scopeScience

MARINE REPORTS 4(2) (2025) : 80-102
DOI: 10.5281/zenodo.18001560
marep@scopesscience.com

MARINE REPORTS

MARINE REPORTS
e-ISSN: 2822-5155
Journal homepage: https://scopesscience.com/index.php/marep/

Received: 18 November 2025; Received in revised form: 17 December 2025
Accepted: 17 December 2025; Available online: 21 December 2025

RESEARCH PAPER

Citation: Anjalie, N.M.I., Nahmagal, K., & Sivashanthini, K. (2025). Diversity and spatio-temporal dynamics of *Caulerpa* J.V.Lamouroux, with two new locality records from Northern Sri Lanka. *Marine Reports*, *4*(2), 80-102. https://doi.org/10.5281/zenodo.18001560

DIVERSITY AND SPATIO-TEMPORAL DYNAMICS OF *Caulerpa* J.V.Lamouroux, WITH TWO NEW LOCALITY RECORDS FROM NORTHERN SRI LANKA

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Abstract

The genus *Caulerpa* is a key component as a primary producer of tropical and subtropical marine ecosystems, yet its diversity and distribution along the northern coast of Sri Lanka remain poorly documented. This study provides a comprehensive assessment of the diversity and spatio-temporal dynamics of *Caulerpa* species at four coastal sites, Mandaitivu, Mathagal, Kankesanthurai, and Point Pedro from July 2024 to June 2025. Monthly sampling using the quadrat-transect method revealed six species: *Caulerpa lentillifera*, *Caulerpa racemosa*, *Caulerpa sertularioides*, *Caulerpa taxifolia*, *Caulerpa serrulata*, and *Caulerpa peltata*. Among these, *C. lentillifera* and *C. serrulata* are reported as new locality records for the Jaffna region, while the distributions of *C. taxifolia* and *C. peltata* are significantly expanded. *C. sertularioides* was the most widespread and dominant species, occurring at all sites, whereas *C. lentillifera* and *C. taxifolia* were rare, each found at only one location. Distinct seasonal patterns were observed, with a complete absence of all species during the northeast monsoon (November–December). Mandaitivu exhibited the highest diversity overall, with peak Simpson diversity (0.375) and evenness (0.946) in March and maximum Shannon diversity (1.121) and species richness (4) in June. Canonical Correspondence Analysis indicated that the growth and distribution of *Caulerpa* species along the northern coast of Sri Lanka are mainly influenced by salinity, temperature, nutrient availability, dissolved oxygen, turbidity, and seasonal monsoonal variability. This study establishes the first detailed baseline of *Caulerpa* diversity in northern Sri Lanka, highlighting its ecological significance and providing a foundation for future conservation and bioprospecting efforts.

Keywords: *Caulerpa* diversity, diversity indices, new records, Northern Sri Lanka, seaweed, spatio-temporal dynamics

Introduction

The genus *Caulerpa* J.V.Lamouroux, a prominent group of green macroalgae (seaweed), is a critical component of tropical and subtropical marine ecosystems. Recognized for its rapid growth, invasive potential (e.g., *Caulerpa taxifolia* in the Mediterranean), and morphological plasticity (feathery, grape-like, etc). *Caulerpa* contributes significantly to primary production, provides habitat and food for marine organisms, and serves as a bioindicator for environmental health (Guiry & Guiry, 2020). Environmental factors, including seawater temperature, salinity fluctuations, light availability, and hydrodynamic conditions, strongly influence the distribution, productivity, and seasonal variability of *Caulerpa* species. Several studies have emphasized how climate-driven changes, such as warming seas and shifts in monsoon patterns, will likely further impact their abundance and spatial distribution (Meinesz, 2007). *C. lentillifera* is known for its rapid vegetative expansion in shallow tropical lagoons, which is greatly determined by external factors such as water temperature, seasonality, weather, and geographical location (Syakilla et al., 2022). *Caulerpa racemosa* occurs pantropically, and its growth and dispersal are greatly affected by the temperature of seawater, which plays an important role in controlling its seasonal growth and physiological functions (Verlaque et al., 2000). Salinity, water temperature, seasonal cycles, and nutrient availability due to upwelling events are major factors affecting growth and distribution patterns of *Caulerpa sertularioides* (Fernández-García et al., 2012). *Caulerpa taxifolia* generally occurs over soft sediment grounds (McKinnon *et al.,* 2009), its growth and distribution strongly dependent upon the temperature of the water (Phillips et al., 2002). The shallow, warm, and sunlit lagoons, sandy-muddy bottoms, and seagrass beds of the Jaffna Peninsula and the Palk Strait are ideal habitats for many *Caulerpa* species. *Caulerpa* species are well-documented in the Gulf of Mannar (to the northwest) and along the southern coast of India, just miles away across the Palk Strait. It is highly unlikely that these algae, which can spread via currents or human activity, would completely skip over the northern coast of Sri Lanka, is almost certainly a reflection of the lack of research and not proof of their actual absence. They are very likely present but have not been formally documented, identified, and published in scientific literature due to the historical constraints prevailed in the country. There has been a slow but steady resurgence of marine research in these previously inaccessible areas. In Sri Lanka, historical biodiversity assessments, such as the one by Silva et al. (1996) documented a rich diversity of 19 *Caulerpa* species. However, subsequent studies have suggested a potential decline, with a comprehensive national survey by Coppejans et al. (2009) reporting only 12 species, and a more recent, localized study in the southern coastal waters by Premarathna et al. (2020a) finding just three: *C. racemosa*, *C. imbricata*, and *C. sertularioides*. Nevertheless, details on precise distribution, exactly where and how abundantly it is distributed is lacking. This apparent contraction in species reports underscores a critical gap in our current understanding: the lack of comprehensive, region-specific diversity studies. While the south has been surveyed, the northern coastal waters of Sri Lanka, particularly around the Jaffna Peninsula, remain relatively under-explored in this context. It is evident from a study by Premarathna et al. (2020b) that he collected *C. racemosa* and *C. sertularioides* from Point Pedro and Kankesanthurai, Jaffna, respectively to examine the cytotoxic effect and wound healing ability of different seaweed species available in Sri Lanka. This research was primarily a pharmacological and biochemical investigation, not a broad ecological survey. According to an incidental study by Abirami et al. (2024), the marine algae *C. peltata*, *C. racemosa*, and *C. taxifolia* were reported only in Kankesanthurai waters. It is important to note that this was not a comprehensive study, and the finding was made incidentally highlighting the need for more systematic surveys in the region. The recent collection of *C. racemosa* in Jaffna for a study on antioxidant properties (Silva et al., 2025) confirms the genus's presence but does not address the full scope of its diversity in the region. A focused study on the diversity and distribution of the green macroalgal genus *Caulerpa* in Northern Sri Lanka is critically important for ecological, economic, and conservation reasons.

The overall objective of the study is to document the previously unreported new *Caulerpa* species to the locality and to comprehensively assess the current diversity, distribution, and abundance of the macroalgal genus *Caulerpa* along the northern coastal waters of Sri Lanka, in order to establish a critical baseline for conservation, sustainable management, and future bioprospecting efforts.

Materials and Methods

Study area

The survey was conducted at four locations along the northern coast of Sri Lanka, namely Mandaitivu, Mathagal, Kankesanthurai (KKS), and Point Pedro. At each location, three replicate sites were selected for sampling, and their precise geographic coordinates were recorded using a handheld Geographical Positioning System (GPS) (Garmin Oregon 750, USA). The sites at Mandaitivu were located at N 09.603067°, E 079.999170°; N 09.603035°, E 079.998891°; and N 09.603331°, E 079.999386°. At Mathagal, the sampling sites were positioned at N 09.603336°, E 079.999372°; N 09.799914°, E 079.959926°; and N 09.800058°, E 079.960654°. The sites at KKS were located at N 09.799610°, E 079.960669°; N 09.816769°, E 080.045700°; and N 09.816479°, E 080.046209°, while those at Point Pedro were situated at N 09.825647°, E 080.251704°; N 09.825897°, E 080.251441°; and N 09.825300°, E 080.251944°. Figure 1 shows the selected areas along the Northern coast of Sri Lanka.

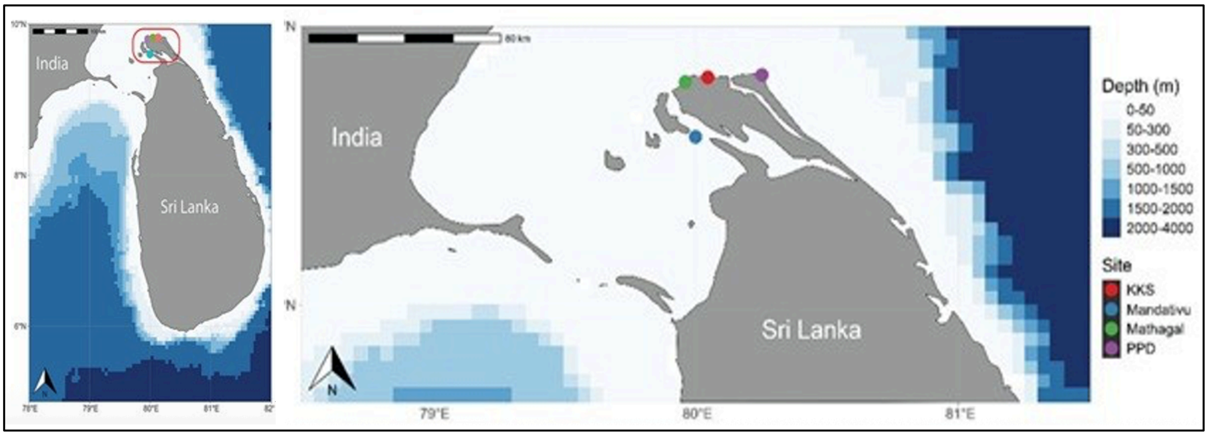

Figure 1. Map showing the study locations in Northern Sri Lanka

Sampling design and sample collection

Monthly field surveys were carried out from July 2024 to June 2025 to collect and identify seaweed samples. At each study location, three permanent sampling sites were established, spaced roughly 50 meters apart. From each site, a 25-meter transect was laid perpendicular to the shoreline, and five quadrats measuring 0.5 m² were placed at 5-meter intervals along the transect line. Table 1 shows the sampling frequency. Seaweed specimens present within each quadrat were gently hand-collected to avoid physical damage, following the standard quadrat–transect sampling technique, and placed in seawater-filled containers for transport to the laboratory at the University of Jaffna for identification (Abirami et al., 2024). Since the objective of the study was to record the diversity of seaweeds, all individuals occurring within the quadrats were collected rather than a predetermined number of specimens. During the study, a total of six distinct species belonging to the genus *Caulerpa* were identified from the selected coastal areas of Jaffna.

Table 1. Sampling design to show the number of sampling sites in each location and sampling frequency.

Location	No. of Sites	Quadrats per Site	Sampling Frequency	Total Quadrats per Site
Mandaitivu	3	5	Monthly × 12 months	60
Mathagal	3	5	Monthly × 12 months	60
Kankesanthurai	3	5	Monthly × 12 months	60
Point Pedro	3	5	Monthly × 12 months	60

Morphological analysis
In the laboratory, specimens were carefully rinsed with fresh water to remove attached sediments, epiphytes, and debris. Morphological characteristics were examined through visual observation, focusing on the overall thallus structure, branching pattern, stolon and rhizoid development, and the shape, size, and arrangement of ramuli (assimilatory branches). Additional attention was given to variations in color and texture.

Taxonomic identification
Species identification was carried out using standard taxonomic keys and descriptions provided in Coppejans et al. (2009): *Sri Lankan Seaweeds – Methodologies and Field Guide to the Dominant Species*, and in The Living Marine Resources of the Western Central Pacific, Volume 1: Seaweeds, Corals, Bivalves and Gastropods (Carpenter & Niem, 1998). Identification details were further verified with updated nomenclature and distributional information available in AlgaeBase (Guiry & Guiry, 2020).

Diversity indices calculation
Diversity indices, the Shannon–Wiener diversity index (H′), Simpson's index (D), species richness, and evenness index (J′), were computed using the PAST software package (Paleontological Statistics, version 3.0). The species abundance data obtained from each sampling site and month were entered into the program to derive the corresponding diversity values.

Statistical analysis
Canonical Correspondence Analysis (CCA) was performed separately for each location to examine the relationship between water quality parameters (wind speed, water temperature, air temperature, salinity, pH, turbidity, phosphate, and dissolved oxygen) in different seasons and species abundance.

Results

Habitat diversity of Caulerpa
The selection of Mathagal, Mandaitivu, Kankesanthurai, and Point Pedro along the northern coast of Sri Lanka was based on ecological and geographical diversity to capture spatial and temporal variations in seaweed distribution. These sites collectively represent a range of habitat types, including sandy, rocky, and muddy substrates, and encompass important environmental gradients such as salinity, temperature, depth, and nutrient levels. The areas differ in exposure

and anthropogenic influence, from the relatively undisturbed shores of Mathagal and Mandaitivu to the moderately impacted semi-urban zone of Kankesanthurai. For example, the Mathagal coast is characterized by a low-lying topography, with occasional rocky cliffs formed where the coast crosses crystalline rock formations. This topography is illustrated in Figure 2a. Their distribution across the coastline ensures adequate spatial coverage, while accessibility and logistical feasibility allowed consistent sampling. Overall, the selected locations provided representative conditions for examining seaweed diversity, abundance, and environmental relationships along the northern coastal ecosystems of Sri Lanka.

Sample collection and identification

A total of six distinct species were i.e. *C. lentillifera*, *C. racemosa*, *C. sertularioides*, *C. taxifolia*, *C. serrulata* and *C. peltata* were confirmed. Of these *C. lentillifera* and *C. serrulata* are new locality records for Jaffna, Northern Sri Lanka. Subsequent to their initial identification in Kankesanthurai, *C. taxifolia* and *C. peltata* were in fact constitute new locality records for a broader area of the Jaffna Peninsula, with confirmed populations in Mathagal, Mandaitivu, and Point Pedro. The specimens were found colonizing both sandy and rocky substrates within the dynamic shallow waters, inhabiting both intertidal and subtidal zones. Occurrence of *Caulerpa racemosa* in the infralittoral fringe, partly air-exposed at extreme low water in association with *Caulerpa sertularioides* and *Acetabularia acetabulum* is illustrated in Figure 2b. Colonies of *Caulerpa lentillifera* and *Caulerpa racemosa* are shown in Figure 2c and d.

Taxonomical hierarchy and distinct morphological characteristics

The taxonomic classification of the studied genus *Caulerpa* is:

Kingdom : Plantae
Phylum : Chlorophyta
Class : Ulvophyceae
Order : Bryopsidales
Family : Caulerpaceae
Genus : *Caulerpa*

The following section explains the taxonomic hierarchy and distinct morphological characteristics for identifying *Caulerpa* species.

Caulerpa lentillifera

Species : *Caulerpa lentillifera* J. Agardh

The thallus is composed of a horizontally branched stolon that gives rise to numerous erect branches. These erect branches are densely covered with short, club-shaped ramuli along most of their length. Each ramulus has a distinct constriction between its stalk and the rounded tip, which serves as a distinguishing feature of this species (Figure 2b and d). *C. lentillifera* showed a stolon diameter of 1.14 ± 0.18 mm, a mean length of 102.06 ± 13.95 mm, and a ramuli diameter of 1.00 ± 0.18 mm. This species shows a broad distribution across tropical marine environments in both the Indian and Pacific Oceans (Coppejans et al., 2009).

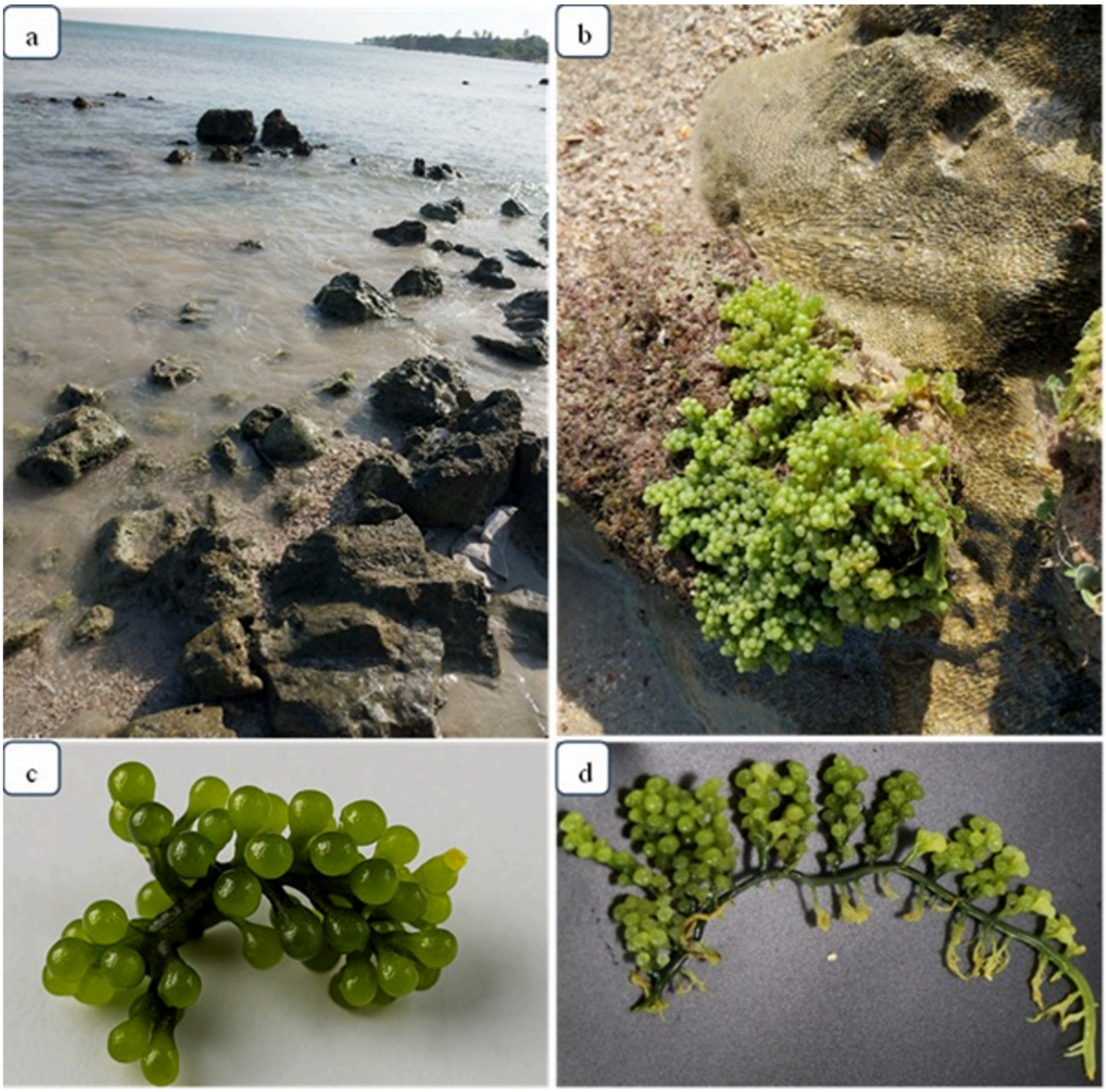

Figure 2. a) Mathagal coast characterized by occasional rocky cliffs formed where the coast crosses crystalline rock formations; b) *Caulerpa racemosa* in the infralittoral fringe, partly air-exposed at extreme low water (Mathagal) in association with *Caulerpa sertularioides* and *Acetabularia acetabulum*; c) *Caulerpa lentillifera* colony; d) *Caulerpa racemosa* colony.

Caulerpa racemosa

Species : *Caulerpa racemosa* J. Agardh

The thallus is composed of a creeping stolon system that gives rise to erect branches. These branches bear numerous short-stalked ramuli, which range from oval to spherical in shape. The ramuli exhibit variable phyllotaxy, being arranged in radial, alternate, pinnate, or irregular patterns along the erect axes, with densities ranging from sparse to dense. A key morphological feature is the diverse form of the ramuli apices, which can appear clavate (club-shaped), turbinate (top-shaped), globose-truncate (spherical with a flattened end), or occasionally discoid (disc-shaped) (Figure 2c). *C. racemosa* had a stolon diameter of 1.14 ± 0.27 mm, with an average length of 62.58 ± 18.00 mm and a ramuli diameter of 1.26 ± 0.33 mm. The species has a pantropical distribution (Coppejans et al., 2009).

Caulerpa sertularioides
Species : *Caulerpa sertularioides* (S.G Gmelin) M.A Howe
The thallus is composed of erect, feather-like branches bearing pinnately arranged, cylindrical ramuli, each terminating in a mucronate tip (Fig. 3a and b). *C. sertularioides* presented a stolon diameter of 0.20 ± 0.058 mm, a mean length of 15.04 ± 1.90 mm, and a branchlet length of 12.22 ± 1.44 mm. This species is distributed across the tropical Indo-Pacific and the tropical eastern Atlantic regions (Coppejans *et al*. 2009).

Caulerpa taxifolia
Species : *Caulerpa taxifolia* (Vahl) C. Agardh
Thallus consists of narrow, erect branches that are generally unbranched or branched and feather-like. The pinnules (ramuli) are arranged pinnately, distinctly flattened, and have a curved, sickle-like shape (falcate) (Figure 3c). *C. taxifolia* showed a stolon diameter of 1.00 ± 0.22 mm, an average length of 38.48 ± 11.25 mm, and a branchlet length of 2.88 ± 0.38 mm. The species occurs throughout tropical oceans worldwide and has been introduced into the Mediterranean Sea (Coppejans et al., 2009).

Caulerpa serrulata
Species : *Caulerpa serrulata* (Forssekal) J. Agardh
The thallus is composed of erect, cylindrical, and generally unbranched axes that arise from a creeping stolon. These axes are densely covered with small, serrated ramuli, arranged in either an alternate or opposite pattern. The ramuli possess pointed or slightly mucronate tips, and this overall morphology confers a distinctive bushy, feathery appearance to the thallus (Figure 3d and e). *C. serrulata* had a stolon diameter of 1.62 ± 0.19 mm, with an average length of 20.52 ± 5.04 mm and a branchlet diameter of 2.20 ± 0.28 mm. This species is distributed in the tropical Indo-Pacific Ocean (Coppejans et al., 2009).

Caulerpa peltata
Species : *Caulerpa peltata* var.
The thallus is composed of a horizontally creeping, branched stolon that gives rise to erect axes. These axes bear numerous short-stalked ramuli, each of which terminates in a flattened disc (Figure 3f and g). *C. peltata* exhibited a stolon diameter of 0.84 ± 0.31 mm, a mean length of 70.34 ± 15.25 mm, and a ramuli (disc) diameter of 1.20 ± 0.22 mm.

Based on the above distinct morphometric characteristic features, the collected species were further authenticated as *C. lentillifera*, *C. racemosa*, *C. sertularioides*, *C. taxifolia*, *C. serrulata* and *C. peltata*. The earlier study, record of *Caulerpa* sp. (Coppejans et al., 2009) in Sri Lanka was confined to a solitary notification which did not elaborate on its specific distribution within Jaffna. The present study establishes *C. lentillifera* and *C. serrulata* as new records for the Jaffna region while significantly expanding their known distribution for *C. taxifolia* and *C. peltata* in the Jaffna peninsula, Sri Lanka.

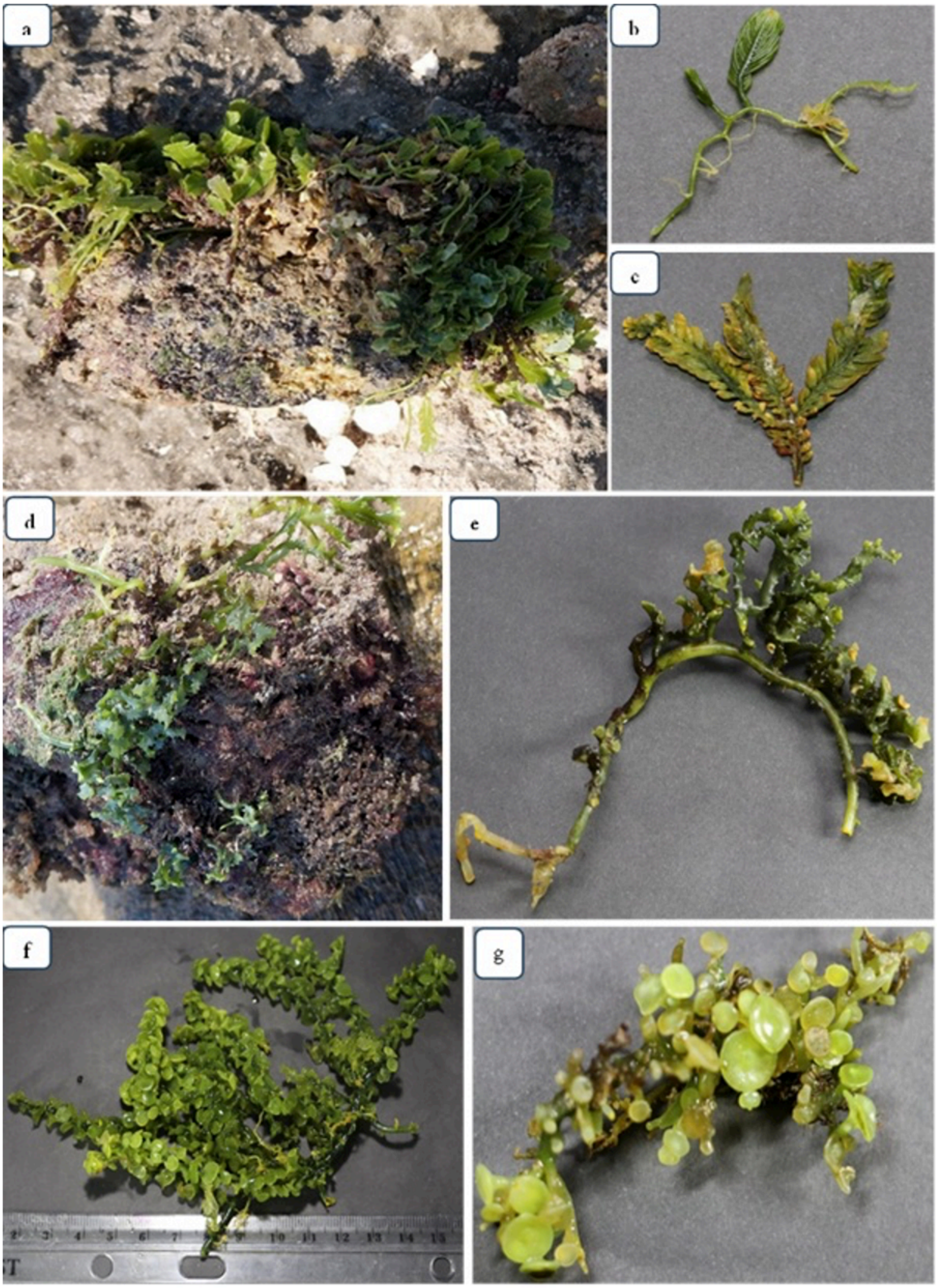

Figure 3. a) Mixed seaweed vegetation under low water level, dominance of *Caulerpa sertularioides* in association with *Halimeda opuntia*; b) *Caulerpa sertularioides* with prostrate rhizomes attached by many rhizoids; c) *Caulerpa taxifolia*; d) *Caulerpa serrulata* in the infralittoral fringe, partly air-exposed at extreme low water (Mathagal) in association with *Caulerpa sertularioides*; e) *Caulerpa serrulata*. f) *Caulerpa peltata*; g) a portion of *Caulerpa peltata*.

Spatial distribution of identified species

Analysis of their spatial distribution revealed distinct patterns across the four sampling locations. *C. sertularioides* was the most widespread species, being present at all four sites. This was followed by *C. racemosa* and *C. peltata*, which were each recorded from three locations. *C. serrulata* demonstrated a more restricted presence, collected from only two locations. In contrast, *C. lentillifera* and *C. taxifolia* appeared to be the least common within the study area, with each found at a single location, suggesting a more niche or limited distribution. A summary of these distributional records is provided in Table 2, offering a clear quantitative overview of species occurrence.

Table 2. The presence (+) or absence (-) of different *Caulerpa* species across four locations in Sri Lanka: Mandativu, Mathagal, KKS, and Point Pedro.

Location	***Caulerpa lentillifera***	***Caulerpa racemosa***	***Caulerpa sertularioides***	***Caulerpa taxifolia***	***Caulerpa serrulata***	***Caulerpa peltata***
Mandaitivu	+	-	+	-	+	+
Mathagal	-	+	+	-	+	+
KKS	-	+	+	+	-	+
Point Pedro	-	+	+	-	-	-

Categorization of Caulerpa species by abundance

The relative abundance of the collected *Caulerpa* species was assessed using two distinct metrics. The first was the raw frequency of occurrence, which represents the number of sampling locations where a particular species was present. The second was the percentage frequency, calculated using the formula: (Number of individuals in each species / Total number of individuals in all *Caulerpa* species). This standardized metric allows for a direct comparison of how widespread each species is across the study area (Magurran,2021). Table 3 summarizes the abundance of the six *Caulerpa* species recorded during the study.

Table 3. Categorization of *Caulerpa* Species by Abundance.

***Caulerpa* Species**	**Presences (out of 4)**	**Percentage Frequency**	**Abundance Category**	**Justification**
Caulerpa lentillifera	1	25%	Rare	Found at only one location (Mandaitivu).
Caulerpa racemosa	3	75%	Common	Also found at three out of four locations (Mathagal, KKS, Point Pedro). Its distribution is very similar to *C. peltata*.
Caulerpa sertularioides	4	100%	Very Common / Dominant	Found at every single location. This is the most widespread and

***Caulerpa* Species**	**Presences (out of 4)**	**Percentage Frequency**	**Abundance Category**	**Justification**
				abundant species in the survey area.
Caulerpa taxifolia	1	25%	Rare	Found at only one location (KKS).
Caulerpa serrulata	2	50%	Common	Found at two locations (Mandaitivu, Mathagal). While not as widespread as the top three, it is still regularly present.
Caulerpa peltata	3	75%	Common	Found at three out of four locations (Mandaitivu, Mathagal, KKS). It is a common and widespread species.

Temporal distribution

Figure 4 visualizes the abundance of six different *Caulerpa* seaweed species over time, across four distinct geographical locations in Jaffna, Sri Lanka (Mandaitivu, Mathagal, Kankesanthurai, and Point Pedro). The primary purpose of the figure is to illustrate the spatial (where) and temporal (when) variations in the population density of these species.

A clear seasonal occurrence is evident, with no *Caulerpa* species recorded during the months of November and December. This indicates a period of low abundance or absence, likely linked to seasonal environmental factors. The data shows species specific abundance peaks that is, different species thrive in different locations and at different times.

The highest abundance of *C. lentillifera* occurred in Mandaitivu during September, while *C. racemosa* peaked in Mathagal in October. *C. peltata* and *C. sertularioides* both reached their maximum densities in Kankesanthurai in March, and *C. serrulata* was most abundant in Mathagal in January. At the community level, the greatest species richness was recorded in Mandaitivu during the month of June.

The graph effectively demonstrates that the distribution and abundance of *Caulerpa* species are not uniform. Instead, they are influenced by a combination of species-specific preferences (each has a unique optimal location and time), spatial factors (different conditions at each site) and temporal/Seasonal factors (changes over the months, including a complete absence in Nov-Dec). This pattern highlights the ecological principle that biodiversity is dynamic and varies across both space and time.

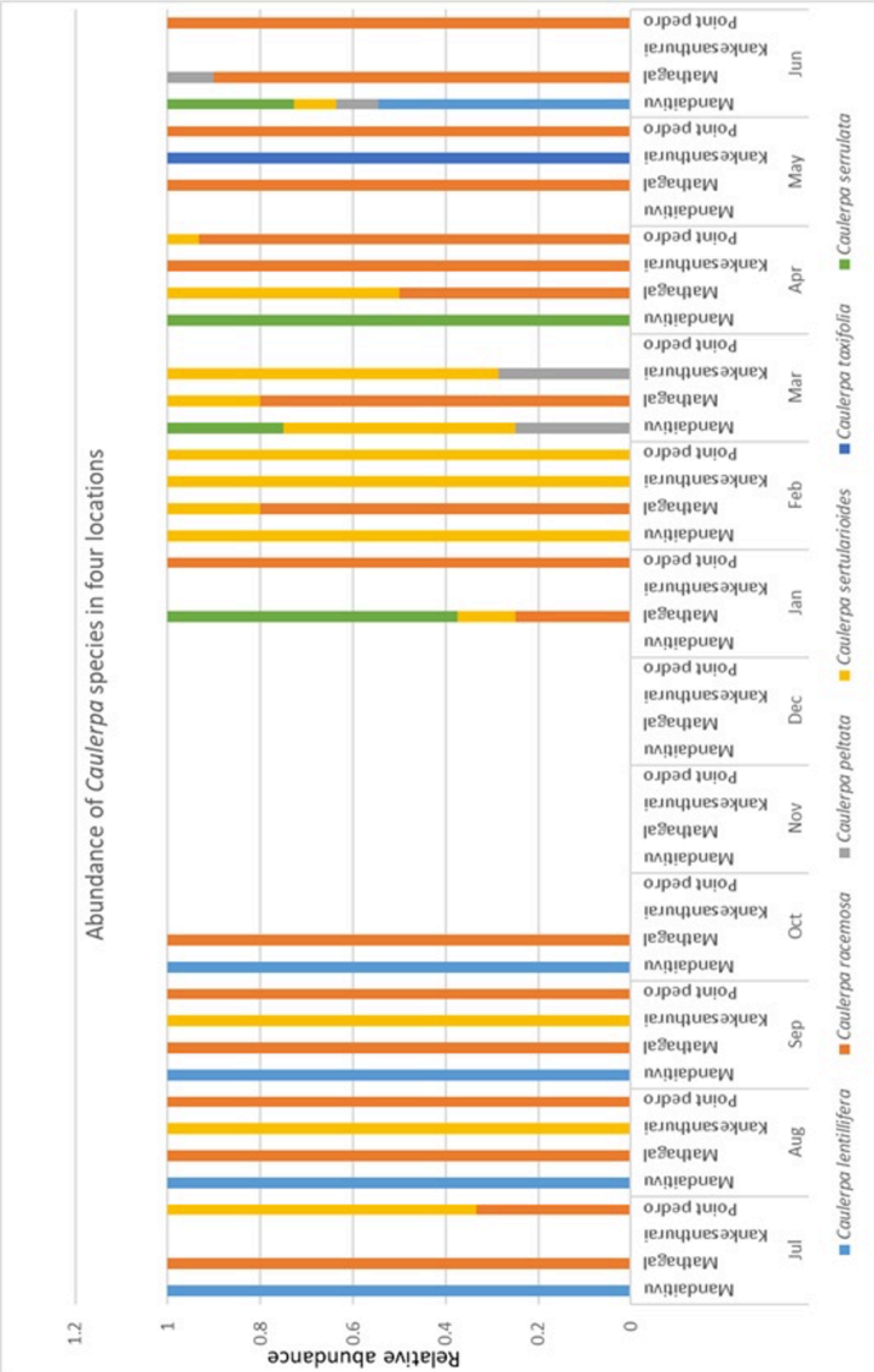

Figure 4. Abundance of six *Caulerpa* species from four locations in Northern Sri Lanka.

Diversity indices

The presented bar graphs in Figure 5 illustrate the monthly variation in species richness and three key diversity indices across four coastal sites from July to June. Species richness was generally low (1-2 species), with two notable exceptions: a peak of 4.0 at Mandaitivu in June and 3.0 at Mathagal in January.

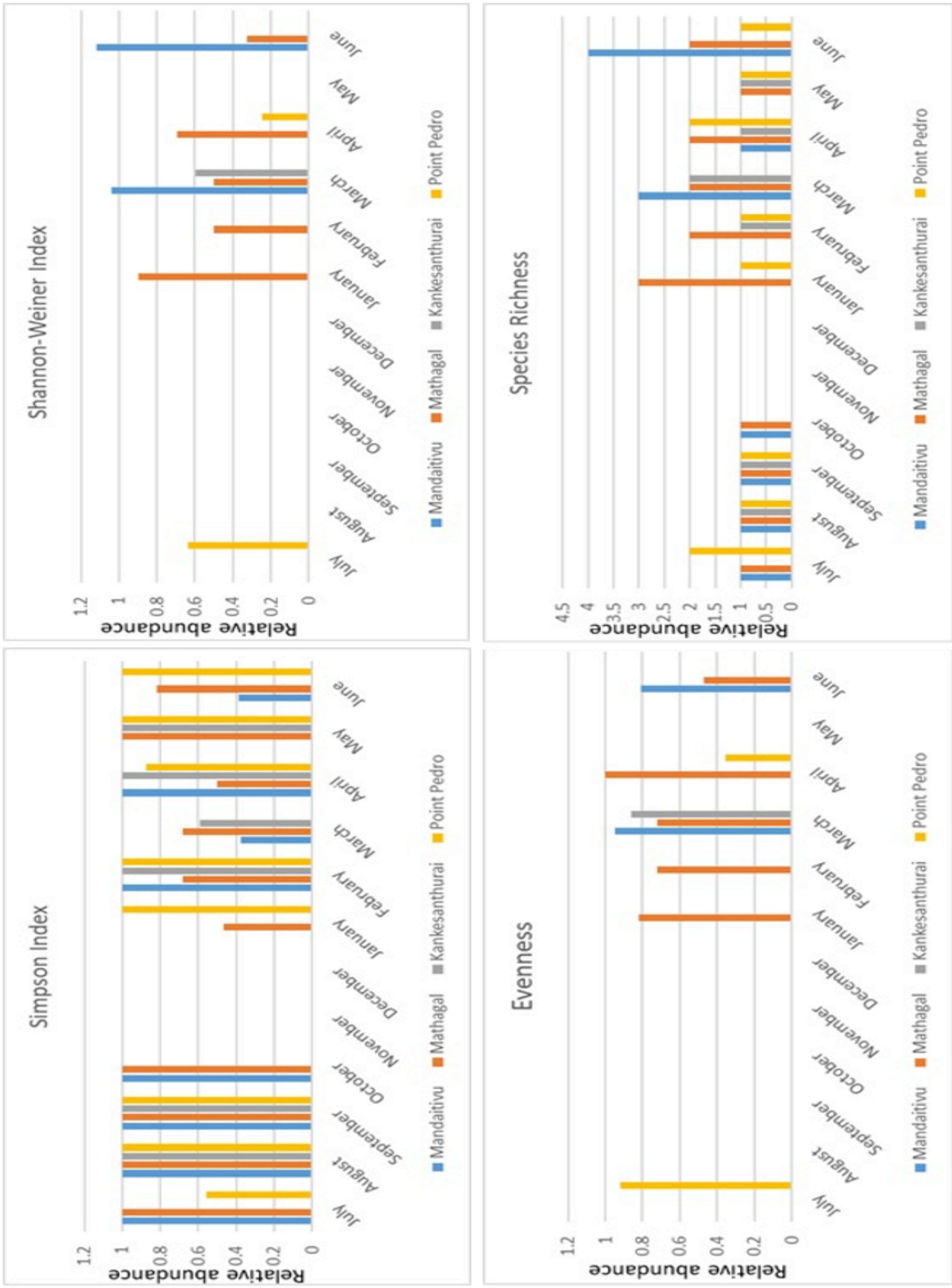

Figure 5. Monthly variation in species richness and three key diversity indices

Crucially, if the Simpson index (D) represents the measure of dominance, its interpretation for diversity is inverse. The high D values (near 1.0) observed across most sites and months (especially July-October) suggest periods of very low diversity where one or two species overwhelmingly dominate the community. Conversely, the lowest Simpson index value recorded at Mandaitivu in June, with the highest species richness (4.0). It actually represents the highest recorded diversity (lowest dominance). This indicates that in June, despite the species being rich, the evenness and abundance distribution favoured a diverse, rather than dominant, community structure. The data also clearly indicates a period of zero species recording for all sites during November and December.

Statistical analysis

Canonical Correspondence Analysis (CCA) revealed that species composition was significantly influenced by the measured environmental variables (permutation test, $p < 0.05$). The strength and type of environmental drivers varied among locations. At Mandaitivu, salinity and temperature were the main factors structuring the community. At Mathagal, species distribution was primarily associated with salinity, pH, and phosphate levels.

In contrast, at Kankesanthurai, salinity, dissolved oxygen, and turbidity were the dominant variables influencing seaweed assemblages. These patterns indicate that each site is shaped by a distinct set of environmental conditions. The CCA ordination diagram for Point Pedro depicts a distinct species grouping based on *Caulerpa* species against the environment. *Caulerpa sertularioides* is dominantly linked to high turbidity and phosphate values in Axis 1, thus preferring nutrient-rich conditions at Point Pedro.

On the contrary, *C. racemosa* is grouped with dissolved oxygen and temperature, which depict a species distribution influenced by high temperatures and high oxygen levels at Point Pedro. The effect of season is also distinct, with the northeast monsoon linked with high nutrient and turbidity values that define species-environment associations. Figure 5, 6, 7 and 8 are the CCA ordinations for four locations.

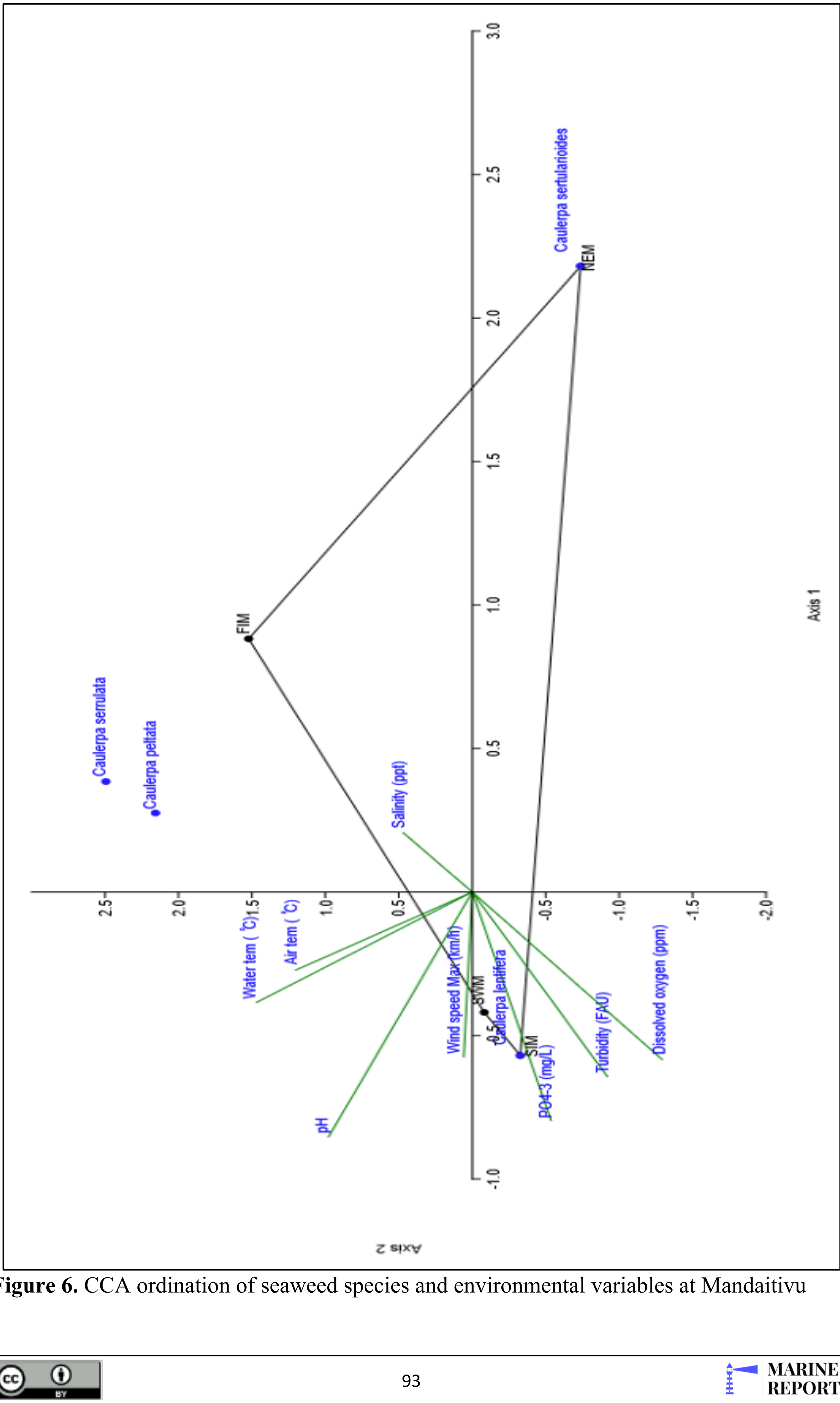

Figure 6. CCA ordination of seaweed species and environmental variables at Mandaitivu

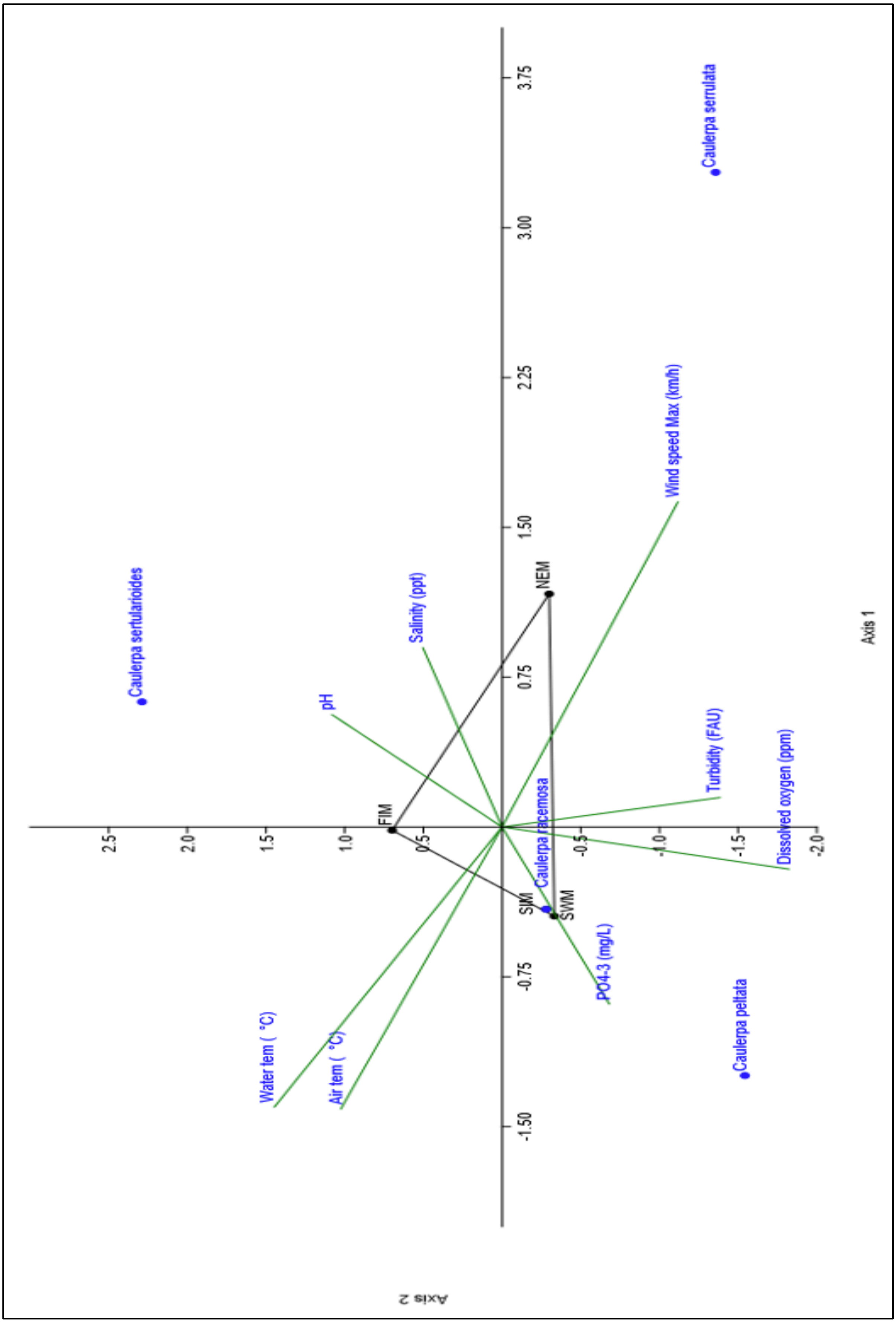

Figure 7. CCA ordination of seaweed species and environmental variables at Mathagal

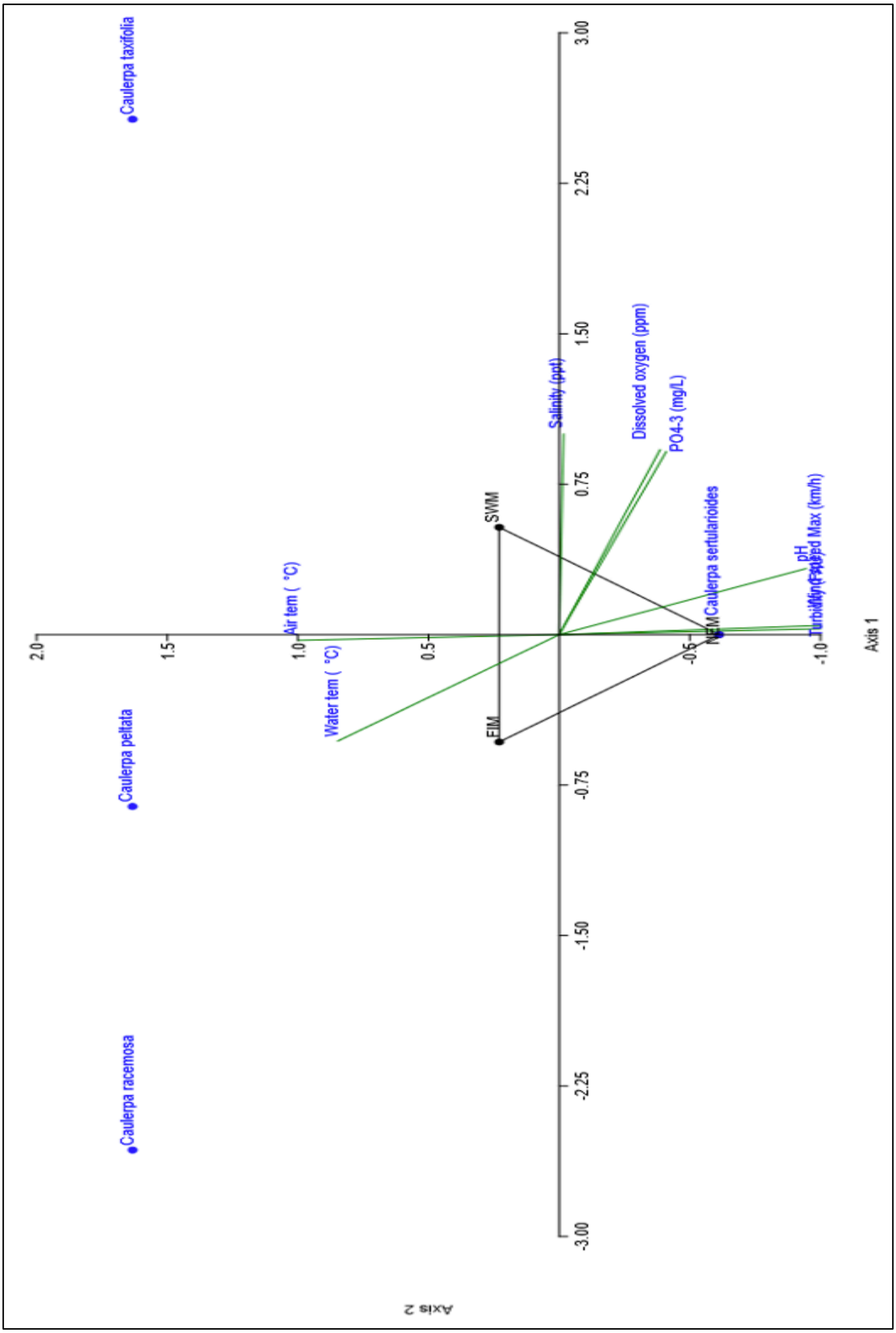

Figure 8. CCA ordination of seaweed species and environmental variables at Kankesanthurai

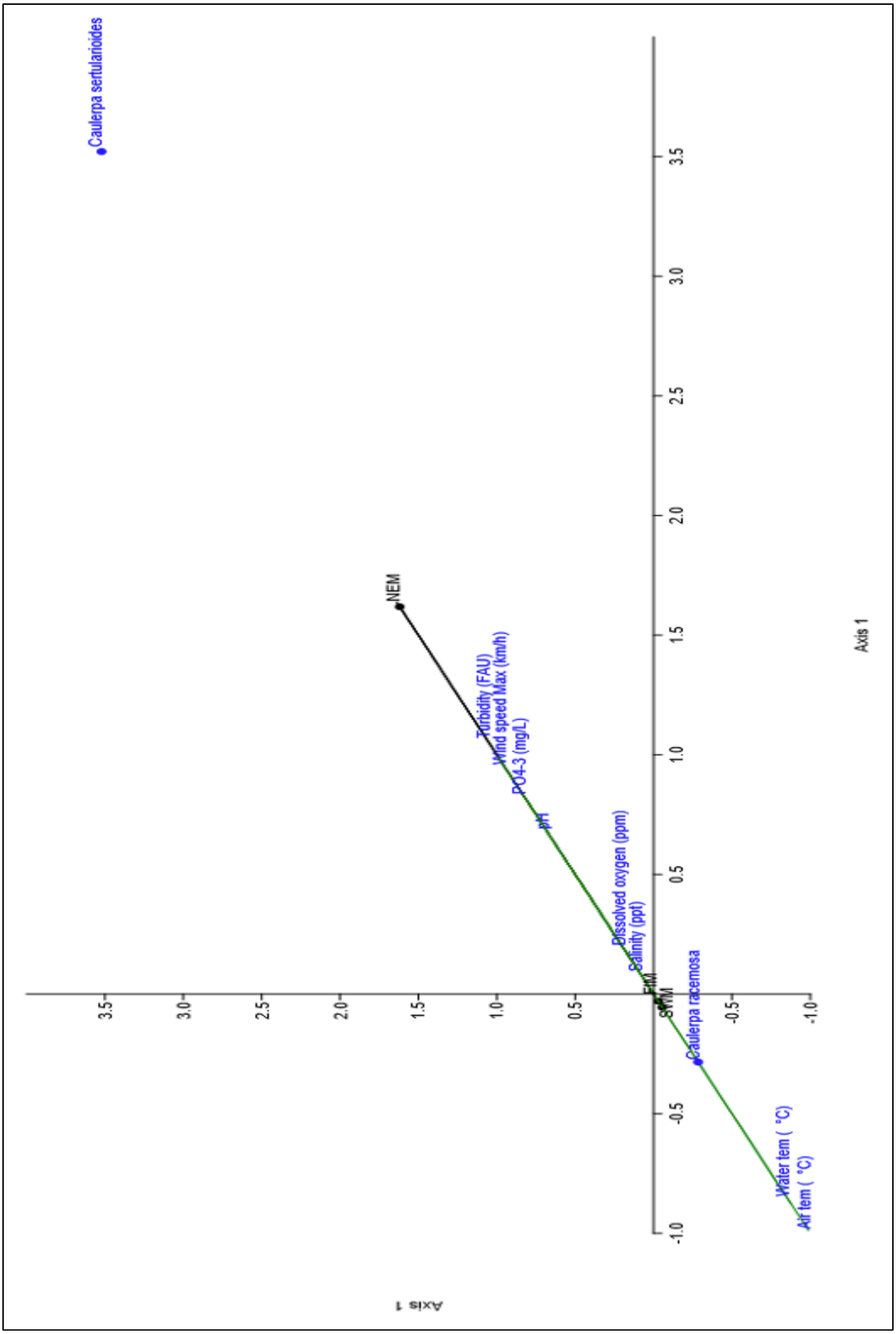

Figure 9. CCA ordination of seaweed species and environmental variables at Point Pedro

Discussion

The present study provides a critical, detailed inventory of the green macroalgal genus *Caulerpa* along the northern coast of Sri Lanka, revealing a previously under-documented marine botanical landscape. Across the four surveyed locations—Mandaitivu, Mathagal, Kankesanthurai, and Point Pedro—six distinct species were meticulously identified, painting a picture of moderate but ecologically vibrant diversity. The documented species—*C. lentillifera*, *C. racemosq, C. sertularioides*, *C. taxifolia, C. serrulata*, and the notable *C. peltata* —represent a fascinating array of forms and adaptations. In the present study, species identification was based on detailed morphological characters, as *Caulerpa* species possess distinctive and well-documented diagnostic features that allow reliable identification at the species level.

Each species presented a unique morphological character within the seascape. *C. lentillifera*, with its delicate, bead-like filaments, offered a more fragile and intricate structure, often swaying in the subtidal currents. *C. racemosa*, often found in dense, verdant mats, was characterized by its grape-like clusters of spherical branchlets, creating a textured carpet over the substrate.

The feather-like fronds of *C. sertularioides* closely resembled miniature underwater ferns, while *C. serrulata* displayed a distinctive, stiff morphology with saw-toothed edges along its upright branches. *C. peltata* was identified by its unique, shield-shaped appendages that terminate its stalks, and the presence of *C. taxifolia*, with its flat, feather-shaped fronds resembling the fronds of a yew tree, was of particular interest given its reputation as one of the world's most invasive marine algae (Coppejans et al., 2009).

The distribution and dominance of these species were far from uniform, revealing a complex interplay of environmental factors. The research uncovered significant spatial and temporal variations. Spatially, the composition of *Caulerpa* communities shifted from one location to another. For instance, some coves exhibited a dominance of *C. racemosa*, blanketing the sandy-rocky bottoms, while other sites, perhaps with stronger water movement, were populated by more robust species like *C. serrulata* or *C. taxifolia*. These patterns were heavily influenced by local environmental conditions and substrate characteristics; the algae's attachment to rocky outcrops, sandy patches, or within seagrass meadows dictated which species could successfully establish and thrive.

Temporally, the populations were dynamic, fluctuating with the seasonal hydrodynamics of the region. The monsoon cycles, with their attendant changes in water temperature, salinity, turbidity, and wave energy, likely governed the growth, reproduction, and seasonal die-back of these algae. A species abundant in the calm, clear waters of one season might recede during periods of heightened turbulence and sedimentation.

The present study is more than a simple checklist; it contributes valuable baseline information to the severely limited body of research on Sri Lankan seaweed flora. By establishing this foundational record, it provides a critical reference point for future ecological monitoring. Understanding the current diversity and distribution of native species like *C. lentillifera* is essential, especially in the context of potential shifts caused by climate change or the spread of non-native species such as *C. taxifolia*. Ultimately, these findings underscore that the northern coast of Sri Lanka hosts an ecologically significant and dynamic assemblage of *Caulerpa* species, whose presence and interactions are key to the health and complexity of its coastal ecosystems.

Spatial Distribution and Habitat Influence

The investigation into the spatial distribution of *Caulerpa* species along the northern Sri Lankan coast reveals a compelling narrative of ecological specialization and adaptation, where the success of each species is intricately dictated by the physical and dynamic character of its habitat. The study revealed that *C. sertularioides* was the most widely distributed species, a true generalist, occurring in all sampled locations and seasons, demonstrating remarkable ecological plasticity. Its presence across all sampled locations and seasons is a direct testament to its broad tolerance for environmental variables, as supported by the work of Coppejans (1992).

Its creeping habit allows effective colonization of both sandy and rocky substrates, explaining its abundance in both sheltered and moderately exposed habitats. In contrast, *C. lentillifera* and *C. taxifolia* exhibited restricted distributions, each being recorded only at specific sites with suitable habitat conditions. The presence of *C. racemosa* and *C. peltata* was more localized but showed seasonal fluctuations, suggesting a preference for intermediate environmental stability.

Habitat diversity among the four sites strongly influenced species composition. Mathagal and Kankesanthurai supported greater species richness due to the presence of mixed rocky and sandy substrates, which provide firm attachment points and favorable hydrodynamics. These areas also experience moderate wave action, promoting nutrient exchange without excessive thallus damage. In contrast, Mandaitivu, characterized by muddy and sandy substrates, supported fewer *Caulerpa* species. The soft sediment may hinder proper holdfast attachment and limit light penetration, reducing diversity. Point Pedro, with its exposed rocky habitat dominated by the forces and currents, occasionally supported *C. sertularioides* and *C. racemosa*, both of which exhibit phenotypic plasticity suited for turbulent waters. Leliaert and Coppejans (2006) showed that species of *Caulerpa* commonly occur in shallow tropical and subtropical marine environments, inhabiting a variety of substrates such as sand, rock, and mud. They also reported that many species are associated with seagrass meadows, reef flats, and lagoonal habitats, where light availability and substrate type strongly influence their distribution.

Temporal Variations and Seasonal Trends

Temporal analysis across twelve months revealed marked fluctuations in *Caulerpa* abundance. The months of November and December showed minimal or no growth, coinciding with the northeast monsoon period. During this season, heavy rainfall and runoff increase turbidity and nutrient loading while reducing light penetration, salinity, and water clarity, conditions generally unfavorable for photosynthetic macroalgae (Jargal et al., 2023). The near-total absence of *Caulerpa* during the Northeast Monsoon (November-December) represents a period of extreme environmental stress that pushes these algae beyond their physiological limits. This "bottleneck" effect is caused by a synergistic confluence of adverse factors such as light deprivation and osmotic shock and nutrient overload and physical scour.

Conversely, from January to October, seaweed abundance progressively increased, particularly from February onward, when hydrological conditions stabilized. The highest abundance was observed in September and October, indicating post-monsoonal recovery and optimal growth conditions. These findings align with Williams and Grosholz (2002), who observed that most *Caulerpa* species exhibit optimal growth at temperatures between 26 – 29 °C with high irradiance and moderate water motion. Recorded water temperatures during the present study (27 – 28 °C) fell within this favorable range, supporting enhanced metabolic and photosynthetic activity.

Distinct seasonal peaks for different *Caulerpa* species were evident. *C. lentillifera* showed maximum abundance in September, while *C. racemosa* and *C. sertularioides* peaked in October. The timing of these peaks likely reflects differences in species' growth and tolerance to environmental conditions. *C. racemosa*, known for its rapid vegetative propagation and adaptability, often dominates following periods of disturbance, while *C. lentillifera* prefers more stable and nutrient-rich conditions. Similar seasonal dynamics were reported by Paul et al. (2014) in Australia, where *C. racemosa* proliferated after monsoon disturbances while *C. lentillifera* dominated in calmer seasons.

Morphological Adaptations and Ecological Significance

The six recorded *Caulerpa* species exhibit diverse morphological traits that enhance their ecological success under varying hydrodynamic regimes. For instance, *C. sertularioides* possesses erect, feather-like fronds that maximize light capture, while its creeping stolons help stabilize sediments. *C. peltata* and *C. serrulata* have flattened, disc-like ramuli that resist strong water movement, allowing persistence in exposed environments. *C. racemosa*, with its characteristic grape-like ramuli, exhibits efficient surface area for photosynthesis and nutrient uptake. These morphological adaptations reflect ecological specialization and plasticity, enabling different *Caulerpa* species to occupy distinct ecological niches. Morphological plasticity within the genus has been widely documented in Coppejans et al. (2009), allowing *Caulerpa* to colonize habitats ranging from shallow to deeper subtidal zones. Morphological measurements of the collected specimens align well with those documented by Coppejans et al. (2009), supporting the identification and confirming the typical species characteristics.

Environmental Drivers and Anthropogenic Factors

Environmental parameters such as temperature, salinity, and nutrient levels played pivotal roles in shaping seaweed distribution. The coastal waters of northern Sri Lanka are subject to monsoonal fluctuations, which significantly alter salinity and turbidity. Sites like Kankesanthurai and Mathagal, being more open to oceanic influence, maintained relatively stable salinity levels, favoring *Caulerpa* growth. In contrast, Mandaitivu, with its lagoonal influence, experienced fluctuating salinity and higher turbidity, reducing overall seaweed abundance. Anthropogenic influences were moderate but noticeable in semi-urban locations such as Kankesanthurai, where occasional wastewater discharge and fishing activities (in Mandaitivu and Mathagal) may contribute to nutrient enrichment, indirectly enhancing algal biomass. However, excessive nutrient input can also lead to epiphytic overgrowth and competition, underscoring the need for balanced nutrient levels for healthy seaweed communities.

Site-specific patterns of separation with respect to environmental drivers discerned in the CCA indicate the prominent role of local hydrographic factors and water quality in determining seaweed assemblage patterns in the area. While the role of salinity as a structuring driver for the seaweed assemblage was universal among the surveyed areas, the role of other drivers, like temperature, nutrients, oxygen, and turbidity, varied significantly among the areas. Such variability in the area of study is consistent with previous research on tropical shallow coastal ecosystems, which indicates that small variations in physicochemical factors can influence the species dominance pattern. Conversely, the association of *C. racemosa* with high temperature and high levels of dissolved oxygen suggests that it prefers warmer, better oxygenated waters, as would be expected for a species with a broad tropical distribution. The distinct seasonal pattern, with the importance of the northeast monsoon in determining levels of nutrients and turbid conditions, further illustrates the importance of monsoonal processes in species-environment interactions at Point Pedro. In total, the CCA analysis reveals that seaweed assemblages in the study area are determined by a combination of spatially discriminable environmental factors, as well as seasonal variability, with differing responses of *Caulerpa* species to gradients of nutrients, temperature, and turbidity. This reveals that it is important to examine both local factors and monsoonal effects when determining the ecology and distribution of tropical coastal seaweeds.

Comparative and Biogeographical Insights

When compared with historical records by Silva et al. (1996), who reported 19 *Caulerpa* species across Sri Lanka, the present study captures a smaller but regionally significant assemblage. The moderate diversity recorded here could reflect localized environmental constraints, limited sampling range, or recent ecological shifts due to climatic and anthropogenic pressures. The continuity underscores the importance of transboundary marine conservation and monitoring efforts in the Indian Ocean region.

Conclusion

Overall, the study reveals that *Caulerpa* diversity and abundance along the northern coast of Sri Lanka are governed by complex interactions between habitat type, environmental parameters, and seasonal dynamics. The observed species distribution reflects the adaptive strategies and ecological roles of *Caulerpa* within these ecosystems. The data generated contribute not only to the national seaweed inventory but also to broader regional understanding of tropical macroalgal ecology in the Indian Ocean. Future research integrating molecular, physiological, and remote-sensing approaches could further reveal population connectivity, species resilience, and responses to climate-induced environmental shifts.

Acknowledgements

The manuscript originates from a part of the M.Phil. research of the first author. Nor-Lanka Blue Project funded the exchange program under NORPART project (DIKU Grant NORPART 2018/10045 at UiT-The Arctic University of Norway, Tromsø) to the first author and the M.Phil. Research. Special appreciation goes to the laboratory staff of Department of Fisheries for their assistance in sample processing and analysis.

Ethical approval

Not applicable.

Informed consent

Not applicable.

Availability of data and material (data transparency)

All relevant raw data are incorporated and presented in this paper.

Conflicts of interest

The authors declare that they have no conflict of interest.

Funding organizations

This project was supported by NORPART project (DIKU Grant NORPART 2018/10045 awarded to UiT-The Arctic University of Norway, Tromsø) in collaboration with University of Jaffna, University of Ruhuna and National Aquatic Resources Development Agency.

Authors' Contribution

Anjalie, N.M.I.: Data curation, formal analysis, investigation, methodology, validation, Writing– Original draft.
Nahmagal, K.: Investigation, supervision, validation, writing – Review and editing.
Sivashanthini, K.: Conceptualization, funding acquisition, investigation, methodology, project, administration, supervision, visualization, Writing – review and editing.

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