Autochthonous Versus Allochthonous Resources in a Tropical Rocky Shore Trophic Web Adjacent to a Marine Riparian Area

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Abstract: Marine riparian areas and coastal vegetation are essential and important to the coastal marine ecosystem, although their interactions and functions are still unknown and ignored in marine ecological studies and integrated management planning. In southeastern Brazil, allochthonous resources derived from riparian Atlantic rainforests bordering rocky shores have been observed in abundance together with the shallow subtidal rocky reef benthos. In this study, we used stable isotopes (δ13C and δ15N) to characterize the main components in a benthic trophic web on a shallow tropical rocky shore, to identify the proportional contributions of allochthonous (marine riparian vegetation—MRV) to autochthonous (phytoplankton and algae) inputs and to test which basal food resources contributed most to the marine community on the Atlantic Forest–rocky coast interface. We found eight major food resources and seventeen consumers that we classified into different groups according to their feeding habits and biology. Although the main source of basal resources in the benthic trophic web in the present study remained autochthonous, the allochthonous resources were assimilated by all consumers. MRV is thus an important resource for some primary consumers and it should be included as a potential source of basal resources in marine ecosystems adjacent to marine riparian areas.

Keywords: coastal marine ecosystem; connectivity; food resources; marine riparian vegetation; stable isotopes; trophic web

1. Introduction

At the border between land and sea, the coastal zone is the region where numerous biological, chemical, physical, geological and meteorological interactions occur and form gradients and where primary production is concentrated [1]. Although terrestrial vegetation, marine phytoplankton and marine macrophytes are parts of distinct environments, they may all represent basal food resources in a coastal marine ecosystem. In some coastal ecosystems, both terrestrially derived (allochthonous) vegetation and autochthonous basal food resources may contribute to the available stock of organic matter. Terrestrial plants have lower energy values and lower protein content (especially dead leaves fallen from the trees) [2,3], while algae have a higher proportion of proteins than plants because they require less fiber for support [4]. Therefore, debris from terrestrial vegetation is less palatable and nutritious to marine species than algae. In mangrove systems, for example, although leaves are much more abundant than other primary resources, their nutritional value is low and they are difficult to digest [5]. Notwithstanding, the bulk of leaves is a significant contribution to the energy budget.
Riparian areas (defined as those bordering water bodies) are highly studied systems as there is a clear linkage between land and stream and freshwater ecosystem functions and wetland ecology [6–10]. In contrast, marine riparian areas, land bordering the sea, have received scant attention [11, 12]. When marine–riparian interactions have been studied, they have mainly focused on marine influences on terrestrial systems, such as marine derived nitrogen enrichment by migrating salmon [13], rather than vice versa. It is known that in certain situations input from terrestrial systems, such as mangroves, saltmarshes, etc., to the adjacent marine area can provide connectivity which enhances invertebrate and vertebrate development in the sea [14–16]. Although marine riparian systems have not been the subject of much scientific investigation, studies suggest that these systems serve similar functions, regardless of their marine or freshwater context [11]. Like shoreline vegetation, marine riparian areas are essential and important to the nearshore marine ecosystem, however their interactions and functions are still largely unknown and are ignored in marine ecological studies and integrated management planning [11, 12, 17]. In addition to social benefits, marine riparian areas provide a variety of ecological functions that integrate the marine ecosystem, such as soil and slope stability, sediment control, wildlife habitat, microclimate formation, water quality improvement, nutrient input and fish prey production and habitat structure and shading provision [11].

Although the nutritional quality and palatability of autochthonous resources, such as marine algae, and allochthonous resources, such as terrestrial vegetation detritus, are recognized, studies on the contribution of marine riparian areas to coastal tropical marine systems are still scarce. Although the Atlantic Forest is the second largest rainforest in South America and an important global biome that is home to 35% of Brazil’s biodiversity, with high levels of endemism, few have previously carried out observations of the availability of allochthonous resources derived from Atlantic marine riparian forests [18–21]. Building upon this, the present study aims to use δ13C and δ15N to characterize the benthic food web in a shallow tropical rocky subtidal coast, estimate the proportional contributions of allochthonous (marine riparian vegetation—MRV) and autochthonous (phytoplankton and algae) food resources to consumers and evaluate which basal food resource contributed the most to the marine community studied at the Atlantic rainforest–coastal interface in Brazil.

2. Materials and Methods

2.1. Study Area

The Ilha Grande Bay (IGB) (22°50′–23°20′ S, 44°00′–44°45′ W) (Figure 1A), located in the south of the state of Rio de Janeiro, Brazil, has a perimeter of approximately 350 km of coastline [22] bordered by the Atlantic rainforest (Figure 1B). This region consists of two bodies of water separated by a constriction between the island and the mainland and is divided into three regions: West Portion, Central Channel and East Portion [23]. The IGB has the largest number of protected areas in the state of Rio de Janeiro [24]. Considered a biodiversity hotspot, IGB has a rich benthic flora and fauna and it is considered a priority area for the conservation of coastal and marine zones [22]. The oceanographic, hydrodynamic and physiographic characteristics of the region and connectivity of coastal ecosystems, input of allochthonous organic matter (Figure 1C,D) and variation of physical and chemical factors are all responsible for its high beta diversity [25] and singular biodiversity [22].

The present study was conducted in Spring 2014 on a rocky shore located in Praia do Abraãozinho (23°08′07″ S, 44°09′05″ W), Ilha Grande, IGB. The shallow wave protected rocky shore, which ends in a sand plain at a depth of ≤7 m, has the Atlantic rainforest as its MRV (Figure 1).
2.2. Field Sampling

The species that had their isotopic compositions analyzed in this study were the most abundant at the study site. The relative abundance of the benthos was estimated by SCUBA diving on the rocky shore at 1–3 m depth; we placed replicate quadrats over the reef and estimated cover (sessile) and density (vagile) species of the benthos in each to calculate mean abundances. We identified and selected the taxa or functional groups with the highest mean percentage cover or density for further studies [26].

The most abundant species of primary producers and macroconsumers were collected in December 2014 for stable isotope analysis of C and N. Three replicate individual/colonies of each species were collected, except for the phytoplankton, zooplankton and the ophiuroid *Ophiothela mirabilis* that, due to their size <1 cm, were collected in greater quantity. For the algae *Padina gymnospora* and the ophiuroid *Ophioderma cinereum*, only two replicates were collected. For a uniform isotopic value and low turnover rates, we used different collection methods that made it possible to collect muscle tissue or calcium carbonate-free samples [27–29]. The encrusting benthic species were removed with the help of hammer and chisel (corals and bryozoans), scissors (sponges and algae) and spatula (ascidians and anemones). Planktonic organisms were collected with nylon plankton nets (25 µm to collect phytoplankton and 68 µm to collect zooplankton). The sediment samples were collected with the aid of a pot and spatula. Leaf litter from the fallen MRV was also collected underwater near the base of the rocky shore. All samples were identified at species level, except for phytoplankton and zooplankton. All samples were frozen immediately after collection and taken to be sorted and prepared in the laboratory.
2.3. Sample Processing for Isotope Analysis

After defrosting the samples, whole collected macroconsumers were screened again to remove the muscle tissue (sea urchins, sea cucumbers, crustaceans and gastropods), the corals had their tissue scraped off, while very small animals, such as ophiuroids, were kept whole and grouped to compose a sample. Sponges, ascidians and anemones had their soft tissue selected. We removed any epiphytes or epizoal of the sampled animals and macroalgae. Sediment samples were filtered with 0.7 \( \mu \text{m} \) GF/F filters (Whatman, Maidstone, Kent, UK). All samples were washed with distilled water so that any contaminants that could influence the isotopic compositions were removed. The samples were oven dried for 48 h at 60 °C. After drying, they were macerated and reduced to a fine powder. We acidified the phytoplankton and zooplankton, the calcified macroalgae \textit{Jania adhaerens} and the ophiuroid \textit{O. cinereum} before carbon isotopic analysis to remove carbonate \[29\]. To remove \( \text{CaCO}_3 \) through acidification, 1 mol L\(^{-1}\) of hydrochloric acid (HCl) was added drop by drop using a pipette, until no more \( \text{CO}_2 \) was released. The carbonate radical in the presence of the \( \text{H}^+ \) ion becomes unstable and decomposes, generating \( \text{CO}_2 \), since this structure is more stable, producing the effervescence reaction when the carbonates are attacked by acids. The samples were then inserted in tin capsules, weighed on a digital balance and analyzed for their isotopic compositions of carbon and nitrogen at the Centro de Energia Nuclear na Agricultura da Escola Superior de Agricultura Luiz de Queiroz, São Paulo University, Brazil (CENA-USP).

Stable isotope analyses were performed using a Delta Plus Continuous Flow Isotope Ratio Mass Spectrometer (CF-IRMS, Finnigan MAT, Bremen, Germany) coupled to an elemental analyzer (CE Instruments Wigan, UK). The isotopic composition is expressed in terms of a delta value (\( \delta \)) in parts per thousand (‰ or ppt) and is obtained according to the formula: \( \delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \cdot 10^3 \), where \( X \) is \( ^{13}\text{C} \) or \( ^{15}\text{N} \) and \( R \) the ratio \( ^{13}\text{C} : ^{12}\text{C} \) or \( ^{15}\text{N} : ^{14}\text{N} \). The standard material for carbon was the Pee Dee Belamite limestone (PDB) and the standard material for nitrogen was atmospheric air \[30\]. The deviation standard of isotopic measurements was estimated at 0.09 for \( \delta^{13}\text{C} \) and 0.21 for \( \delta^{15}\text{N} \) by means of repeated measurements of the internal pattern (sugarcane).

2.4. Group Assignment and Data Analyses

Trophic groups were separated according to their possible food resources \[30–32\] (Table 1). Consumers were separated into guilds according to information about their diet, so resources that are not part of consumption were excluded from the analysis (i.e., we excluded resources that are not autotrophic from the analysis of herbivores). To carry out the separation of consumers into trophic groups, we searched for bibliographical references regarding known feeding habits and diet (Table 1). Using the \( \delta^{13}\text{C} \) and \( \delta^{15}\text{N} \) values of producer and consumer species, the contribution of autochthonous and allochthonous food resources to the consumer’s diet were estimated. Assimilations were also estimated by grouping consumers into trophic groups. For mixing model, the simmr package \[33\] in the R Program \[34\] was used. The simmr package is designed to infer dietary proportions of organisms consuming various food sources from observations on the stable isotope values taken from the organisms’ tissue samples. The analysis is based on a model that provides a combination of possible solutions that can explain consumer value, incorporating the variability of isotopic values of resources, consumer and fractionation. We assumed the isotopic fractionation of +0.5 ± 0.13‰ for \( \delta^{13}\text{C} \) and +2.3 ± 0.18‰ for \( \delta^{15}\text{N} \) for all animals \[35\]. We used concentration-dependent models because elemental carbon and nitrogen concentrations varied substantially between food sources \[36\]. The Brooks–Gelman–Rubin convergence diagnostic provides a numerical convergence summary based on multiple chains (Gelman diagnostic). The Gelman diagnostic values were all close to 1, ensuring satisfactory convergence of the mixing model results (Figures S1 and S2) \[33\].
Table 1. Trophic groups analyzed in the present study separated according to their possible food resources.

<table>
<thead>
<tr>
<th>Taxonomic Group/Species</th>
<th>Comments about Food/Feeding</th>
<th>Resource Potentially Consumed</th>
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<tbody>
<tr>
<td><strong>Suspension Feeders:</strong></td>
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<td>Porifera:</td>
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<td>Desmapsamma anchorata (Carter, 1882)</td>
<td>Occurs via collared cells (choanocytes), which use flagella to move the water to the cell surface, efficiently retaining particles such as phytoplankton, bacterioplankton, heterotrophic eukaryotes, debris and dissolved materials [37,38].</td>
<td>Phytoplankton, zooplankton, particulate MRV, particulate algae, and particulate calcareous algae J. adhaerens.</td>
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<td>Amphimedon viridis Duchassaing &amp; Michelotti, 1864</td>
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<tr>
<td>Mycale (Zygomycale) angulosa (Duchassaing &amp; Michelotti, 1864)</td>
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<td>Cnidaria:</td>
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<tr>
<td>Tubastrea coccinea Lesson, 1830</td>
<td>Feeds on suspended material including phytoplankton, zooplankton, able to filter up to 173 L of water through the body in 24 h [39]. Have the most diverse feeding strategies and may be opportunistic omnivores, suspension feeders, detritivores, deposit feeders or scavengers [40]. Uses a range of benthic invertebrates as hosts, so can keep off the bottom substrate [41]; these relationships suggest it is a suspension feeder [42].</td>
<td>Phytoplankton, zooplankton, particulate MRV, particulate algae, and particulate calcareous algae J. adhaerens.</td>
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<td>Tubastrea tagusensis Wells, 1982</td>
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<td>Chordata:</td>
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<td>Phallusia nigra Savigny, 1816</td>
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<td><strong>Echinoderma:</strong></td>
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<tr>
<td>Ophiothela mirabilis Verrill, 1867</td>
<td>Has both autotrophic and heterotrophic feeding, hosting zooxanthellae, symbiotic dinoflagellates, in its gastrodermal tissues that provide nutrition through photosynthetic products; it is also a suspension feeder on phytoplankton, zooplankton and particulate organic material, although the contributions of each resource are unknown [43].</td>
<td>Phytoplankton, zooplankton, particulate MRV, particulate algae, and particulate calcareous algae J. adhaerens.</td>
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<td>Echinometra lucunter (Linnaeus, 1758)</td>
<td>Sea urchins are herbivores well known to control algae populations [45].</td>
<td>MRV, macroalgae and calcareous algae J. adhaerens.</td>
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<td>Paracentrotus gaimardi (Blainville, 1825)</td>
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<td>Lytechinus variegatus (Lamarck, 1816)</td>
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<td>Mollusca:</td>
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<td><strong>Mixotrophs:</strong></td>
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<td>Cnidaria:</td>
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<tr>
<td>Palythoa caribaeorum Duchassaing &amp; Michelotti, 1860</td>
<td>Feed on fragmented particulate organic matter from the substratum. These holothurians are known to move sediment and feed on microorganisms associated with organic and inorganic material [44].</td>
<td>Sedimentary organic matter, particulate MRV, particulate algae, and particulate calcareous algae J. adhaerens.</td>
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<td><strong>Deposit Feeders:</strong></td>
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<td>Echinodermata:</td>
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<td>Isostichopus badionotus Selenka, 1867</td>
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<td>Holothuria (Halodeima) grisea Selenka, 1867</td>
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<td><strong>Herbivores:</strong></td>
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<td>Echinodermata:</td>
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<td>Mollusca:</td>
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<tr>
<td>Littorina Féussac, 1822</td>
<td>Herbivorous snails [46].</td>
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<td>Omnivore Group I:</td>
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<td>Cnidaria:</td>
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<td>Bunodosoma caissarum Corrêa in Beûm, 1987</td>
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<td><strong>Omnivore Group II:</strong></td>
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<td>Echinodermata:</td>
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<tr>
<td>Ophioderma cinereum Müller &amp; Troschel, 1842</td>
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<tr>
<td>Arthropoda:</td>
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<tr>
<td>Mithrax hispidus (Herbst, 1790 [in Herbst, 1782–1790])</td>
<td>O. cinereum is an omnivorous opportunist that scavenges on carrion, preys on organisms slow enough and small enough to capture, as well as browses on plant debris [40,49]. This crab has an omnivorous diet consisting mainly of algae consumed directly on the substrate, as well as small gastropods, crustaceans, amphipods [50].</td>
<td>Algae, calcareous algae J. adhaerens, MRV, gastropod Littorina sp.</td>
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<td><strong>Omnivore Group III:</strong></td>
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We used the mean percentage contribution of autochthonous and allochthonous material for each taxon by trophic group to explore the consumption relationships of each group, compared the dietary proportions between MRV and each other food resources and estimated a direct probability that the MRV dietary proportion was larger than that of the other food resources. Three species of macroalgae, P. gymnospora, Cladophora sp.
and H. musciformis, were grouped as macroalgae due to the similarity of their isotopic values; however, the calcareous macroalgae J. adhaerens was represented as a separate resource with regard to its isotopic value. Phytoplankton and zooplankton were both combined into what we termed plankton due to overlapping values [31]. Plankton was used for the mixing model of all groups that use both resources. We ran two mixing models for the sea anemone Bunodosoma caissarum, one including the herbivorous gastropod Littorina sp. and the crustacean M. hispidus as two independent food resources and another with both resources combined to reduce the number of resources in the anemone mixing model (“Bunodosoma caissarum model 2”).

3. Results

We identified seven major food resources, among them the MRV, marine sedimentary organic matter, phytoplankton, macroalgae and zooplankton. We also identified seventeen major consumers in the food web, among seven suspension feeders, one mixotroph, two deposit feeders, four herbivores and three omnivores (Tables 1 and S1). MRV, which represents the allochthonous basal food resource, had the lowest isotopic value of $\delta^{13}$C (mean = −30.0; SD = ± 0.6; n = 3) and had a different signature than autochthonous marine resources, which allowed us to differentiate sources in the consumers. The calcareous algae J. adhaerens presented carbon isotopic values (−8.0; ± 0.4; n = 3) that were different from other algae, so it separated from the main algae group (t-test for J. adhaerens and P. gymnospora: \( t = -18.009, \text{df} = 1.601, p = 0.008;\) J. adhaerens and Cladophora sp.: \( t = -37.391, \text{df} = 3.936, p < 0.0001;\) J. adhaerens and H. musciformis: \( t = -27.674, \text{df} = 3.981, p < 0.0001\)). Overall, other marine resources showed similar $\delta^{13}$C values, including marine sedimentary organic matter (Figure 2 and Table S1). Food resources had the lowest average $\delta^{15}$N values (P. gymnospora: 4.5, ± 1.9, n = 3; Cladophora sp.: 6.7, ± 0.6, n = 3; H. musciformis: 6.4, ± 0.3, n = 3; J. adhaerens: 7.4, ± 0.3, n = 3), with the exception of phytoplankton and zooplankton (phytoplankton: 9.8 ± 1.9, n = 2; zooplankton: 8.5 ± 2.0, n = 2), and the lowest values were of MRV (terrestrial vegetation: 1.0 ± 0.5, n = 3). The herbivorous gastropod Littorina sp. and the omnivorous crustacean M. hispidus showed heterogeneous isotopic values, especially for the $\delta^{15}$N, consistent with the higher trophic level occupied by this crustacean in relation to the gastropod (Figure 2 and Table S1).

Figure 2. Isotopic coordinates of $\delta^{15}$N and $\delta^{13}$C of sources and consumers from a tropical rocky shore at Ilha Grande Bay, Brazil. For resources, bars indicate SD around the mean. Each consumer has a color corresponding to the trophic group: orange—suspension feeder; purple—mixotroph; gray—deposit feeder; green—herbivores; pink—omnivores I; blue—omnivores II. Taxa code: MRV—marine riparian vegetation; SOM—marine sedimentary organic matter. For more details on trophic groups, see Tables 1 and S1.
The solitary ascidian *P. nigra* had the lowest $\delta^{15}$N mean value ($6.8 \pm 0.9$, $n = 3$), followed by the ophiuroid *O. mirabilis* ($8.4 \pm 1.0$, $n = 3$) and the sponge *M. angulosa* ($10.6 \pm 0.2$, $n = 3$). The highest $\delta^{15}$N mean value was of the sponge *A. viridis* ($11.3 \pm 0.4$, $n = 3$) (Table S1). Of all the resources, plankton was the most assimilated by the suspension feeders, marine sponges *D. anchorata, A. viridis* and *M. angulosa* and ascidia *P. nigra*. The calcareous algae *J. adhaerens* was the resource most assimilated by *Tubastrea* corals and by the ophiuroid *O. mirabilis*. MRV was assimilated by all consumers and the ascidian *P. nigra* was the suspension feeder that most assimilated MRV, its second most assimilated resource, the first being plankton. The suspension feeders that had the lowest average MRV assimilation were the corals *Tubastrea* (Figure 3 and Table S2). The resource most assimilated by mixotroph *P. caribaeorum* was the calcareous algae *J. adhaerens*, followed by plankton and algae. MRV was the least assimilated resource (Figure 4 and Table S2).

![Figure 3](image-url)
Figure 4. Assimilation web of mixotroph *Palythoa caribaeorum* estimated by mixing model of C and N stable isotopes from a tropical rocky shore at Abraãozinho, Ilha Grande Bay, Brazil. Taxa code: MRV = marine riparian vegetation.

The assimilation of different resources was similar for consumers of the deposit feeding group, where the most assimilated resource was calcareous algae *J. adhaerens*, followed by sedimentary organic matter. MRV was the least assimilated resource (Figure 5 and Table S2). In the herbivore group, the least assimilated resource for sea urchins was MRV. They had the highest assimilation of the calcareous algae *J. adhaerens*, followed by algae, while for the gastropod *Littorina* sp., the most assimilated resource was algae (Figure 6 and Table S2). The average δ¹⁵N value of *B. caissarum* (omnivore group I) was greater than all potential resources, except for the crustacean *M. hispidus* (Figure 7 and Table S2). Even when combining the potential resources of gastropod *Littorina* sp. and crustacean *M. hispidus* to the mixing model of the *B. caissarum*, the percentages of assimilation remained similar to the mixing model with these two potential resources separated. Plankton was the resource most assimilated by the omnivore group I. The average assimilation of MRV and algae were higher than that of *J. adhaerens*, which were the least assimilated resources (Figure 7 and Table S2). Consumers in omnivore group II had a very similar proportional resource assimilation. The most assimilated resource in this group was the calcareous algae *J. adhaerens*. MRV was the least assimilated resource. For the crab, the gastropod *Littorina* sp. was the second most assimilated resource, and for the brittle star, algae was second most consumed resource, followed by the gastropod (Figure 8 and Table S2). The results of the mixing model by trophic groups (Table S3) showed that the average MRV assimilation varied from 4–8% for suspension feeders, deposit feeders, mixotrophs, omnivores II and herbivores to 11% for herbivores and for omnivores I. The mean MRV assimilation by trophic groups obtained from the mixing models by species varied from 7–10% for suspension feeders, mixotrophs and deposit feeders to 11–12% for herbivores and omnivores (Table S2).
Figure 5. Assimilation web of deposit feeder species estimated by mixing model of C and N stable isotopes from a tropical rocky shore at Abraãozinho, Ilha Grande Bay, Brazil. Taxa code: MRV = marine riparian vegetation; SOM = marine sedimentary organic matter.

Figure 6. Assimilation web of herbivorous species estimated by mixing model of C and N stable isotopes from a tropical rocky shore at Abraãozinho, Ilha Grande Bay, Brazil. Taxa code: MRV = marine riparian vegetation.
Figure 7. Assimilation web of the omnivore *Bunodosoma caissarum* estimated by mixing model of C and N stable isotopes from a tropical rocky shore at Abraãozinho, Ilha Grande Bay, Brazil. Taxa code: MRV = marine riparian vegetation.

Figure 8. Assimilation web of omnivores group II estimated by mixing model of C and N stable isotopes from a tropical rocky shore at Abraãozinho, Ilha Grande Bay, Brazil. Taxa code: MRV = marine riparian vegetation.
4. Discussion

This study provides novel insights into the organization and trophic structure of food webs on tropical rocky shores, the identification and relative importance of different basal resources, the contribution of marine riparian vegetation in marine systems at the land–sea interface and trophic niche organization within such communities. All the resources and consumers considered in the present study are quite abundant along the studied tropical rocky shores, which justifies the consideration of each one as a potential food resource [22].

MRV, which represents allochthonous resource, had a lower isotopic value of $\delta^{13}C$ than marine resources. We confirmed the lowest values of $\delta^{13}C$ in MRV, similar to results found in other studies, including $\delta^{13}C$ values from Atlantic rainforest tree leaves [52–56]. The entry of terrestrial organic matter has important consequences for the dynamics of benthic coastal communities [57–59]. Depending on its origin, organic matter which may be imported from the terrestrial environment or locally produced by primary producers differs substantially in its biochemical composition and availability to consumers. The exchange of organic matter across ecosystem boundaries has important consequences for the availability of matter and energy, as it contributes to sediment deposition and mineralization and serves as food for the fauna [60]. In contrast to MRV, algae commonly present the highest $\delta^{13}C$ values among primary producers [52,53].

As major primary producers on rocky reefs, we expected macroalgae (here those other than Jania adhaerens, which is treated below) to be highly assimilated by some consumers, especially due to the palatability, nutritional value and abundance that make macroalgae an important and highly available resource. For example, in flat and shallow rocky reefs in temperate regions, benthic macrophytes such as kelps may dominate organic matter input [61–63]. In fact, macroalgae matter was assimilated to some extent by most consumers but higher assimilation proportions were only found in the herbivorous gastropod Littorina sp. (see below) and the sea urchin Echinometra lucunter. This fact might explain why macroalgae were assimilated in greater proportion by E. lucunter than in the other sea urchins. This species is a rock-borer, often inhabiting burrows scraped with its spines and teeth on rocky substrata [64], which limits its range [65]. It thus depends mainly on a supply of a wide range of larger drifting fragments of algae that are caught up in the holes on the incoming tide or actively caught [66,67].

The present study suggests that although MRV is not the main source of energy for consumers under the waves, it can be consumed to some extent by animals, albeit in different proportions. The results (mean and dispersion) of the mixing model by trophic groups were similar to those of the mixing models by species. The latter was more informative for explaining the differences in assimilation between species of the same trophic group. The primary marine sources of organic matter are phytoplankton, macroalgae and marine magnoliophytes, the first being the dominant resource in oceanic regions. Organic matter in the sea can also be of terrestrial origin, transported to the sea by continental drainage or wind [68]. The southeastern coast of Brazil is characterized by its proximity to the Atlantic rainforest, which contributes debris from terrestrial vegetation to the nearshore coastal ecosystem, especially during the rainy season [69]. In fact, Atlantic rainforest MRV has been estimated to have a mean litterfall of 20–125 g dry weight m$^{-2}$ month$^{-1}$ [70], the upper limit being similar for mangroves in the region [71]. On the studied rocky reefs, large particles of MRV (leaves, twigs, fruits, flowers and their fragments) mainly accumulate (or are most visible) on the bottom nearby the interface with the sandy plain. This material is thus available for mobile herbivores/detritivores, and as it decomposes into smaller fragments, it may also become re-suspended in the water column as particulate organic matter [72]. The large solitary ascidian P. nigra and the gastropod Littorina sp., even though they are part of different trophic guilds, had higher average assimilation of MRV than assimilation of the other resources. Ascidians are suspension feeding organisms while Littorina sp. is a predominantly herbivorous gastropod. However, littorinid snails are known to also consume both angiosperm detritus and the fungi colonizing dead plants, making refractory angiosperm material available as feces to other organisms [73] as well as browsing directly on the surface of rock, inadvertently ingesting detritus [74]. Algae have a
higher proportion of protein than plants [4] and although they were a clearly important resource for *Littorina* sp., in our study, MRV still made up one quarter of their assimilation despite the low nutritional quality and palatability.

Suspension feeders have morphological structures capable of capturing suspended particles as a potential source of food, either items large enough to be seized individually or smaller particles obtained in sufficient quantity through filter feeding [69,75]. Four of the seven suspension feeders, the ascidian and all the sponges had plankton as their main assimilated resource. Plankton was also the main resource for the anemone *B. caissarum*. The second resource most assimilated by the suspension feeders was the articulated calcareous algae *J. adhaerens*.

*Jania adhaerens* was a major and key resource for all three herbivorous sea urchins, the suspension feeding corals *Tubastrea* and brittle star *O. mirabilis*, the mixotrophic *P. caribaeorum*, the deposit feeding sea cucumbers, the omnivorous crab *M. hispidus* and brittle star *O. cinereum*. *J. adhaerens* is a major component of the intertidal to shallow subtidal benthos of the region [76,77] and it is an important component of the algal turf. Algal turfs are a typically low algae layer, several mm to cm high [78], which are a highly productive algal group in the tropics [79,80]. These turfs are ubiquitous on rocky reefs and shores throughout the region [76] and known to cover 29–65% of the shallow subtidal benthos in IGB [81,82]. This species has also been reported as one of the main foods consumed by herbivorous sea urchins [83], as was the case here for the three studied sea urchins. As well as the sea urchins, other vagile invertebrates such as Mithracidae crabs are known to be adapted to consume a wide variety of algae, including calcareous species that commonly co-occur in these habitats [50,84]. In the case of Mithracidae, some species of these crabs are cleaners of fouling algae from hosts to which they associate to escape predation. In the case of mixotrophic *P. caribaeorum* and the other suspension feeders, it is known that epithelial cells of the coralline red algae in general and *J. adhaerens* specifically constantly become senescent, are shed and replaced [85], a mechanism that promotes better nutrient uptake and epiphyte avoidance. This, together with breakage due to wave action, are probably major mechanisms that are responsible for making a supply of ≥ single-cell-sized particles of *J. adherens* available as particulate material in the water column and accessible to suspension feeders.

In isotopic space, as shown in Figure 2, the δ13C values of the sedimentary organic matter were central when compared to the range which the other resources presented (from *Jania adhaerens* to MRV), which may suggest a contribution from multiple sources for the organic matter in the sediment. Marine sediment is usually partially composed of marine derived organic matter but may include terrestrially derived organic matter as well. Terrestrially derived organic matter is higher in marine sediments near the coast, and even seabed sediments deposited in areas remote of the continents may also contain a mixture of organic matter derived from marine and terrestrial processes [86]. It is interesting to note that despite this the deposit feeding sea cucumbers, which inhabit the base of the reef at the sand–rock interface and consume large amounts of sedimentary organic matter, predominately derived their resources from *Jania adhaerens*, which is a highly abundant part of the turf community [22].

Considering that the omnivorous sea anemone *B. caissarum* can consume invertebrates, we considered six potential resources [47]. However, other omnivores such as the crab *M. hispidus* had a higher δ15N value than *B. caissarum*, which indicates that this resource is being consumed in a low proportion. An animal’s 15N:14N ratio is more enriched by 15N than by its food resource, since nitrogen compounds with 14N are excreted more quickly than those with 15N [87]. We determined that plankton was the major resource most assimilated by *B. caissarum* but it is important to highlight that for this species the MRV and macroalage also had higher average assimilation than autochthonous resources such as *J. adhaerens*.

The mixotroph (the mat forming zoantharian *P. caribaeorum*) obtained higher proportions of resources from the three autochthonous resources than the allochthonous one.
This species is also ubiquitous on rocky reefs and shores throughout the region [88] and is known to cover 26–47% of the shallow subtidal benthos in IGB [82,83]. However, as a zooxanthellate organism, it is unclear how much of its energy is obtained from autotrophy rather than heterotrophy through the feeding on suspended material. Certainly, in corals, some of the products of photosynthesis are transferred to the animal host and in some cases, these can provide the majority of the host’s carbon requirements (60–70% for reef corals [89,90]). However, in a comparative study, Sebens (1977) [91] noted that *P. caribaeorum* had more food items than other zoantharians and so the contribution of heterotrophy in *P. caribaeorum* might be somewhat higher.

We estimate that the contribution from the marine riparian vegetation bordering the tropical rocky shore we studied was pervasive, species specific and part of the resources assimilated by benthic consumers. However, this study represents a single observation and was not replicated spatially and temporally, as it was only carried out in the summer season, which hinders the ability to infer seasonal relationships in general. We would recommend further studies of this type be carried out to better examine the generality of our results over space and in systems with other benthic species and community structures. Other coastal ecosystems such as mangroves, estuaries and sandy beaches also receive debris from bordering terrestrial vegetation. Our results corroborate that the contribution of autochthonous resources seems to be the main source in coastal zones [54,92], mangroves [53,93–96], estuaries [52,97] and sandy beaches [20], even though consumers depend on more than one source [54,98]. Most marine riparian areas still lack studies that show the contribution of their vegetation to the marine environment. It should also be considered that multiple resources (the number of sources greater than the number of isotopic types + 1) can influence the robustness of the assimilation results, since all solutions of the assimilated proportion are viable, the contributions of the most commonly used source are underestimated, while the contributions of less used sources are overestimated [31]. We emphasize therefore that the minimum and maximum MRV contributions for consumers were interpreted here, and the variation in the percentage contribution of each resource was reported with the credibility intervals.

In summary, this study provided new information on the trophic organization of the main components of the benthos along the riparian area including coastal vegetation, which are integral and important parts of the coastal marine ecosystem. The results indicate that among the autochthonous resources, algal turfs appear to be the more important basal resource but are not the only components that are part of the basal resources in the benthic food web. Allochthonous resources such as marine riparian vegetation (MRV) were assimilated by all consumers, were an important resource for some primary consumers and should be considered as a potential source of basal resources in other marine ecosystems adjacent to marine riparian areas. Furthermore, we suggest more research should be focused on the marine riparian–shore interface, including the composition of the bottom nearby the interface with the sandy plain and the MOP, as better knowledge will have implications for coastal management, our understanding of nutrient sources and coastal food chain structure.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15060725/s1, Table S1: Mean values and standard deviation (SD) of isotopic carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) ratios of food resources and consumers on a tropical rocky reef adjacent a marine riparian area at Ilha Grande Bay, Brazil; Table S2. Mean of assimilation (%) of each resource per taxon on a shallow tropical rocky shore at Ilha Grande Bay, Brazil; Table S3. Mean of assimilation (%) of each resource per trophic group on a shallow tropical rocky shore at Ilha Grande Bay, Brazil. Figure S1: Diagnostic plots from the R simmr mixing model package with the result of the model fit for each species. Figure S2: Diagnostic plots from the R simmr mixing model package with the result of the model fit for each trophic group.

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References
16. Taylor, M.D.; Gaston, T.F.; Raoult, V. The economic value of fisheries harvest supported by saltmarsh and mangrove productivity in two Australian estuaries. Ecol. Indic. 2018, 84, 701–709. [CrossRef]


33. Parnell, A. *Simmr: A Stable Isotope Mixing Model*; R Package Version 0.4.1; R Foundation for Statistical Computing: Vienna, Austria, 2019; Available online: https://CRAN.R-project.org/package=simmr (accessed on 6 March 2023).


85. Pueschel, C.M.; Judson, B.L.; Wegeberg, S. Decalcification during epibathial cell turnover in *Jania adhaerens* (Corallinales, Rhodophyta). *Phycologia* 2005, 44, 156–162. [CrossRef]
88. Mantelatto, M.C.; Oliveira, A.E.S.; Menegola, C.; Casares, F.A.; Creed, J.C. Depth and grazing intensity are the main drivers of subtidal hardground benthic community structure on tropical south Atlantic reefs. *Mar. Ecol. 2020*, 00, e12586. [CrossRef]