UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Dissertação de Mestrado

Trophic plasticity of a specialist shorebird in response to prey and habitat availability

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Porto Alegre

Novembro de 2021

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Mestre em Ecologia.

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Novembro de 2021

"Não longe d'água, tripudiam com suas pernas brancas, com pescoço encolhido e comprido bico vermelho, quatro bejagüís (Haemantopus palliatus). Com um alto <huit-huit>, que lembra o som de uma flauta, afastam-se voando."

Rudolf Gliesch, 1925

A Fauna de Torres

AGRADECIMENTOS

Resumo: As variações espaçotemporais na disponibilidade de recursos alimentares representam um desafio à sobrevivência de organismos especialistas. O ostreiro Americano (ou só "ostreiro") *Haematopus palliatus* é uma espécie costeira, considerada especialista na predação de moluscos bivalves, contudo, o ambiente e as espécies disponíveis para a sua alimentação variam ao longo da sua distribuição. A plasticidade trófica associada à disponibilidade de presas e habitat em áreas de alimentação e reprodução foi hipotetizada. Entre 2017 e 2021, foram amostrados 100 indivíduos em cinco áreas reprodutivas no sul do Brasil, sendo três compostas de substrato misto (arenoso e rochoso) e duas de substrato arenoso. A disponibilidade de macroinvertebrados bentônicos foi avaliada no substrato arenoso, na zona de mesolitoral. Amostras de músculo de presas potenciais e do sangue de *H. palliatus* foram utilizadas para análise de isótopos estáveis de carbono (δ^{13}C) e nitrogênio (δ^{15}N). A variação espaço-temporal da dieta do ostreiro foi observada através de modelos de mistura e nicho isotópico, sugerindo que é influenciada pela variabilidade de habitats de alimentação, e flutuações nos recursos alimentares. Em praias de substrato misto, o ostreiro apresentou nichos isotópicos mais amplos, sugerindo um aumento na riqueza de presas com a disponibilidade de habitats para o forrageio. A contribuição média de bivalves para a dieta do ostreiro foi de cerca de 60%, mas as espécies preferenciais de bivalves variaram entre as áreas de amostragem. Houve variação interanual na dieta associada à variação na disponibilidade de macroinvertebrados em praias arenosas, em especial de outros grupos taxonômicos (i.e. não bivalves). Portanto, embora o ostreiro seja apontado como especialista em bivalves, a espécie apresentou plasticidade trófica influenciada pela variação temporal na disponibilidade de alimentos e heterogeneidade de habitat de forrageio, moldando a composição da dieta, representando um potencial para adaptação local e diferenciação intraespecífica em aves costeiras residentes.

Palavras-chave: Ostreiro, macroinvertebrados bentônicos, dieta, habitat de forrageio, isótopos estáveis.

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Trophic plasticity of a specialist shorebird in response to prey and habitat availability

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Abstract: Spatiotemporal variations in the availability of food resources represent a challenge to the persistence of specialist species. The American oystercatcher (hereafter "oystercatcher") *Haematopus palliatus* is a coastal species, considered a specialist on bivalves, although available feeding habitats and prey species may vary along its distribution. Trophic plasticity associated with habitat and prey availability in foraging areas was hypothesized. Between 2017 and 2021, 100 individuals were sampled in five breeding areas in southern Brazil, three composed by sandy and rocky, and two sandy only, substrates. On the mesolitoral zone, benthic macroinvertebrate availability was assessed at the sandy substrate. Muscle samples of potential prey and blood of oystercatchers were obtained for analysis of carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes. Spatiotemporal variation in the diet of the oystercatcher was observed through mixing models and isotopic niche, suggesting to be influenced by the variability of feeding habitats and fluctuations in the availability of food resources. In the mixed substrate sites, oystercatchers had a wider isotopic niche, suggesting an increase in prey richness in the available foraging habitats. Bivalves contribution to the diet of the oystercatcher was around 60%, but differences in the preferred bivalve species varied among areas. Interannual variation in the diet associated with variation in macroinvertebrate availability on sandy beaches was observed, especially for non-bivalve prey. Therefore, despite the oystercatcher specialization in bivalves, they presented a trophic plasticity indicated by temporal variations in food availability and heterogeneity of foraging habitats shaping dietary composition, representing a potential local adaptation for intraspecific differentiation in resident shorebirds.

Keywords: oystercatcher, benthic macroinvertebrates, diet, foraging habitat, stable isotopes.

Introduction

Specialization promotes diversification and coexistence as it reduces interspecific competition by decreasing niche overlap between species (Chesson 2000). Specialist species have a narrow trophic niche, and characteristics that limit them to a particular habitat or resource (Amundsen et al. 1996). However, spatiotemporal variations in food availability can influence dietary patterns and even species distribution (Hughes 2000). In this context, intraspecific ability to adjust the diet according to the variability of food resources in time and space has been referred to as trophic plasticity. This may represent an advantage in home range and population size expansion, persistence in areas impacted by human activities, or even be a cause for population differentiation through local adaptation (e.g. Mendes et al. 2009; Michel et al. 2016). Trophic plasticity has been reported in many taxonomic groups, including invertebrates, such as gastropods (Riera 2010), corals (Fox et al. 2019), and echinoids (Michel et al. 2016); as well as in vertebrates, such as amphibians (Arribas et al. 2015), fishes (Feary et al. 2018), mammals (Muñoz et al. 2013), birds (Parrish 2000), and highly invasive species (Almeida et al. 2012; Rolla et al. 2020). Nonetheless, for widespread specialists living in a narrow habitat like shorebirds, spatial and temporal variation in food availability can be a challenge for individual survival and population persistence.

Shorebirds exhibit a variety of bill morphology which is largely associated with their foraging strategies (e.g. prey handling, dietary aspects, and microhabitat selection) (Barbosa and Moreno 1999). For example, Haematopodidae is composed of twelve species distributed mainly on coastal regions which are known to be specialists in predating Bivalve species, assigning them common names associated with the preferred prey in English (oystercatchers), Spanish (*ostreros*), and Portuguese (*ostraceiros*), although other common names have also been used. Oystercatchers are specialized in handling and opening bivalves with its long and sharp bill, which is introduced in between valves to cut the adductor muscle, although they can complement their diet with other macroinvertebrates (Hockey 1996). Most oystercatcher species are strictly distributed over the coastline and, therefore, such limited distribution and high specialization can suggest an intraspecific dietary homogenization. Nevertheless, individual feeding specialization has been documented in some species, such as in the Eurasian oystercatchers (*Haematopus ostralegus*) (van de Pol et al. 2009; van der Kolk et al. 2020).

The American oystercatcher *Haematopus palliatus* (hereafter "oystercatcher") is distributed on the Atlantic Ocean coast, from the northeastern United States to southern

Argentina, and on the Pacific Ocean coast, from northern Mexico to Central Chile (Nol and Humphrey 1994). It forages in sandy and rocky shores, salt marshes, estuaries, river islands and coastal lagoons (Hayman et al. 1986; McGowan et al. 2005; Virzi 2010). Punctual studies about the oystercatcher diet and foraging techniques along the Atlantic coast of South America were carried out through visual observations (Bachmann and Martínez 1999; Fedrizzi 2008; García et al. 2010) fecal analysis (Fedrizzi 2008), and recently prey remains and stable isotopes (Linhares et al. 2022). These studies have shown that even if the diet of the oystercatcher is largely based on bivalves, other prey species are also commonly consumed. However, spatial variation on foraging habitat availability has not yet been considered on a broader geographical scale, although it could shape prey availability and thus composition of oystercatcher diet. Stable isotopes have been widely used to study trophic relationships in a variety of organisms and environments, as such markers enable to estimate dietary variations and contributions of different food sources to an animal's diet (Garvey and Whiles 2017). Stable isotopes also provide spatiotemporal insights into trophic relationships among organisms, reconstructing food webs and providing information on trophic niche variations (Boecklen et al. 2011; Layman et al. 2012). For example, carbon and nitrogen are major components of animal tissues and measurements of its isotopic ratios (δ^{13}C and δ^{15}N, respectively) followed by two-dimensional analysis provide valuable information to estimate contribution of food sources (Parnell and Inger 2021) and isotopic niche (Jackson et al. 2011). Also, δ^{15}N can be used to estimate trophic levels, while δ^{13}C may be used to estimate the flow of distinct origins matter, providing information on foraging areas (Peterson and Fry 1987). Diet composition may also vary according to prey availability, so that assessment of variation in food availability is relevant to estimate its effect on dietary variations in space and time (Huckembeck et al. 2014; Divine et al. 2017). Therefore, the combination of stable isotope analysis and prey sampling to evaluate which resources are available and consumed at a given time and space can provide accurate information to depict a species trophic plasticity.

In this context, the present study aimed to assess if trophic interactions of a widely distributed specialist shorebird vary according to prey and habitat availability in different sites and seasons. Trophic plasticity associated with habitat and prey availability in foraging areas adjacent to breeding sites was hypothesized, challenging the widespread paradigm of oystercatchers as bivalve specialists. Specifically, diet composition was expected to be mostly dominated by bivalves across the study area, but with distinct bivalve and additional prey species among sites with sandy or mixed substrates (sandy and rocky). To evaluate this

hypothesis, a dataset containing carbon and nitrogen isotopic ratios from oystercatcher and macroinvertebrate samples was used, obtained in five breeding sites on sandy and mixed substrate beaches in the southern Brazilian coast, a key conservation site for the species (Clay et al. 2014). Differences in prey availability on the sampled sandy beaches were tested as a potential cause of dietary variation among the sampled areas and seasons.

Materials and methods

Study sites

Fieldwork was carried out on five sandy beaches along 280 km coastline in southern Brazil (Fig. 1) which are breeding sites for oystercatchers. The northern sites, Passo de Torres, Praia Grande and Itapeva are beaches with mixed substrate while the southern sites, Praia das Cabras and Lagoa do Peixe, are composed by sandy substrate only (Fig. 1). The breeding sites in southern Brazil also hold additional landscape elements which are suggested to influence oystercatcher diet: (i) near the mixed substrate area there is a rocky island about 2 km offshore (*Ilha dos Lobos*), which is a marine protected area used as a foraging site by oystercatchers from Praia Grande to obtain *Perna perna* (Linhares et al. 2022); (ii) near the mixed substrate areas and in Lagoa do Peixe there are estuarine systems. However, suitable estuarine foraging environments for oystercatchers, such as mudflats and saltmarshes, are only available in Lagoa do Peixe (Fedrizzi 2008), given the urbanization of the estuarine margins in Passo de Torres and Praia Grande. Final, (iii) Praia Grande, Passo de Torres and Praia das Cabras are urban beaches, while Itapeva and Lagoa do Peixe are protected areas, named *Parque Estadual de Itapeva* and *Parque Nacional da Lagoa do Peixe*, respectively.

Sampling and laboratory procedures

Breeding oystercatchers and chicks were sampled during four consecutive breeding seasons (i.e. September–March) from 2017 to 2021. Birds were caught at night using flashlights and handle nets. Chicks were sampled with a minimum age of three weeks because blood turnover rate for birds is between 15-20 days (Boecklen et al. 2011), in order to ensure that isotopic values in whole blood do not belong to egg nutrients (Ogden et al. 2004). Whole blood samples (~0.1 ml) were collected from the tarsal vein and subsequently stored in microtubes containing anhydrous ethanol. A small drop of blood was also collected on filter paper and used for sexing the birds with molecular methods (Griffiths et al. 1998). Birds were identified with metal rings

to avoid resampling. Macroinvertebrates were sampled on sandy beaches for four out of the five sites, due to logistical constraints at Passo de Torres. Only sandy substrate was sampled because it was common to all sites and allowed resource availability comparison. Sampling occurred in the spring (October and November) of 2019 and 2020, to overlap with the sampling period of oystercatchers during the nesting season. Praia Grande, Itapeva, and Lagoa do Peixe were sampled both in 2019 and 2020, while Praia das Cabras was only sampled in 2019. For each site, ten equidistant points were sampled along a 1 km transect in the mesolitoral zone. Macroinvertebrate samples were obtained with a 20 cm diameter PVC corer inserted 20 cm in the sand, then sieved with a 1 mm mesh (McLachlan and Defeo 2018) and stored into tubes containing 70% ethanol. In the laboratory, samples were analyzed with a stereoscopic microscope and invertebrates were identified at the lowest possible taxonomic level. Samples were identified according to date, site, and sampling point, and individuals were counted to estimate macroinvertebrate abundance.

For stable isotope analysis, whole blood from the oystercatchers, muscle tissue from bivalves, and whole body of smaller prey groups were used. Whole blood of birds has a 15 to 20 days turnover rate and, therefore, stable isotope measurements of this tissue roughly represent what has been assimilated in the last two to three weeks (Boecklen et al. 2011). To remove lipids, prey samples were washed in a Soxhlet extractor during a 6 h cycle, using a 2:1 chloroform:methanol solution as solvent (Logan and Lutcavage 2008; Nunes et al. 2018). Prey and blood samples were then freeze-dried, grounded and subsamples of ~0.7 mg were placed into tin capsules for analysis using isotope ratio mass spectrometry at the *Centro Integrado de Análises* at the *Universidade Federal do Rio Grande* (CIA-FURG, Brazil). Values are provided in δ and expressed in ‰ in the following equation (Bond and Hobson 2012):

$$\delta^{13}\text{C } or \text{ } \delta^{15}\text{N (‰)} = \left(\left(\frac{Rsample}{Rstandard} \right) - 1 \right)$$

The internal standards of the laboratory (glutamic acid and caffeine) were interspersed among unknown samples, and had a standard deviation of 0.1‰ for δ^{13}C and 0.4‰ for δ^{15}N. The international standard for carbon was Vienna Pee Dee Belemnite and for nitrogen was atmospheric air.

Statistical analysis

Univariate differences in isotopic values among areas, years and sexes were assessed with nonparametric Kruskal-Wallis test and a Dunn's test as a post hoc with a Benjamini-Hochberg procedure to control the false discovery rate (Legendre and Legendre 2012) using the "FSA" package (Ogle et al. 2021). Isotopic niches were estimated through a Bayesian framework as implemented in the *SIBER* package (Stable Isotope Bayesian Ellipses in R), from which Standard Ellipse Areas corrected for small sample sizes (SEAc) were evaluated for each site, year and sex and the pairwise overlap value between ellipses was calculated (Jackson et al. 2011). Contribution of different prey to the diet of oystercatchers was estimated with Bayesian mixing models as implemented in the *simmr* package (Stable Isotope Mixing Models in R) (Parnell and Inger 2021). Discriminant factors used in the mixture models were 0.2‰ (±0.4‰) for δ^{13}C and 2.7‰ (±0.4‰) for δ^{15}N as estimated for *Haematopus moquini* (Kohler et al. 2011). Information from previous studies (Fedrizzi 2008; Linhares et al. 2022), field observations and type of substrate were used to select prey types included in the mixing models of each site. *Amarilladesma mactroides, Donax hanleyanus, Emerita brasiliensis, Excirolana armata, Olivancillaria v. auriculata* and Polychaeta were used for all sites. *Perna perna* was included only for sites with rocky substrate (Passo de Torres, Praia Grande and Itapeva; Linhares et al. 2022), and *Tagelus plebeius* was included only for the lagoon-estuarine environment in Lagoa do Peixe (Fedrizzi 2008).

Relative abundance and frequency of occurrence were calculated for the macroinvertebrate to depict variation in food availability for oystercatchers in sandy beaches. Difference in macroinvertebrate composition for the sites was tested with a Permutational Multivariate Analysis of Variance (PERMANOVA, permutations = 999) with abundance data and Bray-Curtis index, and with a Non-Metric Multidimensional Scaling (nMDS), using the Bray-Curtis index using the "vegan" package (Oksanen et al. 2020).

Results

A total of 100 birds were sampled during the breeding seasons from 2017 to 2021 (Table 1, see Table S1). Also, 48.9% of the birds were males and 51.1% were females (n=94, Table 1); and adults represented 74.2% (n=93, Table 1). A Kruskall-Wallis analysis showed significant difference between all areas for δ^{15}N values. However, for δ^{13}C values, significant differences

were found for fewer sites (see Table S2). No significant differences were found between sexes for any site (see Table S3).

Significant interannual differences were found for Praia Grande among all years sampled (2018, 2019, 2020 and 2021) for $\delta^{13}C$ only (see Table S4), and the widest isotopic niche was observed for 2018 (SEAc = 2.35; Fig. 2, see Table S5). At Lagoa do Peixe, significant differences were found between 2020 and 2021 for $\delta^{13}C$ (see Table S6), and isotopic niche was wider in 2020 (Fig. 2, see Table S5). At Itapeva, 2019 and 2020 also differed significantly only for $\delta^{13}C$; and finally, at Passo de Torres the years 2019 and 2020 differed for $\delta^{15}N$ (see Table S6).

Sites with mixed substrate presented wider isotopic niche areas than sites with only sandy substrate. The widest isotopic niche breadth was found at Praia Grande (SEAc = 2.80), and the narrowest niche was found at Lagoa do Peixe (SEAc = 0.46). Itapeva had the second largest niche width (SEAc = 1.31), followed by Passo de Torres (SEAc = 0.77) and Praia das Cabras (SEAc = 0.75) (Fig. 2, see Table S7). The highest isotopic niche overlap among sites occurred between Praia das Cabras and Lagoa do Peixe (0.39, both sandy beaches), followed by Praia Grande and Itapeva (0.37, both mixed substrate beaches and the closest sites) (Table 2).

The macroinvertebrate taxa found in the samples at the sandy beaches were *E. brasiliensis*, *D. hanleyanus*, *A. mactroides*, *E. armata*, Amphipoda and Polychaeta. In 2019, a total of 2,853 macroinvertebrates were counted, whereas in 2020 the total abundance was 5,360 macroinvertebrates. Relative abundance of macroinvertebrates was similar between Praia Grande and Itapeva in 2019, and frequency of occurrence was similar for all places in both years (Fig. 3). Macroinvertebrate composition was similar for all sandy beaches, but abundance differed mainly between northern sites (Praia Grande and Itapeva) and the southern site Lagoa do Peixe. In 2019, bivalve relative abundance was higher at southern sites than at northern. Relative abundance of the crustacean *E. brasiliensis* in 2020 was higher than 2019 for all sites sampled (Fig. 3).

NMDS analysis and PERMANOVA showed similarities between Praia Grande and Itapeva, and significant differences between these areas and Lagoa do Peixe (Fig. 4). For 2019, PERMANOVA analysis showed significant differences between all areas except between Praia Grande and Itapeva, and in 2020 significant differences were found only between Praia Grande and Lagoa do Peixe (see Table S8 and Table S9).

Mixing models indicated that bivalves contributed most substantially to the oystercatcher diet, ranging from 36.7% at Passo de Torres to 88.6% at Praia Grande, with an average contribution of about 60% for all sites (Table 3 and Fig. 5). In sites with a lower contribution of bivalves, some other preys, such as the polychaeta and the crustacean *E. brasiliensis*, assumed greater importance (Table 3 and Figs. 5 and 6). Mixing model results also showed differences in the most consumed bivalve species among sites; the highest contribution of *P. perna* occurred at Praia Grande, *D. hanleyanus* was more important at Praia das Cabras and *T. plebeius* at Lagoa do Peixe (Fig. 6). To analyze differences in the diet between years, mixing models were made for Praia Grande and Lagoa do Peixe. In Praia Grande *P. perna*, *D. hanleyanus* and *E. brasiliensis* varied their contribution between years, while the other species remained similar. At Lagoa do Peixe, *T. plebeius* had a lower contribution in 2021 than in 2020, while *E. brasiliensis* presented a higher contribution in the last sampling period (Fig. 7).

Discussion

The diet of a widely distributed specialist shorebird is proposed to be shaped by variations in food resource availability, which is representative of trophic plasticity both in space and time. Presence of rocky substrate around sandy beaches and locations with heterogeneous estuarine-like landscapes can broaden oystercatcher trophic niches, since hard-bottom habitats represent additional ecological feeding opportunities for oystercatchers. In addition, interannual variations in diet could be associated to the highly dynamic macroinvertebrate community in sandy beaches of the southwest Atlantic Ocean, which is influenced by physicochemical, geological, and hydrological factors (McQuaid and Lindsay 2000; Parise et al. 2009; Coutinho et al. 2016; McLachlan and Defeo 2018). Nonetheless, bivalve preference is confirmed in oystercatchers in all sites, despite the variation in bivalve species and additional prey consumed among distinct sampled areas and years, shedding light on the capacity and constraints for the local adaptation of a specialist predator.

Oystercatchers are restricted to the coastline and preferentially feeds on bivalves, but the consumption of habitat-specific prey species can be indicative of its feeding strategies and habitat use. The use of mudflats was evidenced by the high contribution of *T. plebeius* in Lagoa do Peixe, which occurs in the lagoon-estuarine environment (Holland and Dean 1977) and composes the diet of oystercatchers along with sandy beach prey species, as has been observed in foraging sites in Argentina (Bachmann and Martínez 1999) and previously documented for

Lagoa do Peixe by Fedrizzi (2008). Typical macroinvertebrates of sandy beaches in southern Brazil, such as *A. mactroides*, *D. hanleyanus*, and *E. brasiliensis* (Gianuca 1985) were most consumed by oystercatchers from Praia das Cabras, evidencing that the availability of suitable prey in the sandy beach shapes the diet of that group. Finally, *P. perna* contributed in distinct proportions for the diet of oystercatchers from beaches with mixed substrate, indicating that rocky shores or even coastal islands can be relevant food sources around nesting areas, as previously mentioned by Linhares et al. (2022). In this context, habitat selection in oystercatchers seems to be related to the availability of bivalves, but dietary studies looking at the prey species level can also provide information on habitat use.

Occurrence of oystercatchers in heterogeneous coastal regions may influence trophic niche width since oystercatchers foraging in sites with mixed substrate presented wider isotopic niches than sites with sandy substrate only. Isotopic niche widening could be related to the increased prey diversity provided by foraging areas with distinct landscape elements, which has also been reported for African black oystercatchers (*H. moquini*) using sandy and rocky substrates in South Africa (Scott et al., 2012). The substantially higher contribution of *P. perna* (~70%) to the diet of oystercatchers from Praia Grande, in comparison with the other mixed substrate beaches, is an indicative of frequent use of the rocky substrates nearby as foraging sites. Consuming prey from rocky substrates can be an alternative in case it is not possible to access macroinvertebrates in sandy beaches, due to disturbance for example, which are immediately adjacent to oystercatcher nests and therefore easier to access. Nonetheless, Praia Grande is an urbanized area with massive touristic use during austral spring and summer (Zuanazzi and Bartels 2016), which overlaps with the chick-rearing period for oystercatchers (Linhares et al. 2021). Therefore, human disturbance on sandy beaches can also be a relevant factor shaping the trophic niche and habitat selection by oystercatchers. Also, the increased importance of a rocky shore bivalve (i.e. *P. perna*), which can be captured at the marine protected area of *Ilha dos Lobos* (located 2 km offshore Praia Grande) or nearby rocky shores, can relieve oystercatchers from the pressure of human disturbance on the beachfront, which was thereby suggested to explain the persistence of oystercatchers nesting in Praia Grande (Linhares et al. 2022).

Moreover, although macroinvertebrate availability on the beach may be negatively impacted by human presence (Schlacher et al. 2016; Bom and Colling 2020), no substantial differences were observed in the sandy benthic community between mixed substrate beaches. This suggests that in the presence of the same food resources, the use of prey from rocky

substrate may be a consequence of human disturbance on the sandy beach. Accordingly, Itapeva also has a mixed substrate with macroinvertebrate community in the sandy beach similar to Praia Grande, but the contribution of *P. perna* was lower (~15%) and bivalves of sandy substrates were more important to the oystercatcher diet. This finding suggests that feeding on sandy beaches adjacent to nesting areas can be preferred over more distant rocky substrates when human disturbance is lower. Following the optimal foraging theory (MacArthur and Pianka 1966), prey from the sandy beach may be preferred as they are closer to the nesting areas in fore dunes (Linhares et al. 2021), which allows for quick and easy access to prey during the incubation and chick-rearing periods. However, beaches with heterogeneous landscapes can be advantageous as they allow the use of alternative foraging areas (i.e. rocky shores), which could be crucial depending on the intensity of human disturbance. In contrast, on beaches with only sandy substrate the population persistence may be compromised in case food resources are inaccessible due to human disturbance, which has been referred as the main threat for birds using coastal environments (Dias et al. 2019). Finally, since the studied area is a key conservation site for the species (Clay et al. 2014), it is important to preserve natural sandy beaches from human impacts to ensure reproduction and feeding requirements for oystercatchers in this region.

Interannual dietary variation seems to be associated to temporal fluctuations in prey availability both in rocky and sandy substrate, which can be referred as trophic plasticity. Composition, distribution, and species-specific abundances of benthic community in sandy beaches are highly variable and dependent on complex and multifactorial biotic and abiotic interactions (McLachlan and Defeo 2018). As pointed out, oystercatchers seem to select foraging areas due to the availability of bivalves, but they also opportunistically prey upon additional taxa following its variations in availability. For instance, abundance of *E. brasiliensis* in benthic samples from Lagoa do Peixe increased from 2019 to 2020, as well as its contribution to the diet. On their turn, *D. hanleyanus* followed the opposite trend, as its relative abundance in the sandy substrate decreased from 2019 to 2020, which was also observed for its contribution to the diet during the same period. On rocky substrate, macroinvertebrates such as *P. perna* at *Ilha dos Lobos*, may present fluctuations in availability for oystercatchers due to tidal variations and biological interactions among the benthic community (McQuaid and Lindsay 2000; Coutinho et al. 2016). For example, the rocky island, which is at most 3m above sea level, can stay partially submerged and not accessible for birds during syzygy tides or extreme weather events, such as high energy swell or windstorms (Parise et al. 2009). This

could explain interannual variations of *P. perna* contribution for oystercatchers nesting in mixed substrate sites. In fact, Garcia et al. (2010) reported that during the macroalgal blooms in the San Antonio Bay, Argentina, oystercatchers avoided two prey species with high profitability values, shifting their foraging strategy and feeding onto a suboptimal prey but with a high encounter rate. Therefore, despite the preference and specialization in capturing bivalves, the oystercatcher diet can vary both spatially and temporally following local fluctuations in macroinvertebrate community, illustrating the concept of trophic plasticity (Feary et al. 2018; Fox et al. 2019).

The oystercatcher has been considered a specialist in the literature, but being a specialist or a generalist may depend on which taxonomic level the prey is analyzed. Hughes (2000) classified specialists in two groups, fundamental and local, the first using the same narrow range of resources across multiple spatial scales, and the second using a narrow range of local resources, but varying regionally and/or temporally. Preference on the Class Bivalvia was observed for oystercatchers in all sites but the bivalve species varied on a regional scale, which is representative of a local specialist (Hughes 2000). Local resources for the oystercatcher are constrained by multiple factors, including substrate type, disturbance and variable natural conditions, which affect prey availability and have a fundamental influence on dietary composition (Lawton et al. 2012). In this context, it seems that the availability of bivalves represents a requirement for oystercatcher distribution, which could be tested considering oystercatcher sightings along its home range and the association with benthic invertebrate occurrence. For instance, understanding global patterns of the oystercatcher occurrence and its potential drivers could explain the disjoint distribution of oystercatchers along the Brazilian coast, as well as in other coastal regions of the Americas where the species is absent; as well as to reinforce the role of southern Brazil as a key conservation site for the species (American Oystercatcher Working Group et al. (2020)).

The oystercatcher is an obligate coastal species, which makes it particularly vulnerable to climate change and severe weather (Clay et al. 2014). Besides the reduction in habitat due to the rise in sea-level, climatic changes are also causing alterations in the marine environment such as changes in seawater temperature and ocean acidification. These changes may generate fluctuations in the availability of food resources (Harley et al. 2006; Przeslawski et al. 2008; Birchenough et al. 2015; Coutinho et al. 2016) and make a specialist coastal species even more vulnerable. Modification of intertidal invertebrate communities by human presence or activities, and the loss of breeding sites has already led to the extinction of the Canarian black

oystercatcher in 1913 (Hockey 1987). Severe changes in food availability and nesting areas could threaten oystercatchers in southern Brazil. However, spatiotemporal trophic plasticity of this shorebird should allow adaptation to climate change, as long as there is suitable habitat for breeding and at least some of its preferred prey on the feeding territory.

Conclusions

Trophic plasticity of a specialist shorebird, the oystercatcher, was identified with isotopic analysis and macroinvertebrate sampling. Constrained distribution over the coastline and high specialization could suggest intraspecific homogenization of the oystercatcher diet, but depending on the taxonomic scale analyzed, spatiotemporal trophic plasticity was observed within a 280 km study area. Substrate and habitat availability played an important role in defining oystercatcher diet, so that preferred prey species were used as proxies of its habitat use. Further studies should focus on studying macroinvertebrate and habitat availability along the Brazilian coastline to understand the effect on shorebirds distribution, since it is crucial for persistence of both resident species, such as the oystercatcher, and Nearctic migratory species, which use the Atlantic Flyway and depend on stopover sites for refueling.

Ethical approval: *Instituto Chico Mendes de Conservação da Biodiversidade* (ICMBio) granted sampling permit no. 64234–3. All applicable institutional guidelines for the care and use of animals were followed and approved by the *Comissão de Ética no Uso de Animais* (CEUA/UFRGS).

Conflict of Interest: The authors declare that they have no conflict of interest.

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Table 1 Site with substrate type, sample size (n), total number of adults (A) and chicks (C), total number of females (F) and males (M) and mean ± standard deviation of carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic ratios for whole blood samples of American oystercatchers *Haematopus palliatus* from southern Brazil

Site (substrate)	*n*	A/C	F/M	δ^{13}C (‰)	δ^{15}N (‰)
Passo de Torres (mixed)	9	5/1	5/4	-13.37 ± 0.51	13.34 ± 0.79
Praia Grande (mixed)	42	24/18	20/22	-14.58 ± 0.86	12.69 ± 1.19
Itapeva (mixed)	18	11/3	10/8	-14.75 ± 0.73	13.79 ± 0.57
Praia das Cabras (sandy)	7	5/2	2/2	-14.23 ± 0.28	13.07 ± 0.75
Lagoa do Peixe (sandy)	24	24/0	10/11	-13.90 ± 0.25	12.31 ± 0.68

Table 2 Isotopic niche overlap between foraging sites of American oystercatchers *Haematopus palliatus* from southern Brazil, calculated with SIBER package with ellipses comprising 95% of the data

	Passo de Torres	Praia Grande	Itapeva	Praia das Cabras	Lagoa do Peixe
Passo de Torres	1.00	-	-	-	-
Praia Grande	0.19	1.00	-	-	-
Itapeva	0.22	0.37	1.00	-	-
Praia das Cabras	0.18	0.27	0.29	1.00	-
Lagoa do Peixe	0.13	0.16	0.08	0.39	1.00

Table 3 Contribution (mean ± standard deviation in %) of macroinvertebrates to the diet of American oystercatchers *Haematopus palliatus* in breeding sites along the southern Brazilian coast estimated with Bayesian stable isotope mixing models

Macroinvertebrates	Passo de Torres	Praia Grande	Itapeva	Praia das Cabras	Lagoa do Peixe
Amarilladesma mactroides	12.7 ± 10.6	6.7 ± 9.7	21.9 ± 17.3	24.6 ± 18.6	11.9 ± 7.6
Donax hanleyanus	11.8 ± 9.6	13.2 ± 20.2	21.5 ± 15.7	36.0 ± 20.6	17.2 ± 9.6
Perna perna	12.2 ± 9.9	68.7 ± 23.2	15.3 ± 11.6	-	-
Tagelus plebeius	-	-	-	-	24.6 ± 12.4
Total Bivalves	36.7	88.6	58.7	60.6	53.7
Emerita brasiliensis	17.4 ± 14.5	4.2 ± 4.3	10.4 ± 9.1	17.2 ± 15.1	31.4 ± 15.5
Excirolana armata	13.0 ± 10.7	2.9 ± 2.3	14.3 ± 11.8	9.6 ± 7.9	6.5 ± 5.1
Olivancillaria v. auriculata	8.4 ± 5.5	1.7 ± 1.2	10.9 ± 4.9	4.9 ± 3.5	2.5 ± 1.6
Polychaeta	24.6 ± 11.7	2.6 ± 2.0	5.7 ± 4.3	7.7 ± 6.2	5.9 ± 3.7
Total other prey	63.3	11.4	41.3	39.4	46.3

Figure Captions

Fig. 1 Breeding sites of American oystercatchers *Haematopus palliatus* along the southern Brazilian coast. Rocky substrate with *Perna perna* near to Praia Grande (red arrow); fore dunes and mudflats in Lagoa do Peixe (yellow arrow). Photo: Mar Pedro de Abreu

Fig. 2 Bayesian ellipses representing isotopic niche of the American oystercatcher (δ in ‰). Ellipses comprise 95% of the data. Isotopic ellipses considering all sites (top), distinct years in Praia Grande and Lagoa do Peixe (middle), and intersexual differences (bottom)

Fig. 3 Relative abundance (%) and frequency of occurrence (%) of macroinvertebrates sampled on sandy beaches. PG19 = Praia Grande in 2019; ITA19 = Itapeva in 2019; PC19 = Praia das Cabras in 2019; LP19 = Lagoa do Peixe in 2019, PG20 = Praia Grande in 2020; ITA20 = Itapeva in 2020; LP20 = Lagoa do Peixe in 2020

Fig. 4 Non-Metric Multidimensional Scaling (nMDS) for macroinvertebrate samples obtained in 2019 (left) and 2020 (right) in sandy beaches. PG = Praia Grande; ITA = Itapeva; PC = Praia das Cabras; LP = Lagoa do Peixe. Stress$_{2019}$ = 0.1589; Stress$_{2020}$ = 0.1988

Fig. 5 Sankey diagrams based on Bayesian stable isotope mixing models considering American oystercatchers grouped from 2017 to 2021 (left) and prey species (right) considering (**A**) Bivalvia at the species level; and (**B**) Bivalvia at the Class level. The width of the arrow represents prey contribution to the oystercatcher diet

Fig. 6 Outputs of stable isotope mixing models demonstrating the contribution of each item (source) to American oystercatchers from different sites. Prey = *Donax hanleyanus*, *Amarilladesma mactroides,* Polychaeta, *Emerita brasiliensis*, *Excirolana armata*, *Olivancillaria v. auriculata*, *Perna perna*, *Tagelus plebeius*. Sites = Passo de Torres, Praia Grande, Itapeva, Praia das Cabras, Lagoa do Peixe

Fig. 7 Outputs from stable isotope mixing models demonstrating the contribution of each item (source) in distinct years for American oystercatchers from Praia Grande and Lagoa do Peixe. Prey = *Donax hanleyanus*, *Amarilladesma mactroides*, Polychaeta, *Emerita brasiliensis*, *Excirolana armata*, *Olivancillaria v. auriculata*, *Perna perna*, *Tagelus plebeius*
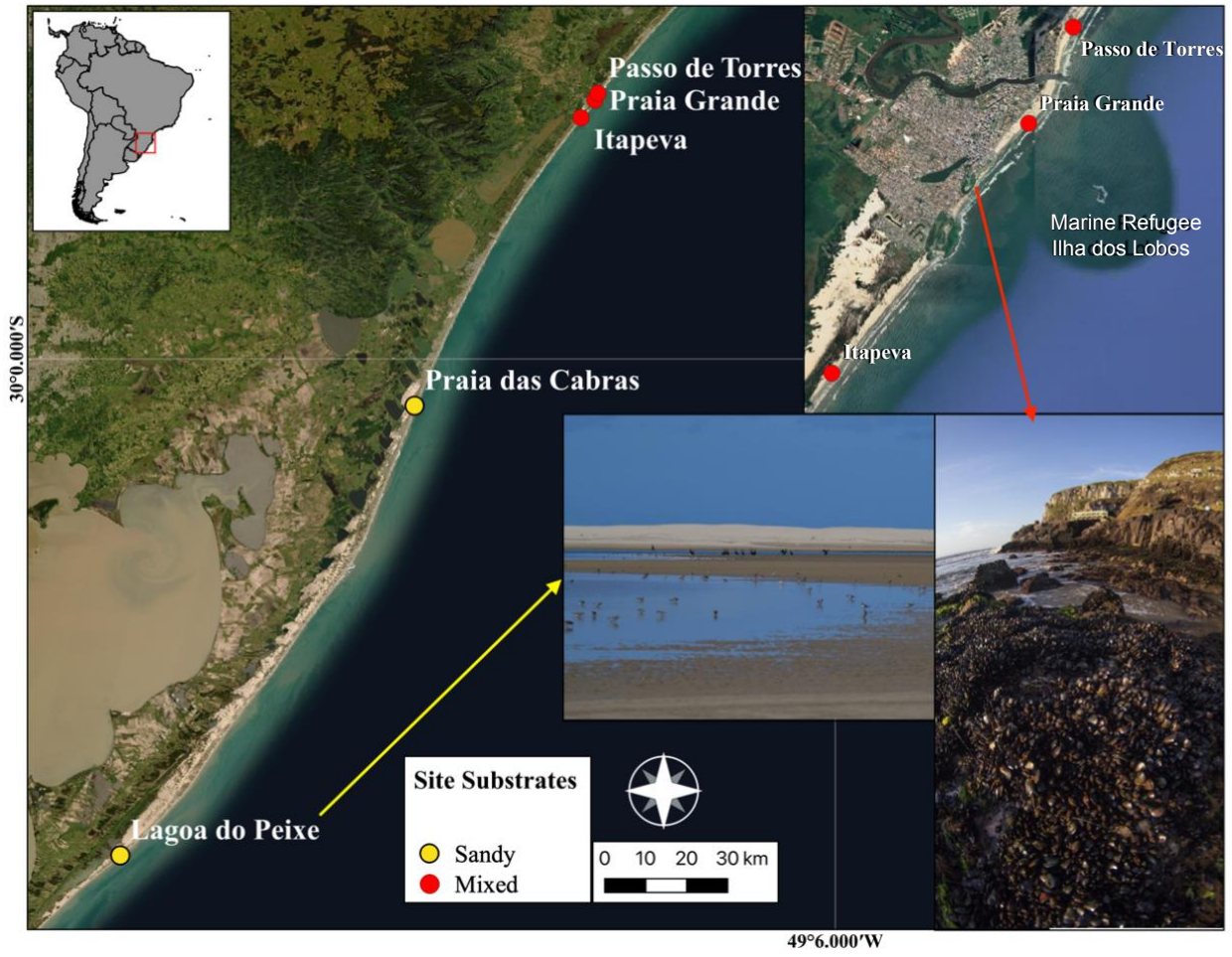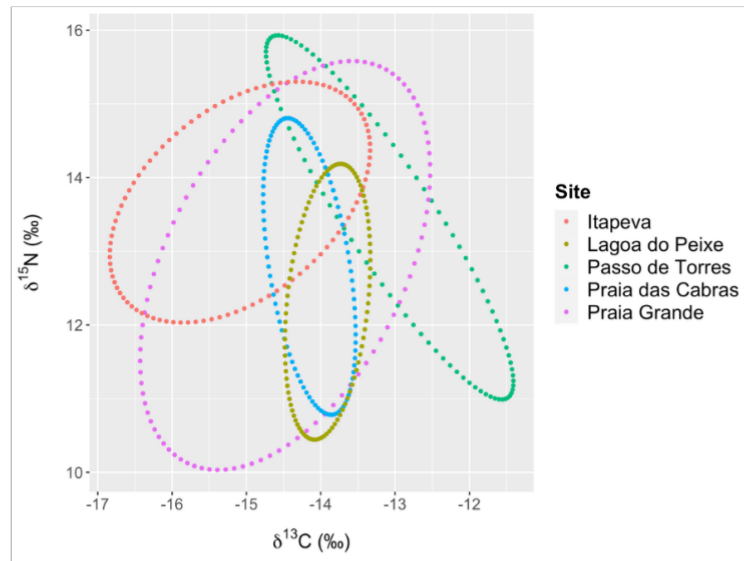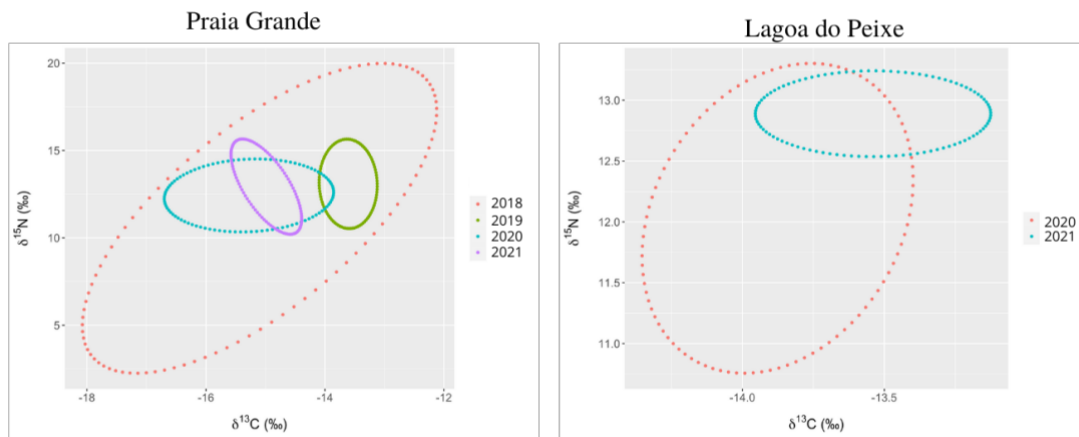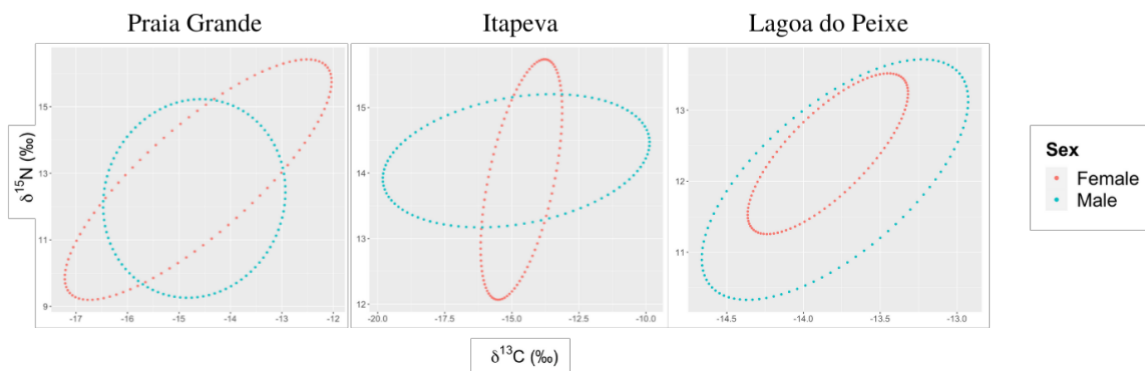
Fig. 1

Sites

Years

Sex

Fig. 2
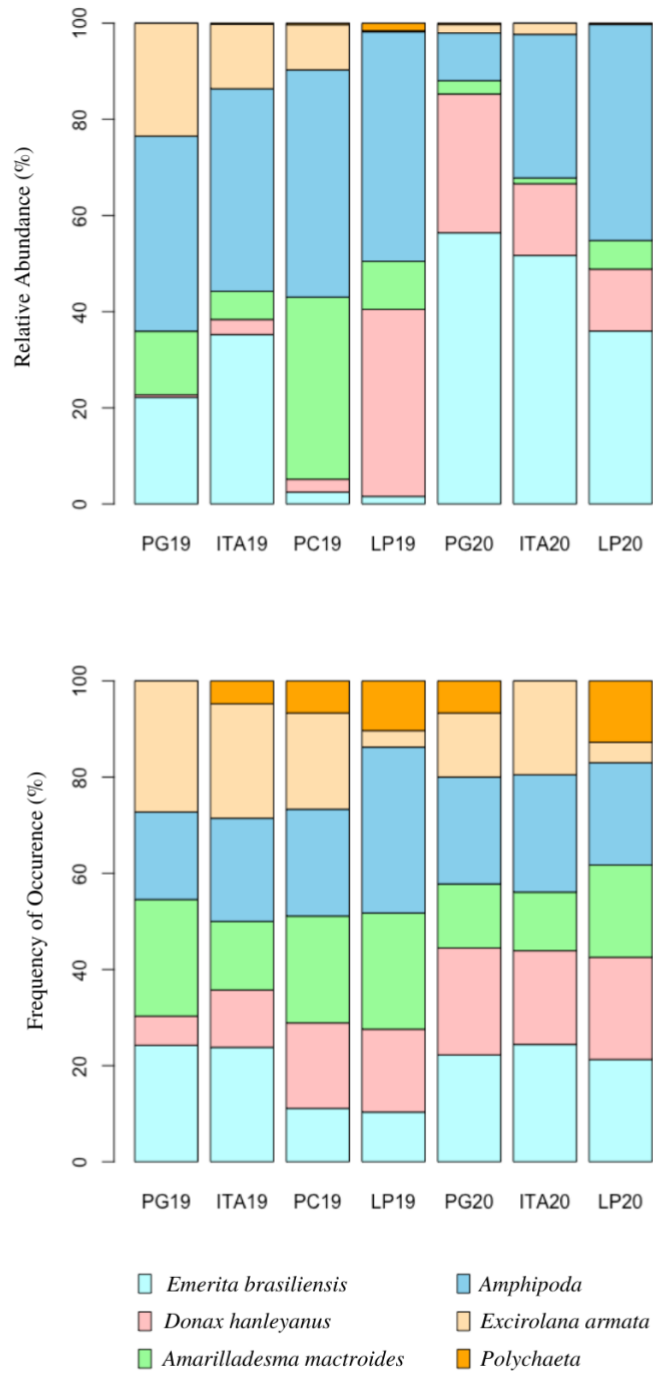
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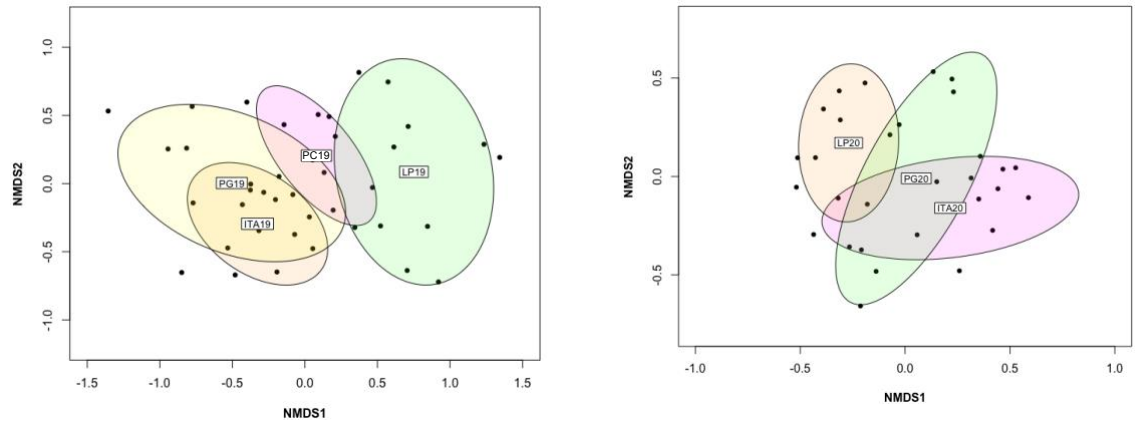
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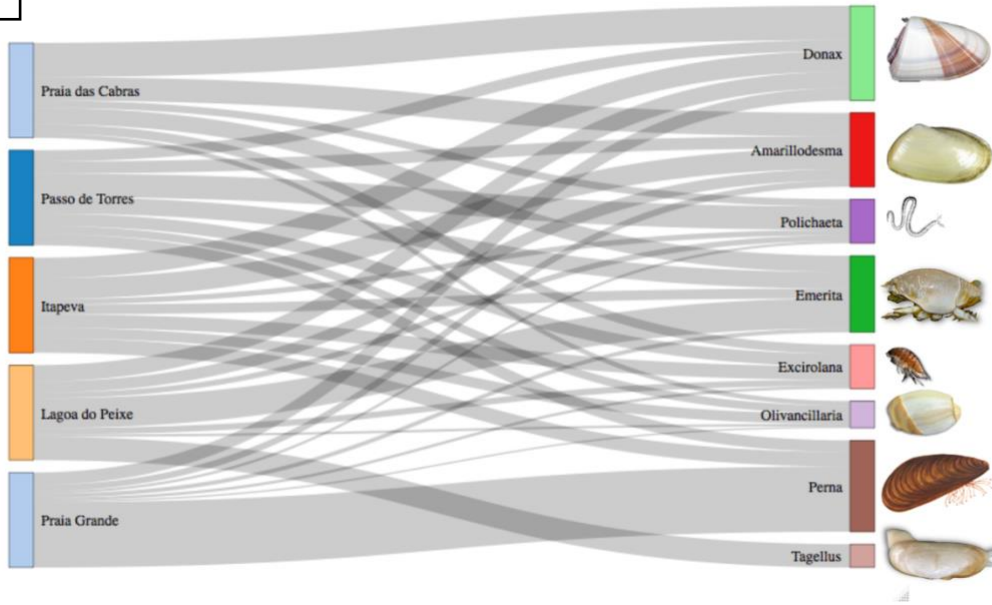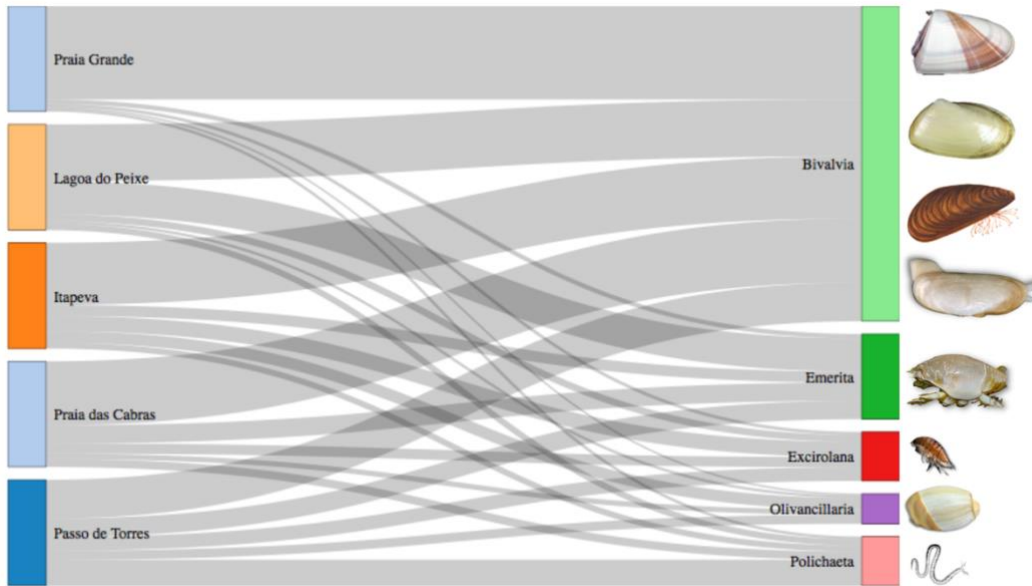
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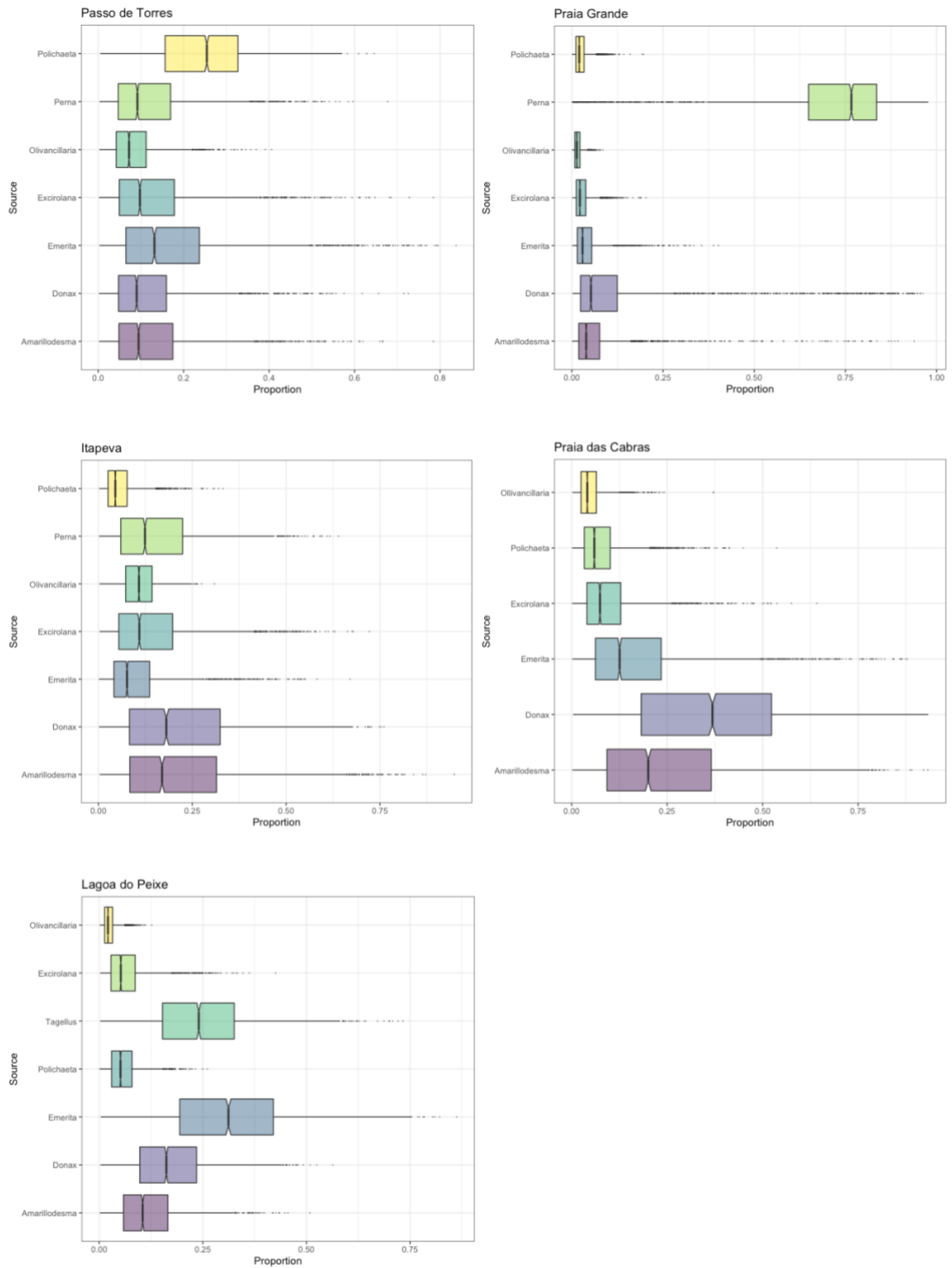
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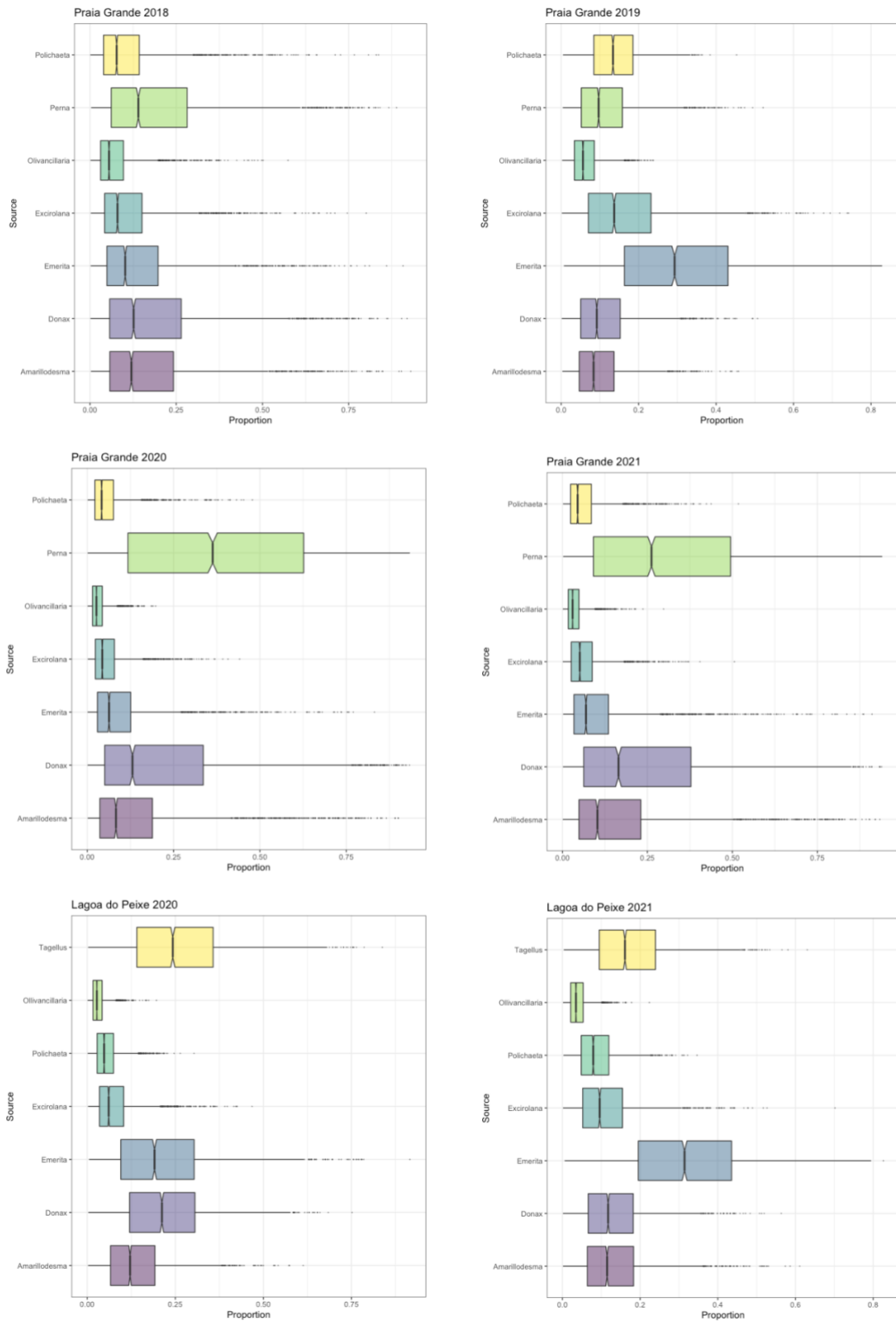
Fig. 7

Supplementary material

Table S1 Identification (ID), season, site, sex, age and nitrogen and carbon isotopic values for each sampled bird (*Haematopus palliatus*)

ID	Season	Site	Sex	Age	$\delta^{15}N$	$\delta^{13}C$
1	2018	Praia Grande	Female	Adult	12,39	-14,12
2	2018	Praia Grande	Female	Chick	9,22	-16,38
3	2018	Praia Grande	Male	Adult	12,75	-13,83
4	2018	Praia Grande	Male	Adult	12,35	-14,78
5	2018	Praia Grande	Male	Adult	12,47	-14,33
6	2018	Praia Grande	Male	Chick	8,96	-15,80
7	2019	Itapeva	Female	Adult	14,03	-13,07
8	2019	Itapeva	Male	Adult	14,10	-13,21
9	2019	Itapeva	Male	Adult	13,81	-13,66
10	2019	Passo de Torres	Female	Adult	13,17	-13,05
11	2019	Passo de Torres	Female	Adult	12,65	-13,05
12	2019	Passo de Torres	Female	Chick	12,50	-13,22
13	2019	Passo de Torres	Female	-	13,06	-13,01
14	2019	Passo de Torres	Male	Adult	13,10	-13,04
15	2019	Passo de Torres	Male	-	12,87	-13,20
16	2019	Passo de Torres	Male	-	13,51	-13,26
17	2019	Praia Grande	Female	Adult	14,31	-13,75
18	2019	Praia Grande	Female	Adult	13,74	-13,44
19	2019	Praia Grande	Female	Adult	13,60	-13,19
20	2019	Praia Grande	Female	Adult	13,81	-13,46
21	2019	Praia Grande	Female	Chick	14,11	-13,73
22	2019	Praia Grande	Female	Chick	12,76	-14,01
23	2019	Praia Grande	Female	Chick	13,18	-13,66
24	2019	Praia Grande	Female	Chick	12,43	-13,82
25	2019	Praia Grande	Male	Adult	14,19	-13,26
26	2019	Praia Grande	Male	Adult	13,34	-13,59
27	2019	Praia Grande	Male	Adult	13,06	-13,34
28	2019	Praia Grande	Male	Chick	13,42	-13,74
29	2019	Praia Grande	Male	Chick	11,80	-13,86
30	2019	Praia Grande	Male	Chick	12,13	-13,69
31	2020	Itapeva	Female	Adult	13,81	-15,33
32	2020	Itapeva	Female	Adult	14,19	-14,75
33	2020	Itapeva	Female	Adult	12,88	-14,87
34	2020	Itapeva	Female	Adult	12,19	-15,07
35	2020	Itapeva	Female	Adult	14,22	-15,02
36	2020	Itapeva	Female	Chick	13,77	-15,40
37	2020	Itapeva	Female	Chick	14,00	-14,76
38	2020	Itapeva	Female	-	13,53	-15,21
39	2020	Itapeva	Female	-	13,58	-15,30
40	2020	Itapeva	Male	Adult	14,87	-14,28
41	2020	Itapeva	Male	Adult	14,10	-14,75
42	2020	Itapeva	Male	Adult	13,98	-15,30
43	2020	Itapeva	Male	Chick	13,99	-15,09

ID	Season	Site	Sex	Age	δ^{15}N	δ^{13}C
44	2020	Itapeva	Male	-	13,71	-15,24
45	2020	Itapeva	Male	-	13,47	-15,20
46	2020	Lagoa do Peixe	Female	Adult	11,76	-13,69
47	2020	Lagoa do Peixe	Female	Adult	12,33	-13,85
48	2020	Lagoa do Peixe	Female	Adult	11,99	-13,94
49	2020	Lagoa do Peixe	Female	Adult	12,09	-14,04
50	2020	Lagoa do Peixe	Female	Adult	12,03	-14,14
51	2020	Lagoa do Peixe	Female	Adult	11,73	-13,89
52	2020	Lagoa do Peixe	Male	Adult	11,33	-13,87
53	2020	Lagoa do Peixe	Male	Adult	12,39	-13,62
54	2020	Lagoa do Peixe	Male	Adult	12,78	-14,19
55	2020	Lagoa do Peixe	Male	Adult	11,59	-14,46
56	2020	Lagoa do Peixe	Male	Adult	11,43	-14,26
57	2020	Lagoa do Peixe	Male	Adult	10,94	-14,10
58	2020	Lagoa do Peixe	-	Adult	11,78	-14,01
59	2020	Lagoa do Peixe	-	Adult	11,88	-14,17
60	2020	Lagoa do Peixe	-	Adult	12,08	-13,81
61	2020	Passo de Torres	Female	Adult	14,24	-14,39
62	2020	Passo de Torres	Male	Adult	14,97	-14,12
63	2020	Praia das Cabras	Female	Adult	13,29	-14,26
64	2020	Praia das Cabras	Female	Chick	12,76	-14,32
65	2020	Praia das Cabras	Male	Adult	13,10	-14,29
66	2020	Praia das Cabras	Male	Adult	13,72	-14,75
67	2020	Praia das Cabras	-	Adult	11,60	-14,05
68	2020	Praia das Cabras	-	Adult	13,86	-13,93
69	2020	Praia das Cabras	-	Chick	13,13	-14,02
70	2020	Praia Grande	Female	Adult	13,21	-15,58
71	2020	Praia Grande	Female	Adult	14,03	-14,43
72	2020	Praia Grande	Female	Adult	12,43	-14,43
73	2020	Praia Grande	Female	Chick	12,11	-15,75
74	2020	Praia Grande	Female	Chick	11,26	-16,14
75	2020	Praia Grande	Male	Adult	12,80	-15,08
76	2020	Praia Grande	Male	Adult	12,84	-15,97
77	2020	Praia Grande	Male	Adult	14,55	-14,77
78	2020	Praia Grande	Male	Chick	12,32	-15,29
79	2020	Praia Grande	Male	Chick	11,08	-15,06
80	2020	Praia Grande	Male	Chick	11,22	-14,92
81	2020	Praia Grande	Male	Chick	12,29	-15,21
82	2020	Praia Grande	Male	Chick	13,19	-15,54
83	2021	Lagoa do Peixe	Female	Adult	13,34	-13,69
84	2021	Lagoa do Peixe	Female	Adult	13,11	-13,61
85	2021	Lagoa do Peixe	Female	Adult	12,98	-13,48
86	2021	Lagoa do Peixe	Female	Adult	12,82	-13,84
87	2021	Lagoa do Peixe	Male	Adult	13,00	-13,84
88	2021	Lagoa do Peixe	Male	Adult	13,08	-13,71
89	2021	Lagoa do Peixe	Male	Adult	12,76	-13,73
90	2021	Lagoa do Peixe	Male	Adult	13,27	-13,59
91	2021	Lagoa do Peixe	Male	Adult	12,90	-14,16

ID	Season	Site	Sex	Age	δ^{15}N	δ^{13}C
92	2021	Praia Grande	Female	Adult	12,33	-14,79
93	2021	Praia Grande	Female	Adult	13,49	-14,64
94	2021	Praia Grande	Female	Adult	12,99	-15,04
95	2021	Praia Grande	Female	Adult	13,58	-15,00
96	2021	Praia Grande	Female	Chick	13,20	-15,16
97	2021	Praia Grande	Male	Adult	13,11	-14,92
98	2021	Praia Grande	Male	Adult	10,84	-14,63
99	2021	Praia Grande	Male	Adult	12,97	-14,93
100	2021	Praia Grande	Male	Chick	13,00	-15,24

Table S2 Univariate differences in carbon and nitrogen isotopic values among areas, assessed with nonparametric Kruskal-Wallis test and a Dunn's test as a post hoc with a Benjamini-Hochberg procedure

Sites	Carbon			Nitrogen		
	Z	P.unadj	P.adj	Z	P.unadj	P.adj
Itapeva – Lagoa do Peixe	-3.52	4.29E-04	0.001	5.38	7.35E-08	7.35E-07
Itapeva – Passo de Torres	-4.39	1.11E-05	0.000	1.51	1.30E-01	1.86E-01
Lagoa do Peixe – Passo de Torres	-1.78	7.48E-02	0.125	-2.71	6.66E-03	2.22E-02
Itapeva – Praia das Cabras	-1.27	2.04E-01	0.292	1.78	7.44E-02	1.24E-01
Lagoa do Peixe – Praia das Cabras	1.24	2.15E-01	0.269	-2.06	3.97E-02	7.95E-02
Passo de Torres – Praia das Cabras	2.44	1.48E-02	0.030	0.35	7.25E-01	7.25E-01
Itapeva – Praia Grande	-1.12	2.61E-01	0.290	3.93	8.35E-05	4.17E-04
Lagoa do Peixe – Praia Grande	3.05	2.25E-03	0.006	-2.22	2.59E-02	6.49E-02
Passo de Torres – Praia Grande	4.02	5.73E-05	0.000	1.34	1.82E-01	2.27E-01
Praia das Cabras – Praia Grande	0.61	5.42E-01	0.542	0.77	4.43E-01	4.92E-01

Table S3 Univariate differences in carbon and nitrogen isotopic values between sexes in Passo de Torres, Praia Grande, Itapeva, Praia das Cabras and Lagoa do Peixe, assessed with a nonparametric Kruskal-Wallis test

	Passo de Torres		Praia Grande		Itapeva		Praia das Cabras		Lagoa do Peixe	
	Carbon	Nitrogen	Carbon	Nitrogen	Carbon	Nitrogen	Carbon	Nitrogen	Carbon	Nitrogen
chi-squared	0.24	0.96	0.5507	2.3162	0.78947	0.63947	0.6	0.6	1.1921	0.12397
df	1	1	1	1	1	1	1	1	1	1
p-value	0.6242	0.3272	0.458	0.128	0.3743	0.4239	0.4368	0.4368	0.2749	0.7248

Table S4 Univariate differences in carbon and nitrogen isotopic values among years in Praia Grande, assessed with nonparametric Kruskal-Wallis test and a Dunn's test as a post hoc with a Benjamini-Hochberg procedure

Praia Grande	Carbon			Nitrogen		
Years	Z	P.unadj	P.adj	Z	P.unadj	P.adj
2018 – 2019	-2.90	3.74E-03	7.47E-03	-2.88	0.003980669	0.023884
2018 – 2020	1.02	3.09E-01	4.64E-01	-1.25	0.212338026	0.318507
2019 – 2020	4.98	6.50E-07	3.90E-06	2.05	0.040358616	0.121076
2018 – 2021	0.27	7.83E-01	7.83E-01	-1.86	0.062246799	0.124494
2019 – 2021	3.65	2.61E-04	7.84E-04	0.99	0.322775173	0.38733
2020 – 2021	-0.82	4.11E-01	4.93E-01	-0.85	0.397153082	0.397153

Table S5 Convex hull Total Area (TA), Siber Ellipse Area (SEA), and Siber Ellipse Area corrected for small sample sizes (SEAc) values for Praia Grande in 2018, 2019, 2020 and 2020, and for Lagoa do Peixe in 2020 and 2021

	Praia Grande				Lagoa do Peixe	
	2018	**2019**	**2020**	**2021**	**2020**	**2021**
TA	2.51	1.19	3.93	0.93	0.92	0.21
SEA	1.88	0.51	1.69	0.49	0.31	0.11
SEAc	2.36	0.55	1.84	0.56	0.34	0.12

Table S6 Univariate differences in carbon and nitrogen isotopic values among years in Passo de Torres, Itapeva and Lagoa do Peixe, assessed with a nonparametric Kruskal-Wallis test

	Passo de Torres		Itapeva		Lagoa do Peixe	
	2019 - 2020		2019 - 2020		2020 - 2021	
	Carbon	Nitrogen	Carbon	Nitrogen	Carbon	Nitrogen
chi-squared	4.2	4.2	7.1053	0.59298	7.3641	15.724
df	1	1	1	1	1	1
p-value	0.04042	0.04042	0.007686	0.4413	0.006654	7.33E-05

Table S7 Convex hull Total Area (TA), Siber Ellipse Area (SEA), and Siber Ellipse Area corrected for small sample sizes (SEAc) values for each of the sites sampled

	Passo de Torres	Praia Grande	Itapeva	Praia das Cabras	Lagoa do Peixe
TA	1.22	9.79	3.09	0.93	1.32
SEA	0.67	2.73	1.23	0.62	0.44
SEAc	0.77	2.80	1.31	0.75	0.46

Table S8 Results of PERMANOVA run with macroinvertebrate abundance data of 2019, pairs, Df= Degrees of Freedom, SumOfSqs = Sum of Squares, F. Model, R2, p.value, p.adjusted. *=significant. PG= Praia Grande, ITA= Itapeva, PC= Praia das Cabras, LP= Lagoa do Peixe

pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted
PG vs ITA	1	0.2348138	1.106.409	0.05790772	0.337	1.000
PG vs PC	1	10.163.767	5.527.583	0.23494053	0.001	0.006*
PG vs LP	1	19.112.580	10.073.824	0.35883334	0.001	0.006*
ITA vs PC	1	0.9966352	5.992.153	0.24975470	0.001	0.006*
ITA vs LP	1	15.808.041	9.181.384	0.33778206	0.001	0.006*
PC vs LP	1	0.9491356	6.599.564	0.26827972	0.001	0.006*

Table S9 Results of PERMANOVA run with macroinvertebrate abundance data of 2020, pairs, Df= Degrees of Freedom, SumOfSqs = Sum of Squares, F. Model, R2, p.value, p.adjusted. *=significant. PG= Praia Grande, ITA= Itapeva, LP= Lagoa do Peixe

pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted
PG vs ITA	1	0.4133734	2.562.981	0.1246405	0.040	0.120
PG vs LP	1	12.428.407	13.615.564	0.4306602	0.001	0.003*
ITA vs LP	1	0.4997600	3.621.771	0.1675057	0.009	0.027