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**Dinâmica Populacional das raias-violas, *Rhinobatos horkelli*,  
*Rhinobatos percellens* e *Zapteryx brevirostris* (Chondrichthyes,  
Rhinobatidae) da Plataforma Continental de São Paulo**

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Palavras-chave: Análise demográfica; Dinâmica Populacional; Raias-viola; Rhinobatidae.

## SUMÁRIO

<b>CONSIDERAÇÕES INICIAIS .....</b>	<b>1</b>
<b>REFERÊNCIAS.....</b>	<b>9</b>
<b>CAPÍTULO.....</b>	<b>19</b>
<b>ABSTRACT.....</b>	<b>20</b>
<b>RESUMO.....</b>	<b>22</b>
<b>1.INTRODUCTION.....</b>	<b>24</b>
<b>2.MATERIAL AND METHODS.....</b>	<b>27</b>
<b>3.RESULTS.....</b>	<b>42</b>
<b>4.DISCUSSION.....</b>	<b>68</b>
<b>5.REFERENCES.....</b>	<b>76</b>

## CONSIDERAÇÕES INICIAIS

As raias-viola, família Rhinobatidae (Chondrichthyes: Rhinobatiformes), apresentam uma distribuição circumglobal, ocorrendo em águas costeiras de regiões tropicais e temperadas (Bigelow & Schroeder, 1953; McEachran & Aschliman, 2004). A família está representada por quatro gêneros: *Aptychotrema*, *Trygonorhina*, *Rhinobatos* e *Zapteryx*. Dentre estes, somente *Rhinobatos* e *Zapteryx* se distribuem ao longo da plataforma continental do Atlântico Sul (Compagno, 1999; Compagno, 2005).

No Brasil a família está representada pelos gêneros *Rhinobatos* e *Zapteryx* e, pelo menos quatro espécies, a saber: *Zapteryx brevirostris* (Müller & Henle, 1841), *Rhinobatos lentiginosus* Garman, 1880, *R. horkelii* Müller & Henle, 1841 e *R. percellens* Walbaum, 1792 (Figueiredo, 1977; Menni & Stehmann, 2000; Vooren *et al.*, 2005). O gênero *Rhinobatos* difere-se de *Zapteryx* basicamente pelo focinho mais longo, com angulação menor do que 90° e pela presença de duas cristas dérmicas projetadas da margem posterior do espiráculo (Bigelow & Schroeder, 1953).

Na costa do Brasil, especificamente na região sudeste-sul, os gêneros *Rhinobatos* e *Zapteryx* são representados por três espécies, *Rhinobatos horkelii*, *Rhinobatos percellens* e *Zapteryx brevirostris* (Menni & Stehmann, 2000). São espécies de hábitos demersais, sendo encontradas usualmente em fundos arenosos ou lamosos da plataforma continental, alimentando-se principalmente de pequenos peixes, crustáceos e pequenos invertebrados (Bigelow & Schroeder, 1953; McEachran & de Carvalho, 2002).

Apresentam como estratégia reprodutiva à viviparidade lecitotrófica (Hamlett *et al.*, 1998).

*Rhinobatos horkelii* (Fig. 01), ocorre desde o Rio de Janeiro até a Argentina (Figueiredo, 1977; McEachran & Carvalho, 2002) e os dados disponíveis sobre a biologia e dinâmica populacional são restritos à plataforma continental do Rio Grande do Sul, onde a espécie foi amplamente estudada na plataforma continental do Rio Grande do Sul (Lessa, 1982; Lessa *et al.*, 1986), e dados residuais da costa norte de São Paulo Ponz-Louro (1995).



Fig 01. Exemplar de *Rhinobatos horkelii* amostrado pelo Projeto Viola (Foto: Camila Mayumi).

De acordo com Vooren *et al.* (2005), *R. horkelii*, classificada pela IUCN como “criticamente em perigo” (IUCN, 2009), é o elasmobrânquio de status populacional mais ameaçado, com abundância atual reduzida à cerca de 16% da original. Ela foi intensamente explorada pela frota pesqueira

industrial da região Sul do Brasil, com perfil de captura marcado por um pico em 1984 (quase 2000 toneladas), seguido de um declínio acentuado nos anos seguintes (entre 200-300 toneladas/ano). Entre 1975 e 1986 estima-se que foram capturados cerca de 2,6 milhões de indivíduos adultos naquela área; com média de 100.000 fêmeas grávidas por ano e considerando-se a média de seis embriões nascidos a cada gestação, calcula-se que foram mortos 6,6 milhões de neonatos em 11 anos (Vooren *et al.*, 2005).

*Rhinobatos percellens* (Fig. 02), distribui-se sobre a plataforma continental do Atlântico ocidental, desde o Panamá até possivelmente o Sul do Brasil (Figueiredo, 1977; McEachran & Carvalho, 2002).



Fig. 02. Exemplo de *Rhinobatos percellens* amostrado pelo Projeto Viola (Foto: Camila Mayumi)

Os dados prévios na literatura indicam que cresce até cerca de 100 cm de comprimento total, vive normalmente sobre substratos não consolidados,

até cerca de 110 m de profundidade, onde se alimenta preferencialmente de invertebrados bentônicos, sobretudo pequenos crustáceos (Bigelow & Schroeder, 1953; Figueiredo, 1977; Menni & Stehmann, 2000; McEachran & Carvalho, 2002). Cervigón & Alcalá (1999), na Venezuela, Shibuya *et al.* (2005), na costa da Paraíba e Durigon (2008), no litoral de São Paulo, estudaram a alimentação de *R. percellens* e, de uma forma geral, verificaram que a dieta é predominantemente composta por crustáceos da família Caridae.

*Zapteryx brevirostris* (Fig. 03), ocorre na plataforma continental do Atlântico Sul ocidental, desde o Rio de Janeiro até a Argentina (Figueiredo, 1977; McEachran & Carvalho, 2002) e foi estudada sob diversos aspectos: reprodução por Ponz-Louro (1995) e Martins (2005), ambos os estudos em Ubatuba, litoral norte de São Paulo; a alimentação foi analisada por Pasquino & Gadig (2004) e Marion (2009), também na costa de São Paulo; a estrutura populacional por Santos *et al.* (2006), Martins (2005) e Pasquino (2006), no Paraná e as duas últimas em São Paulo, respectivamente.

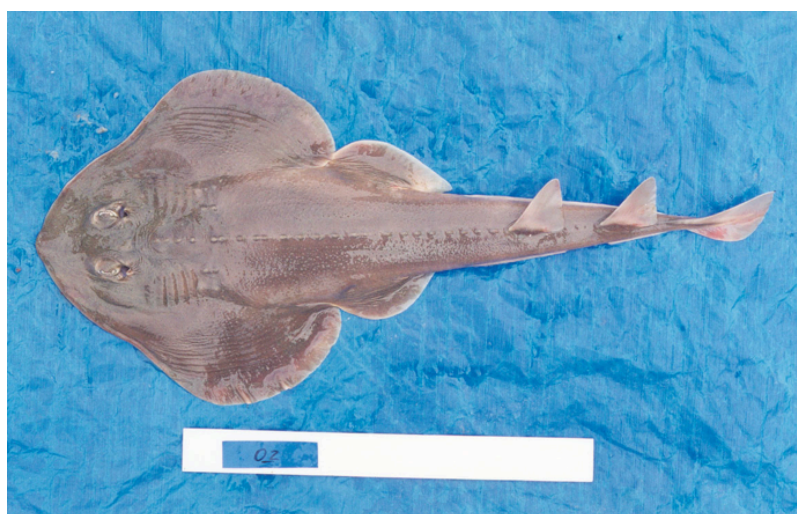


Fig. 03 Exemplar de *Zapteryx brevirostris* amostrado no Projeto Cação (Foto: Fabio dos Santos Motta).

Embora, de uma maneira geral, os Rhinobatidae não constituam o alvo principal da pesca industrial e artesanal, elas são capturadas freqüentemente como fauna acompanhante nas pescarias realizadas pelas frotas de arrasto (simples, duplo e parelhas) (Mazzoleni & Schwingel, 1999; Martins & Schwingel, 2003) e redes de emalhe (Costa & Chaves, 2006), na costa da região sudeste e sul do Brasil.

As raias, seguindo o padrão biológico dos elasmobrânquios, encontram-se entre as espécies menos produtivas sob o ponto de vista pesqueiro, devido às características de seu ciclo de vida que incluem, baixa fecundidade, maturidade tardia e crescimento lento (Walker, 1998). Estas características biológicas refletem em baixas taxas de reprodução e baixas taxas no potencial de crescimento populacional, o que torna as populações mais suscetíveis a sobrepesca (Holden, 1973; Hoing & Gruber, 1990; Sminkey e Musick 1995; Walker & Hislop, 1998; Smith *et al.*, 1998).

Alguns trabalhos têm se concentrado em determinar a vulnerabilidade de algumas espécies de elasmobrânquios (tubarões e raias) através de características de sua história de vida, *i.e.* mortalidade natural, tamanho corporal, idade de primeira maturação sexual, fecundidade e taxa intrínseca de crescimento populacional (Stevens *et al.*, 2000). O aumento da pressão pesqueira em algumas espécies (Hoff & Musick, 1990), principalmente devido a uma crescente procura das nadadeiras de tubarão (Bonfil, 1994), levou ao aparecimento de modelos de população para avaliar o estado destas populações.

Nas duas últimas décadas, a utilização dos modelos de análise demográfica para os elasmobrânquios vem contribuindo de maneira significativa para caracterizar sua vulnerabilidade à exploração (Cortés, 2004, 2007). O principal parâmetro estimado através da análise demográfica é a taxa intrínseca do crescimento populacional ( $r$ ) que avalia o potencial de crescimento da população (Simpfendorfer, 2004). Entre as técnicas utilizadas para analisar essa taxa está o método proposto por Lotka (1907 *apud* Krebs, 1989), baseado na construção de tabelas de vida, a partir da combinação de dados de reprodução e mortalidade (Cortés, 2004).

Um dos aspectos mais importantes da modelagem demográfica é a capacidade de analisar como as populações possam responder aos diversos níveis de mortalidade por pesca (Au & Smith, 1997; Cortés, 1998; Smith, 1998; Simpfendorfer, 1999). Mudanças nos valores deste parâmetro permitem estimar as conseqüências na população sob diferentes cenários teóricos (Beerkircher, 2003), resultando em taxas de crescimento populacional que indicam se a população está crescendo ( $r > 0$ ), em equilíbrio ( $r = 0$ ) ou em declínio ( $r < 0$ ).

Entre alguns dos estudos pioneiros realizados utilizando a análise demográfica destacam-se: Cailliet *et al.* (1992) com *Triakis semifasciata*, na Califórnia; Cortés (1995) com *Rhizoprionodon terraenovae*, também na Califórnia; Cortés & Parsons (1996) e Márquez-Fariáz *et al.* (1998) com *Sphyrna tiburo*, no Golfo do México; Sminkey & Musick, (1996) com *Carcharhinus plumbeus*, na costa oeste do atlântico norte. No Brasil os únicos estudos realizados até o presente foram os de Montealegre-Quijano &

Vooren (2009) com *Prionace glauca* no sul do Brasil e Santana *et al.* (2009) com *Carcharhinus signatus* na costa nordeste do Brasil.

Em um contexto global, devido à pesca predatória, um grande número de espécies foi incluído na lista vermelha das espécies ameaçadas da “International Union for Conservation of Nature and Natural Resources - IUCN” (Camhi *et al.*, 1998). A avaliação realizada em 2008 verificou que 126 espécies de elasmobrânquios estavam incluídas nessa lista como criticamente ameaçadas (CA), ameaçadas (A) ou vulneráveis (V) (IUCN, 2008).

Dentre essas espécies, encontram-se as raias-viola *Rhinobatos horkelli*, *Rhinobatos percellens* e *Zapteryx brevirostris*. De acordo Lessa & Vooren (2007) a população de *R. horkelli* apresenta tendência ao declínio, embora esforços e medidas para sua proteção tenham sido recomendados por Vooren & Klippel (2005). Situação semelhante de tendência ao declínio populacional é observada também para *Z. brevirostris* de acordo com Vooren *et al.* (2006). Uma condição mais delicada é observada para *R. percellens* que devido a falta de dados referentes a captura e a estrutura populacional, impossibilitam uma avaliação sobre a tendência populacional dessa espécie (Casper & Burgess, 2004).

De acordo com o relatório de Avaliação e Ações Prioritárias para a Conservação da Biodiversidade das Zonas Costeira e Marinha do Ministério do Meio Ambiente, ainda é limitado o conhecimento em relação à biodiversidade de elasmobrânquios. Com poucos estudos sobre a dinâmica populacional e avaliação destes estoques na costa brasileira há, portanto a necessidade de pesquisas que visem o conhecimento dos parâmetros básicos da dinâmica populacional das espécies (Lessa *et al.*, 1999).

A estimativa dos parâmetros de idade e crescimento é parte importante no estudo da biologia, e fundamental para o cálculo das taxas de crescimento, mortalidade e produtividade, pois estimativas de crescimento erradas podem levar a situação de sobreexploração dos recursos pesqueiros (Sparre & Venema, 1997; Campana, 2001). Assim, estudos sobre a idade, o crescimento, a estrutura e a capacidade de crescimento populacional são importantes para implementação de programas de manejo pesqueiro e na conservação das espécies, pois se tornam subsídio para o estabelecimento de medidas reguladoras sobre as pescarias.

Portanto, considerando o estado atual de muitas pescarias, a grande diversidade de espécies capturadas e a falta generalizada de recursos para avaliar adequadamente muitos dos estoques tornam-se importante a utilização de ferramentas como as análises, demográfica e de sustentabilidade, capazes de identificar quais as populações já se encontram em perigo ou sobre-exploradas, assim como, auxiliam na elaboração de planos de recuperação mais adequados.

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**Age, Growth and Demographic Analysis of the Guitarfishes,  
*Rhinobatos horkelli*, *Rhinobatos percellens* and *Zapteryx  
brevirostris* in the continental shelf of Sao Paulo**

## ABSTRACT

Guitarfishes (Elamobranchii, Rhinobatiformes) are usually components of the multispecific fishery as by-catch of double-rig, pair and single bottom trawls in the southeast and south of Brazil (Martins & Schwingel, 2003). Considering the lack of life history parameters on the age and population structure studies of these species there is therefore a need for research to enable a proper assessment of the condition of these stocks. We evaluated the structure and the capacity of population growth in the State of São Paulo continental shelf, using the estimated growth and demographic parameters. Were available for this study, 149 samples of *Rhinobatos horkelli*, 752 samples of *Rhinobatos percellens* and 952 samples of *Zapteryx brevirostris*. A sub-sample were used for the age and growth study. The best model that describes the growth of the species was the three parameters von Bertalanffy growth function. Estimated parameters were :  $L_{\infty}=121.71$  ,  $k =0.21$ , and  $t_0 = -1.34$  for *Rhinobatos horkelli* (grouped sex),  $L_{\infty} = 106.99$  ,  $k = 0.17$  and  $t_0 = -1.51$  for *Rhinobatos percellens* (female) ,  $L_{\infty} = 90.69$  ,  $k = 0.24$  and  $t_0 = -1.36$  for *Rhinobatos percellens* (male),  $L_{\infty} = 60.73$  ,  $k = 0.23$  and  $t_0 = - 1.44$  to *Zapteryx brevirostris* (female) and  $L_{\infty} = 57.88$  ,  $k = 0.26$  and  $t_0 = -1.29$  for *Zapteryx brevirostris* (male). Centrum edge analysis and marginal increment suggests the formation of one band-pair (opaque and translucent) per year. The formation of the translucent band should occur from late winter to the end of the spring. Five scenarios were evaluated for estimated the intrinsic rate of population growth. According to the results obtained under natural mortality conditions and in the absence of fishing, population trends of *Rhinobatos horkelli* showed a increase about 9%

per year, *Rhinobatos percellens* about 10% per year and *Zapteryx brevirostris* 3.9% per year. When were considered scenarios with the presence of fishing, all species exhibit a trend of population decline up to 25% per year. Based on these results we suggested a review of the population status, with the major aim of implementing management measures, to protect these species.

## RESUMO

As raias-viola (Elasmobranchii: Rhinobatiformes) são geralmente componentes da captura acessória da pesca multiespecífica de arrasto na região sudeste e sul do Brasil. Considerando a falta de estudos específicos sobre a estrutura etária e populacional dessas espécies há, portanto uma necessidade de pesquisas que possibilitem uma avaliação adequada da condição desses estoques. O presente avaliou a estrutura e a capacidade de crescimento populacional, dessas espécies na plataforma continental do Estado de São Paulo, utilizando para isso o estudo de idade e crescimento e a análise demográfica. Estavam disponíveis para o estudo 149 exemplares de *Rhinobatos horkelli*, 752 exemplares de *Rhinobatos percellens* e 952 exemplares de *Zapteryx brevirostris*. Desse total foi utilizada uma sub-amostra para realização do estudo de idade e crescimento. O melhor modelo que descreveu o crescimento das espécies foi a função do crescimento de três parâmetros von Bertalanffy, sendo que os parâmetros estimados foram:  $L_{\infty}=121.71$ ,  $k=0.21$  e  $t_0=-1.34$  para *Rhinobatos horkelli* (sexo agrupado);  $L_{\infty}=106.99$ ,  $k=0.17$  e  $t_0=-1.51$  para *Rhinobatos percellens* (fêmea);  $L_{\infty}=90.69$ ,  $k=0.24$  e  $t_0=-1.36$  para *Rhinobatos percellens* (macho);  $L_{\infty}=60.73$ ,  $k = 0.23$  e  $t_0 = -1.44$  para *Zapteryx brevirostris* (fêmea) e  $L_{\infty} = 57.88$ ,  $k=0.26$  e  $t_0=-1.29$  para *Zapteryx brevirostris* (macho). Através da análise de borda e do incremento marginal, sugere-se a formação de um par de banda (opaca e translúcida) por ano. A formação da banda translúcida deve ocorrer entre o final do inverno até próximo do final da primavera. Cinco cenários foram avaliados para verificar a taxa intrínseca de crescimento populacional. De acordo com os resultados obtidos sob

condições naturais e com a ausência da pesca a população de *Rhinobatos horkelli* pode aumentar cerca de 9% por ano, *Rhinobatos percellens* cerca de 10% ao ano e *Zapteryx brevirostris* 3.9% ao ano. Em um outro cenário com a presença da pesca, todas as espécies exibem uma tendência de queda populacional de até 25% ao ano. Diante dos resultados obtidos sugere-se a revisão do status populacional visando a implementação de medidas de manejo, com o intuito de proteger as espécies de um provável colapso populacional.

## 1. INTRODUCTION

Guitarfishes (Elamobranchii, Rhinobatiformes) are usually components of the multispecific fishery as by-catch of double-rig, pair and single bottom trawls in the southeast and south of Brazil (Martins & Schwingel, 2003). Despite the recent list that documented the members of Rhinobatidae family as one of the most threatened families of the world's rays (Dulvy *et al.* 2014) detailed biological information are needed to ensure effective management schemes for these species.

Given that guitarfishes possess the same life history characteristics that elasmobranchs in general (e.g. low fecundity, late maturity and slow growth; Walker, 1998) a adequate assessment of these species including growth, mortality rates and projections of population trends are indispensable to the decision makers develop management plans.

Rhinobatidae family contains about 45 benthic species, small- to medium-sized (McEachran & de Carvalho, 2004) occurring in temperate and tropical regions, on the continental shelves and inshore waters (Bigelow & Schroeder, 1953; Compagno, 2005). In the southeastern of Brazil, specifically in the continental shelf of Sao Paulo, the genera *Rhinobatos* and *Zapteryx* are represented by three species, *Rhinobatos horkelli*, *Rhinobatos percellens* and *Zapteryx brevirostris*, ranging from depths 20 to 110 m (Figueiredo, 1977; Menni & Stehmann, 2000). These species has a large geographic distribution, *Rhinobatos horkelli* (Brazilian guitarfish) from Rio de Janeiro to Argentina; *Rhinobatos percellens* (Southern guitarfish) from Panama to southern of Brazil; and *Zapteryx brevirostris* (Shortnose guitarfish) from Rio de Janeiro to Argentina (Figueiredo, 1977; McEachran & Carvalho, 2002).

Age estimates are used to calculate growth and mortality rates, and are fundamental to assess the population status over different scenarios of exploitation. Guitarfishes as many others elasmobranchs, are aged using counts of opaque and translucent growth bands in the vertebral centra (Cailliet & Goldman, 2004; Cailliet *et al.* 2006). Several studies have used different approaches for validation of the seasonality of band deposition; centrum edge analysis (Tanaka & Mizue's, 1979; Yudin & Cailliet, 1990; Carlson *et al.* 1999; Smith *et al.* 2007), and marginal increment analysis (Natanson *et al.* 1995; Conrath *et al.* 2002, Santana & Lessa, 2004).

Although many growth curves are available and used in the ageing studies, the von Bertalanffy growth function (von Bertalanffy, 1938) has been widely used in most of the age and growth studies of elasmobranchs (Cailliet & Goldman, 2004). Recommendations to use a different parameter ( $L_0$ , length at birth) in the von Bertalanffy growth function (Cailliet *et al.* 2006), and advances to incorporate different types of error at the VBGF growth curve are discussed in the literature (Cope & Punt, 2007).

Improvement to estimate the age with more accuracy is a key point to obtain growth parameters more precisely. Age-structured demographic models, requires these estimates to construct life tables. Life tables use the Euler-Lotka equation to make a static projection of population growth based on life history parameters (Simpfendorfer, 2004). In the last decades, the use of demographic models for elasmobranchs has contributed significantly to characterize their vulnerability to exploitation (Cortés, 2004, 2007).

Demographic models have some disadvantages, providing a static picture of the population, and not incorporate some temporal changes (e.g.

somatic growth rates and fertility rates) that can affect recruitment and the natural mortality. However, these models have several advantages because they incorporate the best biological information available of each specie (e.g. age, growth parameters, reproduction and natural mortality) (Cortés, 1998).

Demographic analysis can be used to assess the impact of fishing, to estimate the critical fishing mortality that can affect different ages at the first capture and the change of the intrinsic rate of increase under these scenarios (Chen & Yuan, 2006). These analysis also attempt to provide guidelines as to which portions of the population need more attention and protection (Heppell *et al.* 2000; Cortés, 2002). Although these studies are very important and can provide some insight into the productivity, many factors could complicate the interpretation of the results.

The aim of this study was estimated growth and demographic parameters, of the guitarfishes (*Rhinobatos horkelli*, *Rhinobatos percellens* and *Zapteryx brevirostris*). The specific objectives were 1) determine the growth pattern; 2) determine the periodicity of vertebral band formation, using centrum edge analysis and marginal increment analysis 3) compare growth parameters between the sexes; 4) determine the longevities; 5) determine the mortality rates, and 6) determine the population growth rates through age-structured Life tables.

## 2. MATERIAL AND METHODS

### 2.1 Collection of Samples

The guitarfishes (*Rhinobatos horkelli*, *Rhinobatos percellens* and *Zapteryx brevirostris*) were caught as by-catch from bottom pair trawling of commercial fishery that operating on the continental shelf of Sao Paulo, Brazil. Fishing operation covered the continental shelf from an area to the north of Sao Sebastiao (24°00'S, 45°15'W) to the south of Cananeia (25°10'S, 47°52'W) at depths of 25-50 m (Fig. 04). Samples were collected seasonally from September 2007 to September 2009.

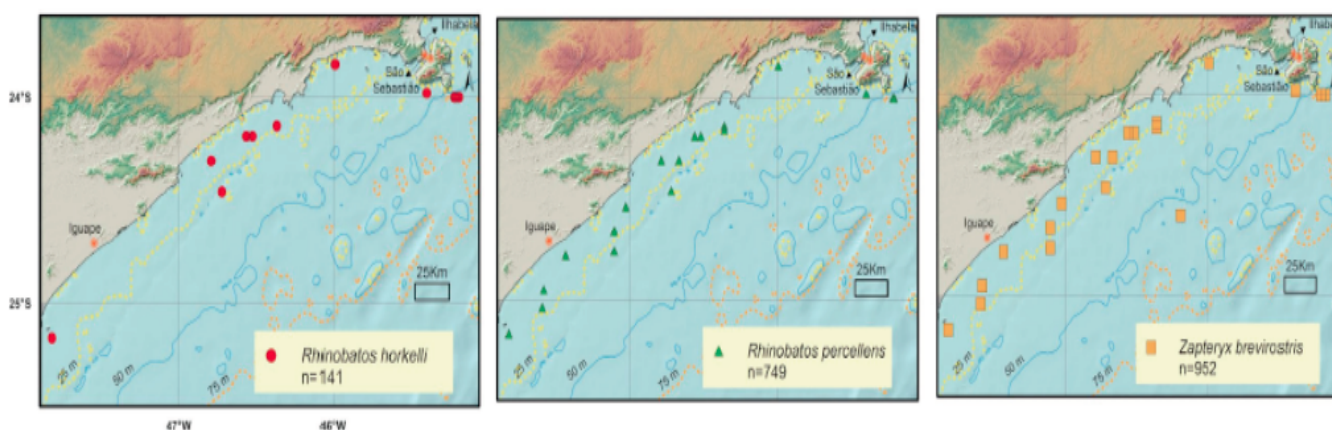


Fig 04. Study Area and capture location of each sample

The bottom pair trawlers used nets that ranged from 40 to 50 m in length and 6 to 8 m in width, with mesh sizes of 150 mm in the body and 100 mm in the codend. For each fishing operation the trawling duration was normally 4.5 h (ranging from 3 to 5 h). Additional specimens of *Zapteryx brevirostris* were used from a previous study conducted at the same area. These specimens were collected during 2002 as part of the BRD Project (*By-catch Reduce Device*) realized by Fisheries Institute of Santos. A sub-sample

of the total catches including all sizes of each specimen were returned whole to Laboratory of Elasmobranch at the University Estadual Paulista “Julio de Mesquita Filho” and stored in a refrigerated container until processing.

## 2.2 Processing of Samples

In laboratory, samples were sexed and total weight (W) was recorded to the nearest 0.1 g. Total length (TL, from the tip of the snout to the tip of the tail, with the tail straightened and aligned to body axis) and the disc width (DW, distance between the wing tips) were measured to the nearest 1.0 mm according to the method of Francis (2006).

A segment of at least 10 vertebrae (post-cephalic) of each individual were removed from the anterior region of the vertebral column, located at the widest point of the body (Fig. 05). Vertebrae from this region are usually largest and provide more accurate age estimation (Officer *et al.* 1996). These vertebral segments were labeled and frozen until the preparation structure process.



Fig 05. *Rhinobatos percellens* #1957 with location of vertebrae removal. Dashed box encompasses the anterior vertebrae area of sampling.

### 2.2.1 Vertebral Structure Preparation

Vertebral samples were defrosted and 5 vertebrae of each specimen were separated into individual centrum, removed the neural and hemal arches and cleaned of excess tissue following standard protocols (Cailliet & Goldman, 2004). One of the 5 centra prepared from each individual was selected for gross sectioning. The other four were labeled and stored frozen as a subsample. For gross sectioning, vertebral centrum were dried and fixed on microscope slides using Crystalbond 509 mounting adhesive (Fig. 06).

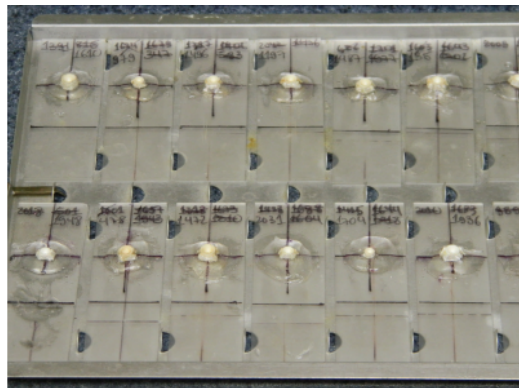


Fig 06. Samples mounted on microscope slides using a Crystalbond 509 mounting adhesive (SPI Supplies, Pennsylvania, USA).

One vertebral centrum of each specimen was sagittally cut using a low speed saw (Buehler™ Isomet, Lake Bluff, IL, USA) with two 4-in diamond blades separated by a spacer. Each centrum was cut along the mid-sagittal axis through the focus resulting in one “bowtie” section of 0.3–0.4 mm thickness. Sectioned centra were stored in vials with 100% ethanol isopropyl. Initial exploration of staining techniques, haematoxylin, crystal violet and silver nitrate were undertaken to enhance band interpretation. However none of these procedures showed a substantial increase in band resolution. Therefore,

vertebrae were read through thin sections without staining. The mean centrum diameter (MCD) was calculated and plotted against TL and age to verify if vertebral growth was in proportion to organism growth. Differences between sexes were assessed based on analysis of covariance (ANCOVA).

### *2.2.2 Age Determination*

Sections were viewed and photographed under a transmitted and reflected light using an AmScope SM-2TZ stereo-zoom dissecting microscope. For thin section, mineral oil was applied before viewing to enhance banding patterns. Photographs were analyzed using Motic Image Plus 2.0® imaging software (Motic China Group Co., Ltd. 1999-2010). The birth mark (age 0) on each vertebral centrum was identifiable as the first distinct band after the focus and is associated with a change of angle on the corpus calcareum (Cailliet & Goldman, 2004).

As has been assumed for some Rhinobatidae species (Lessa, 1982; Timmons & Bray, 1997; Ismen *et al.* 2007; Márquez-Farías, 2007; Basusta *et al.* 2008; Izzo & Gillanders, 2008; Enajjar *et al.* 2012; Nunes, 2012; Wilson *et al.* 2013) each opaque and translucent band pair, thereafter an indirect validation, was interpreted as representing one year of growth (Fig. 07).

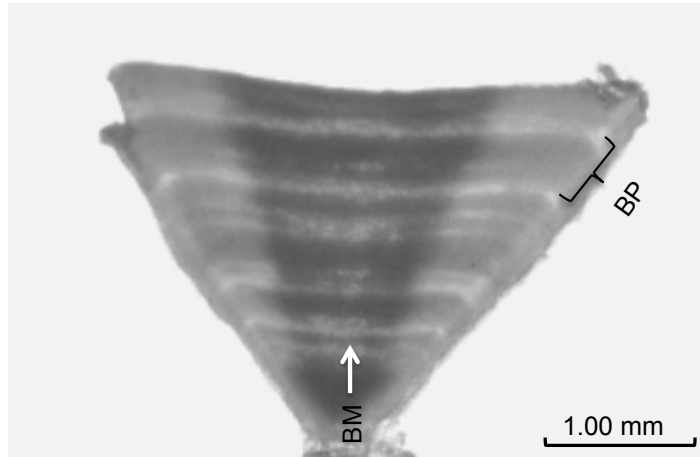


Fig 07. Sagittal thin section of *Rhinobatos percellens* vertebral centrum estimated to be 3 years in age. BM, birth mark; BP, band pair (one opaque band and one translucent band).

Prior to ageing all centra, a subsample comprising the smallest, the intermediaries and largest specimens was read by two readers to ensure that a consensus was reached regarding interpretation of the banding pattern. After established an ageing criteria, one of the readers read all of the centra, without prior knowledge of the size of individual, sex, or previous band counts. The numbers of band pairs was counted two times by the same reader, with counts conducted on different months to ensure independence.

The spacing and clarity of bands and the inflections into the corpus calcareum were used to ensure that true bands, rather than “checks” were being counted. If any of the two readings disagreed by more than 2 years, the sample was recounted and if the agreement was not achieved after a third read, the sample was discarded.

### 2.2.3 Precision and Error Analysis

Precision and error analysis among reads of each vertebral centrum were evaluated for reader consistency and repeatability of age assignment (Campana, 2001). Precision was determined using the following statistical measures: index of average percent error (IAPE; Beamish and Fournier, 1981):

$$IAPE = 100\% * \frac{1}{N} \sum_{j=1}^N \left[ \frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_j} \right]$$

where  $N$  is the total number of samples,  $R$  is the number of reads,  $X_{ij}$  is the  $i^{th}$  age estimate of the  $j^{th}$  individual and  $X_j$  is the mean age estimate for the  $j^{th}$  individual. Lower IAPE value indicates greater precision.

The coefficient of variation (CV; Chang, 1982) that uses the standard deviation rather than absolute deviation of the readings:

$$CV_j = 100\% * \frac{\sqrt{\sum_{i=1}^R \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j}$$

where  $R$  is the number of reads,  $X_{ij}$  is the  $i^{th}$  age estimate of the  $j^{th}$  individual and  $X_j$  is the mean age estimate for the  $j^{th}$  individual. Possible differences between reads were examined using age-bias plot (Campana *et al.* 1995) and contingency tables analyzed by Bowker's test of symmetry were used (Hoenig *et al.* 1995).

#### 2.2.4 Indirect Validation

Periodicity of band pair deposition was assessed using two types of indirect age validation: a qualitative method, centrum edge analysis (CEA) and a quantitative method, the marginal increment ratio (MIR) (Tanaka and Mizue, 1979; Campana, 2001; Cailliet and Goldman, 2004; Cailliet *et al.* 2006; Smith *et al.* 2007). Using CEA the outermost band on the vertebral edge was classified into one of four categories: 1) narrow translucent, 2) broad translucent, 3) narrow opaque, and 4) broad opaque. Band width was determined by comparison with the previous fully formed band pair; a narrow band was classified as their width less than 50% of the previous band pair and a broad band was classified as their width greater than or equal 50% of the previous band pair (Smith *et al.* 2007). The proportion of the edge types was plotted by month to investigate seasonal banding patterns.

The marginal increment ratio (MIR) was calculated according to (Conrath *et al.* 2002):

$$MIR = \frac{MW}{PBW}$$

where *MW* is the margin width of the outermost forming band pair, and *PBW* is the width of the penultimate band pair. Measurements were made on photographs of the thin sections using Motic Image Plus 2.0® imaging software (Motic China Group Co., Ltd. 1999-2010). Age 0 individuals were excluded due to the lack of fully formed band pairs. For MIR analysis, sexes and age classes were pooled. Mean MIR was calculated for each month, and plotted by month versus the edge type to determine the periodicity of band pair

deposition. Differences among months were tested using Kruskal-Wallis test (Smith *et al.* 2007).

### 2.2.5 Growth Modeling

Multiple growth functions were fit to size-at-age estimates for each sex and sexes combined. Only observed size-at-age data were used to construct growth models. Growth modeling was performed for each growth function using the statistical software R (R Development Core Team, 2013). Starting values of each growth model were found using the `vbStarts` ( ) function in the package FSA. Each one of the growth models presented below was performed using the `nls` ( ) function.

The first growth model applied, and the most common used to describe the growth in the age studies of elasmobranchs, was the three parameter von Bertalanffy growth function (3-VBGF):

$$L_t = L_\infty(1 - e^{-k(t-t_0)})$$

where  $L_t$  is the age at length  $t$ ,  $L_\infty$  is the theoretical asymptotic total length,  $k$  is the von Bertalanffy growth coefficient which determines how quickly  $L_\infty$  is attained, and  $t_0$  is the theoretical age at zero length (Ricker, 1979).

The two parameters von Bertalanffy growth function (2-VBGF) incorporates the known size-at-birth and is recommended by presenting a biological meaningful parameter (Cailliet & Goldman, 2004; Cailliet *et al.* 2006):

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt}$$

where  $L_t$  is the age at length  $t$ ,  $L_\infty$  is the theoretical asymptotic total length,  $k$  is the von Bertalanffy growth coefficient, and  $L_0$  is the know length at birth, 29 cm for *Rhinobatos horkelli* (Lessa, 1982; Vooren *et al.* 2005), 20 cm for *Rhinobatos percellens* (Rocha & Gadig, 2012), and 16 cm for *Zapteryx brevirostris* (Ponz-Louro, 1995).

The Gompertz growth function (modified from Ricker, 1979) was the third model applied, and assumes a exponential decrease of the growth rate with size (Cailliet and Goldman, 2004):

$$L_t = L_\infty e\left(-e^{-k(t-t_0)}\right)$$

where  $L_t$  is the age at length  $t$ ,  $L_\infty$  is the theoretical asymptotic total length,  $k$  is the instantaneous growth coefficient when  $t=t_0$ , and  $t_0$  is the time at which the absolute growth rate starts to decrease (i.e. the inflection point in the curve). Finally, a logistic model (modified from Ricker, 1979) was also used:

$$L_t = L_\infty (1 - e^{-k(t-t_0)})^{-1}$$

where  $L_t$  is the age at length  $t$ ,  $L_\infty$  is the theoretical asymptotic total length,  $k$  is the growth coefficient, and  $t_0$  is inflection point of the curve.

Confidence intervals with associated plots and correlation between growth parameters were also performed for each growth model using the statistical method of bootstrap from `nsiBoot` ( ) function. Model performance of growth models were evaluated using Akaike's Information Criteria (AIC). The best model was the one with the lowest AIC value ( $AIC_{min}$ ). The AIC differences were calculated using:  $\Delta_i = AIC - AIC_{min}$  for all growth models. Models with  $\Delta_i < 2$  were considered to have strong support;  $4 < \Delta_i < 7$  have

substantial support; while those with  $\Delta_i > 10$  not have substantial support. The Akaike weight ( $w_i$ ) of each growth model was also calculated to evidence in favor of a model being the best model in the set of candidates (Burnham & Anderson 2002; Katsanevakis, 2006):

$$w_i = \frac{e^{(-0.5\Delta_i)}}{\sum_{i=1}^n e^{(-0.5\Delta_i)}}$$

where  $w_i$  is the Akaike weight and the  $\Delta_i$  is the difference between the AIC and  $AIC_{min}$ . Likelihood ratio test were also applied to determine differences in growth parameters between sexes (Kimura, 1980). Longevity ( $\omega$ ) was also estimated for females and for males separately using two methods. The sizes at which 95% of the  $L_\infty$  is attained were determined as a measure of  $\omega$  following Fabens (1965) and Taylor's (1958):

$$\text{Fabens: } = \frac{5 [\ln(2)]}{k}$$

$$\text{Taylor's: } = t_0 + \frac{\log_e(1-0.95)}{k}$$

where  $k$  is the growth parameter obtained from the results of the three parameters von Bertalanffy growth function.

### 2.3 Life history parameters

Empirical estimation of natural mortality ( $M$ ) not exists for these species, therefore, were used indirect methods for estimating  $M$  and then calculated the survivorship rates. Five mortality estimation methods, which are based on estimates of longevity, age-at-maturity, von Bertalanffy growth function (VBGF) parameters, maximum age, and body weight, were used. Hoenig's (1983) methods derived a equation based on data of teleosts to relating mortality to longevity:

$$\ln(Z) = 1.46 - 1.01\ln(\omega)$$

where  $\omega$  represents the maximum age. For this method based on longevity, the observed ages rather than theoretical maximum ages was used. Pauly (1980) method, uses a estimation based on the asymptotic total length ( $L_\infty$ ) and growth coefficient ( $k$ ) predicted by the VBGF:

$$\log_{10}(M) = -0.006 - 0.279\log_{10}(L_\infty) + 0.6543\log_{10}(k) + 0.4634\log_{10}(T)$$

where  $T$  is the average environmental temperature in Celsius degrees ( $^{\circ}\text{C}$ ) that was fixed at  $24^{\circ}\text{C}$ . Jensen (1996) methods based on Beverton and Holt life history invariants was also used:

$$M = 1.5k \text{ and } M = 1.65/\alpha$$

where  $k$  is the growth coefficient estimated by the VBGF and  $\alpha$  is based upon the median age at maturity. The methods that were described above are age-

independent and they produce identical natural mortality values for all age classes.

The Peterson and Wroblewski (1984) is an age-dependent method based upon ecological theory (Kenchington, 2013) and argues that larger individuals are generally less susceptible to predation. This method uses estimates of total weight ( $W$ ) at age to predict age-specific mortality. We used a conversion factor of 1/5 to obtain the dry weight of the guitarfishes (Cortés, 2002):

$$M = 1.92(0.2W)^{-0.25}$$

Total mortality ( $Z$ ) was estimated using the catch curve from the age frequency distribution, and correspond to the sum of natural mortality ( $M$ ) and fishing mortality ( $F$ ), thus fishing mortality rate ( $F$ ) was obtained from the difference between  $Z$  and  $M$  for each specie. Survivorship rates for each mortality were estimating using the formula described by Ricker (1975):  $S_x = e^{-M}$ , where  $M$  is the total instantaneous rate of mortality of individuals.

Reproductive data used for construction of the life tables were based upon the best information's available in the correlate literature for each species (Table 01). Fecundity ( $m_x$ ) was defined as the mean number of embryos per female per year across all mature ages. Annual fecundities were calculated by the sex ratio at birth and by the reproductive cycle to represent the number of female offspring. For age at first maturity ( $\alpha$ ) were assumed, 5 years for *Rhinobatos horkelli* and 4 years for *Rhinobatos percellens* and *Zapteryx brevirostris*.

Table 01. Summary of life history characteristics used for construct Life tables.

Species	Life History Parameters			References
	Fecundity ( $m_x$ )	Sex ratio (embryos)	Reproductive cycle	
<i>Rhinoabtos horkelli</i>	6	1:1.24	annual	(Lessa, 1982, 1986; Vooren <i>et al.</i> 2005)
<i>Rhinobatos percellens</i>	4.88	1:1	annual	(Rocha & Gadig, 2012)
<i>Zapteryx brevirostris</i>	5	1:1	bienial	(Ponz-Louro, 1995)

## 2.4 Estimation of Demographic parameters

Density-independent, age-structured life tables based on Euler-Lotka equation (Lotka, 1907 *apud* Krebs, 1989) were constructed using the PopTools add-in MS Excel (Hood, 2010). All models were female specific and incorporated the assumption that the intrinsic population growth rates represent a maximum value. Parameters estimated from the life tables were net reproductive rate ( $R_0$ ), generation time ( $G$ ), intrinsic rate of population increase ( $r$ ), finite rate of increase ( $\lambda$ ), and population doubling time ( $t_{x2}$ ) were calculated according to the following equations:

$$R_0 = \sum_{x=1}^w l_x m_x ;$$
$$G = \sum_{x=1}^w l_x m_x x / R_0 ;$$
$$r = \ln(R_0) / G ;$$
$$t_{x2} = \ln(2) / r$$

Using the best parameters obtained that represent the guitarfish population and incorporating the best biological information available was evaluated five possible scenarios. Scenarios were constructed to evaluate the natural mortality ( $M$ ) using the Peterson and Wroblewski (PW) age-dependent method, and the age at first capture with a fixed value of fishing mortality for each specie.

- Scenario A: M age-dependent, constant fecundity and without fishing;
- Scenario B: M age-dependent, constant fecundity and fishing based on the age of the first capture (from catch curve);
- Scenario C: M age-dependent, constant fecundity and fishing after the age at first maturity;
- Scenario D: M age-dependent, survivorship at the first age reduced to 50%, constant fecundity and fishing based on the age of the first capture (from catch curve);
- Scenario E: M age-dependent, survivorship at the first age reduced to 50%, constant fecundity and fishing after the age at first maturity.

### 3. RESULTS

#### 3.1 Collection and Vertebral Preparation

A total of 149 *Rhinobatos horkelli*, 752 *Rhinobatos percellens* and 952 *Zapteryx brevirostris* were collected. Of these, a subset of 123 *Rhinobatos horkelli*, 328 *Rhinobatos percellens* and 400 *Zapteryx brevirostris* were aged through vertebral centra thin sections. Samples size ranged from 45.50 to 98.20 cm TL for females and 55.30 to 99.90 cm TL for males of *Rhinobatos horkelli* (Fig. 08a); from 27.10 to 102.00 cm TL for females and 26.00 to 83.00 cm TL for males of *Rhinobatos percellens* (Fig 08b); and from 14.80 to 59.30 cm TL for females and 16.60 to 52.60 cm TL for males of *Zapteryx brevirostris* (Fig. 08c).



Mean centrum diameter (MCD) indicated that centra increased with the total length and age in each species (Fig. 09).



No significant difference was found between (MCD) with total length and age for *Rhinobatos horkelli* (ANCOVA: F=1.26, p=0.265; ANCOVA: F=0.05, p=0.821 – equ's. 1-2) and between (MCD) and age for *Rhinobatos percellens* (ANCOVA: F=0.688, p=0.688 - equ. 5). Mean centrum diameter regressions were significantly different between sexes for *Rhinobatos percellens* (ANCOVA: F=9.75, p=0.002 - equ's. 3-4) and for *Zapteryx brevirostris* (ANCOVA: F=9.73, p=0.002 - equ's. 6-7; ANCOVA: F=4.83, p=0.028 - equ's. 8-9).

<i>Rhinobatos horkelli</i> :	MCD(mm) = (0.052*TL) – 0.615	(r <sup>2</sup> =0.96)	equ. 1
	MCD(mm) = (0.493*Age) + 1.696	(r <sup>2</sup> =0.88)	equ. 2
<i>Rhinobatos percellens</i> :	MCD(mm) = (0.056*TL) – 0.608	(r <sup>2</sup> =0.94) ♂	equ. 3
	MCD(mm) = (0.061*TL) – 0.777	(r <sup>2</sup> =0.96) ♀	equ. 4
	MCD(mm) = (0.424*Age) + 1.353	(r <sup>2</sup> =0.84)	equ. 5
<i>Zapteryx brevirostris</i> :	MCD(mm) = (0.063*TL) – 0.477	(r <sup>2</sup> =0.92) ♂	equ. 6
	MCD(mm) = (0.069*TL) – 0.552	(r <sup>2</sup> =0.95) ♀	equ. 7
	MCD(mm) = (0.307*Age) + 1.094	(r <sup>2</sup> =0.79) ♂	equ. 8
	MCD(mm) = (0.340*Age) + 1.025	(r <sup>2</sup> =0.87) ♀	equ. 9

### 3.2 Age Determination

Ages were estimated using a total of 118 vertebral sections of *Rhinobatos horkelli* (62 females and 56 males), 318 vertebral sections of *Rhinobatos percellens* (138 females and 180 males) and 388 vertebral sections of *Zapteryx brevirostris* (192 females and 196 males). Each growth band pair was comprised of one wide opaque band and one narrow translucent band. Banding patterns were visible across the intermedialia in most of the thin sections. Banding patterns were visible across the intermedialia in most of the thin sections, however band pairs counts were based on the corpus calcareum. A mean birth mark was measured and identified for each specie, within 1.02

mm from the focus for *Rhinobatos horkelli*, 0.92 mm from the focus for *Rhinobatos percellens* and within 0.63 mm from the focus for *Zapteryx brevirostris*. The largest and oldest female of *Rhinobatos horkelli* in the study measured 98.20-cm TL and was estimated to be 7 years. The largest male of this species measured 99.90-cm TL also was estimated to be 7 years old. Individuals with age 0 were not sampled. The youngest specimen was a female measuring 45.50-cm TL and was estimated at 1 year old. For *Rhinobatos percellens* and *Zapteryx brevirostris*, both female and male samples included age 0 specimens. The largest female of *Rhinobatos percellens* was 102.0-cm TL and 11 years of age. The largest male of this species was 83.0-cm TL and 6 years of age. The largest female of *Zapteryx brevirostris* measured 59.3-cm TL and 9 years old, whereas the largest male of this species was 52.5-cm TL and 8 years of age.

### 3.2.1 Precision and Error Analysis

Of the ageing subset, (4.06%) of *Rhinobatos horkelli*, (3.05%) of *Rhinobatos percellens* and (3.0%) of *Zapteryx brevirostris* were deemed unreadable and were excluded from further analysis. The ages estimates were assigned from the two reads once that did not disagree by more than 2 years. Count precision between read one and read two was very good for each specie; *Rhinobatos horkelli* with 79.66% of age estimates agreement (IAPE = 3.42%, CV = 4.84%), *Rhinobatos percellens* with 78.93% of age estimates agreement (IAPE = 3.49%, CV = 4.94%) and *Zapteryx brevirostris* the highest with 85.05% of age estimates agreement (IAPE = 2.60%, CV = 3.69%). The Bowker's, Evans-

Hoenig test of symmetry detected no bias between the two reads for each specimen aged ( $\chi^2=5.24$ ,  $df=6$ ,  $p=0.39$ ) for *Rhinobatos horkelli*, ( $\chi^2=9.6$ ,  $df=11$ ,  $p=0.56$ ) for *Rhinobatos percellens* and ( $\chi^2=12.92$ ,  $df=8$ ,  $p=0.12$ ) for *Zapteryx brevirostris*. Age bias plot indicated no bias between the two reads for each species aged (Fig. 10).



### 3.2.2 Indirect Validation

Individuals with age 0 or age 1 were excluded from indirect validation methods. The edge type and marginal increment analysis of *Rhinobatos horkelli* were depreciated due to the low sample size and the lack data for certain months (March, June, July, August, October and December) (Fig. 11a). Predominance of narrow opaque bands (NO) occurred in January, February and November. Broad opaque bands (BO) were observed only in April, May, September and November. Narrow translucent edges (NT) were observed only at the spring month (November). Pooled mean monthly MIR values indicated a slight peak in September. Significant differences were found between months using Kruskal-Wallis analysis of ranks ( $\chi^2=17.82$ ,  $df=6$ ,  $p=0.003$ ). Both results suggest, albeit a little bit weak, a band pair deposition from middle-spring onwards (September-November). Seasonal trends were observed in both centrum edge and marginal increment analysis for *Rhinobatos percellens* and *Zapteryx brevirostris*, suggesting that one band pair is produced each year (Fig. 11b,c). The proportion of edge types varied seasonally among the majority of months. Narrow opaque bands (NO) were observed during summer months between December and March and broad opaque bands (BO) increased in proportion from April to September. Narrow translucent bands (NT) were first observed in June for both species and broad translucent bands (BT) increased in proportion in October for *Rhinobatos percellens* and in September for *Zapteryx brevirostris*. Seasonal trends observed in the mean MIR values followed the centrum edge types. Pooled mean monthly MIR values were lower in October and peaked in September for *Rhinobatos*

*percellens* and were lower in November and peaked in August for *Zapteryx brevirostris*. Kruskal-Wallis analysis indicated a significant difference between months for both species: (*Rhinobatos percellens*:  $\chi^2=86.02$ ,  $df=11$ ,  $p=0.000$ ; and *Zapteryx brevirostris*:  $\chi^2=89.88$ ,  $df=11$ ,  $p=0.000$ ). Centrum edge analysis and marginal increment analysis suggest that formation of translucent bands is initiated during September to October for *Rhinobatos percellens*, and during August to October for *Zapteryx brevirostris*.



### 3.2.3 Growth modeling

Growth models parameters are presented in Table 2. Likelihood ratio tests for the four growth models indicated that only the three parameters von Bertalanffy growth function did not indicate significant differences between sexes for *Rhinobatos horkelli* ( $p > 0.05$ ). Therefore, all other data were used for each sex separately for the final curve fitting. Estimates of  $L_{\infty}$  resulting from the three parameter of VBGF model of all species were greater than those obtained for all other models (Table 2). For all species females grow at slower growth rates than males. This sexually dimorphism pattern was not showed only by the two parameter of VBGF for *Rhinobatos horkelli*. Growth parameters estimated for all species that used Logistic model were the lowest values (Table 2). Predictions of  $L_{\infty}$  using the three parameter of VBGF model for all species were similar or slightly greater than the maximum sizes observed in this study.

Table 2. Summary of fitted parameters values; asymptotic total length ( $L_{\infty}$  cm), growth coefficient ( $k$   $\text{cm}^{-\text{yr}}$ ); and theoretical time at which the fish have a length of 0 ( $t_0$ ), with 95% Confidence Interval for (a) *Rhinobatos horkelli*, (b) *Rhinobatos percellens* and (c) *Zapteryx brevirostris*. The 2 VBGF used fixed values for  $L_0$  (*Rhinobatos horkelli*=29.00cm TL, *Rhinobatos percellens*=20.00 cm TL and *Zapteryx brevirostris*=16.00 cm TL) and these were omitted from the table.

Model		$L_{\infty}$	$k$	$t_0$
<b>(a) <i>Rhinobatos horkelli</i></b>				
3 VBGF	Pooled	121.71 (104.33, 139.10)	0.215 (0.130, 0.299)	-1.343 (-1.992, -0.694)
	Females	124.41 (95.79, 153.04)	0.192 (0.079, 0.305)	-1.603 (-2.587, -0.619)
	Males	116.84 (95.57, 138.11)	0.249 (0.109, 0.390)	-1.080 (-2.024, -0.135)
2 VBGF	Pooled	118.63 (111.32, 125.94)	0.232 (0.204, 0.260)	-
	Females	115.47 (104.78, 126.16)	0.239 (0.196, 0.283)	-
	Males	119.12 (109.37, 128.87)	0.235 (0.196, 0.274)	-
Gompertz	Pooled	112.44 (101.83, 123.05)	0.338 (0.250, 0.426)	0.441 (0.281, 0.601)
	Females	113.02 (96.65, 129.39)	0.317 (0.198, 0.436)	0.393 (0.113, 0.673)
	Males	111.21 (96.62, 125.80)	0.357 (0.218, 0.496)	0.437 (0.230, 0.645)
Logistic	Pooled	107.76 (99.93, 115.59)	0.458 (0.367, 0.549)	1.315 (1.057, 1.573)
	Females	107.56 (95.83, 119.29)	0.441 (0.315, 0.566)	1.310 (0.889, 1.723)
	Males	107.78 (96.54, 119.02)	0.466 (0.327, 0.605)	1.286 (0.942, 1.631)
<b>(b) <i>Rhinobatos percellens</i></b>				
3 VBGF	Pooled	102.91 (94.59, 111.22)	0.182 (0.146, 0.218)	-1.570 (-1.911, -1.230)
	Females	106.99 (95.05, 118.93)	0.171 (0.124, 0.218)	-1.512 (-1.993, -1.032)
	Males	90.69 (80.95, 100.42)	0.239 (0.169, 0.310)	-1.362 (-1.830, -0.897)
2 VBGF	Pooled	93.45 (89.51, 97.38)	0.247 (0.226, 0.269)	-
	Females	99.33 (93.15, 105.51)	0.216 (0.189, 0.243)	-
	Males	83.91 (79.39, 88.43)	0.315 (0.275, 0.354)	-
Gompertz	Pooled	91.61 (87.01, 96.22)	0.324 (0.281, 0.366)	0.561 (0.425, 0.697)
	Females	94.40 (88.22, 100.59)	0.315 (0.259, 0.371)	0.767 (0.577, 0.957)
	Males	81.67 (76.35, 86.99)	0.413 (0.330, 0.501)	0.290 (0.124, 0.455)
Logistic	Pooled	86.73 (83.34, 90.12)	0.461 (0.411, 0.511)	1.462 (1.299, 1.624)
	Females	89.12 (84.74, 93.50)	0.459 (0.392, 0.525)	1.695 (1.477, 1.914)
	Males	77.75 (73.94, 81.56)	0.578 (0.483, 0.673)	1.016 (0.855, 1.176)
<b>(c) <i>Zapteryx brevirostris</i></b>				
3 VBGF	Pooled	58.48 (56.17, 60.79)	0.262 (0.232, 0.293)	-1.327 (-1.510, -1.146)
	Females	60.73 (56.90, 64.57)	0.232 (0.192, 0.272)	-1.444 (-1.704, -1.186)
	Males	57.88 (54.51, 61.25)	0.275 (0.227, 0.324)	-1.288 (-1.569, -1.008)
2 VBGF	Pooled	57.37 (55.55, 59.18)	0.284 (0.260, 0.310)	-
	Females	59.21 (56.25, 62.17)	0.255 (0.222, 0.287)	-
	Males	56.71 (54.19, 59.23)	0.299 (0.264, 0.335)	-
Gompertz	Pooled	54.10 (52.69, 55.50)	0.425 (0.389, 0.461)	0.251 (0.154, 0.348)
	Females	55.47 (53.23, 57.71)	0.389 (0.342, 0.441)	0.321 (0.181, 0.462)
	Males	53.69 (51.62, 55.70)	0.440 (0.383, 0.498)	0.206 (0.063, 0.351)
Logistic	Pooled	51.97 (50.90, 53.03)	0.585 (0.541, 0.628)	1.011 (0.913, 1.110)
	Females	52.99 (51.33, 54.67)	0.543 (0.487, 0.600)	1.138 (0.984, 1.292)
	Males	51.69 (50.09, 53.29)	0.598 (0.529, 0.666)	0.934 (0.796, 1.071)

Of the set of candidate models, three parameters von Bertalanffy growth function showed to have strong support for all species with  $\Delta_i < 2$  (Table 3). The two parameters von Bertalanffy growth function also showed to have a strong support ( $\Delta_i < 2$ ) for *Rhinobatos horkelli* and *Zapteryx brevirostris*.

Table 3. Model performance of the candidates growth models for all species based on Akaike Criteria; (k) total number of regression parameters; (AIC) value of the Akaike Information Criteria; ( $\Delta_i$ ) Akaike difference; and ( $\%w_i$ ) Akaike weight.

	Model	k	AIC	$\Delta_i$	$\% w_i$
<i>(a) Rhinobatos horkelli</i>					
	3 VBGF	3	622.31	1.39	29.58
	2 VBGF	2	620.92	0.00	59.27
	Gompertz	3	625.82	4.90	5.13
	Logistic	3	625.50	4.57	6.03
<i>(b) Rhinobatos percellens</i>					
	3 VBGF	3	1809.82	0.00	76.37
	2 VBGF	2	1821.24	11.42	0.25
	Gompertz	3	1812.23	2.41	22.86
	Logistic	3	1819.81	9.99	0.52
<i>(c) Zapteryx brevirostris</i>					
	3 VBGF	3	1642.23	1.40	32.38
	2 VBGF	2	1640.83	0.00	65.11
	Gompertz	3	1647.35	6.51	2.51
	Logistic	3	1662.91	22.08	0.00

Therefore, based on AIC values, biological relevance and for future comparisons, the traditional three parameters von Bertalanffy growth model was chosen and produced the best statistical fit size-at-age for all species (Fig. 12).



Bootstrapping results showed that the distribution of the growth coefficient ( $k$ ) is approximately normally distributed for *Rhinobatos horkelli* (pooled sexes), for *Rhinobatos percellens* (for each sex), and for *Zapteryx brevirostris* (for each sex; Fig. 13). The difference between the asymptotic and bootstrapped confidence intervals are much greater for  $L_{\infty}$  and  $t_0$  for *Rhinobatos horkelli* and *Rhinobatos percellens*, than for *Zapteryx brevirostris*.





The relationship between growth parameters ( $L_\infty$ ,  $k$  and  $t_0$ ) that resulted from the bootstrapping showed the same pattern for all species. The relationship between  $L_\infty$  and  $k$  exhibited a strong correlation (Fig 14). Correlation between  $L_\infty$  and  $t_0$ , and  $k$  and  $t_0$  indicated a similar grouping pattern that was observed between  $L_\infty$  and  $k$ , therefore with  $L_\infty$  increasing,  $t_0$  shows a trend to decrease.





Estimates of the theoretical longevity ( $\omega$ ) were calculated using the three parameters VBGF, determined for males and females for all species of the present study (Table 4). All longevity's estimates were greater than the maximum observed ages. Taylor's method generated the lowest maximum values of age estimates than Fabens (1965). Both methods indicated that females attain greater ages than males.

Table 4. Longevity ( $\omega$  yrs) estimates based on two theoretical methods: Taylor (1958) and Fabens (1965).

	Method	Female ( $\omega$ )	Male ( $\omega$ )
(a) <i>Rhinobatos horkelli</i>			
	Fabens (95% $L_{\infty}$ )	18.24	13.86
	Taylor (95% $L_{\infty}$ )	14.17	10.90
(b) <i>Rhinobatos percellens</i>			
	Fabens (95% $L_{\infty}$ )	20.39	14.50
	Taylor (95% $L_{\infty}$ )	16.11	11.17
(c) <i>Zapteryx brevirostris</i>			
	Fabens (95% $L_{\infty}$ )	15.07	12.60
	Taylor (95% $L_{\infty}$ )	11.59	9.60

### 3.3 Estimation of Life history parameters

Indirect methods for estimating the overall natural mortality ranged from 0.323 to 0.603 for *Rhinobatos horkelli*, from 0.257 to 0.582 for *Rhinobatos percellens* and from 0.348 to 0.468 for *Zapteryx brevirostris* (Table 5). The age-specific Peterson & Wroblewski (1984) generated the highest  $M$  estimates for *Rhinobatos percellens*. Indirect methods of natural mortality ( $M$ ) using age-

independent approach generated the highest rates for *Rhinobatos horkelli* using Hoenig (1983), and using Pauly (1980) for *Zapteryx brevirostris*. Lowest  $M$  estimates for all species were produced by Jensen's (1996) methods. Corresponding  $S_x$  values ranged between 0.547 to 0.828 for *Rhinobatos horkelli*, from 0.559 to 0.818 for *Rhinobatos percellens* and from 0.592 to 0.820 for *Zapteryx brevirostris*.

Table 5. Natural mortality rates ( $M$ ) estimated by age-independent and age-dependent methods based upon the life history characteristics of the guitarfishes (*Rhinobatos horkelli*, *Rhinobatos percellens* and *Zapteryx brevirostris*).  $S_x$  – survivorship rate.

Methods	<i>Rhinobato horkelli</i>		<i>Rhinobato percellens</i>		<i>Zapteryx brevirostris</i>	
	$M$	$S_x$	$M$	$S_x$	$M$	$S_x$
Hoenig (1983)	0.603	0.547	0.382	0.682	0.468	0.626
Pauly (1980)	0.412	0.662	0.367	0.693	0.525	0.592
Jensen (1996 - age)	0.323	0.724	0.412	0.662	0.413	0.662
Jensen (1996 - growth)	0.330	0.719	0.257	0.773	0.348	0.706
Peterson & Wroblewski (1984)	0.485 - 0.189	0.616 - 0.828	0.582 - 0.201	0.559 - 0.818	0.439 - 0.199	0.645 - 0.820

Estimates of total mortality ( $Z$ ) from the catch curve were 0.692 for males and 0.751 for females of *Rhinobatos horkelli*, 0.759 for males and 0.464 for females of *Rhinobatos percellens* and 1.336 for males and 1.027 for females of *Zapteryx brevirostris* (Fig.15). Therefore fishing mortality ( $F$ ) of females calculated from the difference between total mortality ( $Z$ ) and the lowest value of natural mortality ( $M$ ), were 0.428 for *Rhinobatos horkelli*, 0.207 for *Rhinobatos percellens* and 0.679 for *Zapteryx brevirostris*.



### 3.4 Estimation of Demographic Parameters

The estimates of the natural and exploitation scenarios are shown in table 6. It was determined that under natural conditions without fishing, the population of *Rhinobatos horkelli* can increase 9% per year and can double ( $t_{x2}$ ) every 7.41 years. *Rhinobatos percellens* population can increase 10% per year and can double ( $t_{x2}$ ) every 6.73 years, whereas population of *Zapteryx brevirostris* can increase 3.9% per year and can double ( $t_{x2}$ ) every 17.81 years.

With the presence of fishing mortality ( $F=0.42$ ) and age at first capture of 2 years for *Rhinobatos horkelli*, population decrease 25% every 2.73 years (scenario B). The situation for *Rhinobatos percellens* with ( $F=0.20$ ) and age at first capture of 2 years (scenario B) showed a trend of decrease 7% per year every 9.76 years, whereas for *Zapteryx brevirostris* with ( $F=0.68$ ) and age at first capture of 4 years (scenario B) exhibited a population decrease of 25% every 2.67 years.

When the age at first capture was set out after the age of first maturity using the same values of fishing mortality for each species (scenario C), we found an increase of 4% per year of population for *Rhinobatos horkelli* and *Rhinobatos percellens*. However, we found a negative population trend for *Zapteryx brevirostris* with a decrease 4% per year every 14.45 years. The response of scenarios D and E, when was added a survivorship of 50% to the first age class, using the same fishing mortality for each species and changing the age of first as capture as mentioned above, we found the highest population decrease 38% per year for *Zapteryx brevirostris* (scenario D),

followed by *Rhinobatos horkelli* with a decrease 35% per year (scenario D), and *Rhinobatos percellens* decreasing 14% per year.

The results of adding fishing mortality and the change of the age of the first capture for each species can be seen as the drop in the percentage of survivorship rates. Similarly, a drop was observed to the age specific reproductive rates when fishing and an extra natural mortality was included mainly in earlier ages.

According to estimates for scenario B, the population finite rate of increase ( $\lambda$ ) tends to decrease when  $F > 0.10$  considering the age of the first capture for *Rhinobatos horkelli* and *Rhinobatos percellens*. While for *Zapteryx brevirostris* the population finite rate of increase ( $\lambda$ ), tends to decrease when  $F$  ranges from 0 to 0.10. When it was considered that the age of first capture occurs after the age of the first maturity, the finite rate of increase ( $\lambda$ ) tends to decrease when  $F > 0.9$  for *Rhinobatos horkelli*,  $F > 0.3$  for *Rhinobatos percellens* and  $F > 0.2$  for *Zapteryx brevirostris*.

## 4. DISCUSSION

Ageing structures and the subsequent interpretation of the growth is not always consistent and is accompanied of different sources of errors that can affect the assignment of age, resulting in false estimates of growth and mortality rates (Campana, 2001).

Banding patterns in *Rhinobatos horkelli*, *Rhinobatos percellens* and *Zapteryx brevirostris* were relatively easy to interpret due to the vertebral calcification. Growth bands were clear in the most of the samples in the intermedialia; however ages estimates were based mainly on bands in the corpus calcareum. The birthmark was easily discernable in almost all samples. The same pattern for distinguishes growth bands were observed in *Rhinobatos cemiculus* (Enajjar *et al.* 2012) and in *Rhinobatos percellens* (Nunes, 2012).

To deal with sources of error like count of the growth bands, multiple age reads of the age structure are often taken, and the precision of the reads can be quantified (Beamish and Fournier, 1981; Chang, 1982; Campana, 2001). In the present study the index of average percent error between age readings was 3.42% for *Rhinobatos horkelli*, 3.49% for *Rhinobatos percellens* and 2.60% for *Zapteryx brevirostris* and can be well accepted regarding the established 5% thresholds according to Campana (2001). When compared with others age and growth studies of the Rhinobatidae family, the index of average percent error evaluated for *Rhinobatos productus* (Márquez-Farías, 2007) of 6.17% was higher, whereas for *Trygonorrhina fasciata* (Izzo & Gillanders, 2008) 3.56% and for *Rhinobatos percellens* (Nunes, 2012) 2.03% were coincident with the present study.

The annual pattern of band deposition was observed in all studies of

age and growth of Rhinobatidae species using indirect validation methods (Lessa, 1982; Timmons and Bray, 1997; Ismen *et al.* 2007; Márquez-Farías, 2007; Başusta *et al.* 2008; Izzo & Gillanders, 2008; Enajjar *et al.* 2012; Nunes, 2012; Wilson *et al.* 2013) and each opaque and translucent band pair, was interpreted as representing one year of growth. We suggest the same pattern at the present study, based upon the centrum edge analysis and the marginal increment analysis. However due to a limited sampling period and sample size of *Rhinobatos horkelli*, our analysis for this species was a bit weak to suggest a annual band pair deposition, therefore we are supported by Lessa (1982).

Following the recommendations of Cailliet *et al.* (2006) we used both centrum edge analysis and marginal increment analysis of Conrath *et al.* (2002) to support the periodicity of band-pair formation. Significant differences between pooled monthly mean MIR for *Rhinobatos percellens* and *Zapteryx brevirostris* indicated that a single band pair is formed annually. However, validation should be viewed with precaution because when restricting to a single age or size class, we cannot regard the variability of seasonal band deposition patterns that can be obscured using pooled ages (Beamish and McFarlane, 1983; Cailliet *et al.* 2006; Smith *et al.* 2007). Centrum edge analysis also corroborated with the MIR analysis, suggesting that the annual band-pair formation occur between September to October for *Rhinobatos percellens* and between August to October for *Zapteryx brevirostris*.

Of the four growth models used, only two supported the length-at-age based on the difference of AIC criteria ( $\Delta < 2$ ). However, a model can be considered more parsimonious although not represents adequately the trajectory of the growth curves (Pardo *et al.* 2013).

According to Burnham & Anderson (2002) the use of AIC criteria is a good choice when you want to find a more parsimonious model to explain the observed variation in the data. However, maximize all the attributes for a specific model simultaneously is impossible, because the parsimony, precision, accuracy and biological context are not independent attributes (Araya & Cubillos, 2006). At the present study, the growth models of two and three parameters von Bertalanffy growth function were selected as the most parsimonious models for *Rhinobatos horkelli* and *Zapteryx brevirostris*, whereas only the 3 VBGF was chosen for *Rhinobatos percellens*. Although none of the selected models presented  $w_i > 90\%$ , the 3 VBGF was chosen to represent the growth curve for these species since it enables to comparisons with another studies.

Cailliet *et al.* (2006) recommended the uses of the modified two parameters von Bertalanffy growth function with a fixed  $L_0$  (length at birth) based upon a biological meaningful instead the use of the model with  $t_0$ . According to Pardo *et al.* (2013) this model does not represent a benefit for fit the growth curve and not reduces the bias of growth estimates. Ageing error should be considered incorporating different sources of process and observation errors when fitting age growth curves like VBGF growth function (Cope & Punt, 2007).

The Gompertz and Logistic models used at the present study, underestimated the maximum asymptotic length. This has increased the rate at which asymptotic length was reached; therefore, these models produce the highest growth rates.

Comparisons between growth parameters for these species, are possible because the same growth function the 3 VBGF was used in the studies of *Rhinobatos horkelli* (Lessa, 1982), *Rhinobatos annulatus* (Rossouw, 1983), *Rhinobatos productus* (Timmons & Bray, 1997), *Rhinobatos rhinobatos* (Basusta *et al.* 2007), *Rhinobatos productus* (Márquez-Farías, 2007), *Rhinobatos rhinobatos* (Ismen *et al.* 2007), *Rhinobatos cemiculus* (Enajjar *et al.* 2012), and for *Rhinobatos percellens* (Nunes, 2012). Growth rates reported at the present study are within the expected for Batoidea (0.2 - 0.5; Cailliet & Goldman, 2004).

Lessa (1982) was the precursor study that reported the growth parameters  $L_{\infty} = 135.51$ ,  $k = 0.194 \text{ yr}^{-1}$  and  $t_0 = -1.078$  for *Rhinobatos horkelli* in the southern of Brazil. These values were similar to the finds at the present study  $L_{\infty} = 121.71$ ,  $k = 0.215 \text{ yr}^{-1}$  and  $t_0 = -1.343$ . Growth rates estimated for *Rhinobatos rhinobatos* (Başusta *et al.* 2007)  $k = 0.31 \text{ yr}^{-1}$  for males and  $k = 0.134 \text{ yr}^{-1}$  for females; *Rhinobatos productus* (Márquez-Farías, 2007)  $k = 0.44 \text{ yr}^{-1}$  for males and  $k = 0.18 \text{ yr}^{-1}$  for females; *Rhinobatos rhinobatos* (Ismen *et al.* 2007)  $k = 0.29 \text{ yr}^{-1}$ ; and for *Rhinobatos cemiculus* (Enajjar *et al.* 2012)  $k = 0.272 \text{ yr}^{-1}$  for males and  $k = 0.202 \text{ yr}^{-1}$  for females, are within to the values mentioned above for Batoidea corroborating with the values found at the present study for the same group.

Age and growth estimates of *Rhinobatos percellens* in the Southeastern of Brazil differ from the Northeastern of Brazil. Growth coefficients at the present study ( $k = 0.18 \text{ yr}^{-1}$  for combined sexes) are lower than those reported for Northeastern of Brazil ( $k = 0.24 \text{ yr}^{-1}$  for combined sexes, Nunes, 2012). *Rhinobatos percellens* attains larger sizes (102.0 cm TL

for females, observed data) than those in the Northeastern (68.8 cm TL for females). These results suggested a latitudinal pattern in size and growth for this species, with individual from the Southeastern of Brazil reaching maximum ages, growing slowly, and maturity later than those specimens studied in the Northeastern of Brazil.

Growth parameters estimated and the best available biological information were used for constructing life tables and for estimating the demographic parameters, under differences scenarios of exploitation. Demographic analysis is a powerful tool for detected whether a population will increase or decrease and for diagnose of how susceptible it may be under an exploitation scenario (Hoenig & Gruber, 1990; Cortés, 1998, 2004).

In demographic analysis the natural mortality has been estimated for elasmobranch populations using indirect methods (Cailliet, 1992; Sminkey & Musick, 1995; Cortés, 1995; Cortés & Parsons, 1996; Márquez-Farías, 1998). Traditionally, the empirical formulae of Hoenig (1983) had been commonly used to estimate the natural mortality based upon the longevity relationship.

Estimates of natural mortality are difficult to obtain but are necessary to understanding the population dynamics and the responses to disturb (Vetter, 1998). According to Siegfried & Sansó (2009) errors in estimation of mortality affect directly various stock assessment models, therefore, weight and age-based methods are the most adequate to estimate a constant value of  $M$ .

At the present study, we consider all available information about the quality of estimators and we use five indirect methods that exhibited a wide range of the natural mortality estimates. Hoenig method resulted in the highest natural mortality rate for *Rhinobatos horkelli* ( $M = 0.603$ ), and this could be

assigned to the use of our maximum age observed of 7 years, that is lower than the 11 years observed by Lessa (1982). According to Kenchington (2013), this method relies on the maximum observed age and the use of only a single old fish or sampling error introduces a bias to this estimator.

The natural mortality rates for the guitarfish species ranged from 0.257 - 0.603 yr<sup>-1</sup>. These values are higher than almost all other reported values for Batoids studies. Smith *et al.* (2007) reported that natural mortality for *Dasyatis dipterura* ranged from 0.064 - 0.347 yr<sup>-1</sup>. Barnett *et al.* (2013) reported the lowest values for five deepwater skates. However, Márquez-Farías (2007) reported a natural mortality using Hoenig method of 0.42 yr<sup>-1</sup>. This value is similar to those finds at the present study using the same method; therefore, we can suggest that a highest natural mortality is a characteristic of the guitarfish species.

Jensen's methods (1996) showed the lowest natural mortality rates for all species at the present study. Likewise, Barnett *et al.* (2013) observed the lowest natural mortality rates using this method for five deepwater Bering Sea skates. Peterson & Wroblewski (1984) age-dependent method produced the highest survivorship rates when compared with other indirect techniques. Inversely, this method produces the lowest survivorship rates for *Dasyatis dipterura* and could be assigned that this estimator has a limited applicability to benthonic elasmobranchs (Smith *et al.* 2007).

Total mortality was calculated using catch curve method. This analysis is widely applied in data-poor fisheries, which could explain their implementation (Thorson & Prager, 2011). Catch curves relies of some assumptions that can be violated in some circumstances (Schnute & Haigh,

2007). In the present study we support for this analysis, based upon two satisfied assumptions as follow: a constant mortality at age, and a constant selectivity at age (Chapman & Robson, 1960).

The scenarios simulated in the present study were designed to compare an age-dependent natural mortality using the Peterson & Wroblewski (1984) method, with different ages at first capture, adding a constant fishing mortality and decreasing the survivorship rate for the first age class. The survivorship curves reflected a different pattern between all scenarios, except for *Rhinobatos percellens* that exhibited a similar pattern between them. Net reproductive rate showed that the effect of the age at first capture before or among the age at first maturity, reduced by halved or more (*Rhinobatos horkelli*) these rate.

Based on the results of the present study and the actual reality of exploitation in this area, we consider scenario C as the best situation to the *Rhinobatos horkelli* and *Rhinobatos percellens*. However for *Zapteryx brevirostris* we are concerned with the results and the "ideal scenario" is scenario A, without fishing. The result of scenario C for this species produced a value of  $\lambda = 0.95$ , that is out of the pattern reported for others elasmobranchs (Cortés, 2002).

Previous studies regarding demographic of Batoids considering only natural mortality produced the following values:  $\lambda = 1.02$  for *Dasyatis violacea* (Mollet & Cailliet, 2002),  $\lambda = 1.05$  for *Dasyatis dipterura* (Smith *et al.* 2007),  $\lambda = 1.116$  for *Bathyraja taranetzi* (Barnet *et al.* 2013),  $\lambda = 1.110$  for *Bathyraja lindberg* (Barnet *et al.* 2013),  $\lambda = 1.096$  for *Bathyraja minispinosa* (Barnet *et al.* 2013),  $\lambda = 1.079$  for *Bathyraja maculata* (Barnet *et al.* 2013), and  $\lambda = 1.048$  for

*Bathyraja trachura* (Barnet *et al.* 2013). These values are similar to the finds for scenario A for all species.

The value of  $\lambda = 1.043$  for *Rhinobatos horkelli* and  $\lambda = 1.042$  for *Rhinobatos percellens* were obtained in the scenario C and are within the interval reported for other elasmobranch as mentioned above. These values (under fishing pressure) coincide with  $\lambda = 1.074$  reported for *Rhinobatos productus* (Márquez-Farías, 2007), and can strengthen that the genus *Rhinobatos* exhibit a similar characteristic between different species.

The results of the present study based on the growth parameters data, mortality estimation and demographic analysis; provide valuable information to the decision makers regarding the management of the guitarfish (*Rhinobatos horkelli*, *Rhinobatos percellens* and *Zapteryx brevirostris*) in the continental shelf of Sao Paulo.

According to the information presented by the Brazilian Government for the Normative Instrument N°5 of May 2004, only *Rhinobatos horkelli* was included as endangered status. The Government of Sao Paulo State implemented Act N°56.031 on July 2010, and consider that *Rhinobatos horkelli* was collapsed; *Rhinobatos percellens* and *Zapteryx brevirostris* were over-exploited. The last assessment presented in 2012 considers that *Rhinobatos horkelli* is critically endangered, *Rhinobatos percellens* is data deficient and *Zapteryx brevirostris* is vulnerable (Subirá *et al.* 2012).

Therefore, we suggested that our analysis should be taken into account for future changes in the categories assessed for these species of Rhinobatidae family, classified as one of the most threatened families of world's sharks and rays (Dulvy *et al.* 2014).

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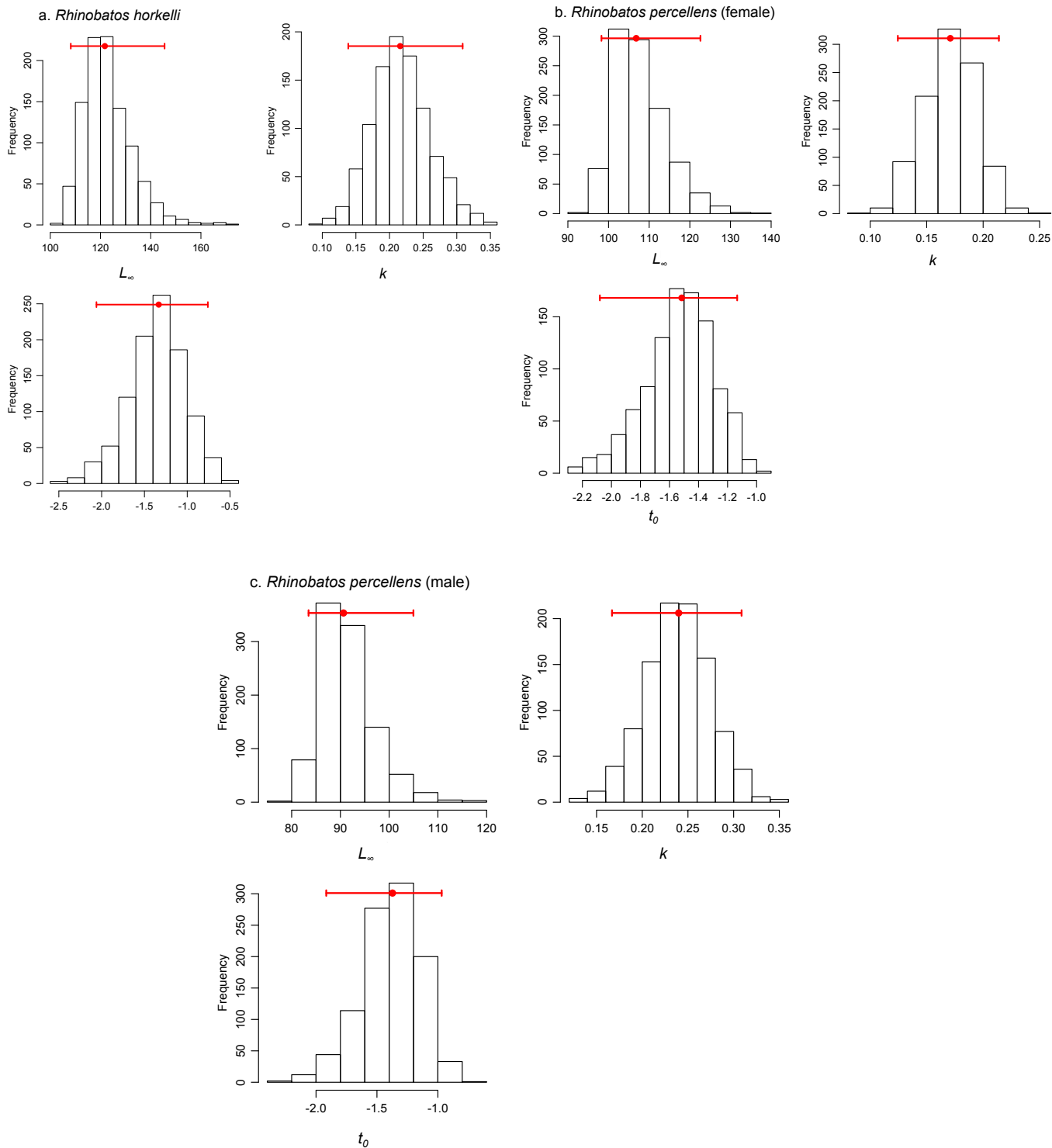


Fig 13. Histograms of the bootstrap results for the three parameters von Bertalanffy growth function. (a) *Rhinobatos horkelli* for pooled sexes; (b) *Rhinobatos percellens* for female; (c) *Rhinobatos percellens* for male; The red horizontal lines represent the 95% bootstrap confidence intervals. (continues)

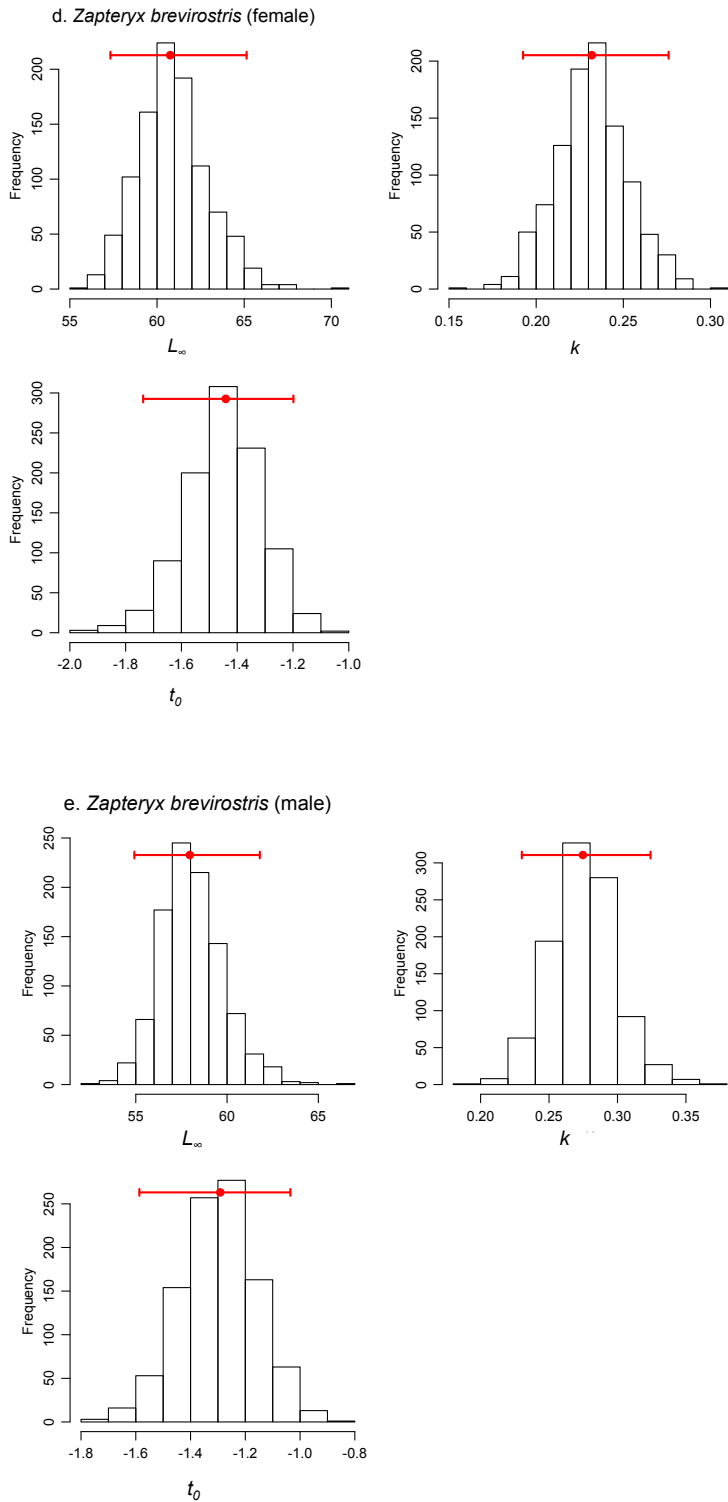


Fig 13. Histograms of the bootstrap results for the three parameters von Bertalanffy growth function. (d) *Zapteryx brevirostris* for female; and (e) *Zapteryx brevirostris* for male. The red horizontal lines represent the 95% bootstrap confidence intervals.

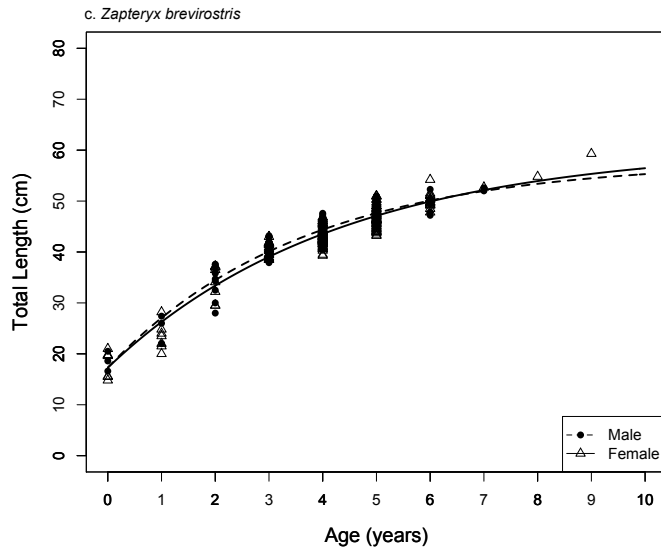
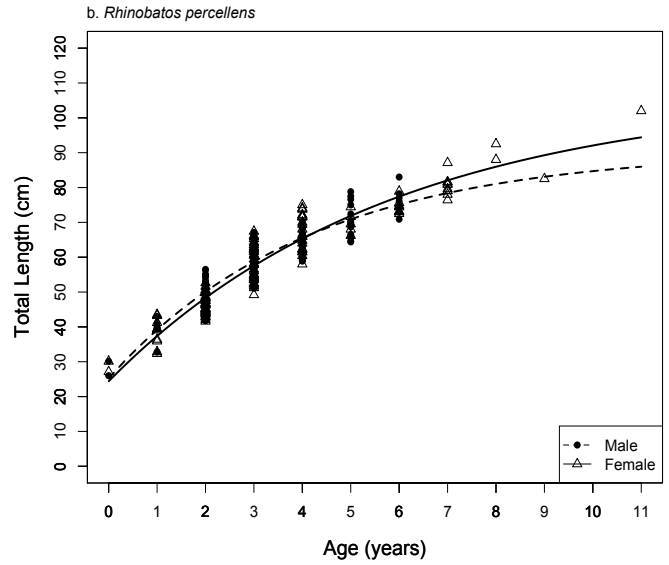
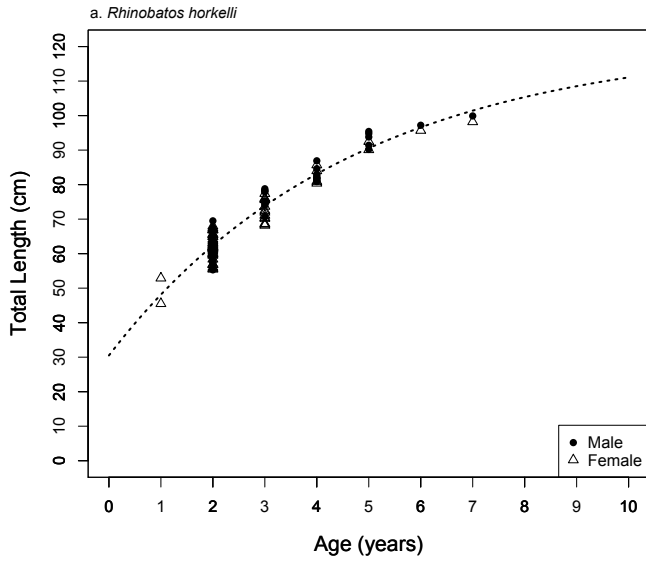


Fig 12. Three parameter von Bertalanffy growth function fitted for size-at-age estimates: (a) *Rhinobatos horkelli*, pooled sexes; (b) *Rhinobatos percellens*, for female and male; and (c) *Zapteryx brevirostris*, for female and male.

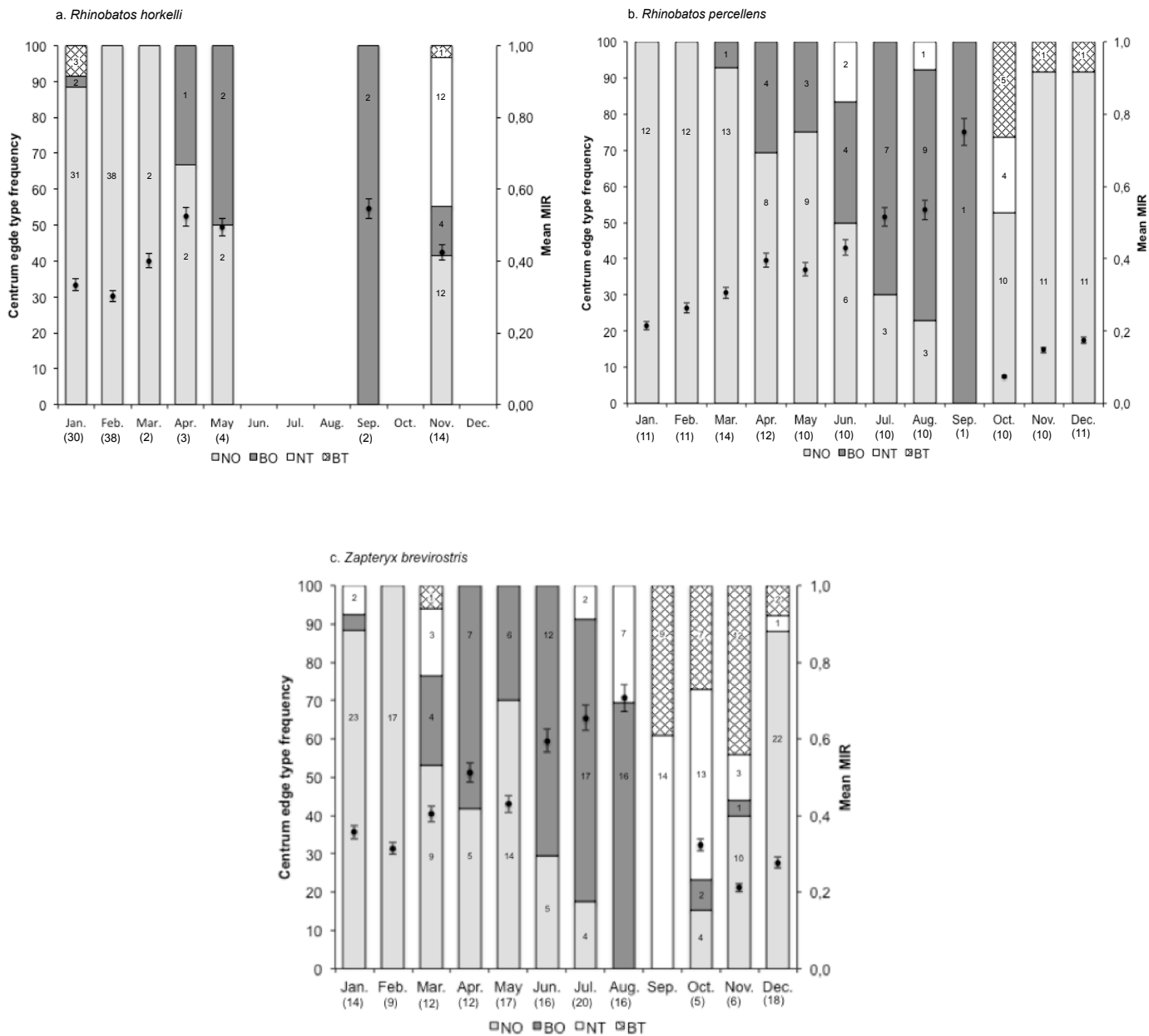


Fig 11. Monthly variation in centrum edge type: (a) *Rhinobatos horkelli* n= 114, (b) *Rhinobatos percellens* n=141, (c) *Zapteryx brevirostris* n=255 and mean monthly marginal increment ratios (MIR)  $\pm 1$  standard error determined from pooled sexes and size classes: (a) *Rhinobatos horkelli* n= 91, (b) *Rhinobatos percellens* n=122, (c) *Zapteryx brevirostris* n=145. Values inside the histogram indicate the number of samples in monthly centrum edge analysis. Samples sizes used for MIR analysis are listed in parentheses below the x-axis. NO - narrow opaque; BO - broad opaque; NT - narrow translucent; and BT - broad translucent.

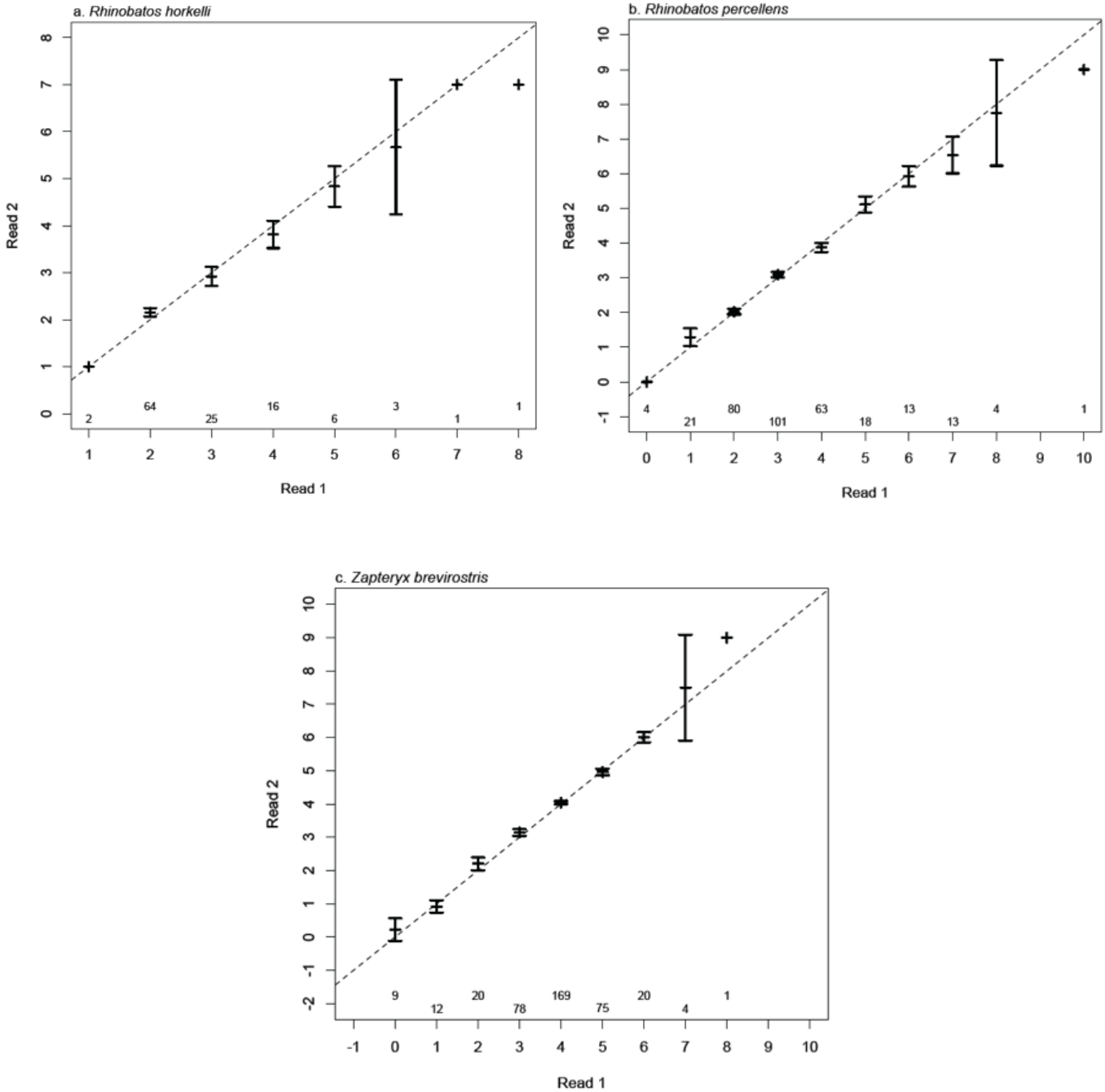


Fig 10. Age bias plot of read one age estimates versus read two age estimates of thin sections: (a) *Rhinobatos horkelli*, (b) *Rhinobatos percellens* and (c) *Zapteryx brevirostris*. Error bars represent standard error and the numbers above x-axis represent the number of specimens aged into the two reads.

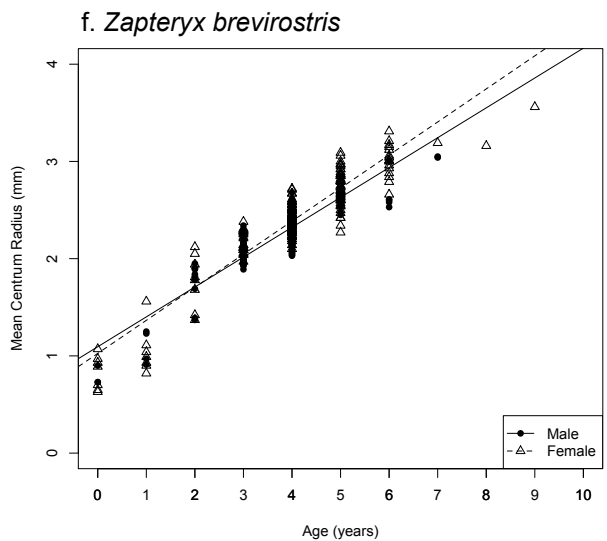
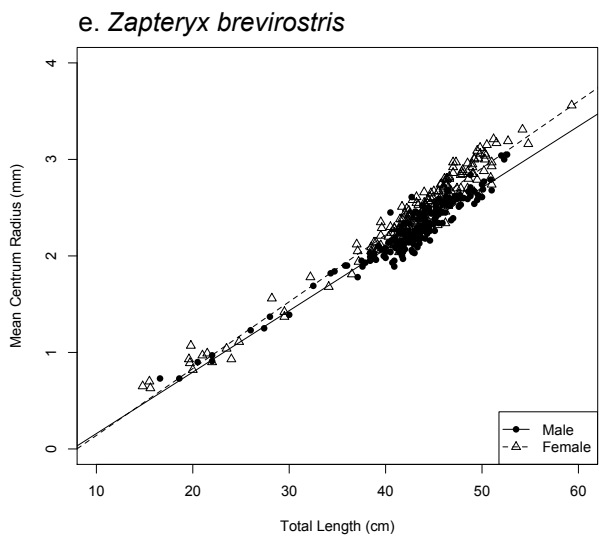
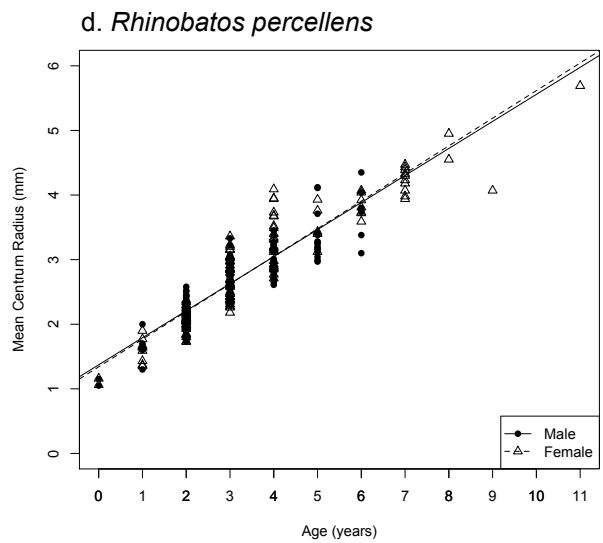
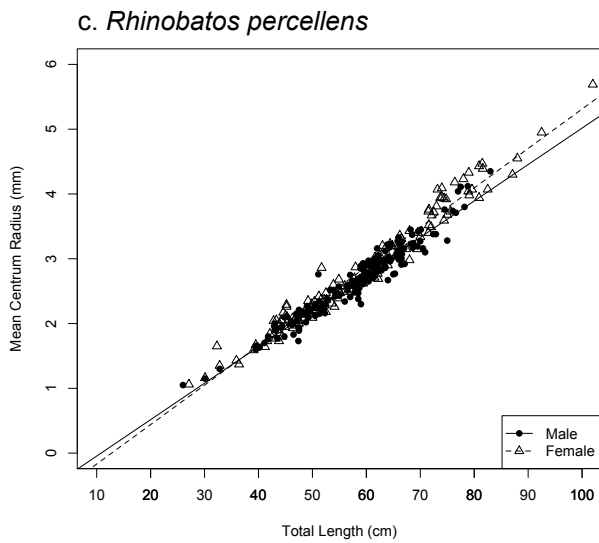
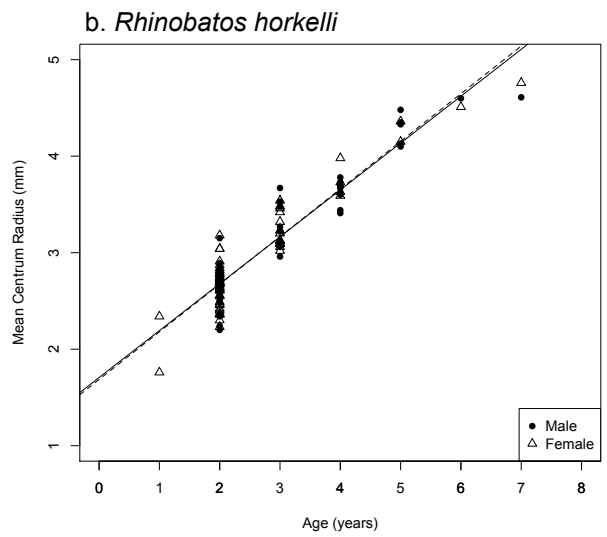
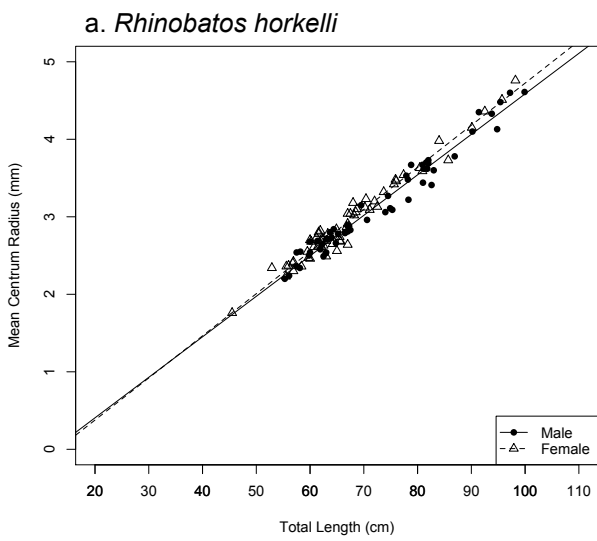


Fig 09. Relationship between mean centrum diameter and (a) size and (b) age for *Rhinobatos horkelli*, (c) size and (d) age for *Rhinobatos percellens* and (e) size and (f) for *Zapteryx brevirostris*. Age estimated from thin sections.

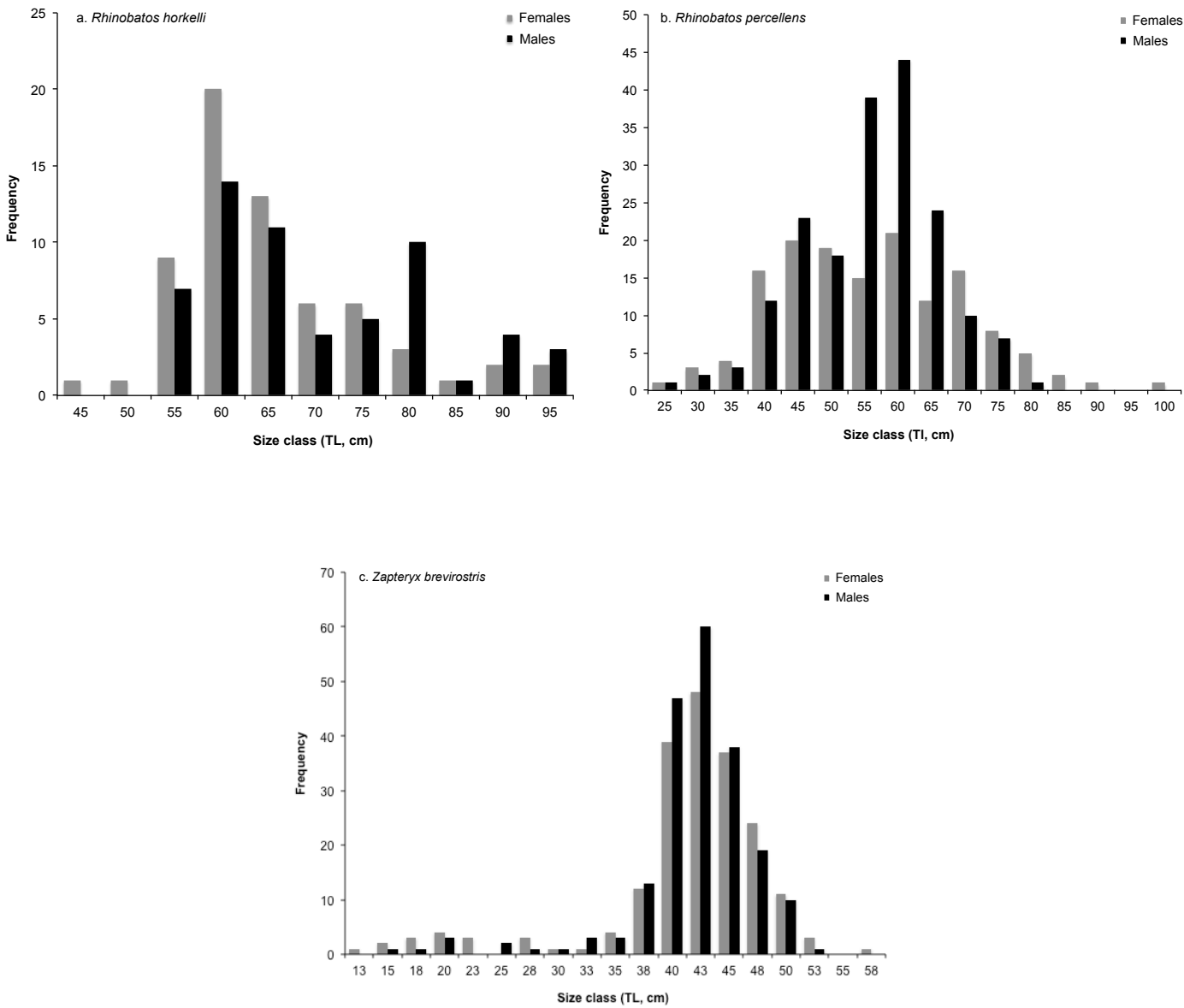


Fig 08. Size frequencies of (a) *Rhinobatos horkelli*, (b) *Rhinobatos percellens* and (c) *Zapteryx brevirostris* – females and males.

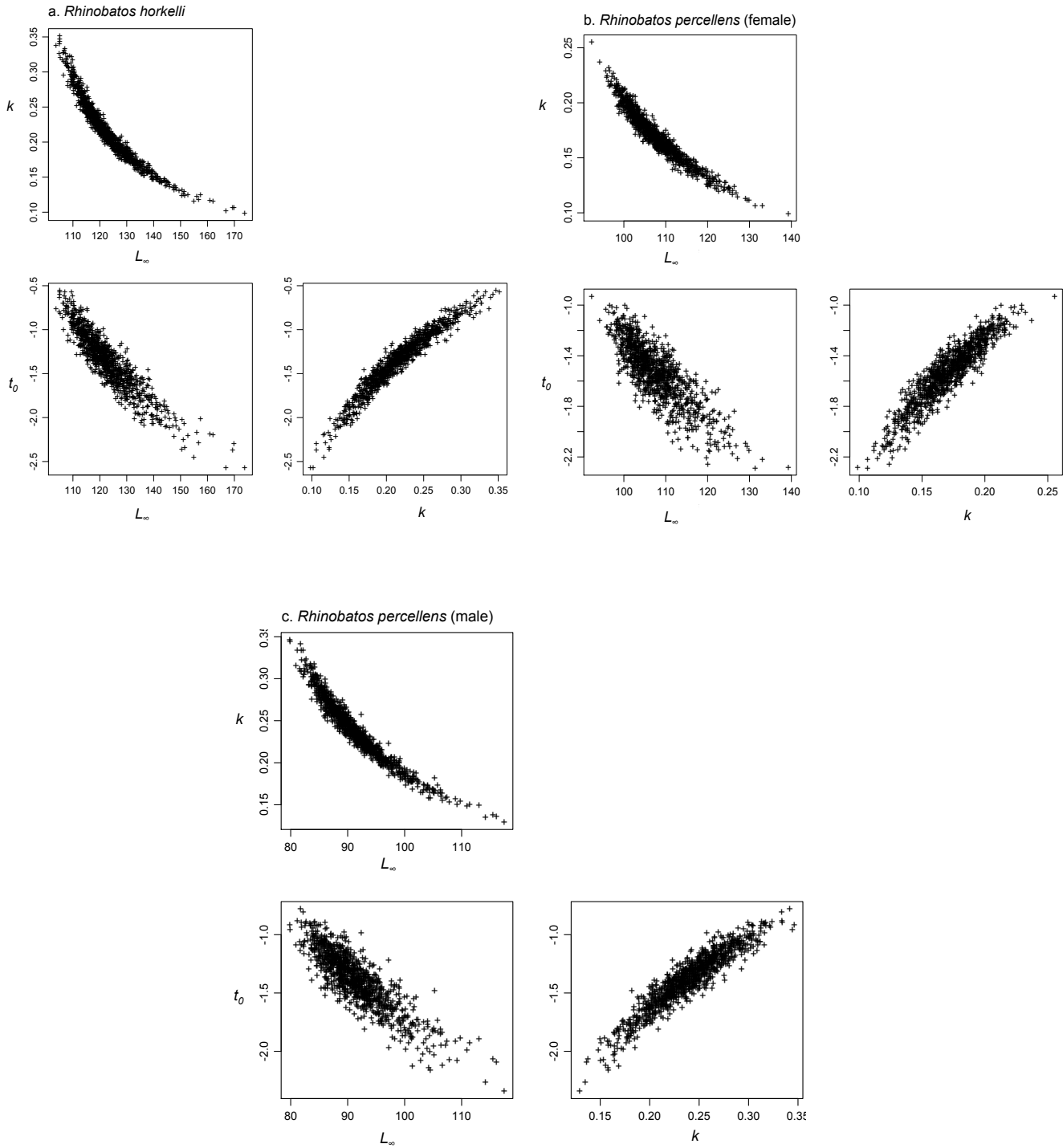


Fig 14. Paired scatterplots for growth parameters ( $L_\infty$ ,  $k$  and  $t_0$ ) resulted from bootstrapping. (a) *Rhinobatos horkelli* for pooled sexes; (b) *Rhinobatos percellens* for female; (c) *Rhinobatos percellens* for male (continue)

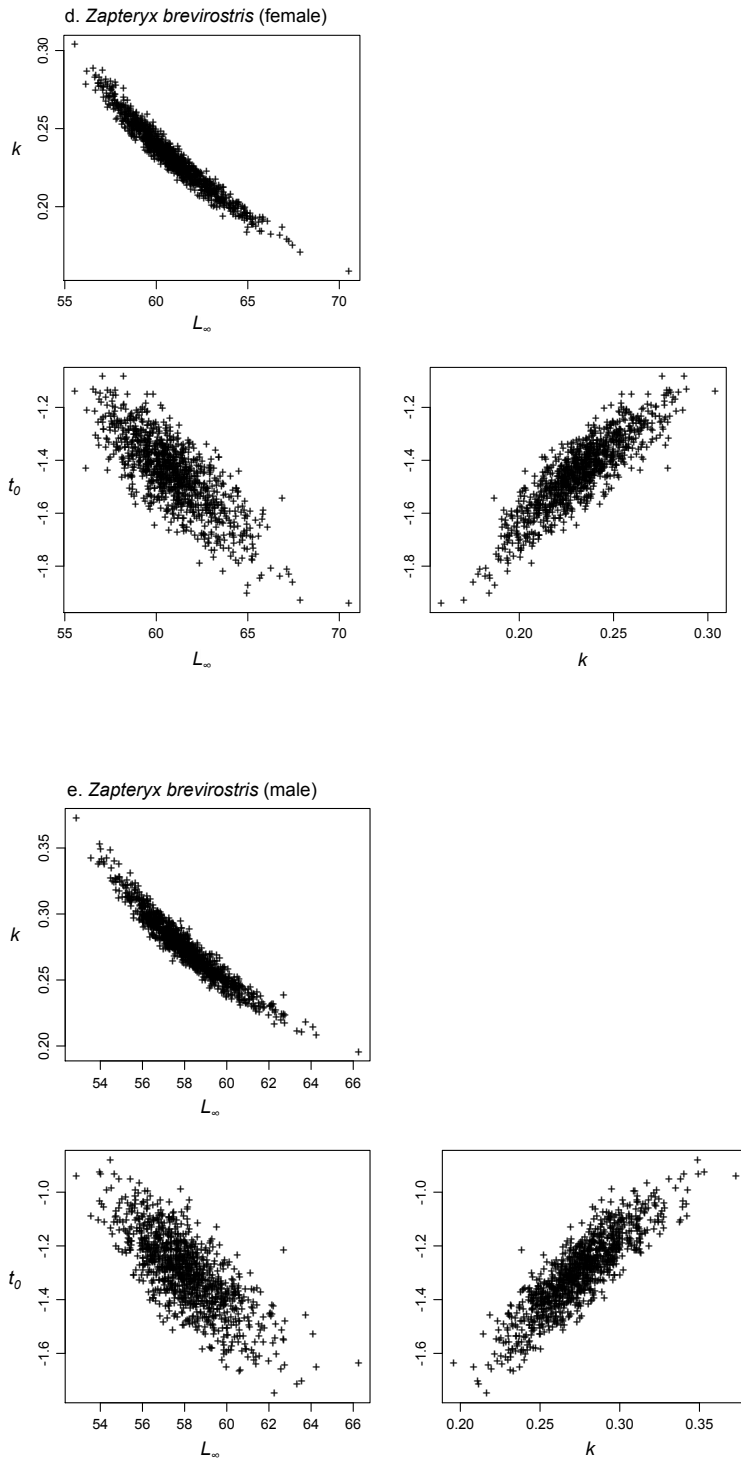


Fig 14. Paired scatterplots for growth parameters ( $L_\infty$ ,  $k$  and  $t_0$ ) resulted from bootstrapping (d) *Zapteryx brevirostris* for female; and (e) *Zapteryx brevirostris* for male.

Table 2. Summary of fitted parameters values; asymptotic total length ( $L_{\infty}$  cm), growth coefficient ( $k$  cm $^{-y}$ ); and theoretical time at which the fish have a length of 0 ( $t_0$ ), with 95% Confidence Interval for (a) *Rhinobatos horkelli*, (b) *Rhinobatos percellens* and (c) *Zapteryx brevirostris*. The 2 VBGF used fixed values for  $L_0$  (*Rhinobatos horkelli*=29.00cm TL, *Rhinobatos percellens*=20.00 cm TL and *Zapteryx brevirostris*=16.00 cm TL) and these were omitted from the table.

Model		$L_{\infty}$	$k$	$t_0$
<b>(a) <i>Rhinobatos horkelli</i></b>				
3 VBGF	Pooled	121.71 (104.33, 139.10)	0.215 (0.130, 0.299)	-1.343 (-1.992, -0.694)
	Females	124.41 (95.79, 153.04)	0.192 (0.079, 0.305)	-1.603 (-2.587, -0.619)
2 VBGF	Males	116.84 (95.57, 138.11)	0.249 (0.109, 0.390)	-1.080 (-2.024, -0.135)
	Pooled	118.63 (111.32, 125.94)	0.232 (0.204, 0.260)	-
Females		115.47 (104.78, 126.16)	0.239 (0.196, 0.283)	-
	Males	119.12 (109.37, 128.87)	0.235 (0.196, 0.274)	-
Gompertz	Pooled	112.44 (101.83, 123.05)	0.338 (0.250, 0.426)	0.441 (0.281, 0.601)
	Females	113.02 (96.65, 129.39)	0.317 (0.198, 0.436)	0.393 (0.113, 0.673)
Males		111.21 (96.62, 125.80)	0.357 (0.218, 0.496)	0.437 (0.230, 0.645)
	Pooled	107.76 (99.93, 115.59)	0.458 (0.367, 0.549)	1.315 (1.057, 1.573)
Females		107.56 (95.83, 119.29)	0.441 (0.315, 0.566)	1.310 (0.889, 1.723)
	Males	107.78 (96.54, 119.02)	0.466 (0.327, 0.605)	1.286 (0.942, 1.631)
<b>(b) <i>Rhinobatos percellens</i></b>				
3 VBGF	Pooled	102.91 (94.59, 111.22)	0.182 (0.146, 0.218)	-1.570 (-1.911, -1.230)
	Females	106.99 (95.05, 118.93)	0.171 (0.124, 0.218)	-1.512 (-1.993, -1.032)
Males		90.69 (80.95, 100.42)	0.239 (0.169, 0.310)	-1.362 (-1.830, -0.897)
	Pooled	93.45 (89.51, 97.38)	0.247 (0.226, 0.269)	-
Females		99.33 (93.15, 105.51)	0.216 (0.189, 0.243)	-
	Males	83.91 (79.39, 88.43)	0.315 (0.275, 0.354)	-
Gompertz	Pooled	91.61 (87.01, 96.22)	0.324 (0.281, 0.366)	0.561 (0.425, 0.697)
	Females	94.40 (88.22, 100.59)	0.315 (0.259, 0.371)	0.767 (0.577, 0.957)
Males		81.67 (76.35, 86.99)	0.413 (0.330, 0.501)	0.290 (0.124, 0.455)
	Pooled	86.73 (83.34, 90.12)	0.461 (0.411, 0.511)	1.462 (1.299, 1.624)
Females		89.12 (84.74, 93.50)	0.459 (0.392, 0.525)	1.695 (1.477, 1.914)
	Males	77.75 (73.94, 81.56)	0.578 (0.483, 0.673)	1.016 (0.855, 1.176)
<b>(c) <i>Zapteryx brevirostris</i></b>				
3 VBGF	Pooled	58.48 (56.17, 60.79)	0.262 (0.232, 0.293)	-1.327 (-1.510, -1.146)
	Females	60.73 (56.90, 64.57)	0.232 (0.192, 0.272)	-1.444 (-1.704, -1.186)
Males		57.88 (54.51, 61.25)	0.275 (0.227, 0.324)	-1.288 (-1.569, -1.008)
	Pooled	57.37 (55.55, 59.18)	0.284 (0.260, 0.310)	-
Females		59.21 (56.25, 62.17)	0.255 (0.222, 0.287)	-
	Males	56.71 (54.19, 59.23)	0.299 (0.264, 0.335)	-
Gompertz	Pooled	54.10 (52.69, 55.50)	0.425 (0.389, 0.461)	0.251 (0.154, 0.348)
	Females	55.47 (53.23, 57.71)	0.389 (0.342, 0.441)	0.321 (0.181, 0.462)
Males		53.69 (51.62, 55.70)	0.440 (0.383, 0.498)	0.206 (0.063, 0.351)
	Pooled	51.97 (50.90, 53.03)	0.585 (0.541, 0.628)	1.011 (0.913, 1.110)
Females		52.99 (51.33, 54.67)	0.543 (0.487, 0.600)	1.138 (0.984, 1.292)
	Males	51.69 (50.09, 53.29)	0.598 (0.529, 0.666)	0.934 (0.796, 1.071)

Table 5. Natural mortality rates ( $M$ ) estimated by age-independent and age-dependent methods based upon the life history characteristics of the guitarfishes (*Rhinobatos horkelli*, *Rhinobatos percellens* and *Zapteryx brevirostris*).  $S_x$  – survivorship rate.

Methods	<i>Rhinobato horkelli</i>		<i>Rhinobato percellens</i>		<i>Zapteryx brevirostris</i>	
	$M$	$S_x$	$M$	$S_x$	$M$	$S_x$
Hoening (1983)	0.603	0.547	0.382	0.682	0.468	0.626
Pauly (1980)	0.412	0.662	0.367	0.693	0.525	0.592
Jensen (1996 - age)	0.323	0.724	0.412	0.662	0.413	0.662
Jensen (1996 - growth)	0.330	0.719	0.257	0.773	0.348	0.706
Peterson & Wroblewski (1984)	0.485 - 0.189	0.616 - 0.828	0.582 - 0.201	0.559 - 0.818	0.439 - 0.199	0.645 - 0.820

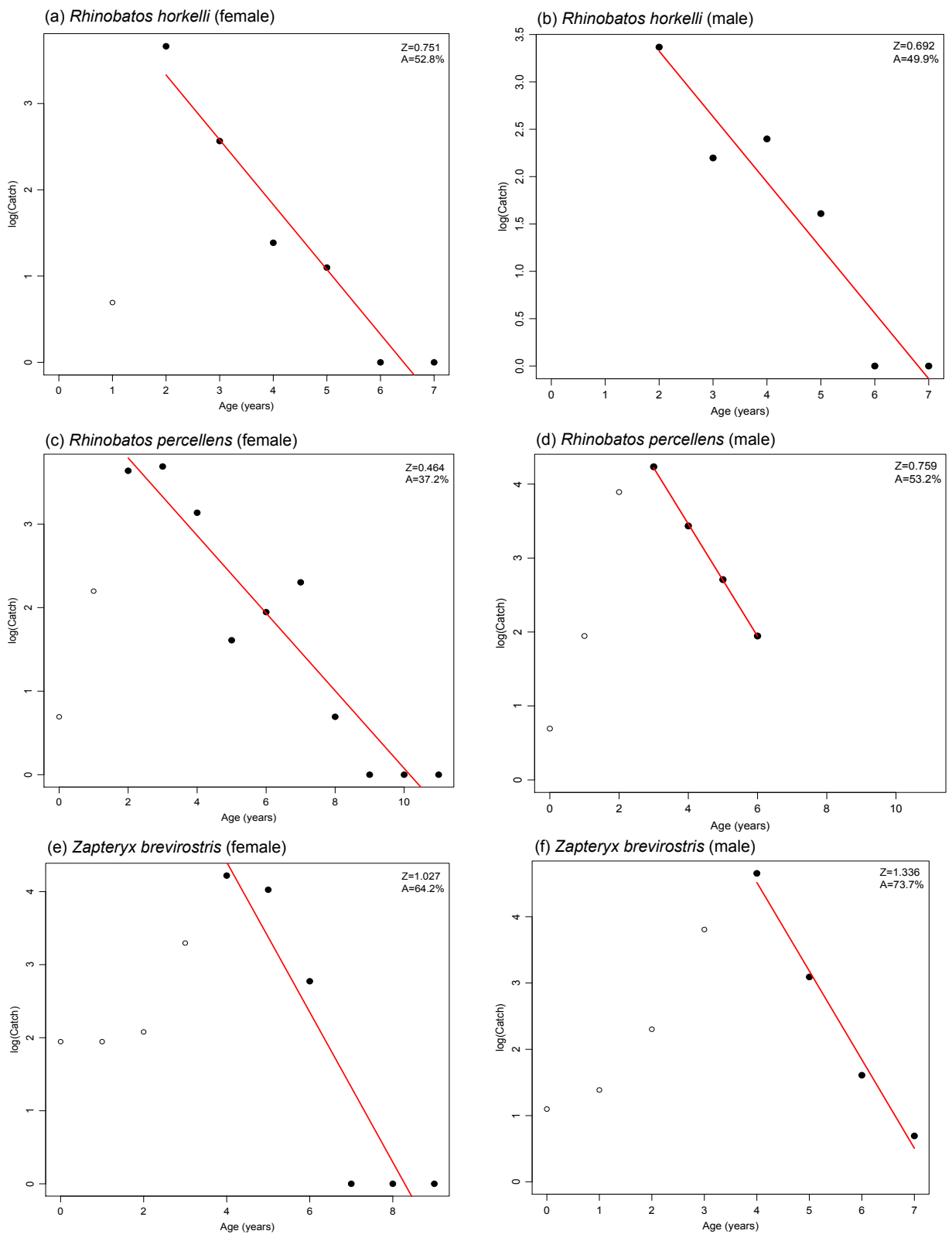


Fig 15. Catch curve for females and males, of *Rhinobatos horkelli*, *Rhinobatos percellens* and *Zapteryx brevirostris*; with the value of (Z) total mortality