



Universidade Federal do Rio Grande
Instituto de Ciências Biológicas
Pós-graduação em Biologia de
Ambientes Aquáticos Continentais



Variabilidade de longo-prazo na abundância e ecologia trófica de juvenis de tainhas associada com impactos naturais e antrópicos no sul do Brasil

Sabrina Radunz Vollrath

Orientador: Alexandre Miranda Garcia

Rio Grande
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Tese apresentada ao Programa de Pós-graduação em Biologia de Ambientes Aquáticos Continentais como requisito parcial para a obtenção do título de Doutora em Biologia de Ambientes Aquáticos Continentais.

Rio Grande
2024

Ficha Catalográfica

V924v Vollrath, Sabrina Radunz.

Variabilidade de longo-prazo na abundância e ecologia trófica de juvenis de tainhas associada com impactos naturais e antrópicos no sul do Brasil / Sabrina Radunz Vollrath. – 2024.

193 f.

Tese (doutorado) – Universidade Federal do Rio Grande – FURG, Programa de Pós-Graduação em Biologia de Ambientes Aquáticos Continentais, Rio Grande/RS, 2024.

Orientador: Dr. Alexandre Miranda Garcia.

1. *Mugil liza* 2. *Mugil curema* 3. Aquecimento dos oceanos
4. *El Niño* Oscilação Sul (ENOS) 5. Efeito da sobrepesca 6. Programa PELD-ELPA I. Garcia, Alexandre Miranda II. Título.

CDU 639.93

Catálogo na Fonte: Bibliotecário José Paulo dos Santos CRB 10/2344



MINISTÉRIO DA EDUCAÇÃO
UNIVERSIDADE FEDERAL DO RIO GRANDE - FURG
INSTITUTO DE CIÊNCIAS BIOLÓGICAS - ICB
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA DE AMBIENTES
AQUÁTICOS CONTINENTAIS



ATA DE DEFESA DE TESE DE DOUTORADO EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS – Nº 001/2024

Às 08h30 (oito horas e trinta minutos) do dia 06 (seis) do mês de fevereiro de 2024 (dois mil e vinte e quatro), via Webconferência no endereço eletrônico: (https://meet.jit.si/defesa_sabrina_06fev_830h_pgbacfurg) reuniram-se docentes, discentes e comunidade em geral, para a Defesa Pública da Tese de Doutorado da acadêmica Sabrina Radunz Vollrath. A Tese intitulada “**Variabilidade de longo-prazo na abundância e ecologia trófica de juvenis de tainhas associada com impactos naturais e antrópicos no sul do Brasil**” foi avaliada pela Banca Examinadora composta pelo Prof^a Dr. Alexandre Miranda Garcia (Orientador); Prof^o Dr. Leandro Bugoni (FURG); Prof^a Dra. Margareth da Silva Copertino (FURG); Prof^a Dra. Nidia Noemi Fabré (UFAL) e Prof^o Dr. André Luiz Machado Pessanha (UEPB). Após a defesa e arguição pública, a Banca Examinadora reuniu-se, para deliberação final, e considerou a acadêmica **APROVADA**. Desta forma, a acadêmica concluiu mais uma das etapas necessárias para a obtenção do grau de **DOUTOR EM BIOLOGIA DE AMBIENTES AQUÁTICOS CONTINENTAIS**. Nada mais havendo a tratar, às 12h00h (doze horas) foi lavrada a presente ata, que lida e aprovada, foi assinada pelos membros da Banca Examinadora, pela Acadêmica e pela Coordenadora do Curso.

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Coordenadora do Curso

Dedico aos meus pais: Celi Radunz Vollrath e Paulo Eroni Vollrath

AGRADECIMENTOS

Agradeço o meu orientador, Profº Dr. Alexandre Miranda Garcia, pelo acolhimento e apoio na minha formação desde o mestrado. Sou imensamente grata por todas as oportunidades de trabalho e aprendizagem que eu tive ao longo desses últimos anos. Agradeço por confiar no meu trabalho, acreditar no meu potencial e por sempre me incentivar a ampliar meus conhecimentos. Foi um privilégio ter sido orientada pelo Garcia e ter tido a oportunidade de aprender e trabalhar junto ao longo da minha caminhada na pós-graduação. Além de ser um exemplo de orientador e professor, também é um excelente amigo. Também gostaria de agradecer sua esposa, Drª Adna Ferreira Garcia, pois junto com o Garcia proporcionaram minhas primeiras oportunidades na pós graduação.

Agradeço minha família por todo apoio e incentivo ao longo de toda minha trajetória acadêmica. Minha mãe Celi e meu pai Paulo são os principais responsáveis por eu ter chegado até aqui, pois me proporcionaram a oportunidade de estudar. Eles são minha fonte de inspiração e exemplos de vida. Agradeço meu noivo Matheus pela paciência, apoio e incentivo ao longo desses anos, inclusive por todas as vezes em que me ajudou com coletas e triagens. Agradeço as minhas irmãs (Rose e Adriana) e irmão (Paulo Ricardo), cunhados (Rogério e Fábio) e cunhada (Carol), sobrinhos (Renan, Ricardo e Bernardo) e sobrinhas (Manuela e Rafaela) por todo carinho e incentivo, vocês tornaram esses anos mais leves. Um agradecimento especial para o meu sobrinho Renan e minha sobrinhas/afilhadas Manuela e Rafaela pela ajuda extra nas coletas e triagens. Eu amo vocês.

Um agradecimento especial para uma amiga, Bianca Possamai, serei eternamente grata pelo acolhimento no laboratório desde o mestrado, pela paciência e por todos os ensinamentos, grande parte do que eu aprendi ao longo da pós-graduação foi graças a ela. Sou grata pela amizade que se construiu, pelo carinho e pela parceria. A Bianca é um exemplo de pesquisadora e uma inspiração para novas meninas/mulheres que desejam entrar para a ciência. Sou sua fã.

Agradeço aos colegas e amigos do laboratório de ictiologia, vocês fazem parte de toda trajetória da minha pós-graduação. Agradeço a parceria para enfrentar os perrengues que passamos juntos com a pandemia do COVID-19, coletas, triagens e processamentos de amostras. Sou grata pelas risadas e conversas que deixaram tudo mais leve ao longo desses anos. Um agradecimento especial para o Leonardo que me auxiliou em praticamente todas as coletas e processamentos de amostras isotópicas, o

Yan pela parceria e colaborações em trabalhos, a Erika pela parceria e longas conversas que tornaram nossas manhãs mais divertidas, e a Amanda, que embora faça pouco tempo que tenha chegado no laboratório, se tornou uma grande amiga e parceira de isótopos estáveis.

Aos colaboradores dos capítulos da Tese. Em especial à Susanne Tanner e ao Patrick Reis-Santos que foram fundamentais para minha aprendizagem com modelagem e na construção do primeiro capítulo da Tese, sou muito grata pelo carinho e paciência que tiveram comigo. À Valéria Lemos e ao Profº João Vieira que foram fundamentais para o desenvolvimento do segundo capítulo da Tese, pela paciência e pelos ensinamentos sobre a pesca. E à Bianca Possamai que foi fundamental na construção e aprendizagem do terceiro capítulo.

À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela concessão da bolsa durante meu doutorado.

Ao programa de Pós-Graduação em Biologia de Ambientes Aquáticos Continentais (PPGBAC) e a Universidade Federal do Rio Grande – FURG por fornecer todos os recursos necessário para o desenvolvimento da Tese.

Por fim, gostaria de ressaltar a importância de todos(as) na construção desta Tese e dizer que eu tenho muita sorte de ter pessoas incríveis ao meu lado. Meus sinceros agradecimentos a todos(as) que participaram de alguma forma dessa etapa da minha vida e formação.

RESUMO

Entender como fenômenos climáticos naturais (e.g., *El Niño* Oscilação Sul - ENOS) e impactos antrópicos (e.g., aquecimento dos Oceanos e sobrepesca) podem afetar a biota é fundamental considerando o cenário atual de mudanças climáticas e perda de biodiversidade. Estudos de longo-prazo são fundamentais para avaliar os efeitos de impactos naturais e antrópicos em espécies de peixes. Nesse sentido, esta Tese teve como principal objetivo utilizar bancos de dados de longo-prazo do programa de Pesquisa Ecológica de Longa Duração no Estuário da Lagoa dos Patos e Costa Marinha Adjacente (PELD-ELPA) para avaliar os efeitos do aquecimento dos Oceanos, eventos ENOS e sobrepesca na abundância e assimilação de fontes basais autóctones (estuário) e alóctones (dulcícola e marinho) por juvenis de espécies de tainhas. O 1º capítulo investigou se estava havendo aquecimento das águas de zonas rasas do estuário e costa marinha adjacente e, caso houvesse, se isso aumentaria a abundância de uma espécie de tainha tropical dada a hipótese de tropicalização da fauna em direção às maiores latitudes devido ao aquecimento global. Os principais resultados desse capítulo foram: (i) houve aquecimento das águas rasas do estuário e costa marinha adjacente; (ii) porém, não houve tendência significativa de aumento da abundância da espécie de tainha tropical (*Mugil curema*) na região; (iii) no entanto, Modelos Aditivos Generalizados mostraram que a abundância da espécie aumenta com o aquecimento da água na região, porém os eventos *El Niños* mascaram esse efeito, diminuindo a abundância da espécie no estuário. No 2º capítulo foi investigado o efeito da pesca dos adultos, principalmente durante a sua migração reprodutiva, na abundância dos juvenis de uma espécie de tainha (*Mugil liza*) com importância comercial. Os principais resultados desse capítulo foram: (i) houve efeito negativo da pesca dos adultos na abundância dos juvenis na costa marinha e no estuário da Lagoa dos Patos; (ii) além disso, foi observado uma defasagem de 1 e 2 meses na costa marinha, ou seja, demora entre 1 e 2 meses para ser observado o efeito da pesca dos adultos na abundância dos juvenis nessa região e 4 meses no estuário. O 3º capítulo investigou variações interanuais e sazonais, associado com a ocorrência de eventos ENOS, na assimilação de fontes basais autóctone e alóctones por consumidores primários. Os principais resultados desse capítulo foram: (i) houve variação interanual, associado com variações sazonais e com eventos ENOS, na assimilação de fontes basais autóctones e alóctones por juvenis de tainha (*Mugil liza*); (ii) entretanto, contrariando o esperado, houve maior assimilação de fontes alóctones marinhas durante períodos chuvosos como inverno-primavera e eventos *El Niños*; (iii) porém, corroborando nossa hipótese inicial, houve maior contribuição relativa de fontes alóctones dulcícolas durante os *El Niños* comparado com as *La Niñas*. Os resultados obtidos nessa Tese destacam a importância de

monitoramentos padronizados de longo-prazo para poder revelar os impactos (muitas vezes complexos e sinérgicos) dos fenômenos climáticos naturais e antrópicos sobre a biota estuarina.

Palavras-chave: *Mugil liza*; *Mugil curema*; aquecimento dos oceanos; *El Niño* Oscilação Sul (ENOS); efeito da sobrepesca, Programa PELD-ELPA

ABSTRACT

Understanding how natural climate phenomena (e.g., *El Niño* Southern Oscillation - ENSO) and anthropogenic impacts (e.g., warming of the oceans and overfishing) can affect biota is fundamental considering the current scenario of climate change and loss of biodiversity. Long-term studies are essential to evaluate the effects of natural and anthropogenic impacts on fish species. In this sense, the main objective of this Thesis was to use long-term databases from the Long-Term Ecological Research in the Patos Lagoon Estuary and Adjacent Marine Coast (Brazilian LTER – Patos Lagoon) program to evaluate the effects of ocean warming, events ENSO and overfishing on the abundance and assimilation of autochthonous (estuarine) and allochthonous (freshwater and marine) basal sources by juveniles of mullet species. The 1st chapter investigated whether there was warming of the shallow waters areas of the estuary and adjacent marine coast and, if so, whether this would increase the abundance of a species of tropical mullet (*Mugil curema*) given the hypothesis of tropicalization of the fauna towards higher latitudes due to warming global. The main results of this chapter were: (i) there was warming of the shallow waters of the estuary and adjacent marine coast; (ii) however, there was no significant trend towards an increase in the abundance of the *M. curema* in the region; (iii) however, Generalized Additive Models showed that the abundance of the species increases with water warming in the region, but *El Niño* events mask this effect, reducing the abundance of the species in the estuary. In the 2nd chapter, the effect of adult fishing, mainly during their reproductive migration, on the abundance of juveniles of a commercially important mullet species (*Mugil liza*) was investigated. The main results of this chapter were: (i) there was a negative effect of adult fishing on the abundance of juveniles on the marine coast and in the Patos Lagoon estuary; (ii) in addition, a lag of 1 and 2 months was observed on the marine coast, that is, it takes between 1 and 2 months to observe the effect of adult fishing on the abundance of juveniles in this region and 4 months in the estuary. The 3rd chapter investigated interannual and seasonal variations, associated with the occurrence of ENSO events, in the assimilation of autochthonous and allochthonous basal sources by primary consumers. The main results of this chapter were: (i) there was interannual variation, associated with seasonal variations and ENSO events, in the assimilation of autochthonous and allochthonous basal sources by juvenile mullet (*Mugil liza*); (ii) however, contrary to expectations, there was higher assimilation of allochthonous marine sources during wet periods such as winter-spring and *El Niño* events; (iii) however, corroborating our initial hypothesis, there was a higher relative contribution from allochthonous freshwater sources during *El Niño* compared to *La Niña* events. The results obtained in this Thesis highlight the importance of standardized long-term monitoring to reveal

the impacts (often complex and synergistic) of natural and anthropogenic climate phenomena on estuarine biota.

Key-words: *Mugil liza*; *Mugil curema*; ocean warming; *El Niño* Southern Oscillation (ENSO); overfishing effect, Brazilian LTER – Patos Lagoon program.

APRESENTAÇÃO

Esta Tese de doutorado segue o modelo sugerido pelo Programa de Pós-Graduação em Biologia de Ambientes Aquáticos Continentais e está estruturada em cinco seções principais. A primeira seção compõe a **Introdução Geral** onde abordo os principais temas conceituais propostos por esta Tese, seguido pelos objetivos que orientaram o trabalho. Os principais tópicos da Introdução Geral são: (i) variações de longo-prazo na abundância e distribuição das espécies causadas por fenômenos climáticos naturais e impactos antrópicos; (ii) monitoramentos de longo-prazo; (iii) impactos dos eventos de *El Niño* Oscilação Sul (ENOS) em peixes; (iv) impacto do aquecimento dos oceanos em peixes; (v) impacto da sobreexploração pesqueira em peixes; (vi) formas juvenis de espécies de tainhas em estuários como modelos biológicos; (vii) o efeito dos eventos *El Niños* na ecologia trófica de consumidores primários e; (viii) objetivos. Essa seção está formatada de acordo com as normas da Associação Brasileira de Normas Técnicas (ABNT).

A segunda seção está apresentada como **Capítulo 1** e é referente ao artigo que utilizou um banco de dados do PELD-ELPA de 23 anos (1997-2019) para investigar o aquecimento das águas rasas (< 2 m) do estuário da Lagoa dos Patos e região marinha adjacente e seu possível efeito no aumento na abundância de uma espécie de tainha com distribuição mais tropical (*Mugil curema*) em um estuário subtropical/temperado. Este capítulo está publicado na *Science of The Total Environment* (STOTEN) e, portanto, formatado de acordo com as normas da revista.

A terceira seção está apresentada como **Capítulo 2** e é referente ao artigo que também utilizou o banco de dados do PELD-ELPA de 23 anos (1997-2019), juntamente com um compilado de bancos de dados disponíveis on-line sobre a pesca da tainha *Mugil liza*, para investigar o efeito da pesca dos adultos durante sua migração reprodutiva na abundância dos juvenis na região costeira e estuário da Lagoa dos Patos. Este segundo capítulo está publicado na *Marine Environmental Research* (MERE) e, portanto, formatado de acordo com as normas da revista.

A quarta seção está apresentada como **Capítulo 3** e é referente ao manuscrito que utilizou o banco de dados do subprojeto PELD-isótopos de 12 anos (2010-2022) e investigou variações sazonais e interanuais associado com a ocorrência de eventos ENOS na assimilação de fontes alimentares basais por juvenis de tainhas (*M. liza*) no estuário da Lagoa dos Patos. Este terceiro capítulo visa ser submetido na *Estuarine, Coastal and Shelf Science* (ECSS) e, portanto, está formatado de acordo com as normas da revista.

A quinta seção compõe as **Considerações Finais e Perspectivas** com as principais conclusões obtidas a partir dos trabalhos desenvolvidos durante a Tese, e com perspectivas futuras.

SUMÁRIO

LISTA DE FIGURAS	xii
LISTA DE TABELAS	xviii
INTRODUÇÃO GERAL	20
OBJETIVO GERAL:	27
OBJETIVOS ESPECÍFICOS:	28
REFERÊNCIAS:	30
CAPÍTULO 1	39
CAPÍTULO 2	96
CAPÍTULO 3	139
CONSIDERAÇÕES FINAIS E PERSPECTIVAS	186
REFERÊNCIAS:	189
ANEXOS	191

LISTA DE FIGURAS

Capítulo 1

Figure 1 (A) Map of Brazil and (B) the location of Patos Lagoon with (C) the sampling stations in the estuarine zone (filled red circles, $n=5$) and the adjacent marine region (filled blue circles, $n=2$). (D) Map of the southernmost state in Brazil showing the location of the river flow stations along the drainage basin of Patos Lagoon (filled black circles).

Figure 2 Mean and standard deviation of the abundance of juvenile white mullet (CPUE – catch per unit effort, i.e, individuals per haul) in the Estuary (red bars) and the Coast region (blue bars). Fish icons further depict the periods of high (January to June) and low abundance (July to December).

Figure 3 Seasonal maps of surface water temperature along the southwest coast of the Atlantic Ocean obtained by satellite images (1° gridded Hadley ISST dataset) together with occurrence records of the white mullet *Mugil curema* (black circles). The black square in the autumn map represents Argentina, where there is only one record of 6 specimens of the white mullet (Castro et al., 2006).

Figure 4 Decomposition of the time series analysis of the (A) surface water temperature from 1997 to 2019 in (B) seasonal, (C) inter-annual and (D) residual components of the Estuary (red lines) and Coast region (blue lines).

Figure 5 Decomposition of the time series analysis of the (A and E) white mullet abundance from 1997 to 2019 into (B and F) seasonal, (C and G) interannual and (D and H) residual components for the Estuary (red lines) and Coast region (blue lines) during the periods of high (January to June; left panels) and low abundance (July to December; right panels). Note that the y-axis scales are different for the high and low abundance periods.

Figure 6 Generalized additive model (GAM) plots showing the partial effects of selected explanatory variables on the abundance of juvenile white mullet in the Estuary (upper panel) and Coast region (lower panel). X-axis are the standardized data with the values scaled to mean zero

and then divided by the standard deviations. The y-axis represents the partial effect of each variable. Shaded areas indicate the 95% confidence intervals.

Supplementary figure 1 Temporal variation (1997-2019) of average values of surface water temperature (°C) in the estuary, Oceanic *Niño* Index (ONI) corresponding to sea surface temperature (SST) anomalies in *Niño* 3.4 (5°N - 5°S, 120°-170°W) in the Pacific Ocean, anomalies of fluvial flow (m³/s) in the Patos Lagoon basin, anomalies of salinity and water transparency (m) in the Estuarine region. Dashed lines indicate the occurrence of *El Niño* events.

Supplementary figure 2 Temporal variation (1997-2019) of average values of surface water temperature (°C) in the Coast region, Oceanic *Niño* Index (ONI) corresponding to sea surface temperature (SST) anomalies in *Niño* 3.4 (5°N - 5°S, 120°-170°W) in the Pacific Ocean, anomalies of fluvial flow (m³/s) in the Patos Lagoon basin, anomalies of salinity and water transparency (m) in the Coast region. Dashed lines indicate the occurrence of *El Niño* events.

Supplementary figure 3 Comparison of salinity in the Estuary (red boxes) and in the Coast region (blue boxes) during *La Niña* and *El Niño* events classified from moderate to very strong ($ONI \leq -1$ and ≥ 1 , respectively) and neutral periods (ONI between -0.4 to 0.4).

Supplementary figure 4 The residuals of generalized additive models for the Estuary and Coast region.

Capítulo 2

Figure 1 (A) Map of Brazil and the location of Patos Lagoon with (B) the sampling stations on the coast (filled blue triangles, n= 2) and estuary (filled red circles, n= 5). (C) Map of the southernmost state in Brazil showing the location of the river flow stations along the drainage basin of Patos Lagoon (filled black circles). And (D) the map of the municipalities where landing data (kg) of industrial and artisanal fishing are obtained in the states of Rio Grande do Sul (RS, green circles), Santa Catarina (SC, orange circles) and São Paulo (SP, pink circles).

Figure 2 Boxplots of intra- and interannual variation of local environmental variables on the coast. The horizontal line in the middle of the boxes indicates the median, the boxes represent

the first and third quartile, vertical lines at the ends of the boxes indicate the minimum and maximum values and the points are the outliers.

Figure 3 Boxplots of intra- and interannual variation of local environmental variables in the estuary. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, vertical lines at the ends of the boxes indicate the minimum and maximum values and the points are the outliers.

Figure 4 Boxplots of intra- and inter-annual variation of climatic (ONI index) and regional (continental water discharge) environmental variables. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, vertical lines at the ends of the boxes indicate the minimum and maximum values and the points are the outliers.

Figure 5 Boxplots of the intra- and interannual variation of $\log_{10}(\text{CPUE}+1)$ of *M. liza* juveniles on the coast (blue boxes) and estuary (red boxes). The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, vertical lines at the ends of the boxes indicate the minimum and maximum values and the points are the outliers.

Figure 6 Decomposition of the time series analysis of the abundance of juveniles *M. liza* from 1997 to 2019 for the coast (blue lines) and estuary (red lines). Boxes A and D represent the seasonality of the data. Boxes B and E indicate the trend of the data. The p values are the results of the linear mixed models that indicate the statistical significance of the trends ($\alpha = 0.05$). And boxes C and F are the residues of the data that were not explained by the analyses.

Figure 7 GAM plots showing the partial effects of selected explanatory variables on the abundance of juvenile mullet on the coast (left panel) and estuary (right panel). X-axis are the standardized data with the values scaled to mean zero and then divided by the standard deviations. The y-axis represents the partial effect of each variable. Shaded areas indicate the 95% confidence intervals.

Figure 8 GAM plots showing the partial effects of landing (kg) with different time-lags on the abundance of juvenile mullet on the coast (left panel) and estuary (right panel). X-axis are the standardized data with the values scaled to mean zero and then divided by the standard deviations. The y-axis represents the partial effect of each variable. Shaded areas indicate the 95% confidence intervals.

Supplementary figure 1 GAM residuals for models with relationship between environmental variables and mullet juveniles on the coast (left panel) and estuary (right panel).

Supplementary figure 2 GAM residuals for models relating landing (capture in kg) with time-lags 1 (left panel) and 2 (right panel) and mullet juveniles on the coast.

Supplementary figure 3 GAM residuals for the model with relationship between landing (capture in kg) with time-lag 4 and mullet juveniles in the estuary.

Capítulo 3

Figure 1 (A) Map of Brazil and (B) location of Patos Lagoon and the fish sampling sites and estuarine basal sources (green square), freshwater (purple asterisk), surf-zone (blue triangle) and marine (orange star) allochthonous basal sources, in addition to sampling sites for temperature, salinity and water transparency in the estuary (red circles). (C) Map of the southernmost state of Brazil showing the location of stations that measure continental water discharge along the Patos Lagoon watershed (filled black circles).

Figure 2 Interannual variation of isotopic values of $\delta^{13}\text{C}$ (top panel) and $\delta^{15}\text{N}$ (bottom panel) of juveniles of the mullet *Mugil liza* in the Patos Lagoon estuary from 2010 to 2022. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, the vertical lines at the ends of the boxes indicate the minimum and maximum values, and the points are the outliers. The symbols below the years indicate which ENSO events occurred in each year. The LN (blue color) indicate the occurrence of *La Niña* events, EN (red color) are *El Niño* events and NE (green color) are Neutral periods.

Figure 3 Seasonal variation of isotopic values of $\delta^{13}\text{C}$ (top panel) and $\delta^{15}\text{N}$ (bottom panel) of juveniles of the mullet *Mugil liza* in the Patos Lagoon estuary from 2010 to 2022. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, the vertical lines at the ends of the boxes indicate the minimum and maximum values, and the points are the outliers.

Figure 4 Stable isotopic ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) and standard ellipse area (SEA) for each season (A) and during ENSO events (B) of juveniles of the mullet *Mugil liza* sampled in the Patos Lagoon estuary from 2010 to 2022.

Figure 5 Variation in standard ellipse area (SEA) of juveniles of the *Mugil liza* during ENSO events in the Patos Lagoon estuary from 2010 to 2022. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, the vertical lines at the ends of the boxes indicate the minimum and maximum values, and the points are the outliers.

Figure 6 Relative median percentage contribution (50%) of carbon sources to mullet juveniles of the *Mugil liza* in the Patos Lagoon estuary from 2010 to 2022. The symbols below the years indicate which ENSO events occurred in each year. The LN (blue color) indicate the occurrence of *La Niña* events, EN (red color) are *El Niño* events and NE (green color) are Neutral periods.

Figure 7 Relative seasonal median percentage contribution (50%) of carbon sources for mullet juvenile *M. liza* in the Patos Lagoon estuary from 2010 to 2022.

Figure 8 Relative median percentage contribution (50%) of carbon sources to juveniles of the *Mugil liza* during ENSO events in the Patos Lagoon estuary from 2010 to 2022.

Supplementary figure 1 Pearson's correlation between environmental variables in the Patos Lagoon estuary from 2010 to 2022.

Supplementary figure 2 Isotopic mixing polygons with the limits of basal source values in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot space over the years in the Patos Lagoon estuary from 2010 to 2022. Mullet juveniles *M. liza* (black filled circles) located outside the region of the 95% mixing polygon were excluded from the annual isotope mixing model analysis.

Supplementary figure 3 Isotopic mixing polygons with the limits of basal source values in seasonal $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot space in the Patos Lagoon estuary from 2010 to 2022. Mullet juveniles *M. liza* (black filled circles) located outside the region of the 95% mixing polygon were excluded from the annual isotope mixing model analysis.

Supplementary figure 4 Isotopic mixing polygons with the limits of basal source values in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot space during ENSO events in the Patos Lagoon estuary from 2010 to 2022.

Mullet juveniles *M. liza* (black filled circles) located outside the region of the 95% mixing polygon were excluded from the annual isotope mixing model analysis.

Supplementary figure 5 Bi-plots of the mean value ($\pm$ SD) of annual carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes in the Patos Lagoon estuary from 2010 to 2022 of mullet juvenile *M. liza* (filled black circles) and autochthonous (estuary SOM) and allochthonous (POM and SOM freshwater, POM marine (surf-zone and offshore) basal food sources.

Supplementary figure 6 Bi-plots of the mean value ($\pm$ SD) of seasonal carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes in the Patos Lagoon estuary from 2010 to 2022 of mullet juvenile *M. liza* (filled black circles) and autochthonous (estuary SOM) and allochthonous (POM and SOM freshwater, POM marine (surf-zone and offshore).

Supplementary figure 7 Bi-plots of the mean value ($\pm$ SD) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes during ENSO events in the Patos Lagoon estuary from 2010 to 2022 of mullet juvenile *M. liza* (filled black circles) and autochthonous (SOM estuary) and allochthonous (POM and SOM freshwater, POM marine (surf-zone and offshore).

Supplementary figure 8 Residuals from the generalized additive model.

LISTA DE TABELAS

Capítulo 1

Table 1 Selected generalized additive models with values of the second-order Akaike information criterion (AICc) and the AIC likelihood weights (AICw) for the Estuary and Coast region. Gray shaded lines represent the selected models with the lowest AICc and highest AICw for the Estuary and Coast region.

Table 2 Predictor variables selected by generalized additive models (GAM) for each sampling area (Estuary and Coast) for explaining variation in abundance of juvenile white mullet. ONI = Ocean Niño Index, Temperature = Surface water temperature, Discharge = River flow in the estuary's drainage basin, df = degrees of freedom and DE = deviance explained (%) of each model.

Supplementary table 1 List of scientific papers containing records of the occurrence of the white mullet in shallow waters along the coast of the southwestern Atlantic Ocean. Latitude of study area and season of occurrence of the species are also shown.

Capítulo 2

Table 1 Mean and standard deviation of fishing landings for adult mullets (x 1000 kg). Landing 1= industrial fishing from SC; Landing 2= artisanal fishing from SC; Landing 3= industrial fishing from RS; Landing 4= artisanal fishing from RS; Landing 5= industrial fishing from Patos Lagoon in RS; Landing 6= artisanal fishing from Patos Lagoon in RS; Landing 7= industrial and artisanal fishing from SP (see Supplementary Table 1). SC, RS and SP denote the code for the names of following Brazilian states: Santa Catarina, Rio Grande do Sul and São Paulo, respectively. The “n” indicates the number of months in each year that had landing data for adult mullets.

Table 2 Generalized additive models of the influence of environmental variables on the abundance of mullet juveniles on the coast and estuary.

Table 3 Generalized additive models of the effect of landing adult fish with different lags (1, 2, 3, 4 and 5) on the abundance of mullet juveniles on the coast and estuary.

Supplementary table 1 Data Source. Databases of mullet fishing landing (capture in kg) occurring along the south and southeastern Brazilian states.

Capítulo 3

Table 1 Seasonal and ENSO events isotopic niche overlap of juveniles of the mullet *Mugil liza* in the Patos Lagoon estuary from 2010 to 2022.

Table 2 Generalized additive model of the influence of numerical (local and regional) and categorical (Global) environmental variables on the SEAc of juveniles of the *Mugil liza* mullet. edf: are the degrees of freedom that reflect the degree of nonlinearity of a curve; Ref. df: are reference degrees of freedom; F: Estimate: Parametric coefficients; Std. error: standard error; p-value: considered statistically significant when $p < 0.5$; R-sq. (adj): adjusts predictors that are not significant in a model; and Deviance explained indicates the model's explainability adjustment for the database used.

INTRODUÇÃO GERAL

O entendimento dos fatores ambientais que controlam a variabilidade de longo-prazo (i.e., interanual e interdecadal) das espécies é um tema importante em ecologia, especialmente no atual contexto de perda de biodiversidade e mudanças climáticas que ameaçam a futura viabilidade das populações e suas funções ecológicas (BARBIER *et al.*, 2011; CARDINALE *et al.*, 2012). Esses fatores, como fenômenos climáticos naturais (e.g., *El Niño*) e atividades humanas que resultam em efeitos deletérios nas populações (e.g. sobreexploração pesqueira) e seus habitats (e.g. aquecimento global), acarretam marcadas variações de longo-prazo na abundância e distribuição das espécies (PAULY *et al.*, 2005; LAST *et al.*, 2010; ABREU *et al.*, 2010; BELARMINO *et al.*, 2021).

Programas de pesquisas com monitoramento de longo-prazo são importantes para investigar, por exemplo, a ocorrência de fenômenos climáticos naturais, mudanças climáticas antrópicas e sobrepesca, e seus efeitos nas espécies (ZHONG *et al.*, 2019; HARVEY *et al.*, 2020; FREIRE *et al.*, 2021). No sudoeste do Oceano Atlântico, estudos com bancos de dados de longo-prazo observaram mudanças na abundância e composição de espécies de peixes associado com o aquecimento da água (ARAÚJO *et al.*, 2018; GIANELLI *et al.*, 2019), podendo inclusive afetar a pesca (GIANELLI *et al.*, 2019). Outros trabalhos demonstram a importância de pesquisas de longo-prazo relacionados à pesca para preservar os ecossistemas, as espécies sobreexploradas e a economia (ALVES *et al.*, 2020; FREIRE *et al.*, 2021; ANDRIGUETTO-FILHO *et al.*, 2022). Também tem sido observadas alterações na abundância de peixes estuarinos residentes e dependentes relacionadas com eventos *El Niño* de diferentes intensidades (BELARMINO *et al.*, 2021; GOWERT *et al.*, 2023). Além disso, monitoramentos de longo-prazo com traçadores químicos naturais (e.g., isótopos estáveis) também permitiram observar mudanças na assimilação de recursos alimentares por consumidores estuarinos associados com a dinâmica dos fatores ambientais, podendo ter influência de eventos *El Niño* (POSSAMAI *et al.*, 2020; LANARI *et al.*, 2021a). Ou seja, os monitoramentos de longo-prazo de populações e comunidades biológicas permitem investigar os potenciais impactos das mudanças climáticas, tanto de origem natural (e.g., o fenômeno *El Niño*) quanto antrópica (e.g., aquecimento dos oceanos devido ao efeito estufa), bem como outros impactos produzidos por atividades humanas como a sobreexploração pesqueira. Portanto, o uso de séries temporais de longo-prazo para avançar na compreensão dos efeitos desses vários fatores sobre a biota, e suas possíveis interações e sinergias, pode gerar

informações importantes para o planejamento de ações mitigadoras dos efeitos da crescente perda de biodiversidade e mudanças climáticas sobre os ecossistemas (LIKENS, 1989; STRONG *et al.*, 2015).

O *El Niño* Oscilação Sul (ENOS) é caracterizado por flutuações naturais na temperatura da superfície do mar no Oceano Pacífico equatorial (MCPHADEN *et al.*, 2006; CAI *et al.*, 2018). Anomalias de temperatura abaixo da média ($\leq -0.5^{\circ}\text{C}$) corresponde a ocorrência de eventos *La Niña*, enquanto acima da média são considerados eventos *El Niño* ($\geq 0.5^{\circ}\text{C}$). Além disso, esses eventos podem ser classificados quanto a sua intensidade como: fracos ($\pm 0,5 - \pm 0,9$), moderados ($\pm 1,0 - \pm 1,4$), fortes ($\pm 1,5 - \pm 1,9$) e muito fortes ($\geq \pm 2,0$). Embora os eventos ENOS se originam no Pacífico tropical, eles afetam o clima globalmente, especialmente através de efeitos atmosféricos remotos que causam anomalias de precipitação e seca em diferentes regiões do mundo (GRIMM *et al.*, 1998; FOLEY *et al.*, 2002; EMMANUEL, 2022), os quais podem desencadear diversos impactos nos ecossistemas e nas suas comunidades biológicas (HOLBROOK *et al.*, 2020; LEHODEY *et al.*, 2020; GILLANDERS *et al.*, 2022). Os eventos *El Niño* e *La Niña* normalmente ocorrem a cada 2 a 7 anos (MCPHADEN *et al.*, 2006). Entretanto, estudos observaram que alterações climáticas e o aquecimento da temperatura superficial da água do Pacífico equatorial oriental podem aumentar a intensidade e a frequência de ocorrência de eventos ENOS (CAI *et al.*, 2018; FREUND *et al.*, 2019; YING *et al.*, 2022).

No sudoeste do Oceano Atlântico, os eventos *La Niña* e *El Niño* estão associados à escassez/excesso de chuvas e à diminuição/aumento da descarga de água continental, respectivamente, o que pode afetar os padrões de salinidade em estuários subtropicais e zonas de arrebentação marinhas adjacentes (GRIMM *et al.*, 1998; ODEBRECHT *et al.*, 2010; CAI *et al.*, 2020). Consequentemente, os eventos ENOS nesta região afetam a abundância de espécies, desde produtores primários até peixes predadores em estuários e costas marinhas adjacentes (GARCIA *et al.*, 2001; LANARI & COPERTINO, 2017; POSSAMAI *et al.*, 2018; GARCIA *et al.*, 2019a; GARCIA *et al.*, 2019b; BELARMINO *et al.*, 2021). Garcia e colaboradores (2001) observaram um aumento na abundância de peixes marinhos dentro do estuário da Lagoa dos Patos durante a *La Niña* e diminuição durante o *El Niño*. Neste estudo observou-se também menor abundância de peixes estuarinos residentes e dependentes, e maior abundância e riqueza de espécies de água doce durante um evento *El Niño* comparado com a *La Niña* (GARCIA *et al.*, 2001). Outro estudo realizado no estuário da Lagoa dos Patos investigou a abundância da ictiofauna antes, durante e depois de um evento *El Niño* e observaram um padrão semelhante, com a redução da abundância de peixes estuarinos

residentes e dependentes, marcada queda na abundância de peixes visitantes marinhos, e aumento de peixes dulcícolas durante o evento *El Niño* na região (GARCIA *et al.*, 2003). No entanto, essas mudanças na assembleia de peixes não foram muito persistentes e a ictiofauna estuarina retornou ao seu estado pré *El Niño* alguns meses depois (GARCIA *et al.*, 2003). Além disso, a abundância de peixes nesta região pode ser modulada pela intensidade do *El Niño*, com impactos mais negativos associados com eventos climáticos de maiores intensidades (BELARMINO *et al.*, 2021; GOWERT *et al.*, 2023). Os eventos ENOS também podem afetar a composição, abundância e riqueza dos produtores primários no estuário (ABREU *et al.*, 2010; TALGATTI *et al.*, 2023) e, conseqüentemente, afetar a cadeia trófica de consumidores estuarinos (GARCIA *et al.*, 2017; POSSAMAI *et al.*, 2020; LANARI *et al.*, 2021a). Estudos prévios no estuário da Lagoa dos Patos (32°S) observaram variações sazonais e interanuais nos valores isotópicos de carbono ($\delta^{13}\text{C}$) e nitrogênio ($\delta^{15}\text{N}$) dos produtores primários e na assimilação de fontes alimentares autóctone (i.e., estuarino) e alóctones (i.e., dulcícolas ou marinhos) por peixes no estuário da Lagoa dos Patos e região costeira marinha, as quais podem estar associadas com a ocorrência de eventos ENOS (GARCIA *et al.*, 2019a; GARCIA *et al.*, 2019b; POSSAMAI *et al.*, 2020; LANARI *et al.*, 2021a).

Entre os impactos antrópicos que podem afetar as assembleias de peixes, o aumento da temperatura das águas dos oceanos associado ao aquecimento global pode expandir a distribuição de espécies marinhas tropicais para regiões subtropicais e temperadas (PUNZÓN *et al.*, 2016). Ou seja, o aquecimento dos oceanos devido ao efeito estufa pode acarretar a diminuição na abundância de espécies que vivem nos trópicos e aumentar sua distribuição e abundância em maiores latitudes (i.e. em direção aos Pólos) (HASTINGS *et al.*, 2020; LAVENDER *et al.*, 2021). Estudos realizados no sudoeste do Oceano Atlântico mostram uma tendência de aumento na temperatura das águas superficiais (ARAÚJO *et al.*, 2018) e a intensificação da corrente do Brasil, que é importante no transporte de águas quentes tropicais em direção ao sul (FRANCO *et al.*, 2020a). Além disso, outros trabalhos sugerem aquecimento das águas costeiras da região através de estimativas com dados oriundos de satélite ou usando abordagens de modelagem climática (ORTEGA *et al.*, 2016; ARAÚJO *et al.*, 2018; GIANELLI *et al.*, 2019), ou por comparação de dados de modelos com dados históricos *in situ* (FRANCO *et al.*, 2020b). Esse aquecimento das águas costeiras poderia promover a expansão da ocorrência de peixes tropicais em direção às regiões de maiores latitudes no Oceano Atlântico (GIANELLI *et al.*, 2019). Por exemplo, Gianelli e colaboradores (2019) utilizaram um banco de dados de longo-prazo e investigaram os desembarques da pesca industrial do Uruguai, e observaram que o aquecimento dos oceanos

levou a uma mudança de espécies associadas a águas mais frias para espécies de águas quentes nos desembarques locais. Outro estudo realizado em uma área de transição entre as regiões tropicais e subtropicais no sudeste do Brasil, observaram mudanças na abundância de espécies de peixes associado com o aquecimento das águas, aumentando a população de algumas espécies e outras diminuindo ou desaparecendo (ARAÚJO *et al.*, 2018). Porém, não existem evidências empíricas, obtidas por meio de monitoramentos *in situ*, sobre a ocorrência desse fenômeno para estuários e suas regiões marinhas adjacentes no sul do Brasil.

Outro impacto antrópico que pode afetar diretamente as assembleias de peixes é a sobreexploração pela indústria pesqueira. A sobrepesca é um dos principais responsáveis pelo declínio das populações de peixes, podendo gerar impactos negativos na economia, segurança alimentar e nos ecossistemas (CRESPO & DUNN, 2017; ABREU-MOTA *et al.*, 2018; RODRIGUEZ *et al.*, 2021). No sul Brasil, a intensa pesca desde a década de 1960 levou à diminuição em torno de 60% nos desembarques de espécies de peixes estuarinas e costeiras (HAIMOVICI & CARDOSO, 2017). Isso fez com que estoques de algumas espécies de peixes fossem classificadas como em colapso, sobreexploradas ou no limite da exploração (HAIMOVICI & CARDOSO, 2017). Estudos demonstraram que a pesca excessiva de indivíduos sexualmente maduros, especialmente antes ou durante os seus eventos de desova, pode ter impactos negativos na abundância de novos recrutas para várias populações de peixes, como o salmão do Pacífico (*Oncorhynchus* spp.) (MUNSCH *et al.*, 2020), Bacalhau do Atlântico (*Gadus morhua*), escamudo (*Pollachius virens*) (MCCAIN *et al.*, 2016), Truta-pintada (*Cynoscion nebulosus*) (NEHEMIAH *et al.*, 2022), peixe-papagaio (*Scarus trispinosus*) (ROOS *et al.*, 2020) e tainha (*Mugil cephalus*) (LAN *et al.*, 2014; LAN *et al.*, 2017). Em geral, estes estudos salientaram que os efeitos sinérgicos da sobrepesca das populações adultas e da dinâmica ambiental são fatores importantes que controlam a abundância de novos recrutas. Uma melhor compreensão da complexa interação entre estes fatores é um passo crucial para fornecer orientações com base empírica para o planejamento de uma gestão pesqueira abrangente e sustentável (PAULY *et al.*, 2002; ABREU-MOTA *et al.*, 2018; MUNSCH *et al.*, 2020).

Monitoramentos de longa duração no estuário da Lagoa dos Patos e costa marinha adjacente nas zonas rasas (<2 m) da região demonstrou que a assembleia de peixes é composta por dezenas de espécies (LE MOS *et al.*, 2022). Garcia *et al.* (2001) observaram a ocorrência de quatro principais grupos de peixes em zonas rasas do estuário da Lagoa dos Patos, sendo eles: peixes estuarinos residentes (*i.e.*, passam todo seu ciclo de vida dentro do estuário), dependentes estuarinos (*i.e.*, passam apenas uma parte do seu ciclo de vida dentro

do estuário), visitantes marinhos (*i.e.*, habitam ambientes marinhos e raramente ocorrem no estuário) e visitantes de água doce (*i.e.*, habitam ambientes dulcícolas e raramente ocorrem no estuário). As principais espécies que ocorrem no estuário e pertencem ao grupo dos peixes estuarinos residentes são a *Atherinella brasiliensis*, *Odonthestes argentinensis* e a *Jenynsia multidentata*. Os principais estuarinos dependentes são *Mugil liza* (anteriormente chamada de *Mugil platanus*), *Micropogonias furnieri*, *Mugil curema* e peixes da família Clupeidae. Os principais visitantes marinhos são *Ulaema lefroyi* e o *Menticirrhus littoralis*. E por fim, os principais visitantes de água doce são o *Parapimelodus nigribarbis* e a *Astyanax eigenmanniorum* (GARCIA *et al.*, 2001).

Além disso, estudos observaram que a ocorrência e abundância das espécies de peixes pertencentes a esses grupos na região podem variar sazonalmente e/ou devido a eventos *El Niño* e *La Niña* (GARCIA *et al.*, 2001; GARCIA *et al.*, 2003). Entretanto, as espécies mais abundantes e frequentes em zonas rasas do estuário da Lagoa dos Patos ao longo de todo o ano são as espécies de tainha *M. liza* e o peixe-rei *A. brasiliensis* (GARCIA *et al.*, 2004). Já na costa marinha adjacente ao estuário da Lagoa dos Patos, um estudo investigou a riqueza e abundância de espécies de peixes na praia do Cassino (<20 m) e observaram uma variação sazonal e interanual (MARTINS *et al.*, 2015). Além disso, encontraram 64 espécies, sendo que as mais abundantes na região são a *M. liza*, *Trachinotus marginatus*, *M. curema*, *Brevoortia pectinata*, *Mugil* sp, *O. argentinensis*, *M. littoralis*, *A. brasiliensis* (MARTINS *et al.*, 2015).

Em relação a relevância para a pesca, Haimovici e Cardoso (2017) discutem sobre as principais espécies de peixes com importância comercial do estuário da Lagoa dos Patos e costa marinha adjacente e suas classificações quanto aos seus estoques, sendo elas a corvina *M. furnieri* (sobrexplorada), a tainha *M. liza* (totalmente explorada), os bagres *Genidens* spp. (colapso), a miraguaia *Pogonias cromis* (colapso), a pescadinha *Macrodon atricauda* (sobrexplorada), a castanha *Umbrina canosai* (sobrexplorada), a maria-mole *Cynoscion guatucupa* (sobrexplorada) e a anchova *Pomatomus saltatrix* (totalmente explorada).

Modelos biológicos apropriados para investigar a influência de fatores ambientais naturais e antrópicos sobre populações numa escala temporal de longo-prazo são as formas juvenis de espécies de tainhas que ocorrem em abundância em estuários e costa marinha adjacente. A ocorrência e a abundância mensal de espécies de tainhas em zonas rasas (<2 m) do estuário da Lagoa dos Patos e sua costa marinha adjacente, juntamente com fatores abióticos (*i.e.*, temperatura, salinidade e transparência da água), vem sendo monitorada mensalmente desde 1996 até os dias atuais por meio do programa de Pesquisas Ecológicas de

Longa Duração (PELD-ELPA) (ODEBRECHT *et al.*, 2017; VIEIRA *et al.*, 2020). Além disso, vem sendo monitorado desde 2010 até os dias atuais os valores sazonais de isótopos estáveis de $\delta^{13}\text{C}$ e $\delta^{15}\text{N}$ dos juvenis de tainha e fontes alimentares basais no estuário da Lagoa dos Patos (LANARI *et al.*, 2021b).

Por exemplo, a espécie de tainha *Mugil curema* é um bom modelo para investigar a hipótese de que com o aumento da temperatura superficial da água, a espécie estaria aumentando sua abundância no estuário da Lagoa dos Patos e na costa marinha adjacente (32°S). Isso porque essa espécie é mais abundante nas zonas tropicais, com uma marcada diminuição em maiores latitudes. No estuário da Lagoa dos Patos e costa marinha adjacente, os juvenis da espécie são registrados apenas no verão e outono quando a temperatura e salinidade estão mais elevadas (VIEIRA, 1991). Essa região parece constituir uma faixa limítrofe na distribuição de *M. curema*, uma vez que os registros de ocorrência ficam mais escassos ao sul, com um único registro de 6 exemplares na Argentina (CASTRO *et al.*, 2006). Além disso, um estudo realizado mais ao norte do sudoeste do Brasil (23°S) em comparação com o estuário da Lagoa dos Patos (32°S), em uma área de transição entre as regiões tropicais e subtropicais, observou uma diminuição na abundância da *M. curema* (ARAÚJO *et al.*, 2018), o que sugere que essa espécie possa estar migrando em direção a regiões subtropicais e aumentando sua abundância no estuário da Lagoa dos Patos e costa marinha adjacente.

Já a espécie *Mugil liza*, que ao contrário de *M. curema*, possui elevada importância comercial na região, é um modelo propício para investigar a hipótese de que a abundância de seus juvenis está diminuindo no estuário da Lagoa dos Patos e na costa marinha adjacente devido a influência de distúrbios climáticos naturais, como o fenômeno *El Niño*, e impactos antrópicos como a sobrepesca dos indivíduos adultos. O ciclo de vida é semelhante ao da espécie *M. curema*, pois *M. liza* também desova no mar e os seus juvenis usam os estuários como zona de alimentação, proteção contra predadores e desenvolvimento dos seus juvenis (VIEIRA, 1991). Porém, ao contrário da espécie de tainha com distribuição mais tropical, *M. liza* ocorre na região durante todo o ano (VIEIRA, 1991). Estudos prévios mostraram que a abundância dos juvenis diminui significativamente no estuário da Lagoa dos Patos durante as fortes chuvas e descarga continental associada a fortes eventos *El Niño* (GARCIA *et al.*, 2004). Já os indivíduos adultos de *M. liza* são importantes na pesca artesanal e industrial aonde sofrem uma alta taxa de exploração (HAIMOVICI & CARDOSO, 2017), sendo que sua captura ocorre principalmente quando elas se agregam para migrar para o ambiente marinho para a reprodução (LE MOS *et al.*, 2014). Além disso, as ovas possuem um alto valor comercial (HAIMOVICI & CARDOSO, 2017). Ou seja, sua captura ocorre principalmente

antes delas desovarem, o que pode levar à diminuição na abundância de juvenis da espécie no estuário da Lagoa dos Patos e na costa marinha adjacente. Além disso, estudos prévios sugerem que a abundância dos juvenis da espécie está diminuindo ao longo dos anos e que isso pode estar relacionado à sobrepesca dos adultos (MARTINS *et al.*, 2015; VIEIRA *et al.*, 2019). Portanto, as populações de *M. liza* podem estar sofrendo o efeito sinérgico de impactos naturais (eventos *El Niño*) e antrópicos (sobrepesca) que poderiam estar acarretando diminuição na abundância dos juvenis nas últimas décadas.

A espécie de tainha *M. liza* também é um bom modelo biológico para investigar a variabilidade temporal (sazonal e longo-prazo) nos elos tróficos que sustentam consumidores primários em estuários e suas possíveis relações com fatores ambientais locais e globais associados com eventos ENOS (POSSAMAI *et al.*, 2020; LANARI *et al.*, 2021b). Isso é possível devido à existência de bancos de dados isotópicos ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$) de longo-prazo (2010-2022) das fontes orgânicas basais assimiladas por juvenis de tainhas no estuário da Lagoa dos Patos. Os isótopos estáveis são utilizados como marcadores que permitem estimar a importância relativa dos recursos alimentares autóctones e alóctones nas cadeias alimentares estuarinas, desde que tenham valores isotópicos distintos. Isso porque esses traçadores químicos naturais permitem inferir a contribuição de cada fonte alimentar assimilada, por meio da comparação das composições isotópicas das fontes alimentares e de seus consumidores (GARCIA *et al.*, 2017; POSSAMAI *et al.*, 2020; LANARI *et al.*, 2021a; Vollrath *et al.*, 2021). Os juvenis dessa espécie são abundantes e frequentes durante todo o ano dentro do estuário (VIEIRA, 1991; GARCIA *et al.*, 2004), o que permite investigar variações sazonais e interanuais nos valores isotópicos assimilados pela espécie. Além disso, os juvenis de *M. liza* são consumidores primários, se alimentando principalmente de diatomáceas, sendo que quando estão na região costeira marinha (i.e., após a desova dos adultos) se alimentam de microalgas presentes na coluna d'água, e quando entram no estuário, mudam sua dieta para microalgas associadas ao sedimento (VOLLRATH *et al.*, 2021).

Estudos prévios sugerem que a assimilação dos consumidores primários estuarinos podem ser afetadas por períodos de maior descarga de água doce continental (i.e., inverno-primavera) e períodos de seca e maior intrusão de água salina (i.e., verão-outono) dentro do estuário, bem como a ocorrência de eventos ENOS que intensificam esses fatores climáticos, que podem aumentar a disponibilidade de fontes basais alóctones de origem dulcícola ou marinha, respectivamente (GARCIA *et al.*, 2017; POSSAMAI *et al.*, 2020; LANARI *et al.*, 2021a). Um estudo realizado no estuário da Lagoa dos Patos observou que períodos de baixa precipitação ou condições de seca (i.e., verão-outono/eventos *La Niña*) podem causar escassez

de nutrientes e afetar o crescimento do fitoplâncton no estuário (ABREU *et al.*, 2010). Em contrapartida, os períodos com elevada precipitação (i.e., inverno-primavera/eventos *El Niño*), que promovem a entrada de água doce na região estuarina, constituem um importante mecanismo de introdução de novos nutrientes no estuário, levando a um crescimento significativo do fitoplâncton (ABREU *et al.*, 2010). Lanari e colaboradores (2021) destacam a importância de usar bancos de dados de longo-prazo e considerar a ocorrência de eventos ENOS em análises de assimilação de recursos alimentares basais, pois os eventos ENOS podem ocasionar sobreposição nos valores isotópicos dos produtores primários de diferentes estações em diferentes anos, levando a interpretações errôneas sobre a assimilação dos consumidores estuarinos.

Nesse contexto, a presente Tese investigou as seguintes questões: (i) Existe uma tendência crescente na temperatura das águas superficiais e, consequentemente, na abundância de espécies de peixes tropicais em um sistema subtropical estuarino e costeiro? (ii) Os eventos climáticos globais (ENOS), os fatores ambientais regionais (vazão dos rios) ou locais (salinidade, temperatura, transparência da água) influenciam a variabilidade da abundância de longo-prazo de uma espécie de peixe tropical em latitudes subtropicais? (iii) Quais as tendências de longo-prazo (1997-2019) na abundância dos juvenis de tainha *M. liza* e suas relações com distúrbios climáticos naturais (eventos *El Niño*) e a exploração pesqueira? (iv) Há variação sazonal e interanual, associado com a ocorrência de eventos ENOS, na assimilação de fontes basais por um consumidor primário, com maior assimilação de recursos alóctones de água doce durante o inverno-primavera e *El Niño* e marinho durante o verão-outono e *La Niña*?

OBJETIVO GERAL

Investigar a variabilidade de longo-prazo na abundância de tainhas e na assimilação de fontes basais autóctones e alóctones dos juvenis de tainhas no estuário da Lagoa dos Patos e na costa marinha adjacente e suas relações com alterações climáticas naturais (i.e., eventos ENOS) e impactos antrópicos (i.e., aquecimento dos oceanos e sobrepesca).

OBJETIVOS ESPECÍFICOS

A partir de banco de dados de monitoramentos padronizados de longo-prazo obtidos pelo programa de Pesquisas Ecológicas de Longa Duração no Estuário da Lagoa dos Patos e Costa Marinha Adjacente (PELD-ELPA) foram investigados: (i) se há aquecimento das águas de zonas rasas do estuário da Lagoa dos Patos e costa marinha adjacente; (ii) caso haja, se há aumento da abundância de uma espécie de tainha (*M. curema*) mais comum em latitudes tropicais nessa região subtropical devido ao aquecimento das águas; (iii) e como os eventos ENOS, fatores ambientais regionais e locais afetam a abundância a longo-prazo dos juvenis dessa espécie em latitudes subtropicais (iv) se há efeito negativo da pesca dos adultos na abundância dos juvenis da tainha *M. liza* na costa e estuário; (vi) se há variação interanual e sazonal, associado com eventos ENOS, na assimilação de fontes basais autóctones e alóctones por consumidores primários como os juvenis da tainha *M. liza*.

HIPÓTESES

Capítulo 1

- 1) Haverá aquecimento das águas superficiais de zonas rasas do estuário da Lagoa dos Patos e costa marinha adjacente;
- 2) Com isso, haverá aumento da abundância dos juvenis de uma espécie de tainha tropical (*M. curema*) em uma região subtropical;
- 3) Eventos ENOS, fatores ambientais regionais e locais irão afetar a abundância a longo-prazo dos juvenis dessa espécie na região.

Capítulo 2

- 1) Haverá uma tendência de declínio a longo-prazo na abundância de juvenis de tainha (*M. liza*) na costa marinha e estuário no sul do Brasil;
- 2) Haverá uma relação negativa entre o número de indivíduos adultos desembarcados pela pesca, principalmente durante a migração reprodutiva, e a abundância de juvenis na região.

Capítulo 3

- 1) A amplitude do nicho isotópico dos consumidores primários (*M. liza*) irá variar de acordo com as estações do ano e eventos ENOS: menor durante o verão-outono/*La Niña* em comparação com o inverno-primavera/*El Niño*;
- 2) Durante o inverno-primavera e eventos *El Niño* haverá maior assimilação de recursos alóctones de água doce e no verão-outono e eventos *La Niña* haverá maior assimilação de recursos alóctones marinhos no estuário.

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CAPÍTULO 1

Complex interactions of ENSO and local conditions buffer the poleward shift of migratory fish in a subtropical seascape

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Este artigo está publicado na revista *Science of The Total Environment* (STOTEN)

<http://dx.doi.org/10.1016/j.scitotenv.2023.165129>

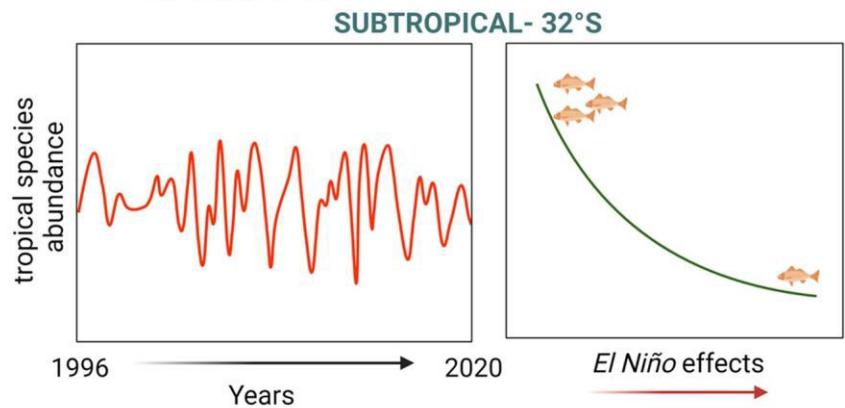
Graphical abstract

BACKGROUND AND HYPOTHESIS



RESULTS

- ☒ Seawater warming
- ☒ Tropicalization
- ☒ *El Niño* buffers global warming effects



Abstract

Ocean warming is associated with the tropicalization of fish toward higher latitudes. However, the influence of global climatic phenomena like the *El Niño* Southern Oscillation (ENSO) and its warm (*El Niño*) and cold (*La Niña*) phases on tropicalization has been overlooked. Understanding the combined effects of global climatic forces together with local variability on the distribution and abundance of tropical fish is essential for building more accurate predictive models of species on the move. This is particularly important in regions where ENSO-related impacts are known to be major drivers of ecosystem change, and is compounded by predictions that *El Niño* is becoming more frequent and intense under current ocean warming. In this study, we used long-term time series of monthly standardized sampling (August 1996 to February 2020) to investigate how ocean warming, ENSO and local environmental variability influence the abundance of an estuarine dependent tropical fish species (white mullet *Mugil curema*) at subtropical latitudes in the southwestern Atlantic Ocean. Our work revealed a significant increasing trend in surface water temperature in shallow waters (< 1.5 m) at estuarine and marine sites. However, against our initial expectation, we did not observe an increasing trend in the abundance of this tropical mullet species. Generalized Additive Models revealed complex, non-linear relationships between species abundance and environmental factors operating at large (ENSO's warm and cold phases), regional (freshwater discharge in the coastal lagoon's drainage basin) and local (temperature and salinity) scales across the estuarine marine gradient. These results demonstrate that fish responses to global climate change can be complex and multifaceted. More specifically, our findings suggested that the interaction among global and local driving

forces dampen the expected effect of tropicalization for this mullet species in a subtropical seascape.

Keywords: Ocean warming, species distribution, *El Niño* and *La Niña* events, tropicalization effect, White mullet *Mugil curema*, southwestern Atlantic Ocean

1. Introduction

Changes in global sea surface temperature and local fluctuations in salinity, hypoxia or acidification are the result of complex multiscale interactions that impact marine and coastal communities worldwide (Parmesan et al., 2011; Pecl et al., 2017; Coni et al., 2021). Global climate change is triggering ocean warming allied to changes in climatic processes and extreme weather patterns linked to phenomena such as fluctuations in the *El Niño* Southern Oscillation (ENSO). However, species' responses to interacting pressures are likely to be complex and to vary in terms of scale and direction, which can potentially amplify or dampen processes such as tropicalization and species future distributions and abundance patterns (Wilbanks & Kates, 1999; Pinsky et al., 2013; Coni et al., 2021). Yet, our understanding of the interactions among global and local factors and their ecological impacts on species distributions is still poor.

El Niño Southern Oscillation (ENSO) is characterized by natural fluctuations in sea surface temperature in the equatorial Pacific Ocean with above- and below-average temperature anomalies classified as *El Niño* and *La Niña* events (McPhaden et al., 2006). Whilst ENSO is situated in the tropical Pacific, it affects the climate globally, especially through precipitation and drought anomalies in different regions of the world (Grimm et al., 1998; Foley et al., 2002; Emmanuel, 2022) that trigger diverse impacts on ecosystems and their biological assemblages (Lehodey et al., 2020; Holbrook et al., 2020; Gillanders et al., 2022).

ENSO can affect primary productivity and disrupt food chains, impacting fisheries that are an important food resource for local communities (McGlue et al., 2020). Increases in sea surface temperature (SST) associated with ENSO can lead

to enhanced fish growth and productivity (Erisman et al., 2021) but disparity among regions is evident, linked to the local outcomes of ENSO weather patterns. For instance, stronger *El Niño* events spur intense rainfall, and negatively impact the growth of grouper (a top predator marine fish) in southern Brazil (Reis-Santos et al., 2021); or change water temperature, salinity and upwelling patterns in north Western Australia that result in decreased fish growth (Ong et al., 2016). ENSO can also impact the reproduction of migratory fish. For instance, on the Southwest Atlantic coast, the colder phase of ENSO (*La Niña*) impacts the abundance of migratory fish associated with the decrease in rainfall and water level and, consequent, reduction in available reproductive areas (Cataldo et al., 2022).

In the southwestern Atlantic, ENSO's warm phase (i.e., *El Niño*) is renowned to be associated with excess rainfall and increased continental water discharge, which may affect salinity patterns in subtropical estuaries and adjacent marine surf zones (Grimm et al., 1998; Odebrecht et al., 2010a; Cai et al., 2020). Consequently, *El Niño* events in this region affect species abundance from primary producers to predatory fish in estuaries and adjacent marine coasts (Possamai et al., 2018; Lanari & Copertino, 2017; Garcia et al., 2019a; Jorge-Romero et al., 2021). Moreover, a recent study suggests that the effects on fish abundance in this region are modulated by the intensity of *El Niño*, with more negative effects decreasing fish abundance associated with stronger climatic events (Belarmino et al., 2021).

Understanding the mechanisms underlying the complex interplays between global and local factors affecting fish assemblages is key. Particularly as climate change and the associated increase in SST of the eastern equatorial Pacific are expected to increase the frequency of strong ENSO events and extreme weather events (Cai et al., 2018; Freund et al., 2019; Ying et al., 2022). Hence, the impacts of

ENSO on fish communities will likely intensify over the coming years and it is critical to better understand how species respond. In addition to the increasing frequency of extreme events associated with stronger ENSO, the increase in SST associated with global warming can also have a direct influence on fish assemblages by expanding the distribution of tropical marine species to subtropical and temperate regions (Punzón et al., 2016). In doing so, this may decrease species numbers and abundance near the tropics against an increase at higher latitudes (i.e., towards the poles) (Hastings et al., 2020; Lavender et al., 2021).

Increasing trends of SST allied to the intensification of the Brazil current transporting warm tropical waters towards the south (Ortega et al., 2016; Araújo et al., 2018; Franco et al., 2020a) may promote the expansion of tropical fish to higher latitudes (i.e., tropicalization) (Araújo et al., 2018; Gianelli et al., 2019; Costa et al., 2021). Higher proportions of cold- to warm-water species have been observed in the landings of Uruguayan industrial fisheries, with these changes being associated with ocean warming (Gianelli et al., 2019). However, there are reports of both increasing and decreasing trends in fish abundance associated with increasing SST and *El Niño* events in coastal areas of the southwestern Atlantic Ocean (Araújo et al., 2018; Gianelli et al., 2019; Belarmino et al., 2021). Therefore, it is critical to understand the interplay between the potential effects of ENSO, associated coastal runoff, and increasing SST in the expected range shift of fish.

The present study used a long-term 23-year time series (1997-2019) of monthly values of surface water temperature and abundance of a tropical mullet (*Mugil curema* Valenciennes, 1836) in a subtropical estuary and its adjacent marine region in the southwestern South Atlantic Ocean to investigate the following questions: (i) Is there an increasing trend in surface water temperature and,

consequently, in the abundance of the tropical fish species in this subtropical estuarine and coastal seascape? (ii) Do global climatic events (ENSO), regional (river flow) or local (salinity, temperature, water transparency) environmental factors mediate long-term abundance variability of a tropical fish species at subtropical latitudes? We hypothesized that: (i) There would be an increasing trend in surface water temperature and the abundance of *M. curema* juveniles in estuarine and marine shallow waters at subtropical latitudes, and (ii) that stronger *El Niño* events would decrease the abundance of *M. curema* juveniles. Overall, this can provide key insights on the interplay between natural climatic phenomena (ENSO) and climate change (ocean warming) on fish populations and potential range shifts.

2. Methods

2.1 Study area and species

The Patos Lagoon in southern Brazil is the largest choked lagoon in the world with an area of 10,227 km² (Kjerfve, 1986). Its estuarine zone covers 10% of the total area, with the lagoon connected to the Atlantic Ocean through a single narrow inlet at the southern point (Seeliger, 2001) (Figure 1). In southern Brazil, the austral summer and autumn are generally characterized by low freshwater discharge and, consequently, increased salinity and less stratified waters in the Patos Lagoon (Marques et al., 2011; Marques et al., 2014). During the austral winter and spring, increased rainfall and freshwater discharge lead to lower salinity and reduce the entry of oceanic waters in the estuarine area of the Patos Lagoon (Marques et al., 2011; Marques et al., 2014). In addition to freshwater discharge, winds are also important for hydrodynamics and stratification in the estuary (Marques et al., 2011;

Marques et al., 2014). However, during *El Niño* events, positive anomalies in precipitation and continental water discharge (i.e., river flow) occur throughout the year. This causes an increase in the freshwater outflow to the ocean and a decrease in seawater inflow (Marques et al., 2011; Marques et al., 2014), leading to near zero salinities in estuarine areas for several weeks or months (Garcia et al., 2004; Belarmino et al., 2021).

The marine surf zone adjacent to the Patos lagoon has an extensive sandy coastline of approximately 220 km mostly characterized by sandy beaches with varying wave regimes (dissipative and intermediate) and a mild average slope (between 1.4° and 1.7°) (da Silva et al., 2008). The surface water temperature in the marine surf zone has a marked seasonality with higher values in the austral summer (21.8°C) and lower values in the austral winter (13.8°C) (Garcia et al., 2019b). Generally, salinity is higher in summer-autumn and decreases in winter-spring associated with increased precipitation and continental water discharge (Mendes et al., 2016). Salinity tends to be lower during *El Niño* events, linked to above-average rainfall in these periods, particularly during strong *El Niño* years (Odebrecht et al., 2010a).

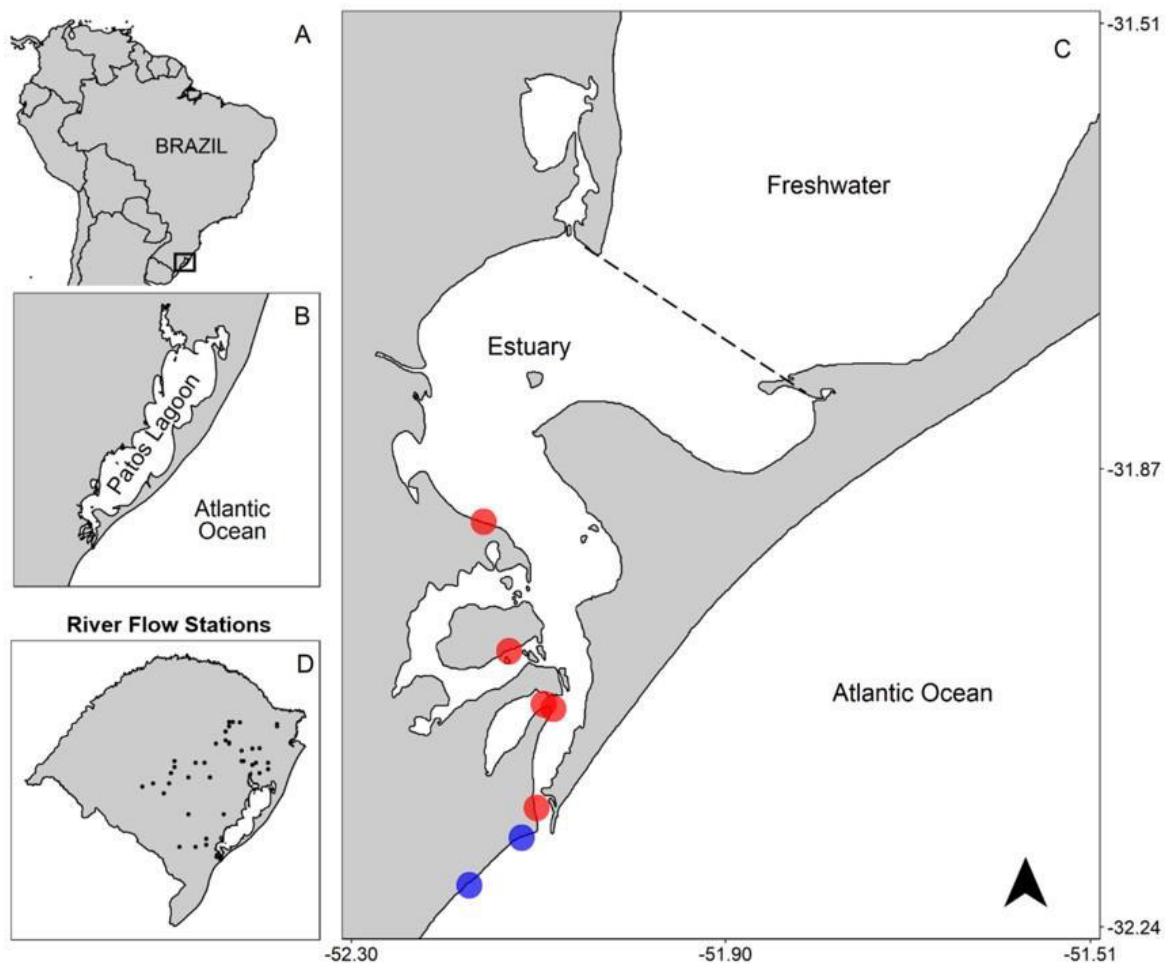


Figure 1. (A) Map of Brazil and (B) the location of Patos Lagoon with (C) the sampling stations in the estuarine zone (filled red circles, $n = 5$) and the adjacent marine region (filled blue circles, $n = 2$). (D) Map of the southernmost state in Brazil showing the location of the river flow stations along the drainage basin of Patos Lagoon (filled black circles).

The white mullet *Mugil curema* is a widely distributed coastal pelagic fish occurring in the Atlantic and Eastern Pacific Oceans (Thompson et al., 1978; Menezes et al., 2003). In the southwestern Atlantic Ocean, this species is most abundant in tropical zones and shows a marked decrease toward higher latitudes. White mullet spawn in the sea and juveniles usually use estuaries as feeding areas

(Vieira, 1991; Mai et al., 2018). In the extreme south of Brazil ($>32^{\circ}\text{S}$), white mullet is reported to occur only as juveniles primarily during summer and autumn when temperature and salinity are higher (Vieira, 1991). This region seems to constitute the southern limit of the distribution range of white mullet, with only one record of occurrence of a few specimens further south (i.e., Argentina) (Castro et al., 2006). Given these characteristics, white mullet juveniles are an excellent biological model to investigate the effects of ocean warming and extreme weather events associated with ENSO on changes in distribution range and abundance patterns.

2.2 Data collection

Since August 1996, ichthyofauna of shallow areas ($<1.5\text{ m}$) has been sampled in five sampling stations in the estuarine area of Patos Lagoon (hereafter, 'Estuary') and two sampling stations in the adjacent marine surf zone (hereafter, 'Coast') (Figure 1). This standardized long-term monitoring is carried out as part of the Brazilian Long-Term Ecological Research (B-LTER) program (Odebrecht et al., 2017; Lemos et al., 2022; Vieira et al., 2022). Fish are sampled with a 9 m beach seine (13 mm mesh in the wings and 0.5 mm mesh in the 3 m center section). Five beach seine hauls are undertaken at each of the seven sampling sites per month. At the time of sampling, the following environmental parameters are measured: water temperature ($^{\circ}\text{C}$) (thermometer), salinity (refractometer), and water transparency (m) (Secchi disc).

The total length (mm) and weight (g) of white mullet were measured, and the mean monthly abundance of the species was expressed as Catch per Unit of Effort (CPUE). Here, we analyzed the long-term time series of monthly abundance of

juvenile white mullets in the B-LTER database from August 1996 to February 2020. All individuals with total lengths ranging from 20 to 150 mm were considered juveniles (Vieira et al., 1991).

Moreover, we conducted an extensive literature review on records of the occurrence (locality and latitude) of the species in each season of the year (i.e., summer, autumn, winter and spring) along the southwest Atlantic Ocean (see Table S1 for references). This occurrence dataset was superimposed on seasonal maps of SST along the southwest Atlantic Ocean.

Monthly mean values of sea surface temperature along the Brazilian coast (0° - 40° S, 32° - 60° W) were obtained from the 1° gridded Hadley ISST dataset (Rayner et al., 2003). Spanning the period from 1997 to 2019, seasonal means (summer: January, February, March; autumn: April, May, June; winter: July, August, September; spring: October, November, December) were calculated for each grid cell.

Monthly averages of river flow (m³/s) were obtained from the Brazilian National Institute of Meteorology (INMET) and Oceanic Niño Index (ONI) values were obtained from the National Oceanic and Atmospheric Administration (NOAA) for the period between August 1996 and February 2020. ONI is the measure of sea surface temperature in the *Niño* 3.4 region (5°N – 5°S, 120° – 170°W) expressed as a three-month running mean that has been used to characterize the occurrence and intensity of the warmer (*El Niño*) and colder (*La Niña*) phases of the ENSO phenomenon. Values above and below 0.5 correspond to the occurrence of *El Niño* and *La Niña* events and their intensities are classified as: weak (0.5-0.9), moderate (1.0-1.4), strong (1.5-1.9) and very strong (≥ 2.0).

2.3 Data analysis

We calculated the mean and standard error of juvenile white mullet abundance for each month (August 1996 to February 2020) to investigate changes in abundance patterns in the Estuary and Coast regions. Given the species' clear seasonal abundance pattern, with juveniles more abundant in summer and autumn (January-June) and absent or rare in winter and spring (July-December) (Vieira, 1991), the dataset of each region was separated into two periods: High Abundance (January to June) and Low Abundance (July to December).

The monthly anomalies of abiotic variables (i.e., ONI, river flow, transparency, salinity, and surface water temperature) were calculated using the mean values for each variable according to the historical dataset (August 1996 to February 2020) as follows: monthly value (e.g., January) minus the respective historical mean for the same month (e.g., average of all Januaries between 1996 to 2020). To better portray the expected changes in salinity along the ENSO phases, we show salinity variation in the Estuary and Coastal regions during *La Niña* and *El Niño* events with intensity classified from moderate to very strong according to the ONI index (≤ -1 and ≥ 1 , respectively) and also during Neutral periods (ONI between -0.4 to 0.4).

Temporal trends in the surface water temperature and abundance of white mullet in the Estuary and Coast regions were investigated using time series analysis, which enabled the decomposition of the components of seasonality, interannual trend and residuals (Crawley, 2012). Time series analysis of the surface water temperature was analyzed considering all months of the year, using only those years of the time series containing all twelve months (i.e., from January to December) (1997 to 2019).

For the abundance of white mullet, the time series analysis was performed separately for the high and low abundance periods and for the Estuary and Coast regions. The statistical significance ($\alpha = 0.05$) of the interannual trend was tested using linear mixed models with interannual trend as fixed factor and time (months/years) as random factor to control for temporal pseudoreplication. Different models (model 1: seasonal+interannual and model 2: only interannual) were compared using the method of maximum likelihood (Crawley, 2012; Belarmino et al., 2021). The analyses were performed in R using the packages “astsa”, “stats”, “lme4”, “magrittr” (Crawley, 2012; Bache et al., 2022; R Core Team 2022; Stoffer & Poison, 2022).

We used Generalized Additive Models (GAMs) to model the relationships between environmental variables and the abundance of white mullet in the Estuary and Coast regions in the period of high abundance (January to June) using a Tweedie error family with log link function (Wood, 2017; Pedersen et al., 2019). We did not model the abundance during the low abundance period (July to December) because the species was nearly or totally absent in colder months, and very low abundances can result in mathematical artefacts and weak statistical inferences. We chose the Tweedie error family because the response variable (CPUE data) contains several zeros (Shono, 2008). Thin plate regression spline smoothers and k-value at most equal to 10 were used to perform the models (Wood, 2017; Pedersen et al., 2019). GAMs were fitted using maximum likelihood estimation with the mgcv R package (Wood, 2017). The “GGally” R package was used to make a correlation matrix plot using Pearson's method (Schloerke et al., 2021). All environmental covariates were maintained in the GAMs, since Pearson correlations among all environmental variables were ≤ 0.5 . To optimise model convergence, environmental

variables were standardized with the values scaled to mean zero and then divided by the standard deviations (Oksanen et al., 2022). Automated model selection (“MuMIn” package, Bartón, 2022) was used to find the most parsimonious final model by constructing and comparing models containing all possible combinations of predictors. The best and most parsimonious model was identified according to the values of the second-order Akaike information criterion (AICc) and the AIC likelihood weights (AICcw) (Bartón, 2022). Residual plots were performed using the “gam.check” function of the “mgcv” package to assess whether the assumptions of the models were met (Wood, 2017). All statistical analyzes were performed in R program (version 4.2.1) (R Core Team, 2022).

3. Results

3.1 Intra-annual patterns in abiotic factors and abundance

Surface water temperature in the estuarine and coastal surf-zone showed a marked seasonality but we found no statistically significant relationship with ONI for the analyzed period (August 1996 to February 2020) ($r = 0.04$; $p > 0.54$ and $r = 0.08$; $p > 0.18$, respectively) (Figure S1; Figure S2). Monthly anomalies of abiotic variables (i.e., ONI, river flow, salinity, transparency and surface water temperature) in the Estuary and Coast regions demonstrated that *El Niño* events were associated with increased river flow in the lagoon’s drainage basin and a subsequent decrease, with approximately 1-2 months lag, in the salinity and water transparency in the estuarine and marine surf-zone regions (Figure S1; Figure S2). In the Estuary, salinity was higher during *La Niña* events and lower in *El Niño* compared to events classified as

neutral (Figure S3). In the Coast region, salinity did not vary during *La Niña*, *El Niño* and neutral events (Figure S3).

The mean abundance of juvenile white mullet during the higher abundance period was 26.19 (± 43.04) and 28.50 (± 53.14) individuals per haul in the Estuary and Coast regions, respectively, compared with a mean of 1.21 (± 3.82) and 1.37 (± 8.82) during the lower abundance period (Figure 2). In the Estuary, the abundance started to increase in January and peaked in February, with a slow continuous decrease in the following months through until June (Figure 2). In the Coast region, abundance started to increase in January, peaked in February and then rapidly decreased until June (Figure 2).

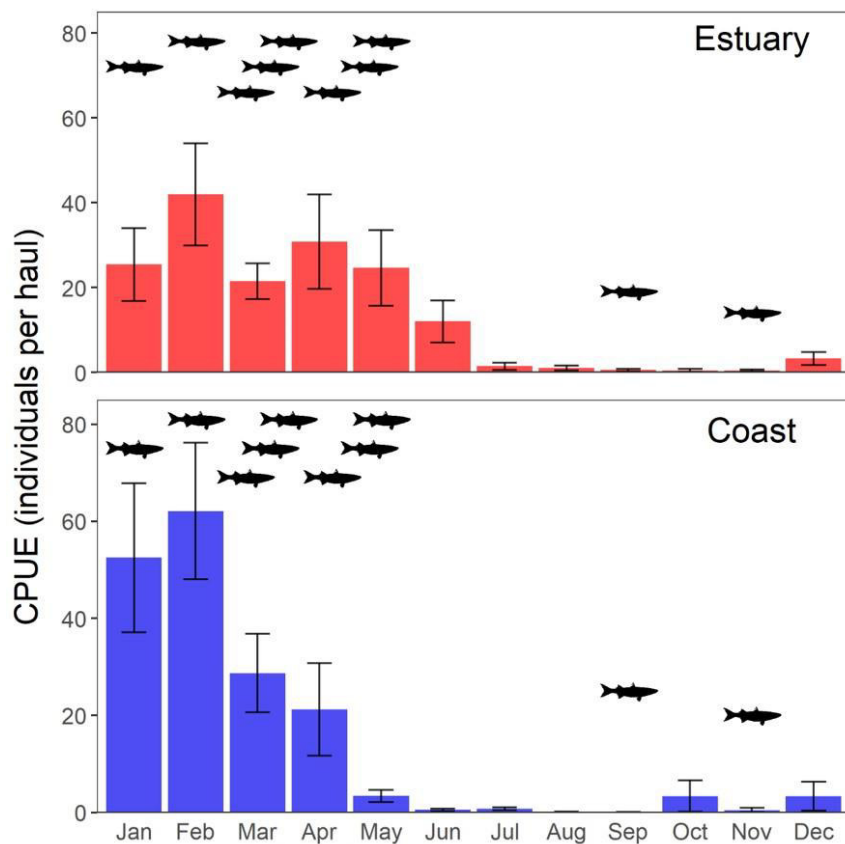


Figure 2. Mean and standard deviation of the abundance of juvenile white mullet (CPUE – catch per unit effort, i.e, individuals per haul) in the Estuary (red bars) and the Coast region (blue bars). Fish icons further depict the periods of high (January to June) and low abundance (July to December).

These results are in agreement with data on the occurrence of the species along the southwestern Atlantic coast obtained from the literature review and the long-term seasonal SST values, which show that white mullet occurs in the extreme south of Brazil only during summer and autumn, when surface water temperatures in shallow areas are higher (Figure 3).

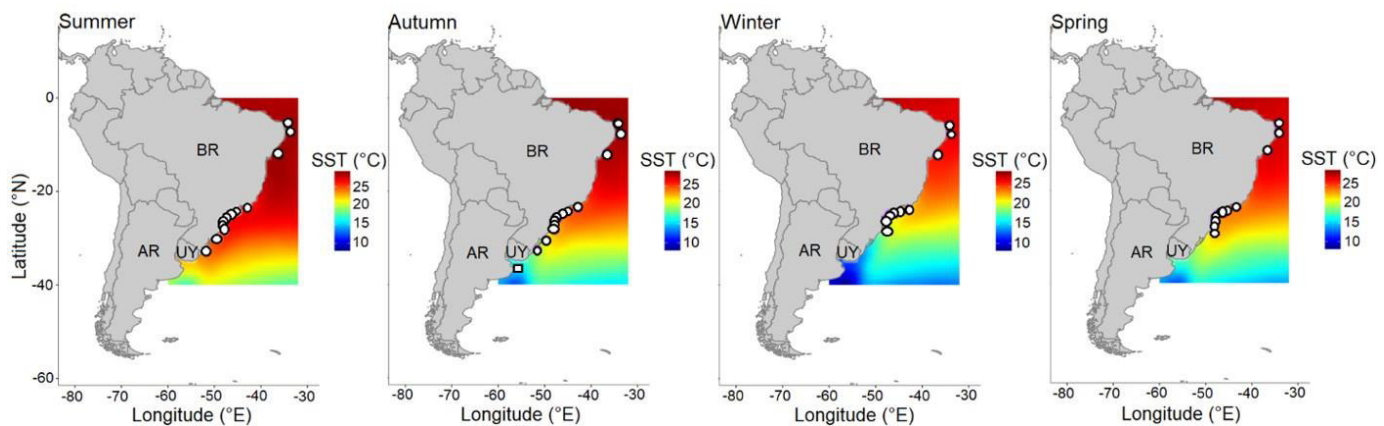


Figure 3. Seasonal maps of surface water temperature along the southwest coast of the Atlantic Ocean obtained by satellite images (1° gridded Hadley ISST dataset) together with occurrence records of the white mullet *Mugil curema* (black circles). The black square in the autumn map represents Argentina, where there is only one record of 6 specimens of the white mullet (Castro et al., 2006).

3.2 Long-term trends in water temperature and abundance

The decomposition of the time series of surface water temperature in the shallow areas of the Estuary and Coast regions revealed marked seasonality and interannual variability (Figure 4A and 4E, respectively). Clear seasonality (Figure 4B and 4F) was observed with higher and lower temperatures in the austral summer and winter months, respectively. The interannual variation in the surface water temperature showed a statistically significant increasing trend through time both in the Estuary ($p < 0.001$) (Figure 4C) and Coast regions ($p < 0.05$) (Figure 4G).

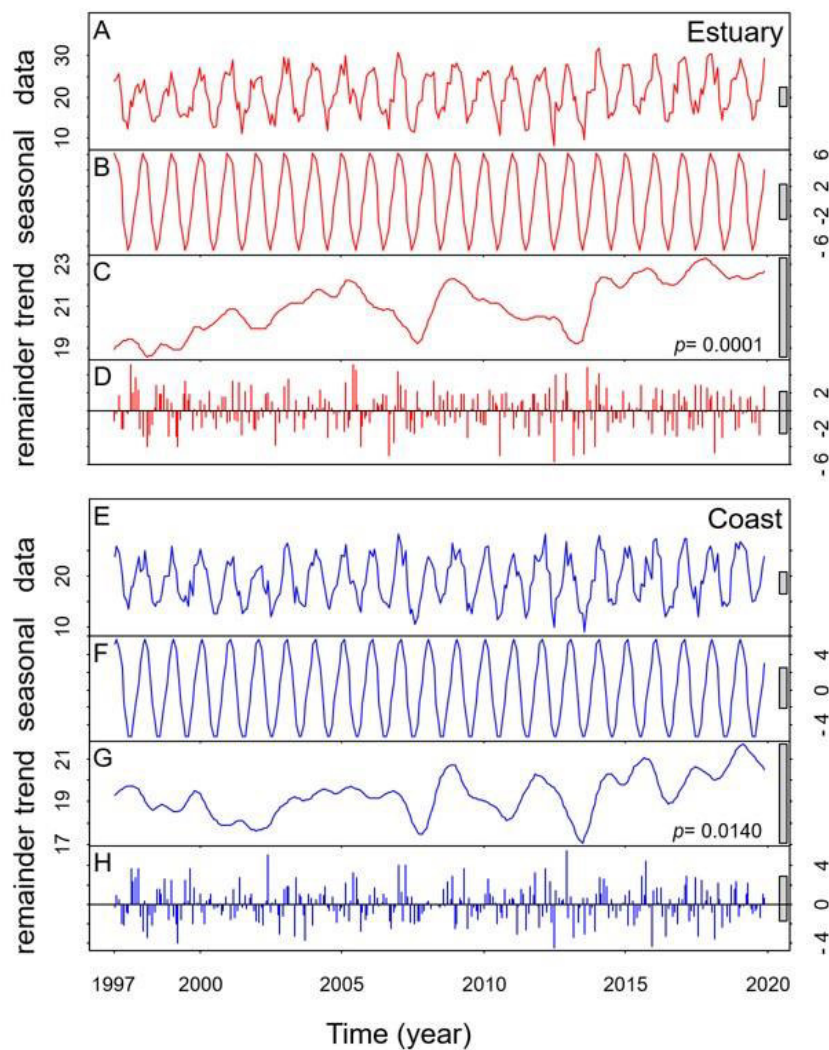


Figure 4. Decomposition of the time series analysis of the (A) surface water temperature from 1997 to 2019 in (B) seasonal, (C) inter-annual and (D) residual components of the Estuary (red lines) and Coast region (blue lines).

The decomposition of white mullet abundance in the high abundance period revealed marked interannual variability in both the Estuary (Figure 5A; left panel) and Coast regions (Figure 5E; left panel). The seasonality component (Figure 5B and 5F; left panel) confirmed the consistent seasonal pattern in the occurrence of the species in both the estuarine and coastal regions, with the highest abundance in February (Figure 2). For the lower abundance period, the time series analysis illustrated the rare occurrence of the species, except for a few conspicuous peaks (Estuary: 1998, 1999, 2004, 2005 and 2015; Coast: 2004 and 2015) (Figure 5A and 5E; right panel). Overall, there was no significant interannual trend in the abundance of juvenile white mullet between 1997 and 2019 for the high or low abundance periods in the Estuary ($p = 0.70$; $p = 0.47$, respectively) (Figure 5C; left and right panel) or the Coast regions ($p = 0.99$; $p = 0.65$, respectively) (Figure 5G; left and right panel).

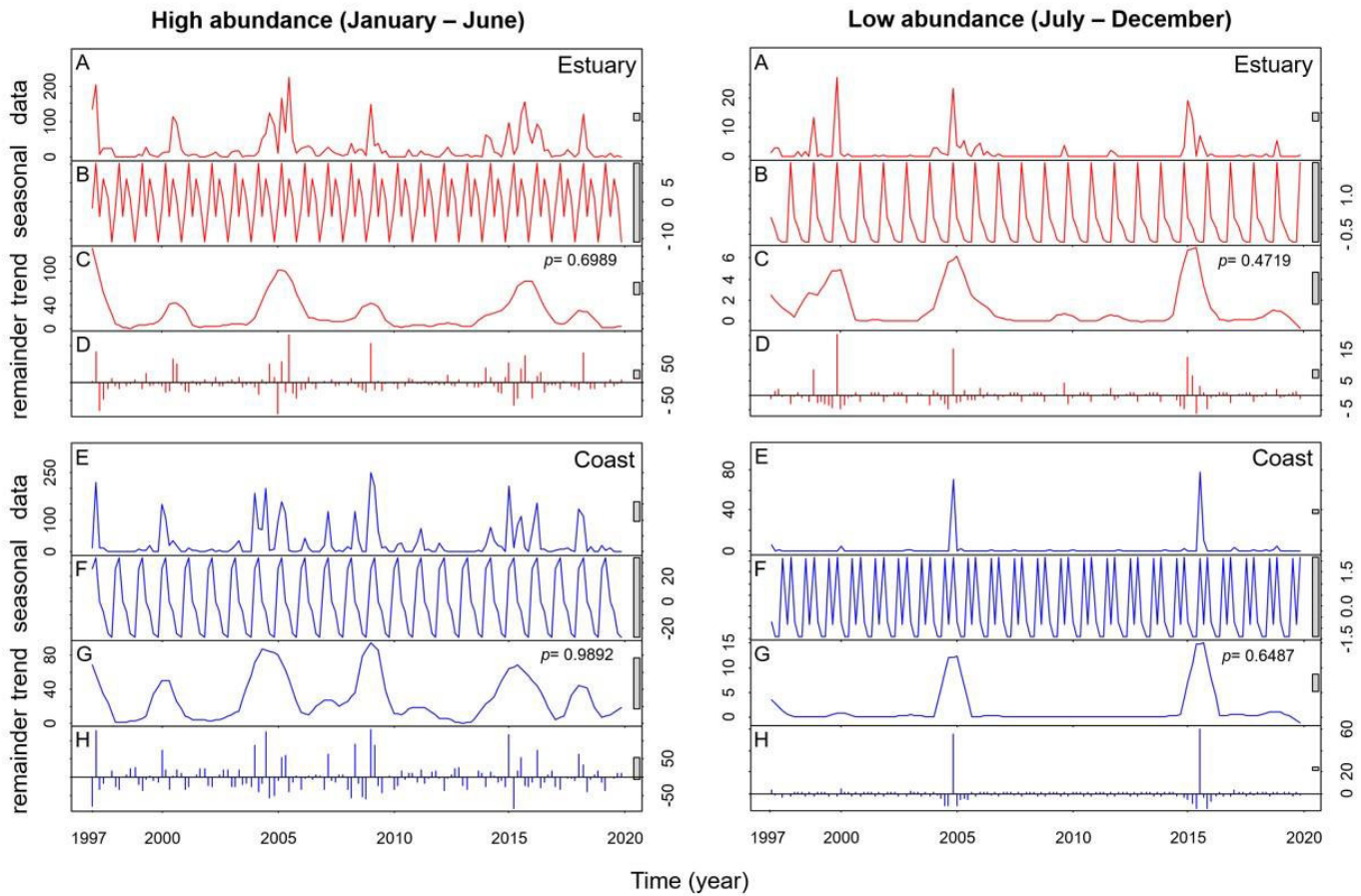


Figure 5. Decomposition of the time series analysis of the (A and E) white mullet abundance from 1997 to 2019 into (B and F) seasonal, (C and G) interannual and (D and H) residual components for the Estuary (red lines) and Coast region (blue lines) during the periods of high (January to June; left panels) and low abundance (July to December; right panels). Note that the y-axis scales are different for the high and low abundance periods.

3.3. Abundance and environmental correlates

The lowest AICc and most parsimonious model revealed that *El Niño*, river flow, surface water temperature and salinity mediated the abundance of white mullet in the Estuary region (Table 1). In contrast, only surface water temperature and river

flow influenced abundance in the Coast region (Table 1) (see Table 1 for all models with $\Delta < 5$ and Figure S4 for information on fit and residuals on models selected). Overall, the best models explained 37.0% and 42.4% of the data variation in the Estuary and Coast regions, respectively (Table 2).

Table 1. Selected generalized additive models with values of the second-order Akaike information criterion (AICc) and the AIC likelihood weights (AICw) for the Estuary and Coast region. Gray shaded lines represent the selected models with the lowest AICc and highest AICw for the Estuary and Coast region.

	Model	AICc	delta	weight
Estuary	s(ONI) + s(Temperature) + s(Salinity) + s(Discharge) + s(Secchi)	1089.44	2.63	0.21
	s(ONI) + s(Temperature) + s(Salinity) + s(Discharge)	1086.81	0	0.79
Coast	s(ONI) + s(Temperature) + s(Salinity) + s(Secchi)	966.29	4.62	0.03
	s(ONI) + s(Temperature) + s(Discharge) + s(Secchi)	965.98	4.31	0.04
	s(ONI) + s(Temperature) + s(Salinity) + s(Discharge)	965.19	3.52	0.06
	s(Temperature) + s(Salinity) + s(Discharge) + s(Secchi)	965.14	3.47	0.06
	s(ONI) + s(Temperature) + s(Salinity)	964.28	2.61	0.09
	s(ONI) + s(Temperature) + s(Discharge)	964.02	2.35	0.10
	s(Temperature) + s(Discharge) + s(Secchi)	963.68	2.01	0.12
	s(Temperature) + s(Salinity) + s(Discharge)	962.86	1.19	0.18
	s(Temperature) + s(Discharge)	961.67	0	0.33

Table 2. Predictor variables selected by generalized additive models (GAM) for each sampling area (Estuary and Coast) for explaining variation in abundance of juvenile white mullet. ONI = Ocean *Niño* Index, Temperature = Surface water temperature, Discharge = River flow in the estuary's drainage basin, df = degrees of freedom and DE = deviance explained (%) of each model.

Sampling area	Parameter	Edf	F-value	P-value	DE
Estuary	ONI	5.306	3.716	0.0016	37%
	Temperature	2.549	6.345	0.0004	
	Salinity	2.476	8.379	0.0000	
	Discharge	2.983	6.255	0.0003	
Coast	Temperature	2.884	32.103	0.0000	42.4%
	Discharge	1.508	7.101	0.0052	

In the Estuary region, the abundance of juvenile white mullet increased with surface water temperature and salinity and, despite a mild increase at low values, abundances decreased with river discharge (Figure 6). The relationship between fish abundance in the estuary and ONI was more complex and non-linear, with a stable trend in abundance for ONI values from -0.5 to -1.7 (i.e., during the colder ENSO phase, *La Niña*) and an increase in abundance in the neutral phases of ENSO (ONI values between -0.5 and 0.5) (Figure 6). In the warmer ENSO phase (*El Niño*), there was a sharp decrease in juvenile fish abundance during weak to strong *El Niño* events (0.5 to 1.6), but the reverse effect with an increase in abundance during strong and in particular very strong *El Niño* events (1.7 to values ≥ 2) (Figure 6). In the Coast region, the abundance of juvenile white mullet increased with increasing surface water temperature and decreased with river discharge (Figure 6).

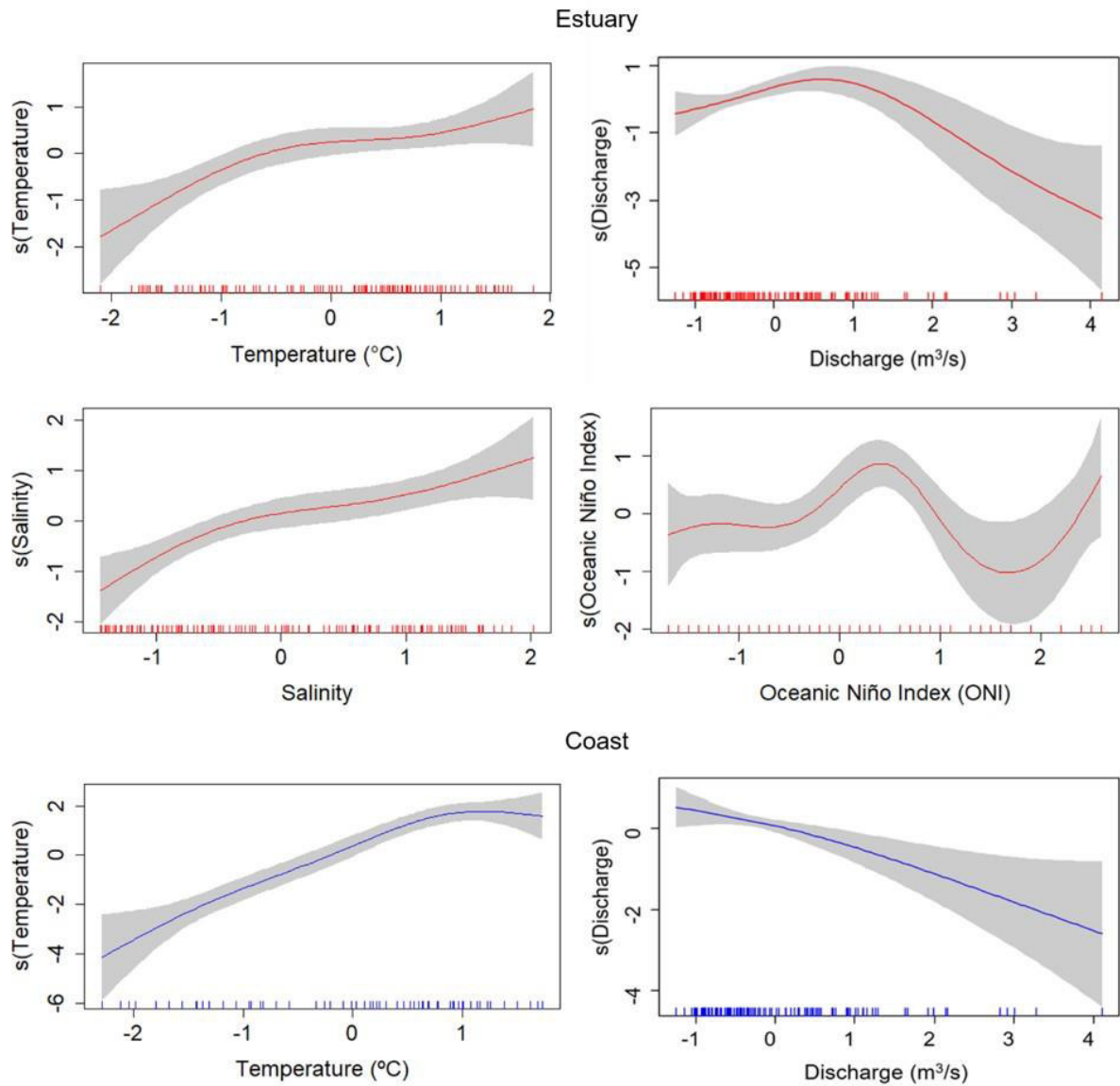


Figure 6. Generalized additive model (GAM) plots showing the partial effects of selected explanatory variables on the abundance of juvenile white mullet in the Estuary (upper panel) and Coast region (lower panel). X-axis are the standardized data with the values scaled to mean zero and then divided by the standard deviations. The y-axis represents the partial effect of each variable. Shaded areas indicate the 95% confidence intervals.

4. Discussion

Our work revealed a significant increasing trend in surface water temperature in shallow waters (<1.5 m) at estuarine and marine sites of a subtropical seascape in the southwestern Atlantic coast (32°S). However, against our initial expectation of a distribution range shift, our 23 years of standardized monthly sampling (1997 to 2019) did not show a clear increase in the abundance of a tropical mullet species (*M. curema*) at this higher latitude, although temperature was positively correlated with white mullet abundance. Our analysis indicates that complex antagonistic interactions among local (temperature, salinity), regional (freshwater discharge) and global (ENSO) factors dampen the expected poleward shift of tropical species.

4.1 Long-term trends in shallow-water temperature but not juvenile white mullet

Our time series analysis corroborated our initial hypothesis of an increasing trend in surface water temperature in the shallow waters (<1.5 m) of the Patos Lagoon estuary and its adjacent marine surf zone. The increase of surface water temperature in the Southwest Atlantic has been estimated through satellite reconstructions or modelling approaches (Ortega et al., 2016; Araújo et al., 2018; Gianelli et al., 2019) or by comparison of model data with historical *in situ* data (Franco et al., 2020b). However, we demonstrate the increase in temperature across the estuarine and coastal seascape using a long-term time series of monthly *in situ* measurements. This warming trend is concerning given that the Patos lagoon is one of the most diverse and productive estuaries in southern South America (Seeliger, 2001; Lemos et al., 2022), and is a key nursery habitat for several commercially important fish species (Haimovici & Cardoso, 2017). Overall, increasing ocean

temperatures together with rising tidal levels can reduce the quality of estuarine habitats, decreasing access and extension of prey-rich habitats, and impacting the recruitment, growth, and survival of juvenile fish (Laurel & Rogers, 2020; Davis et al., 2022), as well as induce changes in estuarine species abundance and composition (Kimball et al., 2020).

In contrast with the observed increasing temperature trend, the analysis of the long-term abundance of white mullet juveniles refuted our initial hypothesis of the species increasing abundance with higher water temperatures. Previous studies had suggested distribution range shifts in the southwestern South Atlantic Ocean associated with warmer water (Izzo et al., 2010; Gianelli et al., 2019; Costa et al., 2021). Aiming to link fish abundance to average monthly sea surface water temperatures (extracted from satellite reconstructions), Araújo et al. (2018) observed a decrease in the abundance of white mullet on estuarine beaches in Sepetiba Bay (22°S, transitional area between tropical and subtropical) and hypothesized a possible southward shift in the population. However, although these authors compiled data in four decades (1980, 1990, 2000 and 2010), the sampling was not continuous or standardized, and there was a lack of further data to validate the suggested range shift. Nonetheless, one study reported the occurrence of six specimens of white mullet in a coastal lagoon in Argentina (37°S) and implied that this could be associated with increased water temperature (Castro et al., 2006) (Figure 3). To our knowledge, this is the only published record of this species so far south, and beyond our study region. Overall, these discrete reports, further highlight the importance of standardized and continuous long-term biological sampling programs linking fish distribution and abundance with environmental parameters to investigate the effects of climate change (Vieira et al., 2022; Cloern et al., 2016). In

particular, it is critical to link environmental change with fish abundance but also disentangle multiscalar effects (from global processes to local factors) and their interaction, i.e., investigating potential effects of global warming together with broadscale climatic phenomena and local environmental variability (Wilbanks & Kates, 1999; Russell et al., 2009; Radinger et al., 2015; Popova et al., 2016). Particularly, as rising temperatures are not the only factor that impact species abundance with others such as salinity, water transparency, freshwater discharge, hypoxia and ENSO events playing a key role (Garcia et al., 2004; Souza et al., 2018; Belarmino et al., 2021; Chermahini et al., 2021).

4.2 Global and local drivers of abundance of juvenile mullets at subtropics

Multivariate responses in the abundance of marine fish to environmental drivers across large time scales are common features (Hansen et al., 2017; Brodie et al., 2021; Salazar et al., 2021), especially in marine migrant species that use estuaries and rivers throughout their life cycle (Garcia et al., 2012; Ward et al., 2015; Erickson et al., 2021). Such complex interplay between biological and physical drivers, which is usually enhanced by non-linear effects of global and local variables operating at distinct time lags (i.e., out of synchrony), poses a challenge when investigating the effects of global warming on fishes (Clews et al., 2010; Moraes et al., 2012). This seems to be the case with juvenile white mullet and the complex and non-linear relationships between abundance and large-scale climate-related (ENSO), regional (rainfall and freshwater discharge) and local factors (water temperature and salinity). More environmental drivers (salinity, surface water temperature, freshwater discharge, and ONI index) influenced species abundance in the estuary than in the

adjacent marine area (surface water temperature and freshwater discharge) which could be related to expected differences in the variability of physicochemical factors between these systems (Day et al., 2012). For instance, temporal and spatial changes in local abiotic factors like salinity are much more marked in the estuary than in adjacent marine surf-zone (Seeliger et al., 1997). Accordingly, our 23 years of *in situ* measurements revealed that salinity values are lower during *El Niño* than *La Niña* and neutral periods inside the estuary, whereas no substantial changes occur in the adjacent marine area (Figure S3). In this sense, species need to cope with the high variability of abiotic factors inside estuaries, while the marine zone offers a more stable habitat with lower physiologic stress.

In both estuarine and marine regions, the abundance of the species was higher with increasing surface water temperature. This higher abundance during warmer months is likely associated with preference for temperatures above 20°C and the higher salinity in the estuary during this period (Vieira, 1991) (Figure 3). River flow in the drainage basin was another factor that influenced the abundance of juvenile white mullet in both regions (i.e., estuarine and coastal), with lower abundance occurring with increasing discharge. In the estuary, *El Niño* events are associated with higher discharge periods, which is associated with a decrease in salinity and subsequent changes in many components of the estuarine biota, from primary producers to top consumers (Odebrecht et al., 2010b; Lanari & Copertino, 2017; Teixeira et al., 2017; Possamai et al., 2018; Belarmino et al., 2021). In addition, prior studies suggest that the high freshwater flow caused by stronger *El Niño* events increases outflow water velocity through the narrow mouth (~700 m wide) of the estuary (Fernandes et al., 2002), which hinders the entrance of juveniles,

such as the mullet species, into the estuary (Garcia et al., 2003; Garcia et al., 2004; Possamai et al., 2020).

In the marine region, increased water discharge from the drainage basin leads to the formation of larger freshwater plumes and enhanced transport of suspended sediments to the inner shelf, as well as contributing to the balance of nutrients in the adjacent coastal plain (Marques et al., 2011; Osadchiev et al., 2020). Freshwater plumes can increase local primary productivity and the abundance of some juvenile and adult fish species nearshore (Kingsford & Suthers, 1994; Smith & Simpkins, 2018). Increases in the abundance of mugilids have been associated with estuarine plumes in southern Brazil (Rodrigues et al., 2015). However, although estuarine plumes increase food availability, they can also lead to decreased abundance of marine fish larvae and be detrimental to growth and individual condition, likely related to higher turbidity and differences in temperature and salinity (Axler et al., 2020).

ENSO had a complex effect on the abundance of white mullet. In the study area, *El Niño* events increase river flow resulting in lower salinity (Figure S3), as well as leading to the formation of a physical barrier that can hinder the entrance of marine estuarine-dependent juveniles into the estuary (Garcia et al., 2003; Garcia et al., 2004). Although the 1997-98 and 2015-16 *El Niño* episodes were very strong (Paek et al., 2017) they had different effects on the abundance, with only the 1997-98 *El Niño* triggering declines in the abundance of white mullet. Both events showed similar strength and evolution (with maximum sea surface temperature anomalies reaching ~2.5°C) but diverged in their decay phase (Lin & Wu, 2019) and the location of the sea surface temperature anomalies in the Pacific Ocean. The 1997-98 event was representative of the Eastern Pacific, while the 2015-16 event was a mixture of the Central and Eastern Pacific types (Paek et al., 2017; Timmermann et al., 2018).

Although the two *El Niño* events are classified as very strong, they caused, for example, distinct anomalies of rainfall, salinity and atmospheric circulation (Paek et al., 2017; Lin & Wu, 2019; Zheng, et al., 2019; de Medeiros & de Oliveira, 2021). These differences in the location of the ENSO anomaly have been shown to affect the abundance of other juvenile fish elsewhere, with the 1997-98 *El Niño* similarly having a more adverse effect on abundance compared with 2015-16 (Lin & Wu, 2019; Belarmino et al., 2021). For example, reductions in precipitation in the Pacific Northwest during the 1997-98 *El Niño* compared with the 2015-16 event, caused a latitudinal change to the salinity front and changes in spawning locations of Japanese eel, as well as decreased recruitment in 1997-98 but increased in 2015-2016 for several species (Lin & Wu, 2019). In the southwestern Atlantic Ocean, the 1997-98 *El Niño* event resulted in higher freshwater input into estuaries compared to the 2015-16 event and may have prevented adults of the Brazilian silverside *Atherinella brasiliensis* from reaching spawning areas (Belarmino et al., 2021), with many individuals also swept out of the estuary due to the increased freshwater discharge (Garcia et al., 2001; Belarmino et al., 2021).

The colder phase (*La Niña*) of the ENSO phenomenon did not influence the abundance of juvenile white mullet in the estuary. The time-series investigated in this study (1997-2019) encompassed several *La Niña* events with differing intensities (Low: 2000-01, 2005-06, 2008-09, 2016-17, 2017-18; Moderate: 1995-96, 2001-12; Strong: 1998-99, 1999-00, 2007-08, 2010-11). *La Niña* events in southern South America have been associated with below-average rainfall and, consequently, lower river flows and higher salinity in the estuary (Grimm et al., 2000; Garcia et al., 2001; Cai et al., 2020), with salinity in the estuary higher during *La Niña* events compared to *El Niño* and neutral events (Figure S3). However, the abundance of juvenile white

mullet was constant regardless of the intensity of these events which is corroborated by the findings of a study on multiple mullet species, including white mullet, that showed no effect of the 1995-96 *La Niña* event on abundances but a significant negative effect of the 1997-98 *El Niño* event (Garcia et al., 2001).

Our findings show that *El Niño* events had stronger impacts on white mullet juveniles than *La Niña* events, but the effects of ENSO warm and cold phases were context-dependent. Globally, *El Niño* and *La Niña* events may be inversely associated with above-average precipitation and droughts depending on the geographical area (Grimm et al., 1998; Ummenhofer et al., 2015; de Oliveira et al., 2022; Nutiprapun et al., 2022). Moreover, the location of the surface water temperature anomaly in the Pacific Ocean and ENSO phase intensities can lead to different climatic and hydrological impacts (Song et al., 2017; Lin & Wu, 2019; Belarmino et al., 2021) and ensuing effects on fish assemblages (Lin & Wu, 2019; Belarmino et al., 2021). The geomorphology of the estuary may influence the abundance of estuarine fish species (Binsong et al., 2014; Hallett et al., 2018). For example, during episodes of excessive freshwater runoff triggered by stronger *El Niño* events, the funneled shape of a subtropical estuary can enhance the flow of freshwater to the sea, amplifying its hydrological effects (Fernandes et al., 2002; Möller et al., 2009). Such interactions highlight the complexity of the effects of *El Niño* and *La Niña* events on local (e.g., salinity and water temperature) and regional (continental water discharge) factors affecting fish estuarine abundance and its potential to mask the effects of poleward shifting tropical fish due to ocean warming.

The observed trend of increasing surface water temperature in the estuary and its adjacent marine region was not accompanied by an increase in the abundance of the tropical-related white mullet at subtropical latitude. We found complex and non-

linear relationships between this species' abundance and large-scale climate-related phenomena, and regional and local environmental variations. Our results demonstrate that species responses to environmental change can be multifaceted and can offset variations occurring at different spatio-temporal scales. The expected effect of rising ocean temperature in increasing the abundance of tropical species towards higher latitudes was counteracted by the cascade of effects resulting from *El Niño* events which ultimately led to decreased fish abundance. Understanding the effects of this complex interplay between global warming and ENSO, together with local conditions, is essential considering that *El Niño* events are expected to increase in both frequency and intensity with climate change (Cai et al., 2018; Freund et al., 2019). Our findings highlight the need to unravel the interactions between ENSO and ocean warming on marine fish species, in particular those that depend on estuaries to complete their life history.

Acknowledgments

We thank Dr. Ana Petry, Dr. André Pessanha and Dr Rogério Vianna for suggestions on the manuscript. SR Vollrath acknowledges the financial support of the National Council for Scientific and Technological Development (CAPES). AM Grimm acknowledges the financial support of the Brazilian National Council for Scientific and Technological Development (CNPq). SE Tanner was supported by Fundação para a Ciência e a Tecnologia (FCT) through CEECIND/02710/2021, UIDB/04292/2020 and LA/P/0069/2020. AM Garcia thanks research fellowship provided by CNPq (Proc. 313008/2021-3). We are also thankful to the Brazilian Long Term Ecological

Research Program (PELD - Pesquisas Ecológicas de Longa Duração) site 8 - Patos Lagoon estuary and adjacent marine region for funding this research.

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Table S1. List of scientific papers containing records of the occurrence of the white mullet in shallow waters along the coast of the southwestern Atlantic Ocean. Latitude of study area and season of occurrence of the species are also shown.

Locality	Latitude (°S)	Season of occurrence	Reference
Rio Potengi estuary – RN, Brazil	05°	Whole year	Oliveira et al., 2011
Mamanguape River estuary – PB, Brazil	06°	Whole year	Medeiros et al., 2018
Rio Vaza Barris estuary – BA, Brazil	11°	Whole year	Araújo & Silva, 2013
Sepetiba Bay – RJ, Brazil	22°	Whole year	Albieri et al., 2010
Santos estuary – SP, Brazil	24°	Whole year	Fernandéz & Dias, 2013
Cananéia – SP, Brazil	25°	Whole year	Fernandéz & Dias, 2013
Atami beach – PR, Brazil	25°	Whole year	Godefroid et al., 2003
Guaratuba Bay – PR, Brazil	25°	Whole year	Pina & Chaves, 2005
Babitonga Bay – SC, Brazil	26°	Summer/Autumn	Vilar et al., 2011
Conceição Lagoon – SC, Brazil	27°	Whole year	Ledo et al., 1993
Tramandaí-Armazém lagoons – RS, Brazil	29°	Summer/Autumn	Vieira et al., 2019
Patos Lagoon estuary/marine surf-zone – RS, Brazil	32°	Summer/Autumn	Vieira, 1991
Mar Chiquita coastal lagoon – BUE, Argentina	37°	Autumn *Only 6 individuals registered	Castro et al., 2006

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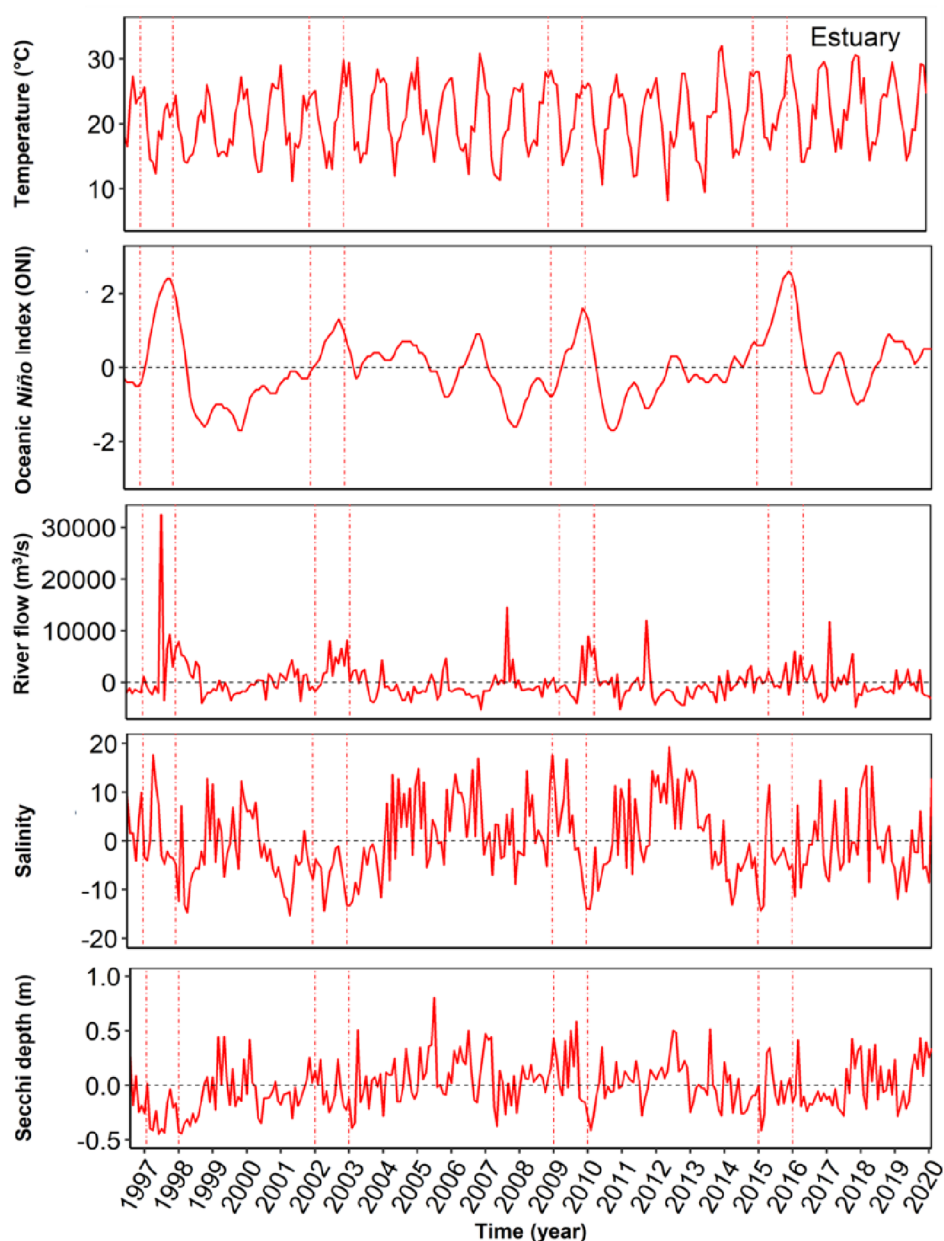


Figure S1. Temporal variation (1997-2019) of average values of surface water temperature (°C) in the estuary, Oceanic *Niño* Index (ONI) corresponding to sea surface temperature (SST) anomalies in *Niño* 3.4 (5°N - 5°S, 120°-170°W) in the Pacific Ocean, anomalies of fluvial flow (m³/s) in the Patos Lagoon basin, anomalies of salinity and water transparency (m) in the Estuarine region. Dashed lines indicate the occurrence of *El Niño* events.

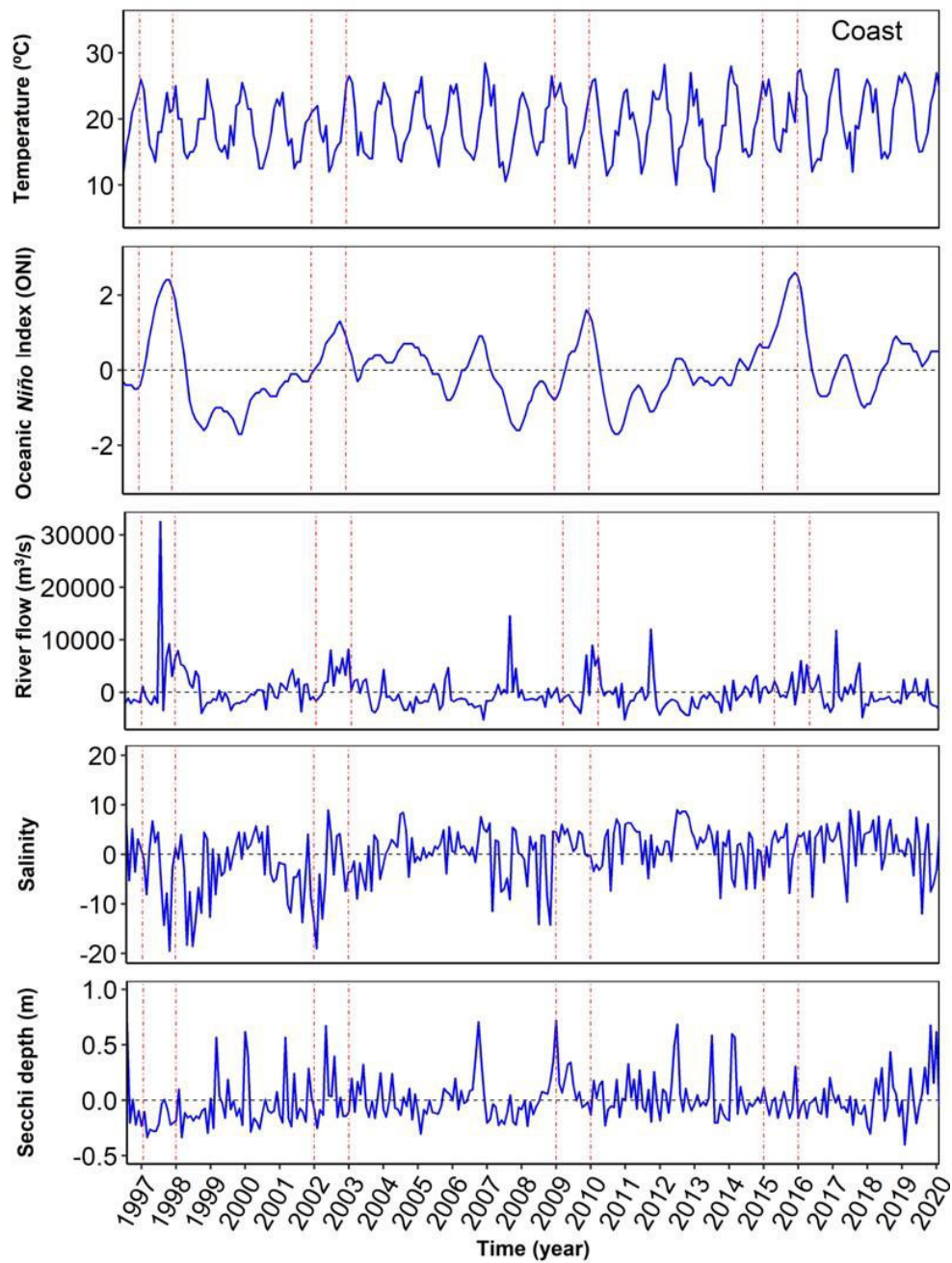


Figure S2. Temporal variation (1997-2019) of average values of surface water temperature (°C) in the Coast region, Oceanic *Niño* Index (ONI) corresponding to sea surface temperature (SST) anomalies in *Niño* 3.4 (5°N - 5°S, 120°-170°W) in the Pacific Ocean, anomalies of fluvial flow (m³/s) in the Patos Lagoon basin, anomalies of salinity and water transparency (m) in the Coast region. Dashed lines indicate the occurrence of *El Niño* events.

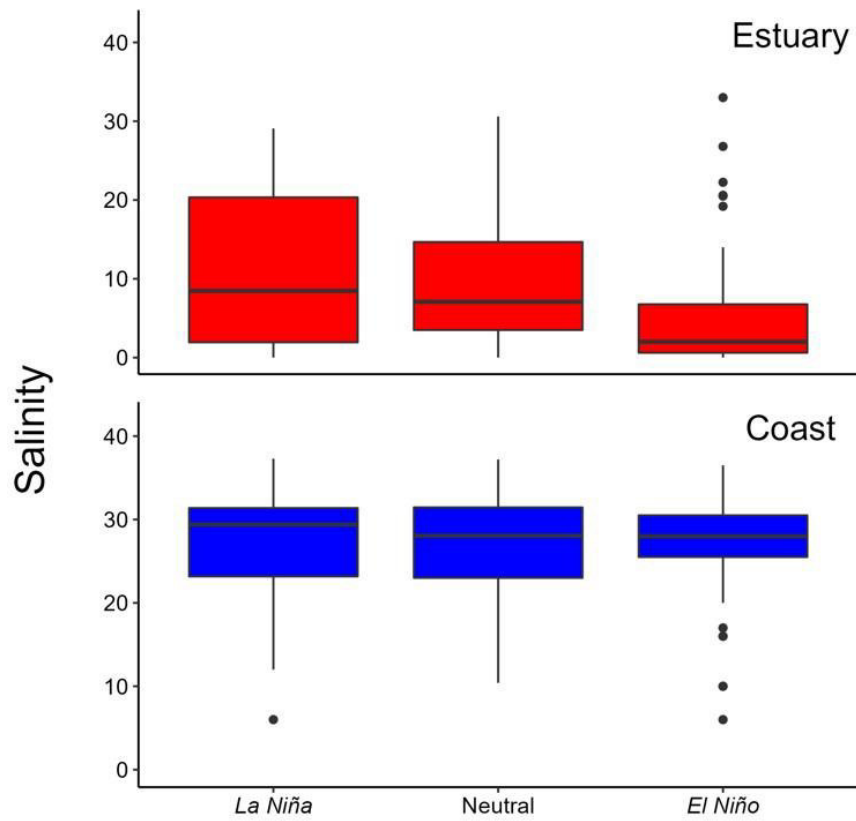


Figure S3. Comparison of salinity in the Estuary (red boxes) and in the Coast region (blue boxes) during *La Niña* and *El Niño* events classified from moderate to very strong ($ONI \leq -1$ and ≥ 1 , respectively) and neutral periods (ONI between -0.4 to 0.4).

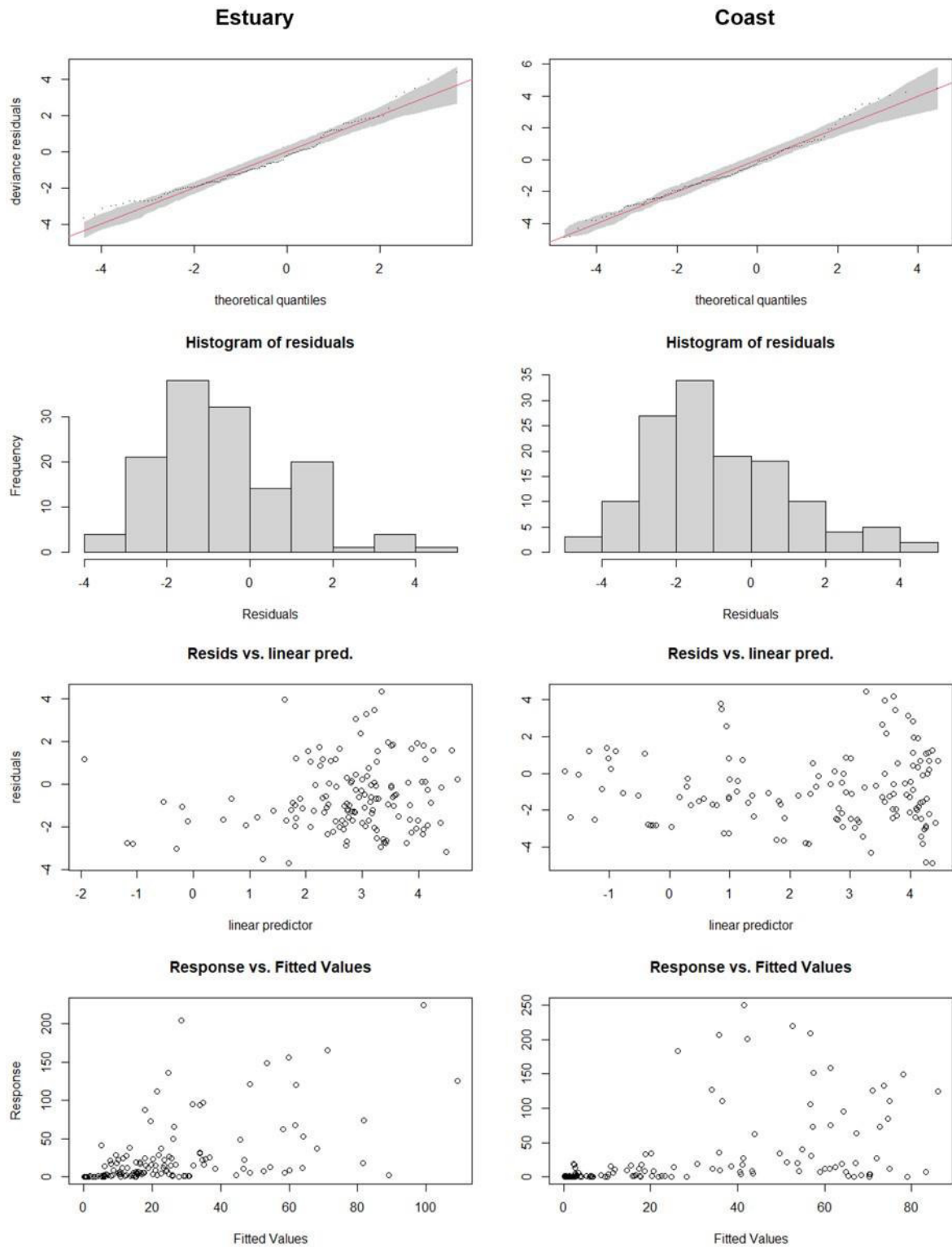


Figure S4. The residuals of generalized additive models for the Estuary and Coast region.

CAPÍTULO 2

Long-term trends in juvenile *Mugil liza* abundance in relation to selected environmental and fisheries influences in southern Brazil

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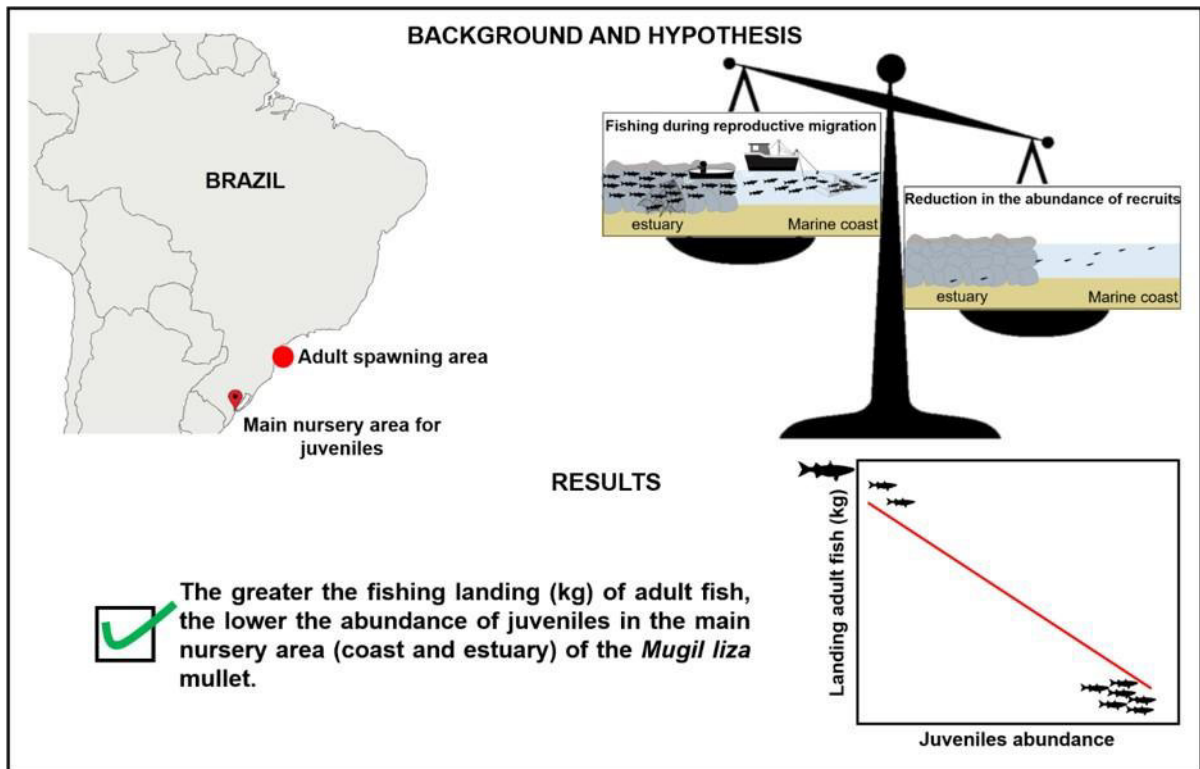
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Este artigo foi publicado na revista *Marine Environmental Research*

<https://doi.org/10.1016/j.marenvres.2023.106290>

Graphical abstract



Abstract

Overfishing constitutes a major threat affecting marine fish population worldwide, including mullet species that have been exploited by fisheries during the reproductive migration in temperate and tropical latitudes for millennia. In the present study, we investigated the relationship of fishing intensity of mullet *Mugil liza* during its reproductive migration and the abundance of their juveniles in an essential nursery ground for the species in the southwest Atlantic Ocean. To carry out this analysis, we used a 23-year standardized long-term time series (1997–2019) of monthly abundance of *M. liza* juveniles, local/regional (water temperature, salinity, water transparency and river discharge) and global (ENSO) environmental factors, along with compilations of fishing landing data for the species. Generalized Additive Models (GAM) revealed the negative effect of fishing adult populations on the abundance of juveniles when they reach the marine surf-zone and after recruiting into the estuary. Our results reinforce the importance of adequate conservation and fishery regulation policies to prevent the species' stock from collapsing.

Keywords: Overfishing; Patos lagoon estuary; Brazilian long-term ecological research (BLTER); GAM models; Coastal waters; Estuaries; Fisheries; Conservation

1. Introduction

Overfishing is one of the most significant drivers of declines in fish populations and can result in reduced biological growth rates, low biomass levels and resource depletion (Roos et al., 2020; Xu et al., 2021; Lucifora et al., 2022). Overfishing also generates negative impacts on the economy, food security and ecosystems (Crespo and Dunn, 2017; Abreu-Mota et al., 2018; Rodriguez et al., 2021). Prior studies have shown that overfishing of sexual mature individuals, especially prior or during their spawning events, can have negative impacts in the abundance of new recruits for several fish population like the Pacific salmon (*Oncorhynchus* spp.) (Munsch et al., 2020), Atlantic cod (*Gadus morhua*), pollock (*Pollachius virens*) (McCain et al., 2016), Spotted Seatrout (*Cynoscion nebulosus*) (Nehemiah et al., 2022), parrotfish (*Scarus trispinosus*) (Roos et al., 2020), and Grey mullet (*Mugil cephalus*) in Taiwan waters (Lan et al., 2014, 2017). In general, these studies pointed out that the synergistic effects of overfishing adult populations and environmental dynamics are important drivers controlling the abundance of new recruits. A better understanding of the complex interplay among these factors is a crucial step to provide empirical-based guidance for planning comprehensive and sustainable fishing management (Pauly et al., 2002; Abreu-Mota et al., 2018; Munsch et al., 2020).

Suitable species models to investigate the relationships among adult fishing exploitation, environmental variability and juvenile abundance in coastal and estuarine zones may be found in the Mugilidae family. Mulletts comprised several species of great ecological and economic importance that has been exploited by fisheries in temperate and tropical latitudes for millennia (Crosetti, 2015). Many species of this family, especially in the set of species collectively denominated “the *Mugil cephalus* complex” (Whitfield et al., 2022), are characterized by their schooling

behavior and their adaption to explore ocean and coastal waters throughout their complex life cycles, which include spawning in ocean waters, recruitment of juveniles in the marine surf zone, and later use of estuaries as nurseries. Their high abundance levels in estuaries have been exploited by several predators (e.g., marine mammals and aquatic birds) as well as sustaining several fisheries (Crosetti, 2015; Santos et al., 2018; Whitfield et al., 2022).

In southwestern Atlantic, one mullet species that has been extensively explored by fisheries is *Mugil liza*, and several authors suggest that there are reasons for concern about the sustainability of the mullet stock (Sant'Ana et al., 2017; Abreu-Mota et al., 2018). In fact, this species has been classified since 2004 as overexploited in the southern Brazilian fisheries (MMA, 2004). *Mugil liza* is a marine migrant estuarine dependent species that reproduces at sea, its larvae drift in the ocean, juveniles recruit to the surf-zone and actively migrate towards estuaries, which are used as feeding areas until they reach maturity (Vieira, 1991; Lemos et al., 2014; Mai et al., 2018). Although there is an artisanal fishery throughout the year in the estuaries, the peak of fishing exploitation, both artisanal and industrial, occurs mainly during their migratory aggregation for reproduction at sea (Lemos et al., 2014). In the last decades, this fishery acquired a high value due to the commercialization of its mature roes considered analogous to caviar, which can reach a value of 40 US\$/kg (IBAMA/ICMBio/CEPSUL, 2007; Haimovici and Cardoso, 2017). Intense fishing before the species' spawning may lead to a decrease in recruits and, consequently, a reduction in the adult stock (Martins et al., 2015; Vieira et al., 2019). For instance, Martins and collaborators (2015) investigated the long-term changes (1996–2012) in juvenile abundance of *M. liza* at the marine surf-zone adjacent to Patos Lagoon Estuary (32°S) and suggest the hypothesis that the decrease in the reproductive

stock and consequent decrease in the recruitment of *M. liza* is related to the increase in fishing effort. However, the authors state that this relationship still needs further investigation because seems to be complex and result of an intricate network of natural and anthropogenic factors.

A common hindrance when investigating the complex relationships between fisheries and its impacts on the recruits is the paucity of long-term standardized time series of fishing captures and, especially, juvenile abundance (e.g., Feyrer et al., 2007). The present study used a 23-year long-term standardized time series (1997–2019) of monthly juvenile abundance of *M. liza* and local, regional and global environmental factors, together with compilations of fishery landing data of *M. liza*, to investigate the effect of fishing in the juvenile recruitment abundance in coastal and estuarine regions in the southwestern South Atlantic Ocean. Based on the expected decline of the adult *M. liza* population, we hypothesize that: (i) there is a long-term declining trend in the abundance of mullet juveniles in their coastal and estuarine nursery grounds and (ii) there is a negative relationship between the number of adult individuals landed during reproductive aggregation and juveniles' abundance in their nursery grounds.

2. Materials and Methods

2.1 Study area

The studied coast region is located at the southern Brazil and is characterized by an extensive sandy coastline of approximately 220 km. This region has varying wave regimes in its marine surf-zone ranging from dissipative and intermediate beaches with a mild average slope (between 1.4° and 1.7°) (Silva et al., 2008). The surface water temperature on the coast has a marked seasonality with higher mean

values in the austral summer (21.8 °C) and lower mean values in the austral winter (13.8 °C) (Garcia et al., 2019). Usually, the salinity is higher in summer-autumn (>27) and lower in winter-spring (<25) due to higher precipitation and increase river flow (Odebrecht et al., 2010; Mendes et al., 2016).

Along this coastline, it is located the Patos Lagoon, which is the largest chocked lagoon in the world with an area of 10,227 km² (Kjerfve, 1986). This lagoon is connected to the Atlantic Ocean through a single and narrow inlet 0.5–3 km in width at its southern end, forming an estuarine area that covers about 10% of the total lagoon area (Seeliger, 2001) (Fig. 1). In this subtropical region, the austral summer and autumn are associated with low freshwater discharge and higher salinity in the Patos Lagoon (Marques et al., 2011, 2014). The opposite pattern is observed during the austral winter and spring, when occurs higher rainfall and freshwater discharge and, consequently, lower entry of oceanic waters into the estuarine area of the Patos Lagoon (Marques et al., 2011, 2014). The ENSO phenomenon can affect the Patos Lagoon estuary. During *El Niño* events there are positive anomalies of precipitation and freshwater discharge causing the estuary to have salinity close to zero for weeks or months (Garcia et al., 2001, 2004; Belarmino et al., 2021). In addition, *La Niña* events are associated with lower rainfall and higher salinity in the estuarine region (Garcia et al., 2001). Thus, ENSO events can affect the abundance of fish species using the Patos Lagoon estuary (Garcia et al., 2001; Belarmino et al., 2021; Vollrath et al., 2023).

There is a highly developed artisanal and industrial fisheries occurring along the coast and estuary of the study area (Haimovici and Cardoso, 2017). In the Patos Lagoon estuary and its adjacent area, *M. liza* is the second most important fishery resource and its capture occurs mainly during its migratory aggregations (Haimovici

and Cardoso, 2017). Inside the estuary, artisanal fishers capture the species with gillnets at the beginning of its reproductive migrations to the coastal waters, where it is caught with gillnets and purse seiners by industrial fishers (Lemos et al., 2016; Haimovici and Cardoso, 2017). Especially in the last two decades, fishing pressure on this species increased due to the high value of its roes (Haimovici and Cardoso 2017). Prior studies have shown a consistent decreasing trend in the abundance of *M. liza* and a high exploitation rate suggesting that the stock is at least fully exploited (Garbin et al., 2014; Sant'Ana et al., 2017; Haimovici and Cardoso, 2017).

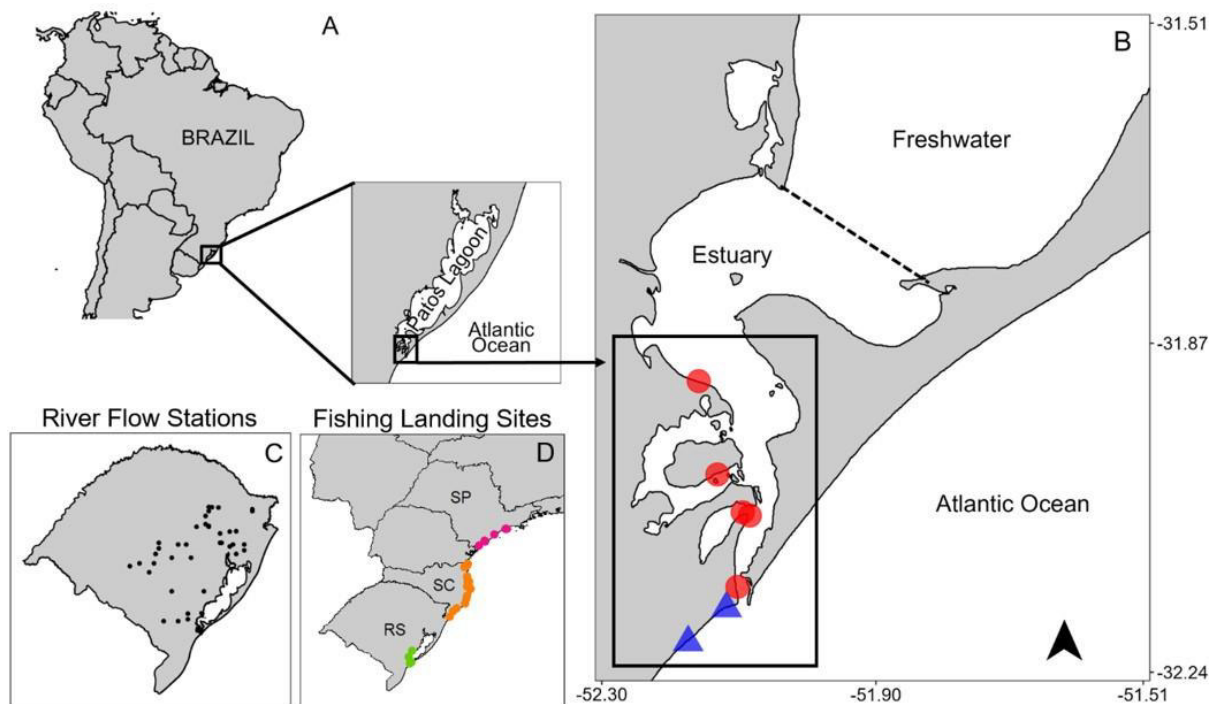


Figure 1. (A) Map of Brazil and the location of Patos Lagoon with (B) the sampling stations on the coast (filled blue triangles, $n = 2$) and estuary (filled red circles, $n = 5$). (C) Map of the southernmost state in Brazil showing the location of the river flow stations along the drainage basin of Patos Lagoon (filled black circles). And (D) the map of the municipalities where landing data (kg) of industrial and artisanal fishing

are obtained in the states of Rio Grande do Sul (RS, green circles), Santa Catarina (SC, orange circles) and São Paulo (SP, pink circles).

2.2 Data collection

Since August 1996, ichthyofauna of shallow areas (<1.5 m) has been sampled monthly at two sampling stations in the marine surf-zone region (hereinafter called 'coast') and at five sampling stations in the estuarine area of Patos Lagoon (hereinafter called 'estuary') (Fig. 1). At the time of sampling, environmental parameters are measured, such as surface water temperature (°C) (thermometer), salinity (refractometer), and water transparency (m) (Secchi disc). This standardized long-term monitoring is carried out as part of the Brazilian Long-Term Ecological Research (B-LTER) program (Odebrecht et al., 2017; Vieira et al., 2022; Lemos et al., 2022). Juvenile fish are sampled with a 9 m beach seine (13 mm mesh in the wings and 0.5 mm mesh in the 3 m center section) and five beach trawl hauls are carried out at each of the seven sampling sites per month. The mean monthly abundance of juvenile *M. liza* was expressed as Catch per Unit of Effort (CPUE). Here, we analyzed the long-term time series of monthly abundance of juvenile mullets in the B-LTER database from August 1996 to February 2020. The remaining months of 2020 and 2021 were not included due to sampling interruptions during the COVID-19 pandemic.

Monthly averages of river flow (m^3/s) (hereinafter called "discharge") were obtained from the Brazilian National Institute of Meteorology (INMET). The Oceanic Niño Index (ONI) values were obtained from the National Oceanic and Atmospheric Administration (NOAA) for the period between August 1996 and February 2020. ONI is the measure of sea surface temperature in the Niño 3.4 region ($5^\circ\text{N} - 5^\circ\text{S}$, $120^\circ\text{E} -$

170°W). Values above and below 0.5 correspond to the occurrence of *El Niño* and *La Niña* events, respectively. The ENSO events intensities are classified as weak (0.5–0.9), moderate (1.0–1.4), strong (1.5–1.9) and very strong (≥ 2.0) (Golden Gate Weather Services, 2023).

Landing data for adult mullet in kilograms (kg) (hereinafter called “landing”) from the southern Brazilian stock (Mai et al., 2014; Lemos et al., 2016) were compiled from five official databases (monthly landing data of artisanal and industrial fishing), which are openly available for consultation between 1996 and 2019 (see Supplementary Table 1). All mullet landing databases were compiled into a single database, in which the monthly landing (kg) was added with the corresponding months and years. Hence, this single database comprised a time series of monthly captures of adult mullets by artisanal and industrial fisheries from 1996 to 2019. For the same period, we have experimental data on monthly abundance of juveniles of *M. liza* on the coast and estuary collected by the B-LTER program.

Ideally, landing data should be tracked by fishing effort to estimate CPUE (caught per unit of effort) and assess the relative impact of fishing (Maccord et al., 2007; Freire et al., 2021). However, it was not possible to compile long-term time series of *M. liza* CPUE. Prior studies highlight that fishing effort data in Brazil are scarce and non-continuous (Sant’Ana et al., 2017), being carried out by several institutions that differed over the years (Sant’Ana et al., 2017; Maccord et al., 2007; Fogliarini et al., 2021; Freire et al., 2021; Machado et al., 2021). Due to the lack of standardization and continuity of such landings databases and their corresponding fishing efforts that would allow estimation of CPUE, some authors argued that other alternative parameters available may be used to allow investigations on fishing trends (Chrysafi and Kuparinen, 2016; Verba et al., 2020; Freire et al., 2021;

Machado et al., 2021). In our study, the alternative available for long-term series was compiling landing data in kg as suggested by Tsikliras et al. (2015), Chrysafi and Kuparinen (2016), Verba et al. (2020) and Freire et al. (2021).

In addition, species that aggregate for reproduction and spawning like *M. liza* (Vieira, 1991; Lemos et al., 2014) may suffer the effect of hyperstability (Lemos et al., 2016), in which the CPUE of the fishery remains constant as the stock decreases, masking the collapse of the fishery (Hilborn and Walters, 1992; Erisman et al., 2011; Sant'Ana et al., 2017). Therefore, Erisman and collaborators (2011) pointed out that CPUE data from fisheries is not the ideal proxy when estimating stock condition in fish that form spawning aggregations. In this scenario, we suggest that the use of fishing landing would be a suitable proxy to evaluate the long-term trends in the relationships between adult fishing and juvenile abundance.

2.3 Data analysis

We used boxplots to observe the distribution over the years (1997–2019) of the juvenile mullet abundances and local (salinity, transparency and temperature water surface), regional (freshwater discharge) and global climatic (ONI index) environmental variables. Regarding the landing data for adult mullets, we tabulated the annual mean and standard deviation from the seven available databases of industrial and artisanal fisheries.

Interannual trends in mullet's juvenile abundance in the coast and estuary regions were investigated using time series analysis, which enabled the decomposition of the components of seasonality, interannual trend and residuals (Crawley, 2012). Time series analysis of juvenile abundance considered all months of the year, using only those years of the time series containing all twelve months

(i.e., from January 1997 to December 2019). The years 1996 (August to December) and 2020 (January and February) were removed from this chart because they had many missing months. The statistical significance ($\alpha = 0.05$) of the interannual trend was tested using linear mixed models with interannual trend as fixed factor and time (months/years) as random factor to control for temporal pseudoreplication. Different models (model 1: seasonal + interannual and model 2: only interannual) were compared using the method of maximum likelihood (Crawley, 2012; Belarmino et al., 2021; Vollrath et al., 2023).

We used Generalized Additive Models (GAMs) to model the relationships between the environmental variables (i.e., temperature, salinity, transparency, freshwater discharge and ONI) and the abundance of juvenile mullets on the coast and estuary considering all months available in the database (i.e., from August 1996 to February 2020). Automated model selection ("MuMIn" package, Bartón, 2023) was used to find the most parsimonious final model with the environmental variables by constructing and comparing models containing all possible combinations of predictors. The best and most parsimonious model was identified according to the values of the second-order Akaike information criterion (AICc) and the AIC likelihood weights (AICcw) (Bartón, 2023).

GAMs were also used to model the relationships between landing and mullet's juvenile abundance in both regions for the same previous period (i.e., August 1996 to February 2020). Landing was introduced in the GAM's environmental variables model in order to avoid loss of explainability and to assess the concomitant effects of environmental and fishing predictors on the response variable. However, the focus of these models was the effect of landing on the abundance of juvenile mullets. Due to the life cycle of the species, in which the adults reproduce in the open sea and the

juveniles drift towards the coast (Vieira, 1991), it is expected that the juveniles will take a certain period of time (probably a couple months) to reach their nursery habitats like, for example, the Patos Lagoon estuary (Lemos et al., 2021). Hence, different models were carried out to test different time-lags (from one to 5 months) between the fishing period of the adults in the sea (i.e., during reproductive migration) and the abundance of juveniles on the coast and estuary.

For all GAMs, the Tweedie error family with log link function was chosen because the response variable (juvenile mullet data) contains several zeros (Shono, 2008). Thin plate regression spline smoothers and k-value at most equal to five were used to perform the models (Wood, 2017; Pedersen et al., 2019). GAMs were fitted using maximum likelihood estimation with the "mgcv" R package (Wood, 2017). The "GGally" R package was used to make a correlation matrix plot using Pearson's method (Schloerke et al., 2021). All environmental covariates were maintained in the GAMs, since Pearson correlations among all environmental variables were ≤ 0.5 . To optimize model convergence, environmental variables were standardized with the values scaled to mean zero and then divided by the standard deviations (Oksanen et al., 2022), with the exception of the variable "ONI" which is already standardized. Considering that the abundance of fish in the estuary presents a delayed response to the climatic and hydrological effects caused by ENSO (Moraes et al., 2012), the ONI variable was considered in the analysis with a time-lag of two months (Belarmino et al., 2021; Vollrath et al., 2023). Residual plots were performed using the "gam.check" function of the "mgcv" package to assess whether the assumptions of the models were met (Wood, 2017). All statistical analyzes were performed in R program (version 4.2.1) (R Core Team, 2022).

3. Results

3.1. Temporal variation in the mullet abundance and environmental variables

Overall, there was much less interannual variation in local variables (especially for salinity and transparency) on the coast (Fig. 2) compared to the estuary (Fig. 3). Furthermore, it was possible to observe that freshwater discharge tended to increase during the same or subsequent year in which the ONI index was higher than 0.5 (i.e., when this index indicated the occurrence of *El Niño* events) (Fig. 4). Finally, there was a marked interannual variability in the juvenile abundance both in the coast and inside the estuary (Fig. 5). The fishing landings of adult mullets vary considerably among years (Table 1). Such complex interannual patterns observed for the abundance (juveniles and landing of adults) and environmental factors precluded a direct observation of the potential influence of the fishery on recruits. Therefore, we employed GAM models to evaluate the concomitant effects of environmental variability occurring at distinct spatial levels (local, regional and global) and the fishery on adult mullets on the abundance of recruits (see subsection 3.3. of the Results).

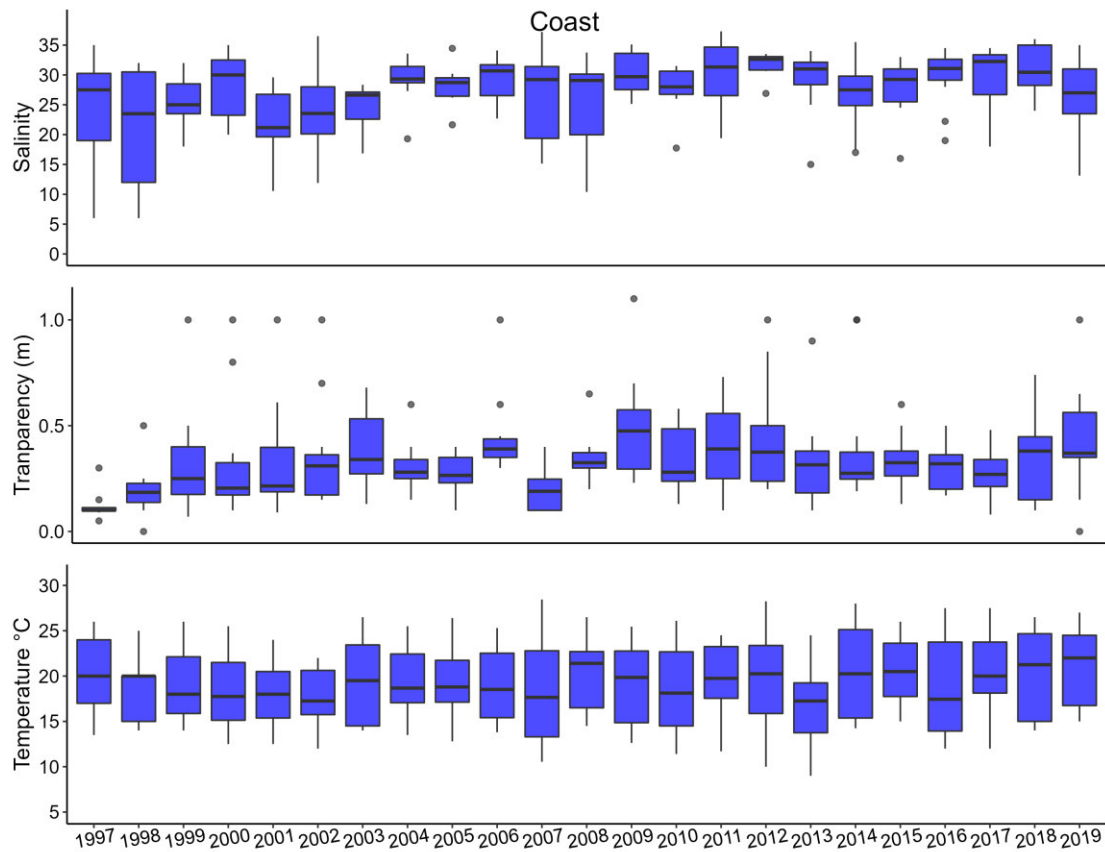


Figure 2. Boxplots of intra- and interannual variation of local environmental variables on the coast. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, vertical lines at the ends of the boxes indicate the minimum and maximum values and the points are the outliers.

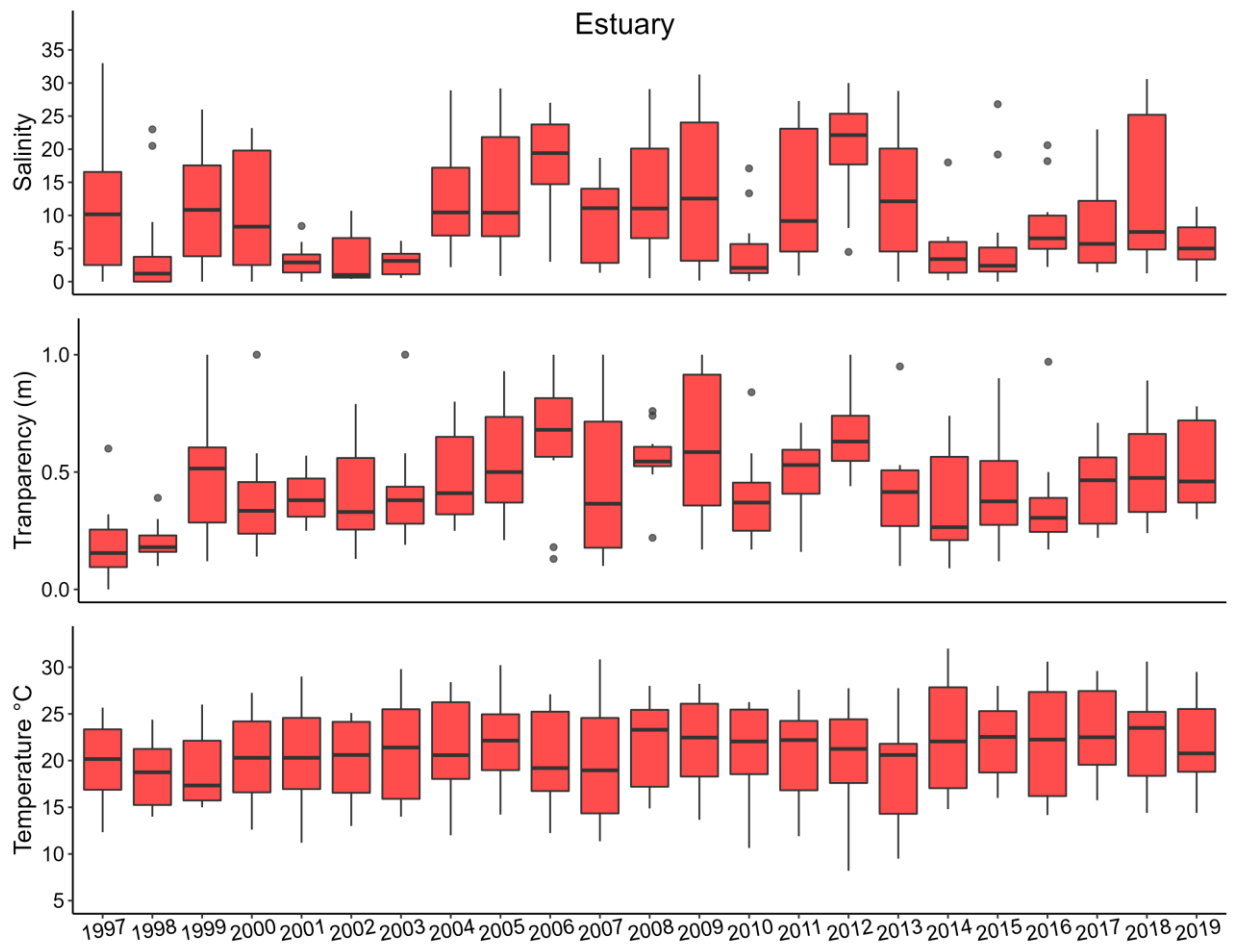


Figure 3. Boxplots of intra- and interannual variation of local environmental variables in the estuary. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, vertical lines at the ends of the boxes indicate the minimum and maximum values and the points are the outliers.

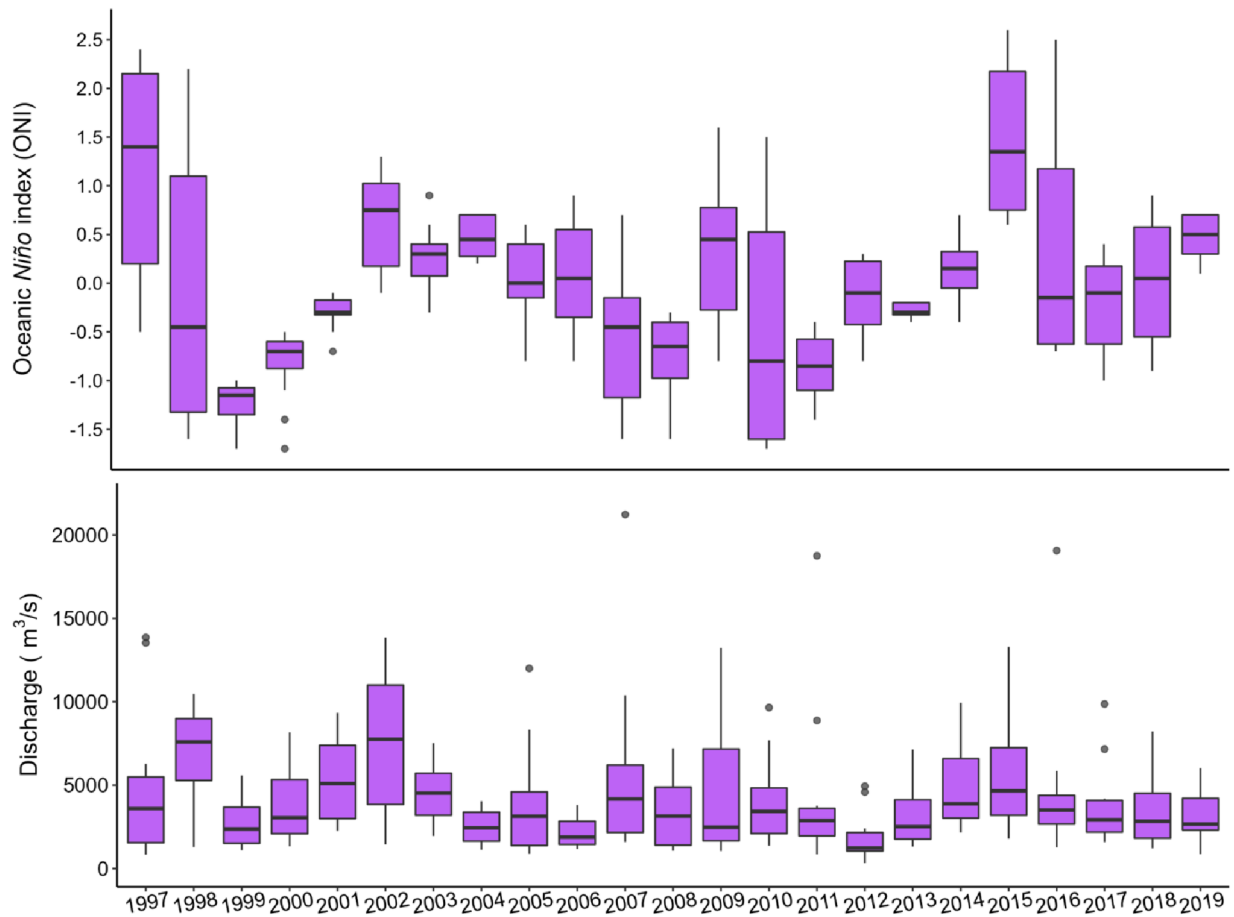


Figure 4. Boxplots of intra- and inter-annual variation of climatic (ONI index) and regional (continental water discharge) environmental variables. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, vertical lines at the ends of the boxes indicate the minimum and maximum values and the points are the outliers.

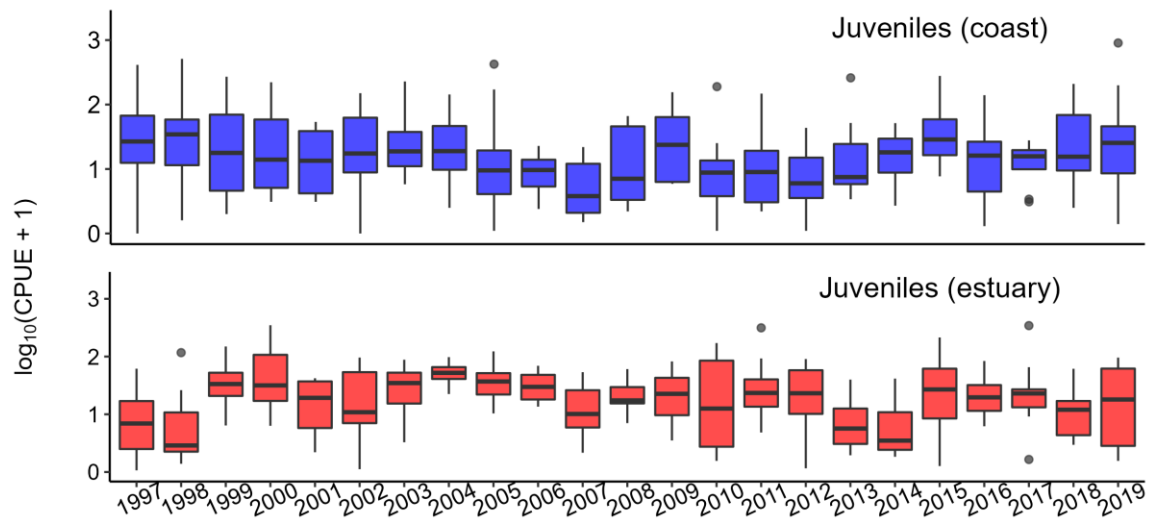


Figure 5. Boxplots of the intra- and interannual variation of $\log_{10}(\text{CPUE}+1)$ of *M. liza* juveniles on the coast (blue boxes) and estuary (red boxes). The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, vertical lines at the ends of the boxes indicate the minimum and maximum values and the points are the outliers.

Table 1. Mean and standard deviation of fishing landings for adult mullets (x 1000 kg). Landing 1= industrial fishing from SC; Landing 2= artisanal fishing from SC; Landing 3= industrial fishing from RS; Landing 4= artisanal fishing from RS; Landing 5= industrial fishing from Patos Lagoon in RS; Landing 6= artisanal fishing from Patos Lagoon in RS; Landing 7= industrial and artisanal fishing from SP (see Supplementary Table 1). SC, RS and SP denote the code for the names of following Brazilian states: Santa Catarina, Rio Grande do Sul and São Paulo, respectively. The “n” indicates the number of months in each year that had landing data for adult mullets.

Year	n	Landing 1	n	Landing 2	n	Landing 3	n	Landing 4	n	Landing 5	n	Landing 6	n	Landing 7
1997	6	242.5 ± 376.9	12	81.1 ± 54.9	12	15.7 ± 40.3	12	74.7 ± 45.4						
1998	9	100.3 ± 211.6	12	68.6 ± 39.9	12	10.5 ± 15.1	12	41.9 ± 20.4				12	19.0 ± 17.0	
1999	10	25.9 ± 53.4	12	8.7 ± 16.5	12	5.3 ± 7.1	12	39.2 ± 36.9				12	15.8 ± 11.0	
2000	11	238.2 ± 501.5	9	59.9 ± 59.9	12	106.3 ± 281.1	12	76.7 ± 101.8				12	18.3 ± 10.8	
2001	9	105.2 ± 187.3			12	28.0 ± 68.8	12	11.1 ± 15.6				12	28.3 ± 40.3	
2002	9	149.8 ± 324.1			12	40.2 ± 90.1	12	13.3 ± 23.6				12	44.9 ± 79.2	
2003	8	310.0 ± 557.6			12	51.8 ± 94.4	12	18.9 ± 17.8				12	32.1 ± 33.6	
2004	6	407.0 ± 649.9			11	50.5 ± 58.9	12	22.2 ± 20.9				12	54.5 ± 90.5	
2005	5	623.1 ± 902.3			12	142.2 ± 276.9	12	37.8 ± 45.1				12	18.7 ± 12.9	
2006	6	180.2 ± 261.2			12	54.9 ± 80.3	12	76.6 ± 178.9						
2007	5	1279.3 ± 1778.8			11	240.2 ± 658.8	12	153.4 ± 198.3						
2008	6	339.7 ± 529.3			11	123.5 ± 214.9	12	69.0 ± 83.6						
2009	6	686.9 ± 1435.6			12	141.4 ± 212.7	12	37.5 ± 31.4						
2010	6	552.3 ± 842.8												
2011	10	282.3 ± 878.3												
2012	8	196.7 ± 358.3							12	22.6 ± 35.9	12	58.0 ± 56.9		
2013	10	122.1 ± 290.5							12	8.1 ± 13.0	12	65.0 ± 55.2		
2014	5	238.2 ± 381.2							12	20.9 ± 61.9	12	18.0 ± 22.9		

2015	2	1002.3 ± 839.4				12	36.1 ± 111.3	12	41.8 ± 43.9
2016	1	839.0 ± 0	5	154.9 ± 17.8		12	15.9 ± 41.0	12	52.1 ± 59.8
2017	2	283.3 ± 307.1	12	415.9 ± 615.3					
2018	1	2973.0 ± 0	12	591.8 ± 699.9					
2019	2	286.2 ± 379.2	12	381.5 ± 247.4					

3.2. Intra- and interannual patterns in juvenile mullet abundance

The time series decomposition of juvenile mullet abundance revealed that the seasonal component in the coast (Fig. 6A; upper panel) was less conspicuous than in the estuary (Fig. 6D; panel below), revealing lower variability across months in *M. liza* juvenile abundance in the coast than in the estuary. No statistically significant interannual decreasing trend in *M. liza* juvenile abundance between 1997 and 2019 was observed on the coast ($p = 0.459$) (Fig. 6B; upper panel) nor in the estuary ($p = 0.910$) (Fig. 6E; below panel).

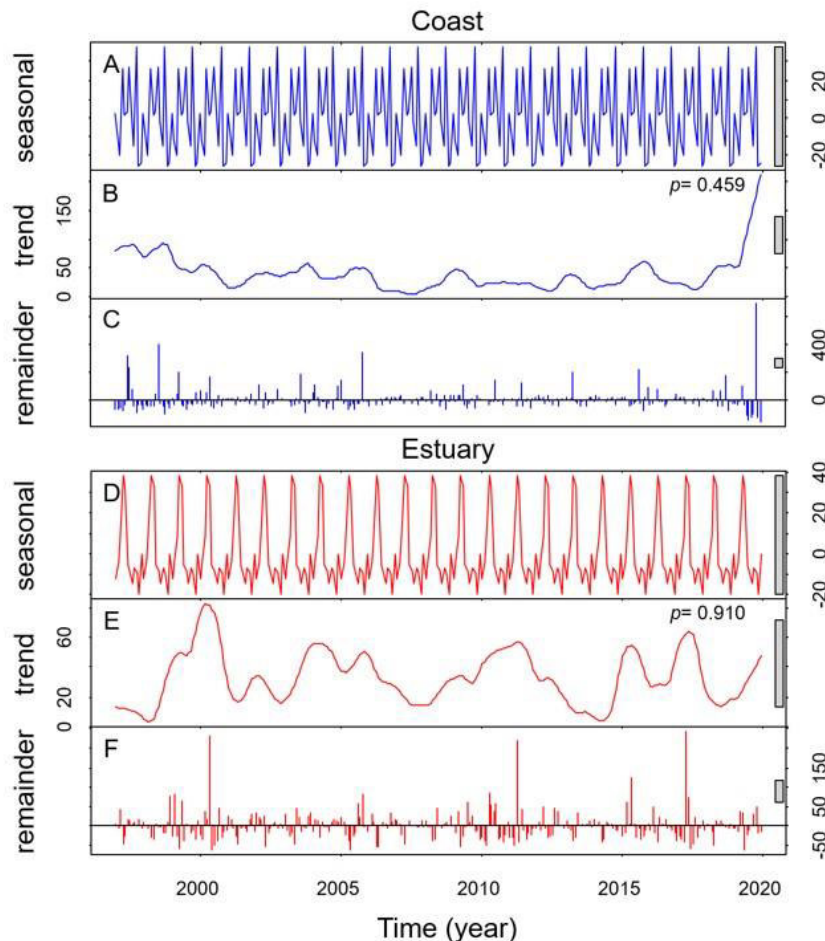


Figure 6. Decomposition of the time series analysis of the abundance of juveniles *M. liza* from 1997 to 2019 for the coast (blue lines) and estuary (red lines). Boxes A and D represent the seasonality of the data. Boxes B and E indicate the trend of the data.

The p values are the results of the linear mixed models that indicate the statistical significance of the trends ($\alpha = 0.05$). And boxes C and F are the residues of the data that were not explained by the analyses.

3.3. Environmental and fishery effects on juvenile abundance

The parsimonious model with the lowest values of the second-order Akaike information criterion (AICc) revealed that only salinity mediated the abundance of juvenile mullets on the coast, however, the model had a low (6.6%) explainability (Table 2). In contrast, temperature, salinity and transparency influenced juvenile abundance in the estuary, resulting in a model with higher explainability (22.8%) (Table 2) (see Supplementary Fig. 1 for information on fit and residuals on models selected). On the coast, the relationship between abundance of mullet juveniles and salinity was non-linear and complex with highest abundance in a few cases when salinity reached its lowest observed values. However, abundance levels remained similar across the remaining salinity range, excepting slight tendencies of increase and decrease abundance when salinity was above its average and when reached its highest values, respectively (Fig. 7). In contrast, relationships between juvenile *M. liza* abundance with the environmental factors showed lesser complex and more linear patterns in the estuary, with an overall positive tendency followed by a stabilization after reaching highest values, especially for temperature and transparency. More specifically, the abundance of juvenile mullets was lower with values below average for salinity, temperature and water transparency, then remains constant with average and above average values, respectively (Fig. 7).

Table 2. Generalized additive models of the influence of environmental variables on the abundance of mullet juveniles on the coast and estuary.

Coast				
Parameter	df	F-value	P-value	DE
Salinity	3.138	3.942	0.0079	
Transparency	1.000	3.600	0.0589	6.62%
Discharge	1.000	2.968	0.0861	
Estuary				
Temperature	3.388	5.744	0.0005	
Salinity	2.839	9.624	0.0000	22.8%
Transparency	3.204	6.262	0.0003	

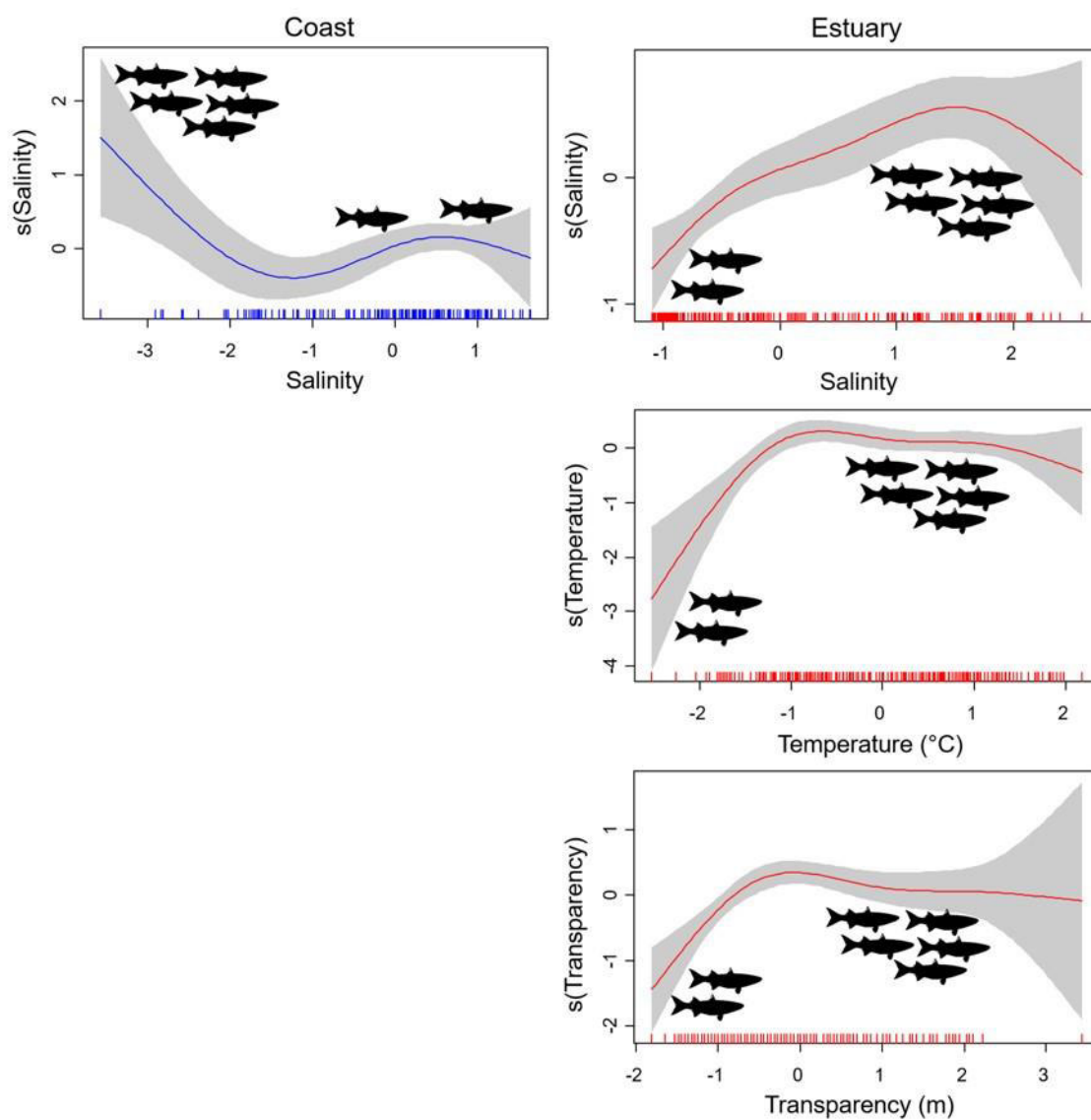


Figure 7. GAM plots showing the partial effects of selected explanatory variables on the abundance of juvenile mullet on the coast (left panel) and estuary (right panel). X-axis are the standardized data with the values scaled to mean zero and then divided by the standard deviations. The y-axis represents the partial effect of each variable. Shaded areas indicate the 95% confidence intervals.

GAM models that include adult landing as predictor showed statistically significant effect of fishing on juvenile mullet both in the coast and in the estuary (Table 3) (see Supplementary Figs. 2 and 3 for information on fit and residuals on models selected). On the coast, the abundance of juvenile *M. liza* decreased significantly with increasing landing with time-lags of one and two months (Table 3; Fig. 8). In the estuary, only time-lag of four months mediated significantly the decrease in the abundance of juvenile mullets (Table 3; Fig. 8).

Table 3. Generalized additive models of the effect of landing adult fish (kg) with different lags (1, 2, 3, 4 and 5) on the abundance of mullet juveniles on the coast and estuary.

Sampling area	Landing	df	F-value	p-value	DE
Coast	Lag 1	2.645	4.378	0.0046	12%
	Lag 2	2.769	4.688	0.0030	11.5%
	Lag 3	1.882	0.484	0.5250	8.07%
	Lag 4	2.871	2.117	0.1658	11.3%
	Lag 5	1.000	1.656	0.1994	9.61%
Estuary	Lag 1	1.000	2.089	0.1497	23.6%
	Lag 2	1.000	0.773	0.3800	24.2%
	Lag 3	1.000	0.012	0.9115	24.5%
	Lag 4	2.970	3.886	0.0074	28.9%
	Lag 5	1.985	1.204	0.2870	23.8%

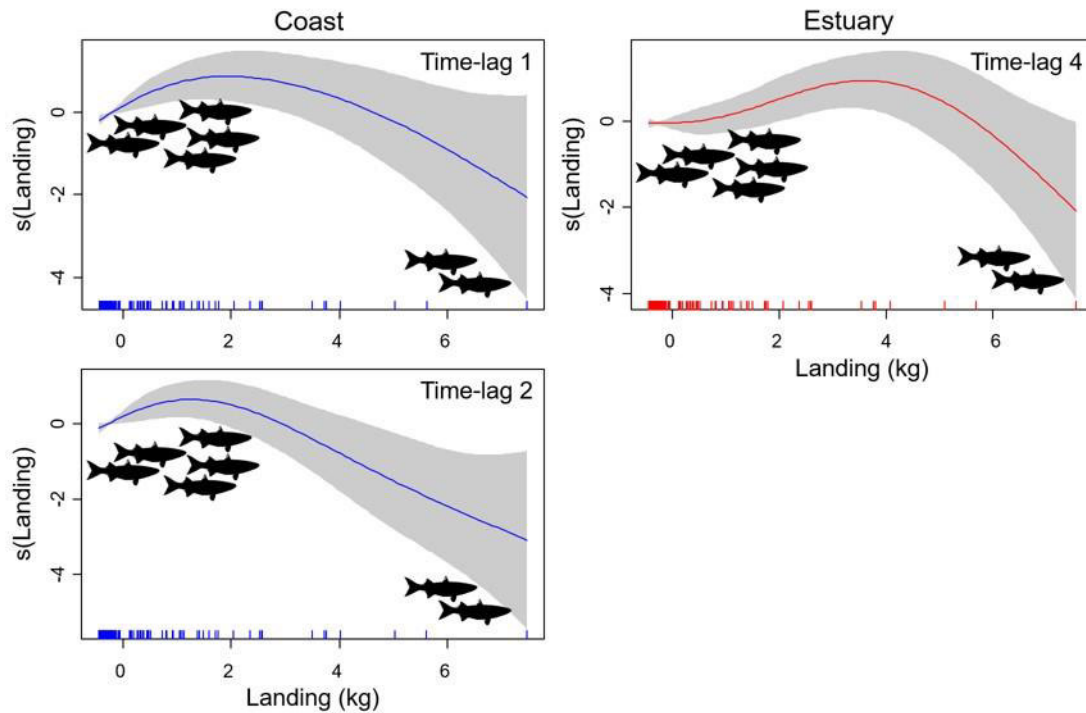


Figure 8. GAM plots showing the partial effects of landing (kg) with different time-lags on the abundance of juvenile mullet on the coast (left panel) and estuary (right panel). X-axis are the standardized data with the values scaled to mean zero and then divided by the standard deviations. The y-axis represents the partial effect of each variable. Shaded areas indicate the 95% confidence intervals.

4. Discussion

4.1. Interannual trend and environmental drivers of mullet juveniles

Regarding long-term trends, our time series analysis did not corroborate our initial hypothesis of declining in abundance of mullet juveniles on the coast and estuary along the studied 23-yrs. Previous studies had suggested an overexploitation of mullet fishing (MMA, 2004; IBAMA/ICMBio/CEPSUL, 2007; Sant'Ana et al., 2017; Haimovici and Cardoso, 2017). In addition, as fishing occurs during the species reproductive aggregation mainly before spawning, it was expected that the abundance of juvenile mullets would be decreasing over the years (Martins et al.,

2015; Vieira et al., 2019). However, it was not possible to see a clear pattern of decrease in the abundance of *M. liza* juveniles over the years either in the coast and inside the estuary. This may be related to influence of environmental variations and/or climatic phenomena that can have positive and negative effects on the abundance of juveniles on the coast and estuary (Belarmino et al., 2021; Vollrath et al., 2023). Therefore, we applied GAM models to investigate how fishing for adult mullet could be affecting the recruitment of juveniles on the coast and estuary after taking into account the potential effects of natural environmental and climatic factors.

On the coast, GAM results revealed that the abundance of mullet juveniles was higher when salinity reached the lowest observed values. In this region, the average salinity was 27.3 (± 6.1). The higher abundance during periods of below-average salinity may be associated with the species' preference for areas with lower salinity, when compared to other sympatric species (e.g., the White mullet *M. curema*) that occur in the region (Mai et al., 2018). Rodrigues and collaborators (2015) observed that salinity is a significant factor for the variation in fish species richness on the coast, but with models showing low explanatory power, as observed in the present study. In addition, they associated the increase in *M. liza* juveniles in this region with the occurrence of the estuarine plume from the Patos Lagoon estuary (Rodrigues et al., 2015), which usually have lower salinity due to input of freshwater discharge in the estuary.

In the estuary, the abundance of *M. liza* juveniles was lower with values below average for salinity, temperature and water transparency. Moreover, the abundance of the species was higher and constant with average and above average values of salinity, temperature and water transparency. Garcia et al. (2003) had already observed that higher abundance of juveniles of *M. liza* (formerly known as *Mugil*

platanus) were associated with mean values of temperature, salinity and water transparency within the estuary.

4.2. Effect of adult fishing on mullet juvenile recruitment

GAMs results corroborated our initial hypothesis that fishing would have a negative effect on the abundance of *M. liza* juveniles in a subtropical region in the southwestern Atlantic Ocean. Considering that the reproductive migration of *M. liza* occurs in the southern states of Brazil (24–26 °S) between April and July, with a peak in June (Lemos et al., 2014), and the highest amounts of adult landing (kg) by artisanal and industrial fishing in the region are during April and July (i.e. period of reproductive migration and before spawning), it was expected that the abundance of recruits in the main nursery area of the species in the southwest Atlantic Ocean had a negative relationship with the fishing of adults (Martins et al., 2015; Vieira et al., 2019). Vieira et al. (2008) have already suggested a decrease in the abundance of both juveniles and adults of *M. liza* in the region.

In the present study, the models with time-lags of 1 and 2 months showed the negative effect of fishing on the recruitment of mullet juveniles on the coast, and only the model with time-lag of 4 months showed the negative effect in the estuary. Vieira and Scalabrin (1991) suggested that recruits took from 2 to 4 months to arrive in the region after spawning at sea. The difference in lag-times duration found on the coast and estuary associated with the effect of fishing on the mullet juveniles' abundance may be related to the life cycle of the species. This is because spawning occurs at sea, larvae and eggs drift to the surf zone by surface currents generated by wind and, finally, they enter estuaries to use them as a feeding and development zone until they reach maturity (Vieira, 1991; Lemos et al., 2014). In other words, juvenile

mulletts arrive and remain for a while first in the coastal region and later enter the estuaries. In addition, the variability in lag-times between 1 and 2 months on the coast may be related to wind. Factors such as wind can influence the arrival and permanence time of recruits in the coast (Bruno et al., 2018). The longshore currents in the study region follow the seasonal wind pattern. Strong winds from the south and southwest predominate between April and August (especially during the passage of cold fronts), causing strong currents towards the northeast (Seeliger et al., 1998). The importance of this wind pattern for the reproductive migration of adult individuals is already known (Lemos et al., 2014). However, during most of the year (September to March), there is a predominance of northeast winds and coastal currents with low intensity but high frequency towards the southwest (Tozzi and Calliari, 2000). These coastal currents can be important for the transport of young mullets along the coast towards the south and their natural variability could help explain the variation in the time lag responses observed in the current study.

Conclusions

Against our initial hypothesis, our long-term (23-yrs) time series analysis did not reveal a significant decrease in the abundance of mullet juveniles of *M. liza* in the coast and estuary of southern Southwestern Atlantic Ocean. However, this finding should be considered with caution because our non-linear models revealed that the abundance *M. liza* juveniles in both regions are influenced by local environmental factors (temperature, salinity and transparency water) and negatively influenced by fishing of the adult stock. Furthermore, our study revealed negative effect of fishing of adult stocks on the juveniles' abundance occurring at different time-lags in the coast and in the estuary. Therefore, if there are no adequate conservation policies and

supervision, the stock of the species tends to collapse. These findings highlight the importance of testing different time-lags when evaluating the effects of fishing on recruitment patterns. Moreover, these results reinforce the importance of long-term time series of standardized in situ sampling of juveniles' abundance and environmental factors in their nursery grounds (Lemos et al., 2022; Vieira et al., 2022) as crucial datasets to reveal the complex long-term effects of fishing on fish populations and to provide sound subsidies for comprehensive and sustainable resource management.

Acknowledgments

SR Vollrath acknowledges the financial support of the National Council for Scientific and Technological Development (CAPES). AM Garcia thanks research fellowship provided by CNPq (Proc. 313008/2021-3). VM Lemos acknowledges the financial support of the Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul - FAPERGS. We are also thankful to the Brazilian Long Term Ecological Research Program (PELD - Pesquisas Ecológicas de Longa Duração) site 8 - Patos Lagoon estuary and adjacent marine coast for funding this research.

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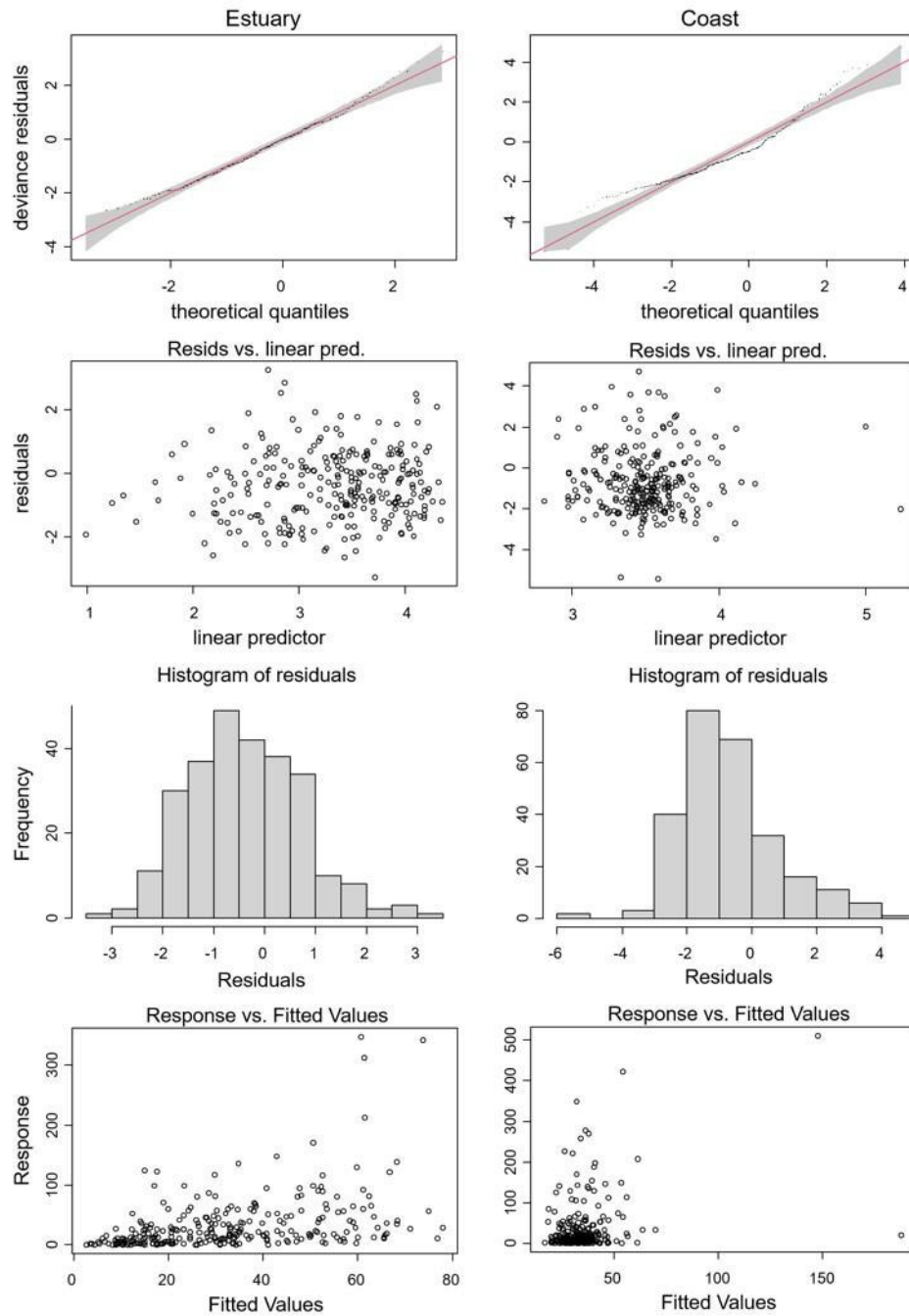
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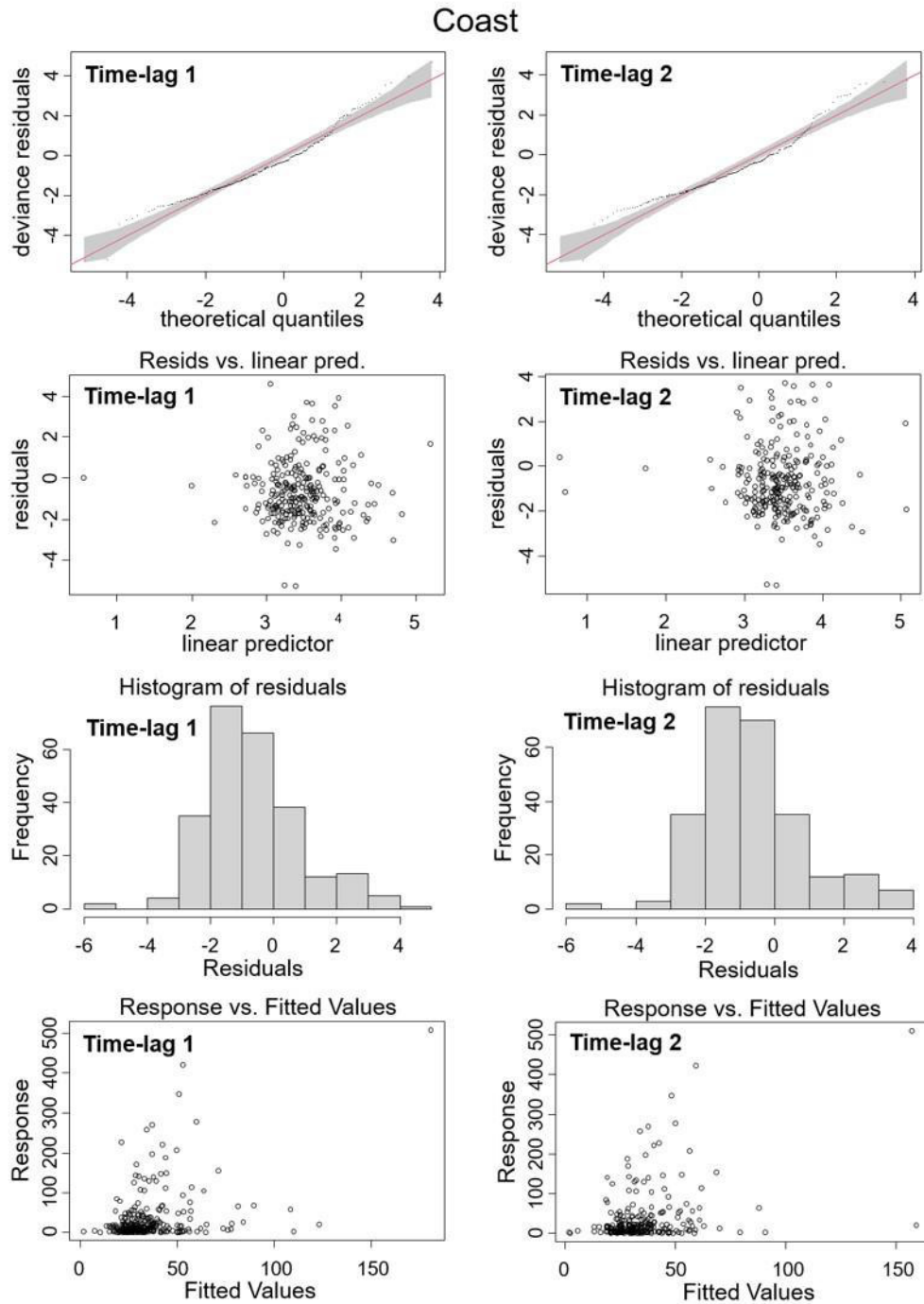
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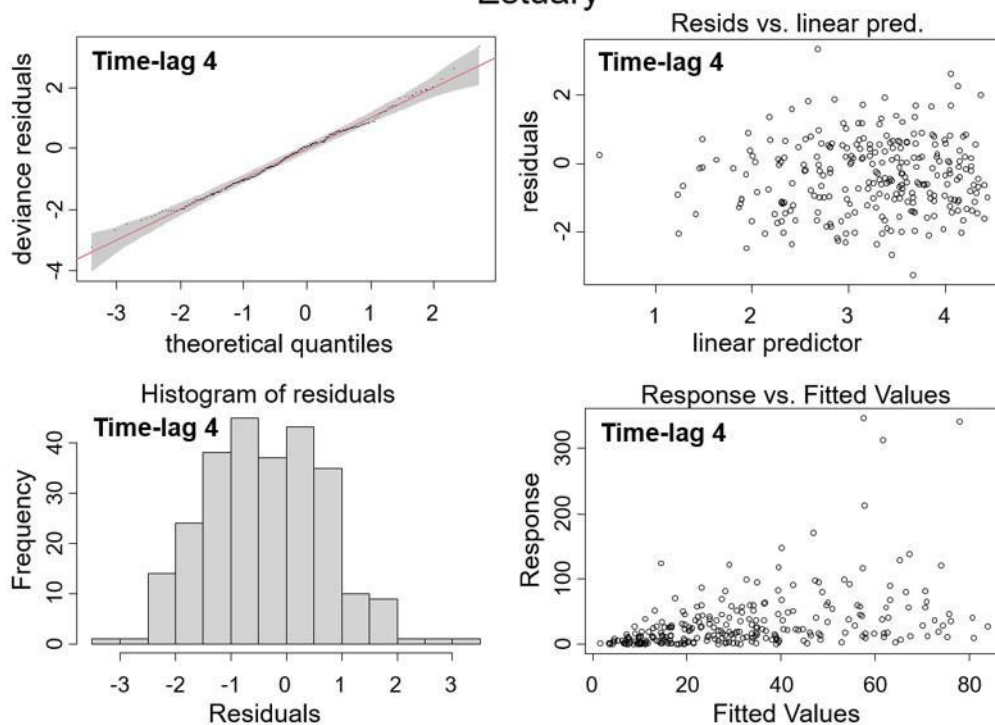


Supplementary Figure 1. GAM residuals for models with relationship between environmental variables and mullet juveniles on the coast (left panel) and estuary (right panel).



Supplementary Figure 2. GAM residuals for models relating landing (capture in kg) with time-lags 1 (left panel) and 2 (right panel) and mullet juveniles on the coast.

Estuary



Supplementary Table 1. Data Source. Databases of mullet fishing landing (capture in kg) occurring along the south and southeastern Brazilian states.

Data Source	Database description (spatial and temporal coverage)	Link
“Projeto de Monitoramento da Atividade Pesqueira em Santa Catarina - PMAP-SC” (UNIVALI/LEMA)	Industrial fisheries database from the state of Santa Catarina from 1996 until 2019.	UNIVALI/LEMA. Estatística Pesqueira de Santa Catarina. Consulta On-line. Projeto de Monitoramento da Atividade Pesqueira do Estado de Santa Catarina. Laboratório de Estudos Marinhos Aplicados (LEMA), da Universidade do Vale do Itajaí (UNIVALI). 2023. Available in: http://pmap-sc.acad.univali.br/ . Accessed on: 10/02/2023.
“Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul” CEPSUL -	Artisanal and industrial fishing database from the state of Santa Catarina from 1993 until 2000.	Informe da Extrativa Marinha em Santa Catarina de 1993 a 2000. Available in: https://www.icmbio.gov.br/cepsul/biblioteca/acervo-digital/38-download/artigos-cientificos/112-

ICMBio		artigos-cientificos.html . Accessed on: 10/02/2023
Fishing landing monitoring program carried out by “Laboratório de Estatística Ambiental - Universidade Federal do Rio Grande” (FURG/LEA)	Artisanal and industrial fishing databases obtained in four cities (Rio Grande, São José do Norte, Pelotas, São Lourenço do Sul) located around Patos Lagoon estuary from 2012 to 2016	Available in: imef.furg.br/o-que-e-o-projeto-estatistica-pesqueira . Accessed on: 10/02/2023
Centro de Pesquisa e Gestão dos Recursos Pesqueiros Lagunares e Estuarinos - Projeto Estatística Pesqueira. CEPERG-ICMBio	Artisanal and industrial fishing database from the state of Rio Grande do Sul from 1997 to 2009.	CEPERG. ICMBIO. Desembarque de pescados no Rio Grande do Sul 1997, 1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007, 2008, 2009. Rio Grande (RS): CEPERG, ICMBIO. Available in: https://www.icmbio.gov.br/cepsul/biblioteca/acervo-digital/38-download/artigos-cientificos/112-artigos-cientificos.html . Accessed on: 10/02/2023
Instituto de Pesca- apta/SAA-SP.	Artisanal and industrial fishing landing occurring along the São Paulo state from 1998 to 2005.	Produção pesqueira marinha do estado de São Paulo. Série Relatórios Técnico São Paulo. Available in: https://www.pesca.sp.gov.br/serie-relatorios-tecnicos . Accessed on: 10/02/2023

CAPÍTULO 3

Temporal change in resource assimilation and isotopic niche of juvenile mullets related to local and remote environmental drivers

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Abstract

Estuaries are areas of brackish water influenced by freshwater from the continent and saltwater from the sea. Local seasonal variations associated, for instance, with temperature and rainfall cycles, and natural climatic phenomena operating at larger interannual scale, such as ENSO events that constitute a remote forcing influencing hydrology patterns worldwide, can affect population dynamics and community composition, including changes in the trophic structure. In the present study, a 12-year time series of seasonal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values of a mullet species (*Mugil liza*) that is a primary consumer in an estuary in southern Brazil was used to evaluate how local environmental variability and ENSO remote climatic effects may affect the use of resources and the isotopic niche of primary consumers. Isotopic values from autochthonous (i.e., estuary) and allochthonous (i.e., freshwater and marine) basal sources were also used to estimate the effects of seasonality and ENSO events on the relative contribution of basal sources to primary consumers. Our results demonstrated that both local environmental variability associated with seasonality and interannual ENSO remote effects on regional hydrology (rainfall and freshwater discharge) affect assimilation of autochthonous and allochthonous basal sources by primary consumers. In addition, this work demonstrates the complexity of evaluating the assimilation of basal sources by primary consumers and the importance of using long-term time series, including seasonal environmental variations and ENSO events.

Keywords: *Mugil liza*; stable isotopes; *El Niño* Southern Oscillation; autochthonous basal source; allochthonous basal sources; trophic connectivity

1. Introduction

Estuaries are ecotones, that is, transition zones, where freshwater from land drainage and saltwater from the sea mix together, making them one of the most biologically productive regions on Earth (Elliott and McLusky, 2002; Kennish, 2002). The dynamism in estuaries abiotic features reflect in different levels of ecosystem organization, from population dynamics and community composition to ecosystem function (Day et al., 2012), including changes in trophic structure (Garcia et al., 2017a; Vinagre et al., 2019; Possamai et al., 2018, 2021). For example, the abundance, species richness and occurrence of algal species, both phytoplankton and microphytobenthos of freshwater or marine origin within the estuary, can be affected on different time scales by winds (hours/days) and freshwater discharge (seasonal/interannual) (Odebrecht et al., 2015; Possamai et al., 2020; Rosa et al., 2023). Therefore, the resources available to consumers vary on different temporal scales and may reflect in their energetic assimilation and role in the food web.

In southern South America, there is a seasonal variation in freshwater discharge to estuarine regions, with a period of low discharge and higher salinity in summer-autumn and higher discharge and lower salinity in winter-spring (Framiñan et al., 1999; Seeliger, 2001; Garcia et al., 2019a; Lanari et al., 2021). Periods of low precipitation or dry conditions in some of these subtropical estuaries can cause nutrient shortages and affect phytoplankton growth in the estuary (Abreu et al., 2010). In contrast, periods with high precipitation, which promotes the entry of freshwater into the estuarine region, are an important mechanism for introducing new nutrients into the estuary, leading to a significant growth of phytoplankton (Abreu et al., 2010). Similarly, hydrology conditions can modify the availability of allochthonous resources to upper trophic levels. During high precipitation, resources of freshwater

origin, such as plants, algae, plankton, and even fish, are pushed to the estuary due to the high discharge, while resources of marine origin are favored introduced into the estuary during low precipitation and windy periods, influencing the diet and energy pathway of estuarine consumers (Garcia et al., 2017b; Possamai et al., 2020).

Climatic phenomena, such as the *El Niño* Southern Oscillation - ENSO, are frequent events that occur approximately at 3 to 5 years and can intensify the effects of meteorological conditions worldwide, including in southern South America (Grimm et al., 1998; Wang et al., 2016; Cai et al., 2020). For example, *La Niña* events are associated with below-average rainfall anomalies, and consequently, lower freshwater discharge and higher salinity in southern South America estuaries (Grimm et al., 1998; Isla, 2008; Possamai et al. 2018). *El Niño* events, on the other hand, present above-average rainfall rates, higher freshwater discharge and lower salinity in the estuary (Grimm et al., 1998). The influence of these events is also observed for the phytoplankton community. Lower chlorophyll-a concentration has been recorded during *La Niña* events and higher concentrations during *El Niño*, which is linked to the depletion of nutrients in marine waters and a higher supply of nutrients from freshwater inflow, respectively (Abreu et al., 2010). However, during strong *El Niño* events, where the precipitation levels may exceed 1.5 folds the annual average, chlorophyll-a levels decrease because of the intense discharge that causes phytoplankton biomass to be washed out of the estuary (Abreu et al., 2010), showing how complex can be these relationships between abiotic factors and biological responses. Benthic microalgae also respond to ENSO events. A seasonal variation in diversity and species richness of benthic diatoms in estuarine areas of this region was associated to ENSO events, and the highest diversity was detected during a

moderate *El Niño* winter (Talgatti et al., 2023). In other words, there is a seasonal variation in these biological components associated with local environmental factors, in addition to interannual variations linked to ENSO remote effects. These two scales of variation can play concomitantly when ENSO events intensify their effects on abiotic factors, which can affect the estuary's primary producers and, consequently, the diet of estuarine consumers at different levels and intensities (Garcia et al., 2017b; Lanari et al., 2021).

Hydrological variation and consequent changes in composition and availability of food resources have an impact on the trophic structure of different ecosystems (Livingston, 1997; Winemiller and Jepsen, 1998; Heng et al., 2018; Possamai et al., 2018; 2020). In floodplains, hydrology plays an important role in connecting habitats during high water season, homogenizing the community, and making terrestrial resources available to aquatic consumers, while in low water periods, these habitats decreased their coverage area, concentrating the aquatic community and increasing the competition for resources (Winemiller and Jepsen, 1998; Heng et al., 2018). In estuaries, river discharge has a strong impact on primary production, which triggers changes in trophic organization in lower trophic levels, indirectly affecting upper levels of estuarine food webs (Abreu et al., 2010; Livingston, 1997; Possamai et al., 2020). Considering climate change has been intensifying the occurrence of extreme climatic events (Freund et al., 2019; Tripathy et al., 2023), understanding how hydrological variation affects lower trophic level organization is key to forecasting changes in resource availability and ecosystem functioning in current and future climate change scenarios.

Stable isotopes of carbon ($^{13}\text{C}/^{12}\text{C}$, expressed as $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, expressed as $\delta^{15}\text{N}$) are used as natural markers that allow estimating the relative

importance of autochthonous and allochthonous food resources in estuarine food chains, as long as they have different isotopic values, because they permit inferring the contribution of each assimilated food source by comparing the isotopic compositions of the sources and of its consumers (Garcia et al., 2007; Garcia et al., 2017b; Possamai et al., 2020; Lanari et al., 2021). However, seasonal and interannual variations in climatic factors, associated with ENSO events, can affect estuary's primary producers, causing variability and overlap in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values of primary producers among different seasons of different years (Lanari et al., 2021). When not considering this variability in producers' isotopic values, researchers may generate erroneous interpretations about the assimilation of resources by estuarine consumers (Lanari et al., 2021). Lanari et al. (2021) highlights the importance of using long-term studies including the interannual effects caused by ENSO events on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values of basal sources to avoid erroneous interpretations about consumer assimilation.

The present study used a 12-year long-term time series (2010-2022) of stable isotope values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from basal food sources (autochthonous and allochthonous) and a primary consumer sampled seasonally to investigate the following hypotheses: (i) the isotopic niche of primary consumers will vary according to the season related to the hydrological period – the isotopic niche breadth during summer-autumn (i.e., dry - lower freshwater discharge) will be smaller in comparison to the more productive winter-spring (i.e., wet - higher freshwater discharge) seasons; and (ii) during *El Niño* events there will be higher availability of allochthonous freshwater resources in the estuary, which will increase the isotopic niche of the primary consumer due to the assimilation of freshwater-derived resources.

2. Materials and Methods

2.1 Study area and species

Patos Lagoon is the largest choked lagoon in the world, covering approximately 10,227 km² (Kjerfve, 1986). The estuarine region covers about 10% of the lagoon's total area (971 km²) and is located in the southern part where the lagoon connects to the Atlantic Ocean by a single and narrow inlet 0.5-3 km wide (Asmus, 1998; Garcia, 1998; Figure 1). This funneled geomorphology reduces the entry of marine water from the Atlantic Ocean and favors the influence of freshwater discharge in this estuary (Asmus, 1998). Freshwater discharge from the drainage basin in the northern part of the estuary can vary between 700–3,000 m³s⁻¹, generally being more intense in winter and spring (Garcia, 1998). In southern Brazil, in years with normal meteorological conditions, summer and autumn are generally associated with low flow of continental water and higher entry of marine waters from the ocean (Marques et al., 2014). In contrast, winter and spring are associated with moderate and strong freshwater discharge conditions that prevent the entry of marine waters into the estuarine region (Marques et al., 2014). The tidal regime has minimal influence in this region, being mainly mixed diurnal with an average amplitude of 0.47 m (Garcia, 1998). However, ENSO events can alter estuary hydrology in southern South America. During years with *El Niño* events, above-average increase in precipitation leads to salinity close to zero in shallow estuarine areas of Patos Lagoon estuary for several weeks or months (Garcia et al., 2004; Grimm and Tedeschi, 2009; Marques et al., 2014; Belarmino et al., 2021). In contrast, years with *La Niña* events have the opposite effect, with below-average precipitation and, consequently, lower discharge of continental water, with an increase in the intrusion of seawater leading to higher salinity in the estuary (Garcia et al., 2001).

One of the most abundant fish species in Patos Lagoon estuary is the mullet *Mugil liza* Valenciennes, 1836 (Mai and Possamai, 2022). This mullet is a marine migrant estuarine dependent species that reproduces at sea, the eggs and larvae drift towards the coast, where the juveniles enter the estuaries to use them as feeding and growth zones until they reach maturity (Vieira, 1991; Lemos et al., 2014, Mai et al., 2018). When juvenile mullet is in the marine region, they feed mainly on plankton (Vollrath et al., 2021). Upon entering the estuary, they change their diet, mainly assimilating detritus and microphytobenthos (Vollrath et al., 2021). In both regions, the predominant microalgae in the species' diet are diatoms (Vollrath et al., 2021), which makes the species a good model to evaluate changes in lower trophic level organization related to hydrological variation in the estuary. In addition of the ecological relevance of juveniles in the shallow waters (< 2 m) of Patos Lagoon estuary (Vieira, 1991, Vollrath et al., 2023), adult forms of *M. liza* constitutes an important source of economical incoming for artisanal fishers in this subtropical estuary (Haimovici and Cardoso, 2017; Vollrath et al., 2024).

2.2 Data collection

Sedimentary particulate organic matter (herein 'SOM estuarine') that can be considered a proxy for microphytobenthos and organic detrital matter in sediments and constitutes the main food source for juvenile mullets, as revealed by prior studies using stomach content and stable isotope analyses (Garcia et al., 2018; Vollrath et al., 2021), was chosen as a representative autochthonous food source of the estuary. This autochthonous source and juvenile mullet *M. liza* individuals were sampled seasonally in a shallow bay (< 2 m) of Patos Lagoon estuary from 2010 until 2022 by

the Brazilian Long-Term Ecological Research program (B-LTER; Garcia et al., 2020), with the exception of 2020 due to the COVID-19 pandemic (Figure 1). The SOM estuarine was obtained by removing the top 2 cm from the surface of the sediment using a core (10 cm diameter). The juvenile mullets were collected using beach seine hauls (13 mm mesh size in the wings and 5 mm in the center of the net).

In addition, allochthonous food sources represented by suspended particulate organic matter (POM: a proxy for phytoplankton and organic matter in the water column; Vollrath et al., 2021) and SOM from the marine and freshwater regions adjacent to the Patos Lagoon estuary also were sampled (Figure 1). The POM offshore was obtained in November 2014 and December 2014 in the coastal area (6 samples) outside the influence of the estuarine plume (Possamai et al., 2020; Figure 1). POM surf-zone was collected in marine locations adjacent to the Patos Lagoon estuary in January, February and March 2018 (nine samples) (Vollrath et al., 2021; Figure 1). In addition, the POM and SOM freshwater were collected during the spring of 2009, summer of 2010 and winter of 2011 in freshwater regions of Patos Lagoon (15 samples) (Possamai et al., 2020; Figure 1). POM was obtained by filtering 0.25-1.00 L of water onto a pre-combusted (450°C for 4 h) Whatman glass fiber filter (0.75 μm). Although we did not collect allochthonous sources in all seasons, the use of these data is justified by the smaller variation in isotopic values of marine and freshwater POM compared to the estuarine (Bouillon et al., 2011; Rosli et al., 2017).

Field collections were carried out near the end of each season considering that the isotopic composition of the muscle tissue of juvenile mullet *M. liza* was derived from food assimilated during the previous months corresponding to each season, being in average 68 and 60 days for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively (Oliveira et

al., 2017). All samples were stored in plastic bags, packed in ice for transportation, and stored in a freezer in the laboratory until processing.

In the laboratory, all samples were processed following standard procedures (Garcia et al., 2007; Hoeinghaus et al., 2011). After thawing the samples, the muscle tissue was removed from the anterodorsal region of juvenile mullet. Samples of muscle tissue and food sources were washed with distilled water, placed in separate sterile Petri dishes, and dried in an oven at 60°C for 48 h. The dried muscle tissue samples and SOM were ground to a fine powder with a mortar and pestle, and the POM was scraped from the most superficial layer of each filter. Subsamples were weighed (between 0.6-0.7 mg for muscle tissues, 10.0 mg for POM and 20.0 mg for SOM) and pressed into ultra-pure tin capsules (Costech Analytical Technologies, Valencia, CA, USA). The analysis was performed using a continuous flow isotope ratio mass spectrometer (EA-IRMS) at the Analytical Chemistry Laboratory of the Institute of Ecology, University of Georgia and at the Analysis Center of the Federal University of Rio Grande (CIA-FURG). Certified standards were used for every twelve samples for calibration. Stable isotopes results are reported as parts per thousand (‰) differences from a corresponding standard (Vienna PeeDee Belemnite for carbon, and nitrogen in air for nitrogen): $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where $R = {}^{15}\text{N}/{}^{14}\text{N}$ or ${}^{13}\text{C}/{}^{12}\text{C}$. The standard deviations for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ obtained from replicate analyses of certified standards, which were analyzed with each sequence, were 0.07‰ and 0.28‰, respectively. We compared interlaboratory measurements by analyzing replicates ($n = 24$) measured in both laboratories. The mean differences for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between laboratories were small (0.26 and 0.28‰, respectively).

Salinity, transparency (m) and water surface temperature (°C) in shallow areas of the Patos Lagoon estuary (5 sampling locations) were obtained monthly by the

Brazilian Long-Term Ecological Research program (B-LTER; Vieira et al., 2022; Figure 1). To estimate the average values of these environmental parameters for each season, a 3-month average was taken for summer (January-March), autumn (April-June), winter (July-September) and spring (October-December) of each year. In addition, the monthly values of river flow (m^3s^{-1}) in the Patos Lagoon drainage basin were provided by the National Water Agency (ANA, 2018). The discharge for each season was calculated as a sum of the monthly average flow (m^3s^{-1}) of the three months that represent each season. The occurrence of monthly *El Niño* Southern-Oscillation events (i.e., *La Niña*, Neutral and *El Niño*) was obtained from the National Oceanic and Atmospheric Administration (NOAA). ENSO events that occurred within 2 or 3 months within the season were considered representative of each season.

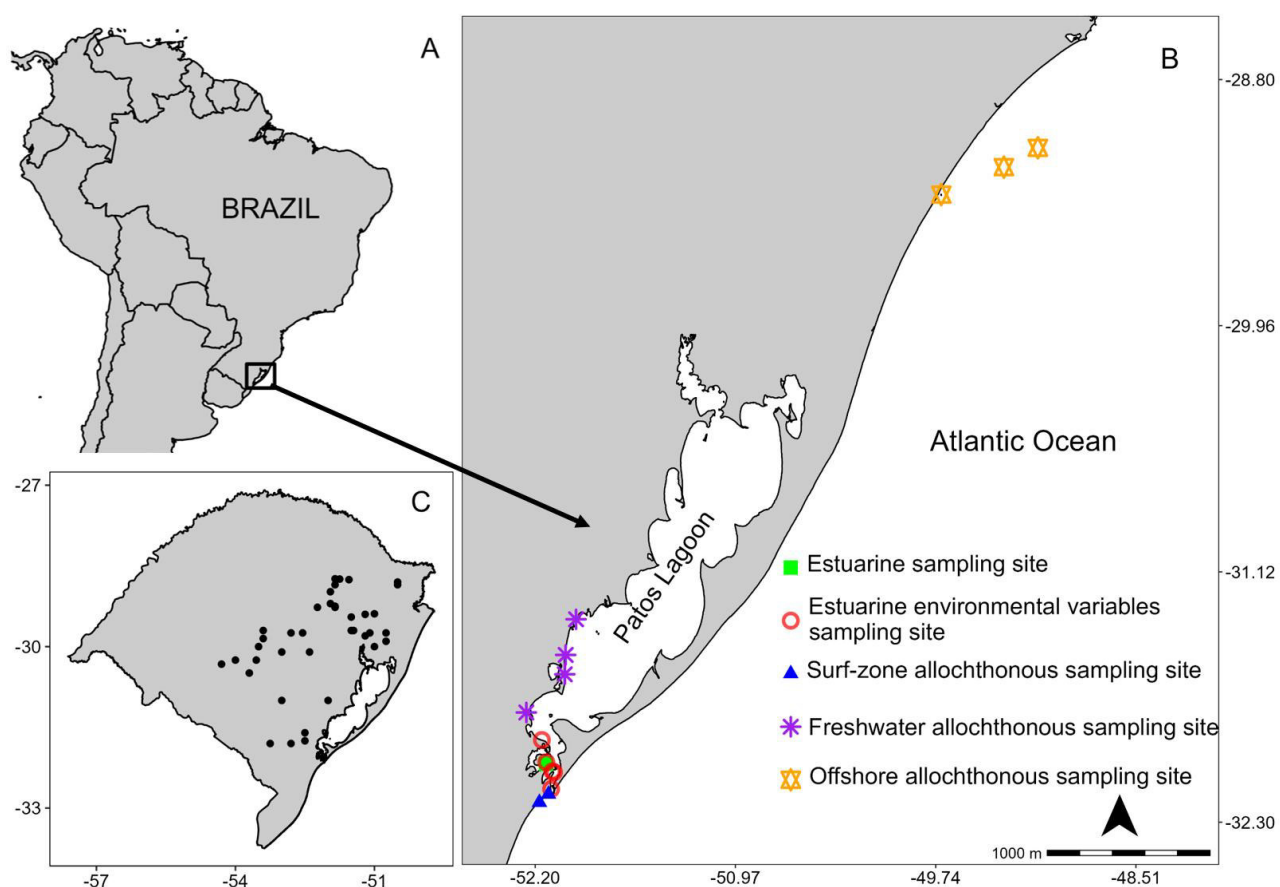


Figure 1. (A) Map of Brazil and (B) location of Patos Lagoon and the fish sampling sites and estuarine basal sources (green square), freshwater (purple asterisk), surf-zone (blue triangle) and marine (orange star) allochthonous basal sources, in addition to sampling sites for temperature, salinity and water transparency in the estuary (red circles). (C) Map of the southernmost state of Brazil showing the location of stations that measure continental water discharge along the Patos Lagoon watershed (filled black circles).

2.3 Data analysis

To estimate the isotopic niche widths and niche overlaps of juvenile *M. liza* among ENSO events (*La Niña*, Neutral and *El Niño*) and seasons (summer, autumn, winter, spring), the corrected standard ellipse areas (SEAc) were computed using the SIBER package (Stable Isotope Bayesian Ellipses) in the R program, considering the default option of 40% of the data variability within each ellipse (Jackson et al., 2011; Jackson, 2023).

The relationships among local (i.e., salinity, transparency, and water temperature), regional (i.e., continental water discharge), and global (i.e., ENSO) driving factors and the isotopic niche breadth (i.e., SEAc) of juveniles of mullet *M. liza* were investigated by a Generalized Additive Model (GAM). The Gamma error family with log link function was used in the modeling (Pedersen et al., 2019). We used thin plate regression spline smoothers and k-value at most equal to five to perform the models (Wood, 2017; Pedersen et al., 2019). GAM was fitted using maximum likelihood estimation with the “mgcv” R package (Wood, 2017). A correlation matrix plot using Pearson's method was made using the “GGally” package (Schloerke et al.,

2021), and values >0.5 or <-0.5 are removed from the modeling. Almost all environmental covariates were maintained in the GAM, except for continental water discharge, which presented a Pearson's correlation equal to -0.6 with salinity and water transparency (see Figure S1). To optimize model convergence, environmental variables were standardized with the values scaled to mean zero and then divided by the standard deviations (Oksanen et al., 2022), except for the "ENSO", which is a categorical variable. Residual plots were performed using the "gam.check" function of the "mgcv" package to assess whether the assumptions of the models were met (Wood, 2017). All statistical analyzes were performed in R program (version 4.2.1) (R Core Team, 2022).

Stable isotopes mixing models were performed to estimate the relative contributions of autochthonous (i.e., estuarine) and allochthonous (i.e., marine and/or freshwater) sources to the diet of juvenile *M. liza* over the years (2010-2022), seasons (summer, autumn, winter and spring) and ENSO events (*La Niña*, Neutral, *El Niño*) (Parnell et al., 2010; Phillips et al., 2014; Vollrath et al., 2021). Mixing models were constructed using the following end-members: 'SOM estuarine' as autochthonous sources, and 'POM and SOM freshwater', 'POM offshore' and 'POM surf-zone' as allochthonous sources. The mean values ($\pm$ standard deviation) of the trophic discrimination factors (TDF) of juveniles *M. liza* were $2.1 \pm 0.7\text{‰}$ for $\delta^{13}\text{C}$ and $3.8 \pm 0.4\text{‰}$ for $\delta^{15}\text{N}$ (Oliveira et al., 2017).

A basic assumption of isotope mixing models is that the isotopic variability of consumers, after accounting for fractionation corrections, are contained within the variability of the assimilated food sources (Phillips et al., 2014). Hence, before running the mixing models, we estimated whether the isotopic variability of juvenile mullet, after accounting for fractionation, was contained in the variability of

assimilated food sources using Bayesian simulations of isotope mixing polygon. Juvenile mullet located outside the 95% mixing polygon region were excluded from the isotope mixing model analysis (Smith et al., 2013; Phillips et al., 2014) (see Fig. S2, S3 and S4). We performed the polygons analysis using the R packages “sp” (Pebesma and Bivand, 2005; Bivand et al., 2013) and “splancs” (Rowlingson and Diggle, 2017).

After selecting only the consumers located inside the sources' isotopic space, we ran Bayesian stable isotopes mixing models in R using the SIMMR package (for biplots, see Fig. S5, S6, and S7). Models used Markov Chain Monte Carlo (MCMC, Parnell et al., 2010; Parnell et al., 2013) with 10,000 interactions in JAGS 4.3.1, using the datasets of individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of juvenile mullet and the mean and $\pm$ standard deviation of isotopic proportions of each food source. Mixture models then create probabilistic comparisons between the given sources and compare dietary proportions between them. We used the median (50%) to summarize the contribution of each food source to juvenile mullet. All statistical tests were performed using R software version 4.2.1 (R Core Team, 2022).

3. Results

3.1. Interannual and seasonal variations of juvenile mullet isotopic composition

Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of juvenile mullet varied along years (Figure 2) and seasons (Figure 3). It was not possible to observe clear interannual patterns in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ related to ENSO events. In some years, carbon and nitrogen showed an inverse relationship, especially in 2011, 2013 and 2015, with higher $\delta^{13}\text{C}$ and lower $\delta^{15}\text{N}$ values and vice-versa. Regarding seasonal changes, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

of juveniles *M. liza* tended to be more enriched in summer and autumn when compared to winter and spring (Figure 3).

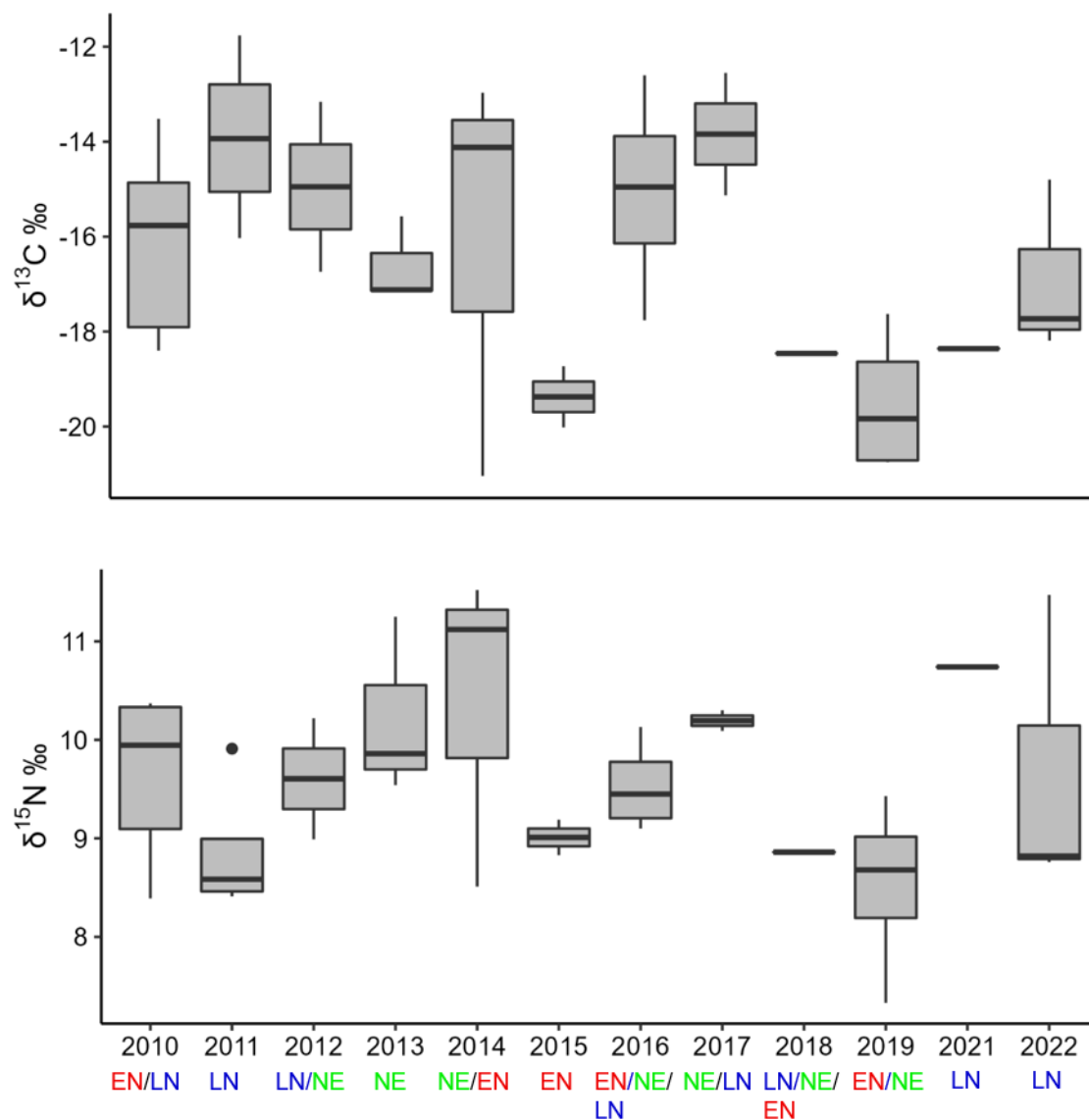


Figure 2. Interannual variation of isotopic values of $\delta^{13}\text{C}$ (top panel) and $\delta^{15}\text{N}$ (bottom panel) of juveniles of the mullet *Mugil liza* in the Patos Lagoon estuary from 2010 to 2022. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, the vertical lines at the ends of the boxes indicate the minimum and maximum values, and the points are the outliers. The

symbols below the years indicate which ENSO events occurred in each year. The LN (blue color) indicate the occurrence of *La Niña* events, EN (red color) are *El Niño* events and NE (green color) are Neutral periods.

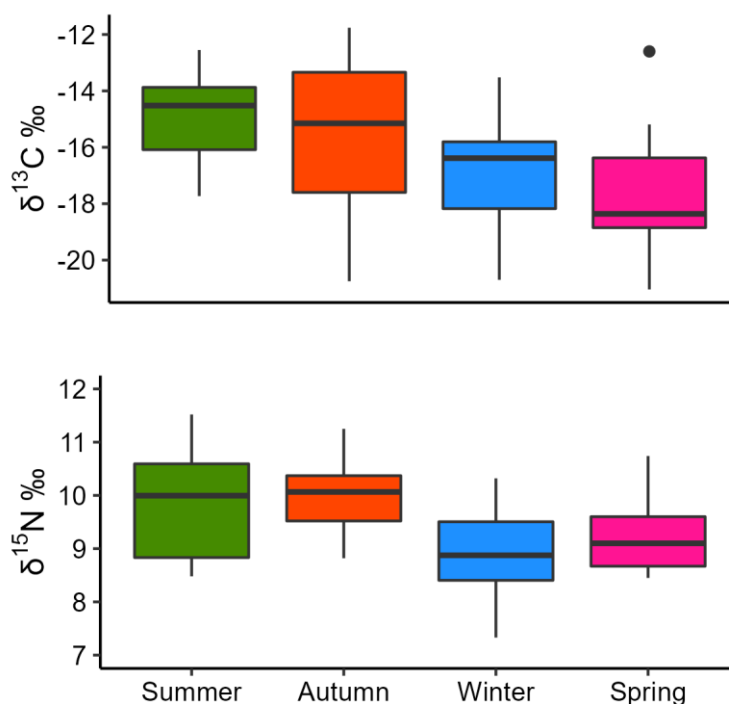


Figure 3. Seasonal variation of isotopic values of $\delta^{13}\text{C}$ (top panel) and $\delta^{15}\text{N}$ (bottom panel) of juveniles of the mullet *Mugil liza* in the Patos Lagoon estuary from 2010 to 2022. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, the vertical lines at the ends of the boxes indicate the minimum and maximum values, and the points are the outliers.

3.2. Isotopic niche of juvenile mullets

The seasonal isotopic niche width (SEAc) of juvenile mullets was higher during summer (14.11 ‰^2) and autumn (11.43 ‰^2) when compared to winter (9.74 ‰^2) and

spring (8.06 ‰²) (Figure 4A). Analyzing the isotopic niche overlap, the highest overlap occurred between summer and autumn seasons, with proportionally low overlap among the other seasons (Table 1; Figure 4A).

Regarding the isotopic niche structure during the different ENSO phases, SEAc was higher during *La Niña* events (13.96) than during *El Niño* (11.90) and Neutral (10.57) events (Figure 4B). Concerning isotopic niche overlap, *La Niña* events and Neutral periods presented the highest overlap, with other periods presenting low overlap (Table 1; Figure 4B).

Table 1. Seasonal and ENSO events isotopic niche overlap of juveniles of the mullet *Mugil liza* in the Patos Lagoon estuary from 2010 to 2022.

Seasons	Overlap
Summer and Autumn	10.8
Summer and Winter	3.7
Summer and Spring	2.1
Winter and Spring	4.5
Winter and Autumn	4.0
Autumn and Spring	2.7
ENSO events	
<i>La Niña</i> and Neutral	8.4
<i>La Niña</i> and <i>El Niño</i>	4.6
Neutral and <i>El Niño</i>	5.1

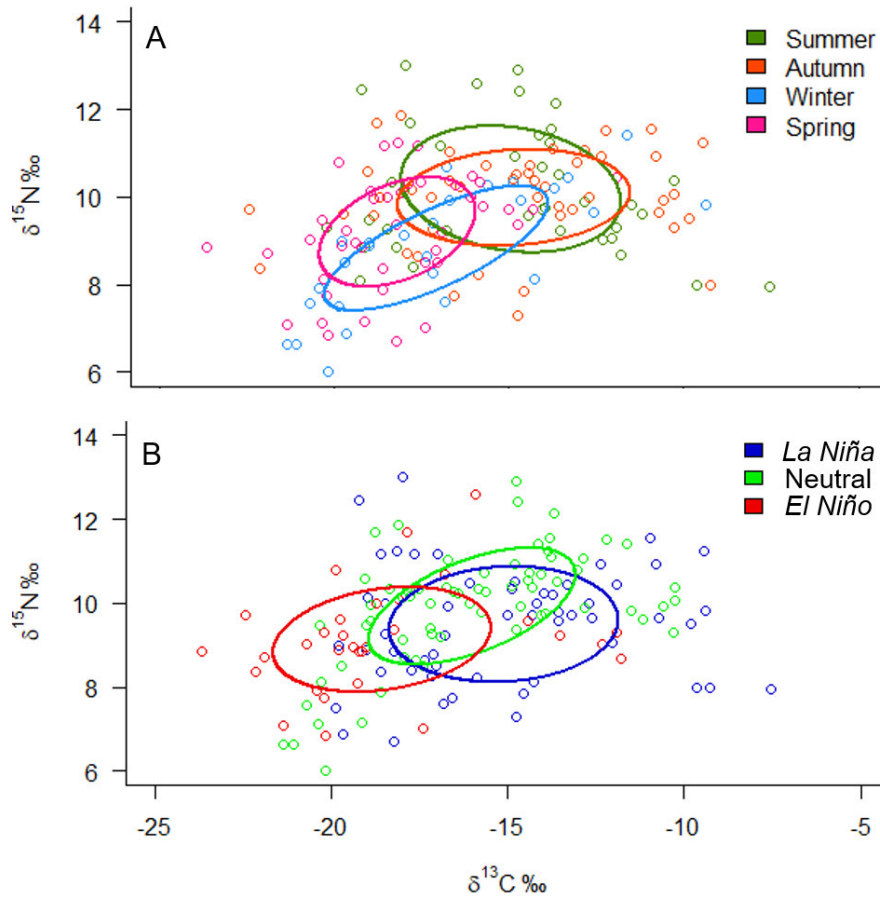


Figure 4. Stable isotopic ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) and standard ellipse area (SEA) for each season (A) and during ENSO events (B) of juveniles of the mullet *Mugil liza* sampled in the Patos Lagoon estuary from 2010 to 2022.

The GAM revealed that only the *El Niño* event and the Neutral period mediated the SEAc of juvenile *M. liza* mullet (Table 2; Figure 5) (see Figure S8 for information on fit and residuals of model). Temperature, a proxy for seasons, did not present any influence on the isotopic niche breadth of juvenile mullets.

Table 2. Generalized additive model of the influence of numerical (local and regional) and categorical (Global) environmental variables on the SEAc of juveniles of the *Mugil liza* mullet. edf: are the degrees of freedom that reflect the degree of nonlinearity of a curve; Ref. df: are reference degrees of freedom; F: Estimate: Parametric coefficients; Std. error: standard error; p-value: considered statistically significant when $p < 0.5$; R-sq. (adj): adjusts predictors that are not significant in a model; and Deviance explained indicates the model's explainability adjustment for the database used.

Numeric variables	edf	Ref. df	p-value	
s(Water temperature)	2.321	2.757	0.335	
s(Water salinity)	1.000	1.000	0.099	
s(Water transparency)	2.716	3.213	0.102	
Categorical variable	Estimate	Std. Error	t-value	p-value
<i>La Niña</i>	0.354	0.369	0.960	0.353
Neutro	-0.926	0.334	-2.771	0.015
<i>El Niño</i>	1.808	0.265	6.817	0.000
R-sq adjusted: 0.512				
Deviance explained: 57.1%				

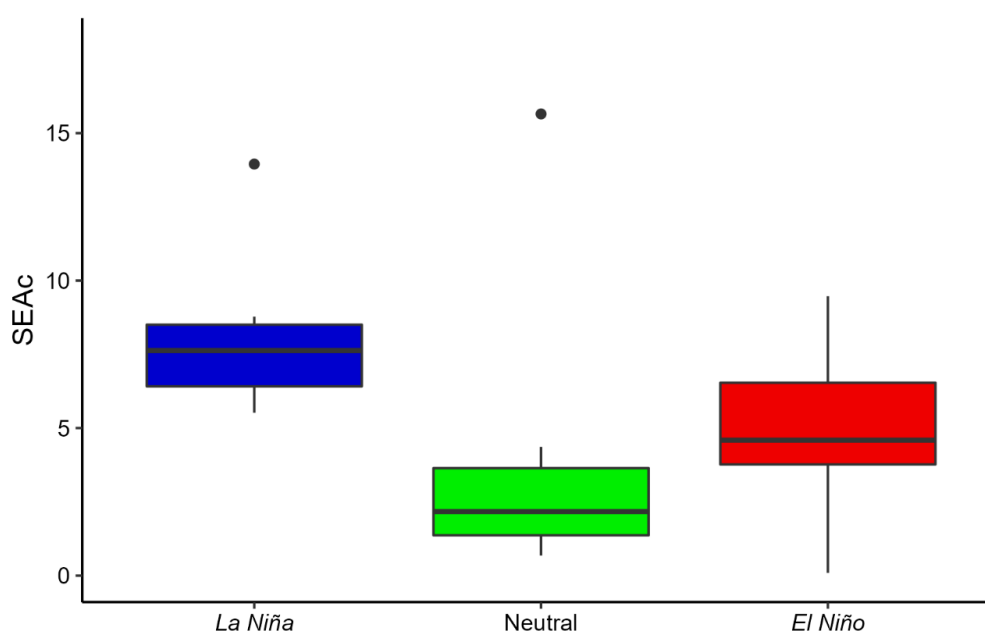


Figure 5. Variation in standard ellipse area (SEA) of juveniles of the *Mugil liza* during ENSO events in the Patos Lagoon estuary from 2010 to 2022. The horizontal line in the middle of the boxes indicates the median, the boxes represent the first and third quartile, the vertical lines at the ends of the boxes indicate the minimum and maximum values, and the points are the outliers.

3.3. Assimilation of primary sources by juvenile mullets

The annual mixing models demonstrated interannual variability in the assimilation of food sources by juvenile mullets from 2010 to 2022 (Figure 6). During 2011 and 2022, which are characterized by the occurrence of *La Niña* events, juvenile mullets showed higher assimilation of sources from marine origin, mainly POM surf-zone (Figure 6). However, although 2021 was also a *La Niña* event year, there was no predominance of assimilation from marine sources (Figure 6). In 2019 had months with the occurrence of *El Niño* and others classified as Neutral, there was the highest assimilation of POM offshore (Figure 6).

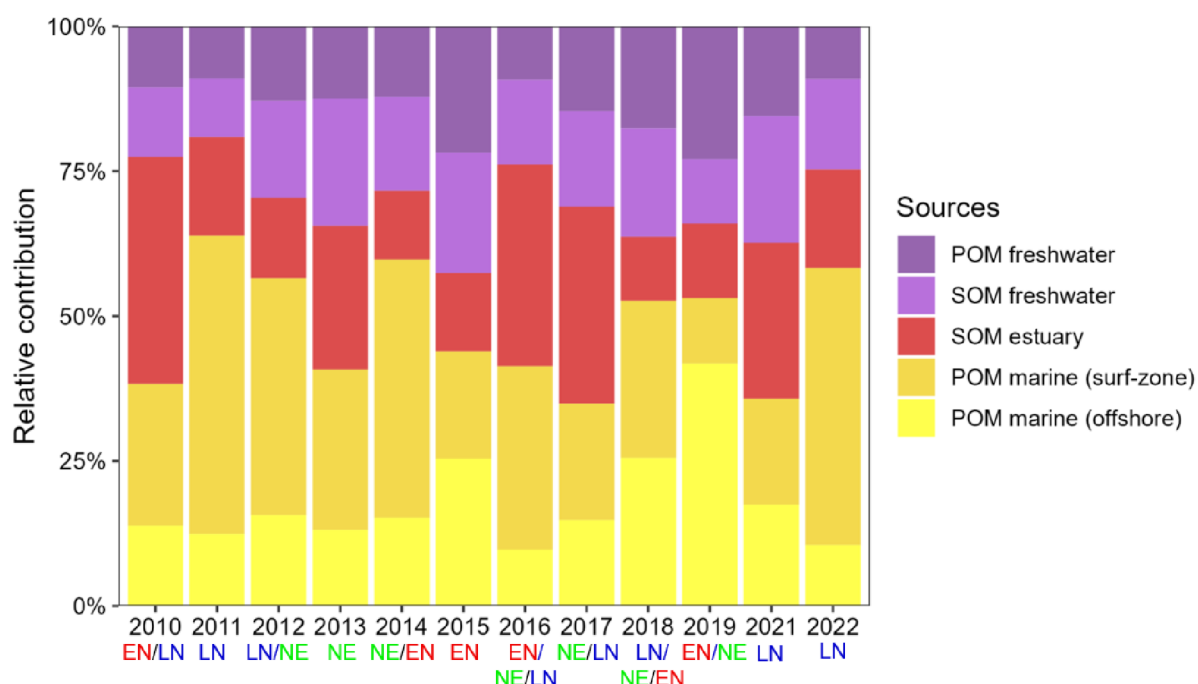


Figure 6. Relative median percentage contribution (50%) of carbon sources to mullet juveniles of the *Mugil liza* in the Patos Lagoon estuary from 2010 to 2022. The symbols below the years indicate which ENSO events occurred in each year. The LN (blue color) indicate the occurrence of *La Niña* events, EN (red color) are *El Niño* events and NE (green color) are Neutral periods.

The seasonal mixing models showed that juveniles *M. liza* had a relative contribution higher than 50% from marine sources in summer, winter and spring (Figure 7). In autumn, although there is a considerable contribution from marine sources, there was more contribution from estuarine and freshwater sources compared to the other seasons (Figure 7). In addition, the POM surf-zone was the source with the highest relative contribution in all stations (Figure 7).

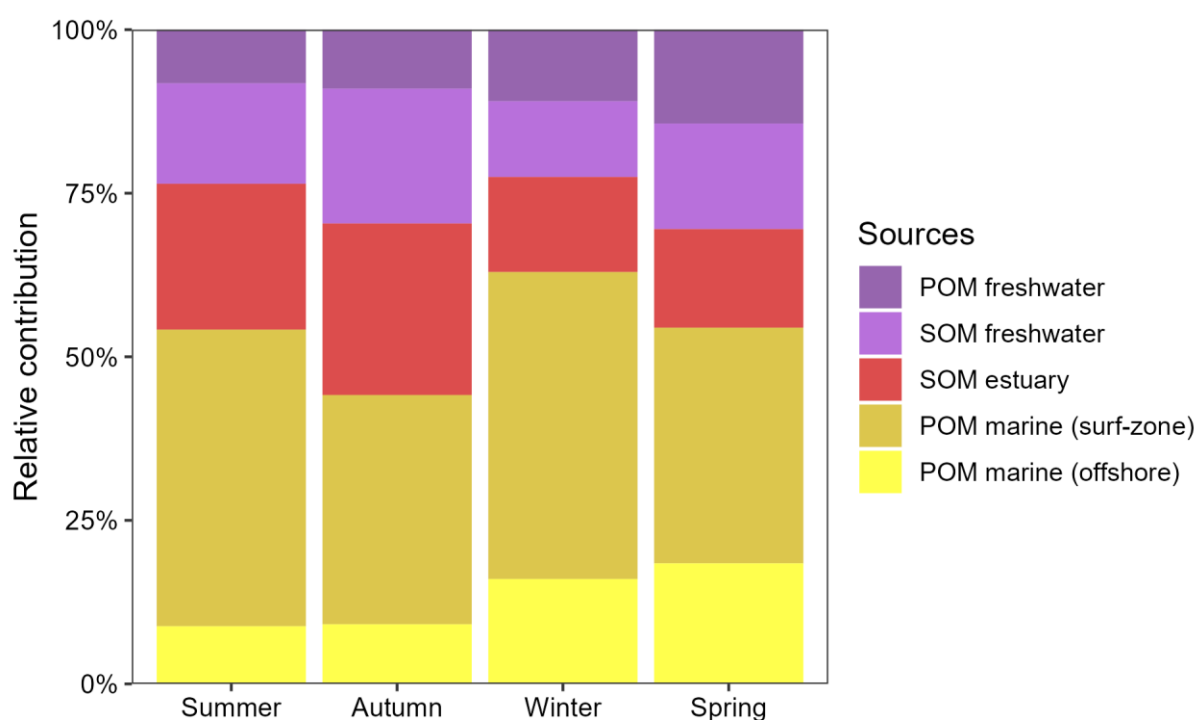


Figure 7. Relative seasonal median percentage contribution (50%) of carbon sources for mullet juvenile *M. liza* in the Patos Lagoon estuary from 2010 to 2022.

The ENSO mixing model showed that during the *La Niña* and *El Niño* events there was higher contribution from marine sources. However, the POM surf-zone was more representative during *La Niña* and the POM offshore during *El Niño* (Figure 8). In addition, during the Neutral period there was higher contribution from freshwater sources, mainly from POM (Figure 8).

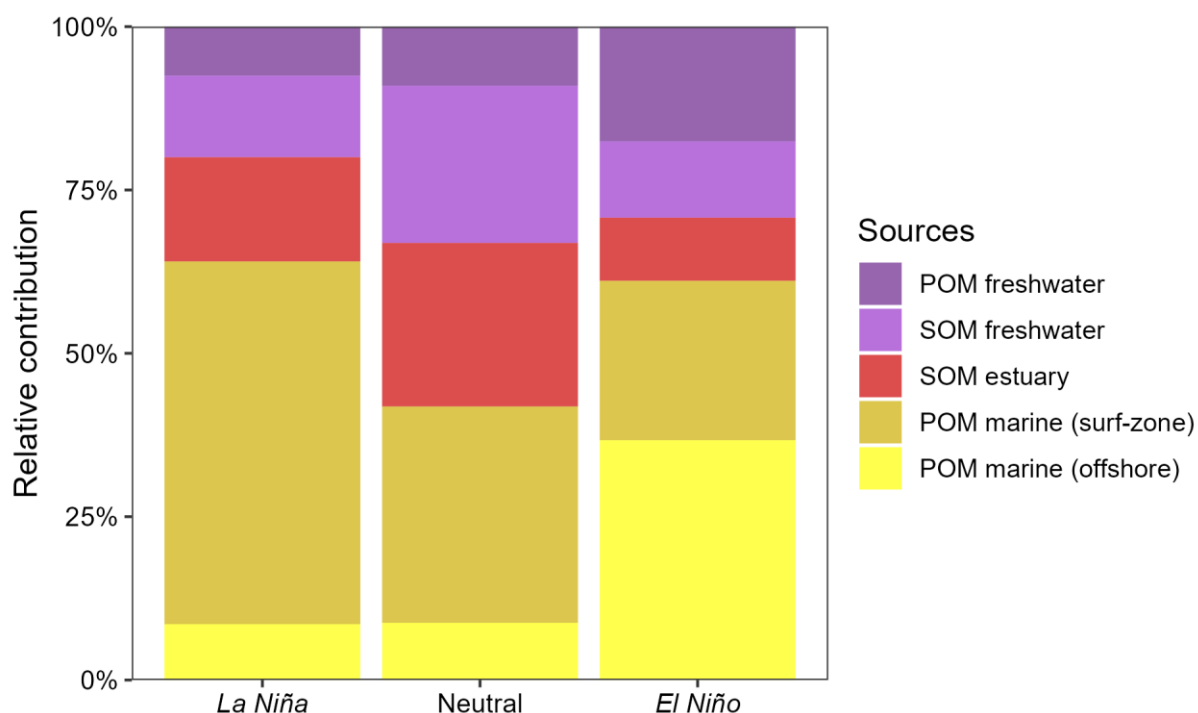


Figure 8. Relative median percentage contribution (50%) of carbon sources to juveniles of the *Mugil liza* during ENSO events in the Patos Lagoon estuary from 2010 to 2022.

4. Discussion

Our results corroborate our initial hypothesis that the annual variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the muscle tissues of juvenile mullets would be associated with

seasonal variations and the influence of ENSO events on the availability of freshwater or marine allochthonous basal sources in the estuary. Seasonal variations in niche breadth of juvenile mullet were also observed. Seasonal variations in hydrology are common in this estuary, which causes variations in composition and abundance of primary producers, which could explain the detected changes in isotopic niche breadth of juvenile mullets (Abreu et al., 2010; Odebrecht et al., 2015; Possamai et al., 2020; Rosa et al., 2023).

In addition, although there is no clear interannual pattern of the influence of ENSO events on the isotopic values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of juvenile mullets, there was an effect of the *El Niño* events and neutral period on the isotopic niche breadth. ENSO events are associated with precipitation anomalies in the region that can affect the isotopic composition of basal sources and reverberate up to consumers along the food chain (Lanari et al., 2021). The interannual variation in assimilation of basal sources by juvenile mullets may be related to temporal variation in physicochemical variables at different scales, which affects the region's primary producers (Abreu et al., 2010; Odebrecht et al., 2015; Possamai et al., 2020; Rosa et al., 2023). Therefore, the abundance, species richness and occurrence of algal species, both phytoplankton (i.e., POM) and microphytobenthos (i.e., SOM) within the estuary can be affected on different time scales by winds (hours to days) and by the discharge of continental water (seasonal/interannual) (Abreu et al., 2010; Odebrecht et al., 2015; Possamai et al., 2020; Rosa et al., 2023). Garcia et al. (2017b) suggest that the intensity in the availability of benthic and pelagic sources that sustain estuarine consumers are not static, that is, they change in response to intra- and interannual variation in the availability of basal production sources. Therefore, this can directly affect the diet and assimilation of juveniles of the mullet *M. liza*, as this species feeds on microalgae

associated with the sediment when they enter estuaries (Garcia et al., 2018; Vollrath et al., 2021).

Regarding the seasonal variation in isotopic values in muscle of juvenile mullets, our results did not corroborate our initial hypothesis of higher niche amplitude in winter-spring than in summer-autumn. Instead, the opposite occurred, with a broader isotopic niche during summer and autumn. The studied subtropical estuary is characterized by lower rainfall in summer-autumn and higher rainfall in winter-spring (Seeliger 2001; Garcia et al., 2019b; Lanari et al., 2021). Therefore, during the summer-autumn there may be a shortage of nutrients affecting the growth of phytoplankton in the estuary due to low precipitation or drought (Abreu et al., 2010), and would be expected smaller niche breadth of primary consumers. On the other hand, during the winter-spring there is a higher intrusion of freshwater into the estuary due to higher precipitation during these seasons, which promotes the entry of nutrients from continent and higher availability of phytoplankton in the estuary (Abreu et al., 2010), which is expected higher niche breadth of primary consumers. However, our results were opposite to what was expected, showing higher breadth niche for juvenile mullets during summer-autumn than in winter-spring. As a potential explanation, Odebrecht et al. (2015) investigated short-term phytoplankton blooms in shallow areas of the Patos Lagoon estuary and observed that saltwater input is as important as the freshwater contribution to the system, because saltwater input can block the freshwater exit from Patos Lagoon, which increases retention time in the estuary, and leads to higher phytoplankton biomass in the region. Therefore, the entry of salt water into the estuary allows blooms of euryhaline phytoplankton species, and the accumulation of biomass would be more likely during periods in which there is an abundance of nutrients and light, that is, mainly during the austral

spring and summer (Odebrecht et al., 2015), which would lead to higher niche breadth among primary consumers during this period. Another hypothesis is that juvenile mullet expands their isotopic niches in summer-autumn, that is, in periods of less algae growth, due to the lack of limited food resources in the region. For example, a study carried out in a coastal brackish lagoon in Spain observed that during the warmer seasons, when there is a reduction in food resources, mullet species expanded their niches breadth by increasing their consumption of algae, although they did not decrease their isotopic niches overlapping due to non-limitation of resources in the region (Cardona et al., 2001). However, although probably there is no limitation of food resources in the Patos Lagoon estuary for juvenile mullet (Vollrath et al., 2023), the lower nutrient input and, consequently, lower growth of algal during the summer-autumn (Abreu et al., 2010), can lead to an increase in niche breadth during these seasons.

Furthermore, excess rainfall associated with the occurrence of *El Niño* events could decrease retention time in the estuary and take most of the estuarine phytoplankton biomass production to the coastal region, reducing the likelihood of phytoplankton bloom development in the estuarine region (Odebrecht et al., 2015) and, consequently, reduce the species' niche breadth. In addition, juvenile mullets did not have a higher proportion of assimilation from freshwater allochthonous sources as expected during periods of higher rainfall and discharge of continental water into the estuary. On the contrary, they had a higher proportion of assimilation from allochthonous sources of marine origin, mainly POM surf-zone during all seasons of the year. Possamai et al. (2020) had already observed a similar pattern for the same species in our studied estuary. They suggest that this higher assimilation of marine resources during periods with greater freshwater discharge into the estuary may be

related to the species' life cycle (Possamai et al., 2020). Mulletts reproduce at sea, eggs and larvae drift towards the coast, and juveniles enter estuaries passively to use this region as a feeding and growth zone (Vieira, 1991; Lemos et al., 2014). Therefore, periods with higher discharge of continental water towards the sea, mainly associated with *El Niño* events, can delay recruitment from the coastal region into the estuary (Possamai et al., 2020).

During *La Niña* events, juvenile mullets presented high assimilation of surf-zone phytoplankton, which was expected considering there is higher intrusion of marine waters into the estuary during these events (Garcia et al., 2019b; Lanari et al., 2021). However, although the opposite pattern occurs during *El Niño* events, with an above-average freshwater discharge into the estuary (Garcia et al., 2019b; Lanari et al., 2021), juvenile mullets also presented an increase in the assimilation of resources of marine origin during these periods. This pattern was different from expected, but when the origin of the marine resources is considered, there is a differentiation in which microalgae community is being used by juvenile mullets during *El Niño* and *La Niña* events. During *El Niño*, the higher contribution is from offshore POM, while during *La Niña* events, the higher contribution to the juvenile mullets come from the surf-zone. Mulletts spawn offshore, and their juveniles can take between 1 and 2 months to reach the coast and 4 months to enter the estuary (Vollrath et al., 2024). Due to the high freshwater inflow during *El Niño* events, it is possible that recruits entering the estuary had higher difficulty to swim against the higher flow and, consequently, delayed their entrance. Thus, they would be staying for a longer time in the coastal marine zone and, when collected inside the estuary, they would be reflecting the carbon consumed in this longer period spent offshore (Possamai et al., 2020). This also could explain the difference in the origin of marine phytoplankton

reflected during *El Niño* and *La Niña* events, considering the intrusion of marine waters to the estuary during *La Niña* events comes from the adjacent coastal area, mainly reflecting surf-zone phytoplankton (Haraguchi et al., 2015).

Although higher assimilation of marine origin phytoplankton occurred during the *La Niña* and *El Niño* events, juvenile mullets presented $\delta^{13}\text{C}$ isotopic values that were lower during the *El Niño* events than during *La Niña*, and low overlap with *La Niña*. Moreover, they also had higher niche breadth during *La Niña*. This may have occurred due to the higher proportion of POM freshwater assimilation during *El Niño* compared to *La Niña*, and the fact that the $\delta^{13}\text{C}$ isotopic values of freshwater basal sources are lower compared to marine basal sources (Garcia et al., 2019b; Lanari et al., 2021). This result corroborates our hypothesis of higher assimilation of freshwater allochthonous basal sources by primary consumers associated with higher continental water discharge into the estuary due to the occurrence of *El Niño* events. In addition, the higher assimilation of freshwater allochthonous basal sources by juvenile mullets during *El Niño* events compared to *La Niña* shows that part of the population is able to enter the estuary during *El Niño* events and assimilate these sources of freshwater origin. This higher distribution in the assimilated proportion of autochthonous and allochthonous basal sources by juvenile mullets during *El Niño* events may also be associated with the intensity of these events. Prior studies have observed that only strong events had a negative effect on the abundance of species within the estuary (Belarmino et al., 2021; Gower et al., 2024; Possamai et al., 2024). During the neutral period, although the highest relative contribution is the POM surf-zone, there is greater assimilation of estuarine and freshwater basal sources compared to *La Niña* and *El Niño* events. This may be related to the life cycle of the species, as after spawning at sea, the juveniles drift towards the coast

and remain until they enter the estuary, where they use it as a feeding and growth area until they reach maturity (Vieira, 1991; Lemos et al., 2014). Therefore, there will be individuals recently arrived from the marine coast that will reflect the sources assimilated from that region. In contrast, there will be other individuals that have already been in the estuary for a longer time that can reflect the estuarine and freshwater sources. This higher assimilation of allochthonous basal sources of freshwater origin during the neutral period may be associated with the seasonality of the region (Abreu et al., 2010), since during this period there is no influence from the occurrence of *La Niña* and *El Niño* events. However, there are potential confounding factors like the mobility of the species, which has a wide tolerance to low salinities (Lisboa et al., 2015). Future studies using natural tracers (e.g., chemical element analyzes in otoliths, Mai et al., 2018) to investigate movement patterns of juvenile mullets inside the estuary would be helpful to better understand the temporal changes in their assimilation of autochthonous and allochthonous sources.

Although the SEAc of juvenile mullets was higher during *La Niña* events, compared to *El Niño* and Neutral periods, the GAM demonstrated that *El Niño* and Neutral events had a significant effect on SEAc. Apparently, during *El Niño* events and neutral periods, there is higher variability in the proportions of relative contributions from autochthonous and allochthonous matter derived from freshwater and marine sources that can influence SEAc than during *La Niña* events. During *La Niña* events, more than 50% of the relative contribution was originated from the POM surf-zone, which coincides with what is expected considering that the species takes between 1 and 2 months to reach the coast and 4 months to enter the estuary (Vollrath et al., 2023) and the higher intrusion of saline waters into the estuary due to the climatic conditions caused by these events (Garcia et al., 2019b; Lanari et al.,

2021). The higher variability in SEAc during *El Niño*, as mentioned in the previous paragraph, may be associated with the species' life cycle (Possamai et al., 2020). Moreover, during the neutral period, the higher variability in SEAc may be related to the seasonality of the region, which may influence the enrichment and growth of phytoplankton in the estuary (Abreu et al., 2010). Additionally, the increase in isotopic niche width during neutral period may be due the stronger signal due to the diet shift from a planktonic and marine-derived consumption to a benthic and estuarine-derived feeding behavior exhibited by juvenile mullets as they migrate from the marine surf-zone into the estuary (Vollrath et al., 2021).

Conclusions

Our study using long-term time series (2010-2022) of stable isotopes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from primary consumer juvenile mullets suggests seasonal and interannual variations in the assimilation of autochthonous (i.e., estuarine) and allochthonous (i.e., freshwater and marine) associated with local and regional environmental factors and remote driving forces associated with natural climate phenomena occurring at global scales (i.e., ENSO events). Contrary to our initial predictions, there was higher assimilation of marine allochthonous sources in rainy seasons and *El Niño* events. In contrast, corroborating our initial hypothesis, there was a higher assimilation of freshwater basal sources by juvenile mullets during *El Niño* events compared to *La Niña* events. These findings highlight the complex effects and interactions between local/regional (e.g., temperature, salinity, water transparency, freshwater discharge) and remote climate factors (ENSO's phases) affecting the assimilation of food resources by estuarine primary consumers. The investigation of such complex

biophysical interactions was only possible due to the availability of long-term time series of abiotic factors and stable isotope tracers ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of food sources and consumers. Moreover, this study highlights the importance of evaluating the impacts of natural climate phenomena, such as ENSO events that tend to increase their frequency and intensity with ocean warming (Cai et al., 2018; Freund et al., 2019), on the structure and functioning of estuarine food webs.

Acknowledgments

SR Vollrath acknowledges the financial support of the National Council for Scientific and Technological Development (CAPES). AM Garcia thanks research fellowship provided by CNPq (Proc. 313008/2021-3). We are also thankful to the Brazilian Long Term Ecological Research Program (PELD - Pesquisas Ecológicas de Longa Duração) site 8 - Patos Lagoon estuary and adjacent marine coast for funding this research.

Funding

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; 001).

Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; Proc. 313008/2021-3).

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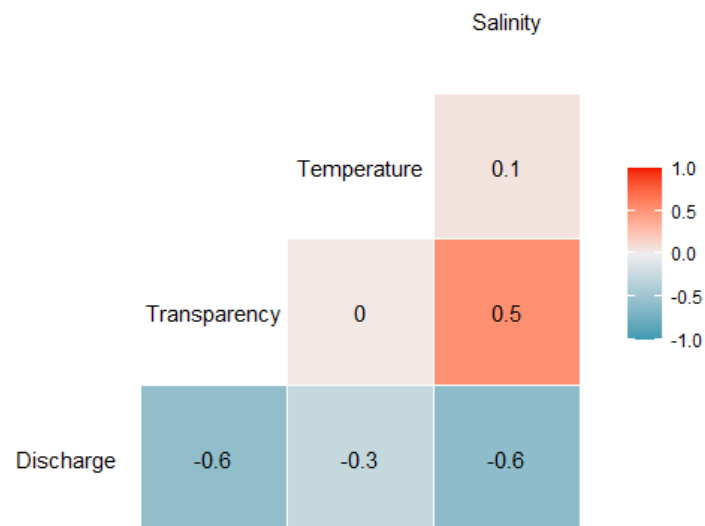


Figure S1. Pearson's correlation between environmental variables in the Patos Lagos estuary from 2010 to 2022.

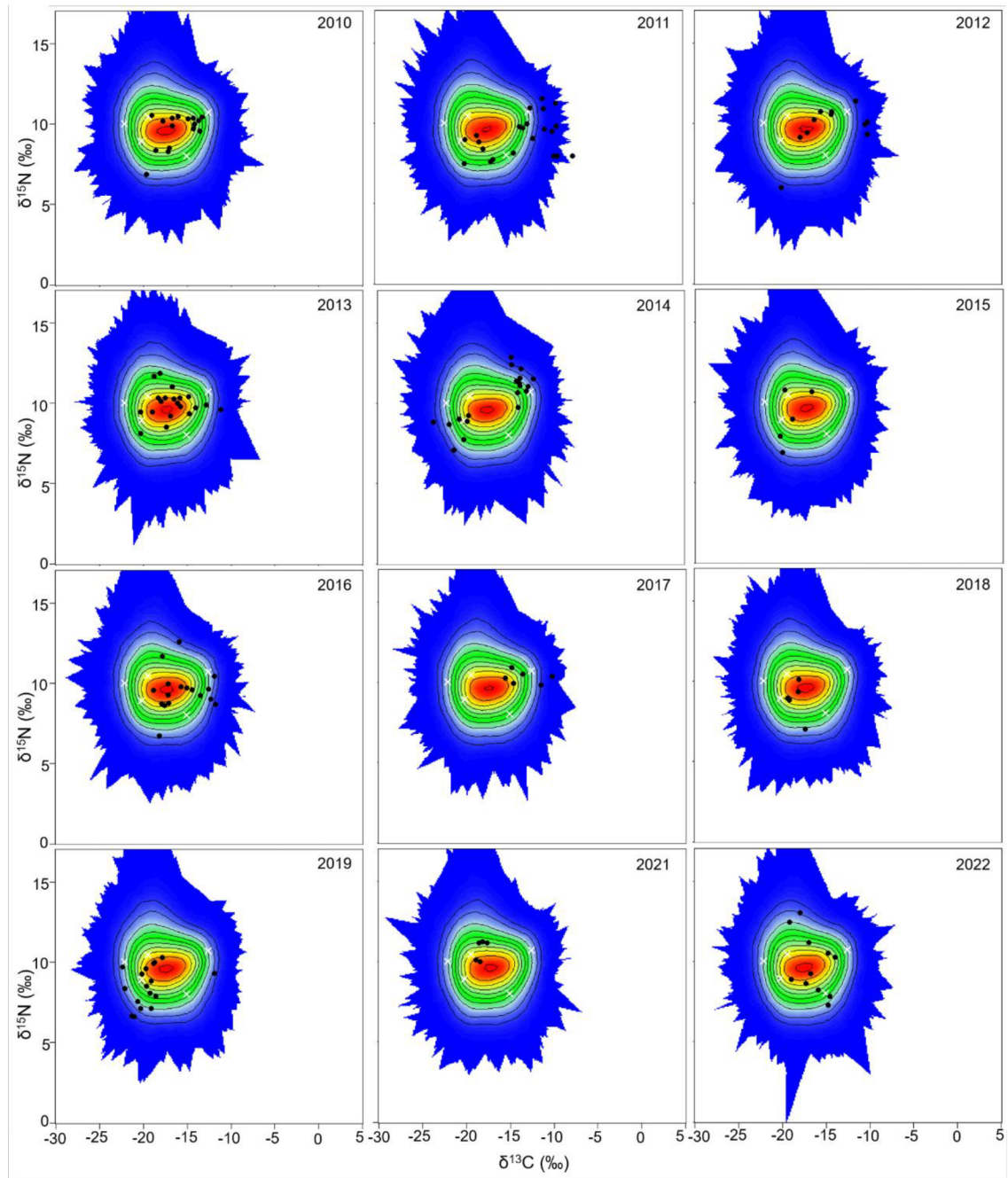


Figure S2. Isotopic mixing polygons with the limits of basal source values in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot space over the years in the Patos Lagoon estuary from 2010 to 2022. Mullet juveniles *M. liza* (black filled circles) located outside the region of the 95% mixing polygon were excluded from the annual isotope mixing model analysis.

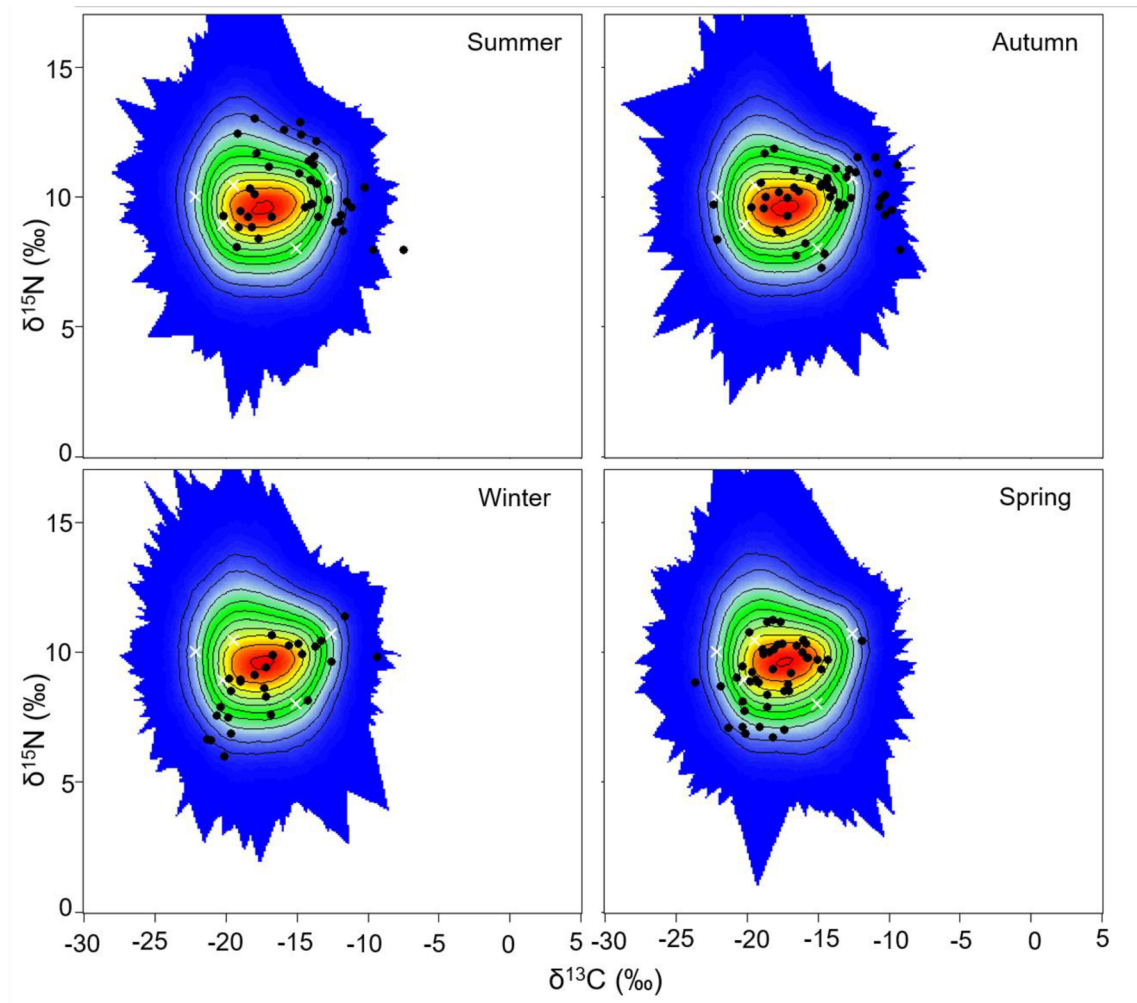


Figure S3. Isotopic mixing polygons with the limits of basal source values in seasonal $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot space in the Patos Lagoon estuary from 2010 to 2022. Mullet juveniles *M. liza* (black filled circles) located outside the region of the 95% mixing polygon were excluded from the annual isotope mixing model analysis.

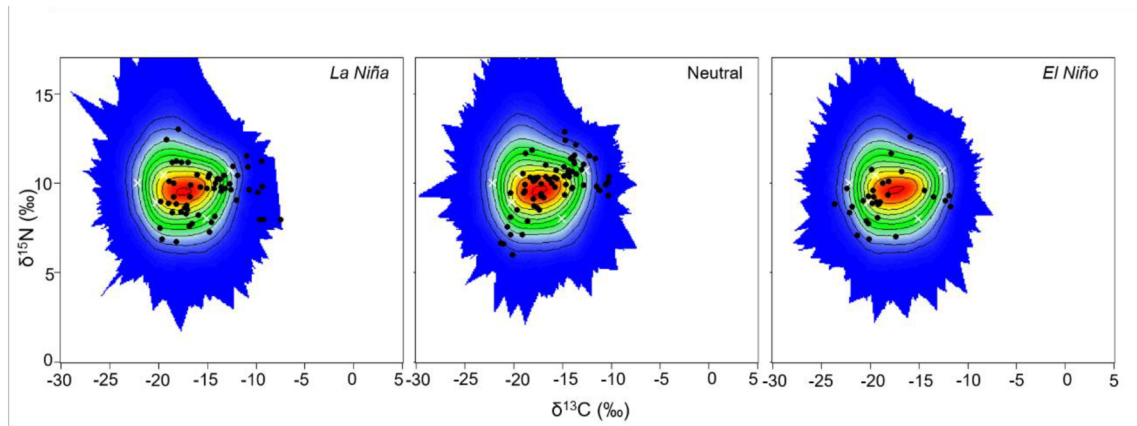


Figure S4. Isotopic mixing polygons with the limits of basal source values in the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot space during ENSO events in the Patos Lagoon estuary from 2010 to 2022. Mullet juveniles *M. liza* (black filled circles) located outside the region of the 95% mixing polygon were excluded from the annual isotope mixing model analysis.

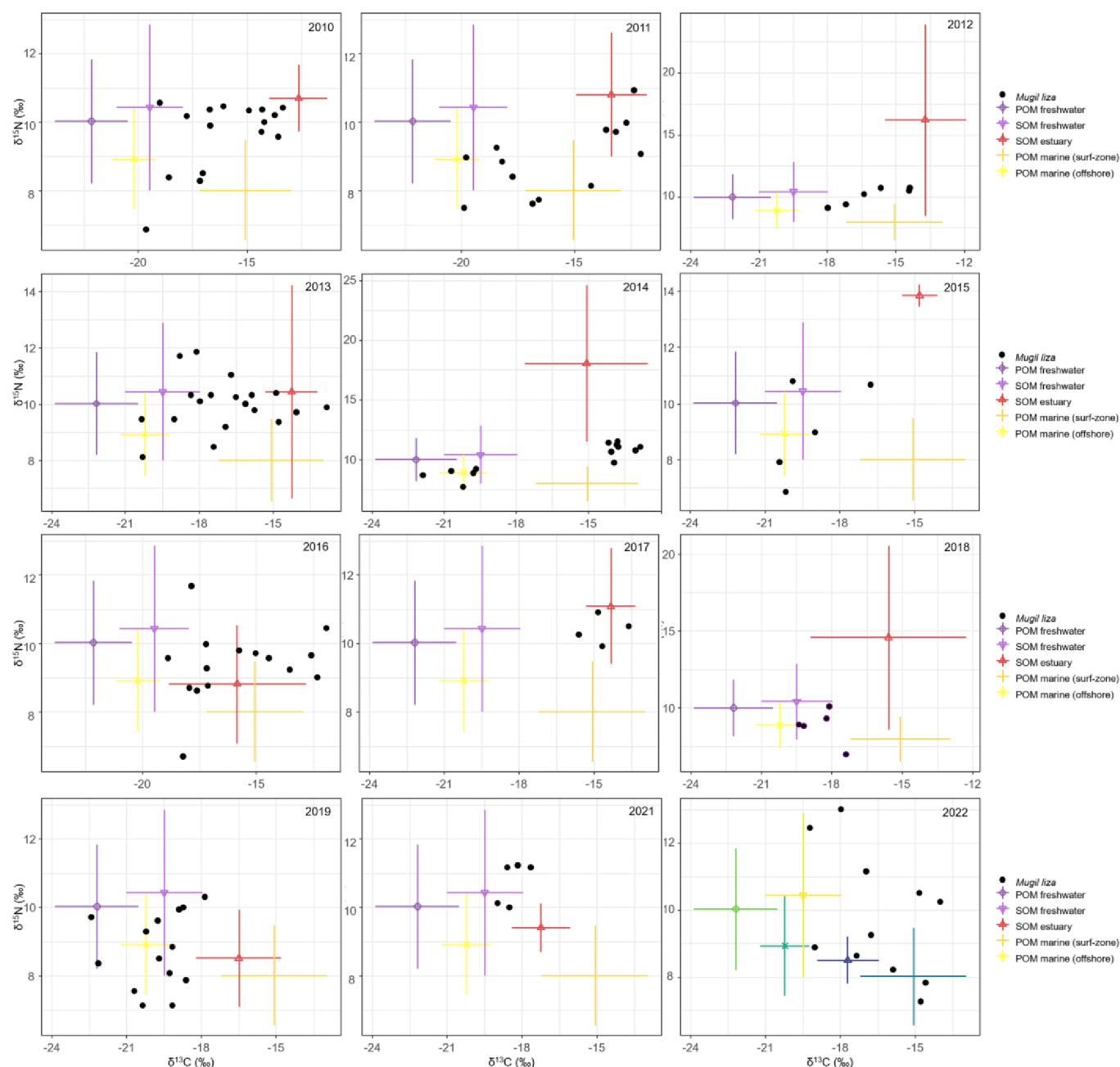


Figure S5. Bi-plots of the mean value ($\pm$ SD) of annual carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes in the Patos Lagoon estuary from 2010 to 2022 of mullet juvenile *M. liza* (filled black circles) and autochthonous (estuary SOM) and allochthonous (POM and SOM freshwater, POM marine (surf-zone and offshore)) basal food sources.

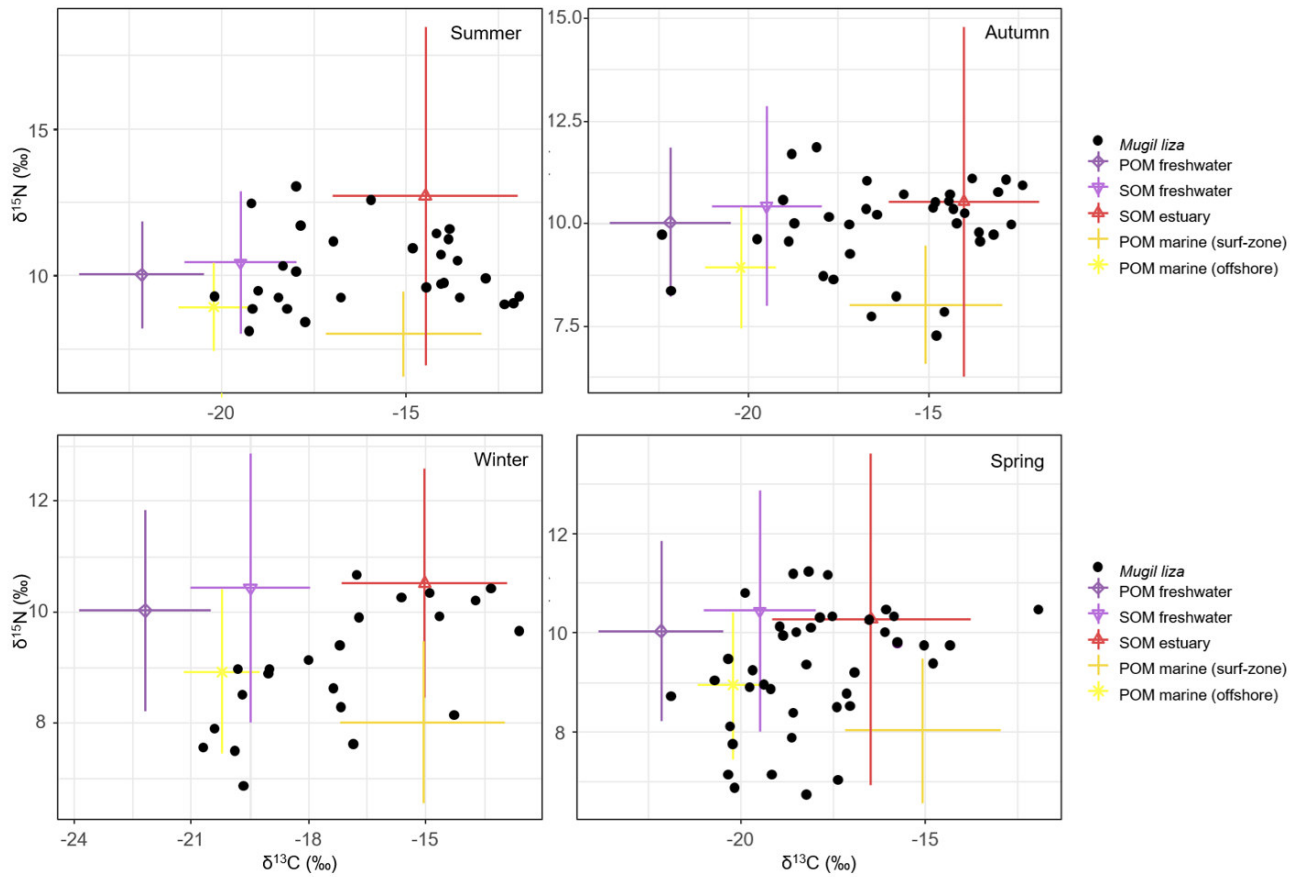


Figure S6. Bi-plots of the mean value ($\pm$ SD) of seasonal carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes in the Patos Lagoon estuary from 2010 to 2022 of mullet juvenile *M. liza* (filled black circles) and autochthonous (estuary SOM) and allochthonous (POM and SOM freshwater, POM marine (surf-zone and offshore)).

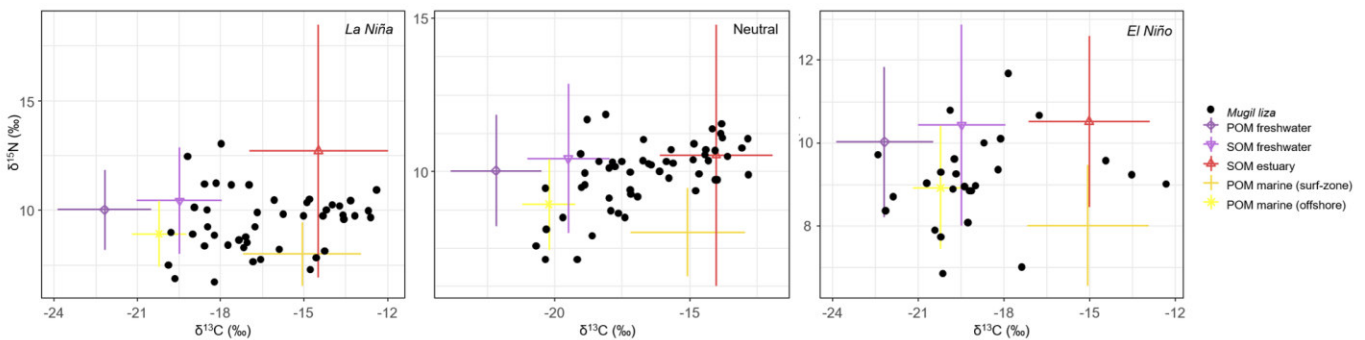


Figure S7. Bi-plots of the mean value ($\pm$ SD) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes during ENSO events in the Patos Lagoon estuary from 2010 to 2022 of

mullet juvenile *M. liza* (filled black circles) and autochthonous (SOM estuary) and allochthonous (POM and SOM freshwater, POM marine (surf-zone and offshore)).

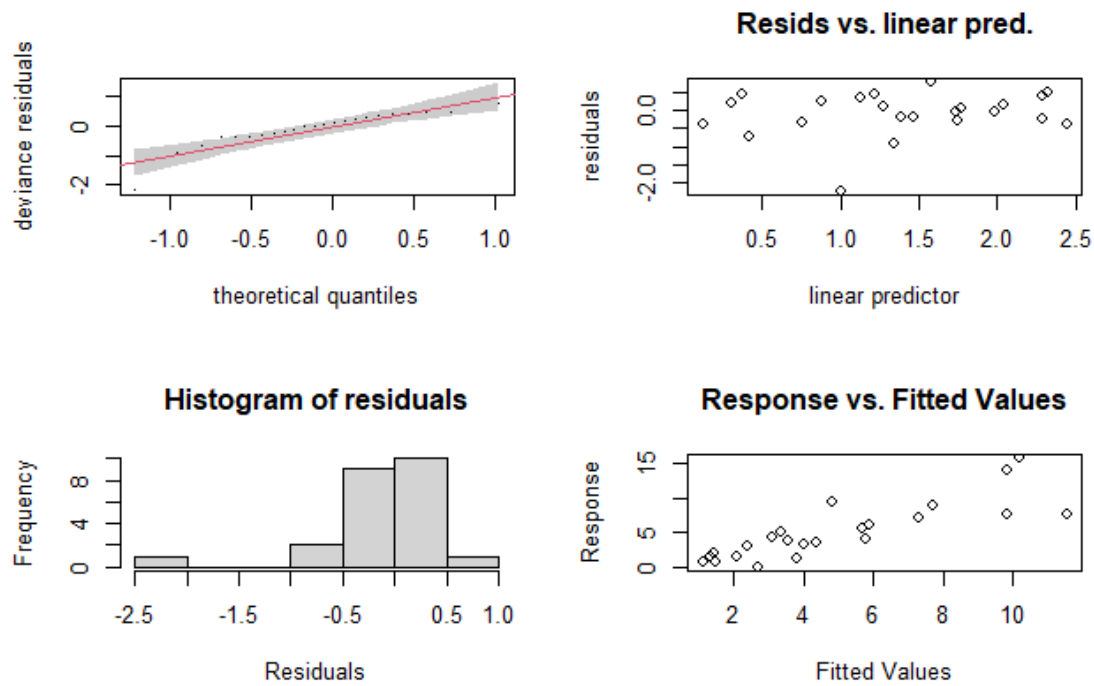


Figure S8. Residuals from the generalized additive model.

CONSIDERAÇÕES FINAIS E PERSPECTIVAS

A principal proposta dessa Tese foi utilizar bancos de dados com séries temporais de longo-prazo que permitiram avaliar os impactos de fenômenos climáticos naturais (i.e., eventos *El Niño* Oscilação Sul, ENOS) e antrópicos (i.e., aquecimento dos oceanos e sobrepesca) na abundância e assimilação de fontes alimentares basais em peixes. Foram utilizados Modelos Aditivos Generalizados (GAM), ou seja, modelos não lineares (WOOD, 2017; PEDERSEN *et al.*, 2019), para estimar os efeitos dos impactos naturais e antrópicos, juntamente com variáveis ambientais locais (i.e., temperatura, salinidade e transparência da água) e regional (i.e., descarga de água continental) em espécies de tainhas (*Mugil curema* e *M. liza*) no estuário da Lagoa dos Patos e costa marinha adjacente (32°S). Isso porque, como mostrado ao longo da Tese, estudos de longo-prazo são extremamente importantes para que seja possível estimar os impactos que as espécies estão sofrendo frente ao aquecimento dos oceanos, aos eventos ENOS (que tendem a aumentar sua frequência e intensidade devido ao aquecimento dos Oceanos; CAI *et al.*, 2018; FREUND *et al.*, 2019) e a pesca excessiva. O conhecimento sobre os impactos e seus possíveis efeitos sinérgicos gerados por esses estudos de longo-prazo podem fornecer informações que alertam e ajudam na criação de legislações adequadas para preservar a biodiversidade.

No primeiro capítulo foi investigado através de uma série temporal de longo-prazo (agosto de 1996 até fevereiro de 2020), com dados coletados mensalmente *in situ*, se estava havendo aquecimento das águas rasas (<1,5 m) do estuário da Lagoa dos Patos e costa marinha adjacente. E caso houvesse aquecimento, se isso poderia aumentar a abundância dos juvenis de uma espécie de tainha (*M. curema*) com distribuição mais tropical na região de estudo que é subtropical. Com essa pesquisa, nós observamos os seguintes resultados (VOLLRATH *et al.*, 2023): (i) Houve aquecimento estatisticamente significativo das águas rasas (<2 m) do estuário da Lagoa dos Patos e costa marinha adjacente. Embora outros estudos já houvessem apontado aquecimento das águas na costa do sudoeste do Oceano Atlântico usando inferências a partir de dados satelitais. Esse estudo foi o primeiro a mostrar esse aquecimento com uma longa série temporal contínua com dados coletados mensalmente *in situ* e de forma padronizada nas zonas rasas do estuário da Lagoa dos Patos e zona de arrebentação marinha adjacente, as quais servem de berçário natural para formas juvenis de várias espécies, incluindo as tainhas; (ii) Embora tenha sido observado o aquecimento das águas da região, a análise de série temporal não mostrou um aumento estatisticamente significativo na abundância dessa espécie na região. No entanto, essa análise mostrou uma variação interanual na abundância da espécie; (iii) A investigação dessa variabilidade interanual através de Modelos Aditivos Generalizados (GAM) permitiu observar

que a abundância dos juvenis de tainha aumenta com a temperatura da água nas zonas rasas do estuário da Lagoa dos Patos e costa marinha adjacente. Por outro lado, a abundância dos juvenis da espécie diminui em anos com ocorrência de eventos *El Niño*. Portanto, esses eventos climáticos acabam mascarando o esperado efeito do aquecimento das águas na abundância da espécie, revelando uma complexa sinergia nos efeitos de fatores climáticos naturais (fenômeno *El Niño*) e antrópicos (aquecimento as águas devido ao efeito estufa); (v) Por fim, este trabalho destaca a importância de séries temporais de longo-prazo para avaliar os impactos do aquecimento dos oceanos em espécies aquáticas, além da necessidade de incluir nas análises os fenômenos climáticos naturais que podem mascarar os efeitos dos impactos antrópicos nas espécies, por exemplo, com o fenômeno da tropicalização da fauna em regiões temperadas.

No segundo capítulo foi utilizado uma série temporal de 23 anos (1997-2019) para investigar os efeitos da pesca, variáveis ambientais de escala global (i.e., eventos ENOS), regional (i.e., descarga de água continental) e local (i.e., temperatura, salinidade e transparência da água) na abundância de juvenis de uma espécie de tainha (*M. liza*) com grande importância comercial. Foi utilizado um compilado de bancos de dados disponíveis *on-line* sobre o desembarque pesqueiro (kg) artesanal e industrial das tainhas no Rio Grande do Sul, Santa Catarina e São Paulo e um banco de dados de longo-prazo (1997-2019) da abundância dos juvenis, para estimar o efeito da pesca dos adultos sobre os juvenis na costa marinha adjacente e dentro do estuário da Lagoa dos Patos, que é a sua principal área de berçário. Nesta pesquisa nós obtivemos os seguintes resultados (VOLLRATH *et al.*, 2024): (i) As análises de séries temporais não apresentaram resultados estatisticamente significativos de que a abundância dos juvenis esteja diminuindo ao longo dos anos na região. Entretanto, houve variação interanual na abundância dos juvenis na costa marinha adjacente e no estuário da Lagoa dos Patos; (ii) Os modelos GAM sugerem que quanto maior é o desembarque pesqueiro (kg) das tainhas adultas, menor é a abundância dos juvenis de tainha na costa marinha e estuário; (iii) Além disso, os GAMs mostraram uma defasagem do efeito da pesca na abundância dos juvenis na costa marinha e estuário. As tainhas adultas são capturadas pela pesca principalmente antes de desovarem no mar. Considerando o ciclo de vida da espécie, que se reproduz no mar, os ovos e larvas derivam em direção à costa, onde entram nos estuários para usarem como zona de alimentação e crescimento (VIEIRA, 1991), é esperado que esses juvenis demorem um tempo para conseguirem chegar na costa e entrar no estuário (VIEIRA & SCALABRIN, 1991). Sendo assim, foi observado uma defasagem de 1 a 2 meses para o efeito da pesca ser observado na abundância dos juvenis na costa e de 4 meses para o estuário; (iv) Por fim, este trabalho destaca a importância de séries temporais de longo-prazo para avaliar os efeitos complexos e concomitantes da variabilidade ambiental e da

sobrepesca sobre a abundância dos juvenis dessas populações de peixes, além de contribuir com dados empíricos que podem auxiliar nos planos de gestão sustentável desses recursos pesqueiros.

No terceiro capítulo foi utilizado uma série temporal de 12 anos (2010-2022, com exceção de 2020 devido à pandemia de COVID-19) de dados sazonais de isótopos estáveis de $\delta^{13}\text{C}$ e $\delta^{15}\text{N}$ no músculo de juvenis de tainhas e fontes alimentares basais, além de variáveis ambientais na escala global (i.e., eventos ENOS), regional (i.e., descarga de água continental) e local (i.e., temperatura, salinidade e transparência da água), para estimar variações sazonais e interanuais na assimilação de fontes basais por consumidores primários (juvenis de *M. liza*), associado com a ocorrência de eventos *La Niña* e *El Niño*. Nesta pesquisa nós obtivemos os seguintes resultados: (i) houve influência da sazonalidade e da ocorrência de eventos ENOS na assimilação das fontes basais autóctone e alóctone pelos juvenis de tainha; (ii) porém, houve maior assimilação de fontes alóctones marinhas nas estações chuvosas e eventos de *El Niño*, contrariando as expectativas prévias; (iii) No entanto, corroborando nossa hipótese inicial, houve maior proporção de contribuição relativa de fontes basais de água doce durante eventos de *El Niño* em comparação com eventos de *La Niña*; (iv) por fim, este trabalho destaca a importância de utilizar bancos de dados de longo-prazo e avaliar os impactos dos fenômenos climáticos naturais, como os eventos ENOS que tendem a aumentar sua frequência e intensidade com o aquecimento dos oceanos (CAI *et al.*, 2018; FREUND *et al.*, 2019), para avançar no entendimento da variabilidade temporal no elos tróficos que sustentam consumidores primários estuarinos.

De modo geral, com base nos três capítulos desenvolvidos ao longo dessa Tese, trago algumas perspectivas para estudos futuros. Primeiramente, os três capítulos destacam a importância de monitoramentos padronizados de longo-prazo de variáveis ambientais e das espécies para avaliar os impactos que podem ser ocasionados por fenômenos climáticos naturais (e.g., eventos ENOS) e impactos antrópicos (e.g., sobreexploração pesqueira e aquecimento dos oceanos) na biota. Além disso, os capítulos 1 e 3 mostraram a necessidade de incluir flutuações climáticas naturais, como por exemplo, a ocorrência de eventos *El Niño*, para estimar a abundância ou assimilação de recursos alimentares, pois um recorte de tempo curto que não incluam essas variações podem gerar interpretações errôneas sobre a dinâmica trófica das espécies. Outro aspecto importante é mostrado no capítulo 1, no qual é possível observar o quanto é complexo estimar os impactos do aquecimento dos oceanos na tropicalização da fauna em maiores latitudes, pois desconsiderando as variações climáticas naturais ocasionadas pelos eventos *El Niños* que podem mascarar o efeito do aquecimento das águas, pode gerar interpretações equivocadas. Já o capítulo 2 mostra a necessidade de monitoramentos padronizados e contínuos da pesca para gerar políticas de gestão e fiscalização adequada para evitar o colapso

de estoques pesqueiros. Além disso, destaca-se a necessidade de incluir características da espécie nos modelos como, por exemplo, o ciclo de vida e o período de captura, para ter um resultado mais coerente com a dinâmica populacional da espécie. Por fim, o capítulo 3 destaca a necessidade de estudos futuros sobre os padrões de movimento dos juvenis de tainha dentro do estuário, os quais poderiam auxiliar na compreensão das mudanças temporais na assimilação de fontes autóctones e alóctones.

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ANEXOS

Anexo 1. Outras publicações realizadas durante o doutorado

1. POSSAMAI, B.; VOLLRATH, S. R.; VIEIRA, J. P.; GARCIA, A. M. Synergistic climatic and anthropogenic effects on marine species turnover in estuarine waters. **Science of the Total Environment**, v. 908, p. 168324, 2024. <https://doi.org/10.1016/j.scitotenv.2023.168324>
2. CONDINI, M. V.; GARCIA, A. M.; BASTOS, R. F.; VOLLRATH, S. R.; BARBOSA, E. F.; OLIVEIRA, R. L.; ALMEIDA, L. L.; HOSTIM-SILVA, M. Hydroclimatic influence on the trophic ecology of Atlantic goliath grouper juveniles (*Epinephelus itajara*) in a tropical estuary using non-lethal methodologies. **Marine Environmental Research**, v. 190, p. 106103, 2023. <https://doi.org/10.1016/j.marenvres.2023.106103>
3. GOWERT, Y.; VOLLRATH, S. R.; VIEIRA, J. P.; GARCIA, A. M. Remote and local environmental factors drive long-term trends of an estuarine-dependent marine fish in a subtropical coastal lagoon. **Estuaries and Coasts**, v. 47, p. 244–257, 2024. <https://doi.org/10.1007/s12237-023-01272-0>