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Discriminação de estoques do pargo-rosa (*Pagrus pagrus* L.) do Atlântico Sudoeste através da análise da forma dos otólitos e avaliação das mudanças do crescimento no Sul do Brasil.

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RESUMO

O pargo-rosa, *Pagrus pagrus* (Linnaeus 1758), é um peixe que habita fundos consolidados e não consolidados de plataforma, sendo alvo da pesca comercial e recreativa ao longo de sua distribuição em ambas as margens do Oceano Atlântico e no Mediterrâneo. No do sul do Brasil foi intensamente explotado na década de 1970, reduzindo drasticamente sua abundância que não mostrou sinais de recuperação após 40 anos. Estudos sobre sua dinâmica populacionais com base em amostragens realizadas entre 1976 e 1985 incluíram a determinação de idades, ciclo reprodutivo e mortalidade além de identificar a existência de dois padrões de marcação de anéis anuais nas escamas (bem marcados e pouco marcadas ou ausentes) o que sugeriu a ocorrência de dois grupos de *P. pagrus* na região. Entre 2015 e 2019 novas amostragens foram realizadas e o material coletado foi utilizado para avaliar possíveis mudanças de crescimento e discriminar os estoques na região através da análise da forma dos otólitos. Quatro grupos de pargo-rosa foram identificados ao longo do Atlântico Sudoeste: um na zona de pesca exclusiva da Argentina, um segundo na zona de pesca da Argentina e Uruguai, incluindo espécimes do sul do Brasil que apresentam bandas de crescimento opacas bem marcadas em seus otólitos (BM), o terceiro grupo no sul do Brasil com bandas opacas pouco marcadas ou ausentes em seus otólitos (PA) e o quarto grupo ao longo do Rio de Janeiro. A diferença na forma entre esses otólitos com marcas de crescimento opacas bem marcadas e pouco marcadas ou ausentes do Sul do Brasil está de acordo com a hipótese de que parte dos pargos-rosa (BM) desovam ao longo do Uruguai enquanto outros são locais (PA) e desovam no sul do Brasil. O crescimento entre 1976-1977 e 2015-2019 no sul do Brasil, não mostrou diferenças significativas. As mudanças na densidade parecem não afetar o crescimento da espécie na região, o qual pode estar relacionado ao seu impacto relativamente pequeno no suprimento geral de alimentos baseados em cadeias tróficas planctônicas.

Palavras-chave: Argentina, Brasil, colapso do estoque, distribuição, escamas, identificação de estoque, microincrementos, morfologia do otólito, recurso pesqueiro, ShapeR, Uruguai.

ABSTRACT

The red porgy, *Pagrus pagrus* (Linnaeus 1758), is a fish that inhabits consolidated and non-consolidated shelf bottoms, being target of commercial and recreational fishing along its distribution on both shores of the Atlantic Ocean and the Mediterranean Sea. In southern Brazil it was intensively exploited in the 1970's, drastically reducing its abundance that showed no signs of recovery after 40 years. Studies on its population dynamics conducted between 1976 and 1985 included age determination, reproductive cycle and mortality, as well as identifying the existence of two patterns of annual growth rings (well-marked and faint or absent), which suggested the occurrence of two groups of *P. pagrus* in the region. Between 2015 and 2019 new samplings were performed and the collected material was used to evaluate possible growth changes and to discriminate the stocks in the region through the otoliths analysis analysis. Four groups of red porgies were identified along the Southwest Atlantic: one in the exclusive fishing zone of Argentina, a second in the Argentine and Uruguayan common fishery zone, including specimens from southern Brazil with well marked opaque growth bands on their otoliths (WM), the third group in southern Brazil with faint or absent opaque bands in their otoliths (FA) and the fourth group along Rio de Janeiro. The difference in shape between these otoliths with well marked and faint or absent opaque growth marks in southern Brazil is in agreement with the hypothesis that part of the red porgy (WM) spawns along Uruguay, while others are local (FA) and spawns along southern Brazil. Growth between 1976-1977 and 2015-2019 in southern Brazil did not showed significant differences. Changes in density appear not to affect the growth of the species in the region, which may be related to its relatively small impact on the general supply of food based on planktonic food webs.

Key-words: Argentina, Brazil, distribution, fishery resources, otolith microincrement, otolith morphology, scales, stock colapse, ShapeR, Sparidae, stock identification, Uruguay.

INTRODUÇÃO

O pargo-rosa, *Pagrus pagrus* (Linnaeus 1758), é uma espécie do sublitoral, demersal, comumente encontrada sobre fundos consolidados e arenosos entre 18 e 200 m de profundidade em regiões temperadas a subtropicais com ampla distribuição em ambas as margens do oceano Atlântico e no Mar Mediterrâneo (Manooch & Hassler 1978; FishstatJ 2018). O pargo-rosa é um predador ativo de invertebrados bentônicos e peixes (Capitoli & Haimovici 1993, Manooch & Hassler 1978). Essa espécie apresenta hermafroditismo protogínico (Alekseev 1983), no qual seu desenvolvimento gonadal pode passar por três sequências: (1) “machos primários”: cujas gônadas desenvolvem tecido testicular e ovariano mas os ovários degeneram antes de atingir a maturidade; (2) “femêas funcionais”: cujo desenvolvimento das gônadas é completado com a maturação da zona ovariana; e (3) “machos secundários”: exemplares que, após uma única ou repetidas desovas como fêmeas, mudam de sexo e se tornam machos funcionais (Fostier et al. 2000).

Pagrus pagrus constitui uma fonte de proteína altamente apreciada, sendo alvo de muitas pescarias comerciais e recreativas ao longo de sua distribuição (Vaughan & Prager 2002, Aristizabal 2007, Labroupoulou et al. 1999, Afonso et al. 2008). Embora *P. pagrus* conste na lista de espécies ameaçadas da IUCN (2014), atualmente não está em um alto risco de extinção para um futuro próximo e, portanto, está listada globalmente na categoria “Menos Preocupante” (*Least Concern*). No entanto, segundo o relatório, as tendências populacionais precisam ser reavaliadas dada a importância econômica da espécie e os complexos requisitos biológicos e ecológicos exibidos por essa. No Brasil, em 21 de maio de 2004 foi publicada a Instrução Normativa MMA nº 5, que incluiu *P. pagrus* na lista nacional das espécies de invertebrados aquáticos e peixes sobrexplotadas ou ameaçadas de sobrexplotação.

No entanto, atualmente na normativa MMA nº 163 de 2015, essa espécie não consta na classificação de espécies em risco.

No Atlântico Sudoeste (SW) o pargo-rosa é comercialmente pescado entre o Espirito Santo no Brasil e a província de Buenos Aires na Argentina (Cousseau & Perrota 2013). As principais área de pesca estão entre o Estado do Espirito Santo e o norte do Rio de Janeiro (19ºS - 23ºS) (Costa et al. 1997); ao sul de Rio Grande do Sul (30ºS - 34ºS) (Haimovici 1998); na zona comum de pesca entre Argentina e Uruguai (34ºS - 39ºS); e na zona de pesca exclusiva da Argentina (39ºS - 41ºS) (Garcia & Molinari 2015).

A heterogeneidade dos estoques de pargo-rosa no Atlântico Sudoeste já foi abordada em alguns estudos. Com base em aspectos de sua dinâmica populacional e pesqueira, Cotrina & Raimundo (1997) discriminaram dois grupos entre a Argentina e o Uruguai. Porrini et al. (2015) utilizaram marcadores microssatélite de DNA e técnicas de marcas corporais para discriminar *P. pagrus* em águas argentinas e uruguaias e, embora a genética não apoiasse a hipótese de estoques distintos, a análise da forma do corpo apontou diferenças. Soares et al. (2018) analisaram as assembleias de parasitas de longa vida em *Pagrus pagrus* do Rio de Janeiro, São Paulo, Rio Grande do Sul e Argentina e identificaram três grupos distintos: um no Rio de Janeiro e São Paulo, outros no Rio Grande do Sul e o terceiro na Argentina. A partir de observações da intensidade das marcas de crescimento em escamas de exemplares provenientes do Rio Grande do Sul, Haimovici (1997) observou patrões de marcação que sugerem a existência de dois grupos. Um primeiro grupo com um padrão de anéis bem marcados que provavelmente desova no norte da zona comum de pesca da Argentina e Uruguai e um segundo grupo com marcação pouco marcadas ou ausente que permanecem durante todo o ano sul do Brasil (Haimovici 1997; Haimovici em prep.). A questão das marcas evidentes (BM) e fracas ou ausentes (PA) nos otólitos e escamas depende de muitos fatores, incluindo deslocamentos para desova entre o sul do Brasil e o Uruguai, para os quais existem apenas evidências indiretas. Estudos espefícos devem ser endereçados para descrever esse aspecto no futuro.

A falha em reconhecer a estrutura de um estoque pesqueiro pode levar a mudanças dramáticas nos atributos biológicos, taxas de produtividade, diversidade genética, bem como levar à sobrepesca e consequentemente a depleção de estoques menos produtivos (Smith et al. 1991). De fato, o estoque de pargos-rosa do Rio Grande do Sul foi intensamente explotado com rede de arrasto a partir da descoberta de concentrações da espécie em profundidades superiores a 80 m (Yesaki & Barcellos 1974). Sua abundância foi sobrestimada e a população intensamente explotada o que levou ao colapso da pescaria de arrasto no inícios da década de 1980. Os desembarques que inicialmente chegaram a 600 t em 1974, diminuíram para níveis inferiores a 500 t anuais na década de 1980 e inferiores a 200 t nas décadas seguintes (Ibama/Ceperg. 2001–2011). Cabe destacar que as estatísticas devem ser tomadas com ressalvas, pois a partir da década de 1980, a espécie foi alvo apenas de pesca com linha de mão por pequenos barcos cujos desembarques raramente são registrados (Haimovici com. pess.). Ainda assim, os desembarques são muito inferiores aos do auge da pescaria e portanto, o pargo-rosa no sul do Brasil foi considerado sobrexplotado nas últimas décadas (Haimovici 1997; Haimovici et al 2006).

A intensa explotação pesqueira continuada pode resultar em mudanças de longo prazo nas taxas de crescimento populacional, tamanho por idade e tamanho máximo, considerada uma resposta típica dependente de densidade devido a um aumento na mortalidade. (Millner & Whiting 1996, Trippel 1995, Law 2000, Audzijonyte et al., 2016). A pesca intensa no sul do Brasil reduziu a abundância da maioria das espécies demersais da região nas últimas décadas (Haimovici e Cardoso, 2016). Associado a esta diminuição na abundância, foram observados aumentos nas taxas de crescimento e tamanho para as espécies demersais costeiras mais abundantes pescadas na região, incluindo *Cynoscion guatucupa* (Miranda & Haimovici 2007), *Macrodon atricauda* (Cardoso & Haimovici 2011, 2014 e 2016*)*, *Umbrina canosai* (Haimvici et al. 2006) e *Micropogonias furnieri* (Haimovici et al. em prep.).

Devido a importância da espécie nos desembarques na época, *Pagrus pagrus* foi intensamente amostrada de 1976 a 1985, período em que 22.964 espécimes foram medidas e 4.407 tiverem sua idade determinada (Haimovici 1987; Haimovici 1998; Haimovici et al. em prep.). A dinâmica populacional, incluindo a taxa de crescimento, ciclo reprodutivo e condição anual e mortalidade antes do colapso foi abordada por Haimovici et al. (em prep.) e fornecer uma linha de base que pode servir para analisar as mudanças na dinâmica populacional sofrida pela espécie.

A determinação da idade é um dos aspectos mais importantes na compreensão da dinâmica do crescimento dos peixes. No entanto, a periodicidade de formação anual das bandas de crescimento nos otólitos está sujeita a várias fontes de erro, sendo que para várias espécies em que as idades foram erroneamente assumidas, resultaram em estimativas imprecisas de taxa de crescimento (Cavole et al. 2018). Além dos incrementos anuais, os otólitos mostram a adição diária de novo material (formação de incremento diário; ver Pannella 1971; Campana & Neilson 1985) o qual pode auxiliar tanto na determinação da idade em espécies que apresentam falsos anéis de crescimento, quanto na validação de leitura de idade para aquelas espécies onde informações de microestrutura e macroestrutura estão atualmente disponíveis (Cavole & Haimovici, 2015; Cavole et al. 2018).

As pesquisas envolvendo otólitos tem aumentado e melhorado constantemente nos últimos tempos (Campana 2005). Os otólitos são concreções acelulares de carbonato de cálcio e outros sais inorgânicos, geralmente considerados imunes à modificação uma vez formados (Green et al. 2009). Alguns estudos demonstraram que os otólitos podem apresentar diferenças morfológicas espécie-especificas (Assis 2005), entre estoques (Tuset et al. 2013) ou populações (Schulz-Mirbach et al. 2011). Estudos ecomorfologicos fornecem informações importantes sobre a questão de como a composição e morfologia do otólito podem estar correlacionadas com diferenças na história de vida (Lombarte et al. 2003; Tuset et al. 2016), taxa de crescimento (Campana & Casselman 1993), gradientes ecológicos, como a temperatura (Lombarte & Lleonart 1993), profundidade da água (Paxton 2000), salinidade(Campana 1999), qualidade alimentar (Gagliano & McCormick 2004), condições estressantes (Reimer et al. 2016), distinções genéticas (Berg et al. 2018) ou separação geográfica (Castonguay et al. 1991; Friedland & Reddin 1994). Portanto, populações ou estoques de peixes com distribuições espaciais distintas, ao longo ou em parte da sua vida, podem ser caracterizadas através da análise morfométrica do otólito, a qual se tornou um método popularmente bem estabelecido (Campana & Casselman 1993; DeVries et al. 2002; Libungan et al. 2015).

A identificação de estoques pesqueiros é um componente integral das avaliações modernas de unidades populacionais e por sua vez, para uma gestão eficaz das pescarias e espécies ameaçadas (Begg et al. 1999). Desta forma, a análise de formas de otólitos pode ser uma ferramenta poderosa para fins de gerenciamento e manejo de estoques (DeVries et al. 2002, Bergenius et al. 2006).

As diferenças na morfologia dos otólitos podem ser avaliadas por diferentes abordagens, como: análise estatística de parâmetros gerais como circularidade, área, comprimento do perímetro, etc (Burke et al. 2008; Paul et al. 2013; Keating et al.

2014); análise de marcas (Cadrin 2013); e análises de forma do otólito (AFO) como as transformações elípticas de Fourier (Campana & Casselman 1993; Burke et al. 2008; Duarte-Neto et al. 2008), e Wavelet (Parisi-Baradad et al. 2005; Libungan & Pálsson 2015). Entre elas, a AFO tornou-se um método popular e bem estabelecido para discriminar peixes com distribuições espaciais distintas ao longo de parte ou durante toda a sua vida (Campana & Casselman 1993; DeVries et al. 2002; Tuset et al. 2013; Libungan et al. 2015). Esse método requer apenas imagens do otólito, das quais a forma pode ser extraída e quantificada em um grande número de variáveis independentes (Stransky 2013; Libungan & Pálsson 2015). O método de Wavelet é útil para detectar diferenças de forma em regiões específicas do otólito; em contraste o método de Fourier fornece informações sobre diferenças gerais na forma do otólito. Portanto, para algumas espécies de peixes, o método de Wavelet pode ser mais efetivo para explicar as diferenças na forma do otólito, enquanto para outras, o método de Fourier pode ser mais poderoso para distinguir populações (Libungan & Pálsson 2015).

A falta de recuperação do estoque de pargo-rosa no sul do Brasil justifica aprofundar os estudos sobre a identificação dos estoques e a dinâmica populacional da espécie na região. O primeiro o objetivo dessa dissertação foi avaliar a forma do otólito como marcador de estoque para *Pagrus pagrus* em uma área com potencial mistura de estoques vizinhos no Atlântico Sudoeste, o segundo foi avaliar se a espécie sofreu alterações de crescimento após o colapso da pescaria no Sul do Brasil. Para isso, caracterizamos os estoques de pargo-rosa capturados no Rio de Janeiro, no Rio Grande do Sul, na zona comum de pesca entre Uruguai e Argentina e na zona econômica exclusiva da Argentina através da análise de forma do otólito. Para a análise de crescimento de *P. pagrus* no sul do Brasil, primeiramente identificamos o período de formação da primeira banda opaca nos otólitos através dos incrementos diários em juvenis e verificamos a correspondência entre bandas de crescimento opaca anual (*annulus)* em seções dos otólitos e anéis de crescimento em escamas previamente validadas. Posteriormente, comparamos o crescimento entre exemplares amostrados antes do colapso da pescaria em 1976 - 1977 e após a forte redução na abundância em 2015 – 2019. Por fim, comparamos o crescimento entre espécimes com bandas de crescimento bem marcadas e pouco marcadas ou ausentes em seus otólitos no último período.

MATERIAL E MÉTODOS

Discriminação dos estoques no Atlântico Sudoeste

Otolitos *Sagittae* de 839 *Pagrus pagrus* foram coletados entre 2015 e 2019 em quatro regiões, abrangendo toda a faixa de distribuição da espécie no Atlântico Sudoeste subtropical e temperado quente: ao longo do Rio de Janeiro (Lat. 22°S - 23°S) e Rio Grande do Sul (Lat. 32°S - 34°S) no Brasil, na zona de pesca comum do Uruguai e Argentina (Lat. 34°S - 39°S) e na zona econômica exclusiva da Argentina (Lat. 39°S - 42°S)

Para os pargos-rosa amostrados em Rio Grande, cortes transversais de 0,20 mm, passando pelo núcleo do otólito, foram obtidos através de uma serra de precisão de baixa velocidade e posteriormente classificados em dois grupos: com bandas de crescimento bem marcadas (BM) e como bandas de crescimento pouco marcadas ou ausentes (PA).

Para cada amostra, o comprimento total (LT; mm) foi registrado e um otólito teve sua superfície capturada por uma câmera AmScope MD500 ampliada 10x vezes sob uma lupa Nikon SMZ800.

Para selecionar um intervalo de comprimento total dos peixes em quem os otólitos apresentam características ontogenéticas semelhantes, a área, perímetro, largura e comprimento do otólito de 70 peixes entre 155 mm e 528 mm foram utilizado em uma análise de agrupamento hierárquico de Ward. Entre os grupos formados, o intervalo de comprimento total de 330 a 370 mm LT, que incluiu 195 indivíduos, teve a melhor sobreposição no conjunto de dados entre os cinco grupos de amostras e foi escolhido para a análise de forma.

O pacote *ShapeR* (Libungan & Pálsson 2015) foi usado para ler as imagens de cada otólito e registrar os contornos da forma como uma matriz de coordenadas. O tamanho dos otólitos foram padronizados para que sua área fosse igual em todas as amostras e assim remover o viés induzido pelo tamanho (Libungan & Pálsson 2015, Libungan et al. 2015).

Os padrões da forma do otólito de cada um dos cinco grupos de amostra: Rio de Janeiro (RJ); Rio Grande do Sul com bandas de crescimento bem marcadas no otólitos (BM) e bandas de crescimento pouco marcadas ou ausentes no otólitos (PA); zona de pesca comum do Uruguai e Argentina (UA); e zona de pesca exclusiva da Argentina (AR), foram calculados através dos coeficientes Wavelet e Elípticas Fourier. Os coeficientes Wavelet foram obtidos com o pacote *wavethresh* (Nason 2012) e os Fourier pelas funções *iefourier* e *efourier* (Claude 2008). Para determinar o número de coeficientes de Wavelet e Fourier necessários para as análises, o desvio dos contornos dos otólitos reconstruídos a partir dos contornos originais foi avaliado no pacote *ShapeR* (Libungan & Pálsson 2015). Utilizando 64 coeficientes de Wavelet e 45 de Fourier, obteve-se uma taxa de erro de 1,5% ou uma precisão de 98,5%.

O crescimento dos peixes afeta a estrutura e a forma do otólito (Geffen 1982; Folkvord et al. 2000; Feet et al. 2002; Fox et al. 2003), por exemplo, otólitos se tornam mais largos com o aumento do tamanho de peixes dentro de um mesmo estoque (Simoneau et al. 2000). A interação entre o comprimento total dos peixes e os coeficientes de Wavelet e Fourier foi investigada por uma análise de covariância (ANCOVA), e quando houve uma interação significativa, esses exemplares foram excluídos da análise para remover a relação alométrica (Libungan & Pálsson 2015).

O formato médio dos contornos dos otólitos reconstruído pelos coeficientes Wavelet normalizados para cada grupo de amostras e suas diferenças foram avaliadas visualmente. Para estimar qual região da forma do otólito apresenta maior contribuição para possíveis diferenças entre os potenciais estoques, a média dos coeficientes e seu desvio padrão foram plotados em um gráfico usando a função *plotCI* do pacote *gplots* (Warnes et al. 2014).

A variação da forma entre os grupos foi comparada com uma análise canônica de coordenada principal (CAP) (Anderson & Willis 2003), aplicada para os coeficientes padronizados de Wavelet e Fourier usando a função *capscale* no pacote *vegan* (Oksanen et al. 2013). A ordenação das médias da forma do otólito dos estoques ao longo dos dois primeiros eixos canônicos foi avaliada graficamente. Uma ANOVA-like como permutação para o teste canônico de coordenadas principais foi usada para avaliar a significância de restrições usando 1000 permutações, também no pacote *vegan* (Oksanen et al. 2013).

Para analisar a precisão da classificação da forma do otólito à origem da amostragem, uma Análise Linear Discriminante (LDA) foi aplicada para os coeficientes padronizados de Wavelet e Fourier (Libungan & Pálsson 2015). O método de classificação LDA discrimina grupos pré-definidos com base na observação amostral de cada grupo (Klecka 1980), e foi calculado através da validação cruzada usando a função *errorest* no pacote *ipred* (Peters & Hothorn 2013), que retorna a probabilidade posterior para os grupos.

Análise de crescimento

Dados biológicos, escamas e 101 otólitos de *P. pagrus* amostrados entre 1976 e 1977 foram disponibilizados para a determinação de idade a partir do programa de amostragem que monitora a pesca demersal costeira na plataforma sul brasileira (28°S a 34°S) realizada pelo Instituto de Oceanografia da Universidade Federal de Rio Grande desde 1976 (Haimovici, 1987, 1998, Haimovici et al., em preparação). De 2015 a 2019, dados biológicos incluindo LT (mm), massa total (W, g) e sexo (macho, fêmea e hermafrodita) além de escamas e otólitos de 574 pargos-rosa foram obtidos a partir dos desembarques de arrastos de fundo, redes de emalhe e pesca de anzóis e linha ao longo do sul do Brasil entre 30°S e 34°S. Além disso, dados e otólitos de 12 *P. pagrus* juvenis provenientes de outras pesquisas foram disponibilizados para o estudo das microestruturas.

As microestruturas (assumidas como incrementos diários de crescimento) de 11 otólitos de juvenis entre 72 e 171 mm LT foram examinadas para auxiliar na determinação do primeiro incremento anual (*annulus*). Os otólitos *sagittae* foram preparados e polidos seguindo os métodos descritos por Cavole & Haimovici (2015). As secções foram examinadas usando uma microscópio com uma ampliação de x 400 (Olympus CX41; www.olympus-ims.com), adequado para o exame de otólitos de crescimento rápido com microincrementos maiores que 2 µm de largura (Campana & Jones 1992). Ao longo das contagens, a luz do microscópio e o foco foram frequentemente ajustados para interpretar corretamente toda a sequência de microincrementos. Os incrementos diários de crescimento foram contados entre o núcleo e a borda externa do otólito ao longo do eixo ventral.

Para a determinação da idade nos adultos, os otólitos sagitais foram seccionados transversalmente (0,2-0,3 mm) através do núcleo com uma serra rotativa de baixa velocidade. Imagens digitais das seções foram tiradas usando um estereomicroscópio com objetivo de 10X em uma câmera com uma resolução de 2048 × 1536 pixels. Os peixes foram classificados em dois grupos com base na legibilidade das seções dos otólitos, um como bandas de crescimento pouco marcadas ou ausentes (PA) e outro com bandas de crescimento bem marcadas (BM).

As faixas alternadas de bandas opacas e translúcidas foram contadas independentemente por dois leitores, se as contagens diferiram, os otólitos foram lidos novamente por ambos os leitores e descartados das análises posteriores se a diferença nas leituras persistisse. As distâncias entre o núcleo e o final das bandas opacas foram medidas com o software livre ImageJ 1.47 (www.imagej.nih.gov) e assumidas a priori como *annulus* (bandas anuais).

Para verificar as determinações de idade, o número de bandas opacas observadas nas seções dos otólitos (*annulus)* foram comparadas com o número de anéis de crescimento nas escamas de 89 pargos-rosa amostrados em 1976-1977, já validados por Haimovici et al. (em prep.).

Entre as 661 amostras ordenadas de forma crescente pelo comprimento total, a cada quarta espécime uma foi retida, resultando em uma amostra de 165 indivíduos medindo entre 72 a 510 mm LT, os quais tiveram a relação linear entre o comprimento total e o eixo ventral do otólito calculado como: L = 0,0084 R + 0,96; R2 = 0,908

Os comprimentos retro-calculados por idade foram obtidos através da hipótese proporcional da escala (Francis 1990) com a fórmula de Fraser-Lee:

$$Li(mm) = \left[(L - a).\left(\frac{Ri}{R}\right)\right] + a$$

em que L é o comprimento total no momento da captura, Li é o comprimento na formação do i-annulus, Ri é a distância entre o núcleo e cada i-annulus e a é o intercepto do raio do otólito na regressão do comprimento do peixe.

O modelo de crescimento de von Bertalanffy ajustado por uma abordagem bayesiana foi utilizado para descrever o crescimento retrocalculado de *Pagrus pagrus* entre as décadas de 1970 e 2010 e entre os otólitos de com bandas bem marcadas e pouco marcadas. Os dados de comprimento por idade (ou o número de bandas por comprimento para *Pagrus pagrus*) foram assumimos como distribuição log-normal: $y_i = \log N\ (\mu_i\,, \sigma^2)$, onde y_i é a distribuição de comprimento com um comprimento médio esperado em uma classe de idade (ou classe de banda) i com variância σ^2.Uma versão logarítmica da equação de von Bertalanffy foi utilizada para conveniência computacional:

$$\mu_i = \log(TL_\infty) + \log(1^{-k(i-t_o)})$$

Priors não informativas foram construídas:

$$p(logTL_\infty) \sim dN(0{,}0.001)\ I\ (-5{,}5)$$

$$p(log\ k) \sim dN(0{,}0.001)\ I\ (-5{,}5)$$

$$p(\log t_0) \sim dU\ (-\ 3{,}0)$$

$$p(\sigma) \sim dU(0{,}5)$$

Distribuições posteriores de cada período de tempo (obtidas através do processo estocástico de Monte Carlo via Cadeias de Markov) foram utilizadas para comparar as estimativas dos parâmetros de crescimento ao longo do tempo e da marcação das bandas nos otólitos. Após 10,000 burn-in, cada segundo valor dos 20.000 restantes foi retido, resultando em uma amostra final de 10.000 iterações na distribuição posterior (log TL∞, log k, log t0) (Kinas & Andrade 2010). A distribuição posterior de cada parâmetro estimado forneceu uma maneira fácil e clara de comparar os resultados entre os períodos e tipos de bandas nos otólitos. O MCMC foi realizado através do *OpenBUGS*, usando os pacotes *R2WinBUGS* (Sturtz et al. 2005) e *BRugs* (Thomas et al. 2006).

Devido ao hermafroditismo protogínico do pargo-rosa nenhuma diferença no crescimento entre os sexos foi observada por Haimovici et al. (em preparação), dessa forma o crescimento foi calculado para os sexos agrupados.

Toda a análise estatística foi realizada no software R (R Core Team 2013), versão 3.3.1.

SÍNTESE DOS RESULTADOS

CAPÍTULO I: DISCRIMINAÇÃO DE GRUPOS DE *PAGRUS PAGRUS* (TELEOSTEI) AO LONGO DO ATLÂNTICO SUDOESTE ATRAVÉS DA ANÁLISE DE FORMA DE OTÓLITOS.

A forma do otólito do pargo-rosa muda ao longo do crescimento. Seis intervalos de comprimento entre indivíduos de 155 a 528mm LT foram identificado através da análise de agrupados, em que o intervalo de comprimento total de 330 a 370 mm foi o mais representado entre os cinco grupos de amostras, portanto foi escolhido para a análise de forma. A reconstrução de Wavelet demostrou diferenças entre as forma média dos otólitos para todos os grupos de amostras, exceto entre Rio Grande com bandas de crescimento bem marcadas (BM) e a zona comum de pesca Uruguaia-Argentina (UA) que mostraram uma forma de otólito muito similar. As maiores variações na forma do otólito foram observadas na *excisura ostii*, seguida pela da borda dorsal. A distância da borda ventral em relação ao centróide do otólito foi maior para o grupo de Rio Grande com bandas de crescimento pouco marcadas ou ausentes (PA) quando comparado com todos os outros grupos de amostras. Houve uma alta sobreposição no *postantirostrum,* no *rostrum* e no *postrostrum* de todos os grupos amostrais. A análise canônica de coordenadas principais (CAP) mostrou que a forma do otólito não foi homogênea entre os grupos para ambos os coeficientes (ANOVA-like, p <0,05), nos quais 95,1% da variação foi explicada ao longo dos dois primeiros eixos para o Fourier e 96,18% para a Wavelet. Em ambas análises canônica de coordenadas principais, a zona de pesca exclusiva da Argentina (AR), Rio de Janeiro (RJ) e PA aparecem em painéis diferentes nos quais não houve sobreposição ao longo de nenhum dos eixos. O desvio padrão dos grupos UA e BM se sobrepõe entre si e exceto entre esses, o teste da ANOVA-like para os coeficientes de Fourier e Wavelet demostraram diferenças significativas entre todos os outros grupos pareados. Entre os grupos que apresentaram diferença significativa, o sucesso de classificação pareada por análise discriminante linear (LDA) foi entre 76% e 96% para o coeficiente de Fourier e entre 76% e 98% para o coeficiente Wavelet. Por outro lado, o sucesso de classificação entre os grupos UA e BM, para os quais o teste da ANOVA-like não foi significativo, atingiu apenas 60 a 61%. As análises gráficas e discussão desses resultados estão aprofundadas no primeiro manuscrito da dissertação, correspondente ao Apêndice I. Este artigo tem título de "Discrimination of red porgy *Pagrus pagrus* (Teleostei) groups along the Southwestern Atlantic by otolith shape analysis", e será submetido à revista Fisheries Research– Qualis A2 (CAPES – Biodiversidade).

CAPÍTULO II: COMPARAÇÕES DE LOGO-PRAZO NO CRESCIMENTO DO *PAGRUS PRAGRUS* (TELEOSTEI) NO SUL DO BRASIL.

Secções finas de otólitos de 12 juvenis medindo de 72 a 171 mm de LT apresentaram um padrão consistente de microincrementos, assumidos como incrementos diários. O número de microincrementos variou entre 114 e 176. O retro cálculo da data de nascimento variou entre 26 de outubro e 27 de janeiro, correspondendo bem à estação reprodutiva de *P. pagrus* no sul do Brasil (Haimovici et al. em prep.). Para um comprimento total médio de 116,6 ± 34,3 mm, o número médio de incrementos diários foi de 146 ± 41 e a distância média entre o núcleo e a borda ventral das secções dos otólitos foi de 1,69 ± 0,22 mm. A relação entre o tamanho médio, o número de microincrementos e o comprimento do eixo ventral das secções dos otólitos levou à conclusão de que a primeira banda opaca terminaria em média a uma distância maior que 1,67 mm ao longo do eixo ventral dos otólitos durante os primeiros meses de vida dos pargo-rosa, visto que a primeira banda anual identificada apresenta uma distância média de 1,84 ± 0,16 mm. Dessa forma, o primeiro *annulus* no otólito foi considerado correspondente a meio ano de vida. A correspondência entre as leituras dos *annulus* nos otólitos e escamas de indivíduos adultos, foi consistente em 53% das comparações e quando somado à contagem que diferiu em um único ano, foi de 93%. As diferenças de um ano entre as leituras em ambas as estruturas foram observadas em 40% dos casos, em que 25% marcaram um ano a mais nos otólitos e 15% nas escalas. No geral, 30% das leituras nas secções do otólito apresentaram mais *annulus* e 17% nas escalas. A correspondência foi considerada significativa, no entanto, para peixes mais velhos, é difícil discriminar anéis na borda das escamas. De fato, um espécime com 12 anéis na escama apresentou 19 bandas opacas correspondentes em seu otólito, dessa forma, outros 12 peixes mais velhos não foram incluídos na comparação, pois a leitura das idades foram consistentes apenas em seus otólitos. No total, 663 *P. pagrus* tiveram sua idade determinada através dos otólitos seccionados,

dos quais 101 indivíduos correspondentes à 1976-1977 e 574 à 2015-2019. Em relação a nitidez dos otólitos, todos os exemplares de 1976-1977 apresentaram banda opacas bem marcada. No período de 2015 a 2019, 263 peixes apresentaram bandas de crescimento opacas bem marcadas e 311 apresentaram bandas de crescimento pouco marcadass ou ausentes. Ambos os padrões de formação de banda ocorreram em quase todos os meses amostrado, sendo que a maior proporção de espécimes com bandas de crescimento bem marcadas foi em setembro (81,6%, n = 77) e a maior proporção de bandas de crescimento pouco marcadas ou ausente em novembro e dezembro (74,2%, n = 184). No primeiro período de 1976 a 1977, o peixe mais velho apresentou 28 *annulus*, já no segundo período (2015 a 2019), 18 *annulus* no otólito com bandas bem marcadas e 10 *annulus* no otólito com bandas pouco marcadas. Os comprimentos médios retro-calculados por idade não diferiram entre os dois períodos e entre os padrões de banda decrescimento no segundo período (*Wilcoxon-Mann-Whitney*, $p > 0,05$). Os parâmetros de crescimento (TL_{∞}, k, t_0) e seus intervalos de credibilidade de se sobrepõem entre os períodos e padrões de bandas de crescimento, indicando que não há diferenças significativas entre as curvas de crescimento analisadas. As análises gráficas e discussão desses resultados estão aprofundadas no segundo manuscrito da dissertação, correspondente ao Apêndice II. Este artigo tem título de "Long-term comparisions in growth of *Pagrus pagrus* **(**teleostei) in southern Brazil", e será submetido à revista Fisheries Research– Qualis A2 (CAPES – Biodiversidade).

CONCLUSÕES

- A forma do otólito do pargo-rosa muda ao longo do crescimento
- A forma do otólito não e homogênea ao longo de sua distribuição no Atlântico sudoeste.

- Os padrões de forma dos otólitos dos estoques de *P. pagrus* podem estar associados a fatores ambientais distintos, a áreas de retenção de larvas ou de desova distintas, e sugerem uma baixa dispersão entre locais geograficamente distantes.
- A forma dos otólitos mostram que os pargos-rosa capturados no Rio de Janeiro são um grupo isolado.
- A dissimilaridade das formas do otólito entre a zona de pesca exclusiva da Argentina e a área de pesca comum do Uruguaia-Argentina, apoia a hipótese da existências de estoques vizinhos distintos.
- A semelhança das formas do otólito entre a área de pesca comum do Uruguaia-Argentina e do Rio Grande com bandas de crescimento nítidas, apoia a hipótese de que o ultimo provavelmente desova no norte da zona comum de pesca do Uruguai e Argentina e se desloca para o Sul do Brasil durante o inverno.
- A grande diferença entre as formas do otólito de Rio grande com bandas de crescimento bem marcadas e pouco marcadas ou ausentes sugere diferentes subgrupos, com distribuição parcialmente sobreposta, cujo grau de sobreposição reprodutiva e geográfica deve ser mais estudada.
- Microincrementos de secções finas de otólitos de *Pagrus pagrus* podem ser assumidos como incrementos diários.
- A primeira banda opaca no otólito se forma entre o final do outono, correspondendo a meio ano de vida.
- Há uma correspondência significativa entre as idades determinadas a partir

de otólitos e escamas, porém é difícil discriminar anéis na borda das escamas em peixes mais velhos. Portanto os otólitos do pargo-rosa são mais indicados para estudos de longevidade.

- Tanto os otólitos com bandas de crescimento bem marcados como os de bandas de crescimento pouco marcadas ou ausentes ocorrerem ao longo do ano no Sul do Brasil, porém com maior proporção de pouco marcadas na primavera.
- A falta de mudanças do crescimento evidencia a baixa influência de fatores denso-dependentes no crescimento de *P. pagrus* no sul do Brasil.
- A falta de mudança no crescimento pode ser atribuída ao impacto relativamente pequeno do pargo-rosa no suprimento geral de alimentos baseado principalmente nas cadeias tróficas planctônicas.

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APÊNDICE I

DISCRIMINATION OF RED PORGY *PAGRUS PAGRUS* (TELEOSTEI) GROUPS ALONG THE SOUTHWESTERN ATLANTIC BY OTOLITH SHAPE ANALYSIS

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ABSTRACT

Otolith Shape Analysis (OSA) is a powerful method for discriminate fish groups that grew under different environmental conditions and therefore it is a potential tool for stock identification and management purposes. We analyzed the otolith shape of *Pagrus pagrus* (Linnaeus, 1758), a coastal sparid fish that inhabits consolidated and sandy shelf bottoms in the southwestern Atlantic, from the four regions in which it is commercially fished: Rio de Janeiro, Rio Grande do Sul in southern Brazil, the Argentine-Uruguayan common fishiery zone and the Argentinian exclusive fishing zone. To address the allometric relationship between fish length and otolith shape we selected a total length range (330 – 370 mm). Elliptical Fourier and Wavelet coefficients were used to compare differences among otolith shapes. Finally, we analyzed the accuracy of the otolith shape classification among the groups. Four groups were identified: one in the Argentine exclusive fishery zone, a second along the Common fishery zone of Argentina and Uruguay which included specimens from Southern Brazil with well-marked opaque bands in its otoliths (MRS), the third group in Southern Brazil with faint or absent opaque bands in its otoliths (FRS) and the fourth group along Rio de Janeiro. The difference in the shape between those otolith with well marked and faint or absent opaque growth marks from Southern Brazil is in accordance with the hypothesis that part of the red porgies (MRS) spawns along Uruguay and other (FRS) spawns locally in southern Brazil.

KEY WORDS: Argentina, Brazil, fishery resources, distribution, otolith morphology, ShapeR, Sparidae, stock identification, Uruguay.

INTRODUCTION

The red porgy, *Pagrus* pagrus (Linnaeus 1758), is a protogynous hermaphrodite coastal sparid fish (Alekseev 1983) commonly found on consolidated and sandy shelf bottoms in temperate and subtropical regions in both margins of the Atlantic Ocean and the Mediterranean Sea. *P. pagrus* is targeted by both commercial and recreational fisheries throughout its distribution (Manooch & Hassler 1978; FishstatJ 2018).

There are four main fishing areas of *P. pagrus* in the Southwestern Atlantic (SW) located from Espirito Santo state in Brazil to Buenos Aires province in Argentina (Cousseau & Perrota 2013). The northern area comprise from 19°S in Espirito Santo to 23^{0}S in the north of Rio de Janeiro (Costa et al. 1997). Another area is located in the south of Rio Grande do Sul, from 30°S to 34°S (Haimovici 1998), following by the one known as the Argentine-Uruguayan common fishery zone (UA) from 34°S to 39°S. The southern area is situated between 39°S to 42°S in the exclusive fishing zone of Argentina (AR) (Garcia & Molinari 2015).

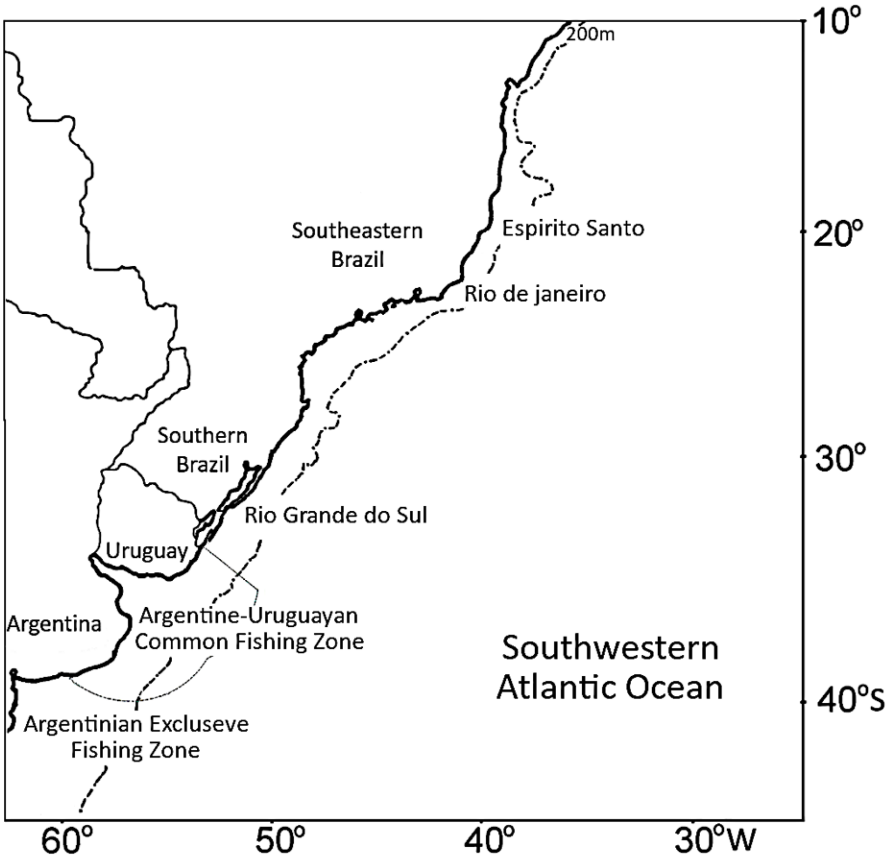

Figure 1. *Pagrus pagrus* principal commercially fished areas in Southeastern Atlantic Ocean. The horizontal sections correspond to the different catch areas.

Ball et al. (2006) compared microsatellites and mitochondrial DNA markers among several stocks of *P. pagrus* of the northeastern, northwestern and southwestern Atlantic and observed differences in two loci the three regions. Within the southwestern Atlantic, the heterogeneity of the stocks of red porgy has already been addressed in several papers. Based in samples collected from 34°S to 42°S Cotrina & Raimundo (1997) discriminated two groups of *P. Pagrus* considering aspects of their population dynamics and fisheries, one in the Argentinian exclusive fishing zone and another in the Argentine-Uruguayan common fishery zone. In the same areas Porrini et al. (2015) used microsatellite DNA markers and body landmarks techniques achieving different results between them. While genetics did not support the hypothesis of distinct stocks, the body shape analysis pointed differences between AR and UA. Soares et al. (2018) analysed the long-lived larval parasites assemblages of *Pagrus pagrus* from Rio de Janeiro, São Paulo along southeastern Brazil, Rio Grande do Sul in southern Brazil and Argentina and identified three distinct groups: one in Rio de Janeiro and São Paulo, other in Rio Grande do Sul and the third in Argentina. In the red porgies from Rio Grande do Sul the pattern of the annuli on the scales was not homogeneous (Haimovici 1997). It has been suggested that those with well-marked growth rings spawn in neighbour waters of Uruguay and feed in winter in Southern Brazil and those with faint rings in their scales remain year round and spawn in southern Brazil (Figure 2; Haimovici 1997; Haimovici in preparation). The same pattern of well marked and faint or absent growth bands was also observed on the sectioned otoliths form Rio Grande do Sul (figure 2).

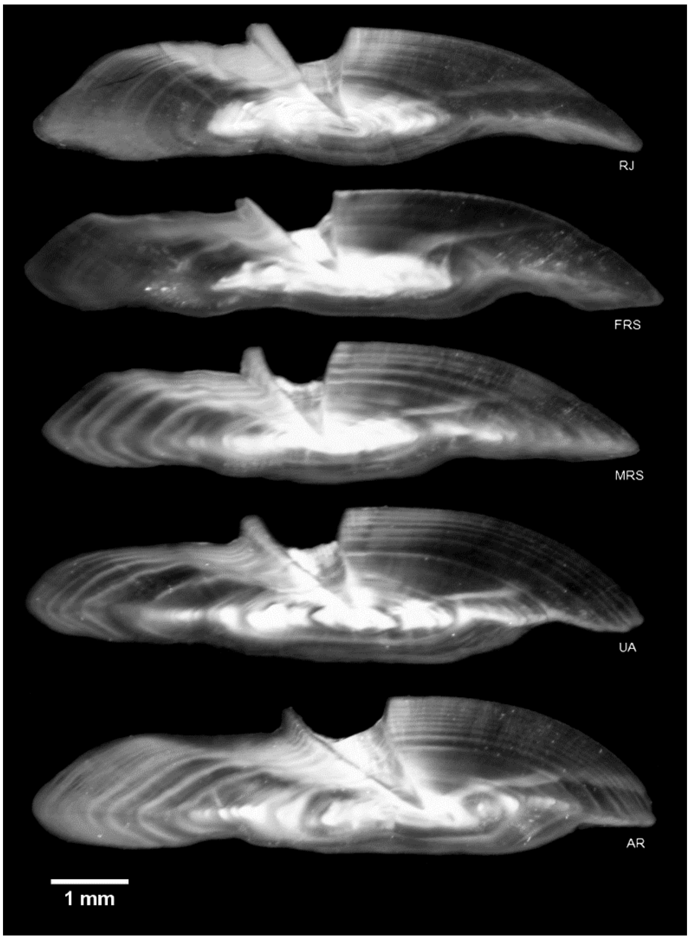

Figure2. *Pagrus pagrus* sagittae otolith sections of 370mm fish size from Rio de Janeiro (RJ), Rio Grande do Sul faint growth opaque bands (FRS) and well-marked growth opaque bands (MRS), the Argentine-Uruguayan common fishery zone (AU), and the Argentinian exclusive fishing zone (AR).

The failure to recognize the stock structure of an exploited species can lead to dramatic changes in the biological attributes, productivity rates, genetic diversity, as well as lead to overfishing and depletion of the less productive stocks (Smith et al. 1991). In fact, the red porgy of Rio Grande do Sul was intensely fished and depleted in a few years after exploratory fishing detected this formerly unexploited stock in 1972, which did not recover in the last decades and are currently considered overexploited (Haimovici 1998; Haimovici in preparation)

Phenotypic divergence along ecological gradients can be made up (to varying degrees) by genetic differences among species or populations as well as phenotypic/developmental plasticity. This also applies to taxon-specific differences in otolith morphology (Schulz-Mirbach et al. 2019). Vignon & Morat (2010) found that the overall 2D outline of otoliths was strongly influenced by environmental factors in the coral reef snapper (*Lutjanus kasmira*) whereas the development of specific shapes of the *rostrum* and the *antirostrum* showed only a low level of variation. Thus different portions of the otolith may show different degrees of phenotypic plasticity. Although environmental factors may induce differences in the fish body and otolith shape (Norton et al. 1995; Cardinale et al. 2004), this last are not affected by short term changes in fish condition (Campana & Casselman 1993). Otoliths are acellular concretions of calcium carbonate and other inorganic salts generally considered immune from modification once formed (Green et al. 2009). Its morphology has been used to identify groups of fish that are likely to have spent a significant part of their lives in different environments and therefore may provide an indirect basis for potential stock separation. (Begg et al. 1999; Bergenius et al. 2006)

The differences in the otoliths morphology can be assessed by different approaches such as statistical analysis of general shape parameters (Burke et al. 2008; Paul et al. 2013; Keating et al. 2014); landmark analysis (Cadrin 2013); and otolith shape analysis (OSA) through the Elliptical Fourier transforms (Campana & Casselman 1993; Burke et al. 2008; Duarte-Neto et al. 2008), and Wavelets (Parisi-Baradad et al. 2005; Libungan & Pálsson 2015). Among these, OSA become a popular and well-established method for discrimination fishes with distinct spatial distributions over part or all of their lifetime (Campana & Casselman 1993; DeVries et al. 2002; Tuset et al. 2013; Libungan et al. 2015). This method requires otolith images from which outlines can be extracted and quantified, so the shape variation patterns within and among groups can be evaluated based on a large number of independent variables (Stransky 2013; Libungan& Pálsson 2015). The Wavelet method is useful for detecting shape differences at specific regions, which could be located at a given angle on the otolith outline; in contrast, the Fourier method only provides information about overall differences in otolith shape, not localized differences. Therefore, for some fish species, Wavelet might prove to be better at explaining shape differences, while for others, the Fourier method might be more powerful to distinguish populations (Libungan & Pálsson 2015).

The aim of this study was to evaluate the otolith shape as a stock marker for *Pagrus pagrus* in an area with potential mixing of neighboring stocks in the Southwestern Atlantic Ocean. To address the allometric relationship between fish length and otolith shape we selected a homogeneous total length range and used both Elliptical Fourier and Wavelet coefficients to compare differences among otolith shapes. Finally, we analyzed the accuracy of the otolith shape classification among the potential stocks.

MATERIALS AND METHODS

Sagittae otoliths of 839 *Pagrus pagrus* were collected between 2015 and 2019 in four regions, covering all the distribution range of the species in the subtropical and warm temperate Southwestern Atlantic Ocean: along Rio de Janeiro (22° S - 23°S) and Rio Grande do Sul (32°S - 34°S) in Brazil, in the Argentine-Uruguayan common fishery zone (34°S - 39°S) and the exclusive fishing zone of Argentina (39°S - 42°S).

Cross-sections of 0.20 mm passing through the otoliths nucleus were obtained with a low-speed precision saw for the red porgies sampled in Rio Grande and classified in two groups: those with well-marked growth bands (MRS) as those with faint or absent growth bands (FRS) (Figure 2).

For each specimen the total length (TL; mm) was recorded and one otolith had its inner surface recorded as a digital image captured with an AmScope MD500 camera magnified 10x times under a Nikon SMZ800 stereomicroscope.

Ward’s hierarchical clustering analysis was used to identify a size range of fishes in which the otoliths had similar ontogenetic characteristics. For this purpose, the area, perimeter, width and length of 70 otoliths of random selected fishes were used, considering the minimum and maximum total length observed (155mm to 528mm TL). Among the formed groups, otoliths of fishes from 330 to 370mm TL, that included 195 individuals, had the best overlap in the dataset among the five samples groups and was chosen for the shape analysis, (Table 1)

Table 1. Latitudes range, year of data collection, total length ranges of the sampled groups of red porgies. OSA: Otolith Shape Analysis.

	Latitude range	Data collection year	Total sampled (TL range = 155 to 528mm)	OSA sample selected (TL range =330 to 37 mm)
RJ (Rio de Janeiro)	22°S - 23°S	2017	174	56
FRS (Rio Grande faint growth bands)	32°S - 34°S	2015-2019	238	45
MRS (Rio Grande well marked growth bands)	32°S - 34°S	2016-2019	249	48
UA (Argentine-Uruguayan common fishery zone)	34°S - 39°S	2018	79	21
AR (Argentinian exclusive fishing zone)	39°S - 42°S	2018	99	25

The *ShapeR* package (Libungan & Pálsson 2015) was used to read the images of each otolith and record the outlines as a matrix of x and y coordinates. To remove size-induced bias, otoliths sizes were standarized so that the otolith area would be equal in all otoliths by dividing the co-ordinates of each otolith with the square root of the otolith area (Libungan & Pálsson 2015; Libungan et al. 2015).

The shape patterns of each of the five sample groups: Rio de Janeiro (RJ); Rio Grande do Sul faint otolith growth bands (FRS) and well-marked otolith growth bands (MRS); Argentine-Uruguayan common fishery zone (UA); and Argentinian exclusive fishing zone (AR) were expressed as the Wavelet/Fourier coefficient. The Wavelet coefficients were obtained with the *wavethresh* package (Nason 2012) and the Normalized Elliptic Fourier technique was performed using the *iefourier* and *efourier* functions (Claude 2008). To determine the number of Wavelet and Fourier coefficientsneeded for the analysis, the deviation of the reconstructed otoliths outline from the original outline was evaluated in *ShapeR* package (Libungan & Pálsson 2015). By using 64 Wavelet and 45 Fourier coefficients, an error rate of 1.5% or an accuracy of 98.5% was obtained.

Fish growth affects the otolith structure and shape (Geffen 1982; Folkvordet al. 2000; Feet et al. 2002; Fox et al. 2003), for example, otoliths become wider with fish size within the same stock (Simoneau et al. 2000). The interaction between the total length of the red porgies and the Wavelet/Fourier coefficients was investigated by analysis of covariance (ANCOVA), and when there was a significant interaction, those coefficients were excluded from the analysis to remove the allometric relationship (Libungan & Pálsson 2015).

The mean otolith shape reconstructed outlines of the normalized Wavelet coefficients for each group of samples were plotted and the differences among the groups evaluated visually. To estimate which part of the otolith outline contributed most to the difference between the potential stocks, mean shape coefficients and their standard deviation (s.d.) were plotted against the angle of the outline from where the coefficients were extracted using the function plotCI from the gplots package (Warnes et al. 2014).

The shape variation among the groups was compared by a canonical analysis of principal coordinate (CAP) (Anderson & Willis 2003), applied on the standardized Wavelet/Fourier coefficient using the *capscale* function in the *vegan* package (Oksanen et al. 2013). Ordination of the stocks averages along the first two canonical axes was evaluated graphically with shape descriptors. An ANOVA-like permutation test for CAP was used to assess the significance of constraints using 1000 permutations, also in *vegan* package (Oksanen et al. 2013).

To analyses the accuracy of the otolith shape classification into their sampling origin, Linear Discriminant Analysis (LDA) was applied on the standardized Wavelet/Fourier coefficients (Libungan & Pálsson 2015). The LDA classification method discriminate predefined groups based on sample observation from each group (Klecka 1980), and was calculated withleave-one-out cross-validation using the *errorest* function in the *ipred* package (Peters & Hothorn 2013), which returns the posterior probabilities for the groups.

All statistical analysis was performed in the software R (R Core Team 2013), version 3.3.1.

RESULTS

Red porgy otolith morphology changes along growth (Figure 3). To minimize biases due to fish size in relation to shape changes, a cluster analysis was applied to the otolith parameters (area, perimeter, width and length) of 70 specimens from the same region covering the total length range of 155 to 528mm. Six total length intervals were clustered (Figure 3), in which the 330 to 370mm total length interval , had the best overlap in the dataset among the five groups of samples, therefore it was chosen for the shape analysis (Table 1).

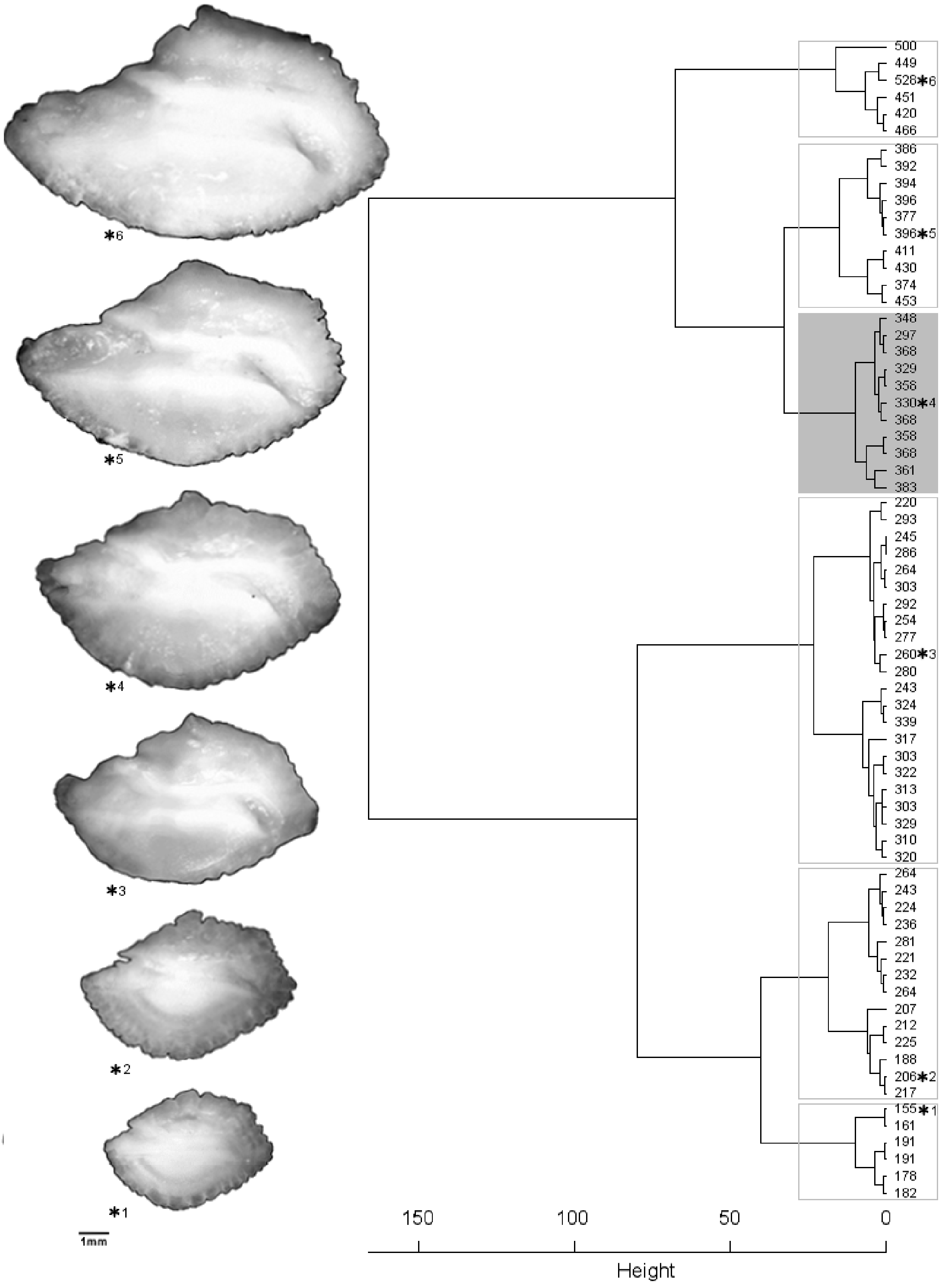

Figure 3. Dendrogram of ontogenetic relationships among otolith area, perimeter, width and length parameters from *Pagrus pagrus* ranging from 155 to 528mm TL, from Rio de Janeiro using the Ward's method of hierarchical clustering analysis based on Euclidean distances. Selected range for the shape analysis in full gray.

The Wavelet reconstruction showed differences among the mean otolith outlines for all samples groups, except between MRS and UA that showed a very similar otolith shape (Figure 4).The larger variation was observed at the *excisura ostii* (angles 130° to 200°) followed by the dorsal edge (angle 90° to 135°). In the ventral edge (angle 225° to 290°) the distance from the otolith centroid was larger in the FRS when compared with all the other samples groups. There was a high overlap in the *postantirostrum* (angle 40° to70°), in the *rostrum* (angle 200° to 225°) and in the *postrostrum* (angle 300° to 320°) of all the samples groups (Figure 4).

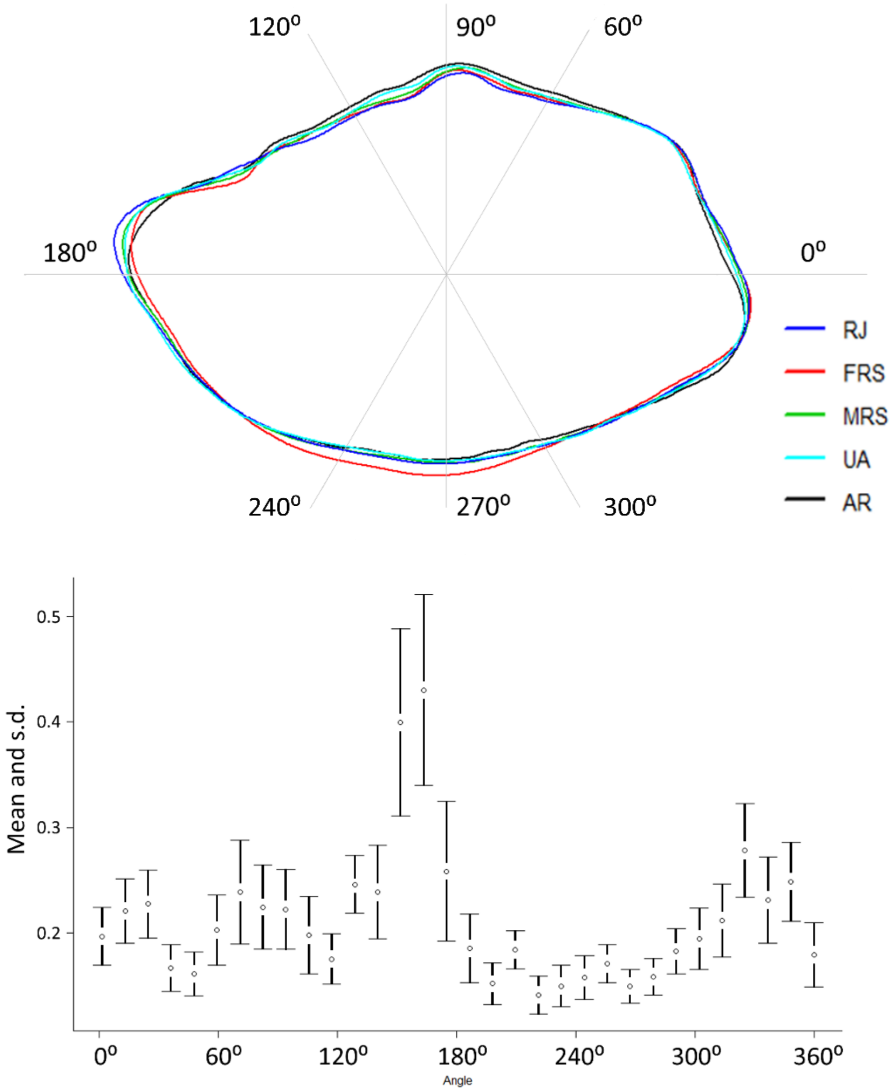

Figure 4. Mean otolith shape based on Wavelet reconstruction for each group (above) and mean and standard deviation (s.d.) of the Wavelet coefficients among all groups (below) of *Pagrus pagrus* sampled in: RJ (Rio de Janeiro); FRS (Rio Grande do Sul faint) and MRS (well-marked otolith growth bands); UA (Argentine-Uruguayan common fishery zone); and AR (Argentinian exclusive fishing zone). Degrees (°) based represent angles on polar coordinates.

The canonical analysis of the principal coordinates showed that otolith shape was not homogeneous among the five sampled groups for both coefficients (ANOVA-like, $p < 0.05$), in which 95.1% of the variation was explained along the first two axes for the Fourier and 96.18% for the Wavelet (Figure 5).

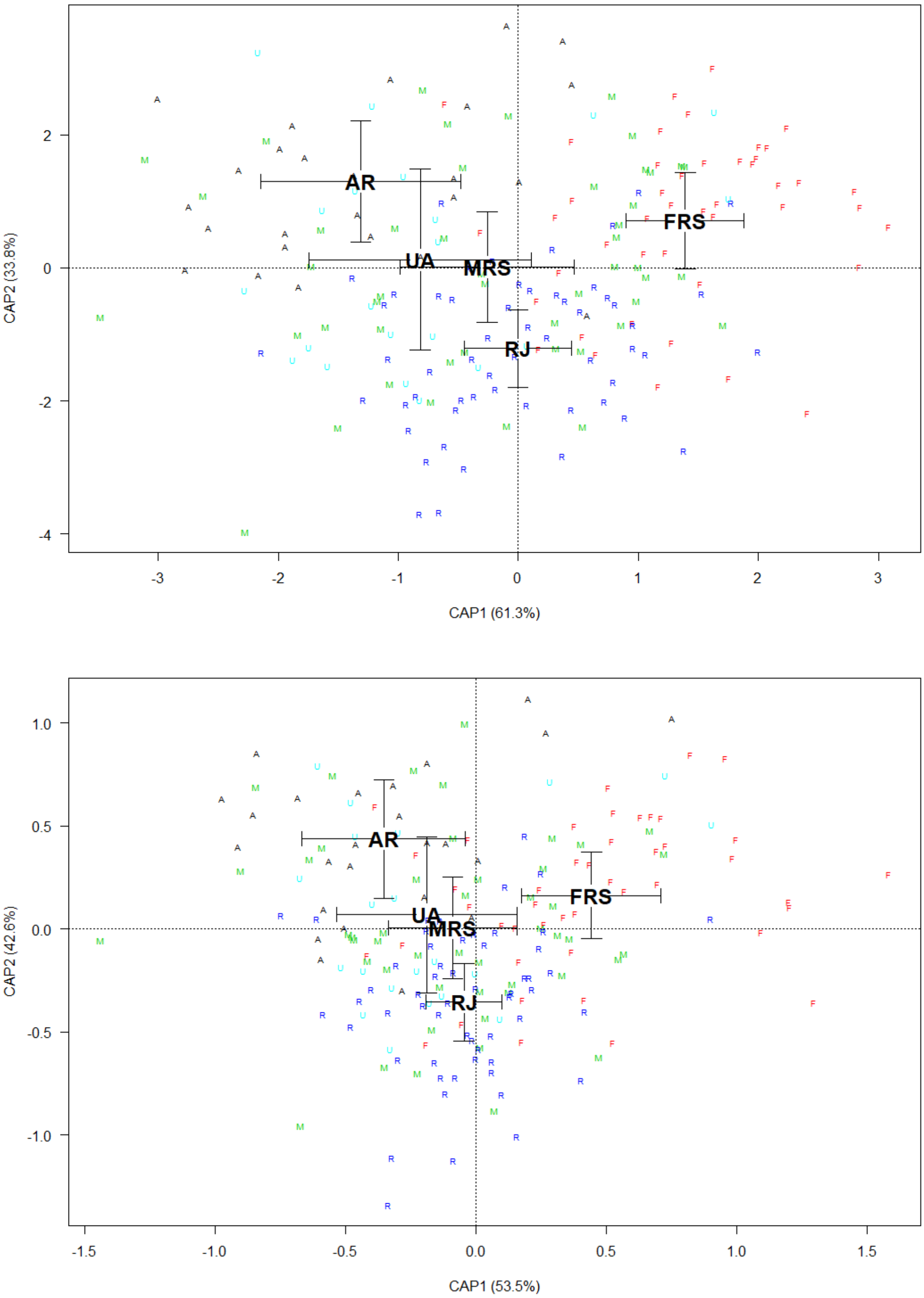

Figure 5. Otolith shape of samples from five red porgy sample groups in the SW-Atlantic using Canonical analysis for Fourier (above) and Wavelet (below) coefficients. Black letters represent the mean canonical coordinates surrounding by standard error for each group: RJ (Rio de Janeiro);

FRS (Rio Grande do Sul faint otolith bands) and MRS (well-marked otolith bands); UA (Argentine-Uruguayan common fishery zone); and AR (Argentinian exclusive fishing zone).

In both CAP, AR, RJ and FRS appear in different panels in which there was no overlap along any of the axes. The standard deviation of both UA and MRS groups overlap among them and with the RJ and AR. Except between UA and MRS, the ANOVA-like permutation test for the Fourier and Wavelet coefficients showed significant differences among all paired groups (Table 2).

Table 2. Analysis of variance (ANOVA)-like permutation test of the otolith shape among *Pagrus pagrus* samples groups in the *a priori* comparisons, and the percentage of classification success (C.s.) of Linear Discriminant Analysis (LDA) of Rio de Janeiro (RJ); Rio Grande faint otolith bands (FRS); Rio Grande well marked otolith bands (MRS); Argentine-Uruguayan common fishery zone (UA); and Argentinian exclusive fishing zone (AR). Statistically significant *p*-values are in bold.

Comparisons		Fourier				Wavelet			
	d.f.	MS	F	*p*	C.s.	MS	F	*p*	C.s.
All populations	4	0.130	8.106	**0.001**		15.910	7.854	**0.001**	
MRS*v*. UA	1	0.003	0.862	0.490	60%	0.673	1.123	0.329	61%
MRS*v*. RJ	1	0.016	4.121	**0.002**	76%	1.178	3.474	**0.002**	76%
MRS*v*.FRS	1	0.038	8.543	**0.001**	78%	4.763	8.725	**0.001**	80%
MRS*v*. AR	1	0.020	4.918	**0.001**	82%	2.483	4.429	**0.001**	80%
UA*v*. AR	1	0.010	2.773	**0.012**	80%	1.120	2.168	**0.023**	77%
UA v. RJ	1	0.015	4.272	**0.001**	83%	1.960	4.153	**0.001**	82%
UA*v*. FRS	1	0.032	7.386	**0.001**	93%	5.000	9.817	**0.001**	94%
AR*v*.FRS	1	0.059	14.163	**0.001**	93%	8.046	16.974	**0.001**	95%
AR*v*. RJ	1	0.054	15.694	**0.001**	96%	5.926	13.365	**0.001**	98%
RJ *v*.FRS	1	0.060	15.343	**0.001**	88%	6.637	14.640	**0.001**	90%
Residual	190	0.764				96.217			

Among the groups that showed significant difference in the ANOVA-like test, the linear discriminant analysis (LDA) pairwise classification success were between 76% and 96% for the Fourier coefficient and between 76% and 98% for the Wavelet coefficient. On the other hand, classification success between the UA and MRS groups, for which the ANOVA-like test was not significant, was of only 60 and 61%.

DISCUSSION

Otolith shape analysis proved to be effective to discriminate both geographically or ecologically distinct groups of *P.pagrus* and together with other tools contribute to support management. As other phenotypically based methods, OSA is more powerful for short-term discrimination processes than presently used genetic markers (Begg et al. 1999). These last are more suitable for long term changes of fully isolated groups, as the case of *P. pagrus* populations among the SWA, NWA, NEA and Mediterranean Sea (Ball et al. 2006), but not for nearby stocks such as those of southern (AR) and northern (UA) Argentina which could not be discriminated by microsatellite DNA markers (Porrini et al. 2015).

Spatial and temporal variations in spawning among fish stocks may contribute to variation in otolith shape, reflecting early life ecological and environmental differences or resource availability during the first year of the individual's life (Burke et al. 2008; Libungan et al. 2015). Temperature is also an important factor that regulates the otolith growth (Lombarte & Lleonart 1993) as well as the food consumption during early life can lead to differed otolith geometry and lobes width (Hüssy 2008). We lack on information on the early growth of *P. pagrus* but in later stages differences in the somatic growth were observed between the northern and southern groups in Argentina by Cotrina & Raimondo (1997) and between AR and UA by Garcia & Déspos (2015).

Castonguay et al. (1991) and Friedland & Reddin (1994), observed that classification success based in the otolith shape increased with increasing geographic distance. Although it is difficult to establish causalities, LDA based in both Wavelet/Fourier coefficient showed increasing classification success as geographic separation increased, except for the group with faint opaque bands form Rio Grande do Sul. Soares et al. (2018) comparing the long-lived parasite communities evidenced the existence of distinct groups of red porgies along Rio de Janeiro, Rio Grande do Sul and northern Argentina. In contrast with otolith shape analysis, this method is not suitable to discriminate geographically coexistent groups, but corroborate the existence of a geographical gradient between red porgies in this region.

It might be possible that the *P. pagrus* inhabiting Rio de Janeiro in the southeastern Brazilian Bight region is a genetically distinct population from those from southern Brazil to Argentina. The segregation between southeastern and southern Brazil fish populations has been observed for other coastal fishes as *Macrodon atricauda* (Rodrigues et al. 2014) and *Micropogonias furneri* (Vasconcellos et al. 2015). However, although *P. pagrus* has a limited migratory behavior (Parker 1990; Afonso et al. 2009) some genetic flux through larval displacement cannot be discarded.

Differences in otolith shape between AR and UA with 80% classification success are in agreement with Porrini et al. (2015) landmarks body shape observations. These authors suggest the presence of two different spawning areas for *P. pagrus* along Argentina coast, which could affect the early stages of development and be responsible for morphological differentiation of adult individuals. Environmental characteristics define two different oceanographic regimes between AR and UA (Acha et al. 2004) with distinct water recirculation, constituting multispecific nursery and feeding areas and favors larval retention (Acha et al. 2004; Militelli et al. 2007).

Differences in otolith shape between UA and MRS were not significant, as seen by both analysis (Wavelet and Fourier). Most of *P. pagrus* catches in the late 1970´s and early 1980´s in southern Brazil were performed by bottom trawlers near the northern Uruguayan border, with catches ten-fold higher during the winters, thus Haimovici (1997) suggest that part of the stock (MRS) is composed by migrants from Uruguayan waters. Despite, long distance migrations of *P. pagrus* are unlikely. Afonso et al. (2009) showed that tagged specimens could move several tenth of km in short periods of time. Limited displacements were shown to occur by Garcia & Molinari (2015) that reported *P. pagrus* seasonal extension of the southward distribution limit from 41ºS to > 42ºS in the warm season and associated it to the species reproduction.

The northward displacement of red porgies from Uruguay could be associated to northward running cold shelf waters under the influence of the inner branch of the Malvinas current that reach their maximum extension towards southern Brazil in winter, mixing the subtropical and subantarctic waters that favor the presence of high concentrations of nutrients (Lucas et al. 2005). The similarity in the shape of the otoliths between UA and MRS support this hypothesis. In addition, Capitoli & Haimovici (1993) found differences in the feeding intensity and diet among *P.pagrus* sampled in winter in southern Brazil near the Uruguayan border, which showed heavier stomach contents and more nutritious prey, than those fished year round in shallow waters and further north.

The otolith shape of the FRS group differed from all the others. Among those fished year round in Rio Grande do Sul, almost one quarter had faint or absent annuli in their scales (Haimovici et al. in preparation). These authors also reported spawning in southern Brazil, supporting the hypothesis that there is a resident stock in the region. The large difference between the outlines of the MRS and FRS suggest different sub-groups, with partly overlapping distribution whose degree of reproductive and geographic overlap have to be further studied.

The otolith shape patterns among *P. pagrus* stocks might reflect environmental effects, which may be associated with discrete retention areas for larvae or different spawning areas, suggesting low dispersal between distant geographical locations. In conclusion, otolith shape can be an additional method to discriminate mixed-stocks for *P.* pagrus.

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APÊNDICE II

LONG-TERM COMPARISIONS ON GROWTH OF *PAGRUS PAGRUS* (TELEOSTEI) IN SOUTHERN BRAZIL

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ABSTRACT

Continued intensive fisheries exploitation may result in long-term changes in individual growth rates. In the 1970’s, a formerly unexploited stock of red porgy (*Pagrus* pagrus L.) along southern Brazil was intensely fished leading to its collapsed few years later, which still did not recover after 40 years. Considering the sharp reduction in the abundance, this work aims to evaluate if the red porgy suffered growth changes after the stock collapse in southern Brazil. The consistency between the validated annual rings in the scales and the opaque bands in the otoliths was verified for samples obtained in the 1976-1977 sampling period. However, opaque bands counts were more precise for aging because rings on the scales got crowded near the edge and led to underestimated ages in specimens aged 10 and older. In contrast, on sectioned otoliths the older aged specimen showed 28 annuli. It was also observed that both in scales and otoliths occurs two patterns of growth marks: well marked (WM) and faint or absent (FA) annulis, which appear year round and may reflect different life styles. Thin otoliths sections of 12 juveniles measuring from 72 to 171 mm LT showed a concentric pattern with 114 to 176 daily microincrements. The birth date back-calculation fell within the spawning season of the species in the region and the end of the first opaque band in the otoliths corresponded in mean to 170 days after the birth, most likely in late autumn. The growth between 1976-1977 (L_∞ = 417; K = 0.31; t_0 = -1.03), before the collapse of the red porgy bottom trawl fishery and 2015-2019 (L_∞ = 440; K = 0.26; t_0 = -1.32), after the sharp reduction in the stock abundance in southern Brazil did not show significant differences. Changes in density appear not to affect the red porgy growth and the lack of growth seems to be related to their relatively small impact on the overall food supply based in the planktonic based food webs.

KEY WORDS: fishery resources; long-term changes; otolith microincrement; scales; stock collapse.

INTRODUCTION

The red porgy, *Pagrus pagrus* (Linnaeus 1758), is a protogynous hermaphrodite coastal sparid fish (Alekseev 1983) commonly found on consolidated and sandy shelf bottoms in temperate and subtropical regions in both margins of the Atlantic Ocean and at the Mediterranean Sea targeted by both commercial and recreational fisheries throughout its distribution (Manooch & Hassler 1978; FishstatJ 2018). In Brazil, *P. pagrus* is mainly exploited along the northern coast of Rio de Janeiro and the southern coast of Rio Grande do Sul (Ávila-da-Silva & Haimovici 2006). Along southern Brazil, exploratory fishing detected a formerly unexploited stock of red porgy in 1972, which was intensively exploited (Yesaki & Barcellos 1974). Its abundance was overestimated and in a few years the intense fishing depleted the stock with catches declined below 500 t per year in the 1980s and below 200 t in the following decades (Figure 1). Due to the drastic decrease of the landings and the lack of a recovery along several decades, the stock of red porgy along southern Brazil is considered to be collapsed (Haimovici & Cardoso 2016)

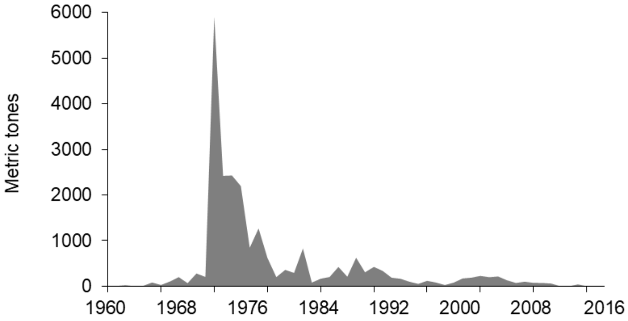

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Figure 1. Recorded landings of *Pagus pagrus* in Rio Grande between 1960 and 2016 (several sources).

Scales and otolith sections have been used to age red porgies. Age determination is one of the most important aspects in understanding fish growth dynamics. Aging is however, subject to various sources of error and for several species annual periodicity of otolith bands has been erroneously assumed, resulting in inaccurate ageing and in optimistic estimates of growth rates (Stevenson & Campana 1992; Cavole et al. 2018). Daily growth increments has the potential to elucidate the growth trajectories in those species with frequent false annuli and checks and can also serve as an age validation process for those species where microstructure and macrostructure information are currently available (Green et al. 2009, Cavole et al 2018).

Pagrus pagrus has been intensely sampled from 1976 to 1985 when the species was intensely fished in southern Brazil. In that period 22.964 specimens were measured and 4.407 aged (Haimovici 1987; 1998; Haimovici et al. in prep). The population dynamics, including ageing, growth, reproductive and condition annual cycle and mortality prior the collapse was addressed by Haimovici et al. (in prep.) and provide a baseline which can serve to analyze the changes in the population dynamics suffered by the species. Few data were collected in the following three decades because the landings were rare.

Along the ageing studies prior the collapse, two patterns of annual ring formation were observed on the scales, one of well-marked annual rings (WM) and a second with faint or almost absent rings (FA) (Haimovici 1997; Haimovici et al. in prep). Similarly, currently this pattern was observed in the otoliths sections (Figure 2). Seasonal and spatial differences in the proportion of specimens with well-marked annual rings and faint annual rings in the scales suggest that most of the well-marked rings in the scales spawns in Uruguay and perform short northward winter displacements to southern Brazil for feeding while those with faint or absent rings in the scales remain year round and reproduce in southern Brazil (Haimovici 1997). The issue of WM and AF marks on otoliths and scales depends on many factors, including spawning shifts between southern Brazil and Uruguay, for which there is only indirect evidence. Specific studies should be addressed to describe this aspect in the future.

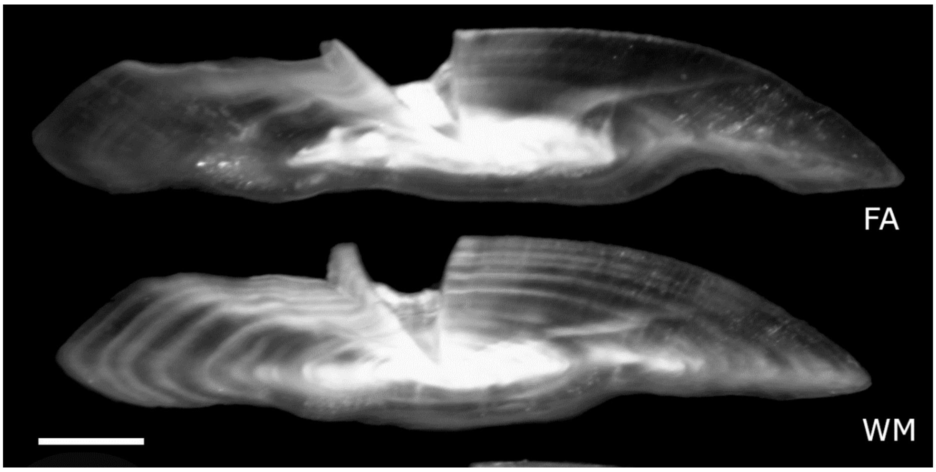

Figure 2. Thin sections of otoliths of two diferent *Pagrus pargus* with 370mm size from southern Brazil examinded with incident ligth over a dark background. Upper panel: faint of absent alternate pattern (AF). Lower panel: well marked alterante opaque and transluscent bands pattern (WM). Scale bar 1 mm.

Continued intensive fisheries exploitation may result in long-term changes in individual growth rates, sizes per age and maximum sizes, since growth rates are highly plastic showing rapid responses to changes in resource availability, temperature and density (Morrongielo & Thresher 2015; Audzijonyte et al. 2016). On the other hand, some changes have been associated with genetic responses to changes in mortality regimes (Trippel 1995, Law 2000, Audzijonyte et al. 2016).

Intense fishing in southern Brazil reduced the abundance of most demersal species in the last decades (Haimovici & Cardoso 2016). Associated to this decreasing abundance, it were observed increases in growth rates and size-at-ages for the most abundant coastal demersal species fished in the region, including *Cynoscion guatucupa* (Miranda & Haimovici 2007) and *Macrodon atricauda* (Cardoso & Haimovici 2011, 2014 and 2016), *Umbrina cansosai* (Haimvici et al .2006) and *Micropogonias furnieri* (Haimovici et al. in prep).

Considering the intense fishery exploitation and the sharp reduction in the abundance of the stock of red porgy in southern Brazil over the years, this work aims to evaluate if the red porgy suffered growth changes after the collapse of the fishery. In this context, first the annual formation of an opaque and a translucent band in the sections of the otoliths were verified by comparing the counts of opaque bands in the otoliths with rings on the scales and by analysing the microstructure of the otoliths of young-of-the-year to aid in the identification of the first annual opaque band. Following the proportions of specimens with well-marked and faint opaque bands in the otoliths were quantified and finally the growth between the specimens sampled between 1976-1977 and 2015-2019 and between specimens with well-marked and faint bands in their otoliths were compared.

MATERIAL AND METHODS

Biological data, otoliths and scales of 101 *P. pagrus* sampled between 1976 and 1977 obtained from the landings of bottom trawlers, hook and line fishing and bottom gill net, were available for ageing from the sampling program that monitors coastal demersal fisheries on the southern Brazilian shelf (28 to 34∘S) carried out by the Oceanography Institute of the University of Rio Grande since 1976 (Haimovici 1987, 1998, Haimovici et al., in prep). From 2015 to 2019, biological data including LT (mm), total mass (W, g) and sex (male, females and hermaphrodite) and scales and otoliths of 574 red porgies were obtained from the landings of bottom trawlers, hook and line fishing and bottom gill net fishing along southern Brazil between 30°S and 34°S (Fig. 3). Additionally data and otoliths of 12 young-of-the-year *P. pagrus* obtained from others surveys were available for microstructure studies.

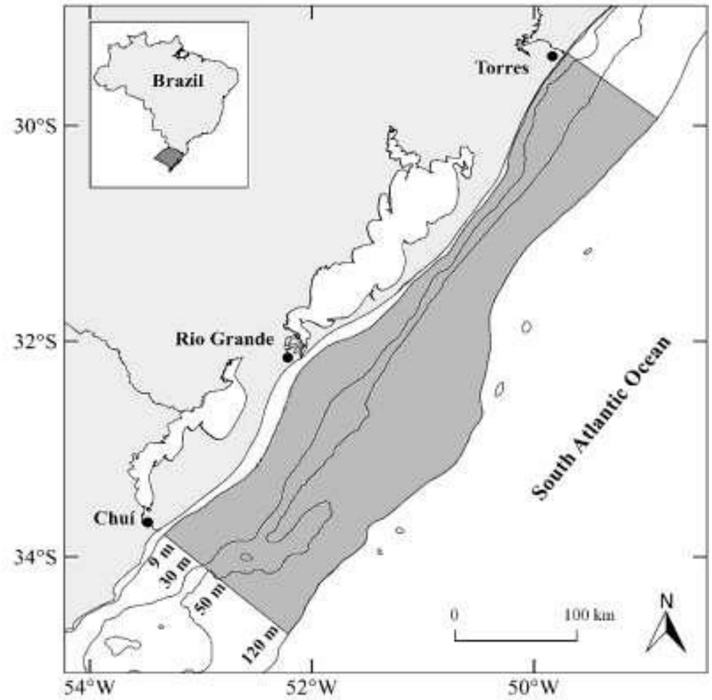

Figure 3. Study area: *Pagrus pagrus* fishing area in southern Brazil.

The microstructure (assumed daily growth increments) of 12 otoliths from specimens measuring 72–171 mm LT were examined to support the identification of the first annual opaque band. Sagittae otoliths were prepared and polished following the methods described by Cavole & Haimovici (2015). Sections were examined using a transmitted light microscopy at x 400 magnification (Olympus CX41; www.olympus-ims.com), suitable for examination of fast growing otoliths with microincrements larger than 2 μm in width (Campana & Jones 1992). Along the counting, the microscope light and focus was frequently adjusted to correctly interpret the entire sequence. Daily growth increments were counted between the otolith core and the outer edge of the otolith along the ventral axis (fig 4).

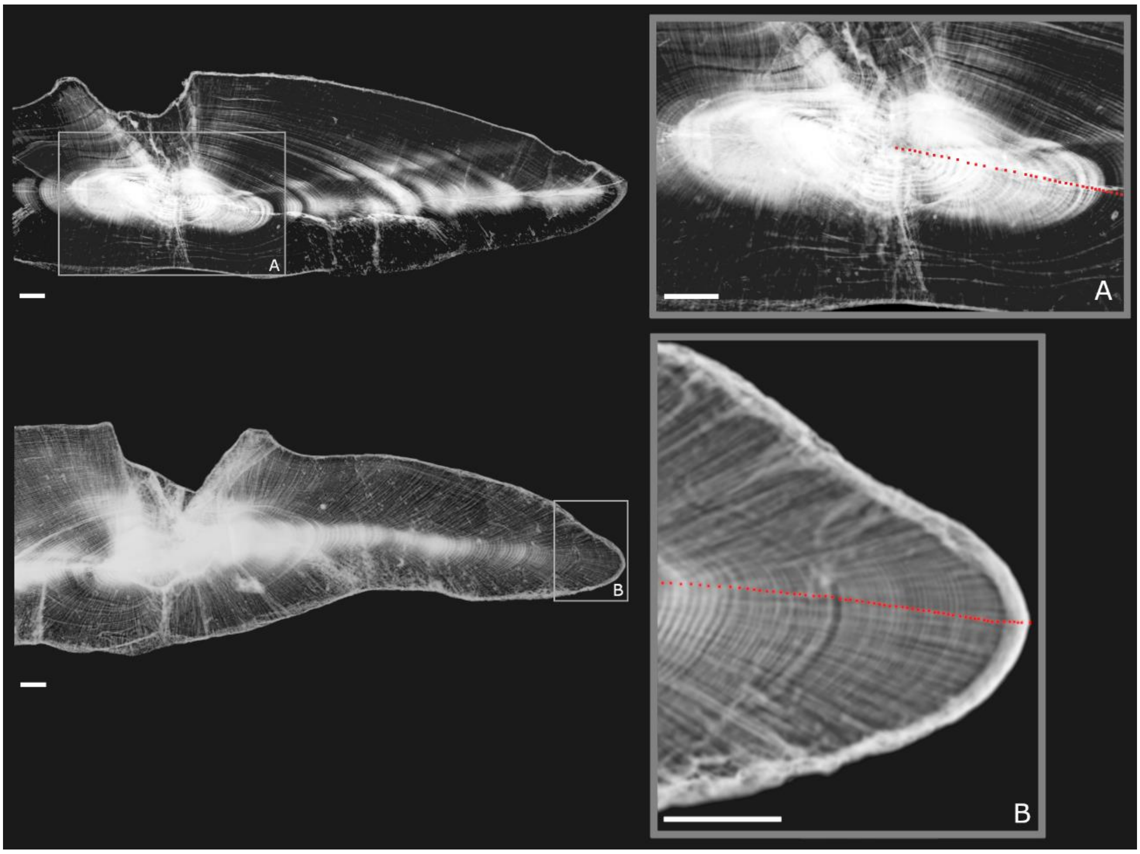

Figure 4. Microincrements in thin otoliths sections from juveniles *Pagrus pagrus*. Figure were produced by overlapping images obtained with a digital camera under a microscope with 10x ocular and a 20x objective focused in different parts of the transect from the nucleus to the border of the section along which the microincrements were counted (red pointed line). (A) Red porgy with 113mm total length showing 155 daily growth increments, evidencing the nucleus microincrements ; (B) Red porgy with 129mm total length showing 161 daily growth increments, evidencing the border microincrements. Scale bars 0.1 mm.

For the macrostructure analyzes, the adults sagittal otoliths were transversally sectioned (0.2–0.3 mm) through the nucleus with a low speed rotary saw. Digital images of the otolith sections were taken using a stereoscopic microscope at ×10 objective power on a camera with a resolution of 2048 × 1536 pixels per inch. The fishes were classified in two groups based on the legibility of the otolith sections as faint or absent growth bands in the otolith (FA) and well-marked growth bands in the otolith (WM) (Figure 2).

Alternate opaque and translucent bands were counted independently by two readers, if counts differed, otoliths were read again by both readers and discarded from further analyses if the difference persisted. The distances between the otolith nucleus and the end of the opaque bands (Fig. 5), assumed a priori as annuli (annual bands), were measured with the free software ImageJ 1·47 (www.imagej.nih.gov).

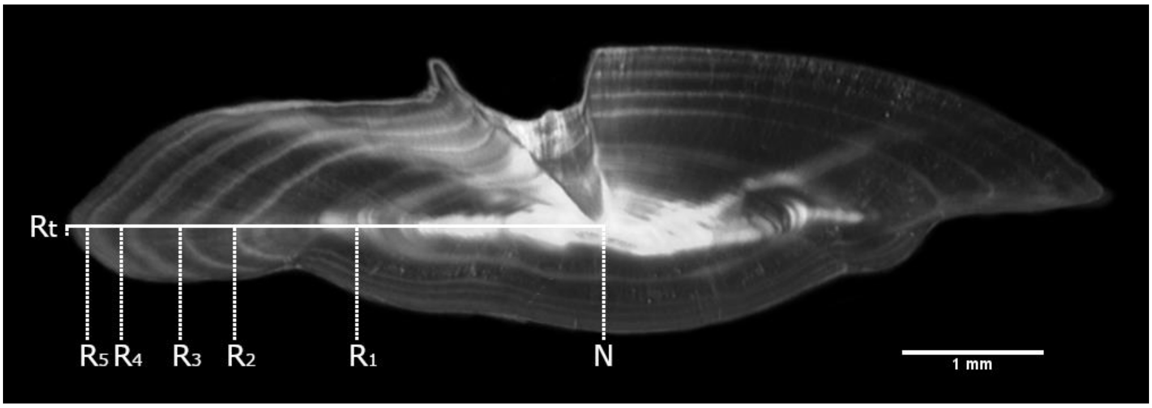

Figure 5. Thin section examined with reflected light of a five-year-old (L: 360 mm) *Pagrus pagrus* from southern Brazil. Dashed white lines indicate the nucleus (N), the end of each opaque band (Ri) and the border (Rt). Solid white line at the ventral axis indicate the measured distance from the nucleus to opaque bands and the border.

To verified the age determinations, the number of opaque bands observed in the otoliths sections were compared with the number of annuli on the scales of 89 red porgies sampled in 1976-1977 already aged and validated by Haimovici et al. (in prep.).

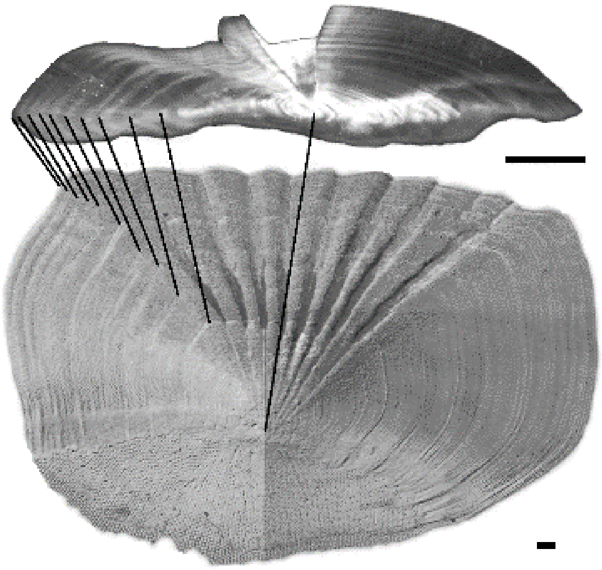

Figure 6. Correspondece between annual rings on the scales with the end of the opaque bands in the thin sections of otoliths of *Pagrus pagrus* form southern Brazil. Scale bars 1 mm.

Among the 661 samples orderly by Total length, every fourth specimens was retained resulting in a final sample of 165 specimens measuring 72 to 510 mm LT witch has the linear relationship between the total length and the otolith ventral axis calculated as $L = 0.0084\ R + 0.96;\ \ R^2$=0.908 (Fig. 7).

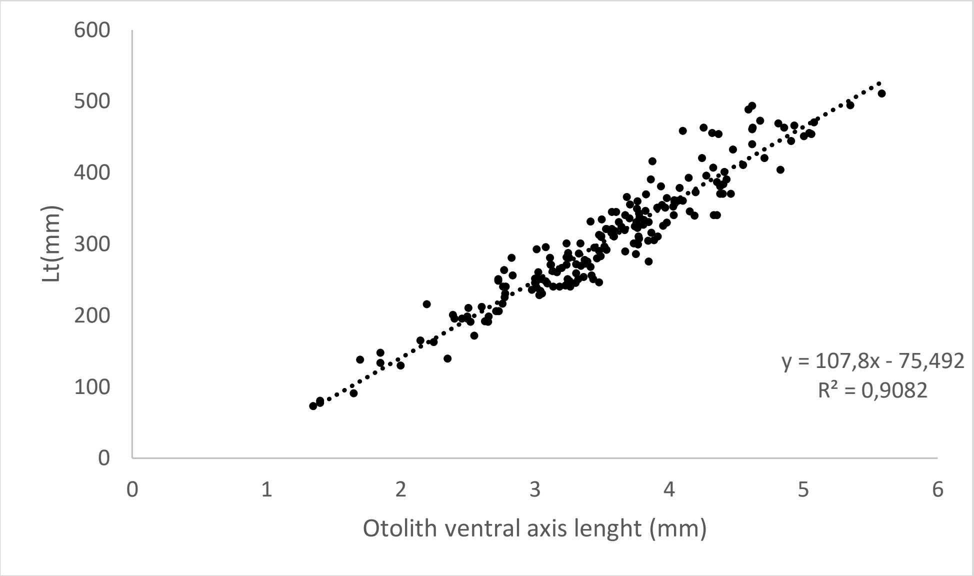

Figure 7. Linear relationship between *Pagrus pagrus* total length and the otolith ventral axis.

Back-calculated lengths-at-age were computed by using the scale proportional hypothesis (Francis 1990) with the Fraser –Lee formula:

$$Li(mm) = \left[(L - a).\left(\frac{Ri}{R}\right)\right] + a$$

in which L is the total length at the time of capture, *Li* is the length at the formation of the ith ring and *Ri* are distances between the focus and each age ring and *a* is the intercept of otolith radius on fish length regression.

The von Bertalanffy growth model adjusted by a bayesian approach was used to describe the growth of *Pagrus pagrus*. The age-length data were assumed (or the number of bands-length data for *P. pagrus*), as log-normal distribution: $y_i = \log N\ (\mu_i\,, \sigma^2)$, where y_i is the length distribution with an average expected length at an age class (or band class) *i* with variance σ^2. A logarithmic version of the von Bertalanffy equation was used for computational convenience:

$$\mu_i = \log(TL_\infty) + \log(1^{-k(i-t_o)})$$

Uninformative priors were constructed:

$$p(logTL_\infty) \sim dN(0{,}0.001)\ I\ (-5{,}5)$$
$$p(log\ k) \sim dN(0{,}0.001)\ I\ (-5{,}5)$$
$$p(\log t_0) \sim dU\ (-\ 3{,}0)$$

The posterior distributions of each time period and pattern of otolith band legibility (obtained via the stochastic process Monte Carlo Markov Chain) were used to compare the estimates of the growth parameters across time and otolith legibility (WM and FA). After 10,000 burn-in runs, every second value of the remaining 20,000 was retained, resulting in a final sample of 10,000 in the posterior distribution p (log TL_∞, log k, log t_0|D) (Kinas & Andrade 2010). The posterior distribution of each estimated parameter provided an easy and clear way to compare the results among periods and otolith pattern. All statistics in this study were run by R version 2.12.0. The MCMC was performed by *OpenBUGS*, using the libraries *R2WinBUGS* (Sturtz et al. 2005) and *BRugs* (Thomas et al. 2006).

Because the red porgy is a protogyneous species and no differences in the growth between sexes was observed by Haimovici et al. (in prep), growth was calculated for pooled sexes.

RESULTS

Thin otoliths sections of 12 juveniles measuring from 72 to 171 mm TL showed a concentric pattern of microincrements assumed to correspond to daily increments. The number of microincrements varied between 114 to 176. Except for one specimen, the birth date back-calculation fell between 26 October and 27 January (table 1). These dates were within the reproductive season of *P. pagrus* in southern Brazil. For a mean total length of 116.6±34.3 mm the number of daily increments was 146±41 and the distance between the nucleus and de ventral border of the otoliths was of 1.69±0.22 mm (Table 1).

Table 1. Back-calculated birth date for juvenile *Pagrus pagrus* based on the number of daily microincrements counted along the otolith thin section ventral axis.

Catch date	Back-calculated birth date	LT (mm)	Daily growth increments	Ventral axis distance (mm)
7-06-1991	27-01-1991	137	131	1.7
7-06-1991	21-01-1991	139	137	1.9
7-06-1991	12-12-1990	133	176	1.9
7-06-1991	28-12-1990	129	161	1.9
7-06-1991	24-12-1990	171	165	1.8
6-07-2001	25-04-2001	164	134	2.0
18-04-2002	16-12-2001	115	123	1.7
18-04-2002	14-11-2001	113	155	1.5
15-04-2008	26-10-2007	90	171	1.7
15-04-2008	28-11-2007	72	139	1.4
15-04-2008	23-12-2007	80	114	1.4
15-04-2008	15-11-2007	77	151	1.4
mean		**116.6±34.3**	**146±41**	**1.69±0.22**

The relationship between the mean size, number of microincrements and the length of the ventral axis of the otolith led the conclusion that first opaque band correspond as half a year, since the first annuli identified at the macrostructure measures 1.84±0.16mm.

The correspondence between the annuli readings on the otoliths and the scales were analyzed for of 89 red porgies sampled in 1976-77 (Table 2). Ageing was coincident in 53% of the comparisons and when added to the counting that differed in a single year, it was 93%. The one-year differences between readings in both structures were observed in 40% of cases, in which 25% marked one year more on the otoliths and 15% on the scales. In general, the otolith sections showed 30% more growth marks and the scales 17%. The correspondence was considered overall good, however for older fishes, it is difficult to discriminate rings in the border of the scales. In fact, a specimen with 12 rings on the scale had 19 opaque bands in their otolith, thus others 12 older fishes were not included in the comparison because of the crowding of the rings in the scales border and they only could be aged on their otoliths.

Table 2. Differences between the readings of annual growth marks in otoliths and scales.

	+ Otolith			Same	+ Scale		
Growth marks	**+7**	**+2**	**+1**	**0**	**+1**	**+2**	**Total**
2			3	5			8
3		2	4	7	3		16
4			5	12	1		18
5			2	9	2	1	14
6			2	5	6		13
7			3	7	1	1	12
8			1				1
9			1				1
10		2	1				3
11				1			1
12	1			1			2
Total	**1**	**4**	**22**	**47**	**13**	**2**	**89**
%	**1%**	**4%**	**25%**	**53%**	**15%**	**2%**	**100%**

All the otoliths aged from 1976-1977 had well marked opaque bands (n= 101). In the 2015 to 2019 period, 263 had well marked opaque bands (size range 190-510 mm, mean 319±57 mm), 311 had faint or absent opaque bands (size range 191-488 mm, mean 322±58mm) and 4 had no discernible growth band pattern. The well-marked and faint or absent band formation patterns occurred in almost all the sampled months (fig. 8).

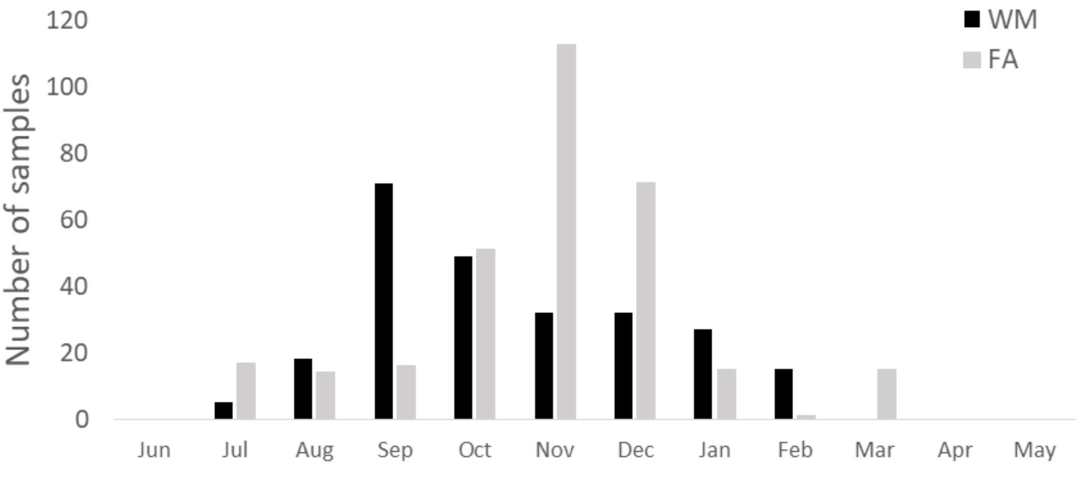

Figure 8. Proportion of *Pagrus pagrus* fished in southern Brazil between 2015 and 2019 with well marked (WM) or faint (FA) annual growth bands on the otolith.

Among the best sampled months, the highest proportion of specimens with well marked growth bands was in September (81.6%, n= 77) and the highest proportion of faint or absent growth bands was observed in November to December (74.2%, n = 184).

In 1976-1977 period the older fish had 28 annuli and in the 2015-2019 period the older aged fish had 18 annuli on their otoliths with well marked growth bands and 10 annuli for those with faint growth bands. The mean back-calculated lengths-at-age did not showed differences (Wilcoxon-Mann-Whitney, $p > 0.05$) between both periods and between well marked and faint opaque bands in the second period (Table 3).

Table 3. Observed mean length (Lt, mm) and back-calculated mean lengths by age of Pagrus pagrus fished in southern Brazil by periods (1976-1977 and 2015-2019) and patterns of bands formation on the otolith, one of well-marked annual bands (WM) and a second with faint bands (FA). n = Number of sampled individuals.

1976 – 1977

Annuli number	n	Observed mean Lt (mm)	Age (years)									
			0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
2	1	240	97	182								
3	11	261	111	200	260							
4	21	314	116	203	266	302						
5	20	341	116	206	261	305	334					
6	18	353	106	202	256	295	325	352				
7	8	360	119	217	275	302	325	344	358			
8	7	370	139	236	280	309	330	346	359	365		
9	4	398	118	203	277	309	332	354	374	386	398	
10	1	410	125	186	245	292	319	337	356	374	390	410
Weighted mean			116	204	265	302	327	347	362	375	394	410
Annual incremets			116	88	61	37	25	19	15	13	19	16
Otolith ventral axis distance (mm)			1.80	2.65	3.20	3.56	3.79	3.98	4.08	4.14	4.25	4.27

2015 – 2019

Annuli number	n	Observed mean Lt (mm)	Age (years)									
			0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
2	41	239	124	209								
3	116	278	122	205	267							
4	181	312	121	200	263	309						
5	87	339	123	204	259	302	335					
6	41	368	126	212	270	309	341	367				
7	37	368	121	206	263	297	323	346	363			
8	18	383	124	211	264	295	324	345	366	382		
9	12	408	127	213	260	299	329	353	373	389	404	
10	16	426	146	237	285	321	348	370	382	397	411	423

Weighted mean			126	211	266	305	333	356	371	390	408	423
Annual incremets			126	85	55	38	29	23	15	19	18	15
Otolith ventral axis distance (mm)			1.84	2.60	3.15	3.52	3.78	3.96	4.09	4.26	4.37	4.47

2015 – 2019 (FA)

Annuli number	n	Observed mean Lt (mm)	Age (years)					
			0.5	1.5	2.5	3.5	4.5	5.5
2	23	261	133	223				
3	90	275	123	205	267			
4	130	315	123	201	265	313		
5	50	329	124	198	251	294	328	
6	14	362	130	208	261	302	335	361
Weighted mean			124	204	258	296	323	348
Annual incremets			124	64	45	34	23	22
Otolith ventral axis distance (mm)			1.83	2.56	3.11	3.50	3.71	3.96

2015 – 2019 (WM)

Annuli number	n	Observed mean Lt (mm)	Age (years)									
			0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
2	18	212	112	192								
3	26	287	119	208	267							
4	51	304	117	198	257	297						
5	37	351	121	211	269	312	344					
6	27	376	124	214	274	313	345	370				
7	35	370	121	207	264	299	324	346	364			
8	18	383	124	211	264	295	324	345	366	382		
9	12	408	127	213	260	299	329	353	373	389	404	
10	15	426	147	235	283	319	344	365	382	397	411	423
Weightd mean			124	210	267	305	335	356	371	390	408	423
Annual incremets			124	70	50	33	27	19	13	17	17	14
Otolith ventral axis distance (mm)			1.84	2.65	3.19	3.54	3.80	3.97	4.09	4.26	4.37	4.47

The growth parameters and their credibility intervals were calculated for the mean back-calculated length-at-age for *P. pagrus* among the periods (1976-1977 and 2015-2019) and patterns of bands on the otolith (WM and FA) (Table 4). The credibility intervals of the growth parameters overlaps among the periods and patterns of growth bands, indicating that there are no significant differences among all growth curves (fig. 9).

Table 4. Von Bertalanffy's growth parameters and their respective credibility interval (*Cr.I.*, $\alpha = 0.05$) for the mean back-calculated length-at-age *Pagrus pagrus* fished in south Brazil by periods and patterns of bands formation on the otolith, one of well-marked annual bands (WM) and a second with faint bands (FA).

Periods	Lower *Cr.I.*	L_∞	Upper *Cr.I.*	Lower *Cr.I.*	K	Upper *Cr.I.*	Lower *Cr.I*	t_0	Upper *Cr.I.*
1976-1977	389	410	433	0.27	0.33	0.39	-0.70	-0.51	-0.35
2015-2019	411	431	455	0.24	0.29	0.34	-0.87	-0.68	-0.51
2015-2019 (WM)	409	431	457	0.24	0.30	0.35	-0.85	-0.64	-0.47
2015-2019 (FA)	366	385	418	0.28	0.36	0.42	-0.80	-0.58	-0.45

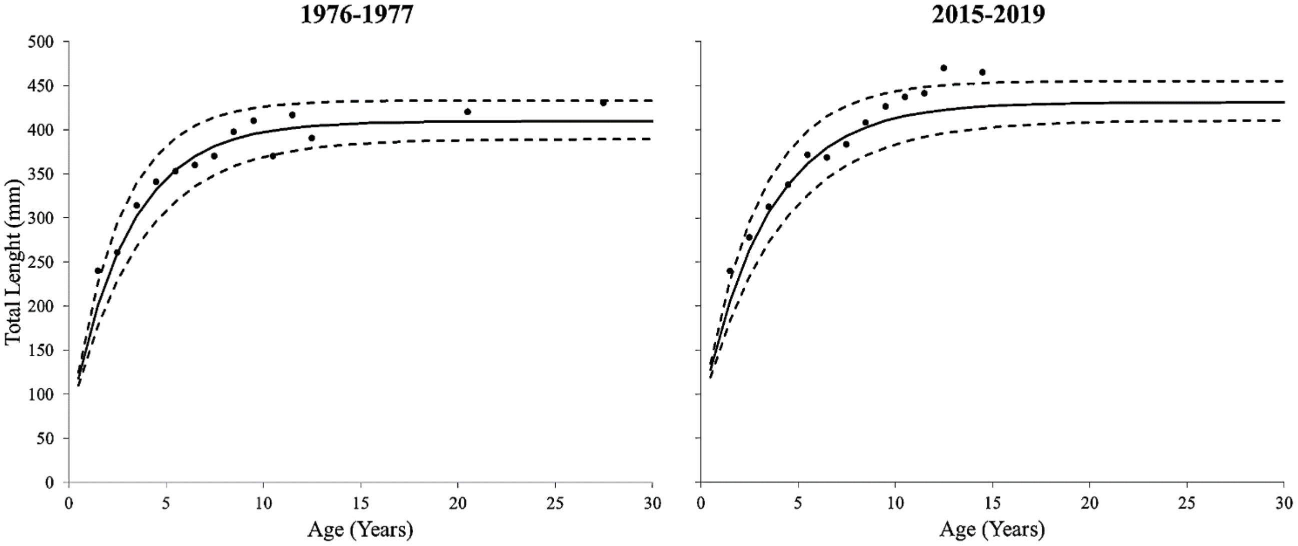

Figure 9. Von Bertalanffy's growth curves for *Pagrus pagrus* mean back-calculated length-at-age in southern Brazil by periods. Full circles indicates the mean observed length at age. Continuous line indicates the regression line. Dashed line indicates the credibility interval ($\alpha = 0.05$).

DISCUSSION

The correct identification of the first annual growth band (annuli) in the otoliths is essential for correct ageing (Campana 1999). Along the first year of life the otolith of the red porgy shows diverse sub-annual bands of different optical densities. Although the daily formation of the otoliths microincrements of young-of-the-year was not experimentally proved, it can be inferred from the equivalence between the number of microincrements, the size of the otoliths, the total length and the back calculated birthday in relation to the spawning season of the red porgy in the region. The mean total length of 117 mm and a mean ventral axis of the otoliths of 1.69 mm corresponded to, in average

150 days after birth (Table 1). The end of the first opaque band (annuli) in the otoliths of red porgies older than one year was shown to form in average 1.84 mm along the ventral axis, corresponding in average to 160 mm back-calculated total length (Table 3) and 170±20 days (Figure 10). The back calculated birth dates of 11 of the 12 sampled young of the year red porgies fell between 26 October and 21 January, within the spawning period of the red porgy in southern Brazil (Haimovici 1998; Haimovici et al. in prep.). Considering the reproductive period and the back-calculated birth dates, the end of the first opaque yearly growth band were estimated to be formed between the late autumn, around 5-7 month after birth.

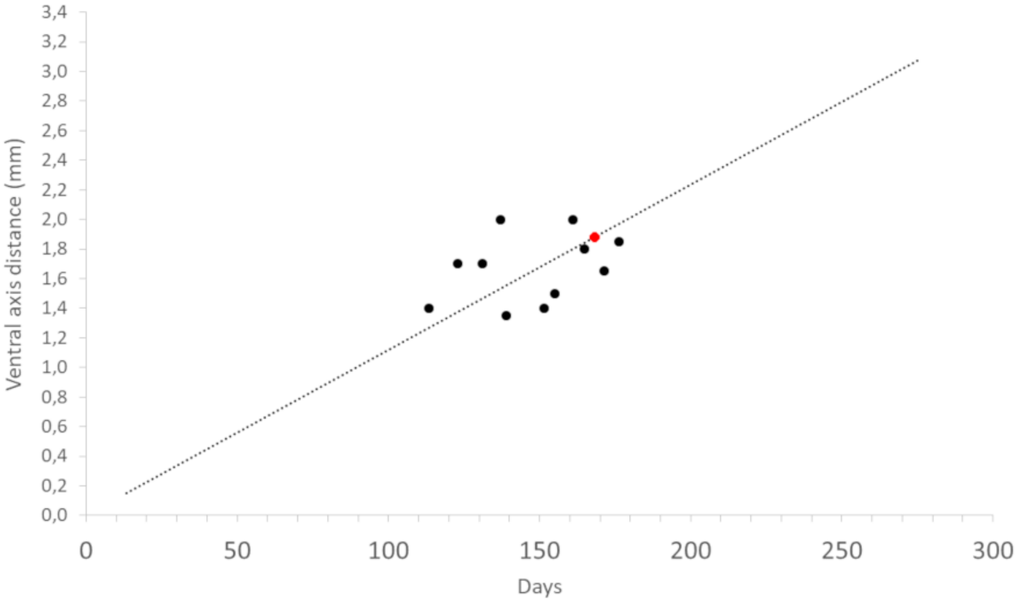

Figure 10. Linear relationship forced by origin between the days of life and the otolith ventral axis of *Pagrus pagrus*. Black full circles indicates the juveniles daily aged. Red full circle indicates the mean end of the first annual opaque band assumed

Several former studies for *Pagrus pagrus* have already validated the annual formation of one ring in the scales (Cotrina & Raimondo 1977, Manooch & Hunstsman 1977; Ávila-da-Silva 1996; Cotrina 1977; Costa et al. 1997) and one opaque band in the otoliths (Pajuelo & Lorenzo 1996; Harris & McGovern 1997; Potts & Manooch 2002; García et al. 2011). Among the different studies, a common pattern of the annuli formation were associated to the increasing water temperatures after the cold seasons. In southern Brazil, the rings in scales become evident in late spring and early summer, in November-December (Haimovici et al. in prep.). In Argentina, rings were reported to become evident in the border of the scales in late spring (Cotrina 1977) and in summer for opaque bands in the otoliths (García et al. 2011).

The seasonality of the opaque band formation was not determined because the lack of samples for part of the year (Figure 8). However, the verification of the annuli formation in the otoliths sections were possible, since 97% of the age readings on the otoliths, the number of opaque bands differed at most in one annuli from the readings on the scales (Table 2), which were already validated by Haimovici et al. (in prep). García et al. (2011) also found a high rate of coincidence between the age readings on otoliths and scales (69.8%) and did not find differences in the von Bertalanffy parameters estimated from readings of both apposition structures. However, these authors preferred to use the otoliths for they analysis, since there is a certain difficulty in reading scales first ring, besides a high degree of regeneration scales. Manooch & Huntsman (1977) also reported that the main problem of aging red porgy with scales was the large number of regenerated scales and a high frequency of false annuli, in contrast, otoliths could be read easily, but they required a lot of labor to prepare. Although, ages could be determined from either otoliths or scales (Potts & Manooch 2002), this last are easier to collect without damaging the fish when sample are obtained from sportive or commercial fishing and a high number of fishes have to be aged for population structure and mortality studies (Haimovici et al. in prep.).

Our results evidenced two patterns of opaque bands in the otoliths of the red porgies in southern Brazil, one with well marked and other with faint or absent opaque bands. These two patterns also appear on the scales and it has been raised the possibility that specimens with well marked rings in their scales could be seasonal migrants that move southward to spawn in Uruguay and those with faint or absent rings in their scales remain year round and spawn in southern Brazil (Haimovici 1997). However faint or absent opaque bands were observed year round, although were more frequent in the warm season (Figure 8) and no differences in the growth of the red porgies with both opaque bands patterns in the otoliths were observed (Table 3 and 4). Further studies to elucidate the causes of the presence of the two patterns of growth bands are necessary for a better understand the stock structure of red porgy in the region.

No substantial changes in the growth of *P. pagrus* were observed between 1976-1977 and 2015-2019 (Figure 9) and either in common fishery zone of Uruguay and Argentina, in the Economic Exclusive zone of Argentina between 1972 -1981 (Cotrina & Raimondo 1997) and 2010-2012 (García & Déspos 2015) nor in the southeaster USA between 1972-1974 (Manooch & Hunstman 1977) and 1989-1998 (Potts & Manooch 2002) (Table 5, Figure 11).

Table 5. Comparison of the von Bertalanffy model parameters in different stocks of *Pagrus pagrus in* southern Brazil, Argentina and Uruguay common fishing zone and southeaster USA.

Authors	Manooch & Hunstman, 1977	Potts & Manooch, 2002	Cotrina & Raimondo, 1997	Cotrina & Raimondo, 1997	García & Déspos, 2015	García & Déspos, 2015	Haimovici et al., in prep.	This study	This study
Region	South-eastern US	South-eastern US	Argentina 35°36°S	Argentina 39°40°S	Argentina-Uruguay 34°39°S	Argentina 39°42°S	Southern Brazil	Southern Brazil	Southern Brazil
Older recorded age	15	18	16	16	16	16	28	28	18
Apposition structure	Otolith	Otolith	Scale	Scale	Otolith	Otolith	Scale	Otolith	Otolith
Sampling period	1972-1974	1989-1998	1972-1981	1972-1981	2010-2012	2011-2013	1976-1978	1976-1977	2015-2019
Infinite length (L_∞) mm	763	774	447	499	443.7	469	434	417	431
Instantaneous growth (k)	0.096	0.09	0.15	0.15	0.15	0.21	0.27	0.31	0.29
Intercept (to) years	-1.88	-1.96	-2.96	-2.81	-2.71	-0.86	-0.32	-1.03	-0.68

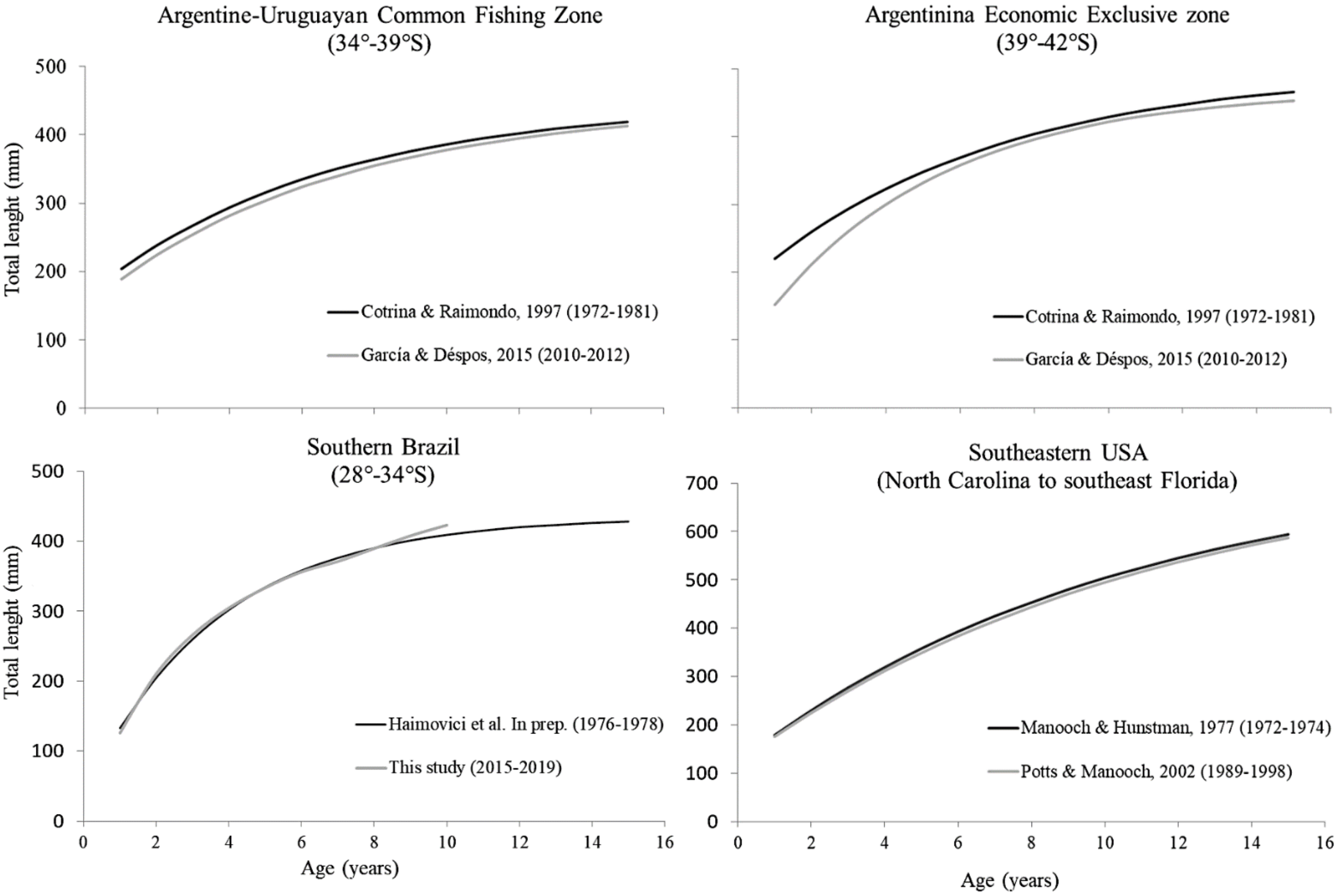

Figure 11. Comparison of the length-at-age back-calculated in different stocks of *Pagrus pagrus* in southern Brazil, Argentina and Uruguay common fishing zone and southeaster USA.

The lack of growth changes of the red porgy before the collapse of the trawl fishery in the 1970-1980´s and the recent period of 2015-2019, suggest that despite large changes in the density there is a low intra-specific competition for food resources. The same lack of growth increases along time was observed in both stocks of red porgy fished in Argentina and Uruguay, where the density oscillated along the last decades (García& Lagos 2011ab; García 2013). A possible explanation for the lack of changes in growth, at least in southern Brazil, is that most of the red porgy´s diet in this region depends on fish and squids that are part of the plankton based food webs (Capitoli & Haimovici 1993). The same lack of growth was observed for the first ages of the stripped weakfish *Cynoscion guatucupa* (Miranda & Haimovici 2007) that feed mostly on zooplankton and small fish (Vieira 1990) and are also part of plankton based food webs.

In contrast, increased growth along the last decades was observed for the most important species in the demersal industrial trawl fishery along southern Brazil: the whitemouth croaker *Micropogonias furnieri* (Haimovici & Ignacio 2005), the argentinian croaker *Umbrina canosai* (Haimovici et al. 2006), the king weakfish *Macrodon atricauda* (Cardoso & Haimovici 2011) and the older stripped weakfish *Cynoscion guatucupa* (Miranda & Haimovici 2007). The density of all this species decreased, but still are the main components of the demersal fishes landing in the region since they comprise, on average, 55% of the demersal fish landings (Haimovici & Cardoso 2016). From 1976 to 1980, at the beginning of its commercial exploitation, *C. guatucupa* and *U. canosai* yielded approximately 1,500 kg per day at sea of pair bottom trawlers while *M. furnieri* and *M. atricauda* yielded, approximately 1,000 kg per day (Haimovici et al. 2006; Haimovici & Cardoso, 2016). These species have a common diet based on less mobile epibenthic and epibenthic invertebrates that form part of the detritus food webs (Haimovici et al. 1989; Vieira 1990; Martins 2000; Cardoso & Haimovici 2016). The higher abundances and densities of these sciaenid fishes imply a high intra-specific competition for food that has been relaxed over time with the intense biomass removal by fishing, resulting in a lower predation pressure and increased availability of food per individual that explain their increased growth as a density dependent process (Cardoso & Haimovici 2016). However, the red porgy, comprised a maximum of 3.2% of the total landings of the region in 1976 and catches per day at sea of the bottom trawlers were of approximately 25 kg in the same time period during the height of the fishery, which shows its lower abundance and natural density in relation to sciaenid fishes (Haimovici et al. 2006). Lower densities implies less intra-specific competition for food, which may explain the absence of changes in growth over time, since food availability per individual may not have been altered.

Therefore, the contrast in the lack of growth response of the red porgy in southern Brazil seems to be related to their relatively small impact on the overall food supply based in the planktonic based food webs since it receives far more energy than the detritus food webs (Christensen & Pauly 1993).

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