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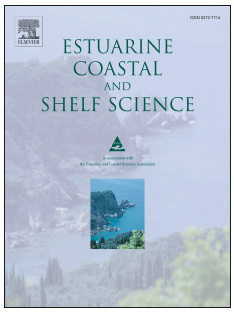

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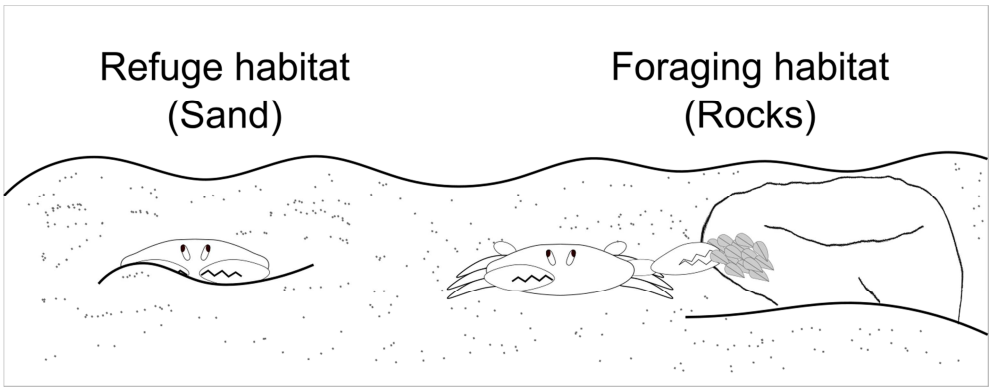

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Patterns of habitat partitioning for the portunid crab *Ovalipes trimaculatus* in costal Patagonian waters.

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Abstract

Animals frequently face trade-offs between their requirements for maximizing growth and minimizing mortality risk. The partition of habitat use in foraging arenas and refuges as an answer to this trade-off has been evaluated in intertidal crabs but is poorly known in subtidal crabs. The subtidal crab *Ovalipes trimaculatus* lives and is captured by artisanal fishermen on sandy bottoms of the San Matías Gulf (Lat 41 °S; Argentina). Whereas these bottoms are poor in potential prey, the nearby rocky outcrops are much richer with relatively high abundance of potential prey for the species. Hence, we investigated if crabs in this area are using rocky bottoms as a foraging arena. Stomach content and stable isotopes analysis show that none of the evaluated prey (small teleosts, echinoderms, mollusks and crustaceans) contributed to more than 10% of *O. trimaculatus* diet, however prey from hard bottoms jointly contributed to 50-80% of the diet. Thus, *O. trimaculatus* is a generalist carnivore that, despite inhabiting mainly open sandy bottoms, uses rocky outcrops habitats as a foraging arena, probably due to their higher prey availability.

Keywords: Stable isotope analysis, Stomach content analysis, Diet, Foraging arena, San Matías Gulf

1. Introduction

Animals frequently face trade-offs between their requirements for maximizing growth and minimizing mortality risk (e.g. Halpin, 2000; Grabowski and Kimbro, 2005). As a result, patterns of empty stomachs and apparent reduced food intake have been observed particularly in fishes (Ahrens et al., 2012). The partition of habitat use in foraging arenas and refuges as a strategy to cope with the compromise between growth and mortality has been mainly identified in fishes (e.g. Werner et al., 1983; Bernot and Turner, 2001), but has received less attention in other aquatic species. In estuarine and marine crabs, movements following the tidal flow represent a trade-off between the higher amount of food at the high intertidal, and the shelter provided underwater (Robles et al., 1989; Holsman et al., 2006). However, the trade-off between foraging and refuging has not been as explored in subtidal crab populations. The Portunid three spot swimming crab *Ovalipes trimaculatus* (De Haan, 1833) is distributed from southern Brazil (Lat 23° S) to San Jorge Gulf (Lat 46° S; Argentina) in the Atlantic Ocean (Vinuesa, 2005), and from southern Perú (Lat 14° S) to Trinidad Channel (Lat 50° S; Chile) in the Pacific Ocean (Retamal, 1981). It inhabits coarse sandy bottoms from 10 to 65 m deep (Fenucci and Boschi, 1975). In the San Matías Gulf (Lat 41° S; Argentina), *O. trimaculatus* is captured by diving fishermen that deploy bait on sandy bottoms the day before fishing. In this area, the seafloor is composed of coarse-sandy bottoms, with zones of mud, sand and shell debris (Servicio de Hidrografía Naval Argentino, 1974). Within this sandy bottom matrix, rocky patches covered by mussel beds (mainly the ribbed mussel *Aulacomya atra*) sporadically occur (Schnack et al., 1996). Fishermen find crabs eating from the bait or shallowly buried in the sand surrounding it. The sandy bottoms where the crabs are commonly found are poor in biodiversity and biomass and look typically poor in potential sources of food for *O.*

trimaculatus. This brings up the question of how this population is sustained. On the contrary, the rocky patches have a very diverse community with high density and biomass that could represent a much more profitable foraging area for *O. trimaculatus* (Narvarte et al., 2012). However, the species has not been described as using this kind of habitat.

Several subtidal crabs show daily foraging movements to the intertidal (e.g. *Cancer productus* L. (Robles et al., 1989); *Necora puber*, *Cancer pagurus* (Silva et al., 2014)) but there is no information on subtidal foraging travels within dissimilar environments. Considering that the sandy-bottom fishery grounds are located in areas with apparently low abundance of potential prey, and that the nearby rocky bottoms are much richer in terms of prey abundances, the question arises whether these individuals could move from sand to rocky bottoms to forage. Hence, the aims of this study are: 1) to determine the diet of *O. trimaculatus,* and 2) to identify the foraging arena of this species in the San Matías Gulf. With this purpose, we studied the *O. trimaculatus* stomach contents and performed C and N stable isotopes analysis (SIA) of *O. trimaculatus* and its potential prey, under the hypothesis that although the species is found inhabiting sandy bottoms it mainly forages in the richer surrounding rocky bottoms.

2. Materials and Methods

2.1. Stomach content analysis

A total of 686 *O. trimaculatus* were captured at the northern part of the San Matías Gulf from April 2013 to December 2014 to perform stomach content analysis. Samples were obtained from depths ranging from 10 to 65 m using bottom trawling and diving. Crabs were immediately frozen after capture and, in the laboratory, were sexed, weighed and measured (carapace width) to the nearest 1 mm. The moult stage was also registered (following Alvarez et al., 2009) and only animals in intermoult stage were used for the analysis, as crabs cease feeding prior to and during moulting (Williams, 1982). The foregut of each crab was removed and the percentage fullness of the cardiac stomach was estimated visually (following Williams,

1981). The contents of the cardiac stomach were stored in 70% ethanol until they were analyzed under stereomicroscope (30X magnification). Most often the items found in the stomachs had undergone high processing by external appendices and extensive grinding by the gastric mill, so they were generally very broken, making a precise identification impossible in most cases, thus, we preferred to classify items with confidence into large groups.

Food items were classified into 12 categories and weighed to calculate a relative weight index (*%W*) for each category as:

$$\%W_i = \frac{\sum_{e=1}^{E} w_{ie}}{W} 100$$

where w_{ie} is the weight of the prey category *i* in stomach *e*, *E* is the number of not-empty stomachs and *W* is the total weight of stomach contents. For each index 95% confidence intervals were calculated using bootstrap resampling (1000 iterations, with replacement). A relative occurrence index (*%O*) was also calculated for each prey category as:

$$\%O_i = \frac{\sum_{e=1}^{E} e_i}{E} 100$$

where e_i= 1 if the stomach presented prey category *i*, or e_i = 0 if the stomach did not present prey category *i* and *E* is the number of not-empty stomachs.

2.2. Availability of prey and stable isotopes analysis

Samples of *O. trimaculatus* and its potential prey from sandy bottom (SB) and hard bottom (HB) communities where taken by diving between November and December 2015 to analyze their natural C and N stable isotopes composition. Different times of sampling is not expected to affect the conclusions given that both methodologies are not directly compared in this study but are both used in a complementary way. For *O. trimaculatus,* five females and five males were captured and immediately frozen. Muscle from one chaela was removed from every crab. To sample SB community, quadrats of 1 m^2 (n = 15) were randomly deployed and sediment and infauna from the first 5 cm deep inside each quadrat were removed using an

airlift pump. At HB, quadrats of 0.25 m^2 (n = 15) were used due to the higher density of benthic organisms in this habitat. Organisms were detached from the rock using a metal spatula.

With these methods we were unable to capture fishes, hence small fishes associated to the benthic communities were sampled by diving using a hand net. Only one fish species of small size and low motility was captured: the "cocherito" *Dules auriga* (Serranidae). This species can be found in both studied habitats (unpub. obs.).

The SB samples were sieved through a 1 mm mesh to separate the sediment from the infaunal community. Individuals larger than 1 mm from both communities were classified to the highest possible taxonomic separation. Each taxonomic group was weighed and individuals were counted. The biomass per m^2 available was compared between habitats using a t- test.

Taxonomic groups with individuals between ~ 1 and 4 cm in size were classified as potential prey if they belonged to a group of items found in the *O. trimaculatus* stomachs or if they had high relative abundance (Table 1). The size criteria was set in order to represent the maneuverability of crab chaelae, as well as an approximation to the size of the items found in stomach contents. The abundance criterion was set to overcome the fact that prey with high digestibility may be underrepresented in stomach content samples.

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Species	Habitat	Type of sample	# individuals per sample	Acid treatment	# Samples $\delta^{13}C$	# Samples $\delta^{15}N$	Prop. in diet (mean, SD)
Tegula patagonica	HB	Mus	5	No	5	5	0.08, 0.07
Ciona robusta	HB	Full	3	No	5	5	0.08, 0.07
Acanthoserolis schythei	SB	Full	1	Yes	3	2	0.08, 0.07
Pachycheles chubutensis	HB	Full	3	Yes	3	3	0.08, 0.07
Leucippa pentagona	HB	Full	1	Yes	3	3	0.07, 0.06
Nereididae (Fam.)	SB	Full	5	No	5	5	0.07, 0.06
Pagurus exilis	SB	Full	1	Yes	3	3	0.07, 0.06
Arbacia dufresnii	HB	Full	1	Yes	3	2	0.07, 0.06
Crepidula sp.	HB	Mus	3	No	5	5	0.07, 0.06
Chaetopleura sp.	HB	Full	5	Yes	3	3	0.07, 0.06
Polynoidae (Fam.)	HB	Full	5	No	5	5	0.06, 0.05
Transenpitar americana	SB	Full	3	No	5	5	0.06, 0.05
Eunicidae (Fam.)	SB	Full	5	No	2	2	0.05, 0.04
Ophioplocus januarii	HB	Full	6	Yes	2	2	0.05, 0.03
Dules auriga	Benthopelagic	Mus	1	No	5	5	0.03, 0.03

Table 1: Potential prey used for SIA identified to the lowest possible taxon. HB, hard bottom; SB, sandy bottom; Full, full body used for SIA; Mus, only muscle used for SIA. "Prop. in diet" is the relative contribution to *O. trimaculatus*' diet according to SIA.

Whenever possible, a sample of muscular tissue was taken from the potential prey species, but in some cases this was not possible due to small size (Table 1). Also, when individuals were too small to obtain an adequate amount of tissue for the analysis, composite samples with at least three individuals were prepared (Table 1). Despite this, some samples were still too small to get confident results, hence some species were less represented in the analysis (Table 1). Samples were dried at 60 °C for 48 h and then ground into a fine powder with mortar and pestle. In cases where carbonate structures could not be mechanically separated from tissues, samples were acidified with HCl 20%.

Determination of total C and N contents and stable isotope analyses were performed by an isotope ratio mass spectrometer at the University of California, Davis. C and N stable isotopes ratios were expressed in δ notation as parts per thousand (‰) according to the following relationship:

$$\delta X(‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where *X* is ^{13}C or ^{15}N, and R_{sample} and $R_{standard}$ are the ^{13}C:^{12}C or ^{15}N:^{14}N ratios of the sample and the standard, respectively (McKinney et al., 1950). The standard reference for C is Pee Dee Belemnite (PDB) and atmospheric N_2 for N. Laboratory internal standards used were G11 (Nylon), G13 (Bovine Liver), G17 (USGS-41Glutamic Acid) and G9 (Glutamic Acid). Replicate measurements of internal laboratory standards indicated measurement standard deviations lower than 0.2 and 0.3 ‰ for$\delta^{13}C$ and $\delta^{15}N$, respectively.

C and N SIA were performed for each sample, except for prey that needed acid treatment, in which case, C SIA was done on acidified samples and N analysis was carried out on independent samples without acid treatment. A mathematical normalization of $\delta^{13}C$ suggested by Post et al. (2007) was applied to account for the presence of lipids in the samples.

To evaluate differences in the diet between sexes, isotopic composition of males and females were compared using ANOVA for $\delta^{13}C$ and $\delta^{15}N$ after confirming normality and homogeneity of variances. To estimate the proportional contribution of the potential sources to the *O. trimaculatus* diet, the MixSIAR model was used (B. Stock and Semmens, 2016). MixSIAR is a Bayesian stable isotope mixing model that incorporates individual and group level diet variability among predators. It is written in the open source languages R (R Core Team, 2016) and JAGS (Plummer, 2003). $\delta^{15}N$ and $\delta^{13}C$ of each individual swimming crab were used as mixture data and the mean and standard deviation values of potential prey items were used as source data. When modeling, discrimination values used for $\delta^{13}C$ and $\delta^{15}N$ were 0.4, 1.3 ‰ and 3.4, 1‰ (mean, SD) (Post, 2002) and concentrations of C and N in the source tissues were considered (Phillips and Koch, 2002). We ran 200,000 iterations with a burning of 50,000, used process residual error term (B. C. Stock and Semmens, 2016) and uninformed priors.

To assess the use of prey from different habitats, sources were grouped *a posteriori* (following Phillips et al., 2005 and Stock et al., 2018) according to their habitat use in SB (n = 18), HB (n = 33) or benthopelagic (n = 5). The main use of combining sources *a posteriori* based on a certain functional similarity is that it is not necessary that the combined sources are similar in their

isotopic signal (Stock et al., 2018). SB and HB groups were composed by the species captured at SB and HB respectively, while 'benthopelagic' was only constituted by the fish *Dules auriga* that is the only species able to move between SB and HB.

3. Results

3.1. Stomach contents analysis

The mean weight of captured crabs was 173.65 g (SD = 64.24 g) with carapace width ranging between 57 and 128 mm (mean = 97 mm, SD = 11 mm). 35% of the sampled crabs were females and 59% of the 686 analyzed stomachs were empty. The diet was mainly carnivore, being algae ~1% of the relative weight and thus considered incidental as well as sediment (~1.5 % mainly sand grains). Most items could not be identified beyond the point of large groups.

In terms of relative weight, crustaceans were the most relevant group contributing more than 50% of the biomass and appearing in 57% of the not empty stomachs (Fig. 1). In the case of crustaceans we found small (<1 mm) pieces of carapace, spines, pieces of segmented appendices. The second best represented group in terms of relative weight and also in relative occurrence were small fishes (10% of weight, occurring in 16% of not-empty stomachs, Fig. 1). In this case, spines and vertebrae of ~1 mm were found. Relative weight and occurrence of the most represented item were around four times higher than those of the second one (*%W* 51 vs 9 % and *%O* 57 vs 16 %, respectively). Despite the uneven distribution, a large variety of invertebrates was found in the stomachs (Fig. 1).

3.2. Availability of prey and stable isotopes analysis

Biomass density of SB (mean = 5.49 $g.m^{-2}$, SD = 2.61 $g.m^{-2}$) was lower than in HB (mean = 15453.53 $g.m^{-2}$, SD = 7748.57 $g.m^{-2}$; t_{14}= 7.72, $P < 0.001$). The three taxa with the largest weight percentage in the *O. trimaculatus* diet (crustaceans, teleosts and polychaetes) were present both in SB and in HB habitats, but different species composed those taxa at the different

habitats (e.g. crustaceans at SB: *Acanthoserolis schythei*, *Pagurus exilis*; crustaceans at HB: *Leucippa pentagona*, *Pachycheles chubutensis*). On the other hand, ascidians, echinoids, ophiuroids and chitons were only present in HB samples.

O. trimaculatus $\delta^{13}C$ values ranged from -16.9 to -15.6 ‰, and $\delta^{15}N$ values ranged from 16.5 to 18.9 ‰ (Fig. 2). No differences were found between the $\delta^{13}C$ and $\delta^{15}N$ of *O. trimaculatus* males and females ($\delta^{13}C$: ANOVA, $F_{(1, 8)}$ = 1.05, *MSE* = 0.16, $P > 0.05$; $\delta^{15}N$: ANOVA, $F_{(1, 8)}$=5.39, *MSE*=0.34, $P = 0.05$) hence data of both sexes were analyzed together. After correcting for lipids, $\delta^{13}C$ of species from SB ranged from -20.2 to -14.5 ‰, and their $\delta^{15}N$ ranged from 12.7 to 17.7 ‰. In the case of $\delta^{13}C$ of species from HB, after correcting for lipids, values ranged from -18.5 to -12.3 ‰, and their $\delta^{15}N$ ranged from 11.1 to 16.0 ‰. The benthopelagic prey $\delta^{13}C$ values, after lipid correction, ranged from -18.2 to -16.6 ‰, and $\delta^{15}N$ from 18.0 to 19.0 ‰ (Fig. 2).

There was no significant correlation in the contribution of the species to the diet (-0.31 was the maximum correlation found between two sources). Source contributions to the *O. trimaculatus* diet was even, the mean contribution of each source ranging between 0.03 (*Dules auriga*) and 0.08 (*T. patagonica, C. robusta, A. schythei, P. chubutensis*) (Table 1).

When sources were combined, species from the HB were represented by 9 sources while species from SB were represented by 5 sources and benthopelagic species by one species. Therefore, these relative abundances represent the new informative prior. Species from HB had a larger combined contribution to the *O. trimaculatus* diet than SB species (Fig. 3), in agreement with the higher abundance of potential prey in HB. The proportional contribution of SB sources ranged from 0.15 to 0.56 (mean = 0.34, 95% confidence interval (CI)) and the contribution of HB from 0.41 to 0.82 (mean = 0.63, 95% CI). *D. auriga,* the benthopelagic species, did not have a relevant contribution to the diet of *O. trimaculatus* (CI 95% = 0.00 - 0.09).

4. Discussion

Our results show that although *O. trimaculatus* lives and is captured mainly in sandy bottoms, it uses rocky bottoms as its foraging arena, a habitat that is not prevalent in this subtidal region (Schnack et al., 1996), in which sandy bottoms are dominant. According to stomach contents analysis and SIA, adult *O. trimaculatus* forage on sandy as well as on hard bottom species. Moreover, SIA indicates that a majority of the *O. trimaculatus* diet is composed of species from hard bottoms. The generalist carnivore diet *O.trimaculatus* presented in this study is similar to that described for the species north of San Matías Gulf (Mar del Plata, 38^{o} S; Fenucci and Boschi, 1975), and is also similar to the diet of other portunid species (e.g. Caine, 1974; de Lestang et al., 2000), although more selective species are also described in the literature (e.g. *Liocarcinus depurator*; Careddu et al., 2017).

Except for small fishes, the most important groups found in stomach contents were present at SB as well as at HB, but their high grade of trituration prevented us from identifying the prey to a better extent. Crustaceans, polychaetes and mollusks were relatively well represented at both habitats but some of the items found in the stomachs were only found at hard bottoms: ascidians, echinoids and ophiuroids. Small fishes were particularly difficult to find during sampling in both environments. Using an alternative method we were able to capture only one species of fish that fits the size of stomach contents and has slow movements. SIA, however, showed that this species is very unlikely to be part of the *O. trimaculatus* diet, as it is too enriched in ^{15}N. The high occurrence of teleost remains in stomachs shows that *O. trimaculatus* consumes fishes at least occasionally, although the method may have overestimated their contribution to the diet due to the indigestibility of bones. Thus, it is possible that *O. trimaculatus* is consuming teleosts with a lower trophic level than *D. auriga*.

We used muscle tissue of *O. trimaculatus* to perform SIA due to its low turnover rate that integrates the diet of the animals at a seasonal scale (Suring and Wing, 2009). However, we

arte not considering what happens with the diet during the rest of the year. Further studies are needed to clarify whether the use of HB as foraging zones is a seasonal or year-round behavior. The results of SIA in terms of proportional contribution of each source are not dependable as some species were under-represented in the analysis (e.g. *Ophioplocus januarii*, but see Table 1 for sample sizes). This was due to the small size of the individuals and the large proportion of carbonate structures in their bodies which resulted in samples with very low mass of C or N (less than 20 µg) to determine their $\delta^{13}C$ or $\delta^{15}N$, even when composite samples were considered. The habitats in which *O. trimaculatus* forages, however, are well represented in terms of replicates due to the grouping of the prey, hence, our conclusions are much more confident in terms of foraging habitat. We applied a mathematical correction for lipid content to $\delta^{13}C$ values proposed by Post (2007) to decrease possible bias caused by lipid presence given that we did not performed lipid extraction. This correction raises some controversy around its accuracy, thus, the proportion of each source in the diet of *O. trimaculatus* should be taken with caution.

Stomach contents analysis depends on the time that the contents remain visible and on the relative digestibility of prey items. Conversely, SIA provides a time- and space-integrated representation of the diet and is useful for studying organisms whose diets are difficult to characterize directly. We conclude from both analyses, in agreement with the literature on the subject, that *O. trimaculatus* is a generalist carnivore, with a wide range of prey. An extensive range of potential prey (15 potential prey types) were considered as possible sources in the SIA mixing model (Phillips et al., 2014), not only including species found in the stomach contents, but also species that were abundant in the study area (e.g. Polyonidae polychaets). Thus, the collection of potential prey was not restricted to the results of the stomach content analysis, rather, we used this analysis as a guide and to assure that all important sources were included in the mixing model. Variability in diet among and within years in the foraging habits of this species is possible, but it was not evaluated in this study.

To our knowledge, there is no record of *O. trimaculatus* using HB in this region. However, the observations from fishermen, local people, scientists or tourists were mainly done during daylight, which may not account to the nocturnal activity of many Portunids (e.g. Caine, 1974; Reigada and Negreiros-Fransozo, 2001). Our results show a prevalence of HB sources suggesting that *O. trimaculatus* moves to HB and forages on them, rather than consuming individuals that incidentally arrive to SB. However, given the higher amount of sources in HB, the proportion of the sources in diet seems to be equivalent to the available sources in each habitat supporting the generalist behavior of the species. It is also possible that *O. trimaculatus* forages from the intersections between both habitats. This brings new insights on the way portunids can partition habitat use, being able to refuge at SB, where they are found by fishers, and approaching HB to forage, where food is much more abundant and profitable. In similar cases, suboptimal foraging (i.e. diminished foraging behavior than the expected by maximum potential rate) has been explained by aversion to competition or predation (e.g. Turner, 1996; Grabowski and Kimbro, 2005). Chemical cues of injured conspecifics, for example, can change freshwater snail habitat use, hence indirectly increasing periphyton abundance on less protected habitats (Bernot and Turner, 2001). The aim of our study was not to evaluate the effect of predators on *O. trimaculatus* habitat use, but at least two species consume *O. trimaculatus* in San Matías Gulf (remains of the species were found in stomach contents of the sea lion *Otaria flavences* and the skate *Sympterygia acuta,* (Barbini and Lucifora, 2016). In the genus *Ovalipes,* the behavior of burying in SB decreases predation risk (Barshaw and Able, 1990), thus, the use of SB as protection from predators rather than as foraging areas is the most plausible hypothesis in the case of *O. trimaculatus*.

In conclusion, our results show that *O. trimaculatus* is a generalist carnivore that, despite inhabiting mainly in open sandy bottoms, also feeds on invertebrates from rocky outcrops, which offer much more prey.

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Figure captions

Fig. 1. A. Relative weight of items found in the stomach contents (n = 280) of *Ovalipes trimaculatus.* Lines represent 95% Confidence Intervals calculated using bootstrap. **B.** Relative occurrence of items in stomachs that were not empty (n = 280).

Fig. 2. $\delta^{13}C$ and $\delta^{15}N$ values for *O. trimaculatus* and sources (mean, SD*). O. trimaculatus'* values were corrected for trophic enrichment. Sources' $\delta^{13}C$ values were corrected for lipids. Filled circles represent sources from benthopelagic environment, filled squares from hard bottom and filled triangles from sandy bottom. Ac, *Acanthoserolis schythei*; Ar, *Arbacia dufresnii*; Ch, *Chaetopleura sp*.; Ci, *Ciona robusta*; Du, *Dules auriga*; Eu, Eunicidae; Cr, *Crepidula sp.*; Pol, Polynoidae; Le, *Leucippa pentagona*; Ner, Nereididae; Op, *Ophioplocus januarii*; Pa, *Pachycheles chubutensis*; Pag, *Pagurus exilis*; Te, *Tegula patagonica*.

Fig. 3. Dietary biomass proportions of aggregated prey from benthopelagic (n = 5), sandy bottom (n = 18), and hard bottom (n = 33) habitats. The aggregate solutions are the sum of the biomass contributions for food sources from each habitat. The aggregate contributions are calculated for all model iterations (in 2% increments), and are expressed as the percent frequency of all possible solutions. The mean proportion of each aggregate distribution is labeled.

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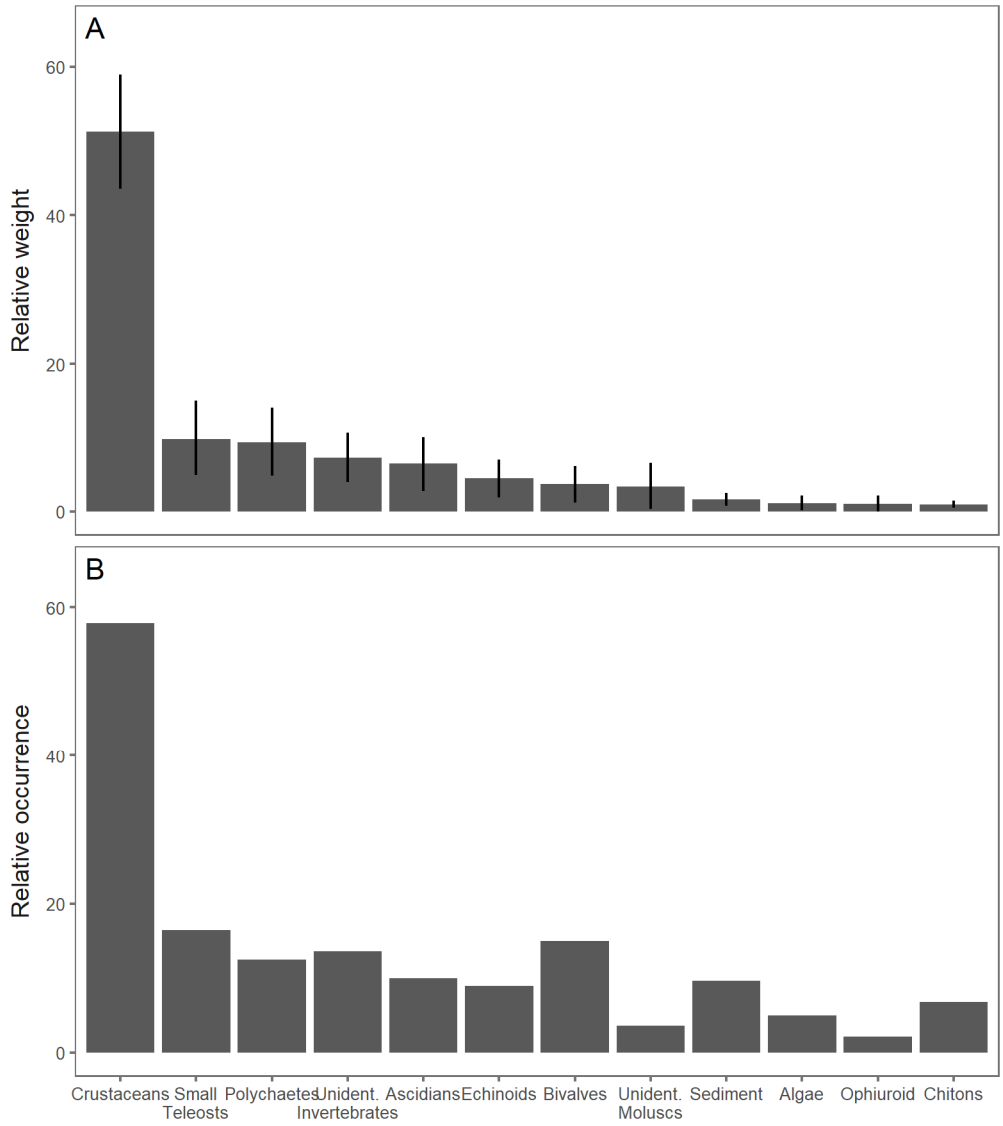

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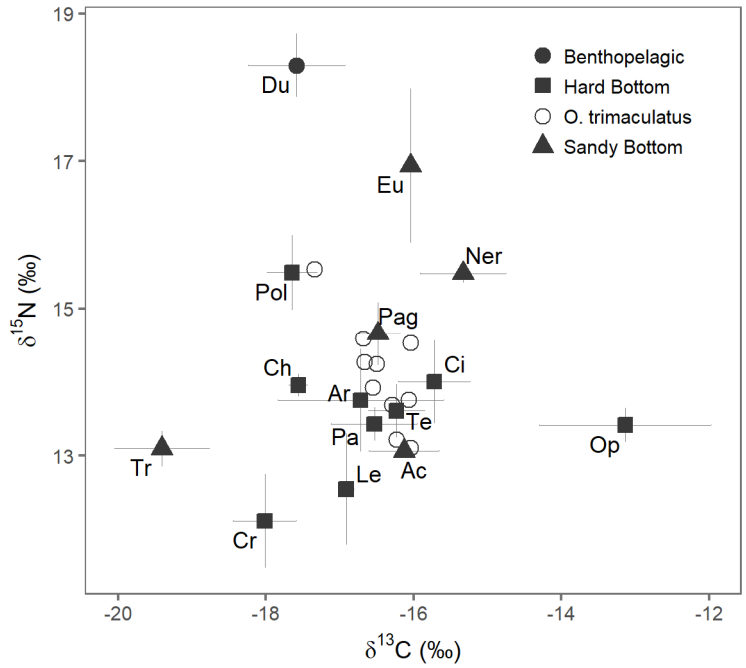

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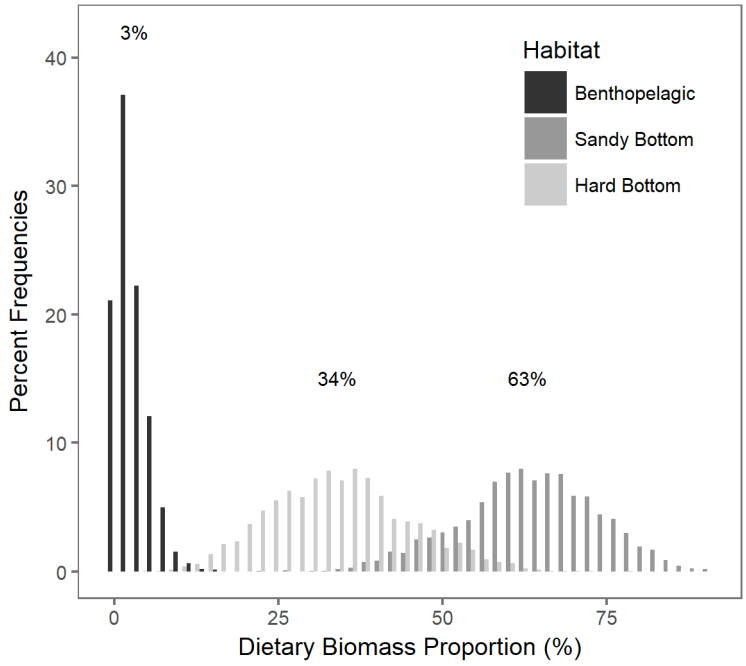

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Highlights

- *Ovalipes trimaculatus* inhabits sandy bottoms, poor in potential preys
- Nearby rocky outcrops are richer, with relatively high abundance of potential preys
- Stomach contents and stable isotopes analysis showed it forages on rocky outcrops
- Neither prey contributed to more than 10% to the diet composition

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