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Research article

Seagrass population dynamics and biodiversity assemblages indicate negative effects of short-term nutrient enrichment in tropical island ecosystem

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ABSTRACT

This study assessed the influence of anthropogenic short-term nutrient enrichment (hereafter enriched) effects on seagrass population dynamics (recruitment, growth rate and mortality), morphometric traits, productivity, and leaf biodiversity assemblages in the islands of Andaman and Nicobar (ANI) of India and contrasted these findings with away from these enriched areas (hereafter pristine). Seagrass (*Thalassia hemprichii* and *Cymodocea rotundata*), and sediment samples were collected in the dry season (October–May) of ANI. Reconstruction techniques, an indirect measurement of plant growth was used to derive leaf plastochrone interval (PI), i.e., number of days required to produce one leaf by the seagrass. Sediment, organic matter (OM) and carbon (C) were quantified using, loss on ignition method and CHNS elemental analyser. The total N in leaves of *T. hemprichii* and *C. rotundata* increased 3.3-fold and 2.4-fold than pristine conditions. Increased N accumulation resulted in higher shoot densities, below ground biomass, and productivity for both seagrasses. *T. hemprichii* and *C. rotundata* took 26.07 and 19.76 days respectively to produce new seagrass leaf under enriched conditions. Low apex densities resulted in lower meadow migration and increased meadow fragmentation under enriched conditions. The above ground-biomass and leaf length of *T. hemprichii* and *C. rotundata* decreased under enriched conditions leading to lower leaf meiofauna abundance. The long-term average recruitment for both *T. hemprichii* and *C. rotundata* increased under enriched conditions resulting in 3.5-fold and 11-fold higher current population growth rates resulting in increased younger plants. Contrastingly, these younger plants did not survive longer under enriched conditions, reducing the long-term seagrass population longevity to 4 years, compared to 6–7 years longevity under pristine conditions. This study highlights that nutrient enrichment in tropical islands benefits seagrass in short-term but reduces seagrass meadow migration, population longevity and biodiversity assemblages, thus reducing seagrass ecosystem service provisions, which calls for urgent monitoring and conservation of seagrass ecosystems of ANI, India.

1. Introduction

Globally, seagrasses form foundational habitats covering 0.1% of the ocean floor, while representing hotspots of coastal biodiversity assemblages, playing an important role in ecosystem functioning and providing critical ecosystem services (Costanza et al., 2014; de Groot et al., 2012; McHenry et al., 2021; Mtwana Nordlund et al., 2016). Seagrasses are key to health of any coastal ecosystems as they provide feeding and breeding habitats for a wide variety of marine organisms, including 20% of global commercially important fish populations. Additionally, they play an active role in removing bacterial pathogens contributing towards health and sustainability of coastal systems (Lamb et al., 2017; Olson et al., 2019; Unsworth, 2018). Other important ecosystem services include coastal sediment stabilization and act as a buffer against coastal erosion (Hilmi et al., 2021; Johannessen, 2022; Mishra et al., 2018; Stankovic et al., 2023; Yau et al., 2023). Further, by sequestering carbon at rates comparable to or greater than terrestrial forests, seagrasses play a vital role in mitigating climate change (Mishra

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et al., 2023; Stankovic et al., 2023). Despite, their ecological importance and highly valuable societal benefits, seagrass ecosystems are declining globally (19.1% year^{-1}), due to various direct threats from local anthropogenic activities such as declining water quality, nutrient enrichment, coastal development and regional and global climate change threats such as rising sea temperatures and marine heatwaves (Dunic et al., 2021; McKenzie et al., 2020; Turschwell et al., 2021). The compounding effect of these multiple stressors may lead to increased meadow fragmentation, degradation or in some cases complete loss of seagrass meadows (Paul Richardson et al., 2018).

Short-term nutrient enrichment due to anthropogenic activities is considered as major driver to local seagrass ecosystem degradation (Wang et al., 2022). The influx of nutrients such as nitrogen (N) and phosphorous (P), from agricultural and industrial run-off, sewage disposal etc., results in subsequent increase in their concentration in water and sediment. The increased nutrient levels promote growth of epiphytic algae or macroalgae that competes with seagrass for nutrient sources (Burkholder et al., 2007; Cabaço et al., 2013). Nutrient influx also increases water turbidity that reduces light availability for seagrass, and results in high organic matter build up, leading to sediment anoxia, ammonium and sulfide toxicity (MacLeod et al., 2023; Mishra and Farooq, 2023; Vieira et al., 2022).

Under such nutrient enriched conditions, seagrass enhance their physiological functions to rapidly uptake the available N and P for higher productivity and increased growth (Helber et al., 2021; Moreira-Saporiti et al., 2023; Yan et al., 2020). However, this increased productivity is dependent on the duration of the nutrient influx (e.g., high or moderate), residence time of nutrients in the environment, surface water quality (e.g., high or low turbidity due to anthropogenic influx) and light availability above seagrass meadows (Jiménez-Casero et al., 2023). To cope of with these stress conditions and maintain growth and productivity, seagrasses depend on their associated microbiota (e.g., Rhodobacteria and Microtrichaceae, Beggiatoaceae). These microbiotas particularly associated with the leaf and root of seagrasses plays crucial role in mitigating the negative effects of the nutrient enrichment (Fuggle et al., 2023; Szitenberg et al., 2022). Beneficial microbial taxa such as Rhodobacteria and Microtrichaceae associated with seagrass leaves and sulfide-oxidizing Beggiatoaceae and denitrifying *Geofilum rubicundun* associated with roots to help reduce nutrient stress and sulfide toxicity, facilitating seagrass survival in nutrient enriched conditions (Fuggle et al., 2023). Additionally, the grazers that feed on leaf epiphytic algae can help in regulating the algal growth on seagrass leaves, thereby reducing the competition for light and nutrients and positively influencing seagrass productivity (Mutchler and Hoffman, 2017; Rodriguez et al., 2022). However, the predators that feed on grazers can indirectly affect the seagrass health by controlling the grazer population (Mutchler and Hoffman, 2017; Rodriguez et al., 2022; Viana et al., 2020; Yan et al., 2020). These biotic interactions along with abiotic factors such as salinity and temperature changes further influence seagrass physiology and response to nutrient enrichment (Helber et al., 2021; Medina-Gómez et al., 2016; Viana et al., 2020). The nutrient enrichment not only affects seagrass health but also has a knock-on effect on seagrass associated biodiversity, that can alter the composition and abundance of leaf and sediment associated meiofauna and macrofauna (Baggett et al., 2010; Yan et al., 2020). Furthermore, under nutrient enrichment conditions, the nutrient uptake efficiency and carbon composition of seagrasses are species-specific (Luo et al., 2022; Viana et al., 2020). For example, the sucrose content in *Enhalus acoroides* leaf increases under N and P enrichment, whereas for *Halophila stipulacae* and *Posidonia oceanica* the sucrose content remained unchanged and decreased respectively (Helber et al., 2021; Pazzaglia et al., 2020). However, in general increase in nutrient contents always increases the amino acids in seagrass leaves (Luo et al., 2022; Yang et al., 2018).

These changes in seagrass nutritional content under nutrient enrichment can alter certain ecosystem services such as carbon sequestration (through reducing refractory organic carbon), and increased palatability for herbivores (high grazing with high nutrient content) and change in associated macrobenthos (Behera et al., 2023; Fang et al., 2022; Ruesink, 2016; Smulders et al., 2022; Su et al., 2020).

In view of the ecological importance of seagrass ecosystems and increasing threat they face, a continuous long-term (i.e., multiple years that includes local seasonal variations) monitoring of seagrass ecosystems under nutrient enrichment conditions is essential to assess the ecological and physiological health (Seagrass Watch, 2024). However, significant knowledge gap remains, particularly in assessing the long-term *in-situ* response of seagrasses to nutrient enrichment in tropical regions such as in the South-America, east Africa, Indo-Pacific and the central Indian Ocean region, where nutrient enrichment due to growing coastal populations and associated anthropogenic activities is increasing (Floyd et al., 2024; Li et al., 2019; MacLeod et al., 2023; Stankovic et al., 2023). More importantly majority of studies related to nutrient enrichment and seagrass response is restricted to few coastal regions (e.g., Atlantic coast of the Europe and the USA, Australia, and China) and few selected species such as *Zostera* sp., and *Thalassia testudinum* (Nordlund et al., 2024; Yang et al., 2018). Furthermore, it is recommended that the response of one species from one geographic location, should not be applied a priori to that species in other regions or to seagrasses in general due to seagrass species showing considerable variations to nutrient enrichment (Touchette and Burkholder, 2000).

Assessing seagrass population dynamics, which includes growth, recruitment and mortality is crucial for understanding their long-term survival rates, and population demography under variable nutrient inputs (Cabaço et al., 2013; Herbert and Fourqurean, 2009; Mishra and Apte, 2020; Yang et al., 2018). 'Reconstruction techniques' which analyze the distinct scars left by abscised leaves of various seagrass provide a unique method to assess population dynamics and demography (Duarte et al., 1994; Perez et al., 1994) under variable environmental conditions over time. However, limited studies have utilized this technique to derive seagrass population dynamics under nutrient enrichment conditions globally (Helber et al., 2021; Herbert and Fourqurean, 2009; Lee and Dunton, 2000).

Therefore, the present study aimed to assess the influence of short-term (i.e., <6 months of a year covering one season) nutrient enrichment on i) morphometrics, population dynamics (growth, recruitment and mortality) and productivity of two seagrass species (*Thalassia hemprichii* and *Cymodocea rotundata*), and ii) variation in seagrass leaf meiofauna abundance and contrast this seagrass response with pristine conditions in a tropical island ecosystem. These seagrass species are chosen for their abundance and their mechanical, physiological and morphological traits that enables them to survive in oligotrophic conditions (Mishra and Apte, 2020; Viana et al., 2020). Additionally, these two species possess vertical rhizome internodes that makes them suitable to be used for calculation of population dynamics, using reconstruction techniques (Duarte et al., 1994). This study also tested the efficiency of these species as early indicators of nutrient pollution using the Nutrient Pollution Index (Yang et al., 2018). This study hypothesizes that nutrient content in seagrass tissues reflect environmental nutrient conditions, and the response of seagrasses to nutrient enrichment is species-specific, focusing on total N (nitrate, ammonium and nitrite) and inorganic phosphate (P) as an indicator of nutrient enrichment (Duarte, 1990). By filling these critical knowledge gaps, our study contributes globally relevant data by presenting the impacts of nutrient enrichment on seagrass population dynamics from an understudied region of the world's oceans. Furthermore, this study will generate species-specific responses and data to fill the existing knowledge gaps of the Indian Ocean region and can be utilized for seagrass research in similar tropical islands globally.

2. Materials and methods

2.1. Study site

The Andaman and Nicobar Islands (ANI) is located of the southeast coast of India in the Andaman Sea, Indian Ocean Region (Fig. 1). The ANI are oligotrophic islands due to the absence of natural riverine systems (Sahu et al., 2013), and experience minimal influence of local anthropogenic input during the wet season (December–April), due to substantial rainfall of 3000–3500 mm (Indian Meteorological Department, 2024). These tropical oligotrophic ANI islands are similar to other islands of the Indian Ocean region like Sri Lanka, Maldives, Cocos Islands of Australia etc., (Buckee et al., 2021; Painter et al., 2023). However, ANI inhabit around 0.4 million coastal communities as of 2023, which have increased significantly in the last decade due to improved facilities and availability of marine resources (Indian Census, 2023). This population growth within few kilometers of the coastal zones has also increased the anthropogenic pollution (e.g., metals and nutrients) and exerting increased pressure on the coastal ecosystems through discharge of domestic, small-scale industrial and untreated anthropogenic waste (VishnuRadhan et al., 2015). Ten out of the 25 seagrass species inhabiting the Indian Ocean Region are found in the ANI (Gole et al., 2024; Mishra et al., 2023) thriving in the intertidal zones up to a depth of 20 m (Bayyana et al., 2020).

For this study, four intertidal seagrass locations were selected: Saheed Dweep (hereafter Neil), Swaraj Dweep (hereafter Havelock), Burmanallah and Haddo Bay (Fig. 1). These locations have individual meadows of both *T. hemprichii* or *C. rotundata*. These locations are influenced by local anthropogenic waste water disposal and nutrient input (hereafter enriched) and the control areas (hereafter pristine) further away from these impacted areas were chosen along the coast of the ANI, India (Fig. 1). The pristine sites were at least 1000 m away from the enriched zones. Mono-specific patches of *T. hemprichii* and *C. rotundata* were sampled from both enriched and pristine sites during low tide at a depth of 0.3 m at each location during April–May 2023 (dry season). The enriched conditions were characterized by high algal growth on both seagrass leaves and sediment (Fig. 2).

2.2. Sediment sampling and processing

At each location a sediment core (n = 5) was collected using a plastic corer (15 cm depth x 5 cm diameter). The sediment corer was pushed down to a depth of 10 cm; further collection of sediment was impeded by the presence of dead corals beds or rocky substrates. These sediment cores were transferred to zip lock bags in the field, stored in dark boxes and sent to the laboratory. In the laboratory, these sediment cores were sectioned at 5 cm interval using a stainless-steel knife and oven dried at 60 °C for 48 h. After drying, the sediment samples were homogenized using a disc mill grinder (Retsch, RS 200, USA) and a fraction was used to analyze the sediment organic matter (OM%) content via loss on ignition (LOI) in a muffle furnace (Howard et al., 2014). Furthermore, 30 mg of sediment was analyzed in duplicates for composition of total carbon (C) and nitrogen (N) elemental concentration using a CHNS Elemental Analyzer (Elementar, UNICUBE). The inorganic P content in the sediment was analyzed using a UV–Visible Spectrophotometer (Perkin Elemer, Lambda 35) following the methods as described in Coastal Ocean Monitoring and Prediction System for Indian Coast (Hansen and Grasshoff, 1983; Kaisary et al., 2012).

2.3. Seagrass sampling and processing

The population dynamics of *T. hemprichii* and *C. rotundata*, including growth, recruitment and mortality, were estimated using plant reconstruction techniques, an indirect measure of plant anatomical growth history and population dynamics changes (Duarte et al., 1994; Short and Duarte, 2001). Reconstruction techniques, involving measuring the internodal length between two consecutive leaf formations have been utilized sparsely in global seagrass population dynamics studies (Cabaço and Santos, 2014; Mendoza et al., 2019; Mishra et al., 2021a; Mishra et al., 2021b; Rollon et al., 2001).

Ten quadrats (20 cm × 20 cm) were collected randomly at both enriched and pristine sites within a depth of 0.3 m during low tide for

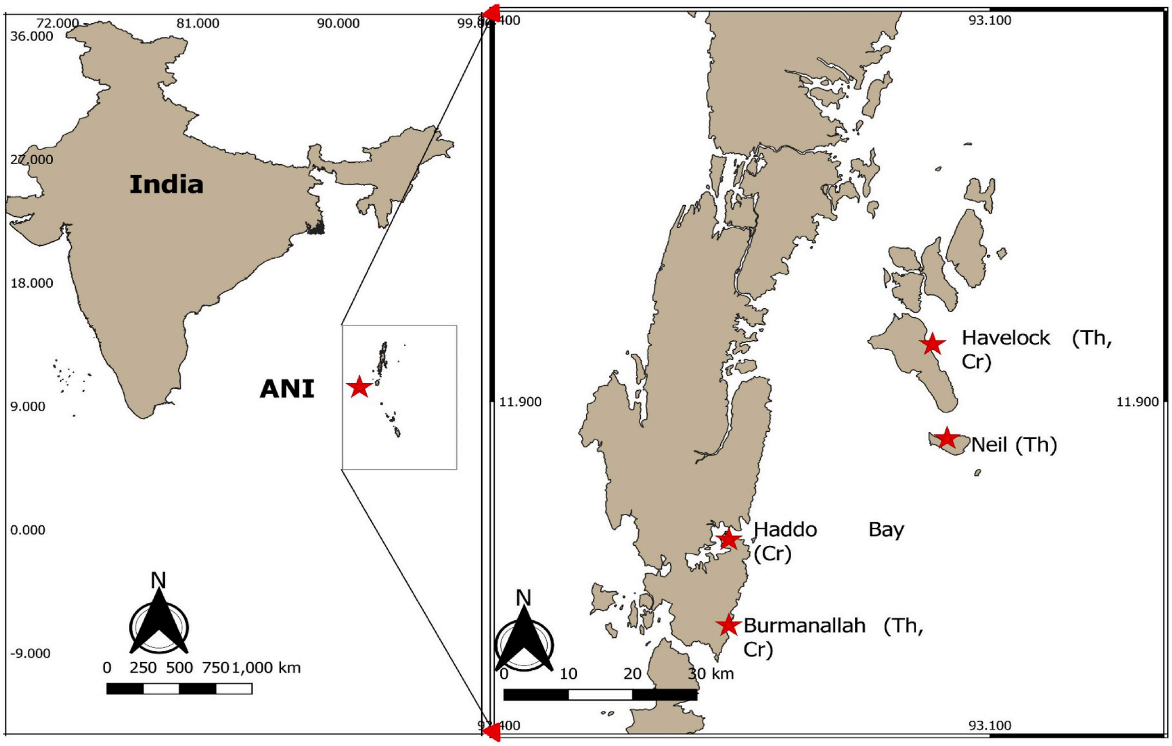

Fig. 1. Map showing the study locations of ANI with *T. hemprichii* (Th) and *C. rotundata* (Cr) presence.

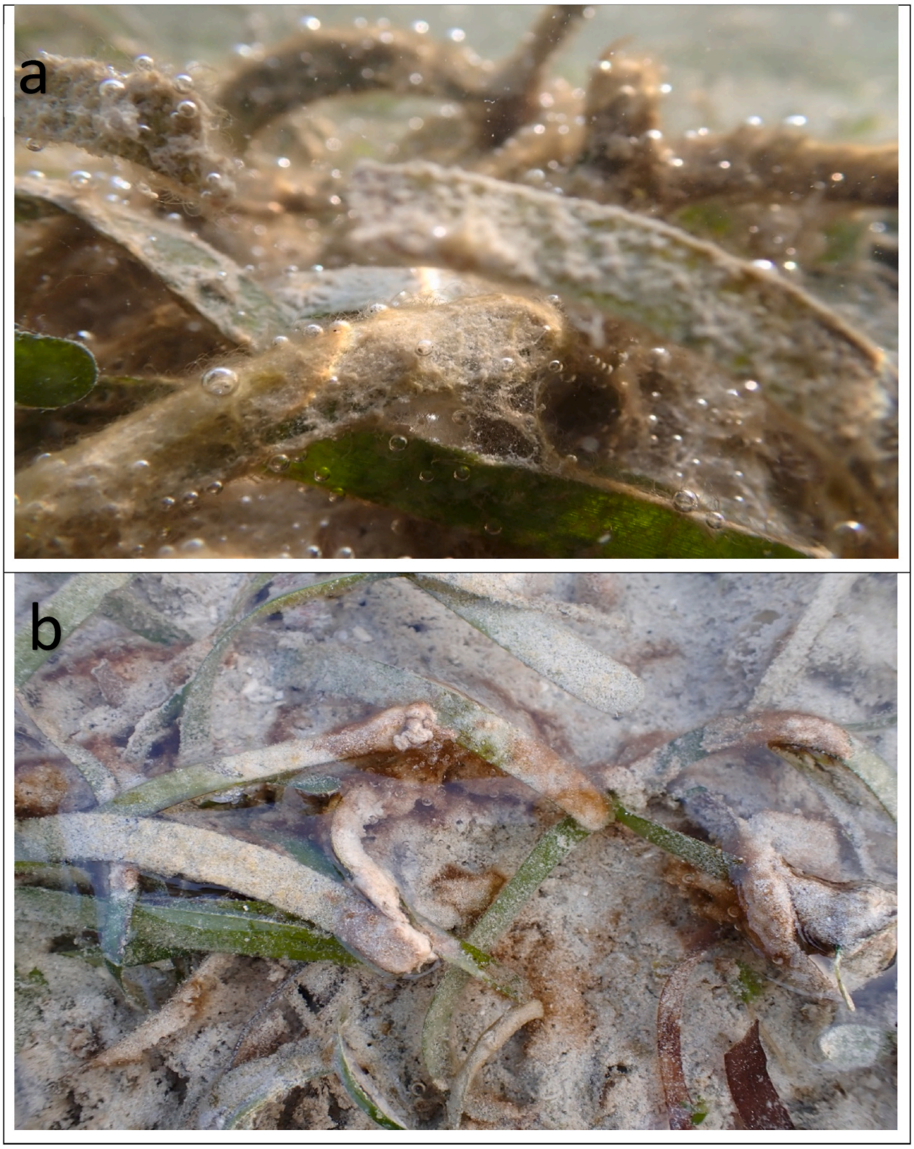

Fig. 2. Algal growth on leaf of a) *T. hemprichii* and b) *C. rotundata* under enriched conditions from the coast of ANI, India.

each seagrass species. A hand shovel was used to dig out seagrass samples up to 10 cm depth. From each quadrat, seagrass leaves, rhizomes and roots were collected, rinsed off carefully in the field with seawater, stored in zip lock plastic bags and brought to the laboratory for further analysis. In the laboratory, the plant samples were washed with deionized water and any debris or organisms attached to the leaves were scrapped of with a glass slide and stored for biomass analysis. From each sample, the density was estimated by counting the number of shoots of physically independent individuals. Morphometric variables such as horizontal rhizome length (cm), leaf length (cm) and width (mm) and internode lengths (cm) were measured using a Vernier Calliper (accuracy ± 0.02 mm). The leaves (above-ground; AG), shoots and roots (below-ground; BG) were separated and dried for 48 h at 60 °C for biomass (g DW m^{-2}) estimates. From these dried biomass samples, 30 mg was used for analysis of total C and N and inorganic P following the same method as sediment samples (see above in section 2.2).

The age of *T. hemprichii* shoots was estimated by counting the number of leaf scars on the vertical rhizomes plus the number of leaves in each shoot multiplied by the leaf plastochrone interval (PI), i.e., the time needed to produce a new leaf. The PI was determined by measuring the sequence of vertical internodal length of *T. hemprichii and C. rotundata* shoots collected from the quadrats plus additional plants collected by hand. The average internodal lengths were plotted against the order of the vertical internodes. These plots show distinct modes, that represent annual growth periods. The average number of leaf scars between modes was used to estimate the leaf PI of both seagrasses (Duarte et al., 1994; Mishra and Apte, 2020; Mishra et al., 2021a). Vertical and horizontal rhizome elongation rates were derived based on the method described by Duarte et al. (1994). The number of leaves per shoot were measured from intact shoots in each sample ($n > 100$/location). The horizontal and vertical rhizome production rates were estimated by multiplying the elongation rates (vertical or horizontal) by density (shoots or apex) and by the specific dry weight of rhizomes (vertical or horizontal), respectively.

The long-term average recruitment (R) was estimated from the shoot age structure using the general model: $N_x = N_0\, e^{-Rx}$, where N_x is the number of shoots in age class x, N_0 is the number of shoots recruited into the population. This model assumes no trend in mortality and recruitment over the lifespan of the oldest shoots in the population, i.e., mortality and recruitment have remained constant over the lifespan of the oldest shoots, with year-to-year random variation (Cunha and Duarte, 2004; Mishra et al., 2021a). The recruitment for the current year of sampling (R_0) was estimated using the method described by Duarte et al. (1994). The population growth rate (*r*) was estimated as: $r = R_0 - M$, where M is the long-term mortality rate, which equals the long-term recruitment rate (R) under the assumptions of near steady state (Fourqurean et al., 2003). Populations were considered growing if *r* is positive ($R_0 > R$), shrinking if *r* is negative ($R_0 < R$), or stable if R_0 is not significantly different from R (Fourqurean et al., 2003).

2.4. Leaf meiofauna processing

For seagrass leaf associated meiofauna were collected from each condition (i.e., pristine and enriched) and species (*T. hemprichii* and *C. rotundata*). Five leaves were collected from each quadrat and were stored in pre-prepared filtered seawater in 100 ml Teflon tubes and brought to the laboratory. In the laboratory, meiofauna were scrapped off from the seagrass leaves with a glass slide and stored in filtered seawater. These samples were passed through <63 μm sieves followed by continuous decantation to remove any debris. The samples were then stained with Rose Bengal dye and were sorted and enumerated under binocular and compound microscopes till group levels using the available identification keys for the region (Naufal and Padmavati, 2018).

2.5. Statistical analysis

The effect of nutrient enriched conditions (pristine vs enriched) on seagrass species (*T. hemprichii* and *C. rotundata*) traits (density, biomass, morphometric features, growth and production estimates) was tested using two -way ANOVA using conditions and species as fixed factors. All data were pre-checked for normality (Shapiro-Wilks test) and homogeneity of variance (F-test). Non-homogenous, data were ln (y) transformed. When significant interactions were detected, the Holm-Sidak test was performed for a posteriori comparison among factor levels. Linear regression was used to derived relationship between sediment N % and P% and seagrass leaf N% and P% and leaf C: N and C:P ratios to derive nutrient pollution index. Sediment P levels in pristine conditions were below detection limit, as a result two-way ANOVA was not tested. Exponential decay regression (single, 2 parameter) model were used to estimate the long-term average recruitment rate (R). The confidence limit allowed its statistical comparison to the present recruitment rate (R_0) as described in Fourqurean et al. (2003). All statistical analysis were carried out using PRISM (Ver. 10.4.1) software. Canonical Correspondence Analysis (CCA) was used to test the relationships between meiofaunal assemblages on seagrass leaves and their relationships with seagrass traits and environmental parameters using PAST software. CCA was used as it is a powerful test for species abundance and their relationships with environmental variables (ter Braak and Verdonschot, 1995). Results are presented as mean ± standard deviation (SD).

3. Results

3.1. Influence of nutrient enrichment on sediment and plant abiotic variables and their relationship

Significant differences were observed in sediment grain size fractions between pristine and enriched condition; sand content (two-way ANOVA; $F_{1,116} = 16.60$, $p < 0.0001$), silt ($F_{1,116} = 5.82$, $p = 0.017$) and clay ($F_{1,116} = 5.82$, $p < 0.0001$) (Tables 1 and 2). Along with OM ($F_{1,56} = 208.3$, $p < 0.0001$), C ($F_{1,56} = 202.1$, $p < 0.0001$) and N ($F_{1,56} = 340.4$, $p < 0.0001$) content also showed significant variation between pristine and enriched conditions (Tables 1 and 2). Under enriched conditions, sediment sand content decreased 1.3-fold for both *T. hemprichii* (56.05 ± 2.51%) and *C. rotundata* (52.39 ± 2.57%). Contrastingly, the sediment silt content increased 1.4-fold for *T. hemprichii* (31.70 ± 2.20%) and by 1.3-fold for *C. rotundata* (29.38 ± 8.47%). Similarly, the sediment clay content also increased 2-fold and 2.6-fold for *T. hemprichii* (12.23 ± 7.31%) and *C. rotundata* (18.21 ± 2.91%) under enriched conditions (Table 1). This increased influx of silt and clay resulted in the increase of sediment OM by 1.4-fold for *T. hemprichii* (39.15 ± 3.44 %) and 1.5-fold *C. rotundata* (40.91 ± 3.09 %) respectively under enriched conditions. Similarly, the sediment C and N increased 1.5-fold and 3-fold for both species respectively (Table 1).

Table 1

Mean ± SD of sediment traits (grain size fractions, OM%, N%, P inorganic %, C %) and density, biomass and morphometric variables of *T. hemprichii* and *C. rotundata* under pristine and enriched conditions from ANI, India. Below Detection Limit (BDL), above-ground (AG), below ground (BG).

Variables	*T. hemprichii*		*C. rotundata*	
	Pristine	Enriched	Pristine	Enriched
Sediment				
Grain size (Sand%)	71.32 ± 20.53	56.05 ± 22.51	71.41 ± 26.17	52.39 ± 22.57
Silt (%)	22.74 ± 16.40	31.70 ± 20.20	21.61 ± 20.56	29.38 ± 18.47
Clay (%)	5.93 ± 3.35	12.23 ± 7.31	6.96 ± 4.23	18.21 ± 2.91
Organic matter (OM%)	27.47 ± 4.35	39.15 ± 3.44	26.18 ± 3.16	40.91 ± 3.09
N (%)	0.24 ± 0.07	0.72 ± 0.13	0.26 ± 0.06	0.81 ± 0.14
C (%)	2.86 ± 1.55	4.40 ± 1.96	2.93 ± 1.85	4.48 ± 1.17
Inorganic P (%)	BDL	0.12 ± 0.03	BDL	0.24 ± 0.17
Seagrass				
Shoot density (ind.m^{-2})	1009.04 ± 316.5	1522.32 ± 718.7	917.31 ± 298.8	1397.62 ± 53.4
Apex density (ind.m^{-2})	171.08 ± 60.82	125.74 ± 47.81	188.61 ± 64.72	103.06 ± 34.88
AG-biomass (g DW m^{-2})	116.85 ± 39.10	79.56 ± 30.00	123.74 ± 38.21	76.98 ± 33.41
BG-Biomass (g DW m^{-2})	221.90 ± 134.00	345.02 ± 101.61	209.68 ± 132.94	328.58 ± 16.3
AG-biomass (N%)	0.54 ± 0.13	1.85 ± 0.29	0.79 ± 0.12	1.94 ± 0.28
AG biomass (inorganic P)%	0.081 ± 0.04	0.16 ± 0.03	0.07 ± 0.01	0.15 ± 0.07
No. of leaves per year	12.33	18.47	12.89	14.02
Leaf length (cm)	16.20 ± 1.66	12.30 ± 1.20	10.83 ± 0.93	9.23 ± 1.03
Leaf width (cm)	0.43 ± 0.19	0.62 ± 0.04	0.26 ± 0.06	0.32 ± 0.05
Leaf elongation rate (cm yr^{-1})	0.39 ± 0.07	0.51 ± 0.185	0.40 ± 0.09	0.63 ± 0.18
Horizontal elongation rate (cm yr^{-1})	1.81	3.63	2.40	8.52
Vertical rhizome production (g DW m^{-2} yr^{-1})	65.86 ± 4.1	138.35 ± 43.23	58.06 ± 38.97	101.25 8.17
Horizontal rhizome production (g DW m^{-2} yr^{-1})	39.24 8.15	83.99 ± 8.50	48.26 ± 4.3	57.51 ± 17.95

Note: Number of leaves per year was derived from Plastochrone interval with a single value, as a result no SD values are provided. Only single values were derived for horizontal elongation, so no SD are presented.

Significant differences were also observed in the total N% in AG-biomass for both seagrass species ($F_{1,56} = 9.27$, $p = 0.003$) and conditions ($F_{1,56} = 441.8$, $p < 0.0001$). The inorganic P% showed significant variation only across conditions ($F_{1,56} = 48.17$, $p < 0.0001$) (Tables 1 and 2). Under enriched conditions, the total N% in AG-biomass of *T. hemprichii* (1.85 ± 0.29) and *C. rotundata* (1.93 ± 0.28) was 3.3-fold and 2.4-fold higher than pristine conditions respectively. This increased accumulation of N in AG-biomass for both seagrass species showed significant positive relationships with sediment N compared to pristine conditions (Fig. 3). Specifically, AG-biomass N versus sediment N showed positive relationship for both *T. hemprichii* ($R^2 = 0.79$, $p < 0.001$) and *C. rotundata* ($R^2 = 0.81$, $p < 0.001$) under enriched conditions, respectively (Fig. 3). Contrastingly, the AG-biomass C: N versus sediment N showed inverse relationships for both *T. hemprichii* ($R^2 =$

Table 2
Results of two-way ANOVA analysis and p values are presented ($p < 0.05$*, $p < 0.001$**, $p < 0.0001$****) for variables presented in Table 1. Not analyzed (NA).

Variables	*Two-way ANOVA*				
	ANOVA Variables	DF	MS	F (DFn, DFd)	P value
Sediment					
Grain size (sand%)	Interaction	1	105.7	F (1,116) = 0.198	0.656
	Species	1	95.39	F (1, 116) = 0.179	0.672
	Condition	1	8817	F (1, 116) = 16.60	**<0.0001**
Silt (%)	Interaction	1	10.77	F (1,116) = 0.028	0.863
	Species	1	88.77	F (1, 116) = 0.244	0.620
	Condition	1	2100	F (1, 116) = 5.82	**0.017**
Clay (%)	Interaction	1	183.9	F (1,116) = 2.62	0.108
	Species	1	368.6	F (1, 116) = 1.15	0.237
	Condition	1	2310	F (1, 116) = 5.82	**<0.0001**
Organic matter (OM%)	Interaction	1	34.92	F (1,56) = 2.77	0.101
	Species	1	0.841	F (1,56) = 0.066	0.796
	Condition	1	2618	F (1,56) = 208.3	**<0.0001**
N (%)	Interaction	1	0.017	F (1,56) = 1.45	0.233
	Species	1	0.044	F (1,56) = 3.75	0.057
	Condition	1	4.066	F (1,56) = 340.4	**<0.0001**
C (%)	Interaction	1	0.265	F (1,56) = 0.015	0.902
	Species	1	4.123	F (1,56) = 0.237	0.628
	Condition	1	3513	F (1,56) = 202.1	**<0.0001**
Inorganic P (%)	NA				
Seagrass					
Shoot density (ind. m^{-2})	Interaction	1	6796	F (1,116) = 0.025	0.8730
	Species	1	292,766	F (1,116) = 1.10	0.2954
	Condition	1	6,170,148	F (1,116) = 23.32	**<0.0001**
Apex density (ind. m^{-2})	Interaction	1	10,100	F (1,116) = 3.54	0.062
	Species	1	165.9	F (1,116) = 0.058	0.809
	Condition	1	107,073	F (1,116) = 37.60	**<0.0001**
AG-biomass (g DW m^{-2})	Interaction	1	278.3	F (1,116) = 0.201	0.654
	Species	1	199.2	F (1,116) = 0.144	0.705
	Condition	1	33,660	F (1,116) = 24.35	**<0.0001**
BG-Biomass (g DW m^{-2})	Interaction	1	88.66	F (1,116) = 0.003	0.95
	Species	1	4107	F (1,76) = 0.159	0.69
	Condition	1	292,858	F (1,76) = 11.35	**0.001**
AG-biomass (N%)	Interaction	1	0.066	F (1,56) = 1.34	0.251
	Species	1	0.461	F (1,56) = 9.278	**0.003**
	Condition	1	21.96	F (1,56) = 441.8	**<0.0001**
AG biomass (P%)	Interaction	1	0.0005	F (1,56) = 0.29	0.58
	Species	1	0.0005	F (1,56) = 0.29	0.57
	Condition	1	0.08	F (1,56) = 48.17	**<0.0001**
No. of leaves per year	NA				
Leaf length (cm)	Interaction	1	0.879	F (1,596) = 0.057	0.121
	Species	1	534.5	F (1, 596) = 345.6	**<0.0001**
	Condition	1	227.8	F (1, 596) = 147.3	**<0.0001**
Leaf width (cm)	Interaction	1	0.013	F (1,596) = 0.054	0.052
	Species	1	1.599	F (1, 596) = 671.7	**<0.0001**
	Condition	1	0.452	F (1, 596) = 190.2	**<0.0001**
Leaf elongation rate (cm yr^{-1})	Interaction	1	0.013	F (1,596) = 0.014	0.061
	Species	1	0.129	F (1, 596) = 5.807	**0.016**
	Condition	1	4.877	F (1, 596) = 219.3	**<0.0001**
Horizontal elongation rate (cm yr^{-1})	NA				
Vertical rhizome production (g DW m^{-2} yr^{-1})	Interaction	1	4292	F (1,76) = 0.544	0.46
	Species	1	10,078	F (1,76) = 1.28	0.26
	Condition	1	66,909	F (1,76) = 8.495	**0.004**
Horizontal rhizome production (g DW m^{-2} yr^{-1})	Interaction	1	6304	F (1,76) = 2.33	0.130
	Species	1	1523	F (1,76) = 0.56	0.454
	Condition	1	14,581	F (1,76) = 5.40	**0.022**

0.65, $p = 0.002$) and *C. rotundata* ($R^2 = 0.86$, $p < 0.001$) under enriched conditions, respectively (Fig. 3). Similarly, under enriched conditions the inorganic P in AG biomass was 2-fold higher in *T. hemprichii* (0.16 ± 0.03 %) and 2.1-fold higher in *C. rotundata* (0.15 ± 0.07%) than their pristine conditions, respectively (Tables 1 and 2). A significant inverse relationship ($R^2 = 0.61$, $p < 0.0006$) between AG-biomass P and sediment P was observed only for *C. rotundata* under enriched conditions (See Supplementary S1).

3.2. Influence of nutrient enrichment on seagrass traits and productivity

3.2.1. Density and biomass

Significant variations were observed in both the shoot density ($F_{1,116} = 23.32$, $p < 0.0001$) and the apex density ($F_{1,116} = 37.60$, $p < 0.0001$) between pristine and enriched conditions (Tables 1 and 2). Under enriched conditions, the shoot density of *T. hemprichii* (1522 ± 71.7 shoots m^{-2}) and *C. rotundata* (1397.6 ± 53.4 shoot m^{-2}) were 1.5-fold higher than respective pristine conditions. Contrastingly, under enriched condition, the apex density of *T. hemprichii* (125.7 ± 7.8 apex m^{-2}) and *C. rotundata* (103 ± 4.9 apex m^{-2}) was 1.3-fold and 1.8-fold lower than respective pristine conditions (Table 1). Similarly, significant differences were also observed for AG-biomass ($F_{1,116} = 37.60$, $p < 0.0001$) and BG-biomass ($F_{1,116} = 11.35$, $p < 0.0001$)) across conditions

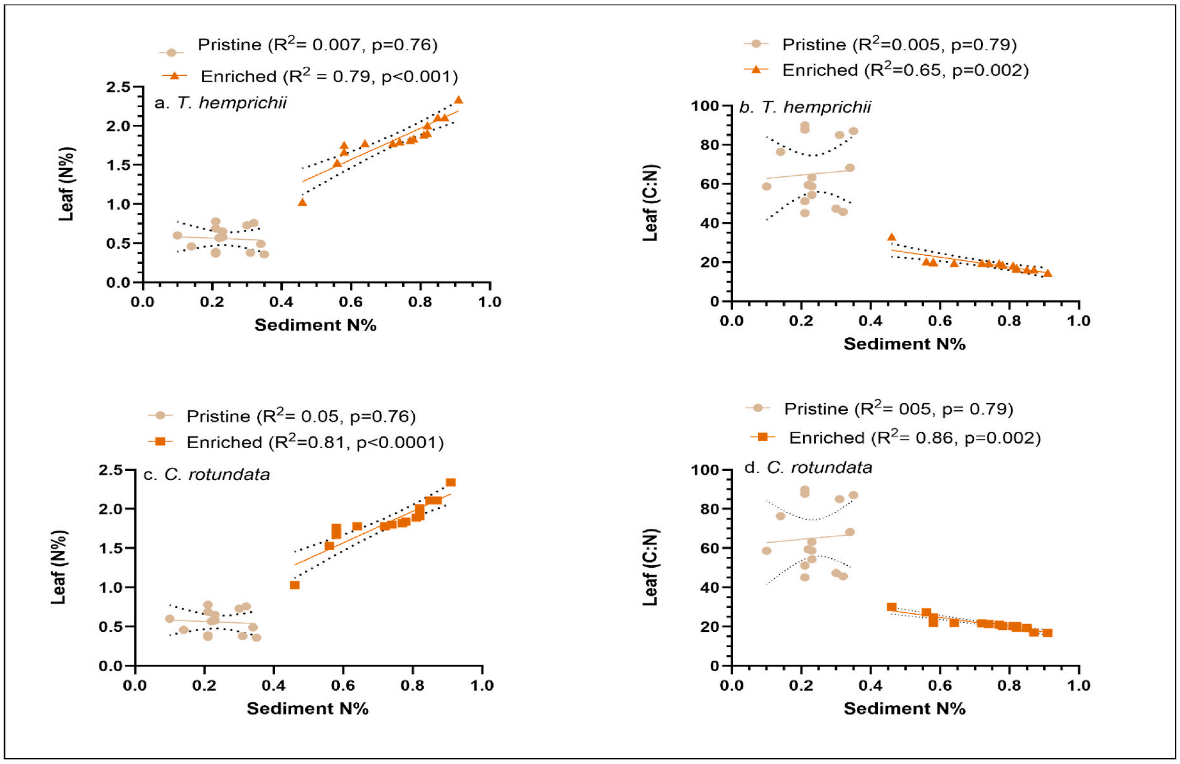

Fig. 3. Relationship between sediment N% and seagrass leaf N% and C:N ratios showcasing both *T. hemprichii* and *C. rotundata* as indicators of nutrient enrichment conditions from our study locations of ANI, India.

(Table 1). Under enriched condition, the AG-biomass of *T. hemprichii* (79.5 ± 3 g DW m^{-2}) and *C. rotundata* (76.9 ± 3.4 g DW m^{-2}) decreased 1.4-fold and 1.5-fold respectively, compared to pristine conditions. Contrastingly, the BG-biomass of *T. hemprichii* (345 ± 10.6 g DW m^{-2}) and *C. rotundata* (328.5 ± 6.3 g DW m^{-2}) increased 1.5-fold under enriched conditions (Table 1).

3.2.2. *Leaf morphometrics and growth*

Significant differences were observed between species and conditions for leaf elongation rates ($F_{1,\,596} = 219.3$, $p < 0.0001$), leaf length ($F_{1,\,596} = 147.3$, $p < 0.0001$) and width ($F_{1,\,596} = 190.2$, $p < 0.0001$) (Tables 1 and 2). Under enriched conditions, the leaf elongation rate increased by 1.3-fold for *T. hemprichii* (0.51 ± 0.18 cm yr-1) and 1.8-fold for *C. rotundata* (0.63 ± 0.18 cm yr^{-1}). Interestingly, this increased elongation rates were not translated to longer leaves, as the leaf length of *T. hemprichii (*12.3 ± 1.2 cm*)* and *C. rotundata* (9.23 ± 1.03 cm) was reduced by 1.3-fold and 1-fold. Contrastingly, the leaf width increased 1.4-fold for *T. hemprichii* (0.51 ± 0.18 cm) and 1.2-fold and for *C. rotundata* (0.63 ± 0.18 cm) respectively under enriched conditions (Table 1).

3.2.3. *Rhizome growth rates and productivity*

The vertical and horizontal rhizome elongation rates of both *T. hemprichii* ($R^2 = 0.63$, $p < 0.0001$; $R^2 = 0.56$, $p < 0.0001$) and *C. rotundata* ($R^2 = 0.68$, $p < 0.0001$; $R^2 = 0.68$, $p < 0.0001$) were significantly different between conditions (See Supplementary S2 and S3). Similarly, the vertical ($F_{1,76} = 8.49$, $p = 0.004$) and horizontal ($F_{1,76} = 5.40$, $p = 0.022$) rhizome production rates were significantly different for both *T. hemprichii* and *C. rotundata* between conditions (Table 1). The vertical elongation rates increased 1.4-fold for *T. hemprichii* (1.56 cm yr^{-1}) and 1-fold for *C. rotundata* (1.33 cm yr^{-1}) under enriched conditions, resulting in increased vertical rhizome productivity of 2-fold for *T. hemprichii* (138.35 ± 43.23 g DW m^{-2} yr^{-1}) and 1.7-fold for *C. rotundata* (101.25 ± 8.17 g DW m^{-2} yr^{-1}) (Table 1). Similarly, the horizontal rhizome elongation rates increased 2-fold for *T. hemprichii* and 3.5-fold for *C. rotundata* under enriched conditions (Supplementary S3), resulting in an increase of horizontal productivity of 2-fold for *T. hemprichii* (84 ± 8.5 g DW m^{-2} yr^{-1}) and 1.2-fold for *C. rotundata* (57.5 ± 17.9 g DW m^{-2} yr^{-1}) (Table 1).

3.3. *Seagrass population dynamics*

The Plastochrone interval (PI), i.e., the number of days required to produce a new leaf was reduced under enrichment for both species compared to pristine conditions, resulting in higher number of leaves

Table 3

Plastochrone interval (PI), age structure and population dynamics of seagrass *T. hemprichii* and *C. rotundata* under the influence of pristine and enriched conditions across our study locations. Mean ± SE are presented for shoot age. Significant differences between conditions (pristine vs enriched) and seagrass species (*T. hemprichii* vs *C. rotundata*) are presented as lowercase and uppercase letters respectively. The exponential coefficient ± SE of the non-linear exponential decay regression is presented for the long-term average recruitment rate (R).

Variables	*T. hemprichii*		*C. rotundata*	
	Pristine	Enriched	Pristine	Enriched
Plastochrone interval (PI)	28.31	26.03	29.6	19.76
Age structure				
Shoot longevity (Yr)	4.87	3.84	6.34	3.91
Shot age (Yr)	1.26 ± 0.04^a	1.05 ± 0.03^b	1.40 ± 0.06^a	1.06 ± 0.03^b
Population dynamics				
Long-term average recruitment (R, Yr^{-1})	0.62 ± 0.10	0.81 ± 0.13	0.69 ± 0.04	0.80 ± 0.05
Present recruitment (Ro, Yr^{-1})	0.64	0.88	0.70	0.91
Population growth rate (r, Yr^{-1})	0.02	0.07	0.01	0.11

being produced by both seagrass species (Tables 1 and 3). The long-term average recruitment (R) for both *T. hemprichii* (0.81 ± 0.13 yr^{-1}) and *C. rotundata* (0.80 ± 0.05 yr^{-1}) increased 1.3-fold and 1-fold, respectively compared to pristine conditions (Fig. 4). Under enriched conditions, the present recruitment (Ro) was 1.4-fold higher for *T. hemprichii* and 1.3-fold for *C. rotundata* populations, respectively (Table 3). Increased Ro > R resulted in 3.5-fold and 11-fold higher population growth rates for *T. hemprichii* and *C. rotundata*, respectively, under enriched conditions compared to pristine conditions (Table 3). However, this increased population growth rates under enriched conditions were not translated into long-term seagrass population longevity for both *T. hemprichii* and *C. rotundata*, as the average shoot age and plants older than four years were mostly present under pristine conditions (Fig. 4).

3.4. Leaf meiofauna abundance

A total of 15 groups of leaf meiofauna were associated with both seagrass leaves under pristine and enriched conditions (Fig. 5). In general, the leaf meiofauna abundance decreased 1.3-fold in *T. hemprichii* meadows and 1.5-fold in *C. rotundata* meadows under enriched conditions. Interestingly, under enriched conditions an increase of 1.6-fold abundance of leaf meiofauna was observed for groups belonging to Nematoda, Amphipoda and Polychaeta in *C. rotundata* meadows. Similarly, within *T. hemprichii* meadows certain species of meiofauna were only observed under enrichment conditions (such as Copepod, Kinorhyncha, Nauplii) and were absent under pristine conditions. (Fig. 5). CCA showed under enriched conditions sediment N%, OM% and leaf width played an important role in meiofauna abundance for both *T. hemprichii* and *C. rotundata* populations (Fig. 6, Supplementary S4).

4. Discussion

There exists a critical knowledge gap in understanding of the effects of nutrient enrichment on seagrass structure and functions of tropical islands, particularly in the Indian-Ocean region (Helber et al., 2021). This study addressed this knowledge gap by examining the growth, productivity, population dynamics and biodiversity assemblage of two tropical seagrass species *T. hemprichii* and *C. rotundata*, under the influence of short-term (<6 months and one season) anthropogenic nutrient enrichment. These findings are contrasted with the response under pristine conditions from the same tropical oligotrophic islands of ANI in the Indian Ocean. Our findings highlight that seagrass responses to nutrient enrichment are species-specific and helps in enhancing the growth, production and population dynamics. On contrary, these positive effects of nutrient enrichment do not translate into increased population longevity of both seagrass species and lead to reduced seagrass apex density (mostly impacting the meadow migration), AG-biomass and leaf length, impacting the overall meadow health and ecosystem services. Similar effect of anthropogenic nutrient enrichment on seagrass population demography has also been observed for other seagrass species like *Halophila ovalis* and *Halodule uninervis* from the coast of India (Mishra et al., 2021b). Furthermore, this reduction in AG-biomass and leaf length also resulted in lower leaf meiofauna assemblages, thus reducing seagrass ecosystem service provisions.

4.1. Effects of nutrient enrichment on sediment traits

Anthropogenic influx brings in the fine sediment particles (<63 μm) into coastal ecosystems and seagrass meadows efficiently trap these finer particles with the help of their long-leaves and dense shoot and rhizome networks (Cozzolino et al., 2021; Mishra and Farooq, 2023; Ricart et al., 2020). These fine grain particles bind OM, thus increasing its concentration under enriched conditions (Jiang et al., 2022; Mishra

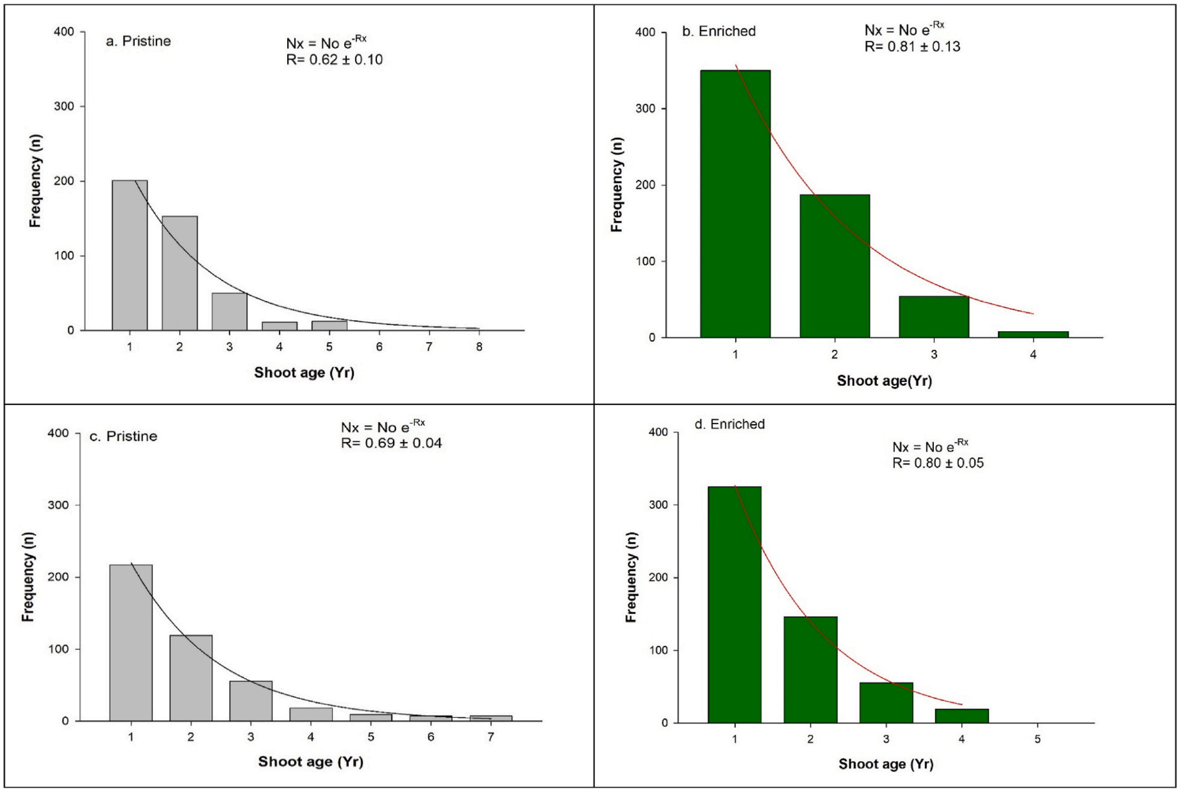

Fig. 4. Age frequency distribution of *T. hemprichii* (a, & b) and *C. rotundata* (c, &d) under pristine and enriched conditions from ANI, India. The long-term average recruitment rate (R) was estimated from the exponential decay regression line fitted to age frequency distribution.

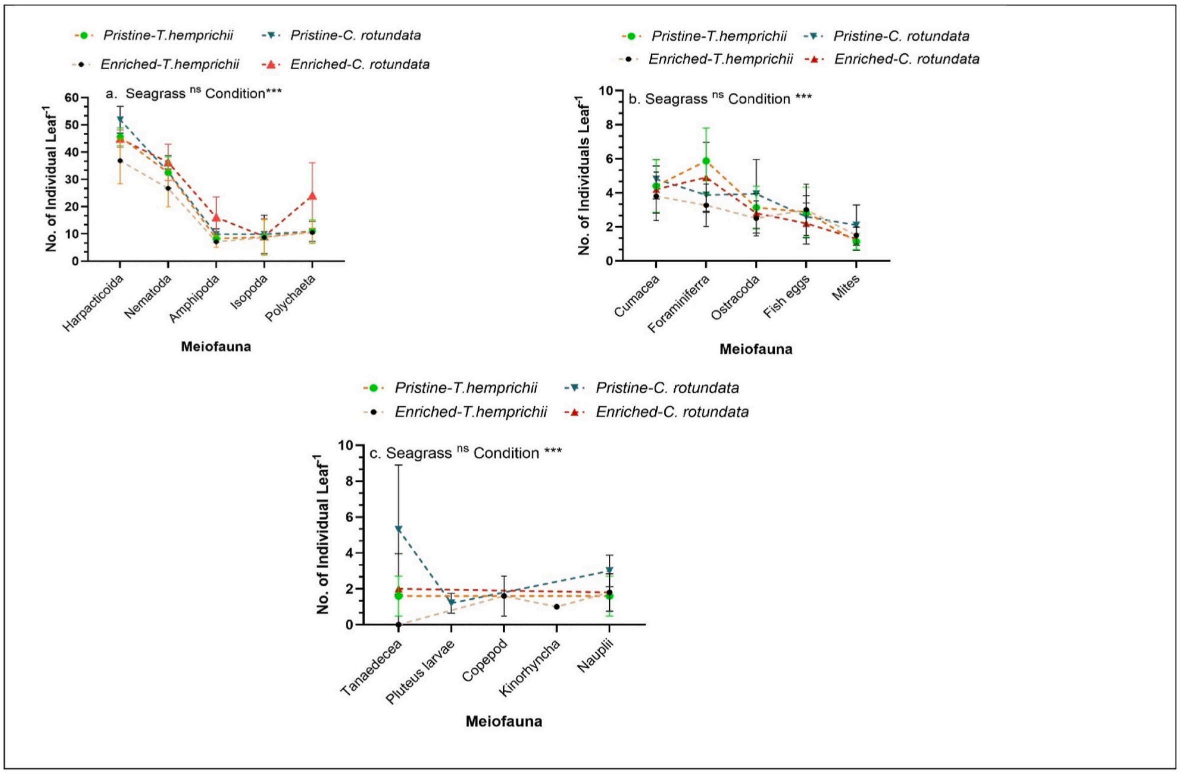

Fig. 5. Meiofauna abundance on leaf of *T. hemprichii* and *C. rotundata* under pristine and enriched conditions of ANI, India. The groups are separated into different graphs for better representation based on the abundance.

and Farooq, 2023; Pandion et al., 2023). In this study, increased silt and clay under enriched conditions has been observed in seagrass meadows of both *T. hemprichii* and *C. rotundata* (Table 1), as a result of anthropogenic influx of local waste water in some locations, small scale industrial waste water and dredging related influx of fine particles at other. Increased turbidity from these anthropogenic activities reduces light availability for seagrass meadows, which significantly reduces the spatial distribution of seagrass meadows resulting in higher meadow fragmentation and reducing the nutrient removal capacity (Li et al., 2019; Wang et al., 2022). The turbidity also increases suspended sediment concentration that may carry additional nutrients (e.g., P) suitable for algal growth and potentially increase the competition with seagrass leaves for N (Vieira et al., 2022; Wang et al., 2022). This was observed in our study sites, with increased algal growth on seagrass leaves, as P levels increased under nutrient enrichment conditions (Fig. 2). This increase in influx of fine particles into seagrass ecosystems from anthropogenic run-off have shown positive influence on the increase in the sediment OM and C content. Additionally, nutrient enrichment also increased algal growth on the sediment and seagrass leaf surface, as observed for *T. hemprichii* and *C. rotundata* meadows from our study locations (Fig. 2) and other tropical island ecosystems (Jha et al., 2014; Libin et al., 2017; Mishra et al., 2023, 2024b). The algal growth and die-offs combined with decaying seagrass leaves may have contributed towards higher sediment OM and C pool in these seagrass meadows, which has been observed for various seagrass meadows globally (Jiang et al., 2022; Qin et al., 2021; Zhang et al., 2022). However, elevated sediment OM can also pose a serious risk by increasing the sediment sulfide levels and impart associated toxicity to seagrass root systems that can lead to seagrass mass mortality (MacLeod et al., 2023; Mishra et al., 2020). This may be one of the reasons for the reduction in apex density and horizontal meadow migration of both seagrass species in this study.

Beneficial seagrass root microbiome (e.g., sulfide oxidizing Beggiatoaceae) can help in mitigating sulfide toxicity and maintaining seagrass functions, as observed in *T. testudinum* (MacLeod et al., 2023). The sediment OM range (26.18–40.91%) in our study is significantly higher than previously reported for ANI's seagrasses and coral reef meadows indicating increased anthropogenic activities (Sachithanandam et al., 2020; Mishra et al., 2023; Mishra and Farooq, 2023). Similarly, the sediment C content observed in this study under enriched conditions (4.40–4.48%) are 2-fold higher than previously observed for *T. hemprichii* meadows of ANI associated with mangroves and 4-fold higher than pristine conditions (Mishra et al., 2023; Mishra and Farooq, 2023), suggesting short-term nutrient enrichment increases sediment C pool. These differences between this study and previous studies of ANI for sediment OM and C pool indicates increase of anthropogenic activities along the coast of ANI and associated input at these locations compared to decade ago as reported by Sachithanandam et al. (2020).

Increased sediment C levels contribute positively contribution to sediment C stocks and seagrass climate change mitigation potential (Liu et al., 2023; Mishra et al., 2023). However, it has been observed that long-term nutrient enrichment can reduce seagrass sediment carbon stocks through several process such as reducing seagrass productivity by increasing the carbon demand for extra ammonium assimilation (Egea et al., 2020) or by the increased competition with algae leading to algal overgrowth and decimation of seagrass leaves (Zribi et al., 2023) resulting in reduction of seagrass derived autochthonous C sources in the sediments. Consequently, long-term nutrient enrichment can also reduce the seagrass sediment C stocks by modifying the decomposition of dissolved organic carbon (that forms a significant portion of sediment C) by altering microbial activity in the sediment (Yamuza-Magdaleno et al., 2024; Yamamuro et al., 2004). Other than these biogeochemical factors, high seasonal temperatures (as observed in summer season in ANI) can increase the decomposition of labile C (e.g., compounds like cellulose and lignin) that are more resistant to microbial decomposition, thus reducing the C storage potential of these tropical seagrasses as observed for *T. hemprichii* across tropical countries (Jiang et al., 2022; Liu et al., 2016; Qin et al., 2021; Zhang et al., 2022). This suggests that effective management of nutrient enrichment is essential to preserve

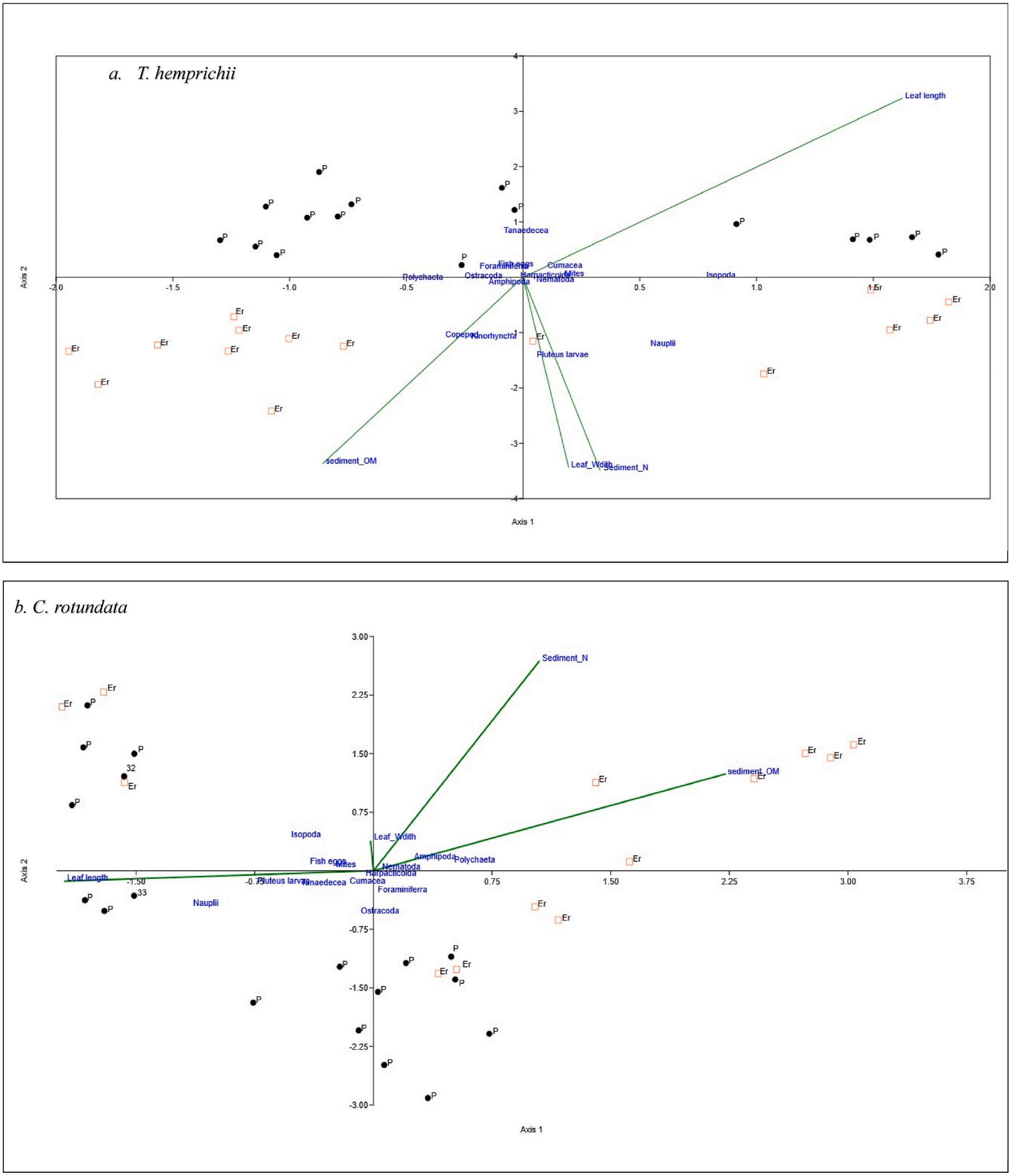

Fig. 6. CCA of leaf associated meiofauna of a) *T. hemprichii* and b) *C. rotundata* with environmental (sediment OM and N%) and seagrass traits (leaf length and width) under pristine (P) and enriched (Er) conditions of ANI, India.

seagrass carbon sequestration capacities.

4.2. Effects of nutrient enrichment on plant traits and population dynamics

Seagrass leaves are considered to be the fast indicators of coastal nutrient conditions due to the rapid utilization of the available N and P in the surface waters towards increasing their primary productivity and growth (Duarte, 1990; Yang et al., 2018). In this study, the low C: N and C:P ratios under enriched conditions, suggests rapid utilization of available N and P for primary productivity and growth for both *T. hemprichii* and *C. rotundata*. Similar trend has been observed globally for various other seagrass species including *T. testudinum*, *Zostera marina*, *Z. japonica*, and *Z. nolteii* (Yang et al., 2018). However, studies assessing this nutrient accumulation in *T. hemprichii* and *C. rotundata* is very limited, though few studies have incorporated response of *C. nodosa* (in the Mediterranean Sea) and *C. serrulata* from the African coast (Supplementary S5). This study uniquely reports the nutrient accumulation potential and the leaf C: N and C:P ratios in *C. rotundata*. Similar nutrient accumulation and indicator potential has been observed in other *Cymodocea* spp., (Fourqurean et al., 2007; Pirc and Wollenweber, 1988; Viana et al., 2020; Yamamuro et al., 2004). It is important to note here, that pristine conditions in this study for both seagrass are of oligotrophic systems, where nutrient supply is highly limited due to lack of rivers and land derived influx (Mishra et al., 2023), thus resulting in very high C:N and C:P ratios, compared to other studies of *Cymodocea* spp., that were located closed to the land-sea interface and received frequent spikes of nutrients even under pristine conditions (Fourqurean et al., 2007; Pirc and Wollenweber, 1988; Yamamuro et al., 2004). Similarly, the range of leaf C:N ratios observed for *T. hemprichii* under enriched conditions (14.66–33.12) were within the range observed for *T. hemprichii* and *T. testudinum* under nutrient enrichment at other locations globally, suggesting species-specific similar mechanisms for nutrient utilization (Govers et al., 2014; Olsen and Valiela, 2010; van Katwijk et al., 2011).

Increase in nutrient availability correlates with positive growth, density and biomass for seagrasses (Cabaço et al., 2013; Herbert and Fourqurean, 2009; Viana et al., 2020). In this study, an increase in density, biomass (only BG), rhizome growth rates, new leaf formation and rhizome productivity of both *T. hemprichii* and *C. rotundata* has been observed under nutrient enriched conditions which is consistent with the global findings for *Thalassia* and *Cymodocea* spp. under nutrient enrichment conditions (Herbert and Fourqurean, 2009; Lapointe et al., 2020a; Medina-Gómez et al., 2016; Viana et al., 2020).

However, the horizontal elongation rate of *C. rotundata* (8.52 cm yr^{-1}) and *T. hemprichii* (3.63 cm yr^{-1}) under nutrient enriched conditions is multifold lower than respective average horizontal elongation rates observed globally for *C. rotundata* (209.9 cm yr^{-1}) and *T. hemprichii* (54.1 cm yr^{-1}) (Cabaço et al., 2013). Reduction in horizontal elongation rates in our study sites can be attributed to anthropogenic influx of metals (e.g., Cu and Pb) and formation of sediment sulfides (due to high OM content, as discussed above in section 4.1) which can exert toxic effects, on seagrass apex formation and most importantly on the seagrass roots, thereby reducing horizontal meadow migration and increasing meadow fragmentation. Further it has also been observed that the vertical elongation rate of *C. rotundata* (1.33 cm yr^{-1}) and *T. hemprichii* (1.56 cm yr^{-1}) under enriched conditions in this study was similar and 2-fold lower than the mean vertical elongation rates observed globally for *C. rotundata* (1.53 cm yr^{-1}), *T. hemprichii* (3.25 cm yr^{-1}) (Cabaço et al., 2013). The lower vertical elongation under nutrient enrichment conditions is generally due to algal proliferation on seagrass leaves, which diverts much of the available energy to new leaf formation instead of vertical elongation of the plant, thus increasing shoot density of the both seagrass species under nutrient enrichment conditions (Table 1). The algal proliferation on seagrass leaves further changes the microbial activity, increases turbidity and associated light limitation which leads to seagrass loss and die-offs (Helber et al., 2021; Lapointe et al., 2020a; Mishra et al., 2021a; Viana et al., 2020). In this study, we observed significant proliferation of algae on the leaves of both *T. hemprichii* and *C. rotundata* (Fig. 2), due to the poor water quality and associated turbidity at our study sites (Sahu et al., 2013; Jha et al., 2015). This algal proliferation hindered growth of seagrass leaves, by increasing inter-specific competition between algae and seagrass for available N and P, resulting in reduction of leaf lengths for both *T. hemprichii* and *C. rotundata* under nutrient enrichment conditions (Table 1). Consequently, this competition reduced seagrass N utilization and photosynthetic production by reducing seagrass leaf surface area and light penetration, explaining the increase of leaf width in both *T. hemprichii* and *C. rotundata* (Table 1).

Furthermore, anthropogenic influx of toxic metals (like Cu and Pb) combined with low pH, can exert toxic effects on leaf growth rates, as observed for *T. hemprichii* and *C. rotundata* from our enriched study sites (Mishra et al., 2024a; Mishra and Farooq, 2022). Combination of algal growth and other confounding factors (e.g., metals, sediment sulfides and seasonal temperatures) can led to decrease in AG-biomass of both *T. hemprichii* and *C. rotundata* under enriched conditions, which has been observed for *T. hemprichii* and other *Cymodocea* spp., elsewhere (Lapointe et al., 2020b; MacLeod et al., 2023; van Katwijk et al., 2011; Westlake et al., 2022) and for *H. ovalis* from the coast of ANI (Mishra et al., 2021a). The reduction in AG-biomass in each seagrass was compensated by increase in BG-biomass for both species under nutrient enriched conditions, which has been observed for various seagrasses under nutrient enrichment conditions (Cabaço et al., 2013; Viana et al., 2020). This increase in BG-biomass also suggests, that both *T. hemprichii* and *C. rotundata* harbor various beneficial root associated microbial communities that help in reducing sediment sulfide toxicity resulting due to increased OM and nutrient input (as discussed earlier). Additionally, both seagrasses are intertidal species, which can regulate their internal plant oxidation mechanisms via water column diffusion during night, driven by tidal subsidy to keep them oxygenated. These seagrasses can increase their spatial root branching to increase oxygen diffusion, which has been mostly observed in *T. testudinum* (MacLeod et al., 2023; Fuggle et al., 2023). However, for *T. hemprichii* in this study, it has been observed that interactions between the seagrass and seagrass associated bivalves exists, which feeds on OM and provides beneficial bacteria for sulfide reductions that helps the seagrass to increase its BG-biomass and persist in nutrient enriched conditions (Mishra and Farooq, 2023). However, this study is limited due to lack of assessment of other anthropogenic pollutants like metals and sediment sulfides, which may have provided better understanding of seagrass response to nutrient enrichment.

Reconstruction techniques provide an advantage in understanding seagrass demography and population dynamics for long-term changes in environmental conditions (Fourqurean and Schrlau, 2003; Herbert and Fourqurean, 2009; Mishra et al., 2021a). In this study, these changes were observed in both *T. hemprichii* and *C. rotundata* under enriched compared to pristine conditions, where the long-term average recruitment (R) for both seagrass species under nutrient enrichment was higher (Table 3). This suggests that both seagrass species under nutrient enrichment were able to increase their vertical rhizome growth rates resulting in higher present recruitment (Table 3). However, these fast growth rates decreased under wet season, when there was a high influx of freshwater into these seagrass meadows and creating similar oligotrophic conditions to the pristine sites. Such conditions, results in low overall population growth rates (Table 3), which is clearly evident for both seagrass species between enriched and pristine conditions. Although, the influx of other anthropogenic contaminants and other confounding factors may also play an important role in reducing the population longevity and demography of both species. This suggests that both seagrass species under nutrient enrichment are subjected to multiple stress conditions due metals or sediment sulfide or reduced water quality combined with high intertidal and seasonal temperatures during low tide resulting in leaf reddening, that can have a negative impact (Mishra and Apte, 2020; Mishra et al., 2021c), resulting in short-living seagrass shoots under enriched conditions (Fig. 4). This may be one of the reasons the population demography of *T. hemprichii* in the islands of ANI is decreasing (Mishra and Apte, 2020). Similar observation of reducing seagrass longevity under nutrient enrichment or anthropogenic contaminants has been observed for *T. testudinum* and *C. nodosa* from the coast of the USA and Europe (Herbert and Fourqurean, 2009; Mishra et al., 2021a).

4.3. Effect of nutrient enrichment on seagrass biodiversity assemblages

Seagrass leaf meiofauna abundance is impacted by the available leaf surface area for attachment and the condition of the seagrass leaves (new vs old). This study observed that seagrass leaf meiofauna abundance decreased under nutrient enrichment conditions, probably due to the extensive algal growth on seagrass leaves and reduction in leaf length for both seagrass species (Table 1). Despite having higher younger plants under enriched conditions, the algal proliferation did not allow a marked differentiation between these younger and older leaves for the meiofaunal settlement. For example, the fish eggs found attached under pristine conditions in both seagrass leaves were absent under enriched conditions (Fig. 6). Simultaneously, the leaf meiofauna composition was altered with certain groups of epiphytic organisms (like Copepods, Konorhyncha, Nauplii, Pluteus larvae) appearing under enriched conditions for *T. hemprichii,* but not in *C. rotundata* leaves, suggesting seagrass-specific relationships with meiofauna abundance (Alsaffar et al., 2020). Similar species-specific meiofauna settlement preferences have been observed for *T. hemprichii* meadows from other study locations of ANI (Naufal and Padmavati, 2018). Furthermore, this suggests algal proliferation under nutrient enrichment and changes in water quality can alter leaf meiofauna abundance by favoring certain groups of organisms compared to others, which can be used as indicators of coastal nutrient enrichment (Hays, 2005; Rodriguez et al., 2022).

Unlike to our study, meiofauna abundance was less affected by nutrient enrichment in *T. hemprichii* and *C. rotundata* ecosystems of Tanzania, whereas the presence of grazers positively influenced the meiofauna abundance under nutrient enrichment conditions. However, the effects of nutrient enrichment on seagrass meiofauna abundance are not straightforward and highly dependent on the availability of grazers or consumers (Alsaffar et al., 2020; Daudi et al., 2012). Thus, the impacts of nutrient enrichment on seagrass are location specific and the presence of grazers affects the structuring and abundance of seagrass meiofauna (Daudi et al., 2012; Hays, 2005; Rodriguez et al., 2022). Though our study sites are known as suitable sites for megaherbivores like Dugongs and Green Sea turtles (D'Souza et al., 2015; Mishra et al., 2021a), no grazing marks were observed on the both seagrass species under nutrient enriched conditions. The increased algal coverage and change in nutritional composition of seagrass leaves under nutrient enrichment, may make them unsuitable for consumption (Armitage and Fourqurean, 2016; Baggett et al., 2010). However, establishing such a direct relationship requires further studies, and this study is limited by not analyzing the various grazers that feed on the algal biomass or the associated leaf meiofauna. Other than these megaherbivores, small grazers like sea urchins, fish sea cucumbers and crabs and their predators constitute healthy trophic cascades that plays an important role in seagrass response to nutrient enrichment and needs to be included in future studies.

5. Conclusions

This study assessed the morphometrical response and population demography of two seagrasses (*T. hemprichii* and *C. rotundata*) response to short-term nutrient enrichment in the under-studied oligotrophic tropical islands of Indian-Ocean Region. The findings of this study indicate species-specific responses of seagrasses to nutrient enrichment. Our results fill the existing knowledge gaps on seagrass research of tropical islands of the global south, which is currently an understudied region for seagrass ecosystems globally. Increase in density, biomass and morphometric features of both seagrasses suggest species-specific short-term positive effects of nutrient enrichment in tropical oligotrophic systems. However, these benefits do not extend to increased population longevity suggesting the negative effects of nutrient enrichment combined with other anthropogenic stressors (e.g., metals, sediment sulfides) and confounding factors (e.g., seasonal high intertidal temperatures), therefore, emphasizing for more such assessments for seagrass ecosystems in tropical islands globally. The nutrient enrichment combined with other confounding factors led to increase in meadow fragmentation and reduction in horizontal meadow migration. Thus, negatively impacting seagrass expansion under nutrient enrichment and lead to algal decimation, and die-offs. This study highlights the reduction in seagrass associated meiofaunal abundance under nutrient enrichment, thus reduction in seagrass ecosystem services provisions. Additionally, the impact of grazers in structuring the meiofaunal assemblages under nutrient enrichment needs to be incorporated for better understanding of these interactions within seagrasses of tropical islands. To avoid seagrass loss in these important tropical islands, continuous monitoring of water quality and seagrass leaf C: N and C:P ratios combined with leaf morphometrics (e.g., length and width) can be utilized as early indicators under nutrient enrichment. These indicators may help in timely interventions for managing the seagrass ecosystems in these oligotrophic island regions, where cultural nutrient enrichment is increasing due to increased anthropogenic activities and human populations. Further studies emphasizing the importance of species-specific seagrass response to nutrient enrichment are essential to assess the impact of long-term (> multiple year and seasonally) nutrient enrichment on seagrass ecosystem services, biodiversity assemblages, trophic interactions, and most importantly seagrass nutritional quality. Long-term monitoring of seagrass ecosystems of oligotrophic tropical islands should include seagrass population demography, root associated microbiomes, interactions of seagrass with sediment associated biodiversity and presence or absence of small mesograzers, and interactions with environmental parameters. These monitoring indicators fit perfectly in the “100 priority questions for seagrass research” which is of utmost priority to halt global seagrass loss and avail the crucial climate change mitigation, food security and habitats for the endangered megaherbivores (e.g., Dugongs and turtles). Preventive measures should focus on minimizing the untreated anthropogenic waste water discharge into these sensitive seagrass ecosystems in small tropical oligotrophic island ecosystems. Most importantly, this study calls for initating quantification of seasonal nutrient input into coastal ecosystems of these islands, where seagrasses are present. This study serves as an initial baseline for future research on the impacts of anthropogenic pollution on seagrass ecosystems of the various tropical islands of the Indian Ocean and for similar other islands ecosystems globally.

CRediT authorship contribution statement

Amrit Kumar Mishra: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Raihana Rasheed:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Syed Hilal Farooq:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.123797.

Data availability

Data will be made available on request.

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