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Factors influencing the feeding habits of the ghost crab *Ocypode quadrata* (Fabricius, 1787) on subtropical sandy beaches

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ABSTRACT

Studies on feeding habits are fundamental to characterising the trophic role that species play in an ecosystem. They also help to understand the dynamics of populations involved in ecological relationships. Among the existing populations on tropical and subtropical sandy beaches in the world, the ghost crab (*Ocypode*) is the most conspicuous invertebrate. Despite its wide distribution, there is arguable information on the trophic ecology of this crab. Our study thus aimed to characterize the diet of the *Ocypode quadrata* on three morphologically distinct beaches in southern Brazil. Considering such factors as environmental differences, seasons, sex, and ontogeny, we evaluated which of these would be responsible for differences in the crab's food composition and quantity of items consumed. In addition, we used the repletion index (RI) to check the presence of food resource throughout the year. The samples were collected monthly, from March 2017 to February 2018, on three subtropical beaches in southern Brazil. We performed the biometry of the crabs, which involved weighing and measuring the size of the individuals, followed by the weighing of the stomachs to calculate the repletion index. We examined the contents of 660 stomachs, which were grouped into major food categories. Feeding index (IAi) indicates that feeding patterns varied only between seasons, demonstrating that the availability of prey is reflected in the diet of the ghost crab. The most significant items in its diet were insects, unidentified organic matter, and crustaceans. The RI tended to increase as the sand temperature increased. An increase in daytime foraging activity during cold months in contrast to a greater night-time foraging during warmer months shows a plasticity in the time of foraging. Finally, we conclude that the variety of prey consumed suggests that the *O. quadrata* has mainly opportunistic detritivorous feeding habits, as well as other feeding modes.

1. Introduction

The animal known as the ghost crab (genus *Ocypode*, Weber 1795) is the most common and notable invertebrate on tropical and subtropical sandy beaches in the world due to its large body size and its burrow-building behaviour, with openings along the supralittoral to dune zones (Brown and McLachlan, 1990; Blankensteyn, 2006; Sakai and Türkay, 2013; Lucrezi and Schlacher, 2014). These crabs play a pivotal ecological role connection in the food webs of beach and dune ecosystems and contribute to the cycle of nutrients as scavengers and deposit-feeders (Wolcott, 1978; Tewfik et al., 2016), while serving as prey for vertebrates (Schlacher et al., 2013). Ghost crabs display high trophic plasticity, occupying a range of trophic levels by feeding on insects, crustaceans, bivalves, macroalgae, diatoms, and marine and terrestrial vascular plants (Branco et al., 2010; Chartosia et al., 2010; Lim et al., 2016; Tewfik et al., 2016; Rae et al., 2019).

Sandy beaches are coastal ecosystems influenced by many abiotic factors (e.g., waves, tides, currents, and wind regimes), which modify hydrodynamic and depositional processes in these environments (Brown and McLachlan, 1990; Veloso et al., 1997). These beaches are classified as reflective, dissipative, and intermediate, depending on the slope, grain size, and wave incidence. These different physical habitat characteristics and climatic factors can influence the activity patterns of such organisms as crabs, which involve digging, feeding, and mating (Palmer,

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1971, 1976). Furthermore, predators, especially birds of prey, which are omnipresent on beaches can also influence crab activity (Branco et al., 2010; Rocha et al., 2021). The variation in beach morphology also affects the structure of the food web. According to Tewfik et al. (2016), high trophic level consumer crabs face intense changes in the availability and accessibility of resources at different levels, just as their own prey do. The food resources of crabs can also be influenced by season, which interferes in prey availability and, consequently, changes the predator's diet throughout the year (Mantelatto and Petracco, 1997). In addition, such intrinsic factors as the reproductive stage and ontogenetic development can result in consumption of different items (Werner and Gilliam, 1984; Lucifora et al., 2009). Thus, studying the natural diet of a species is essential in understanding how the availability and consumption of food items can affect the distribution, migration, and moult cycle (McLaughlin and Hebard, 1961).

The ghost crab *Ocypode quadrata* (Fabricius, 1787) has a wide distribution along the western Atlantic coast, from Rhode Island, USA 42°N 70°W, to Rio Grande do Sul, Brazil 30°S 50°W), and can be found in the different morphotypes of sandy beaches (Melo, 1996). Despite its important role in the trophic structure of ecosystems, studies on feeding habits that involve temporal, ontogenetic, and physical environment conditions are still scarce (Fales, 1976; Morrow et al., 2014; Gomes et al., 2019). A consistent sampling effort is necessary to determine the feeding behaviour of the ghost crab, as data available in the literature rarely cover an entire year. Besides, the behaviour of the species must be related to the physical characteristics of the habitat, as sandy beaches are very dynamic ecosystems (Tewfik et al., 2016).

The transition from narrow (reflective) to wide (dissipative) beach integrates a habitat gradient where *Ocypode* crabs are able to explore. Since these crabs move easily and feed on a variety of food sources, including scavenging carrion (Schlacher et al., 2013) and microphagy (Robertson and William, 1981), they may alternate trophic position or prey preferences in dynamic habitats. Estimating the relative availability of prey in the habitat is an interesting way to predict the items available for high trophic level consumers, such as ghost crabs. Given the wide range of items they explore, an informative way to assess these items is by evaluating their stomach contents. However, certain factors can influence repletion: intrinsic, for example the reproductive seasonality of the species (Chartosia et al., 2010), or extrinsic, in which the number of items ingested may not change seasonally, but rather the quality of resources (Gomes et al., 2019). In these cases, the pattern of feeding activity requires a proper interpretation. These highly dynamic environments reveal that beaches need to be evaluated for the particularities of their habitats, as it is still not clear whether the physical differences that affect the ghost crab's diet can be generalized.

Therefore, our objective was to evaluate the *O. quadrata* diet on three different beaches on the southern Brazilian coast, testing the following hypotheses: (1) Seasonal and physical differences in habitats reflect in the type and quantity of items consumed, and; (2) There is a variation in food items between the seasons, sexes, and ontogeny in the *O. quadrata* diet.

2. Material and methods

2.1. Study area

We performed monthly collections of samples from March 2017 to February 2018 in three distinct Brazilian sandy beaches located on the central-northern coast of Santa Catarina State (Fig. 1). The three areas are located at similar latitudes (26°) to minimize, as much as possible, the influence of climatic conditions on them. The first area, Lagoa de Barra Velha beach (BV) (26°34′56.64″S to 26°37′37.70″S; 48°39′55.38″W to 48°40′49.12″W), is consistent with a "reflective" beach type, showing a sharp slope, coarse sand grains, and a narrow surfing zone with 6 km length and is part of the estuary system of the Itapocú River. Dunes are covered by sand vegetation, comprising shrubs and medium size trees, with mangrove areas nearby. The second area (26°49′36.5″S to 26°54′35.46″S; 48° 37′17.36″W to 48° 38′34.61″W), Navegantes beach (NV), is 10 km long and is characterized as "dissipative" beach type, which presents fine sand grains, gentle slope, and extensive dune area with the Itajaí-açu river that flows into the south end of this beach. The third area exhibits characteristics of an "intermediate" beach type, with intermediate slope, medium grains of sand, and medium surf zone. This beach is known as Brava beach (IT) and is located in the Itajaí municipality (26°55′57.30″S to 26°57′36.02″S to 48°37′35.08″W to 48°37′41.35″W). It is characterized by the presence

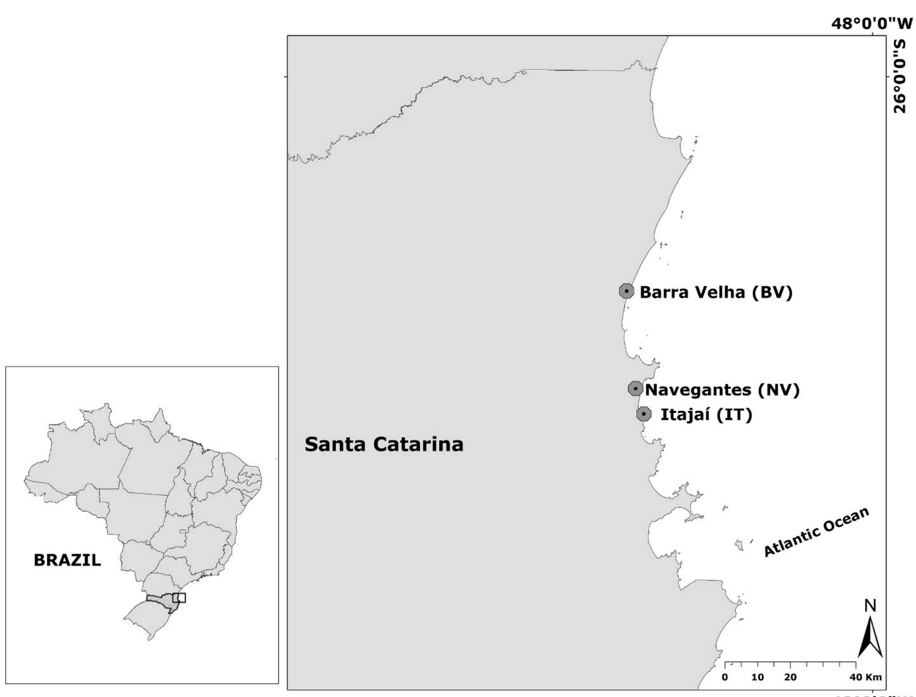

Fig. 1. Study locations along the central-northern coast of Santa Catarina State (Southern Brazil).

of the Cassino da Lagoa nearby, rocky shores at both ends of the beach, with dunes covered by sand vegetation, and is 3 km long.

2.2. Environmental variables

We divided the beaches proportionally into three equal-sized longitudinal sections. Thus, all seasons had biological replicate samples from each sandy beach. We established transects to measure the beach width (distance from the tide line to the end of the coastal vegetation) using a measuring tape, and to calculate the slope, we used the "rise over run" method, i.e., in the transect, two stakes were placed on the shoreline and the foredunes. Then, the perpendicular distance between the two stakes was measured and we obtained a relation between the seaward slope steepness (Emery, 1961). We measured climatic conditions at the beginning and the end of each collection. We recorded air, water, and sand temperatures with a precision thermometer of 0.1 °C and water salinity with an optical refractometer. Also, fresh samples of sand from the respective environments were used to calculate the sand moisture content. For this, an initial reference value (200 g) was weighed for each sample, subsequently placed in an oven at 100 °C for 24 h. A new weighing was then carried out, and we calculated the sand moisture content by the difference between fresh weight and dry weight. We characterized sediment by granulometric analysis using 50 g of sand collected from the three beaches. In the laboratory, the samples were dried in a 60 °C oven for 24 h and sieved with a series of sieves with standard meshes for Wentworth scale (1922), (4.00, 2.00, 1.00, 0.500; 0.250, 0.180, 0125, and 0.063 mm), and adapted to scale phi (φ) according to Krumbein (1934). We implemented the parameters of Folk and Ward (1957) for data and used Sysgran 3 software for statistical analysis (Camargo, 2005).

2.2.1. Specimen samplings

The collection of *O. quadrata* crabs was authorized by the System of Authorization and Information on Biodiversity (SISBIO) under license n°. 57786. We carried out collections at times of ghost crab surface activity, which includes burrow construction and foraging (Jones, 1972; Evans et al., 1976; Lucrezi and Schlacher, 2014). Crabs were collected manually, when they were moving voluntarily on the sandy beach surface, and by excavating the sand at the entrance of burrows containing crabs. Collections were carried out once a month for 2 h, at each sampling site.

In our preliminary study, we did not verify the surface-activity of ghost crabs during cold seasons nights, as higher number were active during the day, building burrows and emerging for foraging. To access a greater number of active crabs throughout the year and to avoid biases, by collecting few (or no) nocturnal individuals who appear to be inactive during cold seasons (most with empty stomachs or few grains of sand: Table A1, Appendix A), we captured them during the day. Thus, collections were performed during the night phase in spring (September, October, and November) and summer (December, January, and February); and, during the day phase, in autumn (March, April, and May) and winter (June, July, and August).

Once captured, specimens were individually placed in plastic bags, properly labelled, and stored in a thermal box with ice cubes to decrease enzymatic digestion and euthanasia. In the laboratory, we separated specimens by sex and analysed them for their maturation stage (Mota-Alves, 1975). We measured the body weight of the crabs with analytical and precision scales for juveniles and adults, respectively. We measured carapace width by a digital calliper with a precision of 0.01 mm. We then separated them into five categories (I to V) according to size (10 mm intervals), and the stomachs were removed, weighed, and stored in 70% ethanol.

2.3. Stomach analysis

Stomach contents were placed in Petri dishes containing 70% alcohol and analysed under a stereo microscope (Zeiss Stemi DV4, Germany). Food items were identified and categorized to the lowest taxonomic level possible using specific literature (Rafael et al., 2012). Items impossible to identify due to digestion were grouped as unidentified organic matter (UOM). After opening the stomach, the degree of repletion was classified into five categories: 1 = empty stomach, 2 = quarter-full stomach, 3 = half-full stomach, 4 = three-quarters-full stomach and 5 = full stomach. The repletion index (RI) was calculated using the formula $RI = (W_e/W_t)$, where "W_e" stands for weight of the stomach and "W_t" for weight of the individual (Santos, 1978). The frequency of occurrence (FO) (Hyslop, 1980) was used for the diet analysis. The method of the feeding index (IAi) (Kawakami and Vazzoler, 1980) was applied for the volume of each food item (Vo) (Albrecht and Pellegrini-Caramaschi, 2003), given by: $IAi = [(Fi \times Vi)/\Sigma (Fi \times Vi)] \times 100$, where F is the frequency of occurrence (%) of the item, and V is the volume (%) of the item.

2.4. Data analysis

To detect statistical differences between environments ($p < 0.05$), variables related to air, sand and water temperatures, water salinity, sand moisture, sand grain size, beach slopes and widths were subjected to analysis of variance (ANOVA), followed by Tukey's post hoc test (Zar, 2010). Since previous studies in sand temperature were shown to be essential for the activity of *Ocypode* crabs (Schoeman et al., 2015; Watson et al., 2018) we used this parameter to verify its effect on the repletion index (RI) among beach morphotypes. To verify the existence of such interactions, we used the monthly average values in a generalized linear model (GLM), applying quasipoisson distribution in the *vegan* package (Oksanen et al., 2020; R Development Core R Core Team, 2020). The Food importance indices (IAi) were subjected to permutational multivariate analysis of variance - PERMANOVA (Anderson, 2001) with 9999 permutations ($p < 0.05$) to detect variations in sex, seasonality, environment, and size class (ontogeny) factors. PERMANOVA (based on the Bray-Curtis dissimilarities) was performed according to the principles of McArdle and Anderson (2001), running sequential, marginal and global tests, detecting precisely which factors were responsible for the differences. Firstly, to have a larger sample volume, all data were grouped into factors "environments" and "seasons", running the analysis for the factors separately and the interaction between them. If no differences between environments were detected, a second round of PERMANOVA, derived from a new rearrangement was run (excluding environment specificity and for a larger sample size) grouping all individuals into males and females (sex factor). When no differences between sexes were detected, the data were regrouped into different size classes (ontogeny factor) to ensure adequate sampling. When significant differences regarding one of the factors were detected, similarity percentage analysis (SIMPER) was used to determine which item contributed most to such differences (Clarke and Warwick, 1994). ANOVA, PERMANOVA and SIMPER analyses were performed using PAST 3.18 software (Hammer et al., 2001).

3. Results

3.1. Environmental variables

The ANOVA analysis did not detect significant differences in the environmental variables related to air ($F_{2\text{-}69} = 0.3289$; $p = 0.7209$), sand ($F_{2\text{-}69} = 0.2582$; $p = 0.7732$), water ($F_{2\text{-}69} = 0.1441$; $p = 0.866$), temperatures and salinity ($F_{2\text{-}69} = 0.2582$; $p = 0.77$), on sandy beaches (Appendix A, Table A2). Conversely, sand moisture was significantly higher in the dissipative beach (NV) when compared to the other two environments ($F_{2\text{-}69} = 15.24$, $p < 0.01$). Considering the morphological and sedimentary characterization of the beaches (Appendix A, Table A3), there were significant differences for the average sand grain sizes (φ values) in the three sites ($F_{2\text{-}14} = 70.22$, $p < 0.01$). As for the beach slopes, the dissipative beach (NV) was significantly lower than the other two environments ($F_{2\text{-}33} = 7.119$; $p < 0.01$). Significant differences were not detected between BV and IT beaches ($p > 0.05$). Additionally, no statistical difference was detected for the average beach width in the three environments ($F_{2\text{-}33} = 3.04$, $p = 0.06$).

3.2. Ghost crab traits

The time when crabs forage was observed during the research. Foraging was nocturnal (spring-summer) and diurnal (autumn-winter). During cold seasons nights crab remained underground and most stomachs were empty or contained some grains of sand (Appendix A, Table A1). A total of 660 individuals was sampled, listed in Table 1.

3.3. Repletion and stomach contents analysis

In the reflective beach (BV) samples, 76% and 71% of male and female stomachs, respectively, contained some food items. In the dissipative beach (NV), 74% of the males and 73% of the females had stomach contents. For the intermediate beach (IT), males and females presented, respectively, 73% and 83% of the stomachs with some content. The repletion index (RI) of the ghost crab population was significantly higher ($F_{2\text{-}624} = 6.238$, $p = 0.020$) in the intermediate beach (IT) (mean ± SE: 0.0232 ± 0.00085), demonstrating more ingestion of food resources than in the dissipative (NV) (0.0203 ± 0.00091) and the reflective beach (BV) (0.0194 ± 0.00069). Throughout the seasons, the repletion indexes generated for the respective sampled environments showed significant differences only for the reflective beach (BV) (Fig. 2), being higher in the months that include spring and summer in BV. This index was statistically significant for both, males ($F_{3\text{-}41} = 8.029$, $p < 0.01$) and females ($F_{3\text{-}72} = 8.929$, $p < 0.01$). These results did not differ in the dissipative (NV) or intermediate (IT) beaches during seasons. Although significant differences between seasons in RI were detected only in the reflective beach, crabs tended to eat more during hot seasons on all beaches.

In fact, GLM analysis detected a significant relationship between RI and sand temperature on the three beaches ($p = 0.0281$), with no significant differences between beach morphodynamics (Fig. 3; Table A4). So, as the sand temperature increases, the stomach repletion of the ghost crab also increases.

3.3.1. Male and female stomachs contents

By analyzing the stomach contents of male crabs captured in the three environments (BV, NV and, IT), we identified 35 items that resulted in ten main food categories, which varied in the frequency of occurrence and volume (mm^3), also varying between seasons (Table A5, Appendix A). In the female stomachs, 30 food items were identified, and then grouped into nine main food categories (Table A6, Appendix A).

3.4. The feeding index (IAi)

The main food categories found in *O. quadrata* stomachs and their respective IAi values are recorded in Table 2. In the stomach samples of male individuals from the reflective beach (BV), the INSECTA category was predominant in spring (0.93), autumn (0.46), and winter (0.60). In summer, the most representative food item was UOM (0.58). For the dissipative beach (NV), the INSECTA was also the most representative category in both, spring (0.99) and winter (0.64) samples. However, the unidentified UOM category achieved greater representation in the summer (0.51) and autumn (0.71) samples. In the analysed stomachs from intermediate beach (IT), the INSECTA category was the most representative in spring (0.92), autumn (0.64), and winter (0.99), while CRUSTACEA was predominant in summer (0.55).

In the female stomachs from the reflective beach (BV), the INSECTA group contributed with the largest share of food items recorded in spring (0.73), summer (0.53), autumn (0.51), and winter (0.63). The same pattern was observed for stomachs from the dissipative beach (NV), in which the INSECTA group prevailed as food content in spring (0.99), summer (0.58), autumn (0.90), and winter seasons (0.98). For the intermediate beach (IT), INSECTA was also the most representative category in spring (0.52), autumn (0.87), and winter (0.57). However, the CRUSTACEA group was prevalent (0.95) in the summer samples as a food resource. When subjecting the results generated by the feeding index (IAi) to PERMANOVA analysis, the factors environment and sex did not result in statistically significant differences (Table 3). However,

Table 1
Morphological characteristics of the ghost crab from the sandy beaches of Barra Velha, Navegantes and Itajaí.

Sites	Sex	Carapace size (mm)	Individuals %
Barra Velha (BV)	Juvenile	9.43 to 14.3 (12.3 ± 2.55)	1.36
Reflective	Female	12.3 to 40.94 (25.96 ± 5.96)	34.84
N = 221	Male	16.94 to 42.8 (30.98 ± 6.16)	63.80
Navegantes (NV)	Juvenile	5.61 to 15.16 (9.48 ± 2.46)	9.14
Dissipative	Female	10.56 to 39.66 (25.97 ± 6.62)	40.32
N = 186	Male	13.18 to 45.01 (30.22 ± 7.77)	50.54
Itajaí (IT)	Juvenile	5.9 to 15.16 (10.47 ± 2.46)	7.11
Intermediate	Female	11.8 to 37.62 (26.13 ± 5.77)	32.41
N = 253	Male	12.6 to 43.22 (25.09 ± 6.45)	60.48

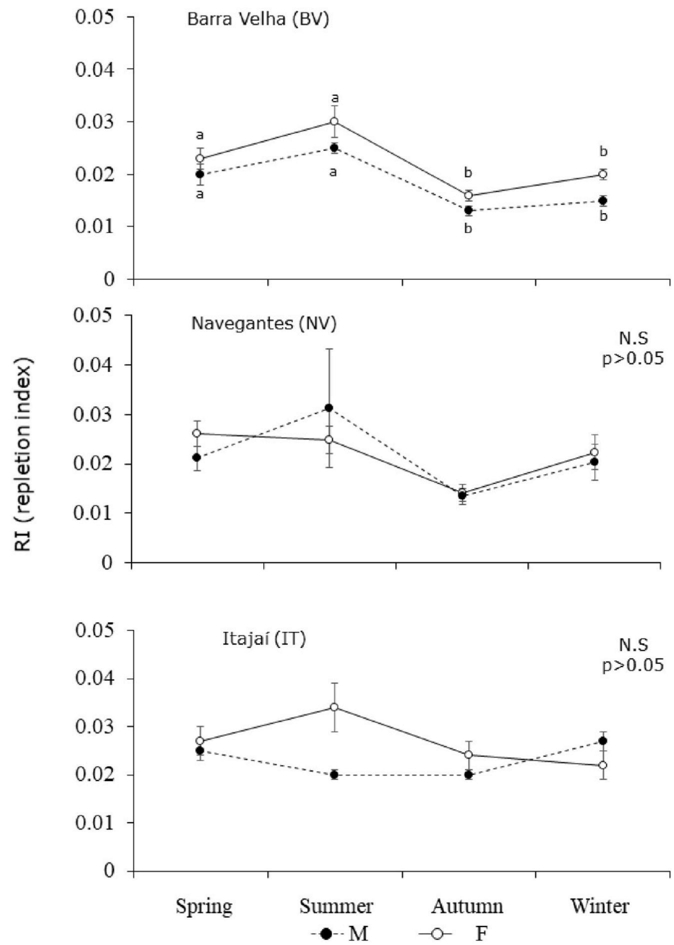

Fig. 2. Mean and standard error of stomach repletion index of male (M) and female (F) of Ocypode quadrata captured in three beach morphologies in southern Brazil: reflective (Barra Velha, BV), dissipative (Navegantes, NV) and intermediate (Itajaí, IT). Legend: N. S – No significant for Tukey Kramer multiple comparison test ($p > 0.05$). Equal letters: no statistical differences of ANOVA: BV – Male ($F_{3\text{-}141} = 8.929$, $p < 0.01$), Female ($F_{3\text{-}72} = 8.029$, $p < 0.01$); NV - Male ($F_{3\text{-}90} = 0.669$, $p = 0.57$), Female ($F_{3\text{-}71} = 2.432$, $p = 0.07$); IT - Male ($F_{3\text{-}149} = 2.531$, $p = 0.06$) and Female ($F_{3\text{-}78} = 1.7\ 02$, $p = 0.17$).

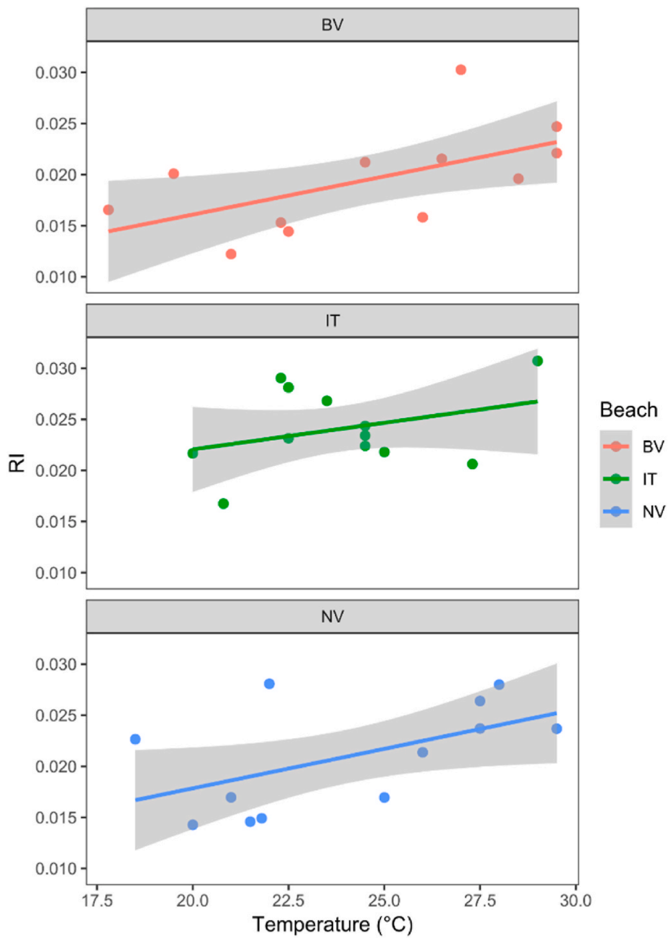

Fig. 3. Generalized linear model relationships between RI and sand temperature of the respective beaches. Legend: (Barra Velha, BV), intermediate (Itajaí, IT) and dissipative (Navegantes, NV) beaches. Statistical parameters are presented in Table A4 (Appendix A).

the resulting composition of feeding indexes differed between seasons. This difference is explained by the values generated for summer, which differed from those generated for the autumn ($F = 6.274$, $p < 0.01$), winter ($F = 3.278$, $p < 0.01$) and spring ($F = 2.534$, $p = 0.03$) seasons.

The diet similarity between sex and environment factors allowed us to group the samples from the three environments for greater representativeness, especially of juveniles, in assessing diet across size classes (ontogeny). For this, we grouped individuals into five size categories (I to V), with an interval of 10 mm between carapace widths (Table A7). It should be noted that category (I) constituted immature individuals. Sand, UOM, Insecta and Crustacea were identified in stomach samples. In category (II), constituted by mixed forms (adults and immatures), mainly sand, UOM, Insecta, Crustacea and plant material were found in stomach samples. The other three categories (III, IV, and V) are constituted only by adult forms. In these larger categories (III–V) more variety of food items was found, but what caught our attention was anthropogenic materials (i.e., plastic, glass, nylon line, paper) in the stomachs. We subjected the food indices of the respective size categories to another round of PERMANOVA analysis and there were no significant differences between them (Table 3).

The result of the SIMPER analysis (Fig. 4) detected which food categories contributed (in percentage) to the differences found between the

Table 3
PERMANOVA test in the diet of Ocypode quadrata. Factors of analysis were environments, seasons, sexes and ontogeny. * significant for $p < 0.05$.

Source	Df	SumOfSqs	R2	F	Pr(>F)
ENVIROMENTS	2	0.275	0.081	1.303	0.267
SEASONS	3	1.044	0.307	3.291	0.005*
ENVIROMENTS vs. SEASONS	6	0.814	0.239	1.284	0.222
RESIDUAL	12	1.268	0.373		
TOTAL	23	3.402	1.000		
SEXES	1	0.167	0.049	1.478	0.240
RESIDUAL	17	1.916	0.563		
TOTAL	23	3.402	1.000		
ONTOGENY	4	0.747	0.292	1.029	0.419
RESIDUAL	10	1.816	0.708		
TOTAL	14	2.564	1.000		

Table 2
Feeding Index (IAi) for sexes of *Ocypode quadrata* captured in three beach morphologies in southern Brazil: Barra Velha (BV), Navegantes (NV) and, Itajaí (IT). Sampling season are shown as Sp - spring, Su - summer, Au - autumn, Wi – winter, UOM - unidentified organic matter. The highest IAi values for each season are in bold.

	BV				NV				IT			
Male	Sp	Su	Au	Wi	Sp	Su	Au	Wi	Sp	Su	Au	Wi
Food category	IAi	IAi	IAi	IAi	IAi	IAi	IAi	IAi	IAi	IAi	IAi	IAi
UOM	0.04	**0.58**	0.16	0.03	<0.01	**0.51**	**0.71**	0.32	0.07	0.13	0.35	<0.01
SAND	<0.01	<0.01	0.17	0.08	0.01	0.01	0.01	0.03	<0.01	0.06	<0.01	<0.01
ANTHROPIC MATERIAL	0.01	<0.01	<0.01	0.05	<0.01	0	0.10	0.01	0	0	<0.01	0
OSTEICHTHYES	0	<0.01	0	0	0	0	0	0	0	0	<0.01	0
PLANT MATERIAL	0.02	0.03	0.10	<0.01	0	<0.01	0	<0.01	0.01	<0.01	<0.01	0.01
ANNELIDA	0	0	<0.01	0	0	0	0	<0.01	0	0	0	0
NEMATODA	0	<0.01	<0.01	<0.01	0	0	0	0	<0.01	<0.01	<0.01	0
MOLLUSCA	0	0	0	0.01	0	0	<0.01	<0.01	0	0	0	<0.01
INSECTA	**0.93**	0.34	**0.46**	**0.60**	**0.99**	0.12	0.19	**0.64**	**0.92**	0.27	**0.64**	**0.99**
CRUSTACEA	0	0.05	0.08	0.24	0	0.36	<0.01	0	0	**0.55**	<0.01	0
	BV				NV				IT			
Female	Sp	Su	Au	Wi	Sp	Su	Au	Wi	Sp	Su	Au	Wi
Food category	IAi	IAi	IAi	IAi	IAi	IAi	IAi	IAi	IAi	IAi	IAi	IAi
UOM	0.16	0.21	0.01	0.17	<0.01	0.01	0.04	<0.01	0.47	0.02	0.01	0.04
SAND	<0.01	0.04	0.04	0.01	0.01	<0.01	0.06	0.01	0.01	<0.01	0.01	0.34
ANTHROPIC MATERIAL	0	0	0	0	0	0	0	0	0	0	<0.01	<0.01
PLANT MATERIAL	0.10	0.21	0.44	0.15	0	<0.01	0	<0.01	<0.01	0	0.06	0
NEMATODA	<0.01	0	0	0	0	0	0	<0.01	0	<0.01	<0.01	0
MOLLUSCA	<0.01	0	0	<0.01	0	0	<0.01	0	0	0	0	<0.01
INSECTA	**0.73**	**0.53**	**0.51**	**0.63**	**0.99**	**0.58**	**0.90**	**0.98**	**0.52**	0.02	**0.87**	**0.57**
CRUSTACEA	<0.01	0.02	<0.01	0.05	0	0.41	<0.01	0	0	**0.95**	0.04	0.05
ARACHNIDA	0	0	0	0	0	0	0	0	0	0	0	<0.01

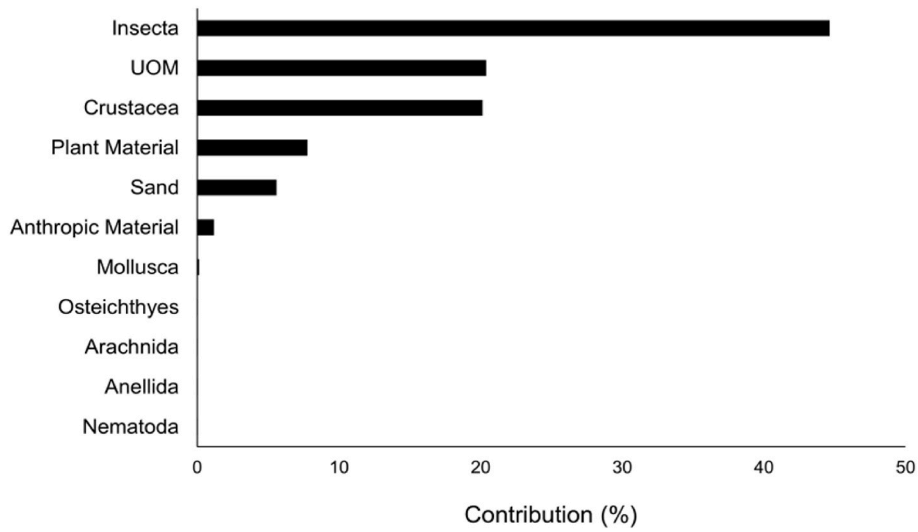

Fig. 4. Similarity Percentage Analysis (SIMPER) to depict the contribution (%) of the food categories of the *Ocypode quadrata*. The analysis shows the food categories that contributed most to the differences in diet.

seasons. The categories were INSECTA (44.65%), ORGANIC MATTER (20.40%), and CRUSTACEA (20.14%), which altogether accounted for 85.19% of the ghost crab's food resource.

4. Discussion

O. quadrata is recognized as being very sensitive to environmental variations, and when subjected to adverse situations, its activity decreases (Wolcott, 1978; Alberto and Fontoura, 1999; Corrêa et al., 2014). In fact, variables such as light and temperature are known to work together with an internal biological timing system to adjust the activity of an organism to a specific time of the day and year (Peschel and Helfrich-Förster, 2011; Vanin et al., 2012). It has been shown that *Ocypode* crab surface activity involves burrow construction followed by foraging and is either diurnal and/or nocturnal (Lucrezi and Schlacher, 2014), depending on species, beach morphodynamics, temperature and moon phases (Jones, 1972; Evans et al., 1976; Pombo et al., 2018; Yong and Lim, 2021). During the coldest seasons, *O. quadrata* enters dormancy on the subtropical sandy beaches of the northern hemisphere (Morrow et al., 2014; Tewfik et al., 2016), but in our study, carried out on subtropical beaches of the southern hemisphere, this species showed prominent diurnal foraging, as already reported in other works (Alberto and Fontoura, 1999; Vinagre et al., 2007; Pombo et al., 2018). That may mean that this crab follows a thermo-energetic rationale, beyond the light/dark cycle, such as *Uca pugilator* (Mat et al., 2017). Further studies should assess the influence of tidal cycles on burrow inundation, particularly during harsh periods of the cold season, to observe if *O. quadrata* displays food hoarding behaviour in burrows and is able to keep stomach repletion during adverse conditions (Yong and Lim, 2021).

According to our statistical results, repletion index (RI) was uniform throughout the year in two of the three beaches (IT and NV). However, in the reflective beach (BV) RI was significantly lower during cold seasons. This result is not a surprise, considering the peculiar physical characteristics of a reflective beach. This leads us to believe that morphodynamics is involved with the decrease in the diversity of resources (Lercari et al., 2010) and the difficulty in accessing them, considering the environmental harshness during cold seasons (Tewfik et al., 2016). The most direct evidence we observed for this seasonal pattern was the positive correlation obtained between repletion index and sand temperature, meaning that temperature exerts influence on feeding rates. Temperature also has effects on metabolism and plays an important role in the activities of *Ocypode* crabs, such as foraging (Weinstein and Full, 1998; Vinagre et al., 2007; Lucrezi and Schlacher, 2014). In fact, we observed that the amount of food ingested by crabs was lower when sand temperatures decreased (and vice versa), regardless of beach type. This effect was more prominent in reflective beach, probably due to the harshness of this beach.

Temporal differences were detected using feeding index (IAi), demonstrating that, in summer, feeding was different from other seasons, without distinction of sexes, ontogeny and beach morphotypes. This temporal variation can be attributed to the variability of food available in both seasonal and daily scales, with fluctuations of prey as well as predator (Leber, 1982). Macrofauna decreases activity in the coldest months, which reflects in the decreasing prey availability to *O. quadrata* (Leber, 1982; Tewfik et al., 2016). The considerable increase in daytime foraging activity during cold months in contrast to a greater night-time foraging during warmer months shows a plasticity in the time of foraging. This may have contributed to the differences in the crabs' diet throughout the year, which leads to questions about the seasonal quality of the diet and its implications for body condition and demographic patterns.

Regardless of the quality of the diet, our results show that *O. quadrata* feeds mainly on insects, crustaceans, and unidentified organic matter throughout the year. Insects are present on sandy beaches and distributed in the dune region (invasive or windblown insects) and the intertidal zone, and are often associated with algae and stranded debris (McLachlan and Brown, 2010). An interesting result was the finding of a higher number of bees (*Apis* sp.), which was also evidenced by Branco et al. (2010), mainly during colder months. On the other hand, during the warmer months, the ghost crab fed more on beetles. This corresponds to the period of highest activity for these insects, which is during the night (Mourglia et al., 2015), while bees are more active during the day (Moore et al., 1998). It is also worth noting that, during our observations and collections, many insects were found dead on the surface (day and night), showing that, alive or dead, they are, indeed, recurrent food resources for *O. quadrata*.

Concerning crustaceans, we found Amphipoda in the stomach of ghost crabs from the three beaches in all seasons, especially summer and winter. This result was possibly due to continuous recruitment and higher densities of Amphipoda in the summer and winter (Cardoso and Veloso, 1996). Amphipoda has also been found in the diet of *Ocypode convexa* (Rae et al., 2019). As for the crustacean mole crab (*Emerita brasiliensis*), this was another food source we found in the ghost crab diet, perhaps due to the increase in population density, mainly in the hottest months (Cardoso et al., 2003). Furthermore, there is evidence that the mole crab is less available on reflective beaches (Defeo and Cardoso, 2002; Defeo and McLachlan, 2011), corroborating our work. A possible explanation is that the accessibility of mole crab by *O. quadrata* on this type of beach is reduced since *O. quadrata* crabs are poor swimmers and tend to avoid the surf zone (Tewfik et al., 2016). As for the high occurrence of UOM as food source, this can be explained by the prey's advanced digestion process or by the soft parts of prey or even clamping behaviour (D'incao et al., 1990; Mantelatto and Christofoletti, 2001), whose leftover components make accurate identification difficult.

Although we have registered plant material in the stomach of some crabs, herbivory was low in the diet of *O. quadrata*, as already reported by Wolcott (1978), Branco et al. (2010), and Gomes et al. (2019). The highest intake of plant material was recorded for autumn and summer samples. The presence of plant material in the ghost crab's diet may originate from the prey's digestive tract or as an alternative to the scarcity of preferred foods (i.e., live prey or animal carrion) (Gomes et al., 2019; Rae et al., 2019). Another item is the nematodes found in the ghost crabs' stomachs, except in juveniles. The nematodes always showed an intact body, which indicates that they were not ingested and, therefore, would be involved with parasitism of *O. quadrata*, as observed by other authors (Turra et al., 2012). As for the role of sand consumption, it is still questionable in the diet of crabs. It may result from accidental ingestion while handling the prey (Branco and Lunardon-Branco, 2002; Gomes et al., 2019), or as an auxiliary particle that helps to grind calcareous prey (Mantelatto and Christofoletti, 2001). Another possibility would be a deposit-feeding behaviour, benefited by adhering organic matter in sediments (microphytobenthos, bacteria and other microorganisms), common in the Ocypodidae superfamily (Robertson and Newell, 1982; D'incao et al., 1990). In our study, sand inside stomachs occurred in all animal sizes, seasons, and environments. We believe that this can be related to the digging habit of this organism, leading to an accidental intake during the prey manipulation at the time of capture. This "accidental intake" can also result in the ingestion of anthropogenic debris, such as plastics.

Solid waste on sandy beaches negatively affects the population density of ghost crabs and their prey (i.e., mole crab, amphipods) (Suciu et al., 2018). It is worth noting that the presence of plastics, and other items of anthropic origin in the stomachs of marine animals, has been frequent in several studies and may be associated with the prominence caused by colours, shapes, and food odours in marine debris. This could lead confusing plastics with prey (Moser and Lee, 1992; Costa et al., 2019a). Some of these plastic items may resemble vegetal material and seaweed. In fact, fishing lines and plastics that we analysed under stereomicroscope had similar colours and shapes to leaf and filamentous algae. It is remarkable the composition of marine debris reported on sandy beaches of Santa Catarina, Brazil that reached 90% of plastic (Widmer and Hennemann, 2010). Since the ghost crab can use marine debris as a food resource (Costa et al., 2019a, 2019b), this poses a potential risk to the species, for example to the marine and terrestrial food web. The relation of *O. quadrata* with debris such as plastics, foam, strings, and other materials has been found associated with crab burrows (Costa et al., 2018). Likewise, we also viewed debris near ghost crab burrows (data not shown) and identified macroplastics and microplastics in the ghost crab stomach, as already demonstrated by Costa et al., 2019b, showing that these crabs could mistakenly identify plastic as a food resource. Furthermore, the interaction with the marine debris tends to increase as individuals of the species *O. quadrata* are larger, and the food resources (crustaceans) are smaller in size (Costa et al., 2019a). In fact, in our work, anthropogenic material was found only in larger ghost crabs, and mainly during the colder seasons, demonstrating detritivorous behaviour. Future studies using length-weight regression for populations with and without plastic should enhance our understanding a of the consequences of plastic ingestion in crab body condition.

5. Conclusions

The different feeding behaviours (i.e., predation, detritivory, deposit-feeding) related to *O. quadrata* along with the variety of food items they consume, suggest a substantial trophic plasticity for this species (Lucrezi and Schlacher, 2014). Taken together, our data indicate, for the three beach types, a tendency toward opportunistic detritivory in this species, since the incidence of insects such as bees (*Apis* sp.) was high in the crab's stomachs, without significant differences between the food resources in these environments. Moreover, other feeding modes, such as predation (mole crab and Amphipoda) were also evident. In fact, metabolism studies suggest that ghost crabs ingest more animal food source (Vinagre et al., 2007), which was also observed in our study. In addition, the presence of anthropic materials demonstrates the negative influence of human activities on this species, and raises awareness of conservation issues.

The relationship between sand temperature and food intake denotes that temperature is an essential factor in crab feeding activity, regardless of beach type. Finally, we concluded that the difference detected in the diet of ghost crabs on the different sandy beaches is more related to the availability of prey that varied throughout the year, since the summer feeding index (IAi) was different from other seasons. The variations in the ghost crab's diet could be related to the change in this crab's activity throughout the year. Regarding beach morphologies and ontogeny, the feeding index did not differ. Complementary studies on population parameters are necessary to understand the dynamics of *O. quadrata* in different environments.

CRediT authorship contribution statement

Julia Gomes do Vale: Visualization, Writing – original draft, Validation, Conceptualization, Funding acquisition, Investigation, Project administration. **Germano Henrique Costa Barrilli:** Project administration, Writing – review & editing, Investigation, Formal analysis, Conceptualization, Methodology. **Samira Chahad-Ehlers:** Writing – review & editing. **Joaquim Olinto Branco:** Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Table A1
Preliminary results of the repletion index (RI) of *Ocypode quadrata* in two captures, one the reflective (Barra Velha) beach and another on the dissipative (Navegantes) beach, in the end of autumn. The collection was nocturnal and diurnal. It is noteworthy that the crabs were not emerging during the night on the sandy beach surface and we had to dig the burrows to find them.

Barra Velha	Repletion	Sex	BW (mm)	RI	Item
1	Empty	Male	38.03 mm	0.016	–
2	Empty	Male	28.84 mm	0.010	–
3	Empty	Female	26.01 mm	0.013	–
4	Quarter full	Female	23.20 mm	0.020	Sand
Navegantes	**Repletion**	**Sex**	**BW (mm)**	**RI**	**Item**
1	Empty	Male	14.00 mm	0.013	–
2	Empty	Female	13.51 mm	0.015	–
3	Quarter full	Male	27.04 mm	0.008	Sand

Table A2
Mean values and standard deviation of the environmental variables recorded on the Barra Velha (BV), Navegantes (NV), and Itajaí (IT) from March 2017 to February 2018.

Season	Beach	Air (°C)	Sand (°C)	Water (°C)	Salinity (%)	Sand Moisture (%)
Spring	BV	23.0 ± 2.45	26.8 ± 2.32	22.5 ± 0.84	34.3 ± 1.15	3.8 ± 2.46
	NV	22.9 ± 1.28	28.2 ± 1.17	23.2 ± 0.41	33.3 ± 1.15	5.2 ± 1.79
	IT	21.0 ± 1.82	25.4 ± 1.74	22.5 ± 0.45	34.7 ± 0.58	2.9 ± 0.72
Summer	BV	28.8 ± 1.17	28.3 ± 1.21	26.2 ± 0.75	32.3 ± 0.58	3.2 ± 0.66
	NV	25.2 ± 0.75	26.3 ± 1.51	25.7 ± 0.52	27.0 ± 5.29	11.5 ± 4.89
	IT	24.2 ± 2.48	25.5 ± 2.95	24.7 ± 0.52	31.7 ± 1.53	3.6 ± 0.29
Autumn	BV	19.7 ± 3.19	20.3 ± 2.23	21.4 ± 2.06	30.3 ± 2.08	5.5 ± 1.27
	NV	21.3 ± 1.21	20.9 ± 1.11	21.8 ± 2.19	28.5 ± 5.89	6.7 ± 2.10
	IT	21.9 ± 2.54	22.3 ± 2.42	21.8 ± 2.32	33.0 ± 2.65	3.6 ± 0.37
Winter	BV	18.6 ± 3.47	22.7 ± 3.14	19.8 ± 0.88	35.0 ± 0	3.5 ± 0.29
	NV	18.1 ± 2.01	20.7 ± 2.07	20.0 ± 0.55	32.0 ± 5.29	3.8 ± 0.64
	IT	19.8 ± 2.25	22.2 ± 1.75	20.2 ± 0.41	34.0 ± 1.73	2.8 ± 0.53

Table A3
Morphological characteristics of sandy beaches of Barra Velha, Navegantes and Itajaí.

Characteristics	Barra Velha	Navegantes	Itajaí
Sand grain (φ)	0.67 ± 0.38	2.65 ± 0.25	1.90 ± 0.06
Sand size	Coarse	Fine	Medium
Width (m)	16.67 ± 7.78	25.33 ± 11.98	19.5 ± 5.2
Slope (°)	5.35 ± 1.77	2.19 ± 1.91	4.5 ± 2.61

Table A4
Results of the generalized linear model to test the effect of temperature and beach type on the repletion index (RI).

Coefficients	Estimate	Std.	t-value	Pr(>|t|)
(Intercept)	−4.91293	0.431565	−11.384	**> 0.001***
Temperature	0.03928	0.01702	2.308	**0.0281***
Itajaí	1.126846	0.699978	1.61	0.1179
Navegantes	0.152991	0.606975	0.252	0.8027
Temperature vs. Itajaí	−0.03678	0.028578	−1.287	0.2079
Temperature vs. Navegantes	−0.00237	0.024244	−0.098	0.9227

Table A5
Frequency of occurrence (FO) and volume (V_o) of food items found in male stomachs of *Ocypode quadrata* captured on the Barra Velha, Navegantes, and Itajaí beaches, southern Brazil. Seasons are expressed as Sp - spring, Su - summer, Au - autumn, Wi - winter. Legend: UOM = unidentified organic matter, UPM = unidentified plant material, N.I = not identified. The highest values of FO and Vo for each season are in bold.

	BARRA VELHA								NAVEGANTES								ITAJAÍ							
	Sp		Su		Au		Wi		Sp		Su		Au		Wi		Sp		Su		Au		Wi	
	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o
UOM	0.13	37.30	0.21	**551.00**	0.15	20.30	0.15	10.50	0.18	0.44	**0.27**	213.60	**0.30**	**110.76**	0.11	100.00	0.17	27.80	0.14	120.00	0.23	396.40	0.05	1.00
SAND	0.13	0.79	0.13	6.20	**0.35**	8.91	**0.33**	14.13	**0.53**	1.59	0.22	3.40	**0.30**	0.90	**0.89**	1.02	**0.24**	1.21	0.20	35.70	0.45	1.99	0.37	0.40
ANTHROPIC MATERIAL																								
Ashes							0.04	0.03																
Line					0.12	<0.01	0.04	0.12					0.04	1.00							0.08	0.10		
Paper							0.04	1.00					0.04	10.00	0.22	2.00								
Plastic	0.06	12.00	0.02	0.10			0.11	24.00	0.06	2.01			0.04	100.00										
Glass					0.03	0.05																		
OSTEICHTHYES																								
Fish scale			0.02	10.0																	0.03	0.01		
PLANT MATERIAL																								
UPM	0.13	13.92	0.06	101.50	0.12	16.38	0.07	3.00			0.02	2.00			0.11	0.03	0.07	0.27	0.05	0.07	0.03	5.00	0.05	6.00
Branch					0.03	12.50	0.04	0.06									0.03	12.50			0.05	30.00		
Spore																	0.03	0.10						
Seed					0.03	0.02											0.10	0.86					0.05	12.50
ANNELIDA																								
Oligochaeta					0.03	0.12									0.11	0.07								
NEMATODA	0.03	0.01	0.04	0.01	0.03	0.02	0.07	0.02									0.10	0.06	0.02	0.02		0.01		
MOLLUSCA																								
Bivalvia							0.04	10.00					0.04	5.00	0.11	0.08							0.05	2.00
Gastropoda									0.06	5.00													0.05	1.00
INSECTA																								
Insecta N.I	**0.28**	119.10	**0.23**	147.80	0.21	34.76			0.35	100.70	0.22	37.25	0.07	1.01			0.21	157.00	**0.22**	155.69	0.10	129.00	**0.42**	190.00
Isoptera																	0.03	10.00						
Diptera							0.04	50.00																
Dermaptera																	0.03	1.00						
Neuroptera																	0.03	25.00						
Larvae of insects													0.04	1.00										
Hymenoptera	0.03	100.00	0.02	50.00							0.02	25.00	0.04	25.00					0.02	5.00	0.03	50.00		
Apis sp.			0.04	75.00	0.03	1.50	0.15	**195.00**	0.18	20.25	0.05	100.00	0.11	10.50			0.07	75.00			0.28	**545.00**	0.16	**200.00**
Bombus sp																							0.05	50.00
Formicidae	0.09	**410.50**	0.02	50.00			0.04	0.01					0.04	0.50	0.22	**100.00**	0.10	**185.00**			0.05	8.02	0.05	1.00
Hemiptera					0.06	18.00							0.04	25.00										
Coleoptera	0.09	200.00	0.08	350.00			0.04	25.00	0.24	**400.00**	0.02	1.00	0.07	75.00			0.10	78.00	0.02	25.00	0.10	8.52	0.05	**200.00**
Elateridae					0.03	10.00																		
Scarabaeidae	0.03	200.00																						
Thysanoptera							0.04	100.00																
CRUSTACEA																								
Crustacea N. I					0.06	<0.01							0.07	3.01							0.03	2.00		
Eggs and larvae of *Ocypode quadrata* (Fabricius 1787)					0.03	0.05							0.04	0.09										
Amphipoda (Talitridae)			0.06	31.00			0.22	63.06					0.04	0.10										
Callinectes sp.					0.03	**50.00**																		
Emerita brasiliensis			0.04	175.00			0.04	0.60			0.07	**550.00**							0.12	**570.25**				

Table A6

Frequency of occurrence (FO) and volume (V_o) of food items found in female stomachs of Ocypode quadrata captured on the Barra Velha, Navegantes, and Itajaí beaches, southern Brazil. Seasons are expressed as Sp - spring, Su - summer, Au - autumn, Wi - winter. Legend: UOM - unidentified organic matter, UPM - unidentified plant material, N.I = not identified. The highest values of FO and V_o for each season are in bold.

	BARRA VELHA								NAVEGANTES								ITAJAÍ							
	Sp		Su		Au		Wi		Sp		Su		Au		Wi		Sp		Su		Au		Wi	
	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o
UOM	0.18	104.10	0.29	72.10	0.26	0.81	0.11	40.00	0.13	0.25	0.13	4.60	0.17	1.25	0.13	0.26	0.29	149.6	0.20	116.80	0.16	14.00	**0.25**	13.05
SAND	0.18	0.34	0.07	50.00	**0.33**	1.90	**0.26**	0.51	**0.63**	1.25	0.22	2.27	**0.50**	0.73	**0.40**	0.89	**0.35**	2.48	0.30	1.64	**0.42**	2.75	0.19	150.10
ANTHROPIC MATERIAL																								
Line					0.04	<0.01															0.05	0.05	0.06	0.01
PLANT MATERIAL																								
UPM	0.12	100.03		**150.00**	0.07	12.56	0.11	35.00			0.03	0.50			0.07	1.00			0.03	0.10	0.10	90.01		
Branch	0.06	<0.01			0.07	90.15																		
Spore					0.04	<0.01																		
Seed											0.03	0.10			0.07	1.00								
NEMATODA	0.06	0.02													0.07	0.02			0.07	<0.01	0.05	0.01		
MOLLUSCA																								
Bivalvia	0.06	1.00					0.05	0.30					0.08	0.20									0.10	2.00
INSECTA																								
Insecta N. I	**0.47**	153.30	**0.43**	122.70	0.15	22.62	0.21	46.50	0.25	82.12	**0.31**	156.18	0.17	**25.01**	0.07	0.25	0.18	13.62	0.13	137.01	0.11	76.00	0.06	50.00
Isoptera									0.06	50.00														
Diptera					0.04	10.00									0.13	12.50	0.06	25.00						
Dermaptera																	0.12	**200.00**						
Insect larvae																					0.05	0.05		
Hymenoptera							0.05	5.00											0.03	100.00			0.13	31.00
Apis sp.					0.04	5.00			0.06	50.00	0.06	150.10	0.10	13	0.07	3.00	0.12	60.00	0.03	25.00	0.32	**385.00**	0.13	**300.00**
Bombus sp.					0.04	30.00									0.13	**220.00**								
Formicidae							0.05	**50.00**							0.07	1.50	0.18	80.00					0.06	25.00
Hemiptera					0.04	**100.00**																		
Coleoptera							0.05	**50.00**	0.31	**269.00**	0.03	30.00			0.07	12.50								
Protura						0.04	<0.01																	
Thysanoptera																							0.06	4.00
Lepidoptera	0.06	**200.00**																						
Orthoptera											0.03	25.00												
	BARRA VELHA								NAVEGANTES								ITAJAÍ							
	Sp		Su		Au		Wi		Sp		Su		Au		Wi		Sp		Su		Au		Wi	
	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o	FO	V_o
CRUSTACEA																								
Crustacea N. I			0.07	25.00							0.03	0.01												
Eggs and larvae of *Ocypode quadrata* (Fabricius 1787)					0.15	0.26	0.05	1.00					0.08	0.07							0.10	60.00		
Amphipoda (Talitridae)	0.06	5.00					0.11	10.05			0.09	160.00											0.10	50.00
Emerita brasiliensis			0.10	0.10							0.13	**214.00**							**0.40**	**2176**			0.10	10.00
ARACHNIDA																							0.10	1.00

Table A7

Feeding index for Ocypode quadrata according to size classes (I -V) in three sampled environments.

	FEEDING INDEX (IAi)														
	Barra Velha (BV)					Navegantes (NV)					Itajaí (IT)				
Food Categories	I	II	III	IV	V	I	II	III	IV	V	I	II	III	IV	V
Organic Matter		0.40	0.24	0.40	0.12	0.98	0.02	0.09	0.28	0.82	0.35	0.52	0.19	0.09	0.01
Sand	1.00	0.02	0.06	0.02	<0.01	<0.01	0.01	0.02	0.01	0.05		<0.01	0.02	0.12	
Anthropic Material			<0.01	0.01	0.01			<0.01	0.01	<0.01			<0.01		<0.01
Osteichthyes			<0.01											<0.01	
Plant Material		0.01	0.11	0.09	0.02		0.01	<0.01	<0.01			<0.01	<0.01	0.01	
Annelida				<0.01			<0.01								
Nematoda		<0.01	<0.01	<0.01	<0.01			<0.01					<0.01	<0.01	
Mollusca			<0.01	<0.01	<0.01				<0.01	0.01				<0.01	
Insecta		0.57	0.57	0.42	0.86	0.02	0.79	0.88	0.40	0.13	0.62	0.47	0.61	0.31	0.17
Crustacea		<0.01	0.01	0.05	<0.01		0.17	0.01	0.30	<0.01	0.02	<0.01	0.18	0.48	0.82
Arachnida														<0.01	

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