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**Declínio populacional da garoupa-verdadeira dentro e fora de uma área
marinha protegida no Atlântico sul ocidental**

Florianópolis

2023

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Orientador: Dr. Sergio Ricardo Floeter

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Declínio populacional da garoupa-verdadeira dentro e fora de uma área marinha protegida no Atlântico sul ocidental

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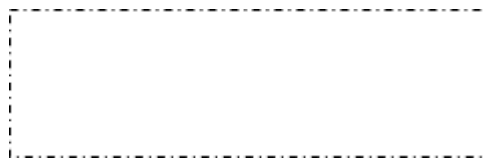
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Florianópolis, 2023.

Dedicado à minha família e a todos aqueles
que têm coragem de fazer ciência.

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Sally Rider

RESUMO

O declínio populacional de espécies é um problema global e as ações humanas são reconhecidas como um dos principais mecanismos responsáveis por esse cenário. Dentro dos ecossistemas marinhos, a pesca tem causado a depleção de diversas populações de peixes. Os predadores de topo estão entre os mais impactados devido ao seu alto valor comercial e a características ecofisiológicas que os tornam vulneráveis à exploração. Predadores de topo são espécies chaves nos ecossistemas marinhos, e sua depleção pode ter impactos na produtividade geral do sistema. Visando contornar essa questão, estratégias têm sido implementadas em todo o mundo com o objetivo de recuperar e beneficiar esse grupo. Entre essas estratégias, as áreas marinhas protegidas (AMPs) são amplamente utilizadas. No entanto, a eficácia de uma área protegida pode ser influenciada por múltiplos fatores, incluindo elementos ambientais e socioeconômicos. Nesse contexto, estudos de caso voltados em avaliar a resposta de populações frente a presença de AMPs são bastante úteis, pois contribuem para uma melhor compreensão dos mecanismos que podem estar por trás da efetividade, ou não, da área protegida. Este estudo teve como objetivo compreender se uma população vulnerável de um peixe predador de topo, sabidamente em declínio, está se beneficiando da presença de uma área marinha protegida no Atlântico sudoeste. A espécie modelo estudada foi a garoupa-verdadeira (*Epinephelus marginatus*), classificada como vulnerável pela IUCN. A AMP em questão é a Reserva Biológica Marinha do Arvoredo, uma área de proteção integral que está em vigor há mais de 30 anos. Foram compilados 16 anos de dados de censos visuais subaquáticos para avaliar as tendências temporais de densidade e biomassa da garoupa-verdadeira dentro e fora da AMP. Para examinar as tendências de densidade e biomassa dentro e fora da AMP foram utilizados modelos Bayesianos de Hurdle-gamma. Além disso, uma análise multinomial para dados proporcionais foi aplicada para investigar possíveis tendências na densidade das classes de vida da espécie. Os resultados revelaram um declínio preocupante na densidade/biomassa da garoupa-verdadeira dentro e fora da AMP ao longo do tempo, acentuado nos últimos cinco anos, indicando que a área protegida não está tendo o efeito esperado para a recuperação populacional da espécie. A classe de vida inicial, os recrutas, mostrou um declínio constante ao longo da série temporal, o que é particularmente preocupante e deve ser melhor investigado. Esses resultados diferem dos encontrados para outras AMPs no Mediterrâneo, onde as populações se beneficiaram significativamente da presença da área protegida. Fatores que podem estar por trás da ineficácia da Reserva Biológica Marinha do Arvoredo para a recuperação da garoupa-verdadeira incluem: atividades de pesca ilegal na região, partes do ciclo de vida da espécie ocorrendo fora dos limites da AMP, mecanismo denso-dependentes e eventos extremos.

Palavras-chave: Conservação; Predador de topo; Área Marinha Protegida; Garoupa verdadeira.

ABSTRACT

The decline in species populations is a global-scale issue and is widely acknowledged that human activities are the primary factors contributing to this scenario. Within marine ecosystems, fishing has been responsible for the depletion of several reef fish populations. Top predators are among the most impacted ones, given their high commercial value and life-history traits that make them vulnerable to exploitation. Furthermore, top predators are keystone species in marine ecosystems, and their depletion can have profound impacts on the overall productivity of the system. Among these, marine protected areas (MPAs) are widely used. However, the effectiveness of a protected area towards population recovery can be influenced by multiple factors, including environmental and socioeconomic elements. In this context, case studies aimed at evaluating the response of depleted populations to MPAs are quite useful, as they contribute to a better understanding of the mechanisms behind the effectiveness or ineffectiveness of the protected area. Thus, this study focused on understanding if a vulnerable top predator species population, known to be declining, benefits from the presence of a marine protected area in the southwestern Atlantic. The species studied is the dusky grouper (*Epinephelus marginatus*), an important predator considered vulnerable to extinction. The MPA is the Arvoredo Biological Marine Reserve, a no-take zone that has been in place for over 30 years. We compiled 16 years of underwater visual census data to evaluate the species' temporal trends in density and biomass inside and outside the MPA. For the analysis, we first applied a resampling method to address the imbalances present in the data. Then, we used Bayesian Hurdle gamma models to examine the density and biomass trends inside and outside the MPA. In addition, a multinomial model for proportional data and a visual analysis were used to investigate differences in life-stage categories between areas. The results revealed a worrying decline in the density/biomass of the dusky grouper both inside and outside the MPA over time, with a marked decrease in the last five years, indicating that the protected area is not having the expected effect on the species' population recovery. The early life stage, the recruits, showed a constant decline throughout the time series, which is particularly concerning and should be further investigated. These results differ from those found for other MPAs in the Mediterranean, where dusky grouper populations greatly benefited from protection. Factors that could be behind the low effectiveness of the Arvoredo Biological Marine Reserve include the non-compliance of fishermen, parts of the species' life cycle occurring outside the MPA boundaries, density-dependent mechanisms and extreme events.

Keywords: Conservation; Top predator; Marine protected area; Southwestern Atlantic; Dusky grouper.

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1 INTRODUÇÃO

O declínio populacional de espécies é um problema preocupante e cada vez mais evidente em todo o mundo (IPBES, 2019; WWF, 2022). Há décadas, estratégias destinadas a remediar essa questão vêm sendo propostas e implementadas, demonstrando ser cruciais para a sobrevivência e conservação das populações afetadas (LOTZE et al., 2011). No entanto, não há uma solução única que se aplique a todas as populações e cenários. Diversos fatores podem ser determinantes na resposta de uma população degradada frente a implementação de uma estratégia de conservação (SALAFSKY et al., 2002; GELL; ROBERTS, 2003). Estes fatores incluem desde questões temporais, como mudanças climáticas (BRUNO et al., 2018); espaciais, como o tamanho da área onde a medida foi implementada (CLAUDET et al., 2008); até biológicas, como a fecundidade dos indivíduos (MIATTA; BATES; SNELGROVE, 2021). Neste contexto, a realização de estudos de caso específicos que avaliam como populações degradadas reagem à implementação de estratégias de conservação é extremamente benéfica (SALAFSKY et al., 2002; GELL; ROBERTS, 2003). Por exemplo, através de estudos de caso é possível entender como diferentes espécies respondem a medidas de proteção, ou como fatores ambientais locais influenciam a recuperação de habitats (LOTZE et al., 2011). Além disso, essas análises fornecem insights valiosos para os tomadores de decisão, que podem utilizar das informações obtidas para desenvolver e aplicar ações de conservação mais efetivas. Isso inclui a escolha de estratégias adaptadas às necessidades específicas de cada ecossistema e espécie, bem como a alocação apropriada de recursos para áreas prioritárias. Ao integrar esses estudos de caso no planejamento e na implementação de políticas de conservação, pode-se alcançar uma abordagem mais holística e adaptativa, aumentando a eficácia global das medidas de proteção ambiental (LOTZE et al., 2011; MARTIN et al., 2012).

No Brasil, a conservação de peixes recifais é uma área que ainda tem muito a evoluir (FLOETER; HALPERN; FERREIRA, 2006; ROCHA; SAMPAIO, 2022). Apesar de o grupo ser essencial como fonte de alimentação para muitas pessoas e desempenhar um papel importante em vários segmentos da economia brasileira (IPBES, 2019, GAMARRA et al., 2023), pouco se sabe sobre o status de conservação de muitas espécies (FLOETER; HALPERN; FERREIRA, 2006; ROCHA; SAMPAIO, 2022). No Brasil, apenas 7.2% das espécies marinhas de peixes estão sob o guarda-chuva de algum instrumento regulatório voltado a sua

proteção (SILVA; SANTOS, 2023). Destas espécies, boa parte não conta com um programa de monitoramento adequado para avaliar os possíveis efeitos das medidas implementadas sob suas populações, sendo os principais programas de monitoramento no país voltados a comunidades e ecossistemas (ROQUE et al., 2018). Dessa forma, existe uma grande demanda por entender se os esforços que já vêm sendo feitos para a conservação dos peixes recifais no Brasil estão sendo efetivos para a recuperação e manutenção das populações.

Dentre as estratégias aplicadas à conservação de peixes recifais no Brasil e no mundo, as áreas marinhas protegidas (AMPs) parecem ter efeitos rápidos e duradouros para a conservação da biodiversidade (CÔTÉ; MOSQUEIRA; REYNOLDS, 2001). Criadas com o intuito de regulamentar e limitar os impactos antrópicos dentro de uma zona específica, AMPs podem ter diferentes enfoques, como a recuperação de ecossistemas degradados ou o manejo pesqueiro (AGARDY, 1994; GAINES et al., 2010). Embora a recuperação de populações específicas nem sempre seja o objetivo central das Áreas Marinhas Protegidas (AMPs), evidências indicam que elas são eficazes nesse sentido (CÔTÉ; MOSQUEIRA; REYNOLDS, 2001). Por exemplo, populações de peixes visadas pela pesca mostram respostas rápidas e benéficas à criação de AMPs. Isso ocorre porque o principal fator limitante para o tamanho dessas populações, a intervenção humana, é eliminado ou minimizado nas AMPs (MOSQUERA et al., 2000; CÔTÉ; MOSQUEIRA; REYNOLDS, 2001).

Um dos grupos de peixes recifais diretamente impactado pela pesca, e cujas populações vêm sofrendo declínios importantes devido à sobre-exploração humana no Brasil e no mundo, são os grandes predadores, como tubarões, garoupas (Epinephelidae) e vermelhos (Lutjanidae) (PAULY et al., 1998; MYERS; WORM, 2003; BENDER et al., 2013). Estes organismos ocupam os mais altos níveis tróficos e exercem papéis chaves na regulação da estrutura trófica e no funcionamento das comunidades (PAULY et al., 1998; HEITHAUS et al., 2008). Ademais, muitas espécies possuem grande valor econômico e cultural, sendo uma importante fonte de renda para as comunidades costeiras (KNIP; HEUPEL; SIMPFENDORFER, 2010; MITCHESON et al., 2013). Contudo, algumas características da sua história de vida os tornam vulneráveis à exploração humana (REYNOLDS et al., 2005). Por exemplo, maturidade tardia e alta longevidade, que propiciam a captura de indivíduos ainda imaturos e diminuem a resiliência frente a distúrbios (REYNOLDS;

IENNINGS; DULVY, 2001). Deste modo, a redução das populações é algo comum, e vem levando a impactos ecológicos e socioeconômicos significativos em diversas regiões (MYERS; WORM, 2003; MITCHESON et al., 2013; DULVY et al., 2021).

Os poucos estudos brasileiros que analisaram séries temporais pesqueiras relatam uma exploração tão intensa de certas espécies de grandes predadores que sua pesca se tornou insustentável, fazendo com que pescadores migrassem destes predadores de topo para níveis tróficos subsequentes (FREIRE; PAULY, 2010; FOGLIARINI et al., 2021). Este fenômeno tende a seguir acontecendo, com a pesca explorando níveis tróficos cada vez menores à medida que os mais altos são exauridos (PAULY et al., 1998). Ecologicamente, essa depleção pode implicar em desbalanços e degradações das teias tróficas atingidas (PINCINATO; GASALLA, 2010; BORNATOWSKI et al., 2014). Assim, a fim de interromper esse ciclo de sobre-exploração e degradação trófica, prevenindo o colapso dos ecossistemas e das pescarias afetadas, é essencial que sejam implementadas estratégias de conservação eficientes para grandes predadores (PAULY et al., 1998; ESSINGTON; BEAUDREAU; WIEDENMANN, 2006).

Estudos de caso focados em avaliar o status populacional de predadores de alto nível trófico e sua resposta frente a estratégias de conservação podem contribuir significativamente para a preservação deste grupo bem como de suas funções e serviços ecossistêmicos (LOTZE et al., 2011; PAULY et al., 2002; HEITHAUS et al., 2008). Tais estudos podem ainda ser chave para quebrar cascatas de sobre-exploração (PAULY et al., 1998). Acompanhar o desempenho das áreas marinhas protegidas pode ainda fornecer insights importantes sobre sua efetividade, o que vem se provando importante para a conservação da biodiversidade marinha no mundo todo (SALA; GIAKOUMI, 2017) e para conservação de espécies cruciais na saúde dos ecossistemas (HAZEN et al., 2019). Dito isso, o Brasil é uma região de grande interesse para estudos com este enfoque, dado que: possui um histórico de depleção de grandes predadores (LOPES et al., 2016); poucos trabalhos deste tipo foram realizados no país (ROCHA; SAMPAIO, 2022; PEREIRA et al., 2022; ANDERSON et al., 2014); e esforços de conservação para os peixes recifais brasileiros demandam uma maior atenção (FLOETER; HALPERN; FERREIRA, 2006; ROCHA; SAMPAIO, 2022). Assim, essa dissertação tem por objetivo entender a dinâmica populacional de uma espécie de peixe predadora emblemática em uma das áreas de preservação integral mais antigas do país, localizada no Sul do Brasil.

O estudo de caso

Este estudo tem como foco a população de garoupa-verdadeira (*Epinephelus marginatus* (LOWE, 1834)) dentro de uma área marinha protegida na região sul do Brasil, mais precisamente na Reserva Biológica Marinha do Arvoredo e zonas adjacentes. A região estudada é uma zona de transição climática subtropical-quente-temperada, sendo influenciada por águas frias vindas do sul e quentes do norte (Figura 1) (ANDERSON et al., 2015; SEGAL, 2017; SILVA; SANTOS, 2023). Dado que a garoupa-verdadeira possui uma preferência por águas subtropicais, esta é uma área importante para a distribuição da espécie no Atlântico sul ocidental (MESA; LOUISY; VACCHI, 2002; LOPES et al., 2019).



Figura 1 – Mapa da região de estudo no litoral sul do Brasil, mostrando as principais ilhas: Ilha do Galé (1), Ilha Deserta (2), Ilha do Arvoredo (MP–A) - porção dentro da Reserva Biológica Marinha do Arvoredo (3), Ilha do Arvoredo (NP–Z) - zona não protegida da Ilha do Arvoredo (4), e Ilha do Xavier (5). A área delimitada por linhas pontilhadas representa a Reserva Biológica Marinha do Arvoredo. A inserção no canto superior esquerdo indica a localização da área de estudo no subcontinente sul-americano.

A garoupa-verdadeira é um peixe predador de alto a médio nível trófico (CONDINI; GARCÍA-CHARTON; GARCIA, 2018), e possui uma importância econômica e cultural significativamente alta para as comunidades costeiras brasileiras (BEGOSSI; SILVANO, 2008a; SILVANO et al., 2017; FOGLIARINI et al., 2021). Suas populações encontram-se em declínio, sendo consideradas vulneráveis em escala global pela IUCN e também nacional pelas avaliações brasileiras (POLLARD et al., 2018; MMA, 2022b). Reconhece-se nacionalmente a importância e a vulnerabilidade da garoupa-verdadeira ao selecioná-la como uma das sete espécies de fauna ameaçadas de extinção estampadas nas cédulas brasileiras (Figura 2). Com relação às estratégias de conservação existentes que podem auxiliar na recuperação da espécie, algumas são relativamente recentes, como é o caso de boa parte da regulamentação pesqueira, implementada em 2018 (MMA, 2018). Por outro lado, existem outras medidas, como as áreas marinhas protegidas, que estão em vigor há décadas (MMA, 2022a), mas mesmo assim pouco se sabe sobre seus efeitos na população (FLOETER; HALPERN; FERREIRA, 2006; ANDERSON et al., 2015; ROCHA; SAMPAIO, 2022).



Figura 2 – Cédula de cem Reais (R\$100,00), Banco Central do Brasil.

A Reserva Biológica Marinha do Arvoredo, uma das mais antigas áreas marinhas de proteção integral do Brasil (MMA, 2022a), tem grande potencial de estar contribuindo para a recuperação da garoupa-verdadeira (ANDERSON et al., 2015; ANDERSON; JOYEUX; FLOETER, 2020). Esta área apresenta três das cinco características que aumentam exponencialmente a efetividade de unidades de

conservação: é uma área no-take, ou seja, onde a extração é completamente proibida; antiga, tendo sido implementada a mais de 30 anos; e de grande extensão, cobrindo 17600 hectares (EDGAR et al., 2014; MMA, 2022a). Além disso, áreas marinhas protegidas tem se mostrado benéficas para a garoupa-verdadeira em outras localidades, onde foram vistos aumentos notáveis na abundância e biomassa da espécie (GARCÍA-RUBIES; HEREU; ZABALA, 2013; HACKRADT et al., 2014; LORENZO; CLAUDET; GUIDETTI, 2016). Estes fatores reforçam a ideia de uma possível contribuição positiva da Reserva Biológica Marinha do Arvoredo para a recuperação da garoupa-verdadeira. No sul do Brasil, região onde a unidade está localizada, a garoupa-verdadeira é um dos principais predadores e um importante recurso pesqueiro (ANDERSON et al., 2015; FOGLIARINI et al., 2021). Desse modo, a efetividade da unidade em recuperar esta espécie pode ser chave para garantir o equilíbrio da comunidade recifal como um todo (HEITHAUS et al., 2008; PINCINATO; GASALLA, 2010), assim como a sustentabilidade das pescarias locais (SILVANO et al., 2017; FOGLIARINI et al., 2021). Ademais, na região sul do Brasil, a presença da garoupa-verdadeira como um dos principais predadores de topo reflete um contexto histórico de depleção de espécies (BORNATOWSKI et al., 2017; LECHETA; AFONSO; CHAVES, 2017; FOGLIARINI et al., 2021). Relatos da década de 50 apontam a forte presença de outros grandes predadores, como meros (*Epinephelus itajara*) e tubarões-mangona (*Carcharias taurus*). Narrativas contam que durante esta época não era incomum que pescarias de apenas algumas horas, feitas por poucos indivíduos, resultassem na captura destas espécies (Figura 2) (SOUZA, 2000).

Contudo, a exploração excessiva resultou na inviabilidade econômica da pesca desses grandes predadores (BORNATOWSKI et al., 2017) e a escassez de registros sugere uma extinção funcional desses organismos na região (ANDERSON et al., 2014; VALIENTE BANUET et al., 2015). Assim, a garoupa-verdadeira, que anteriormente ocupava um nível trófico intermediário como um mesopredador, agora ocupa o topo da cadeia alimentar e se tornou um importante alvo da pesca (BEGOSSI; SILVANO, 2008b; BEGOSSI et al., 2019). Porém, a garoupa-verdadeira parece estar seguindo este padrão de sobre-exploração, dado que pescadores já estão migrando dessa espécie para níveis tróficos menores, devido a baixa abundância de indivíduos (FOGLIARINI et al., 2021). Dito isso, fica clara a importância de se entender se uma das estratégias de conservação mais antigas e

importantes presentes na região está contribuindo para a recuperação da vulnerável população da garoupa-verdadeira, cuja depleção representa a continuidade de um cenário de exploração não sustentável (FREIRE; PAULY, 2010; LECHETA; AFONSO; CHAVES, 2017).



Figura 3 – Resultado de aproximadamente 6 horas de caça submarina na Ilha das Galés, Porto Belo em 1960. Na foto estão os dois pescadores, Vitor Cardoso e Augusto (paulista) e suas caças: 5 cações-mangonas e 3 meros, que totalizaram 720 kg. Foto retirada do livro *O Homem da Ilha e os Pioneiros da Caça Submarina* (Souza, 2000).

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2 CAPÍTULO ÚNICO

POPULATION DECLINE OF THE DUSKY GROUPER INSIDE AND OUTSIDE A MARINE PROTECTED AREA IN THE SOUTHWESTERN ATLANTIC

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Population decline of the dusky grouper inside and outside a marine protected area in the southwestern Atlantic

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Abstract

Understanding the impacts of human activities on marine species over time and how to mitigate them is a major challenge in conserving marine resources. Many fish species, especially marine top predators, are highly depleted and rely on population monitoring and conservation strategies for maintenance. The implementation of Marine Protected Areas (MPAs) is widely accepted as a measure to address this issue. MPAs regulate human activities within their boundaries and can provide crucial information about population recovery when such activities are restricted or managed. In this study, we compiled 16 years of underwater visual census data to evaluate temporal trends in the density and biomass of the dusky grouper (*Epinephelus marginatus*), an important and highly targeted predatory fish, both inside and outside a strict nature Marine Reserve. Our findings reveal a concerning decline in the density and biomass of dusky groupers within and outside the MPA, especially in the last five years of the time series, contradicting initial expectations of positive population trends within the protected area. The recruit life stage showed a constant decline throughout the time series, which is particularly concerning and should be further investigated. We discuss the impacts of human activities on the dusky grouper population, addressing multiple life stages, with a particular focus on juvenile recruits known to settle outside the MPA. Therefore, it is imperative to reevaluate current conservation efforts and conduct further studies to understand the mechanisms driving the observed decline.

Keywords: Conservation, top predator, marine protected area, southwestern Atlantic.

1 Introduction

The rapid growth rate of the human population has led to the expansion and intensification of essential human activities, such as fishing (IPBES, 2019). Fisheries are crucial in providing food and income (IPBES, 2019; Pauly et al., 1998, 2002). However, high human demand for food and other resources has led to unsustainable practices, significantly impacting the environment (Pauly et al., 1998, 2002). A major concern is the depletion of key marine species such as top predators and large herbivores (Stergiou, 2002; Daskalov et al., 2007; Kvamsdal et al., 2023). Many of these species, due to their high commercial value, are prime targets in fisheries (Sadovy de Mitcheson et al., 2013; Fogliarini et al., 2021). Additionally, traits like long lifespans and delayed maturity make them particularly vulnerable to exploitation (Reynolds et al., 2005). As a result, population depletion is a frequent occurrence, posing a significant challenge for conservation efforts (Myers and Worm, 2003; Dulvy et al., 2021; Sadovy de Mitcheson et al., 2013).

The depletion of key marine species like sharks, rays, and certain large fish profoundly impact ecosystem processes (Myers and Worm, 2003; Heithaus et al., 2008). These species are vital for ecological functions including the regulation of trophic webs, nutrient cycling, and habitat structuring, which contribute to the overall productivity of the marine system (Jackson et al., 2001; Jordan, 2009). Additionally, studies indicate that many coastal fish communities, such as sharks and rays, have been so overexploited that their functional roles in the ecosystem are no longer effectively fulfilled (Coleman and Williams, 2002; Heithaus et al., 2008; Bellwood et al., 2012; Payne et al., 2016). Evaluating the population dynamics of the high trophic level species over time and developing comprehensive protection strategies is important to prevent not only their depletion but also their ecosystem-wide impacts (Estes et al., 2011; Sadovy de Mitcheson et al., 2013).

Considering that protection strategies for top predator populations are already implemented worldwide, it is crucial to monitor and evaluate their effectiveness (Camphuysen, 2006; Natsukawa and Sergio, 2022). In this context, marine protected areas (MPAs), widely accepted for protecting marine diversity, play a significant role (Russ and Alcala, 2004; Edgar et al., 2014). MPAs are designed in various forms to meet different objectives, including biodiversity conservation, fisheries management, and ecosystem restoration (Gell and Roberts, 2003; Gaines et al., 2010). These range from no-take zones, where all forms of extraction are prohibited, to multiple-use MPAs, which allow sustainable resource utilization while protecting critical habitats (Gaines et al., 2010; Sciberras et al., 2015). A primary benefit of MPAs is the recovery of targeted fish populations (Marshall et al., 2019; Ovando et al., 2021). However, the success of MPAs in this regard is not guaranteed and depends on multiple factors. These include species traits like longevity and mobility (Hooker et al., 2011; Pilyugin et al., 2016; Miatta et al., 2021), as well as characteristics of the MPAs themselves, such as the level of protection, enforcement, age, size, and type of habitat protected (Claudet et al., 2008; Babcock et al., 2010; Ovando et al., 2021). Therefore, ongoing studies that evaluate the effectiveness of MPAs over time are essential for assessing conservation progress in marine populations (Goldsmith, 2012).

Groupers (Epinephelidae) serve as good models for studies on species conservation and MPA effectiveness, since they comprise top and mesopredators which are highly valued and impacted by fishing (Anderson et al., 2014; Hackradt et al., 2014). It is estimated that approximately 25% of grouper species face

some level of threat according to IUCN criteria, ranging from vulnerable to critically endangered (Sadovy de Mitcheson et al., 2013). In the Mediterranean Sea, the effectiveness of MPAs for grouper conservation has been demonstrated, with benefits including increased biomass, abundance, and positive changes in demographic structure, such as a higher proportion of larger, mature individuals (García-Rubies et al., 2013; Hackradt et al., 2014). However, conservation efforts in the southwestern Atlantic are notably less substantial (Floeter et al., 2006; Anderson et al., 2014, 2020). Given the documented negative impacts of fishing on grouper populations in this region (Floeter et al., 2006; Bender et al., 2014; Silvano et al., 2017; Fogliarini et al., 2021), and the variable effectiveness of MPAs (Gerhardinger et al., 2011; Ferreira et al., 2022), continuous monitoring and research are essential to guarantee the maintenance of these key fish species populations.

Brazil plays a pivotal role in the global conservation of groupers, hosting numerous endangered species (Silvano et al., 2017). Among these, the dusky grouper *Epinephelus marginatus* (Lowe, 1834) is particularly noteworthy. Classified as vulnerable by IUCN standards and Brazilian assessments, this species is not only highly valued by local fishermen but also culturally significant, as evidenced by its depiction on Brazil's 100 Real bills (Silvano et al., 2017; Begossi et al., 2019; Fogliarini et al., 2021). In the Arvoredo Biological Marine Reserve (ABMR hereafter), a critical no-take MPA in southern Brazil, the dusky grouper is a key top predator, having ascended from a mesopredator role due to the depletion of other top predators like the sand tiger shark (*Carcharias taurus*) and the Atlantic goliath grouper (*Epinephelus itajara*) (Souza, 2000; Anderson et al., 2015; Fogliarini et al., 2021). The ABMR is one of the oldest MPAs in the country, spanning over 30 years, however, it is located just 6.5 km from the coast, a proximity that highlights its vulnerability to illegal fishing activities (Godoy et al., 2006; Edgar et al., 2014). Therefore, the survival of the dusky grouper's population in the ABMR region, amidst the vulnerabilities of both the species and the reserve, hinges critically on continuous and effective monitoring (Mosquera et al., 2000; Camphuysen, 2006).

Here, we analyzed 16 years of Underwater Visual Census (UVC) data to achieve two main objectives. First, we aimed to investigate the population dynamics of the dusky grouper (*Epinephelus marginatus*) inside and outside the MPA. Based on previous studies (Babcock et al., 2010; Hackradt et al., 2014), we expected to observe a consistent increase in biomass within the MPA, suggesting its effectiveness as a refuge for the growth and development of dusky grouper populations. Conversely, in areas subject to fishing, we anticipated at least the maintenance of biomass levels, considering the potential spillover benefits from the MPA and existing fishing regulations (García-Rubies et al., 2013; Mourato et al., 2018). Our second objective was to assess differences among the various life stages of the dusky grouper inside and outside the MPA over time. We hypothesized that there would be increased densities of all life stages within the MPA, particularly benefiting larger individuals often targeted by fisheries (Anderson et al., 2014; Fogliarini et al., 2021).

2 Methods

2.1 Study area

The study area encompasses five sites, three inside and two outside of the ABMR (Fig. 1). This MPA is

located in southern Brazil, in Santa Catarina state, and is a no-take Reserve [according to the IUCN category; (Dudley, 2008)] with 17600 hectares and more than 30 years old (IBAMA, 1995). Protected locations correspond to the Galé (27°10'S and 48°24'W), Deserta (27°27'S and 48°33'W), and Arvoredo island (27°16'S and 48°22'W, northern portion). Arvoredo Island encompasses both sites within and outside the marine protected area (MPA). Specifically, one unprotected site is located in the southwest portion of the island (coordinates: (27°17'S and 48°22'W). The other location outside the MPA is Xavier Island (27°36'S and 48°23'W). All locations are characterized by hard substrates including rocky reefs, which end in sandy bottoms at around 12-15 m depth (Aued et al, 2018). The composition of life forms is particularly defined by the temperature dynamics of the region, a subtropical-warm-temperate transition zone (Segal, 2017; Silva et al, 2023). Therefore, the rocky substrate is mainly covered by algal turfs, macroalgae, and zoanthids (Segal, 2017; Aued et al, 2018), and tropical fish communities live side by side with species that can tolerate colder waters (Anderson et al, 2015; Silva et al, 2023).

2.2 Species information

The dusky grouper (*Epinephelus marginatus*; Family Epinephelidae) is one of the most important and emblematic predators in Brazilian southern rocky reefs (Begossi et al, 2019). Their distribution include the southwestern Atlantic transition zone, which presents sub-tropical waters preferred by the species (La Mesa et al, 2002; Lopes et al, 2019). The dusky grouper is a large-bodied monandric protogynous hermaphrodite (Marino et al, 2001), reaching a maximum length of 150 cm (total length) (Reiner, 1996) and weighing up to 60 kg (Menezes and Figueiredo, 1985). This specie is characterized by slow growth and a lifespan of up to 60 years (Reñones et al, 2007). In Brazil, it is believed that the species reaches the first sexual maturity as females at around 46-49 cm (length at first maturity; Andrade et al, 2003), transitioning to males between 9 and 16 years of age (Chauvet, 1988) or earlier (around 7 years; Reñones et al, 2010). Initially classified as near threatened by the IUCN in 1996, its status changed to endangered in 2014 and has been considered vulnerable since 2018 (Pollard et al., 2018). Brazilian assessments have listed it as vulnerable since 2014 (MMA, 2022). In response, Brazil established a recovery plan for the species in 2018 and implemented specific fishing regulations in 2019, including a size limit for catch (minimum 47 cm and maximum 73 cm), a closed fishing season from November 1st to February 28th, and a restriction on the size of fishing vessels to a maximum of 20 feet (MMA, 2018; Mourato et al., 2018).

2.3 Database

We compiled 1,727 Underwater Visual Censuses (UVCs) of fish assemblages in the southwestern Atlantic (SWA), spanning a period of 16 years from 2008 to 2023, sourced from the TimeFISH online repository (Quimbayo et al., 2023) and the Laboratory of Biogeography and Macroecology from the Federal University of Santa Catarina database. Each UVC required divers to perform a 2 × 20 meters belt transect to identify, count, and measure the size (to the nearest centimeter of total body length) of all encountered fish (Floeter et al., 2017). From this data, we filtered the dusky grouper (*E. marginatus*) presence and established the absence over time by

noting occurrences in all transects where the species was observed and recording zeros where it was not (Bacheler et al., 2017). Then, we classified the observed individuals based on several factors: their biology (Andrade et al, 2003; Condini et al, 2013, 2018), geometric progressions (Harmelin-Vivien et al, 1985; García-Charton et al, 2000), previous studies (Félix-Hackradt et al, 2013; Anderson et al, 2020) and the current fisheries regulations in Brazil (MMA, 2018). The categories were as follows: *Recruits* (individuals less than or equal to 10 cm, following geometric progressions and data sensitivity); *Juvenile* (11-30 cm), representing juvenile individuals below the size where fishing pressure increases; *Subadult* (31-47 cm), for individuals that are more attractive to fisheries but have not yet reached the first estimated maturation size; *Adult* (47-73 cm), likely matured and within the legal capture size range; and the *Reproductive Matrix* (above 73 cm), comprising individuals with higher fecundity rates where fishing is restricted. To estimate fish biomass, we used the length-weight relationship formula $W = a * TL^b$, where W represents the total wet weight in grams, 'a' and 'b' are species-specific allometric coefficients (0.0091 and 3.1149 respectively, based on Froese and Pauly., 2023), and 'TL' is the total length in centimeters (Palomares et al., 2020).

2.4 Resampling method

The dataset we utilized exhibits certain limitations, such as gaps in the time series and inconsistent sampling efforts across different years. To account for the potential bias these issues might introduce (Manly, 2006), we employed a bootstrap resampling technique, similar to the process used in rarefaction curve analyses (Magurran and McGill, 2010). Our initial step involved identifying the smallest sample area in the time series, which was 120 m², recorded at the Arvoredo MPA site in 2012. We then randomly selected an equivalent number of transects from all locations and years, estimating the density and biomass of *E. marginatus* for each transect. Due to the variety of transect combinations possible for creating this minimum sample area, we performed bootstrapping 1000 times. This process generated distributions for the estimated metrics (Manly, 2006; Quimbayo et al, 2019; Silva et al, 2023), and we calculated the mean values for density and biomass from these bootstrap distributions for use in further analyses. Ultimately, we created two separate datasets for analysis: The first, a general bootstrap matrix, treated all individuals without distinction in size classes and grouped mean values by years, islands, and protection categories. The second, a life-stage-based bootstrap matrix, went a step further by also grouping mean values according to the life-stage categories of the species. In addition, in this dataset each row represented a single individual of *E. marginatus*. This approach enabled us to conduct a comprehensive analysis, considering both the overall population and the specific life stages of the species.

2.5 Statistical analysis

To understand the relationship between the biomass and density estimates with the year and the protection category, we employed Bayesian gamma-hurdle models with a zero-inflated gamma distribution for the general bootstrap matrix data (Heilbron, 1994; Kroon et al, 2021). This approach was taken as our data showed a large number of absences, represented as zeros. In this case, using a zero-inflated model, which allows for separate modeling of the probability of a zero value and the distribution of non-zero values (Welsh et al.,

1996), provided more accurate estimates and a better fit. The model was implemented using the 'brms' package in R (Bürkener, 2021). Both density and biomass, *i.e.* response variables, and the hurdle component were modeled as a function of year and protection category (protected and unprotected). Bayesian inference was performed with four chains, each consisting of 20,000 iterations. Default priors were used for the biomass model, while for the density model the function 'get_prior' from the 'brms' package was used to define priors. A warm-up period of 10,000 iterations was used, and a thinning rate of one was applied. After discarding the warm-up iterations, a total of 40,000 post-warm-up draws were retained for posterior inference. Summary statistics and credible intervals were computed from the posterior samples for inference and interpretation.

To investigate whether the population structure varies with protection categories and over time, we utilized a multinomial model for proportional data. The analysis was conducted using the life-stage-based bootstrap matrix. Due to the sparse distribution of individuals across each life stage, the continuous 'year' variable was divided into four discrete time periods: 2008-2010, 2011-2014, 2015-2018, and 2019-2023. Utilizing the *multim()* function from R's 'nnet' package, we modeled 'class', representing various life stages, as the response variable, with 'period' (derived from 'year') and 'protection category' (inside or outside the ABMR) as predictors. The fit of the model was assessed using a likelihood ratio test, and the statistical significance of the explanatory variables was evaluated using Wald chi-square tests, from which z-values and corresponding p-values were derived to determine the impact of each predictor on the response variable. Interpretations were drawn from the coefficient estimates, reflecting the change in log odds for each life stage class with unit shifts in predictors. These log odds were then transformed into probabilities, and generalized additive models (GAM) were utilized to elucidate trends through time inside/outside the Marine Reserve. All analyses were conducted in R version 4.2.2 (Team, 2009).

3 Results

3.1 Data Exploration

A visual data exploration (Fig. 1) shows a smaller mean density and an increase in grouper absence frequency in the latest years, especially since 2019. Until 2018 there was only a single island within one year (Arvoredo MPA-2012) where sampling was performed but no dusky grouper individuals were found. From 2019 onwards, all sites inside and outside the protected area had at least one absence recorded, with not even a single specimen recorded at the Arvoredo unprotected site. Density means are also smaller in the last five years, with a mean value of 0.005 individuals/m² per year. This value represents almost 95% reduction compared to the mean density of 1.102 individuals/m² per year in 2007-2018 timeframe (Table S3).

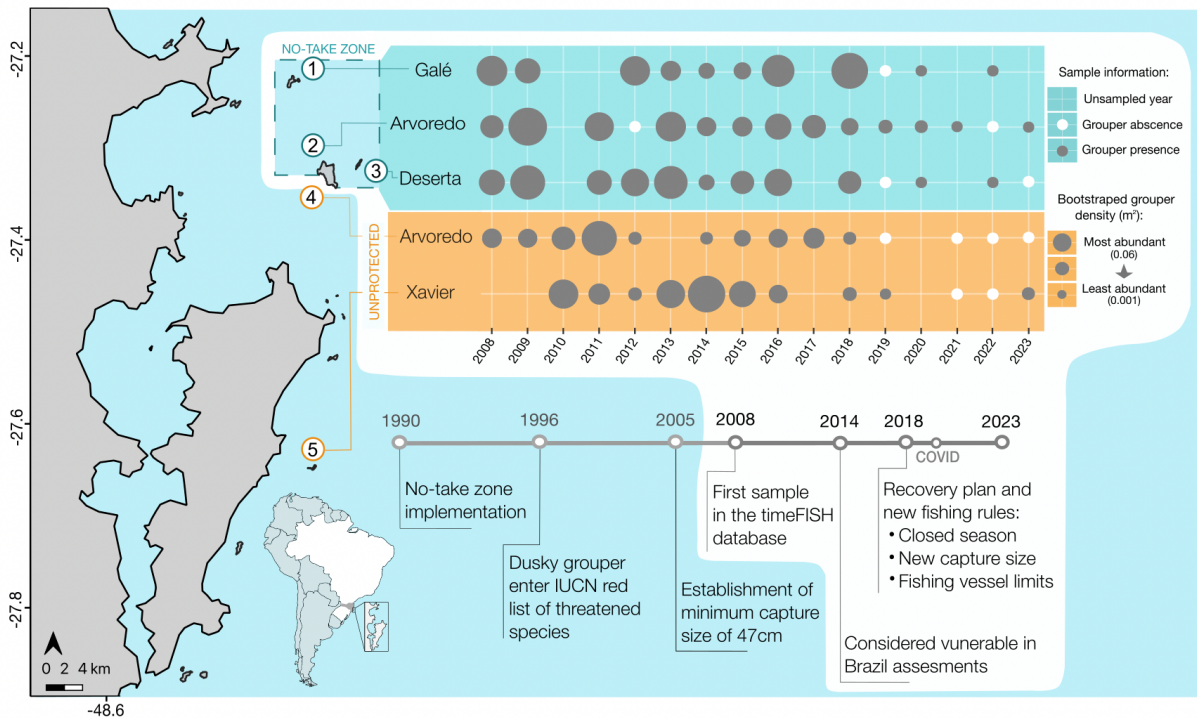


Fig. 1 Study Site Map and Grouper Conservation Timeline. The map on the left displays the sample locations in Santa Catarina: Galé, Arvoredo (protected), Deserta, Arvoredo (unprotected) and Xavier. The ABMR area is delineated with a dashed outline. On the right, an abstract graph shows grouper densities: blue for no-take zones and orange for unprotected areas, with circles depicting the presence (grey) or absence (white) of the species. Circle size varies to reflect population density obtained through resampling; the larger the circle, the higher the density. The timeline at the bottom right details conservation milestones and other relevant information from 1990 to 2023 (see text section 2.1 for references), with the study period highlighted in white to indicate the scope of the data included in the research.

3.2 No-take and unprotected populational trends

The model revealed declining trends in both density and biomass, with no significant differences observed between protected and unprotected areas (Fig. 2; Supplementary Table S1). Density displayed a gradual decline across the study period, with a more pronounced decrease starting from 2019 (Fig.s 1 and 2; Fig. S1; Supplementary Table S2). The downward trend in mean density was associated with both an increase in the frequency of absences and a decrease in the density of individuals over time. This trend is evidenced by a significant positive relationship in the occurrence of zero counts (0.19, lower 95% confidence interval [CI]; 0.77, upper 95% CI) and by a significant negative relationship in the non-zero densities (-1555.82, lower 95% CI; -385.34, upper 95% CI). Biomass remained relatively stable until 2018, before experiencing a notable decrease in recent years. This reduction in mean biomass was attributed to an increasing trend in the absence of individuals over time, as evidenced by a significant and positive probability of encountering zero values (0.2 lower 95% confidence interval [CI] to 0.77 upper 95% CI). Despite the conditional effects suggesting higher

mean values in protected areas, statistical analysis across all models failed to confirm a significant relationship between an area's protection status and the trends observed. Detailed model estimate values and additional information are available in the Supplementary Material, Tables S1 and S3.

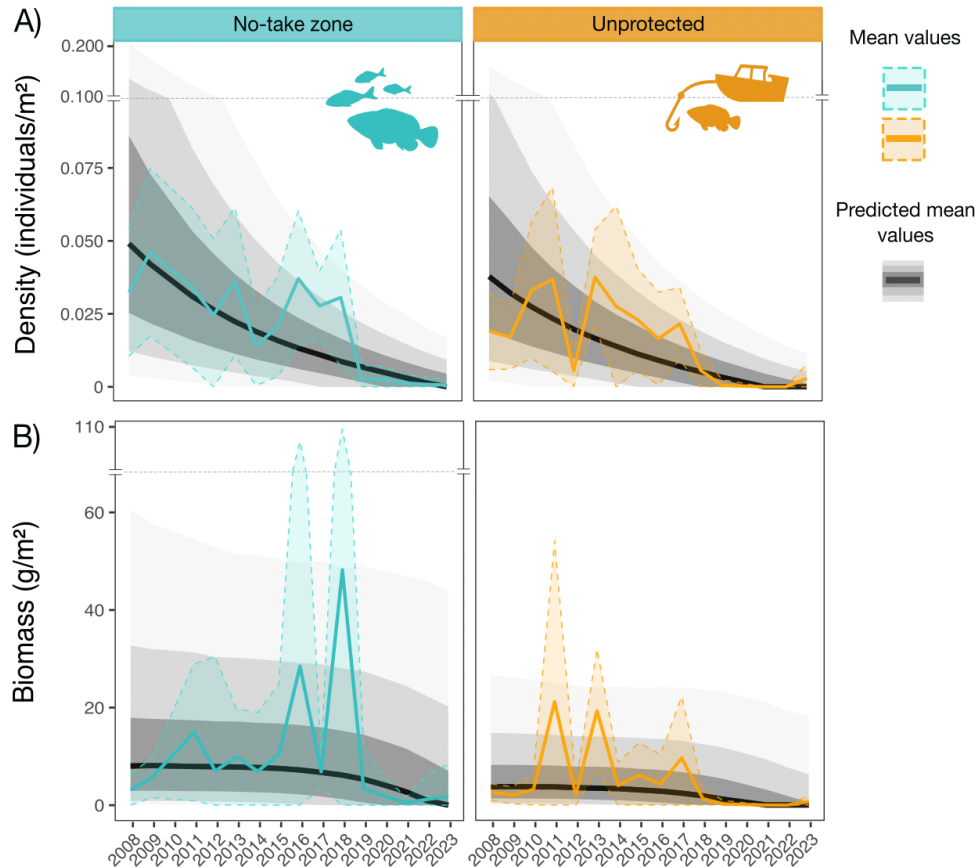


Fig. 2 Temporal trends for dusky grouper mean density (A) and biomass (B) inside (no-take zone) and outside (unprotected) the marine Reserve. The left panels in blue and the right panels in orange display the trends within and outside the Reserve, respectively. The continuous black lines indicate the trends predicted by gamma-hurdle models. The solid colored lines denote the mean values obtained from resampling, while the dashed lines indicate their standard deviations. Grey dashed lines across the panels represent scale breaks, used to display extreme values. The fishes and fishing vessel icons in the graph's top right are graphical representations of the no-take zone and unprotected area, respectively.

3.3 Life stage trends and protection

The multinomial logistic regression analysis, aimed at assessing the effects of protection category and time period on life stage distribution, revealed significant negative predictive effects for the 'Adult' and 'Reproductive Matrix' life stages in the most recent time period (2020-2023), compared to the reference period (2014-2016) and the reference life stage category 'Juvenile' (P-value < 0.001; see Supplementary Table S2 for coefficients). This declining trend is reflected in the mean density histograms (Fig. 3), which demonstrate an absence of 'Recruit' and 'Reproductive Matrix' individuals in the last four years within the no-take zone and in the

last seven years at unprotected sites. Notably, the 'Reproductive Matrix' category was documented only once (2011-2013) outside the ABMR boundaries, as opposed to three times within the marine reserve. Although the histograms suggest a more frequent occurrence of both 'Reproductive Matrix' and 'Recruit' life stages within the MPA compared to outside, the model indicated no significant effect of protection status on the overall distribution of life stages. Taking into account the limitations associated with a restricted sample size, the trends generated by GAM from the multinomial log odds indicate a consistent decrease in the probability of the 'Recruit' life stage over time (Fig. S2). This finding is corroborated by a visual inspection of histograms.

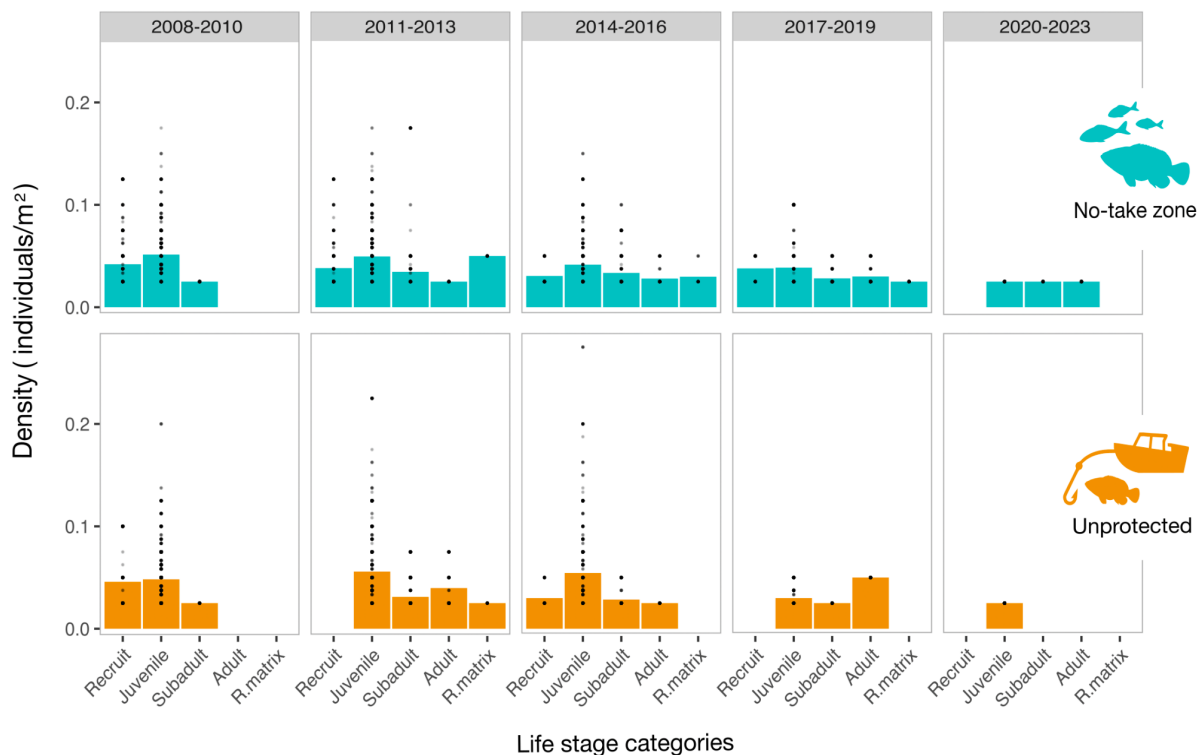


Fig. 3 Life stages mean density for five selected periods inside and outside the no-take zone. Bars represent the mean values obtained through resampling; each black dot corresponds to a single sample from Bootstrap. Life stages categories correspond to Recruit (individuals ≤ 10 cm); Juvenile (individuals between 11-30 cm); Subadult (juvenile individuals between 31-47 cm); Adult (individuals between 47-73 cm); Reproductive Matrix (individuals ≥ 73).

4 Discussion

This study provides valuable insights into the population status of the dusky grouper inside and outside a Marine Protected Area (MPA) in the southwestern Atlantic. Our results present a contrasting scenario to the initial expectations, which relied on the idea that the MPA is highly benefiting the dusky grouper population, leading to higher biomasses and abundances within its boundaries. Instead, we observed declining trends in both density and biomass inside and outside the MPA, especially from 2019 onwards, with no significant statistical

differences between the two areas. We also expected the MPA to exhibit higher densities of all life stages, particularly among large Adults. Although a higher frequency of Recruits and Reproductive Matrices was noted inside the no-take zone, these differences were not statistically significant. It is important to interpret these findings with caution, as sample limitations could be obscuring a more nuanced interpretation. However, the decline in dusky grouper population is undeniable and must be addressed with urgency.

In the Mediterranean Sea, the dusky grouper populations have greatly benefited from protection (García Rubies et al, 2013; Hackradt et al, 2014; Lorenzo et al, 2016). MPAs of similar age and size as the Arvoredo Biological Marine Reserve (ABMR) have shown such improvements that they started to spillover to neighboring unprotected areas through biomass exportation (García-Rubies et al, 2013; Lorenzo et al, 2016). However, the ABMR showed a much different scenario, with declining trends in both density and biomass, similar to those of adjacent unprotected areas (Fig. 2). While variations in the scale and characteristics of the factors causing population depletion might influence the results (Jackson et al, 2001; Edgar et al., 2014), fundamental differences between the ABMR and Mediterranean MPAs could drive the marked disparity in their effectiveness. This is particularly significant considering that the primary cause of population decline – overfishing – is shared by both the Mediterranean and our study region. Additionally, the species have been similarly depleted in both areas (Pollard et al., 2018)."

Although our models did not show statistical differences between protected and unprotected areas, it is probable that the ABMR positively impacts the dusky grouper population. However, this influence may not be consistently strong enough to aid population recovery (Russ and Alcala, 2004; Edgar et al., 2014). Notably, in years like 2016 and 2018, we observed higher biomass within the MPA (Fig. 2), likely due to the exclusive presence of 'Reproductive Matrices' in the MPA during these years (Fig. 3). This is consistent with previous studies using narrower data series and different analytical methods within the ABMR region, which reported higher biomass inside the Reserve, attributed to its role as a sanctuary for larger individuals targeted by fisheries (Anderson et al., 2014, 2020). However, subsequent years of our time series did not show the persistence of these larger individuals or the anticipated reproductive benefits, such as an increase in Recruit life stage (Palumbi, 2004; Beldade et al., 2012; Barneche et al., 2018). As a result, the overall trend within the MPA remained similar to that observed in the adjacent unprotected areas. This highlights the possibility that the ABMR's influence on the *E.marginatus* population fluctuates over time, potentially due to factors yet to be explored (Russ and Alcala, 2004; Edgar et al., 2014).

Factors limiting the ABMR's effectiveness towards dusky grouper recovery might include MPA design issues, such as inadequate consideration of all life cycle stages in the MPA's planning (Grüss et al., 2011). For instance, our analysis demonstrates a persistent decline in the density of Recruits (Fig. 3; Fig. S2). This decrease in smaller sized individuals is a key factor to the overall density reduction, especially until 2018 (Fig. 2), while larger individuals helped maintain stable biomass levels (Condini et al., 2013). Although recruitment in our study area is not well-documented, it is generally believed to occur in coastal habitats such as tide pools and shallow macroalgae beds, predominantly found outside protected areas (Andrade et al., 2003; Cunha et al., 2007; Anderson et al., 2020). Consequently, if self-recruitment within the MPA is insufficient, crucial life stages remain unprotected and vulnerable to threats such as habitat degradation, before reaching the safety of the MPA (La Mesa et al., 2002; Machado et al., 2003; Edgar et al., 2014). However, the observed decline in Recruits could

also be attributed to other factors, including density-dependent mechanisms (Minto et al., 2008), climate change affecting larval survival (Andrello et al., 2014; Silva et al., 2023), or the removal of large, fecund individuals, which are essential for reproduction (Palumbi, 2004; Beldade et al., 2012; Barneche et al., 2018).

Illegal fishing activities within the ABMR boundaries are another potential factor contributing to the Reserve's limited effectiveness in facilitating dusky grouper recovery (Giakoumi et al., 2018). In fact, of the five key features identified by Edgar et al. (2014) as crucial for maximizing MPA benefits, effective enforcement is the only one the ABMR appears to lack (Gerhardinger et al., 2011). The ABMR is known to possess the other four attributes: it is over 30 years old, covers 176 km², and functions as a strict Reserve, isolated from the coast by sand (IBAMA, 1995). In our study, while illegal fishing may be a potential explanation for the overall decline in density throughout the time series, it becomes particularly pertinent in the context of biomass trends (Fig. 2). The reduction in the 'Reproductive Matrices' life stage was primarily responsible for shifting the biomass from relative stability to decline in 2018. Given that fishermen often target these larger individuals, an increase in such activities could account for their observed decline. Moreover, although Brazilian researchers, managers, and environmentalists have long expressed concerns about insufficient resources for conservation strategies (Fernandes, 1992; Gerhardinger et al., 2011), this situation is known to have worsened within the years following the 2018 presidential election (Barbosa et al., 2021), matching the decline present in our data. Taking a closer look into this relationship could be particularly interesting, especially considering that studies have demonstrated that election periods in Brazil can have negative impacts on conservation efforts (Rodrigues-Filho et al., 2015; Ruggiero et al., 2021). However, the possibility of other mechanisms explaining the accentuated biomass decline should not be discarded.

Although our discussions have primarily focused on the ABMR's effectiveness for the dusky grouper population, the factors mentioned above are relevant to the entire population, considering that biomass and density trends were similar both inside and outside the MPA boundaries. In addition to the MPA's presence, the dusky grouper population is also subject to fisheries regulations (Fig. 1), including a minimum capture size of 47 cm established in 2005 (MMA, 2014) and more stringent fishing regulations implemented since 2018 (MMA, 2018). These include a defined closed fishing season, a limited capture size range of 47-73 cm, and restrictions on permitted fishing vessels (MMA, 2018). Such strategies were anticipated to boost biomass and density maintenance of larger individuals in both protected and fishing areas (Gwinn et al., 2015). However, the grouper population's declining trend despite these measures, particularly the pronounced decline right after the 2018 implementation of stricter fishing limits, underscores that important factors are limiting the species recovery. This also reinforces the possibility of non-compliance issues within the local population, a known problem in the state of Santa Catarina (Constantino et al., 2022).

We emphasize the urgent need for further studies encompassing the dusky grouper population, the ABMR and the existent fishing regulations enforcement and surveillance, which can bring fundamental insights for stakeholders, leading to better resource management (Lotze et al., 2011; Martin et al., 2012). Additionally, detailed studies on the life stages and life cycle of the dusky grouper are crucial for understanding the causes behind population decline and for evaluating whether the design of current conservation strategies is comprehensive enough to ensure the species' survival (Hackradt et al., 2014; Anderson et al., 2020). Yet, this task poses challenges, as certain life stages, such as Recruits and Reproductive Matrices are naturally scarce (Seyboth

et al., 2011), a fact exacerbated by their declining numbers (Fig. 3). In fact, we gained first hand on this difficulties. Parallel to this study we attempted to locate and characterize recruitment areas. Despite over 20 hours spent searching tide pools, macroalgae beds, and rocky reefs, including previously known habitat locations (Machado et al., 2003), we did not find any specimens smaller than 15 cm, encountering only five individuals in total. This experience underlines the necessity but also the complexity of studying less abundant life stages, which might require extensive efforts and multiple sampling methods (Bodilis et al., 2003; Ventura et al., 2016).

Our study reinforces how crucial it is to evaluate and monitor conservation strategies and their long-term effects on local populations (Russ and Alcalá, 2004; Goldsmith, 2012). It shows that dusky grouper populations are declining and that neither the marine no-take zone nor the fishing regulations are having the expected outcome for the species maintenance. In the ecosystem, the dusky grouper is already filling gaps created by the depletion of other top predators (Souza, 2000; Fogliarini et al, 2021). Not only exerting important functions such as the top-down control of the food web (Begon and Townsend, 2021) but also serving as a valuable resource for fisheries (Silvano et al, 2017; Begossi et al, 2019; Fogliarini et al, 2021). The depletion of this species can mean the continuity of an unsustainable fishing down the food web scenario, in which fishermen migrate to lower trophic levels due to exhaustion of higher ones (Pauly et al, 1998; Jackson et al, 2001). Therefore, we highlight the importance of reevaluating the strategies in force, focusing on what can be done to change this scenario. We also suggest two main potential contributors to the poor effectiveness of the implemented strategies: non-compliance of the local population and lack of attention to the species' life cycle when designing conservation strategies.

Declarations. The authors declare no conflicts of interest.

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Appendix A: Supplementary Material

Table S1 Effects of year and protection category on dusky grouper population biomass and density, considering the presence of zero-inflation in data, based on gamma-hurdle models. Population-level Effects that start with “hu” correspond to the zero-inflated part of the model, and the presence of (*) indicates the significance of the effects based on the confidence intervals (1-95% CI, u-95% CI). Bulk ESS = Effective Sample Size and Tail ESS = Effective Sample Size for Tail Parameters were used to evaluate the efficiency of the MCMC (Markov Chain Monte Carlo) algorithm used to estimate the parameters of the model. SE = Standard Error refers to the standard deviation of the sampling distribution of the Bayesian posterior estimate of the model.

Hurdle-Gamma models							
Population-level Effects	Biomass						
	Estimate	Est. Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept*	308.21	64.44	180.9	434.07	1	36895	28152
hu_Intercept*	-819.23	249.01	-1355.82	-381.64	1	25216	21308
year*	-0.16	0.03	-0.22	-0.09	1	36861	28069
mpaprotected	0.26	0.23	-0.19	0.7	1	40525	26543
hu_year*	0.41	0.12	0.19	0.67	1	25227	21332
hu_mpaprotected	-0.85	0.81	-2.46	0.72	1	40846	27496
Population-level Effects	Density						
	Estimate	Est. Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept*	-209.72	101.49	-409.8	-12.02	1	44820	29931
hu_Intercept*	-218.27	80.81	-378.98	-60.87	1	26498	22251
year*	0.11	0.05	0.01	0.21	1	44801	30010
mpaprotected	0.42	0.31	-0.2	1.02	1	46576	29560
hu_year*	0.11	0.04	0.03	0.19	1	26520	22225
hu_mpaprotected	-0.4	0.32	-1.04	0.23	1	43010	29284

Table S2 Multinomial logistic regression coefficients for the dusky grouper life stages within the Arvoredo Biological

Marine Reserve. The table reports the coefficients (B), standard errors (Std.Error), Wald statistics, and P-values for each life stage category across different time periods and within the MPA protected area. Negative B values suggest a decline in the likelihood of a life stage category relative to the reference group, while positive values suggest an increase. Statistical significance is indicated by P-values, with significant values represented in bold. This model aims to analyze variations within life stage distributions over time and protection category on the dusky grouper population.

Multinomial model for proportional data												
	Intercept				2008-2010				2011-2013			
	B	Std.Error	Wald	P-value	B	Std.Error	Wald	P-value	B	Std.Error	Wald	P-value
Subadult	-0.228	0.751	-0.879	0.761	-0.503	0.969	0.530	0.603	0.010	0.897	0.520	0.991
R.matrix	-1.565	1.202	-20.970	0.193	-16.024	0.001	20.719	0.000	-0.374	1.129	23.053	0.740
Recruit	-0.661	0.835	-0.535	0.429	0.236	0.930	-0.520	0.800	-0.271	0.998	-0.254	0.786
Adult	-0.508	0.822	-31.986	0.537	-15.856	1393.266	26.952	0.991	0.012	0.952	26.890	0.990
	2017-2019				2020-2023				mpaprotected			
	B	Std.Error	Wald	P-value	B	Std.Error	Wald	P-value	B	Std.Error	Wald	P-value
Subadult	-0.271	0.928	0.233	0.770	-0.508	1.127	-0.004	0.652	0.381	0.670	0.569	0.670
R.matrix	-0.551	1.131	19.528	0.626	-17.075	0.000	-3.868×10¹¹	0.000	1.479	1.187	1.246	1.187
Recruit	-0.775	1.082	-0.952	0.474	-16.805	0.000	-6.814×10¹⁸	0.000	0.690	0.750	0.920	0.750
Adult	-0.058	0.956	26.214	0.952	0.100	1.077	21.964	0.926	0.468	0.760	0.616	0.760

Table S3 Presence of dusky grouper, with mean values and standard deviations (SD) for density and biomass at each site, stratified by year. Data were obtained after resampling procedures. Sites are categorized by island and protection status, with 'Protected' sites situated within the Arvoredo Biological Marine Reserve.

island	protection	location	year	density mean	density sd	biomass mean	biomass sd
Arvoredo	protected	ArvoredoMPA	2008	0.026	0.017	2.280	2.482
Arvoredo	unprotected	ArvoredoNPZ	2008	0.019	0.013	2.557	1.620
Deserta	protected	Deserta	2008	0.031	0.024	1.645	1.700
Galé	protected	Galé	2008	0.041	0.021	5.693	4.020
Arvoredo	protected	ArvoredoMPA	2009	0.056	0.029	6.462	3.420
Arvoredo	unprotected	ArvoredoNPZ	2009	0.018	0.011	2.143	1.790
Deserta	protected	Deserta	2009	0.048	0.027	4.565	3.450
Galé	protected	Galé	2009	0.031	0.022	5.449	4.883
Arvoredo	unprotected	ArvoredoNPZ	2010	0.027	0.017	2.631	2.044
Xavier	unprotected	Xavier	2010	0.039	0.027	3.597	3.850
Arvoredo	protected	ArvoredoMPA	2011	0.039	0.022	16.169	8.549
Arvoredo	unprotected	ArvoredoNPZ	2011	0.049	0.033	30.318	38.900
Deserta	protected	Deserta	2011	0.031	0.031	14.733	18.090
Xavier	unprotected	Xavier	2011	0.022	0.021	7.812	9.370
Arvoredo	protected	ArvoredoMPA	2012	0.000	0.000	0.000	0.000
Arvoredo	unprotected	ArvoredoNPZ	2012	0.005	0.005	2.482	2.490
Deserta	protected	Deserta	2012	0.034	0.026	14.888	37.940
Galé	protected	Galé	2012	0.040	0.021	5.515	3.788
Xavier	unprotected	Xavier	2012	0.006	0.006	1.584	2.106
Arvoredo	protected	ArvoredoMPA	2013	0.039	0.022	16.562	11.590
Deserta	protected	Deserta	2013	0.048	0.027	4.719	3.483
Galé	protected	Galé	2013	0.020	0.018	7.192	6.020
Xavier	unprotected	Xavier	2013	0.037	0.017	19.072	12.909
Arvoredo	protected	ArvoredoMPA	2014	0.019	0.017	7.858	14.000
Arvoredo	unprotected	ArvoredoNPZ	2014	0.004	0.006	1.243	1.960
Deserta	protected	Deserta	2014	0.011	0.011	6.582	10.801
Galé	protected	Galé	2014	0.012	0.011	4.923	6.370
Xavier	unprotected	Xavier	2014	0.053	0.036	7.103	5.080
Arvoredo	protected	ArvoredoMPA	2015	0.020	0.018	3.278	5.158
Arvoredo	unprotected	ArvoredoNPZ	2015	0.012	0.010	6.371	8.270
Deserta	protected	Deserta	2015	0.028	0.019	15.661	15.880
Galé	protected	Galé	2015	0.015	0.012	13.206	17.624
Xavier	unprotected	Xavier	2015	0.033	0.017	5.315	3.832
Arvoredo	protected	ArvoredoMPA	2016	0.033	0.018	9.011	9.410
Arvoredo	unprotected	ArvoredoNPZ	2016	0.018	0.012	6.556	7.487
Deserta	protected	Deserta	2016	0.035	0.022	42.336	92.942
Galé	protected	Galé	2016	0.043	0.027	31.253	38.390
Xavier	unprotected	Xavier	2016	0.017	0.020	2.086	2.770
Arvoredo	protected	ArvoredoMPA	2017	0.027	0.012	6.718	3.241
Arvoredo	unprotected	ArvoredoNPZ	2017	0.022	0.013	9.991	12.870
Arvoredo	protected	ArvoredoMPA	2018	0.013	0.010	5.763	4.760
Arvoredo	unprotected	ArvoredoNPZ	2018	0.004	0.005	1.615	2.550
Deserta	protected	Deserta	2018	0.025	0.018	34.695	50.730
Galé	protected	Galé	2018	0.053	0.018	107.316	39.824
Xavier	unprotected	Xavier	2018	0.007	0.007	1.027	1.381
Arvoredo	protected	ArvoredoMPA	2019	0.007	0.006	10.318	11.630
Arvoredo	unprotected	ArvoredoNPZ	2019	0.000	0.000	0.000	0.000
Deserta	protected	Deserta	2019	0.000	0.000	0.000	0.000
Galé	protected	Galé	2019	0.000	0.000	0.000	0.000
Xavier	unprotected	Xavier	2019	0.001	0.003	0.412	1.030
Arvoredo	protected	ArvoredoMPA	2020	0.005	0.005	1.882	2.174
Deserta	protected	Deserta	2020	0.001	0.003	0.851	1.850
Galé	protected	Galé	2020	0.001	0.003	2.526	5.584
Arvoredo	protected	ArvoredoMPA	2021	0.001	0.003	0.463	1.090
Arvoredo	unprotected	ArvoredoNPZ	2021	0.000	0.000	0.000	0.000
Xavier	unprotected	Xavier	2021	0.000	0.000	0.000	0.000
Arvoredo	protected	ArvoredoMPA	2022	0.000	0.000	0.000	0.000
Arvoredo	unprotected	ArvoredoNPZ	2022	0.000	0.000	0.000	0.000
Deserta	protected	Deserta	2022	0.001	0.003	3.330	8.730
Galé	protected	Galé	2022	0.002	0.003	0.596	1.204
Xavier	unprotected	Xavier	2022	0.000	0.000	0.000	0.000
Arvoredo	protected	ArvoredoMPA	2023	0.001	0.003	3.854	9.280
Arvoredo	unprotected	ArvoredoNPZ	2023	0.000	0.000	0.000	0.000
Deserta	protected	Deserta	2023	0.000	0.000	0.000	0.000
Xavier	unprotected	Xavier	2023	0.006	0.006	1.456	1.632

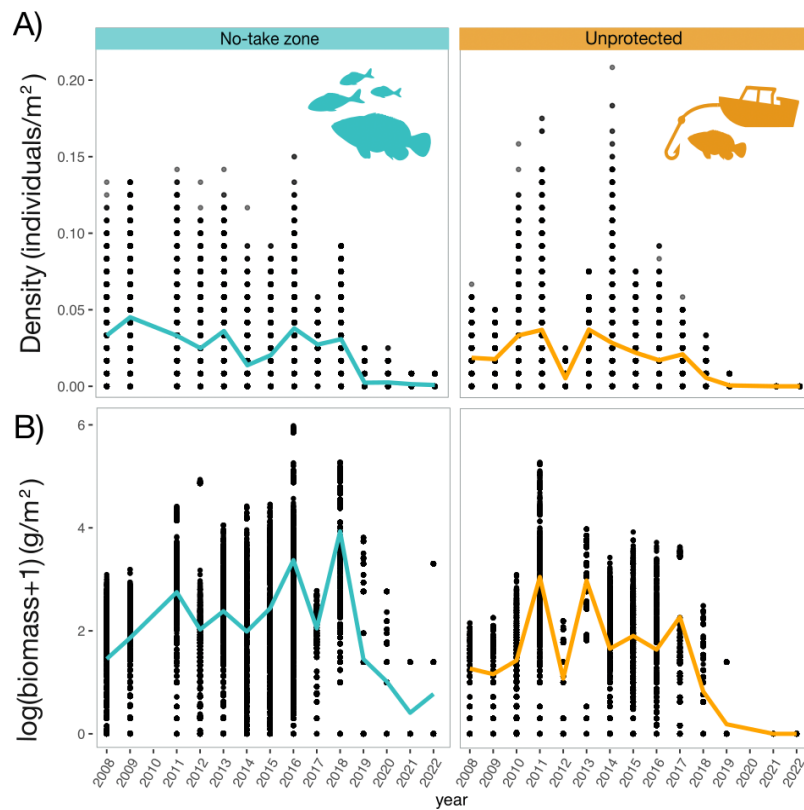


Fig. S1 Bootstrapped mean values for dusky grouper density (A) and biomass (B) inside (blue) and outside (orange) the marine no-take zone. Dots correspond to mean values for each loop of the bootstrap. The continuous lines are the temporal trends given by the mean values of the bootstrap means. Icons in the graphs top right are graphical representations for each protection category.

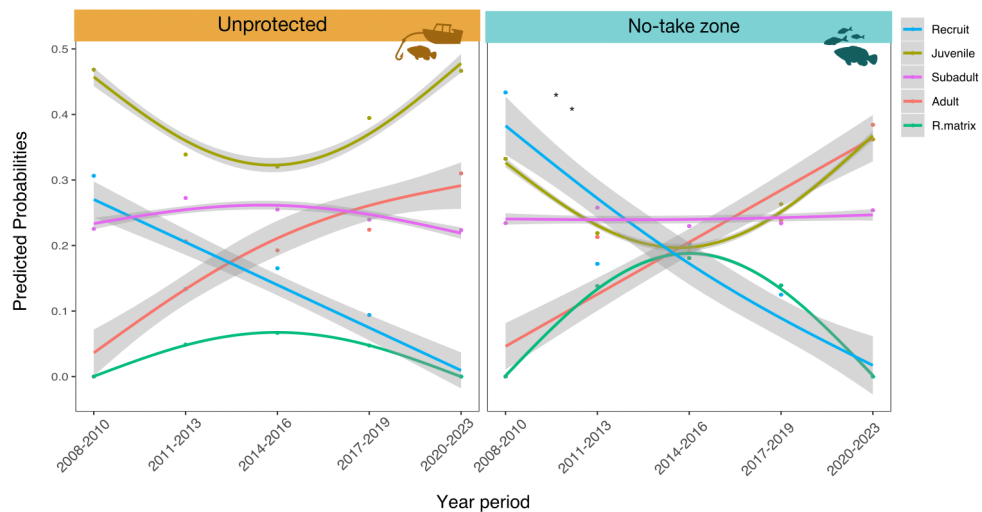


Fig. S2 Temporal trends of life stage categories probabilities inside (blue) and outside (orange) the marine no-take zone, as estimated by a multinomial model and smoothed using Generalized Additive Models (GAM). The x-axis segments the data into specified time periods, while the y-axis quantifies the predicted probabilities of each life stage category. Individual lines represent different life stage categories, with an asterisk (*) denoting those categories, specifically 'Adult' and 'Reproductive Matrix', which exhibited statistical significance in all time periods assessed. Confidence intervals are visualized through the shaded areas surrounding each trend line, offering a 95% confidence level for the predicted probabilities.

3.CONCLUSÃO GERAL

Esta dissertação destaca a importância de não apenas implementar estratégias voltadas para a recuperação de espécies ameaçadas, mas também de monitorá-las a longo prazo para verificar sua eficácia. Embora a garoupa-verdadeira ocorra dentro de uma área marinha de proteção integral e esteja sujeita a regulamentações pesqueiras na região estudada, sua população está em um preocupante declínio, que se intensificou nos últimos cinco anos. A situação é preocupante para todos os estágios de vida, mas ressaltamos o constante declínio de recrutas e baixa abundância de matrizes reprodutivas (BOELTER et al., in prep.). Compreender os mecanismos por trás da ineficácia das medidas implementadas e adaptá-las para que sejam efetivas é crucial para a manutenção e conservação da espécie. Questão urgente para evitar que a garoupa-verdadeira siga o mesmo caminho dos antigos predadores de topo da região, como os meros e tubarões-mangona, que se tornaram raros e funcionalmente extintos.

Os impactos ecossistêmicos e socioeconômicos da redução da espécie já são perceptíveis. Na pesca, a escassez tem tornado a atividade economicamente inviável, levando os pescadores a buscar outros indivíduos de menor nível trófico como alternativa de renda. No ecossistema, os efeitos da perda dessa espécie ainda são pouco estudados, mas é provável que já estejam ocorrendo diversas consequências indiretas, como alterações nas populações de presas (ANDERSON et al., 2014). Destacamos que, mesmo sendo uma espécie emblemática e reconhecida nacionalmente por sua importância e vulnerabilidade (a ponto de estar estampada na nota de cem reais), ainda há uma carência de estudos sobre sua dinâmica populacional e os impactos das estratégias de conservação adotadas para sua recuperação.

O conhecimento, em todas as suas formas, é fundamental para a conservação. Este estudo contribui com informações essenciais para a preservação de uma espécie-chave e amplia a compreensão sobre os efeitos de uma importante unidade de conservação, além de evidenciar lacunas de conhecimento que precisam ser urgentemente preenchidas. Por fim, esperamos que este trabalho não se limite ao papel, mas que tenha um papel ativo na conservação da garoupa-verdadeira em Santa Catarina, evitando assim que a espécie se torne apenas mais uma lenda de pescador ou um personagem de fotografias antigas.

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