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Research Article

Diversity and distribution of seagrasses in Chilika Lagoon: Regional threats and management recommendations

G Rastogi*, P K Tripathy, S P Dash & P R Muduli

Wetland Research and Training Centre, Chilika Development Authority, Balugaon, Odisha – 752 030, India

*[E-mail: rastogigurdeep@gmail.com]

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Studies examining the spatial distribution and abundance of seagrasses are limited in the Indian coastal lagoons. Chilika (Odisha) is the largest brackish water lagoon in Asia which supports the second-largest seagrass meadows in India. A field survey was conducted from 20 locations (n = 57 sites) across the southern, central, and outer channel sectors of the lagoon. A total of six species: *Halophila ovalis*, *H. ovata*, *H. beccarii*, *Halodule pinifolia*, *H. uninervis*, and *Ruppia maritima* were recorded during the study. *Halophila ovalis* (31 sites) and *H. pinifolia* (33 sites) showed wide occurrences in the lagoon. In the southern sector, 46 % of sampled sites demonstrated dense seagrasses (> 70 % cover) with all six species present. In the central sector, 45 % of sites showed medium dense seagrass cover (40 – 70 %) and 4 species were recorded. In the outer channel, 94 % of sampled sites supported dense seagrasses represented by 3 species. Seagrass cover showed a significant positive correlation with salinity (r = 0.489, p-value < 0.01) and plant biomass (r = 0.445, p-value < 0.01). The meadows in the southern and central sectors showed profuse growth of *Stuckenia pectinata*, *Najas indica*, *Gracilariopsis longissima*, and *Chaetomorpha* with seagrasses. Based on DAPSIR (Drivers-Activities-Pressure-State-Impact-Responses) framework, anthropogenic threats to seagrasses included fishing gears, unsustainable fishing methods, including aquaculture, and boat operations. The framework suggested that management responses must include restrictions on fishing gears, illegal aquaculture, and stricter surveillance on boat traffic and water quality. Besides, promoting ecotourism, framing policy actions, stakeholder awareness and community participation were also recognised as crucial responses for effective conservation and protection of seagrasses.

[**Keywords**: Biomass, Conservation, DAPSIR, Macrophytes, Seagrass cover]

Introduction

Benthic macrophytes, especially seagrasses, are efficient "blue carbon" stocks and contribute to climate change mitigation through the uptake of carbon (C) and storing it in their biomass and underneath sediments[1]. These aquatic plants constitute underwater coastal habitats and are referred to as “ecosystem engineers” due to their ability to physically modify their local benthic/pelagic environment[2]. Seagrass meadows, due to increased habitat complexity, are excellent foraging and breeding habitats for various fauna, especially fisheries[3]. It has been shown that the loss of seagrass meadow is invariably associated with the loss of various ecosystem goods and services (*e.g.*, sediment stabilisation and coastal protection, C sequestration, fishery, and tourism)[2,4].

Like other parts of the world[2], seagrass beds in India are also declining due to various anthropogenic and natural stresses[5,6]. For instance, ~ 28 % loss of seagrass cover between the years 2000 – 2004 in the Gulf of Mannar, Tamil Nadu has been attributed to anthropogenic causes[6]. Whereas, nearly 46 % loss of seagrass cover between the years 2004 – 2007 in the Nicobar Islands was primarily due to natural calamities like tsunamis in the Indian Ocean[6]. Restoration and conservation of blue carbon coastal systems (such as mangroves, seagrasses, and salt marshes) have been given high priority by the Indian Government for mitigating climate change through biological C sequestration[7]. Blue C sequestration by seagrasses could be significant due to their large area (~ 517 sq. km) along the Indian coastline[8,9]. It has been estimated in Palk Bay (Tamil Nadu) that 1 sq. km of seagrass meadow has the potential to sequester 13.96 Gg C in the top 1 m of the sediments[8]. In India, a total of 16 species of seagrasses have been reported from diverse coastal systems (such as estuaries, bays, lagoons, backwaters, and open sea)[10]. Of which, the Gulf of Mannar and Palk Bay harbour the highest seagrass species diversity (14), followed by Andaman & Nicobar Islands (12), Lakshadweep Islands (10), Gulf of Kutch, Gujarat (8), and Chilika Lagoon (7)[refs. 5,11]. Since the Gulf of Mannar and Palk Bay support the largest size seagrass meadows (399 sq. km) and the highest species richness, a recent review[12] highlighted that almost 74 % of the published studies from Indian coastal waters are mostly concentrated on these ecosystems. In contrast, lagoonal environments, which are strongly driven by monsoonal freshwater discharge and support a much lower diversity of seagrasses, remain poorly studied[11-13].

Chilika is one of the key Ramsar sites (no. 229) on the eastern coast of India and has immense biodiversity and socioeconomic importance[11]. Based on the geospatial assessment using Landsat 8 OLI data combined with a field survey carried out in the year 2014, the total seagrass area from Indian coastal waters has been estimated to be 517 sq. km[ref. 9]. Of this, Chilika was estimated to contain 85.47 sq. km (April) − 65.12 sq. km (October) of seagrass area with dynamic seasonal changes[9]. Thus based on area, seagrass meadows in Chilika are the second largest after Palk Bay (330 sq. km)[12]. Considering the 85.47 sq. km seagrass area in Chilika, it has been estimated that C biomass could be in the tune of 2.3 – 2.5 Gg, whereas in sediments it could be between 4.5 – 5.7 Gg[ref. 14]. Another study has estimated blue C stock of 2.018±0.673 M gC ha^{-1} in seagrass sediment cores (30 cm) of Chilika[15]. Moreover, an annual C sequestration rate between 10.1 – 16.8 ton CO_2 equivalents per hectare of seagrasses[8] with an estimated economic value of blue C in the tune of Rs. 498 – 828 million per year has also been estimated in Chilika[16]. The provisioning services, such as high fish catches (~16,657 Tons in 2017 – 2018)[16] supporting the livelihood of more than 0.2 million fishermen in Chilika, have been indirectly linked to seagrasses as the majority of spawning grounds have been mapped in the area of seagrass meadows[12,17]. These ecosystem services further stress the need for prompt attention to seagrasses for their conservation and protection in the lagoon.

Google Scholar was used to broadly search literature (peer/non-peer reviewed) on the diversity and ecology of seagrasses in Chilika. Filtering of search results retained merely 10 studies on the theme with field surveys between the years 2000 – 2019 (Table S1). This evidenced the lack of primary data on the seagrasses of Chilika Lagoon. Notably, a recent review[12] has further highlighted this fact through extensive searches made on the SCOPUS database for the period of 1971 – 2022, which resulted in only 16 peer-reviewed articles on Chilika seagrasses. Based on these past studies, a total of 7 species: *Cymodocea serrulata, H. ovalis*, *H. ovata*, *H. beccarii*, *H. pinifolia*, *H. uninervis*, and *R. maritima* have been reported in Chilika (Table S1). Most of the existing studies, except Pattnaik *et al.*[11] and Tripathy *et al.*[13] have a limited spatial coverage and/or lack data on seagrasses abundance and contextual water quality parameters. The scarcity of ground data on seagrasses is mostly due to difficulties in underwater sampling, logistical constraints for sampling in remote locations, and seasonal changes in their distribution and abundance. However, due to the transient nature of seagrass ecosystems, field-based primary data is highly essential for their efficient management and conservation.

Seagrasses in Chilika are also affected by a variety of climatic and anthropogenic drivers[7,12,13]. This lagoon is frequently impacted by the cyclonic storms originating in the Bay of Bengal[18]. Various anthropogenic threats, such as aquaculture, boat traffic associated with tourism/fishing operations, and pollution, negatively impact seagrass meadows[7,12]. These drivers and resulting threats must be examined to monitor their impact on seagrasses to suggest specific management responses for their conservation and protection. Therefore, this study was undertaken to (i) assess seagrass diversity, their abundance, and spatial distribution in relation to water quality and (ii) identify threats and management responses for seagrass conservation and protection using a holistic framework.

Materials and Methods

Study site

Chilika Lagoon (19°28’ – 19°54’ N and 85°06’ – 85°35’ E) is located on the east coast of India in the Odisha State (Fig. 1). It is a shallow lagoon (average water depth ~ 2 m) with a rich diversity of macrophytes, including seagrasses[13,17]. The Northern Sector (NS) of the lagoon is ‘riverine’ due to major (~ 68 – 85 %) freshwater influx from distributaries of the Mahanadi River occurs in this sector[19]. This sector is highly silted and has the lowest salinity regime (< 5 ppt), supporting the luxurious growth of freshwater macrophytes but not seagrasses[13].

The Central Sector (CS) is a ‘brackish’ zone in which the mixing of riverine and marine water occurs[19]. Nalabana, a marshy island of ~ 16 sq. km,

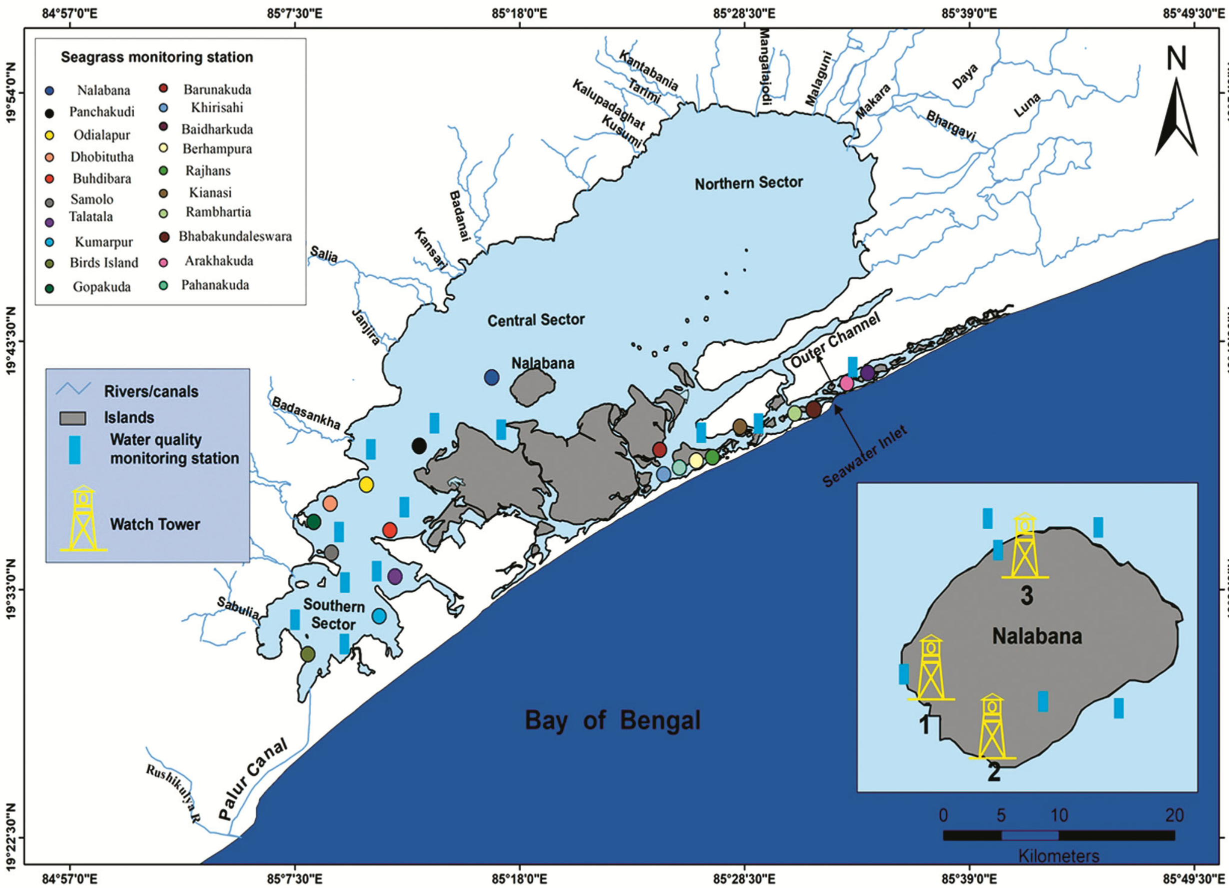

Fig. 1 — Map of Chilika Lagoon depicting seagrass survey (*n* = 20) and water quality monitoring (*n* =18) stations across southern, central, and outer channel sectors. The panel shows the Nalabana Island (and 3 Watch Towers) and the location of water quality monitoring stations in and around it

located in this sector, is a designated Bird Sanctuary under the Wildlife Protection Act, 1972[ref. 20]. Each year, millions of migratory and local birds arrive on this island during winter. Notably, this avian fauna is also a significant source of N and P loading in the lagoon through their guano[20,21], resulting in the luxurious growth of seagrasses, salt marshes, and other halo-tolerant weeds (e.g., *Paspalum*, *Stuckenia*) in this island[13,20]. The Southern Sector (SS) has a stable salinity regime throughout the year due to seawater influx from Palur Canal[19] (Fig. 1). Furthermore, this sector is quite deep (mean depth ~ 3 m) with a high water clarity and photic depth supporting seagrasses, aquatic weeds, and macroalgae[13]. The Outer Channel (OC) sector of the lagoon is 'marine' (except during monsoon) and connected to the Bay of Bengal through several seawater inlets. The salinity is typically high in this sector and has been shown to reach ~ 35 ppt during tidal influx of seawater[19]. This sector supports dense seagrass meadows, mostly in the intertidal zone, creeks, and the shorelines of various islands[13,20].

Seagrass sampling, identification, diversity, and biomass assessment

The seagrass survey was conducted between December 2021 and April 2022. This represents post-monsoon/early winter and is specifically suited for underwater seagrass assessment due to prevailing low wind, calm water, and high water clarity in the lagoon. The ground survey was carried out from 57 sites across 20 broad locations from SS (9 locations, 28 sites), CS (1 location, 11 sites), and OC (10 locations, 18 sites) using a Global Positioning System (GPS) (Fig. 1). Assessment of seagrass distribution and composition in deeper water zones was carried out using a Van Veen Grab sampler (KC Denmark, size 250 cm^2) and a rake mounted on a bamboo pole (Fig. S1a, b).

Seagrass biomass is an indicator of their abundance[22] and was measured from sites located in shallow zones in each sector using a quadrat (50 × 50 cm) sampling method (Fig. S1c, d). Seagrasses (whole plant) were gently separated from sediments and washed repeatedly *on board* to remove associated invertebrates (*e.g*., molluscs), and epiphytic macroalgae (if any). Samples were transported in an ice box to the Wetland Research and Training Centre (WRTC), Balugaon, located on the shoreline of Chilika within 6 – 8 h.

In the laboratory, samples were kept on blotting paper to soak up extra water, and fresh weight (wet weight) was measured. Subsequently, seagrass biomass (g/m^2) in terms of dry weight of samples was measured by keeping the samples in a hot air oven at 50 °C[ref. 23] for 3 days to get a constant weight. The % cover estimated through visual inspection is a simple, coarse, and non-destructive estimate of seagrass abundance[22]. Based on earlier studies from Chilika[9,13], seagrass cover was assigned to dense (> 70 % cover), medium dense (40 – 70 %), and sparse (10 – 40 %). The quadrat (1 per site) was placed in a representative area of the meadow that was selected by the recce survey (Fig. S2). The species composition and % cover of the seagrasses were recorded. The status of various macroalgae and macrophytes associated with seagrasses was also recorded.

The seagrasses were identified based on published keys described in earlier work[5,24]. *Halophila ovalis* was identified through (i) oval leaf shape, (ii) cross-venation > 12 in a leaf, and (iii) smooth leaf margin and hairless leaf surface. The keys for *H. ovata* were (i) transparent leaf lamina, (ii) cross veins 3 – 9 pairs, and (iii) a wide space (0.4 – 0.6 mm) between leaf margin and intra-marginal vein. *Halophila beccarii* was identified through (i) lanceolate leaf shape, (ii) pseudowhorl containing 2 – 6 leaves, (iii) leaf blade shorter than petiole, (iv) no cross venation, and (v) thin and smooth rhizome. Key features of *H. pinifolia* were (i) rhizome with leaf scars, (ii) linear and flat leaf blade up to 20 cm, and (iii) central vein split into two at the leaf tip. The key criteria for *H. uninervis* were (i) leaf blade up to 15 cm long, (ii) linear and flat leaf, and (iii) leaf with 3 distinct points or teeth at the tip and a well-developed lateral tip. Key features of *R. maritima* were (i) delicate, branching stems and long, thread-like leaves, (ii) two flowers, one on top of the other and facing opposite directions constitute inflorescence.

Measurement of physicochemical parameters and statistical analyses

The water quality data from selected long-term monitoring stations which were located close to seagrass sampling sites (9 in SS, 6 in CS (Nalabana Island), and 3 in OC) (Fig. 1) were used to evaluate the broad water quality conditions in proximity to the area of seagrass meadows. The data on physicochemical parameters were collected once each month from December 2021 to April 2022 which included *in situ* recording of Water Temperature (WT), transparency and depth (Secchi Disc), salinity, and pH. Dissolved nutrients [(nitrate (NO_3), nitrite (NO_2), ammonia (NH_4), and phosphate (PO_4)] were measured from water samples using the nutrient autoanalyzer (SKALARSANplus ANALYZER). The detailed protocol for measuring physicochemical parameters was adopted from Srichandan *et al.*[19] and Muduli *et al*.[21]. Besides, the contextual water quality parameters (depth, transparency, WT, salinity, and pH) were recorded from additional shoreline sites in which seagrass biomass and cover were measured. This dataset was used to generate a UPGMA (Unweighted Pair Group Method with Arithmetic Mean) tree using the Jaccard similarity index to reveal clustering between various sites based on their seagrass composition, biomass, and water quality. The statistical significance of the differences in parameters between various sectors (SS, CS, and OC) was tested using one-way ANOVA (p-value < 0.05). Pearson's correlation coefficient (r) was calculated to examine the relationship between seagrass biomass and cover with contextual water quality factors. Shannon's diversity index (H') was calculated to estimate seagrass diversity in each sector. All statistical analyses were performed in the PAST (PAleontological STatistics) program (v 4.03).

Assessment of threats to seagrasses using the DAPSIR framework

The threats and their specific impacts on the status change of seagrass meadows were analyzed using the DAPSIR framework[25] which has been used earlier for suggesting the conservation measures for *H. beccarii* on the Indian coast[10]. DAPSIR is a holistic approach to understand the interactive effect of multiple threats and their cumulative impacts on seagrass meadows[25]. The provisioning services of the lagoon were listed based on the Chilika Integrated Management Plan[17] and field observations (*e.g*., foraging of seagrasses by Chilika buffalo). The assessment of threats to seagrasses in Chilika also included field observations (*e.g*., presence of aquaculture ponds near meadows, deposition of plant debris over meadows after cyclone, and fishing/tourism/foraging activity in

Table 1 — Physicochemical factors measured from water samples collected during the seagrass survey (December 2021 – March 2022). There were 9 water quality monitoring stations in SS (n = 36 samples, 9 stations × 4 months), 3 in OC (n = 12 samples, 3 stations × 4 months), and 6 in CS (Nalabana Island) (n = 24 samples, 6 samples × 4 months). Mean seagrass biomass and cover in 3 sectors (SS n = 19; CS n =11; OC n = 18) is also shown. The value represents mean±SD for each parameter. Mean differences were tested by one-way ANOVA (Welch's F-test) with *Games-Howell post-hoc test*. Means with the same alphabets are not significantly different at PERMANOVA p-value = 0.05

Water parameters	SS	CS	OC	p-value
WT (ºC)	24.76±0.94^{a}	25.88±1.28^{a}	24.71±0.51^{a}	0.117
Transparency (m)	0.70±0.25^{a}	0.48±0.12^{b}	0.70±0.55^{ab}	0.186
Depth (m)	1.52±0.62^{a}	0.75±0.16^{b}	1.75±0.89^{ab}	**0.042**
Salinity	8.13±0.58^{a}	8.69±0.59^{a}	18.40±4.96^{b}	**0.001**
pH	8.52±0.24^{a}	8.47±0.15^{a}	8.41±0.15^{a}	0.678
NO_2 (µmol L^{-1})	0.11±0.07^{a}	0.57±0.57^{b}	0.21±0.01^{b}	**0.006**
NO_3 (µmol L^{-1})	1.39±0.49^{a}	4.98±5.23^{b}	2.15±0.20^{b}	**0.012**
PO_4 (µmol L^{-1})	0.11±0.03^{a}	0.13±0.05^{a}	0.12±0.03^{a}	0.806
NH_3 (µmol L^{-1})	1.73±0.18^{a}	1.90±0.32^{a}	1.90±0.24^{a}	0.428
Seagrass biomass (g/m^2)	116.33±101.43^{a}	101.13±40.39^{a}	105.44±59.23^{a}	0.835
Seagrass cover (%)	59.47±35.66^{a}	65.45±32.36^{a}	96.11±16.50^{b}	**0.001**

seagrass habitats). The data from secondary sources[7,12,13,26-34] on threats from boat/fishing operations, aquaculture ponds, pollutants (oil spills, plastics, and heavy metals), and cyclonic storms were also included in the DAPSIR framework. The specific management responses to mitigate the threats were also recommended for the conservation and protection of seagrasses.

Results

Water quality variation across sectors

Depth, salinity, NO_2, and NO_3 showed significant (ANOVA p-value < 0.05) sectoral variation (Table 1). The salinity of OC (18.40±4.96) was significantly higher than SS (8.13±0.58) and CS (8.69±0.59). The mean dissolved nitrogen concentration (in µmol L^{-1}) in CS (NO_2 = 0.57±0.57, and NO_3 = 4.98±5.23) was higher than SS (NO_2 = 0.11±0.07 and NO_3 = 1.39±0.49). In all sectors, PO_4 concentration was significantly (ANOVA p-value < 0.01) lower than NO_3.

Seagrass diversity, biomass, and cover

Field survey across 20 locations (n = 57 sites) of the lagoon recorded six species namely: *H. ovalis*, *H. ovata*, *H. beccarii*, *H. pinifolia*, *H. uninervis*, and *R. maritima* (Fig. 2) with a wide spatial heterogeneity. All six species were recorded from SS (Shannon's diversity H' = 1.41), whereas only 4 and 3 species were recorded from CS (H' = 1.18) and OC

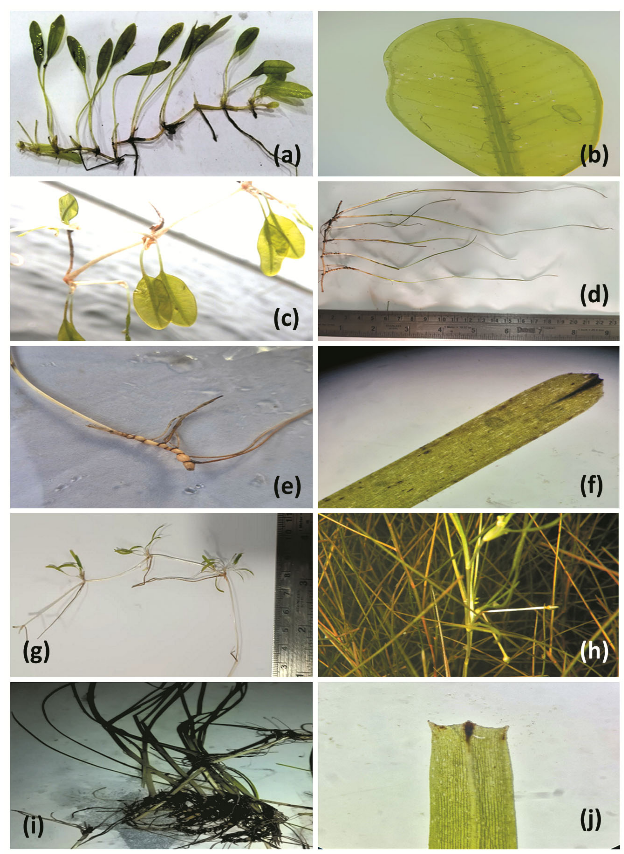

Fig. 2 — Specimen photographs showing (a) *H. ovalis*, (b) Leaf of *H. ovalis* having more than 12 cross venation, (c) *H. ovata*, (d) *H. pinifolia*, (e) Leaf scars of *H. pinifolia*, (f) Leaf tip showing black central vein split into two, (g) *H. beccarii*, (h) *R. maritima*, (i) *H. uninervis*, and (j) Trident leaf tip of *H. uninervis*

(H' = 0.89) sectors, respectively. *Halodule pinifolia* was the most widely distributed species in SS (16/28 sites, Table 2) and OC (14/18 sites, Table 3), whereas *H. ovalis* most widely occurred in CS (9/11 sites, Table 4). *Halodule uninervis* showed restricted distribution in the lagoon and was recorded only from 3 sites [GK1 (in SS); NB1 and NB11 (in CS)] (Tables 2 and 4). *Halophila beccarii* was detected only from 4 sites [OP4 and DT1 sites (in SS); KN and BP2 sites (in OC)]. *Halophila ovata* was limited to only 4 sites (TT2, B11, B12, and GK1) of the SS and was not found in other sectors. The mean seagrass biomass of the 3 sectors did not differ significantly (p-value > 0.05) (Table 1). The seagrass cover showed a significant (p-value < 0.05) variation across 3 sectors, with a higher mean cover (96.11±16.50 %) in OC. Moreover, the cover showed a significant (p-value < 0.05) positive correlation with salinity (r = 0.489) and biomass (r = 0.445) (Fig. 3a). The UPGMA tree showed 3 major clusters composed of sites from various sectors. Some sites, such as DT2, KN, BI1, and KN, formed distinct branches in the tree (Fig. 3b).

Based on the quadrat assessment, 94 % sites in OC contained dense seagrass cover (Table 3), whereas only 46 % sites in SS and 45 % sites in CS contained dense canopy cover (Tables 2 and 4). There was a conspicuous spatial variation in seagrass abundance and distribution across sectors and also within a sector. In SS, dense growth of seagrasses was found in 46.43 % of sites, followed by sparse (32.14 %), and medium dense (21.42 %) (Table 2). The seagrass meadows ranging from mono-specific to mixed beds (Fig. 4a, b) were prevalent throughout the SS shoreline. The GK1 site showed three co-occurring seagrasses (*H. pinifolia*, *H. ovata*, and *H. uninervis*) (Table 2). In some of the sites, *Gracilariopsis longissima* (red algal seaweed) and *Chaetomorpha* were found associated with seagrasses (Fig. 5). *Stuckenia pectinata*, a halotolerant weed, grew profusely over seagrass meadows. *Spongilla alba* was also recorded in some of the meadows located in Kumarpur sites (Fig. 5). The biomass showed a large spatial variation (Table 2). The peak biomass of *H. pinifolia* (315 g/m^2) and *R. maritima* (140 g/m^2) was recorded from the DT2 site. The GK1 site provided the maximum biomass of *H. ovata* (160 g/m^2), while the peak biomass of *H. ovalis* (138 g/m^2) was recorded from the GK2 site. *Halophila beccarii* (20 g/m^2) showed maximum biomass in the OP4 site, while *Halodule uninervis* (11 g/m^2) in the GK1 site.

In CS, long stretches of *H. ovalis* meadows were noted in the navigation channels connecting to Bird Watch Tower no. 1, 2, and 3 of Nalabana Island (Fig. 4c, d). *Gracilariopsis longissima* grew profusely with seagrasses (Fig. 5). Also, it was noted that vigorous growth of *S. pectinata* and *N. indica* (a freshwater macrophyte) formed a top cover on the water surface, resulting in shading over the meadows. The seagrass cover varied from sparse to medium dense to dense across various sites (Table 4). NB10 and NB11 sites near the Watch Tower 3 supported maximum diversity as four species namely *R. maritima*, *H. pinifolia*, *H. ovalis*, and *H. uninervis* were recorded. Peak biomass of *H. ovalis* was recorded from the NB7 site (90 g/m^2), *H. pinifolia* from NB10 site (130.4 g/m^2), *H. uninervis* from NB1 site (140 g/m^2), and *R. maritima* from NB10 site (22.4 g/m^2).

In OC, all 18 sites (except BP2) supported dense seagrass meadows (Table 3). The mono-specific meadows of *H. pinifolia* were recorded from BK, AK, RB, PHK, and BRK sites, while peak biomass was harvested from the RH1 site (247.2 g/m^2) (Fig. 4e). *Halophila ovalis* formed dense mono-specific beds with 100 % cover in BBK and RH2 sites, while peak biomass was obtained from the RH2 site (134 g/m^2). *Halophila beccarii* formed dense monospecific beds in the KN site with a biomass of 73.2 g/m^2 (Fig. 4f).

DAPSIR assessments of threats and management recommendations

The societal needs in terms of fishery and tourism were the major drivers that were linked to key activities such as fishing operations, aquaculture, boat traffic, dredging, and coastal infrastructure projects in lagoon (Fig. 6). These activities were linked to a variety of pressures on seagrasses such as boat scarring, pollution (oil, plastics, and heavy metals), siltation and sedimentation, and changes in water quality (salinity, turbidity, nutrient loading). Climatic drivers were linked to changes in rainfall, tidal flux, and the amount of freshwater inflow into the lagoon. These pressures may cause various state changes such as habitat modification (*e.g.*, fragmentation of meadows), and reduction in cover, biomass, and productivity in seagrasses. The major management response included restriction on fishing gears, boat traffic in seagrass zones, prohibition of illegal

Table 2 — Seagrass diversity, coverage, and biomass along with contextual transparency and depth of water column in SS. Numbers in bold represent peak values of biomass, - Not determined, D - dense, MD - medium dense, and S - sparse

SS/locations	Site code	Composition	Cover (%)	Type	Biomass (g/m^2)	Depth (m)	Transparency (m)	Total distance between sites (km)
Panchakudi	PK1	*H. pinifolia*	20	S	41	0.89	0.45	2
	PK2	*H. ovalis*	30	S	46	1.03	0.43	
Budhibara	BB1	*H. pinifolia*	60	MD	73	0.88	0.21	7
	BB2	*H. ovalis*	90	D	66.33	0.87	0.61	
Kumarpur	KMP1	*H. ovalis*	30	D	103.4	0.77	0.77	1.94
		H. pinifolia	60		83			
	KMP2	*H. ovalis*	80	D	-	0.78	0.78	
		H. pinifolia	20					
	KMP3	*H. ovalis*	60	MD	-	0.87	0.87	
	KMP4	*H. ovalis*	50	MD	-	0.77	0.77	
Talatala	TT1	*H. ovalis*	10	D	28.75	0.89	0.89	4.94
		H. pinifolia	90		105.25			
	TT2	*H. pinifolia*	40	D	-	1.06	1.06	
		H. ovata	60		-			
	TT3	*R. maritima*	40	S	72	0.08	0.08	
	TT4	*H. pinifolia*	50	MD	-	0.80	0.56	
	TT5	*H. ovalis*	20	D	-	0.33	0.33	
		H. pinifolia	80		-			
	TT6	*H. ovalis*	70	D	-	0.72	0.72	
	TT7	*H. ovalis*	70	D	-	0.29	0.29	
Bird Island	BI1	*H. ovata*	60	MD	46.2	0.28	0.28	0.66
	BI2	*H. ovata*	70	MD	-	0.40	0.40	
Odialpur	OP1	*R. maritima*	30	S	18	0.10	0.10	1.72
	OP2	*H. pinifolia*	100	D	282	0.27	0.27	
	OP3	*H. ovalis*	30	S	54	0.26	0.26	
	OP4	*H. beccarii*	10	S	20	0.27	0.27	
Dhobatutha	DT1	*H. beccarii*	10	S	16	0.26	0.26	2.24
		H. pinifolia	20		30			
	DT2	*H. pinifolia*	60	D	315	0.34	0.34	
		R. maritima	40		140			
Gopakuda	GK1	*H. pinifolia*	40	D	90	0.50	0.50	0.82
		H. ovata	50		160			
		H. uninervis	10		11			
	GK2	*H. ovalis*	60	D	138	0.48	0.48	
		H. pinifolia	40		90			
Samolo	SM1	*H. pinifolia*	100	D	103.33	0.26	0.26	1.52
	SM2	*H. pinifolia*	30	S	52	0.27	0.28	
	SM3	*H. pinifolia*	10	S	26	0.26	0.28	

aquaculture, and sensitisation of various stakeholders and local coastal communities. Moreover, regular ground survey of seagrasses along with water quality monitoring is also recommended.

Discussion

In general, seagrasses in Chilika occupied sheltered, calm habitats with high water clarity and low fluctuation in salinity. Therefore, SS, due to its unique geomorphology and sheltered bay habitats, provided an ideal habitat for seagrass meadows. Due to the large spatial separation of SS from the Mahanadi River distributaries, the influence of freshwater discharge was also minimal in this sector, resulting in a stable salinity regime across various seasons[19]. Besides, the dominance of sand content

Table 3 — Seagrass species diversity, coverage, and biomass along with contextual transparency and depth of water column in CS (Nalabana Island). Numbers in bold represent peak values of biomass, D - dense, MD - medium dense, and S - sparse

CS (Nalabana Island)/ locations	Site code	composition	Cover (%)	Type	Biomass (g/m^2)	Depth (m)	Transparency (m)	Total distance between sites (km)
Watch Tower-2	NB1	*H. uninervis*	90	D	140	0.70	0.33	0.6
		H. ovalis	10		16			
	NB2	*H. ovalis*	60	MD	76.4			
	NB3	*H. ovalis*	80	D	78.4			
		H. pinifolia	20		44.8			
Watch Tower-1	NB4	*H. pinifolia*	50	MD	104.4	0.76	0.57	1
	NB5	*H. ovalis*	50	MD	62			
Between Tower-1 and Nuapada	NB6	*H. ovalis*	70	MD	54.4	0.78	0.47	
Nuapada	NB7	*H. ovalis*	10	S	90	0.68	0.43	
Between Nuapada and Tower-3	NB8	*H. pinifolia*	10	D	110	0.53	0.53	
		H. ovalis	90		28			
Watch Tower-3	NB9	*R. maritima*	20	S	15.6	0.26	0.26	0.6
	NB10	*R. maritima*	40	D	22.4			
		H. ovalis	50		76.8			
		H. pinifolia	10		130.4			
	NB11	*H. uninervis*	20	MD	21.6			
		H. ovalis	40		41.2			

Table 4 — Seagrass species diversity, coverage, and biomass along with contextual transparency and depth of water column among in OC sector. Numbers in bold represent peak values of biomass, D - dense, MD - medium dense, and S - sparse

OC/locations	Site code	Composition	Cover (%)	Type	Biomass (g/m^2)	Depth (m)	Transparency (m)	Total distance between sites (km)
Baidharakuda	BK	*H. pinifolia*	100	D	59.2	0.7	0.33	
Arakhakuda	AK	*H. pinifolia*	100	D	50.8	0.05	0.05	
Bhabakundaleswara	BBK	*H. ovalis*	100		78.8	0.36	0.36	
Rambhartia	RB	*H. pinifolia*	100	D	87.6	0.36	0.36	
Kianasi	KN	*H. beccarii*	100	D	73.2	0.38	0.38	
Berhampura	BP1	*H. ovalis*	40	D	40	0.27	0.27	0.5
		H. pinifolia	60		82.4			
	BP2	*H. beccarii*	30	S	16.4	0.26	0.26	
	BP3	*H. ovalis*	50	D	75.6	0.28	0.28	
		H. pinifolia	50		216.4			
Khirisahi	KS1	*H. pinifolia*	80	D	44.4	0.50	0.43	0.5
		H. ovalis	20		7.2			
	KS2	*H. pinifolia*	80	D	44.4	0.68	0.65	
		H. ovalis	20		7.2			
	KS3	*H. ovalis*	30	D	22			
		H. pinifolia	70		34.4			
Rajhans	RH1	*H. pinifolia*	90	D	247.2	0.16	0.16	4.0
		H. ovalis	10		17.2			
	RH2	*H. ovalis*	100	D	134	0.40	0.40	
	RH3	*H. ovalis*	10	D	4	0.35	0.35	
		H. pinifolia	90		108.8			
	RH4	*H. ovalis*	20	D	20	0.40	0.40	
		H. pinifolia	80		127.6			
	RH5	*H. ovalis*	50	D	61.2	0.40	0.40	
		H. pinifolia	50		72.4			
Pahanakuda	PHK	*H. pinifolia*	100	D	125.6	0.42	0.42	
Barunakuda	BRK	*H. pinifolia*	100	D	40	-	-	

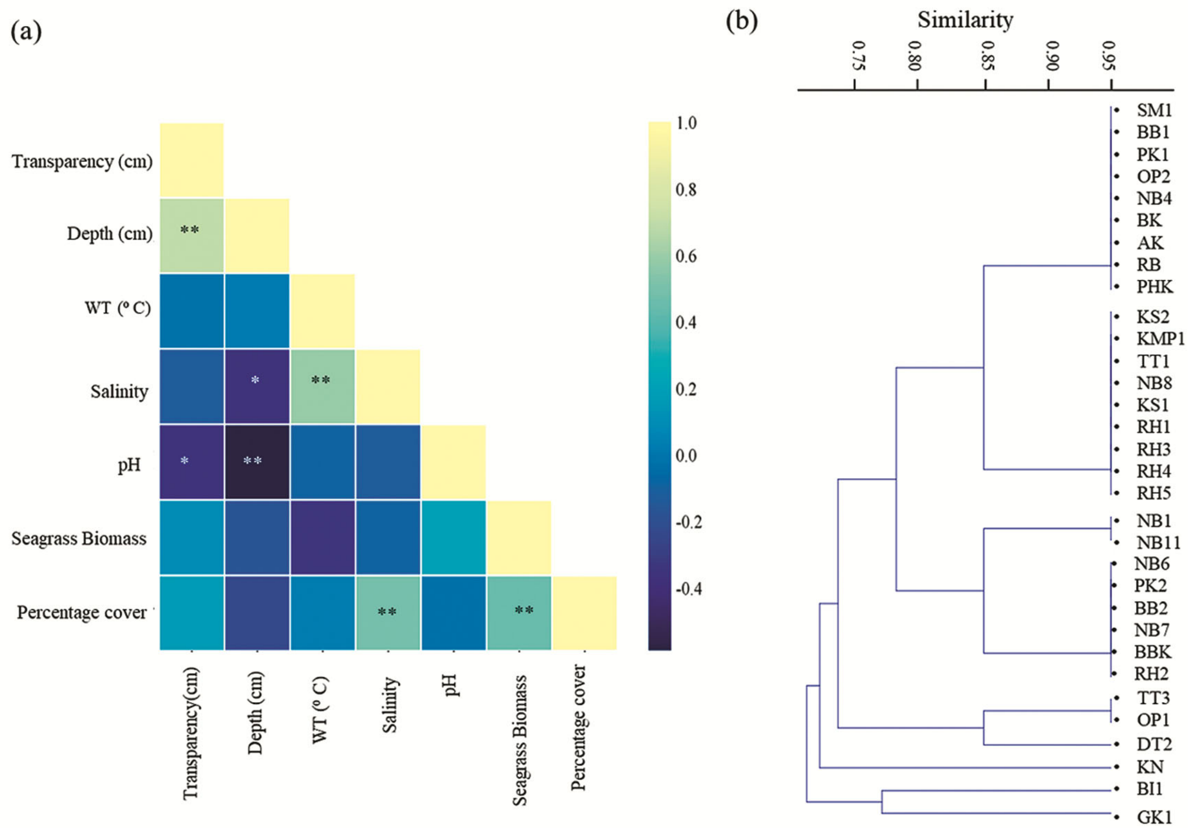

Fig. 3 — (a) Heat map depicting the Pearson's correlations among environmental variables and seagrass biomass and cover. Positive correlations are indicated by pale yellow, while negative correlations are shown in blue, with color intensity corresponding to the strength of the correlation coefficients. Significance levels are denoted by asterisks: * indicates p-value < 0.05, and ** indicates p-value < 0.01; and (b) UPGMA paired group tree constructed, using Jaccard similarity index in past (4.03) software

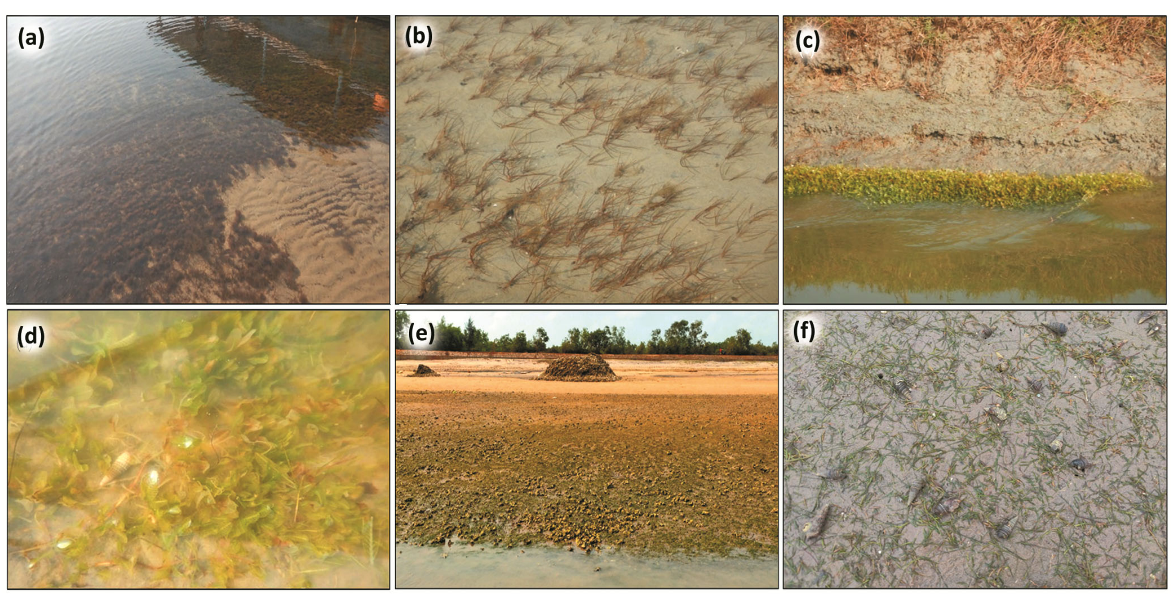

Fig. 4 — Field photographs showing (a) Dense growth of *H. pinifolia* and *H. uninervis* in sandy substratum of Odialpur, SS, (b) Patchy distribution of *H. pinifolia* in SS, (c) *H. ovalis* meadows on the sides of navigation creeks in the Nalabana Island (CS), (d) *H. ovalis* meadow in creek connecting to Watch Tower 1 in Nalabana, (e) A long stretch of *H. pinifolia* in Arakhakuda, OC, and (f) *H. beccarii* in OC

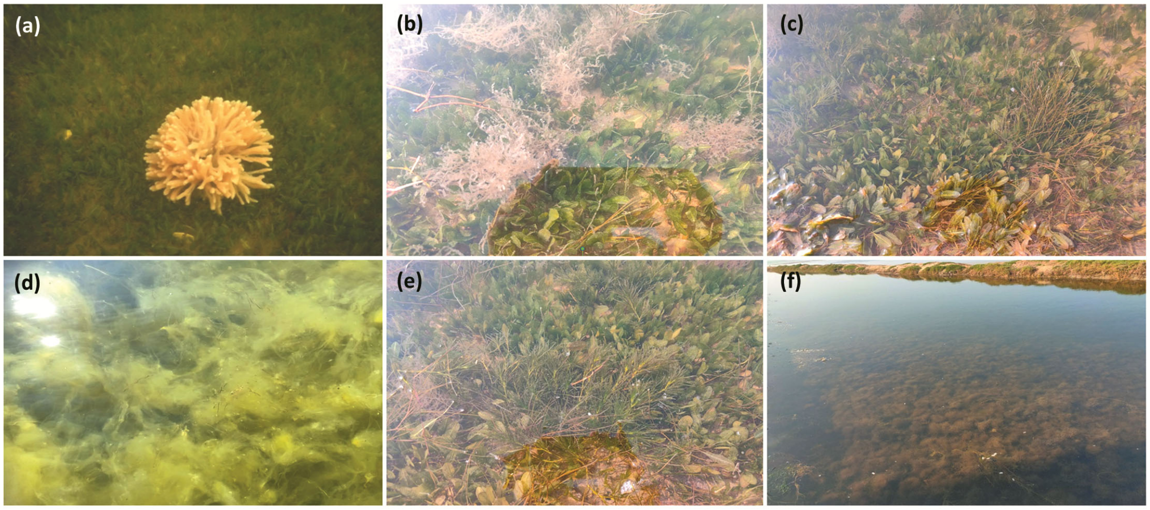

Fig. 5 — Field photographs showing flora and fauna associated with seagrass meadows in Chilika Lagoon. (a) *Spongilla alba* growing over the *H. ovalis* meadows in the southern sector, (b) *H. ovalis* associated with seaweed, *Gracilariopsis longissima*, (c) *H. ovalis* meadows with vigorous growth of *Stuckenia pectinata* near Watch Tower 1 (Nalabana Island), (d) Dense scum of microalgae, *Chaetomorpha* over seagrass meadows in southern sector, (e) *H. ovalis* meadows associated with *Najas indica* near Watch Tower 1, and (f) Vigorous growth of *Gracilariopsis longissima* outcompeting seagrass meadows near Watch Tower 2

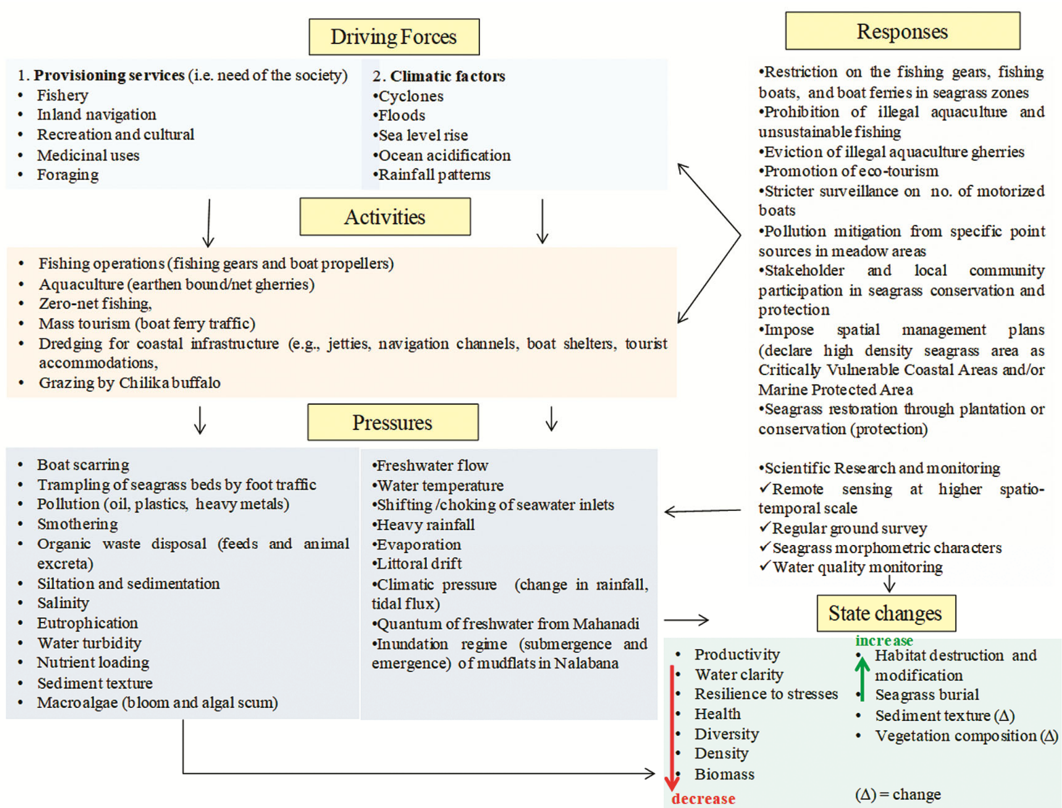

Fig. 6 — DAPSIR framework applied to seagrass ecosystem of Chilika Lagoon. The framework was adapted from Griffiths *et al.*, 2021[ref. 25] and was extended and modified in context to drivers and threats pertinent to Chilika seagrasses. Threats were compiled from primary field observation and secondary sources. Drivers are basic requirements of the society or the climatic/natural factors. Activities include actions that cause threats to seagrasses either directly or indirectly. Pressures are the mechanism(s) through which activity has an effect on seagrass meadows. State changes are changes in the seagrasses or their habitat due to pressure(s). Responses are suggested management actions aimed to stop or mitigate the threat to seagrasses

(93 – 96 %) in bottom sediments of SS, as measured in previous study[20], could also provide a soft substratum required for the expansion of their rhizomes. Results of the current study showed the prominence of dense seagrass beds in most of the sites in SS. When nutrients are high in Chilika, especially after post-monsoon, the growth of macroalgae (*e.g.*, *Chaetomorpha*) can form scum that can drastically reduce the light availability in the water column. Such algal scum is common over seagrass meadows in SS during post-monsoon, however, with seasonal changes in salinity and nutrients, they disappear on their own (field observation). The colonisation depth (*a.k.a*. depth limits) of seagrasses is highly dependent on the depth and transparency of the water column[22]. The higher densities of seagrasses are typically associated with moderate depth and light exposure conditions[22]. As almost all sites in OC (17/18) supported dense seagrass meadows, this indicates an optimal regime of light and other factors (*e.g.*, persistent high salinity) in this sector. The positive correlation of salinity with seagrass % cover further indicated that higher salinity was favourable for their growth.

Seagrasses showed a wide variation in their distribution even at a smaller spatial scale. For instance, different seagrass composition was recorded across NB1 (*H. uninervis* & *H. ovalis*), NB2 (*H. ovalis*), and NB3 (*H. ovalis* & *H. pinifolia*) sites, although these were located within a distance of 0.6 km in Nalabana (CS). UPGMA tree analysis of sites also suggested wide heterogeneity in terms of their seagrass species composition, biomass, and physicochemical parameters. These observations require a closer look at other factors such as sediment texture, nutrients, water clarity and other biological factors which might be underpinning the spatial variations in species composition. To this end, existing literature also shows that seagrass species vary in their adaptation to light and salinity. It has been shown that *H. ovalis* possesses greater adaptation to low light and low salinity conditions than other seagrasses[35], whereas *H. uninervis* is regarded as the species with high salinity tolerance (up to 50 psu)[36]. Therefore, wide occurrences of these two species are justified in Chilika Lagoon, which has a strong seasonal and spatial gradient in physicochemical factors such as turbidity, salinity, and nutrients[19,21]. *Halophila beccarii* showed a narrow distribution in Chilika (4/57 sites) and was recorded only from the SS and OC sectors. This species is considered as 'Vulnerable' in the IUCN Red List (Criterion B2) and is widely distributed on the east and west coast of India, including Andaman and Nicobar Islands[10].

The vigorous growth of *S. pectinata* and *N. indica* over seagrass meadows (Fig. 5) may out-compete them for available open space. In some of the sites near Watch Tower 1 and 2 in Nalabana, seagrasses were almost entirely trapped under the dense growth of these weeds. The overgrowth of macroalgae (*e.g.*, *G. longissima*) and other aquatic weeds in seagrass habitats could be considered as a sentinel of changes in environmental conditions (*e.g.*, nutrient loading and eutrophication) caused by anthropogenic and/or natural factors. For example, higher NO_3 loading in CS (Nalabana) could be mostly due to guano excreted from millions of birds that use Nalabana mudflats as a foraging and feeding ground during winter (October – March) every year[20,21]. Besides the decomposition of macrophytes, especially salt marshes that are highly abundant in mudflats of Nalabana, also contribute to nutrient loading after their decomposition during monsoonal inundation[20].

Overall, seagrass diversity of Chilika recorded here was similar to past studies in terms of number of species (*i.e.* six) recorded (Table S1). Importantly, *C. serrulata* which was reported earlier in the SS (Odialpur/Pathara) by a single study[11], was not traced in the present survey. More detailed comparisons with the latest survey[13] done in 2019/2020 which has some sites in common with the current study, showed changes in seagrass diversity (Table S2). Some species newly appeared; some disappeared, while others remained persistent. For example, *H. ovalis* and *H. pinifolia* were consistently found in Talatala, Kumarpur, Gopakuda, and Panchakudi in both assessments. *Halophila ovata* was confined to Budhibara site in the past survey[13] but was also recorded from Talatala and Gopakuda sites in the current assessment. Notably in CS (Nalabana Island), the appearance of *H. uninervis* was noted while *H. ovata* could not be found (Table S2). These changes in species diversity at the site level could be due to various reasons, such as (i) differences in the scale of sampling in a site, and (ii) a limited dataset for comparison, rather than true ecological changes. This necessitates more in-depth studies involving a larger dataset and wider spatial coverage, including detailed analysis of physicochemical factors (*e.g.*, sediment organic matter, oxidation-reduction potential (ORP), and texture) of their habitat. Also, a closer analysis of seagrass morphometric characters (*e.g.*, root length, shoot length, chlorophyll, and no. of leaves, etc.) would be crucial for detecting finer changes in seagrasses.

Threats to seagrasses and recommended actions

The DAPSIR framework, for the first time, established a cause-consequence-solution relationship, which is helpful to policymakers and wetland managers for the conservation and protection of seagrasses. The framework has provided a cumulative impact of multiple threats, which is crucial for the integrated management of seagrasses by a multitude of stakeholders. The destructive fishing practices (*e.g.*, zero net fishing) and shrimp aquaculture were a major threat to the seagrass meadows (Fig. S3a, b), as also noted in various earlier studies[7,10,26]. Although, aquaculture is prohibited within 1000 m of Chilika, there was encroachment of almost 15500 hectares of area by illegal shrimp culture gherries (enclosures) and earthen embankment (aquaculture ponds). The CDA has freed ~15100 hectares encroached by the illegal shrimp gherries[37], which proved crucial for seagrass expansion and protection in the lagoon.

Oil spills, plastics, and heavy metal pollution

As per data, 6640 registered fishing boats (motorised 2342, and non-motorised 3398) and 900 additional motorised boats are plying in Chilika Lagoon[33]. Although, no quantitative estimates are available on oil spillage from these boats, it does happen from mechanised boats/ferries, especially in shorelines during the re-filling of oil and poor maintenance of engines. Furthermore, anchoring of boats, bottom set fishing net operations, and propellers of motorised boats also cause direct physical damage to seagrass meadows, which could lead to habitat destruction and fragmentation[7,37]. Oil spills can directly kill seagrasses through direct smothering and toxic effects caused by water-soluble fractions of oil[38]. The indirect effect of oil pollution could be *via* reducing the photic depth, causing a decrease in biomass production.

A study carried out in the year 2015[ref. 33] from surface sediments of Chilika Lagoon measured petroleum hydrocarbons (PHC) between 0.18 – 12.13 (mean 3.71±3.94 ppm), which was within the safe limits as per Food and Agriculture Organization (FAO) guidelines (> 70 µg g^{-1} is considered as polluted). Another assessment on total PHC from water and sediments of Chilika in May 2020 during the COVID-19 lockdown period, documented a significant reduction (64 %) in the TPHC level reaching an average of 1.4 µg L^{-1} in water and 0.79 µg g^{-1} in sediments due to restriction in fishing and tourism operations and associated motorised boat traffic[39]. However, as tourism and fishing activities are continuously increasing in the lagoon, the PHC level may rise if not periodically monitored and regulated properly. The key recommendation is the sensitisation of boat operators to the safe handling of fuels and regular maintenance of engines. Many of these operators are unaware of seagrasses and their direct or indirect role in supporting their livelihood through commercial fishery and tourism. Therefore, raising awareness would be a critical step in seagrass conservation through community participation.

The large catchment area (about ~ 4406 sq. km) of Chilika Lagoon is drained by 52 rivers and rivulets passing through urban and agricultural landscapes[17]. Moreover, direct dumping of solid waste, including plastics, occurs from (i) villages around Chilika, (ii) fishing activities (*e.g.*, dumping of abandoned nylon fishing nets and ropes), and (iii) tourism activities. Since seagrass meadows reduce water velocity and increase sedimentation due to their dense canopies, they also trap high amounts of microplastics in their sediments and leaf blades[40]. Importantly, microplastics in the abundances between 7 – 25.2 items/kg in sediments and 26 – 110.7 items/100 L water have been reported from Chilika Lagoon[32]. This study has also shown that fishing and tourism activities largely contributed to the microplastic pollution in Chilika Lagoon. The impact of microplastics on the growth of seagrasses has not been studied in Chilika. However, studies from other parts of the world suggest that microplastics may have a negative influence on seagrasses and epiphytes *via* injury and blockage of light/gas exchange, increase in toxin concentration, and disturbances in metabolic processes, including inhibition of N-fixation by diazotrophs[41]. The recommendation to mitigate plastic pollution requires a 3 R policy (reduce, reuse, and recycle) at the catchment level. Moreover, efficient garbage collection and disposal mechanisms at the source level would be highly essential to stop the dumping of solid wastes into the lagoon. The villagers/tourists/boat operators/fishermen must be sensitised about the microplastics and their bio-accumulation in the food chain and eventually in human beings.

The riverine inputs, especially from Daya and Bhargavi (Fig. 1) are major non-point sources of heavy metals in the Chilika Lagoon. Besides, low-grade paints used in boats, engine fuels, and lead beads of fishing nets also contribute to metals (especially Zn, Cu, Cr, Pb, Ni, and Co)[27,28]. In Chilika sediments, heavy metal accumulation has been detected in the order of Zn > Pb > Cr > Cu > Ni > Co > Cd; however, various pollution indices suggested a low degree of contamination[29]. Importantly, bioaccumulation of Cu and Zn has been reported in seagrasses of Chilika[31]. The data on the physiological responses of seagrasses to metal stress is not available from Chilika. However, studies from other seagrass ecosystems clearly show that heavy metals are toxic in terms of their negative effects on morphology (leaf symmetry, size, etc.), and physiology (photosynthesis, protein synthesis, growth)[42] thereby requiring close monitoring.

Sedimentation, nutrient loading, and eutrophication

Due to the large catchment and changing land use patterns, sedimentation is a big threat to Chilika[17]. A total of 52 rivers/rivulets passing through agricultural and urban landscapes drain a significant load of silt and nutrients into Chilika[17]. Previous measurements[20] from seagrass sediments of SS have recorded a negative ORP (− 82.47±52.08 mv) with a strong odour of H_2S and dark black colouration (Fig. S2c). This indicated highly reducing conditions in benthic sediments due to sulfides produced from the mineralisation of organic matter. Notably, high sulfide concentration in sediments has been attributed to causing seagrass mortality and dieback, globally[43]. Therefore, close monitoring of sulfides in sediments is also required.

Climatic threats

Natural climatic hazards such as cyclones and floods have also been recognised as a major threat to seagrasses in Chilika through direct physical damage and/or indirectly via reduced light availability to seagrasses due to high turbidity[7,26]. Cyclones and super-cyclones originating in the BoB severely impact the hydrology and biodiversity of Chilika[18]. The episodic rainfall accompanying these cyclones brings massive freshwater flow to the lagoon *via* surface precipitation, land surface runoff, and riverine discharge. This has a drastic impact on the overall water quality of the lagoon through changes in salinity, nutrients, and water turbidity, affecting the vegetation of Chilika[18]. Moreover, strong winds during cyclones cause the churning of sediments, leading to physical damage to seagrasses either by tearing up entire plants or through burials of meadows by thick layers of sediment. One such example was *Phailin*, a very severe cyclonic storm (VSCS category 5) which had a landfall near Chilika on 12/10/2013 accompanied by heavy rainfall and surface wind speed of 200 – 210 km/h[18,19]. This VSCS caused a significant reduction in water clarity (transparency) and salinity of the Chilika. The salinity in the SS, which supports dense seagrass meadows, decreased by 7.1 times compared to before *Phailin* month[40]. The overall salinity of the entire lagoon reached 1.72 after *Phailin* which was ~ 10 before the cyclone[30,34]. The salinity returned to its normal regime after almost 5 months of *Phailin* strike. It has been reported that the optimum salinity for the growth of *H. ovalis* is between15 – 35 and can withstand salinity < 10 for a month[44]. The prolonged reduction in salinity, accompanied by excessive sedimentation during *Phailin* resulted in the degeneration of *H. ovalis* meadows[30]. Moreover, it was noted that the reduction in salinity also promoted the proliferation of freshwater weeds in the lagoon, resulting in the competition with seagrasses for space and nutrients[30].

It has also been seen in Chilika that the gusting action of winds and flash floods during cyclone Gulab (September 2021) flushed huge loads of *Eichhornia* from rivers/creeks to the lagoon (Fig. S2d). This floating *Eichhornia* settled over the shoreline on top of seagrass meadows due to wind and currents, and eventually decomposed when the salinity of the lagoon increased. This resulted in a large amount of plant litter settling over the seagrass meadows. The increase in organic matter in both benthic and pelagic compartments would result in increasing turbidity in the overlaying water column and higher algal growth (especially macroalgae) due to eutrophication, which would hamper seagrass biomass production, leading to habitat modification and degeneration.

Overall, the anthropogenic and climatic drivers identified in Chilika are recognised globally as major threats to seagrasses[2]. Notably, seagrasses in Chilika were mostly confined to shallow shoreline areas and intertidal mudflats, making them highly vulnerable to anthropogenic disturbances. There are existing policies and regulations that emphasise the conservation and protection of seagrasses for sustaining fauna such as fishery, dugongs, and sea turtles[7]. For example, National Policy on Marine Fisheries 2017[(ref. 45)] explicitly underscores the importance of seagrasses as habitats for fisheries. Seagrass meadows have been declared as Ecologically Sensitive Areas (ESA) in the Coastal Regulation Zone (CRZ) notification (2011) under the Environment (Protection) Act of 1986, and no construction (except permitted activities) is allowed.

Many of the regional threats (*e.g.*, sedimentation and nutrient loading) are driven by land use patterns in the catchment. Therefore, merely protecting the seagrass habitats in the lagoon would not be an effective measure unless integrated catchment-level planning is implemented. The lack of awareness regarding underwater seagrasses in coastal communities, policymakers, and wetland managers is one of the major challenges in seagrass conservation and management. A greater understanding of socio-economic linkage and seagrass ecosystems would be vital to engage diverse stakeholders, resource users, and policymakers to address various anthropogenic threats and the conflict between conservation goals and livelihood activities. Research and field-guided monitoring of seagrasses should be integrated into the local academic curriculum to raise awareness and ensure societal recognition of these underwater plants. Furthermore, there is no quantitative data available on many pressures, such as the extent of damage to seagrasses by boat scarring, the amount of oil spills, the amount and type of organic waste effluents by aquaculture, and the amount of solid waste (*e.g.*, plastic) entering the lagoon. This requires a comprehensive monitoring of each of these pressures and requires specific studies to assess their impact on seagrass meadows.

Conclusion

The present study reports *H. ovalis*, *H. ovata*, *H. beccarii*, *H. pinifolia*, *H. uninervis*, and *R. maritima* seagrass species from the Chilika Lagoon. *Halophila ovalis* and *H. pinifolia* emerged as the most widely distributed species. Dense seagrass meadows were prominent in SS and OC. DAPSIR framework provided various response actions to be taken up by the policymakers for efficient conservation and management of seagrasses. In Chilika, long-term baseline data are not available for seagrass health indicators (such as biomass, % cover, spatial richness, and morphometrics). Therefore, systematic and periodic field assessment at consistent spatial and temporal scales across multiple years would be essential to detect finer changes in seagrasses.

Supplementary Data

Supplementary data associated with this article is available in the electronic form at https://nopr.niscpr.res.in/jinfo/ijms/IJMS_53(09)595-610_SupplData.pdf

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Conflict of Interest

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

Ethical Statement

Halophila beccarii is considered as ‘Vulnerable’ in the IUCN Red List (Criterion B2). The survey was taken with utmost care to minimize the physical damage to this species.

Author Contributions

GR: Writing - original draft, review & editing; PKT: Field work and assessment; SPD: Writing and data compilation. PRM: water quality assessment. All authors read and approved the final manuscript.

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