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Demersal fish distribution in Northeast Brazil from multifrequency active acoustics and video observation

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Julie SALVETAT

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

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Mar, misterioso mar
Que vem do horizonte
É o berço das sereias
Lendário e fascinante
[Landa das Sereias, Rainha do Mar]

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ABSTRACT

Tropical waters hold major biodiversity hotspots and are priority areas for protection in the context of over-exploration and climate change. Suitable management of marine resources requires comprehensive, spatially explicit, high-quality, and up-to-date data. In that regard, multi-frequency active acoustic is a powerful tool that can provide relevant solutions to the increasing need for comprehensive data. In that framework, this thesis aims at filling some gaps in fish distribution knowledge for two tropical ecosystems of the South Western Tropical Atlantic, an oceanic archipelago, and the neritic coastal ecosystem of Northeast Brazil by using acoustic active methods combined with other approaches. In the first two chapters, we used an innovative integrated method combining acoustic and video data to study fish distribution around the oceanic Archipelago of Fernando de Noronha (FNA). FNA encompasses a marine protected area, preventing extractive biological sampling. Simultaneous scrutinizing of video and echogram allowed discriminating between similar echotypes leading to a classification of all the echoes into ten fish assemblages and two triggerfish species. The most abundant species observed by acoustics was the black triggerfish (*Melichthys niger*). We estimated the *target strength* of this species, a prerequisite for acoustic biomass estimation that we estimated to be 700 tonnes using geostatistics. To provide a detailed comprehensive description of fish distribution and their environment around FNA we analyzed the distribution of fish assemblages in relation to habitat characteristics obtained from acoustic data and video (e.g., depth and sediment type). This comprehensive description allowed highlighting fish hotspots' location and in particular the importance of the shelf-break on the windward side of FNA, which includes well-known fishing hotspots. In contradiction with the expected result, FNA exhibits an asymmetrical fish distribution with a higher concentration on the windward side of the main island as opposed to the higher primary production on the leeward side. These results led us to a revision of the island mass effect for high trophic levels. In the last part of this thesis, we applied the methodology developed above to acoustic data collected continuously along the diel cycle during two surveys performed in different seasons on the neritic environment of the Northeast Brazilian coast. The main objective was to describe the demersal and pelagic fish spatial distribution. For that, we classified fish echoes into eight fish assemblages. The patterns of the distribution of fish total biomass and fish assemblages varied according to the season. The acoustic scape varied along the diel cycle with a higher acoustic response at night due to different gregarious patterns. Many demersal and pelagic fish exhibit diel migrations. This

behavior change is known to affect the acoustic data since fish were more scattered over space and observable at night. Still, the acoustic data highlighted the presence of hotspots along the coast of North-east Brazil in particular a hotspot in the Pernambuco plateau and another in the Rio Grande do Norte shelf. The spatial distribution of fish biomass varied according to season, depth, and distance to the shelf-break. At the end of the manuscript, a discussion is initiated on the perspectives offered by the dataset developed during this thesis, especially for Marine Spatial Planning.

RESUMÉ

Les eaux tropicales contiennent des hauts lieux de biodiversité et sont des zones prioritaires pour la conservation dans le contexte actuel de sur-exploration et de changement climatique. Une gestion adéquate des ressources marines nécessite des données écosystémiques, spatialement explicites, de haute qualité et actualisées. A cet égard, l'acoustique active multifréquence est un outil puissant qui peut apporter une réponse pertinente au besoin croissant de données. Dans ce cadre, cette thèse vise à combler certaines lacunes dans la connaissance de la distribution des poissons pour deux écosystèmes tropicaux de l'Atlantique Tropical Sud-Ouest, un petit archipel océanique et l'écosystème côtier néritique du Nord-Est du Brésil en utilisant des méthodes acoustiques actives combinées à d'autres approches. Dans les deux premiers chapitres de cette thèse, nous avons utilisé une méthode intégrée innovante combinant des données acoustiques et vidéo pour étudier la distribution des poissons autour de l'archipel Fernando de Noronha (FNA). FNA englobe une zone marine protégée, interdisant tout prélèvements. L'examen simultané de la vidéo et des échogrammes a permis de discriminer les échotypes similaires, ce qui a conduit à une classification de tous les échos en assemblages de poissons et en deux espèces de baliste. L'espèce la plus abondante observée par l'acoustique était le baliste noir. Nous avons estimé la target strength de cette espèce, une condition préalable à l'estimation de sa biomasse que nous avons estimée à 700 tonnes en utilisant une méthode géostatistique. Les autres distributions d'assemblages ainsi que la partie "non-poisson" des données ont été analysées en relation avec les caractéristiques de l'habitat obtenues à partir des données acoustiques et de la vidéo telles que la profondeur et le type de sédiment, afin de fournir une description détaillée et complète de la distribution des poissons et de leur environnement autour de l'archipel. Cette description complète a permis de mettre en évidence l'emplacement des hotspots de poissons et en particulier l'importance du plateau continental sur le côté au vent de l'île, qui comprend des hotspots de pêche bien connus à FNA. En contradiction avec le résultat attendu, FNA présente une distribution asymétrique des poissons avec une concentration plus élevée sur le côté au vent de l'île principale par opposition à la production primaire plus élevée sur le côté sous le vent. Cela a conduit à une révision de l'effet d'île pour les niveaux trophiques élevés. Dans la dernière partie de cette thèse, nous avons appliqué la méthodologie développée ci-dessus aux données acoustiques recueillies sur l'environnement néritique de la côte Nord-Est de façon continue de jour comme de nuit et à des saisons différentes. L'objectif principal était de décrire la distribution spatiale des poissons démersaux et pélagiques. Pour cela, nous avons classé les échos de poissons en assemblages de poissons. Le paysage acoustique était très différent la nuit et le jour, avec une réponse acoustique plus élevée la nuit en raison de différences dans les comportements grégaires et dans l'occupation de l'espace. De nombreux poissons démersaux et pélagiques effectuent une migration diurne, qui est associée à l'intensité lumineuse. On sait que ce changement de comportement affecte les données acoustiques. Néanmoins, les données acoustiques ont mis en évidence la présence de hotspots le long de la côte du nord-est du Brésil, en particulier le hotspot du plateau de Pernambuco et celui du plateau de Rio Grande do Norte. La distribution spatiale de la biomasse de poissons varie en fonction de la saison, de la profondeur et de la distance au rebord du plateau. A la fin du manuscrit, une discussion est amorcée sur les perspectives qu'offre le jeu de données développé durant cette thèse, notamment pour le Marine Spatial Planning.

RESUMO

As águas tropicais contêm hotspots de biodiversidade e são áreas prioritárias para proteção no atual contexto de superexploração e mudança climática. O gerenciamento adequado dos recursos marinhos requer dados abrangentes de alta qualidade, espacialmente explícitos e atualizados. A este respeito, a acústica ativa multifreqüencial é uma ferramenta poderosa que pode fornecer uma resposta relevante para a crescente necessidade de dados abrangentes. Dentro desta estrutura, esta tese visa preencher algumas lacunas no conhecimento da distribuição de peixes para dois ecossistemas tropicais no sudoeste do Atlântico tropical, um pequeno arquipélago oceânico e o ecossistema costeiro nerítico do nordeste do Brasil, utilizando métodos acústicos ativos combinados com outras abordagens. Nos dois primeiros capítulos desta tese, utilizamos um método integrado inovador que combina dados acústicos e de vídeo para estudar a distribuição de peixes ao redor do Arquipélago de Fernando de Noronha (AFN). O AFN abrange uma área marinha protegida, proibindo qualquer amostragem. O exame simultâneo de vídeo e ecogramas permitiu a discriminação de ecotipos similares, levando a uma classificação de todos os ecos em assembléias de peixes e duas espécies de peixes cangulo. A espécie mais abundante observada pela acústica foi o cangulo preto (*Melichthys niger*). Estimamos o *target-strength* desta espécie, um pré-requisito para estimar sua biomassa, que estimamos em 700 toneladas usando um método geoestatístico. As demais distribuições do conjunto e a parte não pesqueira dos dados foram analisadas em relação às características do habitat obtidas a partir de dados acústicos e vídeo, como profundidade e tipo de sedimento, a fim de fornecer uma descrição detalhada e completa da distribuição dos peixes e seu ambiente ao redor do arquipélago. Esta descrição abrangente destacou a localização dos pontos de pesca e, em particular, a importância da plataforma continental no barlavento da ilha, que inclui pontos de pesca bem conhecidos do AFN. Em contradição com o resultado esperado, o AFN mostra uma distribuição assimétrica de peixes com maior concentração no lado de barlavento da ilha principal, em oposição à maior produção primária no lado de sotavento e levou a uma revisão do efeito ilha para altos níveis tróficos. Na parte final desta tese, aplicamos a metodologia desenvolvida acima aos dados acústicos coletados no ambiente nerítico da costa nordeste. O principal objetivo era descrever a distribuição espacial dos peixes demersais e pelágicos. Para este fim, classificamos os ecos de peixe em assembléias de peixes. As duas pesquisas foram realizadas em épocas diferentes e mostraram dois padrões diferentes de distribuição e assembleia de peixes. Os dados acústicos costeiros foram coletados durante o dia

e à noite. A paisagem acústica era muito diferente à noite e durante o dia, com uma resposta acústica mais elevada à noite devido às diferenças de comportamento gregário e ocupação de espaço. Muitos peixes demersais e pelágicos exibem movimentos diel. Esta mudança de comportamento é conhecida por afetar os dados acústicos, já que os peixes estavam mais espalhados pelo espaço e observáveis à noite. Ainda assim, os dados acústicos destacaram a presença de hotspots ao longo da costa do Nordeste do Brasil, em particular um hotspot no platô de Pernambuco e outro na plataforma do Rio Grande do Norte. A distribuição espacial da biomassa de peixes variou de acordo com a estação do ano, a profundidade e a distância até o talude. Ao final do manuscrito, é iniciada uma discussão sobre as perspectivas oferecidas pelo conjunto de dados desenvolvidos durante esta tese, especialmente para o Planejamento Espacial Marinho na região estudada.

SYNTHÈSE DES TRAVAUX EN FRANÇAIS (5 pages)

De nombreuses zones d'incertitudes demeurent sur le fonctionnement des écosystèmes marins. En particulier les écosystèmes tropicaux sont peu étudiés. En effet, les pays tropicaux sont majoritairement des pays en voie de développement qui investissent peu dans la recherche alors qu'ils sont aussi très dépendants des écosystèmes marins pour leur sécurité alimentaire mais aussi en tant que source de revenu. Par ailleurs, l'océan est difficile à échantillonner du fait de son immensité, de la diminution de la visibilité et de l'augmentation de la pression avec la profondeur (Dickey-Collas et al., 2017). L'utilisation de sondeurs acoustiques permet de se libérer de ces contraintes et d'échantillonner l'intégralité de la colonne d'eau (Simmonds and MacLennan, 2005). Les méthodes d'échantillonnage d'acoustique active consistent à émettre un son et à enregistrer l'écho de retour qui est caractéristique des organismes ou des structures physiques dans la colonne d'eau, rendant ainsi possible une étude écosystémique (Benoit-Bird et Lawson, 2016). De plus, l'utilisation d'acoustique multifréquence, permet de discriminer différentes communautés, du zooplancton jusqu'au poisson selon leur intensité de réflexion (*target strength*) pour différentes fréquences (Simmonds and MacLennan, 2005; Bertrand et al., 2014; Benoit-Bird and Lawson, 2016).

La zone d'étude englobe le littoral de la région Nordeste du Brésil et l'archipel de Fernando de Noronha (FNA) dont les problématiques de gestion de la mer sont différentes. La région Nordeste est la région la plus peuplée du Brésil et 80% de ses habitants résident sur le littoral qui subit des pressions liées à l'urbanization, la pollution (Oliveira et al., 2014) et l'exploitation commerciale de ses ressources marines (Frédou et al., 2009). A environ 350 km de la côte, FNA bénéficie d'une protection particulière en tant que parc national et aire marine protégée autour de l'île principale qui est également inscrite au patrimoine mondial UNESCO (UNESCO, 2016). A FNA, le tourisme et la pêche artisanale sont les activités économiques les plus importantes (Diegues, 1988; Pedrosa et al., 2018) ce qui engendre des conflits d'usage. En effet la problématique est centrée sur l'équilibre entre la protection de l'environnement marin et un tourisme très important qui vient doubler la population et exercer des pressions sur l'environnement à travers ses activités comme l'utilisation des plages, le tourisme marin avec les plongées et l'augmentation de la demande en poissons pour alimenter les restaurants. Dans ces différents contextes, la planification spatiale marine est essentielle pour assurer la protection du milieu marin et la durabilité des différentes activités liées aux ressources marines.

L’objectif général de cette thèse est de décrire les schémas de distribution des communautés pélagiques et démersales dans le nord-est du Brésil à partir de données acoustiques multifréquences. Cet objectif se décline en trois objectifs spécifiques :

1) Définir les modèles d'occupation spatiale et la biomasse du poisson le plus observé autour de FNA, le baliste noir.

2) Définir les schémas de distribution verticale et horizontale des poissons pélagiques et démersaux à FNA en fonction de l'environnement.

3) Définir les modèles de distribution verticale et horizontale des poissons pélagiques et démersaux le long de la côte nord-est du Brésil en fonction de l'environnement.

Les données issues des campagnes FAROFA ont la particularité de combiner données vidéos et données d’acoustique active. Les données acoustiques permettent d’avoir une sorte de radiographie de ce qui se trouve sous le bateau (poissons, crustacés, algue, etc.) et les vidéos permettent d’identifier précisément les espèces présentes et également le sédiment (sable, roche, coralligène, etc.). Les deux premières années ont été consacrées à l’acquisition et au nettoyage des données mais aussi à l’élaboration de protocoles et de méthodes pour pouvoir traiter à la fois les données acoustiques et les vidéos. Avec la participation aux deux dernières campagnes FAROFA (avril 2018 et avril 2019).

L’exploration des données vidéo a permis de constater que le poisson baliste noir est le plus observé autour de l’iles. L’observation conjointe des vidéos et des données acoustique a permis de repérer sur les echogrammes, les agrégations d’une centaine d’individus de balistes noir, dont la forme est caractéristique. De la même façon, grâce à l’observation combinée des vidéos et des échogrammes, il a été possible de repérer sur les échogrammes les agrégations d’une autre espèce de baliste, le baliste océanique. Ceci a permis d’extraire le *target strength* qui est une valeur acoustique qui permet de caractériser une espèce et d’estimer sa biomasse si on connaît sa taille. Les résultats ont fait l’objet d’un papier intitulé « *In situ* target strength measurement of the black triggerfish *Melichthys niger* and the ocean triggerfish *Canthidermis sufflamen* » qui a été publié dans la revue Marine and Freshwater research en janvier 2020. Ce travail permet de réaliser l’estimation par acoustique de la biomasse du baliste noir dont on a suffisamment de prélèvement pour pouvoir estimer la taille moyenne et qui est une espèce très abondante autour de FNA mais également autour de nombreuses autres îles tropicales. En effet le baliste noir a une distribution circumtropical et prospère particulièrement bien sur les iles isolées, en partie grâce à son alimentation d’omnivore vorace et son comportement opportuniste lui permettant de manger presque tout ce qui est disponible, y compris des œufs de poissons récemment frayés, des fèces et du vomi de dauphins, du plancton, ainsi qu'un large éventail d'algues et d'invertébrés benthique. Cette grande plasticité alimentaire lui permet par exemple d’occuper des niches fonctionnelles non ou peu représentées sur les îles qu’il colonise.

D’autre part l’utilisation d’un algorithme, développé avec l’aide d’un spécialiste (Gildas Roudaut), a permis d’extraire des données acoustique les données relatives uniquement aux poissons. Ceci permet, entre autres, d’obtenir la profondeur à laquelle se situent les poissons sous le bateau le long de son trajet durant les différentes campagnes et donc leur répartition en trois dimensions autour de FNA pour les trois campagnes FAROFA. Les données acoustiques ont l’avantage d’avoir une très haute résolution car elles sont enregistrées toutes les secondes le long du trajet du bateau. De plus, une étude sur la variabilité intra et inter campagne a permis de montrer une forte stabilité des données relatives à la distribution des poissons et de conclure que l’on peut combiner les données issues des différentes campagnes pour faire une cartographie de la distribution des poissons. Une hypothèse forte est que la répartition spatiale des différentes espèces de poissons dépend essentiellement de leur habitat c’est-à-dire la nature du sédiment.

Le travail d’identification (organismes et sédiments) et d’énumération réalisé sur les vidéos des campagnes FAROFA 1, 2 et 3 par différents étudiants que j’ai eu l’occasion d’encadrer, permet d’apporter des éléments de réponses avec notamment la caractérisation de la nature du sédiment. De plus les vidéos fournissent une information complémentaire aux données acoustiques puisqu’elles permettent d’identifier précisément les espèces de poissons détectées par l’acoustique et capture en plus des espèces qui sont susceptibles d’éviter le sondeur. Une cartographie de la distribution des différentes espèces de poissons a été réalisée en parallèle.

En combinant les trois campagnes nous avons une couverture quasi complète de la plateforme continentale jusqu’au talus qui marque le début de la zone océanique. De plus. Ces données à résolution fine permettent d’estimer la distribution des poissons en dehors du trajet du bateau, tout autour de FdN en utilisant des méthodes géostatistiques (kriging) pour interpoler les données. La finesse des données, mais aussi la forme des transects en rayon autour de l’ile ont représenté des challenges considérables que l’encadrement par Nicolas Bez a permis de relever.

Cette interpolation réalisée sur les échos uniquement relatifs aux balistes noirs a permis d’en estimer une biomasse sur l’aire de distribution de l’espèce d’environ 700 tonnes avec un coefficient de variation de 40%.

Une part important du travail sur les données acoustiques relative uniquement aux poissons a consisté à classer à tous les échos de poissons en fonction de leurs caractéristiques (poissons isolés, agrégées ou en bancs, forme du banc, distance des poissons au sein de l'agrégation, taille, profondeur) et des caractéristiques environnementales (ligne de fond, profondeur du fond, pente). Dix assemblages de poissons et les deux espèces de baliste, le baliste noir et le baliste océaniques, ont été déterminés en observant simultanément la vidéo et les echogrammes. La distribution spatiale des échos de poissons et des échos 'non-poissons' mais aussi la distribution spatiale des échos des labels a ensuite été testée par rapport à différents paramètres environnementaux tels que la position par rapport à l'ile et l'arrivée du vent et des courants, la profondeur du fond, les niveaux de protection législatif, le type de sédiment, la pente du talus. L'influence de ces différentes variables a été testée par des analyses univariées et multivariées. Ces résultats sont présentés dans un second article intitulé « Comprehensive spatial distribution of tropical fish assemblages from multifrequency acoustics and video fulfils the island mass effect framework" et qui présente une étude de la distribution es poisson autour de FNA et des caractéristiques environnementales associées. Cette étude apporte une vision revisitée de l'effet d'ile et constitue une première étape vers la compréhension du fonctionnement d'un écosystème marin tropical.

Une partie des traitements de données développées dans les chapitre 1 et 2 ont été transposée à la côte du Nordeste du brésil ce qui a donné naissance au troisième chapitre de cette thèse « Demersal and pelagic fish assemblages distribution along the northeast coast of Brazil from active acoustic data ». Ce dernier chapitre présente sous la forme d'un article est en cours d'amélioration afin d'être soumis à la publication après la thèse. Ce chapitre repose sur les données collectées lors de deux campagnes en mer multidisciplinaires ABRAÇOS I and II. Les deux campagnes ont été menées à des saisons différentes et les données acoustiques côtières ont été collectées de jour comme de nuit. La collecte des données acoustiques a été combinée à l'utilisation de chalut. Les échos de poissons ont d'abord été extraits en utilisant un algorithme multifréquence et ont ensuite été classés en assemblages de poissons en utilisant l'expérience en acoustique acquise et les outils développés pour le chapitre 2. Les résultats obtenus ont permis de cartographier la distribution des poissons de la côte jusqu'au talus. Le centre et le sud du plateau de Pernambuco et une partie de la côte du Rio Grande do Norte ont été mis en évidence comme des hotspots d'abondance en biomasse acoustique de poisson relativement stable durant les deux saisons. La profondeur et la distance au talus ont une influence dans la distribution des poissons. Les migrations verticales nycthémérales des espèces de poissons ont un effet important sur les données acoustiques. Au lieu de former des bancs denses ou bien d'être entièrement dispersés, les poissons vont former des agrégations lâches et jusqu'à former parfois de couches horizontales qui peuvent être denses. Cette modification dans leur comportement grégaire influence positivement la biomasse acoustique mais ne reflète pas une réelle augmentation de la biomasse la nuit.

En conclusion les trois chapitres mettent en évidence le fait que les données acoustiques peuvent être utilisées en milieu tropical pour cartographier la distribution spatiale d'assemblages multi-spécifiques et fournir des données essentielles pour la conservation.

CHAPTER 1. General Introduction

The surfaces of Mars and the moon have been mapped far more extensively than the bottom of our ocean, despite their size and impact on the life of every organism on Earth. The climate change context is urging the need to increase research for ocean conservation as the maintenance of liveable conditions on earth and human wellness depend on it (Lubchenco and Kerry, 2021). Ocean conservation started long after terrestrial conservation for different reasons. Not so long ago ocean resources were believed to be endless just like their capacity to dilute any waste and humans did not believe they could have an impact because of the ocean's vastness (McIntyre, 1995). It is also because of its vastness that oceans are very difficult places to explore and so little is known. Other inherent characteristics that difficult ocean observation such as increased pressure and quick light dissipation with depth making the meters below the surface very dark. There are different ways to sample the ocean but first we need to know where to look. Broad-scale remote sensing via satellites is very helpful, but unfortunately, it only captures the surface of the ocean while thousands of meters below the surface remain unseen. To account for the vertical range, scientists perform *in situ* observations aboard survey vessels or use drifting buoys, gliders, and other tools. Exploration methods have evolved a lot. Nevertheless, gaps in knowledge remain especially in tropical areas. Indeed tropical oceans are very wide; oceans comprise 76% of the world’s tropical area. Tropical coastal ecosystems are also more complex in terms of trophic interactions and hold high biodiversity (Schemske et al., 2009). Another reason why there are still gaps in scientific knowledge about tropical waters is that coastal tropical countries are mostly developing countries that invest less in science than temperate developed countries (Eduardo et al., 2022). Even though developing countries are more reliant on coastal marine ecosystems, the lack of means and gap in scientific knowledge leads to weak governance of highly coveted marine resources. In this thesis, we propose to use acoustic to describe fish distribution in two tropical ecosystems, an oceanic archipelago, and a coastal area, to provide essential information for marine conservation.

1.1. Tropical ecosystems

1.1.1. Tropical ecosystems hold major biodiversity

Marine biodiversity

In contrast with the terrestrial realm, data syntheses at a global scale on the distribution and status of aquatic species are relatively recent (Mittermeier et al., 2011). Marine ecosystems are a huge reservoir of biodiversity, home to hundreds of thousands or more likely millions of species (Mora et al., 2011; Appeltans et al., 2012; Costello et al., 2012). Even though marine species richness is admittedly lower than terrestrial's, life began in the sea and marine species' phylogenetic diversity is broader with most phyla being primarily or exclusively marine (Sala and Knowlton, 2006). One of the most fundamental patterns concerning life on earth is the increase in biological diversity from polar to equatorial regions (Willig et al., 2003; Hillebrand, 2004). Remarkably, tropical areas that are well known for their diversity (Burrows et al., 2011); have among the lowest completeness of all taxonomic inventories (Mora et al., 2008). This raises concerns over the effectiveness of conservation strategies based on data that remain largely precarious (Mora et al., 2008).

Biodiversity hotspot

Within the tropics, many areas are considered biodiversity hotspots i.e. areas of exceptional species richness. These areas are usually defined by one or more species-based metrics (species richness, endemism, and the number of rare or threatened species) or focusing on phylogenetic and functional diversity to protect species that support unique and irreplaceable roles within the ecosystem (Marchese, 2015). In the past three decades, hotspots have been confirmed as priority regions for the efficient conservation of biodiversity more broadly (Mittermeier et al., 2011). There has been a significant effort to identify and map these areas at a global scale, but the resolution of those datasets remains coarse (Morato et al., 2010). Myers's (2000) seminal paper defined 25 global biodiversity hotspots featuring exceptional concentrations of species with exceptional levels of endemism, and that, face exceptional degrees of threat (Myers, 1988). Sixteen of these hotspots were located in the tropics (Myers et al., 2000). Another observed pattern is that marine biodiversity is higher in benthic rather than pelagic systems and on coasts rather than in the open ocean since there is a greater variety of habitats near the coast (Gray, 1997). In tropical coastal ecosystems, hotspots include important habitats such as coral reefs, mangroves, kelp forests, and seagrass meadows (Costello et al., 2022).

Hotspots can have different definitions. For instance, Nelson and Boots (2008) describe a hotpot as “a location where something out of the ordinary has occurred” from an overabundance of species richness to disease or crime. Nelson and Boots (2008) argue that the definition of a hotspot is perhaps less important than the reason for identifying hotspots and that is, understanding the complexity of systems. In ecology, hotspots relate to species or process abundance due to particular environmental conditions shaping ecosystem productivity locally (Bartolino et al., 2011). Identifying biological hotspots is a first step towards understanding mechanisms that generate the observed spatial patterns and is ultimately critical for conservation (Hazen et al., 2013).

Link between biodiversity and ecosystem functioning

Observational evidence supports strong links between species richness and ecosystem functioning, specifically biomass production (Duffy et al., 2017). Indeed, biodiversity is among the strongest predictors of reef fish community biomass, comparable in importance to global temperature gradients and human impacts (Duffy et al., 2016). Lefcheck and collaborators (2021) estimated that high biodiversity is 5.7 times more important in maximizing biomass than the remaining influence of other ecological and environmental factors. Species richness increases community biomass production and suggests that the role of biodiversity in maintaining productive ecosystems should figure prominently in global change science and policy (Duffy et al., 2017). Importantly, diversity and climate are related, with the biomass of diverse communities less affected by rising and variable temperatures than species-poor communities.

As mentioned above, current evidence suggests that there is, in general, a positive relationship between biodiversity and ecosystem functioning, but few studies have addressed tropical ecosystems where the highest levels of biodiversity occur (Clarke et al., 2017). In addition, tropical ecosystems harbor higher diversity and more intense biotic interactions than extratropical regions (Schemske et al., 2009; Freestone et al., 2011; Longo et al., 2019; Inagaki et al., 2020) which makes them even more complex to study.

1.1.2. Ecological process

Tropical habitats

Tropical coastal water host unique habitats such as coral reefs, seagrasses, and mangrove forests. In particular, coral reefs are the most biologically diverse ecosystems per area and their physical complexity and biodiversity are often compared with tropical rainforests (Reaka-Kudla et al., 1996). Their spatial distribution is largely restricted to shallow warm waters and covers 0.2% of the ocean floor but they account for nearly one-quarter of the total known marine biodiversity (Knowlton et al., 2010). In addition to their remarkable biodiversity, coral reefs also provide a wide range of benefits to humans, including fisheries, coastal protection, tourism, recreation, and medicines (Wagner et al., 2020). Concomitantly, shallow-water corals are increasingly being subject to habitat degradation and are particularly vulnerable to global warming (Bongaerts et al., 2017; Rocha et al., 2018). Coral reefs are thus widely regarded as one of the top science and conservation priorities globally and are extensively studied (Knowlton et al., 2010).

Nonetheless, most research is limited to shallow water (<40 m), while light-dependent corals, and the ecosystems they support, extend much deeper, especially in tropical ecosystems (e.g., 150 m in some locations) (Kahng et al., 2016). Deep coral reefs found between 40 and 150 m are called mesophotic coral ecosystems and are lately receiving more attention. The increased number of studies on mesophotic reefs has been favored by advances in technology and by a growing interest in the potential role of mesophotic coral ecosystems as a refuge for shallow-water reef fauna (Kahng et al., 2016). This hypothesis has been contradicted as recent research shows that mesophotic reefs hold distinct fauna from shallow coral reefs that deserve particular specific protection (Bongaerts et al., 2017; Rocha et al., 2018).

Tropical marine ecosystems are composed of a complex mosaic of habitats and interconnected ecological communities that extend from the shoreline to the open ocean (Dahlgren and Marr, 2004). In many tropical regions, coral reefs and seagrass beds form a mosaic of patches within a matrix of sandy sediments (Hitt et al., 2011a). At a broader scale, coral reefs, mangrove forests, and seagrass beds have a symbiotic relationship where they are close and connected through the movements of organisms, nutrients, and other materials (Nagelkerken, 2009; Guannel et al., 2016). Many fish species use more than one habitat along their life cycle and migrate between habitats within a complex seascape as they perform ontogenetic, tidal, and or diel migration between habitats (Krumme, 2009). Habitat heterogeneity has been shown to positively correlate with species richness and is pointed out as a prime factor for choosing among alternative sites for reserves (Roberts et al., 2003).

Flow-topography interactions

Tropical waters are classically very stratified and highly oligotrophic, especially in the open ocean often referred to as a blue desert (de Souza et al., 2013). In this context, anomalies in the topography such as seamounts and oceanic islands also are anomalies of biodiversity and productivity referred to as oases (Cordeiro et al., 2013). They behave like ocean fertilizers and are locally highly productive, biodiverse ecosystems in surrounding oligotrophic waters (Hasegawa et al., 2004; Robinson et al., 2016). Nine of Myers's hotpots were mainly or completely made up of islands; almost all tropical islands fall into one or another hotspot.

Satellite ocean radiometry shows an increase in phytoplankton concentrations in the wake of oceanic Islands (Signorini et al., 1999; Hasegawa et al., 2009). This enhancement of primary productivity is known as the ''island mass effect'' and was first described by Doty and Oguri (1956). Several mechanisms induced by islands can enhance nutrient concentrations allowing phytoplankton to thrive (Fig. 1.1). The interaction between the island topography, wind, and currents causes the ascension of nutrients into the euphotic layer promoting biological production (Andrade et al., 2014). This vertical resurgence of nutrients can be associated with the formation of island-induced wakes, eddies, fronts, filaments, internal waves, upwelling processes, and river discharges or land drainage (Heywood et al., 1996; Leichter et al., 1998; Bucciarelli et al., 2001; Coutis and Middleton, 2002; Caldeira et al., 2005). The nutrient input enhances primary productivity that in turn, attracts higher trophic levels (Gove et al., 2016).

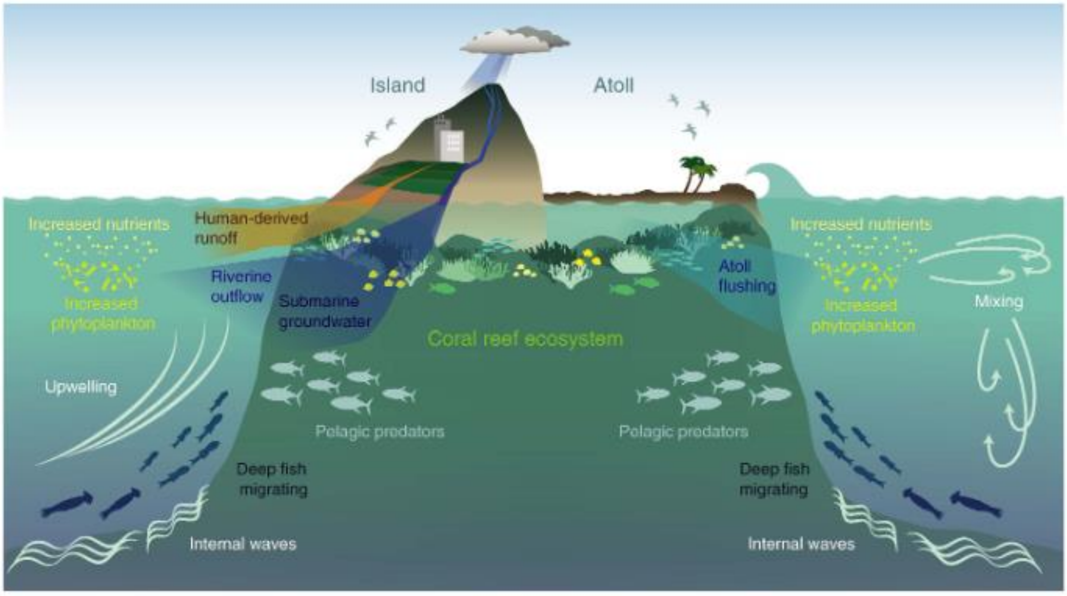

Figure 1.1. Schematic resume of the Island mass effect from Gove et al., 2016

Fishers have long been known for the enhancement of biological productivity in the vicinity of islands (Signorini et al., 1999). Oceanic islands and seamounts are associated with propitious fishing grounds worldwide, hosting abundant and diverse biomass and favoring the congregation of marine predators, such as tunas, dolphins, and seabirds (Morato et al., 2008; Pitcher et al., 2008). Furthermore, oceanic islands and seamounts are important aggregating locations for highly migratory pelagic species (Benoit-Bird and Au, 2003; Musyl et al., 2003) and dispersal stepping stone (Morato et al., 2010; Mazzei et al., 2021, Pinheiro et al., 2017).

Common physical mechanisms are observed in shelf-break where topography-current interactions can form fronts or upwellings promoting primary production that propagates up the food web (Genin, 2004). Aggregations of many organisms are observed over shelf-break, including jellyfish (Graham et al., 2001), krill (Macaulay et al., 1984), copepods (Barange, 1994), and top predators like whales (Murase et al., 2013), tunas (Young et al., 2001) and seabirds (Skov and Durinck, 1998). Shelf-break concentrates diverse fishing resources over a relatively narrow area, sustaining important multi-specific fisheries. Shelf-breaks are also the point of encounter for spawning events of different species of commercially important fish (Frédou and Ferreira, 2005; Heyman and Kjerfve, 2008; Paxton et al., 2021).

1.1.3. Uses and Threats

Fisheries

Marine fisheries contribute substantially to the well-being of people and society, particularly in the tropics where coastal communities depend on fisheries for food security, livelihoods, economic development, and culture (Béné et al., 2016; Lam et al., 2020). In 2020, global capture fisheries production was around 90 million tonnes (FAO, 2022). Approximately 60% of this marine-based food is consumed in the developing world where an estimated 1 billion people rely on fish as their primary source of protein (FAO, 2022). Tropical waters might be oligotrophic but they are also highly productive. Half of the fish catch is made in tropical waters and is consumed both by tropical and temperate human populations. Tropical fisheries substantially contribute to the well-being of societies in both the tropics and the extratropics by telecoupling (Lam et al., 2020).

Overfishing

Fishing precedes all other human disturbances to marine ecosystems (Jackson et al., 2001). There are historical records of marine species brought to extinction or near extinction by overfishing especially large mammals (Bertram and Bertram, 1973; Kenyon, 1977; Jackson et al., 2001) or commercial fish (Hutchings and Myers, 1994). The percentage of stocks fished at biologically unsustainable levels has been increasing since the late 1970s, from 10% in 1974 to 35% in 2019 (FAO, 2022). The implications of unsustainable fisheries extend beyond the simple status of fish populations and economic viability of fisheries to global food security, cultural survival, and even national security (Jennings et al., 2016; Pomeroy et al., 2016; Blanchard et al., 2017). Unsustainable fishing affects fish populations, fleets, and fishery systems (Hilborn et al., 2015; Link, 2018) and has a broad impact on marine ecosystems (Botsford et al., 1997; Jennings and Kaiser, 1998; Jackson et al., 2001; Link, 2018).

Myers and Worm, 2003 showed that 90% of large predatory fish have disappeared from the Atlantic, Pacific, and Indian Oceans since the advent of industrial fishing. Large-bodied fishes contribute disproportionately to ecosystem functioning (Estes et al., 2016), and their selective removal through overexploitation and sensitivity to human disturbance might be expected to have a larger-than-anticipated influence on community productivity compared to random losses (Mellin et al., 2016).

Climate change

Human activities such as energy production, industrial activities, transportation, agriculture, and deforestation produce enormous amounts of greenhouse gas (e.g., CO2 and methane) and are responsible for approximately 1.1°C of warming since 1850-1900 (IPCC, 2022). Climate change induces a wide variety of impacts along with temperature rising such as shifts in current circulation, stratification, nutrient input, oxygen content, ocean acidification, pH falling, sea level rise, reduced or more variable freshwater flow, and severe weather events (Doney et al., 2012). All these have severe impacts on marine life affecting their abundance, diversity, food webs, and human populations. The pace of shifting climate is higher in tropical areas (Burrows et al., 2011). Climate change projections from high-emission scenarios from the Intergovernmental Panel on Climate Change until 2100 show a decrease in global ocean biomass (Cheung et al., 2013; Ariza et al., 2022); the global catch will potentially be reduced in all systems and more substantially in tropical systems (Golden et al., 2016; Capitani et al., 2021). Direct human-induced impacts are also high and increase the tropics' vulnerability to climate change (Halpern et al., 2019).

Coastal ecosystems and habitat destruction

Coastal ecosystems are directly exposed to heavy anthropic pressure as they are the most densely populated regions (Jackson, 2008). Shallow-water tropical marine ecosystems in many areas are degraded, if not destroyed by cumulative effects of exploitation, habitat destruction, and pollution (He and Silliman, 2019). The destruction of critical habitat and the loss of connectivity is particularly detrimental in the tropical seascape. Coral reef ecosystems are particularly susceptible to changes in environmental conditions (Hoegh-Guldberg et al., 2007). Almost 30% of corals have disappeared since the early 1980s, and up to 90% of coral reefs may be gone in the next few decades in the absence of swift conservation action (Hoegh-Guldberg et al., 2018). Other critical habitats such as mangroves and estuaries are increasingly under pressure from climate change and local anthropogenic activities. For instance, eutrophication, land cover change, sea-level variation, and global warming already affect mangrove ecological processes (Ghosh, 2015).

Biodiversity loss

Species are still being described and sampled and advances in molecular methods may add tens of thousands of cryptic species to already described species (Appeltans et al., 2012).

Simultaneously, humans are accelerating the extinction rates of species in both terrestrial and marine environments (Finnegan et al., 2015). Indeed, the world is entering a major extinction spasm with present rates of species extinction reckoned to be between 1000 and 10,000 times the rates seen through most of geological history (Purvis et al., 2000). Humans are altering the composition of biological communities through a variety of activities that increase rates of species extinctions at all scales, from local to global (Hooper et al., 2005). At sea, overfishing, invasive species, habitat loss, pollution, climate change, and ocean acidification pose intensifying threats to marine ecosystems, leading to concerns that a wave of marine extinctions may be imminent with unknown ecological and evolutionary consequences (Jackson, 2008). Especially since biodiversity has been shown to play an important role in ocean resiliency facing degradation and climate change. Even though the ocean covers 70% of the planet, to date 8.2% of the ocean is self-reported by countries as existing in some type of designated MPA (Marine Protected Areas; https://www.protectedplanet.net) and only 2.4% is fully or highly protected from fishing impacts (Marine Protection Atlas; https://mpatlas.org/). Calls are increasing for the more ambitious target of effectively protecting at least 30% of the ocean by 2030 (O'Leary et al., 2016; Jones et al., 2020). Furthermore, the risk of extinction is higher in the tropics (Finnegan et al., 2015) and increases faster (Fig. 1.2). Unfortunately, conservation research is not happening where it is most needed (Wilson et al., 2016).

Poor management, lack of data, limited resources

Sixteen of the 25 hotspots identified by Myer et al., 2000 are located in the tropics, which largely means in developing countries where threats are greatest and conservation resources are scarcest (Myers et al., 2000). Tropics are comparatively less sampled than temperate areas. The higher sampling intensity at mid-latitudes in both hemispheres is not surprising, given the higher funding for marine research provided by developed countries at these latitudes (Mora et al., 2008; Menegotto and Rangel, 2018). Conversely, most developing countries are tropical, with substantially less funding for biodiversity research, as indicated by the fewer number of research vessels and field stations (Costello et al., 2010). Moreover, political instabilities further hinder management action (Granek and Brown, 2005).

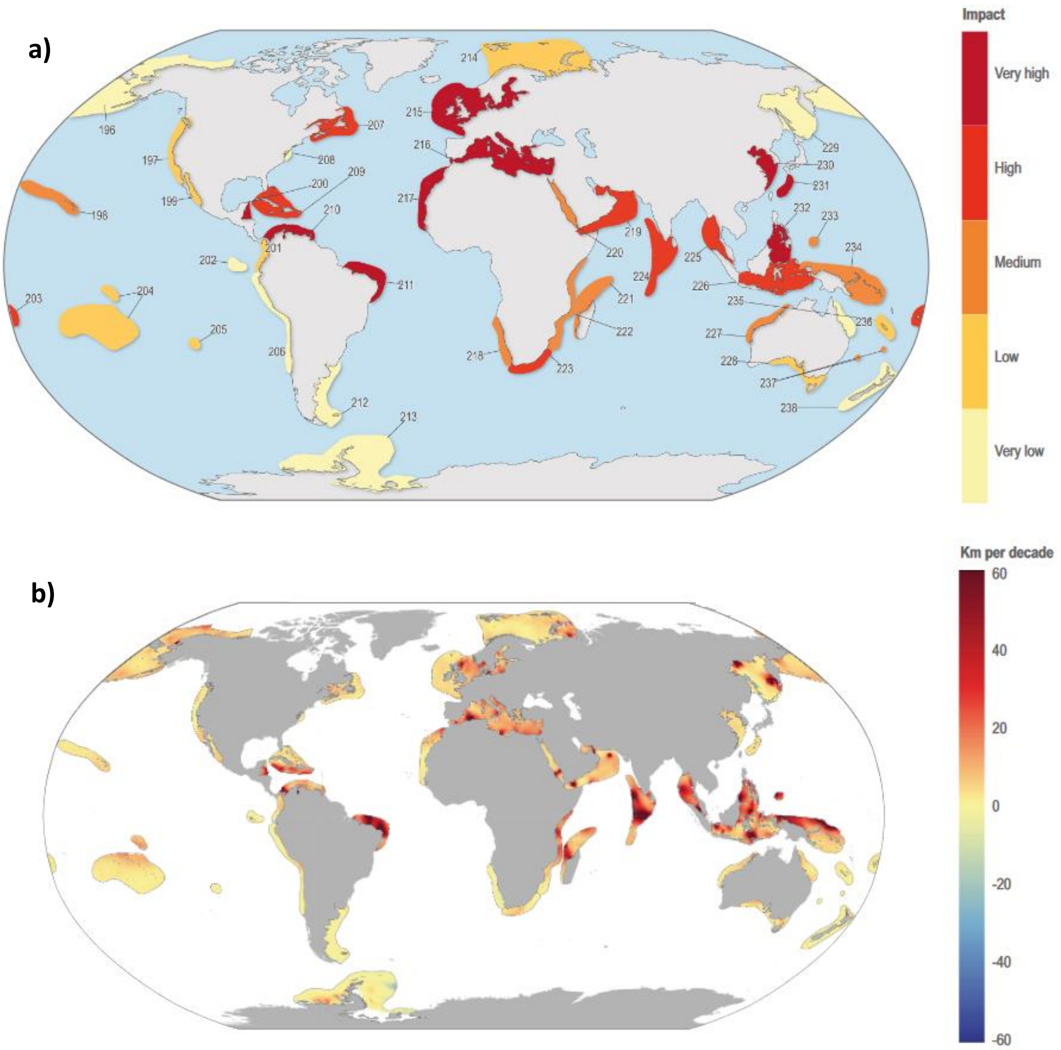

Figure 1.2. Adapted from IPCC (2022). (a) Recent human impacts (land-based, fishing, climate change, and ocean-based stressors) on marine biodiversity hotspots based on Halpern et al. (2015). (b) Climate velocity (in kilometers per decade) in marine hotspots between 1970–2019. Positive and negative velocities indicate warming and cooling, respectively.

1.2. Study area: Northeast Brazil

1.2.1. Brazil is an example of a data-poor and biodiverse tropical ecosystem.

Located in South America, Brazil (Federative Republic of Brazil) is the world's fifth largest country both by geographical area (8.5 million km²) and by population (around 204 million people). Brazil has an exclusive economic zone of 3.56 million km², which includes ecosystems such as coral reefs, dunes, mangroves, lagoons, estuaries, and marshes. The variety of biomes reflects the enormous wealth of flora and fauna of the country: Brazil is home to the greatest biodiversity on the planet. This abundant variety of life represents more than 20% of the total number of species on Earth (UNEP, 2019). Therefore, Brazil is the principal nation among the 17 megadiverse countries (or greater biodiversity). The country owns 3,000 km of coral reefs (Leão et al., 2016) and 9% of mangroves in the world (FAO, 2020).

Some numbers about fisheries in Brazil

A large part of the Brazilian population lives near the coast, a scenario that is more pronounced in the Northeast coastal region. As a result, the Northeast coastal area is under constant anthropogenic pressure from urbanization, pollution (Oliveira et al., 2014), and commercial and artisanal exploitation of marine resources (Frédou et al., 2009). Brazil produced 1.4 million tonnes of fish in 2011, including aquaculture, marine, and continental fishing (MPA, 2011). The Northeast region concentrates the largest number of professional fishers representing 48% of the country's total (MPA, 2011). The northeastern small-scale fishery provides alone 32% of the Brazilian production (Damasio et al., 2015). Artisanal fisheries in northeast Brazil are based on small to medium-sized boats (most of them <12 m long) using sail or small engines, canoes using oars or sail, and sail rafts. There is a large diversity of species and fishing gear/methods used in coastal fisheries in the northeast. In general, gillnets, longlines, and hook-and-line are used in coastal and offshore waters to catch snappers (Lutjanidae), groupers (Serranidae), mackerel (*Scomberomorus spp.*), sardines (Clupeidae), pompanos (Carangidae), tunas and dolphinfish (*Coryphaena hippurus*) (Lucena-Frédou et al., 2021).

Data-poor ecosystem

The historical series of national fisheries statistics started in 1947 with the Ministry of Agriculture, specifically the Hunting and Fishing Division (DPA) and the Brazilian Institute of Forestry Development (IBDF), and officially closed with the last bulletin in 2011 published by the Ministry of Fisheries and Aquaculture which processes the data collected in 2008 (MPA, 2011). In a few states, fish-landing monitoring was maintained through projects like the Projeto de Monitoramento da Atividade Pesqueira (PMAP) from 2008 to 2018 but due to institutional instability national information on fish landing is scarce (Freire et al., 2021). Research has relied on fishers' Local Ecological Knowledge as an effective and low-cost method to generate information in data-poor fisheries (Bender et al., 2014; Previero and Gasalla, 2018). Despite the importance of the activity, the Northeast was one of the regions most affected by the end of fishery monitoring programs in Brazil. More information on fish stocks is needed to support appropriate management actions (Andrew et al., 2007).

1.2.2. Northeast environmental background

Low latitude ecosystem, western boundary currents

Between 10°S and 5°S, along the Brazilian coast, the core of the North Brazilian Under Current (NBUC) transports a South Atlantic water mass characterized by a high oxygen content and high salinity (Arhan et al., 1998; Schott et al., 1998). At ~5°S, the NBUC is reinforced by the central South Equatorial Current (cSEC) that enters the western boundary system. The equatorward transport is thus increased, and the NBUC forms the North Brazil Current (NBC) in the near-surface layer (Fig. 1.3; Dossa et al., 2021).

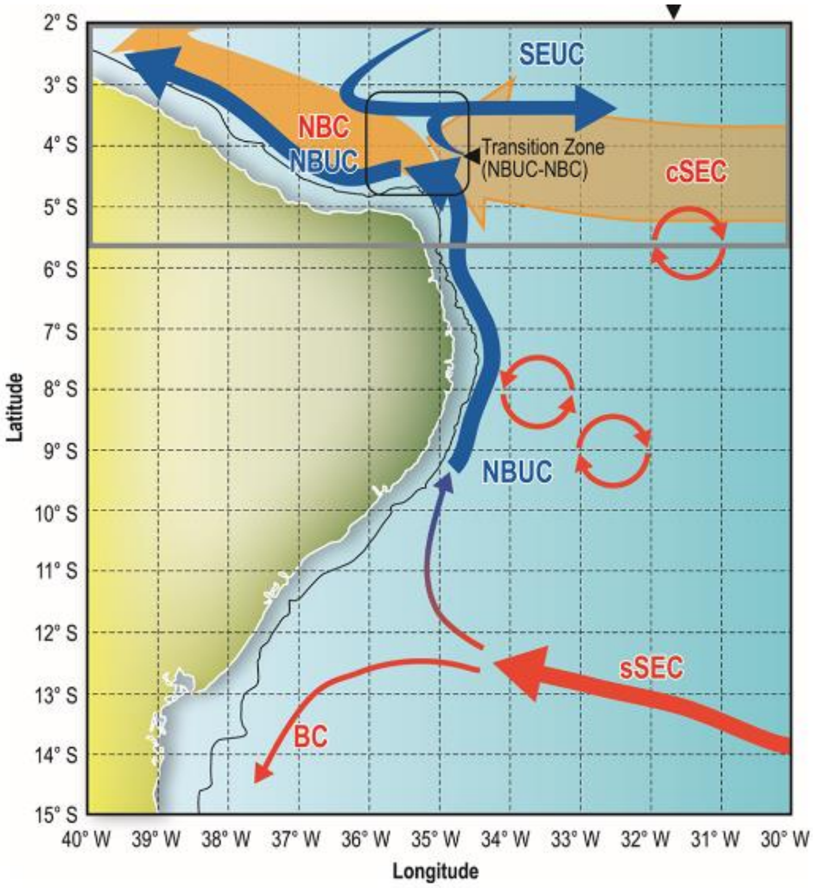

Figure 1.3. Schematic representation of mean currents and eddy generation along the Northeast Brazilian coast from Dossa et al., 2021

Western boundary currents (WBCs) redistribute heat from the equator toward the poles (Todd et al., 2019). Boundary current systems occur where coastal and open ocean ecosystems interact and are highly productive regions, especially in eastern boundary current systems (Chavez, 1995; Chavez et al., 2008). The productivity is lower for WBC systems but geostrophic- and eddy-driven upwellings mechanisms can drive nutrient uplift and increase primary productivity along the coasts (Pelegrí and Csanady, 1991). On narrow continental shelves adjacent to intense western boundary currents, like the Brazilian northeast, the shelf is under the direct impact of deep-ocean circulation, driving significant fluxes across the continental shelf edge (Todd et al., 2019).

Important habitats, coral, rhodolith

The tropical fish fauna of the western Atlantic ranges from about 35°N–28°S (Floeter et al., 2001), and a considerable part of this region (4°N–28°S) is included in Brazilian waters. The largest coralline reefs of Brazil are formed by the rhodolith beds (Amado-Filho and Pereira-Filho, 2012; Horta et al., 2016). The Brazilian coast supports the largest known rhodolith beds (Fig. 1.4) in the world, covering extensive areas of the north, northeastern, and southern Brazilian continental shelf. However, most rhodolith beds remain unexplored or poorly known ecologically largely because the beds occur mostly in mesophotic habitats (30-150 m depth). Due to their broad spatial extension, rhodolith beds may influence ecological processes (e.g. nutrient flow, larval supply) that drive reef fish community structure and dynamics (Mumby et al., 2004).

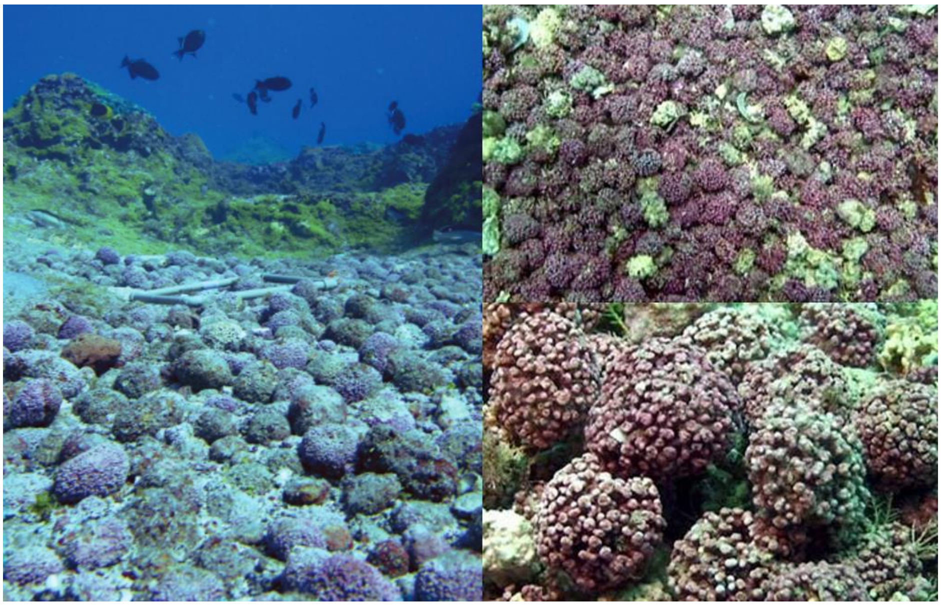

Figure 1.4. Rhodolith bed picture adapted from Horta et al., 2016 and pictures from https://alchetron.com

Relative to other abundant nearshore communities like kelp forests and coral reefs, rhodolith beds have been little investigated by marine ecologists. They provide hard habitat for numerous other marine algae that live on their surfaces, and for invertebrates living on and in the rhodoliths and surrounding sediments (Foster et al., 2013). Rhodoliths can be defined as calcareous nodules composed of coralline red algal material (Corallinophycidae). Crustose coralline red algae are completely calcified encrusting organisms that either adhere tightly to a hard substratum or remain unattached to the seafloor (Broom et al., 2008). Rhodolith beds are among the world's largest photosynthesizer-dominated benthic communities (Mazzei et al., 2021).

The Fernando de Noronha archipelago

Oceanic islands, because of their geographic isolation and their small size suffer less anthropic pressure than the coast, which is often subject to strong demographic pressure resulting in the urbanization of the littoral and pollution. Oceanic islands can be considered almost as pristine environments relative to the coast and are ideal observation research laboratories to study human impact on the marine environment.

Fernando de Noronha archipelago is part of an eponym volcanic ridge (Fernando de Noronha Ridge), developed along an E-W oceanic fracture zone, constituted of Fernando de Noronha archipelago, Atol das Rocas and several seamounts (Almeida, 2006). The oceanic archipelago is located 345 km from the Northeastern Brazilian coast (Fig. 1.5) and is protected by two MPAs that were created at the end of the 1980s: one for the sustainable use of marine and coastal species and the other one as a no-take reserve. Fernando de Noronha archipelago is also recognized as an EBSA ("Ecologically or Biologically Significant Areas"). Indeed, Fernando de Noronha Chain has unequivocal ecological importance due to high biological productivity and for providing important key habitats that are used as nurseries, feeding, breeding, and sheltering sites by various resident and highly migratory species. The area is considered a hotspot due to its high biodiversity and endemism, and Fernando de Noronha and Roca Atol have been designated as a national marine park and biological reserve, respectively, in recognition of their importance in the region.

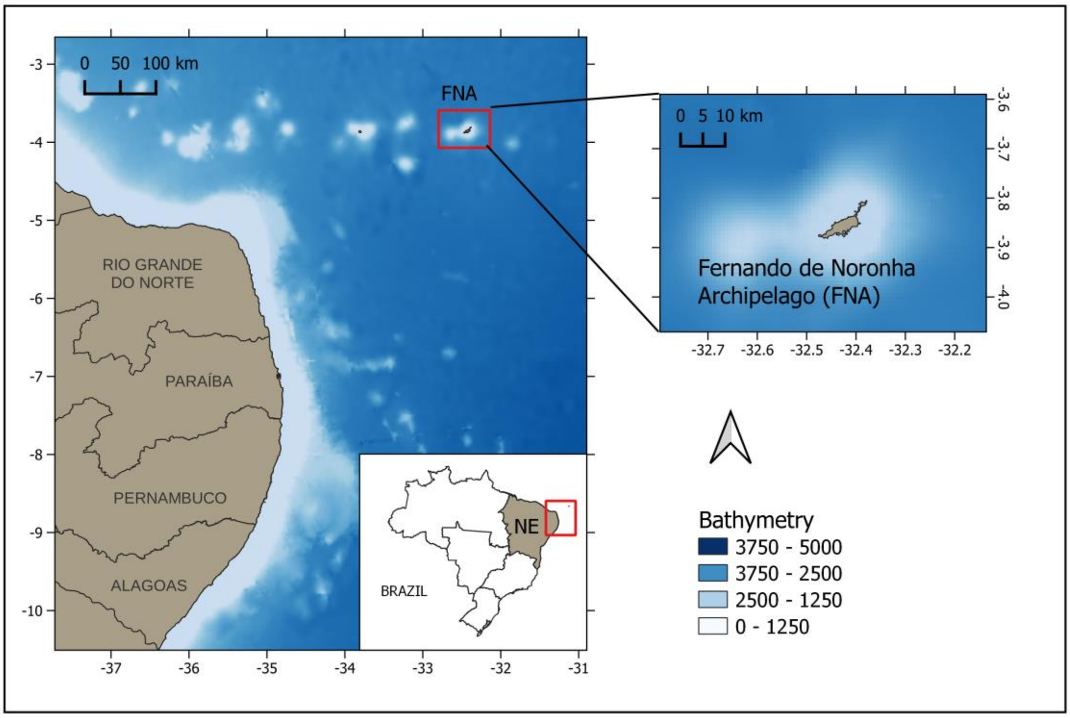

Figure 1.5. Location of the Fernando de Noronha archipelago off Northeast (NE) Brazil

Fernando de Noronha archipelago is almost entirely protected on land and at sea, so it is an ideal place for marine research. On the other hand, it is far from the coast and thus poorly supplied. The local population relies effectively on artisanal fisheries for protein income (Dominguez et al., 2014). The economic activity also relies a lot on tourism, which generates demographic pressure and all its externalities, amplifies the demand for fish and enhances marine related activities such as recreational fishing or diving (Lopes et al., 2017). All of it ultimately amplifies the pressure on fish stock and threatens fish biodiversity. Furthermore, the political context in Brazil is unfavorable for environment preservation and protection politics are changing. In this context it is critical to study and monitor fish distribution around the Island.

1.3. The traditional ways to sample the ocean

Assessing marine systems may be considerably more challenging than assessing terrestrial systems – counting fish stocks, for example, has been compared to "counting trees, except that you do not see them and they move" (Hannesson, 2011). Indeed not only is the surface area of the oceans vastly larger than the Earth's land mass, but marine systems extend into a third dimension. Furthermore, the oceans are dynamic and constantly changing; shifting of populations due to changing ocean and climate conditions may further aggravate this challenge (Cheung et al., 2013; Ariza et al., 2022).

Why do we focus on fish?

Fishes are the most diverse group of vertebrates, play key functional roles in aquatic ecosystems, and provide protein for a billion people, especially in the developing world. Fish assemblage data are often used to help understand how human activities influence marine ecosystems (Hewitt et al., 2005; Caselle et al., 2015) or as a measure of ecosystem health (Díaz-Pérez et al., 2016) and help form the basis for managerial decisions (Topor et al., 2019).

What methods are used?

Fish population assessment can be based on a variety of methods, including fishery-dependant and fishery-independent information; each presenting its set of advantages and limits (Pennino et al., 2016). Fishery-dependent methods such as commercial fish landings data provide long time series and wide spatial coverage all year round. However, they are impaired by gear selectivity and preferential location, and sometimes they lack important details such as the location of fishing grounds and precise species identification (Hilborn and Walters, 2013). Fishery-independent surveys typically consist of field programs involving either stratified trawls and/or acoustic measurements. They have limited coverage in space and time (in terms of seasonality as well as the number of years of available data) but the sampling and collection are scientifically designed and standardized (Hilborn and Walters, 2013). Scientific biodiversity and abundance assessment can also be made using underwater visual census (UVC), videos, bio-logging, acoustic telemetry, or more recently DNA sampling.

In a coastal shallow ecosystem, scientists classically perform direct *in situ* observations through diver-based underwater visual census (UVC) (Bohnsack and Bannerot, 1986) to describe reef fish communities. UVC are widespread and widely used in a variety of manners, from stationary sightings to observations along transects, through direct observation by divers or the use of video operated by drivers (Murphy and Jenkins, 2010; Mallet and Pelletier, 2014). The presence of a diver introduces behavioral bias as some fish species can be attracted while others are diver averse (Kulbicki, 1998; Harvey et al., 2002; Cole et al., 2007), especially large bodied target species (Gotanda et al., 2009; Januchowski-Hartley et al., 2011). Furthermore, scuba diving is limited in time and depth by the diver physiological limits and visibility (Jones and Thompson, 1978; Kimmel, 1985; Michalopoulos et al., 1992). Most studies based on UVC are thus restricted to near shore shallow waters and provide punctual small-scale information whereas species richness and patterns of distribution is heavily influenced by the range of the sampling area (Gray et al., 2004).

To overcome some of these limitations and biases, underwater video techniques, whether stationary or towed, remote-controlled or autonomous, with or without bait, are increasingly being used (Mallet and Pelletier, 2014). The use of video increases sampling range and is more time efficient than diver-based observations (Langlois et al., 2010). Nevertheless, the spatiotemporal range covered remains limited or affected by turbidity and the devices still introduce behavioral bias such as attraction or avoidance (Stoner et al., 2008) and are poor for accessing cryptic species.

1.4. Acoustics as a remedy

Acoustics include a range of different methods using wave propagation to remotely detect organisms or physical change in the water column. Development of acoustic methods is less than a century old, and continues to evolve rapidly (see Horne (2000) for a review).

A little history

The first echo detection of fish by active acoustic was made between the 20s and 30s (Kimura, 1929) and soon after came the first echogram representing the acoustic energy data on a time-versus-depth plot (Sund, 1935). Interest in acoustic methods have grown in importance after the World War II and acoustic tools were designed to specifically study marine animals in the 1960s. Researchers and fishers began use echo sounders to locate and qualitatively visualize distributions, abundances, and behaviors of fish and shrimps (Balls, 1948; Hodgson, 1951). Ultimately, acoustic methods became routinely used for stock assessment of commercial species (Dragesund and Olsen, 1965; Fernandes et al., 2002).

How does active acoustic works?

Sound is a very effective medium with which to perceive marine environments, as the penetration of sound in water is significantly greater than that of light (Fernandes et al., 2002). Sound also propagates very quickly in the water 1500 $m.s^{-1}$ which enables a very quick scanning of the water column. Passive acoustic methods rely on sound wave propagation using hydrophones to listen to the sound emitted by organisms such as whales, dolphins but also shrimps and reef fish. Active acoustic methods differ from passive acoustics with the use of echo sounders to emit sound waves that propagate in the water column and listen to the reflected wave sounds. Indeed echosounders receive the backscattered sound waves from any obstacle it encounters such as the bottom, the surface, bubbles, organisms (fish, crustaceans, gelatinous or algae) or any change of density in the environment such as physical differences between water masses. Each element thus encountered, whose echo is measured, has a characteristic signature. Analysis of the intensity of the sound sent back according to the frequency (frequency response) provides information about the source of biological or physical diffusion (presence of different organisms, discontinuities due to density change). The intensity of the backscattered signal is represented in an echogram using colours; the vertical dimension of an echogram represents the depth and the horizontal dimension can represent the distance covered or the time elapsed as the boat travels (Fig. 1.6b). Today, an increasingly large variety of active acoustic approaches are available for studying life in the ocean (Fig. 1.6a).

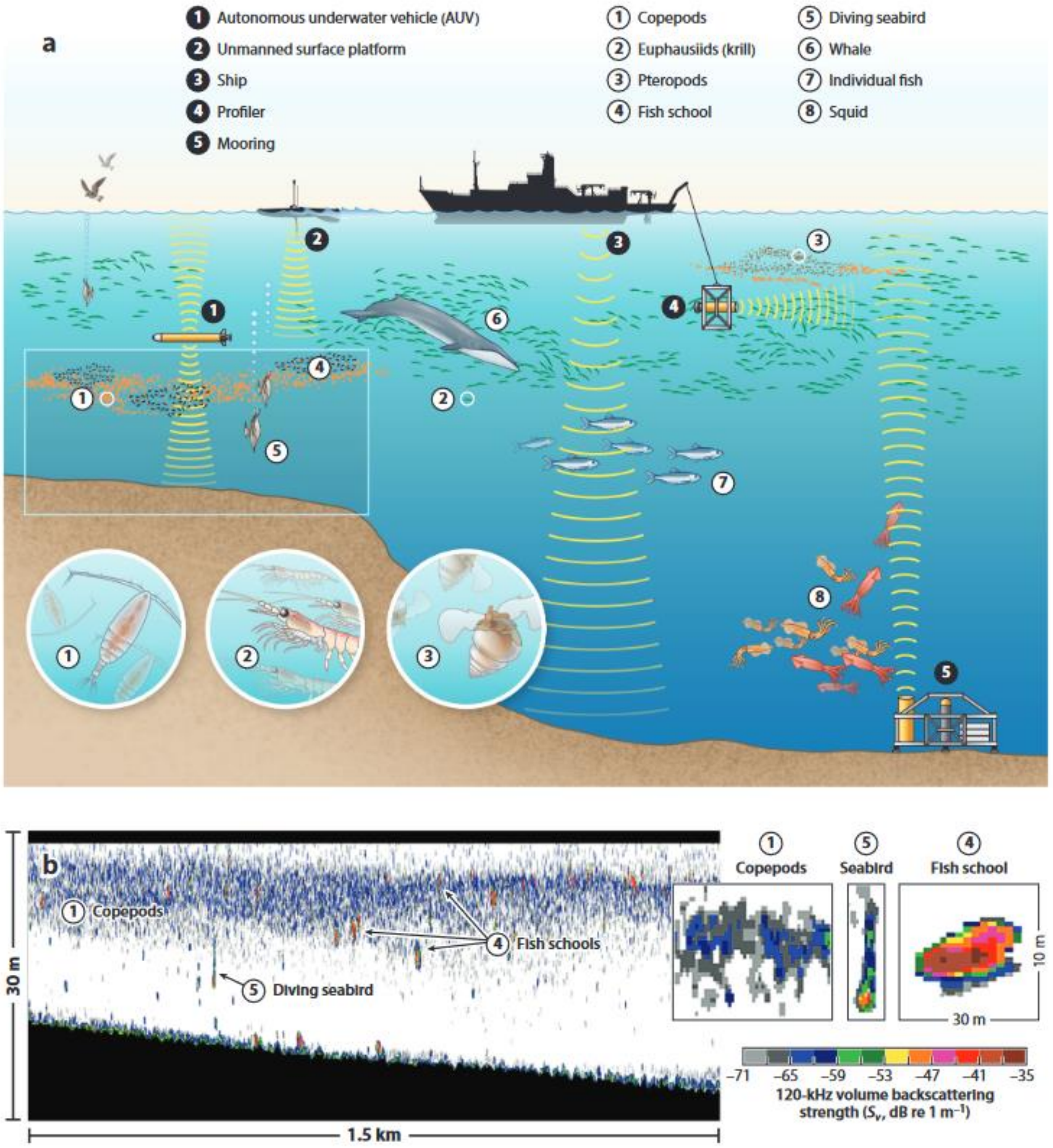

Figure 1.6. Examples of different utilisation of acoustic methods (a); Echograms (b) featuring different types of organisms from Benoit-Bird and Lawson (2016).

Multi-frequency active acoustics use

In particular, multi-frequency acoustics allows discriminating communities, from plankton to fish, whose reflected signal intensity is maximal at different frequencies (Simmonds and MacLennan, 2005; Benoit-Bird and Lawson, 2016).

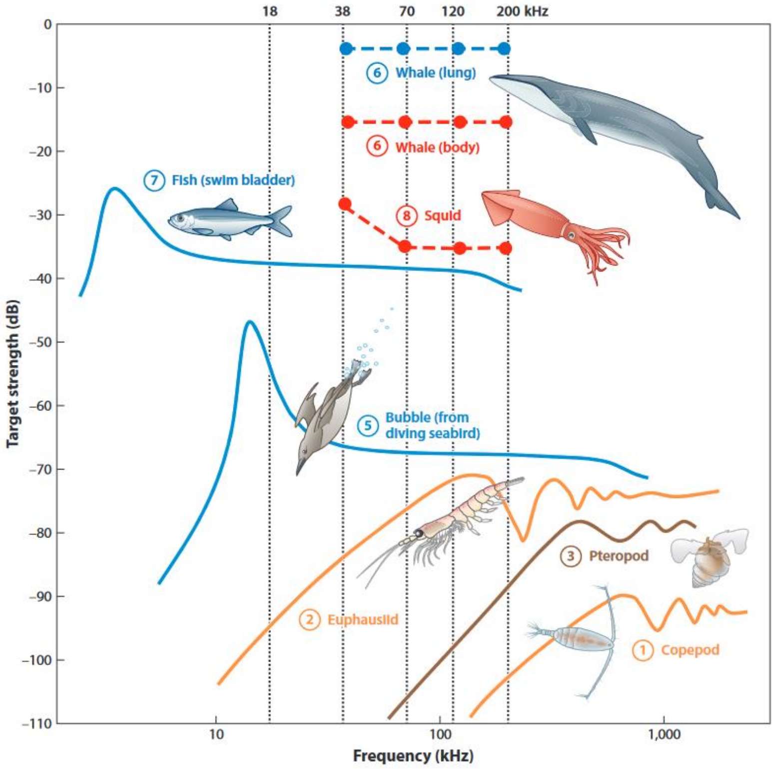

Figure 1.7. Frequency responses characteristic of the different types of animals from Benoit-bird & Lawson, 2016

According to their physical characteristics (shape, presence of swimbladder, etc.), organisms exhibit specific acoustic frequency responses of great value for remote inference of community composition using multifrequency methods. Multifrequency techniques take advantage of the characteristics of the organisms, making possible a classification of the different categories of organisms (Vargas et al., 2017). For example, fish are known to have high backscattering values remaining relatively constant over the usual frequencies (Fig. 1.7). Apart from differences due to presence or absence of swimbladder, fish, as acoustic scatters, are relatively similar, varying principally with size. Crustacean on the other hand have an increasing backscattering response with the frequency, whereas gas-bearing gelatinous have a high backscattering response at low frequency. However, active acoustic methods rely on biological sampling complement and are traditionally combined with trawling or other fishing gears to perform species identification and size measures (Simmonds and MacLennan, 2005). Furthermore, knowledge on individual target strengths (TS) and species composition is a prerequisite to transform acoustic energy into biomass (Simmonds and MacLennan, 2005).

Target strength

Temperate fisheries have developed routine monitoring on temperate pelagic or demersal fish from single-species schools (e.g. as herrings, anchovies, sardines, cod, and walleye Pollock) using acoustics. To convert acoustic density estimates into fish abundance or biomass, a priori or a posteriori knowledge of the mean target strength (TS, in decibels [dB re 1 m^2]) must be available for the size range and species being studied. TS is a specie-specific measure of the amount of acoustic energy backscattered by an individual target (Simmonds and MacLennan, 2005). There is a relationship between TS of a fish and its length (TS-L) and as TS is specie-specific it varie for different species of the same size. The TS is a logarithmic function of the backscattering cross-section (σ_{bs}, in m^2) that mainly depends on the internal physiology – mostly the presence and the shape of the swimbladder - and the body orientation of the fish with respect to the transmitted beam (Simmonds and MacLennan, 2005).

The σ_{bs} is the proportion of reflected intensity (I_R) from the transmitted incident intensity (I_i), measured at a distance from the target (R, [m]):

$$\sigma_{bs} = R^2 \, I_R \, . \, I_i^{-1}.$$

TS describes the same physical measurement in the logarithmic space:

$$TS = 10 \log10 (\sigma_{bs}).$$

To estimate the biomass of a species the relation between TS and length is used:

$$TS = a \log10(L)+b$$

where a and b are constants determined by least-mean-squares regression analysis. As σ_{bs} is approximately proportional to L^2 (Love, 1977), the commonly used equation is:

$$TS = 20\log10(L)+b_{20}$$

The advantages and disadvantages

Contrary to optical methods, acoustic methods are not limited by absence of light. Acoustic instruments allow for continuous sampling with high spatial and temporal resolution. Moreover, they are non-invasive methods and without material extraction (Benoit-bird & Lawson, 2016). Underwater acoustics have an unrealized potential for multicomponent observations that can overcome previous limitations (Bertrand et al., 2014). Only underwater acoustics make feasible the simultaneous collection of qualitative and quantitative data on the distribution and behavior of various communities of an ecosystem, from plankton to large predators as well as abiotic parameters at a variety of spatiotemporal scales (Trenkel et al., 2011).

Acoustic records alone do not allow identifying organisms, specifically. Videos or *in situ* sampling (e.g. plankton net, trawl net or video) are required for echo identification. Frequency dependence can be used to make inferences about the species composition and size distribution of the acoustic scatters. However, while different discrete frequencies allow us to distinguish some functional groups, such as swimbladdered and non-swimbladdered fish, with a high level of confidence, differentiating between fish with similar morphological and physiological characteristics remains challenging (De Robertis et al., 2010; Woillez et al., 2012). Furthermore because it is commonly assumed that the swimbladder accounts for up to 90% of the backscattered energy (Foote, 1985) the body orientation of the sampled fish have a an important influence on the target strength. Fish behavior may lead in several ways to uncertainties in acoustic abundance estimation (Olsen, 1990). Swimbladder volume and TS also vary with depth, which may change on a diel basis due to vertical migration (Godø et al., 2009). Because the ability to discriminate acoustically among taxa remains coarse, acoustics is traditionally used in relatively low-diversity systems such as temperate systems with a few well-defined and acoustically distinct groups (Koslow, 2009).

1.5. Pending questions and Objectives

Active acoustics are not commonly used to describe multi-specific fish assemblages in highly biodiverse tropical ecosystems. Given the sparsity of acoustic studies focusing on tropical demersal habitats, *target strength* estimates for the most tropical fish are yet to be established.

Furthermore, acoustic is not often used to describe multispecific fish assemblages in tropical environments even though active acoustics methodes can help to fill the gap in knowledge providing shelf-scale ecological information. A considerable advantage of acoustic data is the sampling of depths not easily accessible by humans, which allows the study of euphotic and mesophotic depths.

The island mass effect is well described for the low trophic levels such as phytoplankton as the colour of the ocean is a proxy of chlorophyll concentration from which an estimate of primary productivity can be calculated. Planktonic (phyto- and zooplankton) organisms are subject to the hydrography dynamics and can be modelled and their distribution can be inferred from models based on currents and satellite data. On the other hand the distribution of nektonic organisms (i.e. actively swimming organisms) such as fish can be more difficult to infer even for those linked with their prey distribution that might be in the planktonic compartment or relying on planktonic prey (micronekton). Active acoustic provides a high resolution on the horizontal and the vertical dimension along a survey transects allowing fish detection over a large area and over the whole water column.

In particular, there is a gap in fish distribution knowledge in Northeast Brazil because of institutional instabilities in national monitoring.

In the overall context described above, the general aim of this thesis is to describe the distribution patterns of pelagic and demersal communities in northeastern Brazil using multi-frequency acoustic data. This general objective is broken down into three specific objectives:

1) Describe the distribution patterns and biomass of the most observed fish around Fernando de Noronha, the black triggerfish.

2) Describe the vertical and horizontal distribution patterns of pelagic and demersal fish in Fernando de Noronha Archipelago as a function of the environment.

3) Describe the vertical and horizontal distribution patterns of pelagic and demersal fish along the northeastern coast of Brazil.

The first two articles focusing on the Fernando de Noronha archipelago rely on the data collected during three surveys called ‘Fish Acoustics around Fernando de Noronha’ (FAROFA; Bertrand, 2017b, 2018, 2019). Active multi-frequency acoustics coupled with video observation was chosen as a non-extractive method and as the most effective and appropriate tool to describe the distribution of demersal fish around Fernando de Noronha. The third article focus on the Northeastern shelf of Brazil with data from ‘Acoustics along the BRAzilian COaSt’ (ABRAÇOS; Bertrand, 2015, 2017) down to 150 m depth.

CHAPTER 2. Target strength measurement of two triggerfish species

Triggerfish are considered key species in some tropical ecosystems. During the surveys in the tropical oceanic archipelago of Fernando de Noronha, we observed two species of triggerfish, the black triggerfish (*Melichthys niger)* and the ocean triggerfish (*Canthidermis sufflamen)* using underwater videos. The simultaneous scrutiny of underwater videos and active acoustics allowed identifying triggerfish schools in the echograms. For both triggerfish, their schools were monospecific and loose, which allowed for target strength estimation using active acoustics. The black triggerfish was the most observed species, forming a loose school of several hundreds of individuals with different body orientation while the ocean triggerfish formed even loser schools with few individual swimming in the same direction. Black triggerfish are ubiquitous species in tropical water, they have shown a great capacity to colonise and pullulate in remote islands and the ocean triggerfish is an important bycatch of tuna fisheries. To our knowledge, the black triggerfish and the ocean triggerfish had no previous *target strength* estimation, which is a prerequisite for accurate biomass estimations for those species.

Article 1

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In situ* target strength measurement of the black triggerfish *Melichthys niger* and the ocean triggerfish *Canthidermis sufflamen

Julie Salvetat, Anne Lebourges-Dhaussy, Paulo Travassos, Sven Gastauer, Gildas Roudaut, Gary Vargas and Arnaud Bertrand

2.1. Abstract

Triggerfish are widely distributed in tropical waters where they play an important ecological role. The black triggerfish *Melichthys niger* may be the dominant species around oceanic tropical islands, whereas pelagic triggerfish, such as the ocean triggerfish *Canthidermis sufflamen*, can assemble around fish aggregating devices (FADs) where they are a common bycatch of tuna fisheries. In this study we combined acoustic and optical recordings to provide the first in situ target strength (TS) measurement of black and ocean triggerfish. Data were collected in the Archipelago of Fernando de Noronha off north-east Brazil. The mean TS of a 27.8-cm-long black triggerfish at 70 and 200 kHz was -39.3 dB re 1 m^2 (CV = 14.0%) and -38.9 dB re 1 m^2 (CV = 14.4%) respectively. The mean TS values of ocean triggerfish (with a size range of 39–44 cm) at 70 and 200 kHz were -36.0 dB re 1 m^2 (CV = 15.7%) and -33.3 dB re 1 m^2 (CV = 14.0%) respectively. This work opens up the field for acoustic biomass estimates. In addition, we have shown that TS values for ocean triggerfish are within the same range as those of small tunas. Therefore, acoustic data transmitted from FADs equipped with echosounders can introduce a bias in tuna acoustic biomass estimation and lead to increased rates of bycatch.

Keywords: biomass estimation, north-east Brazil, small tuna, target strength–length relationships, tropical ecosystem, underwater acoustics, underwater video.

2.2. Introduction

Triggerfish, which are part of the Balistidae Family and comprise 12 genera and 42 species, are widely distributed in tropical waters of the Atlantic, Pacific and Indian oceans (R. Froese and D. Pauly, FishBase, see https://www.fishbase.de/home.htm, accessed 8 April 2019). Generally associated with coral reefs, triggerfish are an important member of fish assemblages in tropical ecosystems (Vose and Nelson, 1994; Mendes et al., 2019). Several triggerfish have been identified as ‘keystone’ species within coral reef and rocky bottom communities, controlling, by predation, populations of reef-eroding sea urchins (Clemente et al., 2010) and coral-feeding crown-of-thorns starfish *Acanthaster planci* (Rivera-Posada et al., 2014). The diet of triggerfish extends beyond hard-shelled prey because they are opportunistic broad generalists, consuming almost any available food source from plankton, algae, eggs and other fish to the faeces of other organisms (Randall, 1967; Sazima et al., 2003; Morais et al., 2017b). This high trophic plasticity of triggerfish is of special importance for those species that can pullulate (Kavanagh and Olney, 2006; Garcia Júnior et al., 2017; Gerlotto, 2017) and extend their area of distribution to temperate waters (Quigley et al., 1993; Tuponogov, 2015; Brooks et al., 2016). Among the triggerfish, the black triggerfish *Melichthys niger* (Bloch, 1786) has a circumtropical distribution and can form large shoals of more than 100 individuals (Price and John, 1980). Black triggerfish can be the dominant species in terms of biomass around oceanic islands, such as Ascension Island (Lubbock, 1980; Price and John, 1980), Clipperton Atoll (Robertson and Allen, 1996), Trinidad Island (Gasparini and Floeter, 2001), Johnson Atoll (Kavanagh and

Olney, 2006), St Paul’s Rock (Lubbock and Edwards, 1981; Feitoza et al., 2003) and Fernando de Noronha archipelago (FdN) (Sazima et al., 2006). Because of their geographic isolation, remote islands can have high endemism but low taxonomic and functional richness in reef fish assemblages (Pinheiro et al., 2017). Given their high plasticity and abundance, black triggerfish can assume the functional role of virtually missing species, such as roving herbivores. Mendes et al. (2019) suggested that around the Saint Peter and Saint Paul Archipelago, black triggerfish can be considered a functional herbivore and represent an important trophic link between primary productivity and higher levels in the local food chain. However, despite its ecological importance to island ecosystems, the black triggerfish remains one of the least-studied triggerfish (Branco et al., 2013). Triggerfish habitat varies among species. Most triggerfish are associated with coral reefs, but species of the genus Canthidermis are mostly pelagic. Of these, the ocean triggerfish *Canthidermis sufflamen* (Mitchill, 1815) is expanding its distribution with ongoing global warming and the tropicalization of temperate regions. For example, after being first reported in the Canary Islands in the 1990s, it settled there and became commercially exploited (Brito et al., 1995, 2005). In Venezuela, ocean triggerfish have even been estimated to be overexploited by the artisanal fishers of El Tirano, New Sparta State, where those fish have become a low-cost food and protein resource within the current context of high food demand (Alarcón et al., 2017). Despite their use for human consumption, given their low commercial value triggerfish are regularly discarded as unwanted bycatch (Matos-Caraballo et al., 2007; Gastauer et al., 2017). In particular, ocean triggerfish are reported as a common bycatch species within the purse seine tuna fisheries on drifting FADs (DFADs), where triggerfish are known to aggregate (Moreno et al., 2007; Taquet et al., 2007; Romanov, 2008; Lezama-Ochoa et al., 2017, 2018). Bycatch studies around DFADS generally focus on charismatic and vulnerable species (sharks, rays and sea turtles), whereas others non-tuna species are considered of less concern and are not being monitored (Dagorn et al., 2013). Currently nearly 50% of all principal market tunas are caught by purse seiners fishing on DFADs (Fonteneau et al., 2013). Because they are considered to greatly increase purse seine efficiency, DFADs have been extensively deployed since the 1990s, and an estimated 50 000–100 000 DFADs are deployed each year by fishers in tropical waters in the three oceans (Baske et al., 2012). The extensive use of DFADs also raises concerns regarding potential deleterious effects on tuna stocks, high levels of bycatch and threats to the biodiversity of tropical pelagic ecosystems (Bromhead et al., 2003; Morgan, 2011; Dagorn et al., 2013). DFADs are commonly equipped with echosounders that can provide near real-time information to fishers on the accurate geolocation and rough estimates of the biomass of aggregated acoustically located fish

(Lopez et al., 2016). To accurately convert acoustic density estimates into fish abundance or biomass, a priori or a posteriori knowledge of the mean target strength (TS; in decibels relative to 1 m^2,dB re 1m^2) must be available for the size range and species being studied. Moreover, TS plays a role not only as a decisive scaling factor for fish abundance estimates, but also as a tool for fish species identification (Simmonds and MacLennan, 2005), and enables going beyond mono-specific stock assessment of target species, moving towards a more ecosystem-based assessment. In this context, and to open up the field to acoustic ecological studies and biomass estimation, the present study had two main objectives: (1) to make the first in situ TS measurements of the black triggerfish in the FdN; and (2) to investigate the possibility of distinguishing the TS distribution of oceanic triggerfish from that of tuna aggregated around DFADs. In situ TS measurements of black triggerfish were made by combining simultaneous acoustic and optical recordings with fish sampling in the oceanic archipelago of the FdN in north-east Brazil, opening up possibilities for further acoustic in situ biomass estimation. Only there are only two previous studies into the TS of triggerfish: Johnston et al., (2006) conducted caged fish TS measurements on black triggerfish and ocean triggerfish, and Gastauer et al. (2017) used a theoretical model to infer TS. With regard to the second study objective, using the acoustic data to discriminate between species could be a way to reduce bycatch. To test this possibility, we compared published results of in situ TS measurements of tropical tunas of different species and sizes (Bertrand et al., 1999; Bertrand and Josse, 2000; Josse and Bertrand, 2000; Boyra et al., 2018) with those obtained in this study for black and ocean triggerfish.

2.3. Material and methods

Measurements were made in the FdN (3°50’S, 32°25’W), the largest Brazilian oceanic archipelago, 345 km off the northeastern coast of Brazil (Fig. 2.1). Data were collected from 17 to 23 April 2018 during the day within the framework of the second ‘Fish Acoustics around Fernando de Noronha’ (FAROFA2) survey (Bertrand, 2018). Acoustic data were collected continuously throughout the survey with two SIMRAD (Kongsberg maritime AS, Horten, Norway) EK80 echosounders connected to two 78 split beam transducers centred on the frequencies of 70 and 200 kHz and operated simultaneously in narrow band (continuous wave) transmission. Transducers were attached with a stainless-steel pole to the port side of a 10-m-long sport fishing boat (for a detailed description of the setup, see Bertrand et al., 2017). Acoustic data were acquired with transmitted powers of 600 and 90 W for 70 and 200 kHz respectively. With the aim of measuring TS and tracking individual detections, the ping rate was set to ‘maximum’ for a maximum acquisition range of 100 m (on the continental shelf) and to 1 ping s^{-1} off the shelf, where the maximum acquisition range was set to 400 m. Vessel speed was ~2.5 m s^{-1} during acquisition of acoustic data. Because of the rather windy conditions around FdN, pulse duration had to be long enough to improve the signal-to-noise ratio and the maximum range for the two transducers. Thus, the pulse duration was set at 1.024 ms to ensure a good compromise between a pulse long enough to reduce the noise at the maximum range of 400 m at 70 kHz and short enough to separate individual fish by ~40 cm.

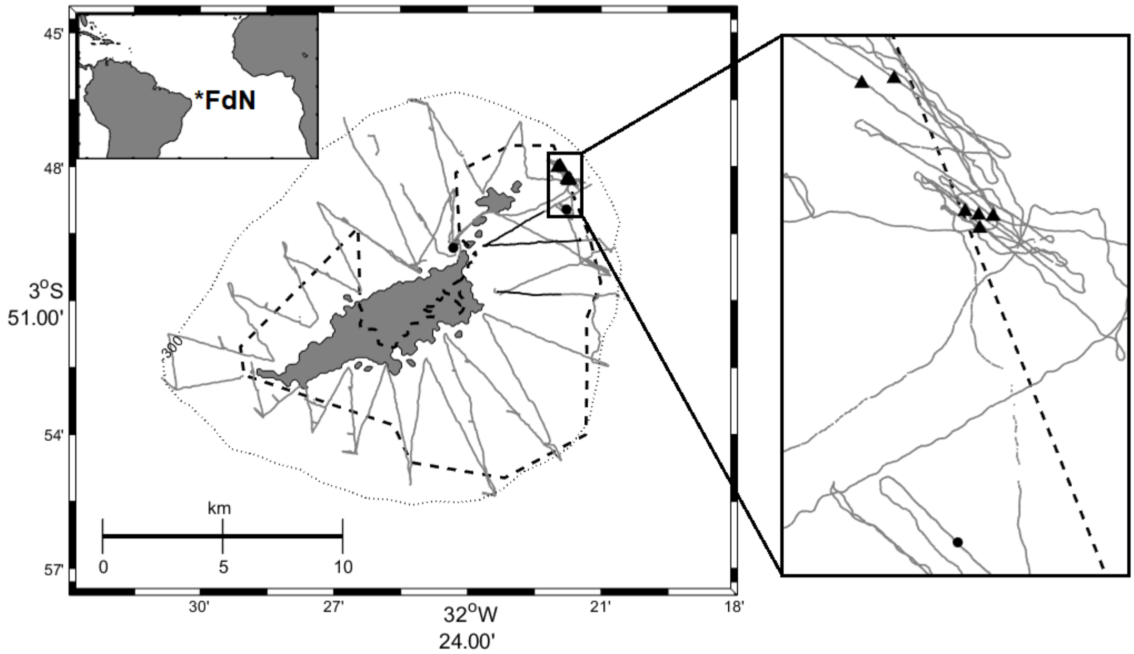


Figure 2.1. Location and selected vertical profile stations around Fernando de Noronha (FdN) for black triggerfish (circles) and ocean triggerfish (triangles) and selected towed video (solid black line). The solid grey line indicates the FAROFA2 acoustic survey, the dashed black line indicates the limits of the Parque Nacional Marinho de Fernando de Noronha (PARNAMAR) and the dotted black line indicates the 300-m isobath.

We chose to use an identical pulse duration at both frequencies to simplify downstream processing. Echosounder calibrations were completed for both frequencies before the cruise in a seawater tank at the Institut francais de recherche pour l’exploitation de la mer (Ifremer) centre in Plouzané, France, using a 38.1-mm tungsten carbide sphere and following the procedures described by Foote (1987). Calibrations were performed for the two pulse durations and transmitted powers used during the survey. Acoustic data were converted to HAC files (McQuinn 2005) using Ifremer’s Hermes software (McQuinn et al., 2005; Trenkel et al., 2009). Processing was completed using the Matecho tool of the Institut de Recherche pour le

Développement (IRD; Perrot et al. 2018) linked to Matlab (MathWorks, Paris, France) and Ifremer's Movies3D software (Ifremer, see https://www.flotteoceanographique.fr/La-Flotte/Logiciels-embarques/HERMES-et-MOVIES3D; Trenkel et al. 2009). Processing steps included a bottom detection with manual correction, removal of transient or attenuated signal (mostly caused by signal blocking due to harsh weather conditions or vessel movement), impulsive noise (instantaneous and sharp signals mainly caused by interference from other acoustic or electrical systems) and background noise (De Robertis and Higginbottom, 2007; Ryan et al., 2015) before the detection of individual fish traces (Soule et al., 1997) or shoals. TS is a logarithmic measure of the amount of acoustic energy backscattered from an individual fish, usually related to fish length (L) as TS – L (Foote, 1979; MacLennan and Menz, 1996; McClatchie et al., 1996; Simmonds and MacLennan, 2005). TS is a logarithmic function of the backscattering cross-section (σ_{bs};m^2) that depends primarily on the internal physiology (mostly the presence and the shape of the swim bladder) and body orientation of the fish with regard to the transmitted beam (Foote, 1980; Hazen and Horne, 2003; Simmonds and MacLennan, 2005). Individual fish TS measurements require the extraction of acoustic single targets (resolvable single echo traces). In this study, single targets were extracted following the methods described by Soule et al. (1997), implemented within Movies3D (Trenkel et al. 2009). Single target detection settings are given in Table 2.1.

Table 2.1. Input parameters in Movies3D for single target detection and tracking algorithms

TS, target strength

Single target algorithm	
Minimum TS threshold (dB m^{-2})	–60.0
Maximum angular one-way compensation (dB m^{-2})	6.0
Maximum phase deviation (phase steps)	8.0
Minimum echo length	0.8
Maximum echo length	1.8
Minimum echo space	1.0

Minimum echo depth (m)	3
Maximum echo depth (m)	120
Tracking algorithm	
Maximum relative speed between acoustic beam and target ($m.s^{-1}$)	8
Maximum holes between two tracked echoes (pings)	1
Minimum single target in track	2
Maximum holes (%)	50

Single target TS discrimination may lead to an overestimation of in situ TS measurements because of the acceptance of multiple echoes (Sawada et al., 1993). To increase the robustness of the results, single successive echoes of each individual fish (Fig. 2.2) were tracked to determine the mean fish TS over a range of pings (Table 1). All TS measurements were compensated for the position of the detected target in the beam. Only tracks encompassing a minimum of two pings were retained. The cohesiveness of the selected tracks was inspected visually within a checking tracks tool developed in Matlab. For each frequency, the mean TS of each fish track was calculated in the linear domain (Eqn 1). The final mean TS of all fish tracks for each frequency was computed as the mean of all mean TS of individual tracks, in the linear domain:

$$\overline{TS} = 10 \log_{10} \left(\overline{s_{bs}}\right) \quad (1)$$

Locations at which single target tracks were extracted were identified through inspection of the video material. Stations with strong dominance and a high density of black or ocean triggerfish were selected to extract TS values from detected acoustic single targets. Optical recordings and echograms were time synchronised. For each selected station, TS values were extracted from 5 min before the beginning to 5 min after the end of the video. It is commonly assumed that the logarithmic TS depends on fish size (Foote, 1979; McClatchie et al., 1996; Simmonds and MacLennan, 2005) following a linear relationship:

$$TS = a \log(L) + b \quad (2)$$

where a and b are constants for a species and a given frequency and L is total length (cm). Here we used Eqn 3, assuming that sbs is proportional to L^2 (Foote, 1979; MacLennan and Menz, 1996; McClatchie et al., 1996; Simmonds and MacLennan, 2005) to estimate the TS–length relationships for the black triggerfish:

$$TS = 20\log(L) + b_{20} \ (3)$$

where b_{20} is the constant of the equation relating TS and fish length with an assumption of a linear relationship with L^2 therefore when the equation is based on 20log(L).

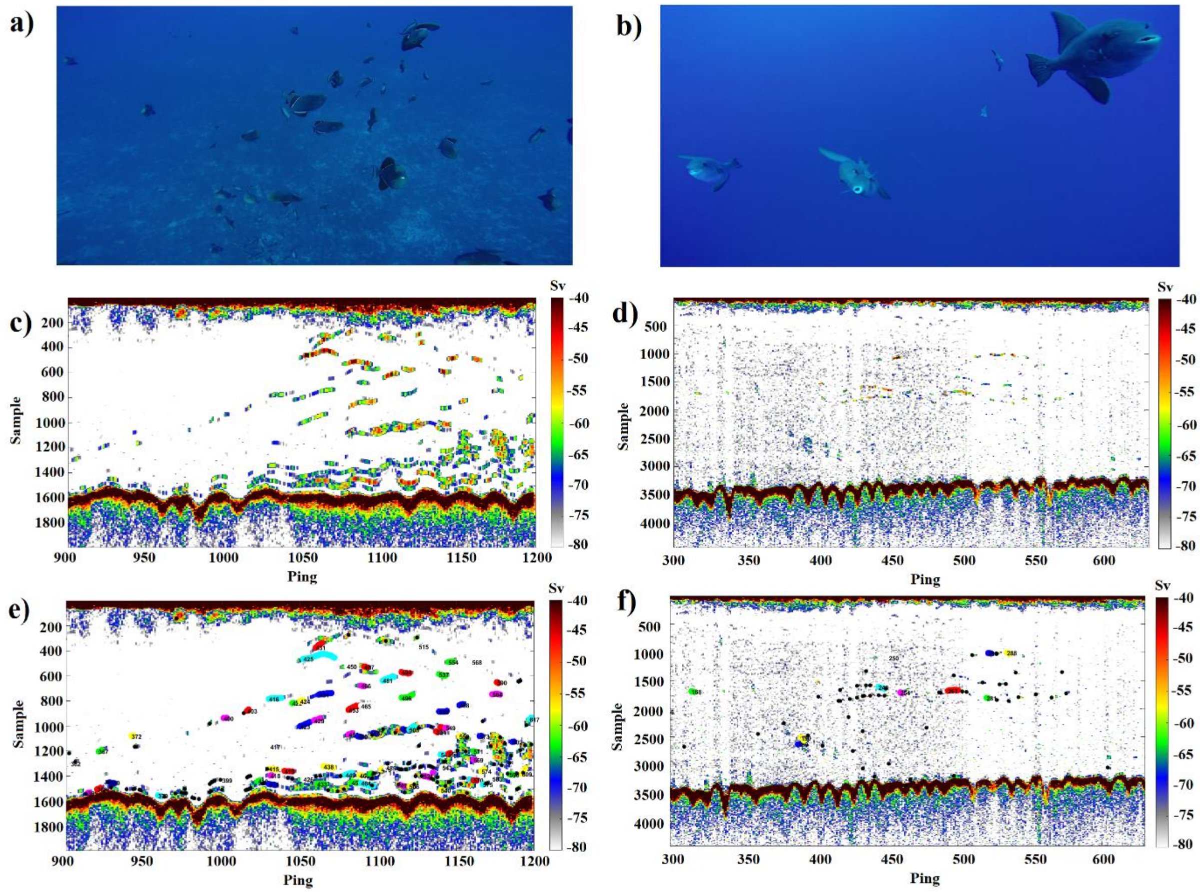


Figure 2.2. Individual fish target extraction. (a, b) Video screenshots showing aggregation of black (a) and ocean (b) triggerfish. (c, d) Corresponding original echograms at 200 kHz for black (c) and ocean (d) triggerfish. (e, f) Tracked individual targets on the respective echograms for black (e) and ocean (f) triggerfish. Data are from the FAROFA2 survey.

Even though Eqn 3 is a controversial approximation, it is still widely used (e.g. Gastauer et al. 2017). We used it here to facilitate comparisons between the present study and other studies. For species identification we obtained video observations in two ways using GoPro Hero 3þ cameras (HD at 1080-pixel equivalent to 2.1 megapixels per frame at 60 frames s1, GoPro, San Mateo, CA, USA). First, we obtained vertical video profiles with a camera fitted on a fishing line (Fernandes et al. 2016) equipped with an electric reel to film at different depths (5–20 m) while adrift. These video stations were located where noteworthy fish aggregations were observed on the echograms and camera depth was defined according to bottom depth and the position of the aggregation. Typical video profiles were 15 min long. In all, videos were obtained from 32 stations. Second, we used a towed video, at vessel speed of 1.5 m s1, on a downrigger along acoustic transects with the video looking down at the bottom. Typical towed videos were 50 min long and 17 profiles were obtained. Black triggerfish were seen in 6 of 32 vertical video profiles and in 7 of 17 towed videos. Ocean triggerfish were observed in 13 of 32 vertical videos and in 1 of 17 towed videos. To extract TS, we selected part of the echogram corresponding to the video records where black and ocean triggerfish were observed forming monospecific shoals. Two vertical video profiles and two towed videos were selected for black triggerfish, whereas six vertical video profiles were selected for ocean triggerfish. Finally, fishing operations using vertical baited handlines and dip nets were occasionally conducted at some stations and between stations to determine the species composition and fish length structure. Time, species and fork length to the closest millimetre were recorded for each fish caught. Because the FdN is protected by a series of legal instruments, including a National Park, Parque Nacional Marinho de Fernando de Noronha (PARNAMAR) where fishing is prohibited (Fig. 2.1), all fishing operations were conducted outside the PARNAMAR. Fishing operations were conducted under permit number 59721-1 from Sistema de Autorização e Informação em Biodiversidade (SISBIO), which authorises fishing outside the marine protected area.

2.4. Results

Black triggerfish were observed shoaling from the shore to the limit of the shelf break (Fig. 2.2a). Ocean triggerfish were observed forming loose shoals close to the shelf break (Fig. 2.2b). In all, 28 black triggerfish were caught in areas where the selected video profiles and TS measurements were performed. The size of the fish was highly homogeneous, with a mean (±s.d.) size of 27.8 ± 1.2 cm (range 26–30 cm; s.d. 1.2 cm) total or fork length (which are alike considering the shape of both species studied). Only three ocean triggerfish were caught measuring 39.0, 44.0 and 44.0 cm, not enough to further estimate the TS–length relationship. In all, 3566 and 6579 single echoes corresponding to 1237 and 1985 tracked fish assumed to be black triggerfish were selected and validated at 70 and 200 kHz respectively. The depth of the echoes varied between 6.6 and 42.1 m (see Fig. S2.1a, available as Supplementary material to this paper). No significant trend in TS according to depth was observed at 70 kHz. However, a significant but weak ($r^2 = 0.0006$) positive relationship was observed between TS and depth at

200 kHz (Fig. S2.2). Mean tracked compensated TS exhibited a unimodal distribution (Fig. 2.3a) with a mean TS of -39.3 ± 5.5 dB (CV = 14.0%) and -38.9 ± 5.6 dB (CV = 14.4%) at 70 and 200 kHz respectively. There was no significant difference in mean TS between 70 and 200 kHz (Mann–Whitney–Wilcoxon test, p = 0.0000). Combining the mean TS with the mean fork length measured for black triggerfish caught during FAROFA2 resulted in b20 values of the TS–length relationship (Eqn 3) of -68.2 and -67.8 dB at 70 and 200 kHz respectively. In all, 249 and 640 single echoes corresponding to 112 and 260 tracked fish assumed to be ocean triggerfish were selected and validated at 70 and 200 kHz respectively. The depth of the echoes varied between 17.2 and 73.7 m (Fig. S2.1b). No significant trend in TS was observed according to depth at 70 kHz, but a significant but weak positive relationship ($r^2 = 0.1162$) between TS and depth was observed at 200 kHz (Fig. S2.3). Mean tracked TS exhibited a unimodal distribution (Fig. 2.3b) with a mean (±s.d.) TS of -36.0 ± 5.6 dB (CV = 15.7%) and -33.3 ± 4.7 dB (CV = 14.0%) at 70 and 200 kHz respectively (Table 2.2).

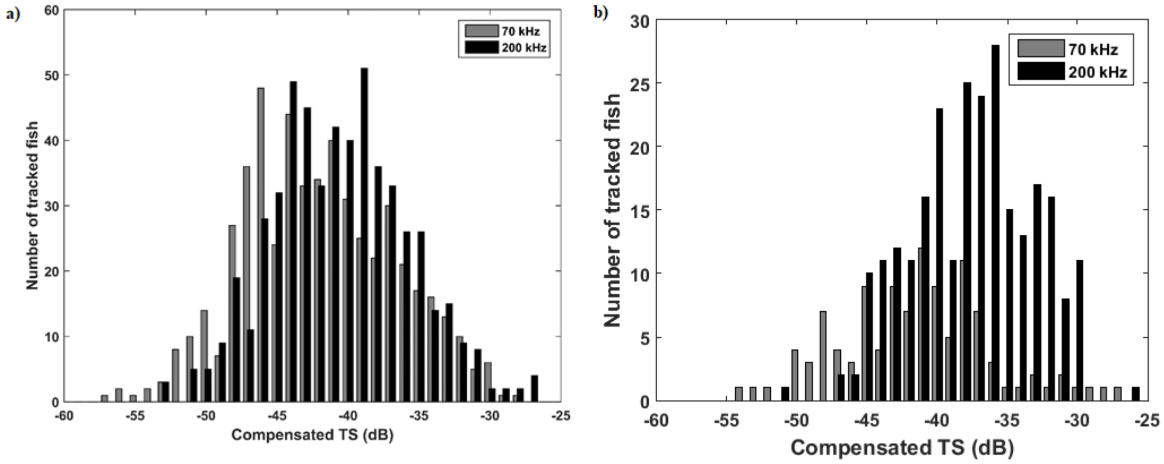


Figure 2.3. Mean target strength (TS) distribution (dB re 1 m^2) of echoes attributed to (a) black and (b) ocean triggerfish at 200) and 70 kHz. Data are from the FAROFA2 survey.

Table 2.2. Overview of target strength (TS) extraction results from FAROFA2 surveys

	Black triggerfish		Ocean triggerfish	
Frequency (kHz)	70	200	70	200
Number of TS values	3566	6579	249	640
Number of tracks	1237	1985	112	260
Mean (±s.d.) TS (dB m^{-2})	–39.3 ± 5.5	–38.9 ± 5.6	–36.0 ± 5.6	–33.3 ± 4.7

CV (%)	14.0	14.4	15.7	14.0

2.5. Discussion

Acoustic methods are one of the most effective and nonintrusive methods allowing the simultaneous collection of continuous high-resolution qualitative and quantitative data on various aquatic organisms in addition to environmental information (Koslow, 2009; Trenkel et al., 2011; Handegard et al., 2013). Registered acoustic data during acoustic cruise are often associated with trawling or trapping because they need biological evidence for species determination or length distribution (Benoit-Bird and Lawson, 2016; Fernandes et al., 2016). In this study we chose to combine acoustic measures with video taping, which is a non-invasive and non-extractive alternative well adapted for protected areas such as most of the FdN. Still, because we had no systems allowing for direct fish size estimation, we had to capture some fish to determine the size distribution. Importantly, black triggerfish have a rapid growth in the first year and slow growth thereafter (Kavanagh and Olney, 2006). This dynamic implies that most individuals in the population are approximately the same size. This was observed in this study, with a very homogeneous size structure. The mean size observed in this study (~28 cm) is comparable to that of sporadic black triggerfish size measurements performed around the FdN at other times (P. Travassos, unpubl. data).

The black and ocean triggerfish are physoclists with a welldeveloped swim bladder encompassing developed anterior lateral lobes (Jones and Marshall, 1953; Chanet et al., 2014). Because the swim bladder accounts for up to 90% of the backscattered energy (Foote, 1985), fish with a swim bladder are known to have a higher backscattering response than fish without a swim bladder. Considering the measured size of the triggerfish, our TS results for both species ranging from -36.0 to -33.3 dB are within an expected range compared with TS values for other fish reported previously (Foote, 1980; Kloser and Horne, 2003; Fässler et al., 2007). Similarly, the b_{20} values estimated for the black triggerfish of 68.2 and 67.8 dB at 70 and 200 kHz respectively fall into the expected range for physoclist fish (Simmonds and MacLennan, 2005). The TS measurements in this study fit between the two unique studies that have reported triggerfish TS, namely those of Johnston et al. (2006) and Gastauer et al. (2017). The measurements of Johnston et al. (2006) were performed along the coast of Puerto Rico on caged fish. These authors found much higher TS at 200 kHz for both species than reported herein, namely a mean TS of -35.8 dB for a 27.9-cm-long black triggerfish (v. -38.9 dB in the present study) and -31.7 dB for a 45.7-cm-long ocean triggerfish (v. -33.3 dB in the present study). Those differences could be due to differences in incidence angle distributions because free-swimming fish change their orientation from time to time as part of their natural behavior (Simmonds and MacLennan 2005), probably more than in a 0.9-m-high cage as used in the study of Johnston et al. (2006). Conversely, Gastauer et al. (2017) used a Kirchhoff-ray mode (KRM) model mapping the swim bladder surface into a digital representation (Clay and Horne, 1994) and estimated a b_{20} of 77.7 dB for triggerfish at 38 kHz, much lower than that observed in the present study. Applying the b_{20} from Gastauer et al. (2017) to a 27.8-cm-long black triggerfish in Eqn 3 would result in a TS of -48.8 dB at -38 kHz, far lower than our estimates (-39.3 and -38.9 dB at 70 and 200 kHz respectively). The samples used by Gastauer et al. (2017) were taken from a commercial trap fishing vessel capturing triggerfish as bycatch in the North-western Demersal Scalefish Fishery in north-western Australia, and the estimate was based on computed tomography scans of three triggerfish with intact swim bladders used as inputs for the KRM. The frequencies used are likely to explain some of the variation, but the difference of almost 10 dB is too high to be due only to the frequency response. Such a large difference can have significant repercussions because it corresponds to a factor of ~10 in biomass estimations. The difference could be due to the fact the equation was fitted for a ‘generic’ triggerfish without species distinction. However, such a large difference is likely to be due primarily to a difference in methodology. For biomass estimates, in situ TS measurements encompassing natural behavior and related tilt angle are recommended (Hazen and Horne, 2003; Simmonds and MacLennan, 2005; Henderson and Horne, 2007); therefore, we believe that our results are more appropriate for such application. We acknowledge that fitting a TS–length relationship using b_{20} (Eqn 3) and thus estimating only one parameter is debatable (e.g. Simmonds and MacLennan 2005). Ideally, TS measurements for different fish sizes would allow estimation of both terms in Eqn 2. Unfortunately, in our case this was very difficult to achieve in situ. Indeed, because triggerfish size distribution is very narrow once adult size is reached, it is virtually impossible to calculate a regression equation of TS as a function of fish length within a given size range. Therefore, the TS–length relationship we propose is questionable but useful for comparison with other studies. DFADs naturally aggregate several pelagic species other than tuna, including ocean megafauna such as sharks, turtles and cetaceans, which can accidentally get caught during the fishing operations. Castro et al. (2002) enumerated over 333 fish species associated with FADs, including black triggerfish, ocean triggerfish and another four species of triggerfish, as bycatch species of the tuna purse seine fishery. Among these, *Canthidermis maculata* can form massive schools of many thousands of individuals around DFADs and represent an important part of the bycatch (Taquet et al., 2007; Romanov, 2008; Lezama-Ochoa et al., 2015). To estimate whether we can discriminate the TS of triggerfish from that of tuna, we compared the TS distributions for both black and ocean triggerfish with the in situ TS reported for tuna of different sizes (Bertrand et al., 1999; Josse and Bertrand, 2000; Boyra et al., 2018). Fig. 2.4a shows tuna TS distribution at 38 kHz with triggerfish TS distribution at 70 kHz, whereas Fig. 2.4b shows black and ocean triggerfish TS at 200 kHz compared with skipjack TS at 200 kHz, because these were the only data available at 200 kHz. Strong overlap can be seen in both graphs. Skipjack, small yellowfin and bigeye tuna are found within the confidence values of the TS for triggerfish (Fig. 2.4), with particular overlap between skipjack and ocean triggerfish (Fig. 2.4b). Large bigeye tuna was the only tuna with a TS distribution different enough to allow for an acoustics discrimination at a sufficiently high level of certainty. Fish behavior can also be useful for species discrimination (e.g. Forget et al. (2015). However, behavioral studies are complex and high-resolution acoustic data are needed, which is not provided by echosounders classically fitted on DFADs. Frequency–response can also be used to discriminate species using acoustic data (Moreno et al., 2019). Fish with swim bladders classically present a decreasing acoustic response with frequency (in the range 38–200 kHz), whereas the opposite is expected for fish without a swim bladder (Fernandes et al. 2006). However, in the present study black and ocean triggerfish, both of which have swim bladders, exhibited a (nonsignificant) increasing response with frequency. This kind of pattern has been reported for other species of fish with swim bladders (Fernandes et al., 2006; Fässler et al., 2007). Under such conditions, frequency–response cannot be a simple way to discriminate triggerfish from tuna, in particular skipjack, because they do not have a swim bladder and are thus expected to have an increasing response with frequency (Boyra et al., 2018; Moreno et al., 2019).

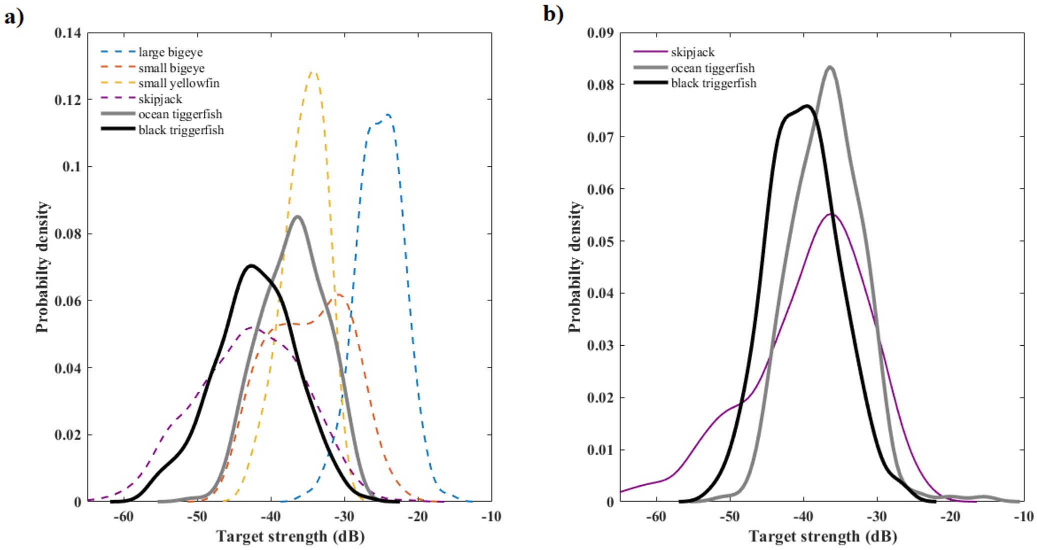
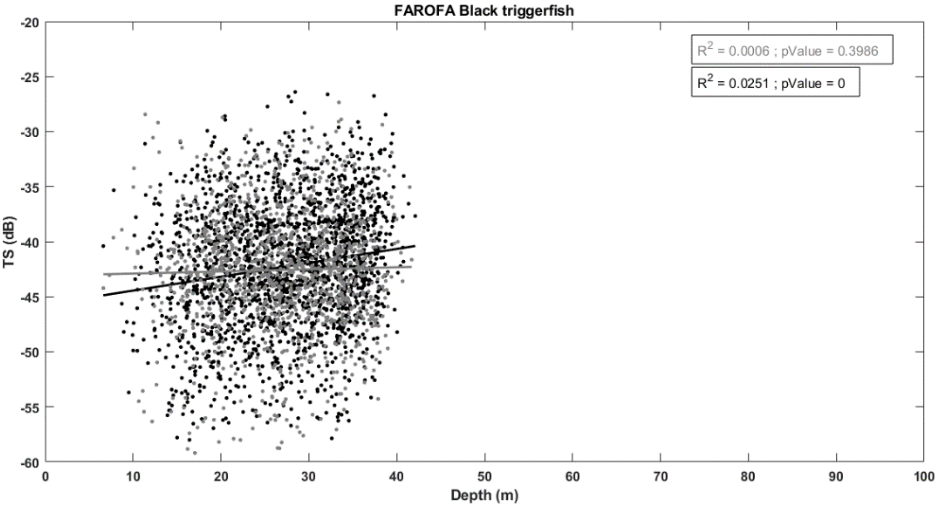


Figure 2.4. (a) Normalised density functions of target strength (TS) distribution (dB re 1 m^2) at 38 kHz for a 60-cm yellowfin tuna and 110-cm bigeye tuna from Bertrand et al. (1999); fish aggregating device (FAD)-aggregated tuna mix dominated by small (,50-cm) bigeye tuna *Thunnus obesus* (92%), *Thunnus albacares* (7%) and *Katsuwonus pelamis* (1%) from Josse and Bertrand (2000); tuna mix dominated by skipjack *K. pelamis* (99%) and *T. albacares* (1%) from Boyra et al. (2018); and at 70 kHz for black and ocean triggerfish from the FAROFA2 survey. TS distributions represented by dotted and solid lines were measured at a frequency of 38 and 70 kHz respectively. (b) Normalised density functions of TS distribution (dB re 1 m^2) at 200 kHz of a tuna mix dominated by skipjack *K. pelamis* (99%) and *T. albacares* (1%) from Boyra et al. (2018) and black and ocean triggerfish from the FAROFA2 survey.

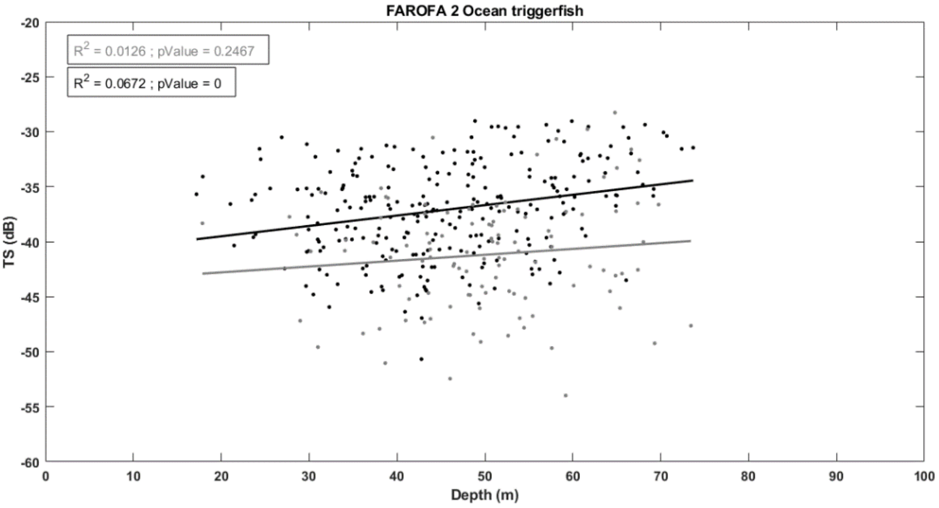
2.6. Conclusion

Through a combination of optical and acoustic methods, the first in situ TS measurements of two important triggerfish species that coexist in the FdN, namely black and ocean triggerfish were computed. The black triggerfish is one of the few reef fish with a circumtropical distribution and it has been seen in remarkably high abundances around remote oceanic islands. The in situ TS measurements we provide here open up the possibility for acoustic biomass estimates, at least for the black triggerfish. Previous studies estimated triggerfish TS experimentally or by using a theoretical model, but in situ acoustic methods allow us to implicitly capture the natural fish behavior and are therefore assumed to be more appropriate for biomass estimations in the wild. Ocean triggerfish are pelagic and can aggregate around DFADs commonly used by commercial tuna purse seine fisheries. We have shown that the TS distributions for both triggerfish strongly overlap those of small tunas, comprising adult skipjacks and bigeye and yellowfin juveniles. Therefore, the use of TS to discriminate small tuna from triggerfish remains challenging.

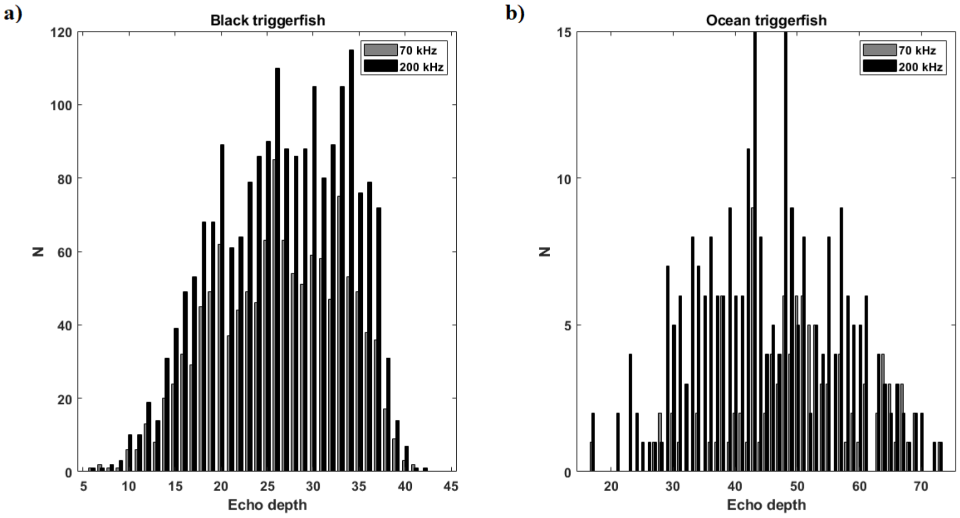
2.7. Supplementary Material



Supplementary Figure S2.1. Depth–TS diagram for black triggerfish in 70 kHz (grey) and 200 kHz (black).



Supplementary Figure S2.2. Depth–TS diagram for ocean triggerfish in 70 kHz (grey) and 200 kHz (black).



Supplementary Figure S2.3. Distribution of the number of individual in function of the depth for a) black triggerfish and b) ocean triggerfish for 70 kHz (grey) and 200 kHz (black).

2.8 Outlook

Prior to this study the *target strength* of the black and the ocean triggerfish were unknown. The black triggerfish (*Melichthys niger*) is ubiquitous and is a very abundant species in many tropical oceanic islands where it might play the key role of functional herbivore where herbivores are virtually absent or overfished. The ocean triggerfish (*Canthidermis sufflamen*) is an important by-catch of tuna industrial fishery using Fish Aggregation Devices. In this first article, we calculated the target strength of both triggerfish species around Fernando de Noronha. Knowledge of the target strength is a prerequisite for biomass estimation and thus to quantify the black triggerfish ecological role and the impact of tuna fishery on ocean triggerfish as a non-targeted by-catch. We point out that the target strength of the ocean triggerfish is very close to the target strength of small tuna species. This result means remote discrimination using active acoustics between tragetted tuna and by-catch triggerfish is very difficult. The black triggerfish biomass is estimated in the second article.

CHAPTER 3. Coupling active acoustics and video to describe the spatial distribution of fish assemblages

In the previous article, we measured in situ *target strength* of the black triggerfish and the ocean triggerfish around Fernando de Noronha archipelago. Those were the only species that formed recognizable monospecific schools identifiable at species level on video footage and on the echograms. In this second article, we use active acoustics and video records simultaneously to classify all fish echoes in multispecific fish assemblages. This gives us the means to provide ecological insight on fish assemblages' spatial distribution around a typical tropical oceanic archipelago such as Fernando de Noronha.

Article 2

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Comprehensive spatial distribution of tropical fish assemblages from multifrequency acoustics and video fulfils the island mass effect framework

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3.1. Abstract

Tropical marine ecosystems are highly biodiverse and provide resources for small-scale fisheries and tourism. However, precise information on fish spatial distribution is lacking, which limits our ability to reconcile exploitation and conservation. We combined acoustics and video observations to provide a comprehensive description of fish distribution in a typical tropical environment, the Fernando de Noronha Archipelago (FNA) off Northeast Brazil. We identified and classified all acoustic echoes into ten fish assemblages and two triggerfish species. This opened up the possibility to relate the different spatial patterns to a series of environmental factors and the level of protection. We provide the first biomass estimation of the black triggerfish *Melichthys niger*, a key tropical player. By comparing the effects of euphotic and mesophotic reefs we show that more than the depth, the most important feature is the topography with the shelf break as the most important hotspot. We also complete the portrait of the island mass effect revealing a clear spatial dissymmetry regarding fish distribution. Indeed, while primary productivity is higher downstream, fish concentrate upstream. The comprehensive fish distribution provided by our approach is directly usable to implement scientific-grounded Marine Spatial Planning.

Keywords: marine tropical ecosystem, mesophotic reefs, marine protected area, biomass estimation, geostatistics, marine spatial planning, fish assemblages

3.2. Introduction

Tropical marine ecosystems hold major biodiversity hotspots (Bowen et al., 2013) and provide a significant share of global fish catch (Lam et al., 2020). Meanwhile, they are increasingly threatened by anthropic pressure including overfishing, global change, invasive species introduction, habitats destruction and pollution (Halpern et al., 2019). In particular, on-going global ocean warming is expected to severely affect species distribution, abundance and extinction rates but also trophic interactions and entire food webs balance (Capitani et al., 2021; Lima et al., 2021). These threats are critical especially for human populations that rely heavily on marine resources and depend on small-scale fisheries (SSF) or tourism for their livelihoods such as tropical developing states or small tropical islands (Sale et al., 2014; Dunstan et al., 2018; Martins and Gasalla, 2018).

Tropical coastal environments form a mosaic of interconnected mega-habitats extending from the shoreline to the open ocean. This complex structure greatly influences the dynamics of fish assemblages (Moura et al., 2013). In recent years, mesophotic reef ecosystems (MREs) have gained attention (Lesser et al., 2009; Bryan et al., 2013; Fukunaga et al., 2016; Kahng et al., 2016; Rocha et al., 2018), not least because their depth may offer protection from anthropic stressors (Bongaerts et al., 2017; Rocha et al., 2018). MREs occur in tropical and subtropical regions and are characterized by the presence of light-dependent corals and associated fauna at depths below 30-40 m extending to 150 m in areas with high water clarity (Fukunaga et al., 2016; Kahng et al., 2016; Rosa et al., 2016). MREs are known hot spots of tropical fish diversity and host fish communities ecologically distinct from shallow water reefs (Medeiros et al., 2021). The mesophotic zone usually encompasses the shelf-break, a transition area from shelf to ocean characterized by a rapid change in the topography with a steep slope. The stiffness of the slope is associated with turbulent mixing enhancing primary productivity and therefore attracting prey and predators (Reid, 2001; Heyman and Kjerfve, 2008; Paxton et al., 2021). It concentrates diverse fishing resources over a relatively narrow area, sustaining important multispecific reef fisheries (Frédou and Ferreira, 2005; Longhurst and Pauly, 2007; Olavo et al., 2011; Eduardo et al., 2018). However, so far few study actually quantified the relative importance of mesophotic reefs for fish and/or in comparison to euphotic reefs, in particular because consistent observations extending from the shoreline to the shelf break are lacking (Silva et al., 2021).

Oceanic islands and shallow seamounts also act as topographic anomalies that trigger complex physical processes increasing primary production and concentrating higher trophic levels. This phenomenon, known as the Island Mass Effect (IME; Doty and Oguri, 1956) is originated by the turbulence created by the island bathymetry, which uplift nutrient-rich water into the photic zone, enhancing primary production (Gove et al., 2016). Oceanic islands and shallow seamounts are important environments for maintaining local biodiversity and non-resident migrating top predatory species (Letessier et al., 2019). IME aggregative effect on top predators supports commercial, artisanal and recreational fisheries (Heywood et al., 1990; Signorini et al., 1999), which play an important role in the local socio-economic life of insular populations(Henry and Lyle, 2003). So far, most studies on the IME focused on physical-biogeochemical processes (Coutis and Middleton, 1999; Cardoso et al., 2020). They showed that primary productivity is most enhanced on the leeward side of islands (Signorini et al., 1999; Tchamabi et al., 2017). However, since fewer studies focused on higher trophic levels, the response of fish is generally depicted as symmetrical around islands (Gove et al., 2016). No studies, for instance, determined if fish follow the pattern of primary productivity and concentrate downstream of islands.

Yet, this kind of knowledge is essential to assist decision making in conservation policies to protect biodiversity and the sustainability of fishing and diverse marine uses. Protective management is generally achieved through the creation of Marine Protected Areas (MPAs) delineating permitted and non-permitted zones according to pre-defined management objectives (Motta et al., 2021). However, in some cases, the consequences of establishing MPAs are not adequately thought out, and a poorly planned MPA can be detrimental for local populations that rely on marine resources (Agardy et al., 2011). Indeed the decision support tools used to design MPAs rely on available data. To coherently manage the use of maritime space and achieve ecological, economic and social objectives, Marine Spatial Planning (MSP) is increasingly used as a strategic alternative aiming at integrating MPAs in a broader context (Shucksmith and Kelly, 2014). MSP is a complex process requiring the use of optimization solvers that ultimately requires large quantities of spatially explicit cross-disciplinary knowledge and data (ecological, legal, social, economic) (Queffelec et al., 2021). One of the main challenges to improve knowledge of tropical ecosystems and their resources and implement MSP is thus the data collection (Rubio-Cisneros et al., 2019).

Comprehensive monitoring is required to provide ground information for sustainable management (Samhouri et al., 2014; Long et al., 2015). Fish assemblage data are often used to help understanding how human activities influence marine ecosystems (Hewitt et al., 2005; Caselle et al., 2015) or as a measure of ecosystem health (Díaz-Pérez et al., 2016) and as a basis for managerial decisions (Topor et al., 2019). A variety of methods is used to assess tropical fish populations, including fishing gears or visual observations, each presenting its own pros and cons (Pennino et al., 2016). Fishery-dependent methods provide long time-series, wide spatiotemporal coverage but are biased by, among other, gear selectivity (Hilborn and Walters, 2013). Scientific fish catches are more reliant but have a limited spatiotemporal coverage (Hilborn and Walters, 2013). Tropical reef fish communities are also classically described via direct *in situ* observations through diver-based underwater visual census (UVC) (Bohnsack and Bannerot, 1986). Scuba diving is constrained by a set of limitations including underwater time and maximal diving depth and visibility (Jones and Thompson, 1978; Kimmel, 1985; Michalopoulos et al., 1992). As a result, most UVC-based studies are restricted to near shore shallow waters and provide punctual small-scale information whereas species richness and patterns of distribution is heavily influenced by the range of the sampling area (Gray et al., 2004). To overcome part of these limitations and bias, underwater video techniques are increasingly used, whether stationary or towed, remotely operated or autonomous, baited or not (Mallet and Pelletier, 2014). The use of video increases sampling range and is more time efficient than diver-based observation (Langlois et al., 2010) but each technique has different limitations and combining underwater video and other sampling methods is therefore recommended (Logan et al., 2017).

Active acoustics, in particular multi-frequency, is a powerful tool allowing simultaneous and continuous observation of the distribution of a variety of marine communities and abiotic characteristics (Koslow, 2009; Bertrand et al., 2014; Benoit-Bird and Lawson, 2016). Acoustics range of observation reaches several hundreds of meters below the surface, which allows prospecting the pelagic domain (Sutton, 2013). However, the ability to discriminate acoustically among taxa remains coarse and works best in relatively low-diversity temperate systems with a few well-defined and acoustically distinct groups (Koslow, 2009). Acoustic species discrimination remains challenging in highly diverse tropical ecosystems. Moreover, acoustics methods needs to be coupled with other observational methods to perform species identification, classically extractive one such as trawls and nets (McClatchie et al., 2000). But trawling can be destructive and is not always possible to operate in topographically complex environments or in MPAs (Cappo et al., 2004; Harvey et al., 2007; Fitzpatrick et al., 2012). To lift out this lock, the combination of acoustic methods with non-extractive optical methods has emerged. These methods were mostly applied in temperate water (Rooper et al., 2010; Jones et al., 2012; O'Driscoll et al., 2012; Fernandes et al., 2016; Gastauer et al., 2017; Blanluet et al., 2019) whereas to date, only few studies focused on tropical waters (Campanella and Taylor, 2016; Domokos, 2021; Villalobos et al., 2021).

In this context, we combine multifrequency acoustic and video observation to provide a comprehensive vision of fish distribution around a tropical oceanic marine ecosystem. The study area, Fernando de Noronha Archipelago (FNA) located ~350 km off the coast of Brazil (Fig. 3.1), is a typical low productivity and high biodiversity system (Hazin et al., 1998; Lessa et al., 1999; Tchamabi et al., 2017), representative of tropical ecosystems. Like many other tropical small islands, the local population of FNA relies on artisanal fisheries for protein income (Dominguez et al., 2014) and the economic activity is mainly based on tourism. Tourism generates demographic pressure and all its externalities, amplifying the demand for fish and enhancing marine related activities such as recreational fishing or diving (Lopes et al., 2017; Outeiro et al., 2019). Beside, FNA is protected by a series of legal instruments regulating the uses of the marine environment and marine resources. Indeed, FNA is bathing in an Environmental Protection Area (EPA) where sustainable use of marine resources and tourism is allowed. The EPA includes a smaller no-take MPA, the "National Marine Park of Fernando de Noronha (PARNAMAR)", covering about 70% of the main island and the coastline from the shore to the 50 m isobaths (Garla et al., 2006).

On the base of three surveys combining multi-frequency active acoustics and underwater videos, we propose to address the questions identified above. Specifically our work includes a series of objectives. First, we aim at providing a comprehensive description of the distribution of the acoustic fish biomass and fish assemblages in FNA. Second, we propose to perform the biomass estimation of the most observed fish, the black triggerfish *Melichthys niger*. Third, we propose to quantify the relative importance of mesophotic reefs for fish in comparison to euphotic reefs. Four, on this background, we propose to complete the portrait of the IME. Finally, we propose to discuss how the comprehensive information gained by such approach can be usable to implement scientific-grounded MSP.

3.3. Material and Methods

Data were collected during three ‘Fish Acoustics around Fernando de Noronha’ (FAROFA) surveys performed on-board a 10-m-long sport fishing boat (see Supplementary Fig. S3.1 online) in September 15-21, 2017 (FAROFA1; Bertrand, 2017), April 17-23, 2018 (FAROFA2; Bertrand, 2018) and April 15-22, 2019 (FAROFA3; Bertrand, 2019). The first survey was conducted during the dry season (August to January) while the two others during the rainy season (March to July). Data were collected during daytime while prospecting over the continental shelf, shelf-break and near offshore area (Fig. 3.1). Video annotations and a degraded resolution of acoustic raw data are published in SEANOE open source platform (Bertrand et al., 2020; Salvetat et al., 2020b).

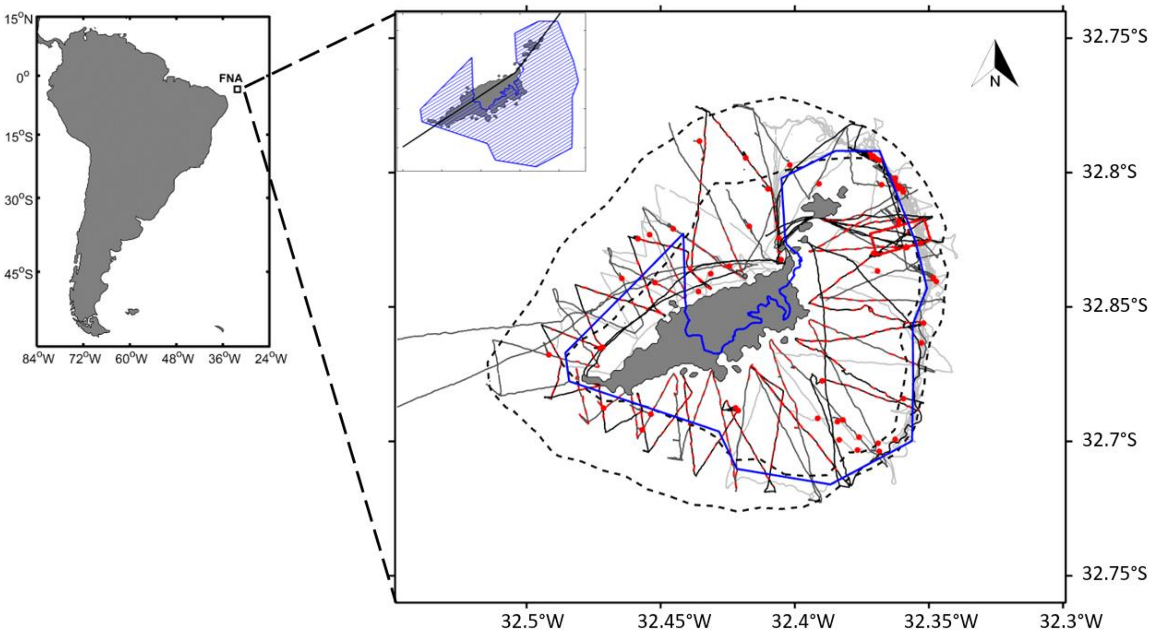


Figure 3.1. Fernando de Noronha archipelago (FNA) (03°51’S, 32°25’W). The blue line delimits the no take MPA PARNAMAR. Acoustic transects are depicted by light grey (FAROFA 1), dark grey (FAROFA 2) and black lines (FAROFA 3); video transects by red dashed lines and video stations by red dots. The black dashed lines depict the 50 and 300 m

isobaths. The insert on the main map shows the PARNAMAR hatched in blue and the black solid line separates the leeward side (L) and the windward side (W). Map was created by the authors using Matlab R2018b (https://fr.mathworks.com/) and m_map mapping package (Pawlowicz, 2020).

Video data

To identify species and bottom habitat characteristics, four different optical systems were deployed: (i) a towed video camera; (ii) a video camera fixed on the transducer support close to the surface; (iii) a video camera deployed vertically; and (iv) a remotely operated vehicle (ROV) (see Supplementary Fig. S3.1 online). The towed video camera and the video camera fixed on the transducer were used to capture videos along transects. Both provided a view of the water column and allowed for substratum identification in shallow water. The towed video was set on a downrigger to deepen the camera, which looked downwards and dragged with a 15 m long rope at a vessel speed of 1.5 m.s^{-1}. The videos captured from the camera fixed on the transducer support were especially useful in very shallow waters. Vertical videos and ROV were deployed during stations whose location was driven by observations of important quantity of fish on the echogram with the purpose of species identification (Fig. 3.1). Vertical videos were made using a camera fitted on a fishing line. The ROV was operated from the vessel with live stream video.

Towed, fixed and vertical videos were captured with a GoPro TM Hero3+ operating in HD at 1,080 p and 30 frames per second during FAROFA 1 and 2 and 60 frames per second during FAROFA 3. ROV videos were performed using a Blue Robotics BlueROV2 system operating in HD at 1,080 p and 30 frames per second. To synchronise acoustic and video observations form the towed video, a delay of 9.7 s was subtracted to the video time to adjust with the echosounder time. Each video was annotated using the Solomon Coder software (Péter, 2019) to identify and enumerate observed species and sediment characteristics classed over nine types (Table 3.1 and see Supplementary Table S3.1 online). For the species censuses, we used the maximum number of individuals (MaxN) of a given species present in a single video frame (Priede et al., 1994). In video stations, the MaxN was directly used on each frame to avoid double counting of individuals. In video transects, the MaxN over 3 seconds of record was used. To estimate the abundance of each taxon observed by video, we used the sum of the maximum values of the MaxN of each video (TMaxN).

Table 3.1. Sediment composition description and code

Composition	Code
Sand	Sa
Large rock+Algae	LrAl
Sand+Unknown	SaUn
Sand+Algae	SaAl
Sand+Stone+Algae	SaStAl
Sand+Large rock+Algae	SaLrAl
Sand+Rhodolith+Algae	SaRhAl
Sand+Coral+Rhodolith+Algae	SaCoRhAl
Sand+Stone+Coral+Rhodolith	SaStCoRhAl

Acoustic data

Acoustic data were collected continuously throughout the survey with two SIMRAD EK80 echosounders connected to two 7° split beam transducers centred on the frequencies of 70 and 200 kHz and operated simultaneously in narrow band (continuous wave) transmission. Transducers were attached with a stainless-steel pole to the port side of a 10-m-long sport fishing boat. The ping rate was set to 'maximum' for a maximum acquisition range of 100 m (over the continental shelf) and to 1 ping s^{-1} off the continental shelf, where the maximum acquisition range was set to 400 m. Vessel speed was ~2.5 m s^{-1} during acquisition of acoustic data and pulse duration was set at 1.024 s. Acoustic data were converted to HAC files using Hermes software (McQuinn et al., 2005; Trenkel et al., 2009). Processing was completed using the Matecho tool (Perrot et al., 2018) and Movies3D software (Trenkel et al., 2009). Details on acquisition and calibration parameters as well as on acoustic pre-processing steps from data acquisition i.e., data conversion, bottom detection, filtering and manual cleaning are available in Salvetat et al. (2020).

Acoustic data processing

To discriminate fish echoes from other organisms, multifrequency approaches, generally rely on the property that swimbladder-bearing fish have, well beyond the resonance of their swimbladder, high and homogenous backscattering response to frequency (Lavery et al., 2007). To discriminate between scatters attributed to fish (fish-like) and those originated by other organisms (no-fish), e.g. gelatinous and crustaceans, we developed an approach based on thresholds on (i) volume backscattering strength Sv (Sv, in dB re 1 m^{-1}; see (MacLennan et al., 2002) for acoustic definitions), (ii) the bi-frequency sum of Sv, and (iii) the variance of Sv. See Supplementary methods and Supplementary Figures S3.2 and S3.3 online for a detailed description of the methodology. To study the horizontal distribution of fish-like and no-fish echoes, we used the Nautical Area Scattering Coefficient (NASC or s_A, in $m^2.nm^{-2}$) (MacLennan et al., 2002), an index of acoustic biomass, for each ping integrated over the water column. Since fish-like and no-fish data were highly correlated at the two frequencies, only the 70 kHz echograms were used for further analyses.

Combining surveys

The three FAROFA surveys were conducted at different seasons and years. To determine whether the surveys could be combined to provide a more comprehensive picture of fish distribution, we verified if, locally, s_A values were sufficiently similar between surveys with regards to the natural variability observed within surveys (see Supplementary Fig. S3.4 online). Punctual comparisons were not possible given that observations of the different surveys were not located at the same geographical points. We thus selected the pixels containing observations from different surveys at a pixel size of 100 m (Fig. 3.2). The inter-survey comparison was based on the difference between the mean $\log10(s_A + 1)$ of different surveys in the selected pixels. Meanwhile, the intra-survey variability was computed by selecting records at least one hour apart within the same grid cell. The inter-survey differences of fish-like $\log10(s_A+1)$ were centred on 0 (Fig. 3.2a) whatever the pair of surveys considered or the pixel size, and were comparable to intra-survey ones. Based on these results indicating a strong spatial stability in the horizontal fish-like $\log10(s_A+1)$ distribution around FNA over years and seasons, we combined the data from the three surveys to provide a comprehensive spatial coverage.

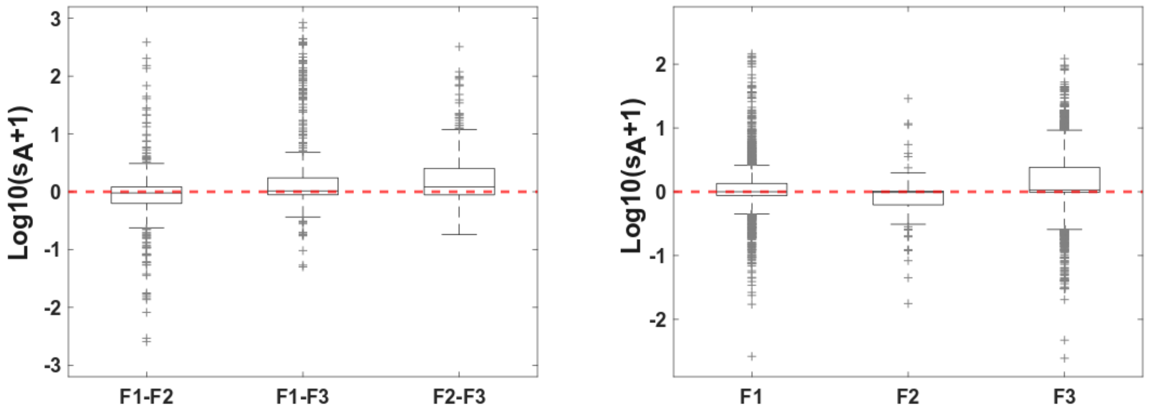


Figure 3.2. Difference between the mean log10(s_A + 1) of different surveys in the selected pixels of 100 m, (a) between surveys, and (b) within a given survey. s_A in m^2.nm^{-2}; F1, F2, F3: FAROFA 1, 2 and 3, respectively.

Spatial distribution

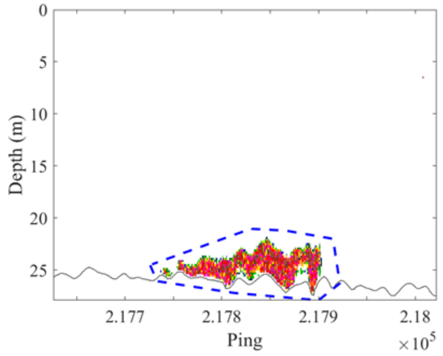
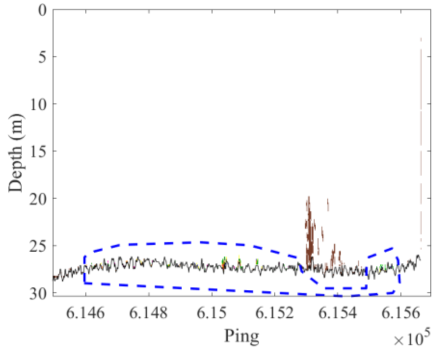
To interpolate the horizontal distribution of fish-like and no-fish acoustic biomass outside acoustics transects around FNA, we applied a tailored geostatistical approach. Spatial interpolation was adapted to face the fact that the domain area was elliptical with radial transects (Fig. 3.3a,b). The geographic reference system was thus irrelevant to describe the orientation between observations. For instance, North-South did not mean the same thing in different parts of the survey area. The relevant orientations to consider were rather parallel or perpendicular to the coast, which required projecting the data in a system conformal to these two main orientations.

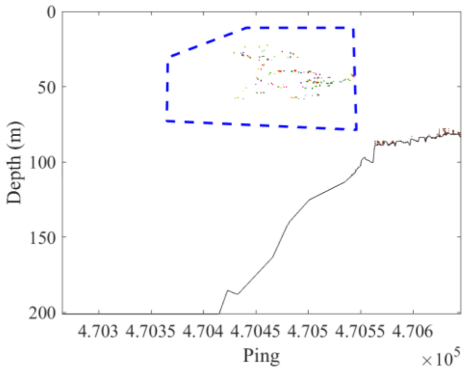
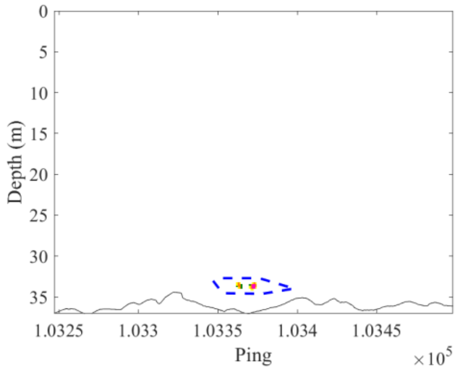
To unfold the sampling area, we covered the domain by a series of trapezes that were then aligned and resized one by one so that the distance perpendicular to the coast ranged from 0 (coast line) to 1 (offshore border of the trapezes), and the distance parallel to the coast ranged from 0 (beginning of the first trapeze chosen conventionally) to the sum of the length of the bases of the trapezes (Supplementary Fig. S3.5 online). This projection was bijective so that we could move back and forth between the geographical space and the unfolded space. In particular, the s_A and the kriging grid cells whose coordinates were defined in the geographical space were projected in the unfold space to compute their variogram and their kriging values. To avoid border effects at the edge of the unfolded system, the starting and ending trapezes were duplicated prior to kriging. So, the interpolation of the left side of the first trapeze was made taking into account the data of the last trapeze also. Interpolations were performed over regular cells of 55 m longitude * 44 m latitude.

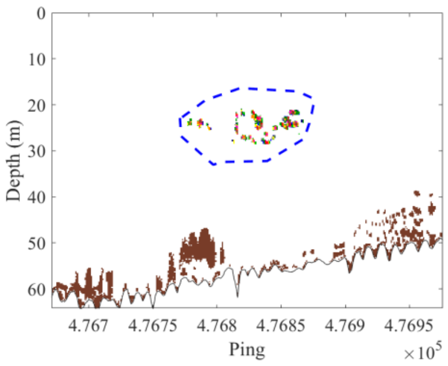
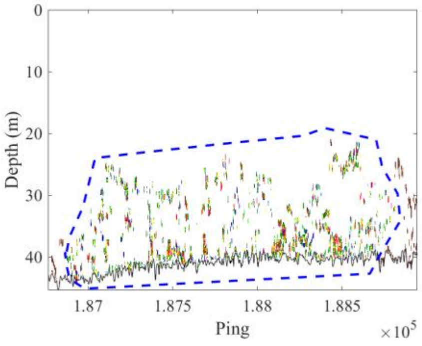
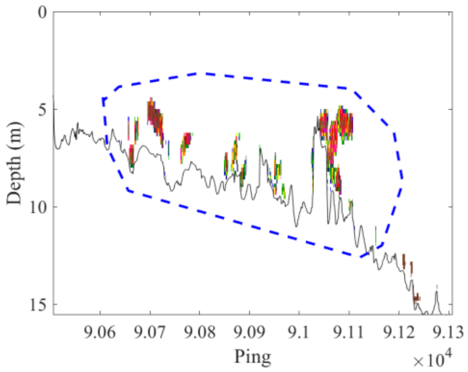
Fish assemblages

Despite the simultaneous acquisition of acoustic and video, except for two triggerfish species, it was not possible to allocate each fish-like echo to a given species. However, consistent fish assemblages with characteristic echotypes were observed on echograms (Table 3.2). To attribute each fish-like acoustic scatter to an assemblage, we labelled all fish-like echoes. Label assignment, hereafter called “labelling”, was based on video observation and the presence of characteristic structures in echograms. Video footages made it possible to identify the species observed simultaneously by the cameras and the echosounder. This experience was then used to label the echograms not monitored by videos. For the three cruises, 70 kHz fish-like echograms were labelled manually by the same operator using the software Matecho (Perrot et al., 2018), which allows drawing polygons to encompass scatters corresponding to a given assemblage. All fish-like echoes inside a polygon were allocated to a given assemblage. In total ten assemblages were defined (Table 3.2). In addition, two species, the black triggerfish *Melichthys niger* and the ocean triggerfish *Canthifermis sufflamen* could be identified on echograms due to their characteristic shoal shape. The black triggerfish forms large loose shoals occupying the whole water column distributed over the shelf from 6 m to 40 m depth exhibiting different body orientations. Ocean triggerfish form smaller looser shoal generally found on deeper depth (~17 to 70 m) close to the shelf-break. The fish-like s_A of each label corresponding to the 10 assemblages and the two triggerfish species was echointegrated over the water column by 25 meters-long elementary sampling distance unit (ESDU).

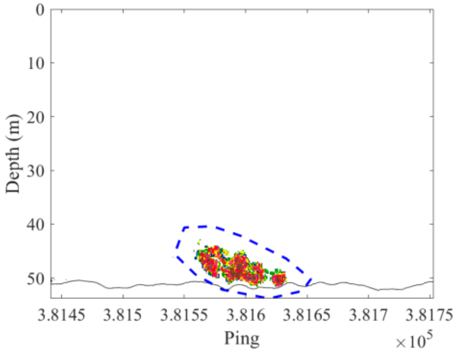
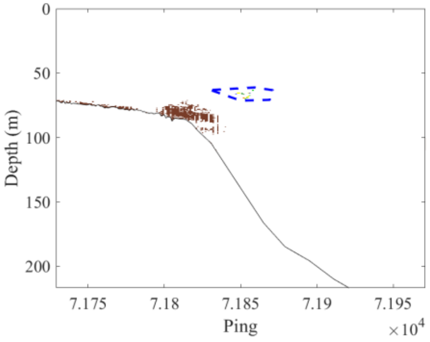
Table 3.2. Description of the fish assemblages and two fish species defined from echotypes (surrounded by a blue dashed line).

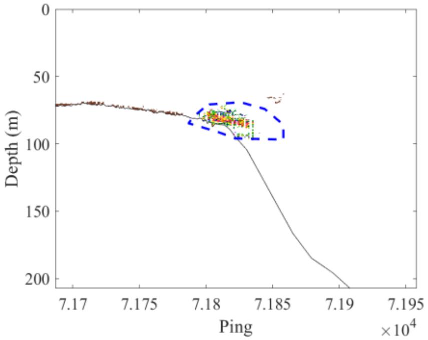
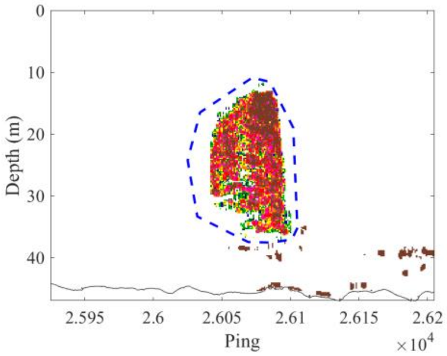
Label name	**Species observed in video**	**Other potential species**	**Characteristics**	**Example of echogram**
bottom small fish school	*Thalassoma noronhanum* *Halichoeres radiatus*	*Xyrichtys martinicensis* (1) *Heteroconger camelopardalis* (1) *Halichoeres dimidiatus* (2) *Xyrichtys incandescens* (3)	Fish school laying on the bottom. The corresponding fish species are hardly visible on video footage since fish quickly hide in the sediment.	
bottom weak fish detection		Crypto-benthic species	Thin layer of benthic fish.	

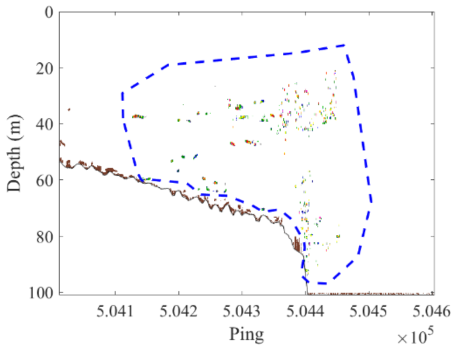
C. sufflamen	*Canthidermis sufflamen*	Loose shoal of fish swimming in the same direction, found close to the shelf-break.	
individual demersal fish	*Lutjanus jocu* *Sphyraena barracuda* *Caranx lugubris* *Caranx latus*	Individual fish on the bottom or in the water column on the shelf.	

loose school			Loose school of unidentified fish over the shelf.	
M. niger	*Melichthys niger*		Big loose shoal with fish exhibiting different body orientations, distributed over the shelf.	
mix reef fish	*Abudefduf saxatilis* *Chromis multilineata* *Melichthys niger* *Sparisoma amplum* *Acanthurus coeruleus*	*Sparisoma axillare (2)* *Sparisoma frondosum (2)* *Sparisoma radians (4)* *Anisotremus surinamensis (3)* *Haemulon parra (3)*	Fish schools and shoals over complex bottom structure formed by coral or rocky reefs.	

	Acanthurus chirurgus *Stegastes rocasensis* *Cephalopholis fulva* *Kyphosus sectatrix* *Cantherhines macrocerus* *Lutjanus jocu* *Thalassoma noronhanum* *Haemulon chrysargyreum* *Balistes vetula* *Paranthias furcifer* *Pseudupeneus maculatus* *Holocentrus adscensionis*	*Haemulon chrysargyreum (3)* *Rypticus saponaceus (3)* *Dermatolepis inermis (3)* *Mycteroperca bonaci (3)* *Epinephelus itajara (3)* *Pomacanthus paru (3)* *Holacanthus ciliaris (3)* *Myripristis jacobus (3)* *Mulloidichthys martinicus (3)* *Pempheris schomburgki (3)* *Centropyge aurantonotus* *Chaetodon striatus (3)*	

		Chaetodon ocellatus (3)		
sand fish			Fish school over flat sand bottom.	
shelf-break large fish	*Sphyraena barracuda* *Caranx lugubris* *Seriola dumerili* *Elagatis bipinnulata* *Thunnus spp* *Caranx spp* *Carcharhinus falciformis*		Individual large fish in the water column over the shelf-break.	

shelf-break school		Mix of reef fish *Paranthias furcifer* *Kyphosus sectatrix* *Caranx lugubris* *Mycteroperca spp. (1)* *Menophorus dubius (1)* *Ginglymostoma cirratum (1)* *Prognathodes guyanensis (1)* Lujanidae	Demersal fish school associated to the shelf-break.	
small pelagics school	*Decapterus macarellus* *Harengula sp*	*Harengula jaguana* (5) *Harengula clupeola* (3)	Fish in dense large school characteristic of small pelagic fish schools.	

small pelagics and predators	*Sphyraena barracuda* *Caranx lugubris* *Seriola dumerili* *Elagatis bipinnulata* *Thunnus spp* *Caranx spp* *Caranx crysos* *Carcharhinus falciformis*	Loose shoal of small pelagic fish in interaction with predators.	

(1) (Barros, 2020)

(2) (Sazima et al., 2005)

(3) (Soto, 2001)

(4) (Krajewski and Floeter, 2011)

(5) (Sazima et al., 2006)

Black triggerfish biomass estimation

The black triggerfish was particularly abundant in observations. The availability of target strength measurement for this species (Salvetat et al., 2020a) opened the field for estimating its biomass. To account for the strong dissymmetry of s_A histograms, we used a non-linear geostatistical approach (Petitgas, 1993; Chiles and Delfiner, 2009; Bez and Braham, 2014). Observations were reduced to 5 classes of acoustic biomass, i.e. null, small, medium, large and very large densities, corresponding to the classes 0,]0-33%],]33%-66%],]66%-95%],]95%-100%], respectively. Each interval was coded by an indicator variable, the first one being nothing but the presence/absence. This coding translated the univariate approach of s_A into a multivariate approach (five disjunctive indicator variables, that reduced to four as they sum to one). This became a real issue given the very large number of s_A data available. To solve this problem, the five spatially mutually correlated indicators variables were transformed into five factors called Min-max Autocorrelation Factors –MAF (Switzer, 1985). These factors are linear combinations of the input georeferenced variables, and are uncorrelated at null and at short distances. Assuming that MAFs were also uncorrelated for larger geographical distances, allowed using them independently from the others. In this context, we performed the global estimation of each of the five MAFs over the study polygon by global kriging (Chiles and Delfiner, 2009) and then recombined them to get the kriging estimates of the mean overall s_A together with its estimation variance (Bez, 2021).

Using all black triggerfish labels, we delineated its area of main presence, concentrated in the east side of FNA. In this area, based on the estimation of the mean overall acoustic value described above, we estimated the biomass by equation (1):

$$Biomass \ = mean\ overall\ s_A * Surface * W / \left(1852^2 * \ 4\pi \ * \ 10^{\frac{TS}{10}}\right) \qquad (1)$$

where the *Surface* corresponds to the total surface of the delineated area (in m^2), W is the triggerfish mean weight estimated at 485 g for 27.8 cm long black triggerfish and TS is the target strength of the black triggerfish at 70 kHz ($TS = -39.3\ dB$ for 27.8 cm long black triggerfish, the mean size during the surveys (Salvetat et al., 2020a)).

Environmental drivers

We investigated the relationships between the fish-like and no-fish acoustic biomasses to a series of categorical environmental variables:

- Wind/current exposure: FNA was categorised in two sides, leeward and windward, according to the exposition to main winds and currents. Indeed, FNA is under the trade wind regime and washed by the central branch of the South Equatorial Current (cSEC) that both flow from east to west (Assunção et al., 2016; da Silva et al., 2021).
- Depth strata: data were classified in two euphotic (upper euphotic: 0-20 m; lower euphotic: 20-40 m) and three mesophotic (upper mesophotic: 40-60 m; mid-mesophotic: 60-80 m and lower mesophotic: 80-100 m) depth strata using the acoustically-detected bottom-depth.
- MPA: data were compared inside and outside the PARNAMAR in the same depth range (0-50 m). The area outside the MPA belongs to the multiple use Environmental Protection Area (EPA).
- Sediment type: the nine sediment types extracted from video observation (Table 3.1).

We used both univariate and multivariate statistics to relate the distribution of the acoustic biomasses log10(s_A+1) of fish-like and no-fish data as well as the acoustic biomasses of the ten assemblages plus the two triggerfish species to the environmental factors. To seek for significant differences in acoustic biomass according to each environmental factor, we used a non-parametric Kruskal Wallis test followed by pairwise Wilcoxon tests since the distribution of the data did not follow a normal distribution.

Classification And Regression Trees (CART; Breiman et al., 1984) were used to explore the relationships between the fish-like acoustic biomass and the fish assemblages (plus the two triggerfish species), and environmental variables. In the first case, we used the rpart package (Therneau et al., 2015) while we used the diet package (Kuhnert et al., 2012) in the second case. The diet package, originally designed to study diet composition, allows a non-parametrical exploratory and predictive approach for identifying complex relationships between environmental variables and assemblages' composition. Classification tree using the diet package uses a bootstrap technique similar to Breiman (1996) and Kuhnert et al. (2010). The diet package also allows visualizing the bagged predictions by mapping the predictions (Kuhnert and Mengersen, 2003). Both trees were pruned to the smallest cross-validated relative error (Breiman et al., 1984).

In addition to the categorical environmental factors, we added two continuous explicative variables, the no-fish acoustic biomass and the bottom local slope (absolute value of the difference between the first and the last depth in a given ESDU relative to the length of the ESDU expressed in %). All statistical analyses were performed with R (R Core Team, 2020).

All statistical analyses were performed twice, including and not the sediment types. Indeed, the sediment types were extracted from video observation and were thus not available for all ESDU but mostly restricted to the shallow areas where video observations are available and the sediment observable.

3.4. Results

Video data

In total, 49h51 of video footage were acquired. Complete information on species identification and sediment classification are available at https://doi.org/10.17882/76019. Video footage allowed the identification of 47 taxa (Table 3.3) from 29 families including one turtle (*Chelonia mydas)*, one dolphin (*Stenella longirostris)*, six elasmobranchs including four sharks (*Carcharhinus falciformis*, *C. perezi*, *Sphyrna lewini* and *Ginglymostoma cirratum*) and two stingrays (*Aetobatus narinari* and *Hypanus americanus)*. We identified thirty-four osteichthyes fish species at specie level, four at genus level (*Harengula sp.*, *Seriola spp*, *Caranx spp*, *Thunnus spp*) and three at family level (*Gobidae sp.*, *Bothidae sp.*, *Ostraciidae sp.)*. For 12 species, only a single individual was recorded. 49 189 fish were recorded using the TMaxN. The most abundant specie, *Harengula sp.* (TmaxN 23529, 47.8%) was observed forming large schools in 2 videos, while the second most abundant species, the black triggerfish *Melichthys niger* (TMaxN 21416, 43.5%) was the fish observed in more videos (48). After those two species, the relative abundance falls with only three species with abundance above 1% of the total abundance: the sergeant major *Abudefduf saxatilis* (TMaxN 1495, 3%), the brown chromis *Chromis multilineata* (TmaxN 636, 1.3%), the ocean triggerfish *Canthidermis sufflamen* (TMaxN 540, 1.1%). After *M. niger* that occurred in 48 videos the species observed in more videos were the barracuda *Sphyraena barracuda* (45), the oceanic triggerfish *Canthidermis sufflamen* (39), the black jack *Caranx lugubris* (22), the blue runner *Caranx crysos* (13), the sergeant major *A. saxatilis* (12), and the dog snapper *Lutjanus jocu* (12).

Beside the fish species, we observed gelatinous (salps, siphonophores and ctenophores), fish larvae (including leptocephalus) and fragments of pelagic algae. These, and likely crustaceans that could not be observed in videos, are the main components of the ‘no-fish’ acoustic data.

Table 3.3. List of species observed in video footage. TMaxN: sum of the maximum number of individuals of a given species present in a single video frame; TV: towed video; TS: transducer support; VP: vertical profile; RV: ROV. The numbers in parenthesis associated with video types indicates the number of videos in which each species was observed.

Class	**Order**	**Family**	**Species**	**TMaxN**	**Video type**
Actinopterygii	Beryciformes	Holocentridae	*Holocentrus adscensionis*	1	TV(1)
	Clupeiformes	Clupeidae	*Harengula spp*	23529	TS(2)
	Perciformes	Acanthuridae	*Acanthurus coeruleus*	8	TV(2),VP(1)
			Acanthurus chirurgus	21	TS(1)
		Carangidae	*Caranx crysos*	189	TV(7),VP(5),RV(1)
			Caranx latus	53	TV(6)
			Caranx lugubris	88	TV(10),TS(1),VP(10),RV(1)
			Caranx ruber	51	VP(3),RV(2)
			Caranx spp	57	TV(2),RV(1)
			Decapterus macarellus	266	VP(1)
			Elagatis bipinnulata	124	TV(3), VP(6)
			Seriola spp	7	VP(5)
		Gobiidae	*Gobiidae sp.*	1	TV(1)
		Haemulidae	*Haemulon chrysargyreum*	149	TV(1)
		Istiophoridae	*Makaira nigricans*	1	TV(1)
		Kyphosidae	*Kyphosus sectatrix*	182	TV(3), VP(1)
		Labridae	*Halichoeres radiatus*	1	TV(1)
			Thalassoma noronhanum	43	TV(2), VP(1)
		Lutjanidae	*Lutjanus jocu*	25	TV(6), VP(5), RV(1)
		Malacanthidae	*Malacanthus plumieri*	4	TV(2)
		Mullidae	*Pseudupeneus maculatus*	1	TV(1)

		Pomacentridae	*Abudefduf saxatilis*	1495	TS(3), TV(5), VP(4)
			Chromis multilineata	636	TS(2), TV(4),VP(2)
			Stegastes rocasensis	17	TV(1), VP(1)
		Serranidae	*Cephalopholis fulva*	18	TV(1), VP(2)
			Paranthias furcifer	57	TV(2)
	Pleuronectiformes	Bothidae	*Bothidae sp.*	1	TV(1)
	Scombriformes	Scaridae	*Sparisoma amplum*	3	TV(1), VP(1)
		Scombridae	*Acanthocybium solandri*	11	TV(2),RV(1)
			Thunnus albacares	1	RV(1)
			Thunnus spp	35	VP(1)
		Sphyraenidae	*Sphyraena barracuda*	106	TV(18), VP(23), RV(4)
	Scorpaeniformes	Dactylopteridae	*Dactylopterus volitans*	2	VP(2)
	Tetraodontiformes	Balistidae	*Balitses vetula*	2	TV(1)
			Canthidermis sufflamen	540	TV(18), VP(20), RV(1)
			Melichthys niger	21416	TS(1),TV(26), VP(19), RV(2)
		Monacanthidae	*Aluterus scriptus*	21	VP(8)
			Cantherhines macrocerus	9	TV(4), RV(1)
		Ostraciidae	*Lactophrys trigonus*	1	VP(1)
			Ostraciidae sp	1	TV(1)
Chondrichthyes	Carcharhiniformes	Carcharhinidae	*Carcharhinus falciformis*	1	VP(1)
			Carcharhinus perezi	1	VP(1)
		Sphyrnidae	*Sphyrna lewini*	1	RV(1)
	Myliobatiformes	Dasyatidae	*Hypanus americanus*	2	TV(1), VP(1)
		Myliobatidae	*Aetobatus narinari*	2	TV(1)
	Orectolobiformes	Ginglymostomatidae	*Ginglymostoma cirratum*	2	TV(2)
Mammalia	Cetacea	Delphinidae	*Stenella longirostris*	1	TS(1)
Reptilia	Testudinata	Cheloniidae	*Chelonia mydas*	3	TS(2)

Fish-like and no fish acoustic biomass

The geostatistical interpolation of fish-like s_A reveals a heterogeneous distribution with the presence of several hotspots, mostly on the windward (east) side of FNA, in the vicinity of the shelf-break (Fig. 3.3c). The lowest fish-like acoustic biomass was observed on the north-western side, in particular at the mid-shelf. The pattern was different for the no-fish acoustic biomass that was concentrated off the shelf-break with a main aggregation on the leeside (Fig. 3.3d).

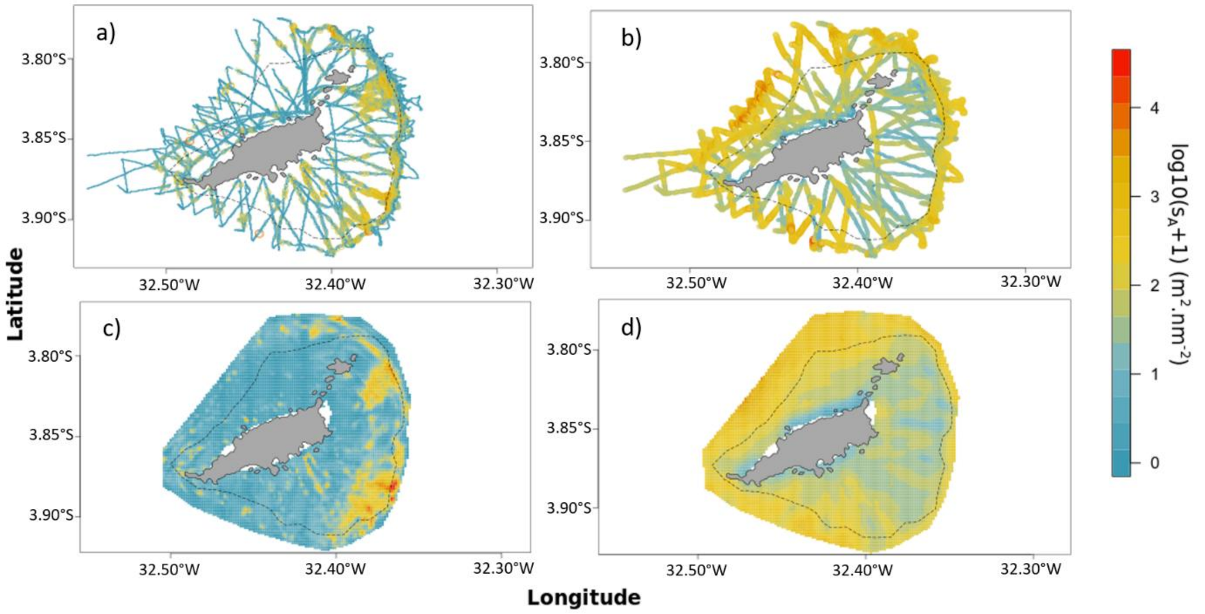


Figure 3.3. Horizontal distribution of the $\log10(s_A+1)$ of fish-like (a) and no-fish (b) echoes along transects. Geostatistical interpolation of fish-like (c) and no-fish (d) echoes. The black dashed lines depict the 50 m isobath. Maps were created by the authors using R (https://www.R-project.org/) and RGeostats package (ParisTech, 2020).

The regression tree relating the fish-like acoustic biomass to the environmental parameters without considering the sediment (Fig. 3.4a) reveals that the main driving factor is the wind exposure with much higher acoustic biomass per ESDU windward ($\log10(s_A+1) = 1.2$ $m^2.nm^{-2}$) than leeward (0.58 $m^2.nm^{-2}$). A second split occurs in the windward side with higher acoustic biomass (1.3 vs. 0.35 $m^2.nm^{-2}$) when the slope is greater than 0.08% meaning that fish-like acoustic biomass is very low in flat areas. When considering the reduced database (restricted to the neritic zone) containing sediment (Fig. 3.4b), the first explicative variable is the sediment.

The most complex sediment (SaStCoRhAl) encompasses a much higher biomass (2.3 $m^2.nm^{-2}$) than the others (0.93 $m^2.nm^{-2}$). For sediments other than SaStCoRhAl, the next splits are wind exposure, sediment types and no-fish biomass with the highest fish-like biomass (1.9 $m^2.nm^{-2}$) distributed windward where the no-fish acoustic biomass ranges between 2.3 and 1.6 $m^2.nm^{-2}$ and over the more complex sediments (SaCoRhAl, SaLrAl, LrAl, SaUn).

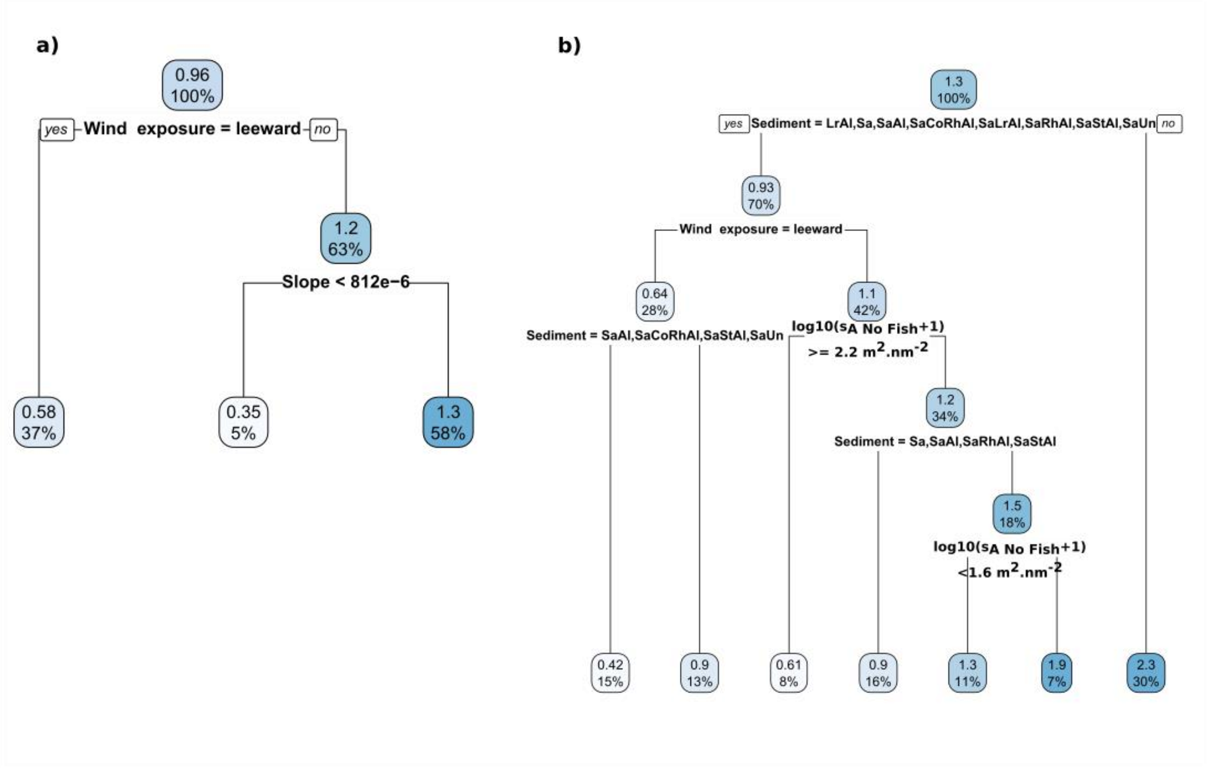


Figure 3.4. Regression tree on values of the fish-like acoustic biomass (log10(s_A+1)) performed on the complete data set (a) and the dataset limited to the locations where sediment was observed (b). The values inside each leaf is the mean fish-like acoustic biomass (log10(s_A+1)) and the corresponding percentage of ESDU.

Univariate analyses provide some additional information (see Supplementary Fig. S3.6 online). Fish-like and no-fish acoustic biomasses significantly varied according to wind and current exposure, protection levels, sediment types, and bottom depth strata. Indeed fish-like acoustic biomass was significantly lower on the leeward even if some ESDU encompassed very high acoustic biomass (log10(s_A +1) up to 6.8 $m^2.nm^{-2}$) in presence of small pelagic schools distributed in the upper mesophotic zone (40-60 m) (see section 3.3). On the opposite, the no-fish acoustic biomass was slightly (but significantly) lower windward (2.1 $m^2.nm^{-2}$) than leeward (2.2 $m^2.nm^{-2}$).

The type of sediment encompassing the highest acoustic biomass was by far the most complex one, SaStCoRhAl (mean log10(s_A+1) = 2.16 $m^2.nm^{-2}$), followed by SaCoRhAl (1.14 $m^2.nm^{-2}$), SaLrAl (1.11 $m^2.nm^{-2}$), LrAl (1.06 m $^2.nm^{-2}$), SaStAl (0.99 $m^2.nm^{-2}$), SaRhAl (0.95 $m^2.nm^{-2}$), while the less complex habitats Sa (0.78 $m^2.nm^{-2}$), SaAl (0.77 $m^2.nm^{-2}$) and SaUn (0.70 $m^2.nm^{-2}$), presented the lowest mean acoustic biomass and a strong dominance of zero values. The no-fish acoustic biomass did not present any clear association with the sediment complexity since the higher acoustic biomass was associated to SaUn (mean log10(s_A +1) = 1.94 $m^2.nm^{-2}$), followed by SaStCoRhAl (1.93 $m^2.nm^{-2}$), SaCoRhAl (1.86 $m^2.nm^{-2}$), SaStAl and Sa (1.77 $m^2.nm^{-2}$), SaAl and SaRhAl (1.66 $m^2.nm^{-2}$), SaLrAl (1.30 $m^2.nm^{-2}$), and LrAl (0.69 $m^2.nm^{-2}$).

Fish-like acoustic biomass was significantly higher (mean log10(s_A +1) = 1.14 $m^2.nm^{-2}$) in the mid-mesophotic zone (60-80 m) that encompasses the upper edge of the shelf-break than the lower euphotic (1.07 $m^2.nm^{-2}$), followed by the upper mesophotic (0.92 $m^2.nm^{-2}$), the upper euphotic (0.87 $m^2.nm^{-2}$) and the lower mesophotic (0.85 $m^2.nm^{-2}$). The no-fish acoustic biomass significantly increased with the bottom depth. It was higher in the lower mesophotic strata (mean log10(s_A +1) = 2.49 $m^2.nm^{-2}$) where dense and strong layers of gelatinous were observed, than in the mid-mesophotic (2.25 $m^2.nm^{-2}$), followed by the upper mesophotic (2.08 $m^2.nm^{-2}$), the lower euphotic (1.84 $m^2.nm^{-2}$), and the upper euphotic zone (1.37 $m^2.nm^{-2}$).

Finally, fish-like acoustic biomass was significantly higher inside (mean log10(s_A +1) = 1.18 $m^2.nm^{-2}$) than outside (0.46 $m^2.nm^2$) the no-take zone. Although less marked, the same trend was observed for the no-fish acoustic biomass (1.88 $m^2.nm^{-2}$ vs. 1.75 $m^2.nm^{-2}$).

Fish assemblages

Fish-like echoes were assigned to ten assemblages and two triggerfish species (Table 3.2). Video observations allowed a good identification of the species present for most of the groups. However, the composition of four groups (bottom weak fish detection, sand fish, loose school, shelf-break school) could not be fully validated by the videos.

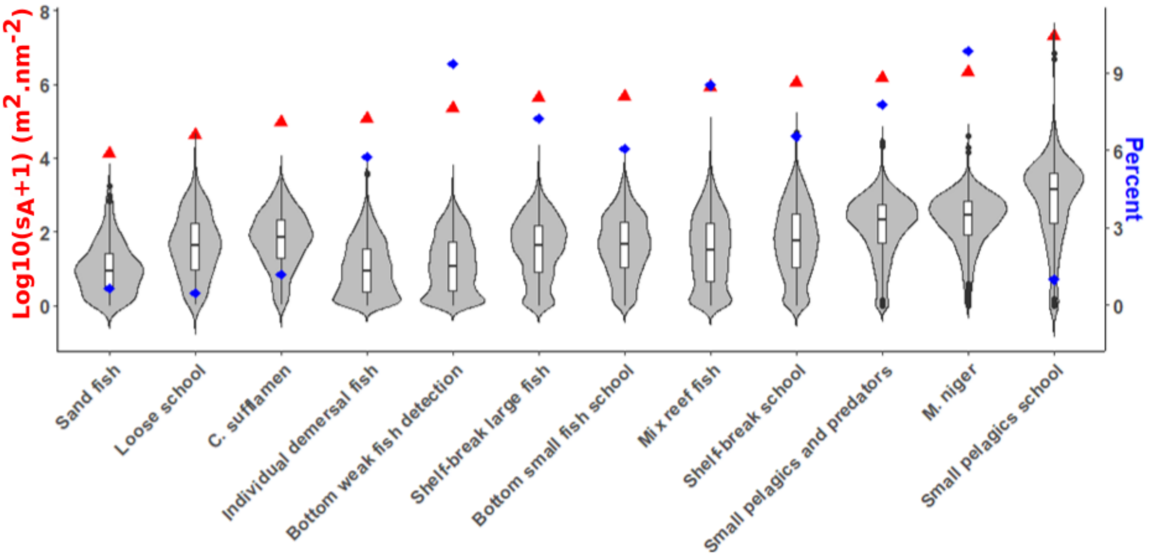


Figure 3.5. Violin plot containing boxplot representing the median (horizontal line), interquartile range, whiskers and outlying points of the acoustic biomass of individual assemblages (in log10(s_A + 1)) by ESDU, their cumulative sum (red triangles) and the percentage of ESDU with presence of each assemblages (blue diamonds).

Small pelagic school presented the highest total acoustic biomass, followed by the black triggerfish (Fig. 3.5). The percentage of ESDU with presence of a given assemblage also mostly followed the trends in acoustic biomass with some notable exceptions. Small pelagic fish school that encompassed the highest acoustic biomass was only observed in 1% of ESDU (Fig. 3.5), indicating that they were concentrated within some large schools. On the opposite, *M. niger* was the most frequently observed assemblage (in 9.9% of ESDU) followed by bottom weak fish detection (9.4%) that ranked eighth in terms of total acoustic biomass.

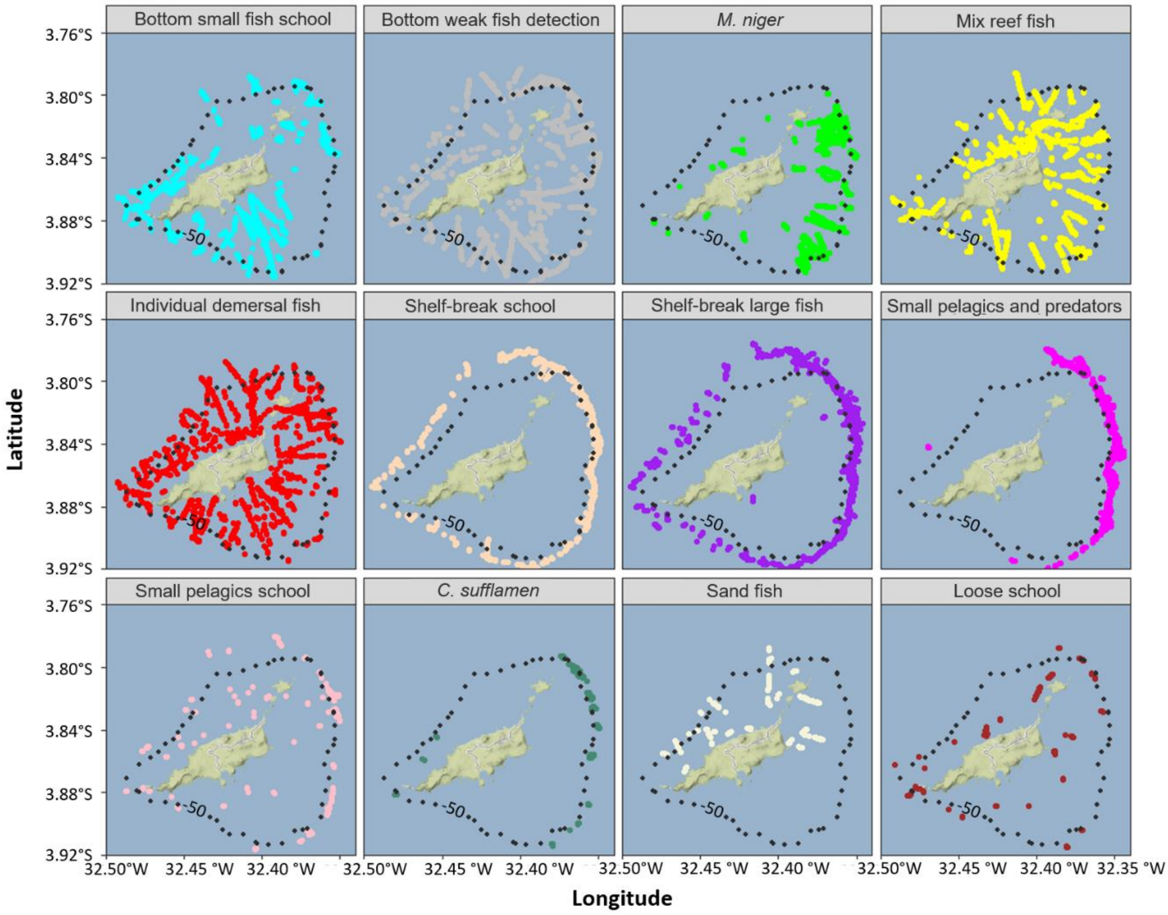


Figure 3.6. Spatial distribution represented by coloured points of the fish assemblages. The black dotted line depict the 50 m isobath. Maps were created by the authors using R (https://www.R-project.org/) and ggmap (Kahle and Wickham, 2013).

Fish assemblages presented specific spatial patterns of distribution (Fig. 3.6). Four assemblages (bottom small fish school, bottom weak fish detection, individual demersal and mix reef fish) presented the most comprehensive distributions over the shelf, all around FNA. The other assemblages associated with the shelf were loose school and sand fish, mostly distributed close to the coast and *M. niger*, mainly distributed on the windward side of FNA. Small pelagic schools were distributed both over the shelf and at the shelf-break. The other groups were mostly associated with the shelf-break, with shelf-break schools and shelf-break large fish distributed all over FNA while small pelagic and predators and C. *sufflamen* were mostly distributed on the windward side.

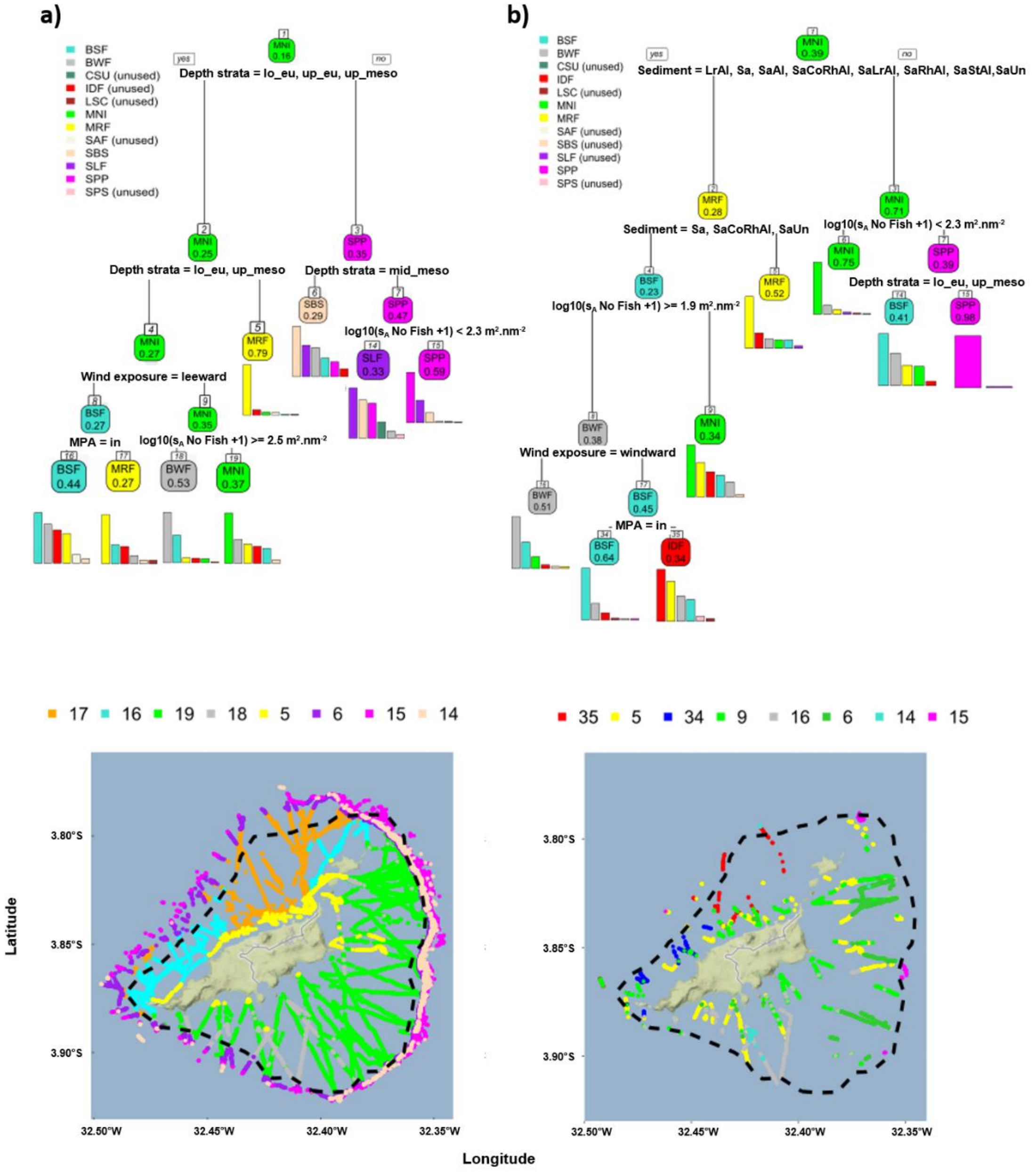


Figure 3.7. Regression tree (a, b) and associated prediction map (c, d) performed on the acoustic biomass (in log10(s_A + 1)) of fish assemblages according to the environmental parameters with the complete data set (a, c) and the dataset limited to the locations with observed sediment (b, d). The fish assemblages identified at each terminal node are those with the highest proportion composition in percent. The composition in assemblage percent for each terminal node is represented by the histogram beneath it. Covariates used to develop the tree were depth strata (up_eu: upper euphotic, lo_eu: lower euphotique, up_meso: upper mesophotic, mid-meso: mid-mesophotic, lo_meso: lower mesophotic), position (wind exposure: windward or leeward), protection level (MPA: in or out) sediment (See Table 3.1 for sediments codes), fish-like and

no-fish acoustic biomass (s_A). Fish assemblages abbreviations were, BSF: bottom small fish, BWF: bottom weak detection, IDF: individual demersal fish, MNI: *M. niger*, MRF: mix reef fish, SBS: shelf-break school, SLF: shelf-break large fish, SPP: small pelagics and predators. Trees were made by the authors using diet package (Kuhnert et al., 2012). Maps were created by the authors using R (https://www.R-project.org/) and ggmap (Kahle and Wickham, 2013).

The regression tree relating the fish-like acoustic biomass to the environmental parameters without considering the sediment (Fig. 3.7a,c) reveals that the main driving factor is depth strata, discriminating between areas shallower (upper and lower euphotic, upper mesophotic) and deeper than 60 m depth (mid and lower mesophotic). Bottom depths shallower than 60 m correspond to the shelf where neritic assemblages dominate: bottom small fish school, mix reef fish, bottom weak fish detection, *M. niger*. Pelagic assemblages logically dominate in deeper areas: small pelagics and predators, shelf-break large fish and shelf-break school. Over the shelf, the next splits of the trees are depth strata, wind exposure, MPA protection and s_A no-fish. Mix reef fish constituted 79% of the assemblages on the upper euphotic strata, it was also the dominant group (27%) in the lower euphotic and upper mesophotic strata on the leeward side outside the MPA. *M. niger* dominates (37%) on lower euphotic and upper mesophotic strata on the windward side with low no-fish acoustic biomass. On the pelagic side, shelf-break large fish dominated (29%) on the mid-mesophotic zone 60-80 m and small pelagic and predators (47%) on the lower mesophotic zone 80-100 m. When considering the reduced database containing sediment information (Fig. 3.7b,d), the first explicative variable was the sediment. On SaStCoRhAl sediment, *M. niger* dominates (73%). For sediments other than SaStCoRhAl, the next splits of the trees are sediment, no-fish acoustic biomass, wind exposure, MPA protection and depth strata. On the sediment LrAl, SaAl, SaRhAl, SaLrAl, SaStAl 52% of the assemblages belong to mix reef fish.

Univariate analyses showed that the percentage of space occupation was substantially higher on the windward side for half of the assemblages (*C. sufflamen,* bottom weak fish detection, shelf-break large fish, shelf- break school, small pelagics and predators, *M. niger*) (Supplementary Fig. S3.7 online). The highest acoustic biomass of all groups corresponded to small pelagics school in the leeward side, followed by *M. niger* in the windward side and mix reef fish in the leeward side.

All assemblages (Supplementary Fig. S3.7 online) varied substantially according to the bottom depth strata. The acoustic biomass percent of presence was higher in the upper and lower euphotic strata for mix reef fish and *M. niger*, respectively. The acoustic biomass and percent of presence of demersal assemblages, sand fish and mix reef fish, decreased with depth. The opposite occurred for pelagic groups shelf-break large fish, shelf-break school, small pelagics and predator, *C. sufflamen* that peaked at mid and lower mesophotic depths, except for small pelagic school that presented highest acoustic biomass in the upper mesophotic zone (40-60 m). Bottom weak fish detection and bottom small fish school, individual demersal fish were distributed and presented higher acoustic biomass either on the lower euphotic or upper mesophotic.

Sediment identification was only possible on shallow water and represented a small portion of the data. In this dataset, some assemblages presented clear association with one sediment (Supplementary Fig. S3.7 online). In particular mix reef fish were strongly related with SaLrAl, *M. niger* with SaStCoRhAl and bottom small fish school with Sa. Mix reef fish and *M. niger*, although showing a higher occurrence on a particular substrate, were the two only groups that appeared on all sediment types.

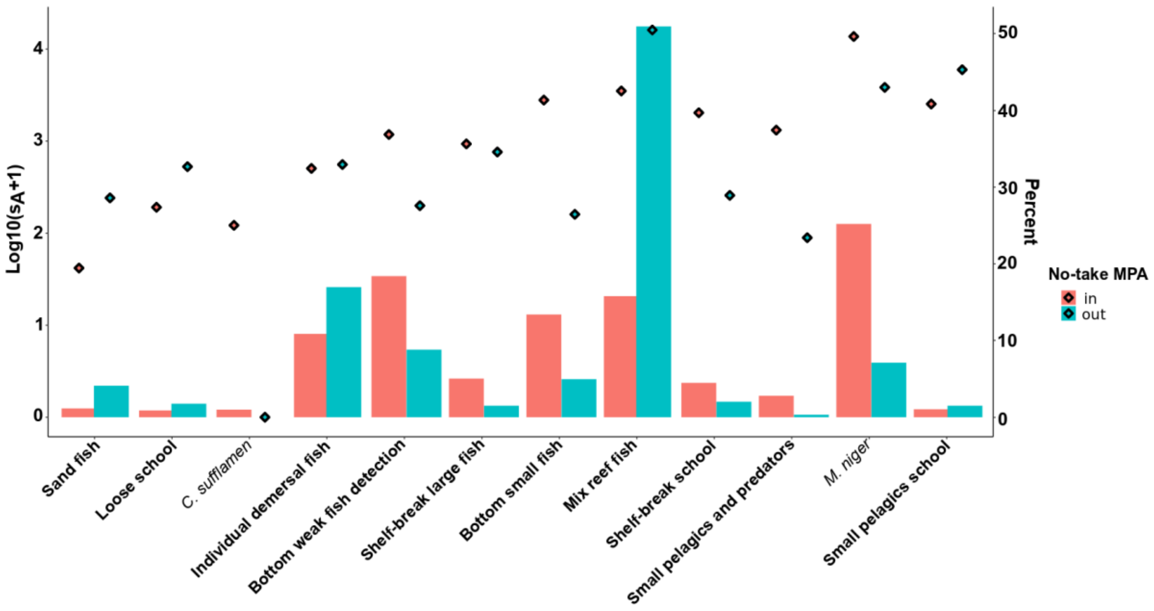


Figure 3.8. Barplot representing the percentage of ESDU with presence of each fish assemblage according to its position regarding the no-take zone and the mean acoustic biomass of each group (log10(s_A+1)) per ESDU (i.e. the total fish acoustic biomass normalised by the number

of ESDU inside and outside the no-take zone) (diamonds).

The no-take MPA effect was clear on fish distribution as six assemblages (bottom weak fish detection, shelf-break large fish, bottom small fish school, shelf-break school, small pelagics and predators, *M. niger*) were more present and had higher acoustic biomass inside the MPA (Fig. 3.8). *C. sufflamen* was virtually absent outside the no-take MPA. The five remaining assemblages (sand fish, loose school, individual demersal fish, mix reef fish and small pelagic school), were all more present and presented higher acoustic biomass outside than inside the no-take MPA.

Black triggerfish biomass

The black triggerfish, the second group in terms of fish acoustic biomass, was mostly concentrated in the East side of FNA. In this area (Fig. 3.9), its actual biomass was estimated to 700 tonnes (19 g.m^{-2}) with an estimated CV of 40%. Its distribution inside the area was heterogeneous and organised in patches.

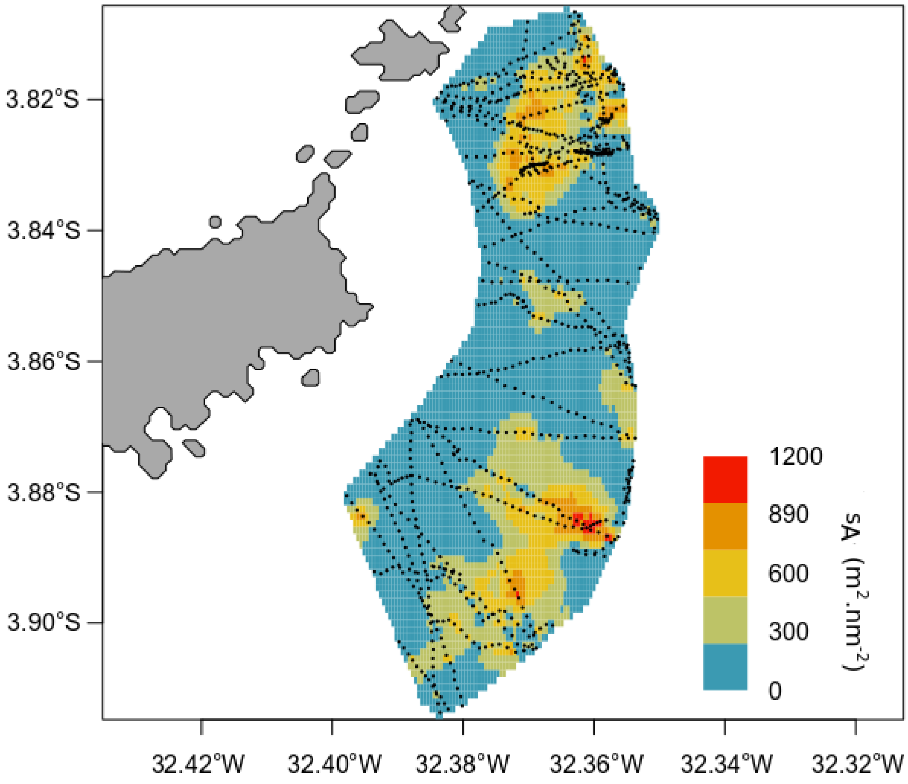


Figure 3.9. Interpolated distribution of the black triggerfish distributed in 5 classes of values of

s_A. The black dashed lines represent the acoustic transects. Map was created by the authors using R (https://www.R-project.org/) and RGeostats package (ParisTech, 2020).

3.5. Discussion

By combining acoustic and video observations, we provided for the first time, a comprehensive vision of tropical fish distribution from the near-shore line to off the shelf-break with a description of (i) fish diversity, (ii) horizontal fish-like and no-fish distribution, and (iii) a focus on the black triggerfish. The data gathered also provided important evidence to (iv) revisit the Island Mass Effect (IME), and (v) give some insights for Marine Spatial Planning (MSP).

Fish diversity

In about 50 h of video footage, we recorded 47 fish species of 29 families (Table 3.3). This is only a small fraction of the ichthyofauna of FNA that, with a total of 250 species and 77 families, harbours the greatest richness of marine fish among the oceanic islands of the South Atlantic (Krajewski and Floeter, 2011; Pimentel et al., 2020). Indeed our objective was not to perform an exhaustive description of the fish diversity but to capture the fish composing the bulk of the biomass. Still, compared with other visual census techniques we observed a similar number of families (27-28; Krajewski and Floeter, 2011; Ilarri et al., 2017; Schmid et al., 2020) but much fewer species (50-66) (Krajewski and Floeter, 2011; Ilarri et al., 2017; Schmid et al., 2020). Only, Soto (2001) depicted much more families (68) and species (167) but his inventory included pelagic species combining visual census, fisheries surveys and literature records. The most diverse families (Serranidae, Labridae and Pomacentridae) are underrepresented in our study since we focused on pelagic and demersal species that can be assessed with acoustics and did not put efforts on filming benthonic and cryptobenthic communities.

In our study, two species, the tropical sardine *Harengula sp.* and the black triggerfish *M. niger* accounted for more than 90% of the fish recorded. This confirm the fact that the biodiversity in FNA is represented by few very abundant species (de Araújo et al., 2020). *M. niger* was the second most abundant and the most often observed species. Such results differ from other studies in FNA. Indeed, most studies (Krajewski and Floeter, 2011; Krajewski et al., 2011; Ilarri et al., 2017) report *Thalassoma noronhanum*, *Haemulon chrysargyreum* and *Stegastes rocasensis* as dominant species. The difference between our and other studies is likely due to our extensive depth coverage compared with other that mostly focused on shallow (<20 m) waters. Only Schmid et al. (2020) observed a dominance of *M. niger* but their study was performed using baited remote underwater video stations and black triggerfish are voracious bold species (Mendes et al., 2019). Even if far form exhaustive, our video records likely provide a robust picture of the main pelagic and demersal species present in FNA and a robust information to complement and identify acoustic observations.

Fish echotypes are known to provide a heuristic description of fish species, assemblages or communities (Petitgas and Levenez, 1996; Burgos and Horne, 2008). Combining video observations with the scrutinizing of acoustic echograms allowed for the identification of consistent fish assemblages (Table 3.2). We acknowledge that, in some cases, some fish echotraces may not have been correctly assigned to the proper fish assemblage. However, since these assignations were sustained by ~50h of video footage we are confident that potential mis-assignation should not have significantly impacted our results.

Comprehensive tropical fish distribution

The algorithm we applied on acoustic data allowed discriminating between fish-like and no-fish echograms. The access to simultaneous video observation and the care taken to validate the algorithm with these images makes us confident that the fish-like echograms do indeed correspond to fish.

The strong stability in acoustic fish biomass distribution between FAROFA surveys (Fig. 3.2), through years and seasons that allowed merging the data from the three surveys, suggests a bottom-up structuration of fish assemblage. Most fish observed by video and acoustics are demersal and pelagic. Demersal fish are classically associated with typical habitat in terms of sediment, benthic composition, structural complexity or depth (Friedlander and Parrish, 1998; Munday, 2002; Russ, 2003; Eduardo et al., 2018) (see also 4.4), which may explain site-fidelity. In the same way, except for *Harengula sp.*, the pelagic fish species were concentrated at the shelf-break, a known hotspot for pelagic fish (Dominguez et al., 2014). Seasonal variations (e.g. rainy vs. dry season) do not imply significant environmental changes. Indeed, the seasonal variation gradient sea surface temperature is minimal (varying from 26.5°C to 28°C) (Tchamabi et al., 2017) and does not seem to significantly impact the distribution of the fish as observed by acoustic. A similar result with no change regarding the season was found in fish predator diet (Martins et al., 2021).

The comprehensive spatial coverage we achieved allows providing the first map of fish acoustic biomass around FNA (Fig. 3.3). Such a picture cannot be completed with classic methods based on visual census or fishing operations (in systems where fishing activity is allowed). More generally, this is the first comprehensive high-resolution map of fish distribution of a tropical system from the near-shore to the shelf-break. To our knowledge at least one example of map of tropical fish biomass was produced from acoustic data covering a fraction of the U.S. Virgin Islands (Costa et al., 2014). However, this study did not use simultaneous video observation limiting the skills of species identification. By combining acoustics and video, we provide the spatial distribution of all acoustically detected fish (Fig. 3.3) but also of a variety of fish assemblages (Fig. 3.6). Our results reveal a strong heterogeneity in the distribution of fish acoustic biomass with the presence of hotspots. This reinforces the fact that punctual observations may miss hotspots in comparison with our extensive continuous sampling. The comprehensive maps we provide have several benefits since they can help defining areas for further sampling strategies, and are key elements for management in particular for implementing MSP (Sale et al., 2014; Outeiro et al., 2019; Queffelec et al., 2021).

Black triggerfish: a key tropical player

In phase with video observations, the black triggerfish was the second most important species in terms of acoustic biomass and the one occupying most space. In its main zone of distribution, we estimated the black triggerfish biomass to 700 tonnes (i.e. 19 $g.m^{-2}$). *M. niger* is one of the very few reef fish with a circumtropical distribution (Kavanagh and Olney, 2006). It is known to form large shoals of more than one hundred individuals and has been reported to exhibit high densities around remote oceanic islands such as Ascension Island (Lubbock, 1980; Price and John, 1980), Clipperton Atoll (Robertson and Allen, 1996), Trinidad Island (Gasparini and Floeter, 2001), Johnson atoll and Porto Rico (Kavanagh and Olney, 2006) or St Peter and St Paul's Rocks (Lubbock and Edwards, 1981; Feitoza et al., 2003). *M. niger* thrives at colonizing and maintaining high population levels at remote location (Kavanagh and Olney, 2006). This is probably due to its long pelagic phase that enables its settlement in remote location and its high plasticity in resource use. Indeed, *M. niger* broad omnivory gives him the potential to forage opportunistically on a variety of prey, including pelagic algae remains or dolphin vomit and faeces(Sazima et al., 2006). In addition, isolated oceanic Islands such as FNA, are impoverished and the functional richness is low (Ferreira et al., 2004; Floeter et al., 2008; Krajewski and Floeter, 2011). *M. niger* has the ability to take advantage of an empty niche as demonstrated by Mendes et al. (2019) at St Peter and St Paul Archipelago where it endorses the functional role of opportunistic grazing herbivore. FNA lacks of large herbivore that are represented by few small Scaridae of the gender *Sparisoma* (Morais et al., 2017a) and roving herbivore by few Kyphosidae and Acanthuridae. In our study we observed one species of parrotfish *Sparisoma amplum* (3 individuals in 2 videos), one species of sea chub *Kyphosus sectatrix* (183 individuals in 4 videos) and one surgeon fish *Acanthurus chirurgus* (11 individuals in 1 videos). Those species are found with higher abundance in southern location of the Brazilian coast such as Abrolhos, Bahia for parrot fish and surgeon fish, or even higher latitude such as Arvoredo Island, Santa Catarina and Arraial do Cabo, Rio de Janeiro for sea chubs (Ferreira et al., 2004).

The black triggerfish is mostly distributed on the northeast side of the Island. This windward pattern of distribution is facilitated by its high swimming abilities (Krajewski and Floeter, 2011). The windward side of FNA also concentrates the more complex sediment, containing reef algal-vermetid barriers along rocky shorelines. *M. niger* directly benefits from this sediment complexity as it lays its eggs in the sand, feeds on epilithic algal matrix (EAM) and sleeps in rocky reef (Walsh, 1987). Adult, *M. niger* is strictly reef-associated as it sleeps in the same hole every night, which attests to a high level of site-fidelity (Walsh, 1984). If the bulk of the *M. niger* occurred in the selected area for biomass estimation, we also observed *M. niger* on the leeward side close to the shore where large rocks occur. In this case, *M. niger* were juvenile associated with other reef fish (e.g. surgeons fish, sergeants). Although edible and appetent, the black triggerfish is not a commercial species and is only consumed occasionally.

Revisiting the Island mass effect (IME)

The IME describes well the higher primary and secondary productivity on the leeside due to turbulent mixing and advection created by eddies on the wake of islands (Caldeira et al., 2002; Martinez and Maamaatuaiahutapu, 2004; Messié et al., 2020). However, the IME on tertiary productivity remains quite unknown or is described as isotrope around the island (Gove et al., 2016). Our data allows us to better describe the IME and propose a new conceptual figure (Fig. 3.10) with an asymmetrical response of the fish distribution.

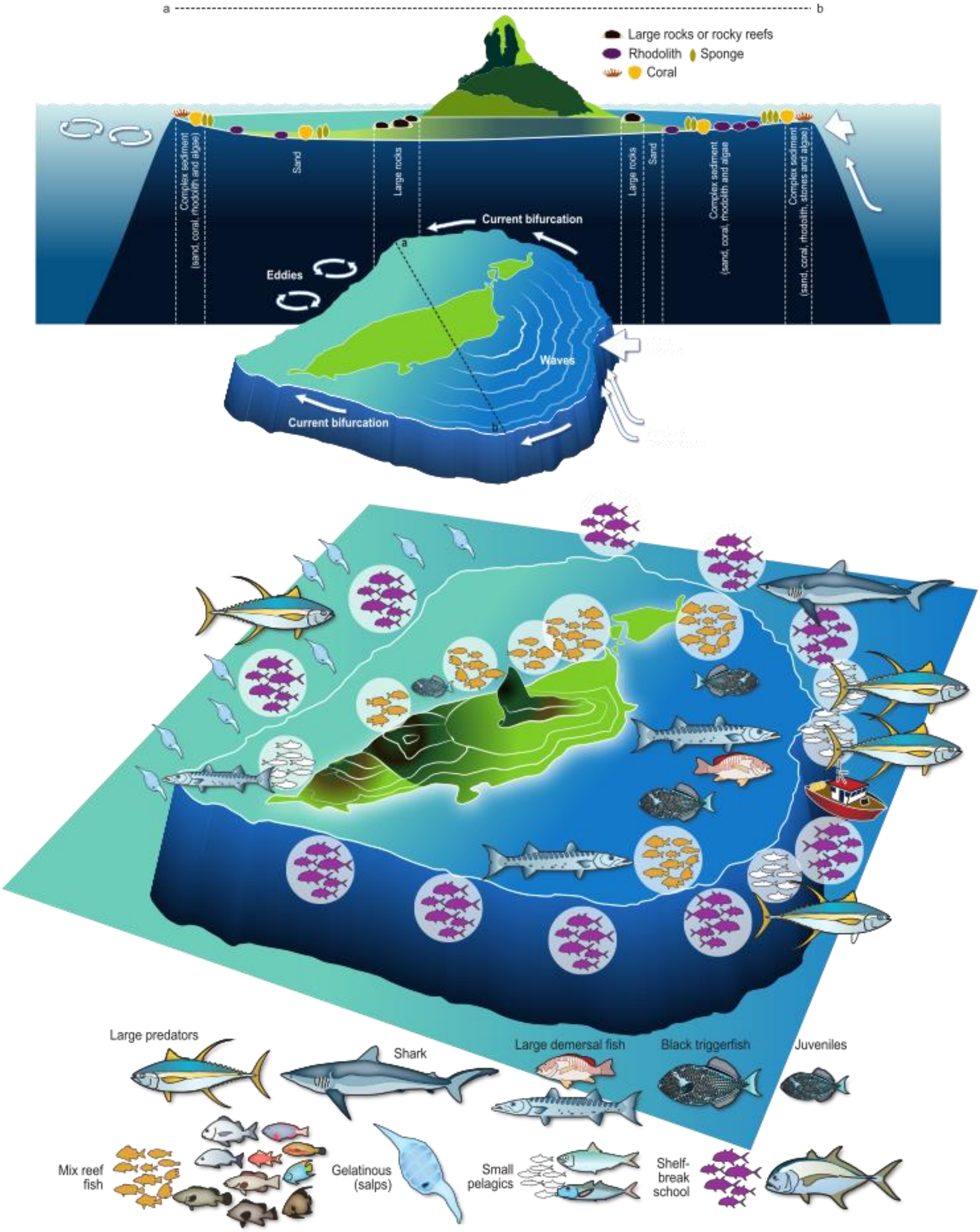


Figure 3.10. Synthetic representation of the island mass effect as illustrated by the case of Fernando de Noronha. Created with Adobe Illustrator software (https://www.adobe.com) by graphic designer Pierre Lopez.

Horizontal fish distribution patterns were very different regarding the position of the archipelago face to the main wind/current flows (windward vs leeward). Overall, fish were much more abundant on the windward side. This is true for most assemblages, especially for pelagic fish and triggerfishes. According to the IME, an overall increase in island-related production is expected. This effect is expected to be more marked on the leeward side due to hydrodynamic retention processes (Heywood et al., 1990; Travassos et al., 1999; de Souza et al., 2013; Gove et al., 2016; Tchamabi et al., 2017). The no-fish acoustic biomass, mostly composed of zooplankton (including gelatinous) was indeed higher on the leeward, in particular off the shelf where dense layers of gelatinous were observed. Lessa et al., 1999 observed a more important concentration of larvae on the west side (leeward) of FNA. Thus, leeward side primary productivity enhancement (Tchamabi et al., 2017) (see also vertical profiles of chlorophyll concentration performed during the FAROFA surveys showing higher concentration in the leeward side; https://doi.org/10.17882/70647) may participate in fish larvae recruitment where the leeside fulfils the conditions of Bakun triade: (i) nutrient enrichment, (ii) concentration of larval food distributions, and (iii) local retention of eggs and larvae (Bakun, 1998; Agostini and Bakun, 2002).

If the IME is well described in terms of turbulent processes and further primary productivity (Signorini et al., 1999), there is a lack of fine scale information on the consequences in terms of fish distribution. We reveal that most pelagic fish are concentrated windward facing the main flow, where the productivity is expected to be lower. This study does not allow concluding about the mechanisms explaining this feature, but we can propose at least three hypotheses. First, the current flow reaching the island topography likely concentrates the flux of particles (Travassos et al., 1999) including zooplankton, favouring the feeding behavior of medium size planktivorous pelagic fish (e.g. *C. sufflamen)* or intermediate predators that feed on small fish, shrimps or invertebrates (e.g. *Caranx crysos*) and are targeted by top predators (e.g. large Scombridae and Carangidae, Istiophoridae and sharks). The aggregation of planktivorous fish on the windward side of island has been observed by Hamner et al. (1988) that described a “wall of mouth” composed by planktivorous fish picking up zooplankton before it reaches the reef (Hamner et al., 1988; Valenzuela et al., 2021). Second, the water is much more turbid leeward than windward where visual predators concentrate. Third, a behavioral pattern consisting in facing the current (reotrope) to keep associated to the island and avoid advection may also play a role.

Interestingly, most demersal assemblages were also more abundant on the windward side. Structural habitat complexity is known to be an important factor for fish richness and abundance (Curley et al., 2002; Eduardo et al., 2018; Ferrari et al., 2018) and higher acoustic biomass was associated with the more complex sediment SaStCoRhAl, a mosaic of different substrates. This may be a consequence of turbulent processes. Indeed, on the windward side, the strong oceanic flow flush soft sediments, favouring the development of complex habitats that concentrate fish (Curley et al., 2002). On the other hand, soft sediments deposit leeward, forming sandy habitats that are less populated (Curley et al., 2002). Wind and current exposure influence the underwater landscape with the windward side, characterized by extensive reef barriers along rocky shorelines, and the leeward side, mainly composed of descending slopes along a rocky shoreline with large scattered boulders and small reefs scattered on sandy habitats (Maida and Ferreira, 1997). This difference in sediment between the windward leeward due to the wind and wave exposure is a common feature observed elsewhere. e.g., in the Madeira Archipelago (Caldeira et al., 2002).

IME effect is thus not just an enhancement of primary productivity though physical process in the leeward side of islands but it also drives the fish distribution by shaping the habitats. Wind and current cause erosion and a transformation of the shoreline and sediment distribution which also impacts the distribution of fish. This results in an anisotropic distribution of fish with schools of small pelagic and associated predators flourishing at the shelf-break on the windward side taking advantage of the vertical mixing, the current and the clear water.

Depth strata

Fish acoustic biomass and assemblage composition varied according to the depth strata. The highest overall fish acoustic biomass was observed on the mid mesophotic zone (60-80 m) that corresponds to the shelf-break. By providing a cross-shore along-depth acoustic biomass estimations of demersal and pelagic fish, we confirm the importance of the bathymetry (Pittman et al., 2009) and quantify and rank the fish distribution among depth strata. Specifically, the shelf-break was a hot spot for five assemblages (Fig. 3.6). Indeed, at the shelf-break, we observed the steady presence of shelf-break schools as well as small pelagics and predators. It is in this area, in particular at the windward, that SSF targeting both demersal and pelagic species concentrate (Costa, 2019). With our results, it is difficult to determine whether the depth and associated light conditions (euphotic vs mesophotic) or the structural characteristic of the vertical zones are the main drivers of diversity and abundance. Indeed, in our case the mid mesophotic zone matches the shelf break. This zone has specific characteristics. It presents a steep slope associated to high structural complexity (Reid, 2001). In addition, by being at the interface of neritic and oceanic domains it concentrates organisms from both domains (Spalding et al., 2007). Mesophotic reefs associated to the shelf-break are thus hot spot for marine life. However, our result do not confirm that mesophotic reefs *per se* (independently of the shelf break) concentrate more life than euphotic ones. Despite their importance, shelf edge reefs are seldom included in marine protected area network, in particular in Brazil (Olavo et al., 2011). Shelf-breaks should thus be considered as important area for biodiversity conservation (Eduardo et al., 2018).

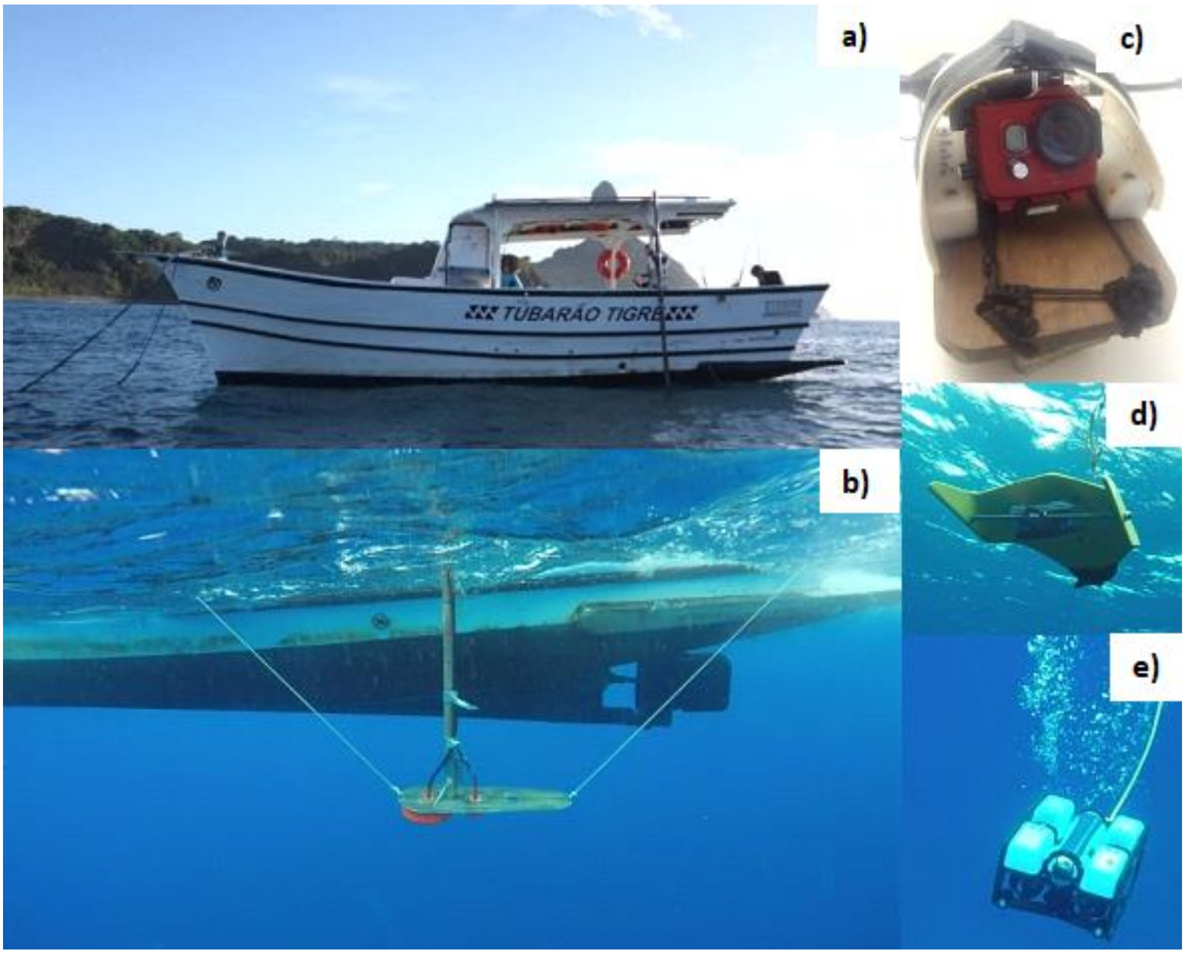
Insights for marine spatial planning

MSP is a natural extension of practices including integrated coastal management and multi-use MPA management (Agardy et al., 2011). MPAs are regarded by many marine scientists as a major management tool needed to tackle fisheries collapse and regular loss of marine biodiversity (Claudet et al., 2006; Caveen et al., 2013; Hernández et al., 2019). Data and analysis should be central to decision-making. The data we provide here have the advantage of being comprehensive. We show that fish acoustic biomass was significantly higher inside than outside the no-take zone (Supplementary Fig. S3.6 online) indicating a potential effect of the MPA. Such positive effect was witnessed by Ilarri et al. (2017) on shallow-reef fish communities. Here, by providing a comprehensive covering of the entire FNA we provide much more robust estimates. If most assemblages had higher acoustic biomass inside than outside the no-take MPA, it is difficult to fully unravel between protection effects and habitat characteristics. Indeed the no-take zone encompasses the entire windward shelf that is characterized by higher bottom habitat complexity while the no-take MPA area encompasses the area close to the port that is susceptible to enhance the productivity through the eutrophication and the presence of rocks and structures. In all cases, with the objective to protect fish biomass and assemblages, the no-take zone seems overall well designed. It covers most of the shelf, protecting reef fish that exhibit high densities in near shore shallow waters areas that classically suffer great anthropic pressure linked to multiple use activities including artisanal and recreational fishing. However, the no-take zone stops at the 50 m isobaths and thus leaves the shelf-break unprotected. As an important zone for biodiversity, foraging and spawning, protecting the shelf-break could favour species reliant on shelf-break mesophotic reefs. However, since most SSF operate at the shelf-break it is important to let a sufficient portion of the shelf-break open to fisheries, in particular for those targeting pelagic species that temporally use FNA as a shelter during their long journey.

3.6. Conclusion

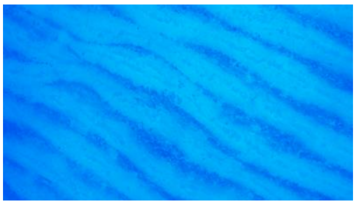
By combining multifrequency acoustic data and video, we provide the first comprehensive description of demersal and pelagic fish distribution of a tropical ecosystem. We also provide the first biomass estimation of the black triggerfish *Melichthys niger*, a key tropical player. More generally, we pictured the distribution of a variety of fish assemblages and related their spatial patterns to biotic and abiotic environmental features. Comparing the effects of euphotic and mesophotic reefs we show that more than the depth, the most important feature is the topography with the shelf break as the most important hotspot. Beyond, this approach allowed us to revisit the IME. We completed the IME portrait and revealed that it is an asymmetric process regarding fish distribution. Indeed, while primary productivity is mostly enhanced in the leeward, higher trophic levels concentrate on the windward side. We also tested for the impact of the no-take MPA of Fernando de Noronha Archipelago on the distribution and acoustic biomass of demersal and pelagic fishes. This MPA protects the most complex habitats that shelter the highest fish diversity and biomass. Still, an important hotspot, the shelf-break, currently unprotected could be partly included given that sufficient space is left for fishing activities, in particular for pelagics. Maintaining pelagic small-scale fisheries in FNA is indeed socially and economically important. More generally, describing fish distribution and associated environmental features is the first step toward understanding how fish communities are spatially structured and is a necessary step to conduct MSP and operate relevant protection policies.

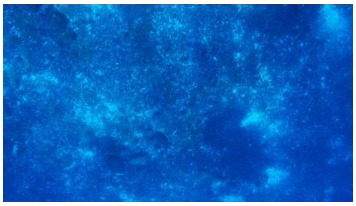
3.7. Supplementary data



Supplementary Figure S3.1. Setting up of operations a) sport fishing boat "Tubarão tigre"; b) acoustic transducers (70 and 200 kHz) attached on a pole; c) vertical video system; d) towed video; e) ROV. Images were obtained by the authors.

Supplementary Table S3.1. Sediment composition name and description. Images were obtained by the authors.

Name	Description	Example of image
Sa	Sand only	
LrAl	Large rocks and algae	
SaUn	Sand and unknown elements	
SaAl	Sand and macro-algae	
SaStAl	Sand, stones and algae	
SaLrAl	Sand, large rocks and algae	

SaRhAl	Sand, rhodolith and algae	
SaCoRhAl	Sand, coral, rhodolith and algae	
SaStCoRhAl	Sand, stones, coral, rhodolith and algae	

Supplementary Material Methods: Acoustic data processing

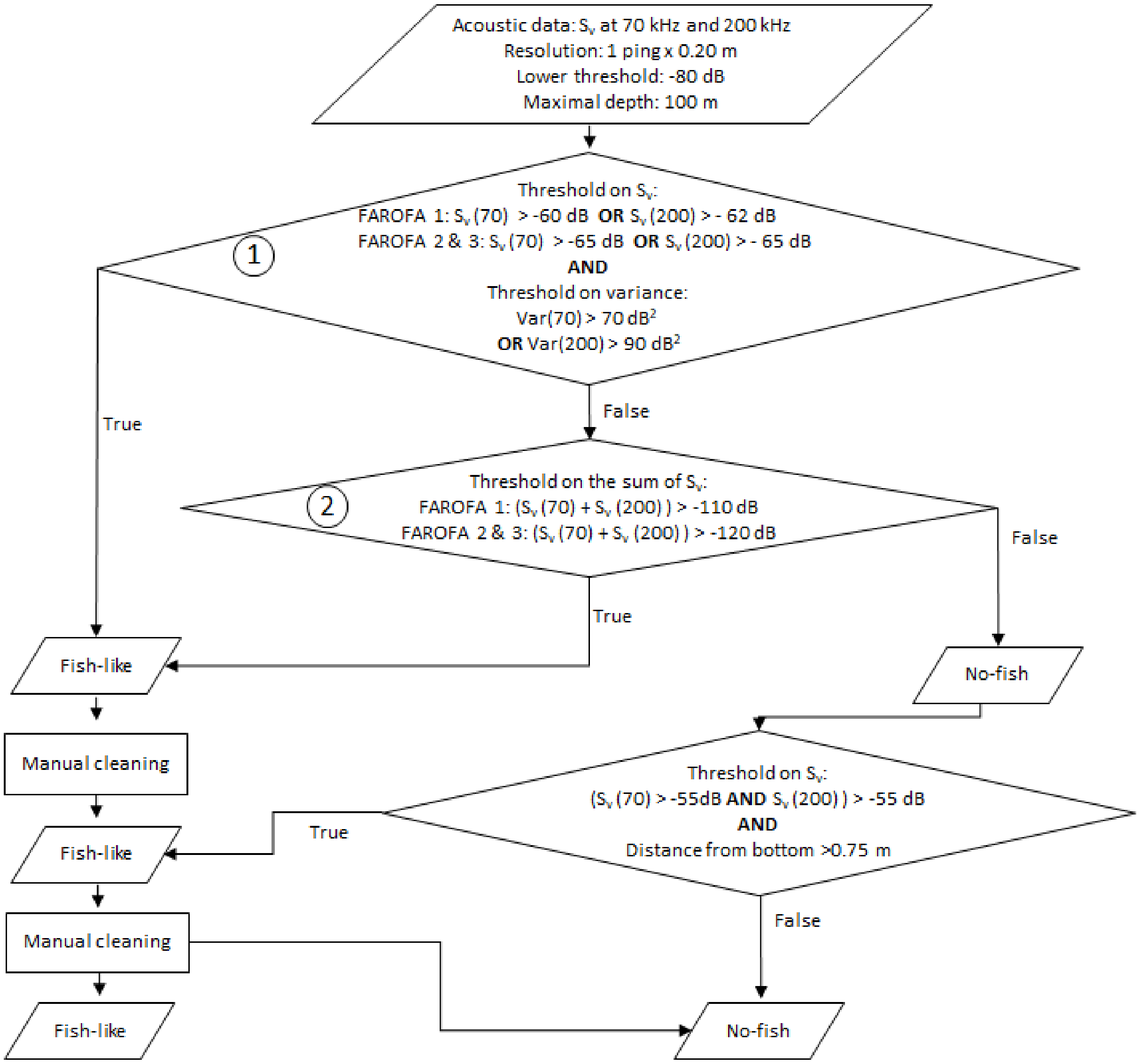
Acoustic data were treated at their highest resolution i.e., 1 ping horizontally and 0.20 m vertically. To discriminate between scatters attributed to fish (fish-like) and those originated by other organisms (no-fish), e.g. gelatinous and crustaceans, we developed an approach based on thresholds on (i) volume backscattering strength Sv (Sv, in dB re 1 m^{-1}; see MacLennan et al. (2002) for acoustic definitions), (ii) the bi-frequency sum of Sv, and (iii) the variance of Sv (see Supplementary Fig. S3.2).

A lower threshold was applied on both frequencies at -80 dB and only the data above 100 m were considered because of the limited vertical range of the 200 kHz. The first step consisted in the application of thresholds on Sv and on the variance of Sv (Supplementary Fig. S3.2). Thresholds on Sv were applied to select echoes strong-enough to be considered as fish. This operation was not sufficient to discriminate between fish-like and no-fish echoes. Indeed, off the shelf-break, we observed continuous homogeneous layers at ~80 m depth. Video records showed that these layers were originated by small gelatinous, likely gas-bearing, that could not be identified. These layers had high backscattering response at both 70 and 200 kHz, preventing their discrimination from fish-like echoes using Sv thresholds only. For that reason, we added a criterion based on the variance of Sv. Indeed, the variance among elementary Sv was significantly higher in ground-thrusted fish echo-traces than in gelatinous layers, at both frequencies (F-test, p=0). Therefore, we calculated the Sv variance of the elementary cells at the centre of the rectangular window of 31 x 5 cells (15 cells before and after, horizontally, and 2 cells above and below, vertically). The size of this window was defined considering the anisotropy of studied processes. Layers are by definition longer than high, while most fish shoals are higher than long in the echograms. The horizontally extended window allows minimising the variance within the layer and maximising the contrast with fish echoes. In case of dense fish school, the thresholds on Sv variance inside the moving window may eliminate the centre of a school where the variance is low. Thus, a second step (Supplementary Fig. S3.2) was necessary on echoes classified as no-fish at the end of the first step. It consisted of a threshold applied on the sum of Sv at both frequencies, complementing the power of discrimination between fish-like and no-fish echoes (Fernandes, 2009; Ballón et al., 2011). This step allowed retaining the dense and homogeneous regions of fish echoes (centre of shoal or very strong isolated echoes) that could be ruled out by the variance threshold.

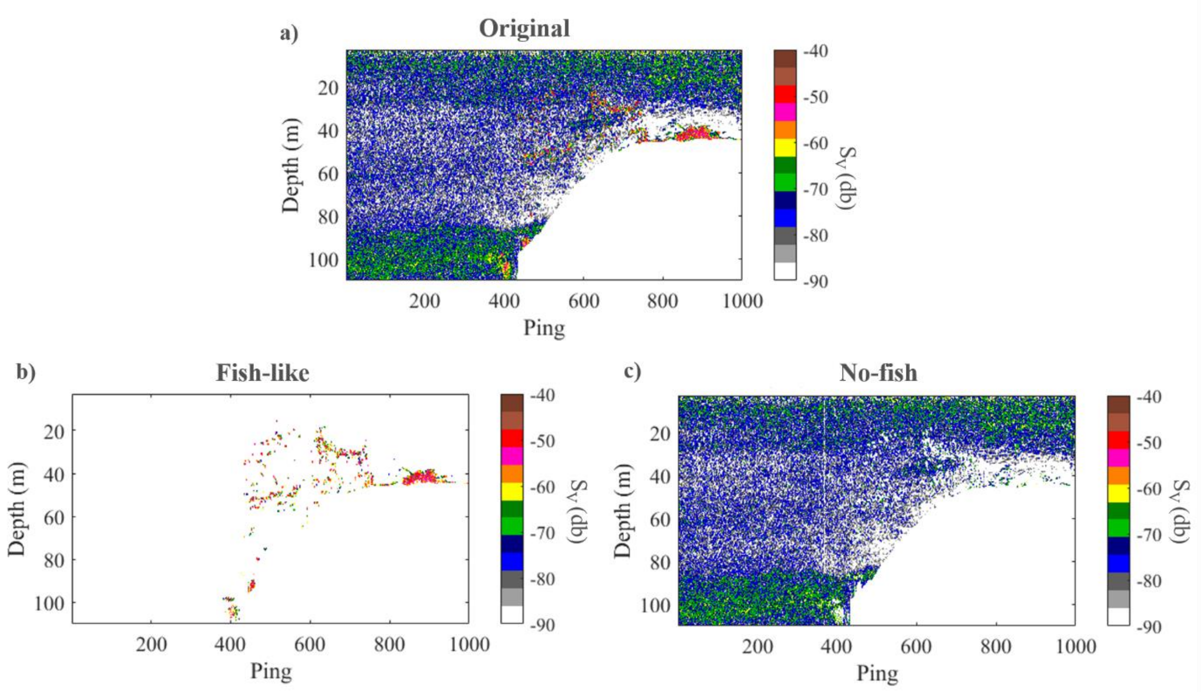
To estimates the thresholds, we applied a sensitivity analysis using the efficiency of the fish discrimination as criteria. The sensitivity analysis was applied over regions selected from video footage containing only gelatinous layers (3 regions) or fish shoals (3 regions). The regions with fish were treated manually to extract fish and served as reference echotrace. Sv thresholds on both frequencies were estimated by setting the variance threshold and the threshold on Sv successively for one frequency at a time for each cruise

During FAROFA 1, weather conditions were harsh and the acoustic data set was noisier and more difficult to clean so different thresholds were used. For FAROFA 1 at 70 kHz, the Sv and variance thresholds (Step 1) were set-up at -60 dB and 70 dB^2, respectively. At 200 kHz, these thresholds were set-up at -62 dB and 90 dB^2, respectively. Ultimately, the threshold on the sum of Sv (Step 2) was set-up at -110 kHz. For FAROFA 2 and 3 at 70 kHz, the Sv and variance thresholds (Step 1) were set-up at -65 dB and 70 dB^2, respectively. At 200 kHz, these thresholds were set-up at -65 dB and 90 dB^2, respectively. Ultimately, the threshold on the sum of Sv (Step 2) was set-up at -120 kHz.

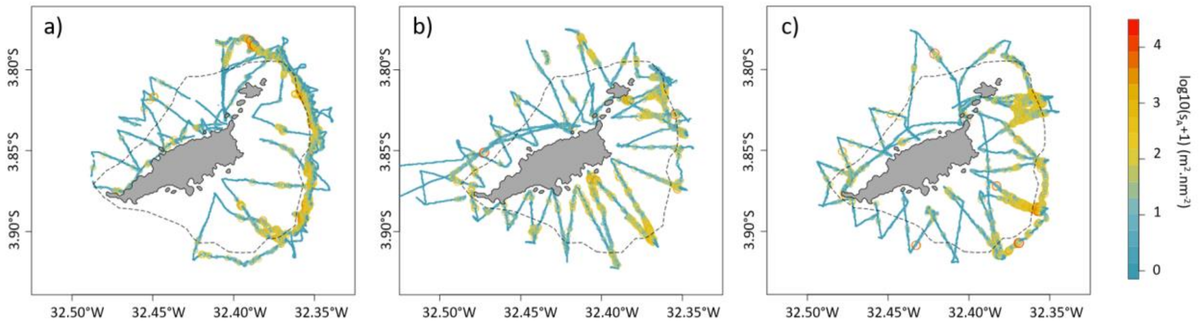
To retrieve residual fish-like still present in the no-fish echograms, additional thresholds (Step 3) were used to retain values above -55 dB in Sv (70) and Sv (200). At the end of these three steps, some manual cleaning (Step 4) of fish-like echograms was necessary to eliminate some portions of gelatinous layers. After applying this process chain to the original acoustic data we obtain fish-like echograms in which we attribute a very low Sv value (-150 dB), far below the detection threshold, to the cells not containing fish-like echoes. By inverting the fish-like mask we obtained the no fish-like echograms where we attributed the same low Sv value (-150 dB) to the cells containing fish-like echoes (see Supplementary Fig.S3.3).



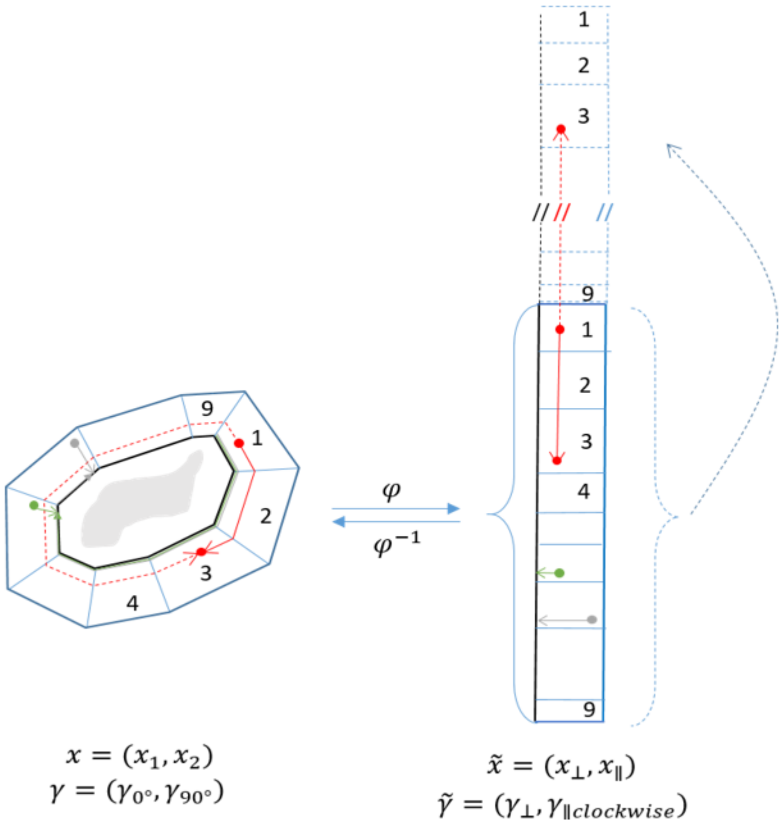
Supplementary Figure S3.2. Summary flowchart documenting acoustic data processing steps.



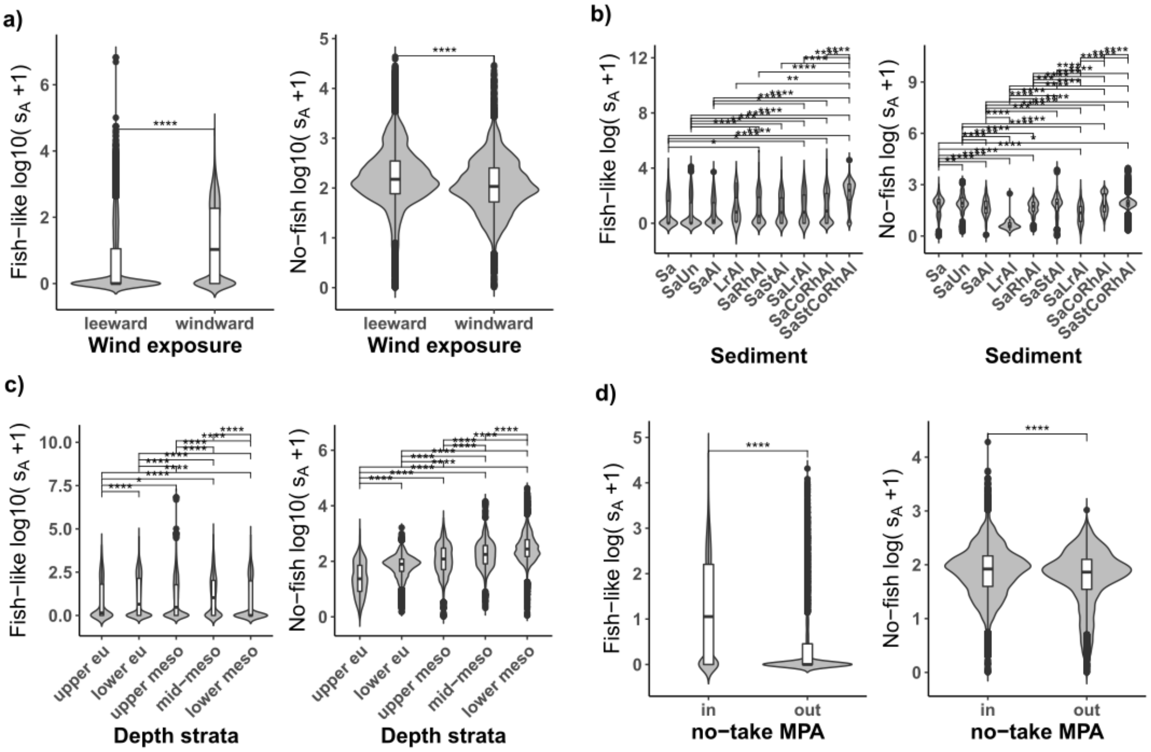
Supplementary Figure S3.3. Examples of an (a) original echogram and its transformation into a (b) fish-like echogram and a (c) no-fish echogram at 70 kHz.



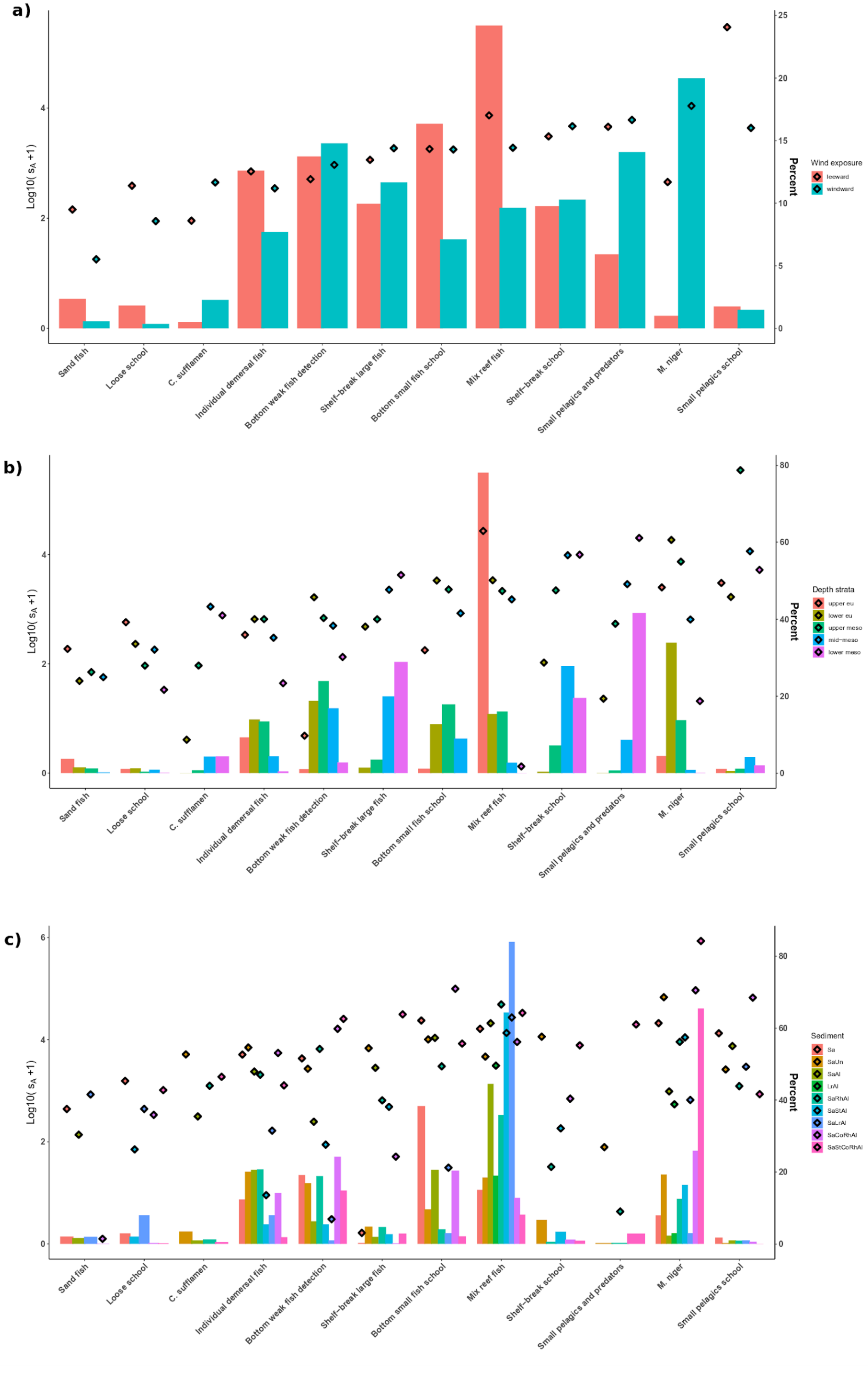
Supplementary Figure S3.4. Fish distribution for FAROFA (a) 1, (b) 2 and (c) 3. The dashed black line depict the 50 m isobaths. Maps were created by the authors using R (https://www.R-project.org/).



Supplementary Figure S3.5. Schematic representation of the algorithm used to unfold the domain area problem prior to variography and kriging. ϕ is the projection function; $x, \tilde{x}$ denote respectively the data coordinates in the geographical space and in the projected space; γ,$\tilde{\gamma}$ denote respectively variogram in the geographical space and in the projected data.



Supplementary Figure S3.6. Violin plot containing boxplot representing the median (horizontal bar), interquartile range, whiskers and outlying points of the fish-like and no-fish biomass (log10(sA+1)) according to (a) the position around FNA, windward vs. leeward; (b) the sediment type; (c) the bottom depth range: upper euphotic (0-20 m), lower euphotic (20-40 m), upper mesophotic (40-60 m), mid-mesophotic (60-80 m), lower mesophotic (80-100 m); and (d) the protection level, i.e., in vs out the no-take zone. The stars indicate the level of significance with (****), (***), (**), and (*), corresponding to p value < 0.0001, < 0.001, < 0.01 and < 0.05, respectively.


a)
Log10(sA +1)
0
2
4
Percent
0
5
10
15
20
25
Wind exposure
leeward
windward
Sand fish
Loose school
C. sufflamen
Individual demersal fish
Bottom weak fish detection
Shelf-break large fish
Bottom small fish school
Mix reef fish
Shelf-break school
Small pelagics and predators
M. niger
Small pelagics school
b)
Log10(sA +1)
0
2
4
Percent
0
20
40
60
80
Depth strata
upper eu
lower eu
upper meso
mid-meso
lower meso
Sand fish
Loose school
C. sufflamen
Individual demersal fish
Bottom weak fish detection
Shelf-break large fish
Bottom small fish school
Mix reef fish
Shelf-break school
Small pelagics and predators
M. niger
Small pelagics school
c)
Log10(sA +1)
0
2
4
6
Percent
0
20
40
60
80
Sediment
Sa
SaUn
SaAl
LrAl
SaRhAl
SaStAl
SaLrAl
SaCoRhAl
SaStCoRhAl
Sand fish
Loose school
C. sufflamen
Individual demersal fish
Bottom weak fish detection
Shelf-break large fish
Bottom small fish school
Mix reef fish
Shelf-break school
Small pelagics and predators
M. niger
Small pelagics school

Supplementary Figure S3.7. Barplot representing the percentage of ESDU with presence of each assemblage according to (a) the wind exposure (leeward vs. windward); (b) the depth strata, and (c) the sediment. The mean acoustic biomass of each group ($\log10(s_A+1)$) per ESDU (i.e. the total acoustic biomass normalised by the number of ESDU in each side) is represented by diamonds (right y-axis).

3.8. Outlook

This chapter displays some of the possibilities of using the combination of active acoustics and videos for a comprehensive monitoring of an oceanic tropical archipelago. The previous *target strength* estimation for the black triggerfish led to its biomass estimation. This work revisited the IME for fish distribution highlighting the concentration over the shelf-break on the windward side of the island. The shelf-break was emphasized as an important hotspot for fish that might require more attention for conservation. The method we used is an original and innovative way to observe protected marine environments at a broad scale and provided a huge amount of data. All the data acquired during FAROFA is open source and should serve as key information conservation wise.

The third article is the transposition of part of the methods and knowledge acquired over the second article to another important area, the coastal neritic ecosystem of Northeast Brazil.

CHAPTER 4. Demersal and pelagic fish assemblages distribution along the northeast coast of Brazil from active acoustic data

In the previous article, we described fish assemblage's distribution around a tropical oceanic archipelago protected by an extensive no-take zone. In this last article, we now explore the fish distribution in a tropical coastal ecosystem, the Northeast of Brazil shelf. The context is quite different since the Northeaster coast is very densely populated and suffers strong anthropic pressure. Most of the fish landing of e Brazil come from Northeastern fisheries, which are mostly artisanal but still quite impactful. Data on fish distribution is lacking in Northeast Brazil and here we propose to use acoustics to provide comprehensive spatially explicit information on the distribution of fish and fish assemblages.

4.1. Abstract

Tropical coastal ecosystems are essential for human wellbeing but increasingly threatened by anthropic activities. This pressure urges the need for comprehensive data to sustain management. Active acoustics (AC) is a powerful tool for mapping fish distribution and collecting ecological information required for proper management. It has been extensively applied in temperate ecosystems; however, the use of AC remains incipient and challenging in highly biodiverse tropical ecosystems. Here, we use AC methods to describe the horizontal distribution of fish and ecological features in a coastal neritic tropical ecosystem of the South-western Atlantic in Northeast Brazil. Data were continuously collected during day and night in two seasons. Fish scatters were classified into eight fish assemblages according to their characteristics. The spatial distribution of fish biomass varied according to season, depth, and distance to the shelf-break. For both seasons fish acoustic biomass was higher at night revealing changes in the spatial occupation of the water column according to the diel cycle.

Keywords: coastal neritic tropical ecosystem, diel migration, Marine Spatial Planning

4.2. Introduction

Tropical coastal regions (TCRs) host highly productive and diverse ecosystems that are priority areas for conservation, including mangrove forests, seagrass beds, and coral reefs (Harborne et al., 2008; Brooks et al., 2020). These ecosystems are usually connected through the exchange of nutrients and movements of organisms, forming a mosaic of patches and environments crucial for species survival (Nagelkerken et al., 2001; Dorenbosch et al., 2005). For instance, TCRs encompass important spawning, feeding, and nursery grounds for many species that support ecological processes and activities of socio-economic relevance, such as small-scale fisheries (Nagelkerken and Velde, 2004; Shan and Jin, 2016). Therefore, the fate of several species, such as demersal fishes, is primarily tied to TCRs. Worryingly, TCRs are increasingly threatened by climatic changes effects such as temperature increase and ocean acidification (Ramírez et al., 2022). Additionally, anthropic activities resulting in habitat destruction are also detrimental to the life cycle of demersal and pelagic fish, especially to those species using the connectivity between ecosystems to undertake ontogenetic, tidal, and or diel migration (Krumme, 2009). Thus, the impact of climate-induced changes on TCRs needs to be considered alongside other human pressures within the conservation framework (Bertrand et al., 2018).

Ecosystem-based approach to conservation through Marine Spatial Planning requires broad spatially explicit data (Coccoli et al., 2018). The analysis of spatial data and in particular the identification of hotspots is fundamental for ecology and conservation studies (Bartolino et al., 2011; Dale and Fortin, 2014). Hotspots are areas where an out of the ordinary event or phenomenon occurs (Nelson and Boots 2008). Biodiversity hotspots (areas of high species richness) are considered priority areas for conservation on a global scale in both terrestrial and marine ecosystems (Myers et al., 2000; Worm et al., 2005). On the other hand, biological hotspots are localized areas where high abundances of organisms are concentrated, typically reflecting areas of high marine productivity that may be appropriate areas for protection in marine systems (Hooker and Gerber, 2004; Davoren, 2007). Identifying biological hotspots is the first step toward understanding mechanisms that generate the observed spatial patterns (Hazen et al., 2013). Fish populations often comprise the largest biomass component in a productive marine ecosystem and mapping fish aggregation is a common strategy to define priority areas for conservation (Hewitt et al., 2005; Polunin et al., 2009; Godø et al., 2014).

Active acoustics (AC) have an unexploited potential for ecosystem-based studies and respond to the need for ecosystem-scale sensing. Indeed, AC provides an important range of data from physics to biology with high spatial and temporal resolution data throughout the water column (Koslow, 2009; Trenkel et al., 2011). Among others, acoustic methods can be used to characterize habitats and study behaviors such as diel migration and schooling associated with spawning or prey-predator interaction (Bertrand et al., 2014; Benoit-Bird and Lawson, 2016).

Indeed, using multi-frequency acoustic data allows for distinguishing between various groups of organisms, such as different types of zooplankton, swimbladder, and non-swimbladder fish (De Robertis et al., 2010). In temperate ecosystems, AC is a standard method to perform stock assessment and evaluate the spatial and temporal distributions of many commercially important fish species (Simmonds and MacLennan, 2005). AC methods require simultaneous biological sampling (e.g., fishing gears, trawl, diver-based visual census or video) for species identification (McClatchie et al., 2000). Therefore, routine monitoring classically uses acoustic-trawl combination and focuses on temperate pelagic ecosystems where pelagic or demersal fish (e.g., herrings, anchovies, sardines, cod, and walleye Pollock) form single-species school (Nakken, 2008; Kotwicki et al., 2009; Boyra et al., 2013; Demer et al., 2013).

In biodiverse warm tropical waters, fish assemblages are often more diverse than in temperate ecosystems, hampering species-specific acoustic assessment (Kracker et al., 2011; Costa et al., 2014; Campanella and Taylor, 2016; Salvetat et al., 2022). Differentiating between fish with similar morphological and physiological characteristics remains challenging (Korneliussen et al., 2009; De Robertis et al., 2010; Woillez et al., 2012). Another drawback of AC in tropical environments is the difficulty in discriminating fish closely associated with bottom relief from bottom echoes, especially in complex benthic structures such as reefs (Taylor et al., 2006). Moreover, to translate acoustic densities into biologically meaningful abundance or biomass estimates, AC methods require biological sampling to identify and measure the species observed (McClatchie et al., 2000). Indeed, biomass estimates from AC data are calculated using the relationship between the species-specific acoustic reflection (target strength) of a given species and its length (Simmonds and MacLennan, 2005). Given the high biodiversity and sparsity of acoustic studies in tropical regions, those relationships still need to be established for most fish species (Costa et al., 2014). Consequently, the use of AC remains scarce in tropical waters and tends to focus on single species' schools of small pelagic fish or grouper spawning aggregations (Fréon et al., 1992; Paramo et al., 2003; Egerton et al., 2017). In such context, our study presented in Chapter 3 was one of the first to propose a comprehensive spatial distribution of tropical fish assemblages in a tropical oceanic archipelago by combining AC with video data (Salvetat et al., 2022).

Indeed, continuous data on tropical fish spatial distribution is lacking worldwide, specifically in South Western Atlantic waters (Miloslavich et al., 2011). Along the Brazilian coast, the highest landed volume of the country comes from small-scale fisheries on the northeast coast, which is also the largest (3000 km) and one of the most densely populated regions (Nóbrega et al., 2009). Solid governance systems and sustainable resource management through Marine Spatial Planning would help the fishing sector to face human-induced impacts (Bertrand et al., 2018). In that regard, there is a growing need to develop comprehensive studies to understand the complexity of tropical marine underlying processes to support MSP decision tools. Traditionally, fish assemblages in this region are studied mostly through underwater visual censing (UVC) (Ferreira et al., 2004; Feitoza et al., 2005) or based on fishery-dependent data (Frédou and Ferreira, 2005; Silva Júnior et al., 2015) providing discrete data. In contrast, AC has the potential to capture a large panel of continuous information at a large-scale and high-resolution.

To date, only one study used active acoustic data from REVIZEE to investigate the distribution and abundance of fish along the northeastern coast (Weigert and Madureira, 2011). Here we propose to use AC to describe the horizontal fish distribution in a coastal neritic tropical ecosystem of Northeast Brazilian. We use data collected during the acoustic "ABRAÇOS" surveys performed along the Northeast Brazilian coast in two contrasting seasons (Assunção et al., 2020; Dossa et al., 2021) in 2015 and 2017. We provide a comprehensive distribution of fish acoustic biomass and highlight where hotspots occur which is essential for Marine Spatial Planning. Additionally, AC data continuously recorded allows observing the change in schooling behavior along the diel cycle. We also modeled the influence of depth and distance to the shelf-break on fish acoustic biomass. Finally, fish echoes classification in fish assemblages provides a more detailed picture of spatial fish distribution and identifies the more important assemblages.

4.3. Material and Methods

4.3.1. Study area

This study was carried out in the western boundary system of the Tropical South Atlantic (SWAT) along the coast of Northeast Brazil between the latitudes 4.5°S and 9.5°S (Rio Grande do Norte, Paraiba, Pernambuco, Alagoas Brazilian States) (Fig. 4.1). The region is characterized by a narrow continental shelf (20–50 km) and a shelf-break between 40–80 m (Knoppers et al., 1999; Vital, 2014). The hydrodynamic in the region is governed by the western boundary current system, which is dominated by the North Brazilian undercurrent and (NBUC) the North Brazilian current (NBC) (Dossa et al., 2021). Strong trade winds and the presence of the NBUC originated from the bifurcation of the southern South Equatorial Current (sSEC) drive the northward transport of oligotrophic saline tropical water along the Northeastern Brazilian continental shelf (Stramma and Schott, 1999; Lumpkin and Garzoli, 2005; Assunção et al., 2020; Dossa et al., 2021). There are two well-defined seasons driven by rainfall: a dry season from September to February called later ‘spring’ and a rainy season between March and August called later ‘fall’.

4.3.2. Survey design

Data were collected during multidisciplinary surveys ABRAÇOS (Acoustics along the BRAzilian COaSt) 1 and 2, carried out on board the RV Antea (35 m long) respectively between Sep 29th - Oct 21st (spring), 2015 and Apr 8th – May 9th (fall), 2017 (Bertrand, 2015, 2017a). Spring 2015 and fall 2017 are representative of canonical spring and fall conditions in terms of thermohaline structure and current dynamics (Assunção et al., 2020; Dossa et al., 2021). For both cruises, the survey track consisted of cross-shore transects between 15 to 30 nm along the coast. Only data recorded on the shelf (depth smaller than 150 m) were retained.

4.3.3. Trawl data

Sampling was conducted at 37 stations over the northeast Brazilian continental shelf, from Rio Grande do Norte to Alagoas (5°-9°S, Fig. 4.2). Hauls were performed between 15 and 65 m depth, for about 5 minutes at 3.2 kt, using a bottom trawl net (body mesh: 40 mm, cod-end mesh: 25mm, entrance dimensions: 28 x10 m); see Eduardo et al. (2018) for further information on sampling procedures. The spatial coverage was alike in both cruises, except for the extreme north area of Rio Grande do Norte, which was only sampled in the second cruise. Tow duration was considered as the moment of the arrival of the net on the pre-set depth to the lift-off time, recorded using 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. Hauls were performed during the day.

The relative indexes of density and biomass (catch per unit of effort – CPUE) were calculated considering the number of individuals and the weight of fish caught per trawled area (ind.km^{-2} – kg.km^{-2}). The trawled area was estimated by multiplying the distance covered by the net through the bottom (in m) with the estimated gear mouth opening obtained through the SCANMAR sensors. In six trawls, the SCANMAR system was not operative, and the average mouth opening (13 m) was used.

Temperature, salinity, and oxygen profiles were collected for each haul using a CTDO (model: SeaBird911). Bottom temperatures were higher during the second survey performed in the fall but overall ranged from 25.5°C to 29.6°C (mean 27.5°C), while salinity and dissolved oxygen varied from 36.4 to 37.5 (mean 36.9) and 4 $mg.l^{-1}$ to 4.4 $mg.l^{-1}$ (mean 4.2 $mg.l^{-1}$), respectively.

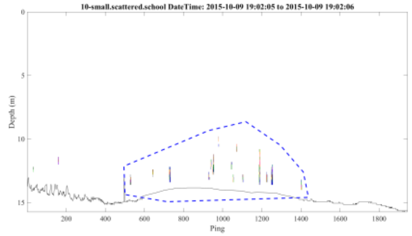
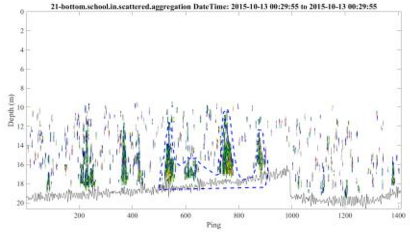
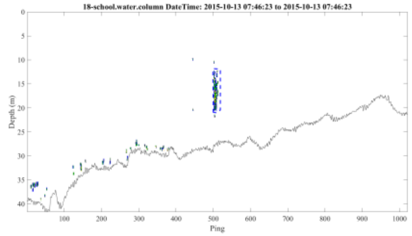
1.1. Acoustic data

Acoustics data were collected continuously along the survey track with a mean vessel speed of 8.5 knots using a Simrad EK60 (Kongsberg Simrad AS) split-beam scientific echosounder at 38, 70, 120, and 200 kHz being interrupted only for fishing hauls and environmental data collection. The echosounder was previously calibrated using a tungsten carbide sphere (Foote, 1987). Raw files were converted to HAC files using Hermes software (McQuinn et al., 2005; Trenkel et al., 2009). Processing was completed using Movies3D software (Trenkel et al., 2009) and Matecho tool (Perrot et al., 2018) to extract the noises, correct the bottom line and for visual scrutinizing. The first 5 m from the surface were excluded to eliminate the near field and the influence of absorption and propagation (Vargas et al., 2017). The result was a matrix (for each frequency) of mean volume backscattering strength (MVBS, in dB re 1 $m^2.m^{-3}$) in two dimensions: vertical samples each 0.2 m and horizontal samples each ping (~1 s) (Vargas et al., 2017).

Fish-like scatters were extracted with a multifrequency algorithm using thresholds on sums and differences of MVBS at the four frequencies deployed (Vargas et al., 2017). For data above 200 m, a threshold over the sum of the four frequencies was used $MVBS_{38+70+120+200} \geq -247$ dB combined with a sum of two frequencies $MVBS_{38+200} \geq -111$ dB. In case $MVBS_{38+200} < -111$ dB when $MVBS_{38+70+120+200} \geq -247$ dB than a threshold on the difference was used $MVBS_{38-70} \geq -4$ dB. Convolutions were used to refine the discrimination and retrieve fish-like scatters from non-fish-like scatters.

The resulting fish-like scatter matrix was used to manually assign a label to all fish-like echoes (Table 4.1). Labelling followed the methodology from (Salvetat et al., 2020a) and was based on characteristic structures in echograms. Indeed, consistent fish assemblages with characteristic echotypes were observed on echograms and eight fish assemblages were defined (Table 4.1). Fish assemblages were identified according to their shapes or the shape of the bottom line. In the echograms, fish were observed individually (Individual demersal fish), forming schools (School, Bottom school, shelf-break school) or aggregations (aggregation, mix reef fish, shelf-break demersal aggregations, shelf-break pelagic aggregations) (see Table 4.1). Three fish assemblages were defined according to their position at the shelf-break, where the bottom-line slope changed sharply (shelf-break school, shelf-break demersal aggregations, shelf-break pelagic aggregations). Mix reef fish correspond to fish above an irregular bottom line. Among schools, some were more than 10 m high and were most likely to be small pelagics. Trawl performed simultaneously with acoustics records served to attribute potential species for the composition of the different assemblages (Table 4.1). For both cruises, 38 kHz fish-like echograms were labelled manually by the same operator using the software Matecho (Perrot et al., 2018), which allows drawing polygons to encompass scatters corresponding to a given assemblage. All fish-like echoes inside a polygon were allocated to a given assemblage.

Table 4.1. Description of labels used to identify the fish assemblages from echotypes

Label name	Example of ecogram	Characteristics	Fish sampled by bottom trawl
School	  	Group of elongated compact schools. Some schools were more than 10 m of height, characteristic of small pelagic fish schools.	Small pelagics : *Chirocentrodon bleekerianus* *Chloroscombrus chrysurus* *Eucinostomus gula* *Eucinostomus argenteus* *Diapterus rhombeus* *Selene sp* *Lycengraulis grossidens* *Opisthonema oglinum* *Selar crumenophthalmus*

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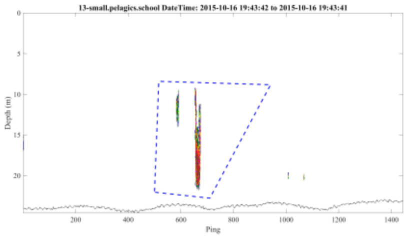

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<td>Individual demersal fish</td>
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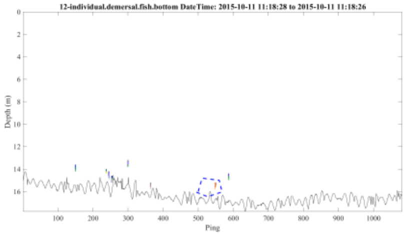

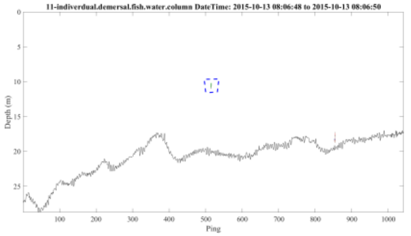

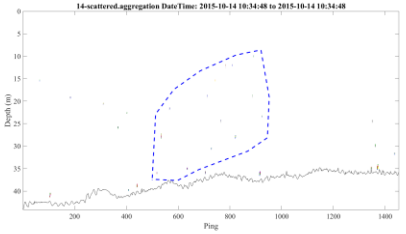

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<td>Individual fish over the bottom or in the water column.</td>
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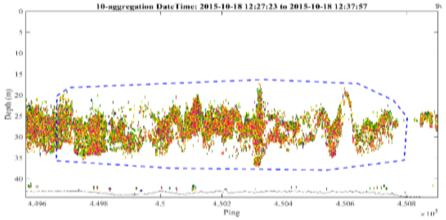
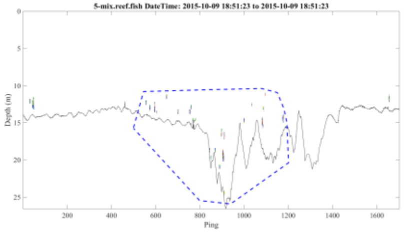
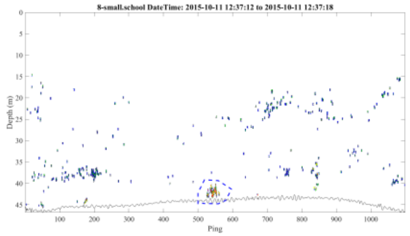
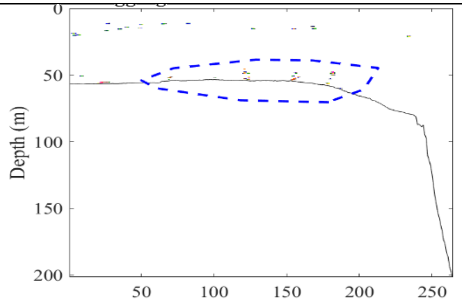
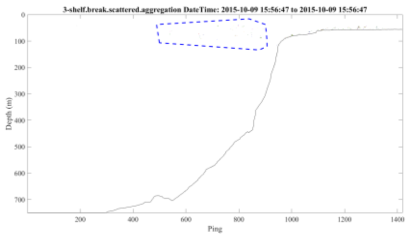
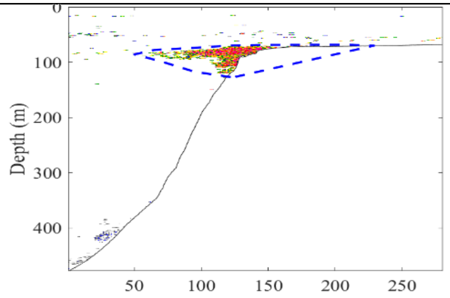
Aggregation		Fish aggregation forming dense layers.	
Mix reef fish		Fish schools and shoals over complex bottom structure formed by coral or rocky reefs.	*Acanthostracion polygonius* *Acanthostracion quadricornis* *Anisotremus virginicus* *Calamus calamus* *Cantherhines pullus* *Chaetodon striatus* *Chilomycterus spinosus* *Diodon holocanthus* *Fistularia tabacaria* *Haemulon aurolineatum* *Haemulon squamipinna* *Halichoeres dimidiatus*

			Lutjanus analis *Lutjanus synagris* *Monacanthus ciliatus* *Myripristis jacobus* *Ocyurus chrysurus* *Pseudupeneus maculatus* *Pomacanthus paru* *Scorpaena brasiliensis* *Stephanolepis hispidus*
Bottom school		School close to the bottom	
Shelf-break demersal aggregations		Demersal fish aggregations close to the shelf-break.	

Shelf-break pelagic aggregations		Scattered fish close to the shelf-break.	
Shelf-break school		Demersal fish school associated to the edge or the slope of the shelf-break.	

To study the horizontal distribution of fish-like scatters, we used the Nautical Area Scattering Coefficient (NASC or s_A, in $m^2.nm^{-2}$), an acoustic biomass index integrated over the water column. Only the 38 kHz frequency was used. The overall fish-like acoustic biomass and the fish-like acoustic biomass of each fish assemblage were echointegrated over the water column by one kilometers-long elementary sampling distance unit (ESDU).

Horizontal distribution of fish-like acoustic biomass was interpolated outside acoustics transects using ordinary kriging (Chiles and Delfiner, 2009). RGeostats package in R (Petitgas et al., 2017; ParisTech, 2020) was used to model data variograms for both cruises. Bi-directional variograms were used (see Fig. S4.1) with the north-south direction representing the along-coast direction and the east–west direction the cross-shelf direction of the transects.

To avoid spatial autocorrelation in statistical tests, fish-like acoustic biomass was averaged in a grid of 0.05 x 0.05 degrees (Fig. 4.1). Non-parametric Kruskal-Wallis and *ad hoc* Dunn tests were used to test for difference in fish acoustic biomass between night and day. Additionally, to evaluate nonlinear relationships between fish-like acoustic biomass and the bottom depth (m) or the distance to the shelf-break (in km), we used Generalized Additive Models (GAMs). GAMs were constructed using the R package ‘mgcv’ (Wood, 2011).

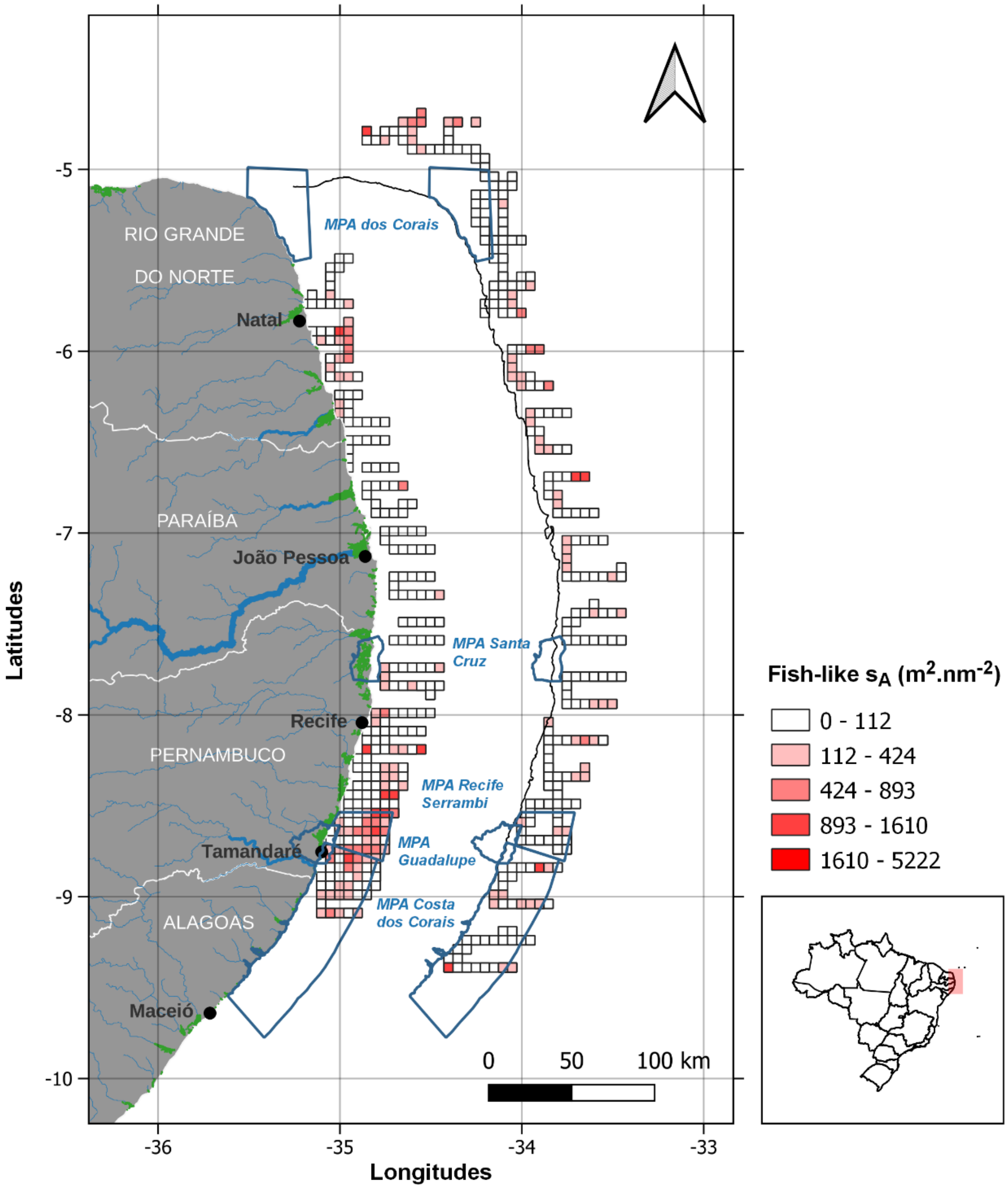


Figure 4.1. Study area and fish-like s_A averaged in a 0.05 x 0.05 degrees grid for ABRAÇOS 1 (left) and 2 (right); the coastline is repeated and represented by a solid black line for ABRAÇOS 2. MPAs limits are represented by solid blue lines. Mangroves are represented in green and rivers in blue with the width of the line proportional to the size of the river.

4.4. Results

Fish catches from bottom trawls revealed the presence of hotspots over the Brazilian Northeastern shelf (Fig. 4.2). The highest CPUEs (in abundance and biomass) were found in one station in the north of Rio Grande do Norte (5°S). In addition, high CPUEs were observed in various stations over the central and south parts of the Pernambuco shelf (8-9°S) when compared with the Paraiba shelf and the north part of the Pernambuco shelf.

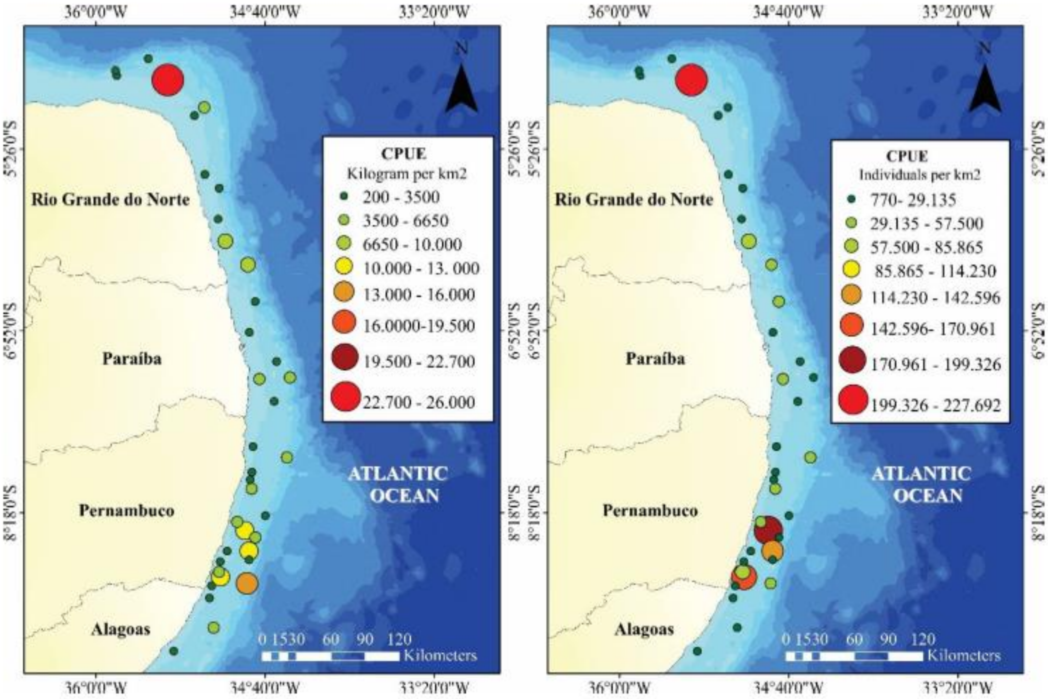


Figure 4.2. Values of catch per unit of effort (CPUE; ind.km^{-2}; kg.km^{-2}) along the study area for both surveys.

The spatial distribution of fish-like acoustic biomass provides continuous information along the survey track and the diel cycle. The distribution of fish-like acoustic biomass was heterogeneous with the presence of several hotspots located in areas varying according to the season (Fig 4.3).

In spring (Fig. 4.3a), two main hotspots were observed, one in the shelf of Rio Grande do Norte south of the city of Natal (6°S - 6.5°S) and a more extensive one in the south in the shelf of Pernambuco state, particularly in front of the city of Tamandaré (7.8°S - 9.2°S). The lowest fish-like acoustic biomass was observed north of Natal (<6°S) and on the shelf of Paraiba (6.5°S - 7.8°S) with, however, two small hotspots over the shelf-break at night.

In the fall (Fig 4.3b), transects extended further north over the shelf of Rio Grande do Norte where we observed a hotspot (5°S) not sampled during the spring survey. The distribution of fish-like acoustic biomass was more homogenous than in spring. As in spring, a hotspot was present south of Natal although it extended further south down to João Pessoa (6°S-7°S). As in spring, the lowest fish-like biomass was found north of Natal (5°S-6°S) and at the transition between the state of Paraiba and Pernambuco (7.5°S). Although less dense, several hotspots were observed in the shelf of Pernambuco fall, south of Recife (8°S-8.5°S) and further south at the transition between Pernambuco and Alagoas state (9°S).

Fish-like acoustic biomass was higher during transect performed during the night than the surrounding transects performed during the day; except for one transect in the fall performed at night located at the transition between Paraiba and Pernambuco shelf (7.5°S). Note that the hotspot in Rio Grande do Norte in fall (5°S) was sampled during the day, only.

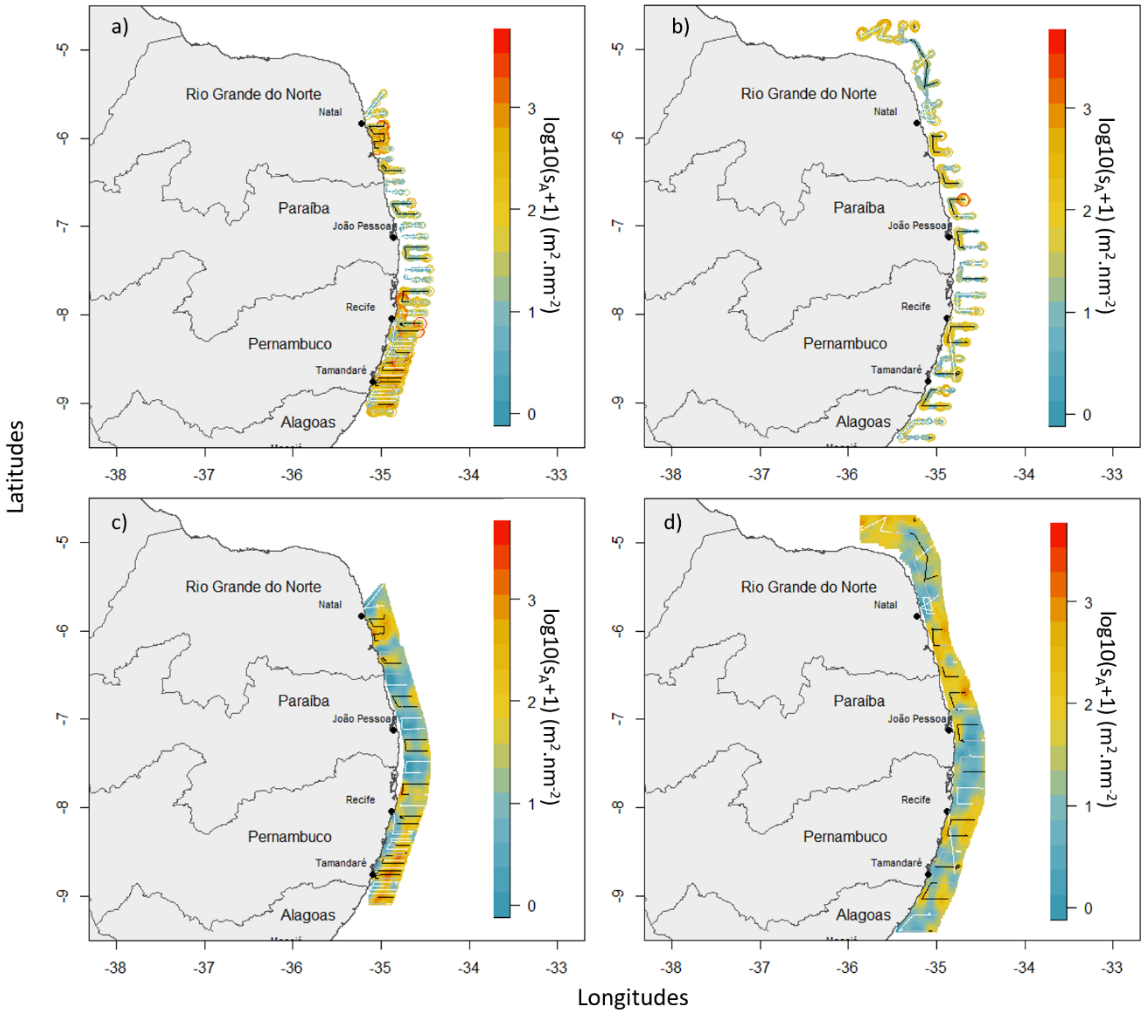


Figure 4.3. Horizontal distribution of fish-like acoustic biomass along transects for spring (a) and fall (b). Geostatistical interpolation of fish-like (c) echoes for spring (a) and fall (b) using kriging. Solid black, white and grey lines represent the transects made during the night, day, and transition phases (sunrise and sunset), respectively.

During the day and fish-like acoustic biomass was not significantly different according to the survey (p=0.389) (Fig. 4.4). At night, fish-like acoustic biomass was significantly higher in spring than in fall (p<0.01). For both surveys, fish-like acoustic biomass was significantly higher at night than during the day (p<0.01).

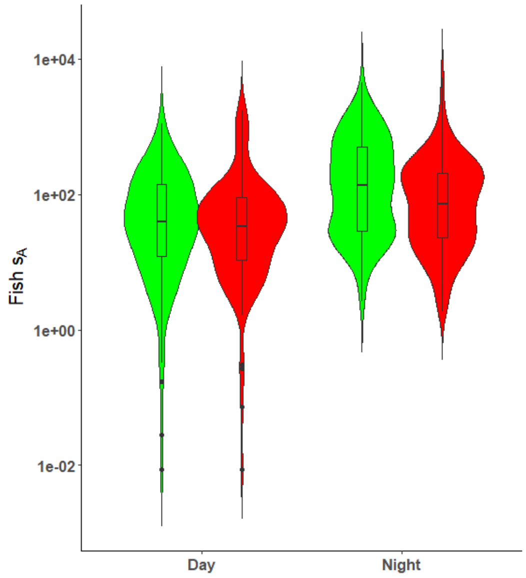


Figure 4.4. Violin plot containing boxplot representing the median (horizontal line), interquartile range, whiskers, and outlying points of fish-like acoustic biomass (s_A) for both cruises and during day and night for spring (green) and fall (red). The y-axis scale is logarithmic.

Fish-like acoustic biomass varied differently with the distance to the shelf-break (Fig. 4.5a-b) and bottom depth whatever the season or the diel period (Fig. 4.5c-d). For both spring and fall, the deviance was better explained by the bottom depth than by the distance to the shelf-break (Table 4.2). During the day in spring, fish-like acoustic biomass increased as we approached the shelf-break. During the day in the fall, the model showed an increase with a local maximum around 35 km then a decrease with a local minimum between 10-20 km and a rapid increase as we approached the shelf-break. At night in spring, fish-like biomass was higher far from the shelf-break (30 km) and decreased before increasing when approaching the shelf-break. At night during fall, the model response to the distance to the shelf-break was flat with a slight increase close to the shelf-break.

Concerning bottom depth (Fig. 4.5c-d), fish-like acoustic biomass peaked around 40 and 70 m during the day in spring. During the day in the fall, fish-like acoustic biomass increased with bottom depth. At night in spring, fish-like acoustic biomass increased with the bottom depth with a local maximum around 50 m which corresponds to the shelf-break. At night this pattern was accompanied by local minimums at 40 m and 60 m; a local maximum was observed at the shelf-break around 50 m depth.

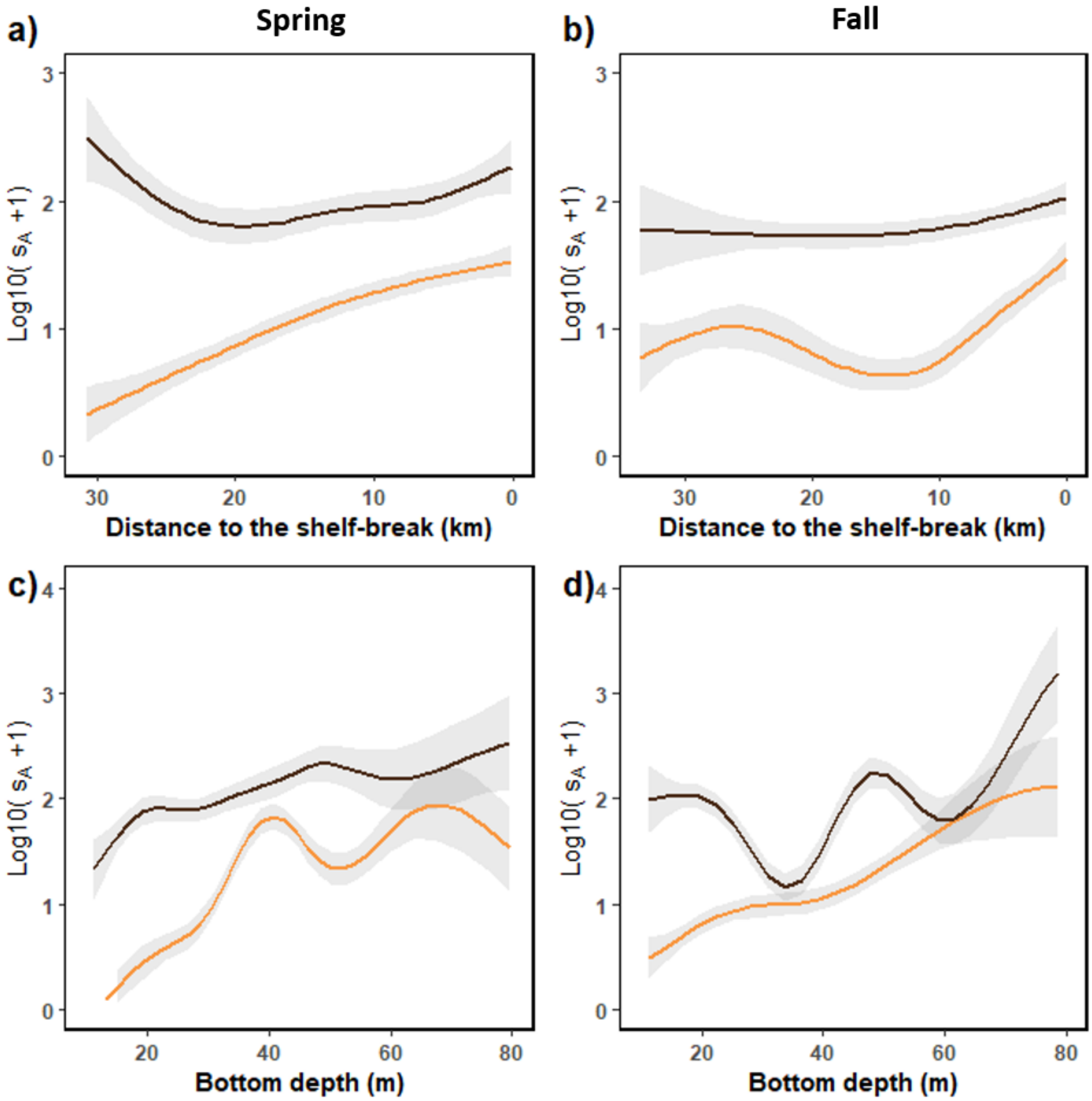


Figure 4.5. Generalised Additive Models (GAMs) results describe the variation of fish biomass according to the distance to the shelf-break for both period day (in orange) and night (in brown)

and both cruises (spring and fall). Solid lines represent smoothed mean relationships from GAM’s and shaded areas are 95% confidence intervals.

Table 4.2. Statistical summary of generalised additive models between the fish-like acoustic biomass (s_A) and two parameters: distance to the shelf-break (distSB) and bottom depth (depth). R^2 is the adjusted proportion of total variability explained by the model; GCV: generalised cross validation score; edf: effective degrees of freedom. All models had a p-value < 0.01.

Survey	Model	R^2	GCV	Deviance explained	Period	edf
ABRACOS 1	Log10(s_A+1) ~ Period + (**distSB**, by= Period)	0.29	0.61	29.5%	Day	2.0
					Night	3.9
	Log10(s_A+1) ~ Period + (**depth**, by= Period)	0.40	0.51	41.2%	Day	8.1
					Night	6.9
ABRACOS 2	Log10(s_A+1) ~ Period + (**distSB**, by= Period)	0.32	0.45	32.8%	Day	4.3
					Night	2.0
	Log10(s_A+1) ~ Period + (**depth**, by= Period)	0.41	0.39	42.3%	Day	5.6
					Night	8.6

In echograms, fish displayed different structures according to the diel period. During the day, we observed a patchy distribution of dense schools (Fig. 4.6a), individual fish and or fish aggregations close to the bottom (Fig. 4.6b). However, at night we observed scattered fish higher in the water column (Fig. 4.6c), sometimes forming dense scattered aggregations (Fig. 4.6d).

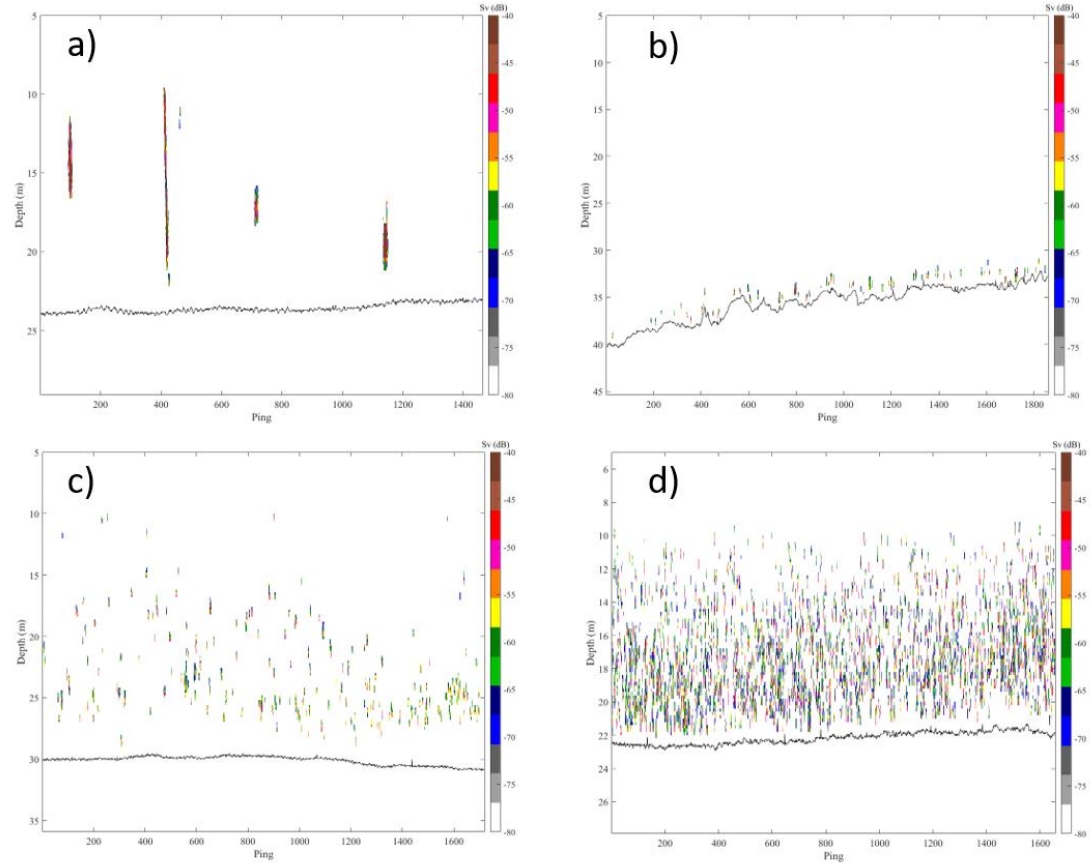


Figure 4.6. Typical fish echograms representing the shoaling structures during the day (a,b) and the night (c,d).

The distribution of fish-like acoustic biomass varied according to the diel period (Fig. 4.7). In both cruises the assemblages School, Mix reef fish and Bottom school had significantly higher values during the day. The other assemblages presented an opposite pattern with significantly higher values at night. At night, Aggregation and Shelf-break school dominated while during the day fish-like acoustic biomass was more evenly distributed among fish assemblages.

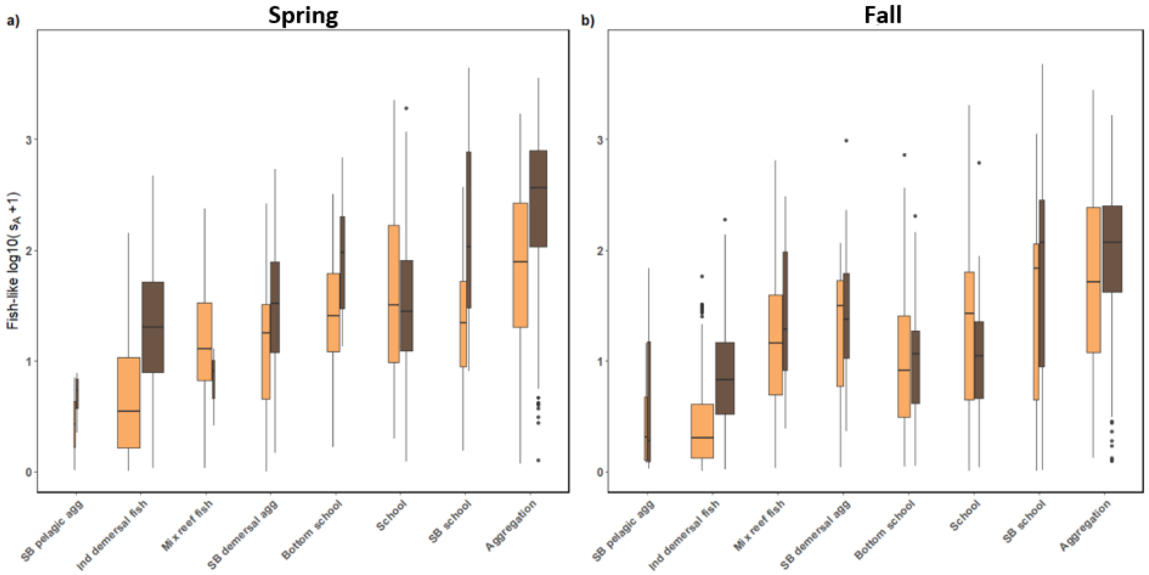


Figure 4.7. boxplot representing the median (horizontal line), interquartile range, whiskers and outlying points of the acoustic biomass of fish assemblages during the day (in orange) and the night (in brown). SB: Shelf-break; agg: aggregation; Ind: individual.

The echoes classification into 8 fish assemblages revealed finer spatial patterns (Fig. 4.8). The assemblages Aggregation, Bottom school and School had a spatial distribution similar to the overall fish-like acoustic biomass in spring and fall. The distribution of individual demersal fish was relatively even along the track of both surveys. In spring, Mix reef fish spatial distribution was restricted to the shelf of Pernambuco while spread all across the survey in fall. Mix reef fish were identified predominantly during the day. Shelf-break demersal aggregation Shelf-break school and Shelf-break pelagic aggregation were, by definition, distributed at the shelf-break. Shelf-break school exhibited high biomass at night over the Pernambuco shelf in spring and over the Paraiba shelf in fall.

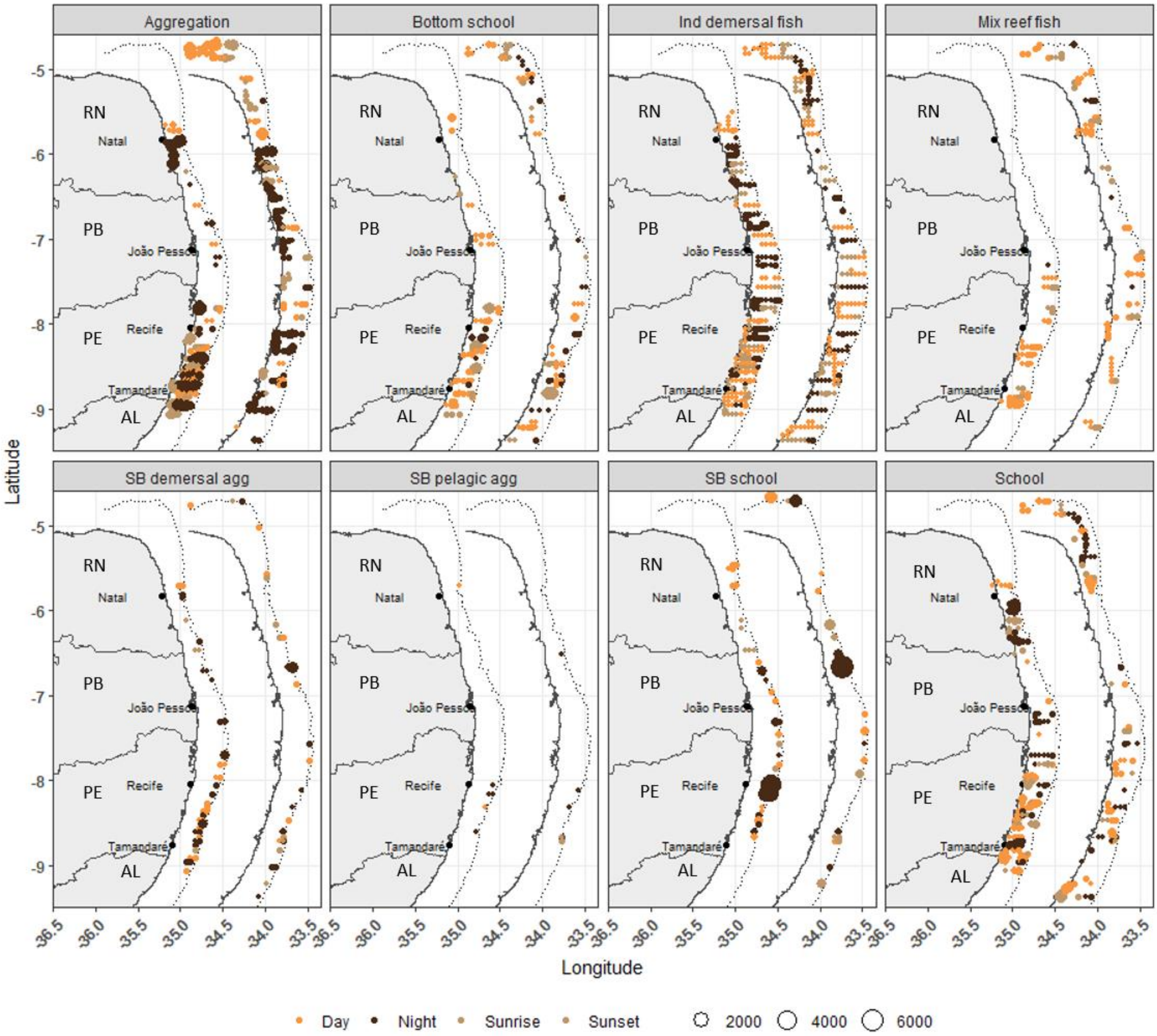


Figure 4.8. Spatial distribution of fish assemblages represented by dots. Dot sizes are proportional to fish-like acoustic biomass (in s_A) and plotted in different colours according to day (orange dots), night (brown dots) and transition phase (sunrise and sunset in beige). The coastline is repeated and represented with a solid black line. The 150 m isobath is repeated and represented with a dotted black line. SB: Shelf-break; agg: aggregation; Ind: individual. RN: Rio Grande do Norte, PB: Paraíba; PE: Pernambuco; AL: Alagoas.

4.5 Discussion

This study is one of the first attempts to map the spatial distribution of multi-specific fish assemblages in a tropical coastal environment using AC. More specifically, we provide the spatial distribution of the acoustic biomass of a variety of fish assemblages in austral spring and fall along the northeast Brazilian coast. Based on that, we point to priority areas for conservation and evaluate seasonal ecological variabilities. Additionally, we test for the efficiency of acoustic tools in ecological assessments (fish acoustic biomass according to bottom depth, distance to shelf-break and diel migration) off tropical coastal regions.

Fish hotspots

The image of the spatial distribution of fish biomass inferred from AC and trawls was similar. Both revealed hotspots in the central and southern part of the Pernambuco shelf and in Rio Grande do Norte (Figs. 4.2 and 4.3). However, the continuous coverage of AC offers more comprehensive continuous and high-resolution observations, providing spatial and temporal data, which cannot be achieved by conventional sampling methods (Stockwell et al., 2006, 2007; Godø et al., 2014). Acoustic surveys also cover a much greater area per unit of time, which makes them more time and cost-efficient and allows large spatial ranges to be studied (Mackinson et al., 2004; Trenkel et al., 2011). Another advantage, AC are not hampered by issues such as water clarity, strong currents or diver depth limits. AC sample continuously along the diel cycle enabling the study of structural changes in the vertical fish distribution in the whole water column along the diel cycle. Still, AC methods are non-invasive and non-extractive whereas bottom trawling is destructive and cannot be used over a protected area and structurally complex substratum like coral or rocky reefs (Taylor et al., 2006; Jones et al., 2012). In addition, it is known that trawling tends to underestimate fish biomass and abundance because of net avoidance (McClatchie et al. 2000) and depth-dependent distribution patterns such as diel migration (Stockwell et al., 2006, 2007).

However, AC cannot discriminate echoes from fish close to the seabed with echoes from the bottom substrata, which exclude some of the demersal fish and most benthonic ones (Mackinson et al., 2004; Rooper and Zimmermann, 2007). Furthermore, to produce accurate biomass estimates, AC methods require ground-truthing (McClatchie et al., 2000). Indeed, AC needs to be coupled with biological sampling to gain species-specific information and for the most accurate calculations of fish lengths and weight (Simmonds and MacLennan, 2005). Trawls allow us to identify and measure fish species, which cannot be done with AC. In areas where trawl is prohibited, video acquisition can be used (Salvetat et al., 2022). A previous study based on ABRACOS data showed that no differences were observed in the assemblage structure identified by trawling or video but differences were observed in fish catchability depending on fish swimming capacity (Barros et al., 2021). Video on the other hand allowed observing the trawling impact on tubular sponges and large branching (Barros et al., 2021).

Seasonal difference

In the study area, spring is a dry season whereas fall is a rainy season, which intensifies river discharges and results in nutrient inputs in coastal waters that increase primary production (Neto et al., 2015; Farias et al., 2022). However, the continental drainage in the region is low and does not reach beyond 16 km offshore (Castro et al., 2006). Furthermore, as a western boundary current system, the northeastern region is under the influence of strong coastward currents carrying oligotrophic oceanic water over most of the shelf (Brandini et al., 1997). Physical variables (e.g. salinity, temperature, oxygen) sampled during the surveys varied between the seasons but were homogenous inside each survey (Assunção et al., 2020; Dossa et al., 2021) over the shelf. The fish acoustic biomass hotspots were roughly consistent between seasons mainly off Natal (spring: 6°S - 6.5°S; fall: 6°S-7°S) and Pernambuco (spring: 7.8°S – 9.2°S; fall: 8°S-8.5°S). However, in spring, the distribution of fish acoustic biomass showed a clear gap between the northern and southern hotspots separated by an area of lower fish biomass, while the distribution was more homogenous in fall. This might be due to a seasonal change in the current intensity. Indeed, using ADCP data from both ABRACOS surveys Dossa et al. (2021) showed that NBUC is weaker during spring than during fall particularly south of 7.5°S over the Pernambuco shelf. This seasonal change in hydrodynamics had an impact on observed cnidarian communities that were oceanic communities over the whole shelf during fall whereas a different pattern was observed in spring with oceanic communities north of 7.5°S and a co-occurrence of coastal and oceanic communities south of 7.5°S in spring (Tosetto et al., 2022).

Topography effects

Overall fish biomass was high at the edge of the shelf-break or at depth concomitant with the shelf-break. This confirms that shelf-breaks are important hotspots for fish biomass (Reid, 2001; Olavo et al., 2011; Eduardo et al., 2018; Salvetat et al., 2022). The sudden change in water depth causes a constriction of the current flow and creates turbulent mixing enhancing primary productivity and therefore attracting prey and predators (Kämpf, 2012; Thévenin et al., 2019; Silva et al., 2022). It concentrates diverse fishing resources over a relatively narrow area, sustaining important multi-specific reef fisheries. Such a pattern is similar to what occurs on the windward side of oceanic islands (Salvetat et al., 2022). Shelf-breaks are also the point of encounter of spawning events of different species of commercially important fish (Frédou and Ferreira, 2005; Heyman and Kjerfve, 2008; Paxton et al., 2021).

There is a hotspot on the Pernambuco shelf that is part of the Pernambuco plateau, a large region of hyper-extended continental crust that extends to approximately 3000 m isobaths (Buarque et al., 2017). Pernambuco plateau exhibits a complex topography with basement lows and highs (Magalhães et al., 2014; Buarque et al., 2016) and displays a system of shelf valleys incised into the continental shelf (Camargo et al., 2015; Silva et al., 2022). Pernambuco plateau shelf valleys and canyons in that region are important morphological features that generate upwelling (Silva et al., 2022). Those shelf valleys are well-known fishing grounds among the local fishers (Camargo et al., 2015; da Silveira et al., 2020).

There is another hotspot on The Rio Grande do Norte eastern shelf. That shelf is 14-30 km wide and reaches its narrowest point adjacent to Natal and widening particularly in the northern sector in the Touros High area where it extends to 75-90 km (Vital et al., 2010). The continental shelf adjacent to Natal also has a complex topography with the Potengi River canyon that is located in front of Natal (Gomes et al., 2020) that might enhance productivity through topography-current interaction in a similar way then in Pernambuco Plateau.

Diel changes in fish behavior

Acoustic transects performed continuously along the diel cycle provide a complete picture of fish behavior. Fish acoustic biomass significantly increased at night in both cruises; while there was no significant variation between spring and fall overall fish biomass during the day. Higher acoustic fish biomass during the night is a classic pattern (Rose, 1992; Fréon et al., 1993; Aglen, 1994; Domínguez-Contreras et al., 2012). Echogram scrutinizing revealed different acoustic landscapes between days and nights with changes in schooling structures. The unique previous study that used AC in this area also observed a significant increase in fish biomass average during the night (Weigert and Madureira, 2011).

Many fish species perform diel migration and the most common pattern being fishes located close to the bottom during the day and higher in the water column at night (Beamish, 1966; Atkinson, 1989; Gauthier and Rose, 2002). Most adult clupeoid and other small pelagic fish species undergo vertical migrations toward the surface at night and disperse (Nilsson et al., 2003; Krutzikowsky and Emmett, 2005; Davoren et al., 2006; Zwolinski et al., 2007). Generally, during the day, they form dense schools to enhance their foraging on mobile prey and they disperse at night because the small-scale collective organization is generally inhibited by low light intensity (Fréon and Misund, 1999). However, some species might adapt their schooling behavior in function of their prey ability. For instance, the Peruvian anchovy (*Engraulis ringens*) has been observed to adopt opportunistic behavior depending on prey availability and feed both during the day and during the night (Bertrand et al., 2008; Espinoza and Bertrand, 2008). While the South Pacific jack mackerel (*Trachurus murphyi)* was observed performing an opposite pattern, forming dense schools to forage on prey during the night and dispersed during the day. Those important migrations and changes in fish schooling behavior according to the diel cycle have a significant impact on acoustic data (Hjellvik et al., 2004; Knudsen et al., 2009). Because part of the fish such as small pelagics is organized in dense fish schools during the day and dispersed at night in larger loose aggregations (Fig. 4.6 c, d) the same fish species occupy more space at night. These changes in the density of fish distribution increase the fish acoustic biomass during the night while not reflecting an actual increase in fish real biomass (Aglen, 1994; Vaz Velho et al., 2010).

Assemblages

To date, Weigert and Madureira, 2011 was the unique study that investigated the fish distribution and abundance in this region using active acoustics. Using the 38 kHz frequency, they classified the echotraces into five functional echo-types (Neritic; Oceanic layer; Myctophidae; Oceanic layer with Myctophidae; and Shelf Break Plume). These echo-types were associated with different species assemblies, mainly small pelagic fishes including micronekton organisms, epi- and mesopelagic organisms with a predominance of Myctophidae and small squids of the Enoploteuthidae family. Here we provide a more detailed classification of the neritic data with 5 fish assemblages on the shelf and 3 pelagic fish assemblages over the shelf-break. This classification can be used to train artificial intelligence for later automatized classification of fish acoustic data (Brautaset et al., 2020; Handegard et al., 2021; Sarr et al., 2021).

Fish forming the assemblages Aggregation, Bottom school and School contributed the most to the overall fish distribution. At night, Aggregation and Shelf-break school were the most important assemblages in terms of fish acoustic biomass. Shelf-break schools are possibly spawning aggregation (Frédou and Ferreira, 2005; Heyman and Kjerfve, 2008; Paxton et al., 2021) or feeding aggregation of nocturnal planktivorous fish taking advantage of the particle flux due to topography-current (Genin, 2004).

A previous study conducted on the oceanic island Fernando de Noronha (Pereira et al., submitted) showed an opposite pattern with an important decrease in fish biomass during the night. The difference can be explained by the difference in the fish species communities. At Fernando de Noronha, the fish community is dominated by the reef fish *Melichthys niger* (Salvetat et al., 2022) which exhibit diurnal behavior and sleeps on the bottom at night (Brewin et al., 2016).

In ABRAÇOS, trawls revealed the presence of different species known to display a diel behavior in particular nocturnal species such as species from the genders Lutjanus and Haemulon but also goatfish and squirrelfish (Meyer and Schultz, 1985; Nagelkerken et al., 2000; Krumme, 2009; Hitt et al., 2011b). Among those, 3 species of the gender Haemulon (i.e. *H. aurolineatum, H. plumierii,* and *H. squamipinna)* were present in most or all areas and were classified as more abundant and frequent for both ABRAÇOS surveys (Cardoso de Melo et al., 2020). Haemulidae are broadly distributed through the Northeast coast of Brazil due to the complex habitat present in this region. Moreover, the grunts family are known to rest over coral colonies during the day and to activate at night feeding on mobile invertebrates in surrounding seagrass beds (Krumme, 2009) and might be responsible for the increase in fish acoustic biomass during the night. Haemulidae (grunts) are suspected to constitute an important part of fish assemblages thus they might display different conformations and fall into different fish assemblages in our classification (Schools, Bottom schools, Aggregations and Individual demersal fish).

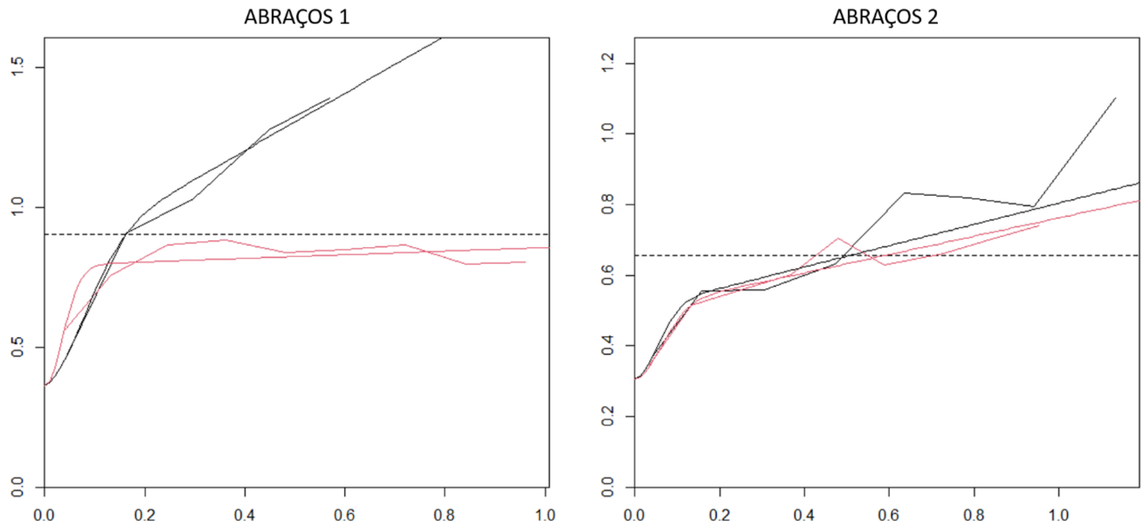
Perspectives for MSP

Brazilian reefs are a conservation priority in the Atlantic Ocean due to high endemism levels (about 25% in fish and 50% in corals) that are concentrated in only 5% of West Atlantic reefs (Moura, 2000). The northeast region is known to host abundant coral reefs (Castro and Pires, 2001; Leão et al., 2016), which motivated the establishment of several MPA in the region but they are multiple-use MPA with a low level of protection (Floeter et al., 2006; Pereira et al., 2021) (Fig. 4.1). Vila-nova et al., 2014 highlighted that the northeast coast, from the state of Paraíba to central northern Bahia (~15°S), had the highest scores of richness in shallow waters (around 10 m). They also emphasized that although there are some very small no-take zones within some multiple-use MPAs in Northeast Brazil, their total area is insufficient when compared to the reef sizes and human pressures (fishing, tourism, urbanization, etc.) existent there (Freire and Pauly, 2010; Freitas et al., 2011). Part of the Pernambuco fish acoustic biomass hotspots falls in two multiple-use MPA with a low level of protection that covers almost the entire shelf, Costa dos Corais and MPA Recife Serrambi. Costa dos Corais is the largest Brazilian coastal multiple-use MPA (135 km along the coast) and covers almost the entire shelf in the south part of Pernambuco and the north part of Alagoas. Only the south part of the shelf of Pernambuco is protected within those two MPA while the biomass hotspot extends in the north up to Recife at 8°S. On the other hand, the extended sampling design in the fall revealed a fish acoustic biomass hotspot in Rio Grande do Norte coastal waters overlap with a biodiversity hotspot revealed by Fonseca et al., 2017. This hotspot falls outside another extended MPA called APA dos Corais. MPA does not completely include either the whole shelf-break nor its mesophotic reefs of fishing activities despite being known as an important spawning aggregation hotspot (Camargo et al., 2015; da Silveira et al., 2020).

4.6. Conclusion

This study is one of the first attempts to describe the spatial distribution of overall fish assemblages using active multifrequency acoustics methods in tropical coastal areas. Indeed, applying fisheries acoustics to assess demersal fish in tropical coastal environments is rarely done for multispecific fish assemblages. Little seasonal variation was observed in the spatial distribution of hotspots. This study goes beyond the definition of fish spatial hotspots with the classification of height fish assemblages. AC methods allowed the rapid acquisition of quantitative spatially explicit data across broad extents to identify both hotspots and areas of low fish occurrence, which is essential information for prioritizing areas of conservation. However, accessing ground truth with biological sampling is mandatory to produce accurate biomass estimation and further studies are needed to estimate the fish biomass.

4.7. Supplementary material



Supplementary Figure S4.1. Bi-directional variogram for both surveys. Direction cross-shelf (west-east, in black) and along the coastline (south-north, in red).

4.8. Outlook

This third article provides a map of the spatial distribution of overall fish acoustic biomass for the Brazilian Northeast coastal neritic environment. Fish acoustic biomass is a proxy of fish biomass but knowledge of specific species' target strength is necessary to provide a precise estimation. The classification of fish echoes in several assemblages based on the shape of fish echoes reflects fish behavior. At night, the conformation of fish in aggregations intensifies which significantly increases the acoustic biomass but might not reflect a real increase in fish biomass.

CHAPTER 5. General Conclusion

5.1. Wrap Up

The present thesis aimed at describing two tropical ecosystems using acoustic data. This was achieved through the completion of three main sub-goals separated into three articles. The first two articles focussed on the oceanic archipelago of Fernando de Noronha using a combination of optics and acoustic data. The third article focussed on the shelf of Northeast Brazil using acoustic data and trawls.

This thesis represents one of the first attempts to describe multispecies tropical ecosystems using acoustics. There are few previous attempts such as Campanella and Taylor (2016) and Costa et al. (2014) in the Virgin Islands; White et al. (2022) in the Gulf of Mexico; Egerton et al. (2018) and Villalobos et al. (2021) in Mexico; Gastauer et al., 2017 in Northern Australia; Domokos (2021) and Benoit-bird et al., 2003 in Hawaii. Those studies usually consider the overall fish acoustic biomass or just one or a few targeted species. The novelty of this study is to consider the overall fish acoustic biomass classified in fish assemblages. We also proposed an original innovative method combining acoustic and video as a non-invasive, non-extractive method adapted to monitor protected areas (Chapters 2 and 3).

The first article was devoted to estimating the target strength of two key species in Fernando de Noronha, the black triggerfish *Melichthys niger* and the ocean triggerfish *Canthidermis sufflamen*. The black triggerfish has been observed in quantity around numerous oceanic islands and we identified that species as the most observed species of Fernando de Noronha. We used video to identify the species aggregations and their shoaling loose conformation allowed us to perform a tracked TS extraction on each individual fish. TS information on tropical fish remains very scarce although there are some studies with TS estimates of commercially important species such as lutjanidae (Benoit-Bird et al., 2003) or groupers (Linares et al., 2013; Egerton et al., 2017). The TS estimation we provided is novel and a mandatory prerequisite to estimate the black triggerfish biomass in Article 2.

The combination of the three surveys around the oceanic archipelago of Fernando de Noronha resulted in an extensive sampling coverage of its shelf and shelf-break. This provided a complete view of spatial fish distribution around the main Island that enabled a revision of the Island Mass Effect with a concentration of fish on the windward side of the Island. It also provided information on overall fish and fish assemblage acoustic biomass at all depths and enabled a comparison between euphotic and mesophotic depths.

The third article describes a coastal neritic ecosystem using a combination of acoustic and trawls. It represents one of the first attempts to describe the spatial distribution of multispecific fish assemblages. Acoustic data allowed for mapping fish’s spatial distribution and investigating a few ecological aspects (influence of bottom depth and distance to the shelf-break). Ultimately, the study emphasized the importance of the Pernambuco plateau and Rio Grande do Norte plateau and their shelf-break.

5.2. Perspectives

There is a need to go towards novel and interdisciplinary approaches for accurate efficient ecosystem-based conservation, (Marchese, 2015). Historically, fish assemblages have been assessed using underwater visual census (UVC) (e.g. Ferreira et al., 2004; Floeter et al., 2006; Anderson et al., 2014 for the Southwestern Atlantic), which provides discrete data. Active acoustics provides comprehensive data to answer the need for large-scale continuous data and ecological insights for suitable management. Indeed, Marine Spatial Planning (MSP) requires large quantities of heterogeneous, multi-sources and spatially explicit data. In particular, marine resource management requires spatially explicit information on fish ecology, habitat and species mapping (Fonseca et al., 2017). The continuous data sets provided by acoustic data in the oceanic archipelago of Fernando de Noronha and along the coast of Northeast Brazil are unprecedented and have great potential for integrated studies.

The Fernando de Noronha dataset and some of the outputs of my work are being used to feed reserve site selection tools developed by Adrien Brunel during his Ph.D (Figs. 5.1 and 5.2). Adrien Brunel developed a code based on exact optimization methods implemented acoustic fish biomass among other input data (i.e. fishing pressure, and bathymetry) to design optimal reserve sites (Fig. 5.2) and serve as decision support tools (Brunel et al., 2022b, 2022a).

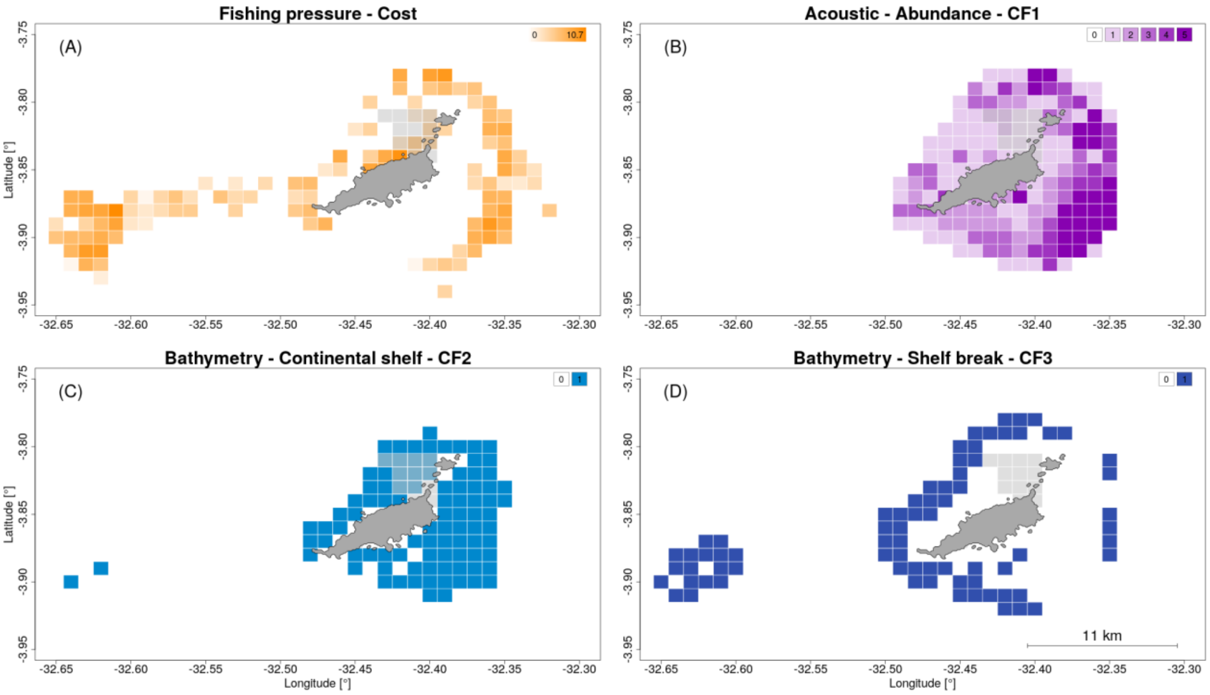


Figure 5.1. from Brunel et al. (2022a). Processed geographical layers feeding the conservation problem. (A) Number of fishing points. (B) Acoustic data interpreted as a fish biomass surrogate. (C) Continental shelf habitat surrogate (0-50 m). (D) Shelf-break habitat surrogate (50-200 m). Transparent grey pixels are the locked-out planning units.

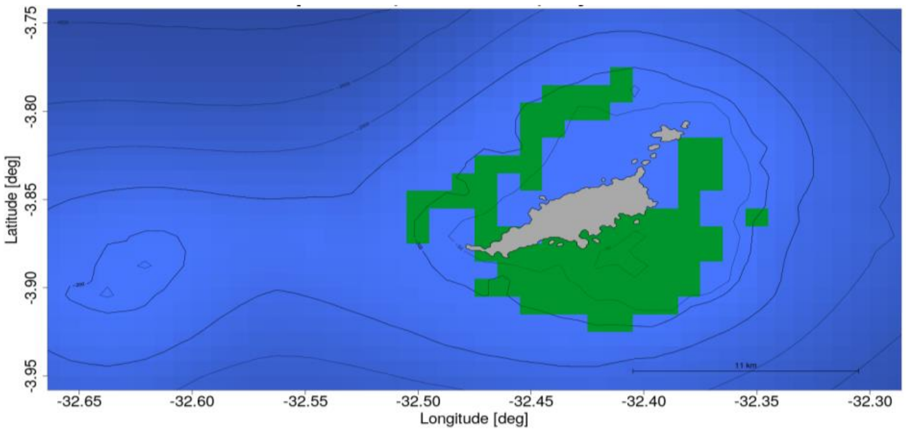


Figure 5.2. Reserve solution in green based on the previous geographical layers.

In Northeast Brazil, active acoustic data allowed identifying critical places with high acoustic biomass. Integrating the hotspot locations with other information can help to understand the underlying ecological mechanisms behind the formation of those hotspots. As an example, a study of plankton dispersal using Lagrangian simulations on different communities with different pelagic life durations was conducted in the Northeast region by Tosetto et al., (Submitted). This study allowed exhibiting recruitment zones that receive and retain larva (Fig. 5.3). Areas of concentration of particles (marks a, b, c, d, Fig. 5.3) appeared in the Rio Grande de Norte region in the north (Touros High) and south (Natal) where we observed high acoustic fish biomass. This pattern of retention might enhance the recruitment and settlement of fish and or prey and participate in the formation of the hotspots we revealed using active acoustics. Further work is necessary to translate acoustic fish assemblages into functional assemblages, taking a closer look at the fish species caught in the trawls.

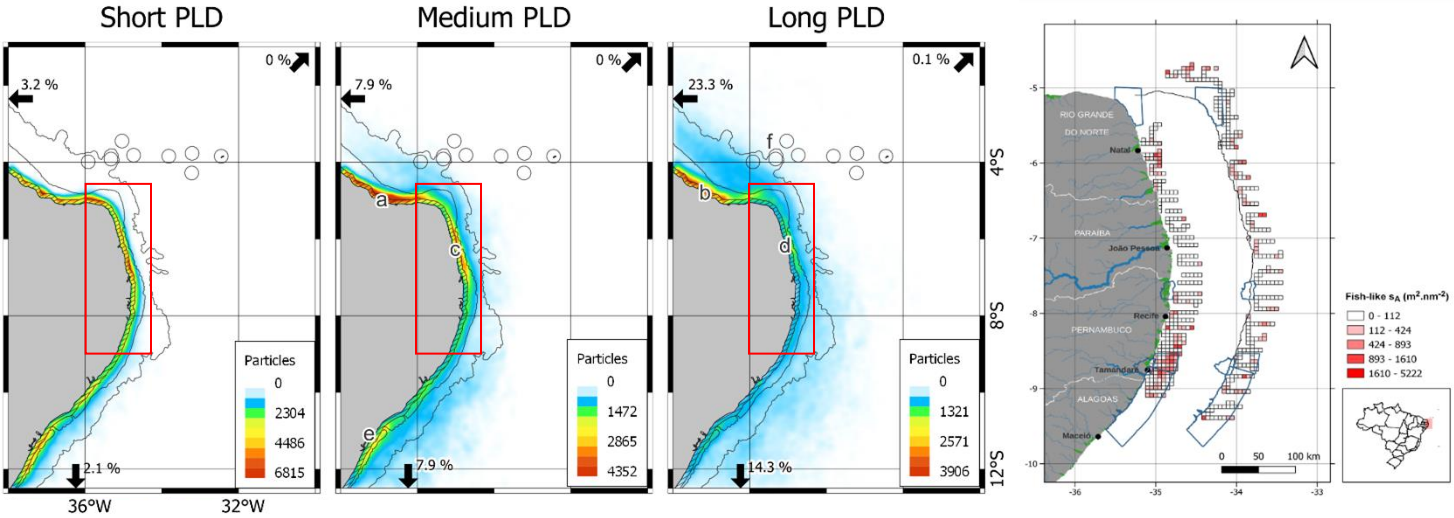


Figure 5.3. Kernel maps of the pooled data (108 runs) of final distribution of particles with short (5 days), medium (15 days) and long (30 days) pelagic life durations (PLD) released over the coast. Dashed zones indicate release area. Arrows indicate export of particles to outside the domain. Red box indicates our study area Fig. 4.1 from chap. 4 is repeated.

One downfall of this method is that annotating video and assigning fish echos to a fish assemblage were both time consuming. The use artificial intelligence has emerged to identify fish in video (Shortis et al., 2016; Villon et al., 2016; Rauf et al., 2019) and there is few very recent studies using IA in the active acoustics field (Brautaset et al., 2020; Handegard et al., 2021; Sarr et al., 2021). The construction of the dataset of annotations and fish assemblage can serve as a database to train artificial intelligence for automated identification and test its efficiency.

Further integration of these data with interdisciplinary studies are needed to provide a better understanding of the biogeochemical impact on fish population. However, this approach developed during this thesis is transposable to other tropical environments to reveal fish spatial distribution. In particular, the combination of active acoustics and video is adapted to monitor strict no-take MPA. Overall, this provides essential information to feed the reflections around creating optimal Marine Spatial Planning.

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