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Article · June 2023

DOI: 10.1016/j.fooweb.2023.e00300

Food Webs 36 (2023) e00300

Contents lists available at ScienceDirect

Food Webs

journal homepage: www.elsevier.com/locate/fooweb

Specialist shorebird respond to prey and habitat availability through trophic plasticity

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ARTICLE INFO

Keywords:
American oystercatcher
Benthic macroinvertebrates
Diet
Haematopus palliatus
Stable isotopes
Trophic ecology

ABSTRACT

Spatiotemporal variations in food availability represent a challenge to the persistence of specialist species. The American oystercatcher (*Haematopus palliatus*) is a shorebird regarded as a bivalve specialist, although foraging habitats and prey species may vary along its distribution. Here, we studied American oystercatcher breeding in sites with variable landscapes to test the effect of temporal and spatial variations in food availability and dietary aspects. Between 2017 and 2021, we sampled oystercatchers ($n = 100$) and macroinvertebrates at the mesolitoral zone in five foraging areas in southern Brazil, three composed by sand and rock substrates (mixed), and two by sandy beach only. We obtained biological samples from oystercatchers and macroinvertebrates for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analysis. In addition, we carried out systematic sampling of macroinvertebrates in sandy beaches at foraging areas to assess prey availability. Main findings showed the oystercatcher diet to be influenced both by the heterogeneity of foraging habitats and temporal fluctuations in availability of food resources. Bivalves contributed ~60% to the diet of oystercatchers, but differences in the preferred bivalve species were detected among areas. In sites with mixed substrates, oystercatchers had a wider isotopic niche, suggesting habitat heterogeneity induced a more varied diet. Finally, we also observed interannual variation in the diet that may be associated with variation in macroinvertebrate availability on sandy beaches, especially for non-bivalve prey. Therefore, both temporal variations in food availability and foraging habitat heterogeneity seem to shape the foraging ecology of oystercatchers in the coastal zone, evidencing trophic plasticity in this specialist shorebird.

1. 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 which limit them to a particular habitat or food 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 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

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https://doi.org/10.1016/j.fooweb.2023.e00300
Received 29 July 2022; Received in revised form 30 January 2023; Accepted 22 June 2023
Available online 24 June 2023
2352-2496/

individual survival and population persistence.

Shorebirds exhibit a variety of bill morphologies associated with their foraging strategies and dietary preferences (Barbosa and Moreno, 1999). For instance, there are twelve species of oystercatchers (Family Haematopodidae) distributed mainly on coastal regions, which are regarded to be specialists in consuming bivalve species. Oystercatchers are specialized in handling and opening bivalves with their long and sharp bill, which is inserted in between valves to cut the adductor muscle, although they can complement their diet with other macroinvertebrates (Hockey, 1996). Assumed foraging specialization and limited distribution of most oystercatcher species along coastlines could suggest dietary homogenization along their range. Nevertheless, distinctive feeding specializations have been documented in some species, such as the Eurasian oystercatcher (*Haematopus ostralegus*), which remarkably exhibits a gradient of bill tip morphologies in response to feeding on soft- or hard-shelled prey (Van de Pol et al., 2009; Van der Kolk et al., 2020), and has been even recorded consuming food from anthropogenic sources, such as bread (van Dijk, 2014). Moreover, dietary variation in relation to sex, day or nightime feeding, chick age, geographical location and macroinvertebrate availability on rocky shores has been reported in African black oystercatchers (*H. moquini*) (Hockey and Underhill, 1984; Kohler et al., 2009; Kohler et al., 2011). Foraging of oystercatchers is spatially constrained during the breeding season due to incubation or chick-rearing duties, despite studies have shown that birds are capable of using foraging areas disjunct from breeding sites if adjacent foraging areas are unavailable (Nol, 1989; Ens et al., 1992; Linhares et al., 2022). Nonetheless, ecological responses of oystercatchers to spatiotemporal variations in prey availability have been poorly investigated, evidencing a knowledge gap for this widely distributed and assumed specialist group of shorebirds.

The American oystercatcher (*H. palliatus*; hereafter “oystercatcher”) is distributed along the Atlantic and Pacific coasts from the United States to southern Argentina (Nol and Humphrey, 1994). The species forages mainly on sandy beaches, but also in 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), food remains and stable isotope analysis in bird tissues (Linhares et al., 2022). However, despite ecological plasticity in using foraging habitats is a key trait for birds inhabiting coastlines in face of climate change and worldwide urban expansion, the effect of temporal and spatial variations in prey availability and dietary composition of oystercatchers has not yet been investigated.

Stable isotopes provide insights into trophic relationships among organisms, reconstructing food webs and providing information on trophic niche variations in space and time (Boecklen et al., 2011; Layman et al., 2012). Carbon and nitrogen are major components of animal tissues, and measurements of their isotopic ratios (δ^{13}C and δ^{15}N, respectively), followed by Bayesian analytical frameworks, provides valuable information to estimate isotopic niches (Jackson et al., 2011) and contribution of different food sources to the diet of consumers (Parnell and Inger, 2021). Moreover, δ^{15}N reflects trophic level of consumers while δ^{13}C may be used to estimate the use of matter from distinct origins, providing information on the foraging habitat (Peterson and Fry, 1987). Diet composition may also vary according to prey availability, so the assessment of variation in food availability is relevant to estimate its effect on dietary composition across scales (Huckembeck et al., 2014; Divine et al., 2017). Stable isotopes have already been used to distinguish between migratory and resident Eurasian oystercatchers in Iceland (Méndez et al., 2020), detect variations in the foraging ecology along biogeographical regions in African black oystercatchers in South Africa (Kohler et al., 2011) and to estimate contribution of prey from different environments around nesting sites in American oystercatchers from southern Brazil (Linhares et al., 2022). The combination of stable isotope analysis with other information, such as prey availability in the environment across temporal and spatial scales, can be a powerful tool to assess variations in the foraging ecology, helping to characterize the trophic plasticity in beach dwelling shorebirds.

In this study, we used carbon and nitrogen stable isotopes in combination with prey sampling to assess whether trophic interactions of American oystercatchers vary according to prey availability and landscape compositions in different sites and years along a ~ 280 km coastline in southern Brazil, a key site for the global conservation of the species (Clay et al., 2014). We hypothesized that the oystercatcher modulates its diet in response to variable prey availability in sandy beaches and the presence of different habitats in the landscape adjacent to breeding sites, such as mudflats and rocky shores. We expected diet composition to be mostly dominated by bivalves across the study area, but with different bivalve species dominating the diet among areas in response to prey availability, as well as consumption of additional prey taxa. For this, we used a stable isotope dataset from 100 oystercatcher individuals and seven potential prey taxa, obtained in five breeding sites with distinctive landscapes, composed by only sandy beaches, or sandy beaches along with mudflats or rocky shores nearby. In addition, we also tested differences in prey availability on the sandy beaches as a potential cause of dietary variation among the sampled areas and seasons.

2. Materials and methods

2.1. Study sites

Fieldwork was carried out on five beaches along a 280 km coastline in southern Brazil, from 29°18’S/49°42’W to 31°21’S/51°02’W (Fig. 1), which are used by oystercatchers as breeding and foraging sites. The southern areas, Praia das Cabras and Lagoa do Peixe, are composed by sandy substrate only, while the northern sites, Passo de Torres, Praia Grande and Itapeva are sandy beaches with the presence of natural or artificial rocky substrates adjacent or nearby, such as slabs and jetties, so we refer to these beaches as mixed substrate sites. These mixed substrate sites also hold additional landscape elements suggested to influence oystercatcher diet, such as a rocky island (Ilha dos Lobos) about 2 km offshore Praia Grande, which is a marine protected area used by oystercatchers for foraging (Linhares et al., 2022); and also an estuarine zone at Lagoa do Peixe, that present suitable foraging environments for oystercatchers, such as mudflats and saltmarshes (Fedrizzi, 2008). There is also an estuary alongside Praia Grande in the mixed substrate area, but it does not present relevant foraging areas for oystercatchers, given that the estuary margins are mostly urbanized. Finally, Praia Grande is an urban beach (Cristiano et al., 2016; Linhares et al., 2021), Passo de Torres is scarcely urbanized nearby, Praia das Cabras is a preserved area due to its distance to urban sites, while Itapeva and Lagoa do Peixe are formally protected areas, as a State Park and a National Park, respectively.

2.2. Sampling and laboratory procedures

Across four consecutive breeding seasons (i.e. September–March), from 2017 to 2021, we sampled adult oystercatchers and chicks at the beaches. We caught birds at night using flashlights and hand nets. Chicks were sampled at a minimum age of three weeks, as the blood turnover rate for birds ranges from 15 to 20 days (Boecklen et al., 2011). This timeframe was chosen to ensure that the isotopic values in the whole blood reflected the assimilated diet of the chicks (Ogden et al., 2004). We collected whole blood samples (~0.1 ml) from the tarsal vein and subsequently stored them in microtubes containing 70% ethanol. A small drop of blood was also collected on filter paper and used for molecular sexing (Griffiths et al., 1998). We identified birds with metal rings to avoid resampling.

We also sampled macroinvertebrates on sandy beaches in four out of the five sites, due to logistical constraints at Passo de Torres. We sampled

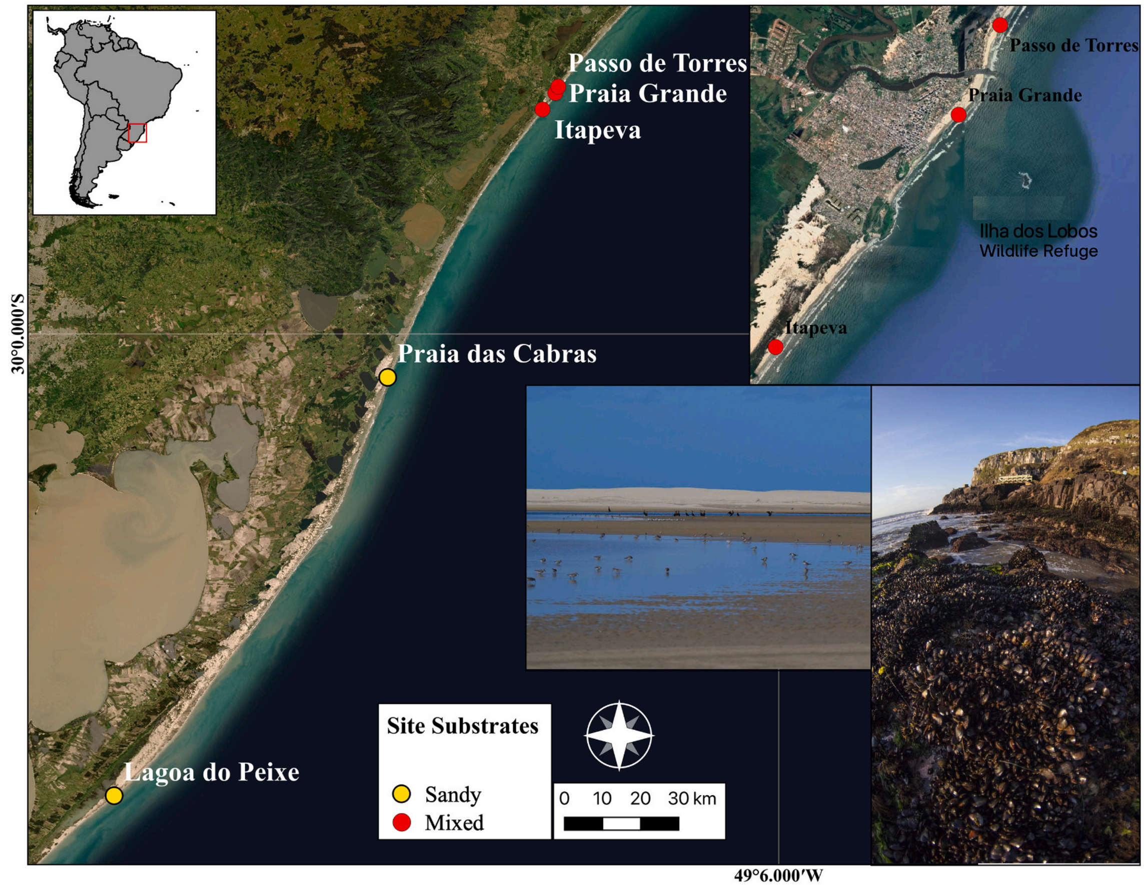

Fig. 1. Breeding sites of the American oystercatcher (*Haematopus palliatus*) along the southern Brazilian coast. Rocky substrate with *Perna perna* near to Praia Grande (red arrow); fore dunes and mudflats at Lagoa do Peixe (yellow arrow). Photo: Mar Pedro de Abreu. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

only sandy substrate because it was common to all sites and allowed comparisons of macroinvertebrate availability. Macroinvertebrate sampling occurred in spring (October and November) of 2019 and 2020, in overlap with the sampling period of oystercatchers during the breeding season. We sampled Praia Grande, Itapeva, Lagoa do Peixe and Praia das Cabras in 2019, and all areas except Praia das Cabras in 2020. For each site, we sampled ten equidistant points along a 1 km transect in the mesolitoral zone. We obtained sandy substrate samples with a 20 cm diameter PVC corer inserted 20 cm deep, then sieved with a 1 mm mesh (McLachlan and Defeo, 2018) and stored invertebrates into tubes containing 70% ethanol. In the laboratory, we analyzed samples with a stereoscopic microscope and identified invertebrates at the lowest taxonomic level possible. We identified samples according to date, site, and sampling point, and counted individuals to estimate macroinvertebrate abundance.

For stable isotope analysis, we used whole blood from the oystercatchers, muscle tissue from bivalves, and whole body of smaller prey groups. 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 2–3 weeks (Boecklen et al., 2011). We washed prey samples to remove lipids 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 - Universidade Federal do Rio Grande* (CIA-FURG, Brazil). Values are provided in δ and expressed in ‰ in the Eq. (1), from Bond and Hobson (2012):

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N}\ (‰) = \left(\mathrm{R_{sample}}/\mathrm{R_{standard}}\right) - 1 \tag{1}$$

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.

2.3. Statistical analysis

We used a nonparametric Kruskal-Wallis test to assess univariate differences in isotopic values among areas, years and sexes, with a Dunn's test as a post hoc and a Benjamini-Hochberg procedure to control the false discovery rate (Legendre and Legendre, 2012) using the *FSA* package in R software (Ogle et al., 2021). We estimated isotopic niches through a Bayesian framework as implemented in the *SIBER* package (Jackson et al., 2011), from which Standard Ellipse Areas corrected for small sample sizes (SEAc) were generated for each site, year and sex, and the pairwise overlap value between ellipses was calculated. We also estimated the contribution of different prey to the diet of oystercatchers with Bayesian mixing models as implemented in the *simmr* package (Parnell and Inger, 2021). Trophic discriminant factors used in mixing models were 0.2‰ (±0.4‰) for δ^{13}C and 2.7‰ (±0.4‰) for δ^{15}N, as estimated for *H. moquini* in South Africa (Kohler et al., 2011). We used information from previous studies (Fedrizzi, 2008; Linhares et al., 2022), field observations and type of substrate to select sources to be included in the mixing models of each site. Based on this data, eight prey species were selected. *Amarilladesma mactroides*, *Donax hanleyanus*, *Emerita brasiliensis*, *Excirolana armata*, *Olivancillaria vesica auriculata* and

Polychaeta were used for all sites. *Perna perna* was included only for sites with rocky substrate (i.e. Passo de Torres, Praia Grande and Itapeva; Linhares et al., 2022), and *Tagelus plebeius* was included only for Lagoa do Peixe considering the lagoon-estuarine foraging environment (Fedrizzi, 2008).

We calculated the relative abundance and frequency of occurrence for the macroinvertebrate in sandy beaches to quantify variation in food availability for oystercatchers. We tested difference in macroinvertebrate composition for the sites with a Permutational Multivariate Analysis of Variance (PERMANOVA; 999 permutations) by using abundance data and the Bray-Curtis index, and with a Non-Metric Multidimensional Scaling (nMDS), using the Bray-Curtis index in the *vegan* package (Oksanen et al., 2020).

3. Results

We sampled a total of 100 birds during the breeding seasons from 2017 to 2021 (Table 1). Most oystercatchers sampled were adults (n = 93) and the average sex ratio was 1:1 (n = 94, Table 1). The lowest mean value of δ^{13}C was detected in Itapeva (−14.75 ± 0.73‰), and the highest in Passo de Torres (−13.37 ± 0.51‰). The pairwise comparison between these sites was significantly different ($Z = -4.39$; $p < 0.05$). The highest δ^{15}N mean value was found in Itapeva (13.79 ± 0.57‰), and the lowest in Lagoa do Peixe (12.31 ± 0.68‰), with these sites differing significantly ($Z = 5.38$; $p < 0.05$). We observed significant differences ($p < 0.05$) in δ^{15}N values for all pairwise comparisons among foraging areas, while significant differences for δ^{13}C values were found for only five out of ten pairwise comparisons (see Table A.1). No significant differences were found between sexes for any site (Table A.2).

We found significant interannual differences in δ^{13}C values for Praia Grande among all years sampled (2018, 2019, 2020 and 2021) (Table A.3), with the widest isotopic niche occurring in 2018 (SEAc = 2.35; Fig. 2, Table A.4). At Lagoa do Peixe, significant differences were found between 2020 and 2021 for δ^{13}C (Table A.5), and isotopic niche was wider in 2020 (Fig. 2, Table A.4). At Itapeva, 2019 and 2020 also differed significantly only for δ^{13}C. The only significant interannual difference in δ^{15}N was detected between 2019 and 2020 for Passo de Torres (Table A.5).

Sites with mixed substrate presented wider isotopic niche than sites with only sandy substrate. The widest isotopic niche width was observed 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, Table A.6). 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 in our dataset) (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. We counted a total of 2853 and 5360 macroinvertebrates in sediment samples in 2019 and 2020, respectively. Relative abundance of macroinvertebrates was similar between Praia Grande and Itapeva in 2019, and frequency of occurrence was similar for all sites 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 southernmost site, Lagoa do Peixe. In 2019, relative abundance of bivalves was higher at the southern sites. 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 Tables A.7 and A.8).

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, Fig. 5). In sites with a lower contribution of bivalves, additional prey, such as Polychaeta and the crustacean *E. brasiliensis*, had greater contribution (Table 3, Figs. 5 and 6). Mixing models also showed differences in the most commonly consumed bivalve species among sites; *P. perna* had the highest contribution in Praia Grande, while *D. hanleyanus* took this position at Praia das Cabras, and *T. plebeius* was the main bivalve species at Lagoa do Peixe (Fig. 6). Differences in the diet between years assessed by mixing models demonstrated that *P. perna*, *D. hanleyanus* and *E. brasiliensis* varied their contribution over the years at Praia Grande, while the other species had stable contributions. 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).

4. Discussion

Our results highlight that the diet of a widely distributed shorebird is shaped by variations in food resource availability in southern Brazil, both spatially and temporally, which demonstrates trophic plasticity of a specialist predator. Presence of rocky substrate and estuarine systems around sandy beaches can influence oystercatcher trophic niches, since these habitats represent additional foraging opportunities for these shorebirds. In addition, interannual variations in the highly dynamic macroinvertebrate communities in sandy beaches along the southwestern Atlantic Ocean seems to induce dietary shifts in oystercatchers; being these temporal variations associated with complex physicochemical, geological, and hydrological factors (McQuaid and Lindsay, 2000; Parise et al., 2009; Coutinho et al., 2016; McLachlan and Defeo, 2018). While maintaining the dietary preference for bivalves, oystercatchers vary their main bivalve species and consume additional prey taxa among the distinct sampled areas and years, shedding light on the capacity and constraints for the local adaptation of this specialist predator.

Oystercatchers are mostly restricted to coastlines, but the consumption of habitat-specific prey species demonstrated here shows additional strategies in foraging and habitat use. The importance of mudflats that are present in the lagoon-estuarine environment at Lagoa do Peixe was suggested by the estimated high contribution of *T. plebeius* (Holland and Dean, 1977), composing 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 this site (Fedrizzi, 2008). Conversely, most common macroinvertebrates inhabiting beaches in southern Brazil, such as *A. mactroides*, *D. hanleyanus*, and *E. brasiliensis* (Gianuca, 1985) formed the bulk of oystercatcher diet at Praia das Cabras, suggesting that the availability of suitable prey in sandy beaches shapes the diet of

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

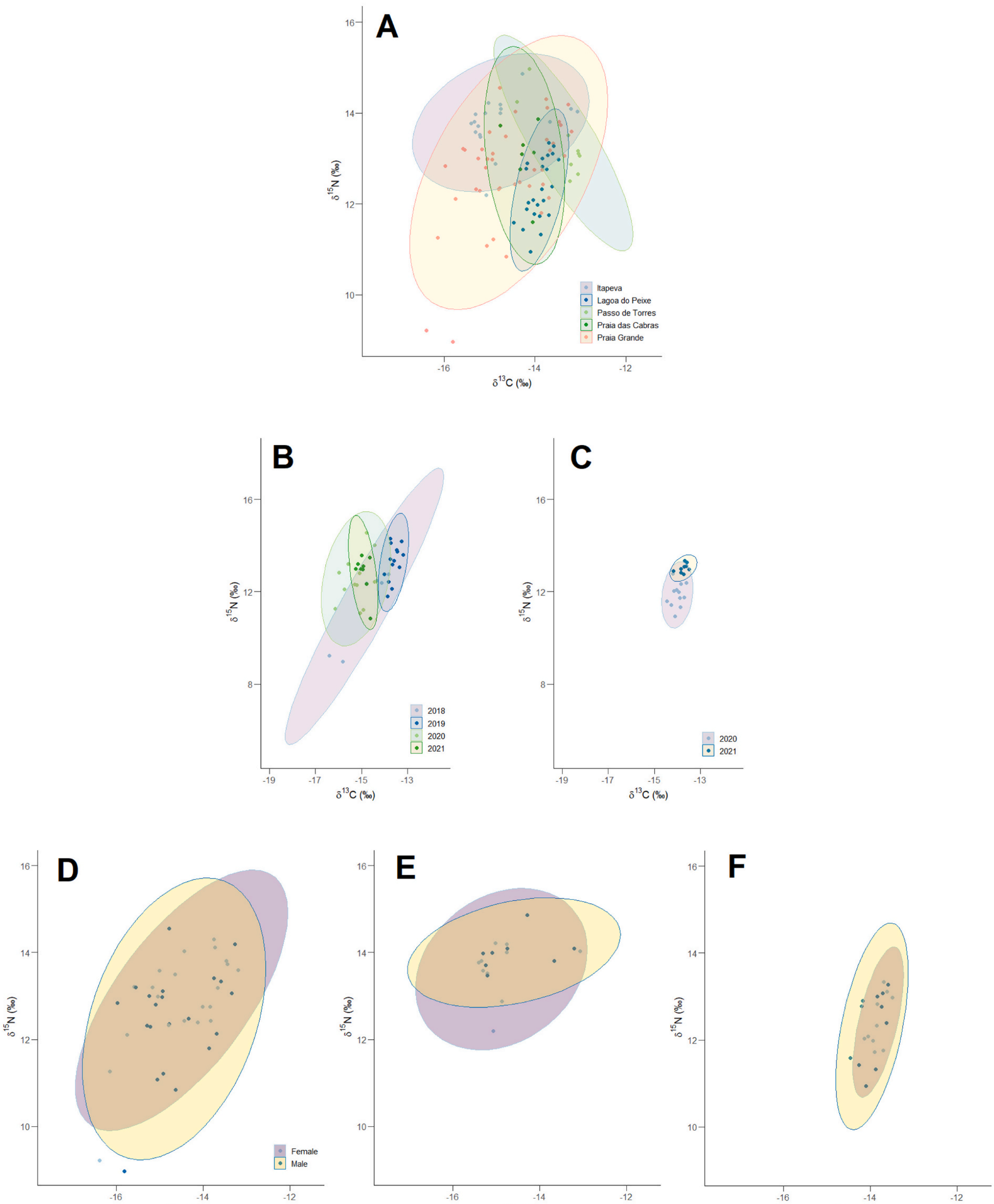

Fig. 2. Bayesian ellipses representing isotopic niche of the American oystercatcher (*Haematopus palliatus*) (δ in ‰). Ellipses comprise 95% of the data. Isotopic ellipses considering all sites (**A**), distinct years at Praia Grande (**B**) and Lagoa do Peixe (**C**), and intersexual differences for Praia Grande (**D**), Itapeva (**E**) and Lagoa do Peixe (**F**).

oystercatchers where they lack other foraging habitats. Finally, *P. perna* contributed in distinct proportions in beaches with mixed substrate, indicating that rocky shores or even islands can provide relevant food sources around nesting areas, as previously shown by Linhares et al. (2022) for Praia Grande during the breeding period. Furthermore, habitat selection by oystercatchers seems to be related to the availability of bivalves in foraging areas.

Availability of alternative habitats influences the trophic niche of oystercatchers as they are able to exploit new resources, revealed by areas with mixed substrate presenting wider isotopic niches than sites with sandy substrate only. Isotopic niche widening may be related to increased prey diversity provided by distinct landscape elements, which has also been reported for African black oystercatchers using sandy and rocky substrates in South Africa (Scott et al., 2012). For instance, the substantially higher contribution of *P. perna* (~70%) to the diet of oystercatchers from Praia Grande, in comparison with the other mixed

Table 2
Isotopic niche overlap between foraging sites of the American oystercatcher (*Haematopus palliatus*) in southern Brazil, calculated with the *SIBER* package. Ellipses comprise 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

substrate beaches, is an indicative of frequent use of the rocky substrates nearby as foraging sites. Consuming prey from alternative rocky areas may be important in urban areas if birds are not able to access the sandy beach foraging habitat due to human disturbance, for example, despite beaches being generally adjacent to oystercatcher nests and, therefore, easier to access. Praia Grande is an urbanized area with massive touristic use during austral spring and summer (Zuanazzi and Bartels, 2016), which overlaps with the breeding period of oystercatchers (Linhares et al., 2021). The increased importance of a rocky shore bivalve (*P. perna*) that can be found at the nearby protected island Ilha dos Lobos (~2 km offshore) or at rocky shores can relieve oystercatchers from the pressure of human disturbance on the beachfront, which was thereby suggested to explain the persistence and success of oystercatchers nesting at Praia Grande (Linhares et al., 2022). In the Eurasian oystercatcher, during critical disturbance thresholds, the frequency at which animals regulate their foraging time and therefore their energetic costs differ between individuals with different foraging strategies, what was suggested to imply in varying levels of sensibility towards anthropogenic and natural threats among individuals (Van der Kolk et al., 2020). Therefore, human disturbance on sandy beaches may be a key factor shaping the foraging choices in oystercatchers.

Macroinvertebrate availability on sandy beaches may be negatively impacted by human presence (Schlacher et al., 2016; Bom and Colling, 2020). However, no substantial differences were observed in the benthic community between mixed substrate beaches sampled in this study. This suggests that, in the presence of similar resources, the use of prey from rocky substrate may be influenced by human disturbance on the sandy beach. Accordingly, Itapeva is located ~3 km from Praia Grande and presents a similar macroinvertebrate community, but the contribution of *P. perna* was remarkably lower (~15%). In Passo de Torres (mixed substrate) the contribution of *P. perna* was also lower (~12%), which can also be explained by the further distance of this site to Ilha dos Lobos (~4 km) and the absence of natural rocky outcrops nearby, besides the short jetty in the mouth of the estuary (~1.5 km). Feeding on sandy beaches may be preferred over more distant rocky substrates when human disturbance is low, as it allows for quick and easy access to prey during the energetically demanding breeding period, which is in accordance with the optimal foraging theory (MacArthur and Pianka, 1966). However, the use of alternative foraging habitats available in heterogeneous landscapes may be crucial depending on the intensity of human disturbance. For example, Eurasian oystercatchers avoid disturbed roosting sites during the tourist season (Van der Kolk et al., 2022). In sandy beaches, persistence of bird populations may be compromised if food resources are inaccessible due to human disturbance, which is the main threat for birds using coastal environments (Dias et al., 2019). Because southern Brazil is a key conservation site for the species globally (Clay et al., 2014), it is important to protect its extensive sandy beaches and associated dunes to ensure breeding and foraging requirements for oystercatchers (Linhares et al., 2021).

Interannual variation in the diet of oystercatchers seems to be

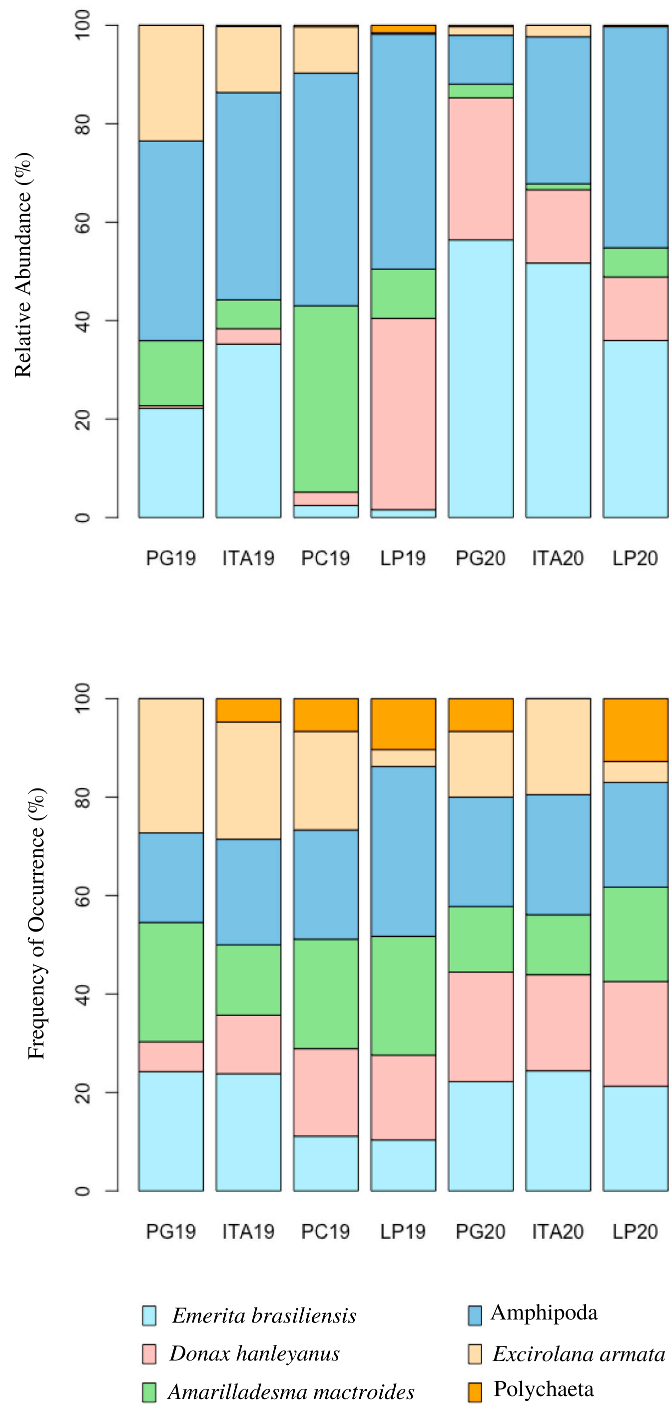

Fig. 3. Relative abundance (%) and frequency of occurrence (%) of macroinvertebrates sampled on sandy beaches. PG19 = Praia Grande in 2019; ITA19 = Itapeva in 2019; PC19 = Praia das Cabras in 2019; LP19 = Lagoa do Peixe in 2019, PG20 = Praia Grande in 2020; ITA20 = Itapeva in 2020; LP20 = Lagoa do Peixe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

associated to temporal fluctuations in prey availability in both rocky and sandy substrate. Composition, distribution, and species-specific abundances of the intertidal benthic community in sandy beaches are highly variable and dependent on complex multifactorial biotic and abiotic interactions (McLachlan and Defeo, 2018). As pointed out, oystercatchers seem to select foraging areas depending on the availability of bivalves, but they also opportunistically prey upon additional taxa following variations in availability. For instance, abundance of *E. brasiliensis* from Lagoa do Peixe increased from 2019 to 2020, as well

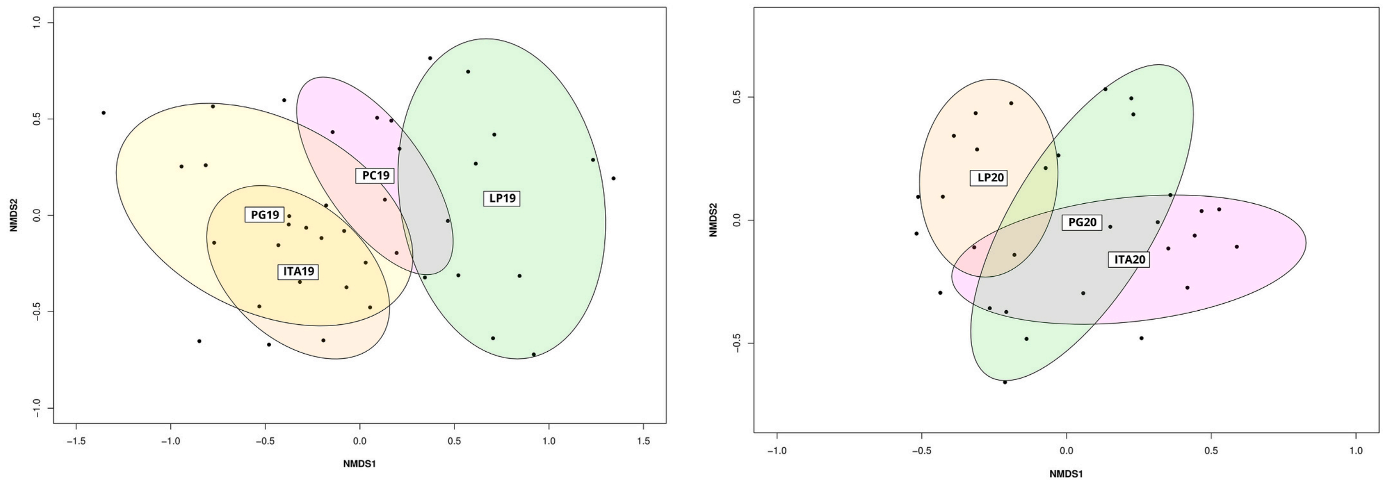

Fig. 4. Non-Metric Multidimensional Scaling (nMDS) for macroinvertebrate samples obtained in 2019 (left) and 2020 (right) in sandy beaches of southern Brazil. PG = Praia Grande; ITA = Itapeva; PC = Praia das Cabras; LP = Lagoa do Peixe. $Stress_{2019}$ = 0.1589; $Stress_{2020}$ = 0.1988.

Table 3
Contribution (mean ± standard deviation in %) of macroinvertebrates to the diet of the American oystercatcher (*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

as its contribution to the diet of oystercatchers. In addition, *D. hanleyanus* followed the opposite trend as its relative abundance decreased from 2019 to 2020, which was also observed in its contribution to the diet during the same period. On rocky substrate, availability of macroinvertebrates for oystercatchers, such as *P. perna* at Ilha dos Lobos, may vary due to tidal variations and biological interactions in the benthic community (McQuaid and Lindsay, 2000; Coutinho et al., 2016). The highest rocks on the island are only about 1.8 m above sea level (Procksch et al., 2023) and can stay partially submerged and inaccessible for birds during syzygy tides or extreme weather events, such as high energy swell or windstorms (Parise et al., 2009). This could in part explain interannual variations detected in *P. perna* contributions for oystercatchers nesting in mixed substrate sites. Moreover, García et al. (2010) reported that during macroalgal blooms in the San Antonio Bay, Argentina, oystercatchers avoided two prey species with high profitability values, shifting their foraging to suboptimal prey but with higher encounter rates. Therefore, despite the preference and specialization in capturing bivalves, the diet of oystercatchers can vary both spatially and temporally following local fluctuations in macroinvertebrate communities linked to multiple biological and environmental factors, illustrating the trophic plasticity concept (Feary et al., 2018; Fox et al., 2019).

The oystercatcher has been considered a diet-specialist in the literature, but the classification of specialist or generalist may depend on the prey taxonomic level 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 at all sites, but the bivalve species varied on a regional scale, which is representative of a local specialist (*sensu* Hughes, 2000). Local resources for the oystercatcher are constrained by multiple factors, including substrate type, human disturbance and variable natural conditions, which affect prey availability and have a fundamental influence on dietary composition (Lawton et al., 2012). The availability of bivalves seems to represent a requirement for oystercatcher distribution, which could be tested on a local scale considering oystercatcher sightings along its home range and the association with benthic invertebrate occurrence. Moreover, understanding potential drivers of the oystercatcher occurrence could explain the disjoint distribution of the species along the Brazilian coast, as well as in other coastal regions of the Americas where the species is absent (American Oystercatcher Working Group et al., 2020).

Moreover, as an obligate coastal species, the oystercatcher is particularly vulnerable to climate change and severe weather (Clay et al., 2014). Climatic change may elevate seawater temperature, induce ocean acidification and sea level rise, which can affect habitat and food resource availability (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 (*H. meadewaldoi*) in 1913 (Hockey, 1987) and several local declines and extirpations have been recorded for *H. palliatus* in the United States (Davis et al., 2001; Clay et al., 2014). However, spatio-temporal trophic plasticity of this shorebird could facilitate its adaptation to climate change, as long as there is suitable habitat for breeding and the occurrence of prey in the nearby foraging territories.

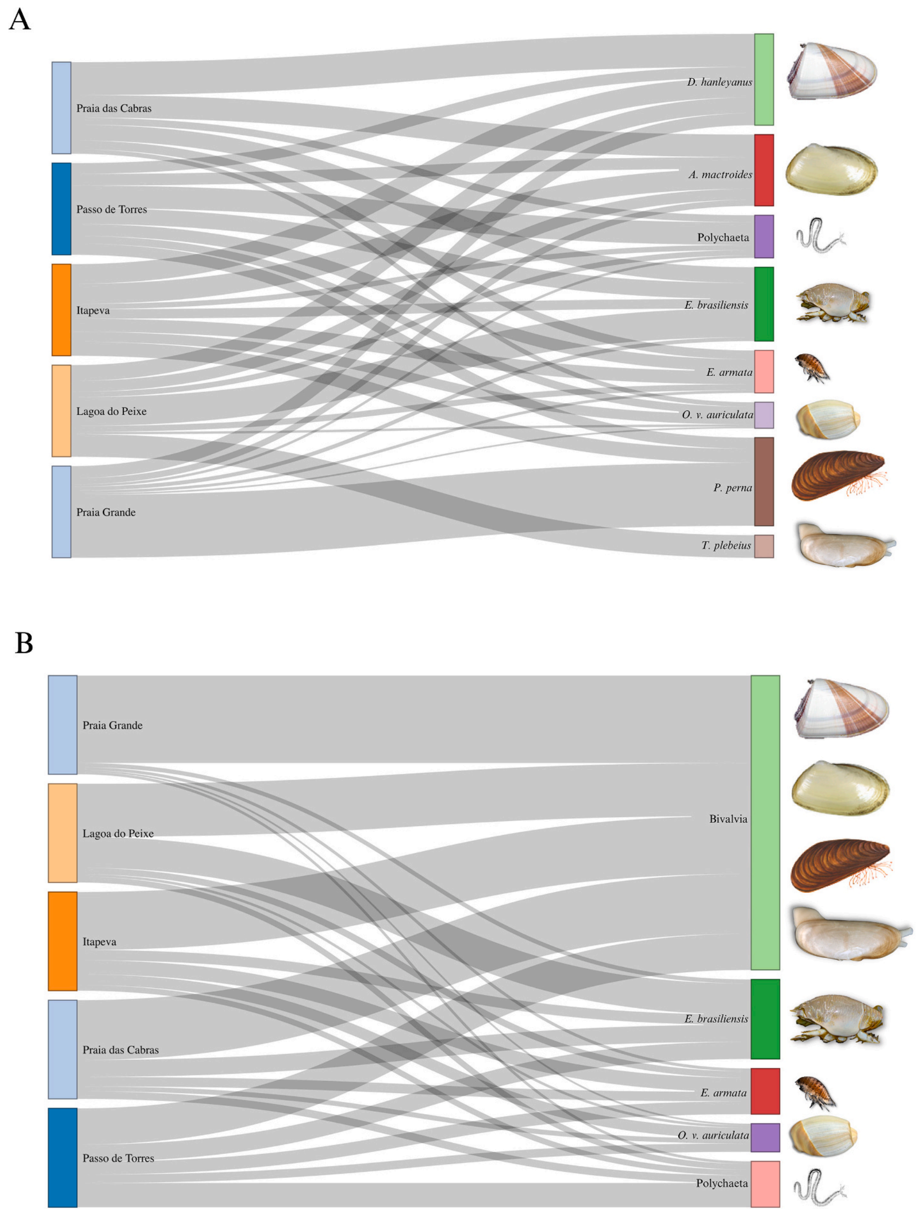

Fig. 5. Sankey diagrams based on Bayesian stable isotope mixing models considering American oystercatchers (*Haematopus palliatus*) from southern Brazil grouped from 2017 to 2021 (left) and prey Species (right) considering (**A**) Bivalvia at the Species level; and (**B**) Bivalvia at the Class level.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

5. Conclusions

Trophic plasticity of a specialist shorebird, the American oystercatcher, was demonstrated 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 level analyzed, spatiotemporal trophic plasticity and local specialization were observed within a 280 km coastline. Substrate and habitat availability played an important role in defining the foraging ecology of oystercatchers, so that profitable 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 the 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.

Funding

This study was partially funded by *Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul* (FAPERGS; 19/2551-0001284-5) and *Fundação Grupo Boticário* (1153-2019). L. Gliesch received a MSc. scholarship granted from *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES; 88887.352874/2019–00) through the *Programa de Pós-Graduação em Ecologia* (UFRGS). B.A. Linhares received a MSc scholarship granted from *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES) through the *Programa de Pós-Graduação em Oceanografia Biológica* (FURG). L. Bugoni is research fellow from CNPq (grant 311409/2018-0).

Ethics approval

Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and *Secretaria do Meio Ambiente e Infraestrutura do Rio Grande do Sul* (SEMA-RS) granted sampling permits no. 64234–3 and DUC-685, respectively.

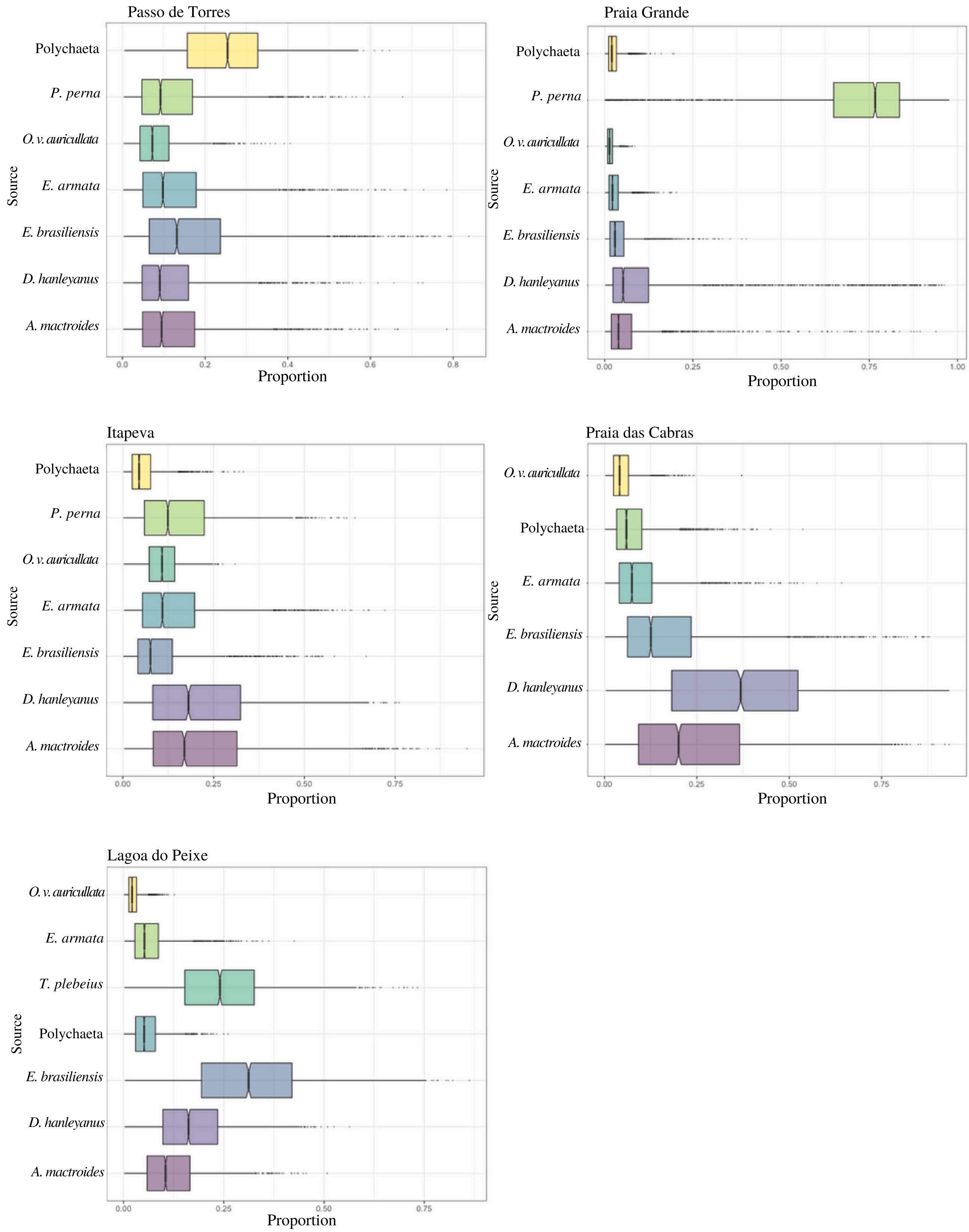

Fig. 6. Contribution of each item (source) to the diet of American oystercatchers (*Haematopus palliatus*) from different sites in southern Brazil. Prey = *Donax hanleyanus*, *Amarilladesma mactroides,* Polychaeta, *Emerita brasiliensis*, *Excirolana armata*, *Olivancillaria v. auriculata*, *Perna perna*, *Tagelus plebeius*.

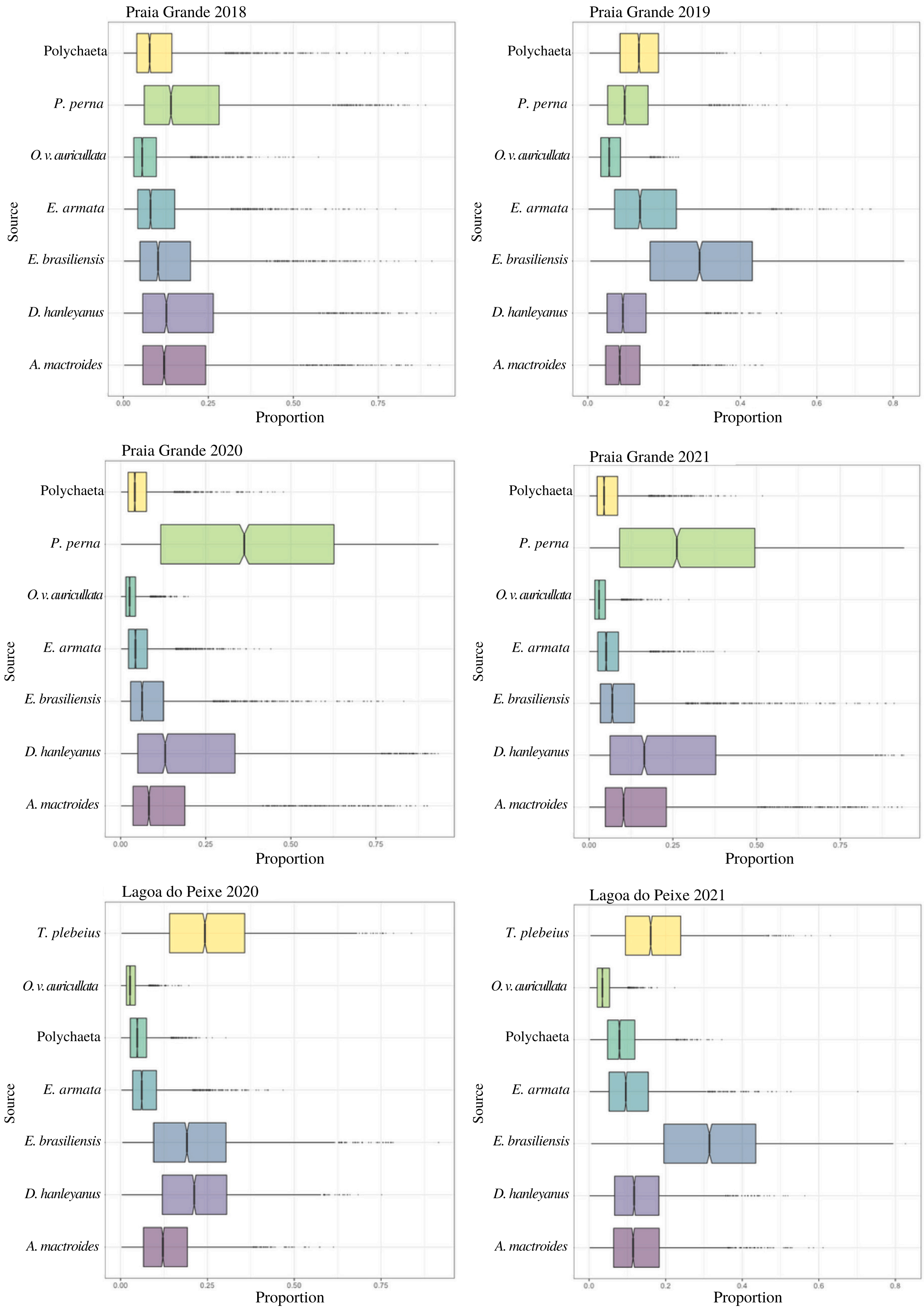

Fig. 7. Contribution of each item (source) in distinct years to the diet of American oystercatchers (*Haematopus palliatus*) from Praia Grande and Lagoa do Peixe, in southern Brazil. Prey = *Donax hanleyanus*, *Amarilladesma mactroides*, Polychaeta, *Emerita brasiliensis*, *Excirolana armata*, *Olivancillaria v. auriculata*, *Perna perna*, *Tagelus plebeius*.

All applicable institutional guidelines for the care and use of animals were followed and approved by the *Comissão de Ética no Uso de Animais* of the *Universidade Federal do Rio Grande do Sul* (CEUA/UFRGS; permit no. 37905).

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Code availability

The code is available at https://github.com/SeabirdEcologyUFRGS/AmericanOystercatcher_TrophicEcology

CRediT authorship contribution statement

Lais Gliesch: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Bruno de Andrade Linhares:** Methodology, Investigation, Data curation, Writing – review & editing. **Carla Penna Ozorio:** Methodology, Investigation, Writing – review & editing. **Paulo Henrique Ott:** Methodology, Investigation, Writing – review & editing, Funding acquisition. **Júlia Jacoby:** Investigation, Formal analysis, Writing – review & editing. **Leandro Bugoni:** Writing – review & editing, Funding acquisition. **Guilherme Tavares Nunes:** Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Data availability

Isotopic and macroinvertebrate datasets are available on GitHub https://github.com/SeabirdEcologyUFRGS/AmericanOystercatcher_TrophicEcology).

Acknowledgements

We are grateful to AP Peppes, CT Bergue, DMM Oliveira, F Caron, G Larre, G Fernandino, G Mendonça, J Gladzik, K Schmidt, L Guaragni, L Pinheiro, L Becker, M Ritter, M Sucunza and PL Martins, for assistance with fieldwork, sample preparation and/or analysis. For further support with fieldwork and sample analysis, we also would like to thank the staff of the *Refúgio de Vida Silvestre da Ilha dos Lobos* (ICMBio), *Parque Nacional da Lagoa do Peixe* (ICMBio), *Parque Estadual de Itapeva* (SEMA/RS), *Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul* (GEMARS), *Centro Integrado de Análises* (CIA/FURG), *Laboratório de Aves Aquáticas e Tartarugas Marinhas* (LAATM/FURG), and *Centro de Estudos Costeiros, Limnológicos e Marinhos* (CECLIMAR/UFRGS). The research group *Observa Litoral* (UERGS/CNPq) also contributed to this study. Mar Pedro Abreu provided the photo of rocky substrate with *P. perna*. We also thank *Centro Nacional de Pesquisa e Conservação de Aves Silvestres* (CEMAVE/ICMBio) for providing metal rings.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2023.e00300.

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