Tropical seagrass under range extension provides similar ecosystem services compared to natural meadows

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Abstract

How range extended meadows of seagrasses compare in ecosystem services with existing meadows is less understood. This study reports for the first time the range extension of three tropical seagrass species, i.e., *Halophila ovalis*, *Halodule uninervis* and *Ruppia maritima* from the Asia's largest brackish water Chilika lagoon into nearby inland areas along the coast of Odisha. Surface water samples, sediment and seagrass biomass of the three species were collected and standard protocols were followed to measure seagrass morphometrics and quantify the sediment carbon (C) and nitrogen (N) stocks. Results indicate high saline conditions favored the establishment of new seagrass meadows. In addition to high salinity, significantly higher sediment N content supported increased growth and morphometrics for the seagrasses except for *H. uninervis* whose growth was limited due to excessive algal growth. Longer leaves were observed in *R. maritima* followed by *H. uninervis* and *H. ovalis*. The mean sediment C stocks in *R. maritima* (6.93 ± 2.28 Mg C ha^{-1}) was the highest followed by the sediment C stocks of *H. ovalis* (1.73 ± 0.97 Mg C ha^{-1}) and *H. uninervis* (1.48 ± 0.26 Mg C ha^{-1}). The combined CO_2 storage and climate change mitigation potential of these newly discovered meadows is 111.73-ton CO_2 per ha with an economic value of US$ 0.009 million. The total N stocks of the three-seagrass meadow was 67.59 ± 4.33 Mg N ha^{-1}, providing additional co-benefits of nutrient retention. Our study highlights better management and monitoring for seagrass meadows from the coast of Odisha.

1. Introduction

Seagrasses provide various ecosystem services and support various trophic networks and ecosystem functions (Stankovic et al. 2021; Mishra et al. 2023). One of the important ecosystem services of seagrass include climate change mitigation through carbon (C) sequestration, with global storage of 140 Mg C ha^{-1} (top 1 m soil), valued at US$ 190.67 ± 30 bn yr^{-1} (do Amaral Camara Lima et al. 2023; Guo et al. 2025). Therefore, conservation, management and restoration of seagrass ecosystems are considered as nature-based solutions (NbS) for climate change mitigation (Macreadie et al. 2021). However, seagrass ecosystems are also the most threatened marine ecosystems globally under anthropogenic disturbances and climate change scenarios (Duarte et al. 2018; Chefaoui et al. 2018).

Seagrass as ecosystem engineers avoid poor or stressful environment (e.g., anthropogenic pollution or under climate change scenarios), by migrating or extending their range to new suitable conditions. This range extension is achieved either through vegetative propagation (e.g., fragment of seagrass shoots that can settle at new habitat) or through reproductive process (Willette and Ambrose 2009; Winters, G. et al. 2020). Seagrasses in their new habitat can alter local biotic and abiotic factors and provide various functions such as sheltering and amelioration of environmental conditions (e.g., temperature oscillations and ocean acidification etc.,) and promote unique biodiversity assemblages (Gorman et al. 2020; Kim et al. 2020; Pavone et al. 2020). For example, the range extension of the seagrass *Halophila decipiens* to new habitats have resulted in the increase of benthic invertebrate biodiversity from the coast of Brazil (Pavone et al. 2020).

Till date the range extension of eight species of seagrasses have been recorded globally with most of these range extension studies limited to the coast of South and North America (Gorman et al., 2020; Pavone et al., 2020; Short et al., 2006 and references there in). Most common reasons for seagrass range extension observed are favorable temperature, good water quality and nutrient conditions and suitable habitat (e.g., availability of fine sediment particles). Few studies from the coast of Florida, USA, and Australia have also indicated natural cyclones or hurricanes and global shipping (use of ballast water) as reasons for range extension of *Halophila johnsonii*, *Halophila decipiens* and *Halophila nigricaulis* (Virnstein and Hall 2009; Smith et al. 2018). Most of these studies have reported the seagrass morphometrics, eco-physiology, reproductive ecology and benthic biodiversity assemblages, whereas the effects of these range extension on ecosystem services such as C storage is not assessed yet (Virnstein and Hall 2009; Smith et al. 2018).

Within this framework, this study aimed at assessing the relationship between water and sediment quality parameters and quantify the ecosystem services (e.g., C and nitrogen (N) stocks) of newly observed three tropical seagrass meadows (*Halophila ovalis*, *Halodule uninervis* and *Ruppia maritima*). These seagrass meadows have extended their range from the Asia's largest brackish water Chilika lagoon, India to nearby saltpan areas or connecting canals. We hypothesize that favorable saline conditions and anthropogenic nutrient enrichment supported the range extension of these seagrasses and can provide similar ecosystem services such as C storage compared to the natural meadows of the lagoon. This study also calculated the economic evaluation of the C storage of this newly discovered seagrass meadows. Additionally, we quantified the N stocks of these newly discovered seagrass meadows that can be integrated as additional co-benefits provided by seagrass ecosystems in nutrient retention.

2. Materials and Methods

2.1. Study site

Palur canal is a 14-kilometer-long channel that connects the southern section of the Chilika lagoon (Fig. 1) to the Bay of Bengal at the Rushikulya river mouth (Suresh et al., 2018). In the Chilika lagoon, six species of seagrass have been identified: *H. ovalis, Halophila ovata, Halophila beccarii, H. uninervis, Halodule pinifolia, and Ruppia maritima* (Acharya et al., 2023). The canal experiences a low tidal influence and is subjected to significant anthropogenic activity; from agricultural runoff, and small-scale shrimp farm effluents

2.2. Sediment sampling and analysis

Six replicate cores were collected using a plastic corer (15 cm depth x 5 cm diameter) from the seagrass meadows at each location (Fig. 1). The sediment corer was pushed down to a depth of 10 cm, and sediment collected were sectioned at 5 cm intervals and were transferred to the laboratory. In the laboratory, the sectioned samples were oven dried at 60°C for 48 h. The sediment dry bulk density (DBD g cm^{-3}) was quantified by multiplying the sediment dry weight with the core volume (Howard et al.

2014). The dried sediment samples were homogenized using a disc mill grinder (Retsch, RS200, USA) and 0.30 mg of each replicate was used for total carbon (C%) and nitrogen (N%) analysis using an Elemental Analyzer (Elementar, UNICUBE). The total C stocks (Mg C ha^{-1}) and N stocks (Mg N ha^{-1}) was calculated by adding the total C stocks in the sediment (top 10 cm only) following the methods described in the Blue Carbon Manual (Howard et al. 2014). The carbon dioxide (CO_2) equivalent was calculated by multiplying 3.67 with the mean sediment C stocks (Mishra et al. 2025a) to derive the CO_2 abatement potential of these newly discovered meadows. The social cost of carbon (SSC) was calculated using the regional approach for India. Recent US$ to Indian Rupees (INR) conversion (IUS$=86.14 INR) was used to estimate the price of CO_2 in INR.

2.3. Plant sampling and Analysis

Six random replicate quadrats (20 cm x 20 cm) were collected from seagrass meadows, where sediment cores were collected (See Supplementary Fig.S1). The seagrass was dug up with a hand-held shovel up to 10 cm depth and transported to the laboratory. In the laboratory, the samples were washed with deionized water and removed of any debris. The individual shoots of each species were counted to calculate the shoot density (ind. m^{-2}) and plants were separated into above-ground (AG; leaves) and below-ground (BG; roots + rhizomes) tissues. Plant morphometrics (n = 20/species) like leaf length (cm), width (cm) and internode lengths (cm) were measured for each species using a Vernier Caliper. After measurement, the plants were oven dried at 60°C for 48 h. Dried plants were grinded in a mortar and pestle and processed for total C and N analysis following the same process for the sediment samples.

2.4. Statistics

A one way-ANOVA was used to test the significant ($p < 0.05$) differences in sediment and plant traits, except leaf width for which an unpaired t-test was used for the seagrass *H. ovalis* and *H. uninervis* only. All data was pre-checked for normality and homogeneity of variance using Shapiro-Wilk and Levene's test respectively. When interactions were detected, Tukey's post hoc test was used. Non-linear regression was to derive relationship between seagrass tissue N content and the log transformed C:N ratios. Principal Component Analysis (PCA) was used to test the relationship between sediment and plant variables. All data is presented as mean ± standard deviation (SD) and all graphs were generated in GraphPad PRISM (ver. 10.4.2).

3. Results

3.1. Sediment variables of the newly discovered meadows

The salinity of the shallow water samples of the Palur canal above the three seagrass meadows were significantly different (See Supplementary Fig. II). The mean highest salinity was observed in the *R. maritima* meadows (28.49 ± 4.12) followed by similar levels in the *H. ovalis* and *H. uninervis* meadows (Supplementary Fig. II). Among the sediment variables, the sediment N content showed significant differences among the sites, whereas no significant differences were observed for sediment total C and sulfur (S) content (Supplementary Fig. II). The highest mean sediment total N was observed in the *H.*

uninervis (2.53 ± 1.26%) meadows, followed by *R. maritima* (2.47 ± 0.86%) and the lowest in the *H. ovalis* (1.53 ± 0.46%) meadows (Supplementary Fig. II).

Significant differences were observed for the sediment C stocks and N stocks for the three seagrass species (Fig. II). Highest mean sediment C stocks were observed in *R. maritima* meadows (6.93 ± 2.28 Mg C ha^{-1}) followed by *H. ovalis* (1.73 ± 0.97 Mg C ha^{-1}) and *H. uninervis* (1.48 ± 0.26 Mg C ha^{-1}) (Fig. IV a). The CO_2 equivalent followed the same pattern as the sediment CO_2 stocks (Fig. IV b). The total economic values of the sediment C stocks of the three newly discovered seagrass meadows were US$ 0.0096 million (Supplementary Table III). The mean sediment N stocks were highest in the *R. maritima* meadows (11.60 ± 3.28 Mg N ha^{-1}) followed by *H. uninervis* (7.15 ± 4.19 Mg N ha^{-1}) and *H. ovalis* (3.78 ± 1.01 Mg N ha^{-1}) (Fig. IV c).

The PC1 and PC2 contributed 40.26% and 21.90% respectively for sediment C stocks, whereas for the sediment N stocks, the PC1 and PC2 explained 37.87% and 23.15% variation respectively (Fig. III, Supplementary Table IV). The sediment C stocks was positively influenced by sediment N content only in the *H. ovalis* meadows, whereas the sediment N stocks was positively influenced by sediment DBD in *H. ovalis* meadows and by sediment N content in *H. uninervis* meadows (Fig. III).

3.2. Plant traits of the newly discovered meadows

High sediment N availability resulted in high N accumulation in the tissues of all three seagrass species, resulting in low C: N ratios (Supplementary Fig. V). Among the seagrass morphometric traits, statistical significance was observed for leaf length, horizontal internode and petiole length, except leaf width (Supplementary Fig. VI). Longer leaves were observed in *R. maritima* (4.77 ± 2.45 cm) followed by *H. uninervis* (4.29 ± 2.01cm) and *H. ovalis* (2.85 ± 0.81cm). Similarly, the horizontal internodes were longer in *R. maritima* (3.85 ± 1.55 cm) followed by *H. uninervis* (1.80 ± 0.40) and *H. ovalis* (0.91 ± 0.40). Contrastingly, the leaf petiole length was longer in *H. ovalis* (3.20 ± 1.56) followed by *H. uninervis* (1.07 ± 0.42 cm) and *R. maritima* (0.98 ± 1.24 cm) (Supplementary Fig.VI).

Statistical significance was observed for the shoot density, total biomass, biomass C and N stocks of the three species (Supplementary Fig. VII). The mean highest shoot density was observed in *H. uninervis* (2130 ± 399 shoots m^{-2}), followed by *H. ovalis* (2125.80 ± 336 shoots m^{-2}) and *R. maritima* (1090 ± 55.63 shoots m^{-2}). Contrastingly, the total biomass was higher in *R. maritima* (37.89 ± 4.55 g DW m^{-2}) followed by *H. uninervis* (13.03 ± 4.04 g DW m^{-2}) and *H. ovalis* (10.52 ± 0.89 g DW m^{-2}). This resulted in higher biomass C stocks in *R. maritima* (0.10 ± 0.01 Mg C ha^{-1}) followed by *H. uninervis* (0.043 ± 0.01 Mg C ha^{-1}) and *H. ovalis* (0.033 ± 0.03 Mg C ha^{-1}). However, for all three seagrass species the biomass N stocks ranged from 0.03 to 0.01 Mg N ha^{-1} (Supplementary Fig.IV).

4. Discussion

Seagrass are ecosystem engineers and can extend their range to new suitable habitats by propagule migration through various natural and anthropogenic activities. In this study, we observed the range extension *H. ovalis*, *H. uninervis* and *R. maritima* to new inland habitats that are connected to the Asia's largest brackish water Chilika lagoon, India. Our results coincide with previous findings from the coast of Odisha, where range extension of *H. ovalis* and *H. uninervis* were previously documented 32 km away from the Chilika lagoon (Mahapatro et al. 2014). In this study, we observed that the salinity of the surface water in our study sites ranged from 13.53 to 28.49 compared to the low range of salinity 8.68 to 10.77 for the seagrasses from the Chilika lagoon (Supplementary Fig. II). This highlights, that these three seagrass species are able to tolerate high salinity levels, especially the *R. maritima* growing in shallow saltpan areas with salinity range of 20.21 to 33.22. Similar levels of mean salinity (28.51) levels have been observed for both *H. ovalis* and *H. uninervis* from other sites of the Odisha coast (Mishra et al. 2021a). One of the major reasons for high salinity in the newly discovered study sites, is the lack of freshwater input during the post- monsoon (January-March) season when our samples were collected. During this period the canal and the surrounding areas are recharged only by the tidal water regimes. Similarly, from the coast of India (e.g., Andaman and Nicobar Islands) both *H. ovalis* and *H. uninervis* inhabit high salinity under oceanic conditions (Mishra et al. 2021b).

Other favorable conditions for seagrass growth included the presence of high sediment N levels (1.53 to 2.53%) in our study sites compared to the seagrass meadows of the Chilika lagoon (0.13 to 0.16%). This resulted in higher N availability for seagrass growth (Supplementary Table III), leading to increased leaf length of *H. ovalis* (max: 6.23 cm), and width (max: 1.27 cm) in this study, compared to the *H. ovalis* of the Chilika lagoon (max leaf length; 4 cm, max leaf width; 0.88 cm) (Fig.S6). Contrastingly, the leaf length (max; 9.82 cm) and width (max; 0.15 cm) of *H. uninervis* was reduced due to increased algal growth on the leaf and sediment surface compared to the Chilika lagoon (max leaf length; 17.56 cm, max leaf width; 0.21 cm). Meanwhile, the horizontal internode length of *H. ovalis* in the Palur canal (0.91 ± 0.42 cm) was shorter compared to the *H. ovalis* internodes (4.21 ± 0.56 cm) in the Chilika lagoon, suggesting the low availability of suitable areas for meadow migration in the Palur canal. This horizontal squeeze in the canal resulted in increased leaf petiole length (3.20 ± 1.56 cm) of *H. ovalis* than the petiole length of *H. ovalis* (1.64 ± 0.04 cm) from the Chilika lagoon, indicating vertical growth of the species due to the horizontal squeeze (Mishra et al. 2021b, a). For *R. maritima* all morphometric traits are reported for the first time from the coast of India; as a result, comparisons were not possible.

The range of sediment C stocks observed in this study for *H. ovalis* (0.82 to 2.75 Mg C ha^{-1}), *H. uninervis* (1.32 to 1.78 Mg C ha^{-1}) and *R. maritima* (5.45 to 9.56 Mg C ha^{-1}) were within the sediment C stocks range (0.99 to 11.9 Mg C ha^{-1}) previously observed for mixed *H. ovalis* and *H. uninervis* from the Chilika lagoon and other coastal ecosystems of India from the top 10–30 cm (Supplementary Table III). Consequently, the sediment C stocks of this study were significantly lower than sediment C stocks (127.08 Mg C ha^{-1}) observed from 1m depth for mixed meadows of the Chilika lagoon (Ganguly et al. 2017). Interestingly, the sediment N content positively influenced the sediment C stocks, showcasing that increased N input leads to higher sediment C storage through possible contribution from algal sources. Secondly, these seagrass ecosystems through their root-rhizome reducing dynamics can filter fine sediment particles thus contributing to allochthonous sources of C (Mishra et al. 2025b). However further studies using stable isotopes of C and N would be required to assess the source contribution into sediment C pool.

The sediment N stocks from seagrass meadows are provided for the first time in India (Fig.II) and it highlights that under range extension seagrass meadows provide additional co-benefits in N retention, which can reduce coastal eutrophication (Kindeberg et al. 2018; Garcias-Bonet et al. 2019). The source of this N is mostly anthropogenic from various shrimp farm discharges and anthropogenic waste discharges, which suggests its terrestrial input. These terrestrial inputs also added finer sediment particles, which were evident from the muddy substrates during sample collection, resulting in positive relationships between sediment DBD and N stocks (Fig.III). However, this study is limited to quantify the economic valuation of sediment N stocks, as N stocks are dependent on various water quality, changes in climate and changes in air quality parameters (Keeler et al. 2016), which were not measured in this study.

This study highlights that, seagrass under favorable conditions can extend their range to new locations and modify the surrounding habitats for colonization and provide additional ecosystem service such as climate change mitigation through C sequestration and nutrient retention. This calls for increased monitoring along the Odisha coast for assessing the presence of new seagrass meadows for better conservation and management and inclusion of these ecosystems in the National Action Plan on Climate Change of India.

Declarations

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Author Contribution

AKM (Amrit Kumar Mishra): Conceptualization, Field work, Methodology, Laboratory processing, Data analysis, Manuscript writing and editing, Funding acquisitionBM (Biswajit Mahari): Field work, Data analysis, Manuscript writing and editingAM (Anjalis Mishra): Field work, Data analysis, laboratory support, manuscript writing and editingSKM (Sandip Kumar Mohakud): Field work, Data analysis, laboratory support, manuscript writing and editingSHF (Syed Hilal Farooq): Conceptualization, laboratory support, manuscript writing and editing, PM (Prasant Mohanty): Conceptualization, manuscript writing and editing, Funding Acquistion

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Data Availability

All data generated in the project are provided as results and supplementary

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Figures

Figure 1

Map of the study location showcasing the study sites from the coast of Odisha, India.

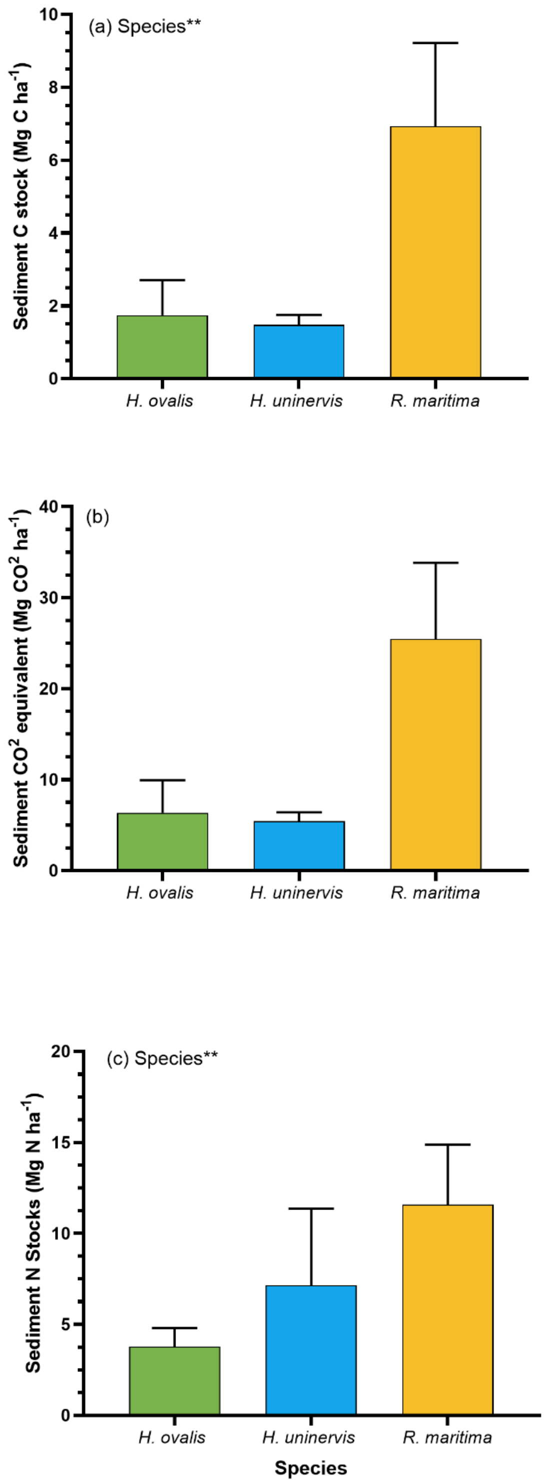

Figure 2

Mean ± SD of sediment C stocks (Mg C ha^{-1}), CO_2 equivalent (Mg CO_2 ha^{-1}) and N stocks (Mg N ha^{-1}) in the newly discovered meadows of our study sites from the coast of Odisha, India. Statistical significance ($p<0.05$) was derived from one-way ANOVA analysis using species as fixed factors. ($p<0.01$**). No statistical analysis was carried out for the CO_2 equivalent values.

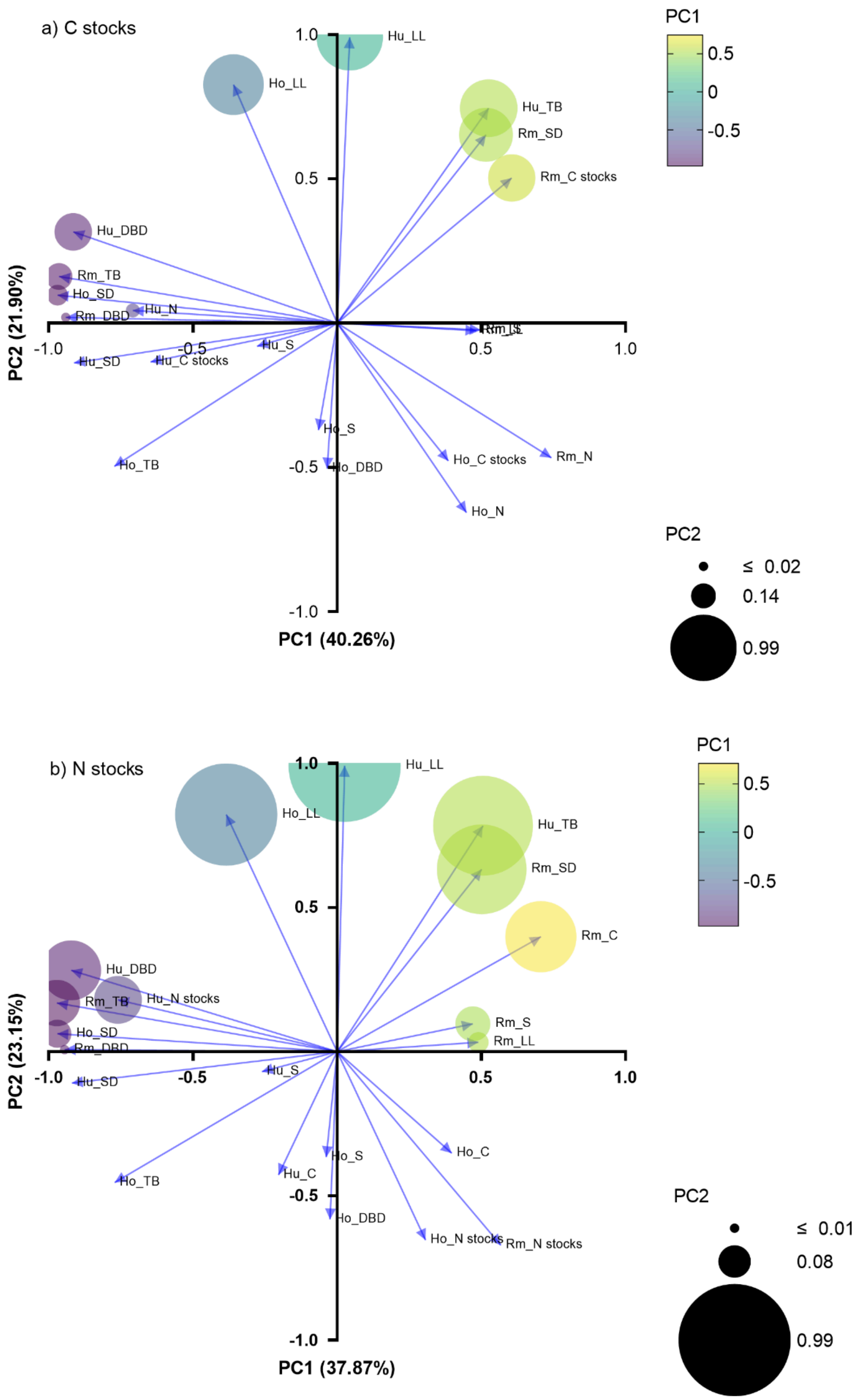

Figure 3

Principal Component Analysis (PCA) of sediment C and N stocks with other sediment and biomass variables of the newly discovered seagrass meadows from the coast of Odisha. The contribution of individual principal components is presented in Supplementary Table S1.

Supplementary Files

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