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Brief Communication

Feeding preference of the sea hares *Aplysia brasiliana* and *A. juliana* from Brazilian littoral: Different trophic specialization

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ABSTRACT

Feeding preference of benthic marine herbivores provides insight into the ecology of the consumers, but also unveiling their trophic relationships and their presumable impact on seaweeds. We present evidence of feeding preferences in the sea hares *Aplysia brasiliana* and *A. juliana*, collected from two distinct locations on the Brazilian coast, based on experiments conducted under experimental laboratory conditions. *Aplysia brasiliana* from Forno Beach primarily consumed *Laurencia dendroidea*, a red seaweed known for its chemical defenses against herbivory, whereas individuals of *A. juliana* from Boa Viagem predominantly fed on palatable green seaweed *Ulva fasciata*. These results suggest that *A. brasiliana* has evolved a dietary counteradaptation to chemically defended seaweeds, while *A. juliana* displays a more generalized feeding preference for palatable seaweeds usually consumed by several marine herbivores.

KEYWORDS: SEAWEED SUSCEPTIBILITY, DIETARY PREFERENCES, FEEDING HABIT, HERBIVORE PREFERENCE

Herbivore feeding preference, or food choice, is a trophic interaction known to strongly influence the distribution and diversity of seaweeds (Lubchenco, 1978). Herbivore responses to dietary changes and shifts in feeding preferences can influence the functional organization of marine communities (Aguilera, 2011). Therefore, understanding the factors that influence herbivore feeding preferences is crucial for predicting their impact on seaweed communities and for understanding the establishment and evolution of plant-herbivore interactions (Poore & Hill, 2006). For example, experiments on herbivore seaweed selection have linked feeding preferences either to environmental conditions (Simoncini & Miller, 2007) or to specific characteristics of individual seaweed species (e.g. Souza et al., 2008).

Sea hares have long served as valuable and well-studied organisms for investigating feeding preferences (e.g., Carefoot, 1967, 1970). Numerous subsequent studies on feeding choice have examined the relative importance of different to seaweed-related aspects, including food abundance (Rogers et al., 1995), biotic interactions (Rogers et al., 2000), nutritional contents (Carefoot, 1970), morphologies (Pennings & Paul, 1992), and the presence of secondary metabolites (Nagle et al., 1998). Despite these effeorts, findings remain inconsistent - likely due to methodological differences and the use of various species from geographic distinct locations.

Sea hares are known for their broad and varied feeding habit, ranging from some specialized species (Paul & Pennings, 1991), while others exhibiting more generalized feeding behaviors (Pennings & Paul, 1992). For example, *Aplysia juliana* feeds on and inhabits the locally abundant green seaweed *Ulva lactuca*. In contrast, *Aplysia parvula* utilizes two chemically rich seaweed species (*Laurencia obtusa* and *Delisea pulchra*) that are less abundant in their environment (Rogers et al., 1995). Similarly, *Aplysia californica* also preferentially feeds on chemically rich red seaweed species, such as *Laurencia* and *Plocamium* (Pennings, 1990a).

Aplysiid species can also exhibit intermediate feeding habit, favoring a limited group of seaweeds but capable of consuming a more varied diet when alternative options are scarc (Carefoot, 1987). For example, the generalist sea hare *Dolabella auricularia* appears relatively unaffected by secondary metabolites present in host seaweeds (Pennings & Paul, 1992), whereas chemicals from the cyanobacterium *Lyngbya majuscula* deter feeding by another sea hare, *Stylocheilus striatus* (Nagle et al., 1998). The nutritional value of seaweeds has been considered important aspect in determining feeding prefrences (Carefoot, 1970), though some studies have found it less influential (e.g., Rogers et al., 1995). Additionally, the low preference of *D. auricularia* correlate negatively with seaweed toughness and calcification (Pennings & Paul, 1992). Regarding the biotic interactions, the abundance of *A. parvula* increases only in the absence of its predator, the pycnogonid *Anaplodactylus evansi* (Rogers et al., 2000).

The sea hare *Aplysia brasiliana* is distributed from western Mexico to Paita, Peru, in the western Pacific, and from Florida to Brazil in the western Atlantic (Nozéres & Kennedy, 2025; Saada et al. 2014). On the other hand, *Aplysia juliana* is a circumtropical species exhibiting the broadest distribution range among sea hares, occurring in all major warm ocean basins worldwide (Uribe et al., 2013). Due to its wide range and feeding habits, *A. juliana* serve as an optimal biological model for studying feeding behavior (Parpagnoh & Fiore, 1994).

In this study, we experimentally evaluated the feeding preferences of sublittoral specimens of *A. brasiliana* and *A. juliana* collected from two subtropical rocky shores contrasting environmental conditions. A total of 13 specimens of *A. brasiliana* (10-11 cm) were collected from a sheltered area at Forno Beach (Búzios, RJ, 22º 46 S; 41º 53 W), and 13 individuals of *A. juliana* (12-13 cm) were collected from Boa Viagem Beach, also a sheltered area in Guanabara Bay (Niterói, 22° 53 S; 43º 07 W), during winter period (August-September 2008). Species identification was confirmed by Dr. Carlo Magenta Cunha, and specimens were ddeposited in the the Zoology Museum at the University of São Paulo under catalog numbers MZUSP 89681 and MZUSP 89679, respectively. Living specimens were maintained in a 100 L recirculating laboratory aquarium at constant temperature (20ºC), salinity (35), and aeration throughout during a three-day acclimation period, during which *Ulva* was provided as food for 15 days.

Five seaweed species from three different phyla were used in feeding-choice experiments involving the two *Aplysia* species: two Rhodophyta (*Laurencia dendroidea* and *Osmundaria obtusiloba*), two Hetrokontophyta (*Dictyota* sp. and *Sargassum* sp.) and one Chlorophyta species (*Ulva fasciata*). Specimens of *Sargassum* sp., *U. fasciata*, and *O. obtusiloba* were collected at Praia Rasa (23º 01 S; 22º 44 W), while *Dictyota* sp. and *L. dendroidea* at Forno Beach; both places are located in Búzios, Rio de Janeiro state. Among these seaweeds, *L. dendroidea* and *Dictyota* sp. are known to produce secondary metabolites - sesquiterpenes and diterpene dictyol-types, respectively – that can inhibit a variey of consumers (Pereira & Da Gama, 2008). *Sargassum* sp. and *O. obtusiloba* possess tough, leathery, and branched thalli, making them less preferred by marine consumers such as sea-urchins, whereas *U. fasciata* is generally more palatable and frequently consumed by various marine herbivores (Souza et al. 2008). Before the assays, seaweeds were maintained under laboratory conditions in 100 L aquaria at 22 ± 2ºC, salinity 32 ± 1%, and irradiance 60-80 μmol photons/m^{-2}.s^{-1}, provided by cool-white fluorescent lamps on a 14:10 h light:dark cycle, without aeration.

Multiple-choice experiments were conducted to evaluate the feeding preference of *A. brasiliana* (over 30h) and *A. juliana* (over 12h), in which the five seaweed species mentioned above were offered simultaneously to specimens of these sea hares. In each experimental aquarium, one pre- weighed specimen of each seaweed (*L. dendroidea*, *O. obtusiloba*, *Dictyota* sp., *Sargassum* sp. and *U. fasciata*) was presented together with one individual of *A. brasiliana* (n= 13 replicates) or *A. juliana* (n= 13 replicates). Detailed wet weights of the seaweeds are provided in Tables S1 and S2 (Supplementary Material). Seaweeds were offered in comparable volumes to the sea hares, though biomass varied due to differences in volume-to-biomass ratios among seaweed species. This approach ensured that similar volumes of each seaweed were equally detectable by both *A. brasiliana* and *A. juliana*. The multiple-choice setup more realistically simulates natural conditions than two-choice tests, as multiple seaweed species are often available to these herbivores in the marine environments. In addition, using living seaweeds allowed simultaneous evaluation of both morphological and chemical characteristics of the seaweed species on the feeding preference of *Aplysia* species.

Simultaneously, control aquaria (also n= 13 replicates) were maintained without herbivores, containing previously weighed specimens of each seaweed species, as described above in the bioassays with the *Aplysia* species (see Table S3, Supplementary Material). These control seaweeds were maintained under the same experimental conditions as the treatment aquaria (with *Aplysia* specimens) to measurement for background biomass changes due to autogenic factors (see Peterson & Renaud, 1989). Initial and final wet weights of all seaweed specimens were recorded in both treatment (with herbivores) and control (without herbivores) setups. Prior to weighing, with excess water was removed by spinning each seaweed specimen in a salad spinner for 10 seconds. Seaweed biomass consumption by *A. brasiliana* and *A. juliana* was calculated using the equation: $[(H_o \times C_f/C_o)-H_f]$, following Cronin & Hay (1996), where H_o and H_f represent initial and final wet weights of the seaweed exposed to herbivory, and C_o and C_f represent the initial and final wet weights of the corresponding control samples. This method incorporates autogenic changes into the consumption estimate. In addition, changes in wet mass of each seaweed species in the presence of sea hares were statiscally tested against control using *t* test to further account for autogenic changes.

To assess the effect of sea hares on wet mass variation of consumed seaweeds, we fitted generalized linear models (glm(consumption ~ taxa). Model validity was assessed through likelihood ratio tests and visual inspection of residuals. Differences between means were evaluated using analysis of deviance tables, followed by Dunnet *post-hoc* pairwise tests to compare each treatment against a control. All data analysis and graphic visualizations were performed in the R environment using RStudio (Rstudio, 2023).

After the end of the experiment, *A. juliana* signifcantly reduced the biomass of *U. fasciata* through consumption (GLM: Deviance = 123.6, Residual deviance = 99.5, P < 0.0001; Figure 1, upper panel), as confirmed by a significant difference in wet mass variation between herbivory and autogenic control (p < 0.0001, *t* test; Figure 1, lower panel). Contrastingly, only *L. dendroidea* was significantly consumed by *A. brasiliana* (GLM: Deviance = 11.8, Residual deviance = 40.7, P < 0.001; Figure 1, upper panel), which was supported by a significant difference from the control condition (p < 0.0001, *t* test; Figure 1, lower panel). These results, consistent across both the consumption equation and comparisons with autogenic controls, indicate distinct feeding preferences: *A. juliana* preferentially consumed *U. fasciata*, while *A. brasiliana* primarily fed on *L. dendroidea*. Studies on feeding preferences in opisthobranch mollusks remain inconclusive, though some evidence point toward food specialization in certain species. In this study, we verified that *A. brasiliana* and *A. juliana* exhibited very distinct feeding preferences. Specimens of *A. juliana* preferentially consumed the green seaweed *U. fasciata*. This preference may be conditioned by food availability in the environment. For example, *A. dactylomela*, a common sea-hare of Hawaiian waters, is considered a red seaweed specialist but feeds almost exclusively on *Ulva* species when they are available in its natural environment (Carefoot, 1987). A general preference for green seaweeds among sea hare species has been widely demonstrated in laboratory experiments – not only invarious *Aplysia* species (Saito & Nakamura, 1961, Winkler & Dawson, 1963, Carefoot, 1967, 1970, 1987, Pennings, 1990 a, b, Rogers et al., 2003), but also in *D. auricularia* (Pennings et al. 1993), and *Bursatella leachii* (Wu, 1980).

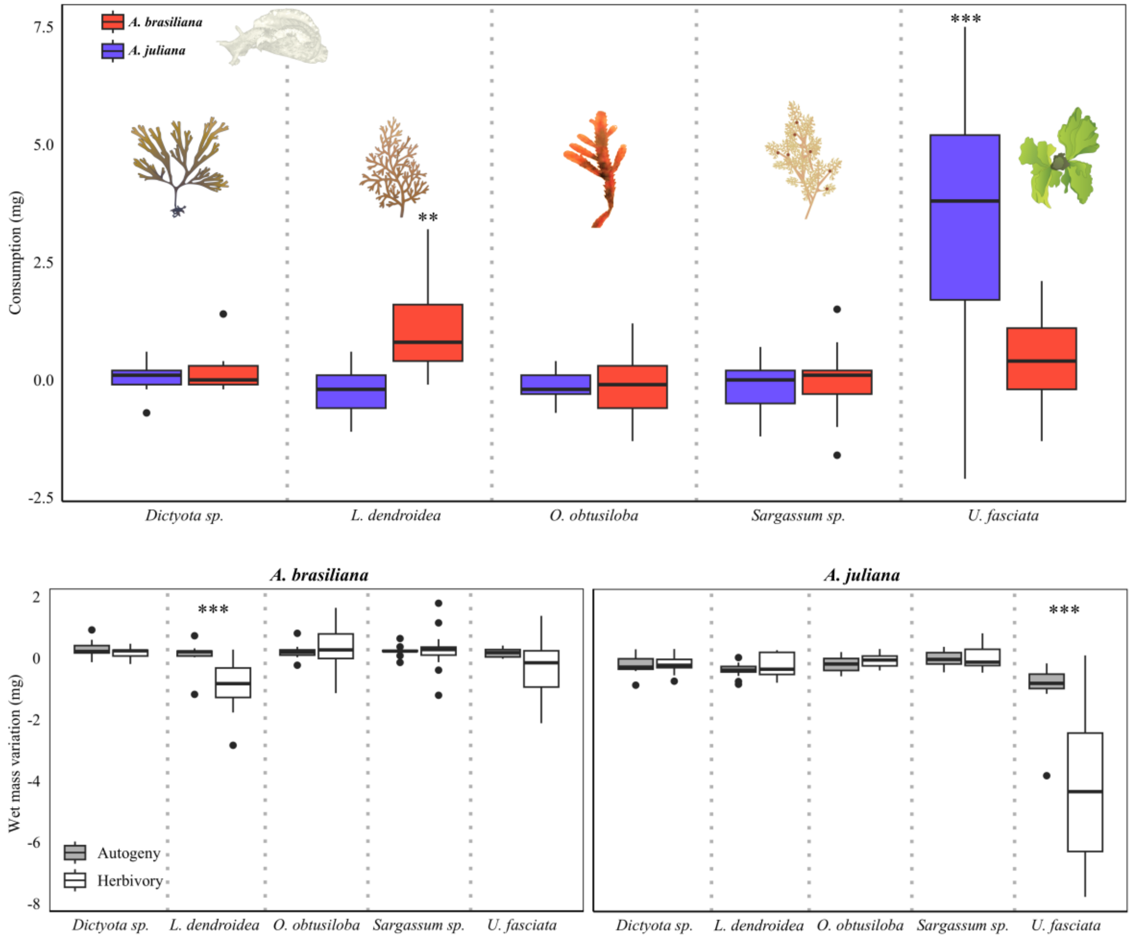

Figure 1. Consumption (mg) of the seaweeds by *A. brasiliana* and *A. juliana* calculated using the equation (upper panel) and comparison of wet mass variation of the seaweeds under herbivory and autogenic conditions in assays with *A. juliana* (lower left panel) and *A. brasiliana* (lower right panel).

Our results suggest that the food preference exhibited by *A. juliana* may be related to the resource availability in the field, as *U. fasciata* is the most abundant seaweed species at the location site (Taouil and Yoneshigue-Valentin, 2002). Similar findings have been reported previously for *A. juliana*, which selectively consumed *Ulva lactuca* – a locally abundant species that lacks defensive secondary metabolites (Rogers et al. 1995). Although secondary metabolites, such as diterpenoid lactone, have already been isolated from *A. juliana*, they are likely diet-derived (Atta-ur-Rahman et al., 1991; Harizani et al., 2016). For some herbivores, food availability may outweigh food quality in determining food choice (Arrontes, 1990). However, *Ulva* species also appear to be high-quality food source for opisthobranchs, as they promote growth and reproduction of the sea hare, such as *A. dactylomela* and *A. kuroadai* (Carefoot, 1980, 1981). Moreover, green Ulvaceae are known to produce chemicals that elicit phagostimulatory responses in *Aplysia* species (Sakata et al. 1985; Frins & Frings, 1965). These seaweeds may thus serve a dual function: provide both a nutritional resource and physical refuge through the structure of their foliose fronds.

Specimens of *A. brasiliana* preferred just a known chemically defended seaweed *L. dendroidea*, with which they are naturally associated-indeed, this was the natural habitat from which the specimens used in our bioassays were collected. Neither *U. fasciata* nor *L. dendroidea* ranks among the most abundant seaweed species at Praia do Forno Beach (The authors, pers. observ.). Despite richness of secondary metabolites in *Laurencia* species, they are selectively grazed by sea hare species. For example, *Aplysia dactylomela* accumulates these chemicals in its digestive gland and uses them as chemical defenses against predators (McPhail et al. 1999; Ginsburg & Paul, 2001). Similarly, the primary host-seaweeds of *Aplysia parvula* - *Laurencia obtusa* and *Delisea pulchra* are relatively scarce in the field but rich in defensive secondary metabolites (Rogers et al. 1995). *Aplysia parvula* sequesters chemicals from *D. pulchra* from its own defense (Rogers et al. 1995). In our study, *A. brasiliana* also appeared to exhibit a degree of specialization, responding positively to chemical signals from *L. dendroidea*, consistent with their natural association (Nocchi et al. 2017).

Although sometimes considered specialists, Aplysiid species are not highly specialized as members of the Sacoglossa order, which are the most specialized herbivores and the only known metazoans that exhibit kleptoplasty - the sequestration and retention of functional chloroplasts from siphonous green seaweeds of the order Bryopsidales (Wade & Sherwood, 2018). For example, while *Aplysia* species may appear to specialize on red seaweeds in the field (Carefoot, 1987), laboratory have repeatedly shown a preference for green seaweeds under controlled conditions (Winkler and Dawson 1963, Rogers et al. 2003). In our study, we found evidence of a close, chemically mediated relationship between *A. brasiliana* and *Laurencia*, which it feeds on and probably obtains protection from consumers. But we also observed a flexibility of feeding by *A. juliana*, which constitutes dietary plasticity and probably optimizes their ability to explore varied seaweed food resources.

DATA AVAILABILITY STATEMENT

Supplementary data to this article (Table S1, Table S2, Table S3) can be found online at: https://doi.org/10.5281/zenodo.16317988.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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AUTHOR CONTRIBUTIONS

R.C.P.: Conceptualization; Supervision; Methodology; Writing – Original Draft; Writing – Review & Editing.
A. C.: Formal Analysis; Methodology; Investigation.
F. V. R.: Formal Analysis; Validation; Writing – Review & Editing
M. V. S. G.: Formal Analysis; Investigation.
D. B. S.: Formal Analysis; Validation; Writing – Review & Editing.

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