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IDADE E CRESCIMENTO DO TUBARÃO ANEQUIM, *ISURUS OXYRINCHUS* (RAFINESQUE 1810), NO ATLÂNTICO SUDOESTE

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RESUMO

O tubarão anequim *Isurus oxyrinchus* é uma espécie frequente na captura incidental da pesca oceânica de espinhel no Atlântico Sul. Apesar disso, estudos de idade e crescimento não têm sido realizados para a espécie na região. O presente estudo forneceu as primeiras estimativas de idade e crescimento do tubarão anequim no Atlântico Sudoeste através da análise de secções vertebrais de 245 exemplares (126 fêmeas, 116 machos e 3 com sexo indeterminado), com uma amplitude de tamanhos de 78 a 330 cm de comprimento furcal (CF). A relação entre o raio da vértebra e o CF foi linear. As análises do incremento marginal não foram conclusivas em relação à periodicidade de formação das bandas de crescimento na área do estudo. Assumindo uma periodicidade anual (uma banda de crescimento por ano), a amplitude de idades estimada foi de 0 a 28 anos. O modelo de crescimento de Schnute, escolhido por sua flexibilidade e ajustado sob uma abordagem bayesiana, forneceu uma boa descrição do crescimento individual para ambos os sexos até os 15 anos de idade. O crescimento no primeiro ano de vida foi 33.9 cm ($ICr_{95\%}$ = 19.9 – 40.8) para as fêmeas e 30.5 cm ($ICr_{95\%}$ = 25.6 - 35.4) para os machos. Até aproximadamente 15 anos de idade, fêmeas e machos apresentaram crescimento semelhante, atingindo ~217 cm CF. A forma sigmoide que apresentaram as curvas de crescimento de ambos os sexos indicou que existe uma mudança no padrão de crescimento em torno dos 7 anos de idade. Os resultados inconclusivos sobre a periodicidade na deposição das bandas de crescimento na área de estudo fazem com que seja necessária a aplicação de técnicas mais robustas de validação no futuro. Enquanto isso, uma abordagem preventiva que assuma um padrão de deposição anual no Atlântico Sudoeste pode ser

utilizada para a avaliação e manejo dos estoques dessa espécie, caracterizada por uma baixa fertilidade e uma maturidade tardia.

Palavras-chave: *Isurus oxyrinchus*, idade e crescimento, modelo de Schnute, abordagem bayesiana.

ABSTRACT

The shortfin mako shark *Isurus oxyrinchus* is a frequent by-catch species in oceanic longline fisheries in the South Atlantic. Despite this, no age and growth studies have been conducted for the species in the region. This study provided the first age and growth estimates of female and male shortfin mako sharks from the western South Atlantic through the analysis of vertebral sections of 245 specimens (126 females, 116 males and 3 with undetermined sex), ranging in size from 78 to 330 cm fork length (FL). A significant linear relationship was found between FL and vertebral radius for sexes combined. Marginal increment analyses were inconclusive about periodicity of growth band deposition and an annual periodicity (one growth band per year) was assumed to make age estimations. Specimens were estimated to be between 0 and 28 years of age. The Schnute growth model (SGM), chosen for its flexibility and fitted with a Bayesian approach, provided a good description of the individual growth for both sexes up to 15 years of age. Shortfin mako growth during the first year of life was 33.9 cm ($ICr_{95\%}$ = 19.9 – 40.8) for females and 30.5 cm ($ICr_{95\%}$ = 25.6 - 35.4) for males. Until approximately 15 years of age, both sexes showed similar growth and reached ~217 cm FL. Sigmoid shaped growth curves obtained for both sexes indicated a change in the growth pattern close to 7 years of age. Inconclusive

results about periodicity of growth band deposition in the study area make necessary the application of more robust validation techniques in the future. Meanwhile, a precautionary approach that assumes an annual deposition pattern in the western South Atlantic can be used for the assessment and management of stocks of this species, characterized by low fecundity and late maturity.

Keywords: *Isurus oxyrinchus*, age and growth, Schnute growth model, Bayesian approach.

1. INTRODUÇÃO

1.1. O tubarão anequim *Isurus oxyrinchus*

O tubarão anequim *Isurus oxyrinchus* (Rafinesque 1810) (**Fig. 1**) é um predador pelágico de grande porte classificado na ordem Lamniformes, na família Lamnidae (Compagno 2001). Apresenta dimorfismo sexual em relação ao tamanho máximo, com registros de até 362 cm de comprimento furcal (CF) para as fêmeas (Bigelow & Schroeder 1948) e de até 270 cm CF para os machos (Bishop *et al.* 2006). Como outros membros da família Lamnidae, *I. oxyrinchus* apresenta endotermia, sendo capaz de manter sua temperatura corporal em até 10°C acima da temperatura da água (Carey & Teal 1969).

I. oxyrinchus ocorre em águas tropicais e temperadas de todos os oceanos, desde a superfície até pelo menos 880 metros de profundidade, sendo mais frequente na camada de mistura (Abascal *et al.* 2011) e em temperaturas de 17 a 22°C (Cliff *et al.* 1990, Casey & Kohler 1992). É uma espécie principalmente oceânica, mas ocasionalmente encontrada perto da costa em regiões onde a plataforma continental é estreita (Stevens 2008). No Atlântico oeste, a espécie tem como limite de distribuição norte as águas do Canadá (aprox. 50°N) onde parece ser um residente sazonal (Campana *et al.* 2005) e como limite sul as águas da Argentina (aprox. 50°S) (Siccardi *et al.* 1981, Cortés *et al. in prep.*).

Estudos de marcação e recaptura no Atlântico noroeste evidenciaram que os anequins fazem deslocamentos de até ~4500 km de distância. No entanto, não há registros de movimentos transequatoriais (Casey & Kohler 1992, Kohler *et al.* 2002), fato que é apoiado por estudos genéticos (Heist *et al.* 1996). Parece ocorrer sobreposição geográfica e intercâmbio genético suficiente entre estoques para considerar o tubarão anequim como

uma única espécie em todo o mundo, não havendo evidência de um estoque genético discreto no Atlântico Sul (Schrey & Heist 2003, Heist 2008).

Assim como as demais espécies de Lamniformes, *I. oxyrinchus* tem uma estratégia reprodutiva vivípara matrotrófica com oofagia como fonte principal de nutrição dos embriões (Gilmore 1993, Mollet *et al.* 2000), embora tenha sido registrada também a adelfofagia (canibalismo intrauterino) (Joung & Hsu 2005). O período de nascimento dura vários meses (Mollet *et al.* 2000, Costa *et al.* 2002, Conde-Moreno & Galván-Magaña 2006), ou eventualmente todo o ano (Duffy & Francis 2001). As ninhadas são de 4 a 20 embriões (Stevens 1983, Costa *et al.* 2002, Joung & Hsu 2005, Semba *et al.* 2011) os quais nascem com um comprimento total de 60 a 70 cm (Gilmore 1993, Mollet *et al.* 2000). Existem diferenças na literatura em relação ao período de gestação da espécie, estimado em 9-13 meses por Semba *et al.* (2011), em 15-18 meses por Mollet *et al.* (2000) e em 23–25 meses por Joung e Hsu (2005). O ciclo reprodutivo parece ser de 3 anos (Mollet *et al.* 2000, Joung & Hsu 2005). O tamanho da maturidade sexual difere entre gêneros, sendo estimado nos machos em 180-185 cm e nas fêmeas em 275-285 cm de comprimento furcal (Francis & Duffy 2005).

I. oxyrinchus é uma espécie de interesse em pescarias comerciais e recreativas. Na pesca recreativa, é cobiçada em países como Nova Zelândia, África do Sul e Estados Unidos (Compagno 2001, Stevens 2008). Na pesca comercial, é capturada de forma incidental principalmente pelas frotas de espinhel de superfície que dirigem seu esforço a atuns (*Thunnus* spp.), espadarte (*Xiphias gladius*) e tubarão azul (*Prionace glauca*). Os exemplares são retidos, e sua carne e nadadeiras, consideradas de alta qualidade, são comercializadas em escala global (Compagno 2001, Clarke *et al.* 2006). No oceano

Atlântico é uma espécie altamente suscetível às pescarias de espinhel de superfície (Cortés *et al.* 2010) e no Atlântico Sudoeste é a segunda espécie de tubarão mais abundante na composição das capturas das frotas de espinhel pelágico, sendo somente superada pelo tubarão azul (Domingo *et. al.* 2002, Montealegre-Quijano *et al.* 2007, Mas 2012). No período de 1982 – 2010, a espécie foi registrada em 59% dos lances de pesca da frota uruguaia de espinhel pelágico (Pons & Domingo 2013 *in press*). Para a mesma frota, operando no Atlântico Sudoeste, não houve uma tendência clara na abundância do anequim baseada em captura por unidade de esforço (CPUE) padronizada no período 1982 – 2010, com uma diminuição entre 2001 e 2008, mas um aumento em 2009 e 2010 (Pons & Domingo 2013 *in press*). Para a frota brasileira de espinhel pelágico, a CPUE padronizada foi relativamente estável entre 1978 e 1990, aumentando em seguida até 2007 (Carvalho *et al.* 2009).

A União Internacional para a Conservação da Natureza (UICN) categorizou a espécie como "vulnerável" em escala global (UICN 2012), embora ainda haja dificuldades para obter estimativas confiáveis do estado atual da espécie, devido ao alto grau de incerteza nas estimativas de captura no passado e a deficiência de parâmetros biológicos importantes, particularmente para o Atlântico Sul (ICCAT 2012).

1.2. Estimação da idade em peixes cartilaginosos (Classe *Chondrichthyes*)

Para avaliar o status das populações dos recursos pesqueiros e poder estimar um nível de exploração sustentável, é fundamental conhecer a estrutura etária das capturas, as taxas de crescimento, as taxas de mortalidade e a longevidade (Ricker 1975). Estudos de

estimação de idade fornecem os dados básicos para gerar esse conhecimento (Campana 2001).

Dentre os métodos que existem para estimar a idade, a esclerocronologia é um dos mais informativos e precisos (Panfili 2002). Esta metodologia objetiva reconstruir a história passada dos organismos a partir do estudo de suas estruturas calcificadas. Pelo fato de crescer por aposição ao longo de toda a vida do peixe, essas estruturas atuam como um registro permanente do crescimento individual (Panfili 2002). Variações na taxa de crescimento se evidenciam pela presença de padrões periódicos associados a processos de biomineralização, também chamados de bandas de crescimento (Panfili 2002). Conhecendo a periodicidade de formação das bandas de crescimento, pode-se associar o número de bandas presentes na estrutura calcificada com a idade do indivíduo.

Em peixes cartilaginosos as estruturas calcificadas utilizadas para a determinação da idade são as vértebras, mas dependendo da espécie, outras estruturas podem ser usadas, como espinhos das nadadeiras dorsais, arcos neurais ou espinhos caudais (Cailliet & Goldman 2004). As vértebras nestes peixes estão constituídas por tecido cartilaginoso, com matriz extracelular mineralizada com cristais de fosfato de cálcio hidroxiapatita (Dean & Summers 2006). Três tipos diferentes de calcificação estão presentes nestas vértebras: areolar, globular e prismático. A cartilagem areolar se apresenta no centro vertebral e os outros tipos dispõem-se cobrindo os arcos vertebrais. A cartilagem areolar compreende um tecido densamente calcificado, formando o que tem sido chamado de “cone duplo” do corpo vertebral (Ridewood 1921). Esta forma de mineralização está disposta em anéis concêntricos e é utilizada com sucesso para determinar a idade dos peixes cartilaginosos (Dean & Summers 2006).

1.3. Estimação dos parâmetros de crescimento

Os dados de estimativas de idade associados a tamanhos individuais observados podem ser ajustados a modelos matemáticos, com o intuito de descrever o crescimento médio dos indivíduos em uma população de peixes. Vários modelos foram propostos para estimar o crescimento em peixes, sendo os mais utilizados o de von Bertalanffy (von Bertalanffy 1938), von Bertalanffy generalizado (Pauly 1979), Gompertz (Gompertz 1825) e Logístico (Ricker 1975). Todos estes modelos assumem um crescimento assintótico, e todos (exceto o modelo de von Bertalanffy) tem uma forma de curva sigmoidal, com um ponto de inflexão. Em peixes cartilaginosos, a maioria dos estudos de idade e crescimento conduzidos utilizaram o modelo de von Bertalanffy, sendo escassos os estudos que exploraram outras possibilidades (Cailliet *et al.* 2006).

Estudos que trabalharam com dados de idade-comprimento de diferentes espécies de elasmobrânquios e que testaram para cada conjunto de dados mais de um modelo de crescimento, incluindo o von Bertalanffy concluíram que, na maioria dos casos, o modelo de von Bertalanffy não era o do melhor ajuste e que várias espécies pareciam seguir trajetórias de crescimento diferentes à descrita por este modelo (Araya & Cubillos 2006, Katsanevakis & Maravelias 2008).

No caso de *Isurus oxyrinchus*, a maioria dos estudos de idade e crescimento conduzidos até o presente utilizaram o modelo de von Bertalanffy de forma exclusiva (Pratt & Casey 1983, Chan 2001, Ribot-Carballal *et al.* 2005, Semba *et al.* 2009, Cerna & Licandeo 2009). No entanto, alguns poucos trabalhos, além de usar o modelo de von Bertalanffy, testaram também outros modelos como o Logístico (Cailliet *et al.* 1983), Gompertz (Natanson *et al.* 2006) ou Schnute (Bishop *et al.* 2006). Quando foi usado mais de um modelo para *I.*

oxyrinchus, o de von Bertalanffy não foi o de melhor ajuste na maioria dos casos (Cailliet *et al.* 1983, Bishop *et al.* 2006, Natanson *et al.* 2006).

Nesse contexto, o uso de um modelo flexível, como o modelo de Schnute (Schnute 1981) se apresenta como uma alternativa interessante já que provê uma formulação que inclui a maioria dos modelos de crescimento como casos particulares. O modelo de Schnute considera não apenas crescimento assintótico, mas também crescimento linear, quadrático, potencial ou exponencial (Schnute 1981). Desta forma, permite que o ajuste dos dados não seja restrito a um único modelo, mas que os próprios dados sejam usados diretamente na escolha do modelo mais apropriado (Schnute 1981).

1.4. A idade e crescimento em *I. oxyrinchus*

Os primeiros estudos de idade e crescimento em *I. oxyrinchus* (Pratt & Casey 1983, Cailliet *et al.* 1983) geraram parâmetros de crescimento com valores contrastantes, como consequência das diferentes interpretações sazonais na formação das bandas de crescimento. Pratt & Casey (1983) consideraram uma periodicidade bienal (2 bandas de crescimento por ano) e Cailliet *et al.* (1983) uma periodicidade anual (1 banda por ano). Desde então, vários estudos de idade e crescimento do tubarão anequim foram realizados em nível mundial, dos quais cinco foram no Pacífico (Hsu 2003, Ribot-Carballal *et al.* 2005, Bishop *et al.* 2006, Cerna & Licandeo 2009, Semba *et al.* 2009) e três no Atlântico Norte (Campana *et al.* 2002, Natanson *et al.* 2006, Ardizzone *et al.* 2006). Todos estes estudos identificaram um padrão anual na formação das bandas de crescimento, embora apenas os estudos no Atlântico Norte (Campana *et al.* 2002, Ardizzone *et al.* 2006, Natanson *et al.* 2006) validaram essas estimativas com o uso das técnicas de bomba de

radiocarbono e marcação e recaptura com oxitetraciclina (OTC). No entanto, recentemente Wells *et al.* (2013) utilizando OTC em exemplares menores de 200 cm CF do Pacífico Norte, evidenciaram que, pelo menos para os primeiros cinco anos de vida, os juvenis de tubarão anequim depositam duas bandas de crescimento por ano.

A alta frequência de ocorrência na captura incidental da pesca oceânica no Atlântico Sul e as características de história de vida -como baixa fecundidade e maturidade tardia- fazem com que o tubarão anequim seja uma espécie suscetível à sobre-explotação. Apesar disso, ainda não há estudos sobre a idade e crescimento desta espécie no Atlântico Sul que forneçam a informação básica para avaliar o estado do estoque na região. No intuito de contribuir para eventuais medidas de manejo e conservação, no presente estudo realizaram-se as primeiras estimativas de idade e crescimento de *I. oxyrinchus* no Atlântico Sudoeste.

2. OBJETIVOS

Os objetivos do presente trabalho foram: 1) Estimar a idade dos tubarões anequim presentes na ZEE do Sul do Brasil, ZEE do Uruguai e águas internacionais adjacentes, através da análise de suas vértebras; 2) Descrever o crescimento somático de *I. oxyrinchus* no Atlântico Sudoeste, segundo o modelo de Schnute, através de uma abordagem bayesiana; e 3) Elaborar uma chave de comprimento-idade da espécie para o Atlântico Sudoeste.

3. MATERIAL E MÉTODOS

3.1. Coleta de dados e material biológico

Tubarões anequim foram amostrados em cruzeiros de pesquisa e de pesca comercial na ZEE do Sul do Brasil e na ZEE do Uruguai, assim como nas águas internacionais adjacentes a ambos os países, entre 24°29´S e 45°50´S e entre 30°02´W e 54°50´W (**Fig. 2**). Os cruzeiros de pesquisa ocorreram entre os anos 1996 e 1999 e os cruzeiros de pesca comercial entre os anos 2004 e 2012. A amostragem abrangeu todos os meses do ano. Inicialmente foi obtida a amostra do Sul do Brasil e posteriormente, com o intuito de acrescentar a representatividade das classes de comprimento pouco frequentes, foram incluídos indivíduos capturados na ZEE do Uruguai. O petrecho de pesca utilizado em todos os cruzeiros foi espinhel de superfície e no caso da pesca comercial, esta foi dirigida a atuns, espadartes e tubarões. Um neonato capturado em águas costeiras do Sul do Brasil foi incluído no estudo.

Para cada tubarão anequim capturado foi registrado o sexo, medido o comprimento furcal (CF) (baseado em Compagno 2001) e coletada uma secção de 3 a 5 vértebras da coluna vertebral. Nos cruzeiros de pesquisa, as vértebras foram coletadas na altura da primeira nadadeira dorsal (11% das vértebras) e nos cruzeiros de pesca comercial na altura da região branquial (89% das vértebras), com o fim de evitar danificar as carcaças que posteriormente seriam comercializadas. Levando em conta que não foram encontradas diferenças nas estimativas de idade realizadas em vértebras de ambas as regiões da coluna do tubarão anequim (Bishop *et al.* 2006, Natanson *et al.* 2006) as amostras foram

agrupadas. A bordo, cada conjunto de vértebras foi fixado em formalina 10% por 24 horas, ou armazenado congelado e posteriormente preservado em álcool 70%.

3.2. Processamento das vértebras e estimação de idade

No laboratório, o excesso de tecido de cada secção da coluna vertebral foi removido com uso de faca. Uma vértebra de cada tubarão foi escolhida para ser processada, da qual foram retirados o arco neural e processos laterais, e removida a cartilagem intervertebral para expor a superfície do centro vertebral. Cada centro vertebral foi seccionado sagitalmente ao nível do foco com uso de uma serra metalográfica de baixa velocidade (Buehler®), provida de uma lâmina de aço diamantado (**Fig. 3a**). Foram obtidas secções com forma de "gravata borboleta" de 0,5 – 0,7 mm de espessura. As secções foram armazenadas em álcool 70% para evitar encolhimento e deformação.

As secções vertebrais apresentam dois tipos de bandas, distinguidas uma da outra pelo seu padrão de calcificação diferente. As diferenças na calcificação causam diferenças nas propriedades ópticas nas bandas, sendo uma opaca e uma translúcida. Um par de bandas, constituído por uma banda opaca e outra translúcida, é interpretado comumente como um ciclo de crescimento, e a periodicidade da sua formação requer validação (Casselman 1983, Cailliet *et al.* 2006). No presente estudo, realizou-se a contagem do número de bandas opacas, portanto quando mencionados os termos "banda" ou "banda de crescimento", refere-se à banda opaca.

Para a estimação da idade, as secções vertebrais foram lidas *in natura* sob luz refletida com uso de um microscópio estereoscópico provido de uma escala micrométrica em um dos oculares e com magnificação de 10x. A leitura de cada secção vertebral consistiu na

contagem do número de bandas opacas que atravessaram a *intermedialia* e na medição do raio de cada banda e da vértebra (RV). As medições dos raios das bandas e do RV foram realizadas desde o foco até a margem externa de cada banda e desde o foco até a margem externa da secção da vértebra, respectivamente, com a escala do ocular posicionada ao longo do eixo transversal da *intermedialia* (**Fig. 3b**).

Para avaliar se a vértebra cresce proporcionalmente com o corpo do animal, foi avaliada a relação entre o raio da vértebra (RV) e o comprimento furcal (CF) através de uma análise de regressão para os sexos combinados. Todas as secções vertebrais foram lidas duas vezes pelo mesmo leitor. Com o intuito de dar maior consistência às interpretações de idade, uma terceira leitura foi realizada por um segundo leitor. As leituras foram independentes entre si, realizadas em tempos diferentes e sem conhecimento prévio do comprimento do animal, sexo, data de captura nem contagem previa.

A segunda leitura do primeiro leitor foi comparada com a contagem do segundo leitor. Quando a diferença foi de duas ou menos bandas, a segunda leitura do primeiro leitor foi a utilizada para fazer estimativa de idade. Secções vertebrais com uma diferença de três ou mais bandas foram re-avaliadas pelos dois leitores com o fim de obter consenso. O número de bandas estabelecido no consenso foi o utilizado para fazer as estimativas de idade. Quando não houve consenso, a vértebra foi classificada como "ilegível" e rejeitada.

Para analisar viés entre leituras foi utilizado o gráfico de viés de idades (Campana *et al.* 1995). A reprodutibilidade das leituras pelo mesmo leitor e entre leitores foi examinada para a amostra total com uso do índice de erro percentual médio (IAPE) (Beamish & Fournier 1981).

Para identificar a periodicidade da formação das bandas de crescimento (as opacas no caso deste estudo) foram realizados dois tipos de análises do incremento marginal: a análise da borda e a análise do incremento marginal relativo (IMR) (Campana 2001). Na primeira, a borda das secções vertebrais foi categorizada como opaca ou translúcida, e as frequências relativas de cada categoria foram comparadas mensalmente ao longo do ano. Períodos com maior frequência de bordas opacas estão relacionados às épocas de formação das bandas de crescimento. Na análise do IMR, a área de crescimento desde a última banda até a borda é expressa como uma porcentagem da largura do último par de bandas (Cailliet & Goldman 2004). O IMR foi calculado para cada secção vertebral segundo Natanson *et al*. (1995):

$$IMR = \frac{(RV - R_n)}{(R_n - R_{n-1})}$$

Onde R_n é o raio da última banda opaca e R_{n-1} é o raio da penúltima banda opaca. O IMR médio foi calculado para cada mês e para cada trimestre e análise de variância (ANOVA) de um fator foi realizada para testar diferenças entre meses e entre trimestres. Meses ou trimestres com valores de IMR médio próximos a 1 foram interpretados como épocas do ano nas quais uma banda de crescimento está prestes a se formar (Campana 2001, Lessa *et al.* 2006).

3.3. Modelagem do crescimento

Uma vez estimada a idade de todos os indivíduos, foi ajustado o modelo de Schnute (1981) ao conjunto de dados de idade-comprimento para ambos os sexos em separado. Este modelo foi escolhido por ter a característica de ser flexível, já que inclui na sua formulação

a maioria dos modelos clássicos de crescimento como casos especiais (Schnute 1981). A equação genérica do modelo usada neste estudo é descrita pela seguinte função:

$$Y(t) = \left[y_1^{\,b} + \left(y_2^{\,b} - y_1^{\,b}\right) \times \frac{1 - e^{-a(t-\tau 1)}}{1 - e^{-a(\tau 2 - \tau 1)}} \right]^{1/b}$$

onde $Y(t)$ é o tamanho de um peixe a uma idade t e a, b, y_1 e y_2 são os quatro parâmetros nos que se baseia o modelo. Os parâmetros a e b estão associados com a forma da curva e os parâmetros y_1 e y_2 representam tamanhos médios esperados que o peixe toma a duas idades diferentes: τ_1 e τ_2. Estas idades são escolhas arbitrarias restritas à condição $\tau_1 < \tau_2$. Neste estudo τ_1 foi fixado como a mínima idade estimada na amostra e τ_2 como 15 anos de idade.

Um conjunto de oito regiões é definido no modelo e cada uma destas regiões está associada a uma determinada forma de curva de crescimento. Combinações específicas dos parâmetros a e b levam a uma ou mais das oito regiões no plano a, b (Schnute 1981). Assim, o modelo pode tomar oito formas de curvas de crescimento diferentes ou uma forma derivada da combinação de mais do que uma região. Estas propriedades paramétricas permitem o uso direto dos dados na seleção de uma curva de crescimento adequada.

Quatro parâmetros adicionais podem existir, mas a sua ocorrência vai depender do tipo de curva que o modelo assuma. Estes são: tau zero (τ_o), tau estrela (τ^*), y estrela (y^*) e tamanho assintótico ($y\infty$). τ_o é uma idade correspondente a um tamanho zero, τ^* e y^* são a idade e o tamanho, respectivamente, onde a curva de crescimento tem um ponto de inflexão e $y\infty$ é o tamanho assintótico.

O modelo de Schnute foi ajustado utilizando uma abordagem bayesiana. Nesta abordagem, as estimativas dos parâmetros de crescimento foram dadas como uma

distribuição de probabilidade posterior a partir da qual foram realizadas as inferências (Kinas & Andrade, 2010). As distribuições posteriores de cada parâmetro, com sua média e intervalo de credibilidade de 95% (*ICr*$_{95\%}$), foram obtidas através do método de simulação estocástica de re-amostragem por importância (SIR) (Rubin 1988) e as *prioris* utilizadas foram não-informativas. Para a aplicação do método SIR foi utilizado o algoritmo descrito por Kinas e Andrade (2010). A probabilidade para cada uma das oito regiões definidas pelo modelo de Schnute, e por tanto, a probabilidade de que o modelo assuma uma forma específica de curva de crescimento, foi obtida com a abordagem bayesiana.

Independentemente da forma da curva de crescimento obtida pelo modelo de Schnute, o modelo de von Bertalanffy foi ajustado com o intuito de facilitar as comparações com a literatura. Um erro multiplicativo foi assumido, o que implicou que os dados de comprimento para cada idade seguem uma distribuição log-Normal, com uma média μ e uma precisão τ: comp [i] ~ logNormal (μ [i], τ), onde μ [i] e a idade [i] foram ajustados na equação de von Bertalanffy, que segue:

$$\mu\,[i] = \log(L\infty) + \log(1-\exp(-k(\text{idade}[i]-t_0)))$$

onde $L\infty$ é o comprimento teórico máximo atingido; k é o coeficiente de crescimento expressado em anos^{-1} e t_0 é a idade teórica que o peixe teria ao comprimento zero.

O modelo de von Bertalanffy foi ajustado para ambos os sexos em separado utilizando uma abordagem bayesiana. As distribuições posteriores de cada parâmetro, com sua mediana e intervalo de credibilidade de 95% (*ICr*$_{95\%}$), foram obtidas através do método de simulação de Monte Carlo com cadeias de Markov (MCMC). *Prioris* não-informativas foram utilizadas com o intuito de dar maior peso aos dados. Para obter uma boa

aproximação, três cadeias de Markov foram simuladas com um total de 600000 ciclos, descartados os primeiros 440000 e retiradas amostras a cada 40 iterações.

O software R (R Core Team, 2012) foi utilizado para fazer as análises estatísticas, simulações e exibições gráficas. O programa OpenBUGS (Thomas *et al.* 2006) e as bibliotecas R2WinBUGS (Sturtz *et al*. 2005) e BRugs (Thomas *et al*. 2006) foram utilizados para ajustar o modelo de von Bertalanffy e obter a amostra da distribuição posterior para cada parâmetro.

4. SÍNTESE DOS RESULTADOS

Foram processadas vértebras de 252 tubarões anequim para a análise de idade e crescimento. Os tamanhos das fêmeas variaram entre 101 e 330 cm CF e os tamanhos dos machos entre 81 e 250 cm CF. Das vértebras processadas, sete foram classificadas como ilegíveis e descartadas, e a estimação de idade foi baseada em 245 indivíduos (126 fêmeas, 116 machos e 3 tubarões de sexo indeterminado). Os 3 tubarões de sexo indeterminado foram incluídos nas estimativas de idade mas não assim nas estimativas de crescimento. Estes tubarões mediram 78, 84 e 105 cm CF.

A relação entre RV e o CF foi linear ($CF = 16.497 + 14.328\ RV$, $r^2 = 0.935$, $P < 0.001$, $n = 252$). A proporcionalidade entre o crescimento da vértebra e o crescimento do animal demonstrou que as vértebras são estruturas de aposição adequadas para descrever o crescimento individual da espécie.

Não foi detectado viés entre as leituras realizadas pelo mesmo leitor até as 18 bandas. A partir desse número, o gráfico de viés mostrou diferenças entre as contagens, evidenciando uma maior dificuldade para interpretar as bandas distais em indivíduos maiores

(possivelmente mais velhos). O IAPE entre as leituras do mesmo leitor foi 11.9% e 14.3% entre leitores. Esses valores foram relativamente altos e evidenciaram algumas dificuldades para reproduzir as leituras em vértebras do tubarão anequim. No entanto, este nível de reprodutibilidade foi considerado aceitável para estudos de idade em tubarões baseados em vértebras que, na sua maioria, foram realizados com coeficiente de variação médios (Chang 1982) maiores a 10% (~ IAPE = 7.1%) (Campana 2001). A posterior reavaliação das secções com uma diferença de três ou mais bandas entre leitores em uma tentativa de chegar a um consenso, ofereceu maior consistência às interpretações de idade.

A análise da borda não mostrou uma tendência clara em relação ao período do ano com maior frequência de bordas opacas e, portanto de formação das bandas de crescimento. Por sua parte, na análise do incremento marginal relativo (IMR) não foram encontradas diferenças significativas no IMR médio mensal ao longo do ano (ANOVA: $F = 0.815$, $P = 0.6145$) nem no IMR médio trimestral (ANOVA: $F = 0.7876$, $P = 0.5021$). Assim, as distintas análises de incremento marginal não foram conclusivas em relação à identificação da periodicidade na formação das bandas de crescimento no Atlântico Sudoeste. A idade foi designada assumindo um padrão anual de deposição das bandas, de acordo com os testes rigorosos de validação realizados para *I. oxyrinchus* no Atlântico Norte (Campana *et al.* 2002, Ardizzone *et al.* 2006 e Natanson *et al.* 2006). Partindo deste pressuposto, uma banda de crescimento representou um ano de idade.

Baseado na contagem de bandas nas vértebras, a idade estimada para os tubarões anequim do Atlântico Sudoeste variou de 0 a 28 anos. O tubarão mais velho foi uma fêmea de 330 cm CF (a fêmea maior da amostra). O macho mais velho teve 18 anos e mediu 241 cm CF. O maior macho (250 cm) teve 17 anos. A fêmea mais velha foi excluída para o

ajuste do modelo, pois seu dado de comprimento-idade ficou afastado do conjunto geral dos dados, tornando-a excessivamente influente no ajuste.

O modelo de Schnute ofereceu uma boa descrição do padrão geral dos dados para ambos os sexos, sendo bem ajustado até ~15 anos. Nas idades maiores, os intervalos de probabilidade posteriores começaram a ser mais amplos, sendo as estimativas menos confiáveis. O ajuste Bayesiano ofereceu uma estimativa precisa dos parâmetros *a*, *b*, y_1 e y_2 para ambos os sexos, com intervalos de probabilidade estreitos (**Fig. 4**).

Os comprimentos estimados pelo modelo de Schnute à idade 0 foram 88.7 cm ($ICr_{95\%}$ = 65.1 - 97.1) para as fêmeas e 81.2 cm ($ICr_{95\%}$ = 71.1 - 89.5) para os machos. Os comprimentos estimados à idade 1 foram 96.9 cm ($ICr_{95\%}$ = 82.9 - 103.8) para as fêmeas e 93.5 cm ($ICr_{95\%}$ = 88.6 - 98.4) para os machos. O crescimento no primeiro ano de vida, estimado a partir da diferença entre o tamanho médio predito pelo modelo para a idade 1 e o tamanho de nascimento reportado para a espécie (63 cm CF, Mollet *et al*. 2000) foi 33.9 cm ($ICr_{95\%}$ = 19.9 – 40.8) para as fêmeas e 30.5 cm ($ICr_{95\%}$ = 25.6 - 35.4) para os machos. Os intervalos de probabilidade mais estreitos para os machos mostraram que as estimativas foram mais precisas para este gênero, possivelmente devido à melhor representatividade de anequins jovens na amostra dos machos.

De acordo com as predições do modelo de Schnute, até os 15 anos de idade, fêmeas e machos atingiram comprimentos similares (217 cm e 216 cm CF, respectivamente). A partir dessa idade, os machos parecem ser maiores que as fêmeas, no entanto as estimativas logo após os 15 anos são pouco precisas.

Para as fêmeas, o 79 % das combinações dos parâmetros *a* e *b* estiveram na região 8 do plano *a*, *b*. A curva dentro desta região apresenta um crescimento assintótico e forma

sigmoide com um ponto de inflexão que indica uma mudança no padrão de crescimento. O ponto de inflexão (τ^*, y^*) se apresentou aos 7 anos de idade e 153 cm de CF. O tamanho assintótico ($y\infty$) foi 244 cm CF ($ICr_{95\%}$ = 220 – 302) e parece ter sido subestimado pelo modelo, em relação ao tamanho máximo que alcançam as fêmeas do anequim.

Para os machos, o 57% das combinações dos parâmetros *a* e *b* favoreceram a região 3. A curva dentro desta região apresenta um crescimento não assintótico e forma sigmoide. As regiões 1, 2 e 8 tiveram probabilidades de 17%, 12% e 14% respectivamente. As curvas associadas com as regiões mais prováveis apresentam um ponto de inflexão que indica uma mudança no crescimento dos machos. Essa mudança no crescimento se apresentou aos 7 anos de idade e 148 cm de CF. Somando as probabilidades das regiões 1, 2 e 8, existe uma probabilidade de 43% de que os machos exibam um crescimento assintótico. O tamanho assintótico estimado foi 261 cm CF ($ICr_{95\%}$ = 216 – 357) , sendo um valor aproximado do comprimento máximo registrado para os machos de tubarão anequim.

O ajuste bayesiano do modelo de Schnute mostrou uma baixa probabilidade para a região 2 para ambos os sexos (5.1% para fêmeas e 12% para machos). Essa região está associada a uma curva de crescimento do tipo de von Bertalanffy. A baixa probabilidade significa que esse modelo não se ajusta bem aos dados. Este fato foi confirmado quando o modelo de von Bertalanffy foi ajustado independentemente ao conjunto de dados comprimento-idade. As estimativas dos parâmetros foram pouco precisas para ambos os sexos, com intervalos de credibilidade amplos. A estimativa do $L\infty$ teve maior sentido biológico para as fêmeas (416 cm; $ICr_{95\%}$ = 293 - 1199) que para os machos (580 cm; $ICr_{95\%}$ = 329 - 1381) embora esses valores tenham sido sobre-estimados de acordo com os tamanhos máximos reportados para a espécie.

5. CONCLUSÕES

O presente estudo forneceu as primeiras estimativas de idade e crescimento do tubarão anequim no Atlântico Sudoeste a partir de uma amostra representativa dos indivíduos capturados nessa região pela pesca de espinhel de superfície. A amplitude de idades estimadas a partir da análise das vértebras foi entre 0 e 28 anos.

A fase do crescimento individual de *I. oxyrinchus* até os 15 anos de idade foi bem descrita para ambos os sexos pelo modelo flexível de Schnute. Dentro da janela de idades descrita pelo modelo, não foi alcançado um tamanho assintótico.

Fêmeas e machos apresentaram crescimento similar e à idade de 15 anos atingiram ~217 cm CF. A forma sigmoide nas curvas de crescimento de ambos os sexos evidenciou uma mudança no padrão de crescimento, que em machos foi perto da idade de primeira maturidade.

Os resultados inconclusivos em relação à periodicidade na deposição das bandas de crescimento na área de estudo, tornam necessária a aplicação de técnicas mais robustas de validação no futuro, devido a que diferentes interpretações em relação à periodicidade, resultam em mudanças nas taxas de crescimento, primeira idade de maturidade e idade máxima. Enquanto isso, uma abordagem preventiva que assuma um padrão de deposição anual pode ser usada em políticas de manejo para esta espécie com características de baixa fecundidade e maturidade tardia.

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7. FIGURAS

Figura 1. A espécie de estudo, o tubarão anequim *Isurus oxyrinchus*, capturado no Atlântico Sudoeste.

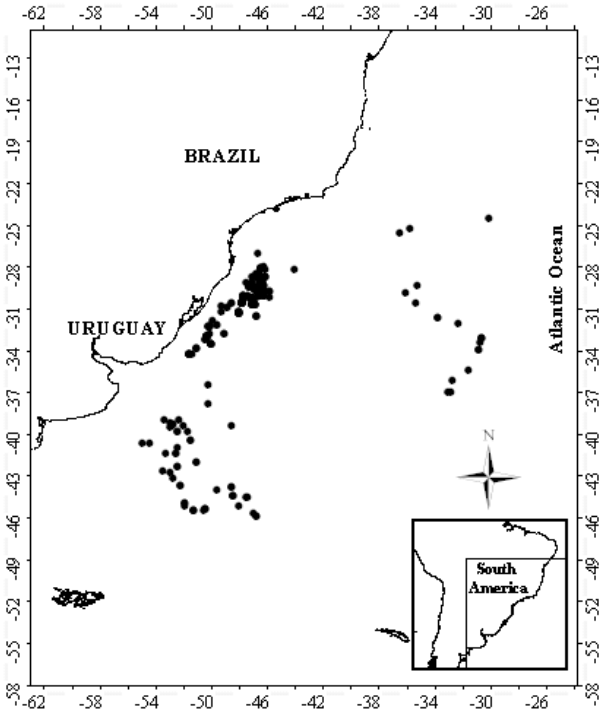

Figura 2. Área de amostragem mostrando as posições de início de cada um dos lances de pesca (pontos pretos) onde foram capturados os tubarões anequim utilizados no presente estudo.

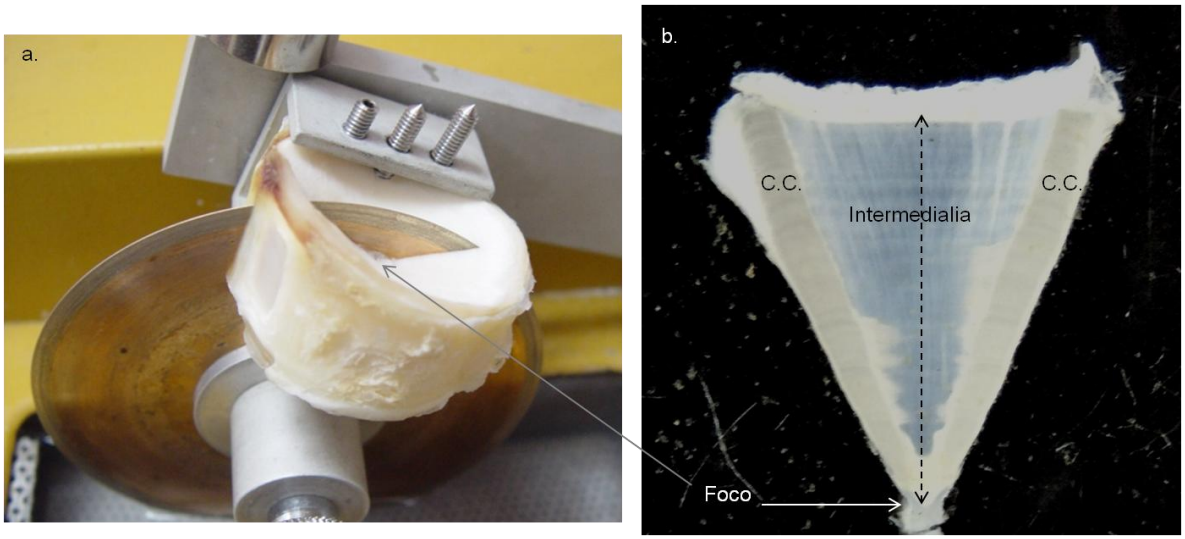

Figura 3. a. Centro vertebral de *Isurus oxyrinchus* seccionado sagitalmente ao nível do foco. **b.** Secção vertebral obtida do corte sagital (se apresenta uma metade). Destacam-se as posições do foco, da *intermedialia* e do *corpus calcareum* (C.C.). A seta pontilhada evidencia onde foi tomada a medida do raio da vértebra.

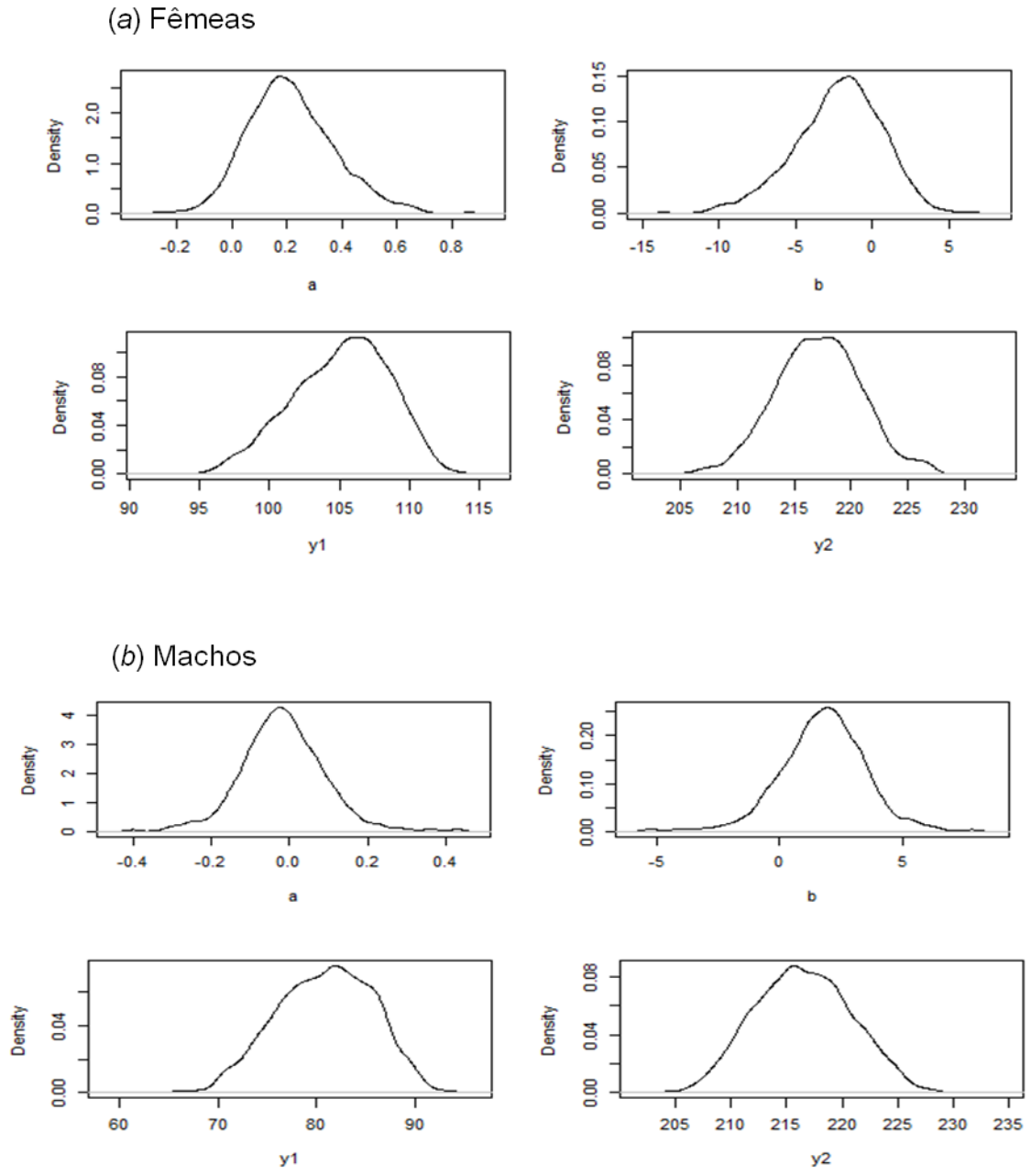

Figura 4. Distribuições posteriores dos parâmetros do modelo de crescimento do Schnute: a, b, y_1 e y_2 para (a) fêmeas e (b) machos do tubarão anequim. y_1 é o tamanho à idade τ_1 que nas fêmeas foi 2 anos e nos machos foi 0 anos; y_2 é o tamanho à idade τ_2 que em ambos os sexos foi de 15 anos.

8. APÊNDICE: MANUSCRITO para o periódico *Fisheries Research*

Age and growth of the shortfin mako shark *Isurus oxyrinchus* in the western South Atlantic Ocean

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Abstract

Age and growth estimates of female and male shortfin mako sharks *Isurus oxyrinchus* from the western South Atlantic Ocean were obtained through the analysis of vertebral sections of 245 specimens (126 females, 116 males and 3 with undetermined sex), ranging in size from 78 to 330 cm fork length (FL). A significant linear relationship was found between FL and vertebral radius for sexes combined. Marginal increment analyses were inconclusive about periodicity of growth band deposition and an annual periodicity was assumed to make age estimations. Specimens were estimated to be between 0 and 28 years of age. The Schnute growth model (SGM), chosen for its flexibility and fitted with a Bayesian approach, provided a good description of the individual growth for both sexes up to 15 years of age. Shortfin mako growth during the first year of life was 33.9 cm ($ICr_{95\%}$ = 19.9 - 40.8) for females and 30.5 cm ($ICr_{95\%}$ = 25.6 - 35.4) for males. Until approximately 15 years of age, both sexes showed similar growth and reached ~217 cm FL. Sigmoid shaped growth curves obtained for both sexes indicated a change in the growth pattern close to 7 years of age. Inconclusive results about periodicity of growth band deposition in the study area make necessary the application of more robust validation techniques in the future. Meanwhile, a precautionary approach that assumes an annual deposition pattern in the western South Atlantic can be used for the assessment and management of stocks of this species, characterized by low fecundity and late maturity.

Keywords: *Isurus oxyrinchus*; age and growth; Schnute growth model; Bayesian approach.

1. Introduction

The shortfin mako shark *Isurus oxyrinchus* (Rafinesque, 1810) is a large lamnid found in tropical and temperate waters worldwide (Compagno, 2001). Primarily oceanic, it occurs from the surface down to at least 880 meters depth, being most closely associated with the mixed layer (Abascal et al., 2011) and with temperatures from 17 to 22°C (Casey and Kohler, 1992; Cliff et al., 1990). The species performs extensive horizontal movements with records of up to ~4,500 km in distance (Kohler and Turner, 2001). Although there is no record of a transequatorial movement in the Atlantic Ocean (Casey and Kohler, 1992; Kohler et al., 2002), sufficient genetic exchange seems to occur between stocks of both hemispheres with no evidence of a discrete genetic stock in the South Atlantic (Heist, 2008; Schrey and Heist, 2003). Makos are born at a size of 63-69 cm in fork length (FL) (Joung and Hsu, 2005; Mollet et al., 2000; Semba et al., 2011) and the maximum sizes reported for the species are of 362 cm FL (Bigelow and Schroeder, 1948) for females and 270 cm FL (Bishop et al., 2006) for males.

Shortfin makos are caught as bycatch in surface pelagic longline fisheries targeting tuna (*Thunnus* spp.), swordfish (*Xiphias gladius*) and blue shark (*Prionace glauca*) and are retained for their valuable meat and fins (Clarke et al., 2006; Compagno, 2001). In the South Atlantic the species is highly susceptible to these fisheries (Cortés et al., 2010), being the second-most common shark species in the catches (Domingo et. al., 2002; Montealegre-Quijano et al., 2007). Whereas a stable trend of the standardized catch per unit of effort was reported for the species in the Atlantic (Carvalho et al., 2009; Mejuto et al., 2009; Pons and Domingo, 2009), there are still difficulties to assess the current status of the stocks there

due to the high uncertainty in past catch estimates and deficiency of important biological parameters, particularly for the southern stock (ICCAT, 2012).

Assessment of the stock status of living resources and estimating a level of sustainable exploitation requires knowledge of the age structure of the population, including individual growth characteristics, mortality and longevity estimates (Ricker, 1975). Age estimation studies provide the basis data to generate this knowledge (Campana, 2001). Age estimations associated with observed individual sizes (age-at-length data) could be fit to growth models to describe the mean growth of individual fish in a population.

Several models have been proposed to estimate growth in fishes, however, in most of age and growth studies of chondrichthyan fishes, only the von Bertalanffy growth model (VBGM) (von Bertalanffy, 1938) was applied (Cailliet et al., 2006). VBGM seems not to provide the best fit to elasmobranch age-at-length data when applied in conjunction with other growth models and several species seem to follow growth trajectories different to the proposed by the VBGM (Araya and Cubillos, 2006; Katsanevakis and Maravelias, 2008).

Despite this, most of the shortfin mako growth studies conducted to date, have used the VBGM uniquely (Cerna and Licandeo, 2009; Pratt and Casey, 1983; Ribot-Carballal et al., 2005; Semba et al., 2009). A few studies used the VBGM, and tested other models such as the logistic (Cailliet et al., 1983), Gompertz (Natanson et al., 2006) and Schnute (Bishop et al., 2006). When more than one model was used, the VBGM did not provide the best fit (Bishop et al., 2006; Cailliet et al., 1983; Natanson et al., 2006 for female data set).

Given this scenario, the use of a flexible model as the Schnute growth model (SGM) (Schnute, 1981) appears as an interesting alternative, since its formulation includes several classical growth models as special cases. The SGM considers not only asymptotic growth,

but also linear, quadratic, power or exponential growth (Schnute, 1981). Thus, it not restrict the observed data to a single model, but allows the data to be used directly in deciding which type of model is most appropriate (Schnute, 1981).

The first studies on age and growth of shortfin mako sharks (Cailliet et al., 1983; Pratt and Casey, 1983) obtained contrasting growth parameters estimates, due to different assumptions on the periodicity of growth band deposition. Pratt and Casey (1983) assumed a biennial (2 growth bands per year) periodicity, whereas Cailliet et al. (1983) assumed an annual periodicity (1 growth band per year). Since then, age and growth studies of shortfin mako sharks have been conducted in the North Pacific (Ribot-Carballal et al., 2005; Semba et al., 2009), South Pacific (Bishop et al., 2006; Cerna and Licandeo, 2009) and North Atlantic (Ardizzone et al., 2006; Campana et al., 2002; Natanson et al., 2006). All these studies reported an annual pattern in growth band formation, but only the studies in the North Atlantic validated the annual periodicity with bomb radiocarbon techniques (Ardizzone et al., 2006; Campana et al., 2002) and one individual chemically-tagged with oxytetracycline (OTC) (Natanson et al., 2006). Recently, Wells et al. (2013) using OTC in specimens <200 cm FL from North Pacific, concluded that at least for the first five years, young shortfin makos deposit 2 growth bands per year.

I. oxyrinchus is a species of low fecundity (Costa et al., 2002; Semba et al., 2011; Stevens, 1983), late maturity (Francis and Duffy, 2005; Mollet et al., 2000) and a reproductive cycle of 3 years (Joung and Hsu, 2005; Mollet et al., 2000). These life history traits added to the fact that is a common by-catch species in the western South Atlantic, make *I. oxyrinchus* a species susceptible to be overexploited. Despite this, there are still no studies on the age and growth for this species in the South Atlantic. In this study, using a

flexible growth model and a Bayesian approach, we provide the first age estimation and analysis of growth for shortfin mako sharks in the western South Atlantic.

2. Materials and methods

2.1. Data and sample collection

Shortfin mako sharks were obtained from research cruises and commercial fishing vessels within the EEZ of southern Brazil and the EEZ of Uruguay, as well as in the international waters adjacent to both countries, between 24°29´S and 45°50´S and between 30°02´W and 54°50´W (**Fig. 1**). Initially, the sample of southern Brazil was obtained. Subsequently, with the aim of increasing the sample size of length classes poorly represented, sharks sampled by the Uruguayan National Observers Program on Board the Tuna Fleet were included. Research cruises took place between 1996 and 1999 and commercial cruises between 2004 and 2012. Six cruises occurred in summer (March/1998, February/2004, March/2005, February/2008, January/2009 and February/2012), three in autumn (June/2004, April/2010 and June/2012), five in winter (July/1997, August/1999, September/2004, July/2005 and August/2006) and three in spring (November/1996, December/2005 and October/2008). The fishing gear used in all cruises was surface pelagic longline and, in the case of commercial fishery, it targeted swordfish, tuna and sharks. One neonate caught in coastal waters of southern Brazil was also included.

All shortfin mako sharks were measured and their sex identified. The fork length (FL) was recorded to the nearest centimeter, as a straight-line distance from the tip of the snout to the fork of caudal fin (Compagno, 2001). For age determination, a section of 3 to 5 vertebrae was removed from the vertebral column. Samples from research cruises were

collected below the first dorsal fin (11% of vertebrae) and samples from commercial vessels were collected over the branchial region (89% of vertebrae) to avoid damaging the carcasses which would later be sold. Since no difference in age estimates was found between vertebrae from the branchial and dorsal regions for this species (Bishop et al., 2006; Natanson et al., 2006), samples were pooled. Vertebrae were stored until analysis either frozen or fixed in 10% formalin for 24 hours and then preserved in 70% ethanol.

2.2. Vertebral processing and age estimation

Excess tissue was cut off from the column sections, and one vertebra was chosen for processing. Neural arch, lateral processes and intervertebral cartilages were removed with use of a blade, to expose the surface of the centrum. Each vertebral centrum was sectioned in a sagital plane through the focus (notochordal remnant, Casey et al., 1985) with an Isomet low-speed saw (Buehler®) provided with a diamond blade. "Bow tie" shaped sections of 0.5 - 0.7 mm thick were obtained. Sections were stored in 70% ethanol to avoid shrinkage and deformation.

When viewed microscopically, vertebral sections show a growth pattern with two types of bands, distinguished by their different calcification pattern (e.g. more and less calcified). Differences in calcification cause different optical properties in the bands, being one opaque and one translucent. A band pair, comprising one opaque and one translucent band, is commonly interpreted as one cycle of growth, and the periodicity on which this band pair is deposited requires validation (Cailliet et al., 2006; Casselman, 1983). In this study, the number of opaque bands was counted and when refers to "band" or "growth band" we will refer to the opaque band.

Vertebral sections were read *in natura*, always submerged in 70% ethanol, using a stereo microscope provided with one ocular with micrometric scale, and under reflected light against a black background. The reading of each vertebral section consisted on counting the number of growth bands that traverse the *intermedialia*, and measuring the radius of each band and of the vertebrae. Under reflected light, the opaque band does not transmit light but reflects it, so this zone appears white (Casselman, 1983). Measurements of each band and vertebral radius (VR) were performed from the focus to the outer edge of each band, and from the focus to the outer edge of the vertebral section, respectively. All measurements were performed with the micrometric scale positioned along the transverse axis of the *intermedialia*. Magnification was held constant at 10x (10 micrometer units = 1 mm).

To assess if vertebra grow proportionally with shark body in this species, the relationship between vertebral radius (VR) and fork length (FL) was assessed with a regression analysis for sexes combined. Two readings of each vertebral section were performed by the same reader. To give additional strength to the age interpretations, a third reading was made independently by a second reader. Band counts were made without knowledge of the fish length, sex, date of capture or number of bands in previous counts.

The second count of the first reader was compared with the single count of the second reader. When the difference was two or fewer bands, the second count of the first reader was used to estimate age. Vertebral sections with a difference in band number of at least three bands were reevaluated by the readers in an attempt to reach a consensus. The number of bands established by consensus was used to make age estimations. If no consensus was reached, the vertebra was classified as “unreadable” and discarded.

Bias was analyzed using the age bias plot (Campana et al., 1995). Reproducibility between readings of the same reader and between readers was tested for the entire sample with the index of average percent error (IAPE) (Beamish and Fournier, 1981).

To identify the periodicity in growth band formation, marginal increment analyses were performed, using two variations of the method: the edge analysis and the mean marginal increment ratio (MIR) analysis (Campana, 2001). In the first, the edge of the vertebral section was classified as opaque or translucent and relative frequencies of each category were compared monthly; whereas in the second, the mean MIR was calculated for each month and for each quarter and analysis of variance (ANOVA) of one factor was performed to test for differences between months and quarters. A significance level of α=0.05 was used in the test. MIR for each vertebral section was calculated according to Natanson et al. (1995):

$$MIR = \frac{(VR - R_n)}{(R_n - R_{n-1})}$$

where R_n is the radius of the last opaque band and R_{n-1} is the radius of the next to last opaque band. Months and quarters with mean MIR values close to one, were interpreted as the time of year in which a growth band formation is close to being completed, and therefore a growth cycle is being closed (Campana, 2001; Lessa et al., 2006). The MIR analysis was conducted both for the overall sample (per month and per quarter of year) and for three age groups: 0-5 years of age, 6-10 years of age and 11-26 years of age (per quarter of year).

From the estimated ages and individual length data observed, two length-age keys (Sparre and Venema, 1995) were constructed, one for females and one for males. The keys

can be used in future studies that aim to determine the age structure of the shortfin mako catches in western South Atlantic fisheries.

2.3. Growth model

The Schnute growth model (SGM) (Schnute, 1981) was fitted to the observed length-at-age data for each sex separately. SGM was chosen because of its flexibility and versatility, as it includes in its formulation most classical growth models -such as von Bertalanffy, Gompertz, Richards and logistic- as special cases (Schnute, 1981). The general equation of the model (case with $a \neq 0$ and $b \neq 0$), used in this study, is described by the following function:

$$Y_{(t)} = \left[y_1^{\,b} + \left(y_2^{\,b} - y_1^{\,b} \right) \times \frac{1 - e^{-a(t-\tau 1)}}{1 - e^{-a(\tau 2-\tau 1)}} \right]^{1/b}$$

where $Y_{(t)}$ is the size of a fish at age t and a, b, y_1 and y_2 are the four parameters which SGM is based. The parameters a and b define the shape of the curve, where a is the relative rate of relative growth (e.g. growth acceleration) and b is the increase or decrease (variation) in growth acceleration. The parameters y_1 and y_2 are expected mean sizes that a fish takes at two particular ages τ_1 and τ_2. These ages are arbitrary choices within the age range of the observed data, restricted to the condition $\tau_1 < \tau_2$. In this study τ_1 was fixed as the minimum estimated age in the sample and τ_2 as 15 years of age.

A set of eight regions is defined in the model and each of these regions is associated with a specific shape of growth curve. Specific combinations of the parameters a and b lead to one or more of the eight regions in the a,b-plane (Schnute, 1981). Therefore, the model can take eight different growth curve shapes or a shape derived of the combination of more

than one region. These parametric properties allow direct use of the data in selecting an appropriate growth curve.

Four additional parameters, defined as tau zero (τ_0), tau star (τ^*), y star (y^*) and asymptotic size ($y\infty$) can exist, but its occurrence would depend on the type of growth curve the model takes. τ_0 is an age corresponding to a projected size zero, τ^* and y^* are the age and the size, respectively, where the growth curve has an inflection point and $y\infty$ is the asymptotic size. To reduce border effects among regions in the *a*,*b*-plane, the lines containing *a*, *b* parameter values near zero were excluded.

Independently of the shape of growth curve that the SGM had taken, the von Bertalanffy growth model (VBGM) was fitted to the observed length-at-age data for each sex separately to facilitate comparisons with the literature. A multiplicative error was assumed which implied that the length data for each age follow a log-Normal distribution, with mean μ and a precision τ: length [i] ~ logNormal (μ [i], τ), where μ [i] and an age [i] were fitted in the von Bertalanffy equation that follows:

$$\mu\,[i] = \log(L\infty) + \log(1-\exp(-k(\text{age}[i]-t_0)))$$

where $L\infty$ is the theoretical maximum length reached; k is the growth coefficient expressed in years^{-1} and t_0 is the theoretical age that a fish would has at length zero.

2.4. Bayesian fit

A Bayesian approach was used to fit the SGM to the data. In the Bayesian approach the estimates of the growth parameters are given as a probability distribution. This probability distribution denoted "*posterior* distribution", is the most complete expression of the

plausibility of different parameter values and the central element to make inference (Kinas and Andrade, 2010). The posterior distribution is the outcome from the combination through Bayes Theorem, of previous information summarized in a distribution named *priori,* with statistical data summarized in the likelihood function. In cases where the posterior distribution cannot be derived analytically, stochastic simulation methods are used instead.

The stochastic method used in this study, named Sampling Importance Resampling (SIR) (Rubin, 1988), uses another probability density (called importance function) "similar" to the posterior, from which samples can be generated easily. A non-central multivariate Student distribution for the SGM parameters vector (a, b, y_1, y_2) with 8 degrees of freedom, centered at the maximum likelihood estimate "m" and with covariance proportional to the inverse Hessian matrix "E" was used as the importance function. The priors were non-informative, chosen to give more relevance to our data. The algorithm described in Kinas and Andrade (2010) was used to implement the SIR method. Firstly, a sample of 50,000 observations from the importance function was drawn. The output of these draws was a matrix of 50,000 rows and 4 columns (one for each SGM parameter). Secondly, the posterior density of the sampled points and the importance densities were calculated. The ratio of both densities was standardized (to add one) and defined "importance weight" for each draw.

In the importance resampling (2^{nd} stage of SIR) a redrawn sample of 4,000 from the first stage sample was obtained, using the importance weights as probabilities. This final sample (a matrix of 4,000 rows and 4 columns) is an approximate random sample of the posterior distribution of interest for (a, b, y_1 and y_2). To assess closeness between the target

posterior distribution and the distribution that provided the importance sample, two diagnostics were used: the one proposed by McAllister et al. (2004) and the entropy relative to uniformity (ERU) proposed by West (1993).

Posterior means were used as SGM parameter estimates and posterior medians as length-at-age estimates, due to asymmetric shaped distribution. Uncertainty about these estimates were expressed in 95% posterior credibility intervals ($ICr_{95\%}$) with lower and upper limits equal to the quartiles 2.5% and 97.5% of the posterior sample, respectively.

From the matrix containing the posterior distributions of the parameters a, b, y_1 and y_2, a new matrix of length predictions was constructed separately for females and males. Each column of this matrix corresponded to the posterior predictive length distribution for a particular age. These predictive distributions were constructed for females and males for different ages (0, 1, 5, 10, 15 and 20 years) and shown in length frequency histograms.

The probability for each one of the eight regions defined by the SGM, and therefore, the probability of the model to assume a specific shape of growth curve, was obtained with the Bayesian approach. Contour plots were constructed to show the posterior probability distribution of the a, b pair.

The VBGM was fitted with a Bayesian approach. Posterior distributions of each parameter, with its median and $ICr_{95\%}$, were obtained using the simulation method of Monte Carlo Markov chains (MCMC). No informative *priors* were used to give more weight to the data. To obtain a good approximation three Markov chains were simulated with a total of 600,000 iterations, burn in of 440,000 and a thinning of 40.

The software R (R Core Team, 2012) was used to do all statistical analyses, simulations and graphical displays. The software OpenBUGS (Thomas et al., 2006) and the libraries

R2WinBUGS (Sturtz et al., 2005) and BRugs (Thomas et al., 2006) were used to fit the VBGM and obtain the posterior sample for each parameter.

3. Results

3.1. Age estimation

Vertebrae from 252 mako sharks (131 females, 118 males and 3 of undetermined sex) were processed for age and growth analysis. Females ranged from 101 to 330 cm FL and males from 81 to 250 cm FL (**Fig. 2**). From the vertebrae processed, seven were classified as unreadable and discarded and the age estimation was made based on 245 individuals (126 females, 116 males and 3 with undetermined sex). The three specimens with undetermined sex were included in age estimates but no in growth estimates. These specimens measured 78, 84 and 105 cm FL.

A significant linear relationship was found between FL and VR for sexes combined ($r^2 = 0.935$, $P < 0.001$) (**Fig. 3**), evidencing proportionality in growth between vertebrae and body. Thus, the vertebrae are suitable structures for describing individual growth in this species.

No age estimation bias was observed within the same reader counts up to 18 bands. From this number on, the age bias plot showed differences between counts (**Fig. 4**) noting a higher difficulty to interpret distal bands in larger (presumably older) individuals. IAPE was 11.9% between counts of the same reader and 14.3% between readers. Although these values expose some difficulties to reproduce readings in vertebrae of shortfin makos, they were considered acceptable, based on that most studies that used vertebrae in sharks did so with mean coefficient of variation (Chang, 1982) exceeding 10% (~ IAPE = 7.1%)

(Campana, 2001). The re-assessment of vertebrae that differed from at least three bands and attempt to reach a consensus between different readers, gave more robustness to age interpretations.

In the edge analysis, some of the vertebral section edges could not be classified as opaque or translucent and were classified as "doubtful." Sections with doubtful edges were discarded, leaving 178 vertebrae for this analysis. The edge analysis for all ages combined showed that there was a progressive decrease in the proportion of the opaque edges from December to April, and December was the month with the highest value of opaque edges. This indicates that growth band deposition could occur in this month (**Fig. 5**). However, sample sizes were small and in the remaining months an unclear trend was observed. Therefore, the analysis was inconclusive about the periodicity pattern of band deposition. The edge analysis per quarter of year was also inconclusive, with a proportion of opaque bands of 34% in quarter 1, 20% in quarter 2, 29% in quarter 3 and 32 % in quarter 4.

The MIR analysis for the overall sample (all ages combined) per month was conducted with a sample of 203 individuals, because the other sections were discarded for difficulties associated with viewing the bands. Growth band deposition appears to be close to being completed in July, when the highest mean MIR value was reached (**Fig. 5**). However, no significant differences were found in mean MIR between months over the year (ANOVA: $F = 0.815$, $P = 0.6145$). Throughout the year, mean MIR was around 0.5 and 0.6, with high standard deviations, which showed that low and high values were present year round (**Fig. 5**). Therefore, the MIR analysis per month for the overall sample was inconclusive about the periodicity pattern in band deposition. The MIR analysis per quarter for age groups was

also inconclusive (**Table 1**) as well as the analysis per quarter for all ages combined (ANOVA: $F = 0.7876$, $P = 0.5021$) (**Table 1**).

Since marginal increment analyses were inconclusive about the periodicity pattern in growth band deposition for shortfin makos in the South Atlantic, age was assigned by assuming an annual pattern, on the basis of the validation tests conducted for shortfin makos in the North Atlantic (Ardizzone et al., 2006; Campana et al., 2002; Natanson et al., 2006). Under this assumption, one growth band represented one year of age.

The first distinctive growth band was defined as the birth band, since it was the only one present in two individuals with size close to the reported size at birth. The mean radius of this birth band was 3.8 mm (s.d. = 0.32 mm, n = 252). In some vertebral sections, a pre-birth band was identified close to the focus, at a radius of ~1.7 mm. The pre-birth band was narrower than the growth bands and was seen as a translucent line in the *corpus calcareum*. The pre-birth band was not considered for age assignation whereas the birth band was regarded as age 0.

Based on vertebral band counts, the age range estimated for shortfin mako sharks of the western South Atlantic was from 0 to 28 years. Young-of-the-year sharks (aged 0) were between 78 and 81 cm. The oldest shark was a female of 330 cm FL (the largest female in the sample) aged in 28 years. The oldest male was 18 years old and measured 241 cm. The largest male (250 cm) was aged 17 years. The oldest female was excluded for the model fitting, since its data point was far removed from the overall data set and was very influential in the fit. Length-age keys, obtained for females and males, are shown in **Table 2**.

3.2. Growth analysis

The SGM provided a good description of the overall pattern of the data for both sexes, with a well fit up to ~15 years (**Fig. 6**). At older ages, the posterior probability intervals started to be wider, becoming the estimates less reliable (**Fig. 6**). The Bayesian fit gave an accurate estimate of the parameters a, b, y_1 and y_2 for both sexes, as shown by the marginal posterior distributions of these parameters with narrow probability intervals (**Table 3**).

Length at age 0, estimated by the SGM, was 88.7 cm ($ICr_{95\%}$ = 65.1 - 97.1) for females and 81.2 cm ($ICr_{95\%}$ = 71.1 - 89.5) for males. Length at age 1 was 96.9 cm ($ICr_{95\%}$ = 82.9 - 103.8) for females and 93.5 cm ($ICr_{95\%}$ = 88.6 - 98.4) for males. Shortfin mako growth during the first year of life, estimated from the difference between the median length predicted by the model for age 1 and the known length at birth of the species (63 cm FL, Mollet et al., 2000), was 33.9 cm ($ICr_{95\%}$ = 19.9 – 40.8) for females and 30.5 cm ($ICr_{95\%}$ = 25.6 - 35.4) for males. The narrower probability intervals for males showed more accurate estimates for this gender, possibly due to the better representation of younger makos in males sample.

The posterior predictive length distributions for the ages 1, 5, 10, 15 and 20 years for females and males shown a similarity in length in both sexes up to 15 years of age (**Fig.7**). At 15 years of age, females reached 217 cm ($ICr_{95\%}$ = 210 – 225) and males 216 cm ($ICr_{95\%}$ = 209 – 225) (**Table 3**). At 20 years of age, males seemed to be larger than females, with a high probability of a difference in length of 20 cm between sexes (**Fig. 7**). However, the estimates after age 15 must be taken with caution, because of their poor accuracy.

The Bayesian fit of the SGM showed for females that 79% of the combinations of the *a*, *b* parameters lied in the region 8 of the *a*,*b*-plane (**Fig. 8**). The curve within this region presents asymptotic growth and is sigmoid-shaped with an inflection point which indicates a change in the growth pattern. The inflection point was at 7 years of age and 153 cm FL (**Table 4**). Asymptotic size was 244 cm FL ($ICr_{95\%}$ = 220 – 302) and seemed to be underestimated in this gender. Although the growth curve defined by the SGM for females had an inflection point and exhibits asymptotic form, the parameters τ^*, y^* and y_∞ were poorly estimated (**Table 4**).

For males, the (*a*, *b*) combinations were in an area that defines more than one region (**Fig. 8**). However, 57% of the *a*,*b* combinations favored the region 3, followed by the regions 1, 2 and 8 which were less probable (**Fig. 8**). Therefore, the shape of the growth curve for males was a combination of the curves associated with these regions. All of the curves associated with the more probable regions, showed an inflection point, which indicated a change in males growth. This change in the growth pattern occurred at 6.7 years of age and 148 cm FL (**Table 4**). Summarizing the probabilities for the regions 1, 2 and 8, there was a probability of 43% that males growth curve reach an asymptote at 261 cm FL ($ICr_{95\%}$ = 216 – 357), which was close to the maximum length reported for this gender (**Table 4**). As with females, although the parameters τ^*, y^* and y_∞ appeared to be relevant in the growth curve shape of males, they were poorly estimated by the SGM (**Table 4**).

The Bayesian fit of the SGM showed a low probability for the region 2 for both sexes (5.1% for females and 12% for males) (**Fig. 8**). This region is associated with the form of a von Bertalanffy growth curve. The low probability means that the VBGM is not the model that better fit the data. This explains why, when VBGM was fit to the data, the parameters

were poorly estimated for both sexes, as indicated the wide credibility intervals (**Table 3**). The estimates of $L\infty$ were more realistic for females than for males (416 cm and 580 cm, respectively); though they were considerably higher to the maximum lengths reported for the species and seemed to be overestimated.

4. Discussion

A representative sample of the shortfin makos caught by the longline fishery in the western South Atlantic was used in this study, with females and males close to the maximum length reported for the species. The largest shortfin mako female caught during 15 years of monitoring by the Uruguayan National Observers Program on Board the Tuna Fleet (PNOFA) was included. Males length classes were better represented than females length classes, since largest females are rarely caught by longline fishery.

On the basis of the age at sexual maturity estimated for makos of the western North Atlantic (18 years for females and 8 years for males, Natanson et al., 2006), all the females sampled in commercial fishing cruises at the EEZ of southern Brazil and international adjacent waters, were juveniles (aged 2 to 12), whereas males were juveniles and adults (aged 1 to 18) (**Fig. 9**).

The low frequency of mature and largest females in the catches of pelagic longline fisheries was observed for the eastern South Pacific (Cerna and Licandeo, 2009), western North Atlantic (Campana et al., 2005) and western South Atlantic (Pons and Domingo, *in press*) representing less than 2% of the females caught. Seldom occurrences in the study area, preference of deeper waters or gear selectivity are factors that can explain the low catches. Another explanation is that a low percentage of the female population survives to

maturity. Wood et al. (2007) taking the upper bound of the annual survival estimated in their work (0.79 with a 95% CI of 0.71-0.87) and assuming the ages at maturity estimated by Natanson et al. (2006), calculated that only 9% of the female mako population would reach reproductive capability in the North Atlantic.

Since most of the data used in age and growth studies of shortfin makos come from longline fisheries, the lack of largest (presumably older) females is a difficulty to model growth in this gender and make it difficult to draw conclusions about female´s asymptotic size.

4.1. Age estimation

The maximum age observed in our study (28 years) was close to the maximum age reported for the species (32 years, Natanson et al., 2006). Based on vertebral band counts, the maximum age of shortfin makos reported was similar in different regions of the world, being between 25 and 32 years of age (29 years for western South Pacific, Bishop et al., 2006; 25 years for eastern South Pacific, Cerna and Licandeo, 2009; 32 years for North Atlantic, Natanson et al., 2006 and 28 years for South Atlantic, present study).

Shortfin mako maximum age estimated, using bomb radiocarbon analysis, was 31 years of age (Ardizzone et al., 2006), which is similar to the maximum age estimate through band vertebral counts. A study in other lamnid shark, the porbeagle (*Lamna nasus*), stated that bomb radiocarbon results supported vertebral age estimates up to ~20 years, but in older sharks vertebral band counts under-estimates age of up to 50% in this species (Francis et al., 2007). This under-estimation could be associated to the difficulty in identifying the increasingly narrow growth bands as the individual growth slows at a point of being

unresolvable (Francis et al., 2007). Similar life history characteristics between shortfin makos and porbeagles suggests that higher longevities than vertebral band counts estimates, could have occurred also in shortfin makos, noting the need to use a combination of methods for age estimation.

All the studies cited above (including the present study) assumed an annual periodicity pattern in band deposition for shortfin makos. However, the interpretation of growth band per year influences the estimated maximum age. If a 2 growth bands per year hypothesis was assumed, the maximum age would decrease to 14 years and if a 2 bands per year for the first 5 years followed by 1 band per year hypothesis was assumed, the maximum age would be 23 years. Long term tagging studies for shortfin makos showed a maximum time at liberty of 13 years for this species (Kohler and Turner, 2001). As the absolute age of this individual was unknown, these results do not support any of the three hypotheses.

Our attempts to determine the periodicity in band growth deposition through different resolutions of marginal increment analyses (overall sample, age groups, per month, per quarter) were inconclusive. Technical difficulties related to measuring and categorizing the distal bands at the margin of vertebrae where they become increasingly narrow (Campana, 2001) may have influenced our results. Months with the smallest sample sizes ($n < 10$) were also the months with the highest or lowest values of mean MIR or percentage of opaque vertebral edges, suggesting bias due to small sample size (Brothers, 1983; Lessa et al., 2006; Santana and Lessa, 2004). Although vertebrae collected between 1996 and 1999 were excluded for these analyses, bias due to a extend sample period, which cause variability on account of annual bands that are not deposited at the same time every year (Brothers, 1983; Lessa et al., 2006; Santana and Lessa, 2004), may have influenced the

results as our samples were collected over a period of 8 years. These biases had already been reported as the causes of inconclusive results about band periodicity pattern in five species of Carcharhiniformes (Lessa et al., 2006).

Whereas marginal increment analyses were inconclusive in this study, they have suggested an annual periodicity in growth band deposition for makos in the North Pacific (Ribot-Carballal et al., 2005; Semba et al., 2009) and South Pacific (Cerna and Licandeo, 2009). Ribot-Carballal et al. (2005) and Cerna and Licandeo (2009) found a high frequency of opaque bands in summer, whereas Semba et al. (2009) identified a high frequency of opaque bands in winter.

Bomb radiocarbon techniques and mark-recapture of chemically-tagged fishes are among the more robust methods of age validation (Campana, 2001; Goldman et al., 2012). Until recently, the most robust evidence of growth band deposition periodicity was that of an annual periodicity provided by these methods for the North Atlantic (Ardizzone et al., 2006; Campana et al., 2002; Natanson et al., 2006) but Wells et al. (2013) raised the discussion with their evidence of biennial deposition for juveniles in North Pacific. As none of these studies validated age for the entire age range of the species, a hypothesis that considers both evidences is one that assumes ontogenetic variation in the periodicity of growth band deposition, with juveniles of at least 5 years of age showing a biennial deposition and older aged individuals an annual deposition (Natanson et al., 2006; Wells et al., 2013). The annual hypothesis was assumed in the present study based on geographical proximity with the studies already conducted in the Atlantic Ocean. However, as uncertainty remains regarding the growth band deposition periodicity in western South Atlantic, the three possible scenarios of growth were presented for discussion: 1 band per

year, 2 bands per year and 2 bands per year for the first 5 years of age followed by 1 band per year (**Fig. 10**).

4.2. Growth analysis

Lengths at age zero predicted by the SGM (88.7 cm for females and 81.2 cm for males) were larger to the reported length at birth for the species. It was expected that estimated length at age zero would not be equivalent to the length at birth but larger, as in this study the estimated age was not corrected with a theoretical birth date, since this date is unknown for the western South Atlantic Ocean.

Growth rate during the first year of life -birth to one year- (33.9 cm/year for females and 30.5 cm/year for males) was slightly slower than the estimated for the North Atlantic (40 cm, Natanson et al., 2006) and for the western South Pacific (39 cm, Bishop et al., 2006) but faster than the reported rate for the eastern South Pacific (16-19 cm, Cerna and Licandeo, 2009). Recently, Wells et al. (2013) with length frequency analyses and a tag-recapture growth model estimated a growth rate for the first year similar to the present study (27 to 36 cm/year) for the North Pacific. The length at age 1 predicted in the present study (96.9 cm for females and 93.5 cm for males) was similar to the estimated for the western South Pacific through SGM (100 cm FL for both sexes, Bishop et al., 2006) and for the eastern South Pacific through modal progression analysis and VBGM (Table 2 in Cerna and Licandeo 2009). Similar growth in the two first years of life was observed for shortfin makos of the western South Atlantic and makos of other regions of the world.

A good description of female and male shortfin mako growth was provided by the Schnute growth model (SGM) up to ~15 years, since data of older individuals were sparse, a frequent problem in age and growth studies for the species. A similar growth for both

sexes was observed until the age of 15 years, from which growth curves become diverging. Previous studies identified differences in growth between sexes at earlier ages (7 years, Semba et al., 2009; 11 years, Natanson et al., 2006).

In contrast to the von Bertalanffy growth model (VBGM), the SGM showed that both females and males growth curves had a sigmoid shape with an inflection point (τ^*, y^*) at which their growth pattern change. An inflexion in growth had already been reported for several elasmobranch species (Araya and Cubillos, 2006; Casey et al., 1985; Katsanevakis and Maravelias, 2008) and also for *I. oxyrinchus* (Natanson et al., 2006). Araya and Cubillos (2006) stated that a two-phase growth model (Soriano et al., 1992) described the growth of several species of elasmobranchs better than the VBGM, and associated this change in growth with age at maturity. This agrees with the shape of male growth curve, in which a change in growth rate occurred at age 7 and 148 cm FL, which is close to the age at maturity (8 years, Natanson et al., 2006) however smaller than the length at maturity (185 cm FL, Natanson et al., 2006). For females, however, the point of inflection could not be related with maturity, since it occurred at age 7 and 153 cm FL, while females reported maturity is at age of 18 years and 275 cm FL (Natanson et al., 2006). However, a better estimation of τ^* is expected for males and an underestimation of this parameter for females, for which older classes are poorly represented. Some authors related the change in growth rate not with maturity, but with a time in life that a change in behavior happens, as a change in feeding habits or a change of habitat (Casey et al., 1985; Soriano et al., 1992). There is no sufficient information in the study area to support any of these hypotheses.

Although the Bayesian fit showed a higher probability of an asymptotic growth curve for females than for males (79% and 43%, respectively), results about asymptotic size for

both sexes must be taken with caution, since after 15 years the model was forced to explain growth with the sparse data available making it difficult to estimate asymptotic size accurately. It is interesting to note that when the SGM was fit with females up to age 18 (the same "window" of age available for males), excluding the three oldest females in the fit, the growth curve shape changed drastically, being the curve of the region 3 the most probable (61% of probability). Similarly, when the oldest female was included in model fitting, the 55% of the *a*, *b* combinations favored the curve of the region 3, showing that it was really very influent in the fit. The growth curve associated with region 3 is not asymptotic and has an inflection point. A no asymptotic growth curve for female shortfin mako sharks had already been reported by Bishop et al. (2006) and may be result of the lack of older females in the samples.

Biologically, asymptotic growth is a fact. Within the phase of growth well described by the SGM (age "window" up to 15 years of age), an asymptote was not reached in any of the two sexes. The flexibility of the SGM allowed describing a phase of the shortfin mako growth without forcing the data to reach an asymptote that, in this study, would be unrealistic, since the species reaches at least 28 years of age. Advantages of the SGM related to modeling growth in shortfin mako sharks had already been identified by Bishop et al. (2006).

The Bayesian fit of the SGM indicated that our data did not respond to a von Bertalanffy growth curve, as the probability of the region associated with this curve (region 2) was low for both sexes. This fact was confirmed when VBGM was fit to the data and wide credibility intervals were obtained for its parameters. Thus, when data of older

individuals is sparse, VBGM probably would not be the best model to be used and uncertainty about its parameter estimates must be taken into account.

In conclusion, this study provided the first estimates of age and growth of the shortfin mako shark in the western South Atlantic Ocean. Growth phase until age 15 was well described with the use of a flexible growth model. A change in growth was observed in both sexes, which in males was close to the age at maturity. Inconclusive results about periodicity of growth band deposition in the study area, make necessary the application of more robust validation techniques in the future, as different interpretations about periodicity results in changes in growth rate, first age at maturity and maximum age. Meanwhile, a precautionary approach assuming an annual deposition pattern can be used in management politics for this species with low fecundity and late maturity characteristics.

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Table 3. Schnute and von Bertalanffy growth parameter estimates by Bayesian fit for female and male shortfin mako sharks. SGM parameter estimates are the posterior means; values within brackets are the 95% credibility intervals (*ICr*95%). Reference ages (τ_1 and τ_2) were 2 and 15 years for females and 0 and 15 years for males. σ is the parameter that describes the error in the model. von Bertalanffy parameter estimates are the posterior medians; values within brackets are the 95% credibility intervals (*ICr*95%).

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TABLES

Table 1. Mean marginal increment ratio (MIR) and standard deviations (s.d.) per quarter of year for the age classes: 0-5 years, 6-10 years and 11-26 years and for all ages combined (n is sample size by quarter).

	0 - 5 years			6 - 10 years			11 - 26 years			All ages combined		
Quarter		**MIR**			**MIR**			**MIR**			**MIR**	
	n	mean	s.d	n	mean	s.d	n	mean	s.d	n	mean	s.d
1	2	0.49	0.23	2	0.46	0.29	35	0.5	0.23	39	0.5	0.23
2	8	0.43	0.29	29	0.52	0.27	14	0.55	0.27	52	0.52	0.27
3	30	0.47	0.21	53	0.6	0.29	8	0.69	0.23	92	0.57	0.27
4	6	0.58	0.33	10	0.55	0.23	4	0.5	0.33	20	0.55	0.27

Table 2. Length-age keys for female (top) and male (bottom) shortfin mako sharks for the western South Atlantic Ocean. Numbers in the centre of the table corresponds to the percentage of individuals within each length class of fork length (FL) in the different age classes. *n* is the total number of individuals in each length class.

Length classes FL (cm)	Age classes (years)																				Mean (years)	S.d.
	n	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**28**		
71-80	0																					–	–
81-90	0																					–	–
91-100	0																					–	–
101-110	6	33	50	17																		2.8	0.75
111-120	5		60	20	20																	3.6	0.89
121-130	14		7	50	29	14																4.5	0.85
131-140	13		8	0	31	23	31	8														5.9	1.32
141-150	20				25	30	30	15														6.4	1.04
151-160	12					58	0	17	17	0	0	8										7.3	1.92
161-170	12					17	33	8	25	8	8											8	1.6
171-180	10						10	30	10	20	20	10										9.4	1.65
181-190	4							25	25	0	0	25	0	25								10.8	2.75
191-200	8									25	25	13	25	0	0	13						12	2
201-210	9									11	44	11	11	11	11							12	1.66
211-220	5											20	0	60	0	0	0	0	0	20		14.8	3.03
221-230	3										33	33	0	0	33							12.7	2.08
231-240	2														50	0	0	0	0	50		17.5	3.54
241-250	0																					–	–
251-260	1																100					–	–
261-270	0																					–	–
271-280	1																	100				–	–
281-290	0																					–	–
291-300	0																					–	–
301-310	0																					–	–
311-320	0																					–	–
321-330	1																				100	–	–

Length classes FL (cm)	Age classes (years)																				Mean (years)	S.d.
	n	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**		
71-80	0																				–	–
81-90	3	33	67																		0.67	0.58
91-100	1				100																–	–
101-110	8		13	25	50	13															2.6	0.92
111-120	9				44	44	11														3.7	0.71
121-130	12				17	42	25	0	17												4.6	1.31
131-140	15					33	27	20	13	7											5.3	1.29
141-150	13					8	23	38	23	8											6	1.08
151-160	11						9	18	18	27	9	18									7.6	1.63
161-170	11							9	18	9	36	27									8.5	1.37
171-180	5								20	40	20	0	0	20							8.8	1.92
181-190	4							25	0	0	0	0	50	25							10	2.71
191-200	8										13	25	38	13	0	0	0	13			11.3	2.12
201-210	11												18	0	45	9	9	18			13.5	1.69
211-220	1															100					–	–
221-230	0																				–	–
231-240	1																100				–	–
241-250	3															33	0	0	33	33	16.3	2.08
251-260	0																				–	–
261-270	0																				–	–

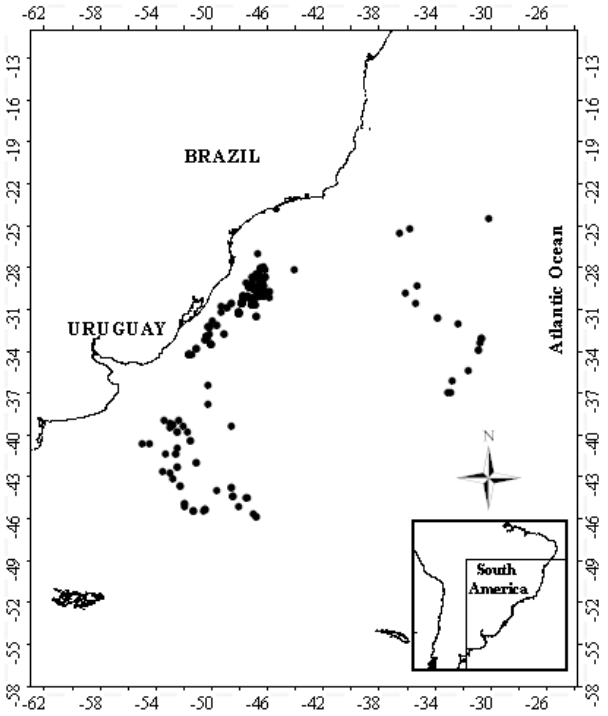
Table 3. Schnute and von Bertalanffy growth parameter estimates by Bayesian fit for female and male shortfin mako sharks. SGM parameter estimates are the posterior means; values within brackets are the 95% credibility intervals (*ICr*95%). Reference ages (τ_1 and τ_2) were 2 and 15 years for females and 0 and 15 years for males. σ is the parameter that describes the error in the model. von Bertalanffy parameter estimates are the posterior medians; values within brackets are the 95% credibility intervals (*ICr*95%).

Growth model		Females (τ =2, τ =15)		Males (τ =0, τ =15)	
	Parameter	Posterior mean	ICr95%	Posterior mean	ICr95%
Schnute	***a***	0.216	[-0.06 ; 0.56]	-0.016	[-0.24 ; 0.21]
	b	-2.2	[-8.36 ; 2.73]	1.76	[-1.78 ; 5.22]
	y	105.1	[97.9 ; 111.0]	80.89	[71.1 ; 89.5]
	y	217.2	[209.8 ; 225.1]	216.47	[208.5 ; 224.7]
	σ	0.083	[0.072 ; 0.094]	0.081	[0.071 ; 0.092]
		Posterior median	ICr95%	Posterior median	ICr95%
Von Bertalanffy	***L*∞**	416	[293 ; 1199]	580	[329 ; 1381]
	k	0.035	[0.0084 ; 0.068]	0.021	[0.0072 ; 0.050]
	to	-6.18	[-9.23 ; -3.99]	-7.52	[-9.41 ; -5.36]

Table 4. Set of parameters defined by the Schnute growth model according to the type of growth curve the model assumed for female and male shortfin mako sharks. Parameter estimates are the posterior medians; values within brackets are the 95% probability intervals (*ICr*95%). τ_o is an age corresponding to a projected size zero, τ^* and y^* are the age and the size, respectively, where the growth curve has an inflection point and $y\infty$ is the asymptotic size. τ_0 and τ^* are in years and y^* and $y\infty$ are in centimeters.

	Females		Males	
Parameter	Posterior median	ICr95%	Posterior median	ICr95%
τ_o	0.029	[-16.3 ; 1.36]	-1.12	[-2.7 ; -0.26]
τ^*	7.0	[2.8 ; 9.8]	6.7	[2.6 ; 10.1]
y^*	153	[112 ; 179]	148	[109 ; 177]
$y\infty$	244	[220 ; 302]	261	[216 ; 357]

FIGURES



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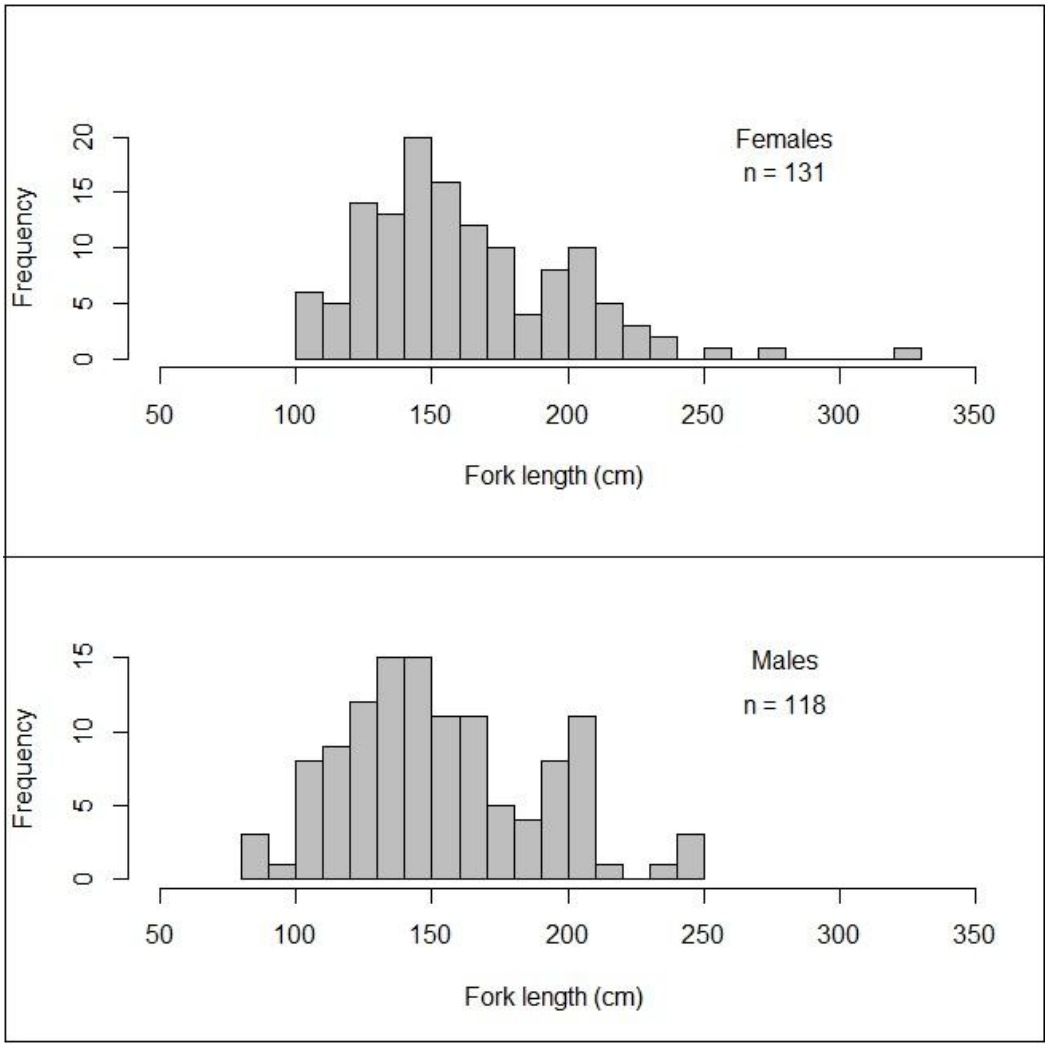

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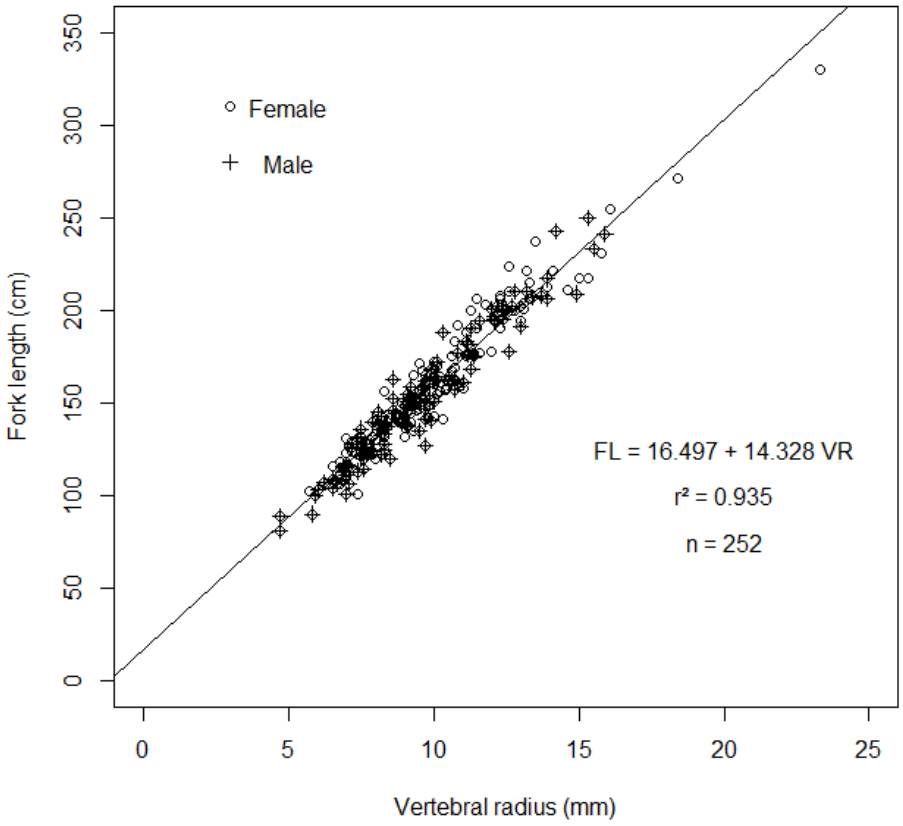

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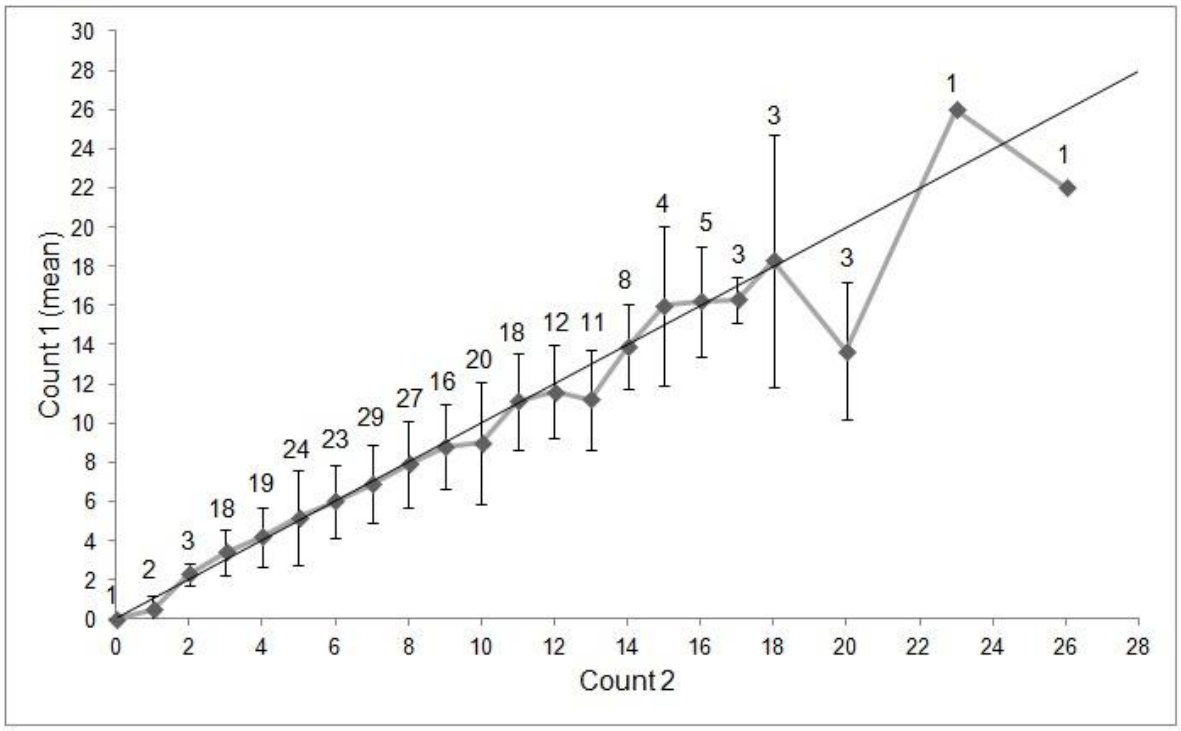

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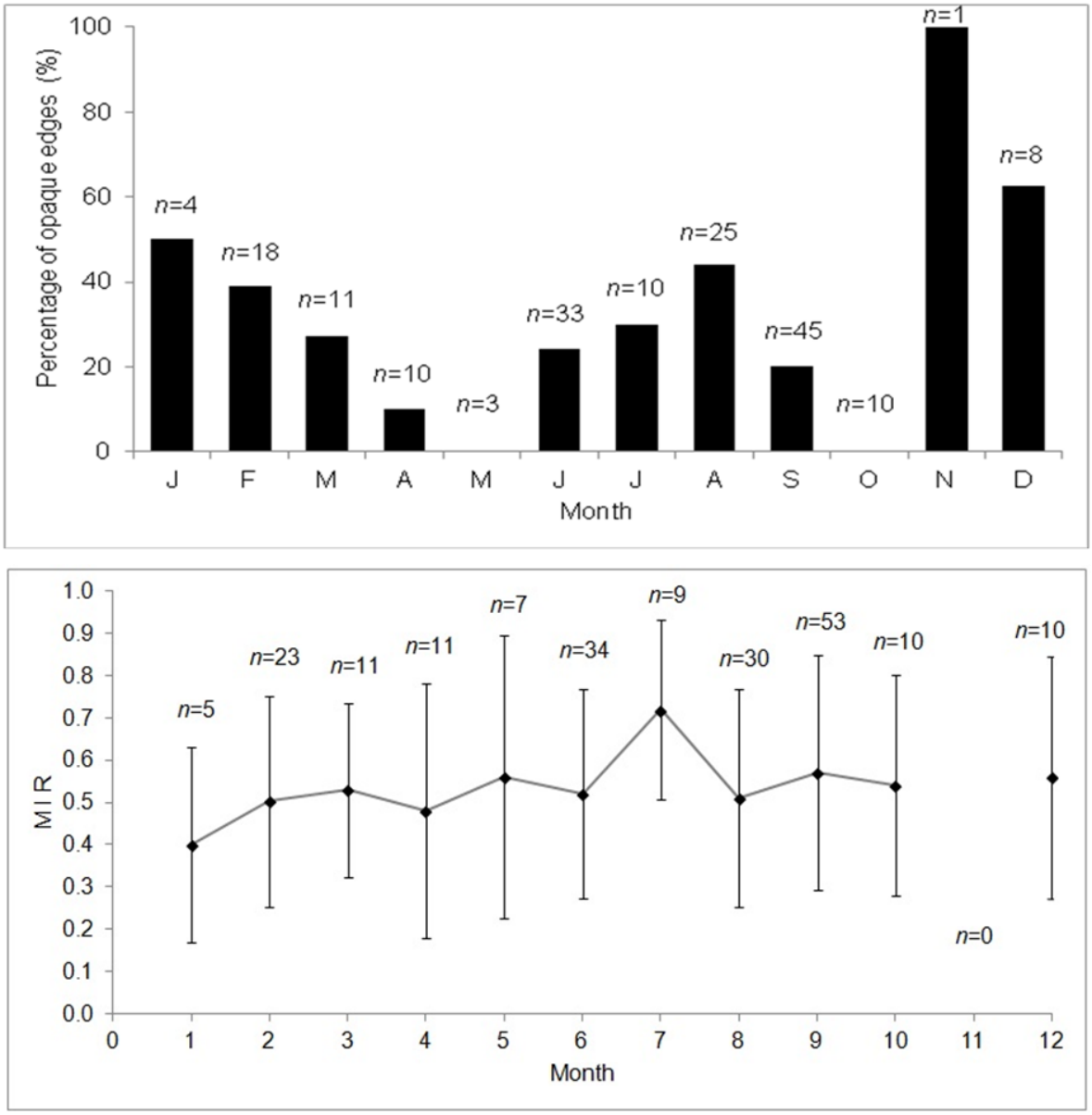

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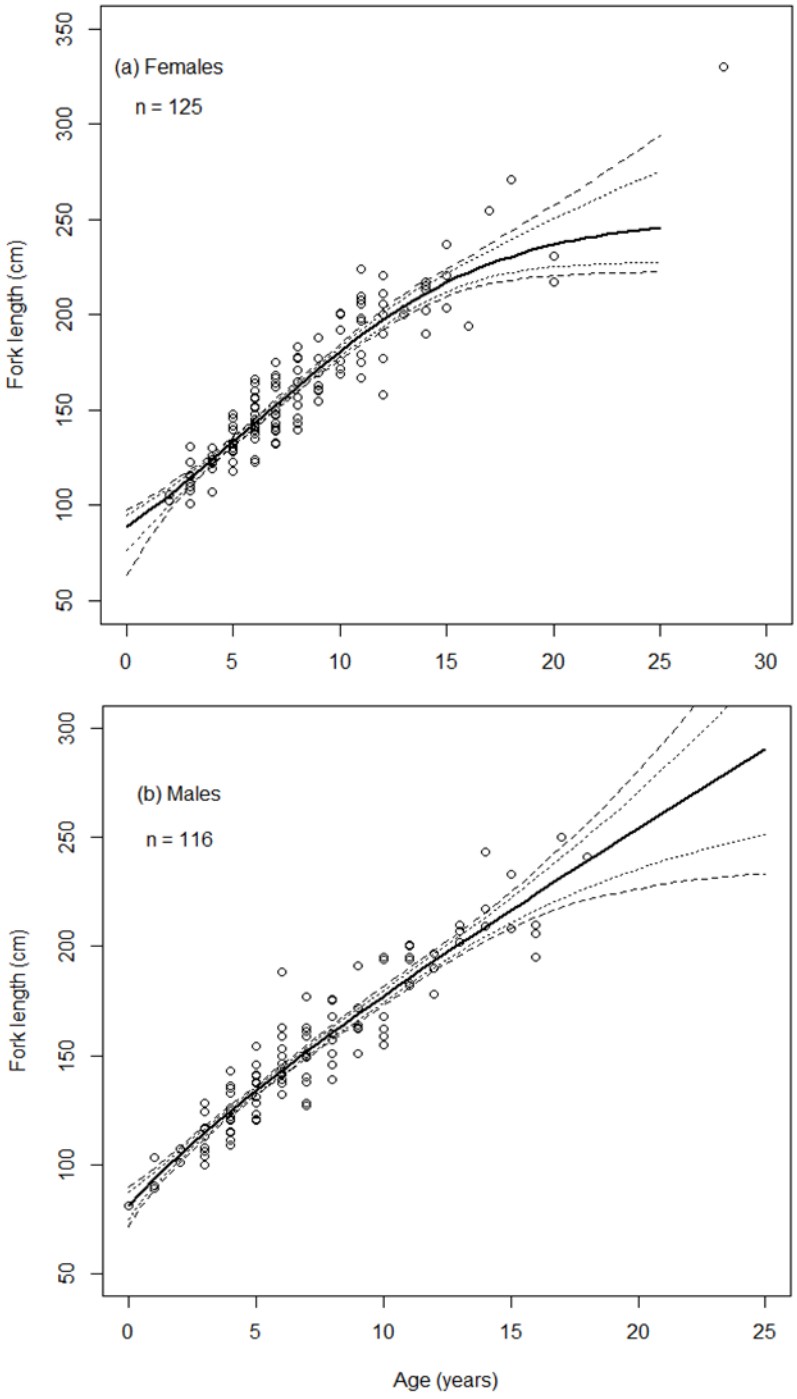

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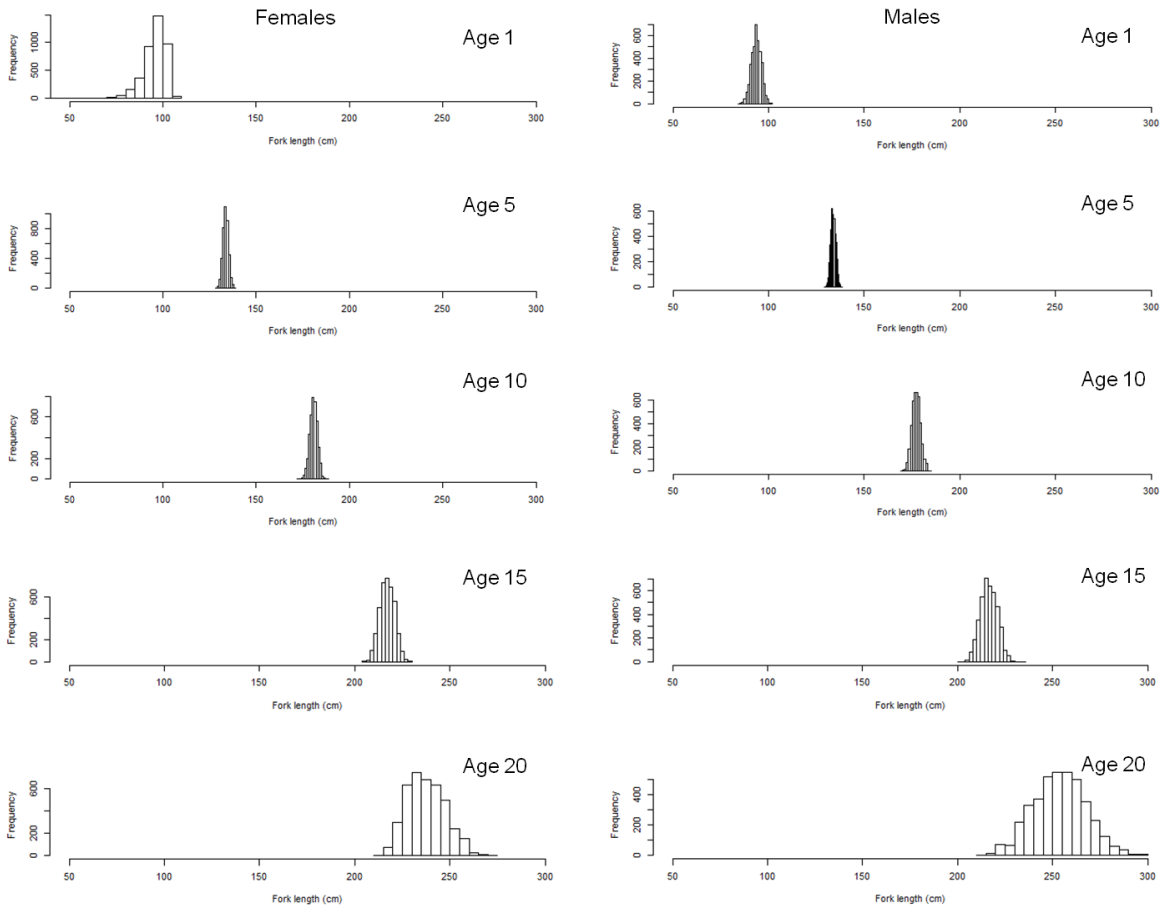

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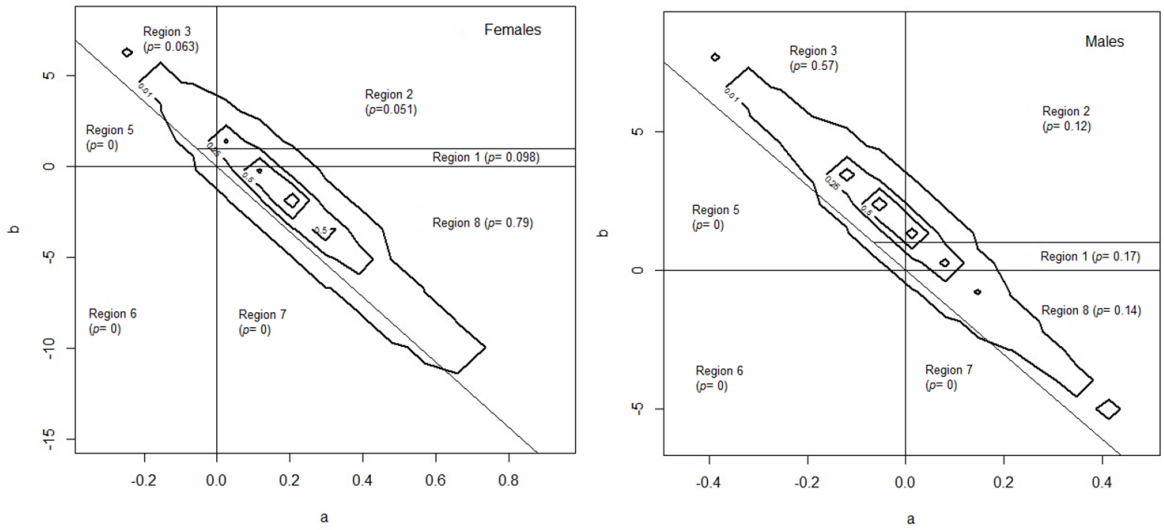

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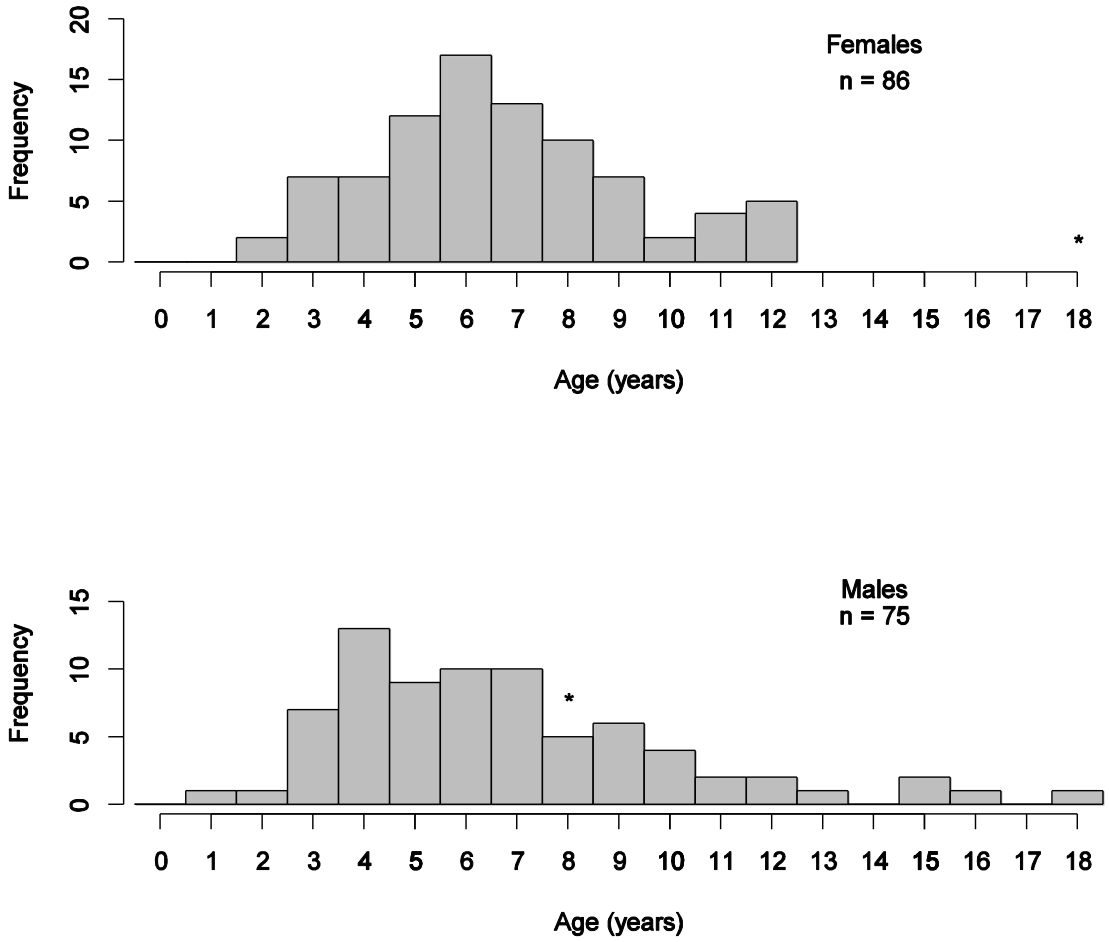

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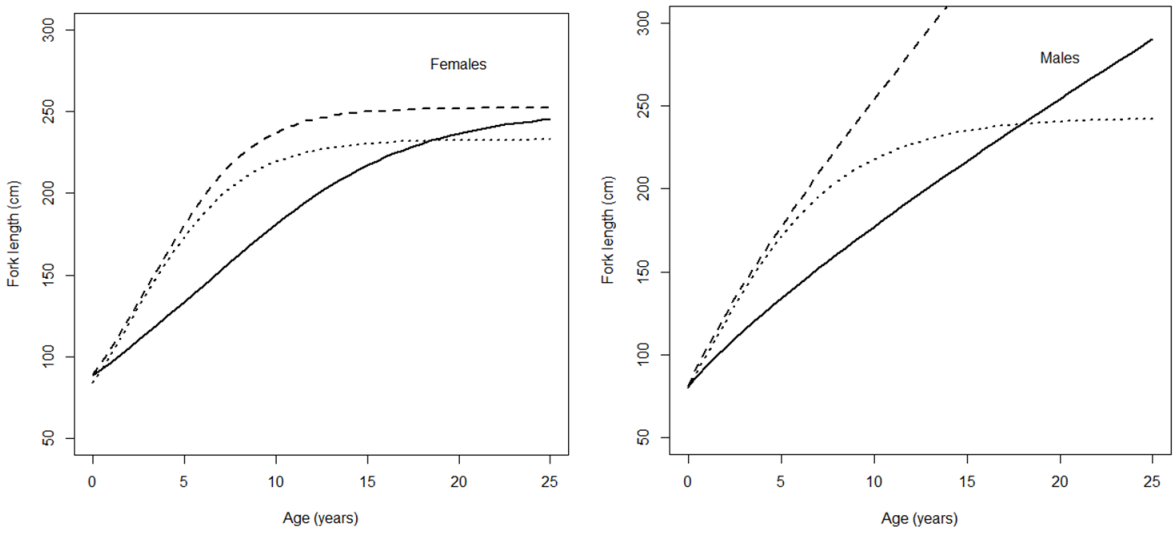

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