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# Diet and food assimilation of the Plata pompano *Trachinotus marginatus* Cuvier, 1832 in a subtropical sandy beach inferred by stomach content and stable isotope analyzes

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## Research Article

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## Abstract

Investigating trophic linkages sustaining consumers is crucial to understanding their functional ecological role in communities and ecosystems. In this work, we combined stomach content (SCA) and stable isotope (SIA) analyses to investigate the trophic ecology of the Plata pompano *Trachinotus marginatus* during a critical phase of its life cycle along a subtropical sandy beach. This species is a conspicuous component of the southwestern Atlantic coast and commonly targeted by coastal fisheries. The diet was described using SCA, whereas the relative importance of food sources sustaining juveniles, as well their food niche structure and trophic position (TP), were evaluated using SIA. Juveniles consumed mainly crustaceans like the hippid crab *Emerita brasiliensis*, although other invertebrates (annelids, insects, molluscs) and fishes (including cannibalism) were also recorded. Although microcrustaceans dominated the diet, SIA showed that more palatable preys without carapaces or shells, like fishes and annelids, were the most assimilated preys in the muscle tissue of juvenile *T. marginatus*. There were marked changes in their isotopic niches (SEAc) and TP across ontogeny. SEAc ranged from 1.41‰$^2$ for smaller individuals (0–40 TL mm) to 0.3‰$^2$ for larger individuals (>80 TL mm). TP ranged from 3.1 (95% CI 2.7–3.6) for smaller to 4.5 (95% CI 3.9–5.1) for larger individuals. SIA suggest that juvenile *T. marginatus* derived most of their primary nutrients from a planktonic food web and, to a lesser extent, from a benthic pathway. Future studies are needed to better understand its functional role in food web of surf-zone ecosystems.


## Introduction

An initial and fundamental step towards understanding the trophic ecology of organisms and its implications for the organization and functioning of biological communities and ecosystems is the study of the species' natural diet (Majdi *et al*., 2018). Fishes are a suitable biological model for trophic ecology studies, due to their wide distribution, diversity and abundance in aquatic ecosystems (Helfman *et al*., 2009). Knowledge about the diet of fish provides information that helps to investigate ecological issues such as the functioning and dynamics of aquatic communities and their food webs, breadth and overlapping of trophic niches, life history and habitat requirements (Gerking, 1994). Furthermore, temporal and spatial analysis of the diet of predatory fish can reveal which predator–prey interactions may have important effects on populations and community structure (Winemiller and Layman, 2005). Among these effects, we can highlight bottom-up and top-down controls along the food web and their consequences for secondary production (Hairston *et al*., 1960; Mittlebach and McGill, 2019), as well as the importance of key species in community regulation (Paine, 1969; Estes *et al*., 2011) and possible impacts related to the introduction of exotic species on native ones (Zaret and Paine, 1973; Begon *et al*., 2006). Regardless of the functional responses at the community and ecosystem levels, it is paramount to initially understand the consumer's food habits to infer the food sources sustaining the species in the food web (Condini *et al*., 2015; Garcia *et al*., 2017a, 2017b; Bastos *et al*., 2022).

A great array of methodological approaches and tools have been employed to investigate fish trophic ecology (Gerking, 1994; Majdi *et al*., 2018; Silveira *et al*., 2020). Traditionally, analyses of the stomach contents (SCA) have been applied to describe the food items consumed and the relative importance of different prey species to the diet (Hyslop, 1980). Despite being a widely used method, it has some limitations like the difficulty in identifying partially digested items and the uncertainty in evaluating the true nutritional role of consumed items, since many items can be refractory to the digestive process and not be assimilated by the predator (Hyslop, 1980; Jepsen and Winemiller, 2002; Silveira *et al*., 2020).

Another method that has been increasingly used to investigate trophic ecology is stable isotope analysis (SIA) (Peterson and Fry, 1987; Fry, 2006; Layman *et al*., 2012). The atomic ratios of stable isotopes in the tissues of predators and their food can be used to understand the pathways of organic matter as it travels among the various consumers along the food chain (Fry, 2006). SIA has been used to infer food assimilation by consumers, including indirect links as the relevance of primary producers as basal sources sustaining carnivorous. It has also been used to estimate the trophic position (TP) of a given species in the food chain (Layman *et al.*, 2012) and other metrics such as the isotopic niche (Jackson *et al.*, 2011). These metrics are useful to help understand important dimensions of the ecological niche, such as the use of food resources and the trophic role of the species in the ecosystem (Newsome *et al.*, 2007; Layman *et al.*, 2012).

The Plata pompano *Trachinotus marginatus* (Cuvier, 1832) is a marine fish of the Carangidae family that is distributed from the coast of Rio de Janeiro in Brazil to the coast of Northern Argentina (Fischer *et al.*, 2011). It is considered a euryhaline species (Sampaio *et al.*, 2003), with the predominant life cycle in the marine environment. In the coastal zone of extreme southern Brazil, during warmer seasons (austral spring and summer), the species reproduce offshore (~40 m deep) and its eggs and larvae are later transported to the shallower inshore waters. Juveniles (<20 mm) are commonly found in the marine surf zone (<2 m deep) of sandy beaches during summer and autumn, which acts as nursery areas for the species. After reaching larger body sizes (>150 mm) in this nursery grounds, they move to the intermediate deep waters (20 m), where they remain until reaching sexual maturity (L50 = 211.5 mm) (Lemos *et al.*, 2011). During its residence in this nursery area, the species is one of the dominant catch components in the trammel net surf-zone fishery (Santos and Vieira, 2016).

Thus, the marine surf zone is an important area for the development of juvenile *T. marginatus* (Monteiro-Neto *et al.*, 2003; Lima and Vieira, 2009; Lemos *et al.*, 2011; Vieira *et al.*, 2019). However, the trophic ecology of this species during its residency in nursery grounds is largely unknown, being restricted only to diet description based on SCA. For example, Monteiro-Neto and Cunha (1990) studied the diet of *T. marginatus* at Cassino Beach in the extreme south of Brazil (32°S) and found that the diet was composed mainly of small planktonic and benthic crustaceans, insects, polychaetes, molluscs, and fish. Currently, no information is available on important aspects of trophic ecology of juvenile *T. marginatus*, such as the primary producers sustaining the species, food niche dimensions and TP along the food chain.

In this context, the present study combined SCA and SIA techniques to investigate the trophic ecology of the species in a marine surf zone in southern Brazil (29°S). Using both techniques allow a more comprehensive and accurate understanding of fish trophic ecology, than solely using traditional methods such as SCA (e.g. Winemiller *et al.*, 2011; Condini *et al.*, 2015). In addition to describing the diet of juvenile *T. marginatus* using SCA, SIA was applied to investigate the relative importance of basal (planktonic and benthic pathways) and prey sources sustaining juveniles, as well as their food niche structure and TP.

## Materials and methods

### Study area

The study was carried out at the marine surf zone of Tramandaí Beach (Figure 1), which is characterized by fine sand and dissipative to intermediate morphodynamics, being directly exposed to waves with medium to high energy (Tomazelli and Villwock, 1991; Toldo *et al.*, 1993; Pereira *et al.*, 2010). Such sandy beaches are important growing sites for juvenile *T. marginatus* along the extensive (~180 km) coastal plain that characterizes southern Brazil (Lemos *et al.*, 2011). The climate in this region is classified as humid subtropical, with higher incidence of northeast winds between September and March, whereas southwest winds predominate between April and August (Nimer, 1977). Precipitation in the region shows a small increase in the winter season (Hasenack and Ferraro, 1989).

### Field collections and sample processing

Sample collection was carried out seasonally at two locations in the surf zone of Tramandaí Beach (Figure 1) during March (autumn), July (winter) and October (spring) 2015 and February (summer) 2016. Fish were collected using beach seine, with the net having the following dimensions: 9 m long, 1.5 m high, 13 mm mesh opening in the wings and 5 mm mesh in the centre (Garcia *et al.*, 2019a). After collection, individuals were preserved in 4% formalin for subsequent stomach contents analysis (SCA) in the laboratory. A total of 282 individuals with an average total length of 55.1 mm (range = 17–136 mm) had their stomach contents analysed. Specimens were collected with the authorization of the SISBIO (Biodiversity Information and Authorization System) of the Chico Mendes Institute for Biodiversity Conservation (ICMBIO) under license number 47567-1.

For SIA, 25 specimens were collected in March 2015, stored on ice in the field and later preserved in a freezer in the laboratory. In addition to fish collections, samples of basal sources as particulate

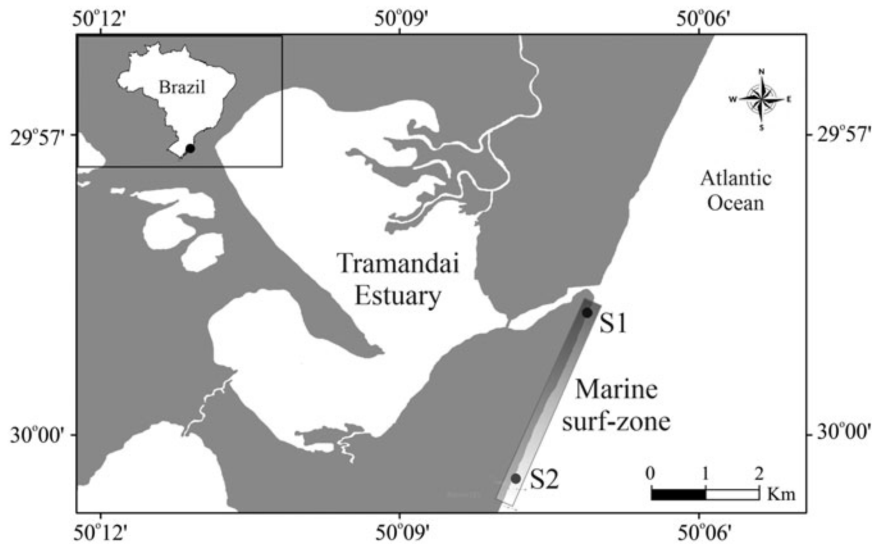


**Figure 1.** Location of the sampling stations (S1 and S2) of *Trachinotus marginatus* in the surf zone of Tramandai (Brazil). The shaded rectangular area denotes the studied marine surf-zone.

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organic matter in suspension (POM) and in sediment (SOM) were also collected at each location for isotopic analysis. POM was obtained by filtering ~1.5 l of water onto a precombusted (450°C, 4 h) Whatman glass-fibre filter (0.75 mm). In order to obtain an SOM sample, about 2 cm of surface sediment was removed using a 10 cm diameter plastic pipe. These organic sources were collected to serve as proxies of the isotopic variability of microalgae and debris (Fry, 2006; Vollrath *et al*., 2021), which constitutes the main sources of primary organic matter sustaining consumers in sandy beaches along the studied coastal plain (Pinotti *et al*., 2014; Garcia *et al*., 2019a, 2019b). Other primary producers, such as floating aquatic macrophytes, seagrasses and macroalgae beds, are usually absent in the sandy beaches of this coastline (Odebrecht *et al*., 2010).

Representative preys of the main food categories (crustaceans, fishes, insects, annelids and molluscs) observed in the food content of *T. marginatus* (see Results) were collected. These comprised (1) hippid crab *Emerita brasiliensis*, (2) juvenile fishes of the mullet *Mugil liza* and *T. marginatus* with TL between 17.0 and 24.5 mm, (3) insects of the orders Hymenoptera, Hemiptera, Coleoptera and Odonata, (4) the polychaeta *Spio gaucha* and (5) the bivalve *Amarilladesma mactroides*. These prey species were sampled in the same studied sandy beach where basal sources (POM and SOM) were obtained, with exception of the insects and annelids that were obtained from the literature (Huckembeck *et al*., 2020 and Garcia *et al*., 2019b, respectively). These studies were carried out in the same coastline of the present study (29°59′S): the former in a sandy dune adjacent to the marine surf zone (31°08′S) and the latter in a sandy beach (32°17′S), respectively. The number of samples obtained for each prey and month/year of their collections are shown at Supplementary Table S1.

In the laboratory, fish were identified and the total length (mm) and total weight (g) of each individual was obtained. Later, each specimen was eviscerated for removal of their stomach, and stomach contents were analysed under a stereoscopic microscope (40×). Food items found within the stomachs were identified at the lowest possible taxonomic level, counted and had their mass measured with a precision scale (0.0001 g) (Hyslop, 1980). For SIA, fish were cleaned with distilled water to remove debris and other materials adhered to the surface, then a sample of muscle tissue in the anterodorsal region of each individual was extracted. After washing, each sample was placed individually in a small glass Petri dish previously sterilized (24 h in HCl) and dried in an oven at 60°C for 48 h. Dried samples remained in the desiccator for a few hours and then grounded to a fine powder with a mortar and pestle. Subsamples were weighed (1–3 mg for animal tissues, 2–3 mg for POM, 25–30 mg for SOM) in tin capsules (Costech, Valencia, CA, USA) and sent to the Stable Isotope/Soil Biology Laboratory, University of Georgia, USA, for analysis of carbon ($\delta^{13}C$) and nitrogen isotope ratios ($\delta^{15}N$). The standard material for carbon and nitrogen were Pee Dee Belemnite (PDB) and atmospheric air, respectively. Results were expressed as delta notation: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$, where $R$ is the ratio between $^{13}C$ and $^{12}C$ or $^{15}N$ and $^{14}N$ (Fry, 2006). Standard deviations for $\delta^{13}C$ and $\delta^{15}N$ replicate analyses of internal standards were 0.11 and 0.10%, respectively. The extraction of lipids in fish samples or mathematical corrections to normalize the data were not performed because C:N ratio of analysed muscle tissues were lower than 3.5 suggesting relatively low levels of lipid content (Post *et al*., 2007; Hoffman *et al*., 2015).

### Data analyses

For statistical analysis, individuals of *T. marginatus* were classified into three size body groups to evaluate potential ontogenetic diet shifts (SCA) and ontogenetic changes in food assimilation (SIA): from 0 to 40 mm (GI), from 40 to 80 mm (GII) and greater than 80 mm (GIII) (see Supplementary Figure S1).

### Stomach content analysis (SCA)

There were no individuals captured in spring; therefore, SCA was carried out only for autumn, winter and summer seasons. The relative importance of food items found in the stomachs was estimated using the alimentary index (IAi) (Kawakami and Vazzoler, 1980) calculated as: IAi = %FO × %W, where %FO represents the frequency of occurrence (i.e. the percentage of the food items found in all analysed stomachs) and %W represents the weight in percentage (i.e. the weight of a food item in relation to the total weight of all food items food found in all analysed stomachs).

Multidimensional non-metric scaling analysis was used to evaluate similarities in diet compositions across body size classes (GI to GIII) of *T. marginatus* and seasons (Borcard *et al*., 2018). For this analysis, prey items were grouped into five broad food categories: annelid, mollusc, crustacean, fish and insect. Differences in diet composition across body size groups and seasons were also evaluated by a permutational analysis of variance (PERMANOVA) test, using a Bray–Curtis matrix of dissimilarity with food item abundance data ($\log(x+1)$ transformed). PERMANOVA was performed with 9999 permutations and $\alpha = 0.05$. These statistical analyses were performed using the Vegan Package in the R software (R Core Team, 2020).

### Stable isotope analysis (SIA)

Changes in $\delta^{13}C$ or $\delta^{15}N$ across size groups of *T. marginatus* were initially evaluated using boxplots and potential differences in average values were tested using the non-parametric Kruskal–Wallis and the Dunn post-hoc tests. These procedures were carried out using ggplot2, dplyr and rstatix packages in the R software (R Core Team, 2020). Isotopic ellipses for each size group were calculated using the standard area of the corrected ellipse (SEAc), which is suitable for relatively small samples ($n < 30$) (Jackson *et al*., 2011). The statistical comparison between the sizes of the ellipses and the degree of overlap between them was made using direct probability and Bayesian estimates. These analyses were performed using the package Stable Isotope Bayesian Ellipses in R (SIBER) in the R software (Jackson *et al*., 2011).

The relative contribution of basal (POM, SOM) and prey sources (crustaceans, fishes, insects, annelids, molluscs) to fish was estimated with Bayesian isotopic mixing models using the Stable Isotope Mixing Models in R (SIMMR) package (Phillips *et al*., 2014; Parnell and Inger, 2016). This approach considers uncertainty and variation in food sources, consumers and isotopic fractionation, employing Gaussian likelihood and Markov chain Monte Carlo (MCMC) to fit the model to the data (Parnell and Inger, 2016). The mean values (and standard deviation) of isotopic fractionation used in the mixing models were 0.54 (0.53) ‰ for carbon ($\delta^{13}C$) and 3.02 (0.47) ‰ for nitrogen ($\delta^{15}N$) (Bastos *et al*., 2017). These fractionation values were multiplied by two for the mixing models with basal sources because the studied fish is a carnivorous consumer and, therefore, is subject to more than one isotopic fractionation in the food chain (Phillips *et al*., 2014; Garcia *et al*., 2019a). The performance of the fitted models was evaluated using the Gelman test, which diagnoses the adequacy of the simulations' fit (Parnell and Inger, 2016). The average values (±SD) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of the fish (consumer), basal and prey sources used in the isotope mixing models are shown in Supplementary Table S1.

The TP estimates for the different size groups of *T. marginatus* were computed with Bayesian models performed using the tRophicPosition package (Quezada-Romegialli *et al.*, 2018) in the R software. The model considered isotopic variability ($\delta^{13}C$ and $\delta^{15}N$) of each individual fish and primary sources (POM and SOM) as two isotopic baselines (Post, 2002). The mean values (and standard deviation) of isotopic fractionation of $\delta^{15}N$ and $\delta^{13}C$ were 3.02 (0.47) and 0.54 (0.53), respectively, which have been suggested for carnivorous fishes (Bastos *et al.*, 2017). Mean TP values and 95% credibility intervals were obtained using MCMC simulations with 10,000 interactions and 10,000 samples in the JAGS 4.3.0 program (Quezada-Romegialli *et al.*, 2018).

## Results

### Diet composition

The stomach contents of 284 individuals of juvenile *T. marginatus* were analysed, of which 36 were empty. In total, 54 prey taxa were identified (Table 1). Crustacean prey were by far the dominant item (IAi > 90%) in the species' diet, both across different size groups and seasons (Figure 2). The main consumed crustacean was the hippid crab *E. brasiliensis*, which dominated the diet during winter (82.3%) and summer (69.8%) but was rare during autumn (0.8%) (Table 1). Among the less abundant food categories in the diet, the consumption of fish preys stands out mainly in autumn (8.3%) by larger *T. marginatus* individuals (>80 TL mm) and annelids in winter (3.4%) by individuals with body sizes between 40 and 80 TL mm (Figure 2). Among the consumed fish that was possible to identify at the genus level were juveniles of both *Trachinotus* spp. and mullet *Mugil* spp. Insects were consumed during summer (0.9%) by smaller individuals (<40 TL mm). Despite their low relative importance in the diet, these terrestrial prey stood out for their high species diversity, being represented by several orders (Hymenoptera, Diptera, Hemiptera, Coleoptera, Trichoptera and Odonata) distributed in 15 families (Table 1).

Overall, comparison of the diet similarity along seasons and body size groups revealed marked overlap patterns (Figure 3). Nevertheless, it was possible to observe differences in diet in some cases. For example, diet similarity between autumn and winter was lower when compared with summer, which had higher intraspecific variability in the diet. A similar pattern was observed for body size groups, with slightly lower diet similarity between individuals with body sizes <40 and >80 TL mm, with intermediate body size individuals indicating comparatively higher intraspecific diet variability (Figure 3). These patterns were corroborated by results of the PERMANOVA test, which revealed statistical differences ($P < 0.005$) both between seasons ($P = 0.0001$) and body size groups ($P = 0.0001$).

### Isotopic niches, assimilation of food sources and trophic position

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios had marked variations among body size groups (Figure 4). There was an increase in both $\delta^{13}C$ and $\delta^{15}N$ with increasing body sizes. Concomitantly, there was a decrease in the isotopic variability around the mean with the increase in individuals' body sizes (Figure 4). Accordingly, the Kruskal–Wallis test revealed statistically significant differences in average $\delta^{13}C$ and $\delta^{15}N$ values across body size groups ($P = 0.0003$ and $P = 0.0002$, respectively). Duncan's post-hoc test ($P = 0.05$) indicated that all groups were statistically different for $\delta^{13}C$, but only group I was statistically different from groups II and III for $\delta^{15}N$ (Figure 4).

Isotopic ellipses areas (SEAc) showed an inverse relationship with increasing *T. marginatus* body sizes (Figure 5A), with highest values (median: 1.41‰$^2$) for smaller individuals (0–40 TL mm), intermediate size (0.76‰$^2$) for individuals between 40 and 80 TL mm and lowest size (0.3‰$^2$) for larger (>80 TL mm) individuals. Credibility intervals (95%) on the SEAc estimates also showed an inverse relationship with increasing body sizes, with higher uncertainty for smaller individuals (0–40 TL mm) (Figure 5B). These patterns were corroborated by direct pairwise probability test that revealed statistically significant ($P < 0.5$) differences in SEAc median values among all size groups.

Isotopic mixing models showed that, regardless of body size group, POM was the primary source that most contributed to *T. marginatus* in the marine surf-zone in comparison with SOM (Figure 6 and Supplementary Figure S2). Mean values of POM contribution ranged from 67.2% (95% CI 38.3–95.7) in larger individuals (>80 TL mm) to 71.3% (95% CI 24.3–97.5) in smaller individuals (0–40 TL mm). In contrast, SOM contribution ranged from 23.6% (95% CI 2.5–75.7) in smaller individuals to 38.1% (95% CI 27.7–48.2). The predominance of POM over SOM was higher for smaller (75.6 vs 24.4%) individuals but become lesser pronounced for intermediate (61.7 vs 38.3%) and larger (66.8 vs 33.2%) ones (Figure 6).

Among prey sources, isotopic mixing models revealed that fishes were the most assimilated in the muscle of smaller (48.1, 95% CI 15.7–74.5) and intermediate (50.3, 95% CI 33.9–63.4) body size individuals of *T. marginatus*. In contrast, annelids were the most assimilated prey by the larger individuals (46.6, 95% CI 13.8–69.1), being also the second most assimilated by intermediate ones (29.6, 95% CI 8.9–46.4). Insects had a relatively noticeable assimilation (22.1, 95% CI 7.9–36.0) only by smaller individuals. Crustaceans and molluscs had negligible assimilations (<10%) across all body size classes of *T. marginatus* (Figure 6 and Supplementary Figure S3).

TP increased with *T. marginatus* body sizes, most notably intermediate (40–80 TL mm) and larger (>80 TL mm) individuals that had values of 4.1 (95% CI 3.6–4.6) and 4.5 (95% CI 3.9–5.1) approximately one trophic level higher than smaller (0–40 TL mm) ones (3.1; 95% CI 2.7–3.6) (Figure 7).

## Discussion

### Changes in diet across seasons and consumer's body size

The diet of juvenile *T. marginatus* in the studied marine surf zone was dominated across all body sizes by small crustaceans, mainly the hippid crab *E. brasiliensis*, which presents a seasonal recruitment pattern in the subtropical beaches of its geographical distribution, with higher abundances during the spring and summer months (Neves *et al.*, 2008; Silva *et al.*, 2008). Although this prey has an escape behaviour of burying itself in the sediment (Cansi, 2007), the high wave action in the surf zone tend to remove them from the sediment, making it available to opportunistic fish predators (Monteiro-Neto and Cunha, 1990). In fact, this prey has been reported as an important food item in the diet of other congeneric species like *T. carolinus* in tropical marine beaches (Niang *et al.*, 2010; Santos, 2010). It is also worth mentioning the consumption of fish prey by larger *T. marginatus* individuals (>80 mm), such as juvenile *Mugil* sp. and specimens of the genus *Trachinotus*, suggesting that intraspecific cannibalism likely occurs in this species. Although it was not possible to identify these predated fish to species level, it is highly likely that these consumed specimens were *T. marginatus* due to its high abundance in the region, compared with other congeneric species (e.g. *T. carolinus*) that are rarely found in this area (Lima and Vieira, 2009; Vieira *et al.*, 2019).

**Table 1.** Frequency of occurrence (%FO), weight (%W) and alimentary index (IAi) values for the food items found in the stomach contents of juveniles of the Plata pompano *Trachinotus marginatus* in the marine surf zone of Tramandaí sandy beach in southern Brazil

| | Autumn | | | Winter | | | Summer | | |
|---|---|---|---|---|---|---|---|---|---|
| Number of individuals | 102 | | | 49 | | | 95 | | |
| Mean (SD) TL (mm) | 48.2 (14.8) | | | 85.2 (20.8) | | | 48.0 (21.4) | | |
| Food items | %FO | %W | %IAi | %FO | %W | %IAi | %FO | %W | %IAi |
| *Phylum Arthropoda* | | | | | | | | | |
| Class Insecta | | | | | | | | | |
| Insects | 7.843 | 0.267 | 0.157 | | | | 3.158 | 0.018 | 0.003 |
| Insect fragment | | | | 2.041 | 0.001 | | 3.158 | 0.013 | 0.002 |
| Order Hymenoptera | | | | | | | | | |
| Hymenoptera | | | | | | | 1.053 | 0.004 | |
| Chalcidoidea | | | | | | | 7.368 | 0.110 | 0.038 |
| Formicidae | | | | | | | 8.421 | 0.075 | 0.030 |
| Order Diptera | | | | | | | | | |
| Diptera | | | | 2.041 | 0.001 | | | | |
| Chironomidae | | | | | | | 1.053 | 0.009 | |
| Culicidae | | | | | | | 2.105 | 0.018 | 0.002 |
| Dolichopodidae | | | | | | | 3.158 | 0.044 | 0.007 |
| Muscidae | | | | | | | 4.211 | 0.289 | 0.057 |
| Order Hemiptera | | | | | | | | | |
| Cicadellidae | | | | | | | 14.737 | 0.206 | 0.143 |
| Order Coleoptera | | | | | | | | | |
| Coleoptera | | | | | | | 1.053 | 0.004 | |
| Dityscidae | | | | | | | 2.105 | 0.092 | 0.009 |
| Elmidae | | | | | | | 9.474 | 0.075 | 0.033 |
| Estafilinideo | | | | | | | 1.053 | 0.004 | |
| Noteridae | | | | | | | 1.053 | 0.009 | |
| Order Trichoptera | | | | | | | | | |
| Hydroptilidae | | | | | | | 1.053 | 0.004 | |
| Order Odonata | | | | 2.041 | 0.026 | 0.001 | | | |
| Class Entognatha | | | | | | | | | |
| Superorder Collembola | | | | | | | 1.053 | 0.004 | |
| Subphylum Crustacea | | | | | | | | | |
| Crustacean | | | | | | | 1.053 | 1.030 | 0.051 |
| Crustacean larvae | 1.961 | 1.158 | 0.170 | | | | 5.263 | 0.088 | 0.022 |
| Crustacean fragment | | | | | | | 3.158 | 0.013 | 0.002 |
| Class Branchiopoda | | | | | | | | | |
| Cladocera | | | | 4.082 | 0.010 | 0.001 | 1.053 | 0.013 | 0.001 |
| Class Malacostraca | | | | | | | | | |
| Superorder Peracarida | | | | | | | | | |
| Order Isopoda | 1.961 | 1.312 | 0.193 | 2.041 | 0.138 | 0.004 | 1.053 | 0.105 | 0.005 |
| Order Mysida | | | | | | | | | |
| Mysidacea | | | | 2.041 | 0.004 | | 5.263 | 1.456 | 0.361 |
| Order Decapoda | | | | | | | | | |
| Decapod larvae | 19.608 | 7.108 | 10.458 | | | | 2.105 | 0.044 | 0.004 |
| Decapod fragment | | | | | | | 6.316 | 0.088 | 0.026 |
| Shrimp | 8.824 | 7.812 | 5.172 | 4.082 | 0.026 | 0.001 | 6.316 | 3.538 | 1.054 |

(*Continued*)

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**Table 1.** (*Continued.*)

| | Autumn | | | Winter | | | Summer | | |
|---|---|---|---|---|---|---|---|---|---|
| Shrimp larvae | 5.882 | 1.628 | 0.719 | | | | 1.053 | 0.009 | |
| Shrimp mysis | | | | | | | 1.053 | 0.022 | 0.001 |
| Shrimp fragment | | | | | | | 2.105 | 0.061 | 0.006 |
| Family Portunidae | | | | | | | | | |
| Callinectes appendix | | | | | | | 1.053 | 0.013 | 0.001 |
| Family Hippidae | | | | | | | | | |
| *Emerita brasiliensis* | 2.941 | 3.824 | 0.844 | 85.714 | 74.303 | 82.289 | 22.105 | 67.010 | 69.849 |
| Abdomen *Emerita* | | | | | | | 1.053 | 0.149 | 0.007 |
| Infraorder Brachyura | | | | | | | | | |
| Brachyura | 4.902 | 1.554 | 0.572 | | | | 1.053 | 0.149 | 0.007 |
| Brachyura larvae | | | | | | | 3.158 | 0.127 | 0.019 |
| Order Amphipoda | | | | | | | | | |
| Amphipoda | 3.922 | 0.045 | 0.013 | 75.510 | 2.454 | 2.394 | 5.263 | 0.070 | 0.017 |
| Amphipoda fragment | | | | | | | 2.105 | 0.031 | 0.003 |
| Suborder Gammaridea | | | | | | | 1.053 | 0.061 | 0.003 |
| Class Maxillopoda | | | | | | | | | |
| Subclass Copepoda | 8.824 | 0.100 | 0.066 | | | | 2.105 | 0.009 | 0.001 |
| Copepoda Calanoida | 0.980 | 0.002 | | 4.082 | 0.003 | | 2.105 | 0.009 | 0.001 |
| Copepoda Cyclopoida | 33.333 | 1.584 | 3.963 | | | | | | |
| *Phylum Mollusca* | | | | | | | | | |
| Class Bivalvia | | | | | | | | | |
| Bivalve | 2.941 | 5.209 | 1.150 | | | | 4.211 | 0.272 | 0.054 |
| *Amarilladesma mactroides* | | | | | | | 2.105 | 0.259 | 0.026 |
| *Phylum Annelida* | | | | | | | | | |
| Class Polychaeta | | | | | | | | | |
| Polychaete | 2.941 | 1.308 | 0.289 | 46.939 | 5.183 | 3.144 | 4.211 | 0.767 | 0.152 |
| *Phylum Platyhelminthes* | | | | | | | | | |
| Class Rhabditophora | | | | | | | | | |
| Digenea | 0.980 | 0.006 | | | | | | | |
| *Phylum Cordada* | | | | | | | | | |
| Subclass Actinopterygii | | | | | | | | | |
| Infraclass Teleostei | 1.961 | 16.701 | 2.457 | | | | | | |
| Order Perciformes | | | | | | | | | |
| *Trachinotus* sp. | 1.961 | 20.647 | 3.038 | | | | 1.053 | 9.558 | 0.474 |
| Order Mugiliformes | | | | | | | | | |
| *Mugil* sp. | 0.980 | 2.739 | 0.202 | | | | | | |
| Others | | | | | | | | | |
| Fish scale | 0.980 | 0.008 | 0.001 | 14.286 | 0.007 | 0.001 | 4.211 | 0.018 | 0.003 |
| Fish larvae | | | | | | | 1.053 | 0.197 | 0.010 |
| Shell fragment | | | | 8.163 | 0.308 | 0.033 | 2.105 | 1.101 | 0.109 |
| Animal rest | 49.020 | 10.712 | 39.402 | 24.490 | 2.014 | 0.637 | 44.211 | 5.827 | 12.148 |
| Vegetable rest | | | | 20.408 | 8.123 | 2.142 | 7.368 | 0.281 | 0.098 |
| Unidentified fragments | | | | 2.041 | 0.005 | | 2.105 | 0.009 | 0.001 |

Values equal to and less than 0.000 are not shown. There were no individuals caught during spring sampling. Number of individuals with no empty stomachs analysed and its mean total length (TL) in mm are shown.

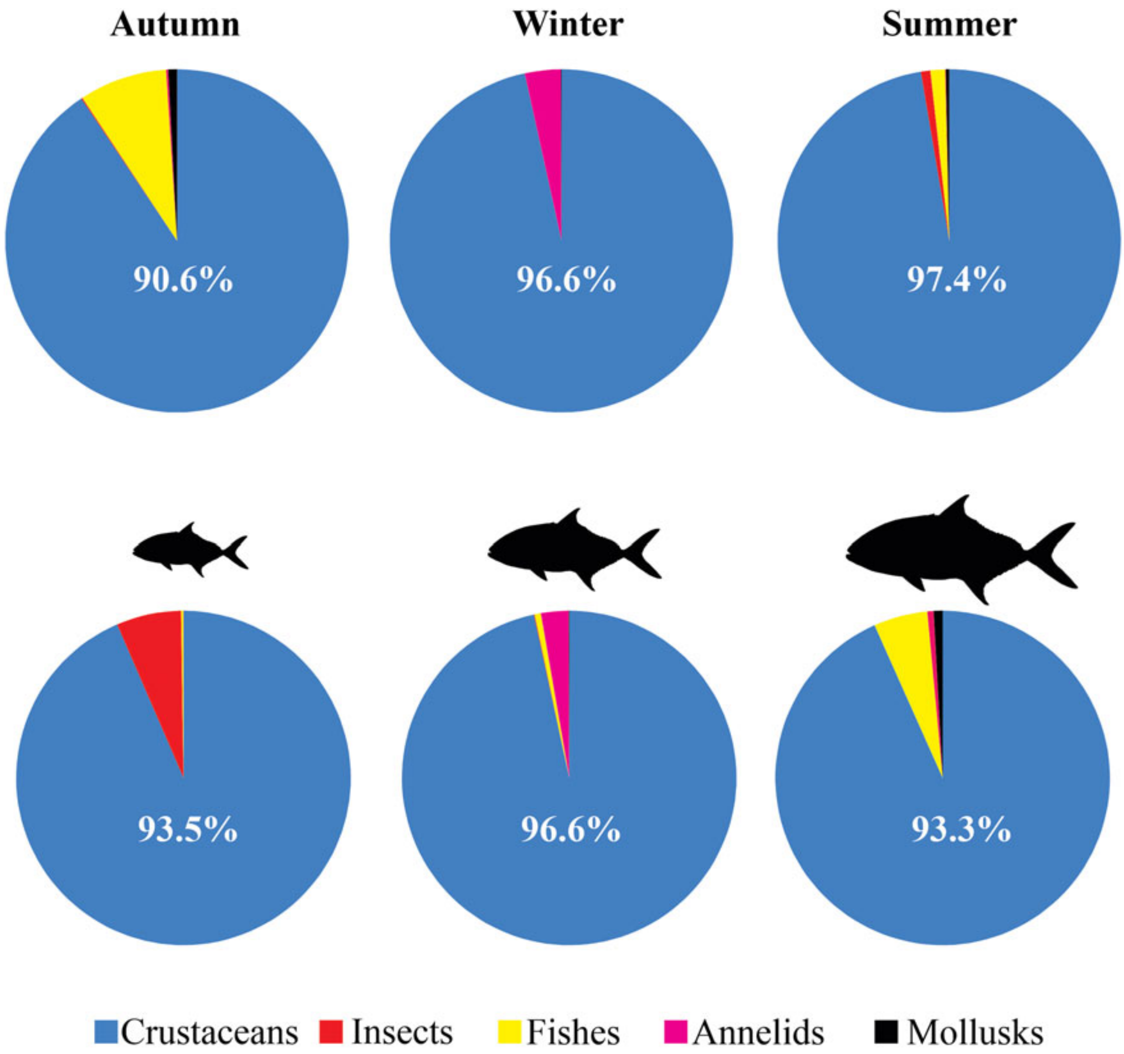


**Figure 2.** Relative importance (based on the IAi) of the food categories found in the stomach content of *Trachinotus marginatus* along the seasons (autumn, winter, summer) and body sizes groups (smaller: 0–40, intermediate: 40–80 and larger: >80 TL mm).

Despite the predominance of crustaceans in the diet of juvenile *T. marginatus* in our study site throughout the year, it was possible to observe temporal and ontogenetic variations in diet composition. Smaller individuals (0–40 mm) also consumed a variety of insects during summer, which coincided with the juvenile recruitment of *T. marginatus* in the surf zone (Lemos *et al*., 2011). This led a greater variability in the diet during summer compared to other seasons. Higher consumption of insects during the warmer season is expected in this subtropical latitude, since this prey usually achieved higher densities during summer when higher temperatures and food availability favour its reproduction (Paschoal, 2013). This may have resulted in a higher density of these preys at this warmer time of year, which were later transported to the marine surf zone.

The transport of terrestrial prey, such as insects, to the studied marine surf zone is probably associated with physical vectors, such as wind, rainfall and continental discharge. Increased rainfall and river flow can lead to an increase in the estuarine plume (Calliari *et al*., 2001; Marques *et al*., 2009), which in turn can carry particulate organic matter (POM) and prey to ocean waters, making them available to marine consumers (Savage *et al*., 2012; Garcia *et al*., 2019b). Winds can also transport terrestrial prey (e.g. insects) from the continental environment (e.g. coastal dunes) directly to the surf zone (Lazzari *et al*., 2008), where they can be ingested by opportunistic carnivorous consumers (Pinotti *et al*., 2014). Additionally, insects are commonly found in sandy marine beaches associated, for example, with macrodebris and decaying vegetation (Gianuca, 1983; Giménez and Yannicelli, 2000). We hypothesized that the occurrence of insects in the dunes that are within a few metres of the surf-zone had facilitated their transport to the sea, where they were consumed opportunistically by *T. marginatus* juveniles.

It is also worth noting that the observed consumption of insects in summer in the present study was somewhat unexpected because this time of year is characterized by low rainfall in southern Brazil. For example, a prior study carried out 300 km south of the present study observed consumption of insects in the winter, when rainfall and freshwater discharge is usually higher (Monteiro-Neto and Cunha, 1990). Such apparent discrepancy may be related to the occurrence of a strong *El Niño* between 2015 and 2016, which increased rainfall and river discharge in the region during our sampling. A prior study in the adjacent Tramandaí-Armazém estuarine complex demonstrated that the hydrological impacts associated with the 2015–16 *El Niño* promoted the consumption of terrestrial-derived material by estuarine fish (Garcia *et al*., 2019c). Hence, it seems reasonable to speculate that this phenomenon may also have contributed to the transport of terrestrial prey, such as insects, to the adjacent marine region, where they were preyed upon by *T. marginatus* juveniles.

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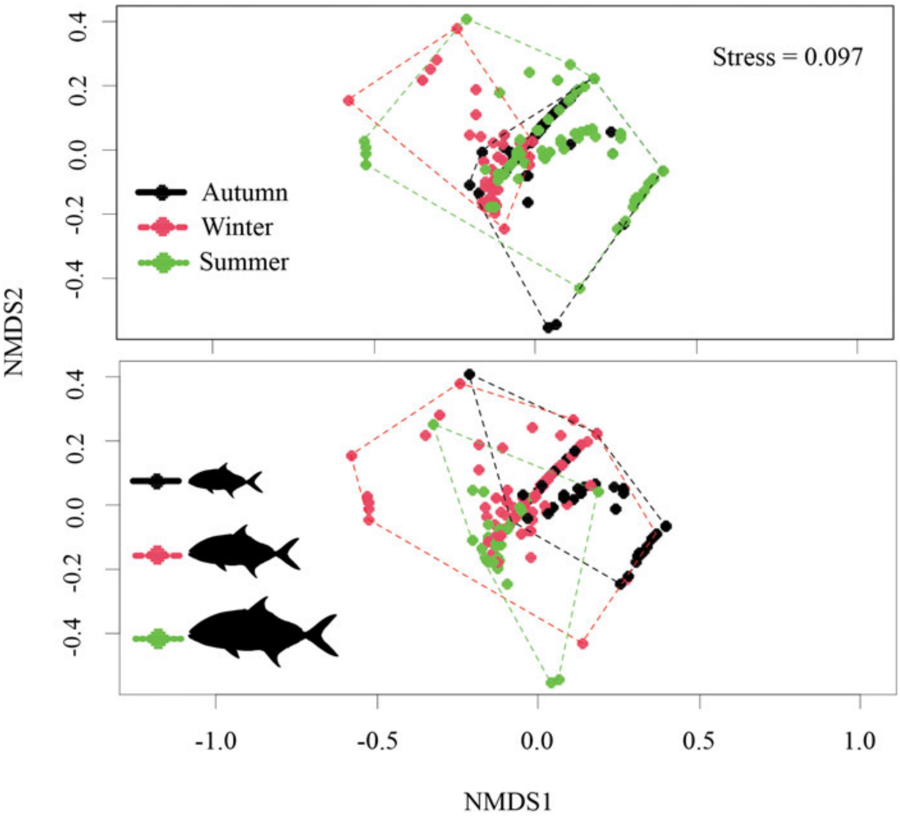


**Figure 3.** Diet similarity among seasons and body size groups (smaller: 0–40, intermediate: 40–80 and larger: >80 TL mm) using multidimensional non-metric scaling analysis (NMDS) based on the IAi of the food categories found in the stomach content of *Trachinotus marginatus*.

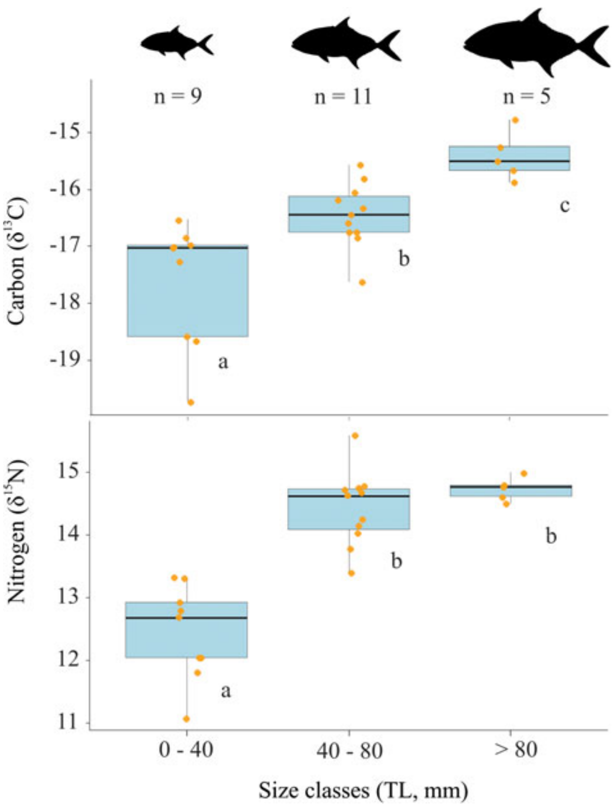


**Figure 4.** Boxplots of carbon (δ13C) and nitrogen (δ15N) isotope ratios among body size groups (smaller: 0–40, intermediate: 40–80 and larger: >80 TL mm) of *Trachinotus marginatus*. The box is the interquartile range, with the lower end being the first quartile (25% of the data) and the upper end the third quartile (75% of the data). The black horizontal line is the median, the vertical line represents the upper and lower limits of the values, and the yellow circles represent each sample.

### *Isotopic niches, assimilation of food sources and trophic position*

Isotopic niche metrics revealed changes in food niche breadth across different body size classes of *T. marginatus* individuals inhabiting surf zone nursery grounds. Isotopic ellipses indicated that the smallest sizes fishes (<40 mm) had larger isotopic niches

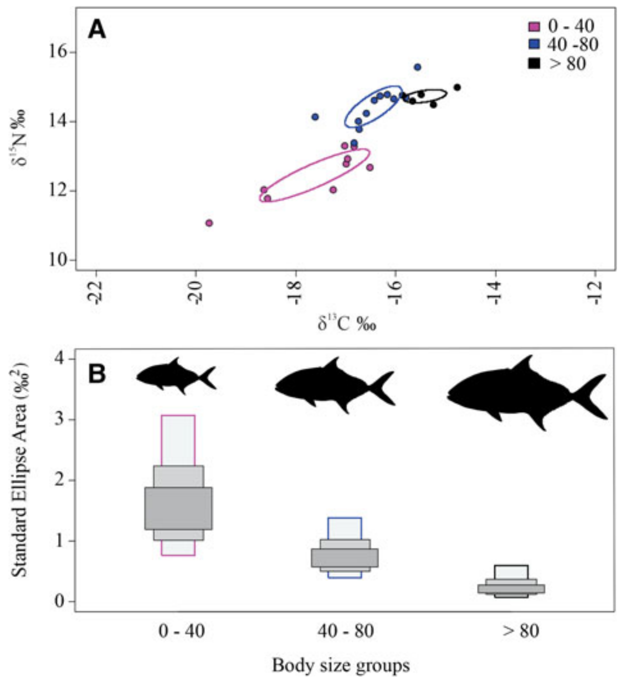


**Figure 5.** Standard ellipse areas (SEA) (A) and their Bayesian estimates (SEAB) (B) for the different body size groups (smaller: 0–40, intermediate: 40–80 and larger: >80 TL mm) of *Trachinotus marginatus*. SEAB's credibility intervals of 95, 75 and 50% are denoted by light grey, grey and dark grey bars, respectively.

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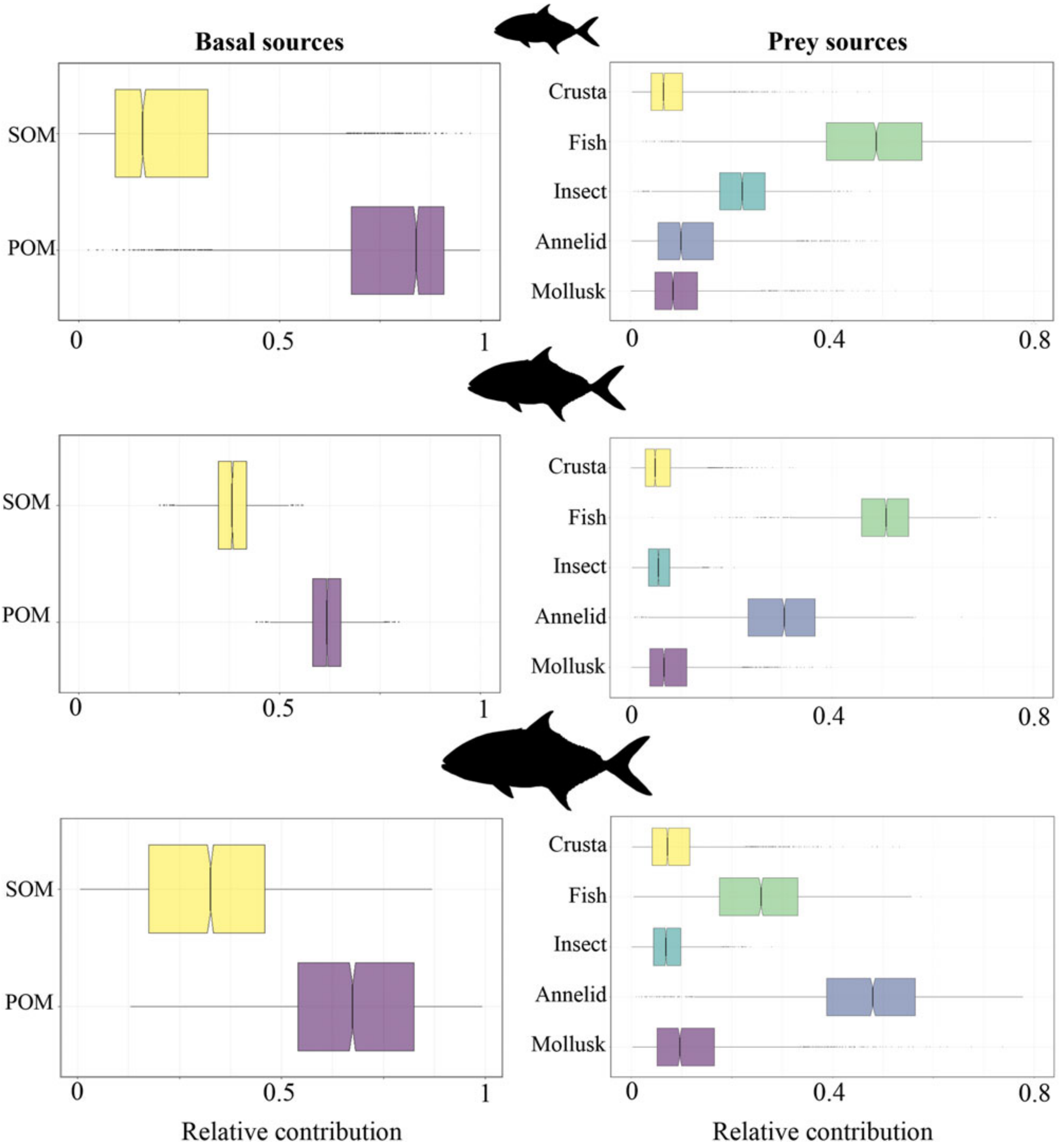


**Figure 6.** Boxplots showing the relative contributions of basal (particulate organic matter in suspension, POM and in sediment, SOM) and prey sources for the different body size groups (smaller: 0–40, intermediate: 40–80 and larger: >80 TL mm). The box boundaries represent the 25th and 75th percentiles, the horizontal line is the median and the whiskers mark the 2.5th and 97.5th percentiles.

suggesting a more diverse diet. In contrast, intermediate (40–80 mm) and larger (>80 mm) individuals had smaller isotopic niches, which could be associated with a less diverse diet. We proposed two non-mutually exclusive hypotheses that could explain the higher isotopic niche observed in the smaller individuals: (i) only smaller individuals consumed terrestrial preys (insects) that tend to have distinct isotopic composition than marine preys (Garcia *et al*., 2019b; Huckembeck *et al*., 2020), which may have contributed to increase the size of their isotopic ellipses, and (ii) considering that the isotopic muscle turnover (i.e. the time the tissue takes to reflect a new food source) of marine fishes is approximately three months (Mont'alverne *et al*., 2016; Oliveira *et al*., 2017), the smaller individuals sampled in the surf zone could be partially reflecting offshore food sources, since they originally migrate (as eggs and larvae) from the deeper coastal zone (40 m) into the surf zone (2 m) in the summer period. Further studies using controlled feeding diet in laboratory and using tags to track their displacement between offshore and surf zone would be needed to evaluate these hypotheses.

Isotopic mixing models showed that, regardless of changes in body sizes, *T. marginatus* individuals inhabiting the surf zone are assimilating more suspended POM than SOM, suggesting they derived primary nutrients mainly from a planktonic food chain. The major intermediate trophic links connecting the carnivorous *T. marginatus* to the base of the food web are probably microcrustaceans, which dominated the fish diet in the surf zone. Most of these crustaceans spend their initial development as planktonic larvae feeding on phytoplankton and/or zooplankton and as

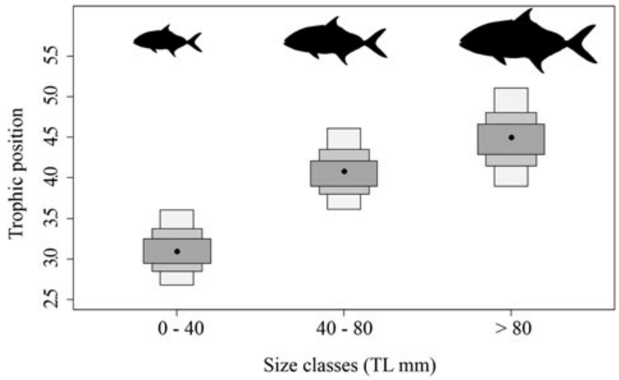


**Figure 7.** Estimates of the trophic position for the different body size groups (smaller: 0–40, intermediate: 40–80 and larger: >80 TL mm) of *Trachinotus marginatus* and their respective credibility intervals of 95% (light grey), 75% (intermediate grey) and 50% (dark grey).

suspension feeders as adults. This pattern seems to be corroborated by other studies showing the importance of POM (a proxy for phytoplankton and POM) for consumers of sandy marine beaches (Bergamino *et al.*, 2011; Pinotti *et al.*, 2014; McLachlan and Defeo, 2017). For example, Garcia *et al.* (2019b) demonstrated that POM represents the main primary source of energy sustaining zoobentivorous fish, such as *T. marginatus*, in the surf zone of Cassino Beach, southern Brazil. Although in relatively lower proportion (~30%), SOM also contributed with primary nutrients to *T. marginatus* juveniles, suggesting that benthic-derived nutrients were complementary sources fuelling the food chain sustaining the species in the marine surf-zone.

Isotope tracers revealed that the most important food item found in the stomach content of *T. marginatus* juveniles, the hippid crab *E. brasiliensis*, was not the most assimilated in their muscle tissues. Rather, ingested prey like fishes and annelids were the most assimilated by juvenile *T. marginatus* in the marine surf-zone. This apparently contrasting findings are not entirely surprising considering that preys protected by carapaces or shells (like the hippid crab and molluscs found in the stomach content) are usually refractory food items less susceptible to digestion and assimilation (Condini *et al.*, 2015). Hence, although the hippid crab *E. brasiliensis* was by far the most observed in stomach contents of juvenile *T. marginatus* (IAi > 90%), this prey probably contributes less (per unit ingested biomass) to assimilated energy due to its slower digestion rates. In comparison, prey like small fish and polychaetes are comparatively more palatable and more prone to be digested and assimilated and, therefore, tended to be observed with less frequency in the stomachs (Gerking, 1994). Hence, our findings based on isotopic mixing models suggested that small fish preys (<25 TL mm) like the mullet *M. liza* and the polychaeta *S. gaucha*, which are abundant in the study area (Pinotti *et al.*, 2014; Rodrigues *et al.*, 2015), represent import food sources sustaining juvenile *T. marginatus* in the marine surf-zone. Isotopic mixing models also corroborated the relative importance of insects for smaller *T. marginatus* individuals (<40 TL mm). As discussed in the prior subsection, insects are abundant in the adjacent dunes and commonly disperse towards the surf-zone, where they are consumed by juvenile *T. marginatus*. Our study with isotope tracers revealed for the first time that such prey can be assimilated in the muscle tissue of fish in the marine surf-zone. Prior works have pointed out evidence of trophic connectivity between terrestrial and marine ecosystems along this extensive subtropical coastline (~500 km) (Oliveira *et al.*, 2014; Garcia *et al.*, 2017b, 2019b). Further investigations are needed to reveal the real extension and implications of such between-ecosystem trophic linkages and its potential to act as trophic subsidies (*sensu* Polis *et al.*, 1997) for fish populations along the southern coastline of the southwestern Atlantic.

TP estimation using SIA revealed that juvenile *T. marginatus* in the surf zone can be considered as tertiary consumers, with a tendency of increasing their TP in the surf zone with increasing body size. Phytoplankton/debris forms the basis of the food chain in the marine surf zone and sandy beach environments (McLachlan and Defeo, 2017). The benthic macrofauna has the role of consuming this primary food on sandy beaches, while in the surf zone this role is shared with zooplankton, assuming the position of secondary consumers in the food chain (Pinotti *et al.*, 2014). In turn, fish are the predators of zooplankton in the surf zone, mainly juveniles, consuming them in the water column where they are most abundant (Pinotti *et al.*, 2014). Thus, juvenile fish tend to be tertiary consumers in this environment (McLachlan and Defeo, 2017). Our findings using SIA corroborates the trophic role of juvenile *T. marginatus* as carnivores acting at higher trophic levels of the food chain in the marine surf zone, which was corroborated by the isotopic mixing models revealing that the species assimilated mainly fish preys.

In conclusion, our findings provided the first description of food habits and food sources sustaining the Plata pompano *T. marginatus* during the early phase of its life cycle in the marine surf-zone. SCA revealed that juveniles fed mainly on the hippid crab *E. brasiliensis*, but also consumed other invertebrates (annelids, insects, molluscs) and fishes (including some cases of cannibalism). However, SIA showed that although microcrustaceans were the most important food item found in the stomach content of *T. marginatus* juveniles, they were not the most assimilated. Rather, more palatable prey without carapaces or shells, like fishes and annelids, were the most assimilated by *T. marginatus* juveniles in the marine surf-zone. SIA also showed changes in their isotopic niches and TP associated both with between-season changes and increment in body sizes during their development in their nursery grounds. Moreover, isotope tracers also allowed to infer that juvenile *T. marginatus* in the surf-zone assimilated most of their primary nutrients from a planktonic food chain and, to a lesser extent, from a benthic pathway. The Plata pompano *T. marginatus* is a conspicuous component of the southwestern Atlantic coast (Lemos *et al.*, 2011; Vieira *et al.*, 2019; Garcia *et al.*, 2019b) and commonly targeted by coastal fisheries (Santos and Vieira, 2016). Therefore, future investigations in other habitats comprising their life cycle (e.g. reproductive sites offshore) are needed to better understand its trophic ecology and functional role in the food web of surf-zone ecosystems.

**Supplementary material.** The supplementary material for this article can be found at https://doi.org/10.1017/S0025315423000711

**Data availability.** Data available at Vieira J. P, Garcia A. M, Lemos V. M (2022). PELD-ELPA Species composition and abundance patterns of fish assemblages at shallow waters of Patos Lagoon estuary. Version 1.11. Sistema de Informação sobre a Biodiversidade Brasileira – SiBBr. Sampling event dataset https://doi.org/10.15468/kci8zb.

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**Author contributions.** A. L. S. A. conceptualized the manuscript, conducted the analyses and figures preparation, and led the manuscript preparation. A. F. S. G. conducted field trips and fish sampling, and contributed to manuscript preparation. E. F. A. helped with preys' identification in the stomach food content analysis and contributed to manuscript preparation. L. A. C. helped with preys' identification in the stomach food content analysis and contributed to manuscript preparation. J. P. V. contributed to project idea, helped with field trips and fish sampling and contributed to manuscript preparation. AMG helped with field trips and fish sampling, contributed with statistical analyses and figure preparation and contributed to manuscript preparation.

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**Competing interest.** None.

**Ethical standards.** Specimens were collected with the authorization of the SISBIO (Biodiversity Information and Authorization System) of the Chico Mendes Institute for Biodiversity Conservation (ICMBIO) under license number 47567-1.

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