UNIVERSIDADE FEDERAL DE SÃO PAULO INSTITUTO DO MAR PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE E ECOLOGIA MARINHA E COSTEIRA - PPGBEMC

ESTRUTURA DAS ASSEMBLEIAS DE PEIXES EM RECIFES SUBTROPICAIS DO ATLÂNTICO SUDOESTE: DIFERENÇAS ENTRE ECOSSISTEMAS RASOS E MESOFÓTICOS E A INFLUÊNCIA DAS CARACTERÍSTICAS DO HABITAT

> Maisha Gragnolati Fernandes Orientador Prof. Dr. Fabio dos Santos Motta Coorientadora Dra. Fernanda Andreoli Rolim

> > Santos - SP 2022

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"Até hoje os xamãs continuam defendendo os seus e a floresta. Mas também protegem os brancos, apesar de serem outra gente, e todas as terras, até as mais imensas e distantes" – Davi Kopenawa

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Resumo

Há um grande aumento na quantidade de pesquisas sendo feitas em recifes mesofóticos tropicais e temperados. No Brasil, esses ambientes foram registrados desde o litoral amazônico até a Cadeia Vitória - Trindade, mas dados de pesca e observações in situ registram a ocorrência dessas formações ao sul do litoral paulista, que permanecem sem descrição na literatura. Existem lacunas de conhecimento sobre a importância ecológica e os serviços ecossistêmicos prestados pelos recifes mesofóticos, mas acredita-se que eles possam fornecer áreas de refúgio para espécies que habitam recifes rasos, muitas vezes ameaçados por estressores naturais e antropogênicos. Este trabalho teve como objetivo investigar a estrutura das assembleias de peixes em recifes subtropicais do Atlântico Sudoeste, buscando compreender as diferenças entre ambientes rasos (< 18m) e mesofóticos (> 18m), bem como avaliar a influência das características locais (profundidade, relevo, temperatura e regime de gestão) na abundância e distribuição das espécies. As assembleias de peixes foram amostradas através de estéreo filmagem remota subaquática com isca (estéreo-BRUV) realizadas na costa centro-sul de São Paulo. Trinta e três lançamentos de estéreo-BRUV foram realizados na primavera de 2021, sendo 15 na zona rasa e 18 na zona mesofótica. Foram registrados 1276 peixes pertencentes a 25 famílias e 66 espécies. Observou-se uma alta substituição de espécies ao longo da coluna d'água. Os grupos tróficos responderam de forma diferente às variáveis de habitat. Carnívoros, herbívoros e onívoros foram influenciados pela profundidade. A média do relevo explicou a abundância de planctívoros e invertívoros sésseis, sendo que estes últimos também responderam à profundidade. Invertívoros móveis responderam principalmente à gestão e à média do relevo. As assembleias de espécies alvo da pesca são diferentes em composição de espécies e abundância entre a zona rasa e funda, embora a biomassa foi proporcional. Os resultados não oferecem evidências de que os recifes mesofóticos do Atlântico Sudoeste subtropical atuem como refúgio para as assembleias de peixes de ambientes rasos. A profundidade, o regime de gestão e o relevo foram as principais características do habitat que influenciaram a estrutura das assembleias de peixes, uma vez que não encontramos uma relação linear entre a temperatura e os atributos da assembleia analisados.

Palavras-chave: Atlântico Sudoeste subtropical, conectividade de habitats, conservação, ecossistemas profundos, BRUVs.

Abstract

There is a current increasing in studies in tropical and temperate mesophotic reefs. In Brazil, these environments have been recorded from the Amazon coast until the Vitória -Trindade Chain, but fishing data and *in situ* observations record the occurrence of these formations until the south of the São Paulo coast, which remain without description in the literature. There are knowledge gaps about the ecological importance and ecosystem services provided by mesophotic reefs, but it is believed that they can provide refuge areas for species that inhabit shallow reefs, often threatened by natural and anthropogenic stressors. This work aims to investigate and describe the vertical structure of fish assemblages in subtropical reefs of the SW Atlantic, seeking for understand the differences between shallow and mesophotic habitats, as well evaluate the influence of local characteristics (depth, relief, temperature and management) in abundance and species distribution. Reef fish assemblages were assessed using Baited Remote Underwater stereo-Videos (stereo-BRUVs) on the south-central coast of São Paulo.

Thirty-three stereo-BRUV deployments were performed in spring of 2021, being 15 in the shallow zone and 18 in the mesophotic zone. 1276 fishes belonging to 25 families and 66 species were recorded. High species turnover was observed along the water column. Trophic groups responded differently to habitat variables. Carnivores, herbivores and omnivores were influenced by depth. The mean relief explained the abundance of planktivores and sessile invertivores, and the latter also responded to depth. Mobile invertivores responded mainly to management and mean relief. Assemblages of fisheries target species were different in species composition and abundance between strata, while biomass were proportional. This fact offered no evidence that mesophotic reefs act as refuges for shallow fish assemblages. Depth, management and mean relief was the main habitat characteristics influencing fish assemblages' structure, since we did not find a linear relationship between temperature and the assemblages attributes analyzed.

Keywords: Subtropical Southwestern Atlantic, habitat connectivity, conservation, deep ecosystems, BRUVs.

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1. Introdução Geral

Ecossistemas recifais são formações tridimensionais biogênicas (e.g., recifes de corais, esponjas, algas calcáreas) ou não biogênicas (i.e., recifes rochosos e recifes artificiais) altamente dinâmicas (Bellwood et al., 2006; Krumholz e Barber, 2011; Coolen et al., 2020). Estão entre os ecossistemas mais diversos e produtivos do mundo, oferecendo bens e serviços ecossistêmicos que contribuem para o bem-estar de grande parte da população mundial (Moberg e Folk, 1999; Hoegh-Guldberg, 2011; Woodhead et al., 2019).

Os recifes do Atlântico Sudoeste subtropical são formações rochosas com a presença de algumas poucas colônias de corais e muito *turf* que crescem associadas às rochas (Aued et al., 2018). Este tipo de formaçãos recifal abriga uma diversidade de peixes que dependem diretamente do substrato para alimentação e abrigo (Jones, 1988). A complexidade destes habitats favorece altos índices de riqueza, abundância e biomassa de peixes (García-Charton e Pérez-Rufaza, 2001; Komyakova et al., 2013; Teixeira-Neves et al., 2015).

A definição de peixes recifais não é um consenso na literatura, podendo ser determinada através dos grupos taxonômicos listados mais comuns em formações recifais ou através de funções ecológicas (Bellwood, 1996, 1998; Bellwood e Wainwright, 2002). Neste estudo, consideramos peixes recifais todos aqueles que utilizam o recife para alguma função, seja residência, abrigo, reprodução, crescimento, alimentação ou limpeza (Bellwood, 1998; Bellwood e Wainwright, 2002).

A sub-província brasileira Leste-Sudeste abriga a maior riqueza de peixes recifais entre todas as sub-províncias do Atlântico Sudoeste, com aproximadamente 326 espécies (Pinheiro et al., 2018). As famílias mais representativas em riqueza e abundância da região subtropical do Atlântico Sudoeste são Haemulidae, Carangidae, Labridae, Serranidae, Epinephelidae e Pomacentridae (Gibran e Moura, 2012; Daros et al., 2018).

É um consenso que o grupo de invertívoros móveis é dominante nas assembleias de peixes recifais do Atlântico Sudoeste subtropical (e.g., Ferreira et al., 2004; Floeter et al., 2007; Gibran e Moura, 2012; Daros et al., 2018, Motta et al., 2021). A grande abundância desse grupo se deve à grande disponibilidade de alimentos em substratos consolidados e inconsolidados (Harmelin-Vivien, 2002), enquanto características do

habitat influenciam a riqueza e abundância dos demais grupos tróficos. Locais protegidos da pesca e perto da costa, por exemplo, tendem a favorecer maior abundância de carnívoros (Gibran e Moura, 2012; Daros et al., 2018; Rolim et al., 2019), enquanto herbívoros e planctívoros tendem a ser mais abundantes em zonas de usos múltiplos (Gibran e Moura, 2012; Motta et al., 2021).

Os estudos prévios citados contribuem para o entendimento das assembleias de peixes e seus atributos ecológicos. Entretanto, estão restritos a profundidades rasas e acessadas pelo mergulho autônomo, criando uma lacuna de conhecimento sobre recifes abaixo dos 30 m de profundidade (conhecidos como recifes mesofóticos) e suas comunidades associadas. A falta de conhecimento sobre as assembleias de peixes em recifes mesofóticos aumenta as incertezas associadas ao planejamento da gestão de ambientes marinhos (Hollarsmith, 2020). Assim, o avanço das investigações sobre diversidade, abundância, biomassa e ecologia das espécies é fundamental para que áreas protegidas possam definir esforços de conservação eficazes (Williams et al., 2019). Considerando que o presente estudo foi realizado na região subtropical brasileira, esperase colaborar com o preenchimento de uma lacuna crítica de conhecimento sobre os recifes mesofóticos em âmbito regional e global.

Os ecossistemas mesofóticos são encontrados entre 30 e 40 m de profundidade, podendo chegar até 150 m em algumas regiões tropicais e subtropicais de águas muito claras, onde habitam organismos pouco dependentes de luz (Kahng et al., 2010; Kahng et al., 2014; Fukunaga et al., 2016; Laverick et al., 2018). Devido à profundidade, ambientes recifais mesofóticos geralmente são considerados menos ameaçados pelos estressores que afetam recifes de águas rasas, como fortes tempestades e a pesca (Baker et al., 2016; Simon et al., 2016; Lesser et al., 2018). Entretanto, evidências mais recentes sugerem que tais ambientes não são imunes a impactos naturais e antrópicos e podem apresentar vulnerabilidade aos mesmos estressores que ameaçam recifes rasos, como aumento da temperatura dos oceanos, branqueamento de corais, introdução de espécies exóticas, acidificação, poluição, turismo, pesca e mineração (Bo et al., 2014; Aguilar-Perera et al., 2016; Baker et al., 2016; Semmler et al., 2016; Rocha et al., 2018; Andradi-Brown, 2019; Francini-Filho, et al., 2019; Woodhead et al., 2019).

Os recifes mesofóticos podem se apresentar como extensões de recifes rasos, favorecendo a conectividade por meio de um gradiente de profundidade (Turner, et al.,

2017; Williams et al., 2019). Acredita-se que estes recifes são capazes de fornecer serviços ecossistêmicos semelhantes aos recifes de águas rasas, mas que também possuem funções ecológicas exclusivas (Baker et al., 2016; Turner, et al., 2017; Woodhead et al., 2019). Dentre os benefícios pode-se destacar a disponibilidade de habitats para espécies de importância ecológica e econômica e a possibilidade de refúgio para aquelas que se encontram sob pressões nos recifes rasos. Nesse contexto, os recifes mesofóticos podem atuar como áreas de recuperação para espécies ameaçadas e/ou sobreexplotadas (Lindfield et al., 2015; Baker et al., 2016, Semmler et al., 2016).

Muitos esforços de pesquisa têm sido direcionados à compreensão da conectividade vertical entre recifes mesofóticos e rasos, sendo esta uma questão essencial para testar a Hipótese do Refúgio dos Recifes Profundos (HRRP) (Lesser et al., 2018). A HRRP se sustenta na ideia de que recifes profundos estão menos expostos a determinadas pressões, ameaças e impactos (naturais e antrópicos) do que os recifes rasos, podendo assim atuar como fontes de organismos viáveis após perturbações (Bongaerts et al., 2010a).

Poucos estudos descreveram a estrutura das assembleias de peixes ao longo de um gradiente de profundidade buscando testar a HRRP. A lacuna de conhecimento a respeito da conectividade biológica entre recifes rasos e mesofóticos é evidente (Rodríguez et al., 2016). Há indícios de que existe uma forte conectividade entre as zonas superiores de recifes mesofóticos (30m) e recifes rasos, e que essa relação pode se estender a níveis mais profundos para algumas espécies (principalmente para aquelas de grande interesse comercial) (Loya et al., 2016). Essa conectividade é favorecida para os peixes devido à capacidade de natação (Loya et al., 2016). Embora esses indícios forneçam suporte à HRRP, diversos estudos encontraram diferentes associações de peixes em diferentes níveis de profundidade, sugerindo um padrão na organização das assembleias (Rodríguez et al., 2016; Rocha et al., 2018; Williams et al., 2019).

Assim, apesar da HRRP fornecer um aspecto importante para guiar os esforços de conservação, mais estudos são cruciais para que a hipótese possa ser sustentada em larga escala geográfica, incluindo diferentes condições oceanográficas e contemplando também recifes rochosos (Bongaerts et al., 2017). O consenso entre grande parte dos estudos é que ainda são necessárias investigações sobre composição taxonômica, preferência de habitat, abundância e distribuição das espécies para explicar os fatores

determinantes da estruturação das comunidades (Loya, et al., 2016; Rodríguez et al., 2016).

A literatura atual sobre ecossistemas mesofóticos é composta majoritariamente por estudos em comunidades coralíneas de ambientes tropicais do Atlântico, principalmente do Caribe (Kahng et al., 2010; Turner et al., 2017). Esses locais apresentam composição estrutural diferente de ambientes subtropicais e temperados (Williams et al., 2019; Soares et al., 2020). Este fator representa um viés no entendimento dos recifes mesofóticos, pois devido aos esforços de pesquisa estarem concentrados em ambientes tropicais não há evidências suficientes para sugerir o papel ecológico de tais ambientes em escala global (Turner et al., 2017). Pouco se sabe sobre ecossistemas mesofóticos subtropicais e temperados, principalmente no que se refere à ecologia de assembleias de peixes, estruturação de habitat e a conectividade vertical entre ambientes rasos e profundos (Williams et al., 2019).

No Brasil, os recifes mesofóticos foram documentados desde a costa Amazônica (5° N) até a Cadeia Vitória - Trindade (21° S), mas dados de pesca e observações *in situ* não publicadas indicam a ocorrência destes ambientes em águas subtropicais (abaixo de 24° S), que permanecem como lacunas críticas de conhecimento (Francini-Filho et al., 2019). A contribuição do Brasil para a compreensão dos recifes mesofóticos se restringe às águas tropicais do país (e.g. Rosa et al., 2016; Simon et al., 2016; Pinheiro et al., 2017; Pimentel et al., 2019; Pimentel et al., 2020; Pinheiro et al., 2020; Silva et al., 2021; Pimentel et al., 2022), tornando-se necessária a investigação desses ambientes em águas subtropicais.

A costa do Estado de São Paulo é composta por uma rede de Unidades de Conservação (UCs) com diferentes contextos e regimes de gestão, que juntas formam a maior rede de Áreas Marinhas Protegidas (AMP) do Brasil, com cerca de 12,055 km² (Motta et al., 2021). Entretanto, apenas 5,7% desse total está sob regime de proteção integral (Motta et al., 2021). O presente trabalho foi realizado em três unidades dessa rede de AMPs: o Parque Estadual Marinho da Laje de Santos, a Área de Proteção Ambiental Marinha Litoral Centro e a Estação Ecológica Tupiniquins.

O Parque Estadual Marinho da Laje de Santos foi criado em 1993 (Decreto Estadual 37.537/1993) compreendendo uma área retangular de 5.000 ha, distante cerca de 33 km da costa central de São Paulo. Sua gestão é feita por meio de um conselho

consultivo em funcionamento desde 2009, um plano de uso público editado em caráter emergencial pela primeira vez em 2010 e revisado em 2019 e o seu plano de manejo concluído no final de 2018. É uma área de exclusão de pesca e conta com um dos melhores pontos de mergulho do litoral brasileiro, recebendo milhares de visitantes anualmente. O parque possui no interior do seu polígono recifes mesofóticos que nunca foram caracterizados na literatura científica.

A Área de Proteção Ambiental Marinha do Litoral Centro (APAMLC) abrange lajes, parcéis submersos e a Ilha da Queimada Grande (IQG). Essa UC é um importante destino turístico para a pesca amadora, caça-submarina e mergulho recreativo do Estado de São Paulo, atividades que não possuem nenhum ordenamento específico no local. Apesar desses múltiplos usos, é destacável como após anos de ação humana essas áreas continuam a sustentar essas atividades. No entorno marinho da IQG foram registradas 210 espécies de peixes recifais (Motta et al., dados não publicados). Vale destacar ainda, o registro de agregação reprodutiva da caranha (Lutjanus cyanopterus) (Motta et al., 2022) e a elevada cobertura de corais (Mussismilia hispida e Madracis decactis) (Pereira-Filho et al., 2019; Grillo et al., 2021) que em determinados pontos é similar àquela dos recifes de coral do Banco dos Abrolhos, o maior e mais diverso complexo recifal do Atlântico Sul (Moura et al. 2003). A administração da APAMLC ocorre através de um conselho gestor. A unidade foi criada em 2008 e teve seu plano de manejo outorgado em junho de 2021. Uma porção marinha de 3 km² no entorno da IQG foi declarada como Área de Interesse para o Turismo (AIT) com o objetivo de compatibilizar as atividades econômicas (recreativas) com a conservação dos recursos naturais.

A ilha da Queimada Pequena é integrante do setor Nordeste da ESEC Tupiniquins que se sobrepõe à APA Marinha do Litoral Centro. A ESEC foi criada em 1986 e seu plano de manejo foi elaborado em 2008. Localizada a 22 km da costa, a pesca, a visitação e o mergulho são proibidos em um raio de 1000 m ao redor da ilha, e seus recifes abrigam uma grande diversidade de peixes. A maior proximidade da costa expõe a Ilha da Queimada Pequena a maiores pressões e ameaças antrópicas, principalmente pelo deságue do Rio Itanhaém e pelo fácil acesso de pescadores. Apesar da área de proteção ao redor da ilha ser muito pequena quando comparada à toda a área protegida em território marinho nacional, sua existência é de extrema importância, uma vez que o pequeno tamanho e pequeno grau de isolamento da ilha a tornam muito frágil frente a interferência humana. O PEM Laje de Santos e a APA Marinha do Litoral Centro abrigam recifes mesofóticos nunca estudados. Neste contexto, a caracterização desses ambientes é fundamental para que os gestores reúnam conhecimento aprofundado de todos os atributos naturais e valores protegidos por essas Unidades de Conservação.

Considerando os desafios logísticos e de segurança envolvidos em profundidades próximas ou superiores aos limites do mergulho recreativo, a maioria dos recifes mesofóticos distribuídos pelo mundo permanecem não descritos e pouco estudados (Kahng et al. 2010; Lesser et al. 2018). Nas duas últimas décadas, os avanços no conhecimento da biodiversidade dos recifes mesofóticos foram possibilitados graças ao desenvolvimento de tecnologias como o mergulho em circuito fechado (*rebreather*), veículos operados remotamente (*Remotely Operated Vehicles - ROV*), submersíveis tripulados e técnicas de filmagem remota subaquática com isca (*Baited Remote Underwater Video - BRUV*) (Kahng et al. 2010; Lindfield et al. 2015).

Os BRUVs representam uma eficiente técnica de amostragem para mensurar a riqueza, abundância, estrutura em comprimento e biomassa de peixes em uma área, bem como avaliar impactos específicos nas assembleias (Watson et al., 2005). Comparado às técnicas de censos visuais, o uso destes sistemas permite mais amostragens no mesmo intervalo de tempo e não exige extenso treinamento (Watson et al., 2005). Adicionalmente, a utilização de BRUVs não compromete a segurança física dos mergulhadores, diminui a possibilidade de alteração comportamental dos peixes e produz estimativas acuradas da abundância e diversidade das assembleias (Langlois et al., 2020). Entretanto, possui capacidade limitada para amostrar pequenas espécies associadas ao fundo devido ao campo de visão das câmeras.

O início do desenvolvimento dos BRUVs se deu devido à capacidade limitada de mergulhadores em fornecer o tamanho preciso de peixes em censos visuais (Harvey e Shortis, 1996). A subjetividade de cada mergulhador na medição dos indivíduos promove um viés no entendimento sobre as pequenas mudanças nos tamanhos dos peixes, tornando necessária a adoção de um sistema de medição imparcial (Harvey e Shortis, 1996). Além da acurácia na medição, os BRUVs não são seletivos com relação ao tamanho dos peixes e atraem grande parte dos indivíduos que estão nos arredores do equipamento (Cappo et al., 2006). Também configuram um método não extrativo e não destrutivo, podendo ser utilizados em diversos tipos de habitat e profundidades (Cappo et al., 2003).

No Brasil, as pesquisas com BRUVs em ambientes marinhos se iniciaram em 2016 no Estado de São Paulo (Rolim et al., 2019a) e se expandiram para outras regiões, como Bahia (Pimentel et al., 2019; Reis-Filho et al., 2019; Moura et al., 2021, Rolim et al., 2022a, Schmid et al., 2022), Pernambuco e Alagoas (Pereira et al., 2021; Bezerra et al., 2022), Fernando de Noronha (Pimentel et al., 2020) e Arquipélago de São Pedro e São Paulo (Pinheiro et al., 2020; Pimentel et al., 2022), contribuindo para o entendimento da diversidade e dinâmica das comunidades de peixes do Atlântico Sudoeste, muitas vezes em locais de difícil acesso a mergulhadores.

Diante do exposto, o presente estudo teve como objetivos:

a) Contrastar a riqueza, abundância, biomassa e grupos tróficos das assembleias de peixes entre ambientes rasos e mesofóticos, buscando testar a hipótese do refúgio dos recifes profundos para o Atlântico Sudoeste subtropical, e

b) Investigar a influência das características do habitat sobre a riqueza, abundância
 e biomassa das espécies de peixes em recifes subtropicais.

Partindo da análise da literatura atual sobre recifes mesofóticos a hipótese deste estudo é que as estruturas das assembleias de peixes de recifes rasos e mesofóticos são diferentes. Devido às diferentes condições do habitat, espera-se encontrar: (1) menor riqueza e maior biomassa em ecossistemas mesofóticos, bem como maior abundância e biomassa de espécies alvo da pesca nesses ambientes (2) variação dos níveis tróficos entre os estratos de profundidade, com maior abundância e biomassa de herbívoros em zonas rasas e de carnívoros em zonas mesofóticas e (3) capacidade dos ecossistemas mesofóticos em fornecer refúgio para espécies de interesse comercial ameaçadas em ambientes rasos.

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FISH STRUCTURE ASSEMBLAGE IN SOUTHWESTERN ATLANTIC SUBTROPICAL REEFS: DIFFERENCES BETWEEN SHALLOW AND MESOPHOTIC ECOSYSTEMS AND THE INFLUENCE OF HABITATS CHARACTHERISTICS

1. Introduction

The current increase in studies of mesophotic coral ecosystems (MCEs) in tropical areas (Garcia-Sais et al., 2010; Kahng et al., 2010; Lindfield et al., 2015; Andradi-Brown et al., 2016; Pinheiro et al., 2016; Rosa et al., 2016; Asher et al., 2017; Lesser et al., 2018; Rocha et al., 2018; Loya et al., 2019; Boland et al., 2020; Pimentel et al., 2022) is a response for the loss of coral coverage in shallow waters due to human activities (Gardner et al., 2003; Hughes et al., 2003, 2007; Pandolfi et al., 2003; Bellwood et al., 2004; Sweatman et al., 2011). Furthermore, the lack of knowledge about these communities encouraged the development of techniques for accessing mesophotic depths, such as rebreathers, remote operated vehicles and baited remote underwater videos (Kahng et al., 2010; Lindfield et al., 2015).

MCEs are light-dependent coral reefs considered typically found in depths varying between 30 – 40 m to over 150 m in tropical and subtropical areas (Kahng et al., 2010, 2014; Hinderstein et al., 2010), which are extensions of their shallow counterparts or isolated submerged reefs (Bongaerts et al., 2010, Williams et al., 2019). Because of the depth, many authors suggested that MCEs are more stable than shallow reefs and act as refuge against human impacts (Feitoza et al., 2005; Lesser et al., 2009, 2018; Bongaerts et al., 2010; Olavo et al., 2011; Lindfield et al., 2015). However, recent studies have showed exposure of MCEs to impacts, as well as ecological differences and disconnection between shallow and deep reefs (Smith et al., 2016; Pinheiro et al., 2021). Indeed, these facts indicate limited capacity of mesophotic ecosystems to serve as refuges for threatened fish species.

Fish fauna transition across a depth gradient was reported in several previous studies, suggesting a well determined pattern in trophic guilds distribution across the water column (Rodríguez et al., 2016; Rocha et al., 2018; Williams et al., 2019). Whereas herbivores are more likely to inhabit shallow reefs due to algae presence, carnivores and zooplanktivores tend to be more abundant in deeper habitats (Feitoza et al., 2005; Brokovich et al., 2008; Kahng et al., 2010, 2014; Bejarano et al., 2014; Pinheiro et al.,

2016; Semmler et al., 2016; Williams et al., 2019; Silva et al., 2021). There is a considerable species turnover in coral reef assemblages as depth increases, and most species exhibit a strong preference for a specific depth zone (Rocha et al., 2018).

Previous studies have characterized the structure of fish assemblages in the subtropical SW Atlantic (Floeter et al., 2001, 2006a, 2006b; Gibran & Moura, 2012, Daros et al., 2018). However, the knowledge on mesophotic reefs is mostly composed by studies on coral communities in the tropical Atlantic, mainly in the Caribbean (Kahng et al., 2010; Turner et al., 2017; Loya et al., 2019). The subtropical SW Atlantic shelters a poor coral coverage, composed mostly by rocky reefs, turf and macroalgae (Aued et al., 2018), a different structural composition of tropical reefs, as well as other subtropical and temperate areas (Williams et al., 2019; Soares et al., 2020;). The ecological role of subtropical and temperate mesophotic ecosystems on a global scale remains uncertain, representing a bias in the global understanding of mesophotic reefs (Turner et al., 2017; Williams et al., 2019; Medeiros et al., 2021). The current lack of information about mesophotic fish assemblages increases management planning uncertainties (Turner et al., 2017; Williams et al., 2019; Hollarsmith et al., 2020), which makes the investigation of these environments a priority. Because of the different benthic coverage of subtropical SW Atlantic, we referred to mesophotic regions in our study as mesophotic ecosystems (MEs) rather than MCEs.

Whereas the lower depth limit of MEs varies by location depending on environmental characteristics (light incidence and temperature, mostly), the fixed upper limit of MEs (30 m) was defined according to maximum safe limits for scuba diving (Kahng et al., 2010, 2014; Lesser et al., 2009; 2018). This consensus does not represent an ecological or physiological boundary for marine organisms (Kahng et al., 2010; Lesser et al., 2018), and it is biologically unjustified. Considering environmental differences between tropical and subtropical areas and that the limits of MEs are not based on ecological factors, we propose a different zonation for MEs in the SW Atlantic, suggesting that faunal zonation should be based on species turnover and light incidence instead of pre-established depth values.

Although depth is an important driver for fish assemblages' structure, other factors associated or not with depth can influence species distribution, such as habitat and structural complexity (Komyakova et al., 2013, Teixeira-Neves et al., 2015, Rolim et al., 2022a), temperature, thermoclines (Buxton and Smale, 1989; Williams et al., 2019) and the management regime (Anderson et al., 2019; Rojo et al., 2019; Rolim et al., 2019;

Motta et al., 2021). In fact, studies have documented the influence of physical, biological and management factors in fish assemblages' structure in subtropical areas (Floeter et al., 2001, 2006a, 2006b; Gibran & Moura, 2012; Teixeira-Neves et al., 2015; Neves et al., 2016; Daros et al., 2018; Rolim et al., 2019; Motta et al., 2021), but the majority of community structure research remains in tropical waters. Understanding patterns and drivers of fish distribution is useful to determine how environmental and habitat changes related to natural and anthropogenic disturbances may affect rocky reef fish assemblages (Neves et al., 2016). This knowledge facilitates prioritization in management planning and definition of priorities areas for conservation.

The access to MEs is difficult since most of its depth range is inaccessible to scuba diving, which pose logistical and safety challenges in field operations. Because of that, these environments are still poorly known and studied (Kahng et al., 2010; Lesser et al., 2018). In the past two decades, progress in knowledge of MEs has been facilitated by the development of rebreather diving and remote underwater filming techniques (e.g., remotely operated vehicles – ROVs and baited remote underwater stereo videos – stereo-BRUVs) (Kahng et al., 2010; Lindfield et al., 2015). Stereo-BRUVs represent a non-destructive and efficient technique to measure species richness, abundance, and biomass of fish assemblages (Watson et al., 2005; Langlois et al., 2020), focusing on target species from fisheries and carnivores, but also recording commercial non-target species and other trophic groups (Rolim et al., 2022b). The use of these systems can also enable the record of apex predators, unusual and new species (Pimentel et al., 2019; Rolim et al., 2019b; Pinheiro et al., 2020).

Our study represents the first assessment on the vertical distribution of fish assemblages using stereo-BRUVs in subtropical reefs of the southwestern Atlantic, as well as provides inferences about the capacity of MEs as refuges. It also expands knowledge about the influence of habitat characteristics (depth, temperature, relief and management regime) on reef species abundance. We aim to contrast richness, abundance, biomass and different trophic groups between shallow (< 18m) and deep strata (> 18m), investigating the capacity of subtropical MEs in serve as refuges for species threatened by fisheries. We also investigated which habitat characteristics influence assemblage's attributes distribution. In case subtropical reefs represent refuge for shallow water species, we hypothesize that: (1) the assemblages of shallow and deep ecosystems are different, with higher richness and abundance in shallow reefs and higher biomass in MEs; (2) trophic guilds herbivores should be more abundant in shallow reefs and

carnivores in MEs and (3) MEs are refuges for target species and present higher biomass due to less fishing pressure.

2. Material and Methods

2.1. Study area

Subtropical SW Atlantic is characterized by seasonal upwellings and the intrusion of South Atlantic Central Water current, which makes the water colder in winter, spring and summer (Cerda and Castro, 2014), mainly from 10m deep, where the thermocline starts. Wet (December – April) and dry (June – August) seasons define a hot and humid climate for the region, depending on the displacement of the tropical and polar anticyclones (Seeliger and Kjerfve, 2001).

São Paulo's coastline has 700 km of extension, comprehending sand beaches, mangroves, estuaries, rocky shores and several islands (Angelo and Lino, 1989). The high industrialization and economic importance of the State favor the presence of almost 20 million of people living less than 100 km from the ocean. These facts contribute to the "very high" index of human impact in the area (Halpern et al., 2008, Magris et al., 2021), as well as the presence of the Santos seaport (the largest of SW Atlantic), commercial fisheries, oil extraction and other human impacts, as pollution and habitat destruction. São Paulo State shelters the highest occurrence of marine endangered species in Brazilian coast (78 species) (Ceretta et al., 2020, Magris et al., 2021). However, only 5.7% of marine territory's State is under no-take MPA regime (Motta et al., 2021).

This study was conducted in three coastal MPAs of São Paulo state, Brazil: 1) in Laje de Santos Marine State Park (Laje de Santos MSP) (corresponding to IUCN Category II: National Park) (24°15' S, 46°10' W) we sampled 16 points, including submerged reefs around the main island (Bandolim, Brilhante, Sul and Novo reefs) (Fig. 1), 2) in Center Coast Marine Environmental Protected Area (Center Coast MEPA) (IUCN Category VI: Protected area with sustainable use of natural resources) (24°29' S, 46°40' W) we conducted 9 BRUV deployments including Queimada Grande Island, Conceição islet and adjacent submerged reefs (Dom Pedro, João Ilhéu, Fora, Conceição and Reis reefs) (Fig. 1) and in the Tupiniquins Ecological Station (ES) (IUCN Category Ia: Strict nature reserve) we sampled 3 points in the Queimada Pequena Island (24°22' S, 46°48' W) (Fig. 1).

Located 36 km from the coast, the Laje de Santos MSP is a no-take area (50 km²) where scuba diving and scientific research are the only public use activities allowed. The main island's relief is very steep, with rocky reefs covered by algae, zoanthids, hydrozoans, ascidians, and sparse colonies of scleractinian corals (Luiz et al., 2008).



Figure 1. Location of sampling stations. ES Tupiniquins: (1) Queimada Pequena Island; Center Coast Marine Environment Protected Area: (2) Conceição Reef, (3) Conceição Rock, (4) Queimada Grande Island, (5) Dom Pedro Reef, (6) Reis Reef; Laje de Santos Marine State Park: (7a) Bandolim Reef, (7b) Brilhante Reef, (8a) Calhaus Rocks, (8b) Laje de Santos, (8c) Sul Reef and (8d) Novo Reef.

Large sand bottoms intersperse the reefs of the Laje de Santos MSP. The park shelters approximately 196 fish species (Luiz et al., 2008), and the giant manta ray (*Mobula birostris*) is the conservation symbol of the area. The maximum depth of reefs in the park reaches approximately 50 m.

The Center Coast MEPA is a multiple-use area (4,530.83 km²) where all types of extractives uses, recreational activities (including spearfishing) and scientific research are allowed, except large pair trawlers and fishing with air compressors. The Queimada

Grande Island (located within the Center Coast MEPA, 35 km from de coast) has a very heterogeneous subtidal substrate, including rocky reefs associated with fringing coral reef and rhodolith bed (Pereira-Filho et al., 2019). The maximum depth of the island is about 20 m and their adjacent submerged reefs can reach 50 m.

Queimada Pequena island is located 22 km from the coast within Tupiniquins ES, a no-take area where only scientific research is allowed. The subtidal substrate is composed of shallow rocky reefs and sandy bottoms, with a maximum depth of 20 m. Only 1 km radius around the island is protected from fisheries and other human activities.

2.2. Data collection

During the spring of 2021 we performed 33 *stereo*-BRUV deployments between 6 and 43 m depth, 15 in the shallow zone (< 18m) and 18 in the mesophotic zone (> 18m). All deployments in shallow zone were in consolidated substrate covered by turf, while 8 samples in mesophotic zone were in unconsolidated substrate, 3 in the water column and 6 in consolidated substrate covered by turf. This difference was driven by local geography and the difficulty in positioning the BRUV in the deep rocky subtrate. Stereo-BRUVs consisted of an aluminum structure with two GoPro Hero 8 Black® video cameras in waterproof housings, each one capable of sampling up to 100 m depth. A 1.5 m arm with a bait box was positioned in the center of the system (Fig. 2a and b). A flashlight was attached to the BRUV. In each deployment we used 800 g of macerated sardine (*Sardinella brasiliensis*) as bait. The stereo-BRUV remained submerged for 60 minutes (Langlois et al., 2020) and we respected the minimum distance of 400 m between deployments (Bond et al., 2018), to prevent assemblage's overlap.

2.3. Video analysis

Before the field operations we conducted the calibration routine in stereo-BRUVs, to obtain accurate measurement of fishes' body size. In a pool, a Seagis® cube was filmed in many positions and the cube's points were marked in CAL® (www.seagis.com.au) software. Through this software we generated a calibration file for each BRUV system, which were used in video analyzes.

All the 33 hours of video were analyzed in the EventMeasure® (www.seagis.com.au) software. However, 1 sample of mesophotic zone and 4 of shallow zone were excluded because we only considered to the analyzes samples with more than 1.5 m of visibility, as well as only fishes less than 7 meters from the cameras (Langlois et al., 2020).

Individuals were classified at the most accurate possible taxonomic level. Relative abundance was estimated by MaxN (i.e., the maximum number of individuals of a same given specie present in a single frame) (Cappo et al., 2004), which prevents the recount of individuals that revisit the bait box. In the moment of each specie's MaxN we measured the total length of each individual. Then, biomass was estimated using the length-weight relationship available in FishBase (Froese & Pauly, 2022). Biomass of species without length-weight relationship was calculated using equations from a similar species from the same family.

Species were classified into trophic groups as carnivorous (CAR), mobile invertebrate feeders (MINV), sessile invertebrate feeders (SINV), herbivorous (HERB), planktivores (PLANK) and omnivores (OMNI) according to Pinheiro et al., (2018). Fish species were also classified in fisheries target and non-target species in the region according to literature (Ávila-da-Silva and Haimovici, 2006; Quimbayo et al., 2021).

2.4. Environmental variables

We considered depth, temperature and relief as environmental variables influencing organism distribution. Depth was measured by the boat's probe at the exact moment that the stereo-BRUV was launched. A profile of temperature along the water column was measured by a mini-CTD from Castaway® at each sample. Is important to highlight that all of our samples remained in the thermocline range (3 - 15 m, with a variation of 6.3°C) or below. Relief was analyzed with a high-definition image of each stereo-BRUV sample. The image was divided in 20 squares in order to measure the relief and benthic coverage. We used benthic coverage only for habitat description purposes. The final measure of each sample was the percentage of the mean and standard deviation relief of each image's square. The classification was based on the CATAMI scheme (Althaus et al., 2015) and on Wilson et al. (2007), adapted from Rolim et al. (2019) (Table 1). Visibility was estimated by measuring the distance to the most distant fish observed at each video.

The depth limits of mesophotic ecosystems (MEs) were defined based on subtropical conditions. The lower limit of MEs is the depth which available light is sufficient to support photosynthesis (i.e., euphotic zone lower limit – 1% of the surface incidence light) (Bongaerts et al., 2010a; Baldwin et al., 2018). To find out the extension of MEs in the subtropical SW Atlantic the diffuse attenuation coefficient of light at 490 nm (Kd490) was used as a proxy for light penetration. Kd490 was obtained from NOAA's Easier Access to Scientific Data database (https://coastwatch.pfeg.noaa.gov/erddap), at 4 km

spatial resolution. We processed these data in software R version 4.1.3 using ncdf4, chron, lattice, RColorBrewer, weathermetrics and raster packages. The lower limits of MEs were calculated for São Paulo's coast and for a random Caribbean tropical area of MCEs, to compare the extension of MEs in both areas. Data were collected for the same month (December of 2021).

We considered changes on fish assemblages, as turnover index and graphic separation of samples (nMDS), to determine the upper limit of MEs in the subtropical SW Atlantic.

Table 1. Habitat-classification based in CATAMI scheme (Althaus et al., 2015) and Wilson et al. (2007) for underwater videos (adapted from Rolim et al., 2019).

Criteria	Habitat description								
	0 – Flat substrate, sand, rubble with few features. $\sim 0^{\circ}$ substrate slope.								
	1 - Some relief f	eatures amongst n	nostly flat substrate/s	and/rubble. <45° sub	ostrate slope.				
Relief	2 – Mostly relie	f features amongst	some flat substrate o	or rubble. ~45° subst	rate slope.				
	3 - Good relief structure with some overhangs. >45° substrate slope.								
	4 - High structural complexity, fissures and caves. Vertical wall. ~90° substrat								
	5 - Exceptional structural complexity, numerous large holes and caves. Vertical wall. $\sim 90^{\circ}$ substrate slope.								
	Unknown								
Field of View	Facing up	Limited							
	Facing down	Open							
Dural	Open Water	Turf	Unconsolidated	Rhodolith	Macroalgae				
Вгоац	Consolidated	Porifera	Consolidated	Stony Corals	Unknown				



Figure 2. Examples of images from the baited remote underwater stereo-videos. (a) Shallow zone accessed in Center Coast Marine Environment Protected Area, with herbivores (*Kyphosus* spp.), carnivores (*Gymnothorax moringa*) and mobile invertebrate feeders (*Haemulon aurolineatum*) fishes, and (b) mesophotic ecosystems accessed in Laje de Santos Marine State Park with carnivores (*Mycteroperca acutirostris*) and mobile invertebrate feeders (*Myliobatis goodei* and *Pagrus pagrus*) species.

2.5. Statistical analysis

Differences between fish assemblages in shallow (< 18 m) (figure 2a) and deep water $(\geq 18m)$ (figure 2b) were investigated using PERMANOVA (Bray-Curtis' index) and visualized through non-metric multidimensional scaling (nMDS). PERMDISP analysis was conducted to identify significant differences between samples of the same depth stratum. A beta diversity analysis based on abundance of individuals (using Bray-Curtis' index) was applied to recognize the level of the dissimilarity between assemblages of the two strata, and the cause of differences (species turnover or nestedness). We conducted this analysis in software R version 4.1.3 using betapart package (Baselga and Orme, 2012; Baselga, 2013). The SIMPER function was used to identify species contributing to observed percentage dissimilarity between depth strata based on species presence/absence and abundance. A second PERMANOVA (using Euclidean distance) was used to compare the differences between assemblages of commercially target species in shallow and deep strata. A Mann-Whitney test was used to detect differences in biomass of this group between strata. The last two analyzes was conducted to infer the capacity of MEs in act as refuges. Statistical analyzes were conducted in R version 4.1.3.

The influence of habitat characteristics (depth, relief, temperature and management regime) on fish assemblages were analyzed using Generalized Additive Mixed Models (GAMM) and a full-subsets multiple regression approach (Fisher et al., 2018). The GAMM was conducted in R version 4.1.3 using the packages mgcv, gamm4, dplyr,

MuMIn and doParallel. Temperature and mean relief were used as continuous variables. Depth (two criteria: shallow and deep water) and management regime (two criteria: notake and open-access) were used as fixed factors, and visibility and distance from shore were used as null variables. Predictor variables adjust to form explanatory models for the distribution of response variables. Models were fitted to overall richness, abundance and biomass, as well as to abundance and biomass of target and non-target species from fisheries and trophic groups. Models that converge results to biomass and abundance were determined, but only abundance models were graphically explored. We used the logarithmic transformation data to reduce the dominant species effects.

Models' selection by the analysis was based on the second-order variant of Akaike's Information Criterion (AIC_c), necessary for small samples, and on AIC_c weights (ω AIC_c). The best models were those with lower values between two units of AIC_c (Δ AIC_c<2) (Burnham and Anderson, 2002) (Table S1). For results interpretation, we adopted the most parsimonious models for each response variable, which showed the lowest effective degrees of freedom (EDF) and greater explanatory power (r²). Models that included Δ AIC_c<2 and depth effects were prioritized despite exhibiting higher EDF and lower explanatory power, since depth effects compose our principal hypothesis.

3. Results

3.1. Upper and lower limits of the mesophotic zone

The proxy Kd 490 indicates the turbidity of the water column (i.e., how visible light in the blue to green region of the spectrum penetrates within the water column) (Wang et al., 2009). The rate of light attenuation at 490 nm is represented by a value of Kd490. The higher the value, the lower the rate of light penetration (Wang et al., 2009). Light at 490 nm reaches 1% of the surface incidence (end of euphotic zone) at a depth 3 times higher in Caribbean than in Laje de Santos island (0.03 for Caribbean and 0.1 for SW Atlantic, converting to 123 m and 43 m depth respectively). Therefore, we propose that both upper and lower limits of MEs are shallower in our region.

3.2. Depth as a structurer of fish assemblages

We recorded a total of 1276 fish's individuals belonging to 25 families and 66 species. The PERMANOVA analysis (p = 0.001) showed two different fish assemblages between depth strata (Fig.3). The PERMDISP (p = 0.9) confirmed that the distances between samples of the same stratum do not show effects of heterogeneity. In this case, assemblages of different samples in shallow habitats were similar, as well as the assemblages of different samples of mesophotic habitats.

The beta diversity analysis identified 73% of difference between strata, with a high level of turnover (87% of all difference) and a low level of nestedness (13%) (Fig. 4). The high species turnover indicates that the two assemblages are distinct both in species and abundance composition.

SIMPER analysis showed that *Haemulon aurolineatum*, *Pagrus pagrus*, *Caranx latus*, *Rhomboplites aurorubens*, *Kyphosus* spp., *Seriola* spp., *Pomacanthus paru*, *Diplectrum formosum* and *Holocentrus adscencionis* accumulated 50% of the differences between strata. *Pagrus pagrus* and *Diplectrum formosum* was the most representative species of the mesophotic zone, while *Haemulon aurolineatum* was mostly recorded in shallow environments.



Figure 3. Non-metric multidimensional scaling (nMDS) showing two different fish assemblages between depths (shallow < 18m and deep > 18m), with a little overlap between strata. (1 - 16) Laje de Santos Marine State Park, (17 - 20); Tupiniquins Ecological Station and (21 - 28); Center Coast Marine Environment Protected Area.

In shallow zones we recorded 764 individuals belonging to 52 species and 20 families. Of these, 33 were only recorded in this stratum. The most abundant species were the tomtate grunt *Haemulon aurolineatum*, the blue runner *Caranx crysos*, and the vermilion snapper *Rhomboplites aurorubens*. They represented almost 50% off all fishes recorded in the shallow zone. We also found *Chromis limbata*, an exotic planktivore from north Atlantic recorded in the area since 2016 (Anderson et al., 2020). Carnivores, mobile invertebrate feeders and herbivores were the most abundant trophic groups, with 302, 284 and 114 individuals each (Table 2).

In mesophotic habitats, 512 individuals belonging to 33 species and 20 families were recorded. We found 30 species of bony-fishes (Actinopterygii) and 3 elasmobranch species (*Myliobatis goodei*, *Pseudobatos* spp. and *Dasyatis hypostigma*). Of these 33 species, 19 were shared with shallow waters and 14 were recorded only in deeper environments. The most abundant specie was the red porgy *Pagrus pagrus*, followed by the vermilion snapper *Rhomboplites aurorubens* and the striped jack *Pseudocaranx dentex*, all commercially targeted species in the SW Atlantic. Together, these species accounted 62% of all individuals recorded in mesophotic ecosystem, and the red porgy represented almost 40% of these. We also recorded an *Heniochus acuminatus*, an exotic species from Indo-Pacific present in the area since 2013 (Luiz et al., 2014). Mobile invertebrate feeders and



Figure 4. Beta diversity of shallow (< 18m) and deep (> 18m) zones. Numbers inside the circles represent the amount of species in each zone. The overlap between circles represents shared species.

carnivores were the most abundant trophic groups, with 254 and 166 individuals each (49% and 32% of total, respectively). Herbivorous species were not recorded in the mesophotic ecosystem (Table 2).

Despite the greater richness and abundance in shallow zone, we recorded a higher biomass in MEs, with nearly 470 kg of fish in shallow waters and 517 kg in deep zones. The second PERMANOVA indicated that the assemblages of target species from fisheries are unique in each depth stratum (p = 0.03). Mann-Whitney test did not revealed differences in biomass of the same group (p = 0.84).

With light attenuation data, species turnover index and differences in fish richness and abundance in water column we established that, in spring, the upper limit of MEs in the SW Atlantic occurs at 18m.

Table 2. Shallow and mesophotic reef fish species and the relative abundance (MaxN) per zone. Presence (X) and absence (-) per area were recorded. Categorization of trophic groups follows Pinheiro et al. (2018). CAR = carnivores, MINV = mobile invertebrate feeders, HERB = herbivores, SINV = sessile invertebrate feeders, PLANK = planktivores and OMNI = omnivores. MSP = Marine State Park, MEPA = Marine Environmental Protected and ES = Ecological Station. SE = shallow ecosystem and ME = mesophotic ecosystem.

Family	Species	Trophic group	Laje de Santos MSP	Center Coast MEPA	Tuipiniquins ES	SE	ME	Targeted from fisheries
Rhinobatidae	Pseudobatos spp.	MINV	Х	-	-	-	2	Х
Dasyatidae	Dasyatis hypostigma	MINV	Х	Х	Х	-	6	Х
Myliobatiidae	Myliobatis goodei	MINV	Х	-	-	-	2	Х
Congridae	Conger orbignianus	CAR	Х	-	-	-	1	-
Muraenidae	Gymnothorax moringa	CAR	-	Х	Х	-	1	-
	Gymnothorax funebris	CAR	-	Х	Х	4	-	-
Holocentridae	Holocentrus adscensionis	MINV	Х	Х	Х	17	2	-
	Myripristis jacobus	MINV	-	-	Х	2	-	-
Serranidae	Serranus flaviventris	MINV	-	Х	Х	2	-	-
	Serranus atrobranchus	MINV	Х	Х	-	-	3	-
	Serranus baldwini	MINV	-	-	Х	1	-	-
	Diplectrum formosum	CAR	Х	Х	-	4	28	_

Family	Species	Trophic group	Laje de Santos MSP	Center Coast MEPA	Tuipiniquins ES	SE	ME	Targeted from fisheries
	Dules auriga	MINV	Х	Х	-	-	2	-
Epinephelidae	Mycteroperca acutirostris	CAR	Х	-	-	-	5	Х
	Epinephelus marginatus	CAR	Х	-	Х	1	3	Х
Malachantidae	Malacanthus plumieri	MINV	Х	-	-	-	2	-
Carangidae	Alectis ciliaris	CAR	Х	-	-	-	2	Х
	Caranx crysos	CAR	Х	Х	Х	128	8	Х
	Caranx latus	CAR	-	Х	Х	45	-	-
	Caranx ruber	CAR	-	Х	-	2	-	Х
	Chloroscombrus chrysurus	PLANK	-	-	Х	26	-	-
	Decapterus spp.	PLANK	-	Х	-	1	-	-
	Pseudocaranx dentex	CAR	Х	Х	Х	8	41	Х
	Seriola lalandi	CAR	Х	-	-	6	-	Х
	Seriola rivoliana	CAR	-	Х	-	1	-	Х
	Seriola spp.	CAR	Х	-	-	30	15	Х
	Trachinotus carolinus	MINV	-	-	Х	1	-	-
Lutjanidae	Lutjanus cyanopterus	CAR	Х	-	-	10	1	Х
	Lutjanus spp.	CAR	Х	Х	-	1	2	Х
	Rhomboplites aurorubens	CAR	Х	Х	-	62	96	Х
Haemulidae	Anisotremus virginicus	MINV	Х	Х	Х	30	8	-
	Anisotremus suringmensis	MINV	Х	-	Х	7	1	-
	Haemulon aurolineatum	MINV	Х	Х	Х	188	37	-
	Haemulon atlanticus	MINV	-	-	Х	2	0	-
	Haemulon parra	MINV	-	-	Х	1	0	-
Sparidae	Calamus spp.	MINV	Х	Х		1	2	-
	Diplodus argenteus	OMNI	Х	Х	Х	8	2	-
	Pagrus pagrus	MINV	Х	Х	-	3	181	Х
Scianidae	Odontoscion dentex	MINV	-	Х	Х	9	-	-
Muliidae	Pseudupeneus maculatus	MINV	X	X	X	2	2	-
Kyphosidae	Kyphosus spp.	HERB	Х	Х	Х	61	-	-
Chaetodontidae	Chaetodon striatus	SINV	-	X	X	9	-	-
	Heniochus acuminatus	SINV	Х	-	-	-	1	-

Family	Species	Trophic group	Laje de Santos MSP	Center Coast MEPA	Tuipiniquins ES	SE	ME	Targeted from fisheries
Pomacanthidae	Pomacanthus paru	SINV	Х	Х	Х	17	12	-
Pomacentridae	Abudefduf saxatilis	OMNI	-	Х	Х	18	-	-
	Chromis limbata	PLANK	-	Х	-	2	-	-
	Stegastes fuscus	HERB	-	Х	Х	19	-	-
Sphyraenidae	Sphyraena guachancho	CAR	-	Х	-	2	-	Х
Labridae	Bodianus pulchellus	MINV	Х	Х	-	2	1	-
	Bodianus rufus	MINV	Х	Х	-	3	-	-
	Halichoeres brasiliensis	MINV	-	Х	-	2	-	-
	Halichoeres poeyi	MINV	-	Х	Х	10	-	-
	Halichoeres spp.	MINV	-	Х	-	3	-	-
	Sparisoma axillare	HERB	-	Х	Х	8	-	-
	Sparisoma frondosum	HERB	-	Х	-	4	-	-
	Sparisoma spp.	HERB	-	Х	-	4	-	-
Bleniidae	Parablennius marmoreus	OMNI	-	Х	-	3	-	-
	Parablennius spp.	OMNI	Х	Х	-	2	4	-
Acanthuridae	Acanthurus spp.	HERB	-	-	Х	17	-	-
Bothidae	Bothus lunatus	MINV	-	Х	-	-	1	-
	Bothus ocellatus	MINV	-	Х	-	-	1	-
	Bothus robinsi	MINV	Х	-	-	-	1	-
Tetraodontidae	Sphoeroides spengleri	MINV	-	Х	Х	7	-	-
	Sphoeroides spp.	MINV	-	Х	-	2	-	-

3.3. Influence of habitat characteristics on fish assemblages

Top GAMM models from each predictor variable are listed in supplementary table S1 and in Figure 5. Considering pre-established metrics of graphic inclusion, for overall biomass, management regime composed the most parsimonious explanatory model (Fig. 6). Most parsimonious models for overall richness and abundance included temperature. Depth and mean relief were also included in explanatory models for overall abundance (Fig. 6). Richness of target species was mostly explained by management regime, depth and temperature, while biomass of the same group was explained by management regime.

Models for abundance of target species included depth and mean relief. In this case, an unexpected result indicated that commercially species were more abundant in shallow and with poor relief structure (Fig. 7). For non-target species, both richness and biomass most parsimonious models included temperature. Richness also included mean relief, as well as abundance of the same group. Non-target species showed higher levels of richness and abundance in habitats with high structural complexity (Fig. 8).

Considering trophic groups (Fig. 9), carnivores abundance tended to increase in shallow habitats. For mobile invertebrate feeders' biomass, mean relief plus management regime were important drivers. Sessile invertebrate feeders and planktivores abundance was mostly explained by mean relief but is important to highlight that while sessile invertebrate feeders' abundance increases with high complexity, planktivores' abundance decreases. SINV also included depth and temperature in explanatory models. The explanatory model for omnivores abundance included depth, with low levels of abundance in deep habitats. For herbivores biomass, management regime and mean relief were the principal drivers of distribution. The most parsimonious model for herbivores abundance included only depth, since we did not record this trophic group individuals in mesophotic zone.

4. Discussion

4.1. Depth as a structurer of fish assemblages

Despite the scientific consensus that MEs begin at 30 - 40 m in tropical areas (Bak et al., 2005; Brokovich et al., 2008; Hinderstein et al., 2010; Kahng et al., 2010; Pinheiro et al., 2016; Rosa et al., 2016; Turner et al., 2017; Rocha et al., 2018, Boland et al., 2020; Brown et al., 2022), our study suggests that in the subtropical SW Atlantic with a non-reef builders' substrate and high light attenuation, the upper boundary of ME can be shallower. Light attenuation is stronger in turbid waters due to proximity to shore and sediment suspension (Lorenzen, 1972). Under these conditions it is expected to find mesophotic communities in depths lower than 30 m (Laverick et al., 2020; Pérez-Castro et al., 2022).



Overall

Richness	X			
Biomass	X		х	X
Abundance	X	Х	Х	

Importance to commercial fisheries

Richness Target Species
Biomass Target Species
Abundance Target Species
Richness of non-Target Species
Biomass of non-Target Species
Abundance of non-Target Species

Х	Х	Х	Х
Х			Х
Х	Х	Х	
Х	Х	Х	
Х	Х		
	Х		

Biomass by trophic group

Carnivores	X		Х	
MINV	X	Х		Х
SINV	X	Х		
Herbivores		Х	-	Х
Omnivores			Х	
Planktivores	X	Х		

Abundance by trophic group



Figure 5. The importance of the predictor variables in distribution of response variables. X = top generalized additive mixed models for each response variable (see Table S1). Colors' intensity indicates the explanatory power of the predictor variables with the relative response variable. Stronger colors indicate stronger relationships.



Figure 6. Plots of the top generalized additive mixed models selected by the parsimonious principle. (A) total richness, (B) total biomass, (C, D, E) total abundance. Gray areas represent 95% confidence intervals. Abscissa axis are in logarithmical scale.

Differences in species composition was the main driver to differentiate shallow and deep strata. Some species were unique in shallow waters, such as some herbivores (e.g. *Stegastes fuscus, Acanthurus* spp., Labridae:Scarini and *Kyphosus* spp.). The convergence between the decrease in light penetration and the increasing depth causes a change in the benthic composition, with shallow reefs dominated by *turf* and macroalgae (Underwood et al., 1991; Aued et al., 2018) and MEs with a predominance of sandy bottoms, favoring the presence of herbivorous fishes in shallow habitats because of food availability and lack of predation. Although the tomtate grunt (*Haemulon aurolineatum*) was the most recorded fish species in the shallow zone (similar to Ferreira et al., 2004; Floeter et al., 2006; Gibran and Moura, 2012; Daros et al., 2018; Rolim et al., 2019 and Motta et al., 2021), it was also found in deeper habitats.



Figure 7. Plots of top generalized additive mixed models for target species selected by the parsimonious principle. (A, B, C) richness, (D) biomass, (E, F) abundance. Gray areas represent 95% confidence interval. Abscissa axis are in logarithmical scale.

This pattern is largely known and found in many studies worldwide (Feitoza et al., 2005; Brokovich et al., 2008, Kahng et al., 2010; Andradi-Brown et al., 2016; Rosa et al., 2016; Pinheiro et al., 2019; Williams et al., 2019; Boland et al., 2020). We suggest that the same occurs with omnivorous fishes. Despite the omnivores distribution in relation to depth is not a consensus for tropical and subtropical areas (Bejarano et al., 2014; Magalhães et al., 2015; Pyle et al., 2016; Rosa et al., 2016; Williams et al., 2019; Pimentel et al., 2022) we believe that food availability (which are directly related to depth) can be the principal driver to abundance distribution of omnivorous fishes.

Our records show that, despite the red porgy (*Pagrus pagrus*) distributes in depths from 0 to 200 m (Froese & Pauly, 2022), it has a greater preference for deeper habitats (> 18 m) than shallower zones (Ávila-da-Silva and Haimovici, 2006; Afonso et al., 2008). Small size individuals (< 25 cm) were mostly found in rocky reefs with a high mean relief, while the majority of medium size individuals (25 - 40 cm) showed a strong relation with the interface between rocky reefs and unconsolidated substrate.



Figure 8. Plots of top generalized additive mixed models for non-target species selected by the parsimonious principle. (A, B and C) richness, (D) biomass, (E) abundance. Gray areas represent 95% confidence interval. Abscissa axis are in logarithmical scale.

This difference of fish body size, i.e., total length, between high complex reefs and unconsolidated substrate may be related to the need for shelter to avoid predation in the early stages of life (Juanes, 2007; Anderson et al., 2022). The adults of the red porgy showed a great association with rhodolith beds (Anderson et al., 2022), but the high proportion and dominance of this species in deep sandy bottoms and rocky reefs of the subtropical SW Atlantic indicates that, despite the strong relation with the substrate type, depth is a very important factor determining the distribution of this species. On the other hand, the sand perch *Diplectrum formosum* (the second most representative species of the mesophotic zone) commonly inhabits sandy bottoms of shallow waters (up to 10 m) (Gibran 2002; 2007), indicating that the *D. formosum* shows a strong relationship with the habitat, inhabiting sandy bottoms despite the depth.



Figure 9. Plots of top generalized additive mixed models for trophic groups selected by the parsimonious principle. (A, B, D, E, H, I, J and K) abundance and (C, F and G) biomass. Abscissa axis are in logarithmical scale.

Fish assemblages of the two depth strata are very different. Indeed, turnover is the main driver of changes in species abundance and composition across depth gradients (Pinheiro et al., 2016, 2019; Rocha et al., 2018; Tuya et al., 2018). The differences between our findings and these previous works remains on species composition of shallow and deep strata. It was expected, since we are providing the first assessment of vertical structure of fish assemblages in the subtropical SW Atlantic, a completely different habitat than those tropical areas of cited previous works. We suspect that, due to the small range of MEs in our subtropical region (only 25 m), our deep community should be compared with the assemblage of upper MCEs, with a reduced number of deep specialist fish species. Also, it could extend until the shelf break because the influence of habitat and temperature. More studies are necessary to investigate if the deep fish assemblage of the subtropical waters of SW Atlantic is unique or if it divides into upper, middle and lower mesophotic fish assemblages along these 25 m of MEs that we have found, considering that the thermocline can influence species distribution.

The decrease in richness and abundance with increasing depth is corroborated by previous studies in tropical coral reefs (Kahng et al., 2010; Komyakova et al., 2013;

Andradi-Brown et al., 2016; Pinheiro et al., 2016; Asher et al., 2017; Tuya et al., 2018; Boland et al., 2020). However, even though we have higher richness and abundance in the shallow ecosystem in the subtropical SW Atlantic, the GAMM analyzes showed that temperature was a main driver of many response variables. Temperature is usually related to depth (Kahng et al., 2012), in which the temperature decreases with depth. However, in this case, because of a sharp and shallow thermocline (3 - 15 m, with a variation of 6.3°C) the temperature of some shallow samples remains almost the same as that of the mesophotic zone. Therefore, the peaks of total richness and abundance, richness and biomass of commercially non targeted species and SINV abundance means that each species show a strong preference for a determined temperature level. We expected a concentration of abundance rates in shallow zones due to the thermocline, following the expectations that marine fish species richness and abundance can be directly related to temperature (Allen et al., 2002). Our unexpected results may be related to physiological affinities of fish species (Manickchand-Heileman and Phillip, 1999; Furukawa et al., 2014; Brazo et al., 2021; Mihelakakis et al., 2021). In fact, nonlinear relationship between species richness and temperature were recorded before in tropical areas (Parravicini et al., 2013).

The fact that shallow waters shelter higher levels of carnivores' abundance was an unexpected result, contrary to several studies in tropical and temperate reefs (Feitoza et al., 2005; Brokovich et al., 2008; Andradi-Brown et al., 2016; Muñoz et al., 2017; Semmler et al., 2016; Pereira et al., 2018; Tuya et al., 2018; Williams et al., 2019; Boland et al., 2020; Silva et al., 2021). Carnivores are usually the main components of target species from fisheries, as apex or meso-predators. Higher abundance of this group in deeper strata is commonly associated with the possible capacity of deep reefs to serve as refuges from overfishing in shallow waters, which is supported by the Deep Reef Refugia Hypothesis (DRRH) (Bongaerts et al., 2010; Bejarano et al., 2014; Lindifield et al., 2015; Smith et al., 2019). In fact, some MEs can act as refuges from disturbances in tropical shallow areas (van open et al., 2011; Garavelli et al., 2018; Morais and Santos et al., 2018). However, we did not make this association for the subtropical SW Atlantic, especially because we found significant differences between assemblages of commercially target species, not indicating a connection between strata for this group. Furthermore, biomass of target species between strata are equivalent, suggesting a similar fishing pressure in both ecosystems.

4.2. Influence of habitat characteristics on fish assemblages

Abundance was mostly explained by mean relief, in which higher complex habitats presented higher levels of abundance. This was also found for total richness, biomass and abundance of non-target species. Indeed, this pattern is commonly found (Teixeira-Neves et al., 2015; Motta et al., 2021; Rolim et al., 2022a), especially because greater habitat complexity decreases rates and effects of competition and predation, since it offers more space, food availability and refuges (Hixon and Mence, 1991; Almany 2004a, 2004b; Graham and Nash, 2013; Komyakova et al., 2013). High complexity and heterogeneity also can promote the coexistence of species with different attributes, specialized on different habitats of the reef, as boulders, caves, vertical walls and sandy bottoms (Depczynski and Bellwood, 2004).

Fish biomass measurement is an important proxy to estimate ecosystem's productivity (Jenkins et al., 2015). This measure can provide the environmental health condition, since it is directly related to the energy flux between trophic groups as well as the provision of ecosystem services, as fishing resources (Cardinale et al., 2006; Forcada et al., 2008; Bar-On and Milo, 2019). In addition, ecosystems with higher biomasses are favored in ecological succession processes after disturbances (Lohbeck et al., 2015). Considering this, our results indicate that in the subtropical SW Atlantic, no-take areas are important to ensure the maintenance of biomass provided by ecological relationships and ecosystem services, including high biomasses of fisheries target species (Rolim et al., 2019a; Motta et al., 2021; Rolim et al., 2022a). The importance of these MPAs in terms of maintenance of natural processes and diversity was also highlighted by considerable higher levels of richness of fisheries target species when compared with open-access areas.

The red porgy and some elasmobranch species are the only mobile invertebrate feeder targeted by fisheries found in this study. The exploitation of median trophic groups follows the phenomenon caused by overfishing of large carnivores and top predators, predicted by Pauly et al. (1998), the fishing down the food webs. It is alarming, since the practice of fishing down marine food webs are unsustainable and may lead to fisheries stocks collapse (Pauly et al., 1998). However, this needs further investigation for effective conclusion in the subtropical SW Atlantic. The great abundance of this species in no-take areas suggests a possible fishing pressure on open-access areas and reinforces the capacity of no-take MPAs in increase the abundance of commercially target species (Rolim et al., 2019a; Motta et al., 2021).

A high variety of sessile benthic invertebrates, such as cnidarians, sponges, hydrozoans etc., which are mostly associated with hard substrate, compose the diet of sessile invertebrate feeders (Ferreira et al., 2004). Our results showed a positive relationship between mean relief and abundance of sessile invertebrate feeder group. Indeed, this was expected, since food availability is positively related to hard substrate. In the same perspective, the negative relationship between mean relief and planktivores abundance which are commonly found in pelagic habitats feeding on macro or micro-zooplankton (Ferreira et al., 2004). These results corroborate that the habitat influences species distribution (Floeter et al., 2006a; Ferrari et al., 2018; Rolim et al., 2022a). In the same way, sessile invertebrate feeders had a strong relationship with shallow habitats. In the studied region, shallow ecosystems are very heterogeneous and harbor great structural complexity, with a coral reef, rocky reefs and rhodolith beds (Pereira-Filho et al., 2019), habitats that offer great food availability to this trophic group.

We can conclude that the limits of ME are variable, depending on oceanographic and biological conditions. The combination of all habitat features acts structuring fish assemblages, and turnover is the main component of beta diversity influencing changes on assemblage composition across the depth gradient. We do not provide scientific basis to support the Deep Reef Refugia Hypothesis (DRRH), but we strongly recommend that further research be done at the species level. Mean relief and management were important drivers of fish distribution. Temperature was an important predictor, but physiological studies on the preference of each species for a certain temperature are necessary. We hope to contribute with scientific data to help MPA managements to know the natural attributes they harbor.

5. Conclusão

As diferenças entre as assembleias de recifes rasos e mesofóticos são causadas principalmente pela substituição de espécies e mudanças nas taxas de abundância ao longo da coluna d'água, o que acarreta na presença de duas assembleias praticamente distintas. A profundidade é um importante fator estruturador da comunidade, sendo limitante para distribuição de herbívoros e onívoros principalmente por estar relacionada a menor disponibilidade de alimento, diretamente associados ao substrato consolidado. Entretanto, há espécies do Atlântico Sudoeste que possuem grande afinidade com habitats mais profundos, como o pargo rosa (*Pagrus pagrus*), que desenvolve essa afinidade ao

longo de sua ontogenia, e o michole de areia listrado (*Diplectrum formosum*), que busca habitats de fundos de areia. Estas duas espécies foram as principais descritoras da assembleia da zona mesofótica subtropical no Atlântico Sudoeste.

Não encontramos ecossistemas mesofóticos atuando como refúgio para espécies ameaçadas pela pesca em recifes rasos, uma vez que a composição de espécies das assembleias entre zonas rasas e fundas é diferente. Além disso, a similaridade entre as biomassas dessas espécies entre ambientes rasos e mesofóticos indica que a pressão de pesca é equivalente em ambas as zonas de profundidade. Entretanto, espécies de peixes possuem diferentes características ontogenéticas e fisiológicas, podendo alcançar variações de profundidade e ótimos de temperatura distintos. Uma espécie generalista de profundidade pode ser mais explorada em zonas rasas, fazendo com que indivíduos maiores permaneçam em regiões mais fundas, nas quais sofram uma menor pressão de pesca. Tal fato seria um indício de refúgio de ambientes mesofóticos para determinadas espécies. Nesse contexto, recomendamos que pesquisas futuras se concentrem na investigação de possibilidade de refúgio para determinadas espécies de peixes compartilhadas entre os dois estratos. A grande riqueza e biomassa de espécies de interesse comercial em áreas protegidas indica que a região sofre pressão da atividade pesqueira e a efetividade das Unidades de Conservação de proteção integral, reforçando a necessidade e importância da manutenção dessas áreas de exclusão da pesca.

O relevo e o regime de gestão também foram importantes preditores da organização das assembleias. Não encontramos uma relação linear entre temperatura e os atributos da assembleia (riqueza, abundância e biomassa), sugerindo que cada espécie possui uma preferência por uma temperatura específica. Neste caso, a termoclina foi encontrada a partir dos 3 metros, fazendo com que todas as amostras permanecessem em águas mais frias do que a superfície e em uma faixa de alta variação da temperatura.

Investigar a estrutura vertical das assembleias de peixes é de extrema importância para a compreensão da diversidade local. Entretanto, mais estudos são necessários para uma descrição robusta dos ecossistemas mesofóticos subtropicais do Atlântico Sudoeste, como por exemplo, a caracterização da comunidade bentônica associada aos recifes rochosos e o mapeamento do assoalho marinho, a fim de entender a distribuição desses recifes na região.

Nosso estudo contribui para o entendimento de que ecossistemas mesofóticos são únicos e que também se encontram ameaçados por atividades antrópicas. É urgente a necessidade de estratégias de gestão visando a conservação desses ambientes considerando suas particularidades. Destacamos a importância do zoneamento tridimensional de Áreas Marinhas Protegidas (Levin et al., 2017), onde áreas mais rasas de Unidades de Conservação de uso sustentável permitam a pesca pelágica, mas onde ecossistemas fundos sejam excluídos dessas atividades a fim de proteger esses ambientes e a biodiversidade associada.

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