

## Effect of habitat attributes on the abundance of *Sargassum*'s epifauna and the feeding habit of an amphipod epifauna from the coast of Western India

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The *Sargassum* bed along the rocky intertidal region is highly productive and serves as a habitat for numerous associated species. In this study, the effect of habitat attributes (algal morphology) on the abundance and diversity of epifauna in *Sargassum tenerrimum* was investigated. Qualitative and quantitative analysis showed that the overall species diversity was high, and *Hyale nuda*, *Gammaropsis* sp. and *Modiolus adriaticus* were the most abundant epifaunal species observed. The abundance of epifauna varied significantly with time. Compared to pre-monsoon months (February to May), post-monsoon (October to January) had a greater diversity of *S. tenerrimum* associated epifauna. The diversity was particularly high in the month of November. Epifauna showed a positive correlation with the characteristic of algal morphology, indicating its influence on abundance and diversity. *Hyale nuda* being the most ubiquitous and abundant epifauna observed, the biotic interaction between *S. tenerrimum* and *H. nuda* was studied further. Close examination of the gut contents of *H. nuda* revealed that they graze and consume the epiphytic microalgae of *S. tenerrimum*, instead of the macroalgal fronds. This suggests that through this relationship, epibiosis in *Sargassum* may remain in control, while the amphipod derives food, shelter and protection from the predators.

[**Keywords:** Abundance, Community structure, Diversity, Epiphytic macrofauna, Epiphytic microalgae, *Hyale nuda*, Seasonal variations]

### Introduction

The intertidal rocky shore is an important marine ecosystem. In the rocky intertidal zone, including the subtidal zone, seaweeds are one of the major producers forming base of the trophic structure. They also function as a habitat former, space occupier, source of food, shelter and protection for a variety of associated organisms, and provide space for settlement<sup>1-4</sup>. Intertidal ecosystems especially rocky shores, experience extreme physical stresses such as desiccation and wave impact. The canopy of seaweeds offers protection from such physical stresses to the associated epifauna, defends against predators, and aids in the settlement of other benthic species<sup>5-6</sup>. Fishes, molluscs, crustaceans, and other epifauna that live on the macroalgal bed are quite diverse and occupy various trophic levels<sup>7-10</sup>.

Various studies showed that the host macroalgal morphological characteristics can affect species diversity because epifauna often chooses algae with more morphological complexity<sup>11-15</sup>. Seaweeds with higher morphological complexity are usually preferred by associated organisms because they provide a greater surface area to inhabit<sup>3,14</sup>. According

to Le Hir & Hily<sup>14</sup>, the complexity of structural habitat is also influenced by seasonal variation in the growth of seaweeds, which may eventually have an impact on associated epifaunal abundance.

*Sargassum* is an important seaweed inhabiting rocky intertidal ecosystems, and their thalli are structurally intricate<sup>16</sup>. It has long, branched thalli with fronds that resemble leaves and air-filled floats (pneumatocysts). These highly branched thalli also give a canopy effect and greater surface area to the associated organisms to inhabit. As a result, seaweeds, particularly *Sargassum* species, play a significant role in the functioning of the intertidal rocky shore ecosystems. A variety of fishes, molluscs, crustaceans, and many other types of species find shelter and refuge in association with *Sargassum* beds. According to previous studies, the epifauna of *Sargassum* spp. is extremely diversified, including filter feeders or detritivores, or carnivores. However, majority of them are herbivores that graze on the host or epiphytic microalgae<sup>7,17-19</sup>).

Considering these characteristics of the seaweeds and their role in the rocky shore intertidal ecosystem, the effect of habitat attributes (macroalgal

morphology) on the seasonal distribution of *Sargassum tenerrimum* associated epifauna was investigated in this study. The abundance of epifauna was analysed from the monthly collected macroalgal samples from the rocky intertidal shore of Anjuna, west coast of India. The mature thalli of *S. tenerrimum* break off due to strong wave action and currents during monsoon months (June to September; author's personal observation); hence, samples from those months were not investigated. Throughout the study, *Hyale nuda*, an amphipod epifauna, frequently appeared. The nature of the interaction was thus of interest. So, in this study, the effect of thalli attributes on the temporal abundance and diversity of epifauna, as well as the biotic interaction between *S. tenerrimum* and *H. nuda* was examined. It is hypothesized that due to the frequent occurrence and abundance of *H. nuda*, this species might be feeding on the fronds of *S. tenerrimum*. The subsequent observations and results have been described in detail in the article.

## Materials and Methods

### Study area

Sampling was done over the course of a year from October 2013 to May 2014 from the rocky intertidal shore of Anjuna, Goa, India, located between 15°34'04" N and 73°44'27" E (Fig. 1). The study area is an exposed and sea-facing rocky intertidal shore with a rich diversity of seaweeds. The substrata is of flat rock and boulders with very little deposition of sand. The samples of *S. tenerrimum*, a brown seaweed, were collected every month during low tide, except for the monsoon months. The seaweed samples of ~ 7 inches long were selected and cut off with a scissor. The samples were kept in a poly bag to prevent the loss of epifauna and brought to the laboratory in an icebox for further investigation. In total, eight months of samples in triplicate were collected for the present study.

### Sample processing and analysis

In the laboratory, the samples were fixed in a buffered Rose-Bengal formalin solution (5 %). The epifauna were removed by repeated washing under running tap water through a 500 µm mesh. After sorting, the epifaunal samples were then preserved in 10 % buffered formalin solution and kept for later identification.

Epifaunal abundance was quantified and analysed under a light microscope (Olympus). In the current

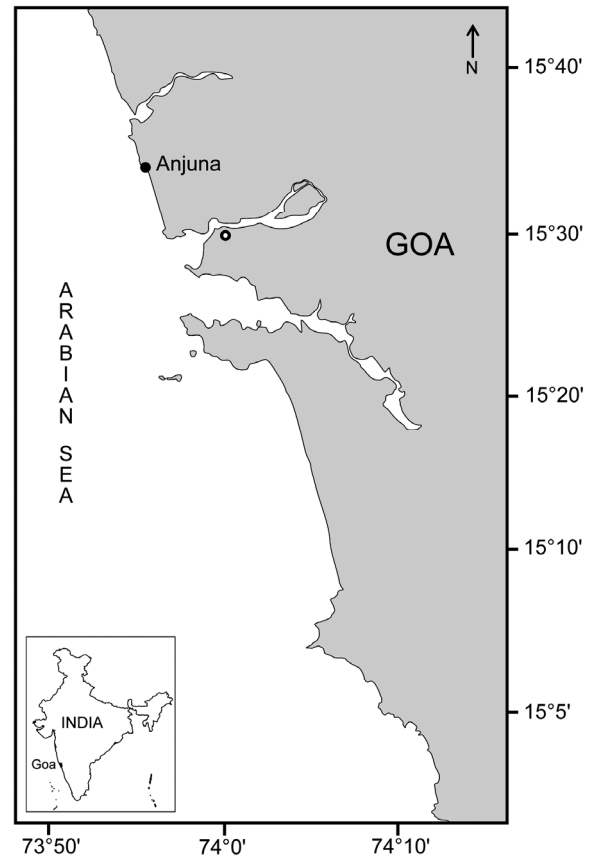


Fig. 1 — Location of the rocky intertidal shore of Anjuna and a sampling site

study, epifauna like hydroids, bryozoans, etc., were not considered as they were not associated directly with *Sargassum* thalli. In the case of fragmented specimens, such as polychaete, only the heads were counted. The epifauna were identified to the lowest possible taxonomic level and to the species level, whenever possible. Epifaunal total abundance was calculated and expressed as the number of individuals per 100 g algal wet weight.

### Effect of habitat attributes

To study the effect of habitat attributes, the algal thalli were dried by blotting with tissue paper, and thereafter the total length of the thallus (LT), the number of thalli (NT), and the fresh weight (FW) of the algal thalli were recorded.

### Analysis of gut content of *H. nuda*

The gut content of *H. nuda* was analysed to examine the nature of interrelationship and interactions with *S. tenerrimum*. The samples of *H. nuda* were preserved with Lugol's solution. In another set, samples of epiphytic microalgae of *S. tenerrimum* were collected by scraping and stored in Lugol's

solution. For the examination of gut contents, this epiphytic microalgae data was used as a reference. Under an inverted microscope, the gut content of preserved *H. nuda* samples was dissected and analysed. The following equation was used to determine the relative abundance ( $A$ ) and the frequency of occurrence ( $F$ ) of microalgae in the gut content<sup>20</sup>:

$$\% F = (n_i/N) \times 100$$

$$\% A = (\sum S_i / \sum S_t) \times 100$$

Where,  $n_i$  is the number of microalgae within the gut content,  $N$  is the total number of microalgae in the gut,  $S_i$  is the number of microalgae found on the thalli of *S. tenerrimum*, and  $S_t$  is the total number of microalgae on *S. tenerrimum* thalli. The epiphytic microalgae from algal thalli and gut contents were identified to the lowest possible taxonomic level using available taxonomic keys<sup>21-22</sup>.

#### Data analysis

One-way ANOVA was used to evaluate epifaunal temporal abundance and species richness. The correlation between the epifaunal abundance and algal morphological characteristics (habitat attributes) was

analysed using Pearson rank correlation. Stat Soft Statistica 8 was used for all the analysis. Bray-Curtis Index and similarity percentage (SIMPER) in PRIMER v.5 (Plymouth Marine Laboratory, Plymouth, UK) was used to analyse the similarity in seasonal distribution of epifauna. Plotting of the similarity results was done using Multidimensional Scaling (MDS). Species diversity was calculated using Shannon-Wiener formula<sup>23</sup>.

$$H' = - \sum_{i=1}^s p_i \times \ln p_i$$

Where,  $p_i$  is the proportion of the entire community made up of individuals of species,  $\ln$  is the natural logarithm,  $s$  is the species richness, and  $H'$  - the species diversity.

#### Results

In this study, a total of 31,962 individual epifauna per 100 g algal wet weight was recorded. They belonged to 25 species representing 8 major taxonomic groups (Table 1). The two groups with the greatest diversity were amphipoda (8 species) and

Table 1 — Monthly numerical abundance (no. of individuals per 100 g of algal wet weight) of epifauna associated with *Sargassum tenerrimum*

Species	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	Total
<i>Hyale nuda</i>	109	547	656	5255	2773	4160	4160	3430	21090
<i>Gammarus locusta</i>	36	36	0	0	0	0	0	0	72
<i>Gammarus</i> sp.	36	145	291	182	0	474	0	182	1310
<i>Maera serratipalma</i>	72	145	0	328	182	0	255	0	982
<i>Gammaropsis</i> sp.	0	109	364	547	255	72	948	255	2550
Gammaridae sp.	109	182	182	145	109	109	0	0	836
<i>Ampithoe</i> sp.	0	0	36	36	182	437	0	291	982
<i>Melita</i> sp.	0	0	145	0	72	36	36	0	289
<i>Platynereis</i> sp	72	218	72	0	0	72	36	36	506
<i>Nereis aibuhitensis</i>	145	218	0	0	0	0	0	36	399
<i>Syllis syllis</i>	145	109	36	0	0	36	72	36	434
<i>Myrianida edwardsi</i>	0	0	0	0	0	36	0	0	36
<i>Lumbrineris</i> sp	0	0	0	0	0	0	0	36	36
<i>Pectinaria papillosa</i>	0	0	0	0	0	36	0	0	36
<i>Owenia fusiformis</i>	0	0	0	0	0	0	0	36	36
<i>Dinamene bidentata</i>	0	36	0	0	0	0	0	0	36
<i>Pentidotea</i> sp.	0	328	0	160	0	36	36	36	596
<i>Mitrella vatovai</i>	36	0	0	0	0	0	0	0	36
<i>Epitonium</i> sp	0	145	0	0	0	0	0	0	145
<i>Diodora gibberula</i>	0	72	0	0	0	0	0	0	72
<i>Brachiodontes variabilis</i>	0	36	0	0	0	0	0	0	36
<i>Modiolus adriaticus</i>	36	583	72	36	36	36	36	36	871
<i>Acanthonyx euryseroche</i>	0	36	36	36	0	0	0	72	180
<i>Ophiactis resiliens</i>	0	72	36	36	36	0	0	0	180
<i>Apseudes chilensis</i>	0	36	0	0	0	0	0	0	36
Total abundance	796	3053	1926	6761	3645	5540	5579	4482	31782

polychaeta (7 species) followed by gastropoda (3 spp.), bivalvia (3 spp.), isopoda (2 spp.), and decapoda (1 sp.). The species of echinoderms and tanaids were also recorded.

The epifaunal diversity and abundance exhibited a significant temporal effect, with diversity being higher in the post-monsoon months of October to December and gradually declining thereafter. From the months of October through December, seen a decline in epifaunal abundance. Amphipoda, polychaeta, and bivalvia were the most common and numerous groups. Among all the groups identified, amphipoda was the most abundant faunal group (Fig. 2). The species diversity as per the Shannon and Wiener index showed that the month of November, with 18 species, had the highest diversity, and the lowest was in the month of April (Fig. 3). However, the species were more evenly distributed in the month of October than in November.

Several amphipod and bivalve species were observed during the course of the study. However, *H. nuda* (amphipoda) was the most common and dominant species in the subsequent months, while, *Modiolus adriaticus* (bivalvia) was the dominant species in November (Table 2). January had the highest abundance of amphipods (~ 5255) (Table 1). Epifaunal diversity ( $F = 5.16, P = 0.003$ ) and seasonal abundance ( $F = 9.84, P = 0.000$ ) varied significantly.

Two separate clusters were revealed by the similarity analysis of the epifaunal distribution (Fig. 4). October and November formed one group, and the other months, December to May, comprised the other. Furthermore, the similarity percentage (SIMPER) showed that the epifauna recorded from December to May had a significant species similarity (67.15 %), while it was 60.61 % in those found between October and November. The dissimilarity between the groups was 58.55 %. Species like *H. nuda* (17.71 %), and *Platynereis* sp. (12.79 %) contributed majorly to the similarity in group 1, whereas *H. nuda* (51.4 %), *Gammaropsis* sp. (14.42 %) and *Ampithoe* sp. (5.97 %) were responsible for the major contribution in group 2 similarity. The dissimilarity between the groups was mainly contributed by *H. nuda* (13.02 %) and *Nereis* sp. (10.14 %). The analysis showed that algal thalli size and branching had an influence on the abundance and species richness of epifauna. There was a positive correlation between the habitat attributes of the macroalga and overall abundance ( $R^2 = 0.459, P < 0.024$ ).

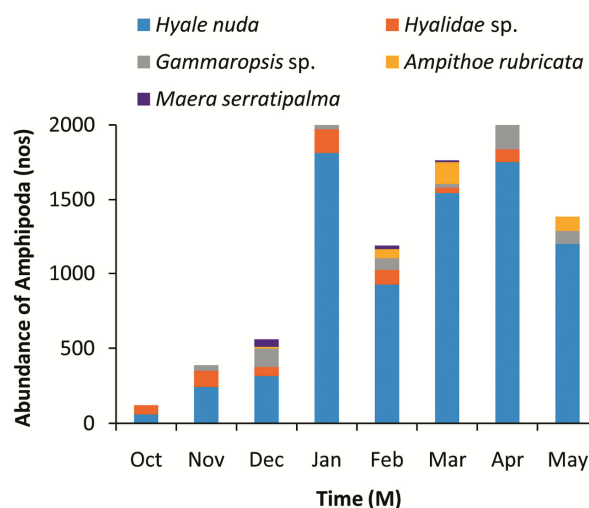


Fig. 2 — Diversity and abundance of amphipoda in association with *Sargassum tenerrimum*

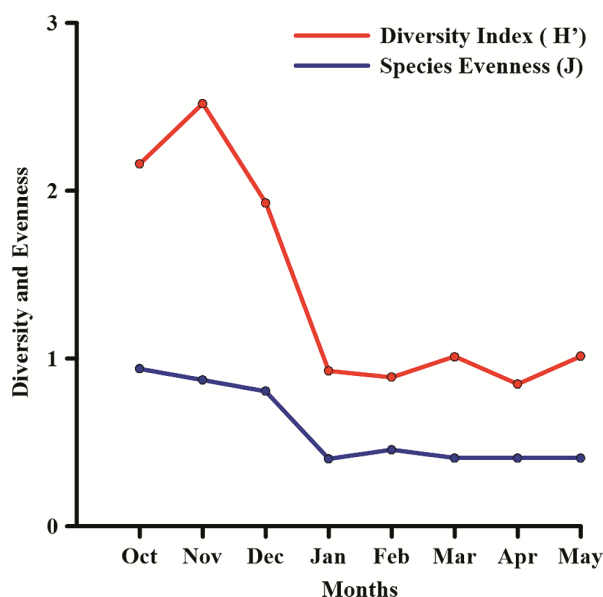


Fig. 3 — Epifaunal species diversity in association with *Sargassum tenerrimum*

Table 2 — Temporal dominance of *Sargassum tenerrimum*'s major epifauna

Time (M)	No. of species	Dominant sp.	Dominance (%)
October	10	Polychaeta spp.	18.2
November	18	<i>Modiolus adriaticus</i>	19
December	11	<i>Hyale nuda</i>	33.5
January	10	<i>Hyale nuda</i>	77.72
February	8	<i>Hyale nuda</i>	76
March	12	<i>Hyale nuda</i>	75
April	8	<i>Hyale nuda</i>	74.5
May	12	<i>Hyale nuda</i>	76.5

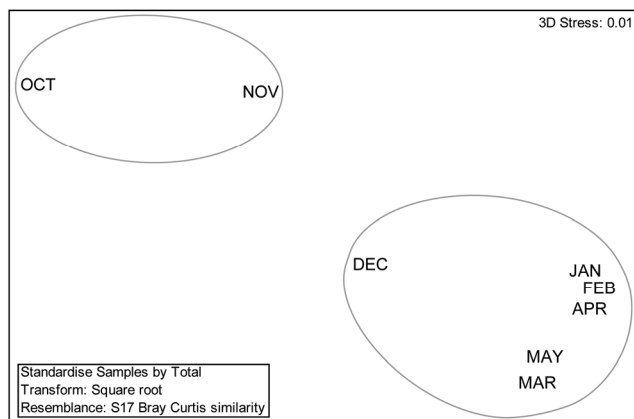


Fig. 4 — Multidimensional Scaling (MDS) plot showing the similarity in temporal distribution of epifauna on *Sargassum tenerrimum*

Table 3 — Epiphytic microalgae of *Sargassum tenerrimum*, their relative abundance and frequency of occurrence in the gut of *Hyale nuda*

Microalgae recorded from the thalli	No. of microalgae recorded from the thalli	Relative abundance and frequency of microalgae in gut content	
		% A	% F
<i>Amphora marina</i>	220	0	0
<i>Chaetoceros gracilis</i>	5	0	0
<i>Dinophysis</i> sp.	10	0	0
<i>Diatoma</i> sp.	4325	1.9	25
<i>Fragillariopsis oceanica</i>	35	0	0
<i>Gymnodinium</i> sp.	3	0	0
<i>Leptocylindrus</i> sp.	40	0	0
<i>Licmophora paradoxa</i>	250	1.5	20
<i>Melosira moniliformis</i>	2	0	0
<i>Navicula oblonga</i>	2975	70.3	100
<i>Nitzschia longissima</i>	10	1.2	15
<i>Pinnularia viridis</i>	65	15.6	60
<i>Streptotheca</i> sp.	20	0	0
<i>Striatella unipunctata</i>	40	0	0
<i>Thalassionema nitzschioides</i>	85	5.7	40
<i>Thalassionema frauenfeldii</i>	10	0	0
<i>Gomposphaeria</i> sp.	25	0	0

The gut content of *H. nuda* exhibited a variety of microalgae. The microalgae recorded in the gut content matched to those found on the thalli of *S. tenerrimum*, which are epiphytic microalgae (Table 3). The two most common epiphytic microalgae on macroalgal thalli were *Diatoma* sp. (N = 1455) and *Navicula oblonga* (N = 1151). *Pinnularia viridis* (~ 63) and *Navicula oblonga* (~ 190) were the most consumed microalgae according to the analysis of gut contents (Table 3).

The gut content did not contain any bits of invertebrates or macroalgal thalli/fronds.

## Discussion

Studies showed that several factors, such as environmental factors, macroalgal habit, food availability, and seasons, may impact the abundance and diversity of algae-associated epifauna<sup>3,24-30</sup>. The present study showed significant temporal variation in the abundance and diversity of *S. tenerrimum* epifauna. The community characteristics were more diverse in the month of November. During this time, the population of amphipoda was comparatively low and the population density of *Modiolus adriaticus* was higher. However, the population of amphipods grew steadily over time and became more abundant. The most diverse and abundant groups in this study were amphipoda, followed by polychaeta, and bivalvia.

The results showed that when there was an increase in the amphipoda population, the characteristics of epifaunal community changed due to a decline in the abundance and diversity of other associated epifauna. This variation could be attributed to a temporally influenced factors as well as interspecific competition. In agreement with this, a study by Gabr *et al.*<sup>31</sup> showed that such variations in diversity and abundance are due to seasonal effects. Although amphipod predation on associated organisms was not investigated in the present study, some studies showed that amphipods have an impact on the abundance of epifauna, such as bivalves, due to predation<sup>32-33</sup>. Conversely, Wakabara *et al.*<sup>34</sup> showed that the morphological adaptation of the species, such as their mobility and ability to attach to the algae, is what causes macroalgal epifauna like amphipods, to dominate.

The most abundant epifauna in the present study were amphipods. *Hyale nuda* was the most common species among them, with a density of about 85 % in January. It was observed that low populations of bivalve and other amphipod species coincided with high abundance of *H. nuda*. This was most probably due to interspecies competition. However, Valério-Berardo & Flynn<sup>35</sup> claimed that the temporary change in community structure is driven by the population dynamics of the dominant species, including predation stress, whereas Ba-Akdah *et al.*<sup>3</sup> reported that the seasonal variation in environmental factors controls the abundance of epifauna and other benthic organisms. In a similar study by Duffy & Hay<sup>36</sup>

showed how a particular species dominance influences a community structure. Resource competition was cited as another reason why the community structure changes. They also observed that grazing amphipods have such a significant effect on the community structure of epifauna that they play an important role in determining the characteristics of the community<sup>36</sup>. A seasonal study on epifauna showed that amphipod population dominance varied over time, and they were more abundant in the winter<sup>35</sup>. In addition, numerous studies showed that tropical amphipod species typically exhibit seasonal abundance<sup>35,37-40</sup>.

According to previous studies, the complex algal morphology has been linked to increased species richness and epifaunal habitat preferences<sup>26,41-42</sup>. In agreement with these studies, a positive correlation ( $R^2 = 0.459$ ,  $P = 0.024$ ) was found between the abundance of epifauna and the highly branched macroalgal thalli. The highly branched thalli increase the space and food availability, which can contribute to greater diversity and abundance. Given that the community structure of epifauna is significantly influenced by the surrounding landscape, the temporal increase in the abundance of epifauna, particularly amphipods, may also be linked to the growth and increased branching of the algae<sup>43</sup>. Additionally, Tavares *et al.*<sup>44</sup> also showed that the choice of marine macrophyte by epifauna is complicated and determined by a variety of factors, including the nutritional value of macroalgae, palatability, value of habitat, availability of microalgae in the environment and protection from the predators.

Amphipods exhibit a variety of feeding strategies, including suspensivory, detritivory, predatory, herbivory, and sometimes omnivory<sup>45</sup>, and these strategies can vary between habitats and seasons within the same species<sup>21,46,47</sup>. In the present study, it was hypothesised that *H. nuda* consumes *S. tenerrimum* fronds or thalli. However, the gut content study showed that they did not consume macroalgal fronds. The results revealed a variety of epiphytic microalgae rather than frond fragments in the gut content. This suggested that they consume the algal epiphytes when grazing. The two main epiphytes found in the gut contents were *Pinnularia viridis* and *Navicula oblonga*. They accounted between 70 and 89 % of the relative abundance and between 85 – 100 % of the frequency of occurrence of the consumed microalgae. *Navicula oblonga* appeared

to be a relatively common species in the gut content, which could suggest that it is a preferred food source. In a related study, Aiken & Kikuchi<sup>48</sup> demonstrated that amphipods graze and consume diatoms.

Although there can be differences in the feeding habits and food sources between species and groups, studies showed that a controlled epibiosis caused by selective epiphyte grazing benefits the host because it improves photosynthesis<sup>6,49</sup>. Buschmann<sup>50</sup> also demonstrated that mobile invertebrates that live on the intertidal macroalgae can use the algae both as food and a place of refuge because they can distinguish between the two in terms of time and space.

### Conclusion

The present study showed that the abundance and diversity of epifauna on *S. tenerrimum* is temporally affected along with the habitat attributes, such as the characteristic of algal morphology. As a result, the diversity was higher in the post-monsoon months, especially in the month of November, than in the pre-monsoon months (February to May). The change in community characteristics of epifauna with increase in the population of amphipoda could be due to interspecific competition as well as temporal factors. The analysis of gut content employed to study the biotic interaction between *S. tenerrimum* and *H. nuda* revealed that *H. nuda* consume epiphytic microalgae of *S. tenerrimum*, and not the fronds of macroalga. This indicated that grazing by *H. nuda* may control the extent of epiphytism on *S. tenerrimum*, while amphipods derive benefits in the form of food, shelter and protection from the predators. However, to understand the trophic dynamics and its consequent impacts on the diversity of macroalgal epifauna, more extensive research on the feeding behaviour of macroalgal epifauna is necessary.

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### Conflict of Interest

There is no conflict of interest.

### Author Contributions

Both the authors have contributed equally.

## References

- 1 Cacabelos E, Olabarria C, Incera M & Troncoso J S, Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae, *Estuar Coast Shelf Sci*, 89 (1) (2010) 43-52. <https://doi.org/10.1016/j.ecss.2010.05.012>
- 2 Pinho D, Bertocci I, Arenas F, Franco J N, Jacinto D, *et al.*, Spatial and temporal variation of kelp forests and associated macroalgal assemblages along the Portuguese coast, *Mar Freshw Res*, 67 (1) (2015) 113-122. <https://doi.org/10.1071/MF14318>
- 3 Ba-Akdah M, Satheesh S & Al-Sofyani A, Habitat preference and seasonal variability of epifaunal assemblages associated with macroalgal beds on the Central Red Sea coast, Saudi Arabia, *J Mar Biol Assoc UK*, 96 (7) (2016) 1457-1467. <https://doi.org/10.1017/S0025315415001678>
- 4 Imchen T & Anil A C, Temporal Effect on the Abundance and Diversity of Intertidal Rocky Shore Macroalgae, *Curr Sci*, 113 (8) (2017) 1593-1596.
- 5 de Oliveira Machado G B, Siqueira S G L & Leite F P P, Abundance, performance, and feeding preference of herbivorous amphipods associated with a host alga-epiphyte system, *J Exp Mar Biol Ecol*, 486 (2017) 328-335. <https://doi.org/10.1016/j.jembe.2016.10.030>
- 6 Machado G B, Ferreira A P, Bueno M, Siqueira S G & Leite F P, Effects of macroalgal host identity and predation on an amphipod assemblage from a subtropical rocky shore, *Hydrobiologia*, 836 (2019) 65-81. <https://doi.org/10.1007/s10750-019-3941-8>
- 7 Duffy J E & Hay M E, Amphipods are not all created equal: a reply to Bell, *Ecology*, 72 (1) (1991) 354-358.
- 8 Taylor R B & Cole R G, Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand, *Mar Ecol Prog Ser*, 115 (1994) 271-282.
- 9 Huang Y M, Amsler M O, McClintock J B, Amsler C D & Baker B J, Patterns of gammaridean amphipod abundance and species composition associated with dominant subtidal macroalgae from the western Antarctic Peninsula, *Polar Biol*, 30 (2007) 1417-1430. <https://doi.org/10.1007/s00300-007-0303-1>
- 10 Jacobucci G B, Tanaka M O & Leite F P P, Temporal variation of amphipod assemblages associated with *Sargassum filipendula* (Phaeophyta) and its epiphytes in a subtropical shore, *Aquat Ecol*, 43 (2009) 1031-1040. <https://doi.org/10.1007/s10452-009-9230-2>
- 11 Duffy J E, Amphipods on seaweeds: partners or pests? *Oecologia*, 83 (1990) 267-276. <https://doi.org/10.1007/BF00317764>
- 12 Hacker S D & Steneck R S, Habitat architecture and the abundance and body size dependent habitat selection of a phytal amphipod, *Ecology*, 71 (6) (1990) 2269-2285. <https://doi.org/10.2307/1938638>
- 13 Lancellotti D & Trucco R, Distribution patterns and coexistence of six species of the amphipod genus *Hyale*, *Mar Ecol Prog Ser*, 93 (1) (1993) 131-141.
- 14 Le Hir M & Hily C, Macrofaunal diversity and habitat structure in intertidal boulder fields, *Biodivers Conserv*, 14 (2005) 233-250. <https://doi.org/10.1007/s10531-005-5046-0>
- 15 Tuya F, Wernberg T & Thomsen M S, The spatial arrangement of reefs alters the ecological patterns of fauna between interspersed algal habitats, *Estuar Coast Shelf Sci*, 78 (4) (2008) 774-782. <https://doi.org/10.1016/j.ecss.2008.02.017>
- 16 Steneck R S, Graham M H, Bourque B J, Corbett D, Erlandson J M, *et al.*, Kelp forest ecosystems: biodiversity, stability, resilience and future, *Environ Conserv*, 29 (4) (2002) 436-459. <https://doi.org/10.1017/S0376892902000322>
- 17 Bell S S, Amphipods as insect equivalents? An alternative view, *Ecology*, 72 (1) (1991) 350-354. <https://doi.org/10.2307/1938929>
- 18 Jacobucci G B, Güth A Z & Leite F P P, Experimental evaluation of amphipod grazing over biomass of *Sargassum filipendula* (Phaeophyta) and its dominant epiphyte, *Nauplius*, 16 (2) (2008) 65-71.
- 19 Huffard C L, Von Thun S, Sherman A D, Sealey K & Smith K L, Pelagic *Sargassum* community change over a 40-year period: temporal and spatial variability, *Mar Biol*, 161 (2014) 2735-2751. <https://doi.org/10.1007/s00227-014-2539-y>
- 20 Yu O H, Suh H L & Shirayama Y, Feeding ecology of three amphipod species *Synchelidium lenorostratum*, *S. trioestegitum* and *Gitanopsis japonica* in the surf zone of a sandy shore, *Mar Ecol Prog Ser*, 258 (2003) 189-199. <https://doi.org/10.3354/meps258189>
- 21 Taylor F J R, Dinoflagellates from the International Indian Ocean Expedition, A report on material collected by the RV 'Anton Bruun' 1963-1964, *Bibl Bot*, 132 (1976) p. 46.
- 22 Tomas C R (ed.), *Identifying marine phytoplankton*, (Academic Press, US), 1997, pp. 858. <https://doi.org/10.1016/B978-0-12-693018-4.X5000-9>
- 23 Shannon C E & Weaver W, *The Mathematical theory of Communication*, (University of Illinois, Urbana, USA), 1963, pp. 117.
- 24 Poltermann M, Growth, production and productivity of the Arctic sympagic amphipod *Gammarus wilkitzkii*, *Mar Ecol Prog Ser*, 193 (2000) 109-116.
- 25 Tanaka M O & Leite F P, Spatial scaling in the distribution of macrofauna associated with *Sargassum stenophyllum* (Mertens) Martius: analyses of faunal groups, gammarid life habits, and assemblage structure, *J Exp Mar Biol Ecol*, 293 (1) (2003) 1-22. [https://doi.org/10.1016/S0022-0981\(03\)00233-8](https://doi.org/10.1016/S0022-0981(03)00233-8)
- 26 Buzá-Jacobucci G & Pereira-Leite F P, The role of epiphytic algae and different species of *Sargassum* in the distribution and feeding of herbivorous amphipods, *Lat Am J Aquat Res*, 42 (2) (2014) 353-363. <https://doi.org/10.3856/vol42-issue2-fulltext-6>
- 27 Gestoso I, Olabarria C & Troncoso J S, Effects of macroalgal identity on epifaunal assemblages: native species versus the invasive species *Sargassum muticum*, *Helgol Mar Res*, 66 (2012) 159-166. <https://doi.org/10.1007/s10152-011-0257-0>
- 28 Veiga P, Rubal M & Sousa-Pinto I, Structural complexity of macroalgae influences epifaunal assemblages associated with native and invasive species, *Mar Environ Res*, 101 (2014) 115-123. <https://doi.org/10.1016/j.marenvres.2014.09.007>
- 29 Tano S, Eggertsen M, Wikström S A, Berkström C, Buriyo A, *et al.*, Tropical seaweed beds are important habitats for mobile invertebrate epifauna, *Estuar Coast Shelf Sci*, 183 (2016) 1-12. <https://doi.org/10.1016/j.ecss.2016.10.010>
- 30 Fulton C J, Abesamis R A, Berkström C, Depczynski M, Graham N A, *et al.*, Form and function of tropical macroalgal reefs in the Anthropocene, *Funct Ecol*, 33 (6) (2019) 989-999. <https://doi.org/10.1111/1365-2435.13282>
- 31 Gabr M K, Ziena F A & Hellal M A, Abundance and diversity of amphipod species associated with macro-algae at Ras-Mohamed, Aqaba Gulf, Red Sea, Egypt, *Egypt J Aquat Biol Fish*, 24 (3) (2020) 1-15. <https://doi.org/10.21608/ejabf.2020.87108>

- 32 Ejdung G & Elmgren R, Predation on newly settled bivalves by deposit-feeding amphipods: a Baltic Sea case study, *Mar Ecol Prog Ser*, 168 (1998) 87-94. <https://doi.org/10.3354/meps168087>
- 33 Ejdung G, Byrén L & Elmgren R, Benthic predator-prey interactions: evidence that adult *Monoporeia affinis* (Amphipoda) eat postlarval *Macoma balthica* (Bivalvia), *J Exp Mar Biol Ecol*, 253 (2) (2000) 243-251. [https://doi.org/10.1016/S0022-0981\(00\)00267-7](https://doi.org/10.1016/S0022-0981(00)00267-7)
- 34 Wakabara Y, Tararam A & Takeda A, Comparative study of the amphipod fauna living on *Sargassum* of two Itanhaém shores, Brazil, *J Crustacean Biol*, 3 (4) (1983) 602-607. <https://doi.org/10.1163/193724083X00265>
- 35 Valério-Berardo M T & Flynn M N, Composition and seasonality of an amphipod community associated to the algae *Bryocladia trysigera*, *Braz J Biol*, 62 (4a) (2002) 735-742. <https://doi.org/10.1590/S1519-69842002000400021>
- 36 Duffy J E & Hay M E, Strong impacts of grazing amphipods on the organization of a benthic community, *Ecol Monogr*, 70 (2) (2000) 237-263. [https://doi.org/10.1890/0012-9615\(2000\)070\[0237:SI0GAO\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2000)070[0237:SI0GAO]2.0.CO;2)
- 37 Lana P C & Guiss C, Influence of *Spartina alterniflora* on structure and temporal variability of macrobenthic associations in a tidal flat of Paranaguá Bay (southeastern Brazil), *Mar Ecol Prog Ser*, 73 (2-3) (1991) 231-244. <https://doi.org/10.3354/meps073231>
- 38 Curvelo R, *A meiofauna vágil associada a Sargassum cymosum* C. Agardh, na Praia do Lásaro, Ubatuba, SP, M.Sc. thesis submitted to Instituto Oceanográfico, Universidade de São Paulo, SP, 1998, pp. 50.
- 39 Flynn M N, Tararam A S & Wakabara Y, Effects of habitat complexity on the structure of macrobenthic association in a *Spartina alterniflora* marsh, *Rev Bras Oceanogr*, 44 (1) (1996) 09-21. <https://doi.org/10.1590/S1413-77391996000100002>
- 40 Flynn M N, Wakabara Y & Tararam A S, Macrobenthic associations of the lower and upper marshes of a tidal flat colonized by *Spartina alterniflora* in Cananéia lagoon estuarine region (southeastern Brazil), *Bull Mar Sci*, 63 (02) (1998) 427-442.
- 41 Anderson M J, Diebel C E, Blom W M & Landers T J, Consistency and variation in kelp holdfast assemblages: spatial patterns of biodiversity for the major phyla at different taxonomic resolutions, *J Exp Mar Biol Ecol*, 320 (1) (2005) 35-56. <https://doi.org/10.1016/j.jembe.2004.12.023>
- 42 Eriksson B K, Rubach A & Hillebrand H, Biotic habitat complexity controls species diversity and nutrient effects on net biomass production, *Ecology*, 87 (1) (2006) 246-254. <https://doi.org/10.1890/05-0090>
- 43 Jungerstam J, Erlandsson J, McQuaid C D, Porri F, Westerbom M, *et al.*, Is habitat amount important for biodiversity in rocky shore systems? A study of South African mussel assemblages, *Mar Biol*, 161 (2014) 1507-1519. <https://doi.org/10.1007/s00227-014-2436-4>
- 44 Tavares M R, Grande H & Jacobucci G B, Habitat and food selection by herbivorous amphipods associated with macroalgal beds on the southeast coast of Brazil, *Nauplius*, 21 (1) (2013) 09-15. <https://doi.org/10.1590/S0104-64972013000100002>
- 45 Goecker M E & Käll S E, Grazing preferences of marine isopods and amphipods on three prominent algal species of the Baltic Sea, *J Sea Res*, 50 (4) (2003) 309-314. <https://doi.org/10.1016/j.seares.2003.04.003>
- 46 Navarro-Barranco C, Tierno-de-Figueroa J M, Guerra-García J M, Sánchez-Tocino L & García-Gómez J C, Feeding habits of amphipods (Crustacea: Malacostraca) from shallow soft bottom communities: Comparison between marine caves and open habitats, *J Sea Res*, 78 (2013) 1-7. <https://doi.org/10.1016/j.seares.2012.12.011>
- 47 Vázquez-Luis M, Sanchez-Jerez P & Bayle-Sempere J T, Does the invasion of *Caulerpa racemosa* var. *cylindracea* affect the feeding habits of amphipods (Crustacea: Amphipoda)? *J Mar Biol Assoc UK*, 93 (1) (2013) 87-94. <https://doi.org/10.1017/S0025315412000288>
- 48 Aikins S & Kikuchi E, Grazing pressure by amphipods on microalgae in Gamo Lagoon, Japan, *Mar Ecol Prog Ser*, 245 (2002) 171-179. <https://doi.org/10.3354/meps245171>
- 49 Amsler M O, Huang Y M, Engl W, McClintock J B & Amsler C D, Abundance and diversity of gastropods associated with dominant subtidal macroalgae from the western Antarctic Peninsula, *Polar Biol*, 38 (2015) 1171-1181. <https://doi.org/10.1007/s00300-015-1681-4>
- 50 Buschmann A H, Intertidal macroalgae as refuge and food for amphipoda in central Chile, *Aquat Bot*, 36 (3) (1990) 237-245. [https://doi.org/10.1016/0304-3770\(90\)90037-L](https://doi.org/10.1016/0304-3770(90)90037-L)