

Sediment organic matter content drives bivalve density in tropical oligotrophic seagrass ecosystem

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Seagrass ecosystems are storehouses of both autochthonous and allochthonous organic matter due to their presence at the land and sea interface. This organic matter acts as a food source and plays an important role in biodiversity assemblages within seagrass ecosystems. The present study assessed the density of the bivalve (*Cardita calyculata*) along a gradient of sediment Organic Matter (OM %) in the mono-specific seagrass meadows of *Thalassia hemprichii* to those in adjacent bare sediments in the Andaman and Nicobar Islands (ANI) of India. The present study also assessed the correlation between sediment OM with *Cardita*'s density and seagrass morphometric traits. *C. calyculata* density was 2-fold higher in *T. hemprichii* meadows (647.7 ± 27.0 ind. m^{-2}) than in the bare sediment (306 ± 14.3 ind. m^{-2}). Bivalve abundance correlated positively with OM in the seagrass meadows but showed no correlation in the unvegetated areas. The root branching of seagrass was higher, leading to increased *C. calyculata* density, suggesting a strong correlation of seagrass meadows with bivalves in nutrient-rich environments. The correlations between *C. calyculata* density and various plant traits were positive. Our study suggests that in the oligotrophic coastal ecosystems of the ANI, the positive influence of sediment OM of seagrass meadows on *C. calyculata* density is significant. Further studies looking at various interactions between seagrass and *C. calyculata* are essential to establish the precise interrelationship between seagrass and the biodiversity of associated faunal assemblages.

[**Keywords:** *Cardita calyculata*, India, Tropical island, Oligotrophic, Seagrass, *Thalassia hemprichii*]

Introduction

Seagrasses are ecosystem engineers that provide various ecological and ecosystem services¹⁻³. Seagrass ecosystems also sustain abundant and diverse benthic fauna compared to other intertidal habitats, providing food and shelter^{4,5}. Bivalves are one of the common benthic organisms associated with seagrass ecosystems due to high concentrations of sediment Organic Matter (OM)⁶⁻⁸. Bivalves prefer the seagrass rhizosphere as a suitable habitat as there is continuous supply of oxygen through the root radial diffusion. In contrast, the bivalves (depending on the species) provide various beneficial services to the seagrasses. For example, the Lucinid bivalves (such as *Loripes lucinalis*, *Luciniscia nassula*, *Loripes orbiculatus*, and *Ctena orbiculata*) that are commonly associated within the sediment of seagrasses, *Cymodocea nodosa*, *Zostera noltei*, *Posidonia oceanica*, and *Thalassia testudinum* help in reducing sulphide toxicity generated from decomposition of sediment OM in the root-adjacent sediments by oxidizing pore

water sulphide^{6,7,9}. Besides reducing sulphide toxicity, the bivalve *L. orbiculatus* also contributes positively to the nitrogen budget in the sediments of *P. oceanica*⁶. Other bivalves, such as hard clams *Mercenaria americanus* help increase sediment nutrient content in *T. testudinum* meadows¹⁰. Such interactions between seagrasses and bivalves play an important ecological role in seagrass persistence and resilience to various human-induced changes.

The seagrass ecosystems of India are part of global bioregion model five in the Indo-Pacific, with highest number of seagrass species^{11,12}. India's seagrass beds occupy estuarine areas to lagoons, bays, backwaters and the open sea systems¹³⁻¹⁸. These seascapes are inhabited by 16 of the 19 seagrass species found in the South and Southeast Asia, covering an area of 517 km² and up to a depth limit of 21 m^(refs. 19,20). Several marine molluscs (including bivalves) inhabit seagrass ecosystems, and these bivalves act as food source and generate livelihood for coastal communities^{21,22}. In India, most of the studies on bivalves in seagrass

ecosystems have showcased higher density of bivalves with respect to the total molluscan diversity²²⁻²⁴. For example, in the oligotrophic seagrass ecosystems of the Lakshadweep Islands (southwest coast of India), the density of bivalves was found to be lower (7.5 %) compared to the total molluscan diversity²⁵; whereas, in the nutrient-rich seagrass ecosystems of Palk Bay of Tamil Nadu (southeast coast of India) bivalve density was higher (20 %) compared to the total benthic diversity²³. Consequently, various other factors (such as sediment OM content, oxygenic sediment and the presence of benthic invertebrates as a food source) also drive the density of bivalves within these seagrass ecosystems are less understood. Sediment OM content plays an essential role in bivalve density in intertidal seagrass ecosystems²⁶. However, a recent study from the intertidal ecosystems without seagrasses on the east coast of India has showcased both positive and negative correlations of OM content with bivalve density. For example, the density of *Paphia malabarica* increased with an increase in sediment OM content, and that of *Meretrix casta* decreased with an increase in sediment OM content in an estuarine habitat²⁶. Consequently, knowledge of how OM content drives the presence of various species of

bivalves within the seagrass ecosystems, is non-existent in the Indian context.

Therefore, the objectives of this study was to assess: (1) the effects of sediment OM content in seagrass (*Thalassia hemprichii*) meadows on the density of the bivalve (*Cardita calyculata*), and (2) derive the relationship between *Cardita* density with various seagrass morphometric traits for habitat suitability. The study assesses whether or not the presence of seagrass influences the presence of *Cardita* bivalves by comparing *Cardita* densities with and without seagrass meadows. The bivalve *C. calyculata* is selected as it is one of the most abundant bivalves found in the intertidal ecosystems of oligotrophic waters of the Andaman and Nicobar Islands (ANI)²⁷.

Materials and Methods

Study site

A survey was conducted within the *T. hemprichii* meadows of the ANI of India. Sampling of seagrass and associated *C. calyculata* bivalves was carried out at three locations: Swaraj Dweep (hereafter Havelock Island), Saheed Dweep (hereafter Neil Island) and Burmanallah (Fig. 1). The sampling was conducted during the dry season (February – March 2019). At

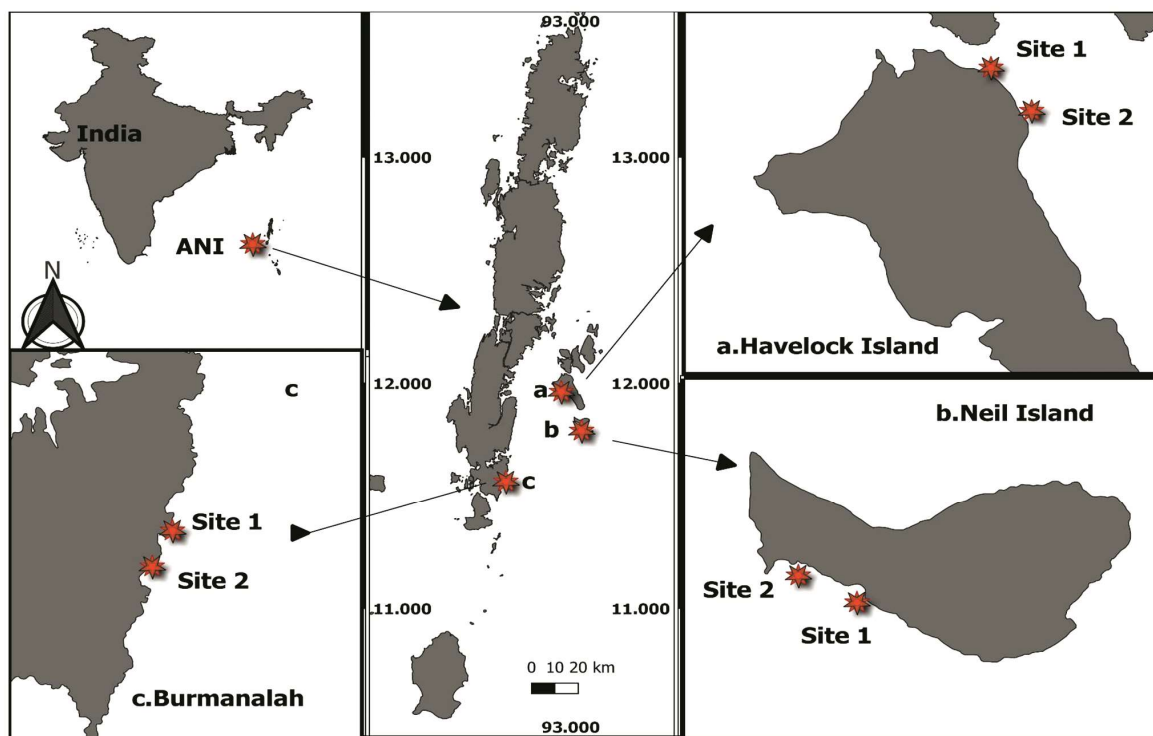


Fig. 1 — Map of study area showing the three locations: a) Havelock Island, b) Neil Island, and c) Burmanallah of ANI, India. The vegetated areas are represented by Site 1 and the Site 2 represents the unvegetated areas of each location, respectively

each location, two sites were selected, one with seagrass vegetation (VG, Site 1) and another without seagrass (UVG, Site 2). A semi-diurnal tidal amplitude of 2.45 m with temperature ranging from 26.3 – 35.7 °C and salinity between 32 – 35 ‰ was exhibited by these study locations¹³. The vegetated sites of Neil and Havelock Islands were 1000 m and 800 m away from the unvegetated sites and were separated by dead coral patches. The mono-specific meadows of *T. hemprichii* were sampled at a depth of 0.5 m during low tide. At Burmanallah, the seagrass site was at 500 m distance from the unvegetated area. The seagrass site was sampled at 0.3 m during the low tide.

Sediment sampling

Ten sediment cores (n = 10) were collected from each quadrat of both sites where seagrass was sampled, using a 5 cm wide and 10 cm long plastic corer. The corer was pushed up to 10 cm into the sediment while sampling and further depth was not possible due to presence of near surface dead coral reef structures or bed rock of volcanic origin¹⁸. Sediment cores were collected in zip-locked plastic bags and transferred to the laboratory in dark boxes. In the laboratory, the sediment samples were placed in aluminium weighing boats and oven-dried at 60 °C for 72 h. These dried sediment samples were sieved for various grain-sized fractions (500, 150, 75, 63 µm). The fine fraction of the sediment (< 75 µm) was used for deriving sediment OM content using the Loss on Ignition (LOI) method²⁸. Five grams of sediment were combusted at 500 °C for 4 h in a muffle furnace (Muffle Furnace-R type, SCIENTECH, SE-130, India). The difference between the weight of the initial (A) and final (B) sample was considered as the fraction of OM expressed as a percentage (%; Eq. 1) of total dry weight.

$$LOI (\%) = \left[\frac{A-B}{A} \right] * 100 \quad \dots (1)$$

Seagrass and bivalve sampling

At each site of all three locations, ten random quadrats (20 cm × 20 cm) were collected from a transect of 30 m perpendicular to the beach at a depth of 0.3 – 0.5 m during low tide. A quadrat and a hand shovel was used to dig out seagrass and associated *C. calyculata* bivalve samples up to 10 cm in depth from the centre of the seagrass meadows. The seagrass meadow edges were avoided. Similarly, the sampling was repeated to collect ten random quadrats

from the unvegetated areas of each site at all three locations. From each quadrat of seagrass meadows, the entire plant (*i.e.*, leaves, rhizomes and roots) were collected. The seagrass tissues were rinsed off carefully in the field with seawater and brought to the laboratory for further analysis. In the laboratory, the seagrass tissues were rinsed carefully again with distilled water, keeping the plant rhizome mat intact to estimate the Root Branching Index (RBI) correctly. The leaves were scrapped of the epiphytes using a glass slide and were dried in an oven at 70 °C for 48 h and weighed to estimate root biomass (g DW m⁻²).

In the laboratory, the live *Cardita* bivalves were separated from the seagrass rhizome mats and were counted to evaluate their density (individuals/m²). The shoot density for *T. hemprichii* was estimated by counting the individual shoots per quadrat^{14,18}. From each quadrat 10 random roots were selected to estimate the maximum root length, and count the number of primary and secondary ramifications. The RBI was calculated as the total number of ramifications divided by the total root length. The seagrass fractions were then rinsed with distilled water, oven-dried at 70 °C for 48 h and weighed. The dried roots were used to derive a Root Weight Ratio (RWR) to express the relative density of roots versus leaves. The RWR was calculated as the root biomass (g DW) divided by the sum of root biomass plus the leaf biomass (g DW).

Statistical analysis

The statistical significance between *T. hemprichii* traits and *Cardita* density was tested using a two-way ANOVA. The seagrass habitat (vegetated and unvegetated areas) and the three locations (Neil, Havelock and Burmanallah) were used as fixed factors. All data were tested for normality (Shapiro-Wilk's test) and homogeneity of variance (F-test). When variances were not homogenous, the corresponding data were root-square transformed. The Holm-Sidak test was performed for a posteriori comparison among factor levels (sites and locations) when there were significant interaction effects. Linear regression analysis was used to derive the correlation between sediment OM content, seagrass traits (root biomass, RWR, RBI and shoot density) and *C. calyculata* density at *p* < 0.05 significance level. The data are presented as mean and Standard Error (SE). All statistical analysis was carried out using SIGMAPLOT (Ver. 11.02) software.

Results

Cardita bivalves were present at all sampling locations of ANI, with variation in density between the vegetated (*T. hemprichii* meadows) and unvegetated areas (bare sediment). *Cardita* density was significant and different among the habitats (two-way ANOVA, $F_{1,54} = 406$, $p < 0.001$) and locations ($F_{2,54} = 175.4$, $p < 0.001$, Fig. 2). The density of *Cardita* bivalves within seagrass meadows ranged from 646.7 ± 22.8 ind. m^{-2} to 1211.0 ± 47.4 ind. m^{-2} , whereas within the unvegetated areas, bivalve density ranged from 298.8 ± 11.6 ind. m^{-2} to 595.2 ± 18.6 ind. m^{-2} . The mean *Cardita* density was 2-fold higher within the seagrass meadows (835.7 ± 30.5 ind. m^{-2}) than in the unvegetated areas (406.2 ± 16.6 ind. m^{-2}). The effect of sediment OM content on the *Cardita* density was significant ($R^2 = 0.80$, $p < 0.001$) and positive within the seagrass meadows but not within the unvegetated areas (Fig. 3). The mean sediment OM content was significantly different ($F_{1,54} = 90.49$, $p < 0.001$) across the seagrass meadows (56.0 ± 3.5 %) and was 1.4-fold higher than unvegetated areas (36.0 ± 2.1 %).

Seagrass traits such as RWR, RBI, root biomass and shoot density varied along the sediment OM gradient (Fig. 4). The relative biomass allocation to roots, as indicated by the RWR, showed no variation with an increase in OM content (Fig. 4a). However, the RBI of the seagrass roots was significantly correlated to the change in OM gradient, meaning higher branching of roots leads to an increase in storage of OM within the *T. hemprichii* sediment (Fig. 4b). These changes in root morphology were visible during the field sampling, where OM-rich sediments were highly branched. However, the obtained RBI was different for *T. hemprichii* plants among the three locations with higher branching at the seagrass meadows of Neil Island (14.07 ± 0.53) followed by Burmanallah (8.5 ± 0.3) and Havelock (3.5 ± 0.14).

This positive relation of RBI ($R^2 = 0.69$) with OM resulted in a significantly increased correlation ($R^2 = 0.82$) of OM gradient with root biomass (Fig. 4b). Similarly, the shoot density of the seagrass meadows was positively correlated ($R^2 = 0.97$) with sediment OM content (Fig. 4d). *Cardita* density was significantly and positively correlated with various plant traits, such as RWR, RBI, root biomass and shoot density (Fig. 5). Positive correlations were observed with root biomass ($R^2 = 0.81$), RBI ($R^2 = 0.88$), shoot density ($R^2 = 0.95$), and RWR ($R^2 = 0.68$).

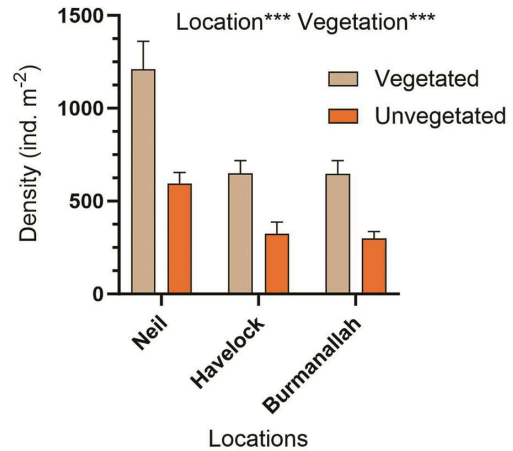


Fig. 2 — Mean density of *Cardita* clams (ind. m^{-2}) in seagrass (*T. hemprichii*) vegetated meadows and unvegetated areas of Neil, Havelock islands and at Burmanallah of ANI, India. Error bars represent standard error. Significant ($p < 0.001$ ***) differences between location and vegetation (VG and UVG) of each location was derived from two-way ANOVA analysis using location and vegetation as fixed factors

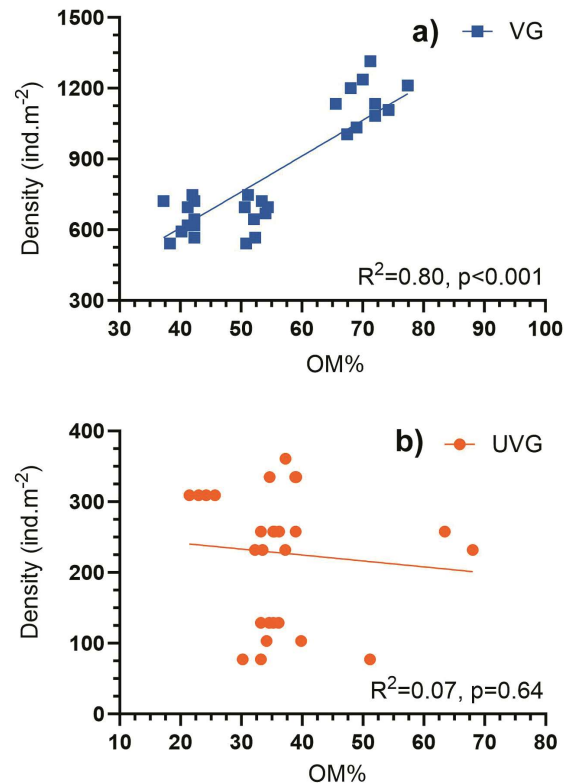


Fig. 3 — *Cardita* abundance and its correlation with organic matter (OM %) in the sediment: a) Vegetated (VG) meadows, and b) Unvegetated (UVG) areas of Neil, Havelock and Burmanallah, of ANI, India. R^2 and p values are presented from linear correlation analysis at significance ($p < 0.05$)

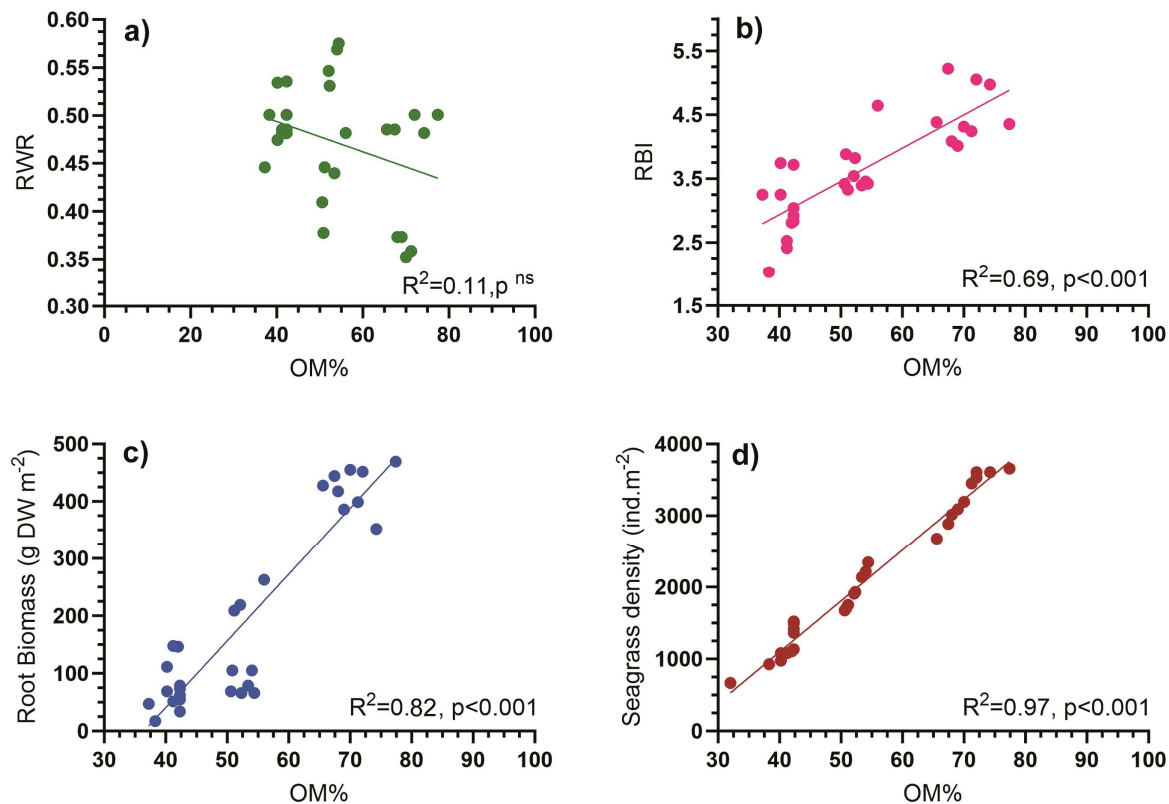


Fig. 4 — Correlation between organic matter content (%) and various *T. hemprichii* traits: (a) Root Weight Ratio (RWR), (b) Root Branching Index (RBI), (c) root biomass (g DW m⁻²), and (d) shoot density (ind. m⁻²). R^2 and p value are presented

Discussion

Seagrass ecosystems can store large quantities of autochthonous and allochthonous OM in their sediments^{18,29}. This sediment OM, drives diverse benthic biodiversity assemblages such as gastropods, bivalves and various other invertebrates^{30,31}. Results of this study show that the density of *Cardita* bivalves increased with increase in sediment OM content in the *T. hemprichii* meadows of ANI. In contrast, the results disagree with a few previous studies that observed a decrease in bivalve density in seagrass meadows with increased sediment OM content. For example, the density of lucinid bivalves decreased in *C. nodosa*, *T. testudinum* and *Z. noltei* meadows with an increase in sediment OM load^{7,32,33}. However, the increase of *C. calyculata* density with an increase in sediment OM in this study indicates the existence of a positive relationship between *T. hemprichii* and *Cardita* bivalves of ANI. This increase in *C. calyculata* density also appears to be positively related to various morphometric features of *T. hemprichii*, especially roots, which are highly branched with higher root biomass in OM-rich

sediments (Fig. 4b & c). Similar to results of present study, high molluscan abundance in *T. hemprichii* meadows was observed in Indonesia in relation to sediment organic matter content and seagrass morphometric traits⁴. A similar correlation of molluscan abundance with sediment organic matter and plant traits was also observed for *P. oceanica* and *Z. noltei* meadows of the Mediterranean Sea^{27,31}.

The study locations of the present study (Neil, Havelock and Burmanallah) receive OM input from the adjacent mangrove ecosystems^{14,18,35}, and the presence of higher density of *Cardita* bivalves could be beneficial for the *T. hemprichii* meadows that otherwise would have been subjected to toxic sulfide produced by decomposition of OM. However, in this study, there is no natural river run-off to the intertidal seagrass ecosystems of ANI, except the mangrove creek at Burmanallah, which brings OM during receding tides^{18,35,36}. Furthermore, the coastal waters of ANI are oligotrophic; as a result, the *T. hemprichii* ecosystems of ANI mainly depend on the nutrients derived from decomposition and cycling of OM within the seagrass ecosystem, and from input of

nutrients from the adjacent mangroves^{18,35,37}. However, as coastal marine sediment lacks free oxygen, the OM stored in the sediment of *T. hemprichii* meadows is decomposed by the bacterial population that uses sulphate in seawater as an electron acceptor instead of oxygen and produces toxic sulphide as a metabolic end product, which is toxic to seagrass. To avoid this toxicity, seagrasses transport oxygen to their roots through radial diffusion^{38,39}. But under warmer conditions, sulphide production can outpace oxygen distribution, resulting in higher sulphide accumulation in seagrass sediment and consequent seagrass mortality^{39,40}. The intertidal *T. hemprichii* ecosystems of ANI are exposed to high temperature and desiccation as a result of which these meadows may be subjected to sulphide stress through decomposition of OM. However, the presence of a higher density of *Cardita* bivalves along the *T. hemprichii* meadows and their positive interactions may help them overcome this stress. Secondly, the *T. hemprichii* population of ANI are found to harbour various bacterial populations that can assist in decomposing OM and reducing sulphide toxicity^{41,42}. Consequently, isotopic sulphur studies of various molluscs associated with the sediment of seagrass ecosystems have revealed a common association of sulphur-reducing bacteria in tissues of various gastropod and bivalves that inhabit sediment enriched with sulphur⁴³. The chemosynthetic bacterial population of *C. calyculata* bivalves, if any, is yet to be catalogued in India, which could have provided meaningful insights. But presence of sulphide stress in the sediment of *T. hemprichii* meadows may be one of the reasons why the population trends of *T. hemprichii* at our study locations are declining¹⁴.

The intertidal seagrass ecosystems possess substantial phenotypical plasticity in their morphological traits. This plasticity aids seagrass adaptation to withstand the intertidal high temperature, desiccation and hydrodynamics⁴⁴. This adaptation strongly influences seagrass interactions with other species^{14,17,45}. As a fast-growing species *T. hemprichii* from ANI shows high resilience to intertidal stress through variation in morphological and reproductive traits^{14,46}. In particular, *T. hemprichii* root morphology and architecture play an important role in seagrass adaptive response to intertidal stress. The roots increase their density and branching frequency when above-ground structures are damaged due to intertidal habitat disturbance^{14,16}. This

adaptation helps optimize seagrass biomass allocation and exploitation of nutrients available in the water and sediment pool⁴⁷. This is evident in the results of present study as the *Cardita* bivalve density, RBI and root biomass of *T. hemprichii* are positively correlated. This positive correlation can influence the various interactions between *Cardita* and *T. hemprichii*. It is evident from previous studies that seagrass roots can facilitate the presence of various species of bivalves, either through providing suitable habitat (by the roots) or through resource facilitation by providing oxygen through root radial diffusion^{40,48}. This is also seen in the present study as *Cardita* bivalves are more abundant in the seagrass meadows than the unvegetated areas. Moreover, the *Cardita* density was positively correlated with various morphometric features of *T. hemprichii* meadows, such as RWR, root biomass and shoot density (Fig. 5) suggesting that plant root traits and density are the major drivers influencing *C. calyculata* density in *T. hemprichii* meadows.

Other factors, such as sediment grain size, pH and salinity, play an important role in OM decomposition and mobilization^{14,18,36,49}. A positive correlation exists between sediment OM content and grain size in the intertidal ecosystems of ANI. This correlation should have the same impact across *T. hemprichii* meadows and unvegetated areas. But the results of this study show that the *Cardita* density varies only along the seagrass meadows. This suggests *T. hemprichii* morphometric traits provide suitable habitat and food and oxygen provisioning for the *Cardita* bivalves unlike the adjacent unvegetated areas. However, the presence of *C. calyculata* in the unvegetated areas suggests, even though low in concentration, OM also facilitates *Cardita* distribution in intertidal ecosystems. One of the other reasons for the presence of *C. calyculata* bivalves in the unvegetated areas could be the abundance of various zoobenthic biomass that serve as a food source for bivalves, which can be in low concentration in the seagrass meadows due to the anoxic environment^{30,31}. Secondly, the sediment grain size of the *T. hemprichii* meadows is high in sand and coral rubble that provides porosity and easy oxygen transfer to the associated *Cardita* bivalves^{14,36} compared to the silty and muddy habitats of the unvegetated areas, where oxygen transfer is low^{31,50}.

The interactions between seagrass species and the associated biodiversity help the seagrasses persist

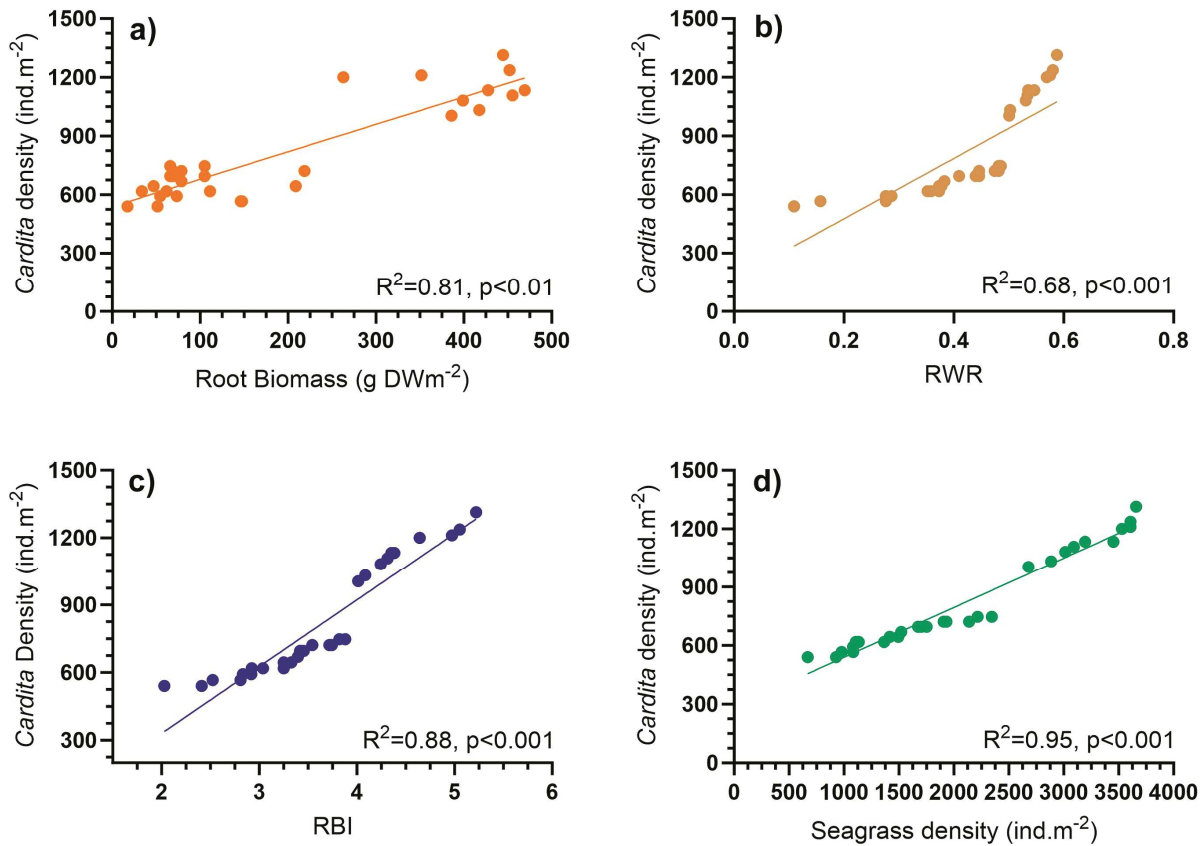


Fig. 5 — Correlation between *Cardita* abundance and various seagrass traits: (a) Root Weight Ratio (RWR), b) Root Branching Index (RBI), c) root biomass (g DW m⁻²), and d) shoot density (ind. m⁻²). R² and p value are presented

under a broader range of conditions³⁰. However, understanding the strength of these interactions under the influence of various stress conditions is important to assess the resilience of both species. Within this framework, the high density of *C. calyculata* bivalves within *T. hemprichii* meadows may help the *T. hemprichii* meadows under various intertidal stress conditions⁴⁸. The results of the present study showcase that the bivalve density is highest at Burmanallah within the *T. hemprichii* meadows where the population dynamics (*i.e.*, growth, recruitment and mortality) of this seagrass is declining¹⁴. This suggests that *Cardita* bivalves may provide beneficial interactions to *T. hemprichii* meadows that can help this meadow sustain intertidal stress and recover, but this reasoning requires further investigation. These interactions between seagrass and bivalves may be disrupted due to the ongoing climate change scenarios, especially ocean acidification and water temperature increase^{17,51}. Weakening of these interactions due to increase in water temperature has been observed for *Z. noltei* associated with lucinid

bivalves³². Consequently, the effects of ocean acidification on marine bivalves and seagrass ecosystem services have been studied separately and there is a need to assess the influence of ocean acidification on various interactions between seagrass and bivalves for India's coastal ecosystems⁵². The Andaman Sea (part of Bay of Bengal) is undergoing rapid ocean acidification and temperature increase⁵³, so studies pertaining to the effects of these changes is necessary for the seagrass and bivalves of ANI.

These island ecosystems are nutrient-poor, but the OM rich sediments may provide the seagrass ecosystems with sufficient nutrients. This also suggests that seagrass ecosystems of ANI have other mechanisms to survive an increase in OM content and the associated sulphide toxicity, as observed for *Z. noltei* ecosystems⁵⁴.

Conclusion

This study shows that OM content in the sediment of seagrass (*T. hemprichii*) ecosystems play an important role in *C. calyculata* bivalve density in

oligotrophic coastal ecosystems. Seagrass ecosystems adjacent to mangroves have a higher input of OM in tropical island settings and play an important role in seagrass-bivalve diversity and interactions. Increased anthropogenic pressure from human activities along the coastline has led to decline of the seagrass ecosystems of ANI^{14,16}. The positive relationship between *C. calyculata* bivalves and *T. hemprichii* can provide resilience for restoration of these seagrass ecosystems, but this proposition needs further investigation. The loss of seagrass ecosystems of ANI can lead to loss of biodiversity assemblages and various other ecosystem services⁵⁵. Therefore, it is critical to understand the various inter-relationships that exist between biodiversity assemblages and seagrass plants and replicate these kinds of studies across various seagrass species of ANI to have a better spatial representation.

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Conflict of Interest

The authors declare that they have no conflict of interest with any organization or funding agencies.

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Ethical Statement

All authors agreed to the ethical principles.

Author Contributions

AKM & SHF: Conceptualization, investigation, methodology, data acquisition, data analysis, writing original draft, reviewing and editing, and funding acquisition. SHF: Supervision & validation.

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