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Inputs for demersal elasmobranch conservation: Marine Protected Areas and coastal regions in focus

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Tese apresentada ao Instituto Oceanográfico da Universidade de São Paulo, como parte dos requisitos para obtenção do título de Doutor em Ciências, Programa de Oceanografia, área de Oceanografia Biológica.

Orientador: Profa. Dra. June Ferraz Dias
Coorientador: Profa. Dra. Elizabeth Ann Babcock

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“[..]
Dorival, vai não
‘Tá cheio de tubarão no mar
Val, vai não
Arranja um emprego no chão
Chorei
Pensando que nunca mais fosse te ver novamente
Chorei
Com medo de tubarão
Das grandes ondas, e do canto da sereia
[...]”

Trecho de “Dorival”
Academia da Berlinda

RESUMO

ABREU, Thamíris Christina Karlovic de. **Contribuições para a conservação de elasmobrânquios demersais:** Áreas de Proteção Marinha e regiões costeiras em foco. 2023. 154 f. Tese (Doutorado) – Instituto Oceanográfico, Universidade de São Paulo, São Paulo, 2023.

O mar territorial brasileiro detém mais de 14% da biodiversidade mundial de elasmobrânquios, dos quais pelo menos um quarto pode ser encontrado em áreas costeiras e sobre a plataforma continental do estado de São Paulo. Apesar da grande biodiversidade e indiscutível relevância para o equilíbrio dos ecossistemas, como reguladores intermediários nas cadeias tróficas, uma parte significativa das espécies permanece pouco estudada, exigindo um conhecimento mais aprofundado sobre sua autocologia (*i.e.*, área de vida, uso de habitat, estrutura e dinâmica populacional). Particularmente, a proteção dos habitats marinhos e de suas espécies ao longo da costa de São Paulo é uma tarefa desafiadora, uma vez que pesquisadores e agentes do governo lutam para cumprir os requisitos de todos os táxons ao longo de seus diferentes estágios vida em meio à intensa e diversa pressão antrópica local (*e.g.*, pesca, poluição química e sonora e atividade portuária). Com base nisso, o principal objetivo da presente tese é fornecer novas informações que possam aprimorar as políticas de conservação e orientar as ações de gestão das Áreas Marinhas Protegidas (AMPs), aumentando sua eficácia para a conservação dos elasmobrânquios demersais. No primeiro capítulo, a relação de dimorfismos morfométricos entre os sexos de uma espécie ameaçada de raia-viola, *Zapteryx brevirostris*, foi exaustivamente investigada em relação às pressões biológicas e ecológicas. Ainda neste capítulo, foi destacada a forte influência da maturação gonadal em tais dimorfismos além de revelar a ocorrência de mudanças ontogenéticas no uso do habitat, alertando para os possíveis impactos das atividades pesqueiras nos *habitat* chave das diferentes fases de vida da espécie. No segundo capítulo, uma abordagem aplicada usando guildas reprodutivas e alimentares, bem como as variações na abundância relativa dos grupos funcionais e das espécies em relação à dinâmica oceanográfica local, caracterizou o papel desempenhado por duas importantes AMPs. Além disso, a eficácia destas para *Z. brevirostris* foi avaliada por meio de indicadores de pesca e comparações de mudanças na composição da ictiofauna ao longo dos anos. O terceiro capítulo estimou a riqueza geral da assembleia demersal nas partes norte e central da plataforma continental do estado de São Paulo, explorando os possíveis efeitos promovidos pela geomorfologia usando diferentes estruturas de modelos de ocupação multi-espécies. A integração de tais resultados pode ser uma ferramenta útil para melhorar o cenário atual de conservação na costa paulista. Enquanto a avaliação da funcionalidade e eficácia das AMPs traz insights sobre como os elasmobrânquios utilizam a região e reforça a importância da implementação de medidas de controle, o entendimento dos padrões de distribuição das espécies permite o estabelecimento de ações de conservação e manejo mais adequadas.

Palavras-chave: Ecologia aplicada, conservação de elasmobrânquios, diversidade funcional, autoecologia, indicadores de pesca, modelos hierárquicos

ABSTRACT

ABREU, Thamíris Christina Karlovic de. **Inputs for demersal elasmobranch conservation**: Marine Protected Areas and coastal regions in focus. 2023. 154 f. Tese (Doutorado) – Instituto Oceanográfico, Universidade de São Paulo, São Paulo, 2019.

The Brazilian territorial sea holds more than 14% of the worldwide elasmobranch biodiversity, of which at least a quarter can be found on inshore areas and over the continental shelf of the São Paulo state. Despite the great biodiversity and undoubted relevance for ecosystem balance as intermediate regulators in the trophic chains, a significant number of the species remains poorly studied, requiring deeper knowledge about their autecology (*i.e.*, home range, habitat use, population structure and dynamics). Particularly, the protection of marine habitats and related species along the São Paulo coast is a challenging task, since stakeholders struggle to accomplish all the taxa conservation requirements throughout their lifespan among intense and diverse anthropogenic stressors (*e.g.,* fisheries, sound and chemical pollution and harbors operation). Based on that, the principal objective of this doctoral dissertation is to provide new information that could enhance conservation polices and guide management actions of local Marine Protected Areas (MPAs), increasing their effectiveness for demersal elasmobranch conservation. In the first chapter, the morphometric dimorphisms between sexes of a threatened guitarfish, *Zapteryx brevirostris*, was investigated regarding biological and ecological pressures. Here the strong influence of gonadal maturation on such dimorphisms is highlighted and ontogenetic changes in habitat use is revealed, warning about the possible impacts of fishing activities in key habitats for its different life stages. In the second chapter, an applied approach using reproductive and feeding guilds as well as variations in the relative abundance of both functional groups and of the species in relation to the local oceanographic dynamic characterized the role played by two major MPAs. Additionally, their effectiveness was assessed by the evaluation of fishery indicators for *Z. brevirostris* and comparisons of changes in ichthyofauna composition over the years. The third chapter estimated the overall richness of the demersal assembly in the north and central parts of the São Paulo's continental shelf, exploring the possible effects promoted by the geomorphology using different structures of multi-species occupancy models. The integration of these findings might be a useful tool to improve the current conservation scenario in the São Paulo coast. While the assessment of the MPAs' functionality and effectiveness bring insights about how the elasmobranchs use the region and strengthen the importance of implementing control measures, the understanding of the species distribution patterns allows the establishment of more suitable conservation and management actions.

Keywords: Applied ecology, elasmobranch conservation, functional diversity, autecology, fishery indicators, hierarchical modelling

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Appendix A

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LISTA DE ABREVIATURAS E SIGLAS

AISP	Parque Estadual Ilha Anchieta
APAM Norte	Área de Proteção Ambiental Litoral Norte
APAM Centro	Área de Proteção Ambiental Litoral Centro
APAM Sul	Área de Proteção Ambiental Litoral Sul
AREISS	Área de Relevante Interesse Ecológico de São Sebastião
AREIG	Área de Relevante Interesse Ecológico do Guará
ATCA	*Atlantoraja castelnaui*
ATCY	*Atlantoraja cyclophora*
BC	Corrente do Brasil
BCC	Corrente Costeira do Brasil
CW	Massa de Água Costeira
DAHY	*Dasyatis hipostigma* (DAHY)
D_{BN}	Distância internasal
D_{IO}	Distância interorbital
D_{IS}	Distância interespiracular
D_{PRO}	Distância pré-oral
F/M	Taxa da mortalidade por pesca em relação à mortalidade natural
GYAL	*Gymnura altavela*
HYGU	*Hypanus gutattus*
HYBE	*Hypanus berthalutzae*
LBSPR	Taxa de potencial de desova baseada no comprimento
L_c	Comprimento mínimo totalmente explotado
L_D	Comprimento do disco
L_{SC}	Comprimento do focinho a cloaca
L_T	Comprimento total
MER	Reserva Extrativista do Mandira
MPAs	Áreas de Proteção Marinhas
MYFR	*Myliobatis freminvillei*
MYCA	*Mustelus canis*
MYSC	*Mustelus schmitti*
MSPLS	Parque Estadual Marinho da Laje de Santos

NABR	*Narcine brasiliensis*
Nfe	Número de fêmeas
Nma	Número de machos
N_{obs}	Número de espécies observados
OEs	Expedições Oceanográficas
OM	Concentração de matéria orgânica
OSs	Estações Oceanográficas
p_i	Probabilidade de detecção da espécie *i*
PSEX	*Psammobatis extenta*
PSHO	*Pseudobatos horkelii*
PSPE	*Pseudobatos percellens*
RHLA	*Rhizoprionodon lalandii*
RIAG	*Rioraja agassizii*
SACW	Massa de Água Central do Atlântico Sul
SPR	Taxa do potencial de desova
SQAL	*Squalus albicaudus*
SQGU	*Squatina gugguenheim*
SQOC	*Squatina oculta*
SSI	Ilha de São Sebastião
TES	Estação Ecológica Tupinambás
TW	Massa de Água Tropical
ZABR	*Zapteryx brevirostris*
WRA	Refúgio da Vida Silvestre de Alcatrazes
W_D	Largura do disco
W_{LS}	Largura do espiráculo esquerdo
W_{LN}	Largura da narina esquerda
W_M	Largura da boca
W_R	Largura do rostro
W_{RN}	Largura da narina direita
W_{RS}	Largura do espiráculo direito
W_T	Peso corpóreo total
Ψ_i	Probabilidade de ocorrência da espécie *i*

SUMÁRIO

1 1 GENERAL INTRODUCTION

1.1 Biodiversity And Conservation Of Demersal Elasmobranchs In The Coast Of The São Paulo State

The Brazilian territorial sea holds more than 14% (Rosa and Gadig, 2014) of the worldwide biodiversity of sharks, skates and rays. Around a quarter of the species can be found on inshore areas and over the continental shelf of the São Paulo state (ICMBio, 2016a; Bachur, 2018), representing a variety of functional guilds in terms of reproductive modes (*e.g.*, oviparous, lecitotrophic and trophonemata/matotrophic) and feeding ecology (*e.g.*, piscivorous, hyperbenthivorous, epibenthic and infauna consumers) (Dias et al., 2021). Over the decades, the local assembly of demersal elasmobranchs has been characterized by at least sixteen families (*e.g.*, Arhynchobatidae, Rhinobatidae and Carcharhinidae) and thirty-two species (Sadowsky, 1965, 1969; Paiva-Filho et al., 1989; Pires-Vanin et al., 1993; Ponz-Louro, 1995; Rocha and Rossi-Wongtschowski, 1998; Luiz et al., 2008; Rossi-Wongtschowski et al., 2008; Contente, 2013; Mattox et al., 2014; Rocha and Dias, 2015; Lamas et al., 2016; Souza et al., 2018), of which are commonly mentioned on scientific studies: the guitarfishes, *Pseudobatos percellens* (Walbaum, 1972), *Pseudobatos horkelii* (Müller and Henle, 1936) and *Zapteryx brevirostris* (Müller and Henle, 1936), the sand skates, *Atlantoraja cyclophora* (Regan, 1903), *Atlantoraja castelnaui* (Ribeiro, 1907), *Psammobatis extenta* (Garman, 1913) and *Rioraja agassizii* (Müller and Henle, 1936) and the stingrays *Hypanus guttatus* (Bloch and Scheider, 1801) and *Dasyatis hypostigma* Santos and Carvalo (2004).

Overall, elasmobranchs occur over sand bottoms up to 100 m deep (Gomes et al., 2019). However, the distribution of some species is broader than that, reaching greater depths across the continental shelf, or is restricted to shallow waters (< 20m), such as *Mustelus canis* (Mitchel, 1815) and *Narcine brasiliensis* (Olfers, 1931), respectively (Rudloe, 1989; Martins et al., 2009; Gomes et al., 2019). They display different habits in association with the sea bottom and rocky shores (*i.e.,* benthic and benthopelagic), exhibiting interspecific as well as intraspecific variations regarding their main habitats. While *N. brasiliensis* and *H. berthalutzae* are estuarine (Rudloe, 1989; Martins et al., 2009) and reef related (Aguiar et al., 2009) throughout their life span, other species, such as the cownose rays, *Rhinoptera bonasus* (Mitchill, 1815) and *Rhinoptera brasiliensis* Müller, 1836 and the guitarfish, *P. horkelii*, show ontogenetic segregations in habitat use, with neonates and juveniles inhabiting sheltered areas along the coast (*i.e.*, bays and estuaries) whereas the adults migrate to deeper waters (Lessa et al., 1986; Rangel et al., 2018).

Furthermore, elasmobranch distribution is heavily influenced not only by the sea floor aspects (Martin et al., 2012; Pennino et al., 2013; Lauria et al., 2015) but also by the water proprieties (Schlaff et al., 2014a) and oceanographic process that shape the local productivity and availability of feeding resources (*e.g.,* Karlovic *et al.*, 2021). In the marine food web, they act as mesopredators (Myers et al., 2007; Bornatowski et al., 2014b), occupying an intermediate trophic level and feeding on a variety of prey items of the benthic megafauna as well as macrofauna (*e.g.,* mollusk, polychaetes and crustaceans) and mobile benthic and pelagic species (*e.g.,* fishes, squids and octopuses) (Vögler et al., 2003; Aguiar and Valentin, 2010; Barbini et al., 2011; Marion et al., 2011; Bornatowski et al., 2014c; Viana and Vianna, 2014; Gianeti et al., 2019b; Queiroz et al., 2023). However, such diversity in habitat use and feeding ecology is not reflected in their life history traits, since they are long-lived species that exhibit late maturity (Compagno, 1990) and low intrinsic rates of population growth (D'Alberto et al., 2019). Some species spend more than a half of their lives to reach maturity and generate few offspring (*e.g., Squatina occulta*, Vooren & Silva, 1991) (Gomes et al., 2019), which prevents the population replacement at the same pace they lose individuals due to natural and fishing mortality (Bornatowski et al., 2014a).

Despite the fact that fishing on threatened elasmobranchs is forbidden in Brazilian waters (MMA, 2014), the majority of the species are caught as bycatch, especially by multispecies fisheries such as longline, gillnets, and otter, double-ring, and pair trawlers. Bornatowski *et al.* (2014c) and Karlovic *et al.* (2021) warned about the impacts of traditional and industrial fisheries over different key habitats (*e.g.,* nursery, reproduction and feeding places) for these species. Owing to these characteristics of the group and the intense anthropogenic pressure in the area (*e.g.,* habitat degradation and pollution by the activities related to the Santos and São Sebastião Ports) (Siqueira et al., 2005; Angelini et al., 2018; Ribeiro, 2020), around 80% of the local species are globally classified in threatened categories (*i.e.,* from vulnerable, endangered or critically endangered classes) (IUCN, 2023). Nevertheless, 25% of them are considered as having insufficient data according to the Brazilian agency (ICMBio, 2016a), preventing the establishment of proper management and conservation actions.

1.2 Sedimentological Aspects And Oceanographic Process In The Area

The São Paulo state coast is 880 km long. The width of the adjacent continental shelf increases from the northeastern part (70 km) to the southeastern one (230 km), with the highest depths varying between 120 and 180 m (Mahiques et al., 2010). Regarding the sedimentological aspects of the area, the São Sebastião island (SSI) is a latitudinal mark between two transition zones, differentiating the north part of the continental shelf. Called the shadow effect, the island acts as a barrier to the incidence of south and southeast waves in the northern inner and mid shelves (up to 50 m deep), promoting a more stable environment (Barcellos and Furtado, 1999). Thus, while the southern inner and mid shelves are predominantly composed by finer grains of sand, due to the direct influence of the energy of waves that carry pelitic sediments and organic particles to the outer shelf, the inverse pattern is observed in the northern zone. There the sediment content is more heterogeneous with higher deposition of mud and retention of terrigenous particles of organic matter, resulting in a richer environment (Gianesella-Galvao and Saldanha-Corrêa, 2003). Additionally, a patchy configuration of different granulometry, including coarser grains of sand, and sorted sediments is observed in the northern outer shelf (Mahiques et al., 1999, 2004; Conti and Furtado, 2006).

The south and central parts of the continental shelf presents a gradient of very fine to fine grains of sand with spots of silt southwards and higher deposition of mud on the central outer shelf (Conti and Furtado, 2006). However, the configuration of the continental areas is also responsible for the complexity of the sedimentological and hydrochemical processes over the shelf. Northwards to the SSI, the Serra do Mar mountain chain is closer to the coast line, limiting the extent of coastal plains and beaches, whereas southwards the mountain chain is more distant from the coast, reflecting in larger drainage systems with high continental runoff potential (*e.g.,* the Ribeira de Iguape river) (Mahiques et al., 1999). This influences significantly the central and south inner shelf, since rivers' outflow changes the water properties, especially in the rainy season, increasing the temperature, lowering salinity and promoting enrichment by the advection of terrigenous organic matter (Moser et al., 2005).

Other forces that drive the regional dynamics are the Brazil Current (BC), the Brazil Costal Current (BCC) and seasonal changes in winds direction. The BC flows southwards along the São Paulo continental shelf break, transporting two major water masses for the region: the warm, salty and oligotrophic Tropical Water (TW, Temperature - $T > 20$ °C and Salinity - $S > 36$) and the deeper, cold and nutrient rich South Atlantic Central Water (SACW, $T < 20$ °C and $S < 36$) (Silveira et al., 2000). A third water mass, the Coastal Water (CW), results from the mixing of the continental drainage and shelf waters, being less saline than the other two ($S < 35$) (Castro-Filho and Miranda, 1998). From late spring through summer, strong north and northeast winds carry superficial waters offshore (*i.e.,* CW and TW). This process promotes bottom inshore intrusions of the SACW over the inner and mid shelves (Castro et al., 1987), lowering water temperatures, raising primary production in the euphotic zone, and enriching the bottom by the input of particulate organic matter (Castro et al., 1987). This increases the diversity as well as abundance of benthic species, being likely a response to the energy surplus by the trophic chain as well as a consequence of the expansion of the SACW's associated species (Pires-Vanin et al., 1993; Muto et al., 2000; Sumida et al., 2005). On the other hand, the BCC acts as a countercurrent to the BC, flowing northwards from the La Plata River and carrying not only colder and less saline waters, but also finer sediments, influencing the sedimentological patterns of the São Paulo's inner and mid shelves (Campos et al., 1999; Souza and Robinson, 2004; Mahiques et al., 2011).

1.3 The Local Mosaic Of Marine Protection Areas And Control Measures

Since 2008 the territorial sea of the São Paulo state has been safeguarded by three major protection areas, the Marine Environment Protection Area of the North, Central and South Coast (*i.e.*, **Figure 1-1**, APAM Norte, APAM Centro and APAM Sul) (São Paulo, 2008c, 2008a, 2008b). All of them are protected areas of sustainable use (*i.e.*, IUCN Category V) (Dudley, 2008), which set zoning regions allowing activities of different intensities (*e.g.*, Zonas de Uso de Baixa escala a Uso Intensivo), including the amateur, traditional and industrial fisheries, aquaculture, extraction of natural resources and tourism (Forestry Foundation, 2019, 2020). The operation of input measures are also regulated by their management plans, such as the restriction of industrial and traditional pair trawlers until the 23.6 m isobath, the specification of months and daylight hours for operation of beach seines (São Paulo, 2009, 2012) and the seasonal closure of fishing on commercial species (SUDEPE, 1984; IBAMA, 2008).

In addition, sixteen Marine Protection Areas (MPAs) are distributed along the coast (**Figure 1-1)**, sheltering inshore areas (*e.g.*, Marine Environment Protection Area of the Comprida island and the Cananéia – Iguape – Peruíbe complex) and insular regions (*e.g.*, The Wildlife Refuge of Alcatrazes – WRA, the Tupinambás Ecological Station – TES, the Marine State Park of Laje de Santos - MSPLS and the no-take zone around the Anchieta island State Park - AISP) (São Paulo, 2008d). They are more restrictive in terms of controlling human activities than the APAs, allowing only supervised visits or educational activities and scientific research (*e.g.*, TES and WRA - IUCN Category Ia, MSPLS and the no-take zone around the AISP - IUCN Category II) and have different objectives, focusing on safeguarding specific ecosystems (*e.g.*, Areas of relevant ecological interest of São Sebastião - AREISS and Guará – AREIG, IUCN Category III) as well as the sustainable use of natural resources by traditional communities (*e.g.*, the Mandira Extractive Reserve – MER, IUCN Category VI). In association with terrestrial protected areas in the surrounding states, they comprise a key network to support ecosystem maintenance, and their relevance has been shown by several studies (*e.g.,* Contente *et al.*, 2020; Karlovic *et al.*, 2021; Motta *et al.*, 2021; Rolim *et al.*, 2019; Santos *et al.*, 2022; Souza *et al.*, 2018).

1.3 Main Objectives And Concise Chapters' Description

As previous mentioned, a significant proportion (*i.e.*, around 25%) of the demersal elasmobranch species are unstudied and even those with sufficient data to be classified in the IUCN or Brazilian red lists are lacking valuable information about their home range, habitat use, population structure and dynamics. This prevents not only the proper assessment of their threatened status (*e.g., P. percellens* is classified as EN based on the population depletion of its congeneric *P. horkelii* - IUCN, 2023) and the establishment of conservation polices, but also can jeopardize the effectiveness of the local MPAs. According to Motta *et al.* (2021) the North, Central and South APAs consists in the most challenging marine conservation initiative in Brazil, due to the complex scenario of intense anthropogenic activities (*e.g.,* Angelini *et al.*, 2018; Barletta *et al.*, 2016; Imoto *et al.*, 2016; Pincinato & Gasalla, 2019), the particularities and requirements of the multiple taxa in the region and the oceanographic processes that change the community seasonally (*e.g.,* Karlovic *et al.*, 2021; Muto *et al.*, 2000; Pires-Vanin *et al.*, 1993; Rodrigues & Pires-Vanin, 2012; Shimabukuro *et al.*, 2016). Thus, **chapter two** aimed to provide new information about a threatened guitarfish, *Z. brevirostris,* elucidating how differences in body morphometry between sexes and throughout the life stages might be related to its development and/or to environmental features, reflecting variations in habitat use. **Chapter three** aimed to assess the role played by two major MPAs located in a transition zone between the central and north parts of the São Paulo coast and evaluate their effectiveness by the enhancement of fishery indicators for *Z. brevirostris*. Finally, **chapter four** aimed to estimate the richness of demersal species in the central and north parts, exploring the shadow effect caused by the SSI, by different structures of multi-species occupancy models.

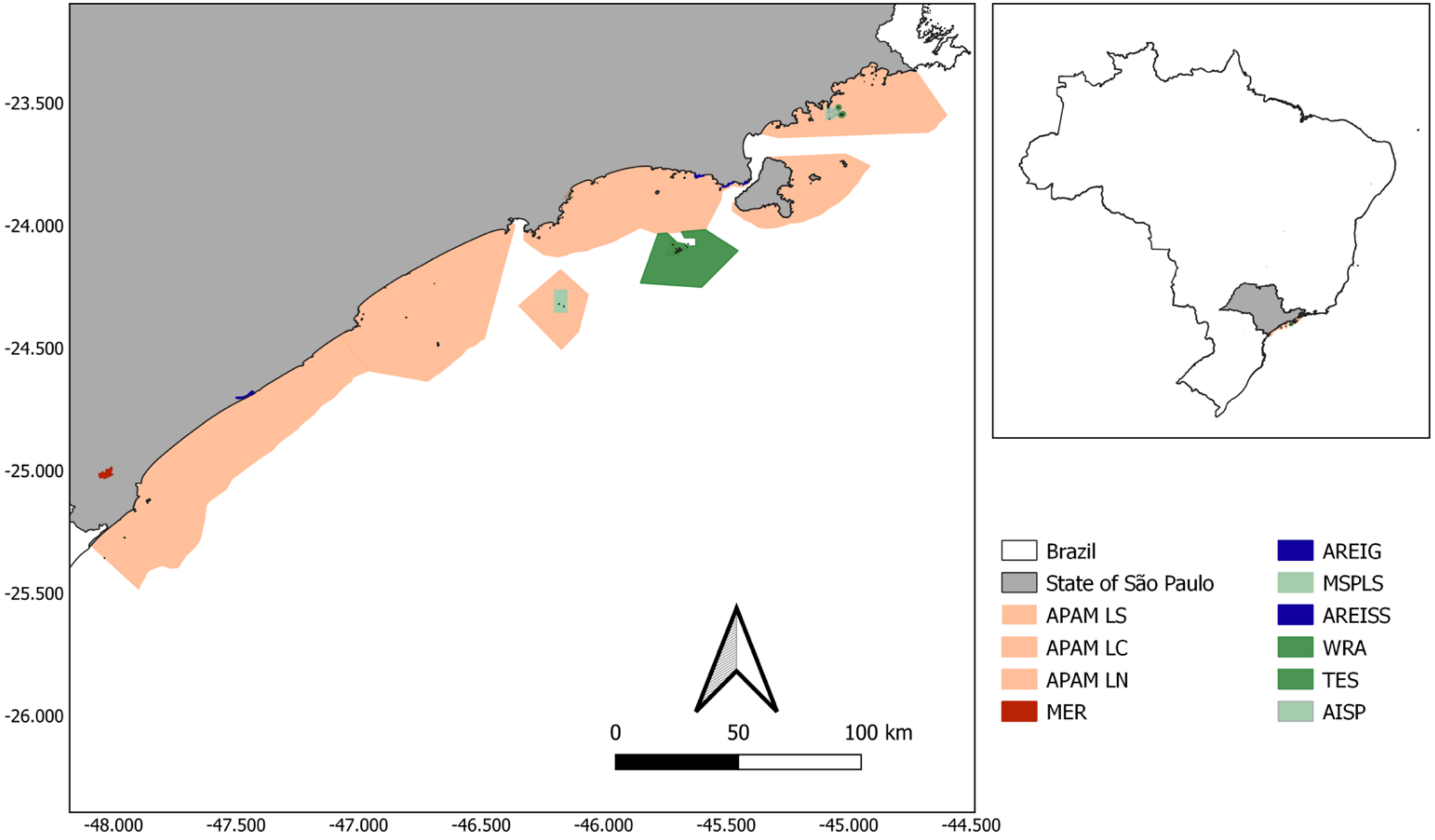

Figure 1-1 Map showing the São Paulo State Coast with the three major Marine Environment Protection Areas (APAMs) and some of the more restrictive MPAs, all colored according to the IUCN classification (Dudley, 2008): Category Ia (dark green), Category II (light green), Category III (blue), Category V (orange) and Category VI (red).

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2 SECONDARY SEXUAL DIMORPHISM AND ONTOGENETIC SHIFTS IN HABITAT USE BY THE LESSER GUITARFISH *ZAPTERYX BREVIROSTRIS*

Abstract

Sexual dimorphisms are generated by divergent process, such as natural or sexual selection and niche convergence. Males and females of the lesser guitarfish, *Zapteryx brevirostris*, present morphologic differences on their discs, and the relationships with the species biology and ecology were unrecognized. Analyzing the morphometry of 201 specimens and the influence of bottom features on the frequencies of 188 specimens among life stages and sexes, we found strong evidence that gonadal maturation leads to dimorphisms on discs and rejected the hypothesis that they were related to ecological pressures. The PCA and PERMANOVA analyses revealed that males and females shared similar body aspects until they reached maturity, mainly due to lower variations of W_D, W_R, L_D, D_{PRO} and L_{SC} at younger life stages. The relationships of these variables with L_T corroborate the former results, showing a changing point around $L_T > 30$ cm where females started to attain larger measurements than males. Moreover, we revealed ontogenetic shifts through the species life stages, with adults from both sexes exploring different habitats than juveniles and subadults. Differences in frequencies of each life stage were better explained by organic matter (OM) with the adults exploring bottom habitats of higher concentrations of OM than juveniles and subadults. These results bring not only new insights about the possible advantages that those morphometric differences provide to males while mating, but also valuable information about the abiotic influences on species distribution, which, along with knowledge of local oceanographic dynamics and benthic community patterns, would inform actions for species conservation.

Key Words: autecology, bottom habitats, body morphometry, elasmobranchs, sediment, Trygonorrhinidae

2.1 Introduction

Secondary sexual dimorphism in elasmobranchs is found in a variety of morphological characters, such as the presence of alar thorns in males (McEachran and Konstantinou, 1996) and differences in morphometry (Kajiura et al., 2005; Rolim et al., 2015), tooth morphology (Kajiura and Tricas, 1996; Gutteridge and Bennett, 2014; Rangel et al., 2014; Silva and Oddone, 2020) and sensory structures (Crooks and Waring, 2013; Kempster et al., 2013). They are generated by divergent process that might act directly or indirectly, setting traits for each sex with sometimes unclear evolutionary origin (*i.e.*, natural or sexual selection and niche convergence) (Hedrick and Temeles, 1989; Shine, 1989). Clear examples are the sexual size dimorphism and sexual differences in feeding structures. While tradeoffs among individual fitness (*i.e.*, mating success, size at maturity and fecundity) and survival (*i.e.*, food competition and predation avoidance) determine body sizes in the two sexes, modified feeding structures may play equal roles on feeding and reproductive strategies (Shine, 1989; Fairbairn, 1997).

Females that are larger and wider as well as heavier than males are commonly reported for batoid species (Braccini and Chiaramonte, 2002; Oddone and Amorim, 2007; Colonello et al., 2012; Tagliafico et al., 2012; Martins et al., 2018; Silva et al., 2018). Particularly for guitarfishes, such aspects are often associated to higher investment in oogenesis and embryo development, resulting in bigger litters of higher body sizes (Vooren and Klippel, 2005; Márquez-Farías, 2007; Rocha and Gadig, 2013; Torres-Huerta et al., 2020). However, this aspect is not universal for the taxa. The lesser guitarfish *Zapteryx brevirostris* (Müller and Henle, 1841) presents similar sizes of first maturity between sexes and no evidence of a size-fitness relationship was reported (Ponz-Louro, 1995; Colonello et al., 2011a), even though the length-weight relationship is sexually divergent (Pasquino et al., 2016).

Regarding differences on feeding structures, only heterodonty was evaluated for *Z. brevirostris*. According to Rangel *et al.*, (2014), females have only shredder teeth, while mature males also presented the grabber type, which in association to alar thorns are used to hold females during mating. On the other hand, different tooth morphologies due to variations on functional ecology are reported for some species, with suggestions that ontogenetic dimorphisms might be associated to changes on diet throughout their life span (Gutteridge and Bennett, 2014; Silva and Oddone, 2020). As Barbini *et al.*, (2011) observed significant differences on diet among juveniles and adults of *Z. brevirostris*, with the occurrence of some items markedly higher for mature females (*i.e.*, cumaceans), obtaining different preys might be a secondary function of the adapted teeth.

A brief notice of morphological dimorphism in specimens of *Z. brevirostris* from Mar del Plata, Argentina, was highlighted by Castello (1971), who described a “sharp concavity on male pectoral fins”. Despite previous works having reported such dimorphism for other species (Leible and Stehmann, 1987; Oddone and Vooren, 2004), to our knowledge it was not reviewed nor thoroughly analyzed about influences on the species biology and autecology. Since this concavity results in a more tapered snout on males, it might facilitate mating by reducing the distance between male’s mouths and females’ pectoral fins. Nevertheless, it also might promote advantages in feeding on animals of the benthic infauna (*i.e.*, invertebrates that live buried in the sediment). Based on this, we investigated the functional role of this concavity and of other body structures related to feeding and reproductive behaviors. We assumed that variations on body measurements would reflect ecological pressures if female’s and male’s main habitats were significantly different throughout the species life stages as well as their bodies. Using data collected from preserved specimens as well as alive ones and assessing differences on frequencies of sexes and life stages by sea bottom features as well as their relationships, we clarify some biological and ecological aspects, providing orientations about how the use of such knowledge (*i.e.*, habitat use x fishing areas) would improve the species conservation, and bring new insights about how the body characteristics could have been modeled by mating behavior.

2.2 Material And Methods

2.2.1 Ethical Statement

This study was reviewed and authorized by the Ethics Committee of Animal Use of the Oceanographic Institute of the University of São Paulo (CEUA IO-USP) and by the Chico Mendes Institute for Biodiversity Conservation (ICMBio): survey permit SISBIO/55824.

2.2.2 Morphology

Body measurements were taken from 110 live specimens collected by expeditions performed at the Alcatrazes Archipelago (24°06′ S and 45°41′ W), southeastern Brazil. Pictures and information regarding sex, total length (L_T, cm), disc width (W_D, cm) and the sharp concavity (*i.e.*, named as rostrum width – W_R, **Figure 2-1**) were obtained from all specimens. Since W_R was not measured on board, we used the open-source software Inkscape (Available at: https://inkscape.org) to obtain this data from pictures taken on board. Through the pictures of each collected specimen and real $W_{D,}$ we estimated a reference measurement of the same variable on the software (W_{Dest}). Then, the ratio between W_D and W_{Dest} were used to estimate W_R through the formula: $W_R = W_{Rest} * (W_D / W_{Dest})$.

To evaluate whether dimorphism was present in other populations, we analyzed 91 preserved specimens deposited at the Museum of Zoology (MZUSP) and at teaching collections of the Institutes of Biosciences and Oceanographic, all based at the University of São Paulo. In addition, 11 body measurements from structures involved on feeding and reproductive behaviors were collected to evaluate whether body changes were related to sexual maturity or feeding divergences. Information regarding the locality of the specimens is on **Appendix A - Table A-1** and the measurements as well as respective abbreviations can be found in **Figure 2-1**.

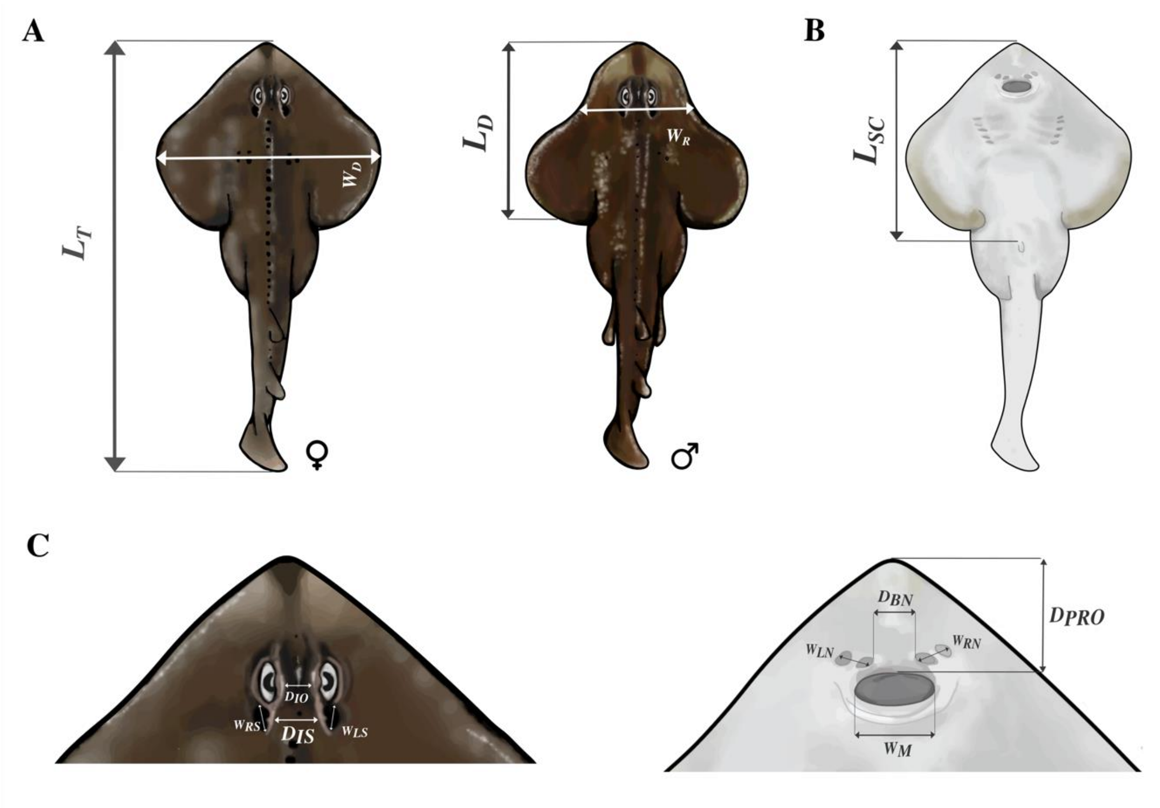

Figure 2-1 Schematic drawing of specimens of *Zapteryx brevirostris* with arrows that represent recorded and estimated morphometric measures: Total length (L_T), disc width (W_D), rostrum width (W_R), disc length (L_D), snout to cloaca length (L_{SC}), interorbital distance (D_{IO}), preoral distance (D_{PRO}), mouth width (W_M), right nostril width (W_{RN}), left nostril width (W_{LN}), distance between nostrils (D_{BN}), interspiracular distance (D_{IS}), right spiracle width (W_{RS}) and left spiracle width (W_{LS}). Draws represents: (A) female and male specimens showing the dimorphism; (B) ventral view of a female specimen and (C) dorsal and ventral views focusing on the anterior part of the species head.

All recorded specimens were grouped into six classes according to sex and L_T: juveniles (17 - 35 cm), subadults (36 - 42 cm) and adults (43 - ~60 cm). Principal component analysis (PCA) was used to assess how the variations in morphometric measurements explain differences among groups. The analysis was applied to ratios between the variables and L_T, that were standardized by z-scaling (Gotelli and Ellison, 2004). Then, to check whether differences between each class combination were significant (*i.e.*, juvenile females *x* juvenile males, juvenile females *x* subadult females, and so on) we set a dissimilarity matrix using Euclidean distances and applied the PERMANOVA (Anderson et al., 2008) test with ten thousand permutations and Bonferroni's correction (Zar, 2009). The PCA and PERMANOVA analysis were performed by the *"prcomp"* and *"adonis2"* functions from the stats (Bolar, 2019) and vegan (Oksanen et al., 2020) packages, respectively, in the R environment (R Core Team, 2023).

Differences between sexes for all measurements were tested by the Mann-Whitney U test for unpaired samples (Zar, 2009). Moreover, to understand the relationships between each measurement and L_T for females and males, we set linear models with interaction effects among continuous and categorical variables (*e.g.,* $W_D \sim L_T * Sex$). The influence of sex on such relationships were evaluated and tested by the t-test and qq-plots and residual plots were used to evaluate issues on regressions fit due to distribution misspecification and heteroscedasticity (Zuur et al., 2009).

2.2.3 Habitat Segregation

Interspecific and intraspecific variations on distribution of elasmobranchs are often related to the sea floor aspects such as sediment composition and rugosity (Karlovic *et al.*, 2021; Lauria *et al.*, 2015; Martin *et al.*, 2012; Pennino *et al.*, 2013), possibly as a response to the occurrence of food items. Thus, datasets generated by expeditions performed on the southwestern Brazilian shelf (23°50'S to 25°23'S and 45°12'W to 46°54'W) in August 2005, February 2006, September 2011 and July 2019 (**Appendix A - Table A-2**), were analyzed to investigate segregations in habitat use by sexes and life stages. Elasmobranchs were collected at 65 sampling locations by 10 to 30 minutes trawls at a speed of two knots, using otter trawl nets with mesh size of 40-60 mm in the body as well as sleeves and 25-30 mm in the cod-end and sediment samples were taken by a van Veen grab.

The sedimentological parameters of the 2005, 2006 and 2011 samples were previously analyzed (Palóczy et al., 2012; Hoff et al., 2015; Shimabukuro et al., 2016). Thus, similar methods in terms of granulometric as well as gravimetric analyses were carried out on the 2019 samples. Particles sizes were measured from 50g samples by the sieve-pipette method (Suguio, 1973) and sediment was classified according to Folk & Ward (1957). In addition, concentrations of organic matter (OM) and $CaCO_3$ were estimated through weight differences after sample digestion by 10% solutions of H_2O_2 and HCl, respectively.

We compared the sedimentological parameters among sexes and species life stages to find variations on habitat use. Differences between males and females were evaluated by the Mann-Whitney U test, and differences among life stages were assessed applying the Kruskal-Wallis H test followed by the pairwise Mann-Whitney U test for unpaired samples with Bonferroni's correction (Zar, 2009). As non-significant differences (U test, $p > 0.05$) were found between males and females (**Appendix A - Figure A-1**), multinomial logistic regression models were fitted only to evaluate the relationships between life stages composition (*i.e.*, adults, subadults and juveniles) and OM and $CaCO_3$ (Fávero, 2017). Models were set considering the fixed effect of variables that previously showed significant differences (H test, $p < 0.05$) among these classes. Moreover, to test the hypothesis that *Z. breviroristris* explores different bottom habitats throughout its life, the models were set considering the subadults as reference class. Thus, we would expect significant differences between subadults and adults as well as subadults and juveniles as a function of the sediment aspects. Before model fitting, we tested collinearity between OM and $CaCO_3$ by the Spearman's coefficient (Zuur et al., 2009, 2010) and both were standardized (mean=0 and variance = 1). The second order Akaike information criterion (AICc) was applied, taking the model of the lowest AICc as the best descriptor of the variations in the species life stages (Burnham and Anderson, 2002). All analysis were performed in R environment (R Core Team, 2023) using the functions "multinom", "coeftest" and "model.sel" from the packages *nnet* (Ripley and Venables, 2022), *lmtest* (Hothorn et al., 2022), *MuMIn* (Bartoń, 2020) for models fit, *p-value* estimation of regression parameters by *Z-tests* and model selection, respectively.

2.3 Results

2.3.1 Morphological Differences Across Life Stages And Between Sexes

The PCA analyses revealed differences among life stages, distinguished mainly by the first principal component (**Figure 2-2**). Adults were separated from the other two stages due to development of the body (*i.e.*, snout to cloaca length - L_{SC}), disc (*i.e.*, disc length - L_D and disc width - W_D) and head (*i.e.*, rostrum width - W_R and pre-oral length - D_{PRO}), being positively loaded on the PC1. Moreover, juveniles were negatively loaded, overlapping with subadults whose presented a gradient, from negative to positive loads, being in the middle of the two stages. The differences explained by PC2 seemed to be related to individual variations on spiracles and nostrils widths.

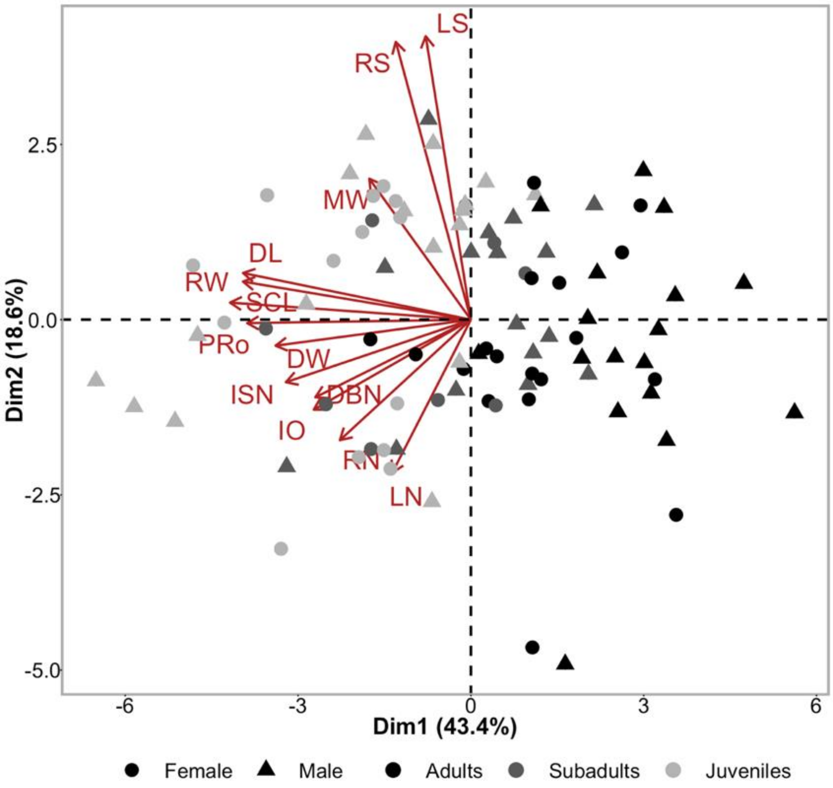

Figure 2-2 Principal component analysis (PCA) differentiating females and males' life stages (juvenile, subadult and adult) by variations in morphometric measurements. All the measurements were divided by L_T and standardized by z-scaling. The initials of body measurements are available on Figure 2-1.

On the other hand, despite the fact that no distinctions between females and males could be visually found on the PCA plot, the PERMANOVA presented significant differences between classes. While the body measurements varied significantly across almost all the life stages for males (**Table 2-1**), females were similar, differentiating only in relation to the older stage (*i.e.*, juvenile females *x* adult females, $p < 0.05$). In addition, when the life stages were compared between sexes, juveniles as well as subadults did not differ whereas adult females and adult males were significantly distinct (**Table 2-1**).

Table 2-1 Results of the pairwise PERMANOVA of the body measurements by life stages and sex combinations.

Source of variation	**df**	**F**	**p-value**
Females			
Adults *x* Juveniles	1	10.66	**<0.01**
Residual	30		
Adults *x* Subadults	1	3.29	0.06
Residual	25		
Subadults *x* Juveniles	1	2.06	1.14
Residual	21		
Males			
Adults *x* Juveniles	1	18.79	**<0.01**
Residual	32		
Adults *x* Subadults	1	6.17	**<0.01**
Residual	31		
Subadults *x* Juveniles	1	4.60	0.10
Residual	31		
Females *x* Males			
Adult females *x* Adult males	1	3.44	**<0.01**
Residual	33		
Juvenile females *x* Juvenile males	1	1.11	5.23
Residual	29		
Subadult females *x* Subadult males	1	2.17	0.79
Residual	23		
Adult females *x* Juvenile males	1	9.57	**<0.01**
Residual	33		

Adult females *x* Subadult males	1	2.15	0.78
Residual	32		
Subadult females *x* Adult males	1	9.65	**<0.01**
Residual	24		
Subadult females *x* Juvenile males	1	1.45	3.32
Residual	24		
Juvenile females *x* Adult males	1	20.63	**<0.01**
Residual	29		
Juvenile females *x* Subadult males	1	6.67	**<0.01**
Residual	28		

Significant differences (corrected Bonferroni p-value<0.05) were highlighted. Notations: evaluated classes for differences in variation (Source of Variation), degrees of freedom (df), F-test (F) and significance in F-test obtained by ten thousand permutations (p-value).

Significant differences between sexes were found in two of the fourteen analyzed measurements (**Table 2-2** and **Appendix A - Figure A-2**). The W_D as well as W_R tend to be wider in females than males (**Figure 2-3**). The relationships of W_D, W_R, $L_{D,}$ D_{PRO} and L_{SC} with L_T showed similar trends. Overall, no differences were found on these lengths between sexes, except to the widths, were juvenile females showed smaller W_D as well as W_R than juvenile males (**Figure 2-4**). However, there is a changing point around $L_T > 30$ cm were females started to attain larger measurements than males (**Figure 2-4**), due to higher growth rates as showed on **Table 2-3** by the estimated $\beta_{LT}{*}_{male}$ and $\beta_{LT}{*}_{female}$.

Table 2-2 Mann-Whitney U test results for differences in body measurements by sex.

Variables	U	p-value
L_T	5120	0.80
W_D	5986	**0.02**
L_D	1208	0.14
W_R	7354	**<0.01**

L_{SC}	1259	0.06
D_{IO}	1184	0.21
D_{PRO}	1218	0.12
W_{M}	1110	0.50
W_{RN}	1146	0.34
W_{LN}	1142	0.36
D_{BN}	1223	0.12
D_{IS}	1216	0.13
W_{RS}	994	0.80
W_{LS}	1014	0.94

Significant differences (p-value<0.05) were highlighted. Notations: analyzed body measurements (Variables), U-test (U) and significance in U-test (p-value).

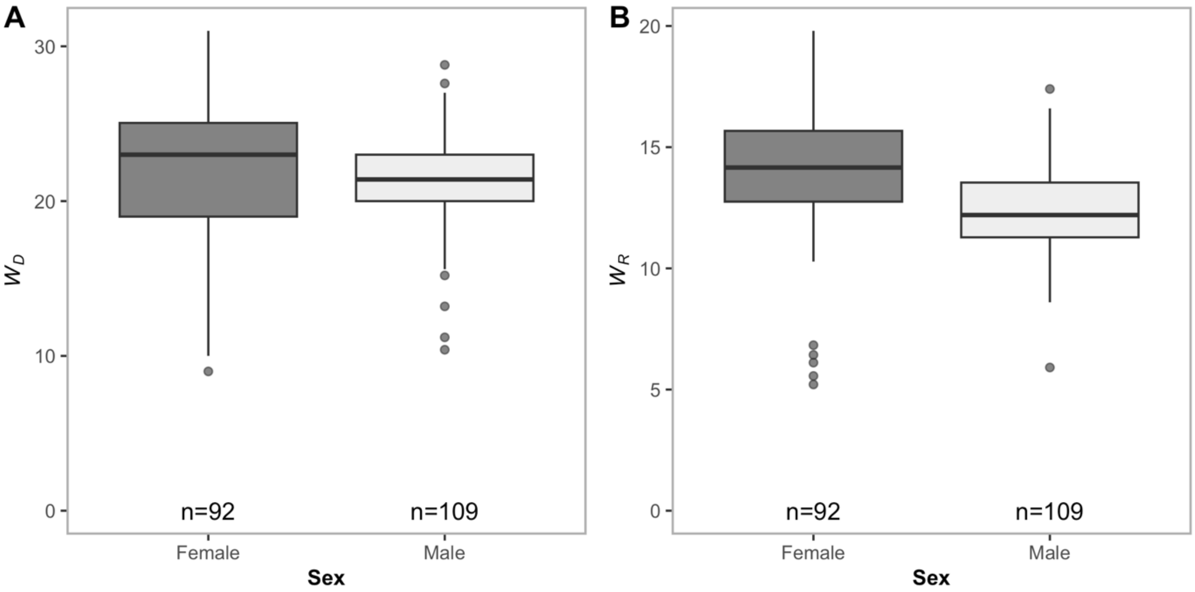

Figure 2-3 Boxplots showing variances in W_D (A) and W_R (B), between females and males of *Zapteryx brevirostris*. Results of the Mann-Whitney U tests are presented on Table 2-2.

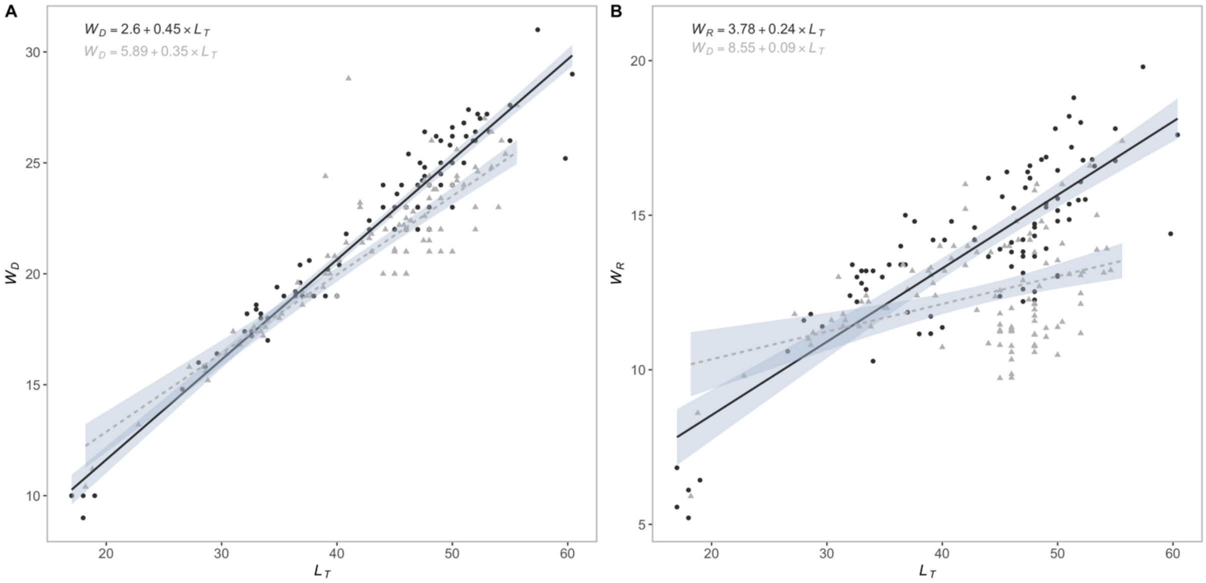

Figure 2-4 Relationships between W_D (A) and W_R (B) with L_T for females (black circles and solid lines) and males (gray triangles and dashed lines) of *Zapteryx brevirostris*. Shaded ribbons represent the 95% confidence intervals of estimated values.

Table 2-3 Estimated parameters from the linear regressions that explain variations in the relationships between body measurements and total length by sex.

Variables	**β**	**SE**	**t-value**	**p-value**
$W_D \sim L_T * \text{Sex}$ ($R^2 = 0.87$)				
Female (intercept)	2.60	0.65	4.01	**<0.01**
L_T * Female	0.45	0.01	30.68	**<0.01**
Male	3.29	0.98	3.34	**<0.01**
L_T * Male	-0.10	0.02	-4.52	**<0.01**
$L_D \sim L_T * \text{Sex}$ ($R^2 = 0.97$)				
Female (intercept)	3.63	0.36	10.11	**<0.01**
L_T * Female	0.37	0.01	43.33	**<0.01**
Male	0.72	0.49	1.45	0.15
L_T * Male	-0.03	0.01	-2.49	**0.01**
$W_R \sim L_T * \text{Sex}$ ($R^2 = 0.57$)				
Female (intercept)	3.78	0.75	5.06	**<0.01**
L_T * Female	0.24	0.02	13.97	**<0.01**
Male	4.77	1.14	4.20	**<0.01**
L_T * Male	-0.15	0.03	-5.74	**<0.01**
$L_{SC} \sim L_T * \text{Sex}$ ($R^2 = 0.99$)				
Female (intercept)	2.70	0.30	9.00	**<0.01**
L_T * Female	0.40	0.01	55.89	**<0.01**

Male	0.80	0.41	1.93	0.06
L_T * Male	-0.04	0.01	-3.90	**<0.01**
$D_{IO} \sim L_T$ * Sex ($R^2 =$ 0.84)				
Female (intercept)	0.05	0.10	0.49	0.62
L_T * Female	0.04	0.00	16.00	**<0.01**
Male	0.18	0.14	1.27	0.21
L_T * Male	-0.01	0.00	-1.49	0.14
$D_{PRO} \sim L_T$ * Sex ($R^2 =$ 0.89)				
Female (intercept)	0.79	0.19	4.26	**<0.01**
L_T * Female	0.09	0.00	19.74	**<0.01**
Male	0.51	0.26	1.97	0.05
L_T * Male	-0.02	0.01	-2.70	**<0.01**
$W_M \sim L_T$ * Sex ($R^2 =$ 0.89)				
Female (intercept)	0.42	0.14	2.93	**<0.01**
L_T * Female	0.06	0.00	18.18	**<0.01**
Male	-0.05	0.20	-0.25	0.80
L_T * Male	0.00	0.00	0.31	0.76
$W_{RN} \sim L_T$ * Sex ($R^2 =$ 0.85)				
Female (intercept)	0.13	0.08	1.60	0.11
L_T * Female	0.03	0.00	15.48	**<0.01**
Male	0.01	0.11	0.11	0.91
L_T * Male	0.00	0.00	-0.09	0.93
$W_{LN} \sim L_T$ * Sex ($R^2 =$ 0.90)				
Female (intercept)	0.10	0.07	1.41	0.16
L_T * Female	0.03	0.00	18.87	**<0.01**
Male	-0.09	0.09	-1.01	0.31
L_T * Male	0.00	0.00	1.12	0.26
$W_{BN} \sim L_T$ * Sex ($R^2 =$ 0.80)				
Female (intercept)	0.16	0.09	1.76	0.08
L_T * Female	0.03	0.00	12.95	**<0.01**
Male	-0.01	0.12	-0.11	0.92
L_T * Male	0.00	0.00	-0.21	0.84
$D_{IS} \sim L_T$ * Sex ($R^2 =$ 0.94)				
Female (intercept)	0.23	0.10	2.43	**0.02**
L_T * Female	0.06	0.00	25.89	**<0.01**

Male	0.00	0.13	-0.01	0.99
L_T * Male	0.00	0.00	-0.62	0.54
W_{RS} ~ L_T * Sex ($R^2 = 0.68$)				
Female (intercept)	0.38	0.10	3.97	**<0.01**
L_T * Female	0.02	0.00	8.94	**<0.01**
Male	-0.08	0.13	-0.61	0.54
L_T * Male	0.00	0.00	0.93	0.35
W_{LS} ~ L_T * Sex ($R^2 = 0.64$)				
Female (intercept)	0.27	0.11	2.40	**0.02**
L_T * Female	0.02	0.00	8.61	**<0.01**
Male	-0.01	0.15	-0.06	0.95
L_T * Male	0.00	0.00	0.27	0.78

Parameters with significant p-value (<0.05) were highlighted. Notations: estimated coefficients (β), standard error (SE), t test (t-value), significance in t test (p-value). Estimates (β) corresponds to intercept for females (Female), slope for females (L_T * Female), difference between male and female intercept (Male) and difference between male and female slope (L_T * Male).

2.3.2 Life Stages Variation By Sediment Aspects

Overall, 188 specimens of which 93 adults, 62 subadults and 33 juveniles were caught across a mosaic of sediments characterized by the predominance of sand and higher concentrations of $CaCO_3$ than OM (**Appendix A - Table A-2**). Comparisons of the sedimentological aspects (**Appendix A - Table A-3**) showed significant differences of $CaCO_3$ ($H = 6.79$; d.f. = 2; $p < 0.05$; **Figure 2-5**) and OM ($H = 14.27$; d.f. = 2; $p < 0.05$; **Figure 2-5**), suggesting that the assumption of changes in habitat use by life stages would be corroborated. The model that best explained (Δ AICc < 2) variations in composition of adults, subadults and juveniles included the variable OM (**Table 2-4**), and the model coefficients supported significant difference between adults and subadults in relation to concentrations of OM (**Table 2-5**).

Table 2-4 Best ranked model for the multinomial model of frequencies of life stages.

Models	**k**	**AICc**	**ΔAICc**	**w**
OM	4	366.30	0.00	0.73
$CaCO_3$ + OM	6	368.89	2.58	0.20
null	2	371.60	5.30	0.05
$CaCO_3$	4	374.50	8.20	0.01

The null model was set without any effect. Notations: number of parameters estimated (k), Akaike's second-order information criterion (AICc), AICci – AICcmin (ΔAICc), Akaike weight (w), concentrations of organic matter (OM) and $CaCO_3$.

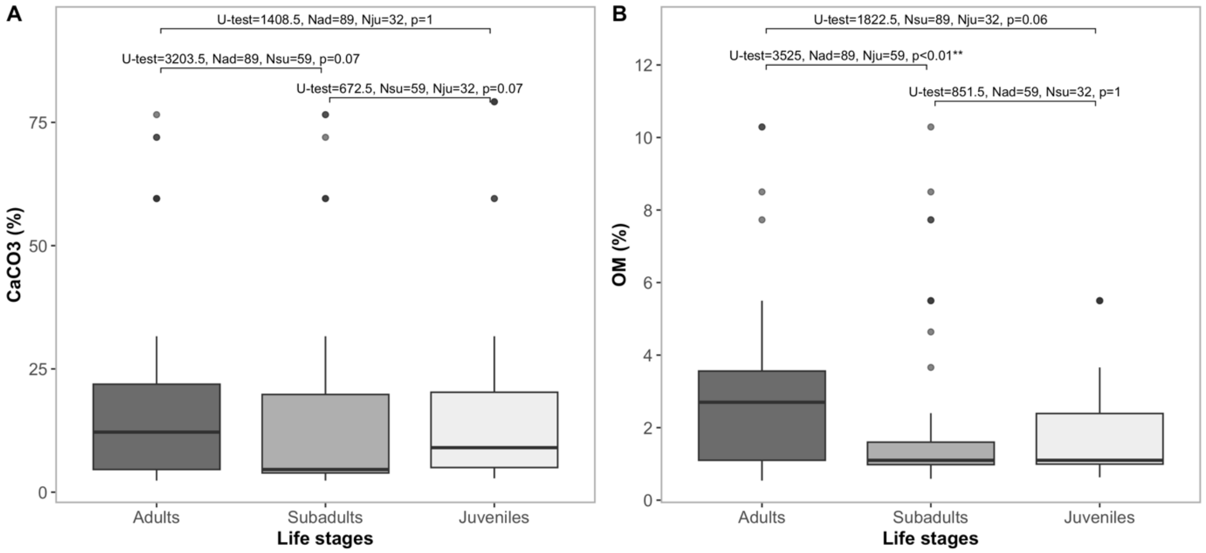

Figure 2-5 Boxplots showing significant differences in concentrations of organic matter (**A**) and $CaCO_3$ (**B**) by life stages. Gray dots are the minimum and maximum values in the data. Results of the Mann-Whitney U tests corrected by Bonferroni are presented.

While subadults and juveniles seemed to explore similar bottom habitats with lower concentrations of OM, the adults showed the opposite pattern (**Table 2-5**). Older specimens were caught at places with higher concentrations of OM and their frequencies increased with the variable (**Table 2-5**). According to the odds ratio, the probability of the caught specimen was an adult, increased around 63% with a unit increment in concentrations of OM (**Figure 2-6**).

Table 2-5 Estimated parameters from the best model that explain differences in frequencies of the life stages by concentrations of organic matter. The subadults class were set as the intercept.

Models	β	SE	Z-value	p-value
Adults	0.42	0.17	2.44	**0.01**
Adults * OM	0.49	0.20	2.46	**0.01**
Juveniles	-0.62	0.23	-2.69	**<0.01**
Juveniles *OM	-0.02	0.29	-0.06	0.95

Parameters were present in the linear predictor scale (logit) and those with significant p-value (<0.05) were highlighted. Notations: estimated coefficients (β), standard error (SE), Z test (Z-value) and significance in Z test (p-value).

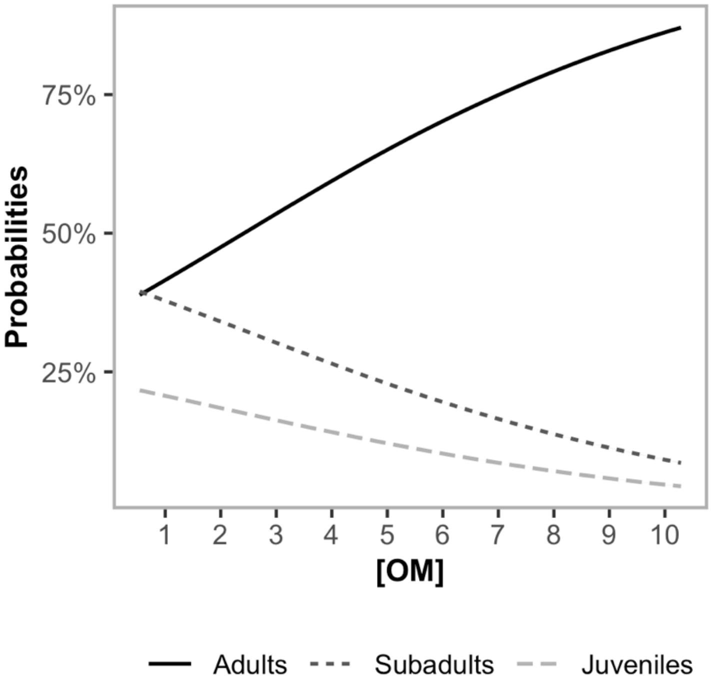

Figure 2-6 Capture probabilities in relation to changes in concentration of organic matter for juveniles, subadults and adults of *Zapteryx brevirostris*.

2.4 Discussion

No evidence that W_R as well as the other body measurements have been shaped by ecological pressures was found. On the contrary, the observed patterns strengthen the assumption that such dimorphisms in the body morphometry are related to changes caused by gonadal maturation and transformations of the female's reproductive system. As elucidated by variations between sexes in the relationships of the body measurements with L_T, some divergences become evident from the L_T = 30 cm. This corresponds to the end of the species second year of life (Caltabellotta et al., 2019), or to our classification, the moment of transition from juveniles to subadults.

The morphometric transformations match the second stage of maturity (*i.e.,* in maturation) for females according to studies of Colonello *et al.*, (2011b) and Ponz-Louro, (1995) who have evaluated the reproductive biology of different populations of *Z. brevirostris*. Immature females (*i.e.,* the first stage) are identified by the absence of differentiated follicles in the ovaries and undeveloped oviducal glands which are barely distinguished from the oviducts. At the second stage (from L_T = 33 cm), there was an augmentation in weight and in diameter of the entire female's reproductive system, especially the ovaries (Ponz-Louro, 1995; Colonello et al., 2011b) due to maturation of follicles in the ovaries and differentiation of the oviducal glands as well as the oviducts to the uterus. For males, transition between the first and the second stages occurred latter, at L_T = 39 cm (Ponz-Louro, 1995). Thus, the earlier beginning in changing the females body morphometry, enhanced by the higher rate of change as they grown (*i.e.*, estimated βs on **Table 2-3**), might be explained by those transformations.

In this sense, the similarities between females and males until they reached maturity, due to the absence of significant variations in body measurements of juveniles and subadults, can be a result of this latter accentuation on the growth rates of such. The energy investment in attaining larger bodies at earlier life stages is a common strategy (Helfman et al., 2009), which results in the development of secondary body parts, such as discs and head structures, occurring at different proportions than the L_T. However, the absence of other studies investigating the development of body structures of *Z. brevirostris* and its congeneric species *Zapteryx exasperata* (Jordan and Gilbert, 1880) and *Zapteryx xyster* Jordan and Evermann, 1896, prevented us from making comparisons.

The wider W_D attained by females were also found in other elasmobranchs (Colonello et al., 2012; Martins et al., 2018; Silva et al., 2018). This dimorphism is usually associated to increases in the uterine fecundity (Martins et al., 2018; Silva et al., 2018) and to a delay in females' maturity due to energetic investment on body development (Oddone et al., 2007, 2008a). However, as elucidated by previous works, no significant differences in L_T between sexes were found and females and males reach maturity at similar sizes (Ponz-Louro, 1995; Colonello et al., 2011b). These differences are possibly related to the reproductive system development and advantages for males during copulation (Pratt and Carrier, 2011).

Besides the wider W_D and W_R, females presented higher growing rates of L_D and L_{SC}, being consistent with the position of the abdominal cavity, placed from the final part of their discs to the beginning of the caudal peduncle (Ponz-Louro, 1995). Since the females' bodies must sustain the significant changes associated with the ovaries, oviducal glands, and uterus as well as the embryos' development, the higher development of such parts is expected. Regarding the males, the tapered snout associated to smaller W_D and W_R as well as the lower growing rates of those parts, could allow a better alignment with females' body, reducing the number of trials of clasper insertion and increasing copulation success. Contrary to the pattern showed by females, the abdominal development of males does not seem to occur at the same rate as the reproductive organs, especially the claspers, even though the reproductive system of both sexes changes significantly in size and weight as they grown (Ponz-Louro, 1995). According to Colonello *et al.*, 2011a, claspers presented a sharp increase, which would compensate the smaller abdomen and becoming anatomically compatible with the body position of females' cloaca. In this sense, such morphometric differences on W_D and W_R as well as L_D and L_{SC} might facilitate the holding and penetrations processes, by reducing the distance between males' mouth and females' pectoral fins and among claspers and females' cloaca, respectively. Nonetheless, further studies associating the species reproductive behavior to body morphometry and individual fitness are necessary to confirm the discussed hypothesis.

As previously, mentioned adult females and males were significant different from each other as well as from juveniles and subadults of the same sex. However, they seemed to share the same habitats in terms of OM concentrations, varying only between adults and the other life stages, which suggests that changes in body morphologies are not related to ecological pressures. Overall, maturity is sharply reached by both sexes, between $LT = 42$ cm and 45 cm (Ponz-Louro, 1995) and this might reflect on differences in diet requirements through life stages, but not necessarily between sexes. The *Z. brevirostris* is a bottom-dwelling predator with a specialized diet, feeding mainly on shrimps, amphipods and polychaetes (Soares et al., 1992; Barbini et al., 2011; Marion et al., 2011; Bornatowski et al., 2014c). However, as they grown proportions of amphipods decrease whereas polychaetes increase (Barbini et al., 2011; Marion et al., 2011). According to studies about the structure and dynamic of communities of polychaetes and amphipods in the southwestern Atlantic, the presence of food items of *Z. brevirostris*, such as specimens of genus *Armandia* and *Ampelisca* (Barbini et al., 2011; Marion et al., 2011), were classified in groups that had their abundances directly and indirectly related to concentrations of OM (Rodrigues and Pires-Vanin, 2012; Shimabukuro et al., 2016), respectively. In this sense, the higher frequency of adults and enhancement in probability due to higher concentrations of OM are explained by the distribution patterns of its prey.

Barbini *et al.*, (2011) identified a pattern in habitat use by the species, being more abundant over sand sediments. Additionally, this seems to be the preferred sediment type for the both prey types formerly mentioned (Rodrigues and Pires-Vanin, 2012; Shimabukuro et al., 2016). As the sampled area were predominantly composed by sand and thus of higher probability of occurrence of its prey, this is a suitable feeding place throughout the different life stages of *Z. brevirostris,* which explains the absence of differences among them. Previous works have also found shifts in habitat use due to changes in prey preferences through sharks and rays' life span (Bethea et al., 2004; Dale et al., 2011; Ketchum et al., 2013). Such changes can be related to different factors such as the necessity of more energetic resources at the maturity stage (Rangel et al., 2021), the trade-off between quantities and quality, leading adults to spend less energy searching for food since they focus on prey of higher trophic levels (Scharf et al., 2000) and reduction of intraspecific competition (Ketchum et al., 2013; Gül and Demirel, 2022).

Considering our findings and the trophic characteristics of their main prey we believe that the differences found might be a strategy by *Z. brevirostris* to reduce competition. Peaks on mating of the lesser guitarfishes occur on summer (Ponz-Louro, 1995), when the abundance of mature specimens increases on the inner shelf, searching for sheltered habitats and more suitable conditions (Karlovic et al., 2021) due to bottom enrichment by the intrusion of the South Atlantic Central Water (Castro et al., 1987; Sumida et al., 2005). This coincides with shifts on its diet, as the relevance of fishes and cephalopods among the adults' prey increased on summer (Marion et al., 2011), probably avoiding dietary overlap. Furthermore, assumptions related to feeding on more energetic items were weakened, since the predominance of food items changed to lower trophic position preys, from subadults eating brachyuran crabs (*e.g., Portunus sp., Callinectes sp., Libinia sp.* and *Persephona sp.*) to adults eating on polychaetes (*e.g.,* Opheliidae, Polynoidae, Aphroditidae and Sigalionidae) (Barbini et al., 2011; Marion et al., 2011), and the fact of the diet of congeneric brachyurans (*e.g., Persephona mediterranea, Portunus spinimanus, Portunus spinicarpus, Callinectes ornatus* and *Libinia spinosa*) also comprises polychates (Petti et al., 1996).

The understanding about ecological patterns in habitat use is mandatory to creation of appropriate conservation actions (Bornatowski *et al.*, 2014; Chapman *et al.*, 2005; Karlovic *et al.*, 2021; Knip *et al.*, 2012; Wiegand *et al.*, 2011), such as the establishment of effective Marine Protected Areas, control and restriction measures and adaptative management. As highlighted by previous studies and strengthened by our findings, the distribution of the lesser guitarfishes is highly associated to its prey, changing in accordance with the effects of oceanographic dynamics over the benthic community. Based on that, the Brazilian southeastern shelf encompasses key habitats throughout the species' life span. However, the operation of bottom trawls only occurs over soft-bottoms, and except for some fishing restrictions imposed over the inner shelf (São Paulo, 2009, 2012) and seasonally active ones on higher bathymetries (SUDEPE, 1984; IBAMA, 2008), it is fair to consider that populations of southeastern Brazil still have been experiencing intense fishing mortality on all their life stages, even though fishing on them is forbidden in Brazilian waters (MMA, 2014). The lesser guitarfish is globally classified as endangered and changes on its growth rate as well as on the intrinsic rate of population growth have been associated to fishery pressures and ineffective or even absent enforcement measures (Caltabellotta, 2014; Caltabellotta et al., 2019), being unable to sustain the impacts provided by this activity (Martins, 2007). Thus, a deeper comprehension about its trophic position, niche and habitat utilization among different life stages as well as updating the assessments about the reproductive biology and ecology are essentials to start improving its conservation status.

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3 FUNCTIONALITY AND EFFECTIVENESS OF MARINE PROTECTED AREAS IN SOUTHEASTERN BRAZILIAN WATERS FOR DEMERSAL ELASMOBRANCHS

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Abstract

Ensuring the efficacy of Marine Protected Areas (MPAs) requires that adequate management strategies be implemented according to the MPA's objectives. Within the scope of species conservation, achieving MPA objectives demands understanding of the role played by MPAs for the target species. In 2014, Brazilian stakeholders and experts set the action plan for elasmobranchs' conservation, which intended to create new protected areas and expand the existing ones. Nevertheless, more than 65% of Brazilian elasmobranch species are threatened by anthropogenic pressures such as fisheries and habitat loss. In addition, their ecological aspects are not well studied, which might jeopardize the success of the proposed actions. To assess the functionality and effectiveness of two no-take MPAs for sixteen demersal species, the Wildlife Refuge of Alcatrazes (WRA) and the Tupinambás Ecological Station (TES), we evaluated the community structure, space-time variations in functional diversity and changes in fishery indicators. Community dynamics were driven by inshore intrusion and time persistent effects of a cold and nutrient-rich water mass, the South Atlantic Central Water, which increased the relative abundance of species, functional groups, and overall diversity. Spatially, the heterogeneity of benthic habitats, due to the action of stronger waves in specific parts of the MPAs, reflects a diverse community of benthic invertebrates, explaining differences in relative abundance and similarities in space use by the functional groups. Regarding effectiveness, the MPAs make up a key network with the surrounding protection areas to support the ecosystem maintenance on the central and northern coast of the São Paulo state. The establishment of the TES has positively influenced the community throughout the years while the recent creation of the WRA may have promoted some improvements in fisheries indicators for a threatened guitarfish. We propose different functions of the Alcatrazes archipelago for each species and suggest some measures to enhance not only elasmobranch conservation but also the MPAs' effectiveness.

Keywords: Alcatrazes archipelago, management strategies, habitat use, community structure, fishery indicators, elasmobranch conservation, functional diversity

3.1 Introduction

For decades, governments have been using Marine Protected Areas (MPAs) to manage use of ocean resources. MPAs can address socioenvironmental issues by supporting traditional fishing communities, avoiding fisheries depletion and marine habitat degradation, and maintaining ecological services (Halpern, 2003; Fox et al., 2012). They are usually employed as a tool for conservation of critical habitats and dependent organisms, accounting for different requirements through a species' life stages that can be safeguarded from anthropogenic disturbances (Claudet et al., 2010; Grüss et al., 2011; Wiegand et al., 2011; Knip et al., 2012; Rolim et al., 2019). Since the accomplishment of multiple objectives is challenging and success indicators, such as fishery sustainability, go beyond the MPA boundaries, coordination between MPA design and other management strategies (e.g., measures of control and restriction, networks of reserves and adaptive management) are mandatory to achieve effectiveness (Fox et al., 2012; Lubchenco and Grorud-Colvert, 2015; Hilborn, 2016).

Previous works have highlighted the importance of adopting multiple strategies, especially when the MPA goals involve long-lived and mobile species like elasmobranchs (Chapman et al., 2005; Wiegand et al., 2011; Knip et al., 2012). For instance, Brazil is home to more than 14% of the worldwide biodiversity of sharks, skates and rays, driving experts and stakeholders to determine that conservation actions including MPAs are needed for the taxon (*i.e.*, The action plan for elasmobranch conservation; ICMBio, 2016a). Currently, at least 65% of the species recorded in Brazilian waters are threatened or have insufficient data (ICMBio, 2016b; IUCN, 2021) and this lack of information might jeopardize the success of conservation and management actions (Gill et al., 2017; Giakoumi et al., 2018).

Among the strategic regions delimited by the action plan (ICMBio, 2016a) two marine reserves call attention: The Wildlife Refuge of Alcatrazes (WRA) and the Tupinambás Ecological Station (TES). They were established three decades apart seeking ecosystems preservation by restriction of human interference (Brazil, 1987, 2016). First, TES was created in 1987 to secure coastal and offshore rock formations, covering two coastal islands in northern São Paulo (i.e., Cabras and Palmas islands) and the islets, shallow flats and submerged pinnacles of the Alcatrazes archipelago. Later, in 2016, the WRA was implemented to shelter a greater area of the archipelago, especially the Alcatrazes island, becoming the largest marine reserve in south and southeastern Brazil. Both are no-take zones and although their delimitations overlap, they have different management plans. TES is the most restrictive, allowing only scientific and educational activities, while the WRA allows supervised visits to general public (ICMBio, 2017; Marconi et al., 2020).

At present, WRA and TES are part of a critical network for biodiversity maintenance that includes adjacent protected areas on the central and northern coasts of the São Paulo state (São Paulo, 2008). It is located at the middle continental shelf, which makes the Alcatrazes archipelago a unique area that interfaces parallel and perpendicular gradients of granulometry and organic matter in relation to the coast (Mahiques et al., 1999, 2004, 2011). Furthermore, it is near temperate and subtropical transition zones, being markedly influenced by mesoscale physical processes that promote seasonal changes in water properties (Castro et al., 1987; Campos et al., 2000). From late spring through summer, the prevalence of north and northeast winds carries superficial waters offshore, composed by the Coastal and Tropical water masses. This process promotes bottom inshore intrusions of the South Atlantic Central Water (SACW), a colder water mass that stratifies the water column (Castro et al., 1987).

The archipelago is ecologically important, presenting greater values of species richness, abundance and biomass of fish assemblages compared to the fished areas inshore, as well as the other no-take areas in the region (Gibran and Moura, 2012; Morais et al., 2017; Rolim et al., 2019). These trends reflect a complex ecosystem primarily regulated by top-down effects, with higher heterogeneity of functional groups when compared to the previously mentioned areas (Rolim et al., 2019). The high abundance of larger individuals of fishery target species (*e.g.,* Epinephelidae, Kyphosidae, Carangidae and Scaridae) suggests a great spillover potential to adjacent zones (Rolim et al., 2019). However, for elasmobranchs, especially the demersal species, the relationship of local species with environmental features is unknown and available information is restricted to community studies that focus mainly in actinopterygians. Approximately seventeen elasmobranch species are reported in the area (Hoff, 2015; ICMBio, 2017; Rolim et al., 2019), which exhibit differences in feeding and reproductive strategies, and behavioral ecology (Lessa et al., 1986; Soares et al., 1992; Vögler et al., 2003; Vooren and Klippel, 2005; Aguiar and Valentin, 2010), highlighting the variety of roles that the WRA and TES MPAs may play according to habitat use by the species.

Obtaining knowledge on the ecology of these species is crucial since fishing pressure and habitat degradation on coastal and inner shelf regions have disturbed the ichthyofauna, resulting in population depletion, diversity loss and ecosystem unbalancing (Imoto et al., 2016; Dias et al., 2017; Prado et al., 2019; Rolim et al., 2019; Trevizani et al., 2019). Thus, the present study aimed to assess the functionality and effectiveness of the two MPAs to assist the decision making process that involves the conservation of demersal elasmobranchs. Our findings are important not only to understand the local and regional dynamics, but also to enhance policies for species conservation, in order to underlie the MPAs' management. We hypothesize that those species use the archipelago for distinct purposes, which would reflect in different population structures. Differences in species distributions and in diversity metrics are also expected throughout space and time. Furthermore, we believe that variations in the relative abundance of functional groups as well as of their species, are related to the seasonal dynamics of the environment and to the heterogeneity of habitats. Finally, we expect that the size structure of a threatened guitarfish changes significantly due to the protection of a newer and larger MPA (*i.e.*, the WRA).

3.2 Material And Methods

3.2.1 Ethics Statement

The animal study was reviewed and approved by the Ethics Committee of Animal Use of the Oceanographic Institute of the University of São Paulo (CEUA IO-USP) and by the Chico Mendes Institute for Biodiversity Conservation (ICMBio) under the survey permit SISBIO/55824.

3.2.2 Sampling

Biotic and abiotic data used in this study were obtained from five oceanographic expeditions performed by the following projects: Contributions to the ESEC Tupinambás Management Plan: oceanography and marine biodiversity (September/2011), Biotic Integrity of the Alcatrazes Archipelago Ecosystems (January/2014) and Geohabitat of the demersal ichthyofauna of the Alcatrazes region: an environmental assessment (September/2015, December/2018 and July/2019). Position of the oceanographic stations was defined according to the objectives of each project. Thus, they were set at different locations throughout the archipelago, except to 2019, when the 2018 stations were re-sampled (**Figure 3-1**). Sampling of sea water and sediments as well as capture of elasmobranchs were carried out at fifty oceanographic stations between 28–53 m depth.

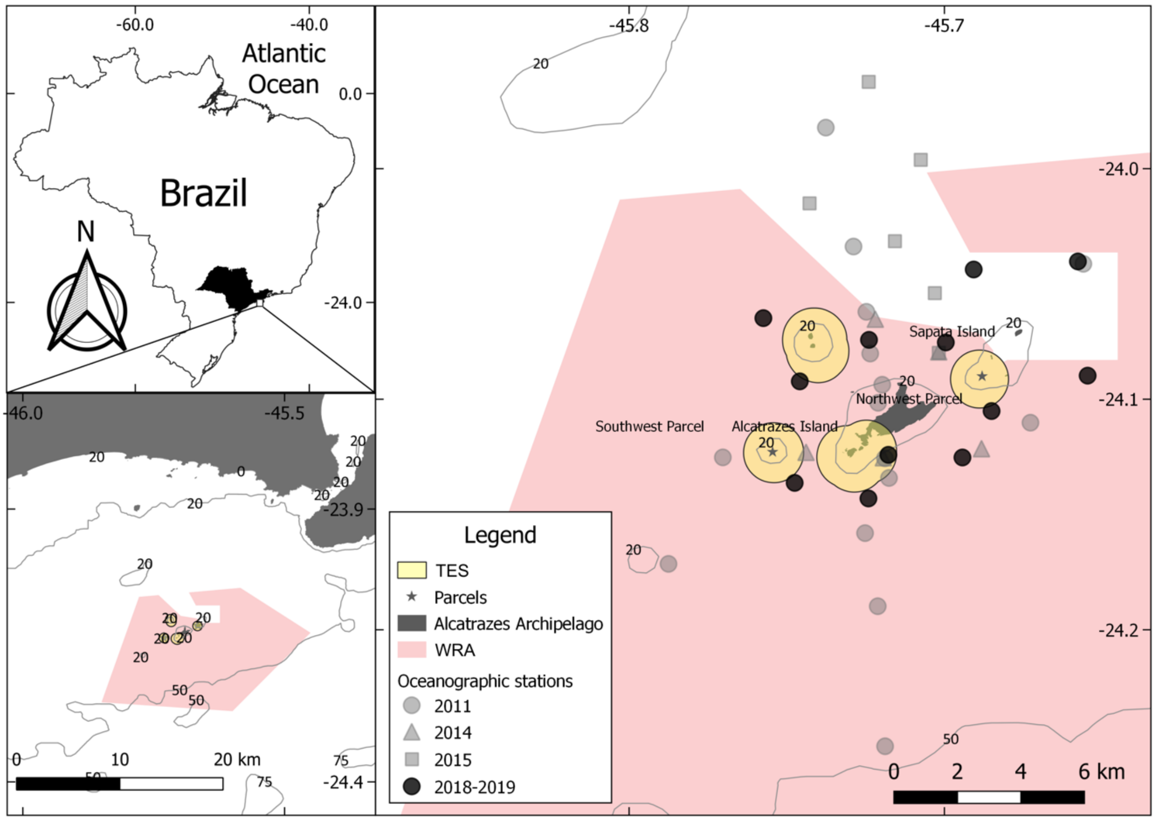

Figure 3-1 Map showing the Alcatrazes Archipelago area, its MPAs delimitations (WRA and TES) and oceanographic stations by expedition.

3.2.2.1 Abiotic Data

The assessment of temperature and salinity data was performed through different methods. Both variables were directly assessed using a conductivity-temperature-depth probe (CTD) (2011 and 2015) and a multiparameter probe (2018). Samples of bottom water taken by Nansen bottles, in 2014 and 2019, were used to measure temperature and salinity values using reversing thermometers and a refractometer, respectively. The sediment mosaic of the MPA region was characterized from samples collected through a van Veen grab in 2011 (Palóczy et al., 2012) and 2019. The area was classified into five zones, calculated as buffers of 2.5, 5, 7.5, 10 and 12.5 kilometers from the center of Alcatrazes island, according to the home ranges of the caught specimens (or nearest taxa, *i.e.*, genus) (Cartamil et al., 2003; Collins et al., 2007; Farrugia et al., 2011; Tilley et al., 2013). These zones were intended to capture any potential changes in benthic ecology with distance from the Alcatrazes island. Species with relatively small home ranges might have home ranges at a finer scale than these zones, while more wide-ranging species would encompass multiple zones.

3.2.2.2 Biotic Data

Demersal elasmobranch specimens were collected through otter trawl nets (20-21 m in the foot rope, 40-60 mm mesh in the body as well as in the sleeves and 25-30 mm in the cod-end), which were operated from ten to twenty minutes at a speed of two knots by the R/Vs Alpha Delphini (IO-USP) and Soloncy Moura (ICMBio). On board, specimens were accommodated in boxes with seawater and information was collected concerning their sex, total length (L_T), disc width (W_D) and total weight (W_T). To ensure correct identification, pictures of each specimen were taken and identification to species level was conducted in accordance with Figueiredo (1977), Viana et al. (2016) and Gomes et al. (2019). After data collecting, all live elasmobranchs were released to the sea. The specimens that did not survive (*i.e.*, less than 5% of the elasmobranch catches) were cooled and brought to the Oceanographic Institute (USP), being stored at the teaching collection. The non-elasmobranch species, such as the actinopterygians, were sacrificed through a solution of 400 $mg.L^{-1}$ of eugenol (Fernandes et al., 2017), cooled and also brought to the Oceanographic Institute to be used as research material in studies of community ecology, reproductive biology and so on.

3.2.3 Hydrographic And Sedimentological Analyses

According to Rossi-Wongtschowski and Paes (1993), the community structure of actinopterygians and elasmobranchs of the northern coast of São Paulo was related to sediment distribution and to the SACW presence. Thus, granulometric and hydrographic analyses were performed, as well as the estimation of calcium carbonate concentrations ($CaCO_3$) of sediment.

In 2014, the refractometer did not operate correctly. Thus, based on the SACW properties, we fixed salinity values at 35.7 to water samples collected at depths where temperature was below 17°C, for this year only. For the whole dataset, values of temperature and salinity of each oceanographic expedition were combined in diagrams and potential densities with pressure equals zero (σ_θ) were calculated. We set diagrams with isopycnal curves through the oce package (Kelley et al., 2021) using $\sigma_\theta = 25.8$ (Stramma and England, 1999; Mémery et al., 2000) as a threshold to identify the SACW presence. To define the sediment type of each oceanographic station, we combined available information about sedimentological parameters of the 2011 samples (Palóczy et al., 2012; Hoff et al., 2015) with data obtained in 2019. Sediment granulometry was determined by application of the sieve-pipette method (Suguio, 1973) to 50g of the 2019 samples, followed by Folk and Ward (1957) classification.

Further, concentrations of $CaCO_3$ were estimated through weight differences after digestion by 10% solution of hydrochloric acid. Gravimetric results were used to characterize the oceanographic stations in accordance with Larsonneur et al. (1982).

Three main factors determine the energy dynamic in the Alcatrazes island surroundings: its Y-shaped morphology, the abrupt change in the bathymetry and the predominance of incident waves from south and southeast. Together, they act as mitigating elements and reflect a more stable environment in the north and towards the coast, due to the indirect incidence of waves as well as energy loss by the decreasing bathymetry. Furthermore, regions are more energetic in the south, with waves varying slightly through the seasons and years (Takase et al., 2021). These factors rule the deposition process in the archipelago, forming sediment features that are sustained over time. Thus, the same characteristics of 2011 and 2019 samples were assumed for unsampled sediments of the other years. Both classifications were applied to the nearest oceanographic stations (**Appendix B - Table B-3**) with distances ranging from 0.38 to 3.17 kilometers.

3.2.4 Ecological Analyses

A bibliographic survey was performed to gather information regarding the size at maturity, reproductive strategies and food items of each species. They were used to classify specimens as juvenile or adult based on the size at first maturity and to identify functional groups through the reproductive and feeding guilds (**Appendix B - Tables B-1 and B-2**). Thus, species were classified into six groups by embryonic feeding method (trophonemata, oviparous or lecithotrophic) and by trophic category (hyperbenthivorous, infauna consumers or piscivorous), according to Elliott et al. (2007). Due to spatial variations in terms of biological and ecological aspects we used information of specimens from the closest regions.

To estimate changes in diversity patterns over time, we calculated species richness, the Shannon-Wiener diversity (H') and the Pielou evenness (J') for each year (Begon et al., 2006). Due to differences in sampling effort among years, instead of comparing raw species counts, we estimated rarefaction curves and species richness through non-parametric estimators (Chao and Chiu, 2016). Those estimators take into account underestimations in richness due to low sampling effort and differences in detection probability of species, since some species might have not been caught despite being present (Chao and Chiu, 2016). Quantities of juveniles and adults, sex ratios, and frequencies of total length/disc width classes were counted for the most abundant species (>25 specimens caught). Deviations from 1:1 of sex ratios and contingency tables of species by life stages were evaluated by chi-square tests (χ^2). Distributions of L_T/W_D frequency classes between sexes were compared by two-sample Kolmogorov-Smirnov tests (Zar, 2009).

Next, to test our hypothesis that species use spatial areas differently, and thus elucidate the roles played by WRA and TES, we conducted a three-step analyses. First, for each oceanographic station, we estimated the Bray-Curtis dissimilarities of the functional group abundances and performed principal coordinate analysis (PCoA) (Borcard et al., 2011) using the *'cmdscale'* function in R. Then, the relationship of the two first ordination scores and buffers were modeled by smoothed splines fitted using the *'ordisurf'* function. This function uses generalized additive models (GAMs) to fit non-linear response surfaces of predictor variables to ordinations (Oksanen et al., 2020). Maps of species' relative abundance by oceanographic expedition were set and compared to the PCoA results to identify spatial-temporal variations in the community composition.

Influences of abiotic features on the abundance of species and functional groups were evaluated through generalized linear models (GLMs). Before model fitting, the predictive variables temperature, salinity, depth, year, seasons, the SACW presence, buffers, sediment type and classes of $CaCO_3$ concentrations were centralized and the collinearity of continuous and ordinal variables were estimated among pairs using the Spearman's correlation coefficient (Zuur et al., 2009, 2010). Since the SACW presence was correlated (>80%) with temperature, and sediment type was correlated (>0.80) with classes of $CaCO_3$ concentrations, only one of each pair of variables was included in each model. According to Larsonneur et al. (1982), sediments with $CaCO_3$ concentrations above 30% are substantially composed of biogenic sources (*i.e.*, animal and vegetal debris), being classified as litho-bioclastic (from 30% to 50%), bio-lithoclastic (from 50% to 70%) and bioclastic (> 70%). Therefore, for model fitting, the sediment variable was set as one of two categories: lithoclastic (up to 30% of $CaCO_3$) and biogenic sediments. Fixed effect models of the count of each species per trawl with the log of swept area (in meters per seconds) as offset term were set up according to prior information about which variables were likely to be relevant for each species (Oddone and Vooren, 2004; Vögler et al., 2008; Menni et al., 2010; Barbini et al., 2011; Palmeira, 2012; Schlaff et al., 2014b). Models were fitted using *'glm'* and *'glm.nb'* functions with Poisson and Negative Binomial error distributions (Zuur et al., 2009). Alternative models were compared by the second order Akaike information criterion (AICc) with ΔAICc < 2 as a threshold to evaluate them regarding their descriptive capacity (Burnham and Anderson, 2002). If more than one model was ranked as plausible, model averaging was applied and parameters estimates were weighted by the Akaike weights (*Wi*) (Burnham and Anderson, 2002). To evaluate the model fits, scaled residuals were analyzed through plots generated by the DHARMa package in R (Hartig and Lohse, 2020). DHARMa residuals are estimated as quantiles of one thousand simulated draws from the distribution used to calculate the likelihood corresponding to each observation. Deviations from the expected values of a uniform distribution as well as of variances in relation to predicted values were compared by qq-plots and residual plots, respectively.

Finally, the WRA effect was assessed through changes in size structure over time only for the most common species: the lesser guitarfish, *Zapteryx brevirostris* (Müller & Henle, 1841). None of the other species had a large enough sample size to calculate these size-based indicators. *Z. brevirostris* L_T data were grouped in two periods (2011-2015 and 2018-2019) according to the MPA establishment in 2016 (Brazil, 2016). We set a linear model with interactions between season and time period (L_T ~ *period*season*) to test whether differences in mean L_T are an effect of the MPA creation or due to sampling different seasons (Zar, 2009). Also, indicators of fishery sustainability for each period were estimated. Fishing mortality relative to natural mortality (F/M) and spawning potential ratios (SPR, defined as the spawning stock biomass relative to unfished SSB) are indicators of stock status. They measure how much higher is the mortality experienced by a fished population and how much lower is its potential fecundity (Goodyear, 1993), respectively, compared to unfished conditions. The F/M indicator was calculated under two different methods with different assumptions about selectivity. First, in the mean length method, total mortality (Z) was estimated by the Beverton and Holt (1957) estimator assuming the same catchability of specimens over the minimum fully exploited size (L_c). The second method, length-based spawning potential ratio (LBSPR), assumes that catchability increases logistically with the length of specimens and estimates the logistic parameters as well as the average F/M and SPR that best fits the length-frequency data, assuming variability in length at age (Hordyk et al., 2015).

Life history parameters were required to estimate fishery indicators. However, most of them have not been calculated for Alcatrazes populations, so we used values of populations from nearby regions. To estimate L_c and other parameters, such as the mean and variance of natural mortality (M), methods proposed by Babcock et al. (2013, 2018) were implemented (**see Appendix B - Table B-4 for details about parameters and indicators**). Uncertainties of parameters' estimates were obtained by ten thousand Monte Carlo simulations. They were performed with bootstrapped samples of the observed length data and values of the life history parameters drawn from a multivariate normal distribution. Then, the 90% confidence interval

(CI) of each indicator was set as the 5% and 95% quantiles of the simulated values (Babcock et al., 2018).

To evaluate whether a difference in mean length should be expected in the before vs. after MPA samples, the necessary time after the establishment of an MPA for the *Z. brevirositris* population to reach an unfished level of the mean length was assessed considering several selectivity assumptions. Life history values of a fished population (**Appendix B - Table B-4**) were used to calculate the numbers (Hilborn and Walters, 1992) and lengths at age (von Bertalanffy growth model, Beverton and Holt, 1957) assuming both natural and fishing mortalities before the WRA, and only natural mortality after its establishment. Then, we calculated the mean length of specimens larger than $L_{c,}$ which is the mean length that is used for the Beverton-Holt estimator, in each year after the founding of the MPA.

All analyses were performed using the R environment (R Core Team, 2020) through the vegan (Oksanen et al., 2020), SpadeR (Chao et al., 2016), MASS (Ripley et al., 2021), MuMIn (Bartoń, 2020), DHARMa, mvtnorm (Genz et al., 2020) and LBSPR (Hordyk, 2019) packages.

3.3 Results

3.3.1 Hydrographic And Sedimentological Features

Temperature and salinity diagrams (**Appendix B - Figure B-1**) showed that the influence of SACW has changed over the years and across the MPA area. The water mass was detected in all years except 2019, which was characterized by higher values of temperature/salinity and homogeneity in the water column with the majority of temperature records from 22.4 to 23.5ºC. Despite the absence of σ_0 reference values in 2014, low temperatures (18ºC<) were verified by reversing thermometers up to 25 meters above the bottom, indicating the presence of SACW. In terms of distribution through the area, the SACW was identified at all oceanographic stations until 2015. Although the 2018 campaign was conducted in summer, the SACW was only detected at oceanographic stations exposed to the open ocean (#08, #09, #10, #11, #12) and in the area between the Sapata and Alcatrazes islands (#05). These variations in the water mass coverage indicate that the intrusion process was beginning, since the samples were collected at the onset of the season. Sediments of both MPAs were defined by fine grains (fine and very fine sand > 85%) and poor $CaCO_3$ composition (*i.e.*, lithoclastic sediments). However, bio-lithoclastic and bioclastic sediments with large quantities of biogenic $CaCO_3$ (making up by 79% of sediment content) were assessed on patches of coarse and very coarse sand. The distribution of these patches was limited to nearby regions of the Alcatrazes island and especially to the island side that is exposed to open ocean (*i.e.*, the south side). Hydrographic and sedimentological compiled data are presented in **Appendix B -Table B-3**.

3.3.2 Diversity And Community Structure

A total of 562 specimens were recorded, belonging to 16 species of seven families. Species richness across all years was estimated as 16.33-17, depending on the estimation method used, with confidence intervals ranging from 16.02-27.05 species (**Table 3-1**). Two families, the Trygonorrhinidae and Arhynchobatidae, were the most common, accounting for almost 85% of the elasmobranchs sampled (**Appendix B - Table B-5**). Trygonorrhinidae was represented by just one species, *Z. brevirostris*, which was recorded in 86% of the oceanographic stations and showed the highest number of individuals caught (n = 257; **Appendix B - Table B-5**). Following *Z. brevirostris*, the Rio skate, *Rioraja agassizii* (Müller & Henle, 1841), made up around 15% of the total sample (n = 81; **Appendix B - Table B-5**) and despite its absence in 2015, the species was recorded in 60% of all oceanographic stations.

According to the estimates of diversity, evenness and species richness, changes in demersal community composition were identified over the time. Overall, the number of observed species and specimens caught were lower (**Table 3-2**) in oceanographic expeditions of smaller sampling effort: the summer of 2014 (five trawls) and spring of 2015 (six trawls). However, rarefaction curves did not reach asymptotes (**Appendix B - Figure B-2**) and the 95% upper confidence interval limits revealed the potential for greater values of estimated richness (**Appendix B - Table B-5**). Diversity and evenness of those oceanographic expeditions were quite similar with higher estimates of the other spring and summer expeditions (2011 and 2018, respectively), which were carried out with a sampling effort almost three times greater (**Table 3-2).** In this sense, a trend in diversity and evenness was observed, with estimates increasing through the seasons, from the lowest ones in the winter (2019' oceanographic expedition) to the highest during the summer (**Table 3-2**).

Table 3-1 Species richness estimates by ChaoSpecies estimators.

Estimators	Estimate	SE	95%CI
	Total		
Chao1 (Chao, 1984)	17.00	1.87	16.09-27.05
Chao1-bc	16.33	0.93	16.02-21.96
iChao1 (Chiu et al., 2014)	17.00	1.87	16.09-27.05
ACE (Chao and Lee, 1992)	16.95	1.48	16.11-24.38
	2011		
Chao1 (Chao, 1984)	9.17	0.53	9.01-12.51
Chao1-bc	9.00	0.79	9.00-11.64
iChao1 (Chiu et al., 2014)	9.17	0.53	9.01-12.51
ACE (Chao and Lee, 1992)	9.84	1.41	9.09-17.14
	2014		
Chao1 (Chao, 1984)	7.00	0.53	7.00-8.55
Chao1-bc	7.00	0.53	7.00-8.55
iChao1 (Chiu et al., 2014)	7.25	0.53	7.02-10.21
ACE (Chao and Lee, 1992)	7.43	0.97	7.03-13.00
	2015		
Chao1 (Chao, 1984)	5.98	2.16	5.07-18.3
Chao1-bc	5.98	2.16	5.07-18.3
iChao1 (Chiu et al., 2014)	5.98	2.16	5.07-18.3
ACE (Chao and Lee, 1992)	7.09	3.51	5.22-25.21
	2018		
Chao1 (Chao, 1984)	12.17	0.53	12.01-15.52
Chao1-bc	12.00	0.82	12.00-14.68
iChao1 (Chiu et al., 2014)	12.17	0.53	12.01-15.52
ACE (Chao and Lee, 1992)	12.43	0.89	12.03-17.36
	2019		
Chao1 (Chao, 1984)	14.46	7.13	10.49-50.53
Chao1-bc	11.49	2.58	10.15-24.95
iChao1 (Chiu et al., 2014)	15.46	5.04	11.17-35.46
ACE (Chao and Lee, 1992)	12.06	2.78	10.28-25.16

Notations: standard error (SE), lower and upper limits of 95% confidence intervals (95% CI).

Table 3-2 Abundance, number of species and ecological index estimates by oceanographic expedition of demersal elasmobranchs.

OEs	n	N	H'	J'
2011	9	98	0.79	0.77
2014	7	95	1.19	0.76
2015	5	58	0.74	0.73
2018	12	196	1.31	0.86
2019	10	101	0.79	0.65

Notations: oceanographic expeditions (OEs), observed number of species (n), abundance (N), Shannon-Wiener diversity (H') and Pielou's evenness (J') indexes.

Altogether, lengths were measured for 554 and sexes for 549 specimens, of which 499 were from six species that had a samples size of at least 25 (**Appendix B - Table B-5**). Species showed significant differences in the distribution of life stage classes ($\chi^2 = 105.6$, df = 5, $p<0.05$). The community was mainly composed of adults for *Z. brevirostris, R. agassizii*, the zipper sand skate, *Psammobatis extenta* (Garman, 1913) and the groovebelly stingray, *Dasyatis hypostigma* Santos & Carvalho, 2004. However, for two species of the Arhynchobatidae family, the spotback skate, *Atlantoraja castelnaui* (Ribeiro, 1907) and the eyespot skate, *Atlantoraja cyclophora* (Regan, 1903), the number of juveniles were substantially higher (over 75% of each species abundance). Deviations in sex ratios from 1:1 were verified of both Arhynchobatidae species, with males outnumbered by females (0.33:1, $\chi^2_{A.\ castelnaui} = 25$, df = 1, $p<0.05$; 0.4:1, $\chi^2_{A.\ cyclophora} = 18.37$, df = 1, $p<0.05$). Concerning the species length ranges, no significant differences among sexes were found for either of these two species ($D_{A.\ castelnaui} = 0.26$, $p>0.05$; $D_{A.\ cyclophora} = 0.26$, $p>0.\ 05$) (**Figure 3-2**).

Conversely, for the other two skate populations, more than 70% of collected specimens were adults. Differences in sex ratios were also verified with more females of *R. agassizii* (0.57:1, $\chi^2 = 7.44$, df = 1, $p<0.05$) and of *P. extenta* (0.54:1, $\chi^2 = 8.84$, df = 1, $p<0.05$). For the latter, L_T frequencies did not differ (D = 0.20, $p>0.05$), however, females of *R. agassizii* exhibited larger sizes (D = 0.43, $p<0.05$) prevailing in L_T classes above 40 cm (**Figure 3-2**). The same pattern was observed for *Z. brevirostris* with more than 70% of the analyzed specimens as adults. The ratio between males and females was equal (0.88:1, $\chi^2 = 0.44$, df = 1, $p>0.05$) and as for *R. agassizii*, females were larger than males (D = 0.19, $p<0.05$). For *D. hypostigma*, there were no differences among sex ratios (0.75:1, $\chi^2 = 2.04$, df = 1, $p>0.05$) and life stage classes were also similar (**Appendix B - Table B-5**). Although the majority of males showed smaller sizes (**Figure 3-2**), no significant differences were found in W_D distributions by sex (D = 0.38, p>0.05).

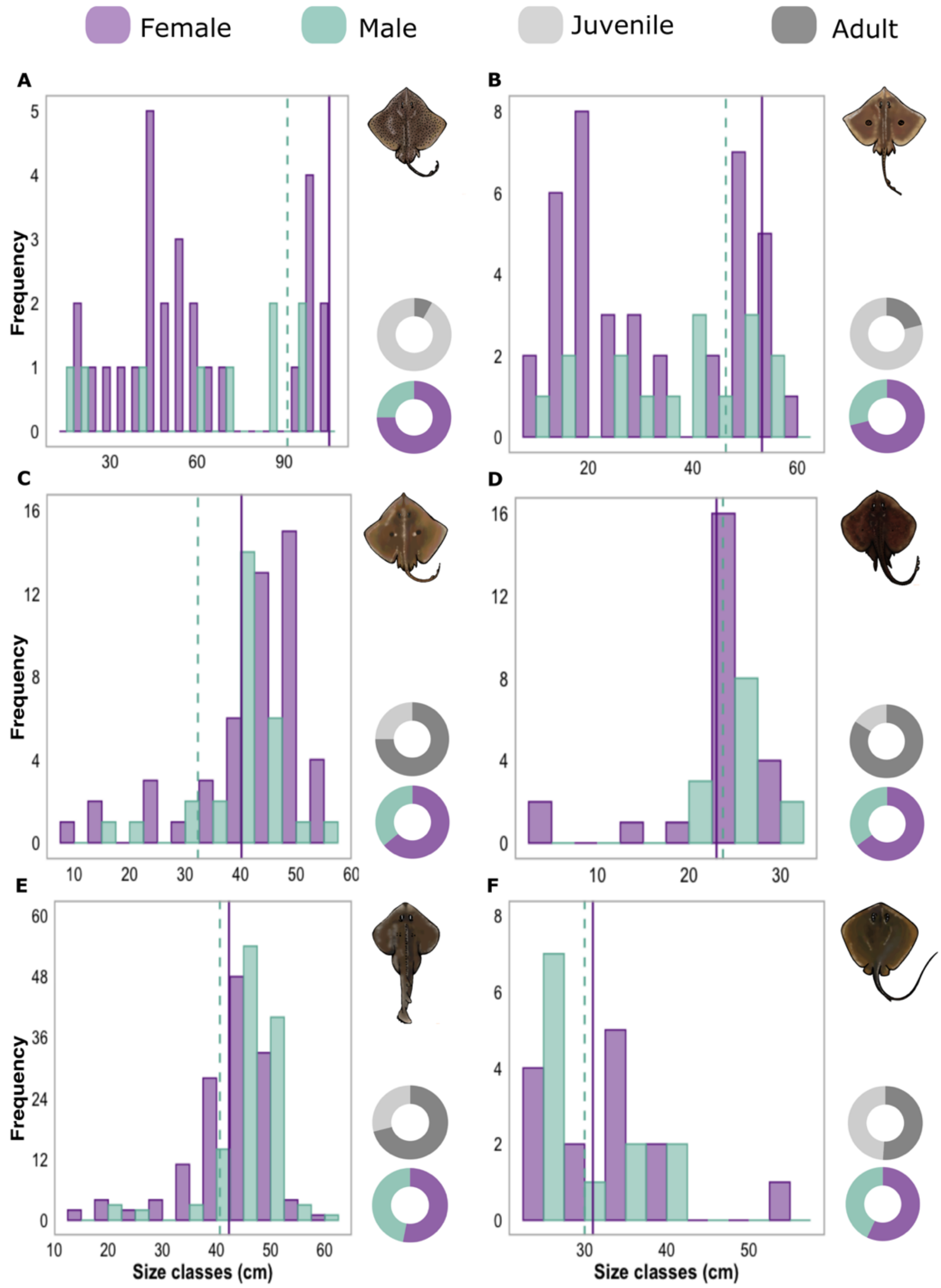

Figure 3-2 Histograms show the total length or disc width frequency classes of females (purple) and males (green) of (A) *Atlantoraja castelnaui*, (B) *A. cyclophora*, (C) *Rioraja agassizii*, (D) *Psammobatis extenta*, (E) *Zapteryx brevirostris* and (F) *Dasyatis hypostigma*. Sizes of first maturity taken from the literature are indicated by purple solid (females) and green dashed (males) vertical lines. Donut charts represent sex ratios and proportions of juveniles and adults.

3.3.3 Habitat Functionality

The first two axis of the PCoA explained 55.6% of the data variance (PCoA1 = 32.4 and PCoA2 = 23.20), being correlated with distances from the Alcatrazes island (*i.e.*, buffers) as shown by the contour lines (**Figure 3-3**). The slight differences in space use by the functional groups appeared to be more related to the species' trophic categories than to their reproductive modes. While the hyperbenthivorous and infauna consumers were common in regions of intermediate distances, the piscivorous species were mainly caught at the farthest oceanographic stations (*i.e.*, those positively loaded on the PCoA1 and negatively loaded on the PCoA2). Regarding the reproductive guilds, such oceanographic stations were also the most different, being separated even from those of other lecithotrophic species (*i.e.*, negatively loaded on the PCoA1). Fifteen individuals of two shark species, the angular angel shark, *Squatina guggenheim* Marini, 1936 and the dogfishes, *Squalus albicaudus* Viana, Carvalho & Gomes, 2016 and *Squalus* sp. were classified as lecithotrophic and piscivore (**Appendix B - Table B-5**). They were caught at seven oceanographic stations that were characterized by low temperatures (µ = 18.1 ºC), presence of the SACW and predominance of finer grains without biogenic $CaCO_3$.

Differences in relative abundances were observed through the archipelago (**Figure 3-4**). In general, the functional groups were present in all regions of the archipelago, however, the region that corresponds to the exposed side of the Alcatrazes island showed higher values of relative abundance and was more heterogeneous in terms of species composition than the northwest side. Some species were widely distributed while occurrence of the other ones was occasional and restricted to certain regions. *A. castelnaui and A. cyclophora* were abundant in the surroundings of the Alcatrazes island and were present through almost the entire sampling period. Similarly, *R. agassizii* and *Z. brevirostris* were ubiquitous in terms of space-time occurrence. However, in 2019 a pattern was identified with concentrations of the skate in the northeast and of the guitarfish in the northwest and south regions. Also, in 2019 large groups of *D. hypostigma* and solitary individuals of the bullnose eagle ray, *Myliobatis freminvillei* Lesueur, 1824 were observed in the northeast region. Still in the northeast, juveniles of *S. albicaudus* were recorded in 2018. Congeneric species, such as the cownose rays and the angel sharks, were not caught together in any of the trawls, indicating possible spatial segregation with the exposed region being mainly used by *Rhinoptera brasiliensis* Müller, 1863 and *S. guggenheim* and the northwest side by *Rhinoptera bonasus* (Mitchill, 1815) and *Squatina occulta* Vooren & Silva, 1991.

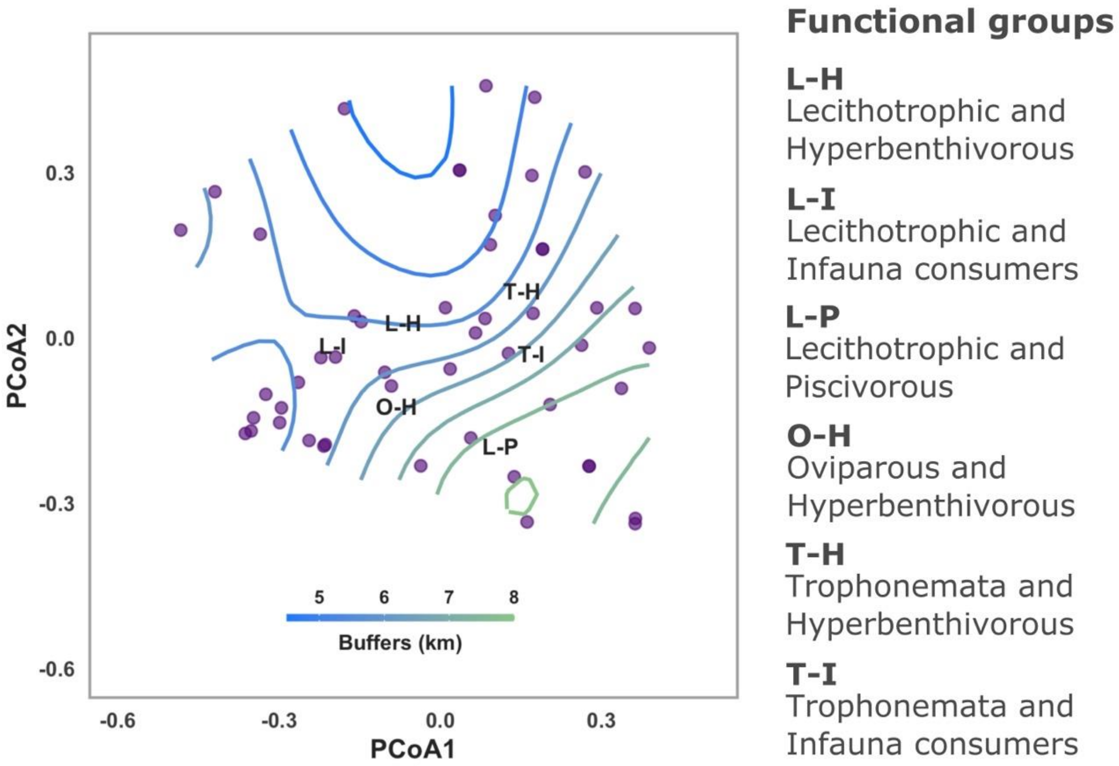

Figure 3-3 Principal Coordinate Analysis (PCoA) results showing the space use configuration by functional groups in relation to distances (km) from the Alcatrazes island. Purple points are the oceanographic stations (OSs), initials represent the functional groups that most contributed to dissimilarities among OSs and the contour lines are the fitted splines of the distances from the Alcatrazes island (*i.e.*, buffers) from closer (blue) to farther (green) zones.

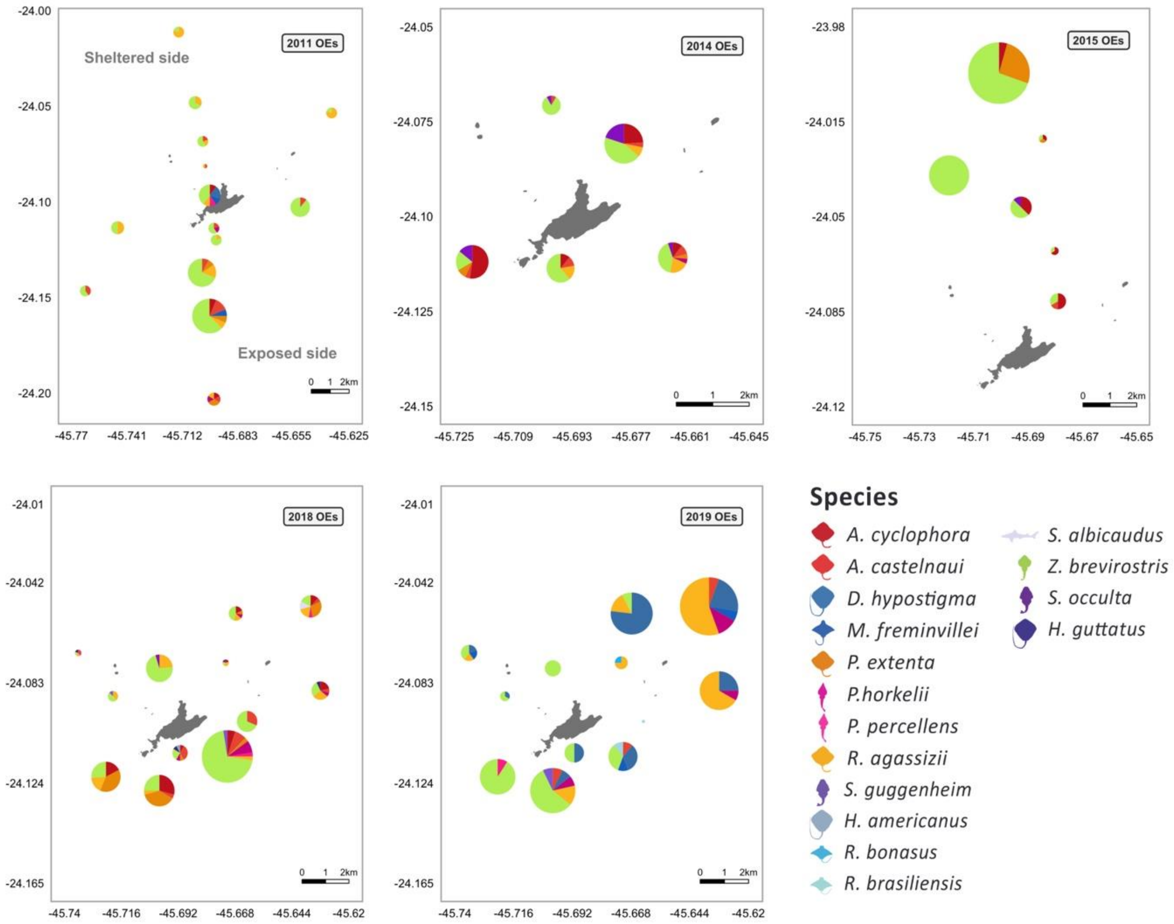

Figure 3-4 Maps of spatial-temporal variation of species relative abundance through the Alcatrazes archipelago. Colors indicate species relative abundance by oceanographic station (OSs) and pie chart sizes represent the contribution of each OS to the total catch by expedition. The sides of the archipelago that are exposed to the open ocean and turned to the continent (sheltered) are present in the first map.

According to the most parsimonious models (ΔAICc<2), temperature and seasons were the predominant variables that explained shifts in abundance of the species and functional groups (**Table 3-3**). Except for the trophonemata-hyperbenthivorous (*i.e.*, species that produce lipid-rich liquid through trophonemas to supplement embryo nutrient provision and feed on benthic invertebrates which live above the sediment, respectively), the relative abundance of all groups was inversely related to bottom water temperature (**Table 3-4**). Moreover, significant differences between summer and spring were found with higher abundances of oviparous-hyperbenthivorous (*i.e.*, species of which embryos depend solely on the yolk-sac reserves, developing inside encapsulated eggs that were deployed in the environment) and lecithotrophic-infauna consumers (*i.e.*, species of which embryos also feed mainly on the yolk-sac reserves, but develop inside the mother uterus and, in later life' stages, feed on benthic invertebrates which live in the sediment) in the former season.

Table 3-3 Best ranked models for the number of individuals of functional groups and species.

Models	**k**	**AICc**	**ΔAICc**	***Wi***
		Lecithotrophic and Infauna consumers		
Seas + Temp	5.00	271.27	0	0.49
Temp	3.00	273.02	1.75	0.21
		Oviparous and Hyperbenthivorous		
Seas + Temp + Buffer	9	243.78	0	0.29
Seas + Dep + Buffer	9	243.81	0.03	0.28
Seas + Temp	5	244.50	0.72	0.20
Seas	4	245.48	1.70	0.12
		Trophonemata and Hyperbenthivorous		
Temp	3	95.92	0	0.62
		Atlantoraja cyclophora		
Temp + Sal	4	121.89	0	0.62
		Atlantoraja castelnaui*		
Seas + Dep + CaCO3	5	104.18	0	0.36
Seas + Dep	4	104.22	0.04	0.36
Seas + CaCO3	4	106.05	1.87	0.14
		Rioraja agassizii		
CaCO3	3	177.14	0	0.61
Seas + CaCO3	5	178.66	1.52	0.28
		Psammobatis extenta		

Sal + Dep	4	106.09	0	0.30
Sal	3	106.17	0.08	0.29
Sal + CaCO3	4	107.47	1.38	0.15
Zapteryx brevirostris				
Seas + Temp	5	269.24	0	0.46
Seas + Temp + CaCO3	6	270.71	1.47	0.22

Log of swept area was included as an offset in all models. Notations: k (number of parameters estimated), AICc (Akaike's second-order information criterion), ΔAICc (AICci – AICcmin), *Wi* (Akaike weight), seasons (Seas), bottom water temperature (Temp), bottom water salinity (Sal), depth (Dep), distance from the Alcatrazes island (Buffer) and CaCO3 classes (CaCO3). * Poisson GLMs were fitted for *A. castelnaui*.

Table 3-4 Estimated parameters of variables from the best models that explain the number of individuals of functional groups.

Variables	***β***	**SE**	***Z*-value**	***P*-value**
Lecithotrophic and Infauna consumers				
Intercept	-7.07	0.20	34.92	**<0.01**
Temp	-0.28	0.13	2.21	**0.03**
Spring	-0.63	0.25	2.43	**0.02**
Winter	0.46	0.59	0.77	0.44
Oviparous and Hyperbenthivorous				
Intercept	-7.34	0.42	17.32	**<0.01**
Temp	-0.25	0.11	2.17	**0.03**
Buffer 5 km	0.64	0.34	1.86	0.06
Buffer 7.5 km	0.97	0.39	2.40	**0.02**
Buffer 10 km	1.23	0.41	2.90	**<0.01**
Buffer 12.5 km	1.51	0.51	2.91	**<0.01**
Spring	-1.11	0.28	3.90	**<0.01**
Winter	-0.64	0.66	0.96	0.34
Dep	0.05	0.02	2.61	**<0.01**
Trophonematas and Hyperbenthivorous*				
Intercept	-9.84	0.35	-28.16	**<0.01**
Temp	0.57	0.13	4.26	**<0.01**

Parameters with significant *P*-value (<0.05) were highlighted. Notations: estimated coefficients (*β*), standard error (SE), *Z* test (*Z*-value) and significance in *Z* test (*P*-value). * Except for Throphonematas and Hyperbenthivorous parameters of other groups were weighted by the Akaike weight (*Wi*) of the best models in which variables were present.

Similar trends were exhibited by the species (**Table 3-5**). For example, the relative abundance of *A. castelnaui* changed seasonally, with higher values in the summer, the same trend seen for its group (*i.e.*, oviparous-hyperbenthivorous). Increases in *A. cyclophora* as well as in the most representative species of lecithotrophic-infauna consumers, *Z. brevirostris*, were related to temperature decrease and, particularly for some skates, salinity had an inverse effect (*e.g.*, *P. extenta*). Spatial variations were mainly explained by depth and differences among buffers. For the oviparous-hyperbenthivorous group, the number of specimens were higher at farther buffers and increased with depth (**Table 3-4**). Overall, the relative abundance of this group, and specifically of *A. castelnaui* (**Table 3-5**), appear to be lower in shallow regions. However, none of the skates varied in relative abundance among buffers and only *R. agassizii* showed significant differences with $CaCO_3$ content (**Table 3-5**). Its lower abundance in biogenic than in lithoclastic sediments might reflect the patterns of the functional group, since oceanographic stations with higher $CaCO_3$ concentrations were found in the vicinity of Alcatrazes island.

Table 3-5 Estimated parameters of variables from the best models that explain the number of individuals of elasmobranch species.

Variables	***ß***	**SE**	***Z*-value**	***P*-value**
		Atlantoraja cyclophora*		
Intercept	-9.95	0.41	-24.18	**<0.01**
Temp	-0.68	0.18	-3.88	**<0.01**
Sal	-3.16	0.90	-3.52	**<0.01**
		Atlantoraja castelnaui		
Intercept	-8.85	0.27	31.79	**<0.01**
Spring	-0.82	0.37	2.19	**0.03**
Winter	-1.54	0.62	2.43	**0.02**
Dep	0.07	0.03	2.36	**0.02**
Bio sed	0.72	0.41	1.71	0.09
		Rioraja agassizii		
Intercept	-8.00	0.26	30.24	**<0.01**
Bio sed	-1.01	0.45	2.20	**0.03**
Spring	-0.70	0.40	1.70	0.09
Winter	-0.08	0.43	0.17	0.86
		Psammobatis extenta		
Intercept	-9.74	0.49	19.51	**<0.01**
Sal	-3.79	1.33	2.79	**<0.01**
Dep	0.09	0.06	1.61	0.11
Bio sed	0.84	0.85	0.96	0.34
		Zapteryx brevirostris		
Intercept	-7.14	0.25	28.20	**<0.01**
Temp	-0.28	0.14	2.01	**<0.05**
Spring	-0.52	0.28	1.81	0.07

Winter	0.28	0.66	0.41	0.68
Bio sed	0.29	0.27	1.03	0.30

Parameters with significant *P*-value (<0.05) were highlighted. Notations: estimated coefficients (*β*), standard error (SE), *Z* test (*Z*-value), significance in *Z* test (*P*-value) and class of sediment composed by biogenic sources (Bio sed). * Except for *A. cyclophora* parameters of other groups were weighted by the Akaike weight (*Wi*) of the best models which variables were present.

3.3.4 MPA Effectiveness For *Z. Brevirostris*

No significant differences in mean lengths of *Z. brevirostris* were identified before and after the WRA MPA establishment when season was included in the model ($\beta_{\text{before+summer}}$ = 44.89 ± 1.33; $\beta_{\text{after+summer}}$ = 45.14 ± 0.77, *t* = -0.19, p = 0.85). On the other hand, there was a significant effect of seasons, with higher mean L_T in summer than in spring (**Table 3-6**). The number of specimens of sizes above L_c, meaning they were susceptible to fishery harvest, was 168 (before MPA: n=65, after: n=103) and the small increase in mean length implied a small decrease in the mean *F/M* for fish larger than L_c estimated by the Beverton-Holt method although the effect was not significant judging by the overlapping confidence intervals. According to LBSPR, which estimates *F/M* of fully selected (*i.e.*, large) individuals, assuming a logistic selectivity curve, the mean estimated fishing mortalities increased and confidence intervals of $(F/M)_{\text{LBSPR}}$ overlapped, being above the overfishing threshold (>1) (**Appendix B - Figure B-3 A**). These numbers are not directly comparable because they correspond to fish of different sizes. Nevertheless, large values of either metric can be taken as evidence of overfishing. The confidence intervals of SPR also overlapped, although the mean increased slightly (current SPR>0.4) (**Appendix B - Figure B-3 B**). According to our simulation, if fishing was completely eliminated, the mean length of guitarfish larger than L_c would be expected to increase after the WRA establishment, reaching the unfished level in approximately five years or six years depending on the assumed selectivity of the fishery (**Appendix B - Figure B-4**).

Table 3-6 Effects of the Wildlife Refuge of Alcatrazes (WRA) establishment and seasons in mean total length (L_T) of the lesser guitarfish.

Variables	***β***	**SE**	***t*-value**	***P*-value**
After WRA + Summer	45.14	0.77	58.75	**<0.01**
Before WRA	-0.25	1.33	-0.19	0.85
Spring	-3.28	1.31	-2.49	**0.01**
Winter	1.95	1.45	1.34	0.18

Parameters with significant *P*-value (<0.05) were highlighted. Summer was the only season in which lesser guitarfish specimens were caught before and after the MPA establishment.

3.4 Discussion

3.4.1 MPA’s Functionality

3.4.1.1 Oceanographic Features Driving The Community Dynamics

Marine communities are usually characterized by a few predominant species that are continuously present and many other species that have relative low abundances and occasional occurrences associated with natural events (Magurran and Henderson, 2003). Our findings showed such patterns with shifts in the Alcatrazes elasmobranch fauna, and consequently in the MPA’s functional diversity, being driven by thermohaline and chemical changes in the water column through the seasons. The inshore intrusion of the SACW is known for lowering water temperatures, raising primary production in the euphotic zone, and enriching the bottom by the input of particulate organic matter during spring and summer. Therefore, increases in diversity metrics were likely a response of the enhancement of feeding resources, given that the energy surplus advantages the benthic megafauna, and is also a consequence of the expansion of the SACW’s associated species (Pires-Vanin et al., 1993; Castro-Filho and Miranda, 1998; Muto et al., 2000). On average, 60% of the species caught are temperate species that are probably related to the water mass (Menni and Stehmann, 2000; Menni et al., 2010). Higher abundances of functional groups in spring and summer (*e.g.,* lecithotrophic-infauna consumers and oviparous-hyperbenthivorous) and their increase with a decrease in temperature, indicate the same association with the SACW. Even though variations could be explained by the input of individuals, the reproductive cycle of such species appears to be synchronized to periods of more suitable conditions. Reported peaks on mating, birth or egg-laying of *A. cyclophora*, *A. castelnaui, R. agassizii, Z. brevirostris*, the Brazilian guitarfish, *Pseudobatos horkelii* (Müller and Henle, 1841) and *S. occulta,* coincides with the timing of the SACW influence (Lessa et al., 1986; Ponz-Louro, 1995; Oddone and Vooren, 2005; Vooren and Klippel, 2005; Oddone et al., 2007, 2008b; Colonello et al., 2011b, 2012). This could enable energy recovery by females and access to food by the newborns.

On the other hand, when the SACW retreats to deeper zones (>100m) in autumn and winter, the Tropical Water mass dominates the middle shelf, increasing the temperature and salinity of the water (Castro-Filho and Miranda, 1998; Campos et al., 2000). Our results show that under the Tropical Water influence, the community became less diverse although some of the recorded species had never been caught before (*e.g.*, *R. bonasus* and *R. brasiliensis*). The cownose rays are trophonemata species that display reproductive traits of high energetic demand to improve likelihood of offspring success (Rangel et al., 2020). Seasonal migrations to nursery areas along the coast have been suggested, with parturition from late spring through summer (Rangel et al., 2018). Thus, the recorded specimens might have been caught while foraging for more energetic resources to improve reserves before mating or during gestation (*e.g.*, Rangel et al., 2021). After stronger SACW events, the availability of potential food items, including higher level species of the benthic megafauna, are more abundant on the middle shelf, making Alcatrazes a productive foraging area (Pires-Vanin et al., 1993; De Léo and Pires-Vanin, 2006; Shimabukuro et al., 2016).

Spatially, while the northwest and northeast parts were predominantly characterized by finer grains and poor $CaCO_3$ content, the south (*i.e.*, part exposed to the open ocean), could be distinguished in two regions: the eastern portion, that is similar to the first two, and the western, with presence of coarse sands and higher $CaCO_3$ concentrations. According to Takase et al. (2021), this region is highly influenced by energetic waves which explains the sediment configuration by the displacement of finer grains to the east. Consequently, the heterogeneity of habitats in the exposed part resulted in a more diverse fauna in comparison to the northern area. Higher abundances of oviparous and hyperbenthivorous species at farther offshore and deeper locations might be related to the distribution of preys. For example, organisms of biogenic source such as mollusks, starfishes and corals, are not part of the *R. agassizii* diet, which like *P. extenta*, feeds significantly on small crustaceans of the benthic macrofauna (Soares et al., 1992; Aguiar and Valentin, 2010; Bornatowski et al., 2014c). Moreover, brachyuran and portunid crabs are main preys of *A. castelnaui* and *A. cyclophora*, respectively (Soares et al., 1992, 2008). Thus, great densities of the macrobenthos on the inner and outer shelf (Pires-Vanin, 2008) and presence of such crabs (*e.g.*, *Persephona punctata*, *Libinia spinosa*, *Portunus spinimanus* and *Callinectes sapidus*), which were found in trawls performed at deeper oceanographic stations, would have attracted the skates to those regions, consistent with our findings. Likewise, spatial differences between angel sharks were probably related to the resource distribution. Abundance of infauna invertebrates (*e.g.*, polychaetes), may be higher in the northwest part due to sediment composition and higher levels of organic matter (Hoff et al., 2015). Thus, whereas *S. guggenheim* are strictly piscivorous, eating demersal and pelagic species (Vögler et al., 2003), the *S. occulta* diet, which consists of polychaetes and nematodes, relies on configurations of benthic habitats (Aguiar and Valentin, 2010; Domingos et al., 2021).

Groupings of mature males (*i.e.*, calcified clasper) of *R. agassizii* and *Z. brevirostris*, in different parts of the archipelago, suggest formation of shoals for reproductive purposes (Paijmans et al., 2019). Although specific evidence of females' maturity stage has not been assessed, the majority of recorded specimens in 2019 were bigger than the published size of first maturity (**Appendix B - Table B-1**). Those results support the reproductive cycle defined by Colonello et al. (2011) and Oddone et al. (2007). Nevertheless, it is possible that the lesser guitarfishes of tropical waters perform two mating periods, since mature males were also recorded during summer oceanographic expeditions. Colonello et al. (2011) previously highlighted the asynchrony of reproductive females when comparing populations from temperate regions and the northern São Paulo coast (Ponz-Louro, 1995). Catches of *D. hypostigma* and *M. freminvillei* at the same oceanographic stations may indicate formation of mixed-species shoals. Despite the fact that both species are hyperbenthivorous and the diet overlap could increase species competition, interspecific associations may also increase foraging efficiency (Paijmans et al., 2019). Stingrays perform foraging traits which expose the benthic fauna (Freitas et al., 2019), facilitating prey catchability.

3.4.1.2 Community Structure And Use Of The MPA

Overall, dissimilarities regarding the population structures from other Brazilian regions may be related to geographical features, sexual segregation and ontogenetic changes in habitat use (Schlaff et al., 2014b). Despite the substantial presence of adults, most of them were individuals just over the reference size of first maturity. In almost all species, juveniles were present, but only *A. castelnaui* and *A. cyclophora* were dominated by them, which will be discussed later. The sex ratio favoring females was similar to what was found with populations of *A. castelnaui,* from the northern coast of São Paulo (Ponz-Louro, 1995) and of *R. agassizii,* along the southeastern Brazil (Oddone and Amorim, 2007). In contrast, the sex ratio of the northern state population of *P. extenta* did not deviate from 1 (Martins et al., 2005) which was not consistent with our findings of a female dominated sex ratio. Furthermore, Martins et al. (2005) found variations in habitat use through the species' life span. This does not seem to be our case as young juveniles, older juveniles and adults were found in Alcatrazes. No significant deviations from 1 were found for *A. cyclophora* in southern and southeastern Brazil (Oddone and Vooren, 2004; Oddone and Amorim, 2007). The evaluated specimens of both studies came from different, and even deeper regions (over 100m), inside of a wider area, which might have caused those disparities. For *Z. brevirostris* and *D. hypostigma,* our results exhibited equal rates between sexes, which agreed with results of the northern guitarfishes evaluated by Ponz-Louro (1995). But, for the last one, no information about population structure was found, pointing out the necessity of efforts to broaden our understanding of the species.

Based on the structure results, evidence of reproductive availability and patterns found in the literature, we propose uses of the MPAs by each elasmobranch although further research regarding species movement ecology is essential to strengthen these conclusions (**Appendix B - Table B-5**). Like other insular regions in Brazil (Wetherbee et al., 2007; Aguiar et al., 2009), Alcatrazes is a nursery area specifically used for development by many species. Early life stages, such as neonates, young of the year and/or juveniles were found, supporting this hypothesis. Juveniles of angel sharks and stingrays (genus *Hypanus*) were found at deeper regions, whereas records of smaller specimens (*e.g.*, *H. americanus* and *S. albicaudus*), indicate that younger animals may use sheltered habitats (Aguiar et al., 2009; Farrugia et al., 2011), such as the shallow zones closer to rock formations and low energetic parts in the northeast. However, for two skates, *A. castelnaui* and *A. cyclopohora*, the area works not only as nursery, but also as mating place, as indicated by the lower frequencies of adults and seasonal records of mature males. The possibility that records of mature specimens of the other species may have been related to migratory behavior hampers the definition that the area was used only for reproduction by them. Thus, as proposed for cownose rays, which are species of large home ranges and exhibit key areas for population maintenance along the coast (Collins et al., 2007; Rangel et al., 2018), we suppose that the MPAs may be a seasonal feeding ground for *M. freminvillei* and *D. hypostigma*.

Connection between the inner and outer shelf may play a critical role in the species' reproductive success, especially for *P. horkelii* and the chola guitarfish, *Pseudobatos percellens* (Walbaum, 1792). Seasonal migrations of *P. horkelii*, from deeper regions (> 100 m) to give birth and mate in coastal zones, is well described by Lessa et al. (1986). This might have been the case of the adult females of both species that were caught in spring and summer. Even though movements of great distances were not reported for *P. percellens*, embryonic diapause, which is a reproductive trait associated with the migratory behavior of *P. horkelii*, was proposed for the former species (Rocha and Gadig, 2013). This may suggest that *P. percellens* also displays such behavior, being consistent with the absence of neonates in our records. Finally, for *R. agassizii*, *P. extenta* and *Z. brevirostris*, all length classes were collected, indicating their resident status. Nevertheless, their presence may be intermittent, particularly for the skates that were absent in some oceanographic expeditions. According to Martins et al. (2005), abundance fluctuations of *P. extenta* was observed in the northern coast, being higher in periods when the species were not recorded in Alcatrazes (*e.g.*, 2009'expedition).

3.4.2 WRA Effectiveness For *Z. brevirostris* And Further Challenges To Conservation Of The Species

Magnitude differences between the methods and uncertainties in fisheries indicators for *Z. brevirostris* may be caused in part by the small sample size, requiring larger datasets to obtain more precise and accurate results, especially for the LBSPR method. Despite the fact that our results did not find a significant positive effect of the WRA establishment, the decrease in mean $F/M_{(ML)}$ and increase in mean SPR may suggest some improvements in fisheries indicators. Our calculation of the expected time to show an improvement in mean length after MPA establishment suggests that under several possible selectivity patterns in the fishery, the WRA effect could be detectable within a few years of the MPA formation. However, further monitoring is needed to estimate the trends of the Alcatrazes population. The WRA is a novel MPA, for which the management plan was defined in 2017 (ICMBio, 2017), starting its initiatives one year before our last sampling campaign. Thus, our short-term evaluation and inconsistent sampling among seasons, might be the reason to the small changes we got in the mean length between periods. Furthermore, *Z. brevirostris* is a relative long-lived species that exhibits late maturity and low intrinsic rate of population growth (Caltabellotta, 2014; D'Alberto et al., 2019), which would increase the estimated times of recovery relative to more short lived species.

As previously mentioned, parts of the archipelago have been being protected by TES and even before its creation, by the Brazilian Navy, which used to perform tactical exercises, forbidding navigation in the surroundings (Hoff et al., 2015). At that time, the demersal fish community was represented by predominance of sole fishes (*e.g.*, *Syacium micrurum*, *S. papillosum*, *Citharichthys macrops* and *Symphurus jenynsi*) and poor diversity of elasmobranchs, with *Z. brevirostris* as the only one in the records (Paiva-Filho et al., 1989). Nowadays, the archipelago shows a well-structured community, with presence of higher-level predators (Rolim et al., 2019) and the apparent improvement of the *Z. brevirostris* population, since the great number of recorded specimens is comparable to other studies that were performed in wider areas along the coast (*e.g.*, Marion et al., 2011; Caltabellotta et al., 2019). In this sense, our results provide a useful baseline for further evaluations of causal effects regarding the WRA. Some studies have pointed out the importance of tracking changes in ecological indicators of a MPA throughout time (Edgar et al., 2004, 2011) and between a control site (Villaseñor-Derbez et al., 2018). However, the historical safeguarding of the archipelago, the influence of physical processes (Castro et al., 1987), the higher complexity of ecological interactions (Rolim et al., 2019) and its great distance from coastal as well as other insular regions, increase the potential sources of variability (Edgar et al., 2014), making difficult the designation of control areas or comparisons with other MPAs.

The relevance of the MPAs for the local ichthyofauna is clear, especially the WRA, which broadened the protection, encompassing the Alcatrazes island and consequently, the essential habitats for elasmobranchs. Furthermore, both areas seem to play pivotal roles for endangered species, as more than 75% of the recorded elasmobranchs are in threatened categories (IUCN, 2023). Both MPAs together encompass an area of approximately seventy thousand hectares (ICMBio, 2017) which would cover the home ranges of the caught species (see section 2.2.1). Nevertheless, ontogenetic differences in their requirements may not be provided, so that for some species the archipelago was used only at specific life stages (*i.e.*, non-resident species). Such differences imply movements to specific habitats outside the MPAs boundaries, raising the threats over the species and consequently affecting the efficiency of the protection areas. Chapman et al. (2005) discovered that the lack of connectivity among adjacent habitat was exposing reef and nursery sharks to the fisheries, demanding additional management measures for species conservation, and some Alcatrazes species may experience similar threats.

Similarly, the intense anthropogenic pressure in the surrounding area may compromise such functionality and thus, the effectiveness of TES and WRA. Alcatrazes is placed between two disturbed areas on the São Paulo coast. To southwest, the Santos Port is the largest port in Latin America and the most important industrial hub in Brazil (Luiz-Silva et al., 2002), producing great concentrations of mercury and plastic pellets, that reach adjacent (*e.g.*, Santos Bay) (Siqueira et al., 2005; Ribeiro, 2020) and even farther regions, such as the archipelago. To northwest and closer to Alcatrazes, the São Sebastião Port will be expanded over the Araçá Bay (Angelini et al., 2018), an important nursery place (Contente et al., 2020). Besides the local impacts, its expansion could also affect the vicinities, disturbing the fauna by the carriage of pollutants and increase in underwater noise (Slabbekoorn et al., 2010; Barletta et al., 2016).

In addition, despite fishery activities being concentrated on the inner and middle shelf (Imoto et al., 2016), including inside the less restrictive protection areas (Carneiro et al., 2013), exploration of deeper zones has been increasing in the past decades (Pincinato and Gasalla, 2019). According to Imoto et al. (2016), great amounts of demersal catches were obtained by industrial fleets in those regions, raising the threat over species that use the archipelago seasonally for feeding or for mating, while also using the surrounding fished area. Currently, fishing of threaten elasmobranchs is forbidden or only allowed for subsistence in Brazilian waters (*i.e.*, species classified as VU) (MMA, 2014). Nevertheless, they are still caught as bycatch by fleets that are known to directly impact the demersal fauna, such as gillnets, and otter, double-ring and pair trawlers. Those activities are controlled in the surroundings of TES and WRA by the management plans of other two protection areas (*i.e.*, Marine Environment Protection Area of the North and Central Coast – APAM Norte and APAM Centro) (Forestry Foundation, 2019, 2020) and different legislations of federal and state level. Inside the APAMs, input measures, such as the restriction of industrial (APAM Centro) and even traditional (APAM Norte) pair trawlers until the 23.6 m isobath as well as the specification of day periods to operation of beach seines (Sao Paulo, 2009, 2012), are applied. Nevertheless, the fishing zonation become less restrictive as distance from the coast increases and despite seasonal closures of catfish and shrimp fishing occur from January to March (SUDEPE, 1984) and March to May (IBAMA, 2008), respectively, gillnets remain allowed (IBAMA, 2007).

Thus, based upon the MPAs use by elasmobranchs and the potential connectivity with other protected areas, we recommend that besides the creation/expansion of marine reserves, fishing control measures should be implemented. Temporal closures in winter as well as extension of the pre-existing ones through all summer months, and limitation of effort (Cochrane and Garcia, 2009), could reduce the pressure on species that make reproductive migrations and/or require larger home ranges (*e.g.*, guitarfishes, eagle and cownoses stingrays). Moreover, economic incentives (*i.e.*, referred to “Seguro Desemprego”, a category of social insurance in Brazil) (Brazil, 2003, 2009, 2015) could be provided to artisanal fishermen during the proposed temporal closures and to those who will not be able to fish or will have to change their techniques due to permanent spatial closures. Last, integrated evaluations of the effectiveness of conservation actions for benthic elasmobranchs and the Alcatrazes ecosystem must consider the associated areas, since they have provide essential services to the ecosystem’s maintenance (Rolim et al., 2019; Contente et al., 2020). If these measures are taken into account, a network with key habitats along the coast (*e.g.*, nursery, reproduction and feeding places) could be developed, assisting the conservation of elasmobranch populations in the southeastern Brazil and consequently, enhancing the WRA and TES efficacy.

3.5 References

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4 ON THE ASSESSMENT OF DEMERSAL ELASMOBRANCH SPECIES RICHNESS USING MULTISPECIES OCCUPANCY MODELS

Abstract

Species richness has been the most addressed measure of biodiversity in the past decades. However, the raw number of species in a community is often an underestimate due to lower abundance or cryptic behavior of some species, that are often not observed in sampling replicates. Among the alternatives that provide best estimates by accounting for imperfect detectability, the hierarchical modelling approach stands out, being used in the assessment of species richness for other taxa, especially reef fishes. In this study, we explore the use of multispecies occupancy models to estimate the richness of demersal elasmobranchs in one of the most complex MPAs networks in Brazil, assessing possible divergences in species distribution due to the particularities of each area. Through the evaluation of different structures of multi-species occupancy models, the effects promoted by the geomorphology were investigated, revealing the equivalence among the north and central coast of São Paulo and a greater richness than previous observed in the former. These findings might contribute to improvement of the current conservation strategies, by providing information on which to base more suitable conservation and management actions.

Keywords: Hierarchical modelling, elasmobranchs conservation, Bayesian analysis, species distribution

4.1 Introduction

Species richness has been the most widely-used measure of biodiversity in the past decades, either because of its straightforward concept (*i.e.*, the number of species) and easily measurement (Marc and Royle, 2009; Chao and Chiu, 2016), but mostly for being the basis of further assessments of diversity patterns (Guisande et al., 2013; Menegotto and Rangel, 2018), disturbance effects, environmental recovery (Barletta et al., 2016; Dias et al., 2017; Viana et al., 2022) and evaluation of management strategies (Rolim et al., 2019; Karlovic et al., 2021; Motta et al., 2021). However, estimating species richness *per se* is problematic. The raw number of species in a community is often an underestimate due to lower abundance (*i.e.*, rare species) or cryptic behavior of some species, and is strongly related to sampling effort (Royle and Dorazio, 2008). Moreover, differences in species detectability are likely influenced by the sampling design, the chosen methodology to collect/record them and the statistical model applied to estimate richness, as their detection probabilities can vary among the sampled places and each species might show different responses to disturbances promoted by the sampling process (Boulinier et al., 1998; Kéry and Schmidt, 2008).

Regarding the marine environment, several factors influence species detectability, such as sampling methods that can only be used in a subset of the habitats in a sampled area (*e.g.,* soft versus hard substrates), unsuitable environmental conditions (*e.g.,* water turbidity and clarity), species behavior (*e.g.,* some species are more curious than others) and their ecological strategies (*e.g.,* schooling species are more detectable) (MacNeil et al., 2008; Bacheler et al., 2014; Coggins et al., 2014). To integrate these sources of variability in species richness, a hierarchical modelling approach that combines community and species level characteristics has been applied. Called a multispecies occupancy model, this structure allows the estimation of the latent number of species in an area, including rare and even unsampled species, based on multiple observations of the species composition at multiple sites (Dorazio and Royle, 2005; Dorazio et al., 2006; Kéry and Royle, 2008; Royle and Dorazio, 2008). While such methods have been applied to reef fishes (MacNeil et al., 2008; Bacheler et al., 2014; Coggins et al., 2014; Harford et al., 2016) , the assessment of other marine taxa still remains in raw counts or uses alternative estimators (*e.g.,* Chao and Chiu, 2016), which despite taking into account imperfect detectability, do not allow the inclusion of such effects (Royle and Dorazio, 2008).

In this study, we explore the use of multispecies occupancy models to estimate the richness of demersal elasmobranchs in one of the most complex networks of Marine Protected Areas (MPAs) in Brazil (Motta et al., 2021): the Marine Environment Protection Area of the

North and Central Coast of the São Paulo state (*i.e.*, APAM Norte and APAM Centro) (São Paulo, 2008b, 2008a). Broadly distributed throughout inshore and continental shelf areas, the local demersal species are exposed to a variety of threats (*e.g.*, fishery, habitat degradation and pollution) (Siqueira et al., 2005; Angelini et al., 2018; Ribeiro, 2020) that occur over their main habitats (*e.g.*, nursery, reproduction and feeding places), affecting different life stages (Bornatowski et al., 2014a; Karlovic et al., 2021). Moreover, the north and central parts of the coast diverge in relation to geomorphological and sedimentological aspects (Mahiques et al., 1999, 2004; Conti and Furtado, 2006), where the north consist in a richer environment due to higher heterogeneity of sediments as well as concentrations of organic matter (Gianesella-Galvao and Saldanha-Corrêa, 2003). As far as we know, the effects of the local dynamics on the diversity patterns of elasmobranchs have not been investigated, although there have been studies of the benthic megafauna as well as macrofauna (Pires, 1992; Soares-Gomes and Pires-Vanin, 2003; De Léo and Pires-Vanin, 2006; Rodrigues and Pires-Vanin, 2012; Shimabukuro et al., 2016) and demersal actinopterygians (Rossi-Wongtschowski and Paes, 1993; Muto et al., 2000; Schmidt and Dias, 2012; Rocha and Dias, 2015). Owing to these factors, our interest lies on obtaining a more accurate estimate of the total richness of demersal elasmobranchs in the region and investigating how the differences among the areas would affect it. We used information collected by the previously mentioned studies and by further prospections in the area. Applying this new analytical approach to the dataset composed only by demersal elasmobranchs and making comparisons with the patterns already identified to other taxa, we were able to clear such matters.

4.2 Material And Methods

4.2.1 Study Area And Data Description

The configuration of the continental and insular areas in the north and central parts of the São Paulo state coast are responsible for the complexity of the sedimentological and hydrochemical processes over the shelf (**Figure 4-1 A and B**). The areas can be physically separated by the presence of São Sebastião island (SSI). As the second largest Brazilian island, the SSI acts as a barrier to the incidence of south and southeast waves in the north shelf regions up to 50 m deep (*i.e.*, inner and mid shelves), promoting a more stable environment (Barcellos and Furtado, 1999). Thus, while the central inner and mid shelves are predominantly composed by finer grains of sand, due to the direct influence of the energy of waves that carry pelitic sediments and organic particles to the outer shelf, the north is characterized by more heterogeneous sediment with higher deposition of mud and retention of terrigenous particles of organic matter in the inner and mid shelves (*i.e.*, the SSI shadow effect) (Gianesella-Galvão and Saldanha-Corrêa, 2003) and a patchy configuration of different granulometry and sorted sediments in the outer shelf (Mahiques et al., 1999, 2004; Conti and Furtado, 2006). Additionally, the southern inner and mid shelves are directly influenced by other two factors: the action of the Brazil Costal Current (BCC) and the retreat of the Serra do Mar mountain chain to the continent, which allowed the formation of larger drainage systems (Mahiques et al., 1999). While the BCC flows northwards, from the La Plata River, carrying finer sediments (Campos et al., 1999; Souza and Robinson, 2004; Mahiques et al., 2011), the presence of rivers of high potential runoff promotes the enrichment of adjacent environments in the central part by the advection of terrigenous organic matter (Moser et al., 2005).

Both areas have been sampled by several oceanographic expeditions since 1980. A massive data set from thirteen cruises of six projects was compiled. The samples included a total of 22 elasmobranch species (**Figure 4-1 C**), of which thirteen and nine show benthic and benthopelagic habits, respectively (Froese and Pauly; Gomes et al., 2019). Overall, the samplings occurred throughout spring, summer and winter months, encompassing a broad depth range (from 8 m to 124 m), and the species were caught using otter trawl nets. Based on the sedimentological characteristics previous described and the fact that the area is seasonally influenced by the bottom intrusion of the South Atlantic Central Water (SACW), the trawl stations were sorted considering their position in relation to the inner (up to 30 m), mid (from 30 to 50 m) or outer shelves (> 50 m) and the season when they were carried out (Castro et al., 1987; Castro-Filho and Miranda, 1998). Here the SACW is considered as an environmental modifier, since its presence on spring and summer months, acts to lower the water temperature and enrich bottom environments, changing the benthic fauna (Pires-vanin and Matsuura, 1993; Muto et al., 2000; Sumida et al., 2005). Thus, a total of eighteen season-area strata were defined (*e.g.*, inner-spring, mid-spring and out-spring for north and central parts) which were sampled from three to twenty-four times. As both MPAs were established in 2008 (São Paulo, 2008a, 2008b) and all the recorded species are long-lived with relatively low intrinsic rates of population growth (*e.g.*, D'Alberto et al., 2019), we assumed that populations would have not had enough time to recover from historical fishing mortality, so that the probability of detection and probability of presence could be considered stable over time, even if they might be influenced by changes in abundance. In this sense, we kept the model assumption that samples must be drawn from closed populations (Dorazio and Royle, 2005; Kéry and Royle, 2008).

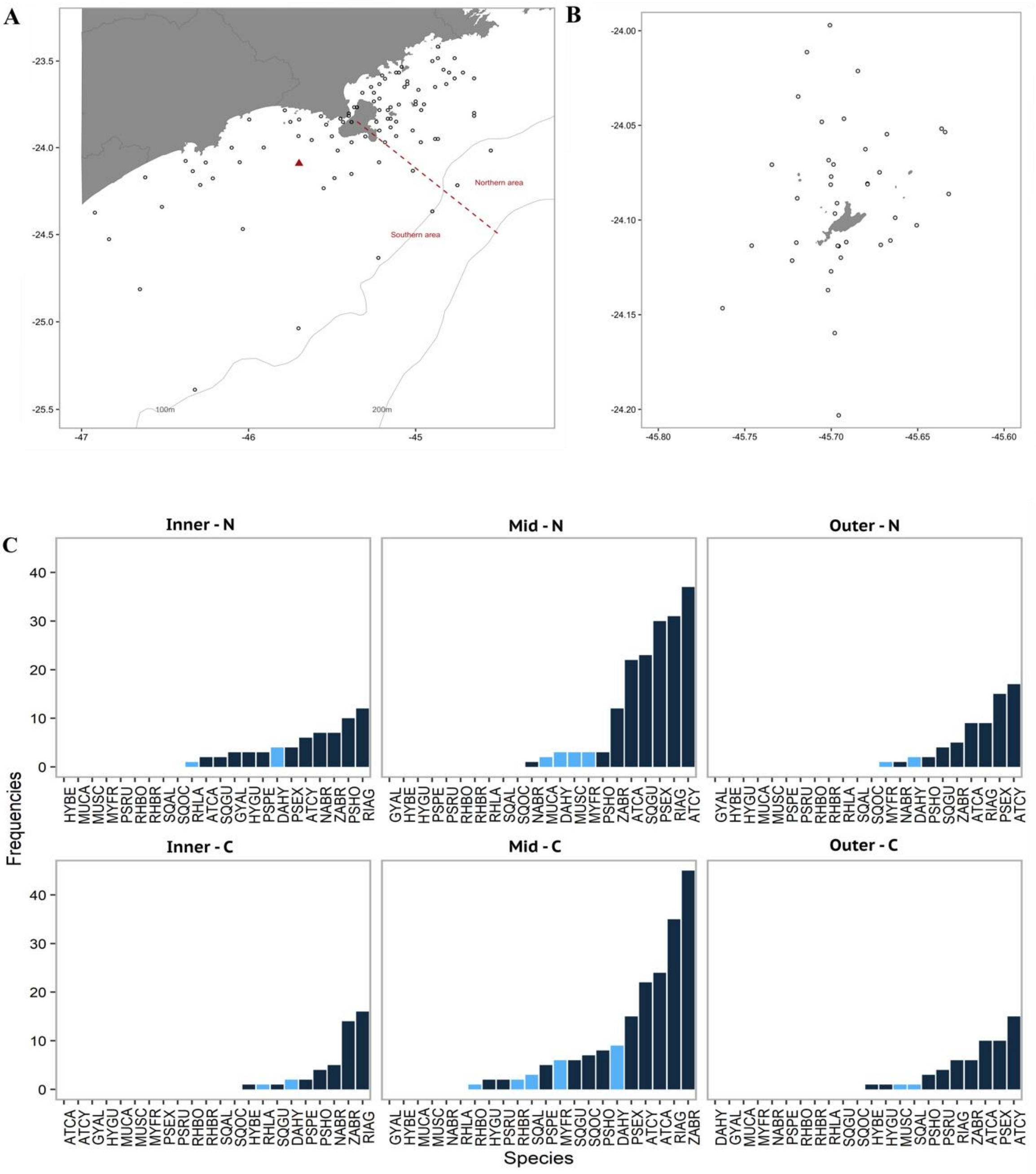

Figure 4-1 Broad view of the study area encompassing the north and central parts of the São Paulo state with all trawl stations (A). The dashed red line marks São Sebastião island, separating the areas and red triangles denotes the Alcatrazes Archipelago with the detailed trawl stations (B). Bellow (C), the graphics shows the frequencies of occurrence of each observed benthic (dark blue) and benthopelagic (light blue) species in the inner, mid and outer shelves of both areas (North and Central). Initials correspond to: *Atlantoraja castelnaui* (ATCA), *A. cyclophora* (ATCY), *Rioraja agassizii* (RIAG), *Psammobatis extenta* (PSEX), *Pseudobatos percellens* (PSPE), *P. horkelii* (PSHO), *Zapteryx brevirostris* (ZABR), *Hypanus gutattus* (HYGU), *H. berthalutzae* (HYBE), *Dasyatis hipostigma* (DAHY), *Narcine brasiliensis* (NABR), *Gymnura altavela* (GYAL), *Mustelus canis* (MUCA), *Mustelus schmitti* (MUSC), *Myliobatis freminvillei* (MYFR), *Squalus albicaudus* (SQAL), *Rhizoprionodon lalandii* (RHLA), *Squatina occulta* (SQOC) and *Squatina gugguenheim* (SQGU).

4.2.3 Model Structure And Fitting

In the Bayesian approach proposed by Dorazio *et al.* (2005, 2006) the unknown richness (N) can be estimated throughout the likelihood of the observed species (n) applying data augmentation (Kéry and Royle, 2008) for the unseen ones. Considering z_i as the latent indicator of the species occurrence, with $z = 1$ when a species is present or $z = 0$ when it is not, z_i consists of a binary variable drawn from a Bernoulli distribution, $z_i \sim$ Bernoulli (Ψ_i), with Ψ_i as the probability of species $\underline{i}$ occurrence. Due to uncertainties in the true state of occurrence of each species i, their detection probability (p_i) given occurrence was estimated using two different structures in terms of variability. In the first one, m_{spec}: Ψ (.) p (.), we assumed that there was no source of variability in relation to the sampled strata, so that p_i was influenced just by the intrinsic characteristics of each species as a normal random effect on the logit scale, logit(p_i)~ Normal (μ_p, $\sigma_p{}^2$). Since their habits would directly influence the detectability (*i.e.*, the chance of being caught), we included habit as a fixed effect, m_{spec}: Ψ (.) p (habit), and μ_{p1} and μ_{p2} were estimated in accordance with the species being benthic or benthopelagic. Besides the species effect on the detection probability, the variability among the strata was accounted in the second structure $m_{spec\&strata}$: Ψ (.) p (.). In this framework, a third Bernoulli random process was added to model the existence of each species in the region (w_i with probability Ω, assumed to be the same for all species). Thus, the conditional probability of a species i occurring in a stratum j given that it existed in the region was modeled as logit(Ψ_{ij})~ Normal (μ_Ψ, $\sigma_\Psi{}^2$) and its detection probability as logit(p_{ij})~ Normal (μ, σ^2) conditional on presence in a stratum. The habit effect was also included in that model structure, generating a fourth model $m_{spec\&strata}$: Ψ (.) p (habit).

On both structures, the data (Y) was the count of number of times each species was observed, and the likelihood assumed a binomial process, with p conditional to the species (i) being present or not (z_i) in the replicates (K) of each stratum (J), being denoted in the first and second structure as:

(1) Y_i ~Binomial (p_i*z_i, J),

(2) Y_{ij} ~Binomial (p_{ij}*z_{ij}, K_j)

Uninformative priors were used in models fit (**Appendix - C** for the models' code). Total richness (N) was obtained by summing the estimated number of species in the occurrence matrix. To elucidate whether the shadow effect promoted by SSI would have influenced the assembly between north and central parts, we also estimated the number of species for both areas (N_{north} and $N_{central}$) and for each stratum (*e.g.*, $N_{in\text{-}su}$, indicates the inner shelf – summer stratum). Comparisons among the posteriors drawn from each model were made to evaluate which structure better estimates richness. Furthermore, the differences among strata were assessed by the overlapping of the estimated richness and 95% credible intervals (CI). The Gelman-Rubin diagnostic (*R-hat* < 1.05) and the effective sample size (*n.effect* > 400) indicated model convergence (Lunn et al., 2012) after we ran two chains with 1,600,000 iterations, discarding the first 10,000 runs and thinning the chains by 10. All models were fitted using the *R2jags* (Yu-Sung Su and Yajima, 2021) package in the R environment (R Core Team, 2023).

4.3 Results

The posterior distributions of total richness revealed significant differences in the precision of the estimate of species richness by each model structure. Models of simpler structure (*i.e.*, m_{spec}) showed right skewed posteriors with longer tails (**Figure 4-2**) and estimates of N at least twice as high as the observed number of species ($N_{obs} = 22$) **(Table 4-1)**. On the other hand, results obtained by those models where p was assumed to vary by species and strata (*i.e.*, $m_{spec\&strata}$), seemed to be more plausible with estimates of N between 30.62 and 34.58 (**Table 4-1**), which were closer to the total number of species reported in the area by previous studies (~ 32 species). Regarding the habit effect on the species detectability, it showed inverse relationships on the estimates, with increases and decreases in N according to each model's structure (**Table 4-1**). However, accounting for the variability in detecting benthic and benthopelagic species among strata seemed to improve estimates, as N became even more similar to N_{obs} with a narrower CI (**Table 4-1**).

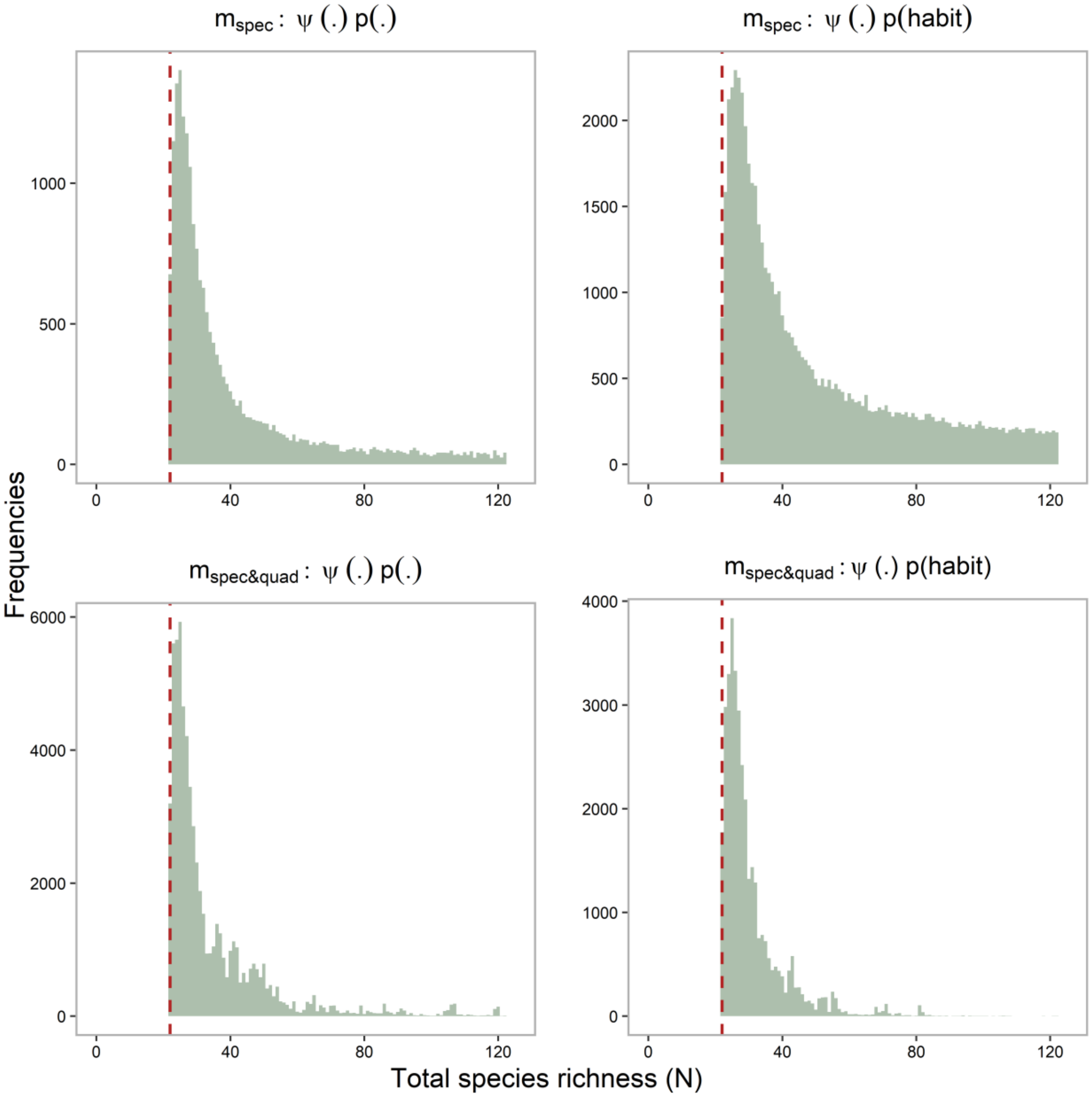

Figure 4-2 Posterior distribution of the total species richness (N) for the model structures considering the detection probability (*p*) varying only by species (m_{spec}) and by species as well as strata ($m_{spec\&quad}$). The fixed effect of the species habit on *p* was considered on both structures. Red dashed lines indicate the observed number of species (N_{obs}).

Table 4-1 Summary of the posterior probability of estimated total species richness (N) for each model's structure.

Models	N_{obs}	μ	sd	2.5%	97.5%	*R-hat*	*n.effect*
M_{spec}:Ψ(.)p(.)	22	40.51	22.62	22	109	1	2800
M_{spec}:Ψ(.)p(habit)	22	49.97	26.93	23	115	1	430
$M_{spec\&strata}$:Ψ(.)p(.)	22	34.58	16.33	22	87	1.01	780
$M_{spec\&strata}$:Ψ(.)p(habit)	22	30.62	9.75	22	56	1.01	4300

Notations: N_{obs} (observed number of species), μ (mean of the posterior distribution), sd (standard deviation), 2.5%-97.5% (95% Bayesian Credible Intervals), *R-hat* (Gelman-Rubin diagnostic) and *n.effect* (effective sample size).

Analyzing the posterior of total richness for the north and central areas (**Figure 4-3**), both structures suggest a higher gap between N_{obs} and N for the north part, from 16 to 29.44-33.34 species, with similar richness between regions (**Table 4-2**). This indicates that there is no effect of the SSI on species richness and such similarities might be explained by the absence of variability among strata (**Figure 4-4**). As pairwise comparisons between estimates obtained for each shelf-season group overlapped between the areas, no significant spatial or seasonal differences were found. Furthermore, the improvement by the inclusion of the habit effect is clear, presenting less skewed distributions of both areas. In this sense, we assumed $m_{spec\&strata}$: Ψ (.) *p* (habit) was the most suitable structure with 30.62 species in the role area (CI = 22 – 56) and 29.44 (CI = 21-55) and 29.73 (CI = 22-55) species in the north and central areas, respectively (**Tables 4-1 and 4-2**).

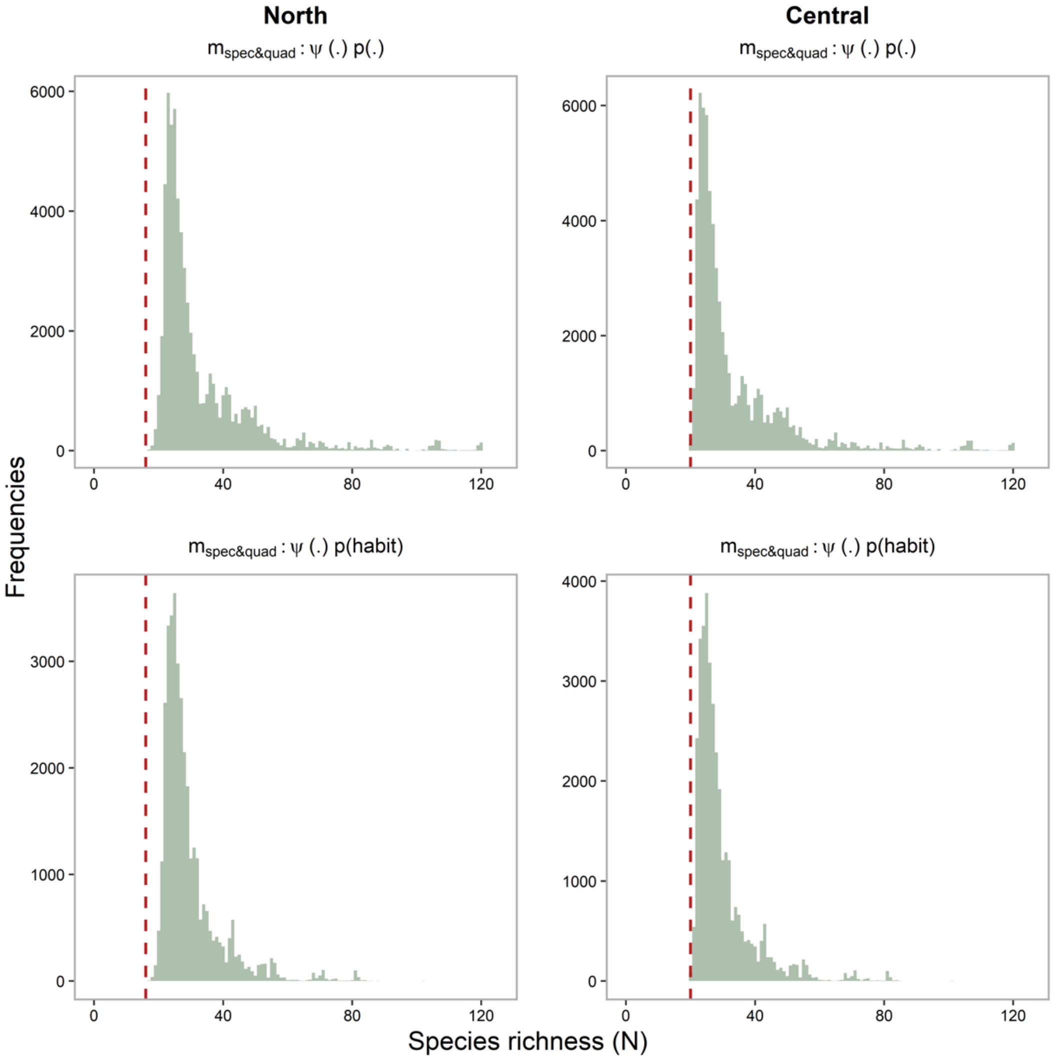

Figure 4-3 Posterior distribution of the species richness in the north (N_{north}) and Central ($N_{central}$) parts of the São Paulo state coast. The fixed effect of the species habit on *p* was considered on the m_{spec} and $m_{spec\&quad}$ model structures. Red dashed lines indicate the observed number of species (N_{obs}).

Table 4-2 Summary of the posterior probability of estimated species richness for the North and Central parts of the São Paulo state coast.

Models	**Coast**	**N_{obs}**	**μ**	**sd**	**2.5%**	**97.5%**	***R-hat***	***n.effect***
M_{spec}:Ψ(.)p(habit)	N	16	33.34	15.93	21	85	1	1400
M_{spec}:Ψ(.)p(habit)	N	20	33.58	15.83	22	85	1	1300
$M_{spec\&strata}$:Ψ(.)p(habit)	C	16	29.44	9.24	21	55	1.01	3700
$M_{spec\&strata}$:Ψ(.)p(habit)	C	20	29.73	9.14	22	55	1.01	3500

Notations: N_{obs} (observed number of species), μ (mean of the posterior distribution), sd (standard deviation), 2.5%-97.5% (95% Bayesian Credible Intervals), *R-hat* (Gelman-Rubin diagnostic) and *n.effect* (effective sample size).

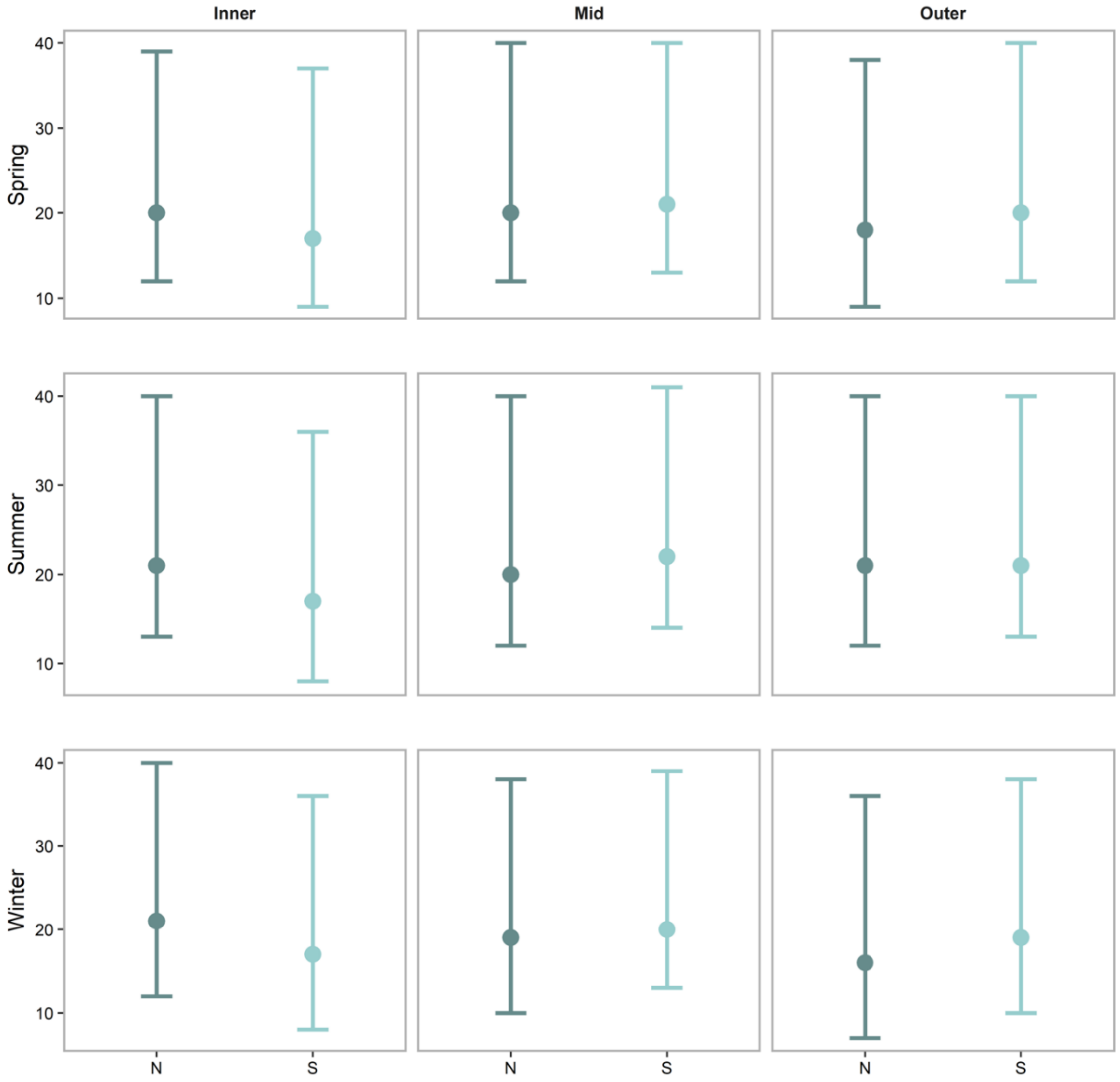

Figure 4-4 Estimates of μ and 95% Bayesian Credible Intervals of the species richness by each one of the eighteen strata. Values were obtained from the most suitable model, $m_{spec\&strata}$: Ψ (.) p (habit).

4.4 Discussion

In the past decades the local assembly of demersal elasmobranchs has been characterized by at least thirty-two species (Sadowsky, 1965, 1969; Paiva-Filho et al., 1989; Pires-Vanin et al., 1993; Ponz-Louro, 1995; Rocha and Rossi-Wongtschowski, 1998; Luiz et al., 2008; Rossi-Wongtschowski et al., 2008; Contente, 2013; Mattox et al., 2014; Rocha and Dias, 2015; Lamas et al., 2016; Souza et al., 2018). Part of them are considered as structural species (*e.g.*, the sand skates: *Atlantoraja cyclophora*, *Psammobatis extenta and Rioraja agassizi*), which are intrinsically related to bottom environments (Pires-Vanin et al., 1993). The analyzed dataset is formed by those structural species, which account for more than a half of the frequencies of occurrence at some parts of the studied area (**Figure 4-1 C**). Nevertheless, the assembly is likely composed by seasonal species (Pires-Vanin et al., 1993; Muto et al., 2000), which have their occurrence associated to environmental factors (*e.g.*, the intrusion of the SACW) as well as by their biological requirements, such as migration to sheltered coastal zones for mating and parturition purposes, and the necessity of larger home ranges in searching for resources (Lessa et al., 1986; Magurran and Henderson, 2003; Collins et al., 2008; Rangel et al., 2018; Karlovic et al., 2021).

Together, the permanent residency of a few abundant species and these multiple factors influencing the distribution of seasonal ones in different periods of the year, might explain the similarities we found between the inner, mid and outer shelves between north and central parts. Whereas the local number of species is expected to broaden due to the expansion of the SACW's associated species (Klippel et al., 2016) during the spring and summer seasons (*e.g.*, *Pseudobatos horkelii*, *Squatina occulta*, *S. guggenheim* and *Mustellus schmitti*), the absence of some species is possibly related to their tropical affinities (*e.g.*, *Hypanus guttatus*, *Rhizoprionodon porosus*). Moreover, similarities suggests that the assembly of both areas are equally influenced by oceanographic process, or that the differences promoted by the stronger SACW's effect in the north are balanced in the central by the energy surplus provided by larger drainage systems. In this sense, our findings would corroborate the results found by Rossi-Wongtschowski and Paes (1993), but for a larger scale, with the assembly composition remaining stable despite seasonal changes in species distribution along the area.

A great species richness in the north part was expected, although it was supposed to be higher than the estimated, as the area presents richer environments due to higher concentrations of organic matter (Gianesella-Galvao and Saldanha-Corrêa, 2003) and strong intrusions of the SACW (Castro et al., 1987; Cerda and Castro, 2014). Neighboring the northern part of the São Paulo coast is Cabo Frio, an area of great importance due to the high fishery productivity promoted by the step topography as well as coastline orientation, which strengthen upwelling effects (Campos et al., 1995; Cerda and Castro, 2014). However, its effects seem to gradually fade southwards, since the abundance of benthic fishes and invertebrates decreases as closer to the SSI (Pires-Vanin, 1993; Muto et al., 2000). This results in a heterogeneous environment in terms of availability of energetic feeding resources which might also reflect on the elasmobranchs, explaining the fact that $N_{central}$ was lower than we expected.

Regarding the differences found among the model's structures, it seems that the variability among sampled areas, such as differences in species occurrence and similarities in terms of composition among strata, must be considered in the hierarchical structure (Royle and Dorazio, 2008). When such sources of variation were incorporated, we allow the model to identify similarities among the north and central strata, since all strata had similar number of observed species and shared the most part of them (**Figure 4-1 C**). Furthermore, the exclusion of important covariates (*i.e.*, missing variables) from the occurrence (z_{ij}) and/or detection (y_{ij}) process might generate inaccurate estimates (Devarajan et al., 2020). This explains the reduction of bias in our estimates after considering whether the observed species were benthic or benthopelagic, making the model able to recognize their relatively equal proportion among strata.

Overall, a strongly relationship between the knowledge about the focal fauna, either in terms of high-quality identification guides and taxonomists, and significant sampling effort, are highlighted as the main causes of low values of diversity indicators worldwide (Costello et al., 2010; Guisande et al., 2013; Menegotto and Rangel, 2018). The poor knowledge about the communities' composition affects the local and worldwide biodiversity conservation (*e.g.*, non-recognition of rare threatened species), as extrapolations for other areas become vague due to the intrinsic bias of the weak estimates and great global variation (Costello et al., 2010). The results present here break the paradigm about the SSI's shadow effect, which were historically imposed due to the local patterns discovered for other taxa (Pires-Vanin, 1993; Muto et al., 2000). Revealing a higher number of species than is commonly observed and the homogeneity among areas, our results drawn our attention to other processes than the sedimentological and oceanographic ones, which in fact seem to act as proxies to the elasmobranch species distribution. Thus, we suggest that the local dynamics of the demersal assembly is driven by the influence of such processes on the occurrence of their main prey and the species life history traits. Finally, we hope that by obtaining estimates using a more precise analytical approach and clearing the patterns of a poorly known and high threatened species, we contribute to improving the taxa conservancy.

4.5 References

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5 CONCLUSIONS

The findings provided on this doctoral dissertation will provide both the academic community as well as the stakeholders with substantial information about the species autecology, their distribution patterns and associations with key habitats along coastal and shelf areas, the relationships with oceanographic processes and the unquestionable relevance of the local MPAs network for the taxa conservation. Despite the great diversity of elasmobranch species along the São Paulo state coast and the fact that a significant number of them are threatened, they remain poorly known. Thus, this huge gap in the knowledge of demersal elasmobranchs was the driving force that inspired the present study. In the second chapter, the detection of a sexual dimorphism, which was briefly mentioned in the literature despite the alarming conservation status of the species (*i.e., Zapteryx brevirostris*), raised questions regarding its potential influence on the species feeding and reproductive ecology. Investigating the relationships among several body measurements, the influence of gonadal maturation on developmental changes in the species' body morphology and differences between sexes, was strengthened. Even though no evidence was found that such dimorphism would influence its feeding habits, for example enhancing the success of females and males in exploring different prey and possibly exploring different habitats (*i.e.,* sexual segregation), ontogenetic changes in habitat was found. This implies that managers should be concerned about the possible impacts of fishing activities in key habitats for its different life stages.

In fact, the currently scenario is troubling. The last assessment made by the Chico Mendes Institute for Biodiversity Conservation showed that some species are depleted by 80% - 90% from their unfished abundance and multiple factors that affect them directly and indirectly (*e.g.,* fisheries, loss of coastal habitats and environmental degradation), are increasing in the region. These are all challenges to sustainable development. Based on that, in the third chapter the principal objective was to provide information that could enhance conservation polices and guide management actions of two important MPAs (*i.e.,* TES and WRA). Understanding the way each species uses the protected environments is essential to increase their success. Thus, the actual effectiveness was assessed by the evaluation of fishery indicators for *Z. brevirostris* and comparisons of changes in ichthyofauna composition over the years. Moreover, through an applied approach using functional diversity and evaluating variations in the relative abundance of functional groups and of the species in relation to the local oceanographic dynamic, the MPAs were characterized as: a residency of sand skates and guitarfishes (*e.g., Rioraja agassizii*, *Psammobatis extenta* and *Z. brevirostris*), nursery and/or reproduction area of several species (*e.g.*, *Z. brevirostris*, *Pseudobatos horkelii*, *Squalus cubensis, Hypanus guttatus*) and a strategic feeding place of highly energetically demanding species (*e.g., Rhinoptera bonasus* and *R. brasiliensis*).

Finally, the largest MPAs in the region (*i.e.,* APAM Norte and APAM Centro) have the challenging mission to ensure the species conservation by the sustainability of extractive activities. However, the effects of the local dynamic on the richness and distribution patterns of demersal elasmobranchs were unrecognized, possibly jeopardizing the management actions. So, revisiting a historical dataset and using different structures of multi-species occupancy models, the effects promoted by the geomorphology were investigated, revealing the equivalence among the north and central parts and a greater richness than previously observed in the former. The integration of these findings might be a useful tool to improve the current conservation strategy in the São Paulo coast. While the assessment of the MPAs' functionality and effectiveness bring insights about how the elasmobranchs use the region and strengthens the importance of implementing control measures, the understanding of the species distribution patterns allows the establishment of more suitable conservation and management actions.

6 APPENDIX A – Supplementary Material Chapter Two

Supplementary Figures

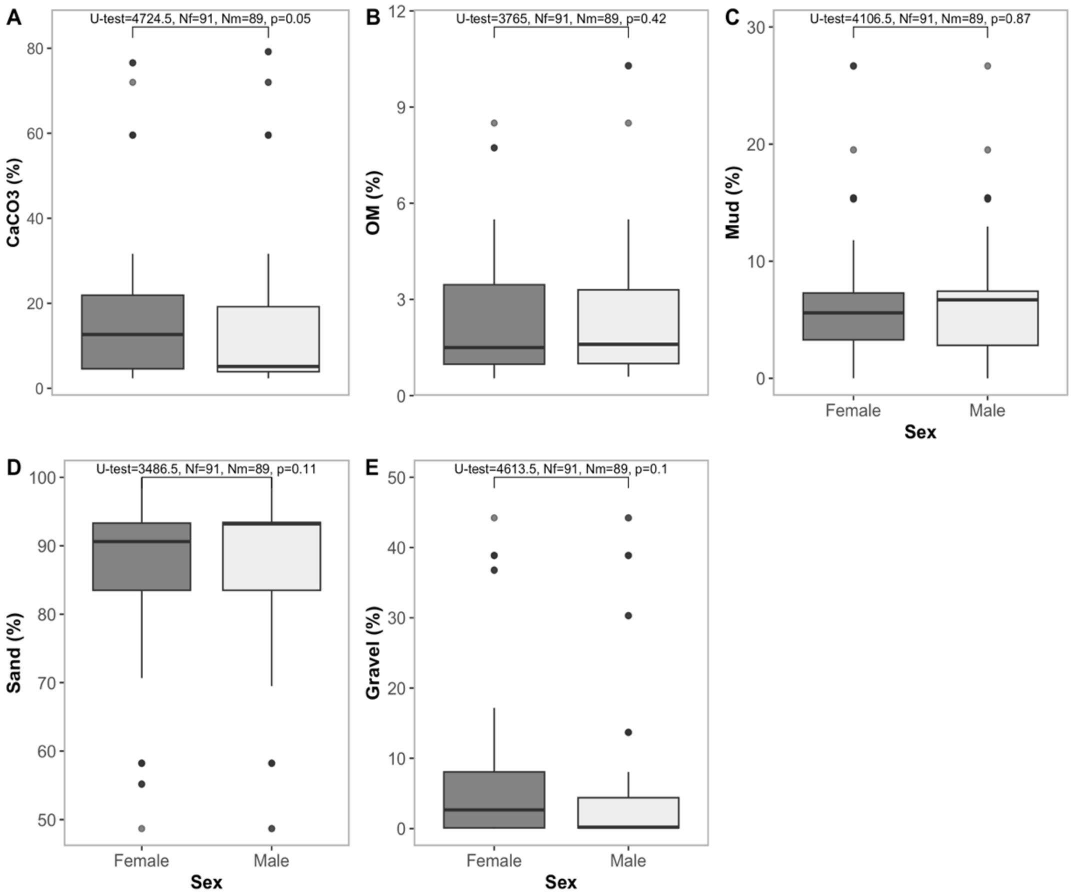

Figure A-1 Boxplots showing no-significant differences in concentrations of $CaCO_3$ (A), organic matter (B) and proportions of Mud (C), Sand (D) and Gravel (E) by sex. Gray dots are the minimum and maximum values in the data. Results of the Mann-Whitney U tests are presented with the sample size by sex: females (Nfe) and males (Nma).

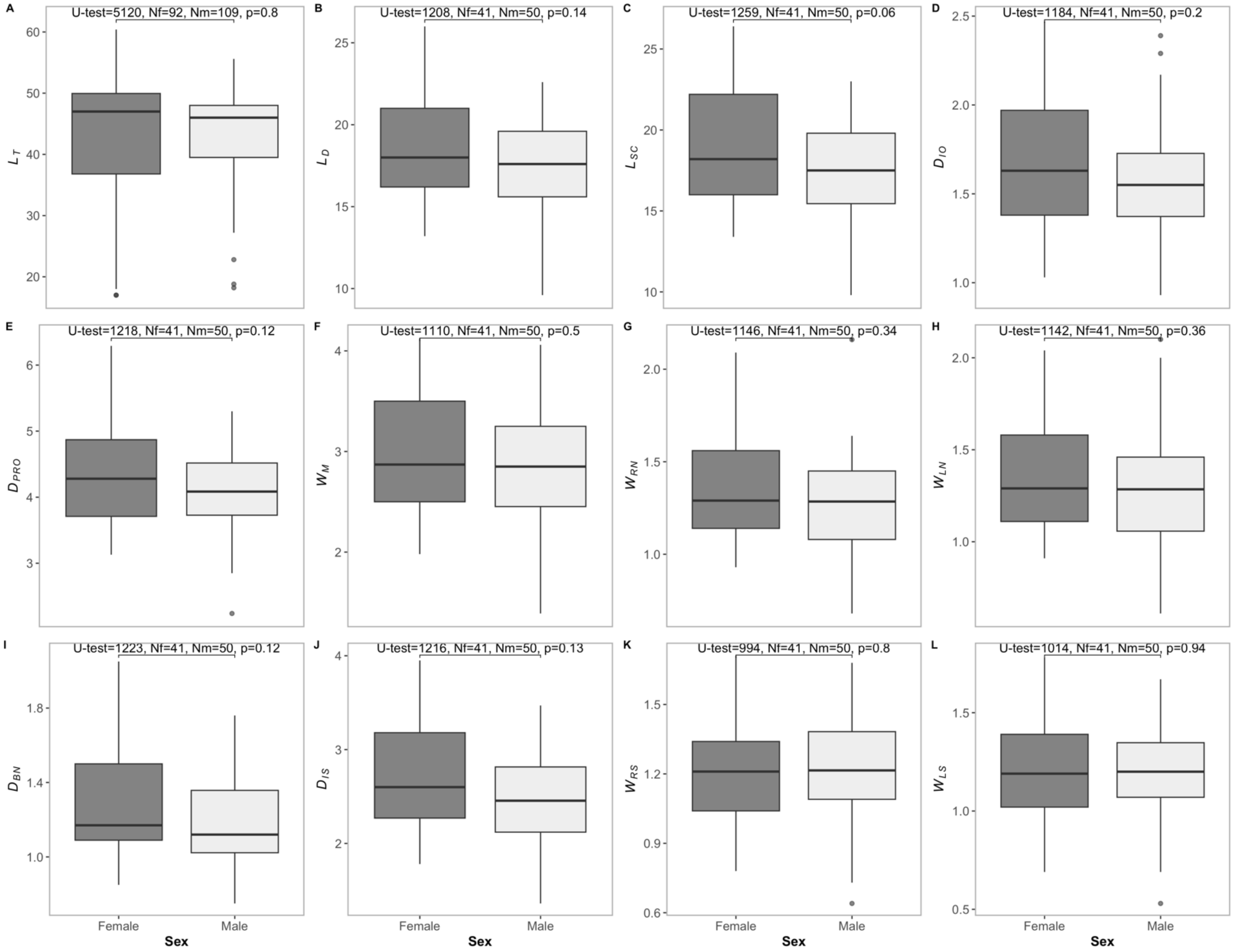

Figure A-2 Boxplots showing no-significant differences in morphometric measurements between females and males of *Zapteryx brevirostris*. Results of the Mann-Whitney U tests are presented with the sample size by sex: females (Nfe) and males (Nma).

Supplementary Tables

Table A-1 Summarized information about the measured specimens of *Zapteryx brevirostris*.

N	Preserved	Collection	ID	F	M	A	S	J	Locality
1	Yes	MZUSP	MZUSP 72777	-	1	-	-	1	Angra dos Reis, State of Rio de Janeiro - Brazil
1	Yes	MZUSP	MZUSP 72775	-	1	1	-	-	Cabo Frio, State of Rio de Janeiro - Brazil
1	Yes	MZUSP	MZUSP 117226	-	1	1	-	-	Coast of Araranguá, State of Santa Catarina - Brazil
1	Yes	MZUSP	MZUSP 117173	1	-	1	-	-	Coast of Florianópolis, State of Santa Catarina - Brazil
2	Yes	MZUSP	MZUSP 69285 and MZUSP 69284	1	1	2	-	-	Âncora Island, coast of Rio de Janeiro - Brazil
1	Yes	MZUSP	MZUSP 72774	-	1	1	-	-	Moela Island, coast of the State of São Paulo - Brazil
6	Yes	MZUSP	MZUSP 117266, MZUSP 117265, MZUSP 117268, MZUSP 117269, MZUSP 117270 and MZUSP 117267	3	3	2	2	2	Macaé, State of Rio de Janeiro - Brazil
1	Yes	MZUSP	MZUSP 3192	-	1	-	1	-	State of Rio de Janeiro - Brazil
1	Yes	MZUSP	MZUSP 47018	-	1	-	-	1	Toque toque beach, coast of the State of São Paulo - Brazil

3	Yes	MZUSP	MZUSP 117276, MZUSP 117275 and MZUSP 117274	3	-	3	-	-	Ubatuba, State of São Paulo - Brazil
42	Yes	OIUSP	-	17	25	14	12	16	Ubatuba, State of São Paulo - Brazil
1	Yes	MZUSP	MZUSP 72778	1	-	-	-	1	São Tomé Bank, State of Espírito Santo - Brazil
6	Yes	MZUSP	MZUSP 72779 and MZUSP 48199 (specimens one to five)	3	3	-	3	3	Uruguai
15	Yes	MZUSP	MZUSP 117231, MZUSP 13049, MZUSP 9737, MZUSP 9962, MZUSP 9961, MZUSP 10376, MZUSP 117308, MZUSP 117311, MZUSP 117312, MZUSP 117309, MZUSP 117283, MZUSP 117306, MZUSP 117313, MZUSP 117314 and MZUSP 117307	7	8	7	5	3	Unspecfied locality
2	Yes	OIUSP	-	2	-	-	-	2	Unspecfied locality
7	Yes	BIUSP	-	3	4	3	2	2	Unspecfied locality
110	No	n/a	n/a	51	59	95	8	7	Alcatrazes Archipelago, State of São Paulo - Brazil

The not preserved species (*i.e.*, lived ones), were released to the sea. N/a stands for not applicable. Notations: Total number of analyzed specimens (N), whether the specimen were preserved and deposited at a collection (Preserved), collections where the specimens are deposited (Collection), specimen' identification number (ID), number of females (F), males (M), adults (A), subadults (S) and juveniles (J) and approximate locality where specimens were caught.

Table A-2 Sedimentological data used to evaluate habitat segregation among age classes and sexes.

Locality	OS	Gravel	Sand	Mud	OM	$CaCO_3$
Santos adjacent shelf	W-1	0.00	93.20	6.80	1.80	5.29
Santos adjacent shelf	W-2	9.40	82.10	8.50	2.20	9.90
Santos adjacent shelf	W-3	0.20	86.30	13.50	3.70	8.68
Santos adjacent shelf	W-4	3.60	83.20	13.30	2.30	19.76
Santos adjacent shelf	W-5	0.00	94.80	5.10	1.20	4.80
Santos adjacent shelf	W-6	1.80	88.30	9.90	1.10	2.30
Santos adjacent shelf	W-7	0.00	84.60	15.40	2.30	3.10
Santos adjacent shelf	W-8	0.10	93.40	6.50	0.90	6.40
Santos adjacent shelf	W-9	0.00	93.20	6.80	1.60	2.80
Santos adjacent shelf	W-10	0.00	99.20	0.00	0.80	5.86
Santos adjacent shelf	W-11	4.40	80.20	15.30	2.00	20.44
Santos adjacent shelf	W-12	0.00	1.50	98.50	9.00	33.17
Santos adjacent shelf	W-13	0.00	91.70	8.30	2.20	3.00
Santos adjacent shelf	W-14	0.00	93.40	6.60	0.90	3.00
Santos adjacent shelf	W-15	0.00	100.00	0.00	0.90	3.33
Santos adjacent shelf	W-16	0.10	93.40	6.70	1.10	3.90
Santos adjacent shelf	W-17	0.00	100.00	0.00	1.20	3.78
Santos adjacent shelf	W-18	0.00	93.30	6.80	1.00	2.35
Santos adjacent shelf	W-19	0.10	100.00	0.00	2.40	3.41
Santos adjacent shelf	W-20	0.30	87.90	11.80	1.50	9.03
Santos adjacent shelf	W-21	10.20	19.30	70.60	6.80	15.30
Santos adjacent shelf	Su-1	0.00	95.00	5.10	1.20	4.30
Santos adjacent shelf	Su-2	1.70	86.60	11.70	5.50	4.60
Santos adjacent shelf	Su-3	0.10	84.70	15.20	2.70	9.40
Santos adjacent shelf	Su-4	4.10	84.10	11.80	2.80	18.50
Santos adjacent shelf	Su-5	0.00	96.50	3.40	4.00	4.50
Santos adjacent shelf	Su-6	0.00	80.50	19.50	8.50	3.00
Santos adjacent shelf	Su-7	0.00	93.30	6.60	5.30	2.20
Santos adjacent shelf	Su-8	0.10	99.90	0.00	0.90	6.30
Santos adjacent shelf	Su-9	0.00	82.00	18.10	6.20	3.20
Santos adjacent shelf	Su-10	0.20	99.80	0.00	1.00	5.13
Santos adjacent shelf	Su-11	1.50	83.00	15.40	2.70	15.62
Santos adjacent shelf	Su-12	0.00	3.80	96.20	12.30	30.04
Santos adjacent shelf	Su-13	0.00	88.70	11.40	4.60	2.65
Santos adjacent shelf	Su-14	0.00	99.90	0.00	0.60	2.99
Santos adjacent shelf	Su-15	0.10	100.00	0.00	1.00	3.70
Santos adjacent shelf	Su-16	0.00	96.50	3.40	1.10	5.10

Santos adjacent shelf	Su-17	0.00	95.00	5.00	2.20	4.50
Santos adjacent shelf	Su-18	0.00	68.20	31.90	7.30	4.15
Santos adjacent shelf	Su-19	0.00	100.00	0.00	1.00	3.99
Santos adjacent shelf	Su-20	0.30	91.20	8.60	1.50	9.30
Santos adjacent shelf	Su-21	0.50	3.60	95.90	17.60	27.04
Alcatrazes Archipelago	Sp-1	0.22	96.55	3.23	0.59	4.41
Alcatrazes Archipelago	Sp-2	17.18	77.64	5.18	1.59	21.90
Alcatrazes Archipelago	Sp-3	4.66	91.95	3.39	0.63	14.01
Alcatrazes Archipelago	Sp-4	0.16	94.24	5.59	0.54	3.24
Alcatrazes Archipelago	Sp-5	23.80	69.84	6.36	2.12	55.81
Alcatrazes Archipelago	Sp-6	4.11	90.61	5.28	1.02	12.66
Alcatrazes Archipelago	Sp-7	44.21	48.68	7.12	4.64	71.97
Alcatrazes Archipelago	Sp-8	38.87	58.23	2.90	0.98	59.55
Alcatrazes Archipelago	Sp-9	2.66	70.67	26.67	3.66	16.48
Alcatrazes Archipelago	Sp-11	9.01	86.51	4.48	0.69	29.45
Alcatrazes Archipelago	Sp-12	13.69	83.49	2.82	0.66	31.62
Alcatrazes Archipelago	Sp-13	36.78	55.18	8.04	7.73	76.56
Alcatrazes Archipelago	Sp-14	6.93	86.16	6.90	1.08	20.87
Alcatrazes Archipelago	Sp-15	8.36	89.09	2.55	0.60	26.79
Alcatrazes Archipelago	W-1	0.72	94.54	4.74	3.27	6.93
Alcatrazes Archipelago	W-2	1.86	90.70	7.44	3.56	12.18
Alcatrazes Archipelago	W-3	0.04	96.40	3.56	2.29	4.68
Alcatrazes Archipelago	W-4	0.14	93.90	5.96	3.75	4.74
Alcatrazes Archipelago	W-5	0.22	71.17	28.60	9.33	13.59
Alcatrazes Archipelago	W-6	0.54	95.08	4.38	4.89	9.27
Alcatrazes Archipelago	W-7	17.70	82.10	0.20	1.60	70.49
Alcatrazes Archipelago	W-8	0.10	98.00	1.90	1.29	4.66
Alcatrazes Archipelago	W-9	8.06	88.66	3.28	3.30	23.18
Alcatrazes Archipelago	W-10	30.30	69.50	0.20	2.39	79.18
Alcatrazes Archipelago	W-11	4.34	91.82	3.84	3.46	18.10
Alcatrazes Archipelago	W-12	6.58	80.46	12.96	10.29	19.19

Except for the data from Alcatrazes Archipelago collected on Winter (W), the sedimentological data were obtained from published works (Palóczy et al., 2012; Hoff et al., 2015; Shimabukuro et al., 2016)(Hoff et al., 2015. Notations: Locality where samples were taken (Locality), number of the oceanographic station with season initials (OS), percentages of gravel, sand and mud in the samples and concentrations of organic matter (OM) e $CaCO_3$, expressed in %.

Table A-3 Results of the Kruskal-Wallis H test of the sedimentological parameters by life stages.

Variables	**H**	**df**	**p-value**
OM	14.3	2	**<0.01**
$CaCO_3$	6.79	2	**0.03**
Gravel	2.68	2	0.26
Sand	2.57	2	0.28
Mud	1.87	2	0.39

Significant differences (p-value<0.05) were highlighted. Notations: analyzed sedimentological parameters (Variables), Chi-squared test (H), degrees of freedom (df) and significance in Chi-squared test (p-value).

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7 APPENDIX B – Supplementary Material Chapter Three

Supplementary Figures

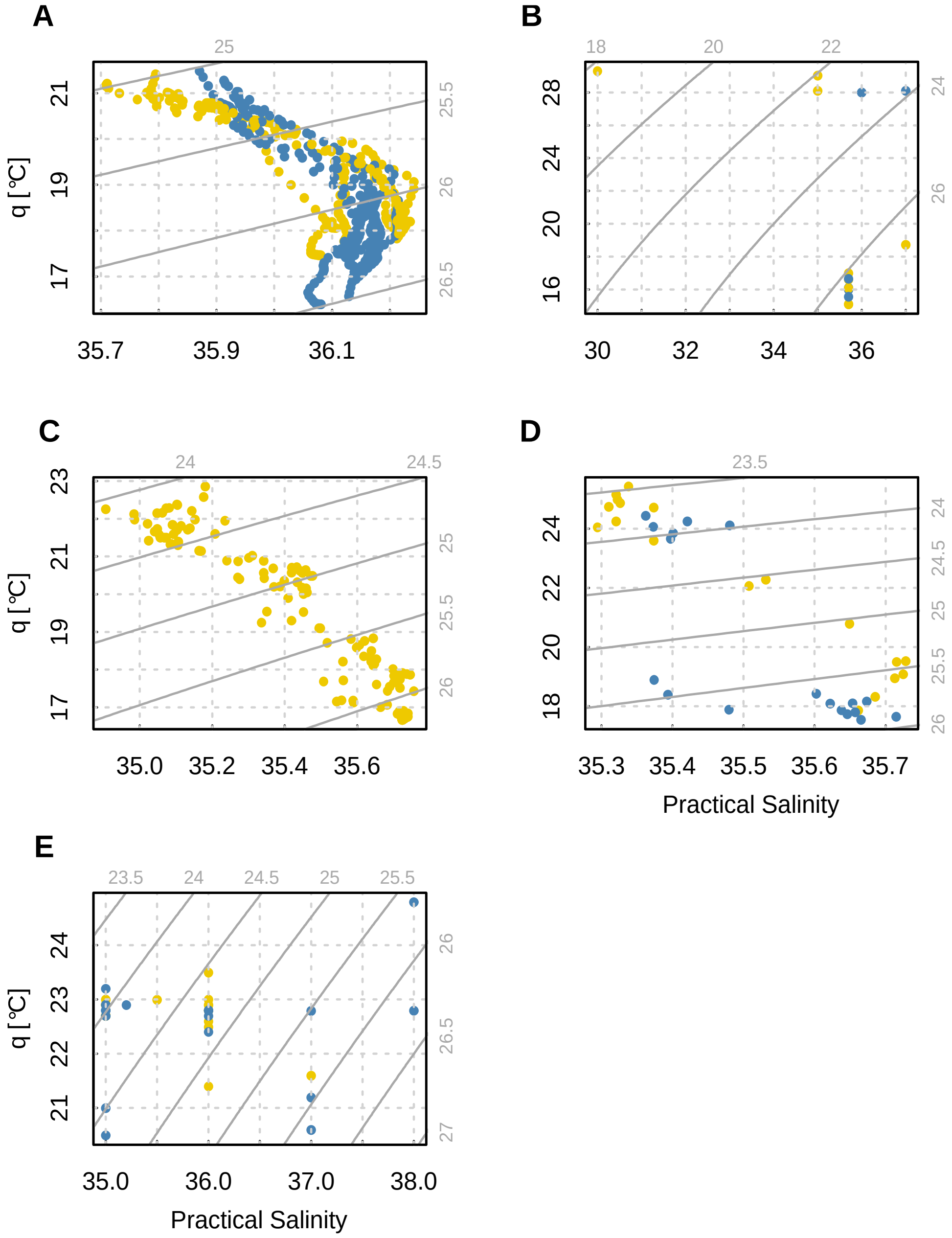

Figure B-1 Temperature-salinity diagrams with potential density lines at zero pressure (σ_θ) by oceanographic expedition: (A) 2011; (B) 2014; (C) 2015; (D) 2018 and (E) 2019. Blue points represent hydrographic data from oceanographic stations in the south and yellow points in the northeast and northwest.

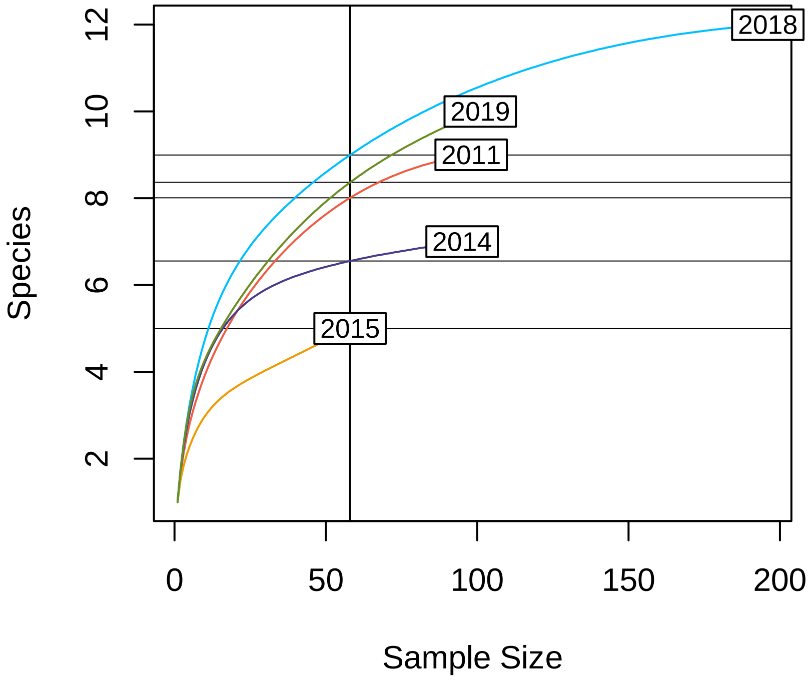

Figure B-2 Sample based rarefaction curves of abundance data by oceanographic expeditions for species richness assessment. Rarefied species richness was obtained through the (Hurlbert, 1971)'s equation using the rarefy function in R.

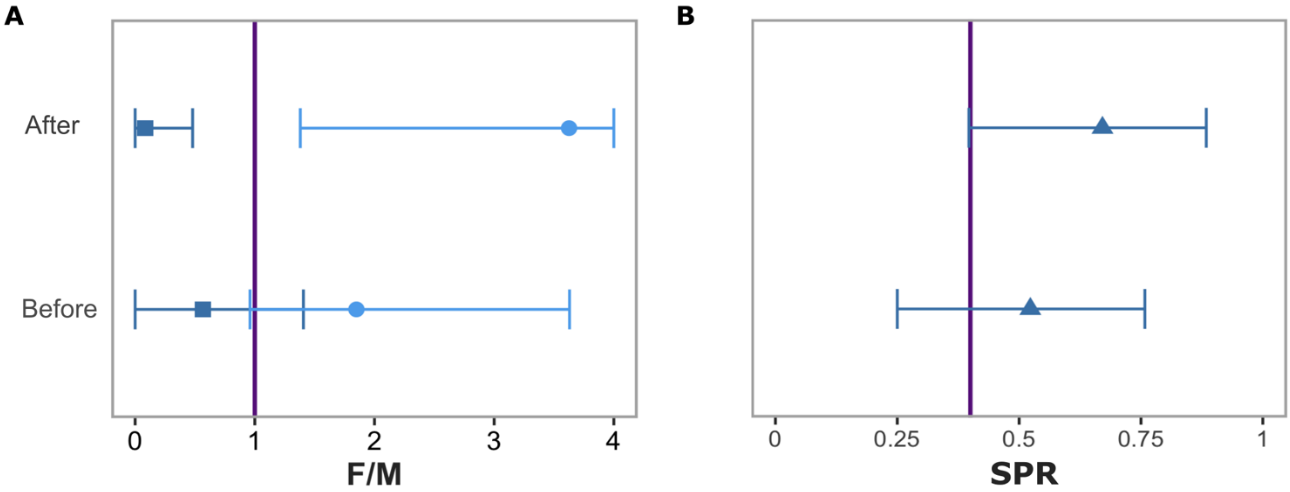

Figure B-3 Mean values of fishery indicators for *Zapteryx brevirostris* before and after the Wildlife Refuge of Alcatrazes establishment: (A) fishing over natural mortalities (*F/M*) estimated through the mean length (dark blue squares) and LBSPR methods (light blue points); and (B) spawning potential ratios (SPR) by LBSPR, all with 90% Monte Carlo confidence intervals. Solid purple lines indicate the overfishing threshold in A and the overfished threshold in B.

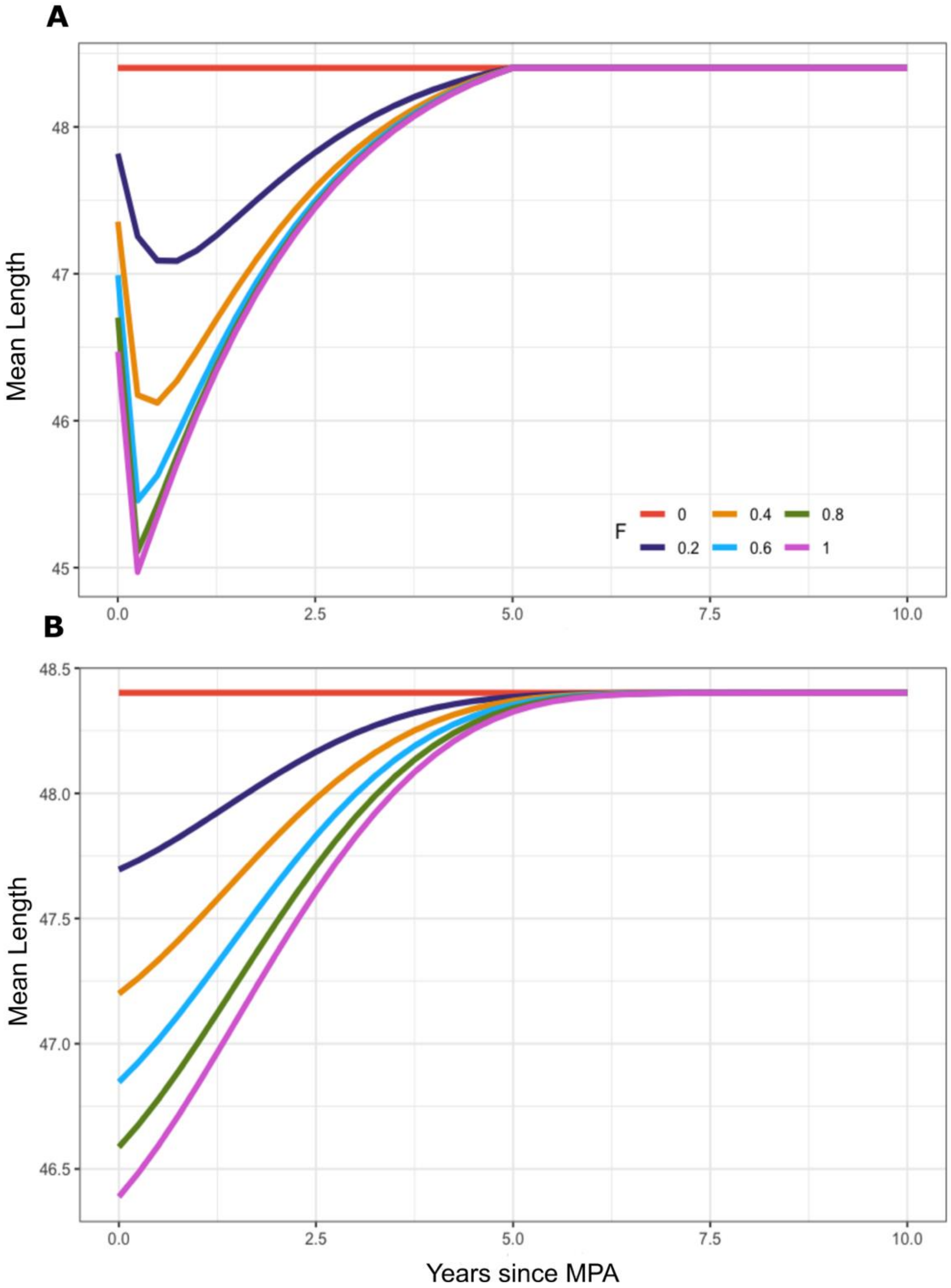

Figure B-4 Assessed mean length of *Zapteryx brevirostris* larger than the minimum fully exploited size (L_c) after the Wildlife Refuge of Alcatrazes establishment assuming: (A) equal fishery selectivity of specimens over L_c = 44 cm (Beverton and Holt, 1957) and (B) logistic selectivity (Hordyk et al., 2015). Line colors indicate the absence (red) and the different levels of fishery pressure that the lesser guitarfishes may have experienced before the MPA creation.

Supplementary Tables

Table B-1 Information on size at first maturity of species caught in Alcatrazes Archipelago.

Species	Sizes at maturity	Study Area	Source
Atlantoraja castelnaui	males = 91.1cm; females = 105.5cm	From Rio de Janeiro to Santa Catarina - Brazil	(Oddone et al., 2008a)
Atlantoraja cyclophora	males = 46.3 cm; females = 53.2 cm	From Rio de Janeiro to Santa Catarina - Brazil	(Oddone et al., 2008b)
Psammobatis extenta	males = 23.7cm; females = 23cm	Ubatuba - Brazil	(Martins et al., 2005)
Rioraja agassizii	males = 32.3 cm; females = 40.14 cm	From Rio de Janeiro to Santa Catarina - Brazil	(Oddone et al., 2007)
Dasyatis hypostigma	males: 30cm; females: > 30cm	Rio de Janeiro - Brazil	(Gomes et al., 2019)
Hypanus americanus	males: 50cm; females: 75-80cm	Rio de Janeiro - Brazil	(Gomes et al., 2019)
Hypanus guttatus	males: 43.5cm; females: 51.3cm	Rio Grande do Norte - Brazil	(Gianeti et al., 2019a)
Myliobatis freminvillei	males: 45cm; females: 58cm	Rio de Janeiro - Brazil	(Gomes et al., 2019)
Rhinoptera bonasus	males: 70 - 80cm; females: 65 - 90cm	Rio de Janeiro - Brazil	(Gomes et al., 2019)
Rhinoptera brasiliensis	Similar to *R. bonasus*	Rio de Janeiro - Brazil	(Gomes et al., 2019)
Pseudobatos horkelii	males: 70.2cm; females: 79.6cm	Sao Paulo - Brazil	(Martins et al., 2018)
Pseudobatos percellens	males: 54.8cm; females: 58.3cm	Sao Paulo - Brazil	(Rocha and Gadig, 2013)
Zapteryx brevirostris	males: 40.62cm; females: 42.3cm	Santa Catarina - Brazil	(Martins, 2007)
Squalus albicaudus	males 40 - 45cm; females: 54 - 61cm	Rio de Janeiro - Brazil	(Gomes et al., 2019)
Squatina guggenheim	males and females: 75cm	Rio de Janeiro - Brazil	(Gomes et al., 2019)
Squatina occulta	males and females: 110cm	Rio de Janeiro - Brazil	(Gomes et al., 2019)

Table B-2 Functional groups according to published information about species reproductive strategies and diet.

Species	**Trophic category**	**Embrionic feeding method**	**Source**
Atlantoraja castelnaui	Zoobentivorous - hyperbenthos	Oviparous	(Soares et al., 1992; Ponz-Louro, 1995; Oddone et al., 2008a; Colonello et al., 2012)
Atlantoraja cyclophora	Zoobentivorous - hyperbenthos	Oviparous	(Soares et al., 1992; Ponz-Louro, 1995; Oddone and Vooren, 2005; Oddone et al., 2008b; Viana and Vianna, 2014)
Psammobatis extenta	Zoobentivorous - hyperbenthos	Oviparous	(Ponz-Louro, 1995; Braccini and Chiaramonte, 2002; Martins et al., 2005; Aguiar and Valentin, 2010)
Rioraja agassizii	Zoobentivorous - hyperbenthos	Oviparous	(Soares et al., 1992; Ponz-Louro, 1995; Oddone et al., 2007; Bornatowski et al., 2014c; Motta et al., 2016)
Dasyatis hypostigma	Zoobentivorous - hyperbenthos	Trophonemata	(Ribeiro et al., 2006; Gomes et al., 2019)
Hypanus americanus	Zoobentivorous - infauna	Trophonemata	(Henningsen, 2000; Ramírez-Mosqueda et al., 2012)
Hypanus guttatus	Zoobentivorous - hyperbenthos	Trophonemata	(Yokota and Lessa, 2007; Aguiar and Valentin, 2010; Gianeti, 2011; Gianeti et al., 2019b)
Myliobatis freminvillei	Zoobentivorous - hyperbenthos	Trophonemata	(Tagliafico et al., 2016; Gomes et al., 2019)
Rhinoptera bonasus	Zoobentivorous - infauna	Trophonemata	(Baldassin et al., 2008; Bornatowski et al., 2014c; Cavalcante et al., 2016)
Rhinoptera brasiliensis	Zoobentivorous - infauna	Trophonemata	(Gomes et al., 2019)
Pseudobatos horkelii	Zoobentivorous - infauna	Lecithotrophic	(Lessa et al., 1986; Soares et al., 1992; Oddone and Vooren, 2005; Martins et al., 2018)
Pseudobatos percellens	Zoobentivorous - hyperbenthos	Lecithotrophic	(Aguiar and Valentin, 2010; Rocha and Gadig, 2013; Bornatowski et al., 2014c)

Zapteryx brevirostris	Zoobentivorous - infauna	Lecithotrophic	(Soares et al., 1992; Ponz-Louro, 1995; Abilhoa et al., 2007; Colonello et al., 2011a; Marion et al., 2011; Bornatowski et al., 2014c)
Squalus albicaudus	Piscivorous	Lecithotrophic	(Soares et al., 1992; Gomes et al., 2019)
Squatina guggenheim	Piscivorous	Lecithotrophic	(Ponz-Louro, 1995; Vögler et al., 2003; Vooren and Klippel, 2005)
Squatina occulta	Zoobentivorous - infauna	Lecithotrophic	(Vooren and Klippel, 2005; Aguiar and Valentin, 2010)

Table B-3 Environmental data used to assess functionality of Alcatrazes archipelago MPAs.

OEs	OSs	Exp	Buff	Seas	Dep	Temp	Sal	SACW	$CaCO_3$%	Sediment type	$CaCO_3$ classes
2011	#01	0	12.5	Spring	31	18.07	36.1	1	4.41	fine sand	lithoclastic
2011	#02	0	2.5	Spring	32.5	17.96	36.22	1	21.9	fine sand	lithoclastic
2011	#03	0	7.5	Spring	31.5	18.2	36.23	1	14.01	fine sand	lithoclastic
2011	#04	0	10	Spring	36.5	17.47	36.08	1	3.24	fine sand	lithoclastic
2011	#05	0	2.5	Spring	28	18.11	36.2	1	55.81	fine sand	bio-lithoclastic
2011	#06	0	7.5	Spring	41.5	17.88	36.13	1	12.66	very fine sand	lithoclastic
2011	#07	1	10	Spring	49	17.34	36.16	1	71.97	very fine sand	bioclastic
2011	#08	1	5	Spring	48	17.1	36.15	1	59.55	fine sand	bio-lithoclastic
2011	#09	1	2.5	Spring	52	17.55	36.13	1	16.48	very fine sand	lithoclastic
2011	#10	1	5	Spring	40	17.5	36.12	1	-	coarse sand	bioclastic
2011	#11	1	12.5	Spring	53	16.4	36.08	1	29.45	fine sand	lithoclastic
2011	#12	1	7.5	Spring	49.5	16.77	36.13	1	31.62	fine sand	litho-bioclastic
2011	#13	1	2.5	Spring	51.5	17.59	36.15	1	76.56	very coarse sand	bioclastic
2011	#14	0	2.5	Spring	39	18.01	36.22	1	20.87	fine sand	lithoclastic
2011	#15	0	5	Spring	31.5	18.2	36.22	1	26.79	fine sand	lithoclastic
2014	#01	0	5	Summer	33	16.4	35.7	1	-	fine sand	lithoclastic
2014	#02	1	2.5	Summer	53	16	35.7	1	-	very coarse sand	bioclastic
2014	#03	0	5	Summer	41	16.1	35.7	1	-	very fine sand	lithoclastic
2014	#04	0	5	Summer	42	16.2	35.7	1	-	fine sand	litho-bioclastic
2014	#05	1	5	Summer	41	15.6	35.7	1	-	fine sand	lithoclastic

2015	#01	0	5	Spring	43	16.8	35.7	1	-	very fine sand	lithoclastic
2015	#02	0	5	Spring	35	16.8	35.7	1	-	very fine sand	lithoclastic
2015	#03	0	7.5	Spring	34	16.8	35.7	1	-	fine sand	lithoclastic
2015	#04	0	10	Spring	32	16.8	35.7	1	-	fine sand	lithoclastic
2015	#05	0	10	Spring	35	16.7	35.7	1	-	fine sand	lithoclastic
2015	#06	0	12.5	Spring	34	16.8	35.7	1	-	fine sand	lithoclastic
2018	#01	0	7.5	Summer	32	19.1	35.7	0	-	very fine sand	lithoclastic
2018	#02	0	5	Summer	40	18.3	35.7	0	-	very fine sand	lithoclastic
2018	#03	0	7.5	Summer	33	19.5	35.7	0	-	very fine sand	lithoclastic
2018	#04	0	10	Summer	36	19.5	35.7	0	-	very fine sand	lithoclastic
2018	#05	0	5	Summer	40	17.9	35.7	1	-	very fine sand	lithoclastic
2018	#06	0	5	Summer	34	19	35.7	0	-	very fine sand	lithoclastic
2018	#07	1	5	Summer	39	18.1	35.6	0	-	coarse sand	bioclastic
2018	#08	1	7.5	Summer	37	18.2	35.7	1	-	fine sand	lithoclastic
2018	#09	1	5	Summer	46	17.8	35.7	1	-	fine sand	litho-bioclastic
2018	#10	1	2.5	Summer	51	17.6	35.7	1	-	very coarse sand	bioclastic
2018	#11	1	5	Summer	41	17.7	35.6	1	-	fine sand	lithoclastic
2018	#12	1	2.5	Summer	48	17.7	35.7	1	-	fine sand	lithoclastic
2019	#01	0	7.5	Winter	34	22.6	36	0	6.93	very fine sand	lithoclastic
2019	#02	0	5	Winter	32	21.4	36	0	12.18	very fine sand	lithoclastic
2019	#03	0	7.5	Winter	34	22.9	36	0	4.68	very fine sand	lithoclastic
2019	#04	0	10	Winter	38	21.6	37	0	4.74	very fine sand	lithoclastic

2019	#05	0	5	Winter	43	22.5	36	0	13.59	very fine sand	lithoclastic
2019	#06	0	5	Winter	37	23	35.5	0	9.27	very fine sand	lithoclastic
2019	#07	1	5	Winter	41	22.8	38	0	70.49	coarse sand	bioclastic
2019	#08	1	7.5	Winter	34	21	35	0	4.66	fine sand	lithoclastic
2019	#09	1	5	Winter	45	22.8	37	0	23.18	fine sand	litho-bioclastic
2019	#10	1	2.5	Winter	46	21.2	37	0	79.18	very coarse sand	bioclastic
2019	#11	1	5	Winter	50	20.6	37	0	18.10	fine sand	lithoclastic
2019	#12	1	2.5	Winter	45	20.5	35	0	19.19	fine sand	lithoclastic

Sampled and published data are presented. Notations, units and sources: Oceanographic expeditions (OEs), oceanographic stations (OSs), exposition to the open sea (Exp), distance from the main island in km (Buff), year seasons (Seas), depth in m (Dep), temperature in ºC (Temp), salinity (Sal), presence/absence of the water mass South Atlantic Central Water (SACW), concentrations of $CaCO_3$ ($CaCO_3$%) - 2011 OSs taken from Hoff et al., 2015, sediment type according to Folk and Ward, 1957 - 2011 OSs taken from Palóczy et al., 2012 and sediment classes ($CaCO_3$ classes) according to Larsonneur et al., 1982. For 2014 and 2015 sediment types and $CaCO_3$ classes, information of the nearest OSs was applied and results of 2018/2019 OEs were shared since the same sample grid was re

Table B-4 Summary of required parameters to fishery indicators estimative by the mean length and LBSPR methods for *Zapteryx brevirostris*.

Parameters/ Indicators	Values	Definition	Use	Source
L_∞	60.37 (1.52)	Asymptotic length estimated through the von Bertalanffy growth curve	Used to estimate M, Z, SPR and $F/M_{(LBSPR)}$, and to assess the necessary time for the mean length recovery	Taken from Caltabellotta et al. (2019)
K	0.24 (0.01)	Growth rate estimated through the von Bertalanffy growth curve	Used to estimate M, Z, SPR and $F/M_{(LBSPR)}$, and to assess the necessary time for the mean length recovery	Taken from Caltabellotta et al. (2019)
t_{max}	9	Maximum observed age	Used to estimate M and to assess the necessary time for the mean length recovery	Taken from Caltabellotta et al. (2019)
t_0	-1.42 (0.07)	Intercept term of the von Bertalanffy growth curve	Used to assess the necessary time for the mean length recovery	Taken from Caltabellotta et al. (2019)
L_c	44	Minimum fully exploited length	Used to estimate Z and to assess the necessary time for the mean length recovery	Estimated by the function of Babcock et al. (2013) to find the mode of length frequency data
L_m	41.46 (2.12)	Median length at first reproduction	Used to estimate Z, SPR and $F/M_{(LBSPR)}$	Taken from Martins, (2007)
$\bar{L}$	before = 46.38 after= 48.49	Mean length above L_c	Used to estimate Z	Mean value of fish lengths higher than L_c
Z	before = 1.41 after = 0.64	Total mortality	Used to estimate $F/M_{(ML)}$	Estimated through equation of Beverton and Holt (1957)

M	0.65 (0.08)	Natural mortality rate	Used to estimate fishing mortality (*ML* and *LBSPR*) and SPR, and to assess the necessary time for the mean length recovery	Estimated through equations of Jensen (1996) and Then et al. (2015)
F	before = 0.78 (0.28; 1.38) after = 0.05 (0; 0.25)	Fishing mortality rate	Used do estimate $F/M_{(ML)}$	Difference between simulated values of Z and M
SL_{50}	before = 51.39 after = 52.89	Length at 50% selection in logistic selectivity curve	Used to estimate SPR and $F/M_{(LBSPR)}$, and to assess the necessary time for the mean length recovery	Estimated using length data through LBSPR models Hordyk et al. (2015)
SL_{95}	before = 61.72; after = 63.44	Length at 95% selection in logistic selectivity curve	Used to estimate SPR and $F/M_{(LBSPR)}$, and to assess the necessary time for the mean length recovery	Estimated using length data through LBSPR models Hordyk et al. (2015)
$F/M_{(ML)}$	before = 1.25 (0.38; 2.50) after = 0.08 (0; 0.49)	Fishing over mortality ratio	Fishery indicator of overfishing whether >1	Estimated through the mean method
$F/M_{(LBSPR)}$	before = 4 after = 3.63 (1.39; 4)	Fishery indicator of overfishing	Fishery indicator of overfishing whether >1	Estimated using length data through LBSPR models Hordyk et al. (2015)
SPR	before = 0.37 (0.15; 0.65) after = 0.67 (0.40; 0.88)	Spawning potentital ratio	Fishery indicator of overfished status whether <0.4	Estimated using length data through LBSPR models Hordyk et al. (2015)

Estimated and published values with standard errors or 95% confidence intervals are presented. L_m of the population was estimated as the mean L_{50} between sexes and ranges were set as the smallest mature specimen and L_{100}, respectively. We used L_m instead of L_{50} on estimates of $F/M_{(LBSPR)}$ and SPR. F/M estimates above 4 were truncated. For more information about simulation procedures see Babcock et al. (2013, 2018).

Table B-5 Summary of demersal elasmobranch species caught in Marine Protected Areas of the Alcatrazes Archipelago and their potential use of the MPAs' habitat.

Species	**Family**	**MPAs use**	**Number of specimens**						**TL or DW (cm)**			
			T	**%**	**F**	**M**	**A**	**J**	**Min**	**Max**	**Mean**	**SD**
Atlantoraja castelnaui (Ribeiro, 1907)	Arhynchobatidae	Nursery/Mating	38	6.8	27	9	3	34	17	106	59.2	28.5
Atlantoraja cyclophora (Regan, 1903)	Arhynchobatidae	Nursery/Mating	56	10.0	40	16	12	44	8.5	58	33.7	15.7
Psammobatis extenta (German, 1913)	Arhynchobatidae	Residence	38	6.8	24	13	31	7	6.6	29	24.3	5.3
Psammobatis sp.	Arhynchobatidae	-	2	0.4	2	-	-	2	6	17	11.5	7.8
Rioraja agassizii (Müller & Henle, 1841)	Arhynchobatidae	Residence	82	14.6	49	29	60	21	9	55	40.2	10.8
Dasyatis hypostigma Santos & Carvalho, 2004	Dasyatidae	Mating/SFG	28	5.0	16	12	14	12	24	53	31.5	7.6
Hypanus americanus (Hildebrand & Shroeder, 1928)	Dasyatidae	Nursery	1	0.2	-	1	-	1	23	23	-	-
Hypanus guttatus (Bloch & Scneider, 1801)	Dasyatidae	Nursery	3	0.5	1	2	-	3	28	50	40.0	11.1
Myliobatis freminvillei Lesueur, 1824	Myliobatidae	Mating/SFG	5	0.9	1	4	3	2	57.2	61	59.4	2.0
Rhinoptera bonasus (Mitchill, 1815)	Rhinopteridae	SFG	1	0.2	1	-	1	-	75	75	-	-
Rhinoptera brasiliensis Müller, 1863	Rhinopteridae	SFG	2	0.4	1	1	2	-	73	85	79.0	8.5
Pseudobatos horkelii Müller & Henle, 1841	Rhinobatidae	SFG	12	2.1	10	2	5	7	34.4	100	74.5	17.2
Pseudobatos percellens (Walbaum, 1792)	Rhinobatidae	SFG	6	1.1	2	4	3	3	46	88	68.4	18.1
Pseudobatos sp.	Rhinobatidae	-	1	0.2	1	-	-	-	62	62	-	-

Zapteryx brevirostris (Müller & Henle, 1841)	Trygonorrhinidae	Residence	257	45.7	137	120	189	68	17	59.8	44.1	7.4
Squalus albicaudus Viana, Carvalho & Gomes, 2016	Squalidae	Nursery	2	0.4	-	2	-	2	23.6	29.4	26.5	4.1
Squalus sp.	Squalidae	-	10	1.8	2	2	1	5	31	50	39.6	6.4
Squatina guggenheim Marini, 1936	Squatinidae	Nursery	3	0.7	3	1	-	4	33	62	51.7	13.2
Squatina occulta Vooren & Silva, 1991	Squatinidae	Nursery	13	2.3	10	2	-	13	42	93	71.6	13.8
Squatina sp.	Squatinidae	-	2	0.4	-	2	-	2	26	39	32.5	9.2
Total			562		327	222	320	234				

Notations: seasonal feeding ground (SFG); total number of specimens recorded (T), relative abundance (%), number of females (F), males (M), adults (A) and juveniles (J), minimum (Min) and maximum (Max) of total length or disc width and respective standard deviations (SD). MPAs use was proposed according to our results of size structure, evidence of reproductive availability and patterns found in the literature.

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8 APPENDIX C – Supplementary Material Chapter Four

Models' code

The code bellow is written for R program and uses R2jags package to run BUGS (Bayesian analysis Using Gibbs Sampling).

```
# The detection/non-detection data is defined in two lists, one for each model structure
# For the simplest structure, the list is composed by the number of strata were each
# species occurred (y), the number of observed (nind) and unseen (nz) species, as
# part of the data augmentation to account for additional species, and the number of
# strata (J)

# For more complex structure, the list is composed by a frequency of occurrence matrix
# of each species by stratum (y), the number of observed (nind) and unseen (nz) species,
# the number of strata (J) and the number of replicates on each stratum (K)

# The fixed effect of the species habit (benthic) is a binary variable with 0 for the benthic
# and 1 for the benthopelagic species

# Load the library

        library(R2jags)

# Load the data for each model

        Data.m1=list(y= c(9, 2, 4, 8, 11, 6, 2, 15, 10, 15, 13, 13, 12, 2, 7, 1, 3, 3, 2 ,4, 1, 1,
                rep(0, 100)), nind=22, nz=100, J=18)

        Data.m2=list(y= c(9, 2, 4, 8, 11, 6, 2, 15, 10, 15, 13, 13, 12, 2, 7, 1, 3, 3, 2 ,4, 1, 1,
                rep(0, 100)), nind=22, nz=100, J=18,
        benthic= c(spec_freq$habit_var, rep(NA, 100))-1))

        Data.m3=list(y= as.matrix(spec_freq[,2:19],122,18),
                nind=22, nz=100, J=18,
                K=c(13, 12, 11, 12, 18, 18, 3, 16, 12,  9, 20, 11, 21, 24, 17, 7, 10, 5))

        Data.m4=list(y=as.matrix(spec_freq[,2:19],122,18),
                nind=22, nz=100, J=18,
                K=c(13, 12, 11, 12, 18, 18, 3, 16, 12,  9, 20, 11, 21, 24, 17, 7, 10, 5),
                benthic=c(spec_freq$habit_var, rep(NA, 100))-1))
```

```
# Set initial values

            init1=list(list(mu=0, tau=1, psi=0.8, z=z), list(mu=1, tau=2, psi=0.5, z=z))

            init2=list(list(mu=rnorm(2),tau=1, psi=0.8, kappa=0.5, z=z),
                        list(mu=rnorm(2),tau=0.6, psi=0.5, kappa=0.2,z=z))

            init3=list(list(mu.alpha = 0, tau.alpha = 1, mu.beta = 0, tau.beta = 1,
                        omega = 0.8, z=z.comp,w=w),
                        list(mu.alpha = 0.1, tau.alpha = 0.2, mu.beta = 0.1, tau.beta = 0.2,
                        omega = 0.5, z=z.comp,w=w))

            init4=list(list(mu.alpha = 0, tau.alpha = 1, mu.beta = rnorm(2), tau.beta = 1,
                        omega = 0.8,kappa=0.5, z=z.comp,w=w),
                        list(mu.alpha = 1, tau.alpha = 0.5, mu.beta = rnorm(2), tau.beta = 0.5,
                        omega = 0.5,kappa=0.5,z=z.comp,w=w))

## Write the models code to a text file
 # Model 1

            write("   model {
                        # set uninformative priors
                                    psi~dunif(0,1)
                                    mu~dnorm(0,0.001)
                                    tau~dgamma(.001,.001)

                        for(i in 1: (nind + nz)){# loop over species
                                    z[i] ~ dbern(psi)
                                    eta[i]~ dnorm(mu, tau)
                                    logit(p[i])<- eta[i]
                                    muy[i]<-p[i] * z[i]
                                    y[i] ~ dbin(muy[i], J)
                        }
                                    # Derived parameters
                                    N<-sum(z[1 : (nind + nz)])
                                    sigma<-sqrt(1  / tau)
                        }", file="m1.txt")

 # Model 2

            write("   model {
                        # set uninformative priors
                                    psi~dunif(0,1) #prior-probability of occurence
                                    kappa ~ dunif(0,1) #prior-effect of unseen species habit
```

```
            # prior for species effect hyperparameters
            for(i in 1:2){
            mu[i]~dnorm(0,0.001)
            }
            tau~dgamma(.001,.001)

        for(i in 1: (nind + nz)){ #loop over species
            #likelihood of the binomial state of habit effect of unseen
            #species
            benthic[i]~dbern(kappa)

            # likelihood of the species true state of occurrence
            z[i] ~ dbern(psi)
            #add 1 to mu be equivalent as its priors
            eta[i]~ dnorm(mu[benthic[i]+1], tau)

            #estimated probability of detection for each species
            logit(p[i])<- eta[i]

            #gets the probability that the species occurred as they exist
            muy[i]<-p[i] * z[i]

            # likelihood for psi (prob. occurrence)
            y[i] ~ dbin(muy[i], J )
        }
            # Derived parameters
            N<-sum(z[1 : (nind + nz)]) # estimated species richness
        }, file="m2.txt")

# Model 3

    write("model{
        # set uninformative priors
            omega ~ dunif(0,1)
            mu.alpha~dnorm(0,0.001)
            tau.alpha~dgamma(.001,.001)
            mu.beta~dnorm(0,0.001)
            tau.beta~dgamma(.001,.001)

        for (i in 1:(nind+nz)) { #loop over sp.
            #likelihood for whether the unseen species exists
            w[i] ~ dbern(omega)

            #prior of the species effect for the probability of occurrence
            alpha[i]~dnorm(mu.alpha,tau.alpha)
```

```
                #prior of the species effect for the detection probability
                beta[i]~dnorm(mu.beta,tau.beta)

        for (j in 1:J) { #loop over quadrats for occurrence
                logit(psi[i,j])<-alpha[i] # prob. Occurrence

                #actual prop. occurrence (given presence)
                mu.psi[i,j] <- psi[i,j]*w[i]
                z[i,j] ~ dbern(mu.psi[i,j]) # likelihood for the actual presence
                logit(theta[i,j])<-beta[i] # prob. detection

                # actual prob. detection (given presence)
                mu.theta[i,j] <- theta[i,j]*z[i,j]
                y[i,j] ~ dbin(mu.theta[i,j],K[j]) # likelihood

        }}

        # loop to estimate richness by strata and by north and central areas

        for(j in 1:J) { Nquad[j]<-sum(z[,j]) }
        for(i in 1:(nz+nind)) {

        #numericall trick to get species by areas 1 if species is found in any
        #quadrats in N vs. C, 0 otherwise
                found.N[i]<-step(sum(z[i,1:9])-0.000001)
                found.C[i]<-step(sum(z[i,10:18])-0.000001)
        }
                N<-sum(w[])
                N.north<-sum(found.N[])
                N.central<-sum(found.C[])
}", file="m3.txt")

#Model 4

write("model{
        # set uninformative priors
                omega ~ dunif(0,1)
                mu.alpha~dnorm(0,0.001)
                tau.alpha~dgamma(.001,.001)
                kappa ~ dunif(0,1) #prior-effect of unseen species habit
                tau.beta~dgamma(.001,.001)

        # prior species effect hyperparameters
        for(i in 1:2){
```

```
		mu.beta[i]~dnorm(0,0.001)
	}

	for (i in 1:(nind+nz)) { #loop over sp.
		#likelihood for whether the unseen species exists
		w[i] ~ dbern(omega)

		#prior of the species effect for the probability of occurrence
		alpha[i]~dnorm(mu.alpha,tau.alpha)

		#prior of the species effect for the detection probability
		beta[i]~dnorm(mu.beta[benthic[i]+1],tau.beta)

		#likelihood of the binomial state of habit effect of unseen
		#species
		benthic[i]~dbern(kappa)

	for (j in 1:J) { #loop over quadrats for occurrence
		logit(psi[i,j])<-alpha[i] # prob. Occurrence

		#actual prop. occurrence (given presence)
		mu.psi[i,j] <- psi[i,j]*w[i]
		z[i,j] ~ dbern(mu.psi[i,j]) # likelihood for the actual presence
		logit(theta[i,j])<-beta[i] # prob. detection

		# actual prob. detection (given presence)
		mu.theta[i,j] <- theta[i,j]*z[i,j]
		y[i,j] ~ dbin(mu.theta[i,j],K[j]) # likelihood

	}}

	# loop to estimate richness by strata and by north and central areas

	for(j in 1:J) { Nquad[j]<-sum(z[,j]) }
	for(i in 1:(nz+nind)) {

	#numericall trick to get species by areas 1 if species is found in any
	#quadrats in N vs. C, 0 otherwise
		found.N[i]<-step(sum(z[i,1:9])-0.000001)
		found.C[i]<-step(sum(z[i,10:18])-0.000001)
	}
		N<-sum(w[])
		N.north<-sum(found.N[])
		N.central<-sum(found.C[])
}", file="m4.txt")
```

```
# Run each model

        m1 = jags(Data.m1,init1, parameters.to.save=c("mu","tau","psi","eta","N"),
                    n.chains = 2,n.burnin = 10000,n.iter = 210000,n.thin=20,
                    model.file = "m1.txt")

        m2 = jags(Data.m2,init2,parameters.to.save=c("psi","mu","eta","N", "tau"),
              n.chains = 2,n.burnin = 10000,n.iter = 150000,n.thin=5,
              model.file = "m2.txt")

        m3 = jags(Data.m3,init3,
        parameters.to.save= c("alpha","beta","N", "Nquad","N.north","N.south")
              n.chains = 2, n.burnin = 10000,n.iter = 1600000,n.thin=50,
              model.file = "m3.txt")

        m4 = jags(Data.m4,init4,
        parameters.to.save= c("alpha","beta","N", "Nquad","N.north","N.south")
              n.chains = 2, n.burnin = 10000,n.iter = 900000,n.thin=50,
              model.file = "m4.txt")

# get the output to see the estimated parameters and evaluate convergence

        round(m1$BUGSoutput$summary,2)
        round(m2$BUGSoutput$summary,2)
        round(m3$BUGSoutput$summary,2)
        round(m5$BUGSoutput$summary,2)
```