theta > 24.5$ $kg.m^{-3}$; Stramma and England, 1999; Gasparin et al., 2014). Below, at the upper part of the thermocline, lies the SUW, with the strongest core in Area 1 (Fig. 3). In subsurface, below the thermocline and down to 500 m, lies the South Atlantic Central Water (SACW; $24.5 < \sigma\theta < 27$ $kg.m^{-3}$; Stramma and England, 1999). The oxygen minimum observed in Area 2 was located at the SACW level indicating a weak renewal in this region (Stramma and Schott, 1999). Finally, the isopycnal $\sigma\theta = 27.1$ kg m^{-3} marks the transition between SACW and AAIW. AAIW is characterized by a local salinity minimum of ∼34.5 and a local oxygen maximum of ∼3–3.5 $ml.l^{-1}$.

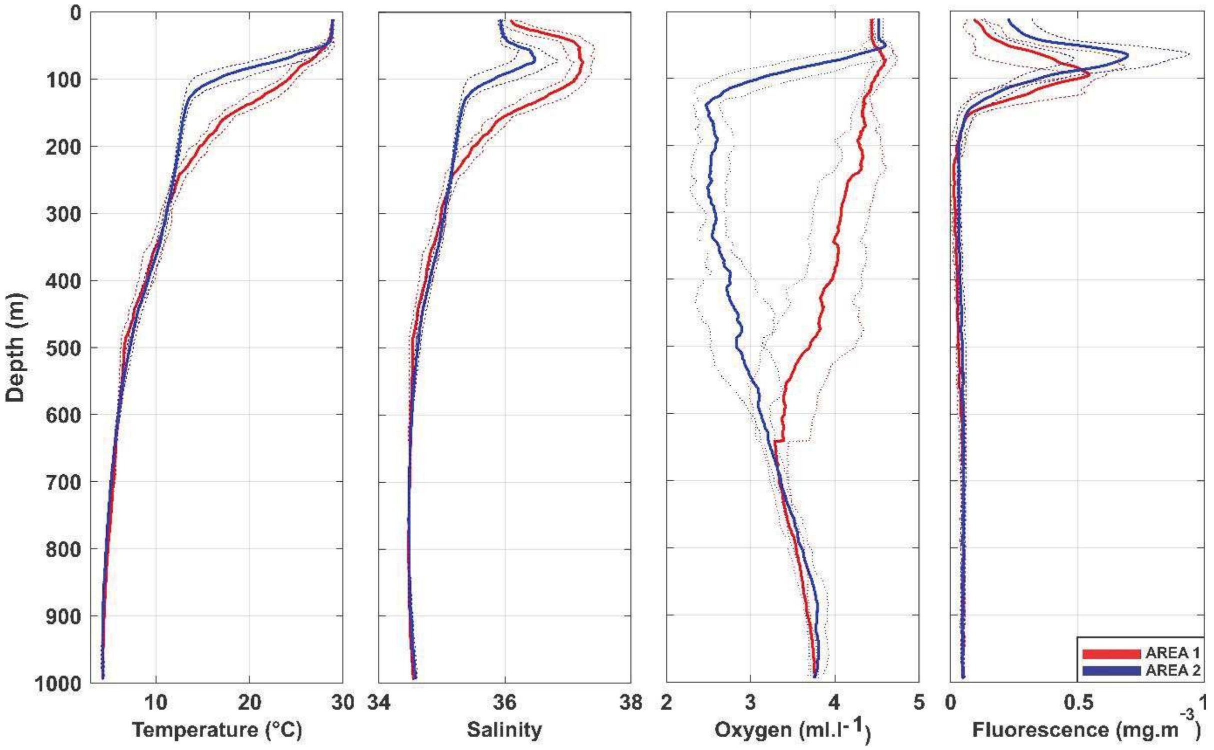

Figure 2. Mean and standard deviation of vertical profiles of temperature, salinity, dissolved oxygen, and fluorescence for the two areas identified off oceanic islands and seamounts of the Southwestern Tropical Atlantic between April and May 2017.

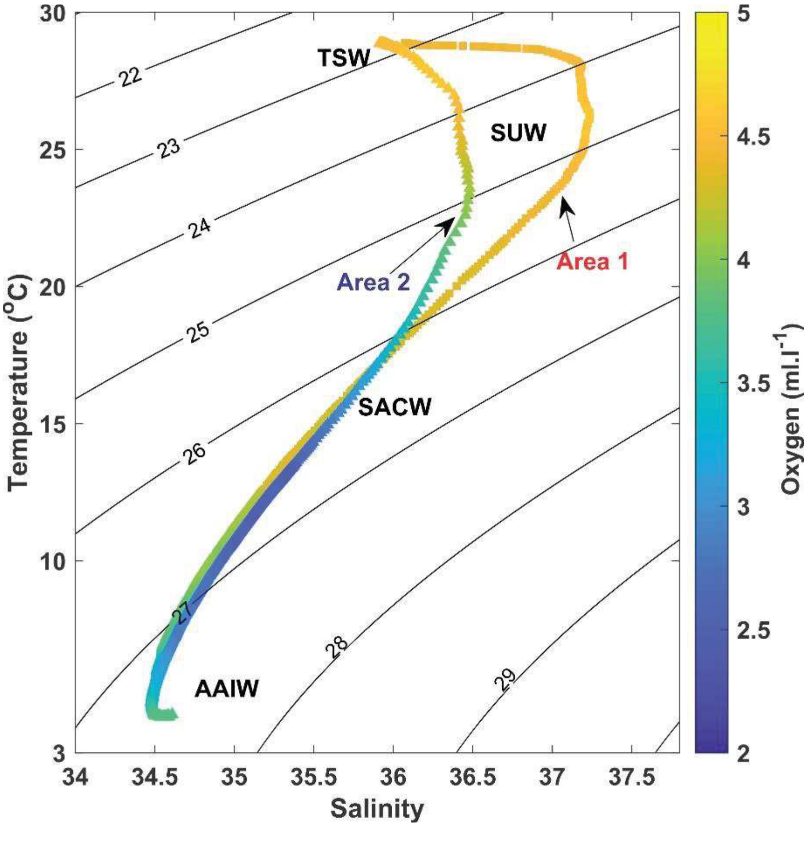

Figure 3. Potential temperature-salinity (TS) diagram showing water-masses diagnosis from the two areas in the SWTA. TSW: Tropical Surface Water, SUW: Subtropical Underwater, SACW: South Atlantic Central Water, AAIW: Antarctic Intermediate Water. The colour of TS-diagram show the oxygen concentration. Isopycnals (kg.m^{-3}) are represented by the transversal black lines along the TS-diagram.

Catch composition and patterns of dominance

In total, 2,268 individuals distributed in 13 genera and 33 species were collected (Table 3). The genus *Diaphus* had the highest numbers of species and specimens (11 species, 60% of the total number of individuals), followed by *Bolinichthys* (4 species; 14% of the total) and *Lampanyctus* (5 species; 6% of the total). Considering the relative importance index (RII), the following seven species (66% of the total number of individuals) were classified as highly abundant or frequent: *Bolinichthys distofax, Diaphus brachycephalus, D. perspicillatus, D. splendidus, Electrona risso, Hygophum taaningi,* and *Lampanyctus nobilis* (Table 3). The other species were highly abundant and rare (8 species, 22% of sampled individuals) and scarce and rare (18 species, 12% of sampled individuals). The standard length and wet weight for all species collected are provided in Table 3 and Supplementary Material 1. The size of specimens ranged from 0.9 cm (*D. brachycephalus*) to 17.8 cm SL (*Lampanyctus lineatum*).

Vertical behaviour

From the 18 species included in vertical migration analyses, 16 presented evidence of diel vertical migration. Only *B. distofax* and *E. risso* did not show any clear indication of vertical migration. Overall, all migrant species presented a polymodal vertical distribution, indicating that species occupy more than one depth strata and/or possibly only part of the population performed diel vertical migration. Additionally, from the 15 species not included in these analyses (low sample number), at least eight were found at epipelagic waters at night, indicating a likely nocturnal vertical ascension. Therefore, at least 72% (25 species) of the collected lanternfishes migrate to epipelagic layers at night. Given the limitations of our gear (see Discussion) and the inherent variability of lanternfishes vertical distribution and movements, interpretation of migration patterns could not be straightforward. However, since some robust patterns emerged, we pictured four general patterns of species vertical partitioning based on the peaks of abundance at day and the shallowest distribution at night.

Pattern 1: This pattern was observed for *B. distofax*, *Ceratoscopelus warmingii*, *Dasyscopelus asper, Diaphus fragilis*, *D. garmani*, *D. lucidus*, *D. perspicillatus*, *D. splendidus*, *H. taaningi*, *Lampadena luminosa*, *L. nobilis*, *L. tenuiformes,* and *Lepidophanes guentheri.* At day, these species peaked and/or were predominant in lower mesopelagic waters (500–1000 m). At night, their distribution expanded up to surface waters, with part of the population migrating to the layer 0–100 m (Fig. 4; Table 3). The thermal and oxygen concentration amplitude ranged between 4–29°C and 2.5–4.4 ml.l^{-1}, respectively.

All these species can cross the thermocline and migrate at night to depths encompassing the fluorescence maximum.

Pattern 2: This pattern was observed for *D. brachycephalus*, *D. dumerilii*, and *D. mollis.* At day, these species peaked and/or were predominant in upper mesopelagic waters (200–500 m). At night, their distribution expanded up to surface waters, with part of the population migrating to the layer 0–100 m (Fig. 4; Table 3). The thermal and oxygen concentration amplitude ranged between 4–29°C and 2.5–4.4 ml.l^{-1}, respectively. These species can cross the thermocline and migrate at night to depths encompassing the fluorescence maximum.

Pattern 3: This pattern was observed for *E. risso*. As for those species from pattern 2, the peak of abundance was in upper mesopelagic waters at day (300–400 m). However, no clear pattern of diel vertical ascension was observed (Fig. 4; Table 3). The thermal and oxygen concentration amplitude ranged between 4.0–9.0°C and 2.8–3.7 ml.l^{-1}, respectively. This species does not seem to cross the thermocline and migrate to depths close to the fluorescence maximum.

Pattern 4: This pattern was observed for *B. distofax.* As for those species from pattern 1, the peak of abundance of this species was observed in lower mesopelagic waters at day (700–800 m). However, no clear pattern of diel vertical ascension was observed (Fig. 4; Table 3). The thermal and oxygen concentration amplitude ranged between 4.0–7.0°C and 3.5–3.7 ml.l^{-1}, respectively. *B. distofax* does not seem to cross the thermocline and migrate to depths close to the fluorescence maximum.

Table 3. Number of collected specimens (N), frequency of occurrence to overall samples (FO%), standard length (mean and range), total wet weight (mean and range), depth, vertical migration (VM) pattern (●: migrant; ○: non-migrant; – migration pattern not established due to small sample number), temperature (T), dissolved oxygen (O), and relative importance index (1: highly abundant and frequent; 2: highly abundant and rare; 3: scarce and frequent; 4: scarce and rare). Temperature and oxygen values correspond to the entire range of species distribution in the study area.

	N	FO%	SL (cm)	TW (g)	Depth (m)	VM	T (°C)	O (ml.l^{-1})	Relative importance index		
									Area 1	Area 2	Total
Benthosema suborbitale (Gilbert, 1913)	13	8	2.4 (1.7–3.0)	1.6 (0.6–2.5)	50–440	–	28–8	4.6–3.1	–	4	4
Bolinichthys distofax Johnson, 1975	85	23	6.2 (3.2–9.1)	4.1 (0.3–10.1)	430–1000	○	7–4	3.5–3.7	1	3	1
Bolinichthys photothorax (Parr, 1928)	54	26	5.3 (2.2–6.7)	2.1 (0.1–3.6)	95–1000	●	25–4	4.5–2.5	3	1	2
Bolinichthys supralateralis (Parr, 1928)	4	8	7.5 (5.0–9.2)	6.5 (1.6–11.0)	95–1000	–	25–4	4.5–2.5	4	4	4
Ceratoscopelus warmingii (Lütken, 1892)	33	36	5.2 (1.8–7.4)	2.0 (0.1–6.2)	50–1000	●	28–4	4.6–2.5	3	3	2
Dasyscopelus asper (Richardson, 1845)	50	21	5.9 (1.4–7.5)	3.7 (0.3–5.1)	25–1000	●	29–4	4.4–2.5	4	3	2
Dasyscopelus obtusirostre (Tåning, 1928)	16	15	6.5 (2.5–8.4)	4.8 (1.5–7.8)	50–800	–	28–5	4.6–2.5	–	4	4
Dasyscopelus selenops (Tåning 1928)	2	3	5.4 (5.0–5.9)	2.2 (2.2–2.3)	95–680	–	25–5	4.5–2.5	–	4	4
Diaphus bertelseni Nafpaktitis, 1966	2	6	8.4 (7.4–9.4)	8.0 (6.7–9.3)	90–385	–	25–9	4.5–3.2	–	4	4
Diaphus brachycephalus Tåning, 1928	454	49	3.8 (0.9–5.4)	1.3 (0.1–2.8)	50–1000	●	28–4	4.6–2.5	1	1	1
Diaphus dumerilii (Bleeker, 1856)	52	31	4.5 (2.9–5.9)	1.3 (0.3–9.3)	65–1000	●	26–4	4.3–2.5	3	1	2
Diaphus fragilis Tåning, 1928	131	36	4.7 (1.4–8.6)	1.9 (0.1–11.7)	65–1000	●	26–4	4.3–2.5	3	3	2
Diaphus garmani Gilbert, 1906	111	15	4.0 (2.5–4.9)	0.7 (0.1–1.3)	65–780	●	26–5	4.3–2.5	4	4	4
Diaphus holti Tåning, 1918	1	3	2.0 (2.0–2.0)	0.1 (0.1–0.1)	385–385	–	9–9	3.2–3.2	–	4	4
Diaphus lucidus (Goode & Bean, 1896)	43	18	7.6 (3.1–9.6)	5.2 (0.3–9.7)	25–800	●	29–5	4.4–2.5	4	4	4
Diaphus mollis Tåning, 1928	41	28	4.8 (2.2–5.9)	1.7 (1.0–2.9)	95–1000	●	25–4	4.5–2.5	3	3	2
Diaphus perspicillatus (Ogilby, 1898)	272	36	4.9 (1.8–6.9)	2.0 (1.0–4.6)	65–1000	●	26–4	4.3–2.5	1	1	1
Diaphus problematicus Parr, 1928	3	5	6.8 (5.2–7.7)	4.0 (1.7–5.8)	430–800	–	8–5	3.1–3.5	4	4	4
Diaphus splendidus (Brauer, 1904)	240	36	5.3 (2.0–8.5)	1.9 (1.0–6.6)	90–1000	●	25–4	4.5–2.5	1	3	1
Electrona risso (Cocco, 1829)	72	36	6.6 (5.0–8.1)	7.4 (3.2–12.4)	385–1000	○	9–4	2.8–3.7	1	1	1
Hygophum hygomii (Lütken, 1892)	2	3	5.3 (5.2–5.4)	2.2 (1.9–2.4)	1000–1000	–	4–4	3.7–3.7	4	–	4
Hygophum macrochir (Günther, 1864)	13	15	4.5 (3.4–5.4)	1.4 (0.4–2.3)	50–800	–	28–5	4.6–2.5	4	4	4
Hygophum taaningi Becker, 1965	104	26	5.1 (2.6–6.6)	1.9 (0.2–3.1)	90–1000	●	20–4	3.7–2.5	1	1	1
Lampadena luminosa (Garman, 1899)	30	8	2.8 (1.9–5.1)	0.5 (0.3–1.4)	90–1000	●	20–4	3.7–2.5	–	4	4
Lampanyctus alatus Goode & Bean, 1896	2	3	3.7 (3.7–3.8)	0.3 (0.2–0.3)	430–430	–	8–8	3.1–3.1	–	4	4
Lampanyctus festivus Tåning, 1928	4	3	8.7 (5.6–12.0)	6.8 (1.3–13.7)	95–95	–	25–25	4.5–4.5	–	4	4
Lampanyctus lineatus Tåning, 1928	4	8	16.5(15.2–17.8)	23.6 (17.2–29.4)	430–1000	–	8–4	3.1–3.7	–	4	4
Lampanyctus nobilis (Tåning, 1928)	279	41	5.7 (1.9–12.1)	1.8 (1.0–13.3)	50–1000	●	28–4	4.6–2.5	1	1	1
Lampanyctus tenuiformes (Brauer, 1906)	22	21	11.1 (4.4–13.6)	16.4 (4.0–46.0)	25–1000	●	29–4	4.4–2.5	2	3	2
Lepidophanes guentheri (Goode & Bean, 1896)	109	41	4.7 (2.2–6.2)	0.9 (0.7–1.7)	25–1000	●	29–4	4.4–2.5	3	1	2
Myctophum nitidulum Garman, 1899	8	13	5.5 (3.8–6.5)	2.5 (0.3–4.1)	50–850	–	28–5	4.6–2.5	4	4	4
Notoscopelus resplendens (Richardson, 1845)	2	5	7.5 (6.7–8.4)	3.1 (2.7–3.5)	430–780	–	8–5	3.1–3.5	–	4	4
Taaningichthys bathyphilus (Tåning, 1928)	10	10	6.2 (5.4–7.1)	1.8 (1.1–2.8)	780–1000	–	5–4	3.5–3.7	4	4	4

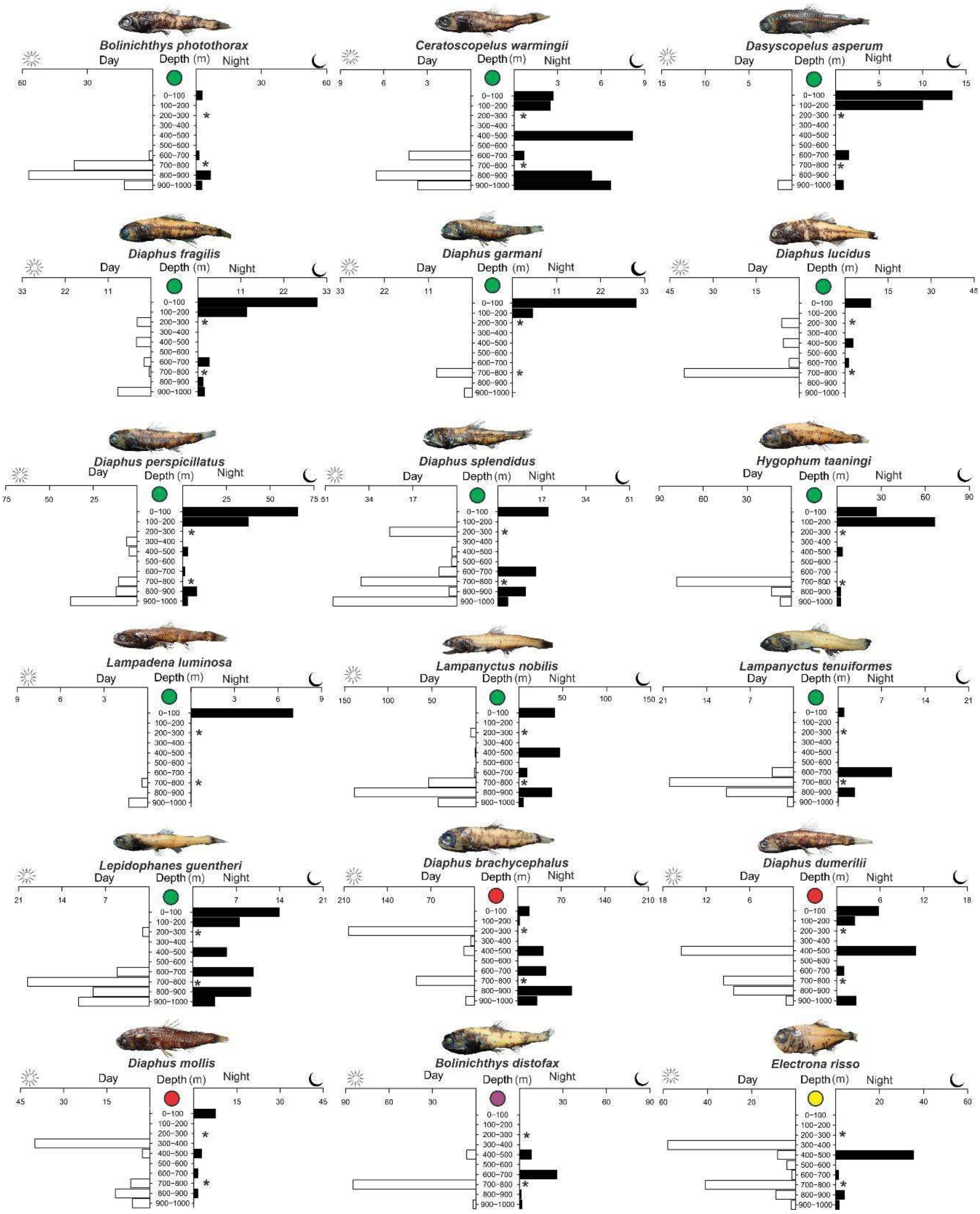

Figure 4. Average of lanternfishes relative abundance (individuals.hour^{-1}) per depth strata and diel period. * Depth strata not sampled. Circles indicate patterns of diel vertical migration: Pattern 1 (green); Pattern 2 (red); Pattern 3 (purple); Pattern 4 (yellow).

Trophic ecology

Mean $\delta^{13}C$ for lanternfishes ranged from -19.20±0.21‰ to -18.19±0.23‰, with a difference of 1‰ separating the most depleted (*D. mollis*) from the most enriched (*H. taaningi*) (Table 5; Fig 5). Conversely, a more extensive range was found among mean $\delta^{15}N$, with 2.4‰ separating the most enriched (*E. risso*: 11.41±0.13‰) and depleted (*D. dumerilii*: 8.99±1.15‰) species (Fig. 5; Supp. Material 2).

Likewise, within lanternfishes prey groups, $\delta^{13}C$ values mostly ranged between -19‰ and -20‰. However, a higher range was found among $\delta^{15}N$ values. Gelatinous organisms presented the highest range of $\delta^{15}N$, varying from 2.99±0.68‰ (*Pyrosoma atlanticum*) to 9.10±0.25‰ (*Siphonophorae sp.*). Crustaceans ranged from 5.9±0.28‰ (*Phronima* sp.) to 7.31±0.50‰ (*Euphausia* sp.). Lastly, $\delta^{15}N$ values of zooplankton ranged from 1.87±0.76‰ (10–20 µm) to 4.94±0.40‰ (>200 µm) (Supp. Material 2). Within predators, the consistency in $\delta^{13}C$ and $\delta^{15}N$ values between the deep-sea species (mean $\delta^{13}C$: -18.7‰; $\delta^{15}N$: 11.85‰) and lanternfishes ($\delta^{13}C$: -18.5‰; $\delta^{15}N$:10.1‰) indicates a likely tight trophic linkage between them. The difference in isotopic values between the epipelagic predators ($\delta^{13}C$: -16.25; $\delta^{15}N$:10.5‰) and lanternfishes, however, indicate a likely weaker trophic linkage (Fig. 5).

Overall, given the set of prey included in our mixing model, fish larvae, euphausiids, and gelatinous organisms seem to have a higher contribution for lanternfishes. Additionally, based on mixing models, it appears that lanternfishes have different patterns of prey importance. For instance, three patterns could be observed (Fig. 6). The first pattern, composed by *D. dumerilii*, *D. mollis*, *E. risso*, *H. taaningi,* and *L. nobilis*, was characterized by a high contribution of Teleostei larvae 15–20 mm (19–23%), *A. tetragona* (18–21%), and *E. gibboides* (14–17%). The second pattern, composed by *D. fragilis* and *L. guentheri*, was characterized by a high contribution of Teleostei larvae 5–10 mm (20–22%), *S. zonaria* (14–15%), *Salpa* sp. (12%), and *E. gibboides* (12–13%; Fig. 6). Finally, the third pattern, composed by *D. brachycephalus* and *D. perspicillatus*, was characterized by a high contribution of Teleostei larvae 5–10 mm (19–24%), Teleostei larvae 15–20 mm (15–18%), and *E. gibboides* (13–16%).

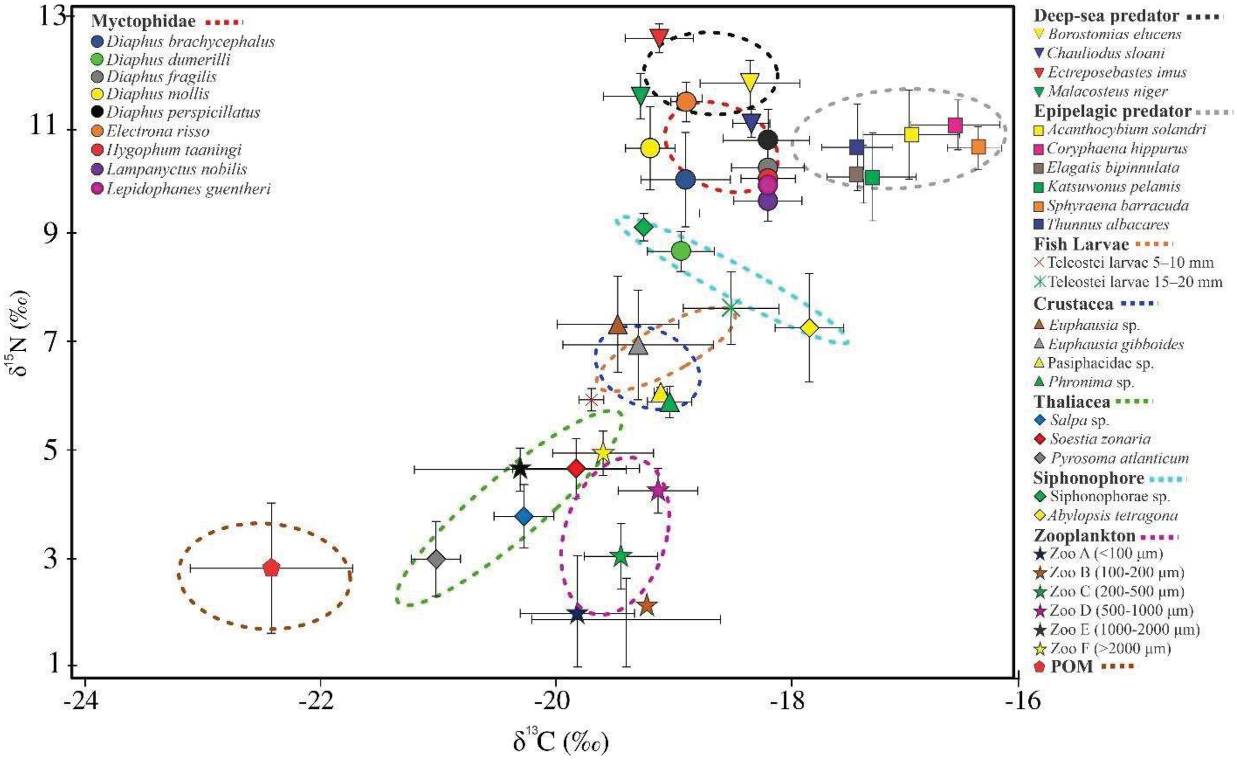

Figure 5. Stable carbon and nitrogen isotope values of lanternfishes and their potential prey and predator from oceanic islands and seamounts of the Southwestern Tropical Atlantic. Dashed lines represent the corrected standard ellipses area (SEAc) for each group.

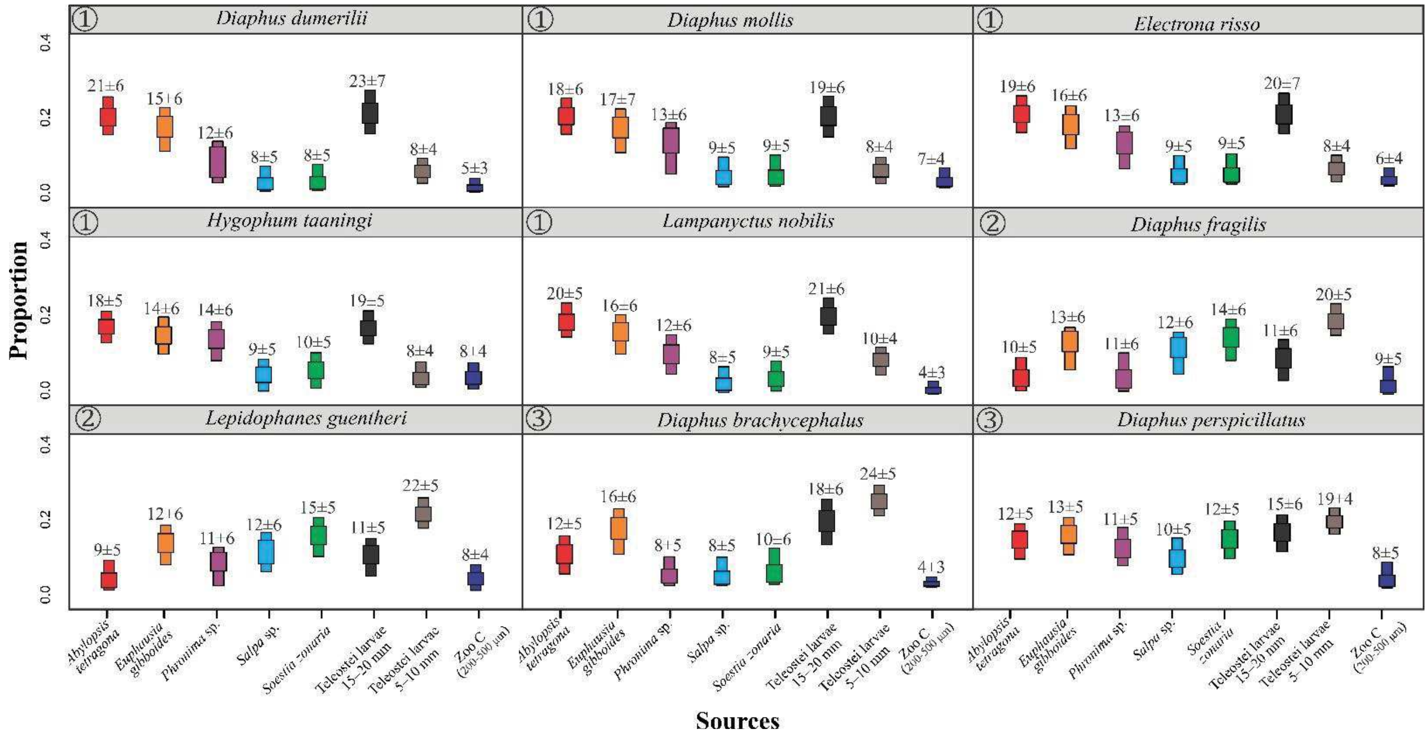

Figure 6. Estimated contribution in % (proportion; mean ± SD) based on stable isotope mixing model of potential prey to the diet of lanternfishes from oceanic islands and seamounts of the Southwestern Tropical Atlantic. Colored boxes represent 25% and 50% quantiles. Numbers in the circles indicate trophic patterns. The trophic

patterns do not reflect a fine-scale description of the diet of lanternfishes but rather demonstrate the likely trophic segregation among species and the expected most important prey groups given the organism included in the mixing model (see Discussion).

Horizontal distribution and assemblage structure

Most species (63%) were found over the entire spatial range (Figs. 7 and 8). Nevertheless, ten species were only captured in Area 2 (*Benthosema suborbitale*, *D. obtusirostre*, *Dasyscopelus selenops*, *Diaphus bertelseni*, *D. holti*, *Lampadena luminosa*, *Lampanyctus alatus*, *L. festivus*, *L. lineatus*, and *Notoscopelus resplendens*), whereas one species was only captured in Area 1 (*Hygophum hygomii*; Fig. 8). The absence of species in one of the areas, however, is probably associated with the sample size, as all these species were also classified as scarce and rare.

Cluster analysis based on the log-transformed dataset exhibited five major assemblages at the resemblance level of 25% (Fig. 9), showing a rather weak but significant difference in the species composition among zones (Areas 1 and 2; ANOSIM R=0.28; $p < 0.01$) and depth categories (Epipelagic 0–200 m, Upper mesopelagic 200−500 m, and Lower mesopelagic 500–1000 m; R=0.15; $p < 0.01$). No significant differences in horizontal distribution were found among diel periods (Day and Night; R<0.01; $p > 0.01$). **Assemblage A** (named Area 2, 0–200 m) included only samples collected in epipelagic waters of Area 2 (Fig. 9). **Assemblage B** (named Area 1, 200–1000 m) encompassed samples collected in mesopelagic waters (upper and lower) of Area 1 (Fig. 9). **Assemblage C** (named Area 1 and 2, 0–200m) encompassed samples collected in both Areas but in epipelagic waters only (Fig. 9). On the contrary, samples from **Assemblage D** (named Area 2, 300–500 m) were restricted to upper mesopelagic waters of Area 2 (Fig. 9). Finally, all samples from **Assemblage E** (named Area 2, 600–1000 m) were collected in lower mesopelagic waters of Area 2 (Fig. 9).

SIMPER analysis showed high dissimilarity levels between assemblages, ranging from 62% to 92% (Supp. Material 3). The following species were considered as consolidating species (cumulatively contributing to over 70% to the dissimilarity between assemblages: *B. distofax*, *B. photothorax*, *D. asper, D. brachycephalus*, *D. dumerilii*, *D. mollis*, *D. perspicillatus*, *D. splendidus*, *E. risso*, *H. taaningi*, *L. nobilis*, and *L. guentheri*). Dissimilarities between assemblages were primarily driven by differences in the average abundance of species, rather than presence/absence. As an example, the high abundances of *D. brachycephalus* on Group A and *L. nobilis* on Group D contributed to as much as 53% of the total dissimilarities between groups (*e.g.,* A–D). However, the absence of *D. perspicillatus* on the group A and B was important for dissimilarities on the interactions B–C (30% of contribution) and A–C (24%) (Supp. Material 3).

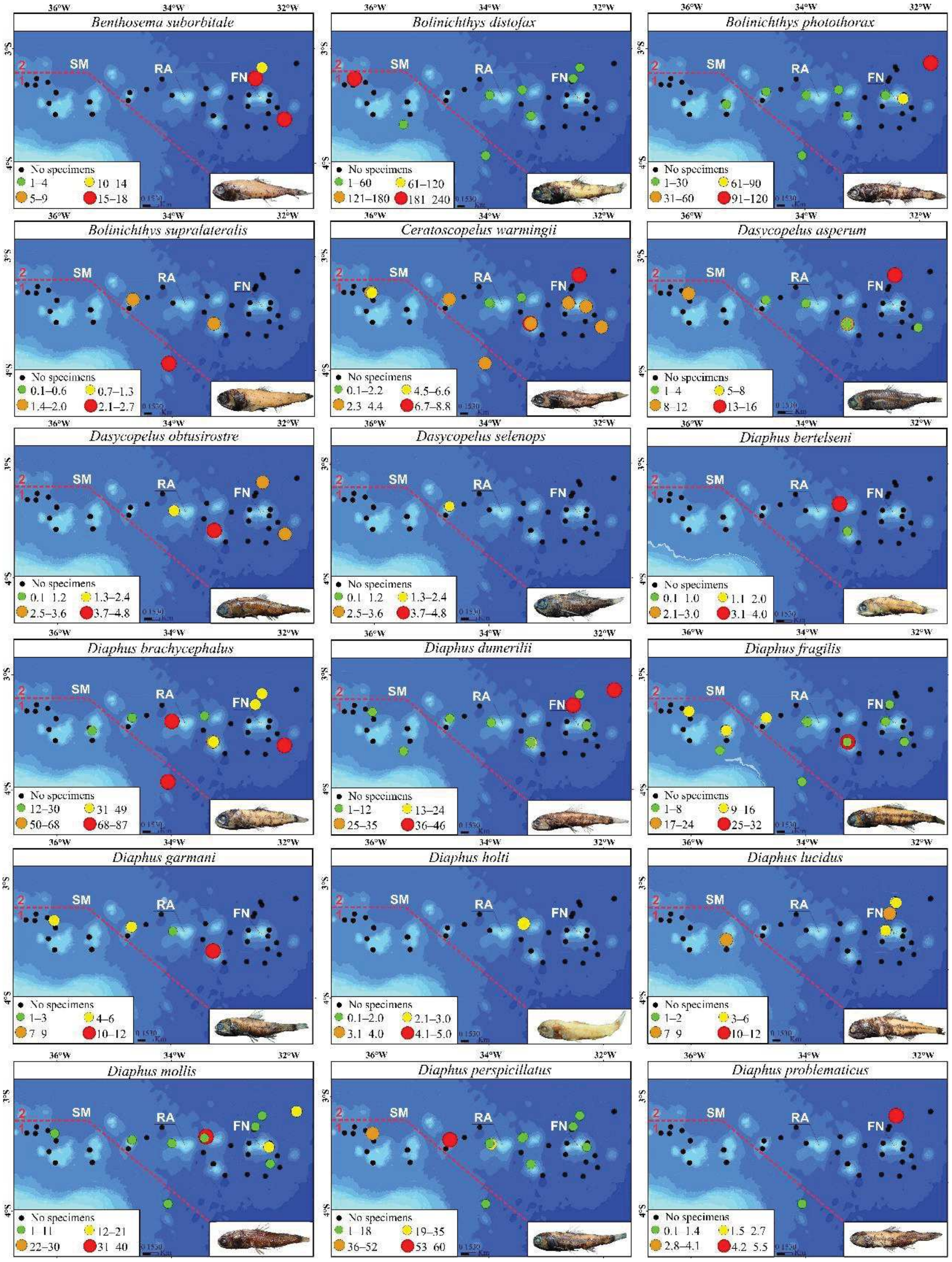

Figure 7. Catch per unit of effort (CPUE; individuals/hour) of lanternfishes from oceanic islands and seamounts of the Southwestern Tropical Atlantic – Part I. Dashed red line shows the limit between Area 1 and Area 2 (adapted from Assunção et al., 2020). SM – Seamounts; RA –Rocas Atoll; FN – Fernando de Noronha Archipelago. Numbers outside the maps indicate the latitude (x axes) and longitude (y axes).

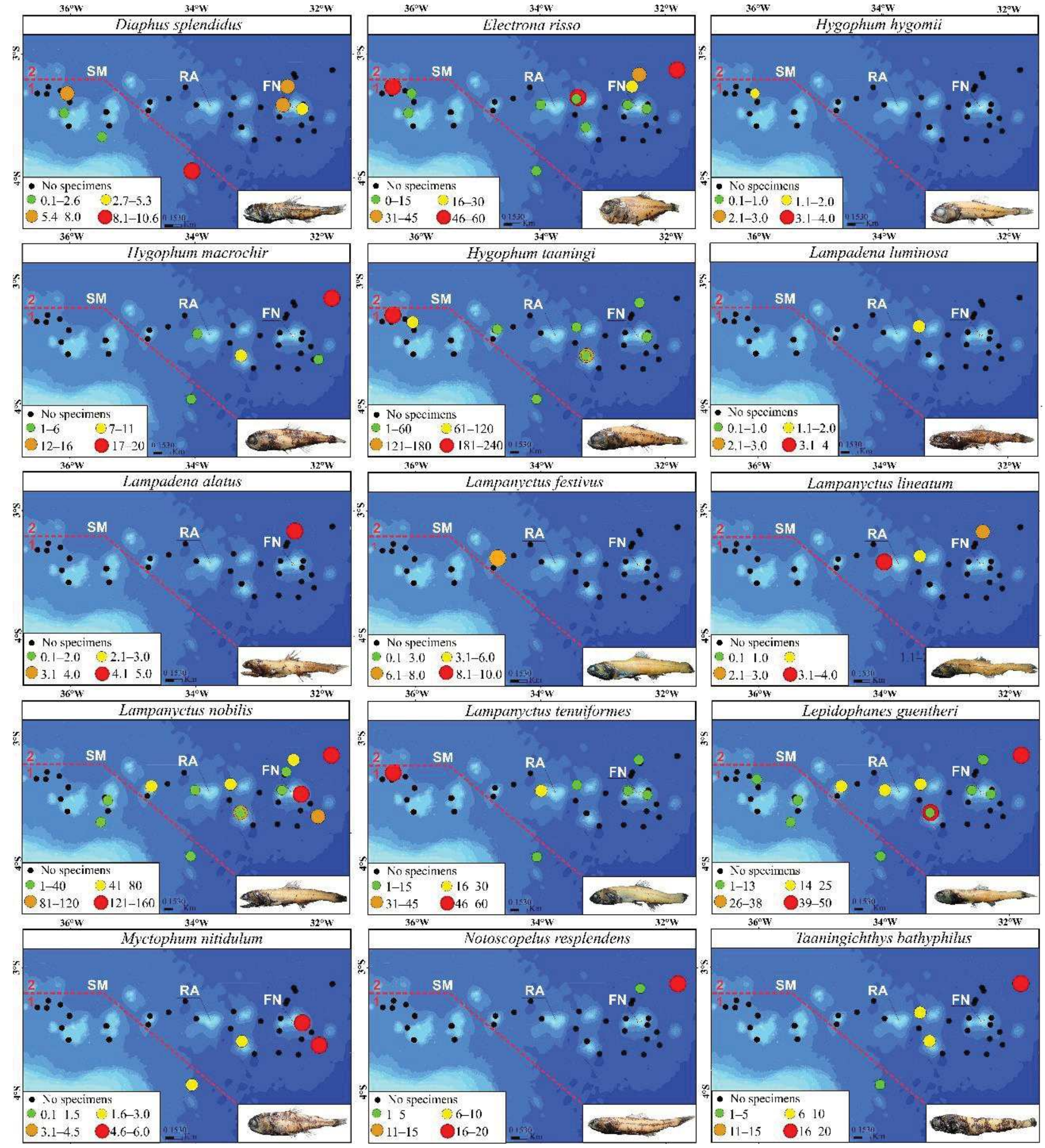

Figure 8. Catch per unit of effort (CPUE; individuals/hour) of lanternfishes from oceanic islands and seamounts of the Southwestern Tropical Atlantic – Part II. Dashed red line shows the limit between Area 1 and Area 2 (adapted from Assunção et al., 2020). SM – Seamounts; RA –Rocas Atoll; FN – Fernando de Noronha Archipelago. Numbers outside the maps indicate the latitude (horizontal) and longitude (vertical).

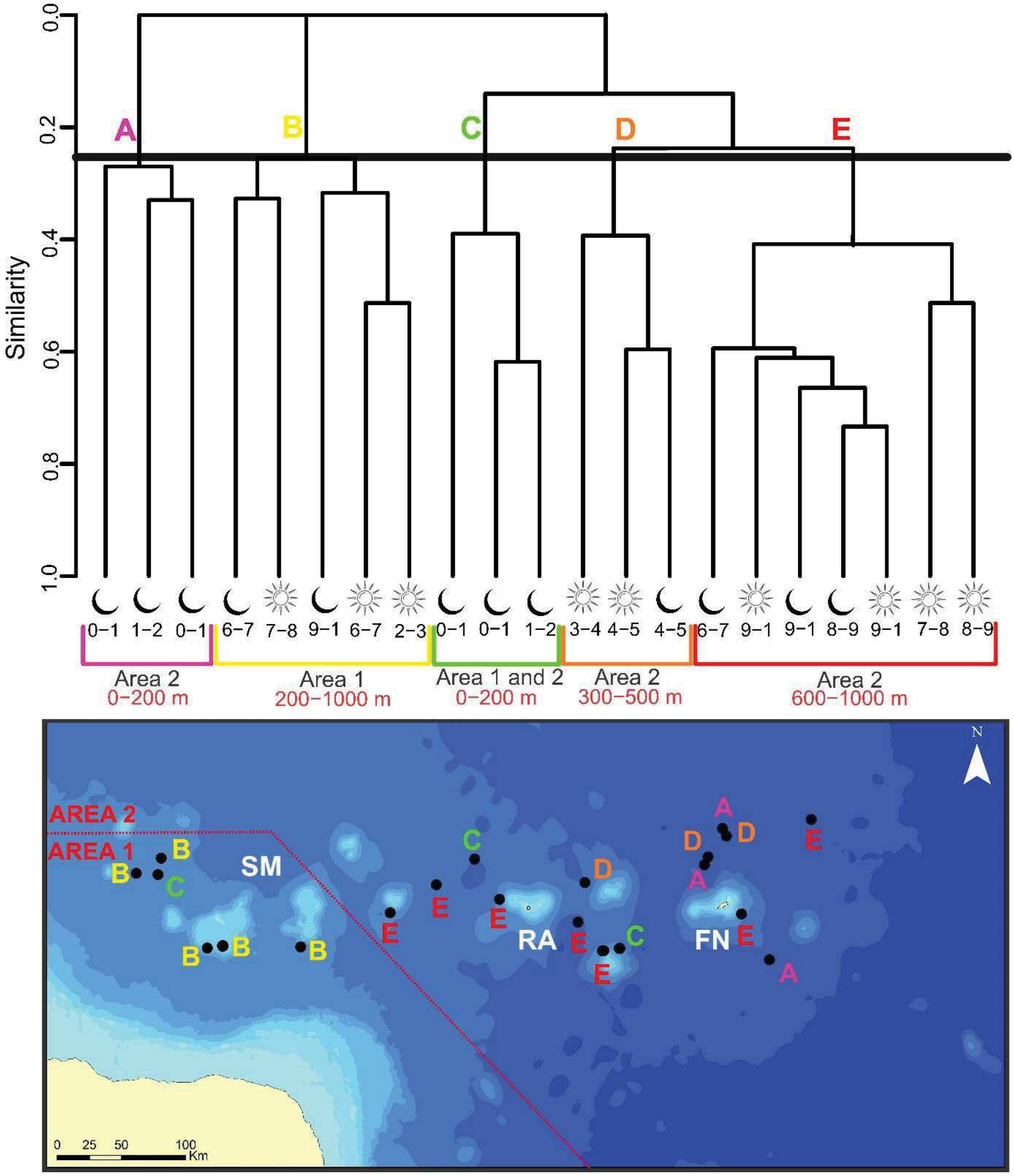

Figure 9. Dendrogram showing assemblages obtained after cluster analysis applied on the Bray Curtis similarities calculated among hauls (abundance data) for lanternfishes from oceanic islands and seamounts of the Southwestern Tropical Atlantic. The variables day period (sun pictogram: Day; moon pictogram: Night), Zone (A1–Area 1; A2–Area 2), and depth (0–1 = 0–100 m; 1–2 = 100–200 m; etc.) are shown. Limits of Area 1 and Area 2 (dashed red line) adapted from Assunção et al., (2020). SM: Seamounts; RA: Rocas Atoll; FN: Fernando de Noronha Archipelago.

DISCUSSION

Here, we investigate the vertical migration and trophic ecology of lanternfishes in the southwestern Tropical Atlantic, as well as the influence of physicochemical factors on their horizontal structuring. For that, we combine information on their species composition, distribution, stable isotopic composition, and habitat. We expose multiple patterns of vertical and trophic behaviour, revealing multidimensional niches, underestimated trophic links, and underling several mechanisms to avoid competitive exclusion. Moreover, we show that lanternfishes are ubiquitous to environmental conditions evaluated here, leading to weak horizontal assemblage segregation.

Sample and analyses drawbacks

Different drawbacks could blur the interpretation of our results. First, any mesopelagic fish sampling is subject to technical hitches, as it includes complex interactions between the features of the gear (*e.g.,* mesh size and mouth-area of the net) and the several body morphologies (*e.g.,* fusiform, eel-like, and compressiform) and behaviours (Kaartvedt et al., 2012; Kwong et al., 2018). As an example, some mesopelagic species present net avoidance behaviour, scaping from the trawls in the same way they run away from predators (Kaartvedt et al., 2012). Additionally, many pelagic organisms exhibit a strong light-escape response in the presence of artificial light from the vessel and may be thus repulsed at night (Ludvigsen et al., 2018; Peña et al., 2019).

Pelagic trawls characteristics also impact the diversity and size of collected specimens. For instance, inter-comparations between gears reveal that the taxonomic composition and contribution of the main size groups to the total catch of pelagic trawls varies between gear types (Kwong et al., 2018). Overall, the gear utilized here enabled capturing a wide number of fish species (206), ranging from 0.3 to 180 cm (L. N. Eduardo, unpubl. data). Nonetheless, lanternfishes composition and size structure we observed may reflect not only the *in situ* biogeographic patterns of this group but also the selectivity of employed gear. Further, although we took precautions to minimize the collection of specimens during the lowering or hoisting (see methodology), our gear did not have an opening-closing mechanism, and the collection of few specimens may have occurred during these processes. Therefore, we focused only on vertical migration patterns, avoiding fine scales analyses and precise delimitations of vertical distribution. Further sampling using different gears (*e.g.,* opening-closing Tucker trawls or MOCNESS nets) may reveal more precise patterns.

Second, diet determination from isotopic mixing models is closely related to the trophic discrimination factor (TDF) and sources utilized to run the analysis (Fry, 2006). Additionally, isotopic incorporation (turnover) in animal tissues is highly variable and can blur the interpretation of isotopic measurements (Fry, 2006). As an example, depending on tissue-specific isotopic turnover, stable isotope measurements may reflect average dietary records that range from days to years (Fry, 2006). In this study, mixing models were performed with the overall goal of assessing the variability in the trophic ecology of lanternfishes. However, the three patterns of prey importance (see Results) defined for lanternfishes were defined solely based on organisms included in the model. Hence, despite carefully selecting TDF values and prey, the inclusion of other prey, gut content analyses, and turnover rates may provide further insights into the trophic ecology of myctophids (Fry, 2006; Olivar et al., 2018).

Third, to increase the robustness of our analysis, all tests were conducted by coupling different size classes, which may lead to loss of information on both vertical and trophic patterns of ontogenetic variation (Catul et al., 2011; Olivar et al., 2015). Therefore, our findings cannot exhaustively describe the ecological aspects of myctophids. Nevertheless, they increase the understanding of a central and understudied deep-sea group, as well as provide new information on important aspects of its ecology.

Species richness and dominance patterns

We collected 13 genera and 33 species of lanternfishes, making it one of the most important mesopelagic fish families in terms of abundance, biomass, and richness (40% of the collected specimens on our samples; L. N. Eduardo, unpubl. data). From those, seven species were dominant (*B. distofax, D. brachycephalus, D. perspicillatus, D. splendidus, E. risso, H. taaningi,* and *L. nobilis*) and accounted for 66% of the total number of individuals. Similar species composition was found in the eastern Tropical Atlantic (Olivar et al., 2017) and eastern coast of Brazil (11°−22° S; Braga et al., 2014), where approximately 30 lanternfish species were found. In these areas, the predominance of few lanternfish species was also observed but with clear differences in the dominant species. For instance, on the eastern coast of Brazil (from Bahia to Rio de Janeiro), *D. garmani* accounted for 84% of all myctophids (Braga et al., 2014), while in our study area, this species was classified as scarce and rare (5% of all specimens). Likewise, in the eastern Tropical Atlantic, *B. suborbitale*, *C. warmingii*, and *H. macrochir* were dominant (Olivar et al., 2017), whereas these species accounted for less than 4% of the total abundance here. These differences in species dominance are likely related to intrinsic biogeographic features (*e.g.,* seabed structure, water masses, and hydrographic fronts), which have been depicted as significant factors driving the structure and composition of myctophid assemblages (Hulley and Krefft, 1985; Hulley, 1992; Olivar et al., 2017). Moreover, fishing gear, sampling strategy, and effort were different among studies, which may affect the overall picture of the biodiversity.

Horizontal distribution and potential influence of physicochemical features

Assunção et al., (2020) divided the study area into two significantly different areas (Area 1 and Area 2) in terms of thermohaline structure and current systems (NBUC/NBC vs. cSEC/SEUC). Additionally, based on our results, differences were also observed in oxygen and fluorescence profiles. Together, all these oceanographic features resulted in significant variations in zooplankton biomass (Figueiredo et al., 2020) and planktonic cnidarians composition (Tosetto et al., 2021). Based on our analyses, it may also partially explain the assemblage structuring of lanternfishes. For instance, assemblage B included only samples performed on mesopelagic waters of Area 1, being dissimilar from other assemblages by the higher abundance of *B. distofax* and low occurrence of *D. brachycephalus* and *D. splendidus*. Indeed, the variability of *B. distofax* distribution has been closely related to oceanographic circulation processes in both the Pacific and Atlantic oceans (Hulley and Duhamel, 2009). However, four other assemblages were also identified, with at least one (Assemblage C) encompassing the two areas. Moreover, a weak explanatory response was found when considering the pre-established areas as a factor. Therefore, although the formation of some assemblages may be driven by oceanographic characteristics of these areas (e*.g.,* current systems, thermohaline structures, and oxygen availability), neither of these set of features alone fully explains lanternfish structuring observed here.

One possible explanation for the weak myctophids horizontal structuring is that, despite the thermohaline structure and stratification at shallow layers (0–300 m) being significantly different between Areas 1 and 2, the thermal gradients between surface and deeper layers were alike. Additionally, water masses below 400 m depth were similar. At the scale of this study, another likely explanation is the high potential of dispersion of myctophids, once vertically migrating species are transported at relatively large horizontal distances depending on the oceanographic conditions through which they travel. Moreover, their ability to actively choose a depth stratum that meets favourable environmental conditions may also be an important factor (Milligan and Sutton, 2020). Similar patterns were observed in the Atlantic, Indian, and Pacific oceans, where environmental characteristics explained only a small portion of the myctophids composition (Flynn and Marshall, 2013; Olivar et al., 2015; Milligan and Sutton, 2020).

Vertical migration, trophic ecology, and niche partitioning

From the 33 lanternfish species collected here, 72% (24 species) were found at epipelagic layers at night, indicating a likely pattern of vertical migration. This agrees with previously information available for these species, where 90% (30 species) of the lanternfishes collected here seem to perform vertical migration elsewhere (Supp. Material 4). Indeed, most myctophids are known to undertake substantial daily vertical migrations, whether to feed, reproduce, or seek refuge (Watanabe et al., 1999; Catul et al., 2011; Sutton, 2013).

All 18 lanternfish species selected to investigate vertical distribution patterns withstand a wide range of environmental conditions (*e.g.,* daily temperatures range up to 25°C) and show a likely pattern of asynchronous migrations (*e.g.,* the entire population might not respond synchronously to diel variation in light intensity). Moreover, we observed high variability of space occupation at both day and night. For instance, while species from Pattern 1 peaked at the upper mesopelagic layers (200–500 m) and partially migrated to the epipelagic layer at night, species from Patterns 3 and 4 seemed to remain at mesopelagic waters full-time (Fig. 4). This agrees with previously information available for these species elsewhere (Supp. Material 4). Interestingly, a similar pattern was found for hatchetfishes (Sternoptychidae; second most abundant mesopelagic fish group in the SWTA). These species are divided into several functional groups with different diet preferences, isotopic composition, and vertical abundance peaks (Eduardo et al., 2020a). Therefore, the two most abundant fish groups of the SWTA (70% of all sampled specimens) seem to be distributed throughout vertical layers and thereby avoiding competitive exclusion (Eduardo et al., 2020a; Sutton, 2013).

Our findings on trophic ecology reinforce this pattern. Despite all the nine species investigated are zooplanktivores (*e.g.,* foraging on fish larvae, gelatinous, and euphausiids), the isotopic mixing models revealed at least three possible patterns of prey importance. For instance, the most important prey for trophic pattern 1 seems to be fish larvae 15–20 mm, *A. tetragona* and *E. gibboides*, whereas the most important prey of pattern 2 are fish larvae 5–10 mm, *S. zonaria*, and *Salpa* sp. Additionally, lanternfishes do not seem to present the same trophic pattern and vertical space occupation. As an example, *D. dumerilii*, *D. mollis*, *E. risso*, *H. taaningi*, and *L. nobilis* were allocated to the trophic Pattern 1, but none of them peaked at the same depth strata at day (Fig. 10). Similar finds were noted in the Southern Ocean and Gulf of Mexico, where most of the lanternfishes presented distinct isotopic niches that differ by at least one of the two niche axes *(e.g*., habitat and trophic level; Hopkins et al., 1996; Hopkins and Gartner, 1992; Hopkins and Sutton, 1998; Cherel et al., 2010). Hence, coupling the information of this study and previous works, it seems that, when living in the same depth layer, the segregation of lanternfishes operate through different feeding habits.

Two other patterns were evidenced in myctophid trophodynamics. First, gelatinous organisms (Siphonophorae and Thaliacea) appeared as important prey for all the nine lanternfish species included in trophic analyses. This pattern diverges from some studies based solely on stomach content analyses and/or not including isotopic and genetic information of gelatinous species (Shreeve et al., 2009; Noord, 2013; Battaglia et al., 2016). Despite some of these studies point out the presence of gelatinous organisms, this type of prey usually does not stand out as an important component of lanternfishes diet since quickly digested gelatinous organisms are often unidentifiable in stomachs, especially after chemical preservation (Robison, 2009). This trophic divergence has also been noted in recent studies applying stable isotopes analyses on mesopelagic species (*e.g.,* McClain-Counts et al., 2017; Eduardo et al., 2020a). For instance, in the SWTA, gelatinous organisms were amongst the main prey of hatchetfishes (Eduardo et al., 2020a). Therefore, it is likely that key trophic relationships between lanternfishes and gelatinous organisms have been globally underestimated due to methodology limitations. This trophic link may also play an important role in the use of resources and niche differentiation. Second, we also found a high trophic contribution of fish larvae, which diverges from previous works (*e.g.,* Bernal et al., 2015). This pattern is likely driven by the local food availability, as the study area includes several coral reefs, islands, and seamounts that could enhance the larvae abundance of several species (CBD, 2014). Indeed, a recent study addressing zooplankton communities in the same location highlights a high biovolume of fish larvae on sample size fractions higher than 2000 µm (Figueiredo et al., 2020).

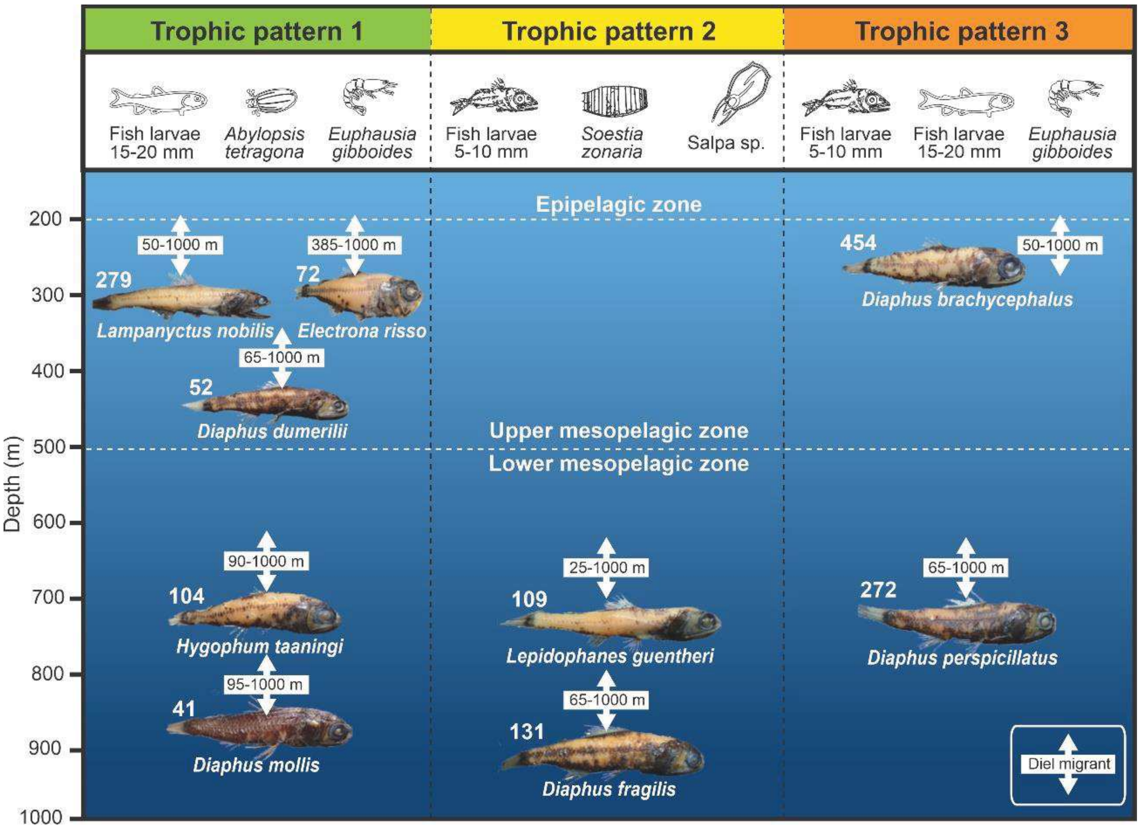

Figure 10. Conceptual model exhibiting vertical niche partitioning of lanternfishes at day. Numbers inside the white boxes indicate the depth range of each species, while numbers outside the boxes indicate the number of specimens sampled. Coloured horizontal lines indicate the peak of abundance of each species at day. It does not necessarily mean that the species are fully partitioned, but rather that their distribution centers are different. Given the limitations of our

methodology (see sample and analysis drawbacks), this model does not intend to provide a precise vision of vertical niche partitioning but rather exemplify how niche differentiation of these species may occur.

Differences in local food availability also seem to reflect in the trophodynamics between myctophids and their potential predators. While lanternfishes may be the most important prey for epipelagic predators in some locations (Karakulak et al., 2009; Battaglia et al., 2013), the SIA results did not evidence a well-defined trophic relationship between these species. Indeed, studies addressing gut content analyses of epipelagic predators over the SWTA show myctophids as a secondary prey, usually after species of Exocoetidae and cephalopods (Albuquerque et al., 2019; Silva et al., 2019; Vaske Júnior et al., 2011). In fact, epipelagic predators included here (*e.g.,* tunas) are mostly opportunistic feeders; therefore, their diet is expected to vary both spatially and temporally (Bertrand et al., 2002; Albuquerque et al., 2019). On the other hand, the isotopic compositions of myctophids and deep-sea predators are well-matched. This is also supported by previous studies of the SWTA (Eduardo et al., 2020b) and elsewhere (Sutton and Hopkins 1996; Butler et al. 2001; Battaglia et al. 2018), where myctophids are the primary prey items of several deep-sea species. For instance, in the study area, lanternfishes constitute up to 85% of the viperfish diet, which is the most abundant mesopelagic micronektivore (Eduardo et al., 2020c). In summary, in the SWTA, myctophids act as a relevant food source for both epipelagic and deep-sea predators. However, the trophic contribution for epipelagic predators is likely lesser, as these species take advantage of several additional epipelagic prey.

Conclusion

Lanternfishes are a highly diverse and abundant fish family of the southwestern Tropical Atlantic, comprising at least 33 species and 40% of all deep-sea specimens collected on our samples. This species composition is comparable to those found in the tropical and subtropical Atlantic but with clear differences in dominance patterns. Species evaluated here showed weak horizontal structuring, suggesting that well-defined assemblages of lanternfishes are not maintained. Although the discrepancies between the two areas considered here (*e.g.,* current systems, thermohaline structures, and oxygen availability) seem to play a role in the structuring of some assemblages, these sets of features alone do not fully explain lanternfish structuring observed here. Therefore, the dispersion of species and their ability to actively select vertical layers and favourable environmental conditions may be overriding the oceanographic features analyzed here.

Lanternfishes present a high variability of trophic and vertical behaviour. Indeed, three possible patterns of prey preference and four patterns of vertical behaviour were observed, showing a likely multidimensional resource partitioning. For instance, based on this study and previous works, it seems that, when living in the same habitat, the segregation of lanternfishes operates through different feeding habits, which diminishes competitive exclusion. Moreover, these species are likely feeding on gelatinous organisms (Thaliacea and Siphonophorae), a trophic relationship usually underestimated (*e.g.,* fragile gelatinous organisms were probably poorly accounted in previous studies based solely on stomach contents). This trophic link may play an important role in the use of resources and thus niche differentiation. Additionally, at least 72% of lanternfishes observed here vertically migrate to the surface to feed at night and actively transport the ingested carbon to deep waters at day, a pathway enhancing the oceanic carbon storage (Cavan et al., 2019). Finally, in the SWTA, myctophids act as a central food source for epipelagic and deep-sea predators. These processes are crucial for maintaining harvestable fish stocks and the connection between shallow and deep-sea ecosystems.

Declaration of Competing Interest

None.

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Trophic ecology, habitat, and migratory behaviour of the viperfish *Chauliodus sloani* reveal a key mesopelagic player

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Mesopelagic fishes are numerically the most important vertebrate group of all world's oceans. While these species are increasingly threatened by anthropogenic activities, basic biological knowledge is still lacking. For instance, major uncertainties remain on the behaviour, ecology, and thus functional roles of mesopelagic micronektivores, particularly regarding their interactions with physicochemical features. Here, we examine the trophic ecology, habitat, and migratory behaviour of the viperfish (*Chauliodus sloani*)—a poorly known and abundant deep-sea species—to further understand the ecology and thus functional role of mesopelagic micronektivores. Moreover, we explore how physical drivers may affect these features and how these relationships are likely to change over large oceanic areas. The viperfish heavily preys on epipelagic migrant species, especially myctophids, and presents spatial and trophic ontogenetic shifts. Temperature restricts its vertical distribution. Therefore, its trophodynamics, migratory behaviour, and functional roles are expected to be modulated by the latitudinal change in temperature. For instance, in most tropical regions the viperfish stay full-time feeding, excreting, and serving as prey (e.g. for bathypelagic predators) at deep layers. On the contrary, in temperate regions, the viperfish ascend to superficial waters where they trophically interact with epipelagic predators and may release carbon where its remineralization is the greatest.

Mesopelagic fishes (200–1000 m depth) are numerically the most important vertebrate group of the world's oceans[1], usually presenting global distribution[2,3], high biodiversity[4], and several adaptations to overcome challenges imposed by the deep-sea[4]. Most of these species vertically migrate to the surface to feed at night and actively transport the ingested carbon to deep waters during daylight[5], a pathway enhancing the oceanic carbon storage and thus global carbon cycles[6–8]. Moreover, they are an important trophic link for the maintenance of harvestable fish stocks[9–11] and the connection between shallow and deep-sea ecosystems[12]. However, while there is a major lack of knowledge regarding their global composition, ecology, and ecosystem functions[13–15], these species are increasingly threatened by anthropogenic activities. For instance, effects of climatic change[16,17], plastic pollution[18], and exploitation of deep-sea resources[15,19] stand to alter the structure and function of deep-sea ecosystems. Therefore, as threats to the diversity and stability increase, the understanding of mesopelagic ecosystems, their processes, and functions is mandatory, especially when sustainability is intended to be achieved[15,20].

Although research on mesopelagic species has considerably advanced over the past few years[3,5,20–24], most works focused on zooplanktivorous groups (e.g. myctophids, sternoptychids), while less attention has been paid to micronektivores (e.g. stomiids) that occupy higher trophic levels[25]. Given their high abundance[26], deep migrations[26,27], great body mass[4], and high predation on migrant zooplanktivorous fishes[23], mesopelagic micronektivores are a crucial component of deep-sea systems that hitherto has been overlooked. Indeed, the trophic ecology, migratory behaviour, and environmental interactions of mesopelagic micronektivores remains poorly known worldwide and unexplored in most oceanic areas[13,15,25]. It is therefore not clear how physical drivers (e.g. temperature, oxygen) structure these communities and how these relationships are likely to change in the

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space and time. Additionally, most of the previous studies addressing the trophodynamics of micronektivores do not include their predators and/or were based solely on stomach contents[25,27,28], while further approaches (e.g. stable isotopes, fatty acids, genetics) are required to provide a comprehensive picture of energy flows across trophic compartments[20]. Clarification of the ecology, vertical behaviour and trophic relationships of micronektivores should provide key knowledge on mesopelagic communities and systems[13–15]. Moreover, it may help to understand how these species might respond under climatic changes[16] and what consequences it may have for their functional role and thus ecosystems health.

In this context, here we examine the habitat, trophic ecology, and vertical migration of the viperfish *Chauliodus sloani* (Stomiiformes: Stomiidae)—a poorly known and abundant deep-sea species[29,30]—to further understand the ecology and thus functional role of mesopelagic micronektivores. For that, we combine several approaches and take advantage of a multidisciplinary deep-sea survey around oceanic islands and seamounts in the western Tropical Atlantic. First, we assess the trophic ecology of the viperfish by coupling stomach content analyses with an extensive stable isotopic data (carbon and nitrogen) of its main probable trophic links, including zooplankton, crustaceans, fish larvae, zooplanktivorous fish, and epipelagic and bathypelagic potential predators. Second, we assess viperfish migratory behaviour by using novel information on its abundance, distribution, and physicochemical characteristics of its habitat (temperature and oxygen). Additionally, we combine our results with previous studies to construct a conceptual model, examining how temperature might influence trophic ecology and vertical movements of the viperfish and thus how latitudinal changes in sea temperature can affect its potential contribution to carbon sequestration.

Materials and methods

Specimens and data collection.

Specimens and data collection are described as follows in[20,31]. Data were collected off northeastern Brazil (Fernando de Noronha Ridge) during the Acoustics along the BRAzilian COaSt 2 (ABRACOS2) survey, carried out from 9th April to 6th May 2017, onboard the French RV *Antea*. Sampling of mesopelagic fishes, crustaceans and gelatinous organisms was conducted during day and night at 33 stations by using a micronekton trawl (body mesh: 40 mm, cod-end mesh: 10 mm) from 10 to 1,113 m (Fig. 1, Suppl. Material 1). Targeted depth was defined for each tow according to the presence of acoustic scattered layer or patches as observed using a Simrad EK60 (Kongsberg Simrad AS) split-beam scientific echosounder, operating at 38, 70, 120 and 200 kHz. Each trawl was performed for about 30 min at 2–3 kt. Tow duration was considered from the moment of the arrival of the net on the pre-set depth to the lift-off time, recorded utilizing a SCANMAR system. The net geometry has also been monitored using SCANMAR sensors, to give headline height, depth, and distance of wings and doors to ensure the net was fishing correctly. As the trawl was not fitted with opening or closing mechanism, the collection of specimens during the lowering or hoisting of the net was reduced as much as possible by decreasing ship velocity and increasing winch speed.

Temperature, salinity, oxygen, and fluorescence profiles were collected using a CTDO (model: SeaBird911 +; Fig. 1). Particulate organic matter (POM) was sampled at 22 stations by filtering seawater from the maximum fluorescence depth (~ 80 m depth) through GF/F filters (47 mm), followed by a dry proceeding of 36 h (40 °C)[32]. Zooplankton samples were collected using bongo nets (four nets fitted with 64, 120, 300, and 500 µm mesh sizes) that were towed from 200 m depth up to the surface at 22 stations. Additional epipelagic sampling, targeting top predators, was performed aboard a sportfishing boat around the Fernando de Noronha Archipelago using hook and line.

Captured organisms were fixed in a 4% formalin solution for one month and then preserved in a 70% alcohol solution. At the laboratory, individuals were identified to the lowest taxonomic level, measured (nearest 0.1 cm of standard length, SL) and weighed (nearest 0.01 g of total weight, TW). Voucher specimens were deposited in the NPM – Fish Collection of the "Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro" (UFRJ). The authors confirm that all methods were approved and carried out in accordance with relevant guidelines and regulations of the Brazilian Ministry of Environment (SISBIO; authorization number: 47270–5).

Vertical distribution, habitat, and migration.

Viperfish vertical behaviour was characterised by using data on diel vertical distribution of abundance, size distribution, and physicochemical habitat. The relative index of abundance (Catch Per Unit of Effort—CPUE) was calculated considering the number and weight of specimens captured per hour, standardized to a similar net-mouth area of 120 m^2 (estimated through SCANMAR sensors). These values, as well as the mean length and weight of specimens, were considered according to the diel period (day/night), and depth strata (10–1000 m, intervals of 100 m). Day was considered to extend from one hour after sunrise to one hour before sunset, while the night was from one hour after sunset to one hour before sunrise. Dawn or dusk samples were discarded when studying day/night vertical distributions. Except for the layers 200–300 and 700–800 at night, where no aggregation of organism was observed through acoustics, all depth strata were sampled at least once (Suppl. Material 1). A two-way ANOVA was performed[33] to determine significant differences in SL and TW between period of the day and depth strata, following the necessary assumptions of normality (Kolmogorov–Smirnov test) and homoscedasticity (Levene's test). Distribution pattern of specimens concerning their environment was analysed by combing data on vertical distributions and mean profiles of temperature and oxygen.

Trophic ecology.

Gut Content (GCA) and carbon and nitrogen Stable Isotopes Analyses (SIA) were implemented to assess the trophic ecology of the viperfish. Both analyses were performed considering three size classes (< 15 cm; > 15 cm; and pooled sizes), based on the viperfish size at sexual maturity (L_{50}:15 cm)[34]. Additionally, we included stable isotopic data on potential viperfish predators to infer whether this species is being consumed by epipelagic and/or bathypelagic species. Based on data availability, local fauna, and literature information[10,12,35,36],

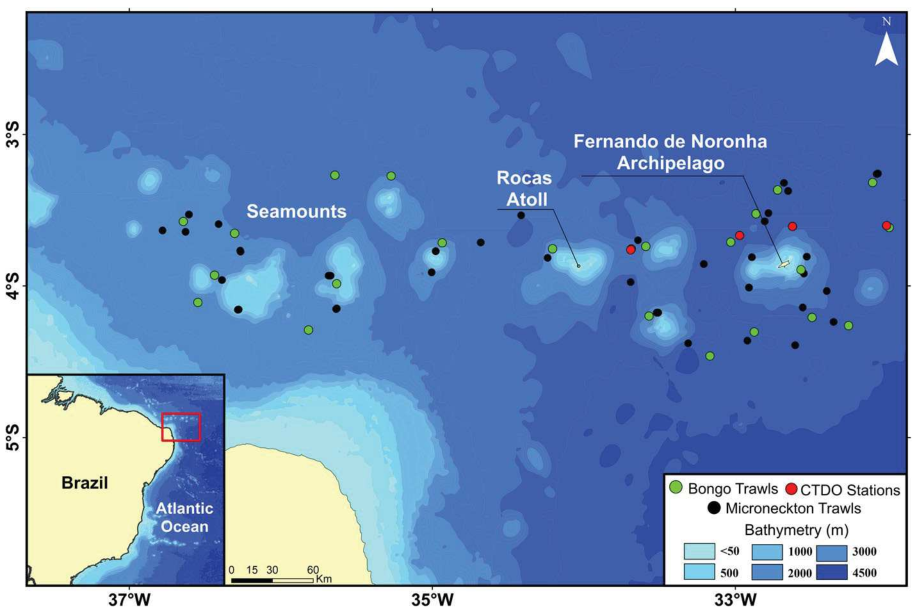

Figure 1. Study area (Fernando de Noronha Ridge) with CTD, bongo, and micronekton-trawl sampling stations. This map was created using the software Qgis 3.14 (https://www.qgis.org/pt_BR/site).

the following species were considered as potential predators and thus included in the analyses: *Ectreposebastes imus*, *Sphyraena barracuda*, *Coryphaena hippurus*, *Elagatis bipinnulata*, *Acanthocybium solandri*, *Katsuwonus pelamis*, and *Thunnus albacares*.

For GCA, each specimen had the stomach extracted and subsequently dissected under the stereoscope for content removal. Contents found in the mouth, oesophagus, and intestines were not considered in this study. Wherever possible, prey-size measurements to the nearest 0.1 mm were carried out with a binocular stereoscope using an ocular micrometric scale. Standard length for fishes; back of eye socket to tip of telson length (excluding terminal spines) for decapods; and tip of rostrum to tip of telson length (excluding terminal spines) for euphausiids were measured.

The vacuity index (VI, %) was calculated as follows: VI = Nv/Ne × 100, where Nv is the number of empty stomachs and Ne the total number of examined stomachs. Vacuity index was calculated for day, night, and both periods together. Dietary indexes for coupled stomachs were calculated to assess the importance of each prey item in viperfish diet: frequency of occurrence (%FO), numerical abundance (%N) and weight percentage (%W)[27]. Additionally, to estimate the niche breadth of viperfish, the Levin's standardized index was calculated as follows: $B_J = \frac{1}{n-1}(\frac{1}{\sum p_{ij}^2} - 1)$, where B_j is the Levin's standardized index for the viperfish, whereas ${p_i^2}_j$ is the proportion in weight of prey i in the diet of predator j and n is the number of prey categories. This index varies from 0 (species that feed on only one item) to 1 (species that feed on the same proportion of all evaluated items)[37]. Size-related differences were evaluated by comparing size classes through the non-parametric permutation procedure ANOSIM (Analysis of Similarity).

SIA were conducted on viperfish and its most probable prey and predator groups, including two fish larvae groups (Teleostei larvae 5–10 mm and Teleostei larvae 15–20 mm); five crustaceans; five gelatinous (divided into Siphonophorae and Thaliacea); eight zooplanktivorous fishes; and seven potential predators of viperfish (Table 2). Samples of Particulate Organic Matter (POM) were also included. For each fish and crustacean, white muscular tissue was extracted and cleaned with distilled water to remove exogenous material such as carapace, scales, and bones. Gelatinous organisms were used in whole. Entire zooplankton samples have been stored in Eppendorf micro tubes. Samples were dried in an oven at 60 °C for 48 h and grounded into a fine powder with a mortar and pestle. To obtain unbiased values of carbon stable isotope composition due to carbonates, zooplankton and POM samples were split in two subsamples. One zooplankton sub-sample was acidified by adding approximately 2 ml of 0.5 mol l^{-1} hydrochloric acid (HCl)[32,38]. POM sub-samples were exposed to hydrochloric acid (HCl) vapour. After 4 h, the filters and zooplankton were dried at 40 °C for 36 h. Untreated sub-samples of POM and zooplankton were analysed for nitrogen stable isotope composition and acidified one for carbon stable isotope composition. Each sample was analysed for carbon and nitrogen stable isotope ratios through a mass spectrometer (Thermo Delta V +) coupled to an element analyser (Thermo Flash 2000, interface Thermo ConFio IV) in the Platform Spectrometry Ocean (PSO, IUEM, France). SIA results for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were derived from the relation of the isotopic composition from the sample and a known standard: $\delta^{13}C$ or $\delta^{15}N = [(Rsample/Rstandard) - 1] \times 10^3$; in which R corresponds to the ratio between ^{13}C:^{12}C or ^{15}N:^{14}N. As differential lipid contents can bias the interpretation of $\delta^{13}C$ values, here we explored the potential lipid bias by using C:N ratios by mass and the relationship between C:N (i.e., lipid content) and $\delta^{13}C$. As samples were not treated to remove lipids before analysis to prevent loss of material, the few prey groups that exhibited C:N dynamics consistent with high lipid content (C:N > 3.5) were normalized using the equation for aquatic animals[31]: $\Delta\delta^{13}C = -3.32 + 0.99 \times C{:}N$, where $\Delta\delta^{13}C$ is the change in $\delta^{13}C$ caused by lipids and C:N is the carbon-to-nitrogen ratio (by mass) of the sample. To investigate the relationship between viperfish and potential prey and predators, isotopic values of carbon and nitrogen were analysed through a bi-dimensional plot. Further, viperfish trophic position (TP) was determined using the following formulae[39]:

$$\mathrm{TP} = \left(\delta^{15}\mathrm{N}_{\mathrm{consumer}} - \delta^{15}\mathrm{N}_{\mathrm{baseline}}\right)/\mathrm{TDF} + \mathrm{TP}_{\mathrm{baseline}}$$

where $\delta^{15}N_{consumer}$ and $\delta^{15}N_{baseline}$ are the $\delta^{15}N$ values of the target consumer and the baseline respectively; TDF is the trophic discrimination factor and $TP_{baseline}$ is the trophic position of the baseline. As POM may be influenced by the co-occurrence of detritus[40] and microzooplankton in the water column[32], primary consumers (TP2) are usually a better isotopic baseline to assess TP. Following the methodology of previous studies on the trophic position of mesopelagic, the baseline utilized was the zooplankton size fraction between 200–500 µm, which were mainly composed of herbivores copepods[32] that act as primary consumers (TP2). To account for uncertainty associated with the index, a Bayesian model was incorporated in the calculation of TP using predict $\delta^{15}N$ values of the viperfish and a TDF of 3.15‰ ± 1.28‰[41]. The R package *tRophicPosition*[42] was run for isotopic trophic position calculations. To explore how trophic levels and carbon source might change across ontogenetic phases, the relationship between fish size and $\delta^{13}C$ and $\delta^{15}N$ were assessed through a least-squares linear regression analysis.

The bayesian mixing model, MixSIAR[43], provide the most accurate estimations of source or prey contributions when tissue and species-specific discrimination factors are used[44]. Using the R package "*SIBER*"[45], we applied mixing models to estimate the relative contribution of viperfish specific-prey utilization. To explore the relationships between source contribution and size, we performed three mixing models considering all size classes. Potential dietary endpoints applicable to viperfish included in mixing models were derived from stomach contents analyses, local fauna (e.g. the most abundant species of myctophids were selected), and published information[27,28,46]. The following prey species were included: i) *Euphausia gibboides* (Euphausiacea), ii) *Diaphus brachycephalus* (Myctophidae), iii) *Diaphus fragilis* (Myctophidae), iv) *Diaphus mollis* (Myctophidae), v) *Hygophum taaningi* (Myctophidae), vi) *Lampanyctus nobilis* (Myctophidae), vii) *Lepidophanes guentheri* (Myctophidae), viii) *Symbolophorus rufinus* (Myctophidae), ix) *Promethichthys prometheus* (Gempylidae).

Results

Oceanographic conditions. Mean hydrological profiles (Fig. 2) revealed the presence of a surface mixed layer, characterized by warm waters (28 °C), extending down to ~ 50 m. Below, a sharp thermocline extended from the lower limit of the mixed layer to 130 m with a thermal difference of 12.3 °C. Vertical profile of salinity showed a layer of saline water within the thermocline, between 80 and 120 m. Dissolved oxygen concentration was homogeneous at the mixing layer, decreased at the upper limit of the thermocline with values less than 2.5 ml l^{-1} at ~ 100 m, ~ 300 m, and ~ 450 m and then increased at depths higher than 550 m. The chlorophyll *a* fluorescence maximum was generally located at the upper limit of the thermocline.

Vertical distribution, habitat, and migration. A total of 304 specimens of viperfish was collected and utilized to investigate vertical habitat and behaviour. The mean and standard deviation of the relative index of abundance were 62.3 ± 87.2 ind.hour^{-1} (0.62 ± 0.86 kg.hour^{-1}), ranging from 2.6 ind.hour^{-1} (0.03 kg.hour^{-1}) to 340 ind.hour^{-1} (3.37 kg.hour^{-1}). Vertically, viperfish were captured only between 400 to 1000 m, showing abundance peaks at 700–900 m (daytime) and 600–700 m (night-time). Both day and night specimens were found between 400 and 1000 m (Fig. 3), suggesting that only part of the population performs diel vertical migration. Additionally, size and weight varied significantly ($p = 0.02$) with the diel period and depth strata, indicating a possible ontogenetic shift on distribution and vertical migration pattern. At daytime, size distribution was heterogeneous among depth layers with larger organisms distributed below 500 m (difference of ± 5 cm/5 g). At night, however, larger individuals seem to migrate upwards, resulting in a more homogeneous size distribution (difference of ± 1 cm/2 g) according to depth layers. Coupling both periods, larger and heavier individuals were found at depths below 500 m (Fig. 4, Suppl. Material 3). *Chauliodus sloani* was captured in temperature ranging from 5 to 12 °C, well below the thermocline zone. Considering dissolved oxygen, the species was caught between 2.5 ml l^{-1} and 3.8 ml l^{-1} (Fig. 3).

Trophic ecology. One hundred and ninety-seven individuals (7–25 cm SL) were dissected for investigation on the viperfish carbon source through GCA. From that, 76 (39%) had stomachs with content and were utilized for further analyses. The vacuity index was 72% for daytime, 50% for night, and 61% for pooled periods. Considering all size classes, *C. sloani* feds largely on myctophids of the genus *Diaphus* (23% by weight, noted hereafter 23%W; 10–30 mm SL) and unidentified myctophids (36%W; 20–36 mm). Unidentified Teleostei (which may also include myctophids) was likewise important (31%W; 11–38 mm), followed by a few specimens of *Hygophum* sp. (3.4%W), *C. sloani* (2.4%W; 38 mm), *Cyclotone* spp. (1.5%W; 27 mm), Gempylidae (0.3%W; 35 mm) and Euphausiidae (0.2%W; 26 mm) (Table 1). No crustaceans were found in stomachs of individuals larger than 15 cm. The low value of Levins standardized index (< 15 cm: 0.22; > 15 cm: 0.30; Pooled Sizes: 0.17) indicated a restricted niche breadth for all size classes, highlighting the strong piscivorous habit of this species. Overall, lager individuals presented a higher niche breadth.

Considering stable isotope analyses, 26 taxa were utilized to assess viperfish trophic ecology (Table 2). Overall, the mixing models and biplot analyses were consistent with GCA, suggesting a tight trophic interaction with fishes, especially myctophids (e.g. *Diaphus brachycephalus* and *Symbolophorus rufinus*) (Figs. 5 and 6). Moreover, the mixing model for all size classes revealed a higher isotopic contribution of euphausiids that could not be

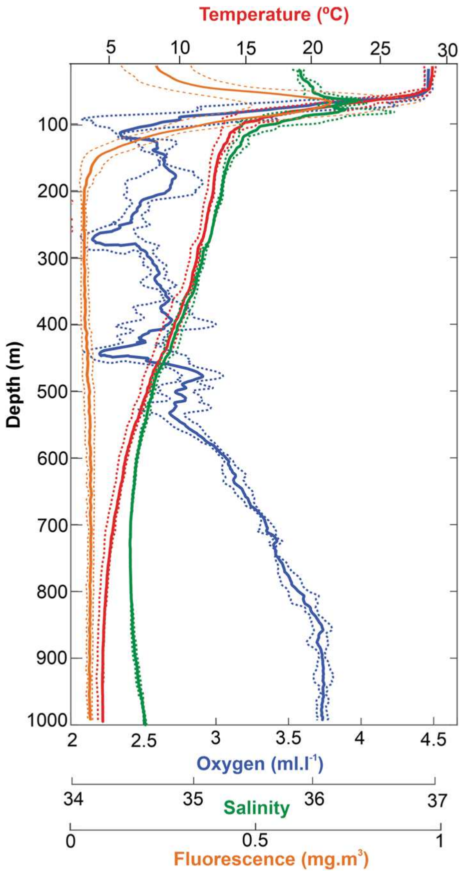

Figure 2. Mean and standard deviation of vertical profiles of temperature (red), dissolved oxygen (blue), salinity (green), and fluorescence (orange) in the study area during the survey.

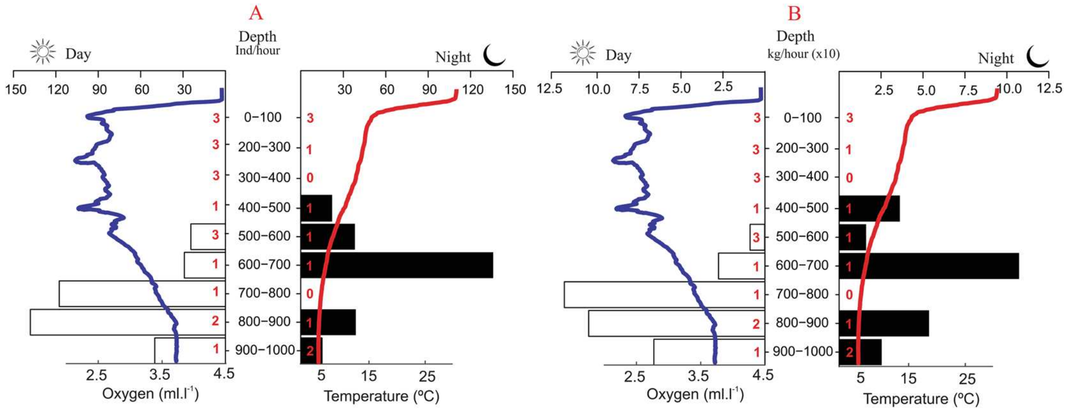

Figure 3. Average relative abundance in individuals.hour^{-1} (A) and kilogram.hour^{-1} (B) per depth strata and day period of the viperfish *Chauliodus sloani*. Coloured lines represent the average vertical profile of dissolved oxygen (blue) and temperature (red) for both day and night times. Red numbers represent the number of trawls per depth strata and period of the day.

observed in GCA (Fig. 5). Mean δ^{15}N values (< 15 cm $= 9.3 \pm 0.6$‰; > 15 cm $= 11.1 \pm 0.7$‰) and trophic levels (TP sia: < 15 cm $= 3.9 \pm 0.1$; > 15 cm $= 4.3 \pm 0.1$; grouped $= 4.1 \pm 0.11$) were significantly different among ontogenetic phases. Considering δ^{13}C values (< 15 cm $= -18.3 \pm 0.2$‰; > 15 cm $= -18.3 \pm 0.1$‰), no significant differences were observed among ontogenetic phases (Suppl. Material 2; Table 2; $p < 0.05$). The consistency in carbon and nitrogen values between the viperfish and the bathypelagic predator *Ectreposebastes imus* indicate a likely tight trophic linkage between them. The difference in δ^{13}C isotopic values between the viperfish and epipelagic predators, however, does not indicate that viperfish could significantly contribute to their feeding regime.

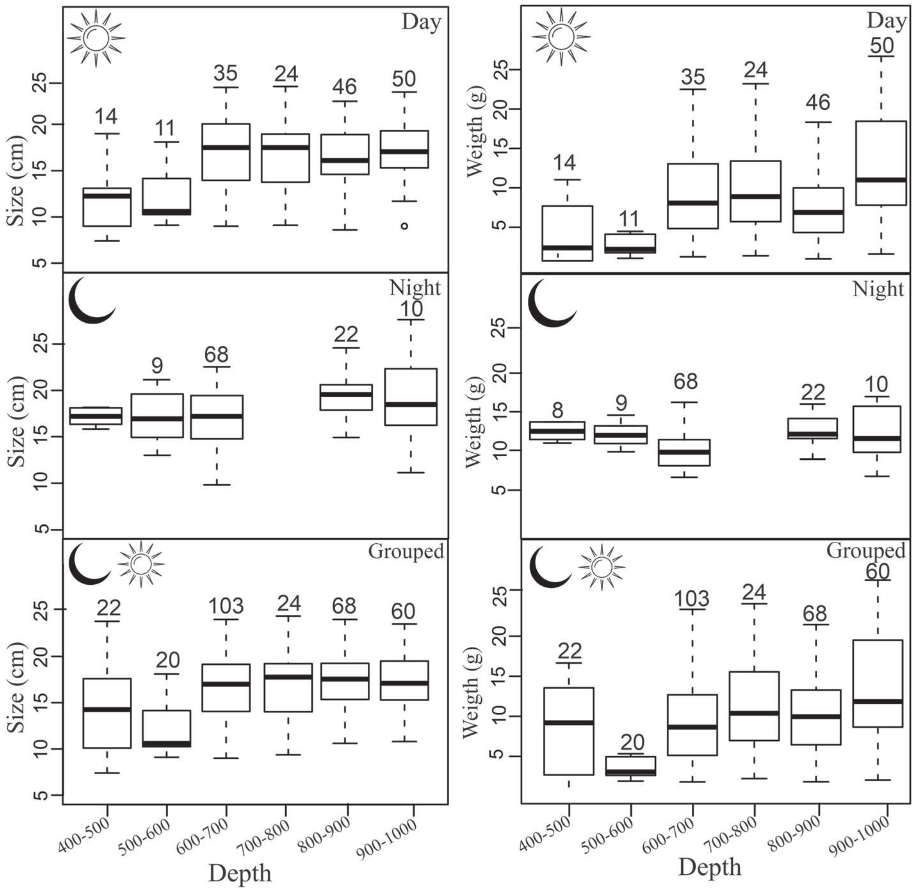

Figure 4. Boxplot of standard length and total weight per size classes and period of the day for the viperfish *Chauliodus sloani*. The depth layer 700–800 m was not sampled at night. Black horizontal lines and boxes represent median values and interquartile ranges, respectively. Dashed lines represent the data range limits. Numbers above the boxes represent the quantity of specimens per depth strata.

		Grouped Sizes			**Size class: 7–15 cm**			**Size class: 15–25 cm**		
		N:197; NSC:76; B_j:0.17			**N:55; NSC:16; B_j:0.22%**			**N:142; NSC:60; B_j:0.30**		
Prey item		**%VI:61; %VD: 72; %VN:50**			**VI:71; %VD78; %VN:58**			**%VI:58; %VD:68; %VN:49**		
Group	Taxa	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W
Crustaceans	Euphausidae	1.3	3.1	0.2	7.1	11.1	2.51	-	-	-
	Decapoda	1.3	0	0.1	7.1	11.1	1.7	-	-	-
Fish	*Chauliodus sloani*	1.3	3.1	2.4	7.1	11.1	29.3	-	-	-
	Cyclotone spp.	1.3	3.1	1.5	-	-	-	2.7	4.3	2.1
	Gempylidae	1.3	3.1	0.7	-	-	-	2.7	4.3	1.0
	Diaphus sp.	2.6	6.2	23.4	-	-	-	5.4	8.7	33.2
	Hygophum sp.	1.3	3.1	3.4	-	-	-	2.7	4.3	4.8
	Myctophidae	15.7	28.1	36.2	7.1	11.1	1.5	24.0	39.1	33.2
	Unidentified Teleostei	39.4	50.0	31.8	71.4	55.5	64.7	49.0	39.1	25.5

Table 1. Diet composition of viperfish *Chauliodus sloani* utilized in gut content analyses and dietary indexes calculated for each prey item: abundance percentage (%N), weight percentage (%W), frequency of occurrence (%F), number of specimens analysed (N), number of stomachs with content (NSC), vacuity index (%VI), vacuity index day (%VD), vacuity index night (%VN) and niche breadth (B_j).

				Standard length (cm)	δ13C (‰)	δ15N (‰)	C:N
Group	**Species**	**Category**	**N**	**Mean ± SD**	**Mean ± SD**	**Mean ± SD**	**Mean ± SD**
Stomiidae	*Chauliodus sloani* (> 15 cm)	–	10	18.1 ± 1.3	− 18.3 ± 0.1	11.1 ± 0.7	3.3 ± 0.1
	Chauliodus sloani (< 15 cm)	–	17	13.6 ± 1.5	− 18.3 ± 0.2	9.3 ± 0.6	3.3 ± 0.1
Setarchidae	*Ectreposebastes imus*	Bat.pred	5	19.1 ± 1.7	− 19.1 ± 0.3	12.8 ± 0.2	4.3 ± 0.2
Sphyraenidae	*Sphyraena barracuda*	Epi.pred	7	151.2 ± 30.0	− 16.2 ± 0.4	10.7 ± 0.5	3.2 ± 0.1
Coryphaenidae	*Coryphaena hippurus*	Epi.pred	6	85.2 ± 12.0	− 16.4 ± 0.4	11.3 ± 0.6	3.2 ± 0.1
Carangidae	*Elagatis bipinnulata*	Epi.pred	6	53.3 ± 10.4	− 19.3 ± 0.2	9.3 ± 0.5	3.4 ± 0.2
Scombridae	*Acanthocybium solandri*	Epi.pred	8	100.0 ± 35.0	− 16.8 ± 0.4	11.0 ± 1.0	3.2 ± 0.1
	Katsuwonus pelamis	Epi.pred	3	44.6 ± 4.1	− 17.2 ± 0.4	10.2 ± 1.0	3.2 ± 0.1
	Thunnus albacares	Epi.pred	12	65.0 ± 20.0	− 17.3 ± 0.2	10.7 ± 1.0	3.1 ± 0.1
Myctophidae	*Diaphus brachycephalus*	prey	10	5.0 ± 2.1	− 18.9 ± 0.3	9.9 ± 0.8	3.4 ± 0.1
	Diaphus fragilis	prey	11	7.3 ± 0.4	− 18.2 ± 0.3	10.2 ± 0.5	3.4 ± 0.1
	Diaphus mollis	prey	5	5.2 ± 0.3	− 19.2 ± 0.2	10.5 ± 0.7	3.4 ± 0.1
	Hygophum taaningi	prey	9	5.5 ± 0.2	− 18.2 ± 0.2	10.0 ± 0.6	3.3 ± 0.1
	Lampanyctus nobilis	prey	7	7.4 ± 1.5	− 18.2 ± 0.2	9.5 ± 0.3	3.3 ± 0.1
	Lepidophanes guentheri	prey	13	5.7 ± 0.6	− 18.2 ± 0.2	9.8 ± 0.7	3.3 ± 0.1
	Symbolophorus rufinus	prey	6	5.7 ± 0.3	− 19.3 ± 0.2	9.3 ± 0.5	3.4 ± 0.1
Gempylidae	*Promethichthys prometheus*	prey	3	14.2 ± 2.0	− 18.4 ± 0.2	10.0 ± 0.1	3.3 ± 0.1
Fish larvae	Teleostei larvae 15–20 mm	prey	6	–	− 18.5 ± 0.4	7.1 ± 0.6	3.2 ± 0.1
	Teleostei larvae 5–10 mm	prey	10	–	− 19.6 ± 0.1	5.9 ± 0.2	3.2 ± 0.1
Crustacea	*Euphausia gibboides*	prey	6	1.5 ± 0.1	− 19.3 ± 1.0	6.9 ± 0.2	3.2 ± 0.1
	Euphausia sp.	prey	3	1.4 ± 0.1	− 19.4 ± 0.5	7.3 ± 0.8	3.2 ± 0.1
	Pasiphaeidae sp.	prey	3	–	− 19.1 ± 0.0	6.0 ± 0.1	3.1 ± 0.1
	Phronima sp.	prey	3	–	− 19.0 ± 0.1	5.8 ± 0.1	3.6 ± 0.2
Siphonophorae	*Abylopsis tetragona*	LTL	3	–	− 17.8 ± 0.2	7.2 ± 1.0	3.3 ± 0.1
	Siphonophorae sp.	LTL	3	–	− 19.2 ± 0.0	9.1 ± 0.2	3.4 ± 0.1
Thaliacea	*Salpa* sp.*	LTL	6	–	− 19.8 ± 0.5	5.4 ± 0.1	4.5 ± 0.7
	Soestia zonaria	LTL	6	–	− 20.2 ± 0.2	3.7 ± 0.5	3.3 ± 0.1
	*Pyrosoma atlanticum**	LTL	11	–	− 18.5 ± 0.2	2.9 ± 0.6	5.4 ± 0.2
Zooplankton		LTL	19	–	− 19.4 ± 0.3	3.0 ± 0.6	4.5 ± 0.5
POM		LTL	17	–	− 22.4 ± 0.6	2.8 ± 1.2	–

Table 2. Number of samples, standard length, and isotopes values of the viperfish *Chauliodus sloani* and its potential predators (Bat.pred–bathypelagic predator; Epi.pred–epipelagic predator), potential prey, and lower trophic levels (LTL). *Species corrected for lipid.

Discussion

Here we analysed the habitat, vertical migration, and trophic ecology of the viperfish *Chauliodus sloani* to further understand the ecology and thus functional role of mesopelagic micronektivores. Among others, we combine our results with previous studies and examine through a conceptual model how latitudinal change in physico-chemical conditions can modulate the viperfish's behaviour. For instance, we show that physical drivers are regulating both patterns of movements and trophic interactions of this species, with possible consequences for ecological processes as energy transfer among vertical oceanic layers. Moreover, we address some of the potential contribution of this species to the oceanic carbon storage. Finally, for the first time we describe the ecology of a mesopelagic micronektivore along the western Tropical Atlantic (WTA), providing further information on an important and poorly known deep-sea species.

Methodological constrains. Some considerations should be made before the interpretation of our results. First, although we took precautions to avoid the collection of specimens during the lowering or hoisting of the net (see methodology), our gear did not have an opening or closing mechanism, allowing the collection of some species during these processes. Moreover, our samples were focused on mesopelagic waters and distribution patterns at layers deeper than 1000 m could not be assessed. Therefore, here we focused on major patterns of vertical behaviour on epipelagic and mesopelagic waters (0–1000 m depth), avoiding precise delimitations of vertical distribution and standing stock calculations. Second, diet determination from isotopic mixing models is closely related to the trophic discrimination factor (TDF) and sources utilized to run the analysis[47]. Hence, despite we carefully selected TDF values and prey groups (see methodology), the inclusion of different prey may provide further insights on the viperfish's trophodynamics[47,48]. Overall, the results presented here are not intended to exhaustively describe the ecological aspects of the viperfish. Instead, they increase the understanding of an important and understudied species, as well as provide novel insights on several aspects of its ecology.

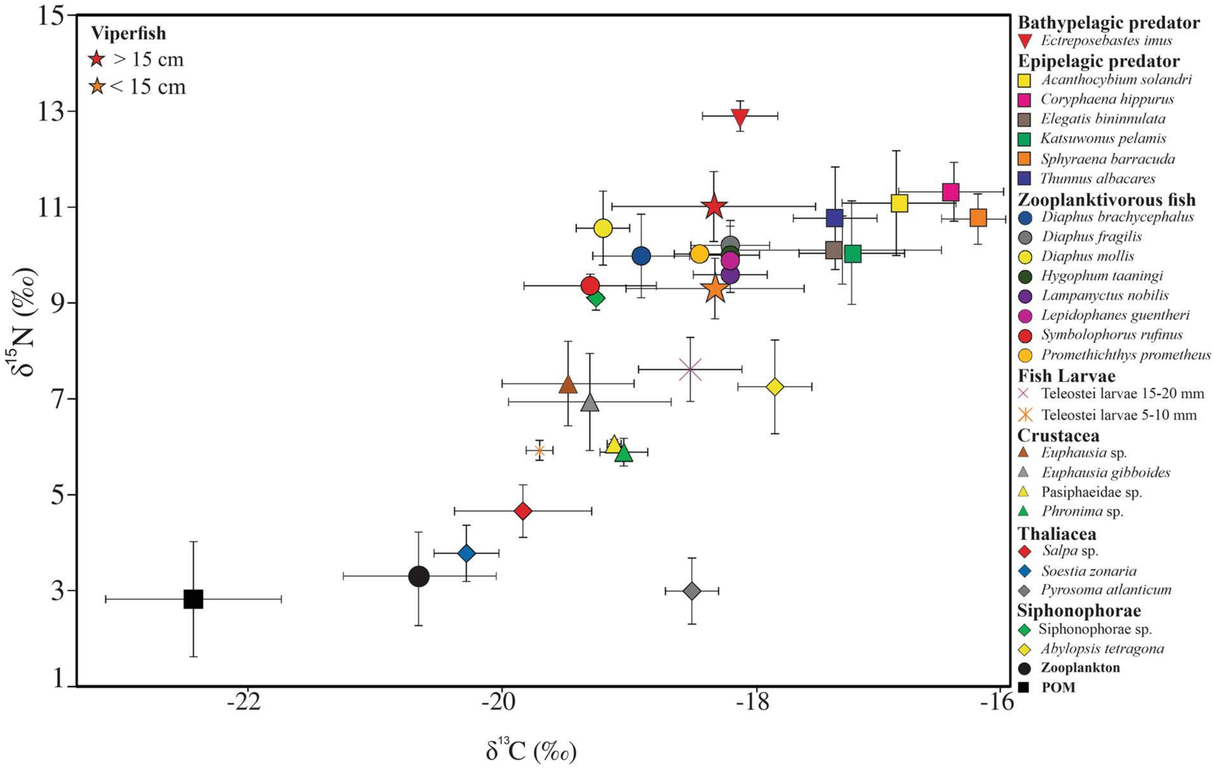

Figure 5. Stable carbon and nitrogen isotope values of particulate organic matter (POM), the viperfish *Chauliodus sloani* and its potential predators, potential preys, and lower trophic levels.

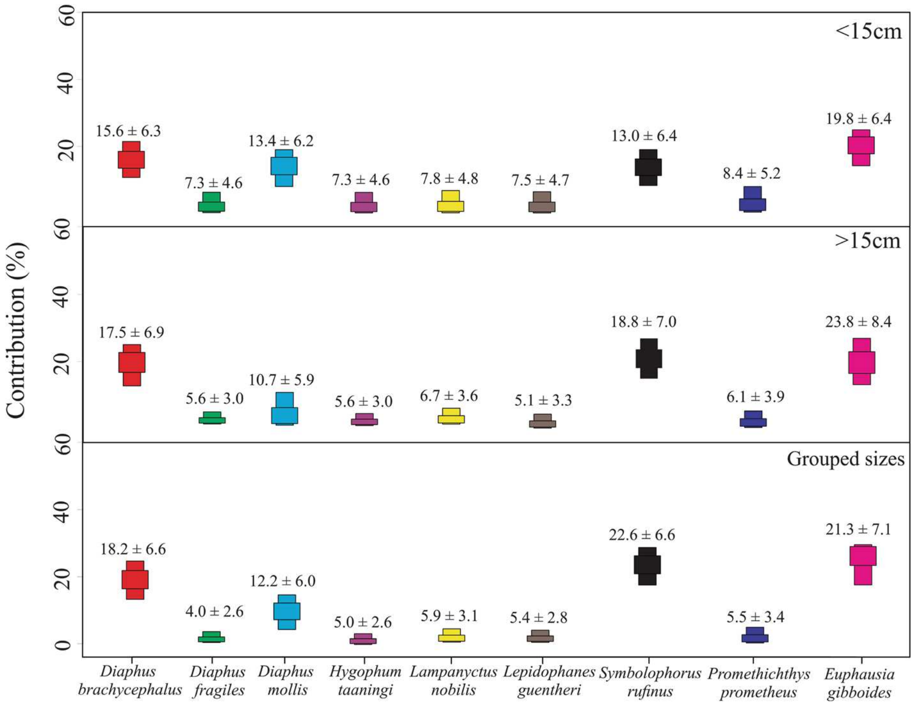

Figure 6. Estimated contribution in % (numbers; mean ± SD) based on stable isotope mixing model of potential prey to the diet of the viperfish *Chauliodus sloani*. Coloured boxes represent 25% and 50% quantiles.

Vertical distribution, habitat, and migration. Based on our data, in the WTA, the viperfish is the most important mesopelagic species in terms of biomass and fifth more abundant (4% of the total; L. N. Eduardo, unpublished data). Indeed, *Chauliodus sloani* represented 13% of the total biomass collected, followed by *Boros-*

Location	Climatic zone	Epipelagic record	Depth range (m)	Temperature range (°C)	References
Western Tropical Atlantic	Tropical	No	400–1000	5–12	This study
South Pacific (Tasmania)	Temperate	Yes	100–900	5–13	74–76
Northeastern Atlantic	Temperate	Yes	100–600	10–12	77,78
Eastern Gulf of Mexico	Subtropical	Yes	150–800	4–15	23
Southwestern Indian Ocean	Subtropical	Yes	100–700	4–15	79,80
Arabian Sea (Somalia)	Tropical	Yes	100–1500	5–15	27
Mid-Atlantic Ridge	Temperate	Yes	50–2900	6–12	81–83

Table 3. List of previous records of the viperfish *Chauliodus sloani*, including the location of occurrence, climatic zone, epipelagic record, depth, and temperature range.

tomias sp. (10%), *Sternoptyx diaphana* (5%), *Melamphaes polylepis* (5%), and *Argyropelecus affinis* (4%)(L. N. Eduardo, unpublished data). The viperfish inhabits depth layers below 400 m, i.e. at temperatures lower than 12 °C and oxygen levels between 2.3 and 3.7 ml l^{-1}. In mesopelagic waters, the abundance of this species peaked at 700–900 m at daytime and 600–700 m at night, indicating a pattern of restricted vertical migration where part of the population seems to migrate upwards at night. Moreover, we evidenced ontogenetic spatial variations (e.g. larger and heavier individuals distributed deeper, below 500 m) and asynchronous patterns of migration, where the entire population does not respond synchronously to diel variation in light intensity (segregating by depth and/or size).

This vertical ascension and size segregation have been previously reported in sub-tropical and temperate zones (Table 3). Interestingly, at all these locations, viperfish has been recorded in epipelagic waters, which was not the case in our data. Oxygen levels and temperature are two oceanic features known to constrict the vertical distribution of mesopelagic fish species[5,49,50]. The viperfish is known to occupy suboxic waters (e.g. 1.0 ml l^{-1})[27], seemingly to support much lower oxygen levels than those reported here. Therefore, vertical distribution differences among oceanic regions may be caused by the warmer epipelagic waters of tropical regions that may be preventing the ascension of this species up to shallow layers. Indeed, by coupling our data with previously information we observe that, independently of the depth, the upper thermal limit of the viperfish ranges from 12° to 15 °C (Table 3). Hence, it is likely that temperature may be shaping the migration patterns of this species. While viperfish ascend to epipelagic waters in sub-tropical and temperate regions, in tropical areas it seems to remain at greater depths. One exception is the record of this species in the superficial tropical waters of Somalia[27]. However, this region is affected by seasonal monsoon conditions and has a strong upwelling, which leads to the cooling of epipelagic waters[51]. This exception reinforces our hypothesis that temperature may be ruling the epipelagic rise of the viperfish.

Trophic ecology.

Differences on the vertical distribution along tropical and temperate regions seems also to reflect in the trophic links of the viperfish. While *C. sloani* represents one of the most important prey items of epipelagic predators in several locations[10,35,36,52], previous studies addressing the trophic ecology of epipelagic predators along the WTA do not mention a trophic relationship with the viperfish[9,53]. Moreover, SIA results do not evidence a well-defined trophic relationship between the viperfish and potential epipelagic predators. It might reflect the low probabilities of predator–prey encounters, as viperfish and epipelagic predators may not be sharing the same vertical space. On the contrary, the isotopic compositions of the viperfish and the bathypelagic predator *Ectreposebastes imus* are well-matched. The trophic link between bathypelagic predator and the viperfish has been also noted worldwide[54–56].

Based on its prey, the viperfish is a predator with a restricted niche breadth that heavily feeds on zooplanktivorous fishes, especially myctophids (at least 50% of prey items). This is supported by the mixing models, which show a potentially high contribution of Myctophidae, especially *Diaphus brachycephalus* and *Symbolophorus rufinus* (Fig. 6). This high contribution of myctophids has been also reported in the Central Mediterranean Sea[28], Pacific Ocean[57], Arabian Sea[27], North Atlantic Ocean[58], and Indian Ocean[59]. Euphausiids were also found as a prey item, both here and in previous studies[57], but in a lesser extension. Larger individuals (> 15 cm; TP_{sia}: 4.3) fed on larger prey and were more enriched in ^{15}N than small specimens (< 15 cm; TP_{sia}: 3.9), reflecting possible ontogenetic trophic shifts and differences on the prey-size consumption.

Overall, considering previous studies and our data, we conclude that myctophids are the most important prey item of the viperfish, followed by few other Teleostei species (e.g. Gempylidae sp., *Cyclotone* spp.), and euphausiids. Following the diel vertical behaviour of zooplankton, most myctophids (including main viperfish prey, e.g. *D. brachycephalus* and *Hygophum* spp.) forage in epipelagic zones at night and vertically migrate and form high-density biological layers in deeper waters in search of predator refuge during daytime[12,60–62]. Indeed, species of Myctophidae are amongst the most important epipelagic zooplankton consumers, feeding up to 30% of their daily stocks[61,62]. Likewise, most of the euphausiids species undergo diel vertical migrations, where they move upwards at night, usually in the layer of maximum chlorophyll concentration, seeking a high density of prey[63,64]. We thus deduce that most viperfish prey are epipelagic migrants that forage on surface waters.

Potential contribution for the Biological Carbon Pump.

The Biological Carbon Pump (BCP) is the active and passive transport of particulate organic carbon produced in the ocean surface by photosynthesis to

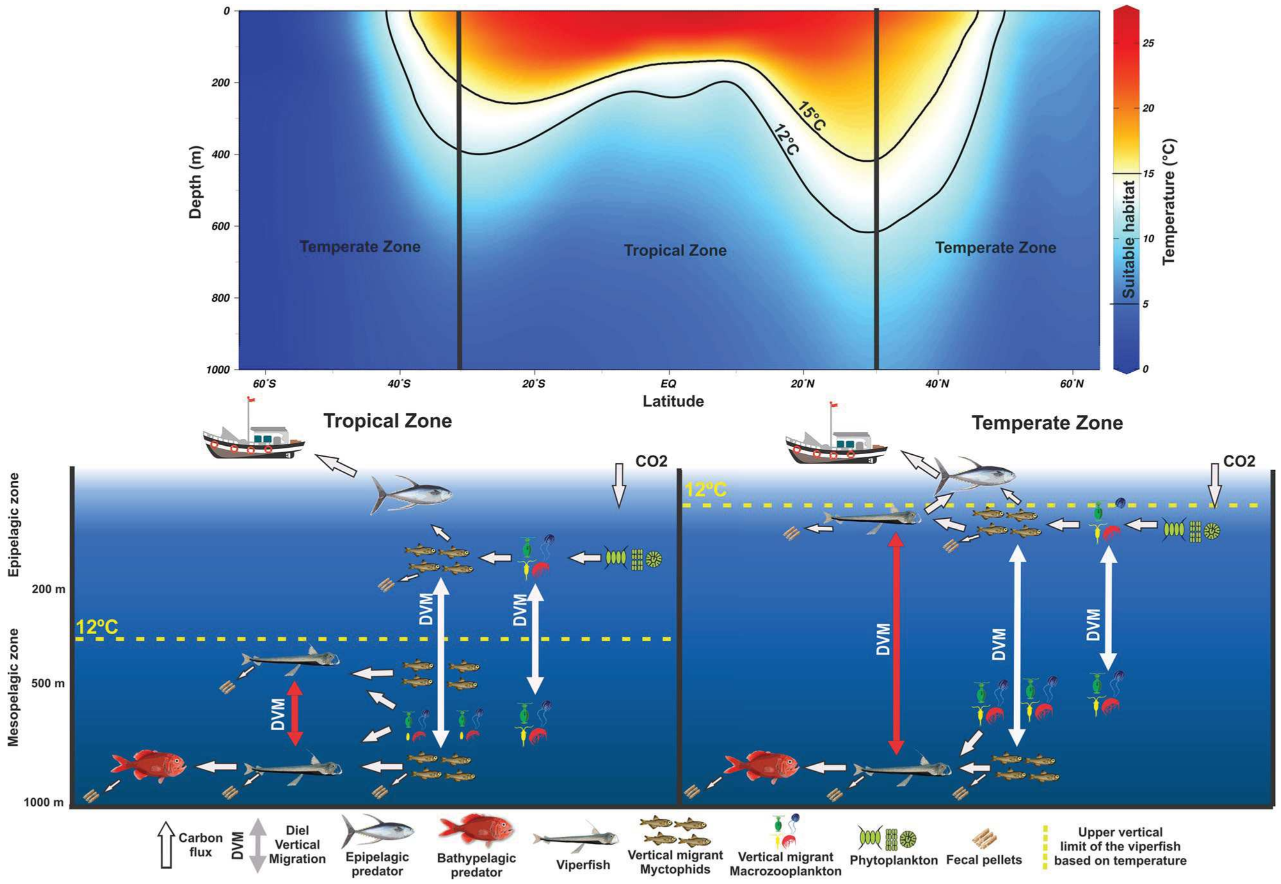

Figure 7. Conceptual model exhibiting global suitable vertical habitat of the viperfish *Chauliodus sloani* based on temperature profiles (Source: Word Ocean Atlas[73]) and differences in the vertical migration and trophic interactions of this species in the tropical and temperate waters. Temperature information from the upper panel refers to the meridional Sect. 30°.

the deep ocean[7,8]. Given their behaviour, high biomass and feeding ecology, mesopelagic micronektivores potentially contribute to the active part of this process[8,65–67]. Indeed, they may be isolated from epipelagic predators and they are directly and/or indirectly (through their prey) connected to epipelagic waters where photosynthetic processes occur[5,23,25,68]. Carbon storage depends on the depth difference between the ingestion of carbon and its release by respiration, excretion, defecation, and mortality[8,62,65,67,69]. For instance, carbon may be sequestered for longer than a year when released at mesopelagic waters, and for up to centuries when egested on deeper-water masses (generally greater than 1,000 m)[6,7]. Conversely, carbon may not be stored when vertical migrants are consumed by epipelagic predators and/or released at surface waters[6,7,70]. Hence, the contribution of mesopelagic micronektivores to the BCP depends on their diel vertical migration as well as the one of their prey and predators[70,71].

Based on our data, the viperfish is the most abundant mesopelagic micronektivore in the WTA. This species remains at deep waters full-time, is away from epipelagic predators, and heavily preys on migrant myctophids, which otherwise would return and release carbon in epipelagic waters. Additionally, at epipelagic waters myctophids are extensively preyed by epipelagic predators. Therefore, this species likely contributes to carbon storage, once it supports the storage of organic matter actively vertically transported through their prey. Moreover, viperfish are preyed by higher trophic levels (e.g. *Ectreposebastes imus*) that perform diel migrations from bathypelagic depth to feed at the lower mesopelagic zone (500–1000 m). This relationship may also accelerates carbon sequestration into the deep-sea. However, the BCP is a complex process[67,69,72] and here we focused only on ecological drivers (vertical behaviour and trophodynamics) that could enhance this activity. Further studies are required to thoroughly investigate the contribution of mesopelagic micronektivores on the BCP. For instance, future investigation should measure and/or estimate the carbon flux of these species through respiration, gut flux, excretion, and mortality[8,65,67,69]. Additionally, to properly understand the extension of this process, estimated carbon fluxes must be contrasted with the gravitational flux of particulate organic matter.

Conceptual model. By combining our results with previous works, we constructed a conceptual model explaining how temperature might influence both trophic ecology and vertical movements of the viperfish (Fig. 7). We observed that temperature (12–15 °C) is likely restricting its upper limit of distribution and thus affecting its vertical habitat and trophodynamics. For instance, in the WTA, and probably most of tropical waters, the viperfish likely stay full-time breathing, excreting, and serving as prey (e.g. for bathypelagic predators) at deep layers (below 400 m). In most temperate regions, however, they ascend to superficial waters where they are consumed by epipelagic predators and release carbon where its remineralization is the greatest (0–200 m). More broadly, based on the viperfish case, we show that the ecology and thus potential contribution of micronektivores to the carbon storage is expected to vary geographically, modulated by the latitudinal change in sea temperature.

Conclusion

Here we combined novel information on the viperfish trophodynamics and migratory behaviour in relation to physicochemical conditions (oxygen and temperature) to further understand the ecology and thus functional role of mesopelagic micronektivores. We demonstrate that, in the western Tropical Atlantic, the viperfish is amongst the most important mesopelagic micronektivore in terms of abundance and biomass. This species remains full-time at deep waters, heavily preys on myctophids, and presents spatial and trophic ontogenetic shifts. Temperature restricts its vertical distribution. Therefore, its ecology and functional roles are expected to be modulated by the latitudinal change in temperature. Moreover, we address some of its potential contribution to carbon storage and suggest further research.

Our findings indicate that the ecology and thus functional role of mesopelagic micronektivores may be more complex than previously thought, providing new perspectives on their trophic ecology, habitat, and migratory behaviour. With the predicted and observed effects of climatic change[16,17], pollution[18], and exploitation of deep-sea resources, we reaffirm that the structure and function of deep-sea ecosystems could undergo changes that, given the current state of knowledge, may go mostly unnoticed by scientists, marine resource managers, and conservation biologists. Studying the variability of biological behaviors of mesopelagic fishes is critical to further understand their ecology, conservation, and thus several ecosystem processes.

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Author contributions

L.N.E. performed analyses and wrote the manuscript with contributions of F.L.F., M.M.M., A.C.S., F.L.L, T.F., F.M. and A.B. A.B. and F.L.F. conceptualized and coordinated the research project. All authors participated to the at-sea survey and/or contributed substantially on biological analyses.

Competing interests

The authors declare no competing interests.

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CHAPTER 2 - OUTLOOK

In this chapter we focused on answering three PRA in which more knowledge is needed to improve the understating of the mesopelagic zone: (ii) links between oceanographic regimes and mesopelagic biomass and biodiversity; (iii) the role of the mesopelagic community in the food web; and (iv) the role of individual species and the community in the sequestration of greenhouse gases. For that, we organized this chapter over three articles proposing a comprehensive study on the ecology of the viperfish, hatchetfishes, Myctophidae. We used information on their abundance, distribution, diversity, and physical and chemical habitat. Additionally, we also included information on their trophic ecology by combing gut content analyses with stable isotope data (carbon and nitrogen) carried out on the mesopelagic fishes and their main trophic links, including zooplankton, crustaceans, fish larvae, and epi- and bathypelagic potential predators. Finally, we constructed conceptual models to describe their niche partitioning, functional groups, and ecosystem roles across large oceanic areas.

In the first article, focused on the hatchetfishes, we defined five functional groups with different diet preferences, isotopic composition, and vertical abundance peaks, revealing a possible high resource partitioning. These groups may respond differently to environmental constraints including oxygen concentration and might present diverse functional roles. As an example, some groups are composed of epipelagic migrants, playing key roles in the transfer of subsurface photoassimilated carbon to deeper waters. Moreover, as consumers of gelatinous organisms, hatchetfishes convert “gelatinous energy” into “fish energy” readily usable by higher trophic levels, including endangered and commercially important species. This is a crucial trophic relationship that has been historically underestimated due to methodology limitations (e.g., quickly digested gelatinous organisms were probably underestimated in previous studies, based solely on stomach contents).

In the second article, focused on the lanternfishes, we show that these species are highly diverse and an abundant fish family of the SWTA, comprising at least 33 species and contributing 40% of all fish collected (in number). We demonstrate that they have different patterns of prey preference and migratory behaviour, leading to multidimensional niches, underestimated trophic links and several mechanisms to avoid competitive exclusion. At least 76% of lanternfishes vertically migrate to the surface to feed at night. Additionally, they are a central food source for epipelagic and deep-sea predators, a pathway enhancing the connection between shallow and deep-sea ecosystems. Finally, we show that lanternfishes are ubiquitous concerning environmental conditions, leading to weak horizontal assemblage segregation.

Finally, in the third article, we focused on the viperfish *Chauliodus sloani.* This species heavily preys on epipelagic migrant fishes, especially myctophids, and presents spatial and trophic ontogenetic shifts. Temperature restricts its vertical distribution. Therefore, through this study case, we demonstrated that the trophodynamics, migratory behaviour, and functional roles of mesopelagic species may be modulated by the latitudinal change in temperature. For instance, in most tropical regions the viperfish stay full-time feeding, excreting, and serving as prey (e.g. for bathypelagic predators) at deep layers. On the contrary, in temperate regions, the viperfish ascend to superficial waters where they trophically interact with epipelagic predators and may release carbon where its remineralization is the greatest.

Together, these findings may provide complementary insights on ecology and thus the functional role of mesopelagic fishes, presenting new perspectives on their trophic ecology, habitat, and migratory behaviour. This information, for instance, may be important to properly answer key ecological questions, including resource use, carbon transportation, and influence of the mesopelagic community in climate change processes.

GENERAL CONCLUSIONS

For more than 200 million years mesopelagic fishes have inhabited earth's oceans, where they lived, evolved, and acquired several adaptations to overcome challenges imposed by the deep-sea (Benton, 2005; Priede, 2017). Over time, these species have become one of the most abundant and diverse fish groups of the world's ocean, contributing to several ecosystem processes (e.g., carbon sequestration, nutrient regeneration, and fisheries production). Yet this zone is poorly understood — physically, biogeochemically, and ecologically (Martin et al., 2020). Even the number of organisms that live there remains a mystery, letting alone their diversity and function. In an ecological context, four priority research areas have been listed to improve the understating of the mesopelagic zone: (i) biodiversity census; (ii) links between oceanographic regimes and mesopelagic biomass and biodiversity; (iii) the role of the mesopelagic community in the food web; and (iv) the role of individual species and the community in ecosystem processes. In this thesis, we focused on answering these questions. For that, we took advantage of the two scientific expeditions of the project ABRACOS, where for the first time the mesopelagic zone of the SWTA was extensively surveyed and thousands of mesopelagic specimens were collected.

(i) Biodiversity census

Previously the project ABRACOS, only a few expeditions have been conducted on the deep-sea of the SWTA. Although these works substantially contributed to the understanding of several species, they were highly sparse and mostly focused on demersal communities. For instance, mesopelagic fishes represented less than 20% of the species recorded on the SWTA (Melo et al., 2020). In this thesis, we demonstrate that a relatively high number of mesopelagic fishes occur in the SWTA, including at least 24 orders, 56 families, and 207 species. From those, nine (4%) are potentially new species and 61 (30%) represented new records for Brazilian waters. Additionally, several species collected are globally rare and had their distribution updated. Five families accounted for 52% of the species diversity, 90% of the specimens collected, and 72% of the total biomass: Myctophidae, Stomiidae, Gonostomatidae, Melamphaidae, and Sternoptychidae. These families are, therefore, the most representative of the mesopelagic fish fauna of the SWTA. This pattern of dominance has also been noted worldwide. Richness and diversity were higher at lower mesopelagic waters (500–1000 m) at daytime, which was enhanced by the presence of bathypelagic species that are probably associated with seamounts. At night, values of richness and diversity increased at epipelagic waters, indicating the ascension of several species at night (e.g., myctophids and sternoptychids). Complementary, novel anatomical data (meristics counts and morphometry) were provided for several species, increasing the basic biological information and overall knowledge for deep-sea species.

(ii) Links between oceanographic regimes and mesopelagic biomass and biodiversity

To investigate the influence of oceanographic features on the ecology and biodiversity of mesopelagic fishes, we took advantage of a set of data combining information on their abundance, distribution, diversity, trophic ecology, and physical and chemical habitat. We observed that hatchetfishes respond differently to environmental constraints, including oxygen concentration and temperature. For instance, during daytime some species (e.g., *Argyropelecus affinis* and *A. sladeni*) were mostly distributed at 400–500 m depth, in the layer presenting the minimum oxygen level. Therefore, during the day, these species were likely in search of predator refuge and/or saving energy by resting in a water mass with low temperature and dissolved oxygen concentration. In the case of lanternfishes, a weak explanatory response was found when considering the influence of different physicochemical scenarios on the assemblage structure of these species. Despite the formation of some assemblages could be partially explained by features of these scenarios, neither of these schemas alone fully explains lanternfish structuring observed here. At the scale of this study, a likely explanation is their ability to actively choose depth stratum that meet favourable environmental conditions. Additionally, many lanternfishes were able to withstand a wide range of environmental conditions (e.g., daily temperatures range up to 25°C).

Finally, through the study case of the viperfish, we combined our results with previous works and constructed a conceptual model explaining how temperature might influence both trophic ecology and vertical movements of this species. We observed that temperature (12–15°C) is likely restricting its upper limit of distribution and thus affecting its vertical habitat and trophodynamics. For instance, in the SWTA, and probably most of the tropical waters, the viperfish likely stay full-time breathing, excreting, and serving as prey (e.g., for bathypelagic predators) at deep layers (below 400 m). In most temperate regions, however, they ascend to superficial waters where they are consumed by epipelagic predators and release carbon where its remineralization is the greatest (0–200 m). More broadly, based on the viperfish case, we show that the ecology and thus potential contribution of micronektivores to the carbon storage is expected to vary geographically, modulated by the latitudinal change in sea temperature.

(iii) The role of the mesopelagic community in the food web

To explore the role of mesopelagic species in the food web, we combined gut content analyses with stable isotope data carried out on the main trophic links of mesopelagic species, including zooplankton, gelatinous organisms, crustaceans, fish larvae, and epipelagic and deep-sea predators. We demonstrate that most lanternfishes and hatchetfishes are acting as mixing of secondary and tertiary consumers, being important predators on the zooplankton community, especially on amphipods, euphausiids, ostracods, copepods, fish larvae, and chaetognaths. Additionally, these species might be species-specific in feeding habits, demonstrating a high degree of resource partitioning. As consumers of Thaliacea and Siphonophorae organisms, these species also convert "gelatinous energy" into "fish energy" readably usable by higher trophic levels. This is a crucial trophic relationship that has been historically underestimated. In the case of the viperfish, we showed a predator with a restricted niche breadth, heavily feeding on zooplanktivorous fishes (specially lanternfishes). Additionally, in the SWTA this species seems to be isolated from epipelagic predators, being mostly predated by bathypelagic species. Finally, we showed that lanternfishes act as a central food source for both epipelagic and deep-sea predators.

(iv) The role of individual especies and community on ecosystem processes

Given their trophic and vertical behaviour, lanternfishes and hatchetfishes contribute to several ecosystem processes of local and global significance. As an example, we could highlight which species in the SWTA vertically migrate to the surface to feed at night and actively transport the ingested carbon to deep waters during daylight, a pathway enhancing the ultimate oceanic carbon storage. Moreover, we showed which species occupy important trophic positions by consuming zooplankton and providing forage for numerous epipelagic and deep-sea predators. These processes, as an example, are crucial for the maintenance of harvestable fish stocks and the connection between shallow and deep-sea ecosystems. Also, we demonstrated that even species remaining in deep waters full-time may have key roles in the ecosystem. As an example, viperfish is amongst the most abundant micronektivore in the SWTA. This species remains at deep waters full-time, is away from epipelagic predators, and heavily preys on migrant myctophids, which otherwise would return and release carbon in epipelagic waters. Therefore, the viperfish likely contributes to carbon storage, once it supports the storage of organic matter actively vertically transported through their prey. Moreover, viperfish are preyed by higher trophic levels (e.g., *Ectreposebastes imus*) that perform diel migrations from bathypelagic depth to feed at the lower mesopelagic zone (500–1000 m). This relationship may also accelerate carbon sequestration into the deep sea.

Combination of research questions

Together, these four RA may also work synergistically and provide new approaches and insights in mesopelagic ecosystems. Indeed, by combining this information we could reveal functional groups and better understand how mesopelagic species are scattered over different patterns of resource use (niche partitioning) and thereby avoiding competitive exclusion. As an example, for hatchetfishes we could define five functional groups with different diet preferences, isotopic composition, and vertical abundance peaks, revealing a possible high resource partitioning and several mechanisms to avoid competitive exclusion. In the case of lanternfishes, we observed three possible patterns of prey preference and four patterns of vertical behaviour. For instance, when living in the same habitat, lanternfish segregation seems to operate through different feeding habits, which diminishes competitive exclusion. Here we focused on the two most abundant families in our samples. However, these features are likely present in most mesopelagic communities. Therefore, we highlight that further investigation on the functional ecology and vertical niche partitioning of mesopelagic species may reveal important information on their evolution, ecology, and ecosystem processes.

Crescent threats

Despite their importance, mesopelagic fishes are increasingly threatened. First, climatic change is rapidly modifying ocean stratification, temperature, acidification, and oxygen levels (Levin et al., 2019; Brito-Morales et al., 2020). Several species, therefore, are expected to be affected. Second, mesopelagic fishes represent one of the last unexplored marine resources, containing fish biomass 100 times greater than the global annual fish catch (Irigoien et al., 2014; Proud et al., 2019). Given the increasing global demand for resources, it is not surprising the rising incentives for the commercial exploitation of deep-sea species (John et al., 2016; Hidalgo and Browman, 2019). Despite not yet used for direct human consumption (e.g. high lipid or wax ester content), some of these species may be used for animal feed, crop fertilizers, and pharmaceuticals (Nair et al., 1982; John et al., 2016). It is not clear the ecological implications of the extensive conventional form of fish exploitation on these species. However, given some of their features (e.g., low fecundity and late maturation), this exploitation may have devastating consequences.

Third, there is a rapidly growing interest in deep-sea mineral exploitation, a potentially multi-billion-dollar industry (Wedding et al., 2015). Equipment and system are already in development and this activity will likely become operational in all world's oceans within the next 20 years (Wedding et al., 2013, 2015). Despite studies have been mainly focusing on seafloor impacts, sediment plumes and noise generated by deep-sea mining may also have extensive ecological effects in deep midwater species (Drazen et al., 2020). And fourth, pollutants and the increasing pervasion of plastics in the marine environment stand to alter the structure and function of deep-sea ecosystems (Drazen and Sutton 2017). As an example, in our study area, preliminary analyses demonstrate high microplastic contamination on lanternfish species (A. K. Justino, unpublished data).

Final message

Information presented here contributes to the overall understanding of the diversity and ecology of deep-sea species. This data may be important for further studies addressing the functioning, conservation, and ecosystem processes of mesopelagic communities. The several discoveries presented here reflect not the efforts of a multidisciplinary research and the high diversity of the SWTA, but also the lack of scientific information on deep-sea waters. The roadmap for the United Nations Decade of Ocean Science recognizes the deep-sea as a frontier of science and discovery (Ryabinin et al., 2019). Additionally, there is an unequal capacity to conduct science among nations, with developing economies facing substantial barriers to participating in deep-sea research (Howell et al., 2020). Consequently, the least-studied parts of the deep-sea are within the Exclusive Economic Zones of the least economically developed countries (Howell et al., 2020). The fact that a French research institution financed our survey and that it is amongst the very few addressing the mesopelagic waters of Brazil reflect these biases. As humans expand resource extraction and habitat impact in the deep ocean, the understanding of mesopelagic ecosystems, their processes, and functions is mandatory, especially when sustainability is intended to be achieved.

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Supplementary Material

Rich and underreported: the diversity of mesopelagic fishes in the southwestern Tropical Atlantic

Supplementary material 1- List of midwater trawls performed during the ABRACOS 1 (AB1) and ABRACOS 2 (AB2) expeditions. FNR: Fernando de Noronha ridge. RN: Rio grande do Norte, PB: Paraíba, PE: Pernambuco, and AL: Alagoas.

Station	Site	Period	Latitude	Longitude	Depth
AB1#1	FNR	Night	-3.772	-32.422	150
AB1#2	FNR	Day	-3.661	-32.218	110
AB1#3	FNR	Night	-3.640	-31.971	60
AB1#4	FNR	Day	-3.908	-32.340	90
AB1#5	FNR	Night	-4.090	-32.180	85
AB1#6	FNR	Day	-4.243	-32.613	85
AB1#7	FNR	Night	-3.960	-32.532	58
AB1#8	FNR	Day	-3.736	-32.895	100
AB1#9	FNR	Night	-3.471	-32.759	105
AB1#11	FNR	Day	-3.750	-33.230	40
AB1#12	FNR	Night	-3.939	-33.511	130
AB1#13	FNR	Day	-3.917	-33.848	110
AB1#14	FNR	Night	-3.983	-34.056	510
AB1#15	FNR	Day	-3.734	-34.000	537
AB1#20	FNR	Night	-3.761	-33.880	60
AB1#21	FNR	Day	-3.657	-33.692	100
AB1#22	FNR	Night	-4.129	-33.790	525
AB1#23	RN	Day	-5.144	-34.713	100
AB1#26	RN	Day	-6.154	-34.576	560
AB1#27	RN	Night	-6.309	-34.979	100
AB1#29	PB	Day	-6.621	-34.760	15
AB1#31	PB	Night	-6.734	-34.440	50
AB1#34	PB	Night	-7.190	-34.266	100
AB1#35	PB	Day	-7.486	-34.425	250
AB1#36	PE	Night	-7.602	-34.338	60
AB1#37	PE	Day	-7.867	-34.495	25
AB1#41	PE	Day	-8.274	-34.680	30
AB1#43	PE	Night	-8.415	-34.844	12
AB1#52	AL	Day	-9.066	-34.801	570
AB1#25	RN	Night	-5.803	-34.951	75
AB2#2	PE	Night	-8.857	-34.728	60
AB2#5	AL	Night	-9.182	-34.758	117
AB2#6	PE	Day	-8.873	-34.599	240
AB2#7	PE	Day	-8.774	-34.742	112
AB2#8	PE	Day	-8.758	-34.785	17
AB2#9	PE	Night	-8.708	-34.745	95
AB2#10	PE	Night	-8.659	-34.761	15
AB2#13	PE	Day	-8.317	-34.428	445
AB2#16	PE	Night	-7.604	-33.993	680
AB2#21	PB	Day	-6.841	-34.306	800
AB2#22	PB	Night	-6.888	-34.762	10
AB2#26	RN	Day	-5.819	-34.813	100
AB2#28	RN	Night	-5.617	-34.785	130
AB2#31	RN	Day	-4.976	-34.951	450
AB2#35	RN	Night	-4.327	-35.497	630
AB2#39	FNR	Night	-4.874	-34.059	800
AB2#40A	FNR	Day	-3.523	-32.528	440
AB2#40B	FNR	Day	-3.520	-32.530	230
AB2#41A	FNR	Night	-3.333	-32.412	430
AB2#41B	FNR	Night	-3.321	-32.428	25
AB2#42A	FNR	Day	-3.258	-31.808	780
AB2#42B	FNR	Day	-3.262	-31.817	50
AB2#44A	FNR	Day	-3.881	-32.293	850
AB2#44B	FNR	Day	-3.872	-32.300	130
AB2#45A	FNR	Night	-4.237	-32.035	30
AB2#45B	FNR	Night	-4.239	-32.021	50
AB2#46A	FNR	Day	-4.142	-32.304	360
AB2#46B	FNR	Day	-4.175	-32.268	440
AB2#48A	FNR	Day	-4.418	-32.964	505
AB2#48B	FNR	Day	-4.440	-32.938	70
AB2#49A	FNR	Night	-4.177	-33.269	1020
AB2#49B	FNR	Night	-4.176	-33.259	90
AB2#50A	FNR	Day	-3.817	-32.599	615
AB2#50B	FNR	Day	-3.812	-32.640	115
AB2#50C	FNR	Day	-3.836	-32.623	58
AB2#52A	FNR	Day	-3.721	-33.419	984
AB2#52B	FNR	Day	-3.699	-33.391	385
AB2#53A	FNR	Night	-3.816	-33.988	610
AB2#53B	FNR	Night	-3.830	-33.962	65
AB2#54A	FNR	Day	-3.771	-34.727	95
AB2#54B	FNR	Day	-3.755	-34.684	1030
AB2#56A	FNR	Day	-3.934	-35.421	110
AB2#56B	FNR	Day	-3.962	-35.406	260
AB2#58A	FNR	Day	-3.948	-36.104	520
AB2#58B	FNR	Day	-3.949	-36.155	90
AB2#58C	FNR	Day	-3.954	-36.183	90
AB2#59A	FNR	Night	-3.634	-36.053	1113
AB2#59B	FNR	Night	-3.643	-36.038	110
AB2#60A	FNR	Day	-3.531	-36.385	449
AB2#60B	FNR	Day	-3.529	-36.356	700

Supplementary material 2- Mesopelagic fish species that could not be identified at species level given their poor condition. Survey (1: ABRACOS 1; 2: ABRACOS 2), number of specimens (N), frequency of occurrence to overall samples (FO%) standard length (mean and range), total wet weight (mean and range), site (PE: Pernambuco; PB: Paraíba; RN: Rio Grande do Norte; FNR: Fernando de Noronha Ridge), depth range, temperature range (T°C), and new records in Brazilian economic exclusive zone

Species	**Survey**	**N**	**FO%**	**SL**	**TW**	**Site**	**Depth range (m)**	**T (°C)**
ANGUILLIFORMES								
Nemichthyidae								
Nemichthyidae sp.	1-2	7	6.1	286(200–480)	5.4(2.4–9.3)	FNR-PE	40–800	4.7–26.6
Serrivomeridae								
Serrivomer sp.	2	2	2.4	236	0.5	FNR	70–900	4.3–25.8
ARGENTINIFORMES								
Bathylagidae								
Bathylagidae sp.	2	5	3.7	79(63–98)	3.3(1.2–4.7)	FNR	430–800	4.6–8.54
STOMIIFORMES								
Gonostomatidae								
Gonostoma sp.	1-2	16	7.3	89(22–198)	8.5(0.3–29.5)	FNR-PB-PE	50–1000	4.3–27.6
Gonostomatidae sp.	2	3	2.4	27	1	FNR	720–780	4.6–4.9
Sternoptychidae								
Sternoptyx sp.	2	72	1.2	25(14–34)	1.6(0.4–4.8)	FNR	110	24.1
Phosichthyidae								
Phosichthyidae sp.	2	5	3.7	57	–	FNR	720–800	4.7–4.9
Stomiidae								
Aristostomias sp.	1-2	23	17.1	85(32–151)	6.3(1.0–19.5)	FNR-PB-PE	60–1000	4.3–26.6
Astronesthes sp.	1-2	9	7.3	51(26–76)	1.8(0.5–3)	FNR-PB-RA	50–900	4.3–26.5
Batophilus sp.	2	1	1.2	16	3.5	FNR	385	9.2
Eustomias sp.	1-2	15	13.4	84(63–134)	3.6(0.6–7.9)	FNR-PB-PE	65–1000	4.3–26.5
Leptostomias sp.	2	3	2.4	109(67–165)	3.2(0.9–5.3)	FNR	90–430	8.5–25.1
Melanostomias sp.	1-2	3	2.4	126(30–176)	12.1(0.3–18.7)	PB-PE	50–680	5.2–26.5
Photonectes sp.	2	1	1.2	79	3.4	FNR	900	4.3
Stomias sp.	2	1	1.2	107	3.3	FNR	610	5.6
AULOPIFORMES								
Notosudidae								
Scopelosaurus sp.	2	4	4.9	69(33–177)	6.2(0.6–22.4)	FNR-PE	100–800	4.7–24.6
Scopelarchidae								
Schopelarchoides sp.	2	1	1.2	75	2.8	FNR	610	5.6
Scopelarchidae sp.	2	1	1.2	76	4.3	FNR	900	4.3
Scopelarchus sp.*	2	1	1.2	27	–	FNR	780	4.6
Paralepididae								
Paralepidiidae sp.	2	1	1.2	23	10.3	FNR	800	4.7
Stemonosudis sp.	2	1	1.2	135	4.7	FNR	780	4.6
MYCTOPHIFORMES								
Myctophidae								
Bolinichthys sp.	2	20	6.1	43(25–76)	4.1(0.5–24.5)	FNR-PB-RN	630–900	4.3–5.6
Diaphus sp.	1-2	276	20.7	32(10–83)	2.0(0.1–9.3)	FNR-PB-PE-RN	60–900	4.3–26.6
Lampadena sp.	1-2	9	2.4	20(13–26)	0.4(0.1–0.8)	FNR	510–780	4.6–6.0
Lampanyctus sp.	1-2	93	19.5	46(21–125)	2.4(0.3–12.6)	FNR-PE-RN	25–900	4.3–28.8
Myctophidae spp.	1-2	138	35.4	40(14–135)	3.0(0.1–25.3)	FNR-PB-PE-RN	25–1000	4.3–28.8
Nannobrachium sp.	2	1	1.2	70	1.73	FNR	610	5.7
Taaningichthys sp.	2	7	6.1	53(43–72)	1.3(0.5–3.6)	FNR	720–800	4.6–4.98
GADIFORMES								
Macrouridae								
Macrouridae sp.	2	2	2.4	275	12.6(4.1–21.1)	FNR	800–900	4.3–4.7
Beryciformes								
Melamphaidae								
Scopeloberyx sp.	2	3	3.7	25(20–32)	2.7(1.9–3.4)	FNR	720–800	4.6–4.9
PERCIFORMES								
Bramidae								
Brama sp.	1	11	8.5	11(08–15)	1.5(0.3–9)	FNR-PB	58–130	15.0–26.6
Caristiidae								
Platyberyx sp.	2	4	3.7	69(41–98)	12.7(2.3–25.1)	FNR-RA-RN	450–720	4.9–8.5
SCOMBRIFORMES								
Gempylidae								
Gempylidae sp.	2	6	6.1	31(12–55)	0.9(0.5–1.2)	FNR-PE	70–800	4.7–25.8
TRACHINIFORMES								
Chiasmodontidae								
Chiasmodon sp.	2	9	8.5	31(16–46)	1.9(0.5–4.4)	FNR-PE	112–800	4.6–24.1
LOPHIIFORMES								
Melanocetidae								
Melanocetus sp.	2	6	6.1	49(20–88)	11.6(2.1–33.2)	FNR-PE	680–900	4.3–5.2
Oneirodidae								
Chaenophryne sp.	1-2	2	2.4	22(17–28)	0.8(0.8–0.8)	PE	510–800	4.7–6.0
Oneirodes sp.	2	1	1.2	15	2.1	FNR	900	4.3
Oneirodidae sp.	1-2	3	3.7	80	–	FNR	40–780	4.6–26.6
Ceratiidae								
Ceratias sp.	2	3	1.2	42(31–51)	2.7(1.4–4.6)	FNR	610–700	5.2–5.6
Ceratiidae sp.	1	1	1.2	30	–	RN	570	6.3
Gigantactinidae								
Gigantactis sp.	1	1	1.2	60	–	FNR	100	24

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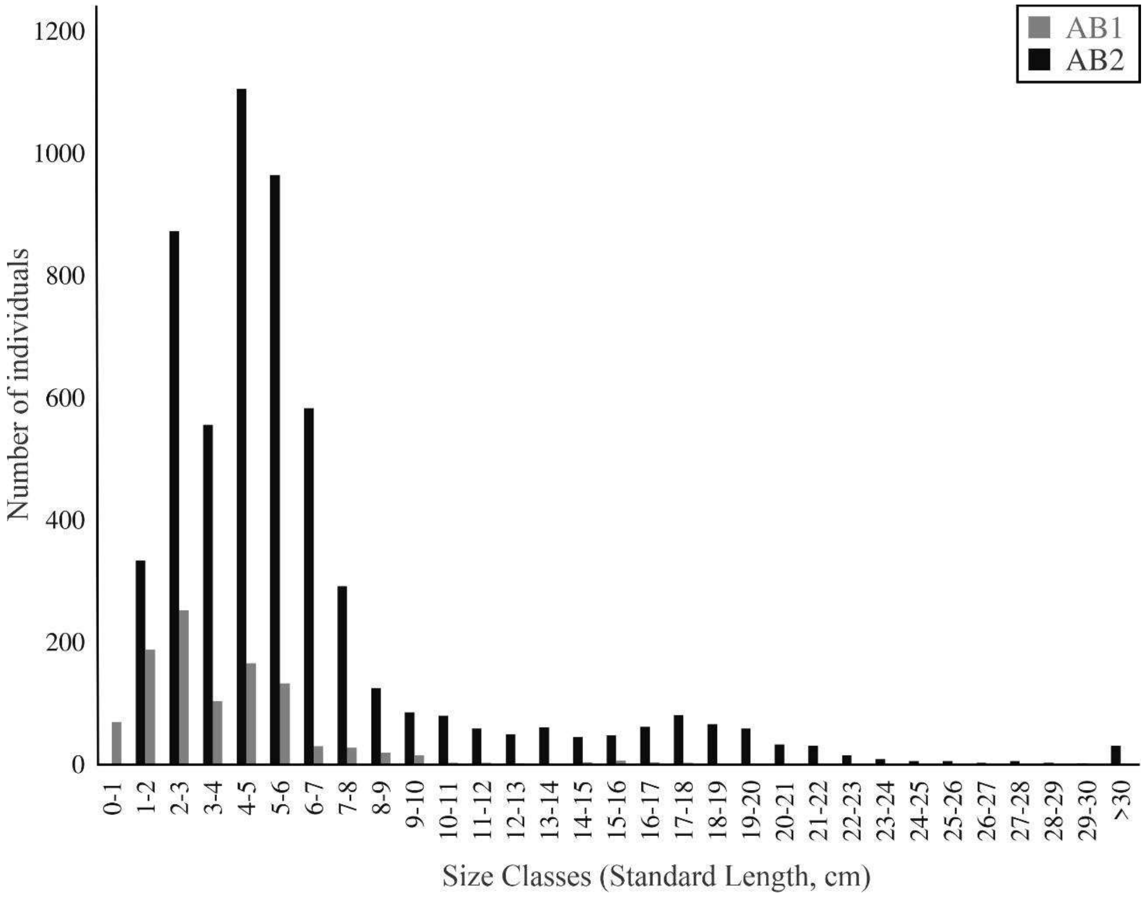


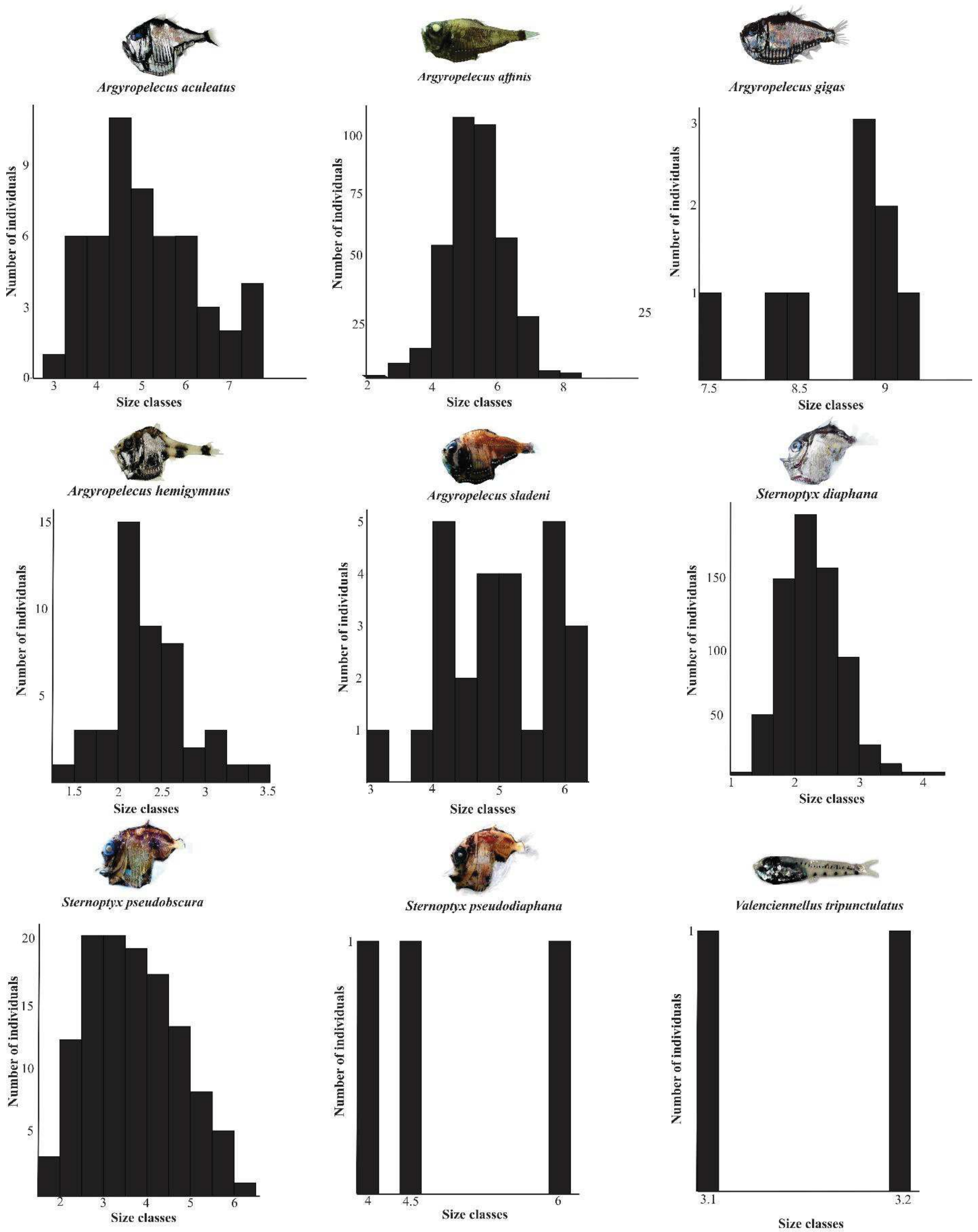
Supplementary material S3- Histogram of mesopelagic species collected on the ABRACOS 1 (mesopelagic trawl) and ABRACOS 2 (micronekton trawl) expeditions.

Hatchetfishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic

Supplementary Material 1 – Number of trawls per depth strata and period of the day.

Depth Strata	Day	Night
10–100	3	3
100–200	3	1
200–300	3	-
300–400	1	1
400–500	3	1
500–600	1	1
600–700	1	1
700–800	2	-
800–900	1	1
900–1000	2	2

Supplementary material 2 – Histogram (Standard length, cm) of hatchetfishes from oceanic islands and seamounts of the western Tropical Atlantic.



Argyropelecus aculeatus

Argyropelecus affinis

Argyropelecus gigas

Argyropelecus hemigymnus

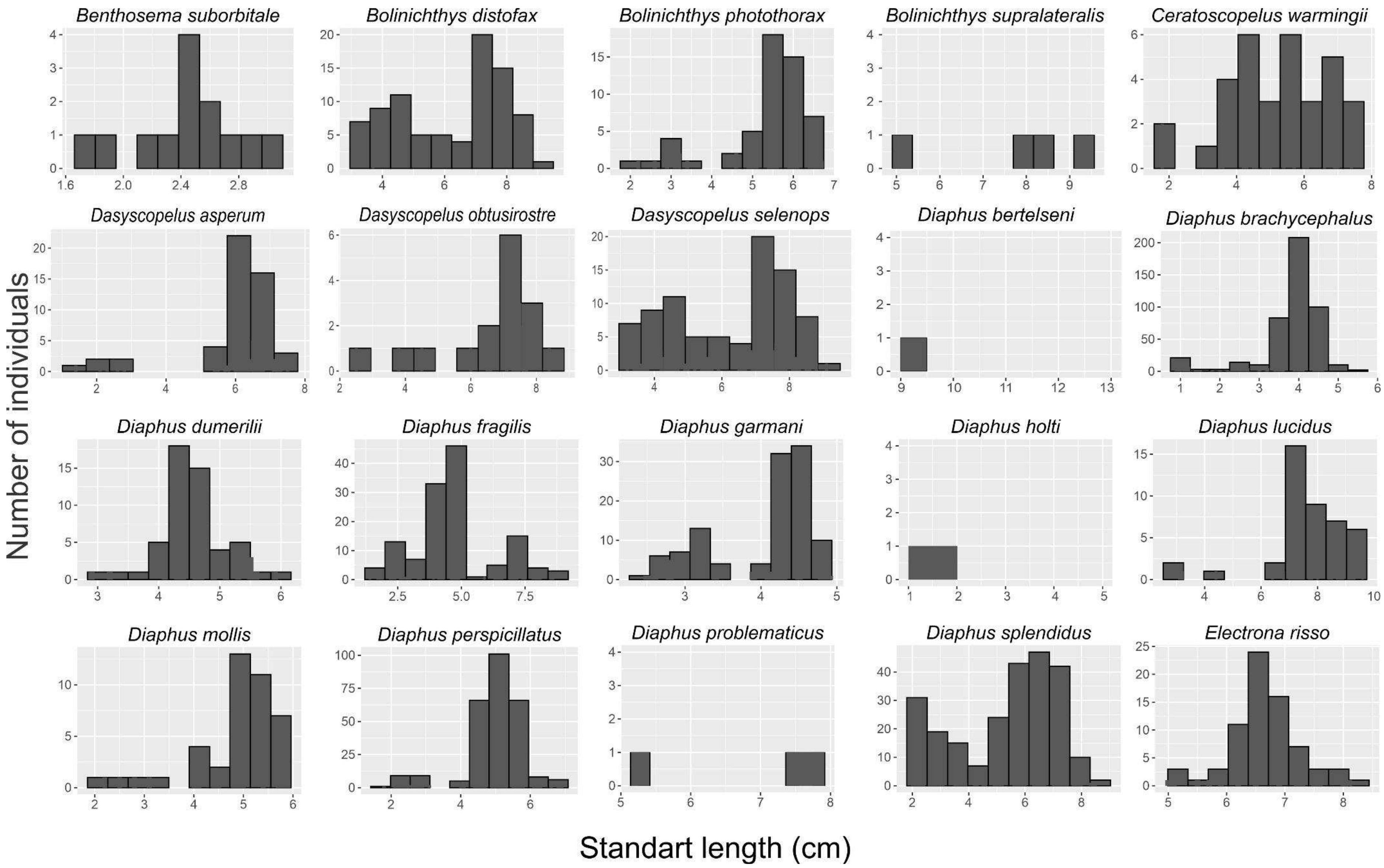
Argyropelecus sladeni

Sternoptyx diaphana

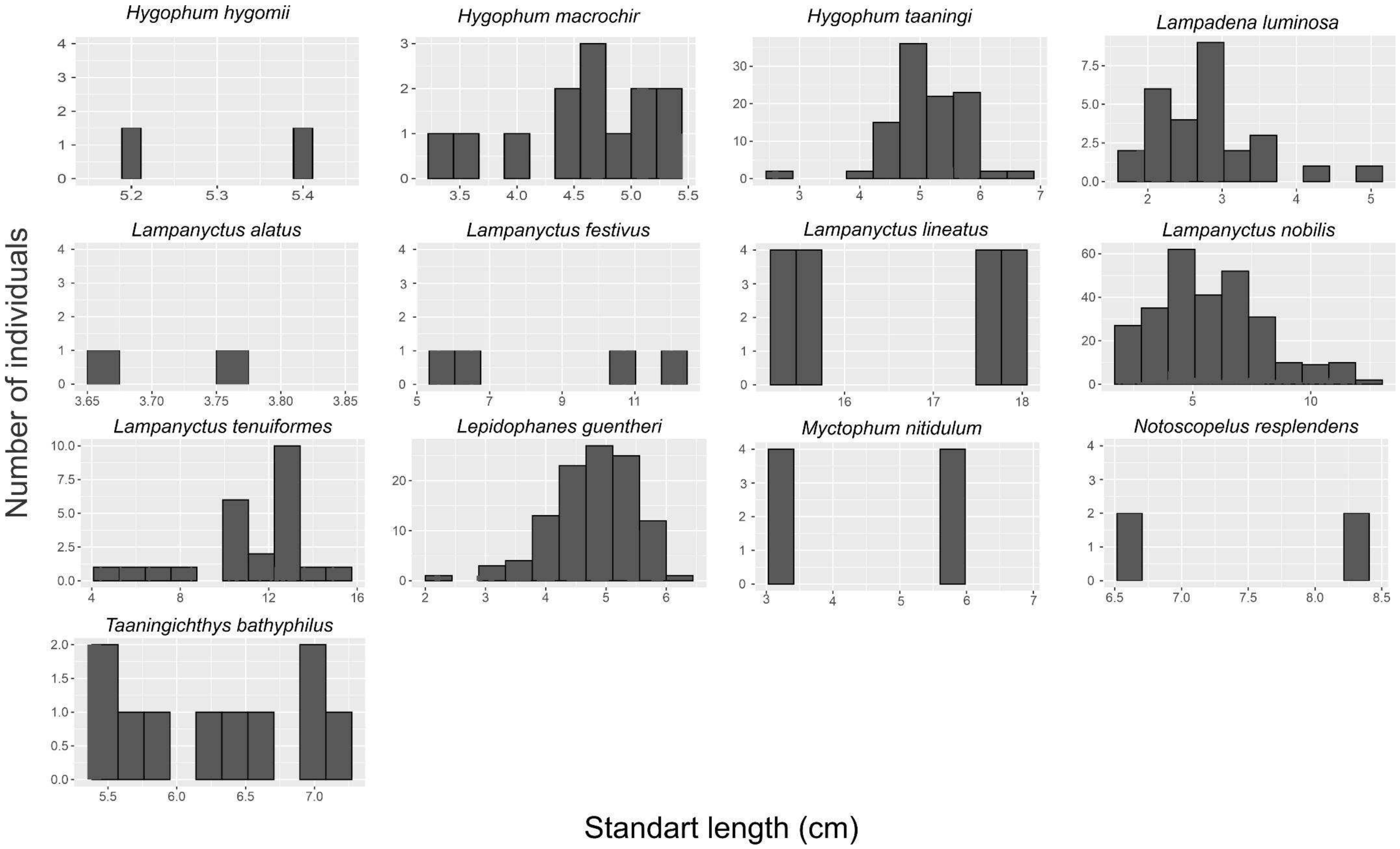
Sternoptyx pseudobscura

Sternoptyx pseudodiaphana

Valenciennellus tripunctulatus



Supplementary material 1– Histogram (Standard length, cm) of lanternfishes from oceanic islands and seamounts of the western Tropical Atlantic. Part I.



Supplementary material 1– Histogram (Standard length, cm) of lanternfishes from oceanic islands and seamounts of the western Tropical Atlantic. Part II.

Supplementary material 2. Number of samples, standard length (cm) and stable isotope values of lanternfishes, potential predator (DP - deep-sea; EP - epipelagic), potential prey, and POM. *Lipid corrected species.

Group	Species	Category	N	SL (cm)	δ^{13}C (‰)	δ^{15}N (‰)	C:N	Trophic level
				Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Myctophidae	*Diaphus brachycephalus*	–	10	5.0±2.1	-18.9±0.4	10.0±0.9	3.4±0.1	3.1±0.3
	Diaphus dumerilii	–	6	16.2±9.5	-19.0±0.5	9.0±1.1	3.5±0.2	2.9±0.3
	Diaphus fragilis	–	11	7.3±0.5	-18.2±0.3	10.2±0.5	3.4±0.1	3.3±0.3
	Diaphus mollis	–	5	5.2±0.3	-19.2±0.2	10.6±0.8	3.4±0.1	3.4±0.3
	Diaphus perspicillatus	–	8	3.2±0.3	-18.2±0.2	10.9±0.7	3.4±0.1	3.3±0.3
	Electrona risso	–	9	5.6±0.1	-18.9±0.1	11.4±0.1	3.2±0.1	3.5±0.3
	Hygophum taaningi	–	9	5.5±0.2	-18.2±0.2	10.0±0.6	3.3±0.1	3.1±0.3
	Lampanyctus nobilis	–	7	7.4±1.5	-18.2±0.3	9.6±0.4	3.3±0.2	3.1±0.3
	Lepidophanes guentheri	–	13	5.7±0.6	-18.2±0.2	9.8±0.7	3.3±0.1	3.1±0.4
Stomiidae	*Borostomias elucens*	DP	9	16.2±1.9	-18.3±0.4	11.9±0.5	3.3±0.1	–
	Chauliodus sloani	DP	10	18.1±1.3	-18.3±0.2	11.1±0.7	3.3±0.0	–
	Malacosteus niger	DP	5	10.7±2.0	-19.2±0.3	11.7±0.5	3.4±0.1	–
Scorpaenidae	*Ectreposebastes imus**	DP	5	19.1±1.8	-19.1±0.3	12.9±0.3	4.3±0.2	–
Sphyraenidae	*Sphyraena barracuda*	EP	7	151.2±30.0	-16.2±0.5	10.7±0.5	3.2±0.1	–
Coryphaenidae	*Coryphaena hippurus*	EP	6	85.2±12.0	-16.5±0.4	11.3±0.6	3.2±0.1	–
Carangidae	*Elagatis bipinnulata*	EP	6	53.3±10.4	-19.3±0.2	9.4±0.5	3.4±0.2	–
Scombridae	*Acanthocybium solandri*	EP	8	100.0±35.0	-16.9±0.4	11.0±1.0	3.2±0.1	–
	Katsuwonus pelamis	EP	3	44.6±4.1	-17.2±0.4	10.2±1.0	3.2±0.1	–
	Thunnus albacares	EP	12	65.0±20.0	-17.4±0.2	10.8±1.1	3.1±0.1	–
Fish larvae	Teleostei larvae 5–10 mm	Prey	10	–	-19.7±0.1	5.9±0.2	3.2±0.1	–
	Teleostei larvae 15–20 mm	Prey	6	–	-18.5±0.4	7.2±0.7	3.2±0.1	–
Crustacea	*Euphausia gibboides*	Prey	6	1.5±0.1	-19.3±1.0	6.9±0.1	3.2±0.1	–
	Euphausia sp.	Prey	3	1.4±0.1	-19.5± 0.5	7.3±0.9	3.2±0.1	–
	Pasiphaeidae sp.	Prey	3	–	-19.1±0.1	6.1±0.1	3.1±0.1	–
	Phronima sp.	Prey	3	–	-19.0±0.2	5.9±0.3	3.6±0.2	–
Siphonophorae	*Abylopsis tetragona*	Prey	3	–	-17.8±0.3	7.2±1.0	3.3±0.1	–
	Siphonophorae sp.	Prey	3	–	-19.2±0.1	9.1±0.2	3.4±0.1	–
Thaliacea	*Pyrosoma atlanticum**	Prey	11	–	-21.5±0.2	3.0±0.7	5.3±0.2	–
	Salpa sp.*	Prey	6	–	-19.8±0.5	5.5±0.5	4.5±0.7	–
	Soestia zonaria	Prey	6	–	-20.3±0.2	3.8±0.6	3.3±0.1	–
Zooplankton	Zoo A (<10 μm)*	Prey	19	–	-19.8±0.5	2.0±1.1	4.7±0.2	–
	Zoo B (100–200 μm)*	Prey	19	–	-19.4±0.5	1.9±0.8	4.6±0.7	–
	Zoo C (200–500 μm)*	Prey	19	–	-19.4±0.3	3.0±0.6	5.6±1.2	–
	Zoo D (5000–1000 μm)*	Prey	18	–	-19.1±0.3	4.2±0.4	4.2±0.4	–
	Zoo E (1000–2000 μm)*	Prey	18	–	-20.3±0.9	4.6±0.4	4.8±0.6	–
	Zoo F (>2000 μm)*	Prey	13	–	-19.6±0.4	4.9±0.4	4.5±0.3	–
POM			17	–	-22.4±0.7	2.8±1.2	–	–

Supplementary material 4 – Literature review on the vertical migration of lanternfishes species found in this study.

Species	Record of epipelagic vertical Migration	References
Benthosema suborbitale (Gilbert, 1913)	Yes	Clarke, (1973); Santos and Figueiredo, (2008)
Bolinichthys distofax Johnson, 1975	No	Clarke, (1973); Hulley, (1990); Hulley and Duhamel, (2009)
Bolinichthys photothorax (Parr, 1928)	Yes	Hulley, (1990); Santos and Figueiredo, (2008)
Bolinichthys supralateralis (Parr, 1928)	Yes	Santos and Figueiredo, (2008); Hulley and Duhamel, (2009)
Ceratoscopelus warmingii (Lütken, 1892)	Yes	Clarke, (1973); Gartner Jr et al., (1987); Santos and Figueiredo, (2008); Watanabe et al., (1999)
Dasyscopelus asperum Richardson 1845	Yes	Hulley, (1990); Santos and Figueiredo, (2008)
Dasyscopelus obtusirostre Tåning, 1928	Yes	Clarke, (1973); Hulley, (1990)
Dasyscopelus selenops (Tåning, 1928)	Yes	Clarke, (1973); Hopkins et al., (1981); Hulley, (1990)
Diaphus bertelseni Nafpaktitis, 1966	Yes	Clarke, (1973); Hulley, (1990); Mundy, (2005)
Diaphus brachycephalus Tåning, 1928	Yes	Clarke, (1973); Santos and Figueiredo, (2008)
Diaphus dumerilii (Bleeker, 1856)	Yes	Gartner Jr et al., (1987); Kinzer and Schulz, (1985)
Diaphus fragilis Tåning, 1928	Yes	Clarke, (1973); Hulley, (1990)
Diaphus garmani Gilbert 1906	Yes	Hulley, (1990); Santos and Figueiredo, (2008)
Diaphus holti Tåning, 1918	Yes	Hulley, (1990); Olivar et al., (2017)
Diaphus lucidus (Goode & Bean, 1896)	Yes	Hulley, (1986); Kinzer and Schulz, (1985); Santos and Figueiredo, (2008)
Diaphus mollis Tåning, 1928	Yes	Hulley, (1990); Kinzer and Schulz, (1985); Santos and Figueiredo, (2008)
Diaphus perspicillatus (Ogilby, 1898)	Yes	Hulley, (1990); Mundy, (2005)
Diaphus problematicus Parr, 1928	Yes	Figueiredo et al., (2002); Hopkins et al., (1981)
Diaphus splendidus (Brauer, 1904)	Yes	Hopkins et al., (1981); Hulley, (1990)
Electrona risso (Cocco, 1829)	No	Battaglia et al., (2016); Moser and Ahlstrom, (1996)
Hygophum hygomii (Lütken, 1892)	Yes	Hulley, (1990)
Hygophum macrochir (Günther, 1864)	Yes	Hulley, (1990); Kinzer and Schulz, (1985); Santos and Figueiredo, (2008)
Hygophum taaningi Becker, 1965	Yes	Hopkins et al., (1981); Hulley, (1990); Santos and Figueiredo, (2008)
Lampadena luminosa (Garman, 1899)	Yes	Clarke, (1973); Hopkins et al., (1981)
Lampanyctus alatus Goode & Bean, 1896	Yes	Hopkins et al., (1981); Hulley, (1990); Kinzer and Schulz, (1985)
Lampanyctus lineatus (Tåning, 1928)	Yes	Hulley, (1990); Zahuranec, (2000)
Lampanyctus festivus Tåning, 1928	Yes	Hulley, (1990)
Lampanyctus nobilis (Tåning, 1928)	Yes	Clarke, (1973); Hulley, (1986)
Lampanyctus tenuiformes (Brauer, 1906)	Yes	Clarke, (1973); Kinzer and Schulz, (1985)
Lepidophanes guentheri Goode & Bean 1896	Yes	(Hulley, 1990; Kinzer and Schulz, 1985)
Myctophum nitidulum Garman 1899	Yes	Hulley, (1990); Kinzer and Schulz, (1985)
Notoscopelus resplendens (Richardson, 1845)	Yes	Hulley, (1990); Kinzer and Schulz, (1985); van der Spoel and Bleeker, (1991)
Taaningichthys bathyphilus (Tåning, 1928)	No	Douglas and Partridge, (1997); Gartner Jr et al., (1987); Hulley, (1990)

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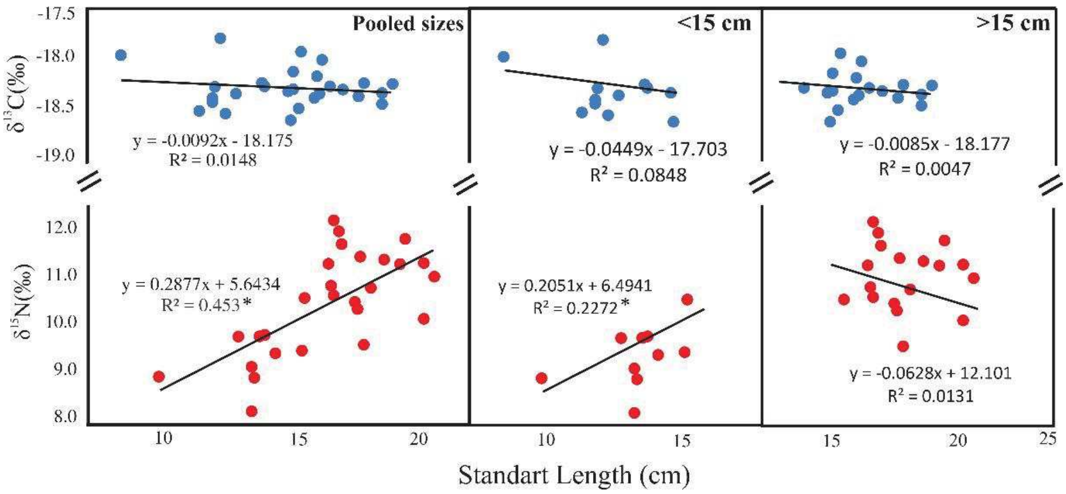
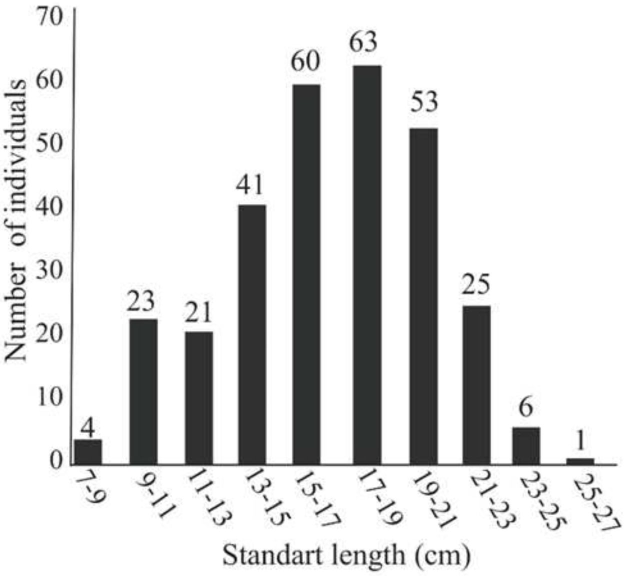
Trophic ecology, habitat, and migratory behaviour of the viperfish *Chauliodus sloani* reveal a key mesopelagic player

Supplementary Material 1 – Number of trawls per depth strata and period of the day.

Depth Strata	Day	Night
10-100	3	3
100-200	3	1
200-300	3	-
300-400	1	1
400-500	3	1
500-600	1	1
600-700	1	1
700-800	2	-
800-900	1	1
900-1000	2	2



Supplementary Material 2 – Results of least-squares regression analysis between standard length (cm) and δ^{15}N and δ^{13}C values of the viperfish *Chauliodus sloani.* * relationships presenting significant statistical differences ($p < 0.05$).



Supplementary Material 3– Histogram of the number of individuals per length. Numbers above bars represent the number of individuals in each size class.

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ORIGINAL ARTICLE

Deep-sea manefishes (Perciformes: Caristiidae) from oceanic islands and seamounts off northeastern Brazil, with comments on the caristiids previously reported in Brazilian waters

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ABSTRACT
The manefishes of the family Caristiidae are rare, poorly known deep-sea species with broad geographical distribution. This study provides new information on the diversity and distribution of this family around the oceanic islands and seamounts off northeastern Brazil, reporting the first records of *Paracaristius nudarcus*, *Platyberyx andriashevi*, *Platyberyx paucus* and *Platyberyx pietschi* in Brazilian waters. Measurements and counts for all specimens examined are provided and compared with those available in the literature. In addition, the identity of caristiids previously reported from Brazil is discussed.

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Introduction

Fishes of the family Caristiidae are rare deep-sea species with broad geographical distribution, occurring in all oceans (Kukuev et al. 2013; Stevenson and Kenaley 2013). The family comprises four genera and 19 species commonly known as manefishes (Kukuev et al. 2013; Stevenson and Kenaley 2013). These species present epipelagic larvae and juveniles, occurring from the surface to the mesopelagic zone, while adults have been reported at depths ranging from 100 to 2000m (Benfield et al. 2009; Stevenson and Kenaley 2011, 2013). The caristiids are characterized by having relatively short heads, steep snouts, large eyes, deep and strongly compressed bodies, very long and high dorsal fins and greatly elongated pelvic fins (Benfield et al. 2009; Kukuev et al. 2013; Stevenson and Kenaley 2013).

Studies on the taxonomy and distribution of caristiids were historically scarce and fragmented. However, a series of taxonomic revisions has been recently conducted (Kukuev et al. 2012, 2013; Stevenson and Kenaley 2011, 2013) and the knowledge on the taxonomy and the distribution patterns was significantly improved. The family Caristiidae is currently divided into two distinctly pronounced groups: Paracaristiinae and Caristiinae. The Paracaristiinae comprises two genera (*Neocaristius* and *Paracaristius*) and five species usually known as ‘small-mouth’ caristiids (Stevenson and Kenaley 2011), while the Caristiinae, in turn, includes two genera (*Caristius* and *Platyberyx*) and 14 species referred to as ‘large-mouth’ caristiids (Stevenson and Kenaley 2013).

In the current study, four species of Caristiidae are reported for the first time in Brazilian waters based on specimens collected around Rocas Atoll, Fernando de Noronha Archipelago, and seamounts off Rio Grande do Norte. Meristic and morphometric data are provided for all specimens examined, and the identity of caristiids previously reported in Brazilian waters is further discussed.

Materials and methods

Most of the material examined in the current study is part of a large collection of mesopelagic invertebrates and fishes sampled during the ABRACOS expeditions (Acoustics along the BRAzilian COaSt), carried out in October 2015 and April 2017, and conducted by the French RV *Antea* off northeastern Brazil, including Rocas Atoll, Fernando de Noronha Archipelago, and

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seamounts off Rio Grande do Norte (Figure 1; Bertrand 2015, 2017). The extensive survey of 80 fishing stations from 0 to 1113 m depth resulted in the collection of 11 specimens of Caristiidae, of which seven where identified at species level. Sampling was conducted using micronekton (body mesh: 40 mm, cod-end mesh: 10 mm) and mesopelagic (body mesh: 30 mm, cod-end mesh: 4 mm) nets. Trawl depth was continuously recorded using a Scanmar depth sensor fitted on the upper part of the trawl mouth. All specimens taken in ABRACOS expeditions are deposited at NPM – Fish Collection of the Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro (Macaé, RJ, Brazil). Additional specimens examined from southern Brazil are deposited at MZUSP – Museu de Zoologia da Universidade de São Paulo (São Paulo, SP, Brazil).

Measurements and counts were mostly taken according to Hubbs and Lagler (1947). In addition, 'preorbital length' and 'predorsal length' were measured along the body axis ('horizontal distance'), from the tip of the snout to a vertical line passing through the anterior margin of orbit (preorbital) and through the dorsal-fin origin (predorsal) (Duane Stevenson and Christopher Kenaley, pers. comm.). This was necessary for comparison with data provided by Stevenson and Kenaley (2011, 2013). Radiographs of specimens were taken using a Faxitron LX-60 to aid fin-rays and vertebrae counts. Specimens were identified according to the keys provided by Stevenson and Kenaley (2011) and Stevenson and Kenaley (2013).

Results

Paracaristius nudarcus Stevenson & Kenaley, 2011

(Figure 2)

Material examined

NPM 4476 (1 specimen, 165 mm SL), RV *Antea*, ABRACOS #41A, Brazil, off northern Fernando de Noronha Archipelago, 03°19′59″S, 32°24′42″W to 03°19′32″S, 32°25′05″W, 0–430 m depth, micronekton trawl net, 26 April 2017, 21:44–22:06 h.

Diagnosis

According to Stevenson and Kenaley (2011), *Paracaristius nudarcus* can be distinguished from *P. aquilus* and *P. nemorosus* by the absence of fingerlike papillae along the dorsal margin of the hyoid arch and at the interhyal-posterior ceratohyal articulation, as well as by the number of dorsal-fin rays (27–31 vs. 30–33) and anal-fin rays (17–20 vs. 15–18). *Paracaristius nudarcus* can be distinguished from *P. maderensis* by the position of the dorsal-fin origin (above orbit vs. posterior to orbit) and by the arrangement of the jaw teeth (single row, except near symphysis vs. multiple rows).

Distribution

Paracaristius nudarcus has been previously reported in the western North Atlantic, eastern South Atlantic, eastern Indian Ocean, and eastern and western Pacific (Stevenson and Kenaley 2011). The specimen reported off northern Fernando de Noronha Archipelago represents the first record of the genus and species in the western South Atlantic (Figure 1).

Remarks

Morphometric and meristic data for the specimen reported herein are within the range to those recorded by Stevenson and Kenaley (2011) (Table I). Upper and lower jaw teeth count of the single specimen examined was not possible as both jaws were damaged.

Platyberyx andriashevi (Kukuev, Parin & Trunov, 2012)

(Figure 3a)

Material examined

NPM 4473 (1, 138 mm SL), RV *Antea*, ABRACOS #44A, Brazil, off eastern Fernando de Noronha Archipelago, 03°52′53″S, 32°17′33″W to 03°52′13″S, 32°26′28″W, 0–850 m depth, micronekton trawl net, 28 April 2017, 12:44–13:17 h. NPM 4475 (2, 23–33 mm SL), RV *Antea*, ABRACOS #40B, Brazil, off northern Fernando de Noronha Archipelago, 03°31′12″S, 32°31′49″W to 03°31′03″S, 32°32′49″W, 0–230 m depth, micronekton trawl net, 26 April 2017, 12:14–12:37 h. MZUSP 93287 (1, 47 mm SL), RV *Atlântico Sul*, Brazil, off Rio Grande do Sul, 32°58′S, 50°35′W, 99 m depth, bottom trawl, 18 November 1983.

Diagnosis

According to Stevenson and Kenaley (2013), *Platyberyx andriashevi* may be distinguished from all congeners by the following combination of characters: 36 or more vertebrae, 31 or more dorsal-fin rays, and 20 or more anal-fin rays. *Platyberyx andriashevi* may be further distinguished from its congeners, except *P. paucus* and *P. pietschi*, by the presence of laterally flattened, blade-like ventral procurrent caudal rays, and an anteriorly directed hook-like process on the third posteriormost ventral procurrent caudal ray.

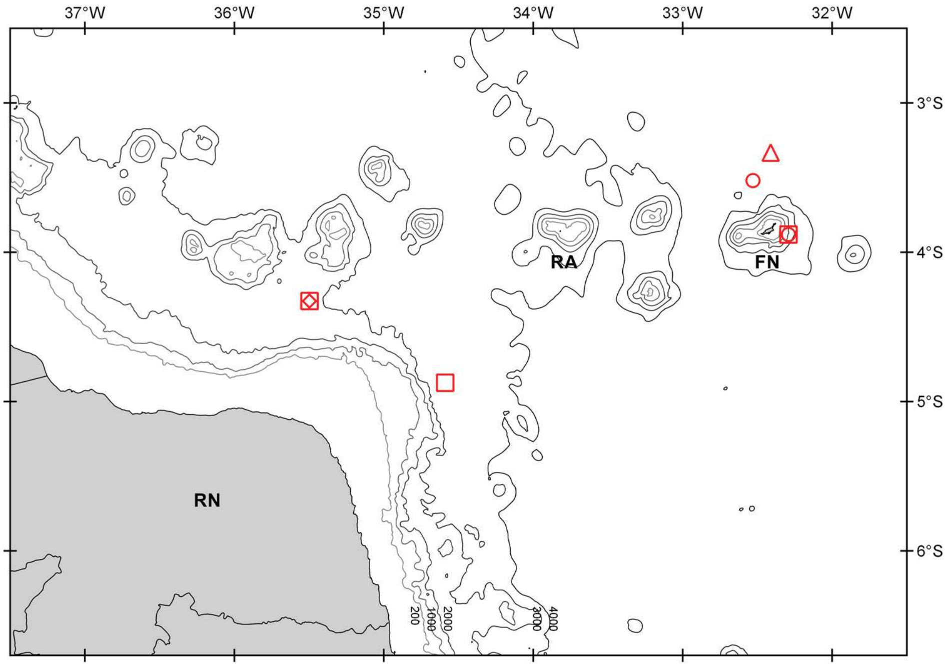

Figure 1. Distribution of fishes of the family Caristiidae around oceanic islands and seamounts off northeastern Brazil: *Paracaristius nudarcus* (open triangle), *Platyberyx andriashevi* (open circles), *Platyberyx paucus* (open squares), and *Platyberyx pietschi* (open diamond). RN – State of Rio Grande do Norte; RA – Rocas Atoll; FN – Fernando de Noronha Archipelago.

Distribution

Platyberyx andriashevi has been previously reported in the north and southeast Atlantic, north and southwest Pacific, and Indian Ocean (Kukuev et al. 2012; Stevenson and Kenaley 2013; Okamoto and Stevenson 2015). The species is herein reported for the first time in Brazilian waters, based on three specimens collected around Fernando de Noronha Archipelago (Figure 1), and one specimen collected off Rio Grande do Sul (previously identified as *Caristius macropus* by Caires et al. 2008).

Remarks

Considering the high meristics and rigidly fixed jaw teeth of *P. andriashevi*, which argue for placement within the genus *Caristius*, the species was first described as *Caristius andriashevi* Kukuev et al. 2012. However, due to the presence of a conspicuous lateral line, and its caudal skeleton similar to that of *P. paucus* and *P. pietschi*, Stevenson and Kenaley (2013) placed the species into the genus *Platyberyx*.

Morphometric and meristic data for the specimens reported herein were within the range of those recorded by Stevenson and Kenaley (2013), except for the peduncle length (8.5–13.0 vs. 12.0–18.9% SL, respectively; Table I). Morphology of gill rakers (two series with small bristles at tip) and ventral procurrent caudal rays (laterally flattened and bladelike) are as those described by Stevenson and Kenaley (2013).

The general colour pattern of the three adult specimens (155–185 mm SL) of *P. andriashevi* was originally described by Kukuev et al. (2012) as body brown, with black fins. The adult specimen (138 mm SL) reported herein has the same colour as described by Kukuev et al. (2012), while the two juveniles (23–33 mm SL) have a light brown body (silvery in life specimens) with five transversal dark stripes along the body (one on eye, one on operculum, two on trunk, and one on caudal peduncle) and whitish fins (Figure 3a).

***Platyberyx paucus* Stevenson & Kenaley, 2013**

(Figure 3b)

Material examined

NPM 4474 (1, 85 mm SL), RV *Antea*, ABRACOS #44A, Brazil, off eastern Fernando de Noronha Archipelago, 03°52′53″S, 32°17′33″W to 03°52′13″S, 32°26′28″W, 0–850 m depth, micronekton trawl net, 28 April 2017, 12:44–13:17 h. NPM 4511 (1, 97 mm SL), RV *Antea*, ABRACOS #35, Brazil, sea mounts off Rio Grande do Norte, 04°19′37″S, 35°29′52″W to 04°18′32″S, 35° 32′20″W, 0–630 m depth, micronekton trawl net, 20 April 2017, 22:35–23:15 h. NPM 4512 (1, 91 mm SL),

Figure 2. *Paracaristius nudarcus* (NPM 4476, 165 mm SL). Scale = 10 mm.

RV *Antea*, ABRACOS #39, Brazil, off Rio Grande do Norte, 04°52′30″S, 34°35′23″W to 04°50′53″S, 34°51′05″W, 0–800 m depth, micronekton trawl net, 24 April 2017, 21:49–22:37 h.

Diagnosis

According to Stevenson and Kenaley (2013), *Platyberyx paucus* can be distinguished from all congeners by the following combination of characters:

Table I. Proportions and counts for *Paracaristius nudarcus*, *Platyberyx andriashevi*, *Platyberyx paucus* and *Platyberyx pietschi* collected off northeastern Brazil (western South Atlantic) and compared with those reported in the literature.

Species	*Paracaristius nudarcus*		*Platyberyx andriashevi*		*Platyberyx paucus*		*Platyberyx pietschi*	
References	Present study	Stevenson and Kenaley (2011)	Present study	Stevenson and Kenaley (2013)	Present study	Stevenson and Kenaley (2013)	Present study	Stevenson and Kenaley (2013)
Standard length (SL, mm)	165 (1)	22–223 (17)	23–138 (4)	32–196 (18)	85–97 (3)	21–100 (4)	53–72 (2)	34–93 (4)
Vertebrae	37 (1)	33–37 (16)	37–39 (3)	36–39 (16)	31–32 (3)	31 (4)	33 (1)	33–35 (3)
Dorsal-fin rays	28 (1)	27–31 (17)	31–35 (4)	31–35 (16)	25–26 (3)	24–26 (4)	30–31 (2)	30–31 (3)
Anal-fin rays	18 (1)	17–20 (17)	21–22 (4)	20–22 (16)	15–17 (3)	15–16 (4)	17–19 (2)	18–19 (4)
Pectoral-fin rays	16 (1)	16–18 (15)	18–19 (4)	17–18 (16)	16–17 (3)	16–17 (4)	18 (2)	17–18 (4)
Vomerine teeth	Absent	Absent	4–7 (4)	3–12 (15)	5 (1)	1–6 (4)	8 (1)	8–10 (4)
Palatine teeth	Absent	Absent	4–12 (4)	3–12 (15)	Absent	Absent	–	6–10 (4)
Upper jaw teeth	–	24–43 (10)	16–22 (4)	12–35 (12)	42–43 (2)	42 (1)	48 (1)	32–45 (3)
Lower jaw teeth	–	16–36 (7)	19–27 (3)	11–26 (7)	42–53 (2)	37 (1)	20 (1)	16–30 (2)
Upper gill rakers	8 (1)	5–8 (16)	6–8 (4)	5–8 (15)	7 (3)	6–7 (4)	6–7 (2)	6–7 (4)
Lower gill rakers	15 (1)	14–16 (16)	11–14 (4)	12–15 (15)	14–15 (3)	14–16 (4)	13–14 (2)	13–14 (4)
Total gill rakers	23 (1)	20–24 (16)	18–22 (4)	18–22 (15)	21–22 (3)	21–23 (4)	20 (2)	19–21 (4)
Measurements in % of SL								
Body depth	58.2 (1)	53.0–77.0 (15)	45.7–48.5 (2)	37.9–49.6 (18)	55.4–57.1 (3)	52.1–68.3 (4)	53.75 (1)	45.6–53.0 (4)
Head length	32.2 (1)	29.0–45.7 (14)	28.6–40.6 (2)	24.2–39.9 (18)	36.7–38.8 (3)	39.9–54.1 (3)	38.9 (1)	33.4–41.3 (4)
Predorsal length	31.5 (1)	–	25.7–30.3 (2)	–	34.5–37.2 (3)	–	34.7 (1)	–
Predorsal length (horizontal)	12.1 (1)	6.5–17.9 (15)	9.4–11.5 (2)	8.3–22.3 (18)	16.5–23.7 (3)	17.2–29.0 (3)	18.9 (1)	16.9–25.9 (4)
Prepectoral length	34.5 (1)	30.4–42.2 (12)	28.6–37.9 (2)	11.6–42.8 (18)	38.2–44.8 (3)	45.8–53.9 (3)	41.3 (1)	39.6–44.4 (4)
Prepelvic length	30.6 (1)	30.5–42.1 (15)	25.5–33.3 (2)	22.4–39.6 (18)	30.6–38.7 (3)	39.3–49.4 (3)	38.9 (1)	36.1–52.7 (4)
Pectoral-fin base	7.9 (1)	6.4–11.9 (15)	6.9–9.1 (2)	5.3–11.5 (17)	7.1–11.0 (3)	7.8–10.6 (4)	9.0 (1)	7.1–9.7 (4)
Preanal length	59.7 (1)	55.5–70.9 (15)	43.0–60.6 (2)	44.6–58.1 (18)	59.3–62.4 (3)	65.3–72.9 (3)	58.1 (1)	54.5–64.7 (4)
Dorsal-fin base	77.6 (1)	72.2–86.3 (15)	75.8–79.7 (2)	65.9–80.8 (18)	62.9–73.8 (3)	61.0–71.7 (4)	73.6 (1)	62.9–68.7 (4)
Anal-fin base	43.3 (1)	34.1–49.6 (15)	31.8–47.6 (2)	31.6–53.3 (18)	34.1–35.7 (3)	29.1–37.7 (4)	33.3 (1)	28.7–37.3 (4)
Peduncle length	16.5 (1)	10.9–16.5 (15)	8.5–13.0 (2)	12.0–18.9 (18)	13.9–17.0 (3)	12.1–14.8 (4)	13.9 (1)	13.5–17.4 (4)
Peduncle depth	15.8 (1)	12.8–17.7 (15)	10.3–10.9 (2)	8.5–12.8 (18)	14.4–15.9 (3)	14.5–16.6 (4)	12.5 (1)	10.7–14.6 (4)
Head length (HL, mm)	53.2 (1)	–	13.4–39.5 (2)	–	32.8–35.6 (3)	–	20.0 (1)	–
Measurements in % of HL								
Upper jaw length	37.6 (1)	34.7–52.8 (13)	64.3–68.7 (2)	58.8–74.7 (18)	45.3–51.8 (3)	49.8–71.0 (3)	67.9 (1)	58.6–69.4 (4)
Lower jaw length	36.7 (1)	39.3–50.4 (13)	51.4–54.5 (2)	52.2–84.6 (18)	39.7–46.1 (3)	48.8–57.3(2)	42.9 (1)	55.6–70.7 (4)
Bony orbit length	38.3 (1)	33.1–45.5 (14)	45.6–52.2 (2)	40.0–52.6 (18)	44.8–50.6 (3)	49.1–51.4 (3)	46.4 (1)	43.7–51.9 (4)
Preorbital length	22.6 (1)	–	14.9–17.7 (2)	–	16.8–20.2 (3)	–	17.9 (1)	–
Preorbital length (horizontal)	13.2 (1)	6.5–17.4 (14)	14.4–14.9 (2)	–	7.6–11.2 (3)	–	10.7 (1)	–

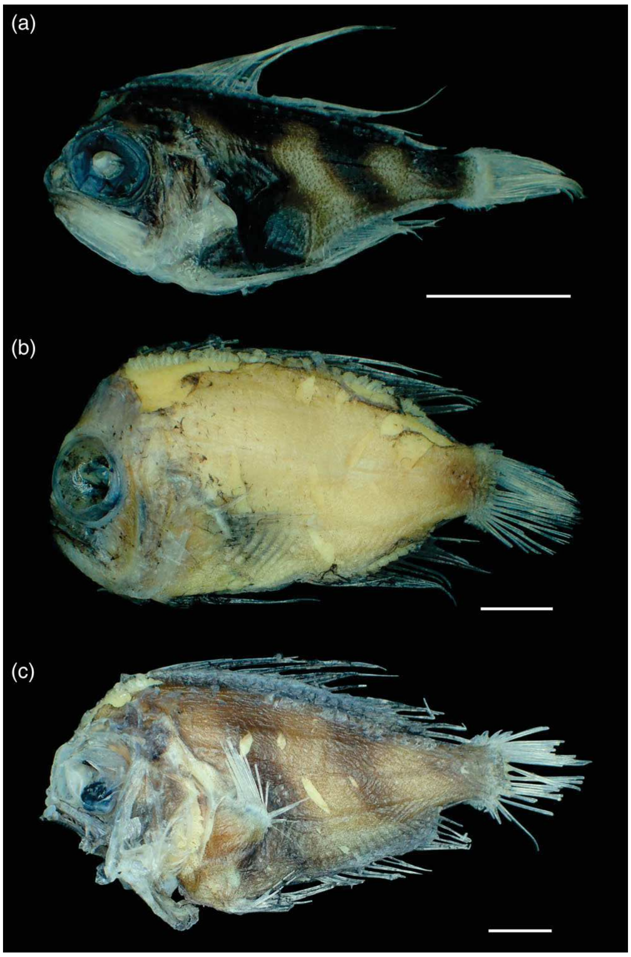

Figure 3. (a) *Platyberyx andriashevi* (NPM 4475, 33 mm SL), (b) *Platyberyx paucus* (NPM 4474, 85 mm SL), and (c) *Platyberyx pietschi* (NPM 4510, 72 mm SL, damaged). Scale = 10 mm.

absence of palatine teeth and lower meristics (31 vertebrae, 24–26 dorsal-fin rays, and 15–16 anal-fin rays). It can be further distinguished from all congeners, except *P. andriashevi* and *P. pietschi*, by the presence of laterally flattened, bladelike ventral procurrent caudal rays, and an anteriorly directed hook-like process on the third posterior-most ventral procurrent caudal ray (Stevenson and Kenaley 2013).

Distribution

Platyberyx paucus is poorly known worldwide, reported from one specimen in the central North Pacific (Hawai'i, western O'ahu Island), and three specimens from the western Central Atlantic (off northern South America) (Stevenson and Kenaley 2013). The current study reports the occurrence of three specimens off Rio Grande do Norte and around Fernando de Noronha Archipelago, which represent the first record of *P. paucus* in Brazilian waters (Figure 1).

Remarks

Most of characters observed in our material ($n = 3$, 85–97 mm SL) are within the ranges presented for the types of *Platyberyx paucus* ($n = 4$, 21–100 mm SL). However, some measurements (head length, lower jaw length, prepectoral length, prepelvic length, and preanal length) of the specimens reported herein were smaller than those recorded by Stevenson and Kenaley (2013) (Table I).

Morphology of gill rakers (two series with small bristles at tip) and ventral procurrent caudal rays (laterally flattened and bladelike) are similar to those described by Stevenson and Kenaley (2013). However, Stevenson and Kenaley (2013) described an anteriorly directed hook-like process on the third porteriormost ventral procurrent caudal ray. In our specimens, this condition was observed in the third and fourth posteriormost ventral procurrent caudal rays. The meaning of this difference is still unknown, as this recently described species is know just from a few specimens.

The specimens recorded herein have a light brown body with dark pigmentation on fins and around the mouth (Figure 3b), which is similar to that reported for the 89-mm holotype of *P. paucus* (Stevenson and Kenaley 2013; figure 1d).

Platyberyx pietschi **Stevenson & Kenaley, 2013**

(Figure 3c)

Material examined

NPM 4510 (1, 72 mm SL), RV *Antea*, ABRACOS #35, Brazil, sea mounts off Rio Grande do Norte, 04° 19′37″S, 35°29′52″W to 04°18′32″S, 35°32′20″W, 0–630 m depth, micronekton trawl net, 20 April 2017, 22:35–23:15 h. MZUSP 86699 (1, 53 mm SL), RV *Atlântico Sul*, Brazil, off São Paulo, 26°19′49″S 45°57′00″W, 600 m depth, midwater trawl, 27 February 2002.

Diagnosis

According to Stevenson and Kenaley (2013), *Platyberyx pietschi* can be distinguished from its congeners, except *P. andriashevi* and *P. paucus*, by the presence of an anteriorly directed hook-like process on the third posteriormost ventral procurrent caudal ray. *Platyberyx pietschi* can be distinguished from *P. andriashevi* by having fewer dorsal-fin rays (30–31 vs. 31–37), anal-fin rays (18–19 vs. 19–22), and vertebrae (33–35 vs. 36–39); and from *P. paucus* by having greater number of dorsal-fin rays (30–31 vs. 24–26), anal-fin rays (18–19 vs. 15–16), pectoral-fin rays (17–18 vs. 16–17), and vertebrae (33–35 vs. 31), respectively.

Distribution

Platyberyx pietschi is a poorly known species, reported only from two specimens from the western Central Atlantic, one specimen from the central Pacific, and one from the western South Pacific (Australia). The species is herein reported for the first time in Brazilian waters, based on a single specimen collected off Rio Grande do Norte (Figure 1), and another specimen collected off São Paulo (previously identified as *Caristius* sp. by Caires et al. 2008).

Remarks

Morphometric and meristic data for the specimen reported herein were within the range of those recorded by Stevenson and Kenaley (2013), except by its dorsal-fin base length (73.6 vs. 62.9–68.7% SL), and lower jaw length (42.9 vs. 55.6–70.7% HL), respectively (Table I).

Morphology of gill rakers (two series with long spikes and small bristles at tip) and ventral procurrent caudal rays (laterally flattened and bladelike) are similar to those described by Stevenson and Kenaley (2013). However, these authors described an anteriorly directed hook-like process on the third porteriormost ventral procurrent caudal ray. In our material, this character was observed in the fourth posteriormost ventral procurrent caudal ray. As this species was just recently described, additional specimens must be examined in order to understand the impact of this difference in the taxonomy of this species.

The specimens recorded herein (53–72 mm SL) have the same colour as the 89-mm holotype of *P. pietschi* (Stevenson and Kenaley 2013; figure 1e): body brown (probably silvery in life specimens) with five transversal dark stripes along the body (one on eye, one on operculum, two on trunk, and one on caudal peduncle), dark dorsal and anal fins, and whitish caudal fin (Figure 3a).

Discussion

Among more than 7000 specimens of mesopelagic fishes caught during the two ABRACOS expeditions (October 2015 and April 2017), only 11 specimens of caristiids were collected, of which four could not be identified due to their poor condition. Of the eighteen species of the family Caristiidae known to date, four have been reported for the first time in Brazilian waters: *Paracaristius nudarcus*, *Platyberyx andriashevi*, *Platyberyx paucus* and *Platyberyx pietschi*.

In addition to the caristiids collected during the ABRACOS expeditions, a few specimens have been previously recorded off Brazilian coast. Caires et al. (2008) recorded two specimens of *Caristius* collected off southern Brazil. The first one (MZUSP 93287) was identified as *C. macropus* (Bellotti 1903), collected off State of Rio Grande do Sul, at 32°58′S, 50°35′W, 99 m depth; and the second (MZUSP 86699) was named as *Caristius* sp., collected off State of São Paulo, at 26°19′49″S, 45° 57′00″W, 600 m depth. The authors, however, recognized the identification of both specimens was tentative due to the lack of updated taxonomic revisions available at that time. Based on the recent reexamination of the specimens reported by Caires et al. (2008), *C. macropus* and *Caristius* sp. are herein reidentified as *Platyberyx andriashevi* and *Platyberyx pietschi*, respectively, extending the known distribution of both species to off southern Brazil.

Carvalho-Filho et al. (2009) also reported another caristiid, named *Caristius* sp., in the stomach content of a tropical pomfret *Eumegistus brevorti* (Poey, 1860)

(Bramidae), caught off State of Bahia, northeast Brazil. Unfortunately, we did not have access to this material and some important characters that allow identification are not clear on the picture (Carvalho-Filho et al. 2009, figure 5) of the half-digested specimen. However, as all known species of *Caristius* have an anti-tropical distribution (Stevenson and Kenaley 2013), it is likely the caristiid reported by Carvalho-Filho et al. (2009) belongs to another genus.

Although we have consistently used two trawl nets (micronekton and mesopelagic), specimens reported herein were caught only with the micronekton net, which has a greater mesh size and seems to have a higher fishing efficiency for caristiids. This has also been found in many mesopelagic studies (e.g. Pakhomov and Yamamura 2010; Heino et al. 2011), where catch efficiency significantly differs among trawl types due to various influences from extrusion through meshes and net avoidance behaviour (Kaartvedt et al. 2012). Thus, we believe the diversity of Caristiidae species observed here is not only a consequence of biogeographic patterns of this group, but also reflects the selectivity of sample methods employed. Further, as most of the Brazilian deep waters remain unexplored the current knowledge on the diversity of Caristiidae occurring in the region is probably underestimated. Additional deep-water sampling over banks, continental slopes, seamounts, and near oceanic islands would likely uncover new information on species composition and distribution of the family Caristiidae.

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Disclosure Statement

No potential conflict of interest was reported by the authors.

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ORIGINAL ARTICLE

Deep-sea smelts, pencil smelts, and barreleyes (Teleostei: Argentiniformes) from oceanic islands and seamounts off northeastern Brazil

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ABSTRACT
New data on the taxonomic composition and distribution of rare deep-sea species of the Bathylagidae, Microstomatidae, and Opisthoproctidae (Argentiniformes) collected off northeastern Brazil, including the Rocas Atoll, the Fernando de Noronha Archipelago, and seamounts off Rio Grande do Norte State are provided. Collections were made by the French RV *Antea* during the ABRACOS 2 (Acoustics along the BRAzilian COaSt) expedition, between April 9 and May 6, 2017. Among the six species of argentiniforms identified, three are reported for the first time in Brazilian waters: *Xenophthalmichthys danae* (Microstomatidae), *Opisthoproctus soleatus* and *Rhynchohyalus natalensis* (Opisthoproctidae). Three additional species previously recorded off Brazil have their geographic distributions extended to the northeastern region of the country: *Dolicholagus longirostris*, *Melanolagus bericoides* (Bathylagidae), and *Winteria telescopa* (Opisthoproctidae). Remarks on other species of the Argentiniformes reported in the Brazilian Exclusive Economic Zone are also provided. A total of 11 genera and 14 species of the order are confirmed to occur in the region.

SUBJECT EDITOR
John Zardus

KEYWORDS
Mesopelagic fishes; seamounts; Rocas Atoll; Fernando de Noronha Archipelago; western Tropical Atlantic

Introduction

The Argentiniformes (Osmeromorpha) includes four families, 22 genera, and 97 species of the strictly marine fishes commonly known as argentines (Argentinidae), deep-sea smelts (Bathylagidae), pencilsmelts (Microstomatidae), and barreleyes (Opisthoproctidae) (Fricke et al. 2020). Fishes of the order are mainly characterized by a forked caudal fin, adipose fin usually present, small mouth, dorsal fin near the body center, maxillae and premaxillae (when present) toothless, supramaxillae absent, endopterygoid teeth absent, metapterygoid reduced, basibranchials 1–3 and pharyngobranchials 2 and 3 toothless (Nelson et al. 2016; Priede 2017). Some members of the Argentiniformes, such as *Bathylagus euryops*, are among the most abundant bathypelagic fishes of the North Atlantic Ocean (Sutton et al. 2008). The Argentiniformes is also crucial to understanding phylogenetic relationships in the Teleostei. The group was considered as sister to the Alepocephaloidei in an expanded Argentiniformes at the base of the Euteleostei (Greenwood and Rosen 1971; Johnson and Patterson 1996). Molecular data, however, indicate that the Argentiniformes is not related to the Alepocephaloidei, but its precise phylogenetic position in the Euteleostei is still a matter of debate (e.g. Wiley and Johnson 2010; Betancur-R. et al. 2017; Hughes et al. 2018). In spite of their ecological and phylogenetic relevance, several species of the Argentiniformes are known from just a few specimens deposited in fish collections, and key aspects of their taxonomy, distribution, biology and ecology remain largely unknown worldwide (Parin et al. 2009; Poulsen 2015; Poulsen et al. 2016).

In this study, we report the occurrence of six mostly rare species of the Argentiniformes collected off northeastern Brazil, including the Rocas Atoll, Fernando de Noronha Archipelago, and the seamounts off Rio Grande do Norte State (Fernando de Noronha Ridge). Three of these species are recorded for the first time in the Brazilian Exclusive Economic Zone (EEZ). Remarks on the species of the Argentiniformes previously reported off Brazil are also provided.

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Materials and methods

Specimens examined in this study are part of a large collection of mesopelagic invertebrates and fishes obtained during the ABRACOS 2 expedition (AB2 – Acoustics along the BRAzilian COaSt), carried out between April 8 and May 9, 2017 (Bertrand 2017). The expedition was conducted by the French RV *Antea* off northeastern Brazil, including the seamounts off Rio Grande do Norte State, the Rocas Atoll, and the Fernando de Noronha Archipelago, at depths ranging from the surface to 1113 m. Temperature (°C) and dissolved oxygen (ml/l) data were collected using a CTDO SeaBird911+. Biological sampling was conducted using a micronekton (body mesh: 40–80 mm, cod-end mesh: 10 mm) trawl net. Trawl depth was recorded continuously using a Scanmar depth sensor fitted on the upper part of the trawl mouth. An open mouth net was employed, but collection of specimens most likely occurred at pre-established target depths, which were defined for each trawl according to the presence of an acoustic scattered layer or patches detected with a Simrad EK60 split-beam scientific echo sounder. Target depth is therefore indicated as capture depth in the species accounts. Fixed specimens were measured for standard length (SL), the distance from the tip of the snout to the posterior end of the hypural plate. All specimens were identified according to Cohen (1964), Ahlstrom et al. (1984), and Carter and Hartel (2003), and subsequently deposited in the NPM – Fish Collection of the 'Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro' (Macaé, Brazil). Other institutional abbreviations follow Sabaj (2020).

Results

Dolicholagus longirostris **(Maul, 1948)**

(Figure 1a)

Specimens examined

NPM 4523, 1 specimen (98 mm), station #44A, off Fernando de Noronha Archipelago, 03°52′53″S, 32°17′33″W to 03°52′13″S, 32°16′28″W, 850 m depth, 4.5°C, 3.5 ml/l O_2, 28 April 2017, 12:44–13:17 h. NPM 4524, 1 (66 mm), #41A, off Fernando de Noronha Archipelago, 03°19′59″S, 32°24′42″W to 03°19′32″S, 32°25′05″W, 430 m depth, 9.0°C, 2.3 ml/l O_2, 26 April 2017, 21:44–22:06 h. NPM 4525, 2 (85–100 mm; Figure 1a), #52A, off Rocas Atoll, 03°43′16″S, 33°25′10″W to 03°42′14″S, 33°24′36″W, 822–984 m depth, 4.5–4.3°C, 3.5–3.7 ml/l O_2, 2 May 2017, 11:47–12:18 h. NPM 4526, 2 (41–65 mm), #42A, off Fernando de Noronha Archipelago, 03°15′28″S, 31°48′29″W to 03°15′28″S, 31°50′41″W, 780 m depth, 6.0°C, 3.0 ml/l O_2, 27 April 2017, 12:23–12:26 h. NPM 4527, 1 (81 mm), #53A, off Rocas Atoll, 03°48′59″S, 33°59′17″W to 03°50′06″S, 33°58′47″W, 610 m depth, 5.8°C, 3.1 ml/l O_2, 2 May 2017, 22:08–22:40 h. NPM 4528, 1 (96 mm), #54B, seamounts off Rio Grande do Norte State, 03°45′17″S, 34°41′04″W to 03°44′39″S, 34°40′05″W, 830–1030 m depth, 4.5–4.3°C, 3.6–3.7 ml/l O_2, 3 May 2017, 13:11–13:47 h.

Diagnostic features

Body slender (body depth 14.1–16.9% SL) and compressed; snout length 4.1–5.6% SL, equal to or greater than one-half eye length; upper margin of operculum extends over the center of the eye, ending in a sharp point; lower lobe of operculum truncate; dorsal-fin origin at the midpoint between the tip of snout and adipose-fin origin; anal-fin base much longer than caudal-peduncle length; pectoral fin low on the body; luminous organs absent; lateral line indistinct; vomer and palatine bearing about 35 conical teeth, dentary with numerous compressed teeth; body and head silver when fresh, absence of dark pigment on the margins of scale pockets (Maul 1948; Cohen 1964; Fujii 1983; McEachran and Fechhelm 1998). Fin rays: D 9–12; A 18–21; P 9–13; V 9–10; branchiostegal rays 2; gill-rakers 21–27; vertebrae 48–53 (Cohen 1964; Ahlstrom et al. 1984; Aizawa and Hatooka 2002; Sutton et al. 2020).

Distribution

Dolicholagus longirostris is a meso- to bathypelagic species with a wide distribution in the tropical and temperate waters of the Atlantic, Pacific and Indian Oceans (Cohen 1964, 1990b; Parin et al. 1974; Fujii 1983; McEachran and Fechhelm 1998; Paxton and Gohen 1999; Porteiro et al. 1999; Aizawa and Hatooka 2002; Carter and Hartel 2003; Moore et al. 2003, 2004; Byrkjedal et al. 2004; Mundy 2005; Evseenko et al. 2006; Shinohara et al. 2009; Kobyliansky et al. 2010; Ross et al. 2010; Sutton et al. 2010, 2020; Bachler 2011; Suntsov and Domokos 2013; Carneiro et al. 2019; Tatsuta et al. 2014; Kenaley and Hartel 2016; Porteiro et al. 2017). The species was previously reported in Brazilian waters based on specimens collected off Pará and São Pedro e São Paulo Archipelago (Judkins and Haedrich 2018) and larvae collected off the mouth of the Amazon river (Campos et al. 2007). Melo et al. (2020, p. 181) also indicated the occurrence of *D. longirostris* in the Brazilian EEZ, without reference

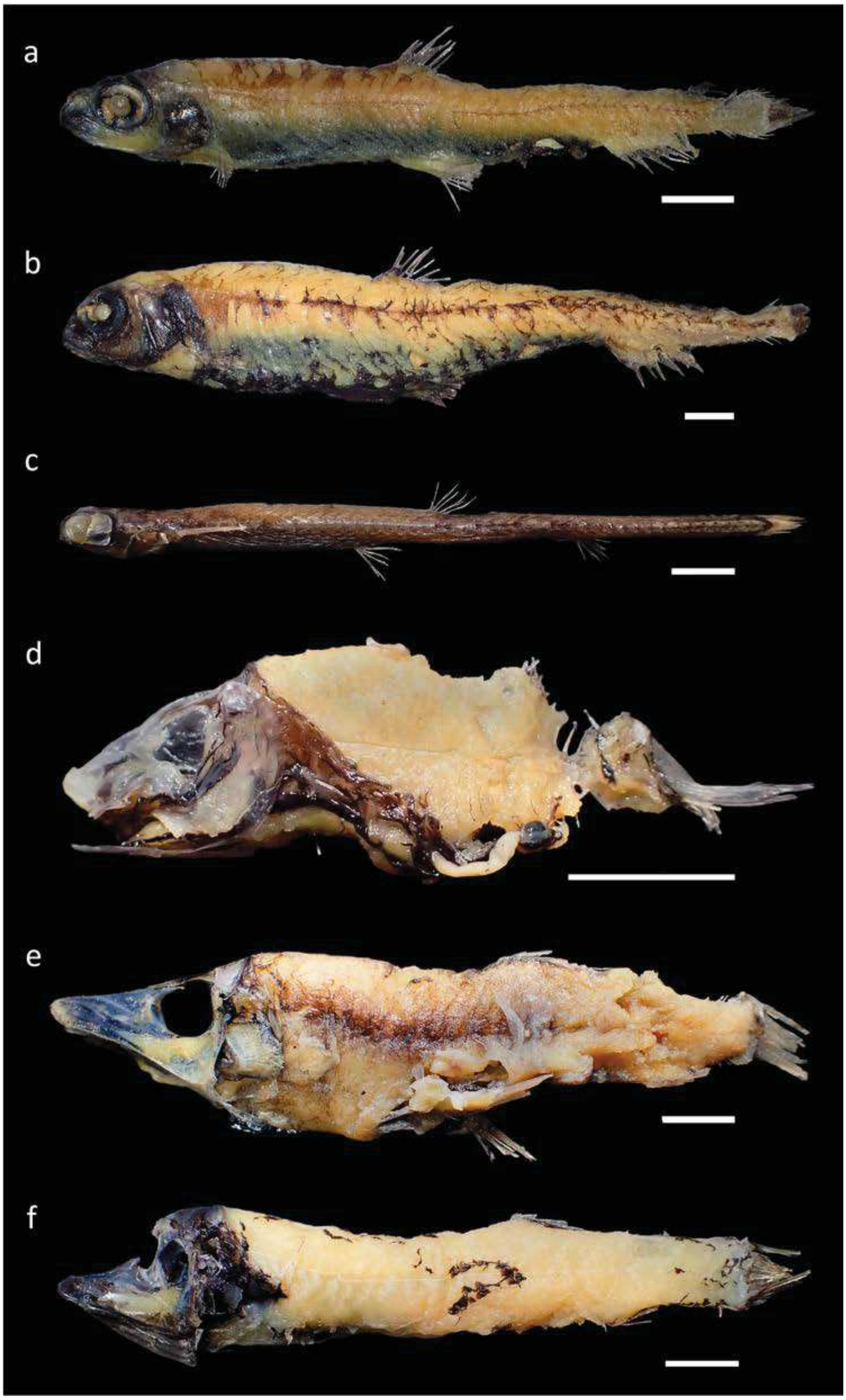

Figure 1. Species of Argentiniformes from oceanic islands and seamounts off northeastern Brazil: (a) *Dolicholagus longirostris*, NPM 4525, 100 mm SL; (b) *Melanolagus bericoides*, NPM 4522, 142 mm SL; (c) *Xenophthalmichthys danae*, NPM 4245, 114 mm SL; (d) *Opisthoproctus soleatus*, NPM 4466, 49 mm SL; (e) *Rhynchohyalus natalensis*, NPM 4221, 109 mm SL; (f) *Winteria telescopa*, NPM 4109, 104 mm SL. Scale = 1 cm.

to supporting literature or voucher specimens. In the current study, eight juvenile and adult specimens (41–100 mm SL) were recorded off the Rocas Atoll, Fernando de Noronha Archipelago, and near the seamounts off Rio Grande do Norte State, between depths of 430 and 1030 m (Figure 2).

Melanolagus bericoides (Borodin, 1929)
(Figure 1b)

Specimens examined

NPM 4520, 5 specimens (128–161 mm), station #54B, seamounts off Rio Grande do Norte, 03°45′17″S, 34° 41′04″W to 03°44′39″S, 34°40′05″W, 830–1030 m depth, 4.5–4.3°C, 3.6–3.7 ml/l O_2, 3 May 2017, 13:11–13:47 h. NPM 4521, 1 (167 mm), #41A, off Fernando de Noronha Archipelago, 03°19′59″S, 32°24′42″W to 03°19′32″S, 32°25′05″W, 430 m depth, 9.0°C, 2.3 ml/l O_2, 26 April 2017, 21:44–22:06 h. NPM 4522, 3 (134–156 mm; Figure 1b), #44A, off Fernando de Noronha Archipelago, 03°52′53″S, 32°17′33″W to 03°52′13″S, 32°16′28″W, 850 m depth, 4.5°C, 3.5 ml/l O_2, 28 April 2017, 12:44–13:17 h.

Diagnostic features

Body slender (body depth 14.8–16.6% SL) and compressed; very short snout (snout length 2.8–3.5% SL); eye diameter lees than 8.0% SL; upper margin of gill opening at or below the level of ventral margin of pupil; dorsal-fin origin ahead of midpoint of body; anal-fin base much longer than caudal-peduncle length; vomer and palatine bearing small, pointed teeth in single row, dentary with minute, compressed teeth; body dark brown or black, with dark pigment on the margins of scale pockets; light mandibular pores surrounded by dark pigment (Cohen 1964, 1986; McEachran and Fechhelm 1998; Sutton et al. 2020). Fin rays: D 9–11, A 19–21, P 9–12, V 9–11; branchiostegal rays 2; gill-rakers

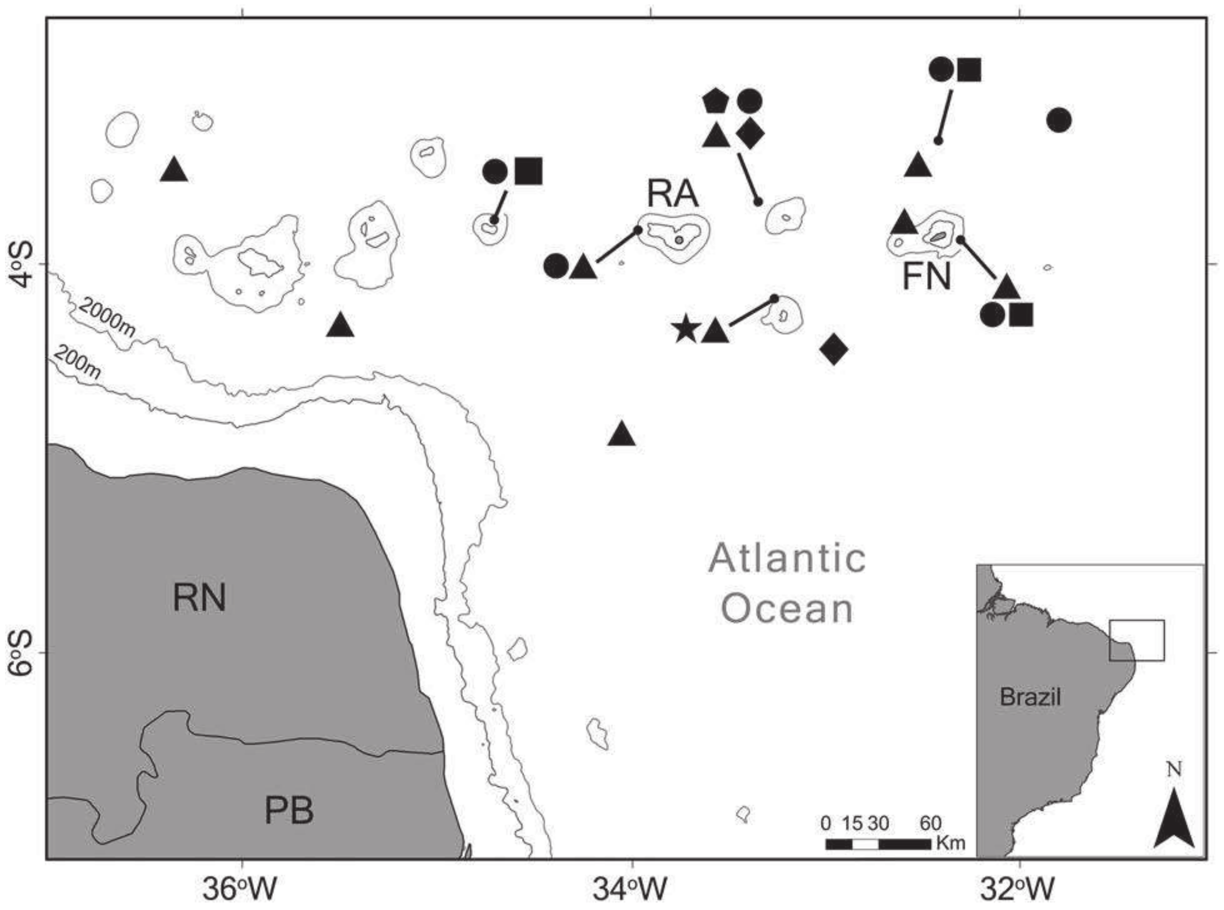

Figure 2. Records of Argentiniformes off northeastern Brazil based on specimens collected during the ABRACOS 2 expedition: *Dolicholagus longirostris* (circle), *Melanolagus bericoides* (square), *Xenophthalmichthys danae* (diamond), *Opisthoproctus soleatus* (pentagon), *Rhynchohyalus natalensis* (star), *Winteria telescopa* (triangle). The small circle at the end of the lines indicates the same trawl haul for different species. FN – Fernando de Noronha Archipelago; PB – Paraíba; RA – Rocas Atoll; RN – Rio Grande do Norte.

25–28; lateral line scale pockets 50–52; vertebrae 48–53 (Ahlstrom et al. 1984; Cohen 1986; Aizawa and Hatooka 2002; Gon and Stewart 2015).

Distribution

Melanolagus bericoides is a bathypelagic species with a circumglobal distribution in the tropical and temperate waters of the Atlantic and Indo-Pacific Oceans (Cohen 1964, 1986, 1990b; Fujii 1983; Uyeno 1984; Miya 1994; Amaoka 1995; Pequeño 1997; Santos et al. 1997; McEachran and Fechhelm 1998; Porteiro et al. 1999; Aizawa and Hatooka 2002; Carter and Hartel 2003; Moore et al. 2003, 2004; Mundy 2005; Shinohara et al. 2005; Gomon 2008; Shinohara 2009; Møller et al. 2010; Carneiro et al. 2019; Gon and Stewart 2015; Kenaley and Hartel 2016; Nión et al. 2016; Porteiro et al. 2017; Sutton et al. 2020). The species was previously reported in Brazilian waters based on specimens collected off Maranhão, São Pedro e São Paulo Archipelago, and Rio Grande do Sul (Figueiredo et al. 2002; Figueiredo and Santos 2003a; Judkins and Haedrich 2018). Melo et al. (2020, p. 181) also indicated the occurrence of *M. bericoides* in the Brazilian EEZ, without reference to supporting literature or voucher specimens. Occurrence of *M. bericoides* in the Brazilian EEZ is therefore extended based on nine specimens (128–167 mm SL) collected off Fernando de Noronha Archipelago and the seamounts off Rio Grande do Norte State, between depths of 430 and 1030 m (Figure 2).

Xenophthalmichthys danae **Regan, 1925**

(Figure 1c)

Specimens examined

NPM 4245, 1 specimen (114 mm; Figure 1c), station #48A, off Fernando de Noronha Archipelago, 04°25′05″S, 32°57′52″W to 04°25′25″S, 32°56′56″W, 505 m depth, 6.8°C, 3.0 ml/l O_2, 30 April 2017, 10:30–10:58 h. NPM 4246, 1 (60 mm SL), #52B, off Rocas Atoll, 03°41′56″S, 33°23′29″W to 03°42′34″S, 33°22′36″W, 385 m depth, 9.5°C, 2.4 ml/l O_2, 2 May 2017, 14:00–14:30 h.

Diagnostic features

Body extremely slender (body depth 6–11.5% SL), subcylindrical anteriorly and more compressed posteriorly; head with a gently descending profile in front of eyes; short, truncated snout (snout length 1.2–2.3% SL); mouth very small; eyes of adults tubular, anteriorly projecting over margin of the head, with sides covered by a silver tissue; anal-fin base much shorter than caudal-peduncle length; lateral line with wider and more adherent scales than rest of body; teeth present on dentary, vomer, and palatine (Cohen 1964; McEachran and Fechhelm 1998; Carter and Hartel 2003). Fin-rays: D 10–12, A 9–10, P 7, V 8–9; branchiostegal rays 3; vertebrae 48 (Gutherz 1964; Ahlstrom et al. 1984).

Distribution

Xenophthalmichthys danae is a rare, mesopelagic species reported from the tropical and temperate waters of the Atlantic, Indian, and Pacific Oceans (Cohen 1964, 1990a; Rass 1962; Gutherz 1964; Fourmanoir 1970; Clarke and Wagner 1976; Karrer 1976; Froese et al. 1996; McEachran and Fechhelm 1998; Paxton and Gohen 1999; Carter and Hartel 2003; Saavedra-Díaz et al. 2004; Mundy 2005; Kobyliansky et al. 2010; Hanel and John 2015; Hartel and Orrell 2016a; Sutton et al. 2020). The species was previously reported in the western North Atlantic, outside the Brazilian EEZ (Menezes 2003: MCZ 66258, 66259). *Xenophthalmichthys danae* is therefore confirmed for the first time in Brazilian waters based on two specimens (60–114 mm SL) collected between the Rocas Atoll and Fernando de Noronha Archipelago, at depths from 385 to 505 m (Figure 2).

Opisthoproctus soleatus **Vaillant, 1888**

(Figure 1d)

Specimen examined

NPM 4466, 1 specimen (49 mm; Figure 1d), station #52B, off Rocas Atoll, 03°41′56″S, 33°23′29″W to 03°42′34″S, 33°22′36″W, 385 m depth, 9.5°C, 2.4 ml/l O_2, 2 May 2017, 14:00–14:30 h.

Diagnostic features

Body compressed and short (body depth 35.7–40.2% SL); eyes tubular, directed upward; belly with a flattened, scaly, ventral sole from head to anus; sole length approximately 90% SL; snout slightly pointed, not protruding into a tube (10–15% SL); dorsal-fin base approximately 20% SL; anal fin rudimentary, often absent or not visible; bioluminescent bacteria present in a rectal bulb producing a pale blue light (Cohen 1964; Carter and Hartel 2003; Stewart 2015; Poulsen et al. 2016). Fin rays: D 10–13, A 0–3, P 12–14, V 9–10; branchiostegal rays 2; gill-rakers 12; vertebrae 31 (Cohen 1964; Ahlstrom et al. 1984; Heemstra 1986; Stewart 2015).

Distribution

Opisthoproctus soleatus is a mesopelagic species with a circumglobal distribution in the tropical and temperate waters of the Atlantic and Indo-Pacific Oceans (Cohen 1964; Backus et al. 1969; Fourmanoir 1970; Parin et al. 1974; Krefft 1976; Heemstra 1986; Quéro 1990; Rivaton et al. 1990; Santos et al. 1997; Vinnichenko 1997; Paxton and Gohen 1999; Randall and Lim 2000; Vakily et al. 2002; Carter and Hartel 2003; Moore et al. 2003; Byrkjedal et al. 2004; Mundy 2005; Kobyliansky et al. 2010; Fricke et al. 2011; Flynn and Pogonoski 2012; Hanel and John 2015; Stewart 2015; Hartel and Orrell 2016b; Porteiro et al. 2017; Carneiro et al. 2019). Melo et al. (2020) included *O. soleatus* in their list of species occurring in the Brazilian waters, but previous known records of the species in the western South Atlantic are actually outside Brazilian EEZ (Parin et al. 1974; Krefft 1976; Figueiredo and Santos 2003b). Therefore, *O. soleatus* is confirmed for the first time in the Brazilian EEZ based on a single specimen (49 mm SL) collected off Rocas Atoll, at 385 m depth (Figure 2).

Rhynchohyalus natalensis **(Gilchrist & von Bonde, 1924)**

(Figure 1e)

Specimen examined

NPM 4221, 1 specimen (109 mm; Figure 1e), station #49A, off Rocas Atoll, 04°10′38″S, 33°16′07″W to 04°10′58″S, 33°15′04″W, 770–1020 m depth, 4.8–4.3°C, 3.5–3.7 ml/l O_2, 30 April 2017, 21:17–21:52 h.

Diagnostic features

Body elongated; head translucent and elongated; snout length larger than eye length; eyes tubular, black, directed upward, and separated by a very narrow interorbital space; suborbital light organ present (visible on fresh specimens); mouth very small, terminal, and toothless; vomer with a band of teeth; pelvic fin large, its origin anterior to dorsal-fin origin; distance between verticals of pelvic and dorsal fin origins 6.4–11.3% SL; anal-fin origin posterior to dorsal-fin origin (Cohen 1964; Heemstra 1986; Stewart 2015; Prokofiev and Kukuev 2020). Fin rays: D 10–13, A 7–10, P 14–20, V 11–12; branchiostegal rays 4; gill-rakers 27–32; lateral line scales 39–41; vertebrae 40 (Cohen 1964; Ahlstrom et al. 1984; Heemstra 1986; Aizawa and Hatooka 2002; Stewart 2015; Prokofiev and Kukuev 2020).

Distribution

Rhynchohyalus natalensis is a rare, bathypelagic species known from the tropical and temperate waters of the Atlantic, off South Africa, central Indian Ocean, southeastern Australia, New Caledonia, New Zealand, Japan, and Hawaiian Islands (Cohen 1964; Backus et al. 1969; Clarke and Wagner 1976; Heemstra 1986; Quéro 1990; Rivaton et al. 1990; Vinnichenko 1997; Williams and Koslow 1997; Porteiro et al. 1999; Aizawa 2002; Carter and Hartel 2003; Mundy 2005; Hartel et al. 2008; Fricke et al. 2011; Flynn and Pogonoski 2012; Hanel and John 2015; Stewart 2015; Hartel and Orrell 2016b; Carneiro et al. 2019; Prokofiev and Kukuev 2020; Sutton et al. 2020). The species is reported for the first time in Brazilian waters based on a single specimen (109 mm SL) collected off the Rocas Atoll, at depths ranging from 770 to 1020 m (Figure 2).

Winteria telescopa **Brauer, 1901**

(Figure 1f)

Specimens examined

NPM 4109, 2 specimens (104–104 mm; Figure 1f), station #52A, off Rocas Atoll, 03°43′16″S, 33°25′10″W to 03°42′14″S, 33°24′36″W, 822–984 m depth, 4.5–4.3°C, 3.5–3.7 ml/l O_2, 2 May 2017, 11:47–12:18 h. NPM 4146, 2 (62–105 mm), #49A, off Rocas Atoll, 04°10′38″S, 33°16′07″W to 04°10′58″S, 33°15′04″W, 770–1020 m depth, 4.8–4.3°C, 3.5–3.7 ml/l O_2, 30 April 2017, 21:17–21:52 h. NPM 4147, 7 (80–109 mm), #50A, off Fernando de Noronha Archipelago, 03°49′01″S, 32°35′56″W to 03°47′33″S, 32°36′51″W, 615 m depth, 6.0°C, 3.0 ml/l O_2, 1 May 2017, 10:48–11:29 h. NPM 4301, 1 (83 mm), #35, seamounts off Rio Grande do Norte, 04°19′37″S, 35°29′52″W to 04°18′32″S, 35°32′20″W, 630 m depth, 5.9°C, 3.1 ml/l O_2, 20 April 2017, 22:35–23:15 h. NPM 4462, 11 (84–118 mm), #53A, off Rocas Atoll, 03°48′59″S, 33°59′17″W to 03°50′06″S, 33°58′47″W, 610 m depth, 5.8°C, 3.1 ml/l O_2, 2 May 2017, 22:08–22:40 h. NPM 4463, 1 (107 mm), #44A, off Fernando de Noronha Archipelago, 03°52′53″S, 32°17′33″W to 03°52′13″S, 32°16′28″W, 850 m depth, 4.5°C, 3.5 ml/l O_2, 28 April 2017, 12:44–13:17 h. NPM 4464, 2 (51–103 mm), #39, off Rio Grande do Norte State, 04°52′27″S, 34°35′23″W to 04°50′53″S, 34°51′05″W, 650–800 m depth, 5.6–4.8°C, 3.2–3.4 ml/l O_2, 24 April 2017, 21:49–22:37 h. NPM 4465, 1 (64 mm), #40A, off Fernando de Noronha Archipelago, 03°31′21″S, 32°31′40″W to 03°31′31″S, 32°30′41″W, 440 m depth, 8.6°C, 2.8 ml/l O_2, 26 April 2017, 10:43–11:06 h. NPM 5409, 3 (78–99 mm), #60B, seamounts off Rio Grande do Norte, 03°31′43″S, 36°21′20″W to 03°31′47″S, 36°22′26″W, 670–700 m depth, 5.5–5.3°C, 3.3–3.4 ml/l O_2, 6 May 2017, 12:49–13:19 h.

Diagnostic features

Body elongated, cylindrical, compressed at caudal peduncle; snout pointed and short, its length less than or equal to eye length; eyes tubular, directed forward, and separated by a very narrow interorbital space; suborbital light organ absent; mouth very small, terminal, and toothless; dorsal fin posterior to midpoint of body; pelvic-fin origin anterior to dorsal-fin origin; anal-fin origin posterior to dorsal-fin origin; small scale pockets on body marked with black edges (Heemstra 1986; Stewart 2015). Fin rays: D 8–9, A 7–9, P 12–14, V 7–10; branchiostegal rays 3; lateral line scales 34–38; vertebrae 33–36 (Heemstra 1986; Aizawa 2002; Stewart 2015).

Distribution

Winteria telescopa is a meso- to bathypelagic species known from the tropical and temperate waters of the Atlantic and Indo-Pacific Oceans (Haedrich and Craddock 1968; Clarke and Wagner 1976; Krefft 1976; Parin et al. 1976; Heemstra 1986; Quéro 1990; Williams and Koslow 1997; Paxton and Gohen 1999; Aizawa 2002; Vakily et al. 2002; Carter and Hartel 2003; Mundy 2005; Shinohara et al. 2009; Kobyliansky et al. 2010; Flynn and Pogonoski 2012; Kuriiwa et al. 2014; Tatsuta et al. 2014; Hanel and John 2015; Stewart 2015; Hartel and Orrell 2016b; Sutton et al. 2020). The species was previously reported in Brazilian waters based on a few specimens collected off São Pedro e São Paulo Archipelago (Haedrich and Craddock 1968; Krefft 1976; Parin et al. 1976; Judkins and Haedrich 2018; Melo et al. 2020; Sutton et al. 2020). The distribution of *W. telescopa* in the Brazilian EEZ is therefore extended based on 30 specimens (51–118 mm SL) collected off Rocas Atoll, Fernando de Noronha Archipelago, and the seamounts off Rio Grande do Norte State, between depths of 440 and 1020 m (Figure 2).

Discussion

Among more than 9,000 pelagic fishes collected during the ABRACOS expeditions, only 51 specimens were unquestionably identified as members of the Argentiniformes. Five species reported here are represented by just one to nine specimens, with *Opisthoproctus soleatus*, *Rhynchohyalus natalensis*, and *Xenophthalmichthys danae* regarded as rare on a global level. *Winteria telescopa*, in turn, is represented by more than half of the total number of specimens of Argentiniformes identified. This situation, where seemingly locally abundant deep-sea species are misrepresented in fish collections, most likely reflects the overall lack of studies on the deep-sea fauna of the western South Atlantic and Brazil, in particular, as recently discussed by many authors (e.g. Lima et al. 2011; Mincarone et al. 2014; Nielsen et al. 2015; Reis et al. 2016). In this context, studies on meso- and bathypelagic fishes collected during the ABRACOS expeditions, now published in a series of papers, are contributing to the understanding of the diversity and distribution of rare or poorly documented species (Eduardo et al. 2018, 2019a, 2019b, 2020a, 2020b, 2020c; Mincarone et al. 2019).

Other species recorded here for the first time in the Brazilian EEZ were supposed to occur in the region based on their presumably wide geographic distributions. That is the case of *Xenophthalmichthys danae*, which was previously included in a list of the Brazilian marine fishes based on specimens collected in international waters relatively distant from the Brazilian EEZ (Menezes 2003). The microstomatids *Microstoma microstoma* (Risso, 1810) and *Nansenia pelagica* Kawaguchi & Butler, 1984 were also reported by Menezes (2003) as occurring off Brazil, but as in the case of *X. danae*, records of those species are not in the Brazilian EEZ. The single record of *Nansenia atlantica* Blache & Rossignol, 1962 in Brazil, in turn, was based on a juvenile specimen (NPM 1843) collected off Rio de Janeiro State (Costa and Mincarone 2010). However, this specimen was examined by the authors and re-identified as *Chlorophthalmus agassizi* Bonaparte, 1840 (Aulopiformes: Chlorophthalmidae). *Nansenia atlantica* was also included in a recently published list of Brazilian deep-sea teleosts (Melo et al. 2020) likely based on this erroneous identification. Therefore, the only species of the Microstomatidae whose occurrence is confirmed to date in Brazil is *X. danae*.

The opisthoproctids *Opisthoproctus soleatus*, *Monacoa grimaldii* (Zugmayer, 1911) and *Dolichopteryx longipes* (Vaillant, 1888) were also previously included in lists of the Brazilian fauna based on their wide geographic distributions and occurrence in other portions of the western South Atlantic outside the Brazilian EEZ (Krefft 1976; Figueiredo and Santos 2003b; Poulsen et al. 2016; Melo et al. 2020). Among these species, only the occurrence of *Opisthoproctus soleatus* is so far confirmed in Brazilian waters, based on records presented here. Three further opisthoproctids were previously reported in the Brazilian EEZ: *Dolichopteryx rostrata* Fukui & Kitagawa, 2006 based on a single specimen (MCZ 66339) recorded off northwestern Rocas Atoll (Judkins and Haedrich 2018); and *Dolichopteroides binocularis* (Beebe, 1932) and *Dolichopteryx anascopa* Brauer, 1901, both based on specimens collected off Rio Grande do Sul State (Figueiredo et al. 2002). However, the single specimen identified by Figueiredo et al. (2002) as *D. anascopa* (MZUSP 78212,

Table I. Species of Argentifinormes reported in the Brazilian Exclusive Economic Zone.

Taxa	References
Argentinidae	
Argentina brasiliensis	Kobyliansky (2004), Bernardes et al. (2005), Melo et al. (2020)
Argentina georgei	Lins Oliveira et al. (2015), Melo et al. (2020)
Glossanodon polli	Cohen (1958, 1990a)
Glossanodon pygmaeus	Cohen (1958), Figueiredo and Menezes (1978), Andreata and Séret (1996), Figueiredo et al. (2002), Melo et al. (2020)
Bathylagidae	
Bathylagus gracilis	Judkins and Haedrich (2018)
Dolicholagus longirostris	Campos et al. (2007), Judkins and Haedrich (2018), Melo et al. (2020), this study
Melanolagus bericoides	Figueiredo et al. (2002), Figueiredo and Santos (2003a), Judkins and Haedrich (2018), Melo et al. (2020), this study
Microstomatidae	
Xenophthalmichthys danae	This study
Opisthoproctidae	
Dolichopteroides binocularis	Figueiredo et al. (2002, as *Dolichopteryx binocularis*), Parin et al. (2009), Melo et al. (2020, as *Dolichopteryx binocularis*)
Dolichopteryx rostrata	Judkins and Haedrich (2018)
Dolichopteryx sp.	Figueiredo et al. (2002, as *Dolichopteryx anascopa*)
Opisthoproctus soleatus	This study
Rhynchohyalus natalensis	This study
Winteria telescopa	Haedrich and Craddock (1968), Krefft (1976), Parin et al. (1976), Judkins and Haedrich (2018), this study

36 mm SL) most likely refers to another species. *Dolichopteryx anascopa* is currently known only from the holotype, collected near the Coco Island, Indian Ocean (ZMB 17428) and one additional specimen collected near the Suruga Seamount, west Mariana Ridge, western North Pacific (NSMT-P 95484) (Parin et al. 2009; Mizusawa et al. 2015). The total number of gill rakers reported for the these specimens (31–32) is much higher than the number reported by Figueiredo et al. (2002) for the specimen identified as *D. anascopa* (11–12). Actually, the number of gill rakers and other meristic data provided by Figueiredo et al. (2002) for that specimen are very similar to those described for *Dolichopteryx trunovi* Parin 2005, another rare species reported in temperate waters of the South Atlantic and South Pacific, between 35° and 53° S (Parin 2005; Parin et al. 2009; Prokofiev 2020).

Occurrence of the bathylagids *Dolicholagus longirostris* and *Melanolagus bericoides* in Brazilian waters is also confirmed. Another bathylagid recorded in the Brazilian EEZ, but not collected in this study, is *Bathylagus gracilis* Lönnberg, 1905, known from four specimens (MCZ 61905) collected off Rio Grande do Sul State, southern Brazil (34°43′S, 49°28′W) (Judkins and Haedrich 2018). The only family of the Argentiniformes not represented in the ABRACOS collection off northeastern Brazil is the Argentinidae. Four species of the family are reported for Brazil: *Argentina brasiliensis* Kobyliansky 2004, recently described for the southeastern and southern Brazil based on specimens formerly identified as *Argentina striata* Goode & Bean, 1896 (Carvalho 1950; Figueiredo and Menezes 1978; Kobyliansky 2004; Bernardes et al. 2005); *Argentina georgei* Cohen & Atsaides, 1969, from the western Central Atlantic and recently recorded off Rio Grande do Norte State (Lins Oliveira et al. 2015); *Glossanodon polli* Cohen 1958, from the eastern and western Tropical Atlantic, including a few records off the mouth of the Amazon river (Cohen 1958, 1990a); and *Glossanodon pygmaeus* Cohen 1958, known from the western Atlantic, including some records off northern, southeastern and southern Brazil (Cohen 1958; Figueiredo and Menezes 1978; Andreata and Séret 1996; Figueiredo et al. 2002). Summing up, the presence of four families, 11 genera, and 14 species of the Argentiniformes is confirmed in the Brazilian Exclusive Economic Zone (Table I).

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Deep-sea anglerfishes (Lophiiformes: Ceratioidei) from off northeastern Brazil, with remarks on the ceratioids reported from the Brazilian Exclusive Economic Zone

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The deep-sea anglerfishes of the suborder Ceratioidei (Lophiiformes) are represented by about 170 valid species with some of the most extraordinary morphological and reproductive adaptations among vertebrates, including extreme sexual dimorphism and male parasitism. Here we report on the diversity and distribution of rare ceratioids collected during the ABRACOS (Acoustics along the BRAzilian COaSt) expeditions off northeastern Brazil and the Fernando de Noronha Ridge (Rocas Atoll, Fernando de Noronha Archipelago, and associated seamounts). *Chaenophryne ramifera*, *Oneirodes anisacanthus*, *O. carlsbergi*, *Gigantactis watermani*, and unidentified specimens of *Caulophryne*, *Dolopichthys*, and *Rhynchactis* are recorded for the first time in the Brazilian Exclusive Economic Zone. *Ceratias uranoscopus*, *Melanocetus johnsonii*, and *Chaenophryne draco* have their distributions extended in Brazilian waters. *Caulophryne*, *O. anisacanthus*, and *G. watermani* are also recorded for the first time in the western South Atlantic. The specimen of *G. watermani* reported here represents the third known specimen of the species, and variations of its escal anatomy in relation to the holotype are described. Based on specimens examined and a review of records in the literature, 20 species of the Ceratioidei, in addition to unidentified species of *Caulophryne*, *Dolopichthys*, and *Rhynchactis*, are confirmed in the Brazilian Exclusive Economic Zone.

Keywords: Distribution, Fernando de Noronha Archipelago, Rocas Atoll, Seamounts, Taxonomy.

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Os peixes-pescadores de profundidade da subordem Ceratioidei (Lophiiformes) são representados por cerca de 170 espécies válidas que apresentam algumas das adaptações anatômicas e reprodutivas mais extraordinárias entre os vertebrados, incluindo extremo dimorfismo sexual e parasitismo masculino. No presente estudo reportamos sobre a diversidade e distribuição de espécies raras de Ceratioidei coletadas durante as expedições ABRACOS (*Acoustics along the BRAzilian COaSt*) realizadas ao largo do nordeste do Brasil e na Cadeia de Fernando de Noronha (Atol das Rocas, Arquipélago de Fernando de Noronha e montes submarinos associados). *Chaenophryne ramifera*, *Oneirodes anisacanthus*, *O. carlsbergi*, *Gigantactis watermani* e espécimes não identificados dos gêneros *Caulophryne*, *Dolopichthys* e *Rhynchactis* são registrados pela primeira vez na Zona Econômica Exclusiva brasileira. *Ceratias uranoscopus*, *Melanocetus johnsonii* e *Chaenophryne draco* tiveram suas distribuições estendidas em águas brasileiras. *Caulophryne*, *O. anisacanthus* e *G. watermani* também são registrados pela primeira vez no Atlântico Sul ocidental. O espécime de *G. watermani* reportado aqui representa o terceiro espécime conhecido da espécie, e variações anatômicas de sua esca em relação à do holótipo são descritas. Com base nos espécimes examinados e na revisão de registros na literatura, 20 espécies de Ceratioidei, além de espécies não identificadas de *Caulophryne*, *Dolopichthys*, and *Rhynchactis*, são confirmadas na Zona Econômica Exclusiva brasileira.

Palavras-chave: Arquipélago de Fernando de Noronha, Atol das Rocas, Distribuição, Montes submarinos, Taxonomia.

INTRODUCTION

The Ceratioidei (Lophiiformes) includes 11 families, 35 genera and about 170 valid species of fishes commonly known as deep-sea anglerfishes (Pietsch, Orr, 2007; Pietsch, 2009; Ho, Shao, 2019; Fricke *et al*., 2021). Adults and larvae of the group are remarkable in a number of features, including their anatomical diversity and extreme sexual dimorphism in which males are often obligatorily attached to females, with fusion of tissues and sharing of circulatory systems (Pietsch, 2009; Swann *et al*., 2020). Members of the Ceratioidei are also externally recognized by the absence of pelvic fins, scales usually absent (but prickles, spines or plates variably present), gill openings narrowly constricted and forming a tube-like structure that opens posteriorly, denticular bones present in dwarf males, usually 12–28 pectoral-fin rays, 8–9 caudal-fin rays, and females with an illicial apparatus usually tipped by a modified esca containing a globular, bacteria-filled photophore (Pietsch, 2009). Female ceratioids are also typically short and deep, with a nearly globular body in the Caulophrynidae, Melanocetidae, Himantolophidae, Diceratiidae, and Linophrynidae, or with a more elongate and somewhat laterally compressed body in the Centrophrynidae, Ceratiidae, Gigantactinidae, Neoceratiidae, Thaumatichthyidae, and some members of the Oneroididae (Pietsch, 2009).

Despite representing one of the most ubiquitous deep-sea groups of vertebrates in the meso- and bathypelagic zones, new species of deep-sea anglerfishes continue to be described, mostly from still poorly explored regions of the world (Ho, Shao, 2004; Stewart, Pietsch, 2010; Pietsch, Kenaley, 2011; Prokofiev, 2014a,b; Ho *et al*., 2016; Rajeeshkumar *et al*., 2017; Ho, Shao, 2019). With about 7,500 km of coastline in addition to some biogeographically relevant oceanic island complexes (Reis *et al*., 2016), the Brazilian Exclusive Economic Zone (EEZ) stands out in the western South Atlantic as one of such poorly known regions in terms of its deep-sea biota. Indeed, this area includes several Ecologically or Biologically Significant Marine Areas that encompass hotspots of biodiversity and endemism (CBD, 2014).

Part of the northeastern Brazilian coast and adjacent oceanic islands and seamounts were recently explored by the RV *Antea*, resulting in the collection of more than 9,000 specimens of mesopelagic fishes (Bertrand, 2015, 2017). Studies based on these collections have contributed significantly to the understanding of the deep-sea fauna of different groups in the region (Eduardo *et al*., 2018, 2019, 2020a,b; Mincarone *et al*., 2019, *in press*; Afonso *et al*., *in press*). This study, part of an ongoing effort to report on the still puzzling deep-sea fauna of the western South Atlantic, focus on the diversity of deep-sea anglerfishes collected off northeastern Brazil, including oceanic islands and seamounts. Remarks on the taxonomy and distribution of previous records of the Ceratioidei in the Brazilian EEZ are also presented.

MATERIAL AND METHODS

Specimens examined in this study are part of a large collection of mesopelagic invertebrates and fishes collected during the ABRACOS expeditions (Acoustics along the BRAzilian COaSt), carried out between 30 September and 20 October 2015 (ABRACOS 1 - AB1; Bertrand, 2015), and between 9 April and 6 May 2017 (ABRACOS 2 - AB2; Bertrand, 2017). Both expeditions were conducted onboard the French RV *Antea* off Rio Grande do Norte to Pernambuco States and along the Fernando de Noronha Ridge, formed by the Fernando de Noronha Archipelago, the Rocas Atoll, and the seamounts off Rio Grande do Norte and Ceará States (Jinno, Souza, 1999). The survey comprised 82 fishing stations, between the surface and 1,113 m depth. Sampling was conducted using micronekton (body mesh 40–80 mm, cod-end mesh 10 mm, height 24 m, width 24 m) and mesopelagic (body mesh 30 mm, cod-end mesh 4 mm, height 8.4 m, width 12.6 m) nets. Trawl depth was continuously recorded using a Scanmar depth sensor fitted on the upper part of the trawl mouth. An open-mouth net was employed, but collection of specimens most likely occurred at pre-established target depths, which were defined for each trawl according to the presence of an acoustic scattered layer or patches detected with a Simrad EK60 split-beam scientific echo sounder. At the target depths, trawling activity lasted for about 30 minutes. Target depth is therefore indicated as capture depth in the species accounts presented herein. Specimens were identified based on Pietsch (2009). Only female specimens were examined and, unless stated otherwise, distributional data refers to female specimens. All specimens collected were deposited in the Fish Collection of the Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro (NPM, Macaé, Brazil). Other institutional abbreviations follow Sabaj (2020).

RESULTS

CERATIIDAE

Females of the Ceratiidae are distinguished by having an elongate, laterally compressed body; mouth almost vertical to strongly oblique; 2 or 3 club-shaped caruncles (low fleshy appendages) on the dorsal midline just anterior to the soft dorsal fin; dorsal-fin rays 4 or (rarely) 5; 4 anal-fin rays; 15–19 pectoral-fin rays; caudal fin rounded, with 8 well-developed rays (the ninth or lower-most ray reduced to a small remnant in *Ceratias*); the pterygiophore of the illicium emerging anteriorly well behind the tip of the snout and posteriorly on the back, near the soft dorsal-fin origin; males obligatory sexual parasites as adults (Pietsch, 2009).

Ceratias Krøyer, 1845

Diagnosis. *Ceratias* differs from *Cryptopsaras*, the only other genus of the Ceratiidae, by 9 caudal-fin rays, the ninth or ventral-most ray reduced to a small remnant (*vs*. 8 caudal-fin rays), and by the absence of a spine on the anterodorsal margin of the subopercle (Bertelsen, 1951; Pietsch, 1986, 2009). Metamorphosed females of *Ceratias* are further differentiated from those of *Cryptopsaras* by having a long illicium, 19.0–28.2% SL (*vs*. illicium reduced to a small remnant, nearly fully enveloped by tissue of the esca), and by the number of club-shaped caruncles on the dorsal midline of the trunk just anterior to the origin of the soft dorsal fin (2 *vs*. 3) (Pietsch, 1986, 2009).

Ceratias uranoscopus Murray, 1877

(Figs. 1A, 2)

Diagnosis. Metamorphosed females of *Ceratias uranoscopus* differ from those of *C. holboelli* Krøyer, 1845 and *C. tentaculatus* (Norman, 1930), the other two known species of the genus, by the absence of distal escal appendages (*vs*. presence of a single distal escal appendages or a pair of distal escal appendages), and by the lack of vomerine teeth (*vs*. present or nearly always present) (Pietsch, 1986, 2009).

Geographical distribution. *Ceratias uranoscopus* is widely distributed in the Atlantic and Pacific. It is also known from the Indian Ocean based on three specimens collected off South Africa, India, and the Arabian Sea (Pietsch, 1986, 2009; Rajeeshkumar *et al*., 2016). In the Atlantic, it is reported from off Nova Scotia in the west to approximately 40°S off Cape Town in the east (Pietsch, 2009). The species was previously reported in Brazilian waters based on a specimen (129 mm SL) collected off southeastern Saint Peter and Saint Paul Archipelago (MCZ 42845, 0°03'N 27°31'W) (Pietsch, 1986; Menezes *et al*., 2003; Melo *et al*., 2020). In the present study, a single specimen is reported nearby Fernando de Noronha Archipelago, at 850 m depth (Fig. 2).

Remarks. Three additional small (31–51 mm SL) specimens of *Ceratias* (NPM 4974, NPM 4978, NPM 4979) were also collected during the ABRACOS expeditions, but identification was only possible to genus. They were collected around Rocas Atoll (610 m depth) and near the seamounts off Rio Grande do Norte State (670–700 m depth) (Fig. 2).

In addition to *Ceratias uranoscopus*, *C. holboelli* and *C. tentaculatus* were previously reported in the western South Atlantic (Sutton *et al*., 2008; Porteiro *et al*., 2017). *Ceratias holboelli* is widely distributed in the Atlantic and Indo-Pacific, with records in the Atlantic ranging between 68°N and 14°S. The species was recorded in Brazilian waters based on a single specimen collected off Ilhéus, Bahia State (MNRJ 30701, 14°36'36"S 38°49'21"W; Pietsch, 2009; Fig. 2). This specimen was previously identified as *C. uranoscopus* by Costa *et al*. (2007). Melo *et al*. (2020) also listed *C. uranoscopus* in Brazilian waters based on this misidentification. *Ceratias tentaculatus* is restricted to the Southern Hemisphere with two records in the western South Atlantic, one off northern Argentina (ISH 435/71, 38°20'S 54°33'W), and another off Rio Grande do Sul State, close to the Brazilian EEZ (ISH 1657/68, 35°16'S 49°26'W) (Pietsch, 1986). *Ceratias tentaculatus* has also been briefly mentioned as occurring off Uruguay (Nión *et al*., 2016).

Cryptopsaras couesii Gill, 1883 is known from the Atlantic, Indian and Pacific Oceans (Pietsch, 2009). The species was also reported in Brazilian waters based on specimens collected off Pará State (MCZ 147828, 01°24'N 45°24'W) and off Saint Peter and Saint Paul Archipelago (MCZ 45065, 00°58'S 27°34'W; MCZ 76502, 00°34'N 30°43'W) (Pietsch, 1986; Edwards, 1993; Menezes *et al*., 2003; Sutton *et al*., 2008; Pietsch, 2009; Porteiro *et al*., 2017; Melo *et al*., 2020; Fig. 2). Larvae of *C. couesii* have also been recently reported off Trindade Island (20°27'36"S 29°26'16"W; Stocco, Joyeux, 2015).

Material examined. NPM 5060, 1, 76 mm (Fig. 1A), RV *Antea*, sta. AB2/44A, 3°52'52.5"S 32°17'33.3"W to 3°52'13.4"S 32°16'28.0"W, 850 m, 28 Apr 2017, 12:44–13:17 h.

HIMANTOLOPHIDAE

Females of the Himantolophidae are distinguished by having a short, deep body, globular; lower jaw unusually blunt, extending anteriorly beyond the upper jaw; illicium thick and stout, esca unusually large and anatomically complex, the pterygiophore of the illicium fully embedded in the dermis of the head; low and rounded wart-like papilla covering the snout and chin; sphenotic spines well developed, spines absent on quadrate, articular, angular and preopercular bones; jaw teeth numerous and short, arranged in several close-set longitudinal series, vomer broad and toothless; skin of specimens larger than 30–40 mm SL, with large, widely spaced bony plates, each bearing a single median spine; 5–6 dorsal-fin rays, 4 anal-fin rays, 14–18 pectoral fin-rays, 9 caudal-fin rays; males free-living, apparently never parasitic on females (Bertelsen, Krefft, 1988; Pietsch, 2009).

Himantolophus Reinhardt, 1837

Diagnosis. *Himantolophus* is the only genus in the family. In addition to the diagnostic features of the Himantolophidae, females and males are distinguished by the absence of the parietal bone throughout life (*vs*. parietal present or lost during metamorphosis in females of the gigantactinid genus *Rhynchactis*), and by the presence of a triradiate pelvic bone (sometimes also present in the oneirodid genus *Chaenophryne*) (Pietsch, 2009).

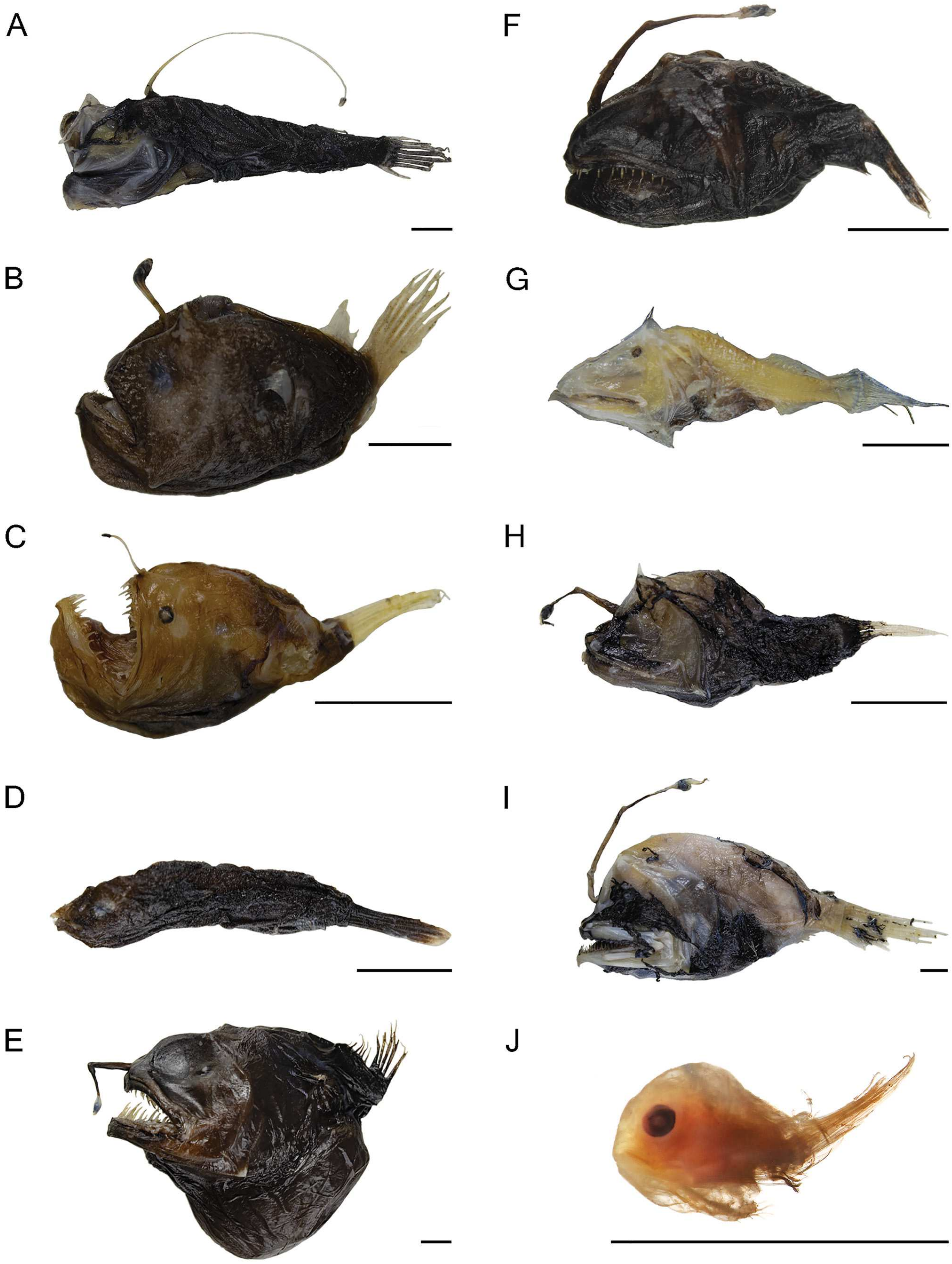

FIGURE 1 | Species of the Ceratioidei reported in this study: **A**. *Ceratias uranoscopus*, NPM 5050, 76 mm SL; **B**. *Himantolophus* sp., NPM 4959, 37 mm SL; **C**. *Melanocetus johnsonii*, NPM 4970, 19 mm SL; **D**. *Thaumatichthys* sp., NPM 4985, 32 mm SL; **E**. *Chaenophryne draco*, NPM 4954, 90 mm SL; **F**. *Chaenophryne ramifera*, NPM 4955, 32 mm SL; **G**. *Dolopichthys* sp., NPM 4980, 35 mm SL; **H**. *Oneirodes anisacanthus*, NPM 4977, 30 mm SL; **I**. *Oneirodes carlsbergi*, NPM 4953, 98 mm SL; **J**. *Caulophryne* sp., NPM 3835, 6 mm SL. Scale bars = 10 mm.

Himantolophus sp.

(Figs. 1B, 2)

Geographical distribution. A total of 13 larvae and juvenile specimens were collected off Rio Grande do Norte State, the Fernando de Noronha Archipelago, Rocas Atoll, and the seamounts off Rio Grande do Norte State, between 35 and 1,113 m (Fig. 2).

Remarks. Due to the immature nature of the specimens collected in this study, identification was possible only to genus. It is also possible that those specimens represent more than one species. *Himantolophus* currently includes 20 species distributed among five species groups, with representatives of all groups occurring in the Atlantic Ocean (Bertelsen, Krefft, 1988; Pietsch, 2009; Stewart, Pietsch, 2010; Pietsch, Kenaley, 2011; Fricke *et al*., 2021). Two species of *Himantolophus* were previously reported in Brazilian waters: *Himantolophus macroceras* Bertelsen & Krefft, 1988, known from five specimens reported from the central Atlantic, including one collected off Saint Peter and Saint Paul Archipelago (MCZ 58177, 0°10’N 27°30’W; Bertelsen, Krefft, 1988); and *Himantolophus groenlandicus* Reinhardt, 1837, widely distributed in the Atlantic, with one specimen reported off Saint Peter and Saint Paul Archipelago (MCZ 49841, 1°02’N 29°04’W; Bertelsen, Krefft, 1988; Fig. 2). A third species, *Himantolophus paucifilosus* Bertelsen & Krefft, 1988, might also occur off Brazil (Melo *et al*., 2020; see Discussion).

Material examined. NPM 3840, 1, 9.5 mm, RV *Antea*, sta. AB1/5, 4°05’23.9”S 32°10’49.0”W to 4°04’33.4”S 32°11’53.1”W, 85 m, 2 Oct 2015, 21:18–22:48 h; NPM 3841, 3, 8.5–13 mm, RV *Antea*, sta. AB1/12, 3°56’19.0”S 33°30’39.2”W to 3°56’35.8”S 33°32’00.3”W, 130 m, 5 Oct 2015, 21:24–21:54 h; NPM 4959, 1, 37 mm (Fig. 1B), RV *Antea*, sta. AB2/39, 4°52’26.9”S 34°35’22.9”W to 4°50’52.8”S 34°51’04.7”W, 650–800 m, 24 Apr 2017, 21:49–22:37 h; NPM 4961, 1, 24 mm, RV *Antea*, sta. AB2/42A, 3°15’28.1”S 31°48’29.1”W to 3°15’27.8”S 31°50’40.6”W, 780 m, 27 Apr 2017, 12:23–12:26 h; NPM 4964, 1, 21 mm, RV *Antea*, sta. AB2/44A, 3°52’52.5”S 32°17’33.3”W to 3°52’13.4”S 32°16’28.0”W, 850 m, 28 Apr 2017, 12:44–13:17 h; NPM 4968, 1, 24 mm, RV *Antea*, sta. AB2/49A, 4°10’38.1”S 33°16’07.4”W to 4°10’58.0”S 33°15’03.8”W, 770–1020 m, 30 Apr 2017, 21:17–21:52 h; NPM 4973, 1, 19 mm, RV *Antea*, sta. AB2/53A, 3°48’58.7”S 33°59’17.1”W to 3°50’05.8”S 33°58’46.5”W, 610 m, 2 May 2017, 22:08–22:40 h; NPM 4982, 1, 29 mm, RV *Antea*, sta. AB2/59A, 3°38’01.6”S 36°31’46.3”W to 3°38’36.1”S 36°17’49.7”W, 700–1113 m, 5 May 2017, 21:57–22:37 h; NPM 4984, 1, 30 mm, RV *Antea*, sta. AB2/59A, 3°38’01.6”S 36°31’46.3”W to 3°38’36.1”S 36°17’49.7”W, 700–1113 m, 5 May 2017, 21:57–22:37 h; NPM 5221, 1, 18 mm, RV *Antea*, sta. AB1/4, 3°54’29.9”S 32°20’24.8”W to 3°53’19.3”S 32°19’26.3”W, 90 m, 2 Oct 2015, 14:00–14:30 h; NPM 5223, 1, 50 mm, RV *Antea*, sta. AB1/23, 5°08’36.7”S 34°42’48.5”W to 5°08’02.8”S 34°44’40.4”W, 35–100 m, 9 Oct 2015, 10:35–11:20 h.

MELANOCETIDAE

Females of the Melanocetidae are distinguished by having a short, deep body, globular; mouth large, opening oblique to nearly vertical; numerous well-developed teeth on jaws; vomer usually well-toothed, with a single row of up to 12 teeth; head smooth and rounded, spines absent on the sphenotic, quadrate and articular bones; illicium emerging on snout, its supporting pterygiophore fully embedded in skin of head; body smooth, dermal spines or spinules absent; dorsal fin long, with 13–16 (rarely 12 or 17) rays, anal fin short, with 4 (rarely 3 or 5) rays, and 15–23 pectoral-fin rays; males may attach temporarily to females (Pietsch, 2009).

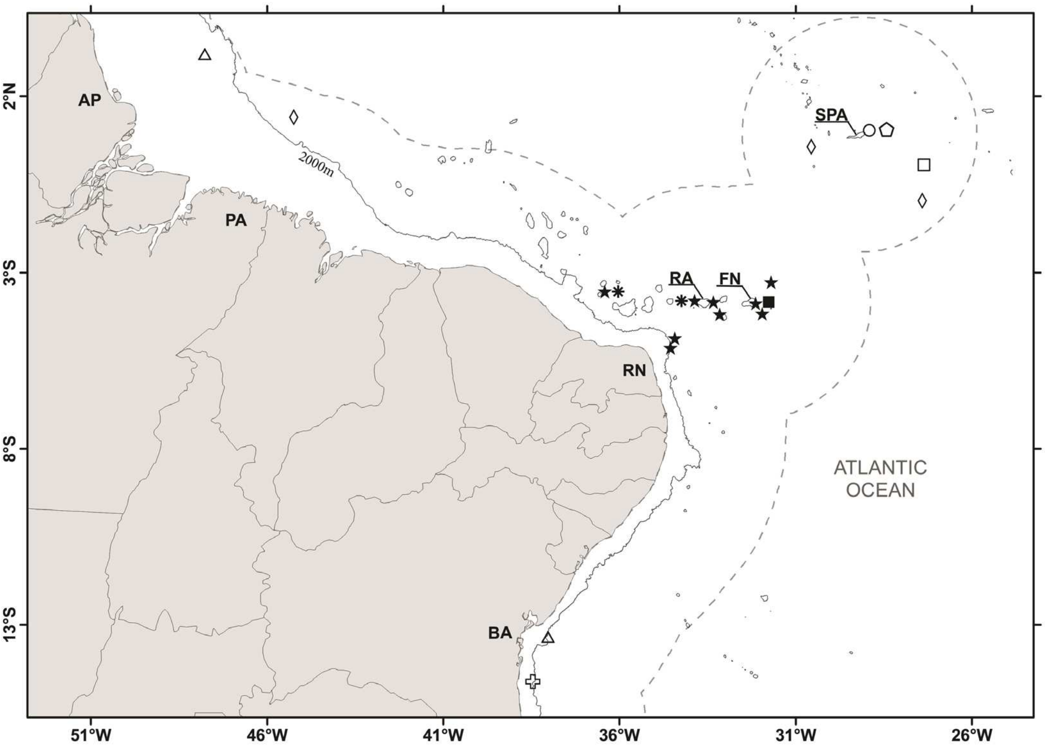

FIGURE 2 | Records of the Ceratiidae, Diceratiidae and Himantolophidae in Brazilian waters: *Ceratias uranoscopus* (square), *Ceratias holboelli* (cross), *Ceratias* sp. (asterisk), *Cryptopsaras couesii* (diamond), *Bufoceratias wedli* (triangle), *Himantolophus groenlandicus* (pentagon), *Himantolophus macroceras* (circle), *Himantolophus* sp. (star). Full symbols represent specimens collected during the ABRACOS surveys and open symbols are records from the literature (see text). Selected Brazilian States and islands are: AP – Amapá, PA – Pará, RN – Rio Grande do Norte, BA – Bahia; SPA – Saint Peter and Saint Paul Archipelago, FN – Fernando de Noronha Archipelago, RA – Rocas Atoll. Dashed line represents the outer limit of the Brazilian Exclusive Economic Zone.

Melanocetus Günther, 1864

Diagnosis. *Melanocetus* is the only genus in the Melanocetidae; diagnostic features are as those of the family (Pietsch, 2009).

Melanocetus johnsonii Günther, 1864

(Figs. 1C, 3)

Diagnosis. Metamorphosed females of *Melanocetus johnsonii* differ from congeners by the nearly straight anterior margin of the vomer; least outside width between frontals 13.5–28.6% SL; 48–134 teeth on upper jaw, 32–78 on lower jaw; length of longest tooth in lower jaw 8.4–25.0% SL; width of pectoral-fin lobe 10.7–17.8% SL; width of escal bulb 4.3–8.6% SL; length of illicium 32.4–60.8% SL; esca with posterior and usually anterior crests; skin with minute spinules over most of body; integument relatively thick (1.55 mm) (Pietsch, Van Duzer, 1980; Pietsch, 2009).

Geographical distribution. *Melanocetus johnsonii* occurs in the Atlantic, Pacific and Indian oceans. It was previously reported in Brazilian waters based on specimens collected off Saint Peter and Saint Paul Archipelago (MCZ 42849, 0°24'N 27°32'W; Pietsch, Van Duzer, 1980), Espírito Santo State (MNRJ 30702, 20°27'40"S 39°38'06"W; MNRJ 30703, 19°43'40"S 38°39'50"W; Pietsch, 2009), and Trindade Island (ISH 2352–1968, 21°04'S 30°08'W; Pietsch, Van Duzer, 1980; Menezes *et al*., 2003; Pietsch, 2009). The five specimens identified here were collected off Fernando de Noronha Archipelago and seamounts off Rio Grande do Norte State, between depths of 58 and 1,113 m (Fig. 3).

Remarks. Six additional juvenile (20–88 mm SL) specimens of *Melanocetus* collected in this study were only identified to genus (NPM 4956, NPM 4957, NPM 4967, NPM 4971, NPM 4976, NPM 4983). They were collected off Pernambuco State, Fernando de Noronha Archipelago, and near the seamounts off Rio Grande do Norte State, between depths of 680 and 1,113 m. *Melanocetus murrayi* Günther, 1887, with a circumglobal distribution, was recorded off Brazil, around Saint Peter and Saint Paul Archipelago (MCZ 42847, 1°20'30"S 27°37'30"W) and off northern Trindade Island (ISH 1180–1968, 17°33'S 28°13'W) (Pietsch, Van Duzer 1980; Menezes *et al*., 2003; Pietsch, 2009; Melo *et al*., 2020; Fig. 3).

Material examined. NPM 3837, 1, 10.5 mm, RV *Antea*, sta. AB1/7, 3°57'36.1"S 32°31'56.7"W to 3°56'48.1"S 32°31'05.3"W, 58 m, 3 Oct 2015, 19:22–19:52 h; NPM 3838, 1, 13.5 mm, RV *Antea*, sta. AB1/9, 3°28'15.4"S 32°45'31.5"W to 3°27'36.5"S 32°46'43.9"W, 105 m, 4 Oct 2015, 21:17–21:47 h; NPM 4970, 2, 14–19 mm (Fig. 1C), RV *Antea*, sta. AB2/52A, 3°43'16.2"S 33°25'09.8"W to 3°42'14.2"S 33°24'36.2"W, 822–984 m, 2 May 2017, 11:47–12:18 h; NPM 4981, 1, 17.5 mm, RV *Antea*, sta. AB2/59A, 3°38'01.6"S 36°31'46.3"W to 3°38'36.1"S 36°17'49.7"W, 700–1113 m, 5 May 2017, 21:57–22:37 h.

THAUMATICHTHYIDAE

Females of the Thaumatichthyidae are distinguished by having an elongate body; esca bearing 1–3 large toothlike denticles (bony hooks); upper jaw extending forward far beyond the lower jaw, premaxillae bearing numerous hooked teeth; upper arm of opercle divided into two or more branches; males and larvae of *Lasiognathus* are unknown, metamorphosed males of *Thaumatichthys* are unusually slender and elongate, apparently never parasitic on females (Pietsch, 2009).

Thaumatichthys sp.

(Figs. 1D, 3)

Diagnosis. Metamorphosed females of *Thaumatichthys* differ from those of *Lasiognathus*, the only other recognized genus of the family by having the body strongly depressed dorsoventrally (*vs*. body compressed laterally); a broad and also depressed head (*vs*. head narrow); pterygiophore of illicium short, completely hidden beneath skin of

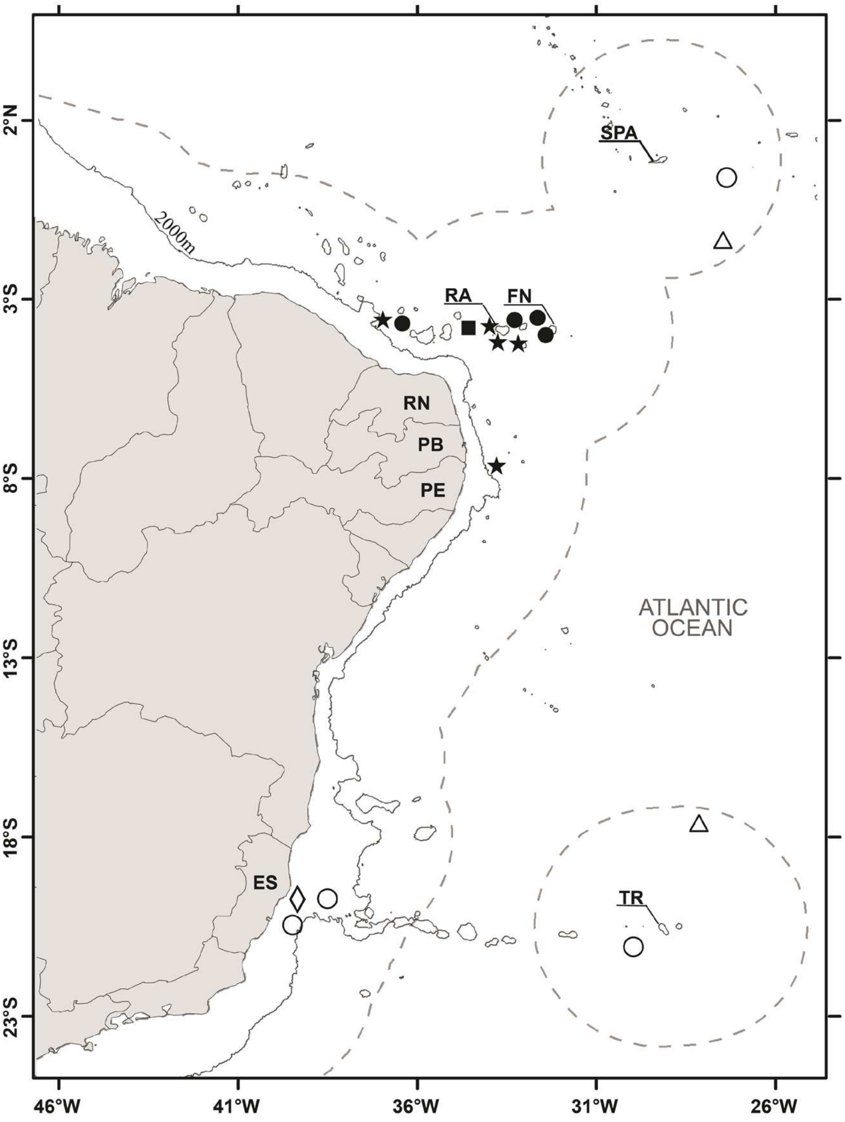

FIGURE 3 | Records of the Melanocetidae and Thaumatichthydae in Brazilian waters: *Melanocetus johnsonii* (circle), *Melanocetus murrayi* (triangle), *Melanocetus* sp. (star), *Thaumatichthys binghami* (diamond), *Thaumatichthys* sp. (square). Full symbols represent specimens collected during the ABRACOS surveys and open symbols are records from the literature (see text). Selected Brazilian States and islands are: Rio Grande do Norte, PB – Paraíba, PE – Pernambuco; ES – Espírito Santo; SPA – Saint Peter and Saint Paul Archipelago, FN – Fernando de Noronha Archipelago, RA – Rocas Atoll, TR – Trindade Island. Dashed line represents the outer limit of the Brazilian Exclusive Economic Zone.

head (*vs*. pterygiophore of illicium long, anterior tip emerging on snout from between frontal bones); illicium also short, embedded within the esca (*vs*. illicium long, greater than 35% SL); esca hanging from roof of mouth, bearing a single dermal denticle (*vs*. esca at the tip of illicium, with 2 or 3 large toothlike denticles); skin on ventral and lateral surfaces of head, body and tail covered with close-set dermal spinules (*vs*. skin naked, dermal spinules absent); 6 or 7 dorsal-fin rays (*vs*. 5), and 4 anal-fin rays (*vs*. 5) (Bertelsen, Struhsaker, 1977; Pietsch, 2009).

Geographical distribution. A single specimen collected at the seamounts off Rio Grande do Norte State, between depths of 830 and 1,030 m (Fig. 3).

Remarks. *Thaumatichthys* has three valid species, with only *Thaumatichthys binghami* Parr, 1927 reported from the western Atlantic, in the Bahamas, Gulf of Mexico, Caribbean Sea, and off Espírito Santo State, Brazil (MNRJ 30710, 19°45'S 39°30'W; Pietsch, 2009; Fig. 3). The single juvenile specimen recorded here could not be identified to species, but might be *T. binghami*.

Material examined. NPM 4985, 1, 32 mm (Fig. 1D), RV *Antea*, sta. AB2/54B, 3°45'17.2"S 34°41'04.0"W to 3°44'39.2"S 34°40'04.5"W, 830–1,030 m, mid-water trawl, 3 May 2017, 13:11–13:47 h.

ONEIRODIDAE

Females of the Oneirodidae are distinguished by having a short, deep to moderately elongate and laterally compressed body; mouth oblique to nearly horizontal, jaws equal anteriorly; illicium with a bulbous distal light organ; pterygiophore of the illicium usually emerging anteriorly on the snout, extending posteriorly on the back behind the head only in *Oneirodes*; top of head usually bearing sharp sphenotic spines, absent only in *Chaenophryne* and short in *Ctenochirichthys*; quadrate and articular spines usually well developed; skin smooth, dermal spines or spinules absent except in *Spiniphryne*; 4–8 dorsal-fin rays, 4–7 anal fin-rays, 13–30 pectoral-fin rays; a narrow, spatulate, anterodorsally directed process that overlaps the posterolateral surface of the respective sphenotic present in metamorphosed females; males usually free-living, non-parasitic, but two species apparently with facultative sexual parasitism (Pietsch, 2009).

In addition to the species reported below, three other oneirodids have been recorded in the Brazilian EEZ: *Microlophichthys microlophus* (Regan, 1925), collected off Saint Peter and Saint Paul Archipelago (MCZ 47566, 0°02'N 27°30'W to 0°03'N 27°31'W; MCZ 47567, 1°20'S 27°37'W; Pietsch, 2009); *Oneirodes notius* Pietsch, 1974, off Rio Grande do Sul State (MZUSP 78220, 31°04'S 49°15'W; Figueiredo *et al*., 2002); and *Pentherichthys atratus* (Regan & Trewavas, 1932), collected off Fernando de Noronha Archipelago (MCZ 42852, 5°42'S 32°25'W; Pietsch, 2009) and Saint Peter and Saint Paul Archipelago (MCZ 47569, 1°20'S 27°37'W; MCZ 97115, 4°3'12"N 29°37'36"W; Pietsch, 2009) (Fig. 4).

Chaenophryne Regan, 1925

Diagnosis. Metamorphosed females of *Chaenophryne* differ from other genera of the Oneirodidae by the presence of blunt protuberances on the dorsal surface of the head, sphenotic spines absent (*vs*. protuberances absent and sphenotic spines present), opercle only slightly concave posteriorly (*vs*. opercle deeply notched posteriorly), pelvic bones triradiate to broadly expanded distally (*vs*. pelvic bones rod shaped, with or without slight distal expansions), bones, especially those closely associated with the external surface of the head, highly cancellous (*vs*. not cancellous in other ceratioids), and illicium pterygiophore long, 70–82% SL (*vs*. less than 50% SL) (Pietsch, 1974, 1975, 2009).

Chaenophryne draco Beebe, 1932

(Figs. 1E, 4)

Diagnosis. Among the five valid species of *Chaenophryne*, *C. draco*, *C. longiceps* Regan, 1925 and *C. ramifera* Regan & Trewavas, 1932 are reported from the Atlantic Ocean (Pietsch, 1975, 2009). Females of *Chaenophryne draco* differ from all other congeners by the absence of anterolateral escal appendages (*vs*. esca with 1–3 anterolateral appendages on each side), and ratio of number of teeth in upper and lower jaws in specimens 20 mm or larger (1.08–1.45 *vs*. 0.76–1.30). The species is further distinguished from *C. longiceps* by having esca with an unpaired internally pigmented anterior appendage (*vs*. esca with a pair of internally pigmented anterior appendages); width of escal bulb 2.1–6.6% SL in specimens larger than 20 mm (*vs*. width of escal bulb 5.3–11.4% SL in specimens larger than 20 mm); pectoral-fin rays 16–19, rarely more than 18 (*vs*. 17–22, rarely less than 18). *Chaenophryne draco* also seems to differ from *C. ramifera* by a slightly shorter illicium (24.0–36.4% SL *vs*. 32.8–47.4% SL) and by fewer dorsal-fin rays (6–8 *vs*. 7–8) (Pietsch, 1975; Pietsch, 2007, 2009).

Geographical distribution. *Chaenophryne draco* is widespread in the Atlantic, Indian, and Pacific Oceans. In the Atlantic, it has been reported from Greenland to Cape Verde, with additional records from off Cape Town, South Africa, and off Espírito Santo State, Brazil (MNRJ 30707, 19°43’40”S 38°39’50”W; Pietsch, 1975, 2009; Sutton *et al*., 2008; Porteiro *et al*., 2017). The species reported here is based on two specimens collected off Pernambuco State and near the seamounts off Rio Grande do Norte State, between depths of 680 and 984 m (Fig. 4).

Material examined. NPM 4954, 1, 90 mm (Fig. 1E), RV *Antea*, sta. AB2/16, 7°36’15.0”S 33°59’30.0”W to 7°36’49.3”S 33°57’18.7”W, 680 m, 14 Apr 2017, 21:53–22:39 h; NPM 4969, 1, 55 mm, RV *Antea*, sta. AB2/52A, 3°43’16.2”S 33°25’09.8”W to 3°42’14.2”S 33°24’36.2”W, 822–984 m, 2 May 2017, 11:47–12:18 h.

Chaenophryne ramifera Regan & Trewavas, 1932

(Figs. 1F, 4)

Diagnosis. Females of *Chaenophryne ramifera* are distinguished from those of *C. longiceps* by having a single, elongate, internally pigmented, anterior escal appendage (*vs*. esca with a pair of internally pigmented, anterior appendages), medial escal appendages absent (*vs*. medial escal appendage or appendages present), width of escal bulb 4.5–6.5% SL in specimens 20 mm or larger (vs. 5.3–11.4% SL in specimens 20 mm or larger), pectoral-fin rays 16–19 (vs. 17–22, rarely less than 18); they are also distinguished from C. draco by having two or three filamentous, anterolateral escal appendages on each side (vs. esca without anterolateral appendages), and by the ratio between number of teeth in upper jaw to number of teeth in lower jaw 0.76–0.98 (vs. 1.08–1.45) (Pietsch, 1975, 2007, 2009).

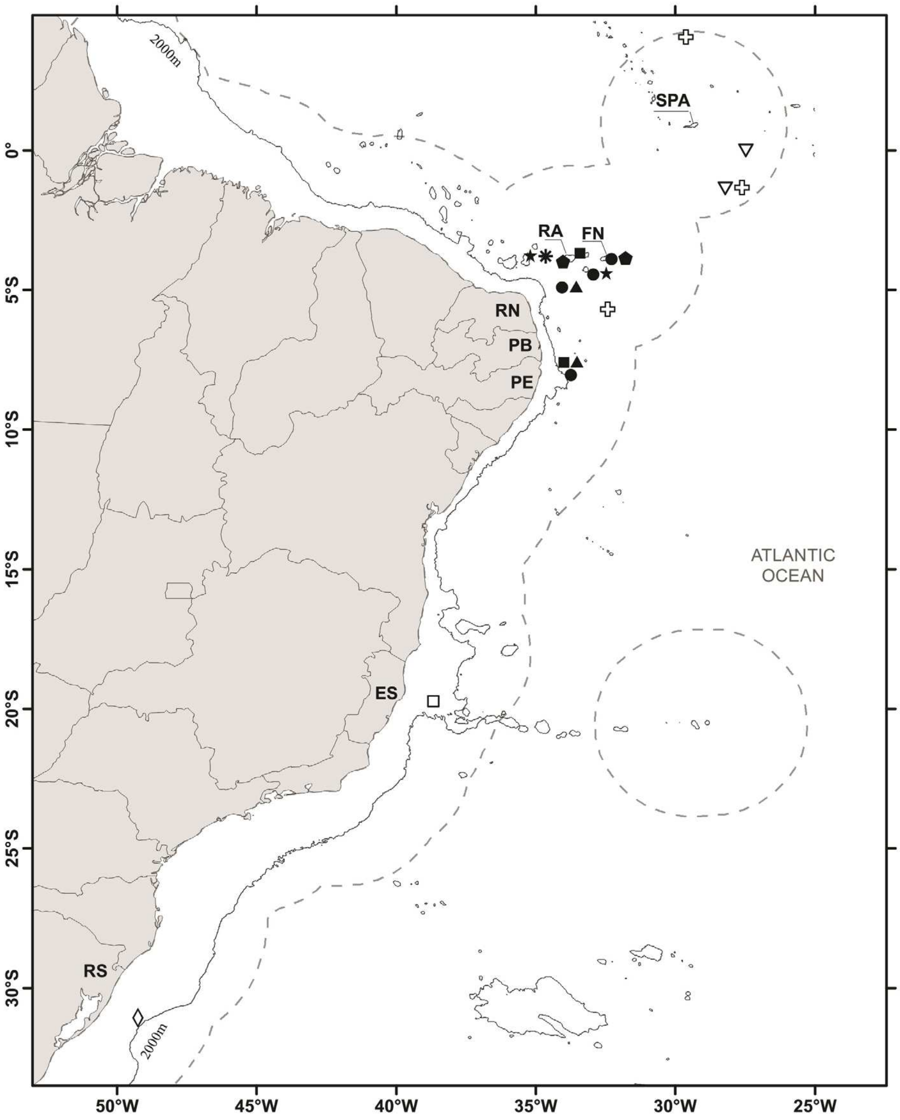

FIGURE 4 | Records of the Oneirodidae in Brazilian waters: *Chaenophryne draco* (square), *Chaenophryne ramifera* (circle), *Chaenophryne* sp. (pentagon), *Dolopichthys* sp. (asterisk), *Microlophichthys microlophus* (upside-down triangle), *Oneirodes anisacanthus* (star), *Oneirodes carlsbergi* (triangle), *Oneirodes notius* (diamond), *Pentherichthys atratus* (cross). Full symbols represent specimens collected during the ABRACOS surveys and open symbols are records from the literature (see text). Selected Brazilian States and islands are: Rio Grande do Norte, PB – Paraíba, PE – Pernambuco; ES – Espírito Santo, RS – Rio Grande do Sul; SPA – Saint Peter and Saint Paul Archipelago, FN – Fernando de Noronha Archipelago, RA – Rocas Atoll. Dashed line represents the outer limit of the Brazilian Exclusive Economic Zone.

Geographical distribution. *Chaenophryne ramifera* occurs in the Atlantic, Indian and Pacific Oceans. In the Atlantic, the species has been reported between 35°N off North Carolina and 12°S off Angola, with records near the Brazilian EEZ off Saint Peter and Saint Paul Archipelago (Pietsch, 1975, 2009). *Chaenophryne ramifera* is recorded for the first time in the Brazilian EEZ based on specimens collected off Fernando de Noronha Archipelago, Rocas Atoll, Rio Grande do Norte, and Pernambuco States, between depths of 505 and 850 m (Fig. 4).

Remarks. Two other specimens of *Chaenophryne* (NPM 4963, 28 mm SL; NPM 5219, 17 mm SL) could not be identified to species due to their extremely small sizes. They were collected from off Fernando de Noronha Archipelago and Rocas Atoll, between depths of 510 and 850 m (Fig. 4).

Material examined. NPM 4955, 1, 32 mm (Fig. 1F), RV *Antea*, sta. AB2/16, 7°36'15.0"S 33°59'30.0"W to 7°36'49.3"S 33°57'18.7"W, 680 m, 14 Apr 2017, 21:53–22:39 h; NPM 4958, 1, 40 mm, RV *Antea*, sta. AB2/39, 4°52'26.9"S 34°03'32.3"W to 4°50'52.8"S 34°05'06.5"W, 650–800 m, 24 Apr 2017, 21:49–22:37 h; NPM 5061, 1, 44 mm, RV *Antea*, sta. AB2/44A, 3°52'52.5"S 32°17'33.3"W to 3°52'13.4"S 32°16'28.0"W, 850 m, 28 Apr 2017, 12:44–13:17 h; NPM 5062, 1, 50 mm, RV *Antea*, sta. AB2/48A, 4°25'05.3"S 32°57'52.1"W to 4°25'24.9"S 32°56'55.5"W, 505 m, 30 Apr 2017, 10:30–10:58 h.

Dolopichthys Garman, 1899

Diagnosis. Females of *Dolopichthys* differ from those of *Chaenophryne* by the presence of sphenotic spines (*vs*. absence of sphenotic spines), opercle deeply notched posteriorly (*vs*. opercle not deeply notched posteriorly), pelvic bones rod shaped, with or without slight distal expansion (*vs*. pelvic bones triradiate or greatly expanded distally); from *Oneirodes*, *Tyrannophryne*, *Phyllorhinichthys*, *Microlophichthys*, and *Danaphryne* by having the dorsal margin of frontal bones nearly straight (*vs*. dorsal margin of frontal bones strongly convex) and subopercle long and narrow, ventral end strongly oval (*vs*. subopercle short and broad, ventral end nearly circular); from *Ctenochirichthys*, *Leptacanthichthys*, *Chirophryne* and *Puck* by the pectoral-fin lobe broad, shorter than the longest pectoral-fin rays (*vs*. pectoral-fin lobe narrow, longer than longest pectoral-fin rays); from *Bertella* by having the hyomandibula with a double head (*vs*. hyomandibula with a single head); from *Dermatias* by the depth of caudal peduncle less than 20% SL (*vs*. greater than 20% SL); from *Lophodolos* by the illicial apparatus emerging near the tip of snout, between the frontal bones (*vs*. illicial apparatus emerging from the dorsal surface of head, between or behind sphenotic spines); from *Pentherichthys* by having the lower jaw with a symphysial spine (*vs*. lower jaw without a symphysial spine, ventral margin of dentaries at symphysis concave), and caudal-fin rays without internal pigment (*vs*. caudal-fin rays internally pigmented); and from *Spiniphryne* by the skin naked or the presence of only minute, widely spaced dermal spinules, visible only with the aid of a microscope in cleared and stained specimens (*vs*. skin covered with close-set dermal spinules) (Pietsch, 2009).

Dolopichthys sp.

(Figs. 1G, 4)

Diagnosis. As for genus.

Geographical distribution. All seven valid species of *Dolopichthys* occurs in the Atlantic Ocean and two of them were reported from the western South Atlantic near the Brazilian EEZ: *Dolopichthys danae* Regan, 1926, and *D. pullatus* Regan & Trewavas, 1932 (Pietsch, 1972, 2009). The small specimen of *Dolopichthys* reported here and identified only to genus, however, represents the first record of the genus in Brazilian waters. The specimen was collected near the seamounts off Rio Grande do Norte State, between depths of 830 and 1,030 m (Fig. 4).

Material examined. NPM 4980, 1, 35 mm (Fig. 1G), RV *Antea*, sta. AB2/54B, 3°45’17.2”S 34°41’04.0”W to 3°44’39.2”S 34°40’04.5”W, 830–1,030 m, 3 May 2017, 13:11–13:47 h.

Oneirodes Lütken, 1871

Diagnosis. *Oneirodes* is the largest genus of the Ceratioidei, with 35 currently recognized species. Metamorphosed females of *Oneirodes* differ from those of all other genera of the Oneirodidae by having the posterior end of the pterygiophore of the illicium protruding from the dorsal midline of the trunk behind the head (*vs.* posterior end of the pterygiophore of the illicium not protruding from the dorsal midline of the trunk behind the head) (Pietsch, 2009).

Oneirodes anisacanthus Regan, 1925

(Figs. 1H, 4)

Diagnosis. Females of *Oneirodes anisacanthus* differ from those of its congeners, except *O. plagionema*, *O. kreffti*, *O. posti*, *O. rosenblatti*, *O. dicromischus*, *O. luetkeni*, *O. carlsbergi*, and those of the *O. schmidti* group, by the presence of a well-developed lateral escal appendage (*vs.* esca with lateral appendage minute or absent). *Oneirodes anisacanthus* differs from *O. plagionema* by the posterior escal appendage about one-third the length of escal bulb (*vs.* posterior escal appendage minute), anterior appendage anterodorsally directed, bearing numerous short filaments, and 2 unpigmented tapering filaments on anterior margin near the distal tip (*vs.* anterior appendage narrow, elongate, and anteroventrally directed, bearing a single short distal filament); from *O. kreffti* and *O. posti* by the esca without elongate medial appendages (*vs.* esca with 2 or 3 medial filaments more than twice the length of escal bulb); from *O. rosenblatti* and *O. dicromischus* by the lower jaw with fewer than 90 teeth in specimens greater than 45 mm, fewer than 60 teeth in specimens greater than 25 mm (*vs.* lower jaw with more than 90 teeth in specimens greater than 45 mm, more than 60 teeth in specimens greater than 25 mm), 3–9 (usually fewer than 8) teeth on vomer in specimens greater than 25 mm (*vs.* 8–14, usually more than 9 teeth); from *O. luetkeni* and *O. carlsbergi* by the presence of teeth on the epibranchial of the first gill arch (*vs.* epibranchial teeth absent); and from species of the *O. schmidti* group by the anterior escal appendage internally pigmented, anterolateral appendages absent (*vs.* anterior appendage without internal pigment, usually two pairs of filamentous anterolateral appendages) (Pietsch, 1974, 2009; Orr, 1991; Prokofiev, 2014a,b; Ho *et al.*, 2016; Rajeeshkumar *et al.*, 2017; Ho, Shao, 2019).

Geographical distribution. *Oneirodes anisacanthus* is widespread in the Atlantic Ocean, with records from off eastern Greenland, the Caribbean Sea, Madeira, Gulf of Guinea, and off Cape Town, South Africa (Pietsch, 1974, 2009). The two specimens collected around the Fernando de Noronha Archipelago and the seamounts off Rio Grande do Norte State, between depths of 505 and 1,030 m (Fig. 4), represent the first record of the species in Brazilian waters and in the western South Atlantic.

Material examined. NPM 4965, 1, 48 mm, RV *Antea*, sta. AB2/48A, 4°25’05.3”S 32°57’52.1”W to 4°25’24.9”S 32°56’55.5”W, 505 m, 30 Apr 2017, 10:30–10:58 h; NPM 4977, 1, 30 mm (Fig. 1H), RV *Antea*, sta. AB2/54B, 3°45’17.2”S 34°41’04.0”W to 3°44’39.2”S 34°40’04.5”W, 830–1,030 m, 3 May 2017, 13:11–13:47 h.

Oneirodes carlsbergi (Regan & Trewavas, 1932)

(Figs. 1I, 4)

Diagnosis. *Oneirodes carlsbergi* differs from its congeners, except *O. luetkeni*, by the presence of teeth on the epibranchial of the first gill arch (*vs*. teeth absent). It differs from *O. luetkeni*, reported only from the eastern Pacific, by the number of teeth on the epibranchial of the first gill arch (1–5 *vs*. 6–17), number of toothed pharyngobranchials (two pairs of tooth-bearing pharyngobranchials *vs*. a single pair of tooth-bearing pharyngobranchials), ratio of lengths of dorsal and ventral forks of opercle (0.51–0.61 *vs*. 0.60–0.71), and esca with a tapering and internally pigmented anterior appendage (*vs*. anterior appendage without internal pigment, anterolateral appendage represented by a broad membranous flap) (Pietsch, 1974, 2009; Orr, 1991; Prokofiev, 2014a,b; Ho *et al*., 2016; Rajeeshkumar *et al*., 2017; Ho, Shao, 2019).

Geographical distribution. *Oneirodes carlsbergi* seems to have a circumtropical distribution between approximately 18°N and 8°S (Pietsch, 2009; Ho *et al*., 2016; Ho, Shao, 2019). One specimen recorded far from this presumably circumtropical range was collected off the Irish Atlantic slope (Pietsch, 2009). Other records in the Atlantic Ocean range from 17°49’N to 5°34’S, and include two records near the Brazilian EEZ (ISH 660/66, 5°34’S 26°58’W; ISH 924/68, 3°00’S 26°16’W) (Pietsch, 1974, 2009). In the present study *O. carlsbergi* is reported for the first time in Brazilian waters based on two specimens collected off Pernambuco State and Rocas Atoll, between depths of 650 and 800 m (Fig. 4).

Material examined. NPM 4953, 1, 98 mm (Fig. 1I), RV *Antea*, sta. AB2/16, 7°36’15.0”S 33°59’30.0”W to 7°36’49.3”S 33°57’18.7”W, 680 m, 14 Apr 2017, 21:53–22:39 h; NPM 4960, 1, 18.5 mm, RV *Antea*, sta. AB2/39, 4°52’26.9”S 34°03’32.3”W to 4°50’52.8”S 34°05’06.5”W, 650–800 m, 24 Apr 2017, 21:49–22:37 h.

CAULOPHRYNIDAE

Females of the Caulophrynidae are distinguished by having a short, deep body, more or less globular; mouth large, lower jaw usually extending posteriorly beyond the base of the pectoral-fin lobe; jaw teeth unusually large; epibranchial and ceratobranchial teeth absent; illicium without a bulbous bacteria-filled light organ, the pterygiophore of the illicium fully embedded beneath skin of head; skin smooth and naked, spines or dermal denticles absent; lateral-line structures unusually well-developed, sense organs at the tips of cutaneous papillae; dorsal- and anal-fin rays apparently free, not interconnected by membrane, and usually longer than 60% SL; and 8 caudal-fin rays. Larvae of the Caulophrynidae are also distinguished in the Ceratioidei by the presence of pelvic fins, which are absent at all stages in other families of the suborder. Males are probably facultative parasites on females (Pietsch, 2009).

Caulophryne Goode & Bean, 1896

Diagnosis. Metamorphosed females of *Caulophryne* can be distinguished from those of *Robia*, the only other genus of the family (known from a single, 41 mm SL female collected in the western Central Pacific), by having a considerably shorter illicium (less than 130 mm *vs*. about 270 mm) and by a larger number of dorsal- and anal-fin rays (14–22 dorsal-fin rays, the longest ray > 70% SL *vs*. 6 dorsal-fin rays, the longest ray < 65% SL; 12–19 anal-fin rays, the longest ray > 60% SL *vs*. 5 anal-fin rays, the longest ray < 40% SL) (Pietsch, 2009).

Caulophryne sp.

(Figs. 1J, 5)

Diagnosis. Same as for genus.

Geographical distribution. Species of *Caulophryne* have been reported from the Atlantic, Indian and Pacific Oceans between approximately 65°N and 50°S (Pietsch, 2009). Three of the four currently recognized species of the genus are known from the Atlantic Ocean: *Caulophryne jordani* Goode & Bean, 1896, known from the North Atlantic up to about 5°N; *Caulophryne pelagica* (Brauer, 1902), recorded in the Atlantic at a single locality off Cape Verde Islands; and *Caulophryne polynema* Regan, 1930, recorded in the North and South Atlantic to 28°S off Africa, with no records in the western South Atlantic (Pietsch, 1979, 2009). The extremely small specimen of *Caulophryne* sp. reported here was collected off Rio Grande do Norte State, between depths of 35 and 100 m, and represents the first record of the genus in Brazilian waters and in the western South Atlantic (Fig. 5).

Material examined. NPM 3835, 1, 6 mm SL (Fig. 1J), RV *Antea*, sta. AB1/23, 5°08'36.7"S 34°42'48.5"W to 5°08'02.8"S 34°44'40.4"W, 35–100 m, 9 Oct 2015, 10:35–11:20 h.

GIGANTACTINIDAE

Females of the Gigantactinidae are distinguished by having an elongate, laterally compressed body; a long slender illicium, with highly variable lengths (less than SL to

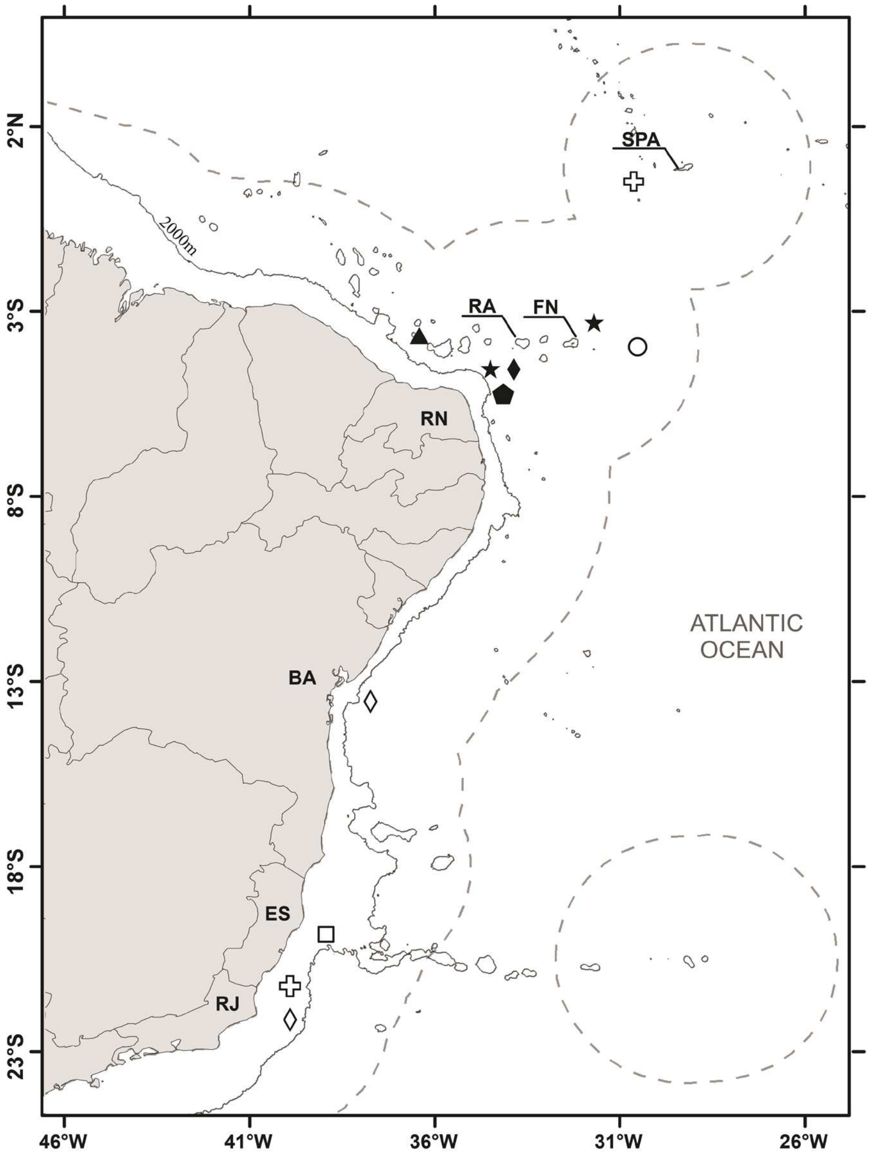

FIGURE 5 | Records of the Caulophrynidae, Gigantactinidae, and Linophrynidae in Brazilian waters: *Caulophryne* sp. (pentagon), *Gigantactis longicirra* (square), *Gigantactis vanhoeffeni* (cross), *Gigantactis watermani* (triangle), *Gigantactis* sp. (diamond), *Rhynchactis* sp. (star), *Linophryne arborifera* (circle). Full symbols represent specimens collected during the ABRACOS surveys and open symbols are records from the literature (see text). Selected Brazilian States and oceanic islands are Rio Grande do Norte, BA – Bahia, ES – Espírito Santo, RJ – Rio de Janeiro; SPA – Saint Peter and Saint Paul Archipelago, FN – Fernando de Noronha Archipelago, RA – Rocas Atoll. Dashed line represents the outer limit of the Brazilian Exclusive Economic Zone.

nearly five times SL) emerging from the anteriormost tip of the snout; length of head less than 35% SL; mouth nearly horizontal, upper jaw extending slightly beyond lower jaw; epibranchial and ceratobranchial teeth absent; caudal peduncle unusually long and slender, more than 20% SL; 3–10 dorsal-fin rays, 3–8 anal-fin rays; caudal fin usually incised posteriorly, 9 caudal-fin rays, usually highly elongate. Males are probably free living, never parasitic (Pietsch, 2009).

In addition to the species recorded here, two species of the family have been previously reported in Brazilian waters: *Gigantactis longicirra* Waterman, 1939 and *G. vanhoeffeni* Brauer, 1902. *Gigantactis longicirra* is known from the Atlantic and Pacific oceans. In the Atlantic, it occurs in the Gulf of Saint Lawrence, Canada, south along the New England slope to the Gulf of Mexico, Caribbean Sea, off Venezuela, and in the Gulf of Guinea. A single specimen was also collected off Espírito Santo State, Brazil (MNRJ 30700, 19°48'29"S 39°02'21"W; Pietsch, 2009). *Gigantactis vanhoeffeni* is known from the Atlantic, Indian and Pacific Oceans, with records in the Atlantic ranging from off western Greenland to the South Atlantic, including the Gulf of Mexico, Caribbean Sea, Cape Verde Islands, Gulf of Guinea, and off South Africa (Bertelsen *et al*., 1981; Sutton *et al*., 2008; Pietsch, 2009; Porteiro *et al*., 2017). In Brazil, *G. vanhoeffeni* was recorded based on specimens collected off Saint Peter and Saint Paul Archipelago (MCZ 61049, 0°34'N 30°43'W) and off Espírito Santo State (MNRJ 30708, 21°12'18"S 40°00'53"W; Costa *et al*., 2007; Pietsch, 2009; Mincarone *et al*., 2017; Melo *et al*., 2020: 188, as "*verhoeffeni*") (Fig. 5).

Two additional records of *Gigantactis* sp. in Brazilian waters are also known, one consisting of a female collected off Bahia State (MNRJ 30699, 13°30'28"S 38°38'59"W; Costa *et al*., 2007), and a female larva, collected off Rio de Janeiro State (DZUFRJ 1286, 22°06'52.3"S 39°48'46.2"W; Bonecker *et al*., 2014) (Fig. 5).

Gigantactis Brauer, 1902

Diagnosis. Metamorphosed females of *Gigantactis* are distinguished from those of *Rhynchactis*, the other genus of the family, by the absence of pelvic bones and by having 5–9 dorsal-fin rays (rarely 4–10) and 4–7 anal-fin rays (rarely 8) (*vs*. 3–4 dorsal-fin rays, rarely 5, and 3–4 anal-fin rays). They further differ from those of *Rhynchactis* by the following characters: frontal and parietal bones present (*vs*. absent), premaxilla well developed, with teeth present throughout their length (*vs*. premaxilla represented by a remnant bearing 0–2 teeth), maxilla reduced to threadlike remnants (*vs*. maxillae absent), dentary with several rows of strong recurved teeth (*vs*. dentary toothless or with only minute teeth), a single hypohyal (*vs*. two hypohyals), all caudal-fin rays unbranched (*vs*. 9 caudal-fins rays, 2 simple + 4 branched + 3 simple), skin spinulose (*vs*. skin covered with minute spinules in larger specimens, but juveniles naked), snout produced in front of mouth, illicium originating at its tip (*vs*. snout truncated, illicium origin slightly behind its tip), and esca consisting of an expanded luminous bulb (*vs*. absence of bulbous, terminal, escal light organs) (Bertelsen *et al*., 1981; Pietsch, 2009).

Gigantactis watermani Bertelsen, Pietsch & Lavenberg, 1981

(Figs. 5, 6A, 7)

Diagnosis. Twenty species of *Gigantactis* are recognized (two of doubtful validity: *G. ovifer* Regan & Trewavas, 1932 and *G. filibulbosus* Fraser-Brunner, 1935), of which 14 are reported for the Atlantic. *Gigantactis watermani* differs from *G. elsmani*, *G. kreffti*, and *G. perlatus* by the length of the illicium (130–490% SL, rarely less than 200%, *vs*. 60–120% SL); from *G. golovani*, *G. macronema*, and *G. gargantua* (North Pacific and eastern South Indian ocean) by the escal filaments (distal escal filaments simple, without posterior filaments on or below its base *vs*. esca with distal filaments branched, several filaments emerging from and below its base); it further differs from *G. gargantua* by the pigmentation of distal escal filaments (heavily pigmented for more than one-half their length *vs*. lightly pigmented for less than one-fifth their length) and position of proximal escal filaments (restricted to the anterior margin of the escal bulb *vs*. not restricted to the anterior margin of escal bulb); from *G. ios*, *G. longicauda*, *G. macronema*, *G. microdontis* (eastern Pacific), and *G. savagei* (eastern North Pacific) by the presence of a group of anterior filaments arising from the base of esca (*vs*. absence), escal bulb structure (distal part of escal bulb bearing four or five pairs of stout filaments along posterior margin *vs*. filaments of distal part of escal bulb different from above), and length of caudal-fin rays (second and seventh greater than 50% SL *vs*. longest caudal-fin rays less than 40% SL); from *G. herwigi* by the number of filaments at esca base (10 *vs*. less than 10), number of pair of filaments on the distal part of escal bulb (four or five, each with a pigmented swollen base *vs*. four, each gradually tapering and only faintly pigmented at base); from *G. longicirra* by the number and length of the dorsal-fin rays (4–7, all about equal in length *vs*. 8–10, the first and last distinctly longer than intermediate rays) and length of the first and eighth caudal-fin rays (less than 40% *vs*. 60–100% SL); and from *G. gibbsi*, *G. gracilicauda*, *G. meadi*, *G. vanhoeffeni*, and *G. paxtoni* (western South Indian Ocean and western South Pacific), by the absence of a darkly pigmented, spinulose distal prolongation in the esca (*vs*. presence of dark pigment) (Pietsch, 2009).

FIGURE 6 | Species of the Gigantactidae reported in this study: **A**. *Gigantactis watermani*, NPM 4424, 170 mm SL; **B**. *Rhynchactis* sp., NPM 4425, 113 mm SL. Scale bars = 10 mm.

Geographical distribution. Only two metamorphosed females of *Gigantactis watermani* were previously known, one from the eastern Tropical Atlantic (ISH 2330/71, 1°04’N 18°22’W) and another from the western Tropical Pacific, off New Caledonia (Pietsch, 2009). The specimen collected off seamounts of Rio Grande do Norte State, between depths of 700 and 1,113 m, represents the third known female specimen of the species and the first record in the South Atlantic (Fig. 5).

Remarks. Morphological and meristic data of the specimen agree with the description provided by Bertelsen *et al.* (1981) for the holotype, but some slightly differences were noted in its escal anatomy. The esca is bilaterally asymmetric, with four stout, tapering filaments present on the left side and five filaments present on the right side. The base of the most proximal filament of the right side is, however, reduced, with the structure mostly represented by the swollen, dark pigmented proximal part and a tiny unpigmented narrow tip (Fig. 7). In addition, the left filament of the most distal pair of filaments is secondarily branched, resulting in three filaments for this pair. In the holotype, the filaments of the most distal pair have a single branch. Bertelsen *et al.* (1981) also indicated the presence of 12 narrow unpigmented filaments on the anterior margin base of the escal bulb, but 14 filaments are present in the specimen examined (Fig. 7), a number that is within the range noted by Pietsch (2009: 467) for the species.

One additional small-sized specimen (NPM 3836, 6 mm SL) of *Gigantactis* collected off Rio Grande do Norte State, between depths of 35 and 100 m, was identified only to genus (Fig. 5).

Material examined. NPM 4424, 1, 170 mm (Fig. 6A), RV *Antea*, sta. AB2/59A, 3°38’01.6”S 36°31’46.3”W to 3°38’36.1”S 36°17’49.7”W, 700–1,113 m, 5 May 2017, 21:57–22:37 h.

Rhynchactis Regan, 1925

Diagnosis. See “Diagnosis” of *Gigantactis.*

Rhynchactis sp.

(Figs. 5, 6B)

Geographical distribution. Two specimens were collected off Rio Grande do Norte State and Fernando de Noronha Archipelago between depths of 650 and 800 m (Fig. 5). As discussed below, they could not be identified to species, but represent the first record of the genus in Brazilian waters.

Remarks. Of the three valid species of *Rhynchactis*, two occur in the Atlantic: *Rhynchactis leptonema* Regan, 1925 and *Rhynchactis macrothrix* Bertelsen & Pietsch, 1998 (Pietsch, 2009). Both species are poorly represented in collections and their geographic distributions are poorly known (Pietsch, 2009). *Rhynchactis leptonema* has been collected in a few localities of the Atlantic and Pacific (off Hawaii and Taiwan). In the Atlantic, it is known from the holotype collected in the western Tropical Atlantic (ZMUC P92133,

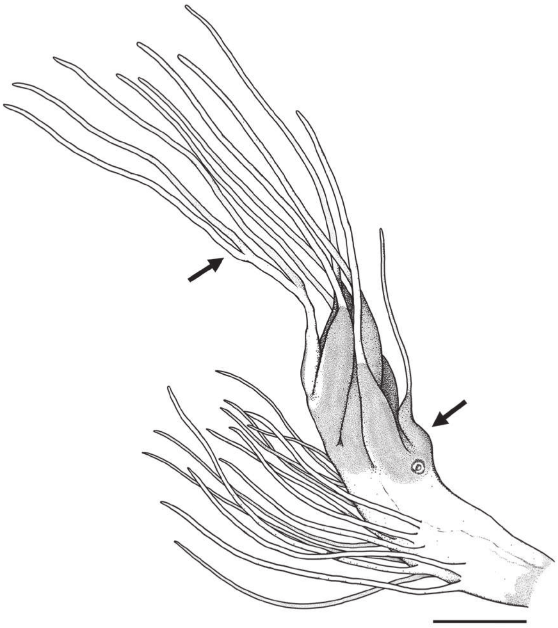

FIGURE 7 | Esca of *Gigantactis watermani*, NPM 4424, in left ventrolateral view. Arrows indicate the secondary branching of the left filament of the most distal pair of filaments (upper left) and the reduced base of the most proximal filament of the right side (lower right). Scale bar = 5 mm.

8°19’N 44°35’W). *Rhynchactis macrothrix* is also known from widely spread localities in the Atlantic and the western Indian and western Pacific Oceans. In the Atlantic, it is known from three specimens: the holotype collected in central equatorial waters (ISH 605/74, 7°55’N 32°41’W), and two specimens collected off Bermuda and in the Gulf of Mexico (Bertelsen, Pietsch, 1998; Pietsch, 2009).

The larger specimen reported here (NPM 4425, 113 mm SL; Fig. 6B) is in overall good condition but while it retains the full length of the illicium, the skin of the structure has been lost. The illicium length (208% SL) clearly indicates that it is not *R. leptonema* (maximum 177% SL; Bertelsen *et al*., 1981), being more similar in that respect to *R. microthrix* (210% SL; Bertelsen, Pietsch, 1998). The smaller specimen (NPM 5014) is an unidentified juvenile.

Material examined. NPM 4425, 1, 113 mm (Fig. 6B), RV *Antea*, sta. AB2/42A, 3°15’28.1”S 31°48’29.1”W to 3°15’27.8”S 31°50’40.6”W, 780 m, 27 Apr 2017, 12:23–12:26 h; NPM 5014, 1, 42 mm, RV *Antea*, sta. AB2/39, 4°52’26.9”S 34°35’22.9”W to 4°50’52.8”S 34°51’04.7”W, 650–800 m, 24 Apr 2017, 21:49–22:37 h.

DISCUSSION

Nine of the 11 families of the Ceratioidei are confirmed in Brazilian waters, with four species (*Chaenophryne ramifera*, *Gigantactis watermani*, *Oneirodes anisacanthus*, and *O. carlsbergi*) and three genera (*Caulophryne*, *Dolopichthys*, and *Rhynchactis*) reported here for the first time. Three other species (*Ceratias uranoscopus*, *Chaenophryne draco*, and *Melanocetus johnsonii*) have their distributions extended in the Brazilian Exclusive Economic Zone.

Species of other ceratioid families previously recorded in Brazilian waters but not collected in the ABRACOS expeditions are *Bufoceratias wedli* (Pietschmann, 1926) (Diceratiidae), and *Linophryne arborifera* Regan, 1925 (Linophrynidae). *Bufoceratias wedli* is widely distributed along the eastern and western coasts of the Atlantic Ocean. It was listed by Asano Filho *et al*. (2005) among other fishes trawled off Amapá State, without reporting voucher specimens. Based on that report, Klautau *et al*. (2020) recently included the species in their inventory of the deep-sea teleosts of the Brazilian north coast. Three additional specimens of *Bufoceratias wedli* were subsequently reported off Salvador, Bahia State (MNRJ 30705, 13°19'57"S 38°19'39"W; MNRJ 30706, 13°21'50"S 38°16'41"W; MNRJ 30709, 13°17'35"S 38°17'36"W; Costa *et al*., 2007; Pietsch, 2009). *Linophryne arborifera* was reported in Brazilian waters based on a specimen collected off eastern Fernando de Noronha Archipelago (MCZ 44171, 3°55'S 30°38'W; Bertelsen, 1980). Melo *et al*. (2020: 188) also included *Himantolophus paucifilosus* (Himantolophidae) and *Neoceratias spinifer* Pappenheim, 1914 (Neoceratiidae) in their list of the deep-sea fishes off Brazil. The record of *H. paucifilosus* was based on paratypes and other specimens collected in international waters off northern South America in the vicinities of the Brazilian EEZ (ZMH 138226, 1°N 26°W; ZMH 138231, 2°N 35°W; ISH 640–1974, 2°30'N 34°52'W; Pietsch, 2009). That is also the case for *Neoceratias spinifer*, known from only two records in the South Atlantic, one near the Brazilian EEZ (MCZ 51292, 10°20'31"N 30°32'31"W; Pietsch, 2009). Both species therefore probably occur in Brazilian waters, but have not yet been recorded in the country's EEZ.

Summing up, a total of 23 species of the Ceratioidei, across 15 genera and nine families, occur in the Brazilian Exclusive Economic Zone (Tab. 1). Most of those species were reported along the northeastern coast and off oceanic islands. Given that most of the Brazilian coast has not been sufficiently explored in terms of its deep-sea fauna, these numbers are certainly an underestimate, reinforcing the need for more deep-water surveys in the Brazilian EEZ and in the western South Atlantic overall. Exploring deeper waters and trawling for longer distances will certainly result in an increase in the number of deep-water fishes known from the region.

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TABLE 1 | Confirmed records of the Ceratioidei in the Brazilian Exclusive Economic Zone. Asterisk indicates records based on larval and/or small juvenile specimens only.

Species	Distribution	References
Ceratiidae		
Ceratias holboelli Krøyer, 1845	Circumglobal	Pietsch (2009); Melo *et al.* (2020)
Ceratias uranoscopus Murray, 1877	Circumglobal	Pietsch (1986); Menezes *et al.* (2003); Melo *et al.* (2020); this study
Cryptopsaras couesii Gill, 1883	Circumglobal	Pietsch (1986); Menezes *et al.* (2003); Melo *et al.* (2020)
Himantolophidae		
Himantolophus groenlandicus Reinhardt, 1837	Atlantic and probably Indian and Pacific oceans	Bertelsen, Krefft (1988); Melo *et al.* (2020)
Himantolophus macroceras Bertelsen & Krefft, 1988	Atlantic Ocean	Bertelsen, Krefft (1988); Melo *et al.* (2020)
Diceratiidae		
Bufoceratias wedli (Pietschmann, 1926)	Atlantic Ocean and off Sumatra	Asano Filho *et al.* (2005); Costa *et al.* (2007); Pietsch (2009); Klautau *et al.* (2020); Melo *et al.* (2020)
Melanocetidae		
Melanocetus johnsonii Günther, 1864	Circumglobal	Pietsch, Van Duzer (1980); Pietsch (2009); Menezes *et al.* (2003); Melo *et al.* (2020); this study
Melanocetus murrayi Günther, 1887	Circumglobal	Pietsch, Van Duzer (1980); Menezes *et al.* (2003); Melo *et al.* (2020)
Thaumatichthyidae		
Thaumatichthys binghami Parr, 1927	Atlantic	Pietsch (2009); Melo *et al.* (2020)
Oneirodidae		
Chaenophryne draco Beebe, 1932	Circumglobal	Pietsch (2009); Melo *et al.* (2020); this study
Chaenophryne ramifera Regan & Trewavas, 1932	Circumglobal	This study
Dolopichthys sp.*	Off northeastern Brazil	This study
Microlophichthys microlophus (Regan, 1925)	Circumglobal	Pietsch (2009); Melo *et al.* (2020)
Oneirodes anisacanthus Regan, 1925	Atlantic	This study
Oneirodes carlsbergi (Regan & Trewavas, 1932)	Circumglobal	This study
Oneirodes notius Pietsch, 1974	Circumglobal in Southern Hemisphere	Figueiredo *et al.* (2002); Menezes *et al.* (2003); Melo *et al.* (2020)
Pentherichthys atratus (Regan & Trewavas, 1932)	Circumglobal	Pietsch (2009); Melo *et al.* (2020)
Caulophrynidae		
Caulophryne sp.*	Off northeastern Brazil	This study
Gigantactinidae		
Gigantactis longicirra Waterman, 1939	Atlantic and Pacific	Pietsch (2009); Melo *et al.* (2020)
Gigantactis vanhoeffeni Brauer, 1902	Circumglobal	Costa *et al.* (2007); Pietsch (2009); Mincarone *et al.* (2017); Melo *et al.* (2020)
Gigantactis watermani Bertelsen, Pietsch & Lavenberg, 1981	Atlantic and Pacific	This study
Rhynchactis sp.	Off northeastern Brazil	This study
Linophrynidae		
Linophryne arborifera Regan, 1925	Atlantic	Bertelsen (1980)

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ETHICAL STATEMENT

The authors state that all methods were approved and conducted in accordance with guidelines and 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 the Ordinances 178 (08/09/2015) and 4 (24/01/2017).

COMPETING INTERESTS

The authors declare no competing interests.

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Taxonomy and Distribution of Deep-Sea Bigscales and Whalefishes (Teleostei: Stephanoberycoidei) Collected off Northeastern Brazil, Including Seamounts and Oceanic Islands

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Despite the increasing number of studies on the systematics of the Stephanoberycoidei (bigscales, pricklefishes, gibberfishes, hispidoberycids, and whalefishes) globally, knowledge about the diversity and distribution of the group in the western South Atlantic still remains fragmentary. In this study, we present new anatomical (meristic and morphometric) and distributional data for 18 species of the Stephanoberycoidei based on the examination of 150 specimens recently collected during the ABRACOS (Acoustics along the BRAzilian COaSt) expeditions off northeastern Brazil, including the Rocas Atoll, Fernando de Noronha Archipelago, and the seamounts off Rio Grande do Norte State, and additional museum specimens. In the Melamphaidae, remarks on the taxonomy of *Melamphaes polylepis* and of the *Poromitra crassiceps* and *P. megalops* species groups are made based on specimens examined. In addition, *Scopeloberyx opercularis*, currently considered as a junior synonym of *Scopeloberyx robustus*, is recognized as a valid species. Among the species identified, nine have their distributions extended in the western South Atlantic based on confirmed records: *Melamphaes polylepis*, *M. typhlops*, *Poromitra megalops*, *Poromitra* sp., *Scopeloberyx opercularis*, *Scopeloberyx opisthopterus*, *Scopelogadus mizolepis*, *Cetostoma regani*, and *Rondeletia loricata*. Eight further species are reported for the first time in Brazilian waters: *Cetomimus* sp. 1, *Cetomimus* sp. 2, *Ditropichthys storeri*, *Gyrinomimus bruuni*, *Melamphaes eulepis*, *M. leprus*, *M. longivelis*, and *Melamphaes* sp. Additional remarks on the taxonomy and distribution of the Stephanoberycoidei in the western South Atlantic are also provided.

THE Stephanoberycoidei comprises 23 genera and about 94 species of mostly meso- and bathypelagic teleosts commonly known as bigscales, pricklefishes, gibberfishes, hispidoberycids, and whalefishes (Nelson et al., 2016; Fricke et al., 2020a). Fishes of this suborder usually have a short to moderately long and somewhat compressed body, the subocular shelf and orbitosphenoid are absent, basibranchial tooth plates are also absent, with the exception of the copular tooth plate in the Cetomimidae, ossification is reduced to thin laminar bones on the surface of an extensively cartilaginous neurocranium, the supramaxillae are absent or reduced, and the extrascapular, when present, is greatly enlarged, partially or entirely covering the parietal bone (Johnson and Patterson, 1993; Moore, 1993; Wiley and Johnson, 2010; Nelson et al., 2016).

Until recently, the Stephanoberycoidei was recognized as an order (Stephanoberyciformes), distinct from the Beryciformes (e.g., Johnson and Patterson, 1993; Nelson, 2006; Wiley and Johnson, 2010), but there is growing evidence indicating that the former is a subgroup of the latter based on both morphological (Stiassny and Moore, 1992; Moore, 1993) and molecular data (Miya et al., 2005; Near et al., 2012; Betancur-R. et al., 2013; Dornburg et al., 2017). Relationships within the Stephanoberycoidei are also contentious: the Melamphaidae, traditionally recognized as a family of the Stephanoberycoidei or Stephanoberyciformes (e.g., Johnson and Patterson, 1993; Moore, 1993; Wiley and Johnson, 2010), has been proposed as the sister group of the Berycidae in the Berycoidei (Miya et al., 2005; Near et al., 2012; Betancur-R. et al., 2013; Dornburg et al., 2017). However, for purposes of this study, we follow Moore's (1993) traditional arrangement of the Stephanoberycoidei, including the families Melamphaidae, Stephanoberycidae, Hispidoberycidae, Gibberichthyidae, Rondeletiidae, Barbourisiidae, and Cetomimidae. The Mirapinnidae and Megalomycteridae, also traditionally included in the Stephanoberycoidei (e.g., Moore, 1993; Nelson, 2006), are no longer recognized as valid since members of those families are now regarded as larvae and males, respectively, of the Cetomimidae (Johnson et al., 2009; Nelson et al., 2016).

Several contributions have been made on the systematics and biogeography of the Stephanoberycoidei in the last decades (e.g., Ebeling, 1962; Ebeling and Weed, 1973; Keene, 1973, 1987; Keene et al., 1987; Paxton, 1989; Kotlyar, 1996, 1999, 2004a, 2004b, 2008a, 2011a, 2013, 2014, 2019; Merrett and Moore, 2005; Bartow, 2010; Mincarone et al., 2014). However, knowledge of the diversity and distribution of the group in the western South Atlantic remains fragmentary, despite the apparent relative abundance of some stephanoberycoids in deep-sea environments (Günther, 1887; Keene, 1987; Campos et al., 2008; Costa and Mincarone, 2010; Mincarone et al., 2014; Judkins and Haedrich, 2018). This study reports on new anatomical and taxonomic data of mostly rare species of the Stephanoberycoidei recently collected off northeastern Brazil. The extensively long Brazilian coastline (c. 7,500 km; e.g., Reis et al., 2016) and associated Exclusive Economic Zone (EEZ) encompasses a substantial portion of the Tropical western South Atlantic. Therefore, a review of the distribution of the species recorded

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in this study in the Brazilian EEZ is also provided, with references to additional records in the western South Atlantic.

MATERIALS AND METHODS

Most specimens examined in this study are part of a large collection of mesopelagic invertebrates and fishes sampled during the ABRACOS expeditions (Acoustics along the Brazilian Coast), carried out between 30 September and 20 October 2015 (ABRACOS 1–AB1; Bertrand, 2015), and between 9 April and 6 May 2017 (ABRACOS 2–AB2; Bertrand, 2017). Both expeditions were conducted by the French RV *Antea* off northeastern Brazil and included collections along the Fernando de Noronha Ridge (Rocas Atoll, Fernando de Noronha Archipelago, and seamounts off Rio Grande do Norte State). The survey comprised 82 fishing stations, between the surface and 1,113 m depth, and resulted in the collection of more than 9,000 fish specimens. Sampling was conducted using micronekton (body mesh 40–80 mm, cod-end mesh: 10 mm) and mesopelagic (body mesh: 30 mm, cod-end mesh: 4 mm) nets. Trawl depth was continuously recorded using a Scanmar depth sensor fitted on the upper part of the trawl mouth. An open-mouth net was employed, but pre-established target (maximum) depths were defined for each trawl according to the presence of an acoustic scattering layer or patches detected with a Simrad EK60 split-beam scientific echo sounder. At the target depths, trawling activity lasted for about 30 minutes. Therefore, collection of specimens most likely occurred at target depths, which are indicated as capture depths in the species accounts.

Measurements and counts followed Hubbs and Lagler (1947) with adjustments by Ebeling (1962) for the Melamphaidae and Paxton (1989) for the Cetomimidae. Cranial bone nomenclature followed Kotlyar (1991). Vertebrae and dorsal- and anal-fin ray counts were obtained through a Faxitron LX-60 Cabinet X-ray System. Unless stated otherwise, gill raker number refers to the total number of rakers in the first gill arch. Species identifications were based on descriptions and taxonomic keys provided by Goode and Bean (1895), Parr (1934, 1946), Harry (1952), Rofen (1959), Bigelow (1961), Ebeling (1962), Abe and Hotta (1963), Richardson and Garrick (1964), Abe et al. (1965), Maul (1969), Ebeling and Weed (1973), Fedorov et al. (1987), Paxton (1989), McEachran and Fechhelm (1998), Moore (2003), Paxton and Trnski (2003), Kotlyar (2004b, 2004c, 2005, 2008a, 2008b, 2009a, 2009b, 2009c, 2010, 2011a, 2011b, 2012a, 2012b, 2013, 2014, 2015a, 2015b, 2015c, 2016a, 2016b, 2016c, 2019, 2020), Iwasaki (2009), and Mincarone et al. (2014). Institutional abbreviations follow Sabaj (2020).

RESULTS

Melamphaidae

The Melamphaidae (bigscales) is the largest family in the Stephanoberycoidei, comprising five genera and about 72 species of meso- and bathypelagic fishes (Ebeling and Weed, 1973; Kotlyar, 2004a, 2005, 2010, 2012b, 2013, 2016c). Species of the group are reported from all oceans except the Arctic and the Mediterranean Sea (Ebeling, 1962; Kotlyar, 2004b, 2004c, 2005, 2008a, 2008b, 2009b, 2009c, 2010, 2011a, 2011b, 2012a, 2012b, 2013, 2019; Moore, 2016; Sutton et al., 2020). Juveniles occur in shallow oceanic waters, whereas adults occur below 100–200 m to depths greater than 3,000 m (Ebeling, 1962; Keene, 1987; Kotlyar, 2004a; Mincarone et al., 2014). In the Brazilian EEZ, ten species of the Melamphaidae were previously recorded: *Melamphaes hubbsi*, *M. polylepis*, *M. typhlops*, *Poromitra crassiceps*, *P. megalops*, *Poromitra* sp., *Scopeloberyx opisthopterus*, *Scopeloberyx robustus*, *Scopelogadus beanii*, and *Scopelogadus mizolepis* (Günther, 1887; Keene, 1987; Campos et al., 2008; Costa and Mincarone, 2010; Mincarone et al., 2014; Judkins and Haedrich, 2018). Records of 11 species of the Melamphaidae in the western South Atlantic are provided, four of them new in the Brazilian EEZ.

***Melamphaes eulepis* Ebeling, 1962**

Figure 1A, Table 1

Melamphaes eulepis Ebeling, 1962: 70 (type locality: off Ghana, 00°31′S, 11°02′W, about 200 m depth; holotype: ZMUC P41141).

Specimens examined.—NPM 5007, 3, 35.2–45.6 mm, RV *Antea*, sta. AB2/41A, 03°19′59.1″S, 32°24′42.1″W to 03°19′31.8″S, 32°25′04.6″W, 430 m, 26 April 2017, 2144–2206 h; NPM 5008, 3, 42.0–45.0 mm, sta. AB2/49A, 04°10′38.1″S, 33°16′07.4″W to 04°10′58.0″S, 33°15′03.8″W, 770–1020 m, 30 April 2017, 2117–2152 h; NPM 5009, 2, 41.5–45.1 mm (Fig. 1A), sta. AB2/53A, 03°48′58.7″S, 33°59′17.1″W to 03°50′05.8″S, 33°58′46.5″W, 610 m, 2 May 2017, 2208–2240 h; NPM 5224, 2, 45.5–46.8 mm, sta. AB2/54B, 03°45′17.2″S, 34°41′04.0″W to 03°44′39.2″S, 34°40′04.5″W, 830–1030 m, 3 May 2017, 1311–1347 h.

Diagnosis.—*Melamphaes eulepis* differs from all congeners by the presence of bone expansions on the head ridges. It also differs from all congeners, except *M. spinifer*, by having almost all body scales intact in preserved specimens. *Melamphaes eulepis* differs from *M. spinifer* by the number of pores in the angular portion of the cheek (3–4, usually 3 vs. 4–5, usually 5) and total number of vertebrae (28–30 vs. 26–29, usually 27; Kotlyar, 2016c).

Distribution.—*Melamphaes eulepis* has a circumtropical distribution, except for the eastern Pacific (Kotlyar, 2014). In the Atlantic Ocean, the species is reported between 27°N and 7°S, including the Gulf of Mexico and the Caribbean Sea (Ebeling, 1962; Keene, 1987; Kotlyar, 2014; Moore, 2016; Sutton et al., 2020). In the western South Atlantic, the species was previously known based on a single record made southeast of São Pedro e São Paulo Archipelago (ISH 606/66—01°24′S, 26°W; Keene, 1987). The ten specimens reported herein therefore represent further confirmation of the occurrence of the species in the western South Atlantic and the first records in Brazilian waters. They were collected off the Fernando de Noronha Archipelago, Rocas Atoll, and near the seamounts off Rio Grande do Norte State, at depths ranging between 430 and 1,030 m (Fig. 2).

Habitat.—*Melamphaes eulepis* is a mesopelagic species, with adults and juveniles occurring at a minimum depth of 150 and 200 m, whereas adults probably occur below 700 m at night (Ebeling, 1962; Keene, 1987).

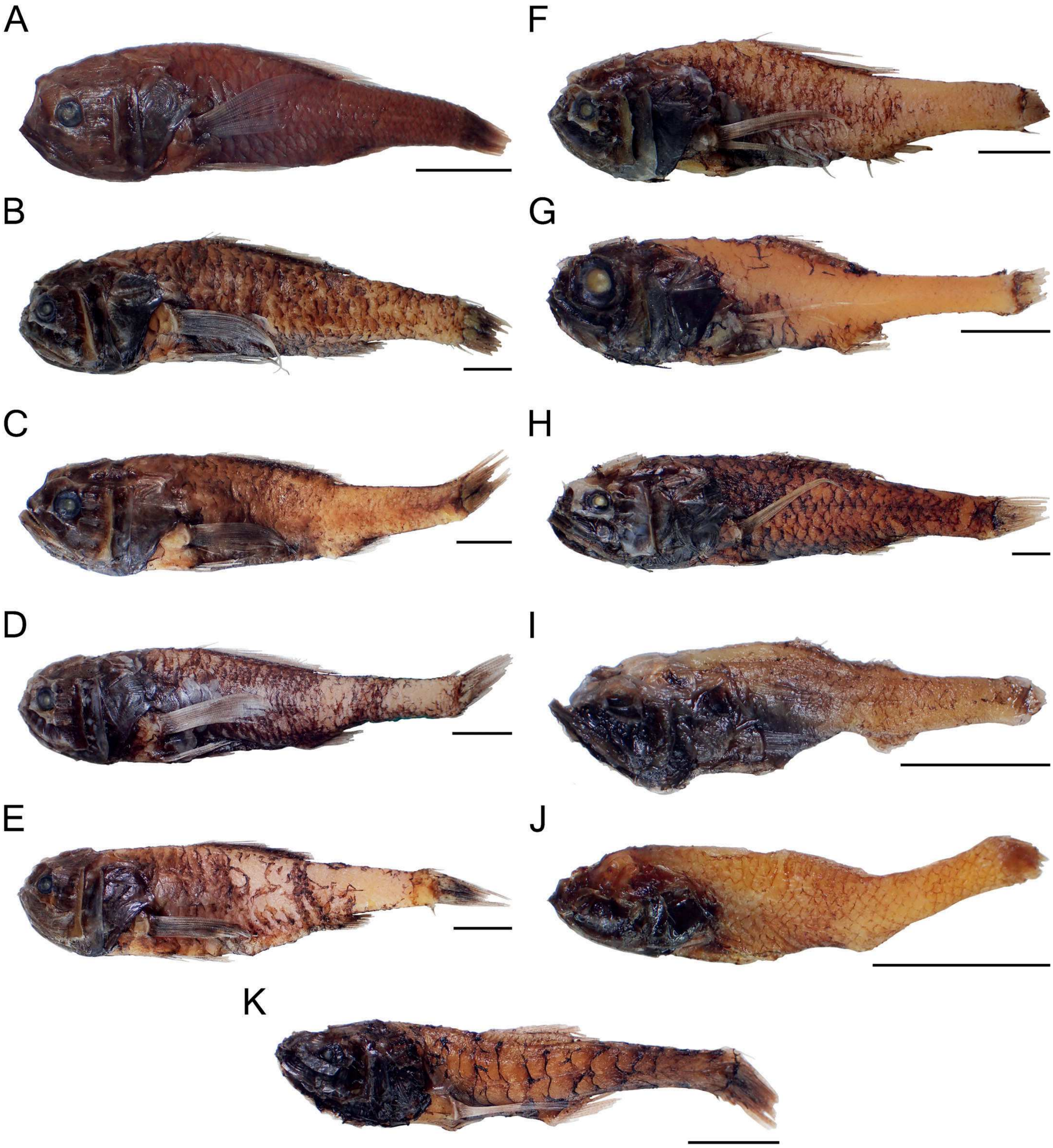

Fig. 1. Species of Melamphaidae reported in this study: (A) *Melamphaes eulepis*, NPM 5009, 45.1 mm SL; (B) *Melamphaes leprus*, NPM 5227, 90 mm SL; (C) *Melamphaes longivelis*, NPM 5229, 75.2 mm SL; (D) *Melamphaes polylepis*, NPM 5228, 49.0 mm SL; (E) *Melamphaes typhlops*, NPM 5225, 60.3 mm SL; (F) *Melamphaes* sp., NPM 5826, 61.9 mm SL; (G) *Poromitra megalops*, NPM 5632, 57.0 mm SL; (H) *Poromitra* sp., NPM 5331, 120.0 mm SL; (I) *Scopeloberyx opercularis*, NPM 5987, 32.0 mm SL; (J) *Scopeloberyx opisthopterus*, NPM 5985, 25.0 mm SL; (K) *Scopelogadus mizolepis*, NPM 5990, 49.0 mm SL. Scale bar = 1 cm.

Table 1. Morphometric and meristic data of species of *Melamphaes* reported in this study.

Species	*M. eulepis*	*M. leprus*	*M. longivelis*	*M. polylepis*	*M. typhlops*	*Melamphaes* sp.
n	10	1	2	37	7	1
Standard length (SL, mm)	35.2–46.8	90.0	73.8–75.2	36–70.2	37.3–71.0	61.9
Measurements in % SL						
Head length	36.9–40.0	35.6	36.0–36.7	31.6–39.9	33.7–35.1	34.9
Head width	18.3–21.1	17.1	16.9	14.5–17.5	15.3–17.5	16.2
Eye diameter	5.3–6.0	4.8	6.2–6.3	3.9–5.6	4.1–5.5	4.8
Postorbital length	23.2–26.7	22.3	23.5–24.7	20.0–25.1	22.4–22.8	22.9
Snout length	9.1–10.3	8.6	8.4–9.4	6.9–9.3	7.5–8.6	8.1
Upper jaw length	17.2–18.8	17.0	18.0–18.1	14.5–17.6	16.6–18.2	16.5
Body depth	27.7–31.5	24.4	25.9	21.3–27.6	23.0–26.1	25.8
Prepectoral length	34.7–40.7	36.8	37.2–38.3	32.0–36.9	33.6–35.7	35.1
Prepelvic length	34.4–43.1	37.7	38.6–39.9	34.7–39.7	36.6–39.5	—
Predorsal length	43.7–49.9	43.1	41.3–42.8	40.6–45.4	39.9–42.6	43.3
Preanal length	62.5–73.8	63.9	71.8–74.8	60.6–71.1	70.0–72.6	67.9
Dorsal-fin base length	25.6–31.6	30.6	29.4–30.6	22.9–29.0	23.5–28.7	26.2
Anal-fin base length	7.7–11.1	11.1	8.9–10.2	8.0–11.4	7.3–10.0	9.7
Caudal peduncle length	22.7–25.5	23.1	21.4–23.0	21.3–30.6	17.9–24.1	26.3
Caudal peduncle depth	9.3–10.5	9.6	9.3–9.5	7.8–10.1	7.9–9.7	9.7
Counts						
Gill rakers (upper + angle and lower)	4+13–14	6+16	4+14	5–6+15–17	4+11–13	5+15
Gill rakers (total)	17–18	22	18	20–23	16–17	20
Dorsal-fin rays	III,14–16	III,15	III,17–18	III,13–15	III,15	III,14
Anal-fin rays	I,8	I,8	I,8	I,7–8	I,8	I,8
Pectoral-fin rays	15	15	15	14–15	15	15
Pelvic-fin rays	I,7	I,7	I,7	I,7	I,7	I,8
Principal caudal rays (upper/lower)	8–10/8–9	10/9	9/8–9	8–11/7–10	8–10/8–9	10/9
Procurrent caudal rays (upper/lower)	3–4/3	4/4	5/3	—	—	—
Vertebrae (precaudal + caudal)	12–13+16–18	11+16	12+17	11+17–19	12–13+14–16	11+18
Vertebrae (total)	28–30	27	29	28–30	26–28	29

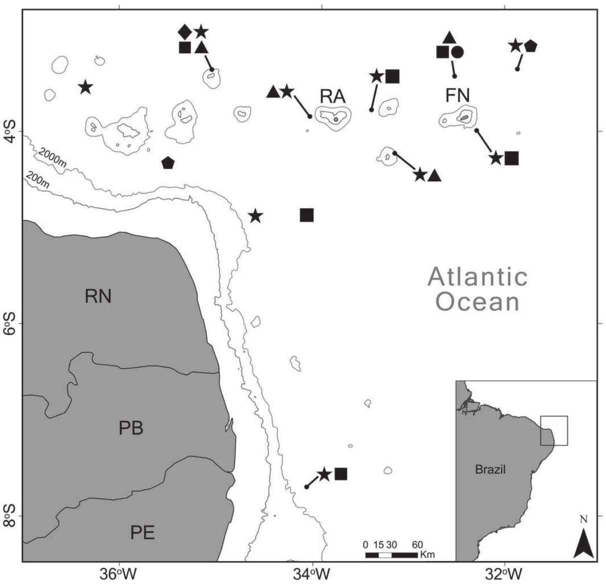

Fig. 2. Records of *Melamphaes eulepis* (triangle), *M. leprus* (circle), *M. longivelis* (pentagon), *M. polylepis* (star), *M. typhlops* (square), and *Melamphaes* sp. (diamond) off northeastern Brazil collected during the ABRACOS surveys. Tip of arrow indicates same collection locality for different species. FN–Fernando de Noronha Archipelago; PB–Paraíba; PE–Pernambuco; RA–Rocas Atoll; RN–Rio Grande do Norte.

Melamphaes leprus Ebeling, 1962

Figure 1B, Table 1

Melamphaes leprus Ebeling, 1962: 60 (type locality: north of Ascension Island, 03°45′S, 10°00′W, about 350 m depth; holotype: ZMUC P41172).

Specimen examined.—NPM 5227, 1, 90 mm (Fig. 1B), RV *Antea*, sta. AB2/41A, 03°19′59.1″S, 32°24′42.1″W to 03°19′31.8″S, 32°25′04.6″W, 430 m, 26 April 2017, 2144–2206 h.

Diagnosis.—*Melamphaes leprus* differs from all congeners, except *M. falsidicus*, *M. macrocephalus*, *M. pachystomus*, and *M. polylepis*, by having 20 or more gill rakers (rarely 19), width near the median region of the larger gill rakers approximately equal to the space between rakers, I, 7 pelvic-fin rays, posttemporal spine absent, and presence simultaneously of 14–15 rays in the pectoral fin and 11 precaudal vertebrae. *Melamphaes leprus* differs from *M. macrocephalus* by the number of transverse series of scales (31–33 vs. 25–28) and by the relative position of the pelvic and pectoral fins (pelvic fin originates after pectoral-fin origin vs. pelvic-fin origin is anterior to pectoral-fin origin). It differs from *M. falsidicus* and *M. polylepis* by the absence of spurs on the haemal arch of the first caudal vertebra (vs. spurs present), and from *M. pachystomus* by the anal-fin origin (in line with the third or fourth dorsal-fin ray, counting from the last ray vs. posterior to the last dorsal-fin ray) and by the number of vertebrae (27 vs. 28–29; Kotlyar, 2011b, 2012b).

Distribution.—Ebeling (1962) described *Melamphaes leprus* based on ten specimens from the eastern Tropical Atlantic, collected between 11°N and 4°S. Subsequently, Keene (1987) reported a wider distribution for the species in the Atlantic, from 17°N to 13°S, and from 29°W to 11°E, with only three records in the western South Atlantic. Kotlyar (2011b) also reported on a single specimen from the Gulf of Guinea, eastern Atlantic. The single specimen reported herein was collected off the Fernando de Noronha Archipelago, at 430 m depth, and represents the fourth record of the species in the western South Atlantic and the first record in Brazilian waters (Fig. 2).

Habitat.—*Melamphaes leprus* is a meso- to bathypelagic species, with juveniles and half-grown specimens captured at the upper limit of the mesopelagic zone, between 150 and 300 m at night (Ebeling, 1962). One adult specimen was captured in bottom trawling at 1,550 m depth (Kotlyar, 2011b).

Melamphaes longivelis **Parr, 1933**

Figure 1C, Table 1

Melamphaes microps longivelis Parr, 1933: 16 (type locality: off Acklins Island, Bahama, western Atlantic, 22°31′N, 74°26′W, 10,000 feet [3048 m] wire out; holotype: YPM 2833).

Specimens examined.—NPM 5229, 1, 75.2 mm (Fig. 1C), RV *Antea*, sta. AB2/42A, 03°15′28.1″S, 31°48′29.1″W to 03°15′27.8″S, 31°50′40.6″W, 780 m, 27 April 2017, 1223–1226 h; NPM 5230, 1, 73.8 mm, sta. AB2/35, 04°19′36.6″S, 35°29′51.6″W to 04°18′32.4″S, 35°32′19.8″W, 630 m, 20 April 2017, 2235–2315 h.

Diagnosis.—*Melamphaes longivelis* differs from all congeners, except *M. eulepis* and *M. spinifer*, by having 17–19 (more often 18) gill rakers, width near the median region of the larger gill rakers less than three-quarters of the space between the rakers, eye diameter equal to or larger than the suborbital bone width, anal-fin origin in line with or posterior to the last dorsal-fin ray origin (less than the width of one scale pocket), caudal peduncle depth substantially more than two times in the caudal peduncle length, and III,17–18 dorsal-fin rays. *Melamphaes longivelis* differs from *M. eulepis* and *M. spinifer* by having less than half (rarely more) body scales present in preserved specimens (vs. all, or almost all, body scales present in preserved specimens; Kotlyar, 2015a, 2016c).

Distribution.—*Melamphaes longivelis* occurs in the Atlantic Ocean, with confirmed records restricted to the eastern and western North Atlantic (Kotlyar, 2015a; Sutton et al., 2020) and the eastern South Atlantic (Sutton et al., 2020). Keene (1987) reported two specimens of *M. longivelis* in the western South Atlantic off southeastern São Pedro e São Paulo Archipelago, but his report was made before Kotlyar's (2015a) revision of the species complex. Therefore, the two specimens collected off the Fernando de Noronha Archipelago and off Rio Grande do Norte State, between depths of 630 and 780 m (Fig. 2) represent the first confirmed records of *M. longivelis* in the western South Atlantic. Records of the species in the region prior to Kotlyar's (2015a) revision (e.g., Ebeling, 1962; Moore, 2003) require confirmation.

Habitat.—*Melamphaes longivelis* is a mesopelagic species, with juveniles recorded in depths shallower than 150 m and adults below 500 m (Ebeling, 1962; Keene, 1987; Kotlyar, 2015a).

Melamphaes polylepis **Ebeling, 1962**

Figure 1D, Table 1

Melamphaes polylepis Ebeling, 1962: 43 (type locality: South of Sri Lanka, 05°21′N, 80°38′E, about 2250 m depth; holotype: ZMUC P41178).

Specimens examined.—NPM 5228, 2, 49.0–60.5 mm (Fig. 1D), RV *Antea*, sta. AB2/42A, 03°15′28.1″S, 31°48′29.1″W to 03°15′27.8″S, 31°50′40.6″W, 780 m, 27 April 2017, 1223–1226 h; NPM 5231, 2, 46.3–57.6 mm, sta. AB2/60B, 03°31′43.0″S, 36°21′19.8″W to 03°31′46.8″S, 36°22′25.7″W, 670–700 m, 6 May 2017, 1249–1319 h; NPM 5233, 4, 59.0–67.3 mm, sta. AB2/52A, 03°43′16.2″S, 33°25′09.8″W to 03°42′14.2″S, 33°24′36.2″W, 822–984 m, 2 May 2017, 1147–1218 h; NPM 5234, 2, 52.6–56.8 mm, sta. AB2/16, 07°36′15.0″S, 33°59′30.0″W to 07°36′49.3″S, 33°57′18.7″W, 680 m, 14 April 2017, 2153–2239 h; NPM 5237, 8, 60.5–69.0 mm, sta. AB2/44A, 03°52′52.5″S, 32°17′33.3″W to 03°52′13.4″ S, 32°16′28.0″W, 850 m, 28 April 2017, 1244–1317 h, 1244–1317 h; NPM 5238, 4, 64.1–66.4 mm, sta. AB2/53A, 03°48′58.7″S, 33°59′17.1″W to 03°50′05.8″S, 33°58′46.5″W, 610 m, 2 May 2017, 2208–2240 h; NPM 5239, 2, 36.0–66.0 mm, sta. AB2/49A, 04°10′38.1″S, 33°16′07.4″W to 04°10′58.0″S, 33°15′03.8″W, 770–1020 m, 30 April 2017, 2117–2152 h; NPM 5241, 2, 37.0–60.6 mm, sta. AB2/54B, 03°45′17.2″S, 34°41′04.0″W to 03°44′39.2″S, 34°40′04.5″W, 830–1030 m, 3 May 2017, 1311–1347 h; NPM 5242, 11, 58.2–70.2 mm, sta. AB2/39, 04°52′26.9″S, 34°35′22.9″W to 04°50′52.8″S, 34°51′04.7″W, 650–800 m, 24 April 2017, 2149–2237 h.

Diagnosis.—*Melamphaes polylepis* differs from all congeners, except *M. falsidicus*, *M. macrocephalus*, *M. pachystomus*, and *M. leprus*, by having 20 or more (rarely 19) gill rakers, width near the median region of the larger gill rakers approximately equal to the space between rakers, I,7 pelvic-fin rays, posttemporal spine absent, and presence simultaneously of 14–15 pectoral-fin rays and 11 precaudal vertebrae. *Melamphaes polylepis* differs from *M. falsidicus* by the number of transverse series of scales (30–36 vs. 29–30) and the eye diameter (10.0–16.3% HL vs. 16.4–19.2% HL). It differs from *M. leprus*, *M. macrocephalus*, and *M. pachystomus* by the presence of spurs on the haemal arch of the first caudal vertebra (vs. spurs absent; Kotlyar, 2011b, 2012b).

Distribution.—*Melamphaes polylepis* has a circumglobal distribution, except for the eastern Pacific Ocean (Kotlyar, 2011b). It was originally reported from the North Atlantic between the equator and 20°N, the Indian Ocean and Indonesia between 15°N and 15°S, and the North Pacific between 34°N and 6°N (Ebeling, 1962). Ebeling (1962) also reported the species from the South Pacific, at 30°56′S, 109°17′W, based on a single specimen that might actually represent *M. pachystomus* (Kotlyar, 2011b). Keene (1987) recorded *M.*

polylepis from 32°N to 18°S in the Atlantic Ocean, including the southeastern Caribbean Sea and the western South Atlantic, from eastern São Pedro e São Paulo Archipelago to northern Trindade Island (ISH 484/66, 17°36′S, 28°53′W), off the central Brazilian coast. Further records of the species in Brazil were also made off Bahia and Espírito Santo States based on two specimens collected between depths of 837 and 1,051 m (Mincarone et al., 2014), and off northeastern Brazil (Eduardo et al., 2020a). The 37 specimens examined here were collected off Pernambuco State, the Fernando de Noronha Archipelago, the Rocas Atoll, and the seamounts off Rio Grande do Norte State, between depths of 610 and 1,030 m (Fig. 2).

Habitat.—*Melamphaes polylepis* is a meso- and bathypelagic species, with specimens captured by open-mouth nets at depths down to 4,228 m (Ebeling, 1962; Keene, 1987; Keene et al., 1987; Kotlyar, 2011b). According to Ebeling (1962), juveniles and subadults probably occur at depths below 200–300 m. Keene (1987) reported on vertical migration of juveniles between 500 and 800 m during the day, and mainly between 100 and 400 m at night.

Remarks.—In his unpublished Ph.D. dissertation, Keene (1987) described "*Melamphaes indicoides*" based on specimens collected in the Atlantic. The species, which was never formally described and is, therefore, not valid, is morphologically similar to *M. polylepis*, differing by the number of diagonal series of scales (8 vs. 9–10, respectively). Subsequently, Bartow (2010), based on the examination of only five specimens, proposed that "*Melamphaes indicoides*" and *M. polylepis* might also differ by the following characters (numbers in brackets refer to mode values for counts or mean values for measurements): number of dorsal- (III,15–16 [III,15] vs. III,13–15 [III,14]) and caudal-fin rays (25–27 [25] vs. 27–29 [28]), number of gill rakers on the first gill arch (20 vs. 20–23 [21]), number of scale in horizontal series (25–31 [28] vs. 33–35 [34]), number of scales in diagonal row (5–8 [7] vs. 8–10 [9]), HL (29.76–32.44% [30.92%] SL vs. 35.0–41.4% [37.5%] SL), distance between the end of dorsal fin to caudal-fin origin (27.38–32.83% [30.37%] SL vs. 33.1–36.6% [35.0%] SL), postanal length (25.56–30.77% [28.43%] SL vs. 35.6–41.3% [38.1%] SL), orbit to cheek angle length (10.77–13.75% [12.68%] SL vs. 9.6–11.7% [10.8%] SL), and caudal peduncle length (19.72–23.21% [21.21%] SL vs. 26.6–30.7% [28.3%] SL). The specimens recognized as *M. polylepis* in the current study are partially damaged but might represent the same species provisionally named by Keene (1987) as "*Melamphaes indicoides*." More in-depth taxonomic studies in the *M. polylepis* species complex are necessary.

***Melamphaes typhlops* (Lowe, 1843)**

Figure 1E, Table 1

Metopias typhlops Lowe, 1843: 90 (type locality: off Madeira; neotype: BMNH 1864.11.8.1 [designated by Ebeling, 1962]).

Specimens examined.—NPM 5225, 1, 60.3 mm (Fig. 1E), RV *Antea*, sta. AB2/54B, 03°45′17.2″S, 34°41′04.0″W to 03°44′39.2″S, 34°40′04.5″W, 830–1030 m, 3 May 2017, 1311–1347 h; NPM 5226, 1, 37.3 mm, sta. AB2/41A, 03°19′59.1″S, 32°24′42.1″W to 03°19′31.8″S, 32°25′04.6″W, 430 m, 26 April 2017, 2144–2206 h; NPM 5232, 1, 65.7 mm, sta. AB2/52A, 03°43′16.2″S, 33°25′09.8″W to 03°42′14.2″S, 33°24′36.2″W, 822–984 m, 2 May 2017, 1147–1218 h; NPM 5235, 1, 61.6 mm, sta. AB2/16, 07°36′15.0″S, 33°59′30.0″W to 07°36′49.3″S, 33°57′18.7″W, 680 m, 14 April 2017, 2153–2239 h; NPM 5236, 1, 68.2 mm, sta. AB2/44A, 03°52′52.5″S, 32°17′33.3″W to 03°52′13.4″S, 32°16′28.0″W, 850 m, 28 April 2017, 1244–1317 h; NPM 5240, 2, 67.5–71.0 mm, sta. AB2/39, 04°52′26.9″S, 34°03′32.3″W to 04°50′52.8″S, 34°05′06.5″W, 650–800 m, 24 April 2017, 2149–2237 h.

Diagnosis.—*Melamphaes typhlops* differs from congeners, except *M. contradictorius*, *M. eurous*, *M. inconspicuus*, *M. indicus*, *M. janae*, *M. kobylyanskyi*, *M. longivelis*, *M. parvus*, *M. proximus*, and *M. succedaneus*, by having 19 or fewer (rarely 20) gill rakers, width near the median region of the larger gill rakers less than three-quarters of the space between rakers, eye diameter equal to or larger than suborbital bone width, anal-fin origin posterior to the vertical through the last dorsal-fin ray origin, and less than half of body with scales present in preserved specimens (rarely more). *Melamphaes typhlops* differs from *M. contradictorius*, *M. inconspicuus*, *M. janae*, *M. kobylyanskyi*, *M. longivelis*, *M. parvus*, *M. proximus*, and *M. succedaneus* by the distance between anal-fin origin and the vertical through the last dorsal-fin ray origin (usually equal to the width of one to one and a half scale pocket vs. less than the width of one scale pocket) and number of gill rakers on the lower portion of the first gill arch (10–11 vs. 12–14 [a single specimen with 12 in the present study]). It differs from *M. eurous* and *M. indicus* by having gill rakers of the fourth branchial arch present as reduced, flat or slightly convex, patches (vs. gill rakers of the fourth branchial arch in the shape of short knobs; Kotlyar, 2016a, 2016c; this study).

Distribution.—*Melamphaes typhlops* occurs in the Atlantic Ocean, from 41°N to 28°S, including the Gulf of Mexico (Ebeling, 1962; Keene, 1987; Keene et al., 1987; Kotlyar, 2016a; Moore, 2016; Sutton et al., 2020). In the western South Atlantic, the species was previously known from 22 specimens collected off southern São Pedro e São Paulo Archipelago and off the central to southeastern Brazilian coast, with some records inside the country's EEZ (Keene, 1987; Mincarone et al., 2014). Seven specimens collected between depths of 430 and 1,030 m off the Fernando de Noronha Archipelago, the Rocas Atoll, the seamounts off Rio Grande do Norte State, and off Rio Grande do Norte and Pernambuco States are reported here (Fig. 2).

Habitat.—*Melamphaes typhlops* is a meso- to bathypelagic species, with post-larvae captured between the surface and down to 100 m, juveniles between depths of 150 and 1,000 m, and adults below 500 m (Ebeling, 1962; Keene et al. 1987; Kotlyar, 2016a).

***Melamphaes* sp.**

Figure 1F, Table 1

Specimen examined.—NPM 5826, 1, 61.9 mm (Fig. 1F), RV *Antea*, sta. AB2/54B, 03°45′17.2″S, 34°41′04.0″W to 03°44′39.2″S, 34°40′04.5″W, 830–1030 m, 3 May 2017, 1311–1347 h.

Diagnosis.—The only specimen identified here as *Melamphaes* sp. differs from all other species of the genus, except *M. ebelingi*, *M. nikolayi*, and *M. occlusus*, by the number of pelvic-

Table 2. Morphometric and meristic data of species of *Poromitra*, *Scopeloberyx*, and *Scopelogadus* reported in this study.

Species	*Poromitra megalops*	*Poromitra* sp.	*Scopeloberyx opercularis*	*Scopeloberyx opisthopterus*	*Scopelogadus mizolepis*
n	28	27	1	4	19
Standard length (SL, mm)	25.0–59.0	48.0–121.0	32.0	25.0–32.0	37.0–70.0
Measurements in % SL					
Head length	32.9–39.7	39.3–44.8	39.0	29.0	34.8–38.6
Head width	11.7–14.5	12.8–16.1	–	–	–
Eye diameter	8.8–12.7	4.3–6.8	6.3	–	–
Postorbital length	17.3–23.0	23.7–28.3	–	–	–
Snout length	4.5–6.9	8.8–11.3	–	–	8.0–10.7
Upper jaw length	13.2–18.3	16.4–19.2	–	–	–
Body depth	22.3–26.7	20.7–26.3	–	–	20.4–22.9
Prepectoral length	35.6–41.3	39.6–47.2	43.8	–	35.2–43.0
Prepelvic length	32.0–36.3	39.8–44.5	–	–	36.9–39.8
Predorsal length	42.0–46.3	44.7–50.8	–	–	41.4–44.8
Preanal length	55.1–62.7	61.9–72.8	–	–	57.6–60.2
Dorsal-fin base length	20.8–25.0	23.6–28.9	–	–	17.6–20.2
Anal-fin base length	8.4–11.8	8.7–12.2	–	–	9.0–11.1
Caudal peduncle length	28.9–34.4	19.4–25.3	22.8	–	29.1–34.9
Caudal peduncle depth	5.8–7.6	7.7–10.0	–	–	8.1–9.4
Counts					
Gill rakers (upper + angle and lower)	6–8+16–20	9–11+21–23	18+8	3–4+11–13	7–8+15–17
Gill rakers (total)	23–27	30–34	26	14–17	22–25
Dorsal-fin rays	II–III,11–12	III,11–12	–	–	II,11
Anal-fin rays	I,9	I,8	I,7	–	I,8
Pectoral-fin rays	12–14	14–15	–	–	13–14
Pelvic-fin rays	I,7	I,7	–	I,7–8	–
Principal caudal rays (upper/lower)	10/8–10	9–10/9–10	–	–	–
Procurrent caudal rays (upper/lower)	3/3	3/3	–	–	–
Vertebrae (precaudal + caudal)	10+19–20	10–11+15–17	–	–	–
Vertebrae (total)	29–30	26–27	26	25	24–25

fin rays (I,8 vs. I,7). *Melamphaes* sp. differs from *M. ebelingi* by the number of vertebrae (29 vs. 26–27) and by the presence of spurs on the haemal arch of the first caudal vertebra (vs. spurs absent). It differs from *M. occlusus* by the number of gill rakers (20 vs. 22) and by the number of dorsal-fin rays (III,14 vs. III,16), and from *M. nikolayi* by the presence of spurs on the haemal arch of the first caudal vertebra (vs. spurs absent) and by the number of precaudal vertebrae (11 vs. 12; Ebeling, 1962; Keene, 1973; Bartow, 2010; Kotlyar, 2012b). Kotlyar (2015c) reported on the occurrence of one spine and eight soft rays in one side of the pelvic fin of a single specimen of *M. lentiginosus* (typical condition: I,7 pelvic-fin rays), but the specimen reported in the present study differs from *M. lentiginosus* by the number of gill rakers (20 vs. 15–17; Table 1).

Distribution.—Known only from a single specimen, collected near the seamounts off Rio Grande do Norte State, between depths of 830 and 1,030 m (Fig. 2).

Remarks.—This specimen most likely belongs to a new species, which will be described in a forthcoming study.

Poromitra megalops **(Lutken, 1877)**

Figure 1G, Table 2

Melamphaes megalops Lutken, 1877: 176 (type-locality: south of Azores, eastern North Atlantic [stomach content]; holotype: ZMUC 84).

Specimens examined.—NPM 5632, 9, 32.5–57.0 mm (Fig. 1G), RV *Antea*, sta. AB2/53A, 03°48′58.7″S, 33°59′17.1″W to 03°50′05.8″S, 33°58′46.5″W, 610 m, 2 May 2017, 2208–2240 h; NPM 5927, 2, 46.5–53.0 mm, sta. AB2/52A, 03°43′16.2″S, 33°25′09.8″W to 03°42′14.2″S, 33°24′36.2″W, 822–984 m, 2 May 2017, 1147–1218 h; NPM 5928, 1, 53.0 mm, sta. AB2/49A, 04°10′38.1″S, 33°16′07.4″W to 04°10′58.0″S, 33°15′03.8″W, 770–1020 m, 30 April 2017, 2117–2152 h; NPM 5929, 1, 54.5 mm, sta. AB2/39, 04°52′26.9″S, 34°03′32.3″W to 04°50′52.8″S, 34°05′06.5″W, 650–800 m, 24 April 2017, 2149–2237 h; NPM 5931, 2, 33.0–42.0 mm, sta. AB2/35, 04°19′36.6″S, 35°29′51.6″W to 04°18′32.4″S, 35°32′19.8″W, 630 m, 20 April 2017, 2235–2315 h; NPM 5933, 5, 35.0–59.0 mm, sta. AB2/44A, 03°52′52.5″S, 32°17′33.3″W to 03°51′43.6″S, 32°16′20.0″W, 850 m, 28 April 2017, 1244–1317 h; NPM 5937, 1, 34.0 mm, sta. AB2/59A, 03°38′01.6″S, 36°03′10.6″W to 03°38′07.9″S, 36°02′22.6″W, 700–1113 m, 5 May 2017, 2157–2237 h; NPM 5938, 6, 47.0–59.0 mm, sta. AB2/54B, 03°45′17.2″S, 34°41′04.0″W to 03°44′39.2″S, 34°40′04.5″W, 830–1030 m, 3 May 2017, 1311–1347 h; NPM 6089, 1, 25.0 mm, sta. AB1/22, 04°07′44.8″S, 33°47′24.5″W to 04°07′00.7″S, 33°48′57.9″W, 525 m, 8 October 2015, 2132–2212 h.

Diagnosis.—*Poromitra megalops* differs from all congeners, except *P. jucunda* and *P. macrophthalma*, by the eye diameter (2.9–3.2 in HL vs. 4.0–17.2 in HL; Kotlyar, 2010). According to Kotlyar (2010), *P. megalops* differs from *P. macrophthalma* by the number of gill rakers (26–28 vs. 21–24), in addition to

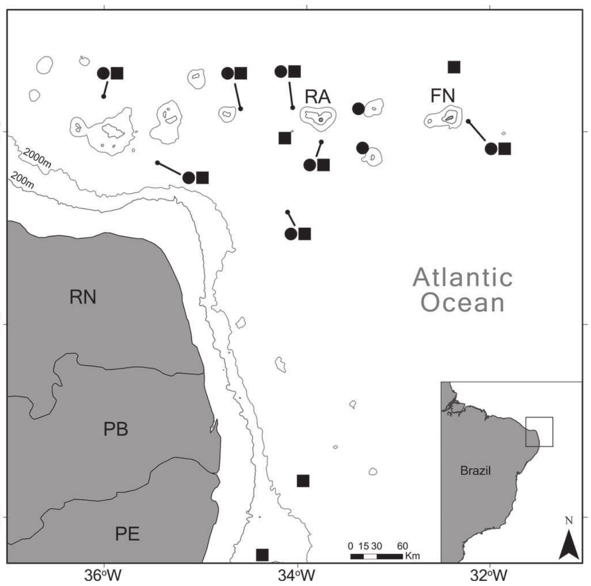

Fig. 3. Records of *Poromitra megalops* (circle) and *Poromitra* sp. (square) off northeastern Brazil collected during the ABRACOS surveys. Tip of arrow indicates same collection locality for both species. FN–Fernando de Noronha Archipelago; PB–Paraíba; PE–Pernambuco; RA–Rocas Atoll; RN–Rio Grande do Norte.

number of pyloric caeca (6 vs. 4–5), number of spines on the posterior margin of the preopercle (2–15 vs. 0–1), and width of the angular region of the preopercle (11.6–13.4% HL vs. 7–12% HL), and from *P. jucunda* also by the number of gill rakers (26–28 vs. 23–25; but see Remarks, below).

Distribution.—*Poromitra megalops* has a circumtropical distribution, being more common in the eastern Atlantic, Indo-Pacific and eastern Central Pacific (Ebeling and Weed, 1973; Keene, 1987; Moore, 2016; Sutton et al., 2020). Previous records in the western South Atlantic were restricted to nine specimens collected off southeastern São Pedro e São Paulo Archipelago and by one further isolated record made at 32°49′S, 26°26′W (Keene, 1987; Judkins and Haedrich, 2018). The species was also recorded off Ascension Island, middle Atlantic, based on two specimens (Keene, 1987). Ebeling and Weed (1973) reported intraspecific variation between populations from the Atlantic and eastern Central Pacific and those of the Indo-Pacific. Kotlyar (2010), however, proposed that those different populations should be recognized as distinct species, restricting *P. megalops* to the Atlantic, except the western South Atlantic (see Remarks, below). In Brazilian waters, the species was previously reported off São Pedro e São Paulo Archipelago (01°20′S, 27°37′W; 01°44′S, 27°44′W; Keene, 1987; Judkins and Haedrich, 2018). In the current study, *P. megalops* is reported from 28 specimens collected off the Fernando de Noronha Archipelago, the Rocas Atoll, and from the seamounts off Rio Grande do Norte State, between depths of 525 and 1,113 m. This also represents the largest single collection of *P. megalops* in the western South Atlantic made to date (Fig. 3).

Habitat.—The species is meso- to bathypelagic, with adults usually occurring below depths of 400–500 m (maximum depth 1,113 m; this study). Juveniles and post-larvae occur in shallow waters down to 150–200 m (Ebeling and Weed, 1973; Keene, 1987; Keene et al., 1987).

Remarks.—*Poromitra macrophthalma* was recognized as valid until recently, when Ebeling and Weed (1973) proposed that the species is a junior synonym of *P. megalops*. According to them, specimens previously assigned to *P. macrophthalma* would represent a different morphotype of *P. megalops* restricted to the Indo-Pacific, only slightly distinct from the Atlantic and middle to eastern Pacific remaining population of the species in the number of anal-fin rays (I,8–10 vs. I,9–10), number of gill rakers in the lower portion of the first gill arch (14–18 vs. 16–20), number of vertebrae (26–28 vs. 28–30), and number of dorsal-fin spines (usually II vs. usually III). Subsequently, Kotlyar (2010) revalidated *P. macrophthalma*, restricting its distribution to the Indo-Pacific. He furthermore restricted the distribution of *P. megalops* to the Atlantic and described *P. jucunda* from the Central and eastern Pacific. According to Kotlyar (2010), *P. megalops* differs from *P. jucunda* by the eye diameter (31.3–34.0% HL vs. 24.2–32.6% HL) and number of gill rakers (26–28 vs. 23–25). However, eye diameter of some specimens of *P. megalops* from the Atlantic examined by Keene (1987) is also around 20% HL, with number of gill rakers ranging from 22 to 28. The eye diameter and gill raker counts of some specimens identified herein as *P. megalops* also fall within the range proposed by Kotlyar (2010) for *P. jucunda* (eye diameter 24.3–37.5% HL and number of gill rakers on the first branchial arch 23–27; Table 2). Separation between *P. megalops* and *P. macrophthalma sensu* Kotlyar (2010) is also problematic. According to Kotlyar (2010), *P. megalops* differs from *P. macrophthalma* by the following characters: number of gill rakers (26–28 vs. 21–24), number of pyloric caeca (6 vs. 4–5), number of spines on the posterior margin of preopercle (2–15 vs. 0–1), and width of the angular region of the preopercle (11.6–13.4% HL vs. 7–12% HL). However, specimens identified here as *P. megalops* have 23–27 gill rakers, 1–5 inconspicuous spines on the posterior margin of the preopercle, and width of the angular region of the preopercle from 10 to 16.5% HL (Table 2). Summing up, data available from specimens identified here as *P. megalops*, in association with information provided by Keene (1987) and Kotlyar (2010), suggest that *P. macrophthalma* and *P. jucunda* might not be valid. If correct, the situation would be similar to the one proposed by Ebeling and Weed (1973), in which a single species of the group (*P. megalops*, the senior synonym), with a circumglobal distribution, should be recognized. However, a more thorough taxonomic study of this group of species is necessary, based on examination of more specimens from the Atlantic and Indo-Pacific Oceans.

***Poromitra* sp.**

Figure 1H, Table 2

Specimens examined.—NPM 3189, 1, 110.0 mm, RV *Antea*, sta. AB1/14, 03°58′57.4″S, 34°03′23.1″W to 03°57′43.5″S, 34°04′50.5″W, 510 m, 6 October 2015, 2140–2226 h; NPM 3190, 4, 59.5–72.0 mm, sta. AB1/22, 04°07′44.8″S, 33°47′24.5″W to 04°07′00.7″S, 33°48′57.9″W, 525 m, 8 October 2015, 2132–2212 h; NPM 3198, 1, 48.0 mm, sta. AB1/51, 08°56′29.5″S, 34°29′03.5″W to 08°59′05.6″S, 34°28′35.2″W, 45–200 m, 19 October 2015, 2209–2335 h;

NPM 5331, 3, 100.0–120.0 mm (Fig. 1H), sta. AB2/53A, 03°48′58.7″S, 33°59′17.1″W to 3°50′05.8″S, 33°58′46.5″W, 610 m, 2 May 2017, 2208–2240 h; NPM 5926, 1, 59.0 mm, sta. AB2/16, 07°36′14.4″S, 33°59′33.8″W to 07°36′49.3″S, 33°57′18.7″W, 680 m, 14 April 2017, 2153–2239 h; NPM 5930, 2, 65.0–111.0 mm, sta. AB2/35, 04°19′36.6″S, 35°29′51.6″W to 04°18′32.4″S, 35°32′19.8″W, 630 m, 20 April 2017, 2235–2315 h; NPM 5932, 2, 51.5–66.5 mm, sta. AB2/39, 04°52′26.9″S, 34°03′32.3″W to 04°50′52.8″S, 34°05′06.5″W, 650–800 m, 24 April 2017, 2149–2237 h; NPM 5934, 6, 81.0–121.0 mm, sta. AB2/41A, 03°19′59.1″S, 32°24′42.1″W to 03°19′31.8″S, 32°25′04.6″W, 430 m, 26 April 2017, 2144–2206 h; NPM 5935, 1, 62.0 mm, sta. AB2/44A, 03°52′52.5″S, 32°17′33.3″W to 03°51′43.6″S, 32°16′20.0″W, 850 m, 28 April 2017, 1244–1317 h; NPM 5936, 1, 62.0 mm, sta. AB2/59A, 03°38′01.6″S, 36°03′10.6″W to 03°38′07.9″S, 36°02′22.6″W, 700–1113 m, 5 May 2017, 2157–2237 h; NPM 5939, 5, 62.0–85.0 mm, sta. AB2/54B, 03°45′17.2″S, 34°41′04.0″W to 03°44′39.2″S, 34°40′04.5″W, 830–1030 m, 3 May 2017, 1311–1347 h.

Diagnosis.—Kotlyar (2008a) defined five species groups of *Poromitra* based on the anatomy of the preopercle. The specimens of *Poromitra* sp. examined here are more similar to those of the *P. crassa* and *P. crassiceps* species groups (Kotlyar, 2008a). However, *Poromitra* sp. differs from *P. crassa* (the single species in the *P. crassa* species group) by the number of dorsal-fin rays (III,11–12 vs. III,10), number of gill rakers (30–34 vs. 23–25), and body depth (20.7–26.3% SL vs. 31.5–34.2% SL; Kotlyar, 2008a). In the *P. crassiceps* species group, *Poromitra* sp. differs from *P. coronata* by the number of dorsal-fin rays (III,11–12 vs. III,10), from *P. rugosa* and *P. decipiens* by the relative position of pelvic and pectoral fins (pelvic-fin origin is beneath or slightly anterior to pectoral-fin origin vs. pelvic fin originates after pectoral-fin origin), and from *P. curilensis* by the number of dorsal-fin rays (III,11–12 vs. III,12–14), anal-fin origin (in line with the second to fifth dorsal-fin ray origins vs. in line with the sixth to seventh dorsal-fin ray origins, counting from the last ray), and extension of the posterior margin of the upper jaw (extending beyond the posterior margin of the eye vs. in line with the posterior margin of the eye). See Remarks for further details.

Distribution.—The 27 specimens identified in this study as *Poromitra* sp. were collected off the Fernando de Noronha Archipelago, Rocas Atoll, seamounts off Rio Grande do Norte State, and off Rio Grande do Norte and Pernambuco States, between depths of 45 and 1,113 m (Fig. 3). The species was previously reported off Espírito Santo and Rio de Janeiro States, southeastern Brazil, at depths between 837 and 1,762 m (Mincarone et al., 2014).

Remarks.—The specimens identified here as *Poromitra* sp. represent the same species also recognized as *Poromitra* sp. by Mincarone et al. (2014). Those authors concluded that *Poromitra* sp. belongs to the *P. crassiceps* group of Kotlyar (2008a, 2008b), and this conclusion is supported in the present study based on the new specimens examined. According to Kotlyar (2008a, 2008b), only two species of the *Poromitra crassiceps* group occur in the western Atlantic Ocean, *P. crassiceps* and *P. kukuevi*. *Poromitra crassiceps* differs from *Poromitra* sp. by the number of dorsal- (III,12–13 vs. III,11–12 [a single specimen with 12]) and anal-fin rays (I,9–10 vs. I,8), number of vertebrae (27–29 vs. 26–27), and relative position of pelvic and pectoral fins (pelvic fin originates after pectoral-fin origin vs. pelvic-fin origin is beneath or slightly anterior to pectoral-fin origin). Despite similarities in terms of shape of the preopercle, number and presence of spines in the preopercle, and counts of pectoral-, pelvic-, dorsal-, and anal-fin rays, *P. kukuevi* (which was described based on a single and possibly juvenile specimen) differs substantially from *Poromitra* sp. in the number of gill rakers (26 vs. 30–34, respectively). Measures and counts of 12 specimens identified as *Poromitra* sp. by Mincarone et al. (2014) are in accordance with those presented here, except by the number of vertebrae (26 vs. 26–27, respectively; Table 2). This variation is interesting, since the single known specimen of *P. kukuevi* also has 27 vertebrae (Kotlyar, 2008b). Mincarone et al. (2014) indicated that the taxonomic situation of at least part of the *Poromitra crassiceps* group is complex, concluding, among other things, that *P. kukuevi* might be a junior synonym of *P. indooceanica*, which has priority over the former by six printed pages (Kotlyar, 2008b). This situation renders the proper identification of *Poromitra* sp. as even more problematic. Bartow (2010) also noted the current taxonomic complexity of the genus *Poromitra* in the Atlantic, especially of the species included in the *Poromitra crassiceps* group. Keene (1987), in his unpublished Ph.D. dissertation, informally described a distinct Atlantic species of the genus and provisionally named it as "*Poromitra gibbsi*" (not *Poromitra gibbsi* Parin and Borodulina, 1989, which is a valid and distinct species), with records along the western South Atlantic, including off Brazil. Measurements and counts of "*Poromitra gibbsi*" *sensu* Keene (1987), such as number of vertebrae (25–27) and dorsal-fin rays (III,10–12), are similar to those reported for *P. glochidiata*, *P. indooceanica*, *P. kukuevi*, and *P. unicornis*, all of them included in the *Poromitra crassiceps* species group of Kotlyar (2008a). Meristic and morphometric data of the specimens identified here as *Poromitra* sp. also fall within the ranges and description provided by Keene (1987) for his "*Poromitra gibbsi*." Therefore, it is possible that the species recognized by Kotlyar (2008a) as *P. kukuevi*, in addition to "*Poromitra gibbsi*" *sensu* Keene (1987) and *Poromitra* sp. *sensu* Mincarone et al. (2014) and this paper, might represent the same Atlantic species. The taxonomic problems of the *Poromitra crassiceps* group can be properly addressed only with a major global review of the group, including the examination of a substantial number of specimens and the type material of all nominal species included in the complex.

Scopeloberyx opercularis Zugmayer, 1911

Figure 1I, Table 2

Scopeloberyx opercularis Zugmayer, 1911: 8 (type-locality: off Portugal, 36°07′N, 10°18′W, 0–4740 m depth; holotype: MOM 0091-1179).

Specimen examined.—NPM 5987, 1, 32.0 mm (Fig. 1I), RV *Antea*, sta. AB2/42A, 03°15′28.1″S, 31°48′29.1″W to 03°15′26.4″S, 31°48′22.9″W, 780 m, 27 April 2017, 1223–1226 h.

Diagnosis.—According to Keene (1987), *Scopeloberyx opercularis* differs from all congeners, except *S. rubriventer*, by the horizontal distance between the pelvic- and pectoral-fin

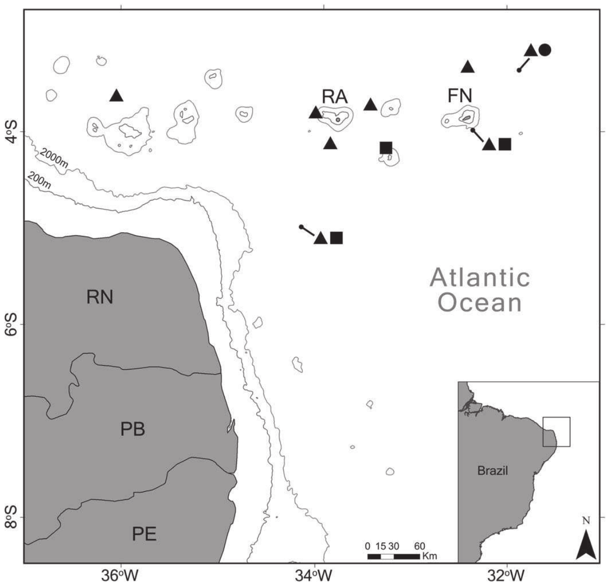

Fig. 4. Records of *Scopeloberyx opercularis* (circle), *Scopeloberyx opisthopterus* (square), and *Scopelogadus mizolepis* (triangle) off northeastern Brazil collected during the ABRACOS surveys. Tip of arrow indicates same collection locality for different species. FN–Fernando de Noronha Archipelago; PB–Paraíba; PE–Pernambuco; RA–Rocas Atoll; RN–Rio Grande do Norte.

origins (5% SL or less vs. 7.5% SL or more) and number of gill rakers (23 or more [rarely 22] vs. 21 or fewer [rarely 22]). *Scopeloberyx opercularis* differs from *S. rubriventer* by the HL (39.0–44.9% SL vs. 46.1–47.8% SL; Keene, 1987; this study). In a recent review, Kotlyar (2004b, 2004c, 2005) described three species of *Scopeloberyx*: *S. bannikovi*, *S. pequenoi*, and *S. rossicus*. *Scopeloberyx opercularis* differs from *S. bannikovi* and *S. pequenoi* by the number of gill rakers (23–26 vs. 15–16) and from *S. rossicus* by the number of vertebrae (25–28 [usually 26] vs. 23–25 [usually 24–25]; Keene, 1987; Kotlyar, 2004b, 2004c, 2005; this study). Kotlyar (2004a, 2004b) also recognized *S. opercularis* as a junior synonym of *S. robustus*, and this conclusion is generally accepted (e.g., Kotlyar, 2004a, 2004b; Mincarone et al., 2014). However, the present study follows Keene (1987) and Moore (2003, 2016), which consider *S. opercularis* as a valid species (see Remarks). In addition to characters indicated previously, *S. opercularis* also differs from *S. robustus* by the number of gill rakers (23–25 vs. 19–22; Keene, 1987; this study).

Distribution.—*Scopeloberyx opercularis* occurs in the western Tropical Atlantic between 28°N and 5°S, including the Gulf of Mexico and south of Caribbean Sea, and in the eastern Atlantic between 39°N and 16°S (Keene, 1987). Keene (1987) indicated records of the species in Brazilian waters off southeastern São Pedro e São Paulo Archipelago (01°20′S, 27°37′W; 01°44′S, 27°44′W), in addition to records outside the Brazilian EEZ. The species was also recorded in Brazilian waters off northern Bahia State (Mincarone et al., 2014; as *Scopeloberyx robustus*). In the present study, a single juvenile specimen was collected off the Fernando de Noronha Archipelago, at 780 m depth (Fig. 4).

Habitat.—According to Keene (1987), most specimens of *S. opercularis* were captured below 700 m depth, and there is no evidence of migratory behavior. The species is, therefore, apparently meso- to bathypelagic.

Remarks.—*Scopeloberyx opercularis* is currently considered as a junior synonym of *S. robustus* (e.g., Ebeling and Weed, 1973; Maul, 1973; Fricke et al., 2020a), but there is still some controversy in the literature about the validity of the species. The synonymy of the two species was followed in the recent revision of Kotlyar (2004b), who concluded that variations in the anal-fin origin in relation to the dorsal-fin origin, number of transverse series of scales, and number of pyloric caeca indicated "a sub-species level of difference between the fishes from the Atlantic Ocean and the Indo-Pacific." However, Keene (1987), in his unpublished dissertation, recognized *S. opercularis* as a distinct and valid species based on the examination of 162 specimens distributed throughout the Tropical Atlantic. Moore (2003, 2016), probably following Keene (1987), also considered the species as valid. Mincarone et al. (2014) accepted that synonymy but indicated that most characters of the single specimen identified by them as *S. robustus* collected off Bahia State, central coast of Brazil, were in accordance with the description of *S. opercularis* provided by Keene (1987). Identification of the specimen examined here is also in accordance with the diagnosis of *S. opercularis* provided by Keene (1987) based on the number of gill rakers: 6–7+16–18 = 23–25 (8+18 in our specimen, including one rudimentary raker in the upper branch) vs. 5–6+14–17 = 19–22 in *S. robustus* according to Kotlyar (2004b, 2004c, 2005). In addition, the eye diameter of the juvenile specimen examined herein (6.3% SL) is within the range for *S. opercularis* (4.2–4.9% in adults and 5.7–6.4% in juveniles) and differs from values proposed for *S. robustus* by Keene (1987; 2.5–3.5% in adults and 4.2–5.8% in juveniles). Therefore, and following Keene's (1987) diagnosis and taxonomic conclusion, we propose that *S. opercularis* is a valid species. With the revalidation of *S. opercularis*, and following Keene (1987), distribution of *S. robustus* is restricted to the North Atlantic between about 30–40°N, and the Tropical and Subtropical Atlantic, east of 30°W, including one record in Brazilian waters, off southeastern São Pedro e São Paulo Archipelago (01°44′S, 27°44′W).

***Scopeloberyx opisthopterus* (Parr, 1933)**

Figure 1J, Table 2

Melamphaes opisthopterus Parr, 1933: 18 (type-locality: off Cat Island, Bahamas, 24°29′N, 75°53′W, 7000 feet [2134 m]; holotype: YPM 2816).

Specimens examined.—NPM 5985, 1, 25.0 mm (Fig. 1J), RV *Antea*, sta. AB2/49A, 04°10′38.1″S, 33°16′07.4″W to 04°10′58.0″S, 33°15′03.8″W, 770–1020 m, 30 April 2017, 2117–2152 h; NPM 5988, 1, 32.0 mm, sta. AB2/39, 04°52′26.9″S, 34°03′32.3″W to 04°50′52.8″S, 34°05′06.5″W, 650–800 m, 24 April 2017, 2149–2237 h; NPM 5989, 2, 29.0–30.0 mm, sta. AB2/44A, 03°52′52.5″S, 32°17′33.3″W to 03°51′43.6″S, 32°16′20.0″W, 850 m, 28 April 2017, 1244–1317 h.

Diagnosis.—*Scopeloberyx opisthopterus* differs from all congeners, except *S. microlepis*, by the horizontal distance between the verticals through the ventral margin of the pectoral fin and the origin of the pelvic fin (4.1–9.9% SL vs. 0–5.9% SL). *Scopeloberyx opisthopterus* differs from *S. microlepis* by the number of pelvic-fin rays (6–8 [rarely 6] vs. 6) and number of vertebrae (25–27 vs. 27–29; Kotlyar, 2005).

Distribution.—*Scopeloberyx opisthopterus* has a circumglobal distribution, occurring in both sides of the Atlantic Ocean from off the United Kingdom to approximately 10°S off Africa (Kotlyar, 2005; Sutton et al., 2020). The species was previously reported in Brazilian waters off São Pedro e São Paulo Archipelago (Keene, 1987; Judkins and Haedrich, 2018). Other records in the western South Atlantic were also restricted to the region of São Pedro e São Paulo Archipelago, but outside the Brazilian EEZ (Keene, 1987; Judkins and Haedrich, 2018). The four specimens collected off the Fernando de Noronha Archipelago, between depths of 650 and 1,020 m (Fig. 4), represent an extension of the distribution of the species in the western South Atlantic.

Habitat.—*Scopeloberyx opisthopterus* is meso- to bathypelagic, with larger post-larvae and all other stages inhabiting depths between 800 and at least 1,550 m, whereas smaller post-larvae occur between 50 and 300 m (Keene et al., 1987).

Scopelogadus mizolepis (Günther, 1878)
Figure 1K, Table 2

Scopelus mizolepis Günther, 1878: 185 (type-locality: south of New Guinea, off Aru Island; Molucca Islands, Indonesia, Arafura Sea, western Pacific, 05°41′S, 134°04′30″E, 800 fathoms [1463 m] depth; holotype: BMNH 1887.12.7.9).

Specimens examined.—NPM 5990, 3, 37.0–49.0 mm (Fig. 1K), RV *Antea*, sta. AB2/41A, 03°19′59.1″S, 32°24′42.1″W to 03°19′31.8″S, 32°25′04.6″W, 430 m, 26 April 2017, 2144–2206 h; NPM 5991, 1, 54.5 mm, sta. AB2/52A, 03°43′16.2″S, 33°25′09.8″W to 03°42′14.2″S, 33°24′36.2″W, 822–984 m, 2 May 2017, 1147–1218 h; NPM 5992, 5, 42.0–58.0 mm, sta. AB2/42A, 03°15′28.1″S, 31°48′29.1″W to 03°15′26.4″S, 31°48′22.9″W, 780 m, 27 April 2017, 1223–1226 h; NPM 5993, 1, 43.0 mm, sta. AB2/59A, 03°38′01.6″S, 36°03′10.6″W to 03°38′07.9″S, 36°02′22.6″W, 700–1113 m, 5 May 2017, 2157–2237 h; NPM 5994, 3, 46.0–70.0 mm, sta. AB2/44A, 03°52′52.5″S, 32°17′33.3″W to 03°51′43.6″S, 32°16′20.0″W, 850 m, 28 April 2017, 1244–1317 h; NPM 5995, 2, damaged–45.0 mm, sta. AB2/39, 04°03′32.3″S, 34°35′22.9″W to 04°50′52.8″S, 34°05′06.5″W, 650–800 m, 24 April 2017, 2149–2237 h; NPM 5996, 3, 37.0–40.0 mm, sta. AB2/53A, 03°48′58.7″S, 33°59′17.1″W to 03°50′05.8″S, 33°58′46.5″W, 610 m, 2 May 2017, 2208–2240 h; NPM 6090, 1, 40.0 mm, sta. AB1/22, 04°07′44.8″S, 33°47′24.5″W to 04°07′00.7″S, 33°48′57.9″W, 525 m, 8 October 2015, 2132–2212 h.

Diagnosis.—Four species of *Scopelogadus* are currently considered as valid, with only *S. beanii* and *S. mizolepis* occurring in the Atlantic (Fricke et al., 2020a). *Scopelogadus mizolepis* differs from *S. beanii* by the number of gill rakers 21–26 (6–8+15–18) vs. 26–32 (8–10+18–22; but see Remarks), and by the stomach noticeably darkened posteriorly (vs. stomach not darkened posteriorly; Sutton et al., 2020).

Distribution.—*Scopelogadus mizolepis* occurs in all oceans except the eastern Pacific (Kotlyar, 2020). In the Atlantic, the species is reported between 43°N and 30°S (Ebeling and Weed, 1973; Keene, 1987; McEachran and Fechhelm, 1998; Moore, 2016; Sutton et al., 2020). Several records are known in the western South Atlantic and also off Ascension Island (Keene, 1987; Judkins and Haedrich, 2018). In Brazilian waters, the species was previously reported off São Pedro e São Paulo Archipelago, Vitória-Trindade Seamount Chain (Keene, 1987), Rocas Atoll, Fernando de Noronha Archipelago (Judkins and Haedrich, 2018), and off Rio de Janeiro State, southeastern Brazil (Costa and Mincarone, 2010; Mincarone et al., 2014). The 19 specimens identified here as *S. mizolepis* were collected near the Fernando de Noronha Archipelago, Rocas Atoll, and the seamounts off Rio Grande do Norte State, between depths of 430 and 1,113 m (Fig. 4).

Habitat.—The species is meso- to bathypelagic, with adults collected below 500 m and post-larvae and juveniles collected between depths of 50 and 300 m (Ebeling and Weed, 1973; McEachran and Fechhelm, 1998).

Remarks.—There is some inconsistency in values of the number of gill rakers on the first gill arch presented by Kotlyar (2020) in his recent review of *S. mizopelis*. In the diagnosis (Kotlyar, 2020: 4), it is stated "on first branchial arch, 16–24 (usually 19–21) rakers," whereas in the description, presented a few lines later in the same page, it is mentioned "(6–8)+1+(12–17) = 19–25" as the number of gill rakers on the first gill arch. Variation in the number of gill rakers on the first gill arch of the 19 specimens of *S. mizolepis* examined here (22–25; Table 2) is in accordance with values presented by both Kotlyar (2020: description) and Sutton et al. (2020).

Two subspecies of *Scopelogadus mizolepis* were recognized by Ebeling and Weed (1973): *Scopelogadus mizolepis bispinosus* (Gilbert 1915), from the eastern Tropical Pacific, and *Scopelogadus mizolepis mizolepis* (Günther 1878), from the Tropical Atlantic and Central Pacific. These subspecies are not considered herein, as in Iwasaki (2009) and Mincarone et al. (2014). However, according to Kotlyar (2020), the two subspecies of *S. mizolepis* proposed by Ebeling and Weed (1973) actually represent species that await formal recognition at that level.

Cetomimidae

The Cetomimidae (whalefishes) includes meso- and bathypelagic fishes occurring in all oceans between 52°N and 72°S (Paxton, 1989). After Johnson et al.'s (2009) study, the number of species in the family became rather uncertain, as molecular data revealed that species belonging to the Mirapinnidae and Megalomycteridae are, in fact, larvae and males, respectively, of the Cetomimidae, which was previously known only by females. About 21 to 26 nominal species belonging to nine genera have been recognized as valid in the Cetomimidae (Paxton, 1989; Johnson et al., 2009; Nelson et al., 2016; Fricke et al., 2020b), with several species still lacking formal description (Paxton, 1989; Nelson et al., 2016). The Cetomimidae comprises one of the most species-rich groups in the bathypelagic zone (1,000–4,000 m) and it is suspected that this is the most abundant fish family below 1,800 m (Paxton, 1989; Nelson et al., 2016). However, records of the family in the western South Atlantic are still scarce (e.g., Paxton, 1989; Mincarone et al., 2014). Cetomimid fishes are mainly recognized by an elongated body, enormous mouth extending far behind eye, reduced or rudimentary eyes, absence of scales, and pelvic fins totally absent in females, usually absent in males, and jugular in juveniles (Paxton, 1989; Johnson et al., 2009; Mincarone et al., 2014; Nelson et al., 2016).

***Cetomimus* sp. 1**

Figure 5A, Table 3

Specimens examined.—NPM 5004, 1, 65.1 mm, RV *Antea*, sta. AB2/16, 07°36′14.4″S, 33°59′33.8″W to 07°36′49.3″S, 33°57′18.7″W, 680 m, 14 April 2017, 2153–2239 h; NPM 5005, 1, 62.5 mm (Fig. 5A), sta. AB2/42A, 03°15′28.1″S, 31°48′29.1″W to 03°15′26.4″S, 31°48′22.9″W, 780 m, 27 April 2017, 1223–1226 h.

Diagnosis.—*Cetomimus* has no single, derived character that distinguishes it from other genera of the Cetomimidae (Paxton, 1989). Three free branchial arches are present in *Cetomimus*, and also in *Rhamphocetichthys* and *Gyrinomimus*. *Cetomimus* differs from *Rhamphocetichthys* by having a cavernous lateral-line system formed by large canals pierced by wide pores on the head and body (vs. absence of these canals), a much shorter, rounded snout (vs. elongated and pointed snout), and by the absence of ventral pharyngeal tooth plates (vs. presence of ventral pharyngeal tooth plates). *Cetomimus* is most similar to *Gyrinomimus*, differing from this genus by the shape of teeth (short, in indistinct diagonal rows vs. long, in distinct, usually longitudinal, rows) and by the shape of the vomerine tooth patch (round or elliptical and dome shaped vs. rectangular or laterally elongate and flat; Paxton, 1989).

Distribution.—Species of *Cetomimus* are reported from the Atlantic and Indo-Pacific Oceans, ranging from 41°N to 57°S in the Pacific and from 41°N to 40°S in the Atlantic (Paxton, 1989). Two specimens badly damaged during the trawl (NPM 5004 and 5005) were collected off Pernambuco State and the Fernando de Noronha Archipelago, between depths of 680 and 780 m (Fig. 6). Those specimens represent the first confirmed records of the genus *Cetomimus* in Brazilian waters and some of the few records in the western South Atlantic.

Habitat.—Species of *Cetomimus* are meso- to bathypelagic, ranging from depths between 500 and approximately 3,300 m (Paxton, 1989; Tolley et al., 1989; Angulo, 2015; Paxton et al., 2016). Juvenile specimens have been recorded in shallow waters (Paxton et al., 2016).

Remarks.—*Cetomimus* currently includes seven nominal species, and at least five species await description (Paxton, 1989). The seven species considered as valid are: *Cetomimus compunctus*, from the western North Pacific and the western South and eastern Central Atlantic (Paxton et al., 2016); *Cetomimus craneae*, from Bermuda (Harry, 1952); *Cetomimus gillii*, from the Atlantic, eastern Pacific, and western Indian Oceans (Angulo, 2015; Paxton et al., 2016); *Cetomimus hempeli*, from the Atlantic Ocean and possibly the North Pacific (Paxton et al., 2016); *Cetomimus kerdops*, from the Bahamas (Parr, 1934; Moore and Boardman, 1991); *Cetomimus picklei*, from the eastern South Atlantic (Paxton and Bray, 1986); and *Cetomimus teevani*, from the western Atlantic (Harry, 1952). The identification at the species level of the two specimens reported here based on the ABRACOS collection (NPM 5004 and 5005; *Cetomimus* sp. 1) was not possible due to their poor state of preservation. Both specimens are somewhat distorted, and the skin is almost completely unattached to the remaining integument. Another specimen of the genus (MNRJ 26794) was identified as *Cetomimus* sp. 2 (Fig. 5B), collected off Espírito Santo State, southeastern Brazil (19°42′34.1″S, 38°32′01.8″W to 19°42′41.1″S, 38°36′57.7″W), between depths of 875 and 942 m. The skin of specimen MNRJ 26794 is also damaged, compromising the observation of lateral-line pores and flaps and of the cavernous tissue. Nevertheless, some measurements were successfully obtained, in addition to the number of vertebrae, and of the dorsal-, anal-, and pectoral-fin rays (Table 3). *Cetomimus* sp. 1 differs from *Cetomimus* sp. 2 in the shape of the vomerine tooth patch (oval vs. triangular, with its anterior tip narrower) in addition to meristic and morphometric data provided in Table 3. Therefore, at least two species of the genus occur in Brazilian waters, one of them recorded off northeastern Brazil (NPM 5004 and 5005, *Cetomimus* sp. 1) and the other collected off Espírito Santo State (MNRJ 26794, *Cetomimus* sp. 2).

***Cetostoma regani* Zugmayer, 1914**

Figure 5C, Table 3

Cetostoma regani Zugmayer, 1914: 4 (type locality: eastern Atlantic, 30°45′30″N, 25°47′W, 0–2000 m depth; holotype: MOM 0091-1729).

Specimens examined.—NPM 3185, 1, 81.0 mm (Fig. 5C), RV *Antea*, sta. AB1/22, 04°07′44.8″S, 33°47′24.5″W to 04°07′00.7″S, 33°48′57.9″W, 525 m, 8 October 2015, 2132–2212 h; NPM 5001, 1, 96.8 mm, sta. AB2/54B, 03°45′17.2″S, 34°41′04.0″W to 03°44′39.2″S, 34°40′04.5″W, 830–1030 m, 3 May 2017, 1311–1347 h; NPM 5002, 2, 85.2–113.7 mm, sta. AB2/42A, 03°15′28.1″S, 31°48′29.1″W to 03°15′26.4″S, 31°48′2.9″W, 780 m, 27 April 2017, 1223–1226 h; NPM 5151, 1, 95.0 mm, sta. AB2/44A, 03°52′52.5″S, 32°17′33.3″W to 03°51′43.6″S, 32°16′20.0″W, 850 m, 28 April 2017, 1244–1317 h.

Diagnosis.—*Cetostoma regani* is the single species of the genus, and it differs from other genera of the Cetomimidae by the number of dorsal-fin rays (29–37 vs. 13–22), number of anal-fin rays (26–34 vs. 13–20), dorsal- and anal-fin bases elevated in relation to the body (vs. not elevated), predorsal length (1.7–2.0 in SL vs. 1.3–1.6 in SL), a very long, narrow copular tooth patch present as three separate dentigerous plates (vs. one solid plate), the gill slit behind the angle of fourth gill arch tiny and tubular (vs. gill slit behind the ventral arm of fourth gill arch either elongate or absent), numerous small skin ridges along the belly from the pectoral-fin base to the anus (vs. absence of skin ridges), and the fin membrane between last ten anal-fin rays voluminous and curtain-like (vs. fin membrane between posterior anal-fin rays not voluminous and not curtain-like; Paxton, 1989).

Distribution.—*Cetostoma regani* has the broadest distribution of all cetomimids, occurring in the Atlantic and Indo-Pacific Oceans (except the eastern South Pacific), from 50°N to 40°S (Paxton et al., 2016). The species was previously recorded in Brazilian waters off São Pedro e São Paulo Archipelago, North Atlantic, at 02°41′N, 28°56′W, 0–ca. 1,100 m depth (MCZ 42844), and at 00°17′N, 27°31′W, 0–ca. 300 m depth (MCZ 42843; Paxton, 1989). In this study, five specimens were

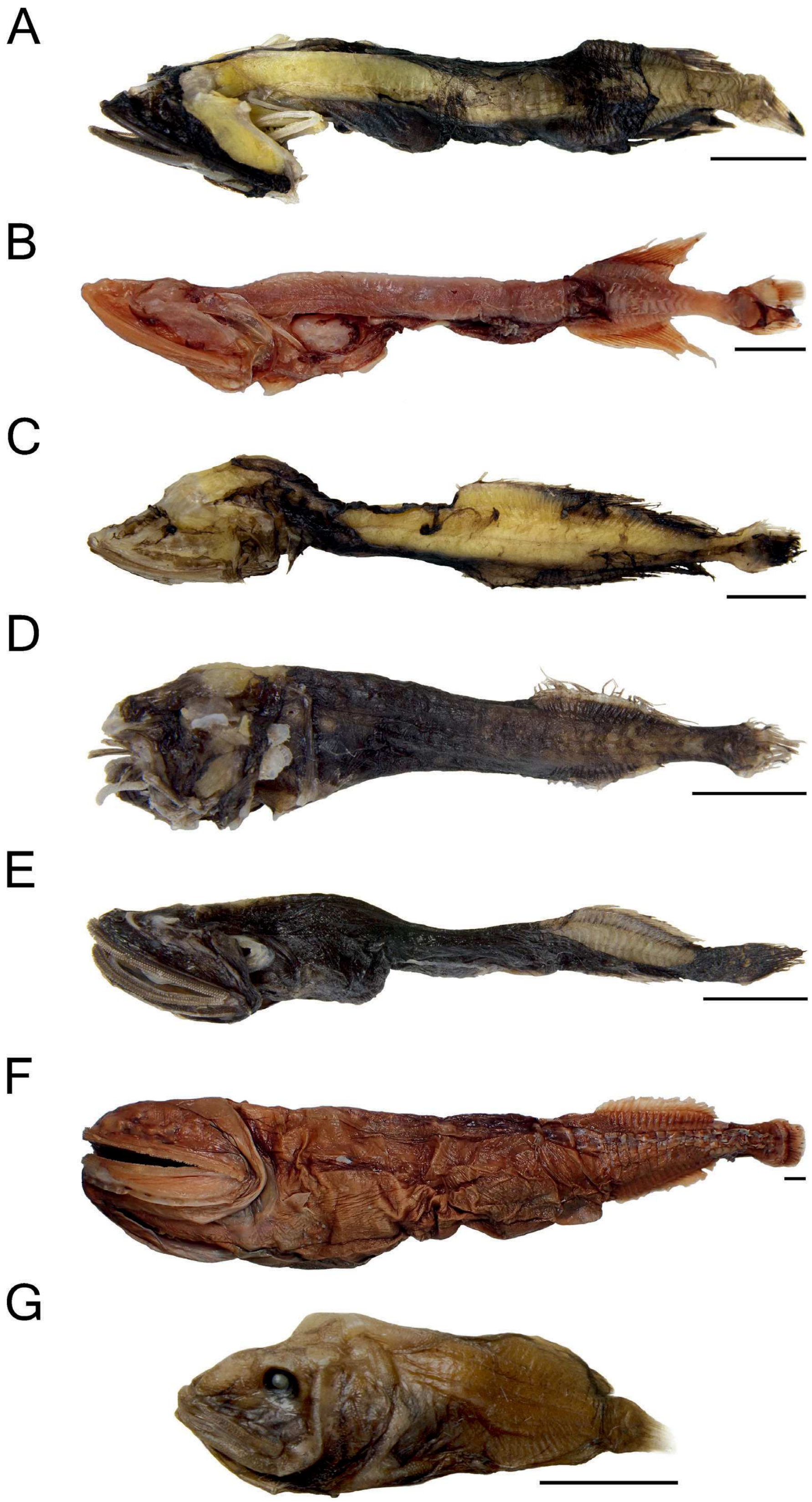

Fig. 5. Species of Cetomimidae reported in this study: (A) *Cetomimus* sp. 1, NPM 5005, 62.5 mm SL; (B) *Cetomimus* sp. 2, MNRJ 26794, 92.0 mm SL; (C) *Cetostoma regani*, NPM 3185, 81.0 mm SL; (D) *Ditropichthys storeri*, NPM 5003, 49.0 mm SL; (E) *Gyrinomimus bruuni*, NPM 5000, 66.2 mm SL; (F) *Gyrinomimus* cf. *bruuni*, MNRJ 26793, 305.0 mm SL; (G) *Rondeletia loricata*, NPM 3197, 32.3 mm SL. Scale bar = 1 cm.

Table 3. Morphometric and meristic data of species of Cetomimidae and Rondeletiidae reported in this study (d = damaged).

Species	*Cetomimus* sp. 1	*Cetomimus* sp. 2	*Cetostoma regani*	*Ditropichthys storeri*	*Gyrinomimus bruuni*	*Gyrinomimus* cf. *bruuni*	*Gyrinomimus* sp.	*Rondeletia loricata*
n	2	1	5	1	2	1	1	3
Standard length (SL, mm)	62.5–65.1	92.0	81.0–113.7	49.0	60.0–66.2	305.0	95.0	32.3–78.4
Measurements in % SL								
Head length	d–30.1	26.0	21.4–28.0	33.7	25.5–26.9	27.9	34.8	44.2–45.9
Head width	7.2–10.7	–	6.4–7.6	16.5	–	16.4	19.5	17.2–19.8
Eye diameter	–	–	–	–	–	1.0	1.7	6.5–7.4
Postorbital length	–	–	–	–	–	22.0	24.2	16.4–20.0
Snout length	–	9.5	11.9	–	10.6–10.7	8.4	11.6	18.6–20.0
Upper jaw length	d–29.9	23.0	16.1–19.6	–	24.3–26.4	23.0	32.6	25.0–26.0
Body depth	12.9–13.3	–	6.9–9.0	21.8	–	23.3	–	32.1–37.5
Prepectoral length	36.2–38.7	–	23.2–29.5	36.1	27.7–30.7	30.0	–	43.3–48.5
Prepelvic length	–	–	–	–	–	–	–	60.1–69.3
Predorsal length	72.6–75.0	66.0	54.5–58.8	69.4	74.0–75.5	71.5	67.4	66.6–72.8
Preanal length	73.6–76.0	66.0	55.8–60.0	70.4	74.6–76.7	72.1	–	68.1–74.0
Dorsal-fin base length	16.3–16.4	13.0	32.2–40.2	26.7	15.7–15.9	17.0	18.0	19.4–27.9
Anal-fin base length	16.0–16.9	13.9	26.3–32.7	20.4	13.6–13.8	16.6	19.0	16.6–27.9
Caudal peduncle length	9.9–11.5	10.8	9.5–12.7	15.3	8.3–9.0	10.5	12.0	7.7–10.8
Caudal peduncle depth	5.4–5.9	3.3	3.3–4.3	6.0	5.1–5.2	4.4	7.4	8.3–12.4
Head length (HL, mm)	d–17.1	23.9	–	–	d–17.8	85.0	33.1	–
Measurements in % HL								
Copular tooth plate length	d–29.2	33.5	–	–	d–27.0	27.0	30.2	–
Copular tooth plate width max.	d–7.6	6.7	–	–	d–19.1	10.6	13.6	–
Copular tooth plate width min.	d–5.8	4.2	–	–	d–7.9	5.3	12.0	–
Copular tooth plate ratio (max/min)	d–1.3	1.6	–	–	d–2.4	2.0	1.1	–
Counts								
Dorsal-fin rays	15–16	18	30–34	21	20	19	16	11–12
Anal-fin rays	16	17	27–32	16	18–19	18	15	11–12
Pectoral-fin rays	15–20	16	17–20	18	16–18	16	18	7–8
Pelvic-fin rays	–	–	–	–	–	–	–	4–6
Principal caudal rays (upper/lower)	7–8/9	–	7–9/7–10	6/7	8/9–10	8/9	8/9	10–11/10
Procurrent caudal rays (upper/lower)	2–3/2–3	–	–	3/2	3/2	5/4	5/3	5/2–3
Vertebrae (precaudal + caudal)	32+17	33+21	22–26+23–26	22+17	36–38+19–21	38+20	–	10–11+15–16
Vertebrae (total)	48–49	54	48–50	39	57	58	48	25–27
Jaws teeth rows (upper/lower)	–	–	–	–	d–3–4/3–4	6–9/7–10	3/3	–
Vomerine teeth rows	–	–	–	–	2	indistinct	3	–

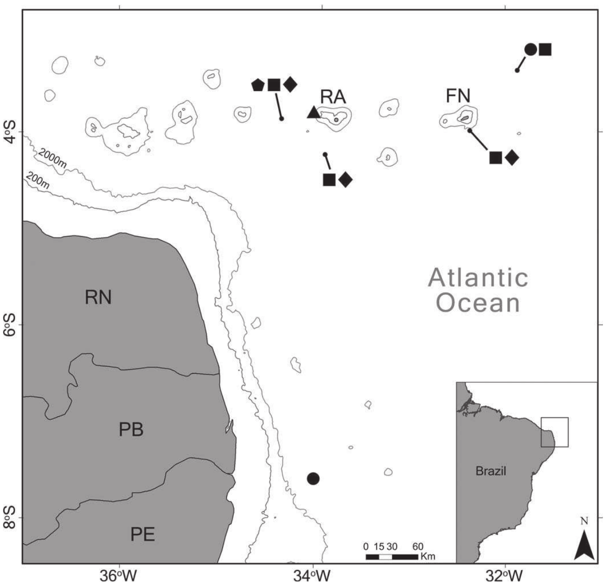

Fig. 6. Records of *Cetomimus* sp. 1 (circle), *Cetostoma regani* (square), *Ditropichthys storeri* (triangle), *Gyrinomimus bruuni* (pentagon), and *Rondeletia loricata* (diamond) off northeastern Brazil collected during the ABRACOS surveys. Tip of arrow indicates same collection locality for different species. FN–Fernando de Noronha Archipelago; PB–Paraíba; PE–Pernambuco; RA–Rocas Atoll; RN–Rio Grande do Norte.

collected off the Fernando de Noronha Archipelago, the Rocas Atoll, and the seamounts off Rio Grande do Norte State, between depths of 525 and 1,030 m (Fig. 6). In addition, another specimen identified as *C. regani* (MNRJ 26795), collected off Espírito Santo State (21°12′17.6″S, 40°00′53.0″W to 21°09′34.6″S, 40°00′27.7″W) between depths of 1,333 and 1,390 m, extends the occurrence of the species further south in Brazilian waters. Specimens reported here also represent some of the few confirmed records of the species in the western South Atlantic (Paxton, 1989).

Habitat.—Females of *Cetostoma regani* are meso- to bathypelagic, with adults collected between 100 and 3,700 m, whereas juveniles are reported from shallow waters (Paxton, 1989; Paxton et al., 2016). Males are bathypelagic (Paxton et al., 2016).

Remarks.—In this study, only females were collected. The absence of males might be related to the depth of collections (maximum 1,113 m), which did not reach the bathypelagic zone.

***Ditropichthys storeri* (Goode and Bean, 1895)**

Figure 5D, Table 3

Cetomimus storeri Goode and Bean, 1895: 453 (type locality: western North Atlantic, 39°03′15″N, 70°50′45″W, 1535 fathoms [2807 m] depth; holotype: USNM 35634).

Specimen examined.—NPM 5003, 1, 49.0 mm (Fig. 5D), RV *Antea*, sta. AB2/53A, 03°48′58.7″S, 33°59′17.1″W to 03°50′05.8″S, 33°58′46.5″W, 610 m, 2 May 2017, 2208–2240 h.

Diagnosis.—*Ditropichthys storeri* is the single species of the genus, differing from all other genera in the Cetomimidae by having fully developed, club-shaped gill rakers, a pair of thin dermal folds along the abdomen, and anal lappets connected as an unbroken fold of skin containing lappet scales over the anal-fin base (Paxton, 1989).

Distribution.—*Ditropichthys storeri* has a circumglobal distribution between 45°N and 45°S (Paxton et al., 2016). The absence of the species in some regions may be related to the lack of collecting efforts (Paxton, 1989). The species was previously recorded in the western South Atlantic in five localities off Uruguay and Argentina (Paxton, 1989). A single specimen of *D. storeri* was collected off the Rocas Atoll, at 610 m depth (Fig. 6). This represents the first record of the species in Brazilian waters and one of the few confirmed records in the western South Atlantic (Paxton, 1989).

Habitat.—Small specimens of *D. storeri* (<40 mm) are mesopelagic, occurring from 650 to 1,000 m, whereas larger specimens (>60 mm) are bathypelagic, occurring from 1,000 to approximately 5,000 m (Paxton et al., 2016).

***Gyrinomimus bruuni* Rofen, 1959**

Figure 5E, Table 3

Gyrinomimus bruuni Rofen, 1959: 257 (type locality: off Kenya, 05°25′S, 47°09′E, over 4820 m depth; holotype: ZMUC P23452).

Specimens examined.—NPM 5000, 2, 60.0–66.2 mm (Fig. 5E), RV *Antea*, sta. AB2/54B, 03°45′17.2″S, 34°41′04.0″W to 03°44′39.2″S, 34°40′04.5″W, 830–1030 m, 3 May 2017, 1311–1347 h.

Diagnosis.—*Gyrinomimus* differs from other genera of the Cetomimidae, except *Rhamphocetichthys* and *Cetomimus*, by having three free branchial arches (vs. four). *Gyrinomimus* differs from *Rhamphocetichthys* by having a round snout (vs. beak-like snout), and by the presence of tooth plates on the second and third branchial arches (vs. plates absent). It differs from *Cetomimus* by having jaw teeth arranged in distinct longitudinal rows (vs. jaw teeth arranged in indistinct diagonal rows), by the length of the teeth (except the newest teeth) more than three times the width of its base (vs. less than two times the width of its base), and by the shape of the vomerine tooth plate, which is flat and rectangular or oval (vs. domed and round or rarely oval; Paxton, 1989). *Gyrinomimus bruuni* differs from its congeners by the following characters: number of dorsal-fin rays (19–20 vs. 14–17 in *G. andriashevi*, *G. grahami*, *G. myersi*, and *G. parri*); number of anal-fin rays (18–20 vs. 14–17 in *G. andriashevi*, *G. grahami*, *G. myersi*, and *G. parri*); number of lateral-line pores (19 vs. 14–15 in *G. myersi* and *G. parri*, and 23 in *G. andriashevi*); and pectoral-fin length (6.2–9.8% SL vs. 2.9% SL in *G. andriashevi*; Parr, 1934; Richardson and Garrick, 1946; Rofen, 1959; Bigelow, 1961; Fedorov et al., 1987; Paxton, 1989).

Distribution.—*Gyrinomimus bruuni* has a circumglobal distribution between 30°N and 10°S (Paxton, 2003). This is the first report of this species in Brazilian waters, and it is based on two specimens collected off the Rocas Atoll, between depths of 830 and 1,030 m (Fig. 6). Those specimens also represent one of the few records of the genus in the South Atlantic and apparently the first confirmed record of the species in the region (see Remarks).

Habitat.—Maximum depth reported for the species is 1,805 m (MNRJ 26793, this study). Other species of the genus are bathypelagic, captured between 1,594 and 2,350 m (Mincarone et al., 2014; Paxton et al., 2016).

Remarks.—In addition to *G. bruuni*, four other species of *Gyrinomimus* are currently regarded as valid: *G. andriashevi*, from the Antarctic Ocean; *G. grahami*, cosmopolitan in the South Hemisphere; *G. myersi*, circumglobal; and *G. parri*, from the western Atlantic and western Pacific (Paxton, 1989; Paxton et al., 2016; Fricke et al., 2020a). Two species groups of *Gyrinomimus* in the North Atlantic are recognized: the *bruuni* species group, with *G. bruuni* and two undescribed species, and the *myersi* species group, with *G. myersi*, *G. parri*, and one undescribed species (Moore et al., 2003; Paxton et al., 2016).

Mincarone et al. (2014) reported the first specimen of *Gyrinomimus* in Brazilian waters (MNRJ 36421, 95 mm SL), collected off Rio de Janeiro State, southeastern Brazil. This specimen was highly damaged and its identification at the species level was not possible. A comparison made between the specimens reported here as *G. bruuni* with the one reported by Mincarone et al. (2014) as *Gyrinomimus* sp. clearly indicates that the latter belongs to a different species. *Gyrinomimus* sp. differs from *G. bruuni* by the following characters: three distinct gill arches bearing well-developed holobranchs, a reduced gill slit behind the ventral arm of the third arch, near the angle vs. four distinct gill arches bearing well-developed holobranchs, a relatively well-developed gill slit behind the ventral arm of the third arch; holobranchs on fourth gill arch highly undeveloped, in the shape of tubercles vs. holobranchs more developed (0.5 times length of holobranchs on first gill arch) and with a regular shape; number of dorsal-fin rays (16 vs. 20); number of anal-fin rays (15 vs. 18–19); number of distinct teeth rows on vomer (3 vs. 2); number of vertebrae (48 vs. 57); middle portion of preural centra distinctly constricted vs. centra only slightly constricted; HL (34.8% SL vs. 25.5–26.9% SL); upper-jaw length (32.6% SL vs. 24.3–26.4% SL); predorsal length (67.4% SL vs. 74.0–75.5% SL); dorsal-fin base length (18.0% SL vs. 15.7–15.9% SL); anal-fin base length (19.0% SL vs. 13.6–13.8% SL); caudal-peduncle length (12.0% SL vs. 8.3–9% SL); and caudal peduncle depth (7.4% SL vs. 5.1–5.2% SL; Table 3).

In addition to *G. bruuni* and *Gyrinomimus* sp., another specimen of the genus (MNRJ 26793, 305 mm SL) collected off Rio de Janeiro State, from 21°28′36.7″S, 39°40′18.2″W to 21°25′31.4″S, 39°40′26.6″W, between depths of 1,790 and 1,805 m, was tentatively identified as *Gyrinomimus* cf. *bruuni*, but it may represent an undescribed species (Fig. 5F, Table 3; Paxton, 1989; J. Paxton, pers. comm.). Morphometric and meristic data comparing *G. bruuni* "stricto sensu" (NPM 5000, 2 specimens) and *Gyrinomimus* cf. *bruuni* (MNRJ 26793) are presented in Table 3. Other characters that differ between *G. bruuni* and *Gyrinomimus* cf. *bruuni* are: the shape of preural centra (middle portion of the centra only slightly constricted vs. distinctly constricted) and the number of teeth rows on upper (3–4 vs. 6–9, increasing anteriorly) and lower jaws (3–4 vs. 7–10, increasing anteriorly). *Gyrinomimus* cf. *bruuni* also has cavernous tissue up to above the third anal-fin ray, about three anal lappets, about 21–22 lateral-line pores, and the length of the holobranchs on the fourth arch is 0.54 the length on those of the first arch (J. Paxton, pers. comm.; present study). A further specimen of *Gyrinomimus* (MCZ 50688), collected off Rio Grande do Sul State, southern Brazil, in 1967, referred to as *Gyrinomimus* sp. by Mincarone et al. (2014), still seems to be lost.

Rondeletiidae

The Rondeletiidae includes only two species, *Rondeletia bicolor* Goode and Bean 1895 and *Rondeletia loricata* Abe and Hotta 1963 (Paxton et al., 2001). Both species are meso- and bathypelagic in tropical and temperate waters, with *R. bicolor* occurring in the Atlantic and Pacific Oceans, and *R. loricata* having an almost circumglobal distribution (Paxton and Trnski, 2003; Kobyliansky et al., 2020). *Rondeletia* is mainly recognized among the Stephanoberycoidei by having the following combination of characters: large mouth with jaws not extending beyond the posterior margin of eye; pelvic fins with five or six soft rays; lack of teeth on basibranchials; lateral line as vertical rows of papillae without supporting internal scales; and lack of external body scales (Paxton and Trnski, 2003).

Rondeletia loricata Abe and Hotta, 1963

Figure 5G, Table 3

Rondeletia loricata Abe and Hotta, 1963: 43, Pls. 11 (figs. 1–7), 12 (figs. 8–9) (type locality: off Kesennuma, Miyagi Prefecture, Japan, 750 m depth; holotype: ZUMT 52196).

Specimens examined.—NPM 3197, 1, 32.3 mm (Fig. 5G), RV *Antea*, sta. AB1/22, 04°07′44.8″S, 33°47′24.5″W to 04°07′00.7″S, 33°48′57.9″W, 525 m, 8 October 2015, 2132–2212 h; NPM 4144, 1, 78.4 mm, sta. AB2/54B, 03°45′17.2″S, 34°41′04.0″W to 03°44′39.2″S, 34°40′04.5″W, 830–1030 m, 3 May 2017, 1311–1347 h; NPM 4228, 1, 46.4 mm, sta. AB2/44A, 03°52′52.5″S, 32°17′33.3″W to 03°51′43.6″S, 32°16′20.0″W, 850 m, 28 April 2017, 1244–1317 h.

Diagnosis.—*Rondeletia loricata* differs from *R. bicolor* by the number of vertical rows of lateral-line pores (14–19 vs. 24–26), the lack of a bony sphenotic hook over the orbit (vs. presence of a bony sphenotic hook), and supratemporal and cleithrum with large posterior extensions (vs. absence of large posterior extensions; Paxton, 1974; Paxton and Trnski, 2003).

Distribution.—*Rondeletia loricata* has an almost circumglobal distribution, being reported from 60°N to 50°S in all oceans (Paxton, 1974; Bast and Klinkhardt, 1990; Kotlyar, 1996; Paxton et al., 2001; Paxton and Trnski, 2003; Kharin, 2006; Balanov and Kharin, 2009; Møller et al., 2010; Mincarone et al., 2014). Records of the species in the western South Atlantic are restricted to off Argentina and Brazil (Figueroa et al., 1998; Mincarone et al., 2014). The species was first reported in Brazilian waters by Mincarone et al. (2014), based on three specimens collected off Bahia and Espírito Santo States, between depths of 837 and 1,049 m. *Rondeletia loricata* is recorded here based on three specimens collected off Rocas Atoll, the Fernando de Noronha Archipelago, and seamounts off Rio Grande do Norte State, between depths of 525 and 1,030 m (Fig. 6).

Table 4. Species of the Stephanoberycoidei recorded in Brazilian waters. * The four specimens of *B. rufa* (and only known records of the species off Brazil) reported as missing by Mincarone et al. (2014) have now been located, in lots MNRJ 42181, 42182, 42183, and 42184.

Species	Distribution	References
Barbourisiidae		
Barbourisia rufa	Circumglobal	Mincarone et al. (2014)*
Cetomimidae		
Cetostoma regani	Circumglobal, except eastern South Pacific	Paxton (1989), present study
Cetomimus sp. 1	off northeastern Brazil	present study
Cetomimus sp. 2	off Espírito Santo, Brazil	present study
Ditropichthys storeri	Circumglobal	present study
Gyrinomimus bruuni	Circumglobal	present study
Gyrinomimus cf. *bruuni*	off Rio de Janeiro, Brazil	present study
Gyrinomimus sp.	off Rio de Janeiro, Brazil	Mincarone et al. (2014); present study
Gibberichthyidae		
Gibberichthys pumilus	western Tropical Atlantic	Asano Filho et al. (2005); Mincarone et al. (2014)
Melamphaidae		
Melamphaes eulepis	Circumtropical, except eastern Pacific	present study
Melamphaes hubbsi	Tropical South Atlantic	Judkins and Haedrich (2018)
Melamphaes leprus	Tropical Atlantic	present study
Melamphaes longivelis	Circumglobal, except eastern Pacific	present study
Melamphaes polylepis	Circumglobal	Keene (1987); Mincarone et al. (2014); Eduardo et al. (2020a); present study
Melamphaes typhlops	Atlantic	Keene (1987); Mincarone et al. (2014); present study
Melamphaes sp.	off Rio Grande do Norte, Brazil	present study
Poromitra megalops	Circumtropical	Keene (1987); Judkins and Haedrich (2018); present study
Poromitra sp.	off Brazil	Mincarone et al. (2014); present study
Scopeloberyx opercularis	Tropical Atlantic	Keene (1987); Mincarone et al. (2014, as *S. robustus*); present study
Scopeloberyx opisthopterus	Circumglobal	Keene (1987); Judkins and Haedrich (2018); present study
Scopeloberyx robustus	Circumglobal, except eastern Pacific	Keene (1987); Judkins and Haedrich (2018)
Scopelogadus beanii	Circumglobal	Judkins and Haedrich (2018)
Scopelogadus mizolepis	Circumglobal	Keene (1987); Costa and Mincarone (2010); Mincarone et al. (2014); Judkins and Haedrich (2018); present study
Stephanoberycidae		
Acanthochaenus luetkenii	Atlantic, Indian and South Pacific	Mincarone et al. (2014)
Stephanoberyx monae	western Atlantic	Mincarone et al. (2014)
Rondeletiidae		
Rondeletia bicolor	Atlantic and Pacific	Mincarone et al. (2014)
Rondeletia loricata	Circumglobal	Mincarone et al. (2014); present study

Habitat.—The species is meso- to bathypelagic, with most records of adults below 400 m, with a maximum record of 1,200 m depth (Paxton et al., 2001; Kharin, 2006; Balanov and Kharin, 2009). Larvae (3.5–4.6 mm SL) are captured in shallow waters, between 8 and 40 m, and juveniles (<20 mm SL) are captured between 110 and 175 m (Paxton et al., 2001).

DISCUSSION

Scientific expeditions conducted since the last decades of the 20th century resulted in new records and new species descriptions of several groups of deep-sea fishes in Brazilian waters, substantially contributing to the understanding of this important component of the diversity in the western South Atlantic (e.g., Figueiredo et al., 2002; Melo, 2008; Santos and Figueiredo, 2008; Carvalho-Filho et al., 2010; Melo et al., 2010; Lima et al., 2011; Braga et al., 2014; Pinheiro et al., 2015; Eduardo et al., 2018, 2019a, 2019b, 2020a, 2020b; Mincarone et al., 2019, 2020). However, knowledge on the deep-sea fish diversity of the western South Atlantic is still insufficient (Paxton, 1989; Mincarone et al., 2014; Nielsen et al., 2015; Reis et al., 2016). The eight new records and nine range extensions of species of the Stephanoberycoidei reported here for Brazil, for instance, were based on two relatively short deep-sea collecting campaigns, indicating that a substantial diversity of deep-sea fishes is still waiting to be discovered and properly studied in the region.

With the new records presented here, a total of 26 species of the Stephanoberycoidei are reported from off Brazil (Keene, 1987; Paxton, 1989; Mincarone et al., 2014; Judkins and Haedrich, 2018; Table 4). Based on the distribution of melamphaids reported by Ebeling (1962) and Keene (1987), other species of the family that potentially occur in Brazilian waters are: *Melamphaes suborbitalis* (recorded in the central Atlantic and off Rio da Prata, between Uruguay and Argentina); *M. microps* (south of 27°S, near the Brazilian EEZ off Rio Grande do Sul State); *M. simus* (central Atlantic); and *Sio nordenskjoldii* (south of 32°S, off Uruguay). *Scopeloberyx nigrescens*, which was considered as a junior synonym of *Scopeloberyx robustus* by Kotlyar (2004b), but considered as valid by Moore (2003, 2016), was also reported from the central Atlantic and, if valid, also potentially occurs off Brazil (Keene, 1987).

The complex taxonomic scenario revealed by the examination of relatively few specimens of *Melamphaes*, *Poromitra*, and *Scopeloberyx* in this study indicates that the systematics of certain components of those genera are still in need of revision, despite Kotlyar's extensive taxonomic work (e.g., Kotlyar, 2004b, 2004c, 2005, 2008a, 2008b, 2009a, 2009b, 2009c, 2010, 2011a, 2011b, 2012a, 2012b, 2013, 2014, 2015a, 2015b, 2015c, 2016a, 2016b, 2016c). Part of the problem might be due to the fact that a substantial number of species in the group have been described based on relatively few specimens or even on a single specimen in some cases, as previously noted by other authors (e.g., Ebeling, 1962; Bartow, 2010). This situation is quite common for deep-sea organisms and might not necessarily represent a problem in itself when species are unambiguously distinct from congeners or are presumably rare or with relatively restricted geographic ranges, for instance. However, some species of the Melamphaidae, particularly those of the genera *Melamphaes*, *Poromitra*, and *Scopeloberyx*, are apparently abundant and have presumably large geographic ranges. Therefore, descriptions or taxonomic revisions of components of those genera based on relatively few specimens patchily distributed over large areas have a worrying tendency of neglecting relevant anatomical variation. The experience accumulated in the last decades indicate that extensive taxonomic studies including proper examination of the type series and a large, truly representative number of specimens on a global scale are required for a more coherent and realistic taxonomic scenario of the group to emerge. In this context, and also based on the results presented by Mincarone et al. (2014), more investments in deep-sea collections in historically neglected regions such as the South Atlantic are still necessary in order to properly assess the diversity of the Stephanoberycoidei.

DATA ACCESSIBILITY

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