



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

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ABSTRACT

Feeding preferences of benthic marine herbivores provides insight into their ecology, as well as their trophic relationships and potential impact on seaweeds. We present evidence of feeding preferences in *Aplysia brasiliiana* and *A. juliana* sea hares, collected from two distinct locations along the Brazilian coast, based on laboratory experiments. *Aplysia brasiliiana* from Forno Beach primarily consumed *Laurencia dendroidea*, a red seaweed known for its chemical defenses against herbivory, whereas *A. juliana* from Boa Viagem predominantly fed on *Ulva fasciata*, a palatable green seaweed. These results suggest that *A. brasiliiana* has evolved dietary counteradaptations to chemically defended seaweeds, while *A. juliana* displays a more generalized preference for palatable seaweeds commonly 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 shape herbivore feeding preferences is crucial to predict their impact on seaweed communities and to understand the establishment and evolution of plant-herbivore interactions (Poore and Hill, 2006). For example, experiments on herbivore seaweed

selection have linked feeding preferences either to environmental conditions (Simoncini and Miller, 2007) or to specific characteristics of individual seaweed species (e.g., Souza et al., 2008).

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

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Sea hares are known for their broad and varied feeding habits, with some species being more specialized (Paul and Pennings, 1991), while others exhibit more generalized feeding behaviors (Pennings and 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* preferentially feeds on chemically rich red seaweed species, such as *Laurencia* and *Plocamium* (Pennings, 1990a).

Aplysiid species can also exhibit intermediate feeding habits, favoring a limited group of seaweeds but capable of consuming a more varied diet when alternative options are scarce (Carefoot, 1987). For instance, the generalist sea hare *Dolabella auricularia* appears relatively unaffected by secondary metabolites present in host seaweeds (Pennings and 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 an important aspect in determining feeding preferences (Carefoot, 1970), although 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 and Paul, 1992). Regarding biotic interactions, the abundance of *A. parvula* increases only in the absence of its predator, the pycnogonid *Anaploactylus evansi* (Rogers et al., 2000).

The sea hare *Aplysia brasiliiana* is distributed from western Mexico to Paita, Peru, in the western Pacific, and from Florida to Brazil in the western Atlantic (Nozères and Kennedy, 2025; Saad et al., 2014). Conversely, *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* is an optimal biological model to assess feeding behavior (Pargagnon and Fiore, 1994).

In this study, we evaluated the feeding preferences of sublittoral specimens of *A. brasiliiana*

and *A. juliana* collected from two subtropical rocky shores with contrasting environmental conditions. A total of 13 specimens of *A. brasiliiana* (10–11 cm) were collected from a sheltered area at Forno Beach (Búzios, Rio de Janeiro State, 22° 46 S; 41° 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; 43° 07 W), during winter (August–September 2008). Species identification was confirmed by Dr. Carlo Magenta Cunha, and specimens were deposited in 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 (20°C), salinity (35), and aeration throughout 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-preference experiments involving the two *Aplysia* species: two Rhodophyta (*Laurencia dendroidea* and *Osmundaria obtusiloba*), two Heterokontophyta (*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 (23° 01 S; 22° 44 W), while *Dictyota* sp. and *L. dendroidea* were collected at Forno Beach—both sites 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 variety of consumers (Pereira and 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 ± 2°C, salinity 32 ± 1‰, and irradiance 60–80 μmol photons/m²·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. brasiliiana*

(over 30h) and *A. juliana* (over 12h), in which the five seaweed species aforementioned were simultaneously offered to specimens of these sea hares. In each experimental aquarium, one pre-weighed specimen of each seaweed was presented together with one individual of *A. brasiliiana* (n= 13) or *A. juliana* (n= 13). 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, although biomass varied due to differences in volume-to-biomass ratios among species. This approach ensured that similar volumes of each seaweed were equally detectable by both *A. brasiliiana* and *A. juliana*. The multiple-choice setup more realistically simulates natural conditions than dichotomous tests, as multiple seaweed species are often available to these herbivores in marine environments. Additionally, using living seaweeds enabled the simultaneous evaluation of both morphological and chemical characteristics of the seaweed species on the feeding preferences of *Aplysia* species.

Simultaneously, control aquaria (n= 13) were maintained without herbivores, containing previously weighed specimens of each seaweed species, as previously described in the bioassays with the *Aplysia* species ([Table S3, Supplementary Material](#)). These control seaweeds were maintained under the same experimental conditions as the treatment aquaria (with *Aplysia* specimens) to account for background biomass changes due to autogenic factors (Peterson and 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, excess water was removed by spinning each seaweed specimen in a salad spinner for 10 seconds.

Seaweed biomass consumption by *A. brasiliiana* and *A. juliana* was calculated using the equation $[(H_o \times C_i/C_o) - H_f]$, following Cronin and Hay (1996), in which H_o and H_f are the initial and final wet weights of seaweed exposed to herbivory, and C_o and C_i represent the initial and final wet weights of the corresponding control samples. This method incorporates autogenic changes into the consumption estimate. Moreover,

changes in wet mass of each seaweed species in the presence of sea hares were statistically tested against control using a *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 ($\text{glm}(\text{consumption} \sim \text{taxa})$). Model validity was assessed using likelihood ratio tests and visual inspection of residuals. Differences between means were evaluated using analysis of deviance tables, followed by Dunnett's *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 (Posit, 2023).

After the experiment, *A. juliana* significantly reduced the biomass of *U. fasciata* via 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 controls ($p < 0.0001$, *t*-test; Figure 1, lower panel). Conversely, only *L. dendroidea* was significantly consumed by *A. brasiliiana* (GLM: Deviance = 11.8, Residual deviance = 40.7, $p < 0.001$; Figure 1, upper panel), which was supported by a significant difference from controls ($p < 0.0001$, *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. brasiliiana* primarily fed on *L. dendroidea*.

Studies on feeding preferences in opisthobranch mollusks remain inconclusive, although some evidence points toward food specialization in certain species. In this study, we found that *A. brasiliiana* and *A. juliana* exhibited very distinct feeding preferences. *A. juliana* specimens preferentially consumed the green seaweed *U. fasciata*. This preference may be conditioned by food availability in the environment. For example, *A. dactylorella*, a common sea-hare of Hawaiian waters, is considered a red seaweed specialist but feeds almost exclusively on *Ulva* species when these are available in its natural habitat (Carefoot, 1987). A general preference for green seaweeds among sea hare species

has been widely demonstrated in laboratory experiments—not only in various *Aplysia* species (Carefoot, 1967, 1970, 1987; Pennings, 1990a,

1990b; Rogers et al., 2003; Saito and Nakamura, 1961; Winkler and Dawson, 1963) but also in *D. auricularia* (Pennings et al., 1993).

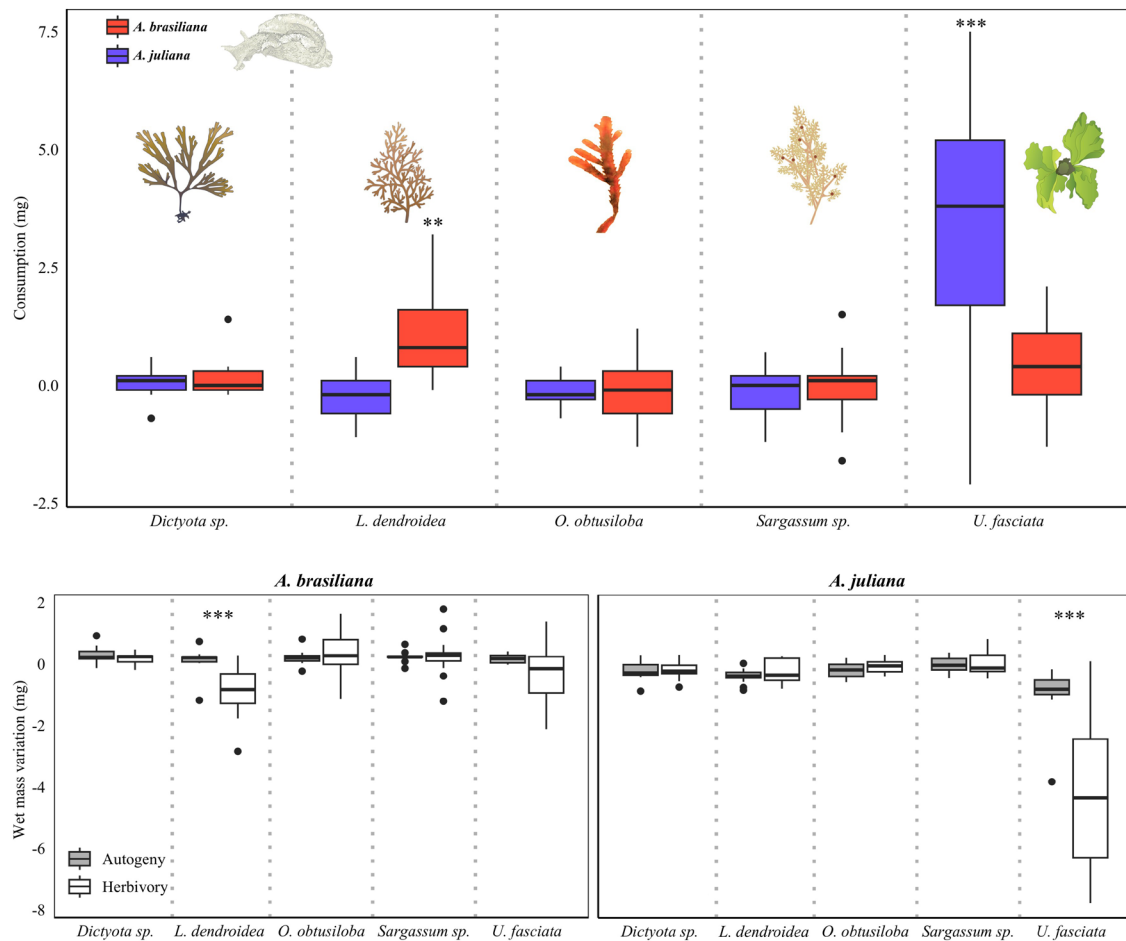


Figure 1. Consumption (mg) of seaweeds by *A. brasiliiana* and *A. juliana*, calculated using the consumption equation (upper panel). Wet mass variation of seaweeds under herbivory and autogenic conditions is shown for assays with *A. juliana* (lower left panel) and *A. brasiliiana* (lower right panel).

Our results suggest that the feeding preference of *A. juliana* may be related to resource availability in the habitat, as *U. fasciata* is the most abundant seaweed species at the study site (Taouil and Yoneshigue-Valentin, 2002). Similar findings have been reported 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 lactones have 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 feeding choice (Arrontes, 1990). However, *Ulva* species also appear to be high-quality food sources for the opisthobranch, as they promote growth and reproduction of the sea hares 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 (Frings and Frings, 1965; Sakata et al., 1985). These seaweeds may thus serve a dual function: providing both a nutritional resource and physical refuge through the structure of their foliose fronds.

A. brasiliiana specimens preferred only one 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 (authors, pers. observ.). Despite the 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 (Ginsburg and Paul, 2001; McPhail et al., 1999). 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). *A. parvula* sequesters chemicals from *D. pulchra* for its own defense (Rogers et al., 1995). In our study, *A. brasiliiana* 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, Aplysiidae species are not as 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 Bryopsidales order (Wade and Sherwood, 2018). For example, while *Aplysia* species may appear to specialize on red seaweeds in the field (Carefoot, 1987), laboratory studies have repeatedly shown a preference for green seaweeds under controlled conditions (Rogers et al., 2003; Winkler and Dawson, 1963). In our study, we found evidence of a close, chemically mediated relationship between *A. brasiliiana* and *L. dendroidea*, from which it feeds and probably obtains protection from consumers. We also observed flexible feeding by *A. juliana*, indicating dietary plasticity that may optimize its ability to exploit varied seaweed food resources.

AI USE DISCLOSURE

Artificial intelligence tools (ChatGPT) was used exclusively to refine the English language

of this manuscript. The content was carefully reviewed by the authors to ensure consistency and correctness, and the authors are fully responsible for the final version of the manuscript.

DATA AVAILABILITY STATEMENT

All data are available from the corresponding author upon reasonable request.

SUPPLEMENTARY MATERIAL

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

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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., D. B. S.: Formal Analysis; Validation; Writing – Review & Editing.

M. V. S. G.: Formal Analysis; Investigation.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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