Research Square

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A broad-scale biometrical response of a pristine meadow, Posidonia oceanica, to winter and summer conditions in the north-eastern Mediterranean coast

Erhan Mutlu (emutlu@akdeniz.edu.tr)
Akdeniz University
Güler Sıla Duman
Akdeniz University
Doğukan Karaca
Akdeniz University
Yaşar Özvarol
Akdeniz University
Ahmet Şahin
Karadeniz Technical University

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Abstract

The concept of the present study was derived from a study to ground-truth the acoustical echo energy of the seagrass biometrics in order not to use any destructive method and was scoped to study the estimated environment-related biometrical distribution of a pristine marine phanerogam, *Posidonia oceanica* meadow, along the entire Turkish Mediterranean coast. This study also provided the first knowledge on the broad-scale extent of the meadow from a significant coast length in the Mediterranean Sea. For this purpose, two surveys were conducted covering bottom depths of 5–35 m in the critical seasons (winter and summer 2019) of a subtropical coast for the growth dynamics of the meadow. The meadow samples were collected in a frame of 0.4 x 0.4 m by SCUBA divers, which was a destructive method. The physicochemical and optical environments of the water were evaluated with the biometrical dynamics of the meadow. Orderly, season, region, bottom types, and bottom depths dictated the biometrical distribution. The meadow shoot density showed the environment to be in good ecological condition without changing the average shoot density in season. Other biometrics grew 2-fold higher in summer compared to winter (water temperature and salinity). The region influenced by the Aegean Sea had lower biometrical values than the other two regions. Hard (rock and *matte*) and soft (sand and mud) benthic environments differentiated the biometrics as follows: Contrary to the morphometric variables, the density biometrics decreased linearly from the hard bottom to the soft bottom. The density dynamics were partially contrasted with the morphometrical dynamics. Rhizome-related biometrics were independently governed by the leaf-related biometrics, especially by nitrogen-based nutrients in near-bottom water. The optical parameter, especially PAR, a certain percent of the daylight was effective during the growth of the biometrics. The present study provided the first knowledge on a broad-scale biometrical distribution from the entire Turkish Mediterranean coast to the seagrass studies.

Introduction

Of the seaweeds, a phanerogam, *Posidonia* spp., has been sustained favorably in the poor-nutrient marine environment and formed colonial life in the world seas (Walker 2000). An endemic species of the Mediterranean Sea, a meadow, *Posidonia oceanica* (Linnaeus) Delile, 1813 was well adapted to ultra-oligotrophic habitats in the Eastern Mediterranean (Marba et al. 1996). Therefore, *P. oceanica* suggested useful information and data about the health and ecological status of the seas. This seagrass meadow ecologically functioned to sustain niches such as oxygen sources, biotope (epiphytes), habitat, shelter (protectors of prey), direct (herbivore fish and turtle) and indirect (epiphytes) food, and control of invasive seaweeds (Boudouresque and Meinesz 1982; Peirano et al. 2005). Furthermore, the seagrass induced increase in diversity and production of invertebrate and osseous fishes, favored the organisms with different food webs as compared to unvegetated marine environments (Edgar and Shaw, 1995), and ultimately, expanded their community spatially (Den Hartog 1977).

Monitoring the seasonality of their growth dynamics over the years has presented suggestions for temporally acute, chronic, and drastic changes in their corresponding prevailing environment. Such data were often used for planning environmental measures by marine ecologists, biologists, and species

managers and protectors (Marba et al. 2002; Orth et al. 2006; Gobert et al. 2009). Besides, water temperature, salinity, and bottom depth dictated their seasonal population dynamics under the good ambiance of the sea (Gobert et al. 2006). Seasonal population dynamics were derived from some biometrics of theirs such as leaf and rhizome length, width, and elongation in contrast to the unchanging shoot density in a pristine environment (UNEP/MAPRAC/SPA 2015). The growth of the *Posidonia* population dynamic began in the month (late autumn-early winter) when new leaves occurred (Gobert et al. 2006; Mutlu et al. 2022a). The bottom depth induced a slight difference in the growth dynamic (Caye and Rossignol, 1983). This difference was more pronounced at shallower and greater bottom depths than 15 m (Mutlu et al. 2022a). The Mediterranean meadow has exhibited apparently spatiotemporal dynamics under clean environmental conditions (Mutlu et al. 2022a), but has not performed the spatiotemporal dynamics under poorly-stated ecological environments in a year (e.g. Marba et al. 1996; Guidetti et al. 2002; Sghaier et al. 2006; Pagès et al. 2012; Montefalcone et al. 2016). The interannual dynamic could be high depending on potential environmental sources such as nutrients, carbon (Alcoverro et al. 1997), and light (Gobert et al. 2003).

Of many predicted environmental variables stimulating the population dynamics, bottom substrates (hard; rock and *matte* or soft; gravel, sand, and mud) differed statistically in the biometrics of *P. oceanica* (Catucci and Scardi 2020; Gnisci et al. 2020). During their early development, each of the bottom types produced specific root hairs for itself (Borg et al. 2009; Alagna et al. 2015), and hence the dispersal type (regular or binomial distribution and types) and depthwise boundary of the meadow were shaped according to the bottom types (Colantoni et al. 1982; Marbà et al. 2002; Vacchi et al. 2012; Tomasello et al. 2018). Such a specific peculiarity of early-developed hairs sustained the specimens of the specific type in addition to the hydrodynamic (De Falco et al. 2008) and anthropogenic effects shifting the upper boundary of *P. oceanica* (Montefalcone et al. 2019).

Posidonia oceanica has been subjected to lots of environmental studies (Marbà et al. 1996; Short and Neckles 1998; Peirano et al. 2005; Gobert et al. 2009), research of local biometrical dynamics under different marine environments prior to the 2000s(Caye and Rossignol 1983; Wittmann 1984; Pergent and Pergent-Martini 1990; Bay 1984; Marba et al. 1996; Via et al. 1998), followed by experimental studies on biology under controlled marine medium in field and lab (Borg et al. 2005; Fernandez-Torquemada and Sanchez-Lizaso 2005; Leoni et al. 2006; Diaz-Almela et al. 2009; Planes et al. 2011; Terrados and Medina-Pons 2011; Marín-Guirao et al. 2013; Tomasello et al. 2016), and then detection and mapping using the remote sensing systems (Fornes et al. 2006; Borfecchia et al. 2013; Corbí et al. 2018). All previous studies were conducted mainly in the West Mediterranean Sea, but the studies in the East Mediterranean Sea were carried out between the Greek and Italian coasts (Vacchi et al. 2017). However, the Turkish Mediterranean coast, which has a significant coastline in the eastern Mediterranean Sea, has not been exclusively studied (Vacchi et al. 2017). Recently, some local biometrical studies have been conducted on *P. oceanica* (Turna et al. 2017; Olguner and Mutlu 2020, Mutlu et al. 2022a) and on *Cymodocea nodosa* (Ucria) Asch as a seagrass (Mutlu et al. 2022b) along the Turkish Mediterranean coast.

The present study was indeed conducted to calibrate and ground-truth the seagrass using the acoustical technique; therefore, the destructive method was used here for the collection of the *P. oceanica* sample. Some methodological suggestions were available for describing the destructive effects: sampling more than 1000 shoots (Mutlu et al. 2023), more than 20 orthotropic shoots (Pergent et al. 1995), and cutting leaves above the ligule inside more than one-third of the sampling quadrant (Gobert et al. 2020). Therefore, some preliminary acoustical algorithms were developed (Mutlu and Balaban 2018; Olguner and Mutlu 2020) and some studies have been published for the seagarss acoustics (Mutlu and Olguner 2023a, b, c) to no longer conduct the destructive sampling.

In terms of the ecological derivations and status of *P. oceanica* in the marine environment considering the chronological lack of broad-scale knowledge comprising the southern Turkish coastal waters (Vacchi et al. 2017), which have a variety of bottom types (rock, *matte*, sand, and mud), this study is aimed at determining the biometrics (density and plant traits; morphometrics)-environment relationship (physiochemical and optical variables) of *P. oceanica* in the infralittoral zone along the entire Turkish Mediterranean coast in winter (biometrics at minima) and summer (biometrics at maxima) conditions.

Material and Methods

The sample collection was performed to calibrate the acoustical data with the biometrical data of *P. oceanica* distributed along the Turkish Mediterranean coast in winter 2018–2019 (December-January) and summer 2019 (June-July) (Fig. 1). The materials collected in the present study would help to stop using the destructive methods to sample the seagrasses under protection (Mutlu and Balaban 2018; Balaban and Mutlu 2020; Mutlu and Olguner, 2023a, b, c). Each seasonal survey lasted 1.5-2 months due to the acoustical tracking using a split-beam scientific transducer and echosounder operated at a sound frequency of 206 kHz (DT series, BioSonics Inc., USA), which guided the present study to sample the bottom inhabited by *P. oceanica*. In winter and summer, the materials were taken from surface and near-bottom waters for the basic physical environmental parameters. Besides, materials for the chemical and optical parameters were supplied from the waters only in summer since population dynamics were stable in stagnation conditions at minima and maxima in summer, resulting in differences in the biometrics among the regions (bays), bottom depths, and bottom types (Fig. 1b-d). The present materials, provided by a destructive-method of SCUBA sampling, were used here to determine the spatiotemporal and ecological distribution of the Mediterranean meadow or seagrass on a broad-scale along the north-easternmost coast of the Mediterranean Sea.

Sample collection

Sample collection was considered for the ecological study of *P. oceanica* with the biometrical and environmental variables provided from 48 stations in winter and 100 stations in summer (Fig. 1c, d). The sampling bottom depth varied between 5 m and 35 m, but generally between 10 and 30 m due to the security of “R/V Akdeniz” in the shallower waters and the daily diving limitations of SCUBA divers at the

greater depths. Non-sampled space (ground) was not inhabited by *P. oceanica*, as instantaneously estimated by the acoustical study.

Sampling the meadow material

Posidonia samples were collected by SCUBA divers at each station in time (season) and space (bays and bottom depths). The divers used a quadrant measure of 0.4 x 0.4 m for collecting the meadow with their horizontal rhizome as much as possible. Three replicates were performed at each station.

After collection of the seagrass, the sample of each replicate was preserved in a borax buffered-formaldehyde solution of 4% in concentration in the plastic jar for later biometrical measurements at the lab. On the course of the ship R/V Akdeniz, sampling bottom depth was designed to cover and match all the bottom depths (overall, 10-to-30 m; generally, 10, 15, 20, 25, 30 m) located close to the next station.

During each dive, the bottom type was visually classified as rock, *matte*, sand, or mud by the divers (Fig. 1b).

Sampling the environmental material

During sampling at the stations, water samples were taken from the surface and near-bottom depths with a 5 liter Nisken bottle. The physical hydrographical parameters were then measured on board using a multi-parameter probe (YSI, HiTech, USA). The physical parameters were water temperature (^{o}C), salinity (PSU), pH, and dissolved oxygen (mg/l). The dissolved oxygen was not measured in summer since its probe malfunctioned.

From the water samples, 1 liter of water was filtered for each filter of CF/C and CF/F for measurements of the chemical variables performed at the lab: nutrients, total suspended matter, and chlorophyll-*a*, respectively. The chemical parameters were nutrients (NO_2, NO_3, NH_4, SiO_2, and PO_4 in $mg.l^{-1}$), chl-*a*, and total suspended matter. All water samples and filters were frozen at -20 ^{o}C for later studies at the lab.

Furthermore, the optical variables were photosynthetically active radiation (PAR, %) and Secchi disk depth (in m) measured on board. PAR was profiled from the surface to a depth of 50 m by a multi-parameter logger and PAR ampoule (LiCor, USA).

Laboratorial studies

Seagrass biometrics

Leaves of *P. oceanica* were collected in each sampling period to measure seagrass morphometrics or plant traits (leaf length and width, vertical rhizome length and thickness, sheath length and width). The density biometrics were leaf area (LA cm^2 per sampling frame; leaf length x leaf width), shoot density, number of leaves per shoot, leaf area index (LAI $m^2.m^{-2}$), inter-shoot (nodal) distance, and leaf biomass ($g.m^{-2}$). Leaf biomass was estimated from the length-weight and LAI-weight regression equations established in a previous study (Mutlu et al. 2022a).

Environmental variables

In the laboratory, nutrients were measured following the standard procedures: Ammonium (NH_4 mg.l^{-1}), nitrate (NO_3 mg.l^{-1}), nitrite (NO_2 mg.l^{-1}), silicate (SiO_2 mg.l^{-1}), and phosphate (PO_4 mg.l^{-1}) were measured using the methods of 4500-NH_4 B, 4500 $N0_3$-E, 4500 $N0_2$-B, 4500-SiO 2, and 4500-P E, respectively (APHA 1999).

For the estimates of total suspended solids the material was dried in an oven at 60 ^{o}C for 24 h and then weighed before the weight of the dried membrane was subtracted from the total dry weight). Chlorophyll *a* (chl-*a*) was estimated using a method described by Lorenzen (1967). Secchi disk depth was recorded once at each station.

From the PAR data at each station, the percent of PAR which reached the seagrass bed was estimated referring to measure at the sea surface and light extinction rate (K) and a depth (KD) where the minimum end of the exponential curve occurred with the depth was determined as optical environmental parameters.

Bottom types

Besides the classification by the divers, the bottom type and bathymetry were determined acoustically to identify the boundaries of the distribution depth. For this purpose, Visual Bottom Typer (VBT, ver. 1.10, Biosonics Inc.) was used. VBT was configured according to the grain size distribution of the sediment. The bottoms of the stations were acoustically classified as rock coded as 1, sand (slime, 2 and rough, 3), and mud (slime, 4 and rough, 5).

Statistical study

The statistical analyses were performed to test the differences in the biometrics by season, region, bottom type, and bottom depth using univariate parametric analyses and three-way analyses of variance (3-way ANOVA). The interaction of season x region x bottom depth could not be afforded since the factorial design of a 3-way ANOVA was not suitable for the present data matrix due to the absence of repeats for each factor. This could be achieved under ill-condition of the model, but it was not forced or attempted for the statistical solution. Before the analyses, the variance-mean dependence of the variables was checked to ensure a random distribution in the data. The data were then $\log_{10}$-transformed before the analyses. A univariate analysis, Spearman rank correlation, was used to estimate the degree of the relationships between the biometrical and environmental parameters in winter and summer. The statistical tool MatLab (vers. 2021a, Matworks Inc.) was used for the statistical analyses above.

Of the multivariate analyses, the principal component analysis was applied to the environmental variables and biometrical variables of *P. oceanica* to determine the components inducing classification of the variables for the study area. The data was normalized prior to the analysis using PRIMER 6 (vers. 6.1.13) + PERMANOVA + (1.0.3). For grouping the sampling stations based on the normalized biometrics,

the triangle matrix using Euclidean distance was estimated using the biometrical rectangular matrix (stations vs. biometrics) for the Cluster and non-parametric dimensional scaling (nMDS) analyses between stations and the biometrical variables. Between-biometrical cluster analysis was performed to see the type of relation for their dynamics among the biometrical variables in space and time using PRIMER 6. The canonical correspondence analyses (CCA) were chosen after the gradient length of the biometrics was estimated using CANOCA (CANOCA ver. 4.5) to establish and explain biometrical data and the biometrics-environment relationship using only physical parameters in winter and all the environmental parameters in summer. The Monte Carlo test was then used to validate the relationship significantly at the stations classified by season, regions, bottom type, and bottom depths at $p < 0.05$.

The surface area of coverage by *P. oceanica* was estimated using Surfer 12 (Golden Software).

Results

Study area and environment

Half of the stations in regions 3 were influenced by the water of the Aegean Sea, and more than half of the stations in region 2 were located in Antalya Gulf, regarding the water rim current, respectively. Region 2 was set around the Atlantic rim current of the Levant water to influence the environmental parameters (Fig. 1).

Sampling bottom depth varied generally between 10 m and 30 m, but 5 and 35 m were rarely included in the samplings (Fig. 1). Regional average bottom depth was 17.9 m and 20.8 m in region 3 (Muğla), 19.5 m and 18.9 m in region 1 (Antalya), and 16.0 m and 18.4 m in region 2 (Mersin) in winter and summer, respectively (Fig. 1). The bottom type was composed mainly of sand and mud in region 3, rocks in region 1, and *matte* of *P. oceanica* and mud in region 2 (Fig. 1).

Contrary to the variation, average sea surface salinity increased from the west to the east of the study area and varied between 37.2 and 38.9 PSU in winter. In summer, it was at its minima in region 1 (Antalya), at its maxima in region 3 (Muğla), followed by region 2 (Mersin), and lower than that in winter. Near-bottom water salinity was lower in summer (36.0-37.2 PSU) than in winter (38.4–38.8 PSU) and increased from the west to the east in contrast to their standard deviation.

Sea surface temperature increased from 16.7 ^{o}C in the west to 18.8 ^{o}C in the east in winter, and from 24.9 ^{o}C (region 3) to 26.9 ^{o}C (region 1), followed by 26.0 ^{o}C (region 2), in summer. Near-bottom water temperature showed a similar regional trend in sea surface temperature in winter and summer and varied between 16.9 ^{o}C and 19.6 ^{o}C in winter and between 23.5 ^{o}C and 25.4 ^{o}C in summer.

Dissolved oxygen, which was measured only in winter (the probe of oxygen was malfunctioned in summer), was measured to be similar in sea surface and near-bottom waters and increased from east (9.3 mg/l) to west (9.8 mg/l).

Inherently, the surface water was denser in winter than summer for a subtropical region of the present study area. In winter, sea surface water was denser on the set of the rim water current (more temperate and saline) than semi-enclosed gulfs (Antalya, Yeşilova, and Hisarönü Gulf; less saline and temperate). In summer, sea surface water trended to increase water density from the east to the west of the study area. The east was slightly more saline and temperate, which decreased the density, whereas the west was less temperate, which increased the density as compared to the west and east, respectively. This suggested that the west was under the influence of the Aegean Sea, which was expected to change the biometrics.

Of the nutrients which were measured only in summer, the highest $NO_2 + NO_3$ was measured on average in region 2, followed by regions 3 and 2. The concentration of $NO_2 + NO_3$ varied between 2.17 mg/l and 2.69 mg/l in surface waters and between 1.64 mg/l and 1.87 mg/l in near-bottom waters. Concentrations of PO_4 and SiO_2 of the sea surface waters increased slightly and strictly from the west to the east, respectively in contrast to the regional concentration of NH_4. Near-bottom PO_4 was at its maxima in region 2 (9.61 mg/l), followed by region 3, and was at its minima in region 1 (6.34 mg/l). The concentration of near-bottom SiO_2 varied between 27.2 mg/l in region 2 (easternmost) and 37.4 mg/l in region 3 (westernmost). NH4 was measured to be maximum in region 3 and minimum in region 1, followed by region.

The following measurements were performed only in summer. Sea surface and near-bottom total suspended matter were weighed to be maximum (0.085 mg/l) and minimum (0.045 mg/l) in region 3, respectively, and to be similar values (0.05 mg/l) in region 2, respectively. Sea surface chlorophyll-*a* was the lowest in region 2 (0.53 µg/l), which was doubled in region 1 (1.12 µg/l).

Of the optical variables, Secchi depth tended to increase from the east to the west, particularly in summer as partially contrasted to the %PAR. Secchi depth varied between 3 m and 29.5 m in winter and 4 m and 32 m in summer. The maximum PAR which arrived at the bottom was estimated to be 30%, and the PAR was around 3.07% (region 2) and 3.95% (region 3) on average. Average depth where the minimum end of the exponential decreasing curve vs depth occurred was at its maxima in region 1 (KD: 10.69 ± 3.20 m), followed by region 3 (8.81 ± 3.36 m), and at its minima in region 2 (6.88 ± 3.77 m).

A multivariate analysis, PCA, revealed a summary of the spatiotemporal characteristics of the environmental measurements (Online Resource 1). The basic descriptive physical oceanography of the study area was differentiated by the regions in season, but it was more pronounced in summer. Overall, regions 1 and 2 were more saline and temperate than region 3. Like the dissolved oxygen, water temperature (surface and near-bottom) explained this difference with a variance of 45.8% in winter on PCA1, and bottom depth and sea surface pH explained that on PCA2 (Online Resource 1, 2). These variables explained the apparently regional difference in summer on PCA1, but open water was more clear than the shallower waters as a function of Secchi disk depth on PCA2 (Online Resource 1, 2). However, water salinity was not effective in explaining the difference in both winter and summer (Online Resource 1, 2).

The chemistry with the basic parameters was measured only in summer and was dominantly characterized with nutrients from near-bottom waters on PCA1 and nutrients from sea surface water on PCA2, besides sea surface chl-*a* and total suspended matter (Online Resource 1). There was no regional difference, but there was a depthwise difference (open and coastal waters). However, these differences were explained by a low percent variance of 16.7% on PCA1 and 14.8% on PCA2 (Online Resource 1, 2).

Biometrics of Posidonia oceanica

The surface area covered by *P. oceanica* was estimated to be about 321.5 km^2 of a total survey area of 1106.2 km^2 along the coast of the study area. About two-fifths of the study area (Datça to Taşucu, Fig. 2) was devoid of *P. oceanica* along the Turkish Mediterranean coast (Fig. 2). *Posidonia oceanica* was last found at Datça in the west and at Sipahili Cove in the east. *P. oceanica* was no longer found along the further eastern coast of the Turkish coast (Fig. 1a). The Mediterranean meadow inhabited a variety of bottom types along the Turkish Mediterranean coast; *matte* and mud in Mersin Bay, rock in Antalya Gulf, and sand and mud in Muğla Bay and the west of Antalya Bay (Figs. 1b, 2). However, hard substrates (*matte* and rock) restricted the vertical distribution of the meadow, i.e., 9.5-to-24.5 m on *matte* and 0.5-to-28.5 m on rock, depending on the occurrence of hard substrates. The maximum distributional extension was determined to be 43.5 m in Muğla Bay (Göçek, Fethiye) (Figs. 1, 2). However, the depthwise extension of the meadows was not significantly different among the bottom types (ANOVA, $p = 0.753$) in winter and ($p = 0.749$) in summer at $p < 0.05$. Overall, the depth limits were shallower in the hard bottoms than in the soft bottoms.

Spatiotemporal distribution

The biometrics of *P. oceanica* consisted of the density (biomass: BL, leaf area index: LAI, shoot density: TS) and morphometric (inter-nodal distance: SD, number of leaves per shoot: LNo, vertical rhizome + sheath length: SL, leaf length: LL, and width: LW) parameters for their distribution in space (bottom depth and bays) and time (winter and summer).

The density distribution

Leaf biomass (BL) varied between 12.7 g/m^2 and 2901 g/m^2 a year. Maximum biomass was estimated to be 654 g/m^2 in winter (Fig. 3a) and was measured to be about four-fold higher in summer than in winter (Fig. 3b). The mean biomass was calculated to be 257.9 ± 169.6 g/m^2 (X ± SD) in winter and 573.9 ± 423.5 g/m^2 in summer. The highest biomass was measured on hard substrates in winter and summer (Fig. 3); 354 ± 46 g/m^2 on rock and 402 ± 140 g/m^2 on *matte* in winter and 804 ± 74 g/m^2 and 906 ± 150 g/m^2, respectively, in summer. These values were about 2-fold lower on soft substrates than on hard substrates in both seasons. Bottom types differentiated the biomass significantly in both seasons at $p < 0.05$ (ANOVA, $p = 0.045$, 0.00014, respectively), but the bottom depth induced a significant difference in

the biomass only in summer ($p = 0.035$). Muğla Bay inhabited the lowest biomasses as compared to Antalya and Mersin bays in winter and summer (Fig. 3).

The minimum shoot number (TS) was 63 shoots/m^2 in winter (Fig. 4a) and 19 shoots/m^2 in summer (Fig. 4b), and the maximum number was 844 and 1094 shoots/m^2, respectively (Fig. 4). The average shoot density was estimated to be similar in winter (360 ± 198 shoots/m^2) and summer (316 ± 189 shoots/m^2). Similar to the biomass distribution, the shoot density was significantly different among the bottom types (436–517 shoots/m^2 on hard substrates) and (223–309 shoots/m^2on soft bottoms) on average in both seasons and was different among the bottom depths only in summer at $p < 0.05$ (Table 1). The shoot density was slightly higher in winter than in summer on both substrates (Fig. 4).

There was no significant difference in the shoot density between seasons (Fig. 5b), but the shoot density was significantly different among the regions (bays, Fig. 5a) and bottom depths (Fig. 5c) at $p < 0.05$ (Table 1). The shoot density was significantly higher in Antalya and Mersin bays than in Muğla Bay (Fig. 5a) and decreased gradually with the bottom depths (Fig. 5c).

LAI (m^2/m^2) varied between 0.08 estimated in winter and 15.26 in summer; the average LAI was 1.48 ± 0.95 in winter and 3.11 ± 2.20 in summer (Fig. 5b). The LAI was significantly higher in summer than in winter, and in Mersin than Antalya and Muğla bays (Fig. 5a, b). Three-way ANOVA showed that there was a significant difference in LAI only by regions (bays) and seasons since the LAI differed significantly by depth only in summer at $p < 0.05$ (one-way ANOVA). Therefore, only the interaction of region x depth differentiated the LAI significantly (three-way ANOVA). The LAI was less than 2 on soft substrates and greater than 2 on hard substrates in winter, and these values were doubled in summer, respectively. The LAI decreased gradually from 4 at 5 m to 1 at 35 m by depth (Fig. 5c).

Table 1
Results of a 3-way ANOVA for differences in the shoot density (TS) and LAI among the regions, seasons, and bottom depths. The bold p values were significantly different at $p < 0.05$.

Factors	TS	LAI
Region	**0.0001**	**0.0039**
Season	0.0927	**$1.2*10^{-5}$**
Depth	**0.0204**	0.1557
Region x Season	0.2470	0.0734
Region x Depth	0.9242	**0.0307**
Season x Depth	0.2471	0.2301
Region x Season x Depth		No test

The morphometrical distribution

Vertical rhizome + sheath (SL) was significantly different among regions, seasons, and bottom depths at $p < 0.05$ (Table 2, Fig. 6). The SL increased from Antalya (5.7 cm) to Mersin (6.05 cm), followed by Muğla (6.1 cm on average), and decreased from winter (6.1 ± 1.5 cm) to summer (5.8 ± 1.4 cm) (Fig. 6a, b). Bottom types significantly differed the SL in both winter and summer. The highest average SL was measured on *matte*, and the lowest SL was recorded on rock. The soft bottoms seemed to have longer SL (5.7–6.4 cm on average) in both winter and summer as compared to overall hard substrates. In the depthwise distribution, the shortest SL was found at 5 m, and the longest SL occurred at 20, 30 m, and 35 m (~ 6.5 cm). The SL at 5 m increased 1 cm more at 10 m and then decreased from 10 m to 25 m excluding the exceptional depths (Fig. 6c).

One of the indications of the density parameters, inter-nodal (shoot) (SD) distance, was overall significantly different by space (bays and bottom depths) and time (seasons) (three-way ANOVA) (Table 2). However, the distance was not significantly different among the bottom depths in winter as a one-way ANOVA was applied to the distance data. The distance varied between 2 cm and 11 cm in both seasons, but the average distance was 5.2 ± 1.7 cm in winter and 5.0 ± 1.5 cm in summer (Fig. 6b). Regarding the bottom types, inter-nodal distance ranged from 5.2 ± 0.19 cm to 6.4 ± 0.74 cm on hard substrates and from 5.9 ± 0.26 cm to 5.9 ± 0.24 cm on soft substrates in winter, and from 5.2 ± 0.11 cm to 5.6 ± 0.22 cm and 4.5 ± 0.15 cm to 5.1 ± 0.15 cm, respectively, in summer. The distance was significantly higher in Mersin Bay than Muğla Bay (Fig. 6a), in winter than summer (Fig. 6b), and at bottom depths of 15 m and 30 m than 25 m (Fig. 6c).

Table 2
Results of a 3-way ANOVA for differences in the morphometrical variables; vertical rhizome + sheath (SL), leaf length (LL), leaf width (LW), inter-nodal (shoot) distance (SD), and number of leaves per shoot (LNo) of *P. oceanica* among the regions, seasons, and bottom depths. The bold p values were significantly different at $p < 0.05$.

Factors	SL	LL	LW	SD	LNo
Region	**$6.2*10^{-8}$**	**$1.0*10^{-244}$**	0.0824	**0.0462**	0.5745
Season	**$2.1*10^{-29}$**	**0**	0.3801	**$2.6*10^{-5}$**	**$6.5*10^{-89}$**
Depth	**$3.5*10^{-32}$**	**$2.2*10^{-105}$**	0.2609	**0.0378**	**$2.9*10^{-31}$**
Region x Season	**0.0118**	**$4.9*10^{-63}$**	0.5397	0.0758	**$2.3*10^{-6}$**
Region x Depth	**$1.6*10^{-30}$**	**0**	**0.0051**	0.1270	**$1.5*10^{-9}$**
Season x Depth	**$1.3*10^{-5}$**	**$4.7*10^{-16}$**	0.6056	0.0849	**$6.9*10^{-6}$**
Region x Season x Depth		No test			

The maximum leaf length (LL) was recorded as 188 cm on sandy bottoms in summer, followed by ~ 120 cm on rocky bottoms in both winter and summer. The LL was significantly different among the regions, seasons, bottom types, and bottom depths at $p < 0.05$ (Table 2, Figs. 6, 7). The LL was significantly shorter in Antalya than on the Mersin and Muğla coasts (Figs. 6a, 7), shorter in winter than summer (Figs. 6b, 7), and trended to decrease by bottom depths at $p < 0.05$ (Fig. 6c). However, the LL had the longest leaves at 25 m, followed by 10 m and 35 m. Bottom types indicated different differences in LL as compared to the other morphometrics and density variables. In winter, the average LL was similar on rock and mud and on sand and *matte*, whereas the LL varied between 25.8 cm and 26.7 cm on rock, sand, and mud, but the highest LL occurred on *matte* (30.5 cm) in summer (Figs. 6b, 7). The LL was significantly higher in summer than in winter (Figs. 6b, 7), the average LL varied between 7.6 cm and 24.5 cm (13.2 ± 3.3 cm on the grand average) in winter and between 11.3 cm and 49.5 cm (25.4 ± 6.6 cm) in summer (Figs. 6b, 7).

The leaf width (LW) was significantly different among the bottom types in summer, while there was no significant difference in the LW among the bottom types in winter. The LW tended to increase from the hard substratum to the soft substratum, and this trend was significantly more pronounced in summer. The widest leaves were measured on mud, and the narrowest leaves were on rock. The LW was not significantly different by seasons, regions, or bottom depths (three-way ANOVA, Table 2; Fig. 6). Seasonal average LW varied between 0.7 cm and 1.0 cm in winter (0.8 ± 0.1 cm on the grand average) and between 0.6 cm and 1.2 cm in summer (0.8 ± 0.1 cm) (Fig. 6b)

Average number of leaves per shoot (LNo) remained at 4.1–4.2 leaves/shoots on four bottom types in winter with an average value of 4.2 ± 0.6 leaves/shoots, slightly increased to 4.6–5.1 leaves/shoots on hard substrates, and to 4.7–4.8 leaves/shoots on soft bottoms by the summer with 4.9 ± 0.5 leaves/shoots. However, there was no significant difference in LNo among the regions (Fig. 6a, Table 2).

The LNo was significantly differentiated by seasons (Fig. 6a) and bottom depths at $p < 0.05$, increased from 5 m to 15 m of the bottom depths, and then trended to decrease (Fig. 6c, Table 2). However, the LNo was significantly and exceptionally higher at 25 m and 35 m than at the other depths (Fig. 6c).

Ecological distribution

Of a series of multivariate analyses to determine ecological properties of *P. oceanica* biometrics, the PCA analysis showed that the biometrics were dispersed depending mainly on season on PCA1 and bottom type on PCA2 (Online Resource 3). Seasonal differences were contributed by biomass, and LAI positively correlated with PCA1 scores, whereas bottom type based-differences positively correlated with shoot density, and leaf width and rhizome + sheath length negatively correlated with PCA2 scores (Online Resource 3, 4). Leaf length differed PCA scores on both PCA axes. Both axes were explained with a cumulative variance of 57.4% (38.5% on PCA1) (Online Resource 4). An expected cumulative variance of 95% for a better explanation was reached at PCA5.

Overall, the biometrical variables of *P. oceanica* were clustered into two groups: the rhizome + sheath-related biometrics and the leaf-related biometrics (Fig. 8). The leaf-related biometrics were grouped into two clusters composed of individual morphometrical and density variables (Fig. 8).

The biometrics were significantly different among the regions, seasons, bottom types, and bottom depths at $p < 0.05$ (Four-way PerMANOVA) (Online Resource 5). Only the interaction of region x bottom type x depth differed the biometrics significantly at $p < 0.05$ (Monte Carlo test) (Online Resource 5).

The biometrics of *P. oceanica* were clustered primarily by season (Fig. 9b, e), followed secondarily by bottom type (Fig. 9a, e). The biometrics on only rock were distinguished as occurring in both winter and summer. The effect of the bottom types was more pronounced in summer than winter (Fig. 9c, e). In summer, the bottom types were shifted from soft bottoms through a mixture of soft-hard bottoms to hard bottoms in the order of bottom hardness (Fig. 9c, e). The bottom depth affected the biometrical distribution slightly, whereas the biometrics at bottom depths of 15 m and 20 m were scattered on the nMDS plot in both winter and summer (Fig. 9a, e). Regional biometrics occurred (Fig. 9d, e).

Seasonal discrimination occurred in the biometrics of *P. oceanica* in relation to the physical parameters of the sea surface and near-bottom waters. This discrimination was significantly validated by the Monte Carlo test (F: 49.16, p: 0.0020 on CCA1, and F: 6.764, p: 0.0020 on all CCA axes). CCA1 compounded the seasons (Fig. 10a), and CCA2 compounded regions (bays) (Fig. 10b). This regional difference was more pronounced in summer and in the order from the east to west of the study area. The biometrics of *P. oceanica* contrasted the density biometrics against the morphometrics (Fig. 10a, b). On the CCA1, the water temperature was positively and negatively correlated with the density biometrics and most of the morphometrical parameters, respectively, and was positively correlated with sea surface pH, followed by near-bottom salinity, which was negatively correlated with the region on CCA2 (Online Resource 6). Furthermore, Secchi depth and bottom depth were correlated with the regions on CCA2 (Online Resource

6, Fig. 10a, b). Seasonal and regional discriminations were explained with a high cumulative variance of 71.1% and 95.9% of the total variance, respectively (Online Resource 6).

Individual seasonal CCA showed that regional trends occurred in both winter and summer, but this was more pronounced in summer (Fig. 10). The biometrical distribution of *P. oceanica* was similar in winter and summer to the contrasts that occurred in the annual CCA. In winter, the regional difference was correlated with water temperature, followed by water dissolved oxygen, was explained with a percent variance of 76.3%, and was significantly validated by the Monte Carlo test (F: 16.031, p: 0.0140). Near-bottom dissolved oxygen was positively correlated with the CCA2, which was explained by a cumulative variance of 91.0% (Online Resource 6, Fig. 10c, d, and F: 1.766, p: 0.0100). In summer, most of the physical parameters of the water explained the biometrical contrast only on CCA1 with a variance of 86.4% (Fig. 10e, f, Online Resource 6). Of the environmental parameters, Secchi depth and bottom depth were correlated with the biometrics, and water temperatures (sea surface and near-bottom) were substantially correlated with the biometric contrast on CCA1 (Fig. 10e, f, Online Resource 6). This was validated by the Monte Carlo test (F: 29.096, p: 0.0020).

In summer when the optical and chemical environmental parameters were added to the measurements of the physical parameters and the discrimination was more pronounced, the Secchi depth and bottom depth discriminated the biometrical contrasts, and the NO_3 concentration of surface and near-bottom waters affected the biometrical distribution on CCA1 (Fig. 11, Online Resource 6). This biometrics-environment relationship was explained with a percent variance of 82.6% and was significantly validated by the Monte Carlo test (F: 39.299, p: 0.0040). On CCA2, the sea surface temperature and PO_4 concentration were slightly correlated with the biometrics whose biomass, LAI, LL, LNo, and LW were positively correlated on CCA2 (Figs. 10e, f, 11). The density and morphometrical variables were negatively and positively correlated with CCA1, respectively, as similar contrasts occurred in winter and summer to the physical parameters (Figs. 10e, f, 11).

However, the species (biometrics) data were overall explained with lower variances in winter, summer, and the year than the species-environment relationship (Online Resource 6).

The biomass, LAI, LNo, and LL were positively correlated with most of the physical parameters and were negatively correlated with water salinity (sea surface and near-bottom) in the year (Table 3). However, LW and SD were correlated with none of the physical parameters at $p < 0.05$. Near-bottom salinity, Secchi, and bottom depth were positively and negatively correlated with the TS, respectively. The SL was negatively correlated with the water temperatures at $p < 0.05$ in the year (Table 3).

In summer, the NO_3 concentration of the water was negatively correlated with the density biometrics of *P. oceanica* at $p < 0.05$ (Table 3). The LNo was negatively correlated with the nutrients of near-bottom waters but was not correlated with the SiO_2 of the water (Table 3). However, none of the morphometrical biometrics was correlated with the chemical and optical variables of the water. Water temperature was

negatively correlated with SL, whereas the LL was negatively correlated withthe sea surface temperature at $p < 0.05$ (Table 3).

Table 3

Coefficients of Spearman correlation between the biometrics and environmental parameters in winter and summer (see Online Resource 4 for the abbreviations of the biometrics and see Online Resource 2 for the abbreviations of the environmental parameters). Bold coefficient was significantly correlated at $p < 0.05$ ($n = 48$ in winter, and $n = 100$ in summer

Winter + summer	SL	LL	LW	SD	TS	BLAI	LAI	LNo
SS	0.077	**-0.361**	0.018	0.092	0.105	**-0.187**	-0.158	**-0.311**
ST	**-0.224**	**0.536**	0.023	0.008	0.071	**0.497**	**0.471**	**0.491**
SpH	-0.073	**0.301**	-0.035	0.042	-0.006	**0.286**	**0.258**	**0.302**
NS	0.043	**-0.566**	-0.155	0.110	**0.226**	**-0.239**	**-0.212**	**-0.449**
NT	**-0.195**	**0.580**	-0.049	0.019	0.141	**0.559**	**0.532**	**0.421**
NpH	-0.013	**0.299**	-0.032	0.079	-0.050	**0.213**	**0.191**	**0.354**
Sec	0.015	**0.295**	0.071	-0.052	**-0.189**	0.058	0.047	**0.357**
De	0.131	0.064	0.128	0.116	**-0.308**	**-0.205**	**-0.217**	0.161
Summer								
SS	0.162	0.069	0.177	0.113	-0.068	-0.009	0.011	-0.074
ST	**-0.264**	**-0.216**	-0.038	0.120	**0.234**	0.172	0.166	**0.210**
SpH	-0.051	-0.109	-0.031	0.183	0.166	0.156	0.168	0.154
NS	-0.088	0.012	-0.188	0.146	0.164	0.150	0.135	-0.189
NT	**-0.206**	-0.069	-0.192	0.151	**0.374**	**0.343**	**0.333**	0.028
NpH	0.024	-0.041	-0.050	0.191	0.067	0.098	0.106	**0.305**
Sec	0.025	-0.093	0.060	0.003	**-0.420**	**-0.398**	**-0.402**	**0.203**
De	**0.215**	0.066	0.112	0.127	**-0.445**	**-0.322**	**-0.329**	**0.258**
Ssi	0.019	0.011	0.136	0.010	-0.055	0.009	0.023	0.146
SNO_3	0.000	-0.052	0.172	-0.085	**-0.403**	**-0.385**	**-0.367**	0.110
SPO_4	-0.016	-0.141	-0.020	0.065	-0.008	-0.100	-0.101	0.074
SNO_2	-0.122	-0.045	0.087	0.039	0.010	-0.020	0.003	0.042
SNH_4	0.071	-0.111	-0.130	0.110	-0.102	-0.088	-0.111	0.131
$SNO_2 + NO_3$	-0.126	-0.069	0.093	0.024	-0.045	-0.076	-0.054	0.080
Nsi	-0.050	-0.012	0.029	-0.130	-0.054	-0.044	-0.030	0.000

Winter + summer	SL	LL	LW	SD	TS	BLAI	LAI	LNo
NNO_3	0.098	0.016	0.057	-0.112	**-0.277**	**-0.285**	**-0.274**	**-0.244**
NPO_4	0.009	-0.019	0.003	-0.065	-0.130	-0.161	-0.141	**-0.258**
NNO_2	0.041	0.012	0.066	-0.164	-0.045	-0.029	-0.008	**-0.215**
NNH_4	0.095	-0.011	-0.023	-0.156	-0.160	-0.112	-0.107	0.114
$NNO_2 + NO_3$	0.094	0.030	0.093	-0.132	-0.076	-0.054	-0.030	**-0.251**
STSM	0.075	-0.095	-0.128	0.027	-0.088	-0.180	-0.183	-0.070
NTSM	0.031	-0.070	-0.194	0.136	0.044	-0.045	-0.075	-0.108
Chl-*a*	-0.159	-0.199	-0.133	-0.104	**0.205**	0.134	0.127	0.204
PAR	0.073	0.092	-0.015	0.007	0.144	0.186	0.185	-0.019

Discussion

The study area was ultra-poor in nutrients and assigned as the most ultra-oligotrophic waters in the Mediterranean Sea (Sisma-Ventura et al. 2017). Mutlu et al. (2022a) showed that seasonal cyclic biometrics were observed in the middle part of the Antalya Gulf and occurred in good concordance with some of the different *Posidonia* indicators, i.e., shoot density at certain bottom depths (UNEP/MAPRAC/SPA 2015), determined for the ecological status by Fernández-Torquemada et al. (2020).

Posidonia oceanica was found to be in the third-fifth of the survey coasts and inhabited four main bottom types: rock, *matte*, sand, and mud, whereas around one-third of a small area (Antalya Gulf) comprising a single bottom type of rock of the Levant Turkish coast was inhabited by the meadow (Mutlu et al. 2022a). *Posidonia oceanica* was spatially found in depths varying between 0.5 m (only rock, Antalya Gulf) and 43.5 m (only soft bottom, Muğla Bay). The vertical extension of the meadow depended on the extension of the occurrence of rock and *matte* on the hard substrates. Prior to hydrographical parameters, substrate type was categorized as the main factor for the meadow to re-colonize on the ground via vegetative fragments by Alagna et al. (2019) owing to the development of specific seedlings and root hair to trap for each substrate type (Balestri et al. 2015; Pereda-Briones et al. 2018; Tomasello et al. 2018). Therefore, the lower depth limit of the meadow was extended down to 29.5 m on rock and down to 24.5 m on *matte*. Furthermore, the upper limit of their extension began at 0.5 m on rock (Antalya Bay) and 9.5 m on *matte* (Mersin Bay). The limits were determined, regardless of bottom types, to vary between 0.5-1 m and 33–43 m in the western Mediterranean Sea (Colantoni et al. 1982; Marbà et al. 2002).

The present study area has a very large surface and has been exposed to different atmospheric, hydrographic, and water movement (especially water velocity) conditions, which have all affected the spatiotemporal seedling and bathymetrical limits for expansion of the meadow. For instance, *Zostera marina* was favored at ground level with a water velocity of 14 $cm.s^{-1}$, *P. oceanica* with 20 $cm.s^{-1}$, and *Cymodocea nodosa* with 21 $cm.s^{-1}$ on sand (Pereda-Briones et al. 2018), besides the vice versa effect of the meadow reducing the velocity, erosion of the sediment, and dispersion of biogenic materials and carbonate particles (De Falco et al. 2003, 2008; Pereda-Briones et al. 2018).

Spatiotemporal distribution

The biometrics of the meadow changed with different environmental variables in the Mediterranean Sea; e.g., shoot density was differentiated majorly by geographical coordinates and seafloor depths, and subsequently by wind, bottom type, and gradient (Catucci and Scardi 2020; Gnisci et al. 2020).

The average biomass was doubled in summer compared to winter. The highest biomass was estimated on *matte*, followed by rock, and the average biomass was two times less on soft bottoms than on hard substrates. The biomass decreased gradually with the bottom depths. Regional distribution was relatively characterized by high biomass in Antalya and Mersin and low biomass in Muğla Bay, whose majority of sampling stations were influenced by Aegean waters.

According to seagrass shoot density considered for the ecological status of the Mediterranean marine environment (UNEP/MAP-RAC/SPA 2015; Gobert et al. 2009), the present study's coasts comprising Antalya Gulf were a more pristine environment in 2019 compared to a previous study in Antalya Gulf in 2011–2012 (Mutlu et al. 2022a) since the number of shoots per square area did not change between winter and summer (360 ± 198 shoots/m^2 and 316 ± 189 shoots/m^2, respectively) and was above the threshold of the shoot density determined by UNEP/MAP-RAC/SPA (2015). Therefore, a calcareous alga, *Hydrolithon boreale*, abundantly appeared in 2019 (Mutlu et al. 2023). The shoot density was differentiated by the bottom depths, bottom types, and regions; the shoot density was doubled on hard substrates as compared to that on soft bottoms. Therefore, the shoot density was higher in Antalya and Mersin bays than Muğla Bay. The shoot density decreased slightly with bottom depths, as Mutlu et al. (2022a) determined a logarithmic reduction of the number of shoots by bottom depth.

As a function of leaf length and width and the number of leaves and shoots per area (m^2), the LAI distribution was very similar to the biomass distribution by bottom depth, bottom type, season, and region. LAI estimated in the present study was low on rock as compared to sand and *matte*, similar to the findings denoted by Sghaier et al. (2006) and Maida et al. (2013). Bottom coverage by the meadow changed the biometrical variation (Gnisci et al. 2020) and was different on the substrate types: coverage > 75% on rock and 50–75% on sand, fine sand, and eroded *matte* (Sgorbini et al. 2002). Contrasted to the present study and a study by Mutlu et al. (2022a), there were no significant monthly differences in LAI owing to no seasonal difference in the shoot density (Bay 1984; Wittmann 1984; Guidetti et al. 2002). Nevertheless, the LAI were differentiated by seasons, whereas the shoot density did not differ in time in a

year in a good ecological environment (Mutlu et al. 2022a) but decreased by bottom depth (Gobert et al. 2003). Bottom types differed the LAI, being lower on rock by a factor of 42% than sand by 23% and *matte* by 32% (Giovannetti et al. 2008; Maida et al. 2013), since the rock was favorable for better anchorage by the root hairs and had comparatively low nutrients (Touchette and Burkholder 2000).

Vertical rhizome + sheath-related biometrics, the SL and SD, were differentiated by season, region, bottom types, and depth. They were characterized by high values in winter, on *matte*, in Muğla and Mersin, and at greater depths. The vertical rhizome was at its minima in length in September and at its maxima in July (a difference of 1.2 cm) in Levant Sea (Mutlu et al. 2022a) coinciding with a period of occurrence of new and mortality of aged rhizome, respectively (Piazzi et al. 1999). Earlier mortality of the rhizomes occurred in Antalya Gulf, which had a unique substrate, rock (Mutlu et al. 2022a), since a dynamical strategy of the rhizome developed a low limit in length with a low maximum age due to shrinkage on rock compared to other bottom types (Maida et al. 2013; Tomasello et al. 2016). A further reason for the mortality was the water salinity reaching a value over 39 PSU (Fernandez-Torquemada and Sanchez-Lizaso 2005). This salinity occurred in late summer-early autumn in the study area, particularly in the eastern half of the study area (Mutlu et al. 2022a). Sheath length increased with the occurrence of high water nitrogen content occurring in April/May (Mutlu et al. 2022a). Nevertheless, higher nutrients than the optimum concentration negatively affected growth in elongation (Leoni et al. 2006).

Of the leaf-related biometrics, the LL was different among the regions, seasons, bottom types, and bottom depth. The LL was significantly shorter in Antalya than on the Mersin and Muğla coasts, in winter than in summer. The LL decreased spatially by bottom depths, increased temporarily from winter (15 ^{o}C) to spring (21 ^{o}C) at lower salinity than 39 PSU, decreased little by July (27 ^{o}C and salinity, 39 PSU), and decreased further by August (28 ^{o}C)-September (29 ^{o}C) at salinities close to ~ 40 PSU in Antalya Gulf, Turkey (Mutlu et al. 2022a). High mortality followed by high salinities (Fernandez-Torquemada and Sanchez-Lizaso 2005), the length decrement continued until December (18 ^{o}C) (Mutlu et al. 2022a), as occurred in the other studies (Vasapollo and Gambi 2012). Overall, length growth was different in time with the following elements: leaf type, bottom type, and depth, and started with the occurrence of an increase in the water temperature (Caye and Rossignol 1983; Bay 1984; Gambi et al. 1989; Zupo et al. 1997; Via et al. 1998; Guidetti et al. 2002; Sghaier et al. 2006; Maida et al. 2013). Herbivorous turtle and fish changed the biometrics of the meadow (Lal et al. 2010; Steele et al. 2014).

The LW was not different by seasons, regions, or bottom depths as Sghaier et al. (2006) estimated a similar spatial gradient off Tunisia Bay (1984). The LW tended to increase from the hard substratum to the soft substratum, and this trend was significantly more pronounced in summer. However, the leaf width was not significantly differentiated by the substrate types (Maida et al. 2013). On rocky substrate, leaf width was at its maxima in August (39.5–39.9 PSU), followed by a decrease from September to November/December (~ 40 PSU) in Antalya Gulf (Mutlu et al. 2022a), as suggested by Marín-Guirao et al. (2013), with exposure to higher salinity (43 PSU) for the quarter year inducing a reduction of 22% in leaf width.

There was no significant difference in LNo among the regions, whereas the LNo was differentiated by seasons and bottom depths. The LNo was higher in summer than winter, on hard bottoms than soft bottoms, in shallower waters than 20 m, and at depths greater than 20 m. Pergent and Pergent-Martini (1990) suggested the existence of a balance in LNo occurring between a period of autumn deriving leaf foliage and late summer and autumn deriving high leaf induction. However, the LNo was not found to be significantly different by season in the Adriatic Sea (Guidetti et al. 2002). On the Sicilian coast (Giulia et al. 2007), similar winter and summer numbers of leaves per shoot were estimated to the present study depending on seasonality of the salinity. There were differences in LNo between different substrates, with LNo being two times higher on soft bottom (sand) than hard bottom (rock) in the field study (Sghaier et al. 2013) and in the lab study (Alagna et al. 2015).

Ecological distribution

During the present study, two different factors were considered to differ the biometrics-environment relationship of the meadow: bottom-related and water-related parameters. Besides the bottom types and substratum (Pereda-Briones et al. 2018) for the meadow to form a specific root structure (Balestri et al. 2015; Tomasello et al. 2018) and to persist on a certain substrate (Montefalcone et al. 2016; Pereda-Briones et al. 2018), in contrast to findings established by Balestri and Lardicci (2008), hydro-dynamical elements differed expansion of the meadow on bottom (Vacchi et al. 2012; Mutlu et al. 2022a) as the meadow was highly colonized in hard bottoms prevailed by more active hydrodynamic surf-zone (Montefalcone et al. 2016). This explained the existence of *depauperate* coasts of the meadow along the coasts of Dalaman, Finike, Patara, İztuzu, the western coast of Antalya Gulf, and Taşucu Bay (Fig. 1b), which were exposed to high-surf zones and were devoid of hard bottoms. As ahuman-sourced effect (Montefalcone et al. 2019), the coasts of Antalya and Muğla have been actively used by tourists and pleasure craft with their litter and anchorage during the summers (Mutlu et al. 2020b).

Ballesta et al. (2000) related the dispersal type of the meadows to the bottom coverage and types: continuous type occurred with coverage > 50%, and mosaic type with coverage < 50% on hard substrates (rock and *matte*). Using the acoustical records, we observed different dispersal types depending on bottom types and depths: continuous on soft bottoms, reticulate and patchy type on hard bottoms, reticulate and patchy in shallower waters (< 10 m) and deeper waters (> 20 m), and continuous distribution in the intermediate waters (10–20 m). Borga et al. (2005) observed patches on rocky and/or sandy substratum in the shallower waters (2–4 m), reticulate beds in 5–10 m on bare sand, and reticulate to continuous beds in 11–13 m, and Borg et al. (2009) observed continuous beds extending down to 25–30 m and reticulate or patchy beds in deeper waters (> 25 m). Furthermore, total organic carbon (TOC) negatively affected the temporal and seasonal dynamics of the rhizome-related biometrics (Mutlu et al., 2022a).

The biometrical variables of *P. oceanica* were clustered into two groups: the rhizome + sheath-related biometrics and leaf-related biometrics. The leaf-related biometrics were grouped into two clusters composed of individual morphometrical and density variables. The biometrics of *P. oceanica* contrasted the density biometrics against the morphometrics. The biometrics of *P. oceanica* were clustered primarily

by the season (temperature and salinity), followed secondarily by the bottom type (region). The bottom depth affected the biometrical distribution slightly, whereas the biometrics at bottom depths 15 m and 20 m were highly variable in both winter and summer. Pirc (1986) and Mutlu et al. (2022a) determined a depth of 15 m as an exceptional zone characterized by lower photosynthetic activity than that at 5 m and 30 m because of solar irradiance compared to higher and lower than an optimum PAR of 10–32% (Mutlu et al. 2022a).

The regional difference was more pronounced in summer ordering sampling stations from the east to west of the study area. In winter, the regional difference was derived from water temperature, followed by water dissolved oxygen. In summer, Secchi depth and bottom depth were related with the biometrics, and water temperatures (sea surface and near-bottom) induced the biometrical contrast. Mutlu et al. (2022a) outlined the limiting thresholds of the environment such as water temperature up to 28.8–29.3 ^{o}C, corresponded with salinity up to > 39 PSU and optical PAR between < 10% and > 32% for *P. oceanica* to survive in space of a pristine gulf, Antalya, Levant Sea. Furthermore, the NO_3 concentration of surface and near-bottom waters affected the biometrics. The second component in summer was characterized as follows: the sea surface temperature and PO_4 concentration accelerated regional and depthwise differences in the biometrics of the BL, LAI, LL, LNo, and LW. In summer, the correlation analysis showed that the NO_3 concentration of the water was negatively correlated with the density biometrics of *P. oceanica*. The LNo was negatively correlated with the nutrients of near-bottom waters but was not correlated with the SiO_2 of the water. However, none of the leaf-related morphometrical biometrics was correlated with the chemical and optical variables of the water. The water temperature was negatively correlated with the SL, whereas the LL was negatively correlated with the sea surface temperature. Mutlu et al. (2022a) showed that nitrogen concentration in sea surface water was negatively correlated with leaf width and positively correlated with LNo in a pristine gulf, Antalya. Temporally, poor nutrient occurred in autumn, reducing the growth of the meadow, and limiting nutrient for growth was more pronounced in late spring and summer (Alcoverro et al. 1997). The inter-nodal distance was affected by optical and some physicochemical parameters of the waters at the surface and near-bottom (mostly temperature, salinity, PO_4, and $NO_2 + NO_3$) (Mutlu et al. 2022a). There was a temporal utilization of the nutrients by the meadow; nitrogen-based nutrient was utilized mostly in winter and early spring by the roots (Lepoint et al. 2002) due to its high concentrations in the water (Mutlu et al., 2022a). NH_4 played a crucial role in the seasonal growth of the meadow and was preferentially six-fold higher than NO_3 utilized by the roots (Lepoint et al. 2002).

Conclusion

Winter and summer surveys (before August when the leaves started to be sheared, Mutlu et al. 2022a) were still effective in observing environment-related biometrical dynamics of *P. oceanica* as compared to the seasonal studies. About one-third of the surface area of the Turkish Mediterranean coast was covered by the meadow. The shoot density did not change between winter and summer and remained above the reference shoot density to show good status for the marine environment. Other biometrical density

variables, leaf biomass and LAI, were doubled in summer compared to winter. There were regional differences in the biometrics of the meadow, and this was also attributed to the occurrence of different bottom types at each region. The bottom of Muğla Bay was composed of sand and mud, that of Antalya Bay was composed of rock, and that of Mersin Bay was composed of *matte* and mud. The morphometrical variables responded differently to the seasons and regions, but the morphometrics tended to decrease with bottom depth. A bottom depth of around 15 m was distinguished by high variance in the biometrics. Interactions of the biometrics were differently derived in a year; rhizome-related biometrics was differentiated from leaf-related biometrics, consisting separately of the density and morphometrical variables. Throughout the entire Turkish Mediterranean coast, the meadow was first affected by season (salinity and temperature), region owing to the different bottom types, and then bottom depth. *Posidonia oceanica* alone was partly offered to classify the benthic zonation since hard substrates dictated the depthwise distribution of the meadow depending on the occurrence of each hard bottom type. In winter, the meadow interacted with the temperature and oxygen of the water in the large-scale survey area. Nitrogen based-nutrients were related to the seasonal growth dynamics of the meadow, but silicate was not utilized by the meadow. The optical parameters (Sechhi depth and percent PAR) were not correlated with the biometrics since a certain percentage of light optimized the biometrics, as suggested by Mutlu et al. (2022a) (10% < PAR < 30%). Overall, the density variables were contrasted to the morphometrical variables during the growth dynamics of the meadow. The biometrical dynamics of pristine *P. oceanica* were considered an annual mirror of coastal environmental studies.

Declarations

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Ethical Approval. not applicable since the present study is on aquatic plant.

Competing interests. The authors declare no conflict of interest.

Authors' contributions E.M. acquired the financial support, analyzed the data and wrote the main manuscript text, S.G.D. and D.K. performed the biological and environmental measurements, and Y.Ö. and A.Ş. collected biological and environmental materials. All authors reviewed the manuscript.

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Availability of data and materials The data and material will be available if requested by the Journal.

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Figures

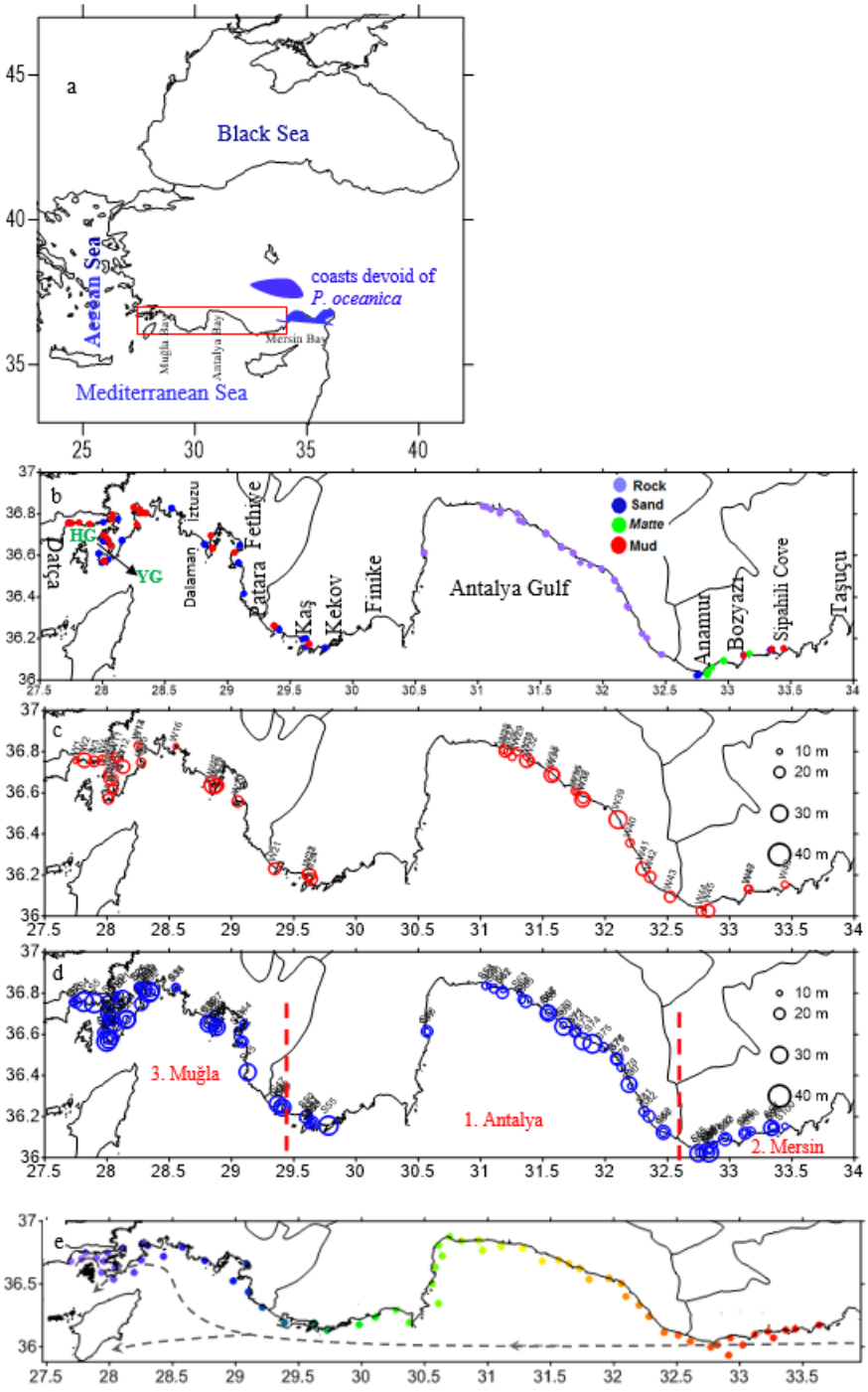

Figure 1

Study area and regions, bays (a, d), bottom types (b), sampling stations for *P. oceanica* and bottom depths in winter (c), summer (d), and regional classification of the stations with the rim water current (e). YG is Yeşilova Gulf, and HG is Hisarönü Gulf.

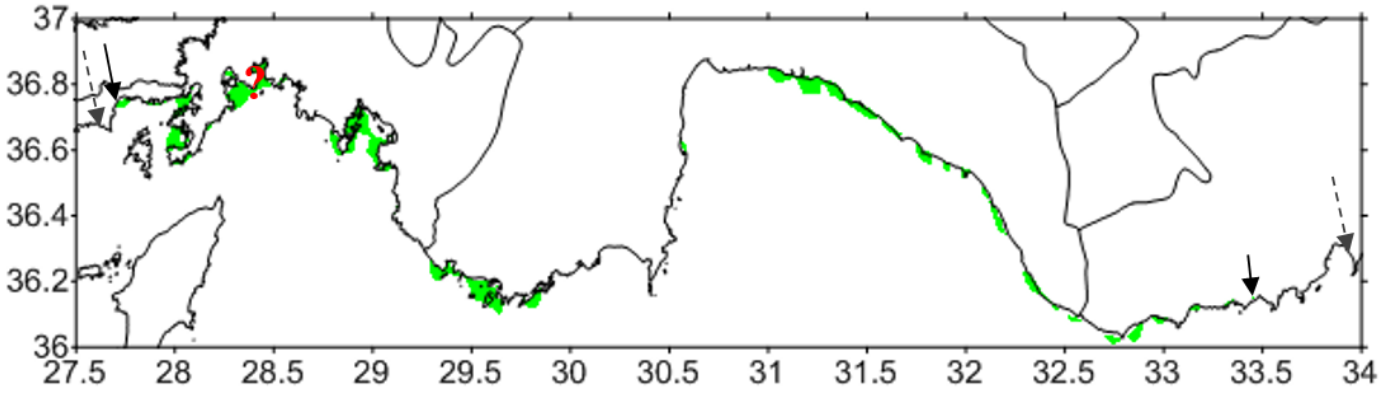

Figure 2

Distribution of the occurrence of *P. oceanica* (green patches) along the Turkish Mediterranean coast. The occurrence was shown from the pooled data in both winter and summer. Dashed line arrows show the borders of the study area, and the non-dashed arrows show the ends of the occurrence of *P. oceanica*in the study area. The mark **?** showed a small cove which is forbidden to entry.

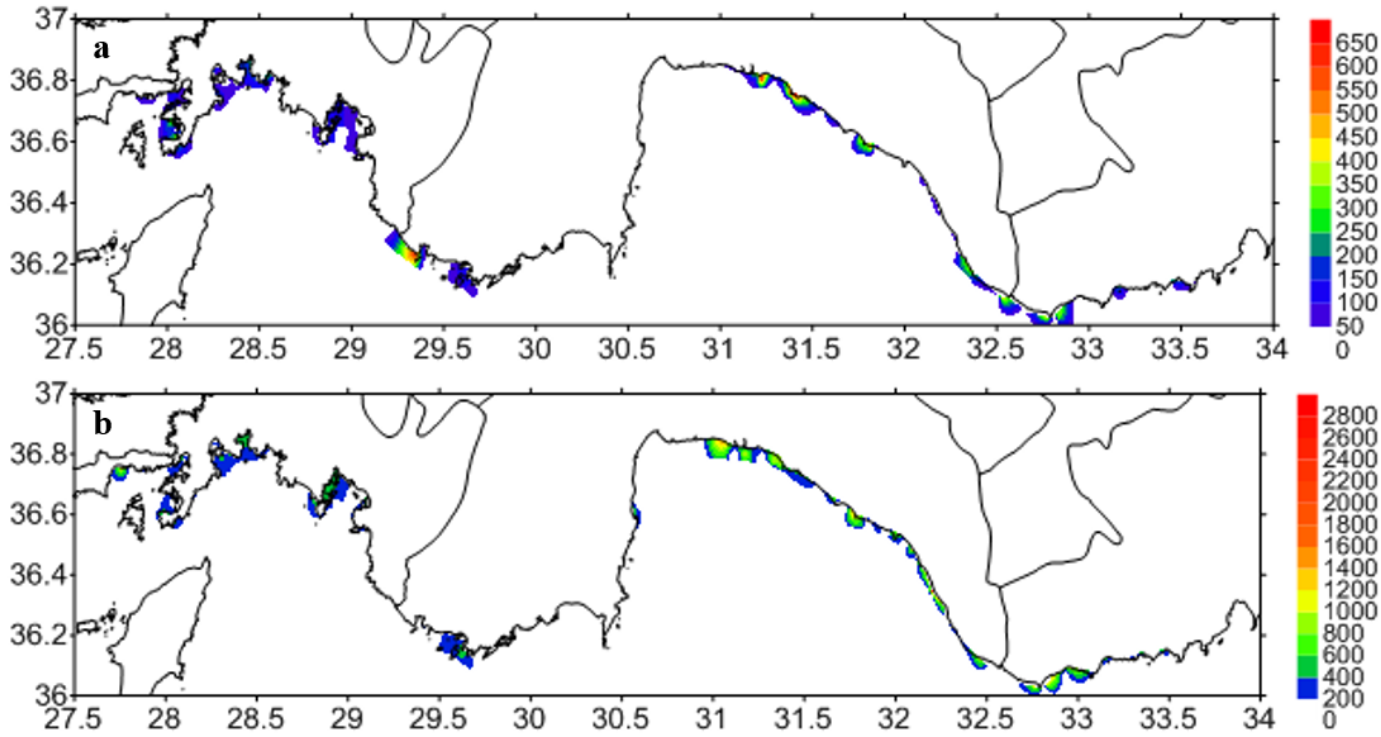

Figure 3

Distribution of leaf biomass (g/m2 on the color bar) of *P. oceanica* along the study area in winter (a) and summer (b).

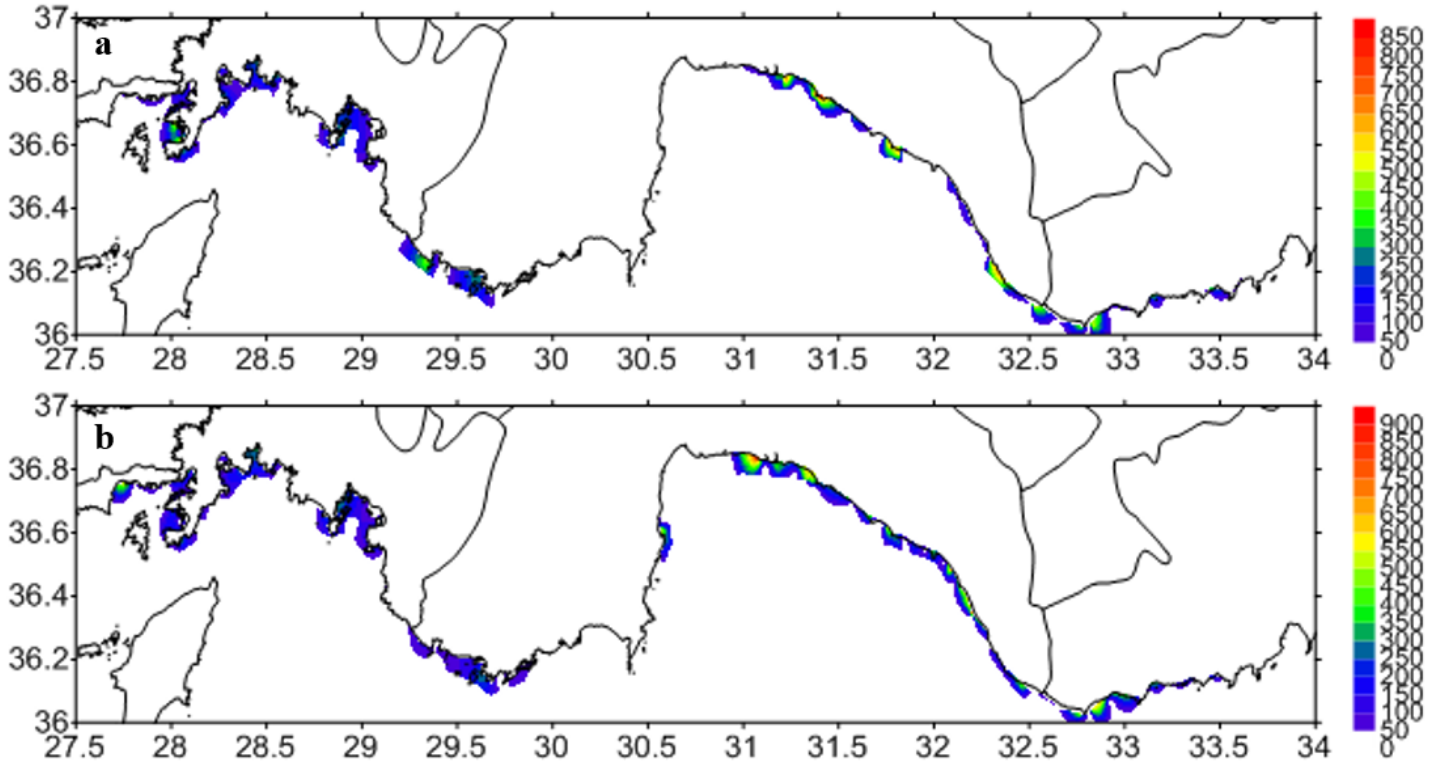

Figure 4

Distribution of the shoot density (shoots/m^2 on the color bar) along the Turkish coast in winter (a) and summer (b).

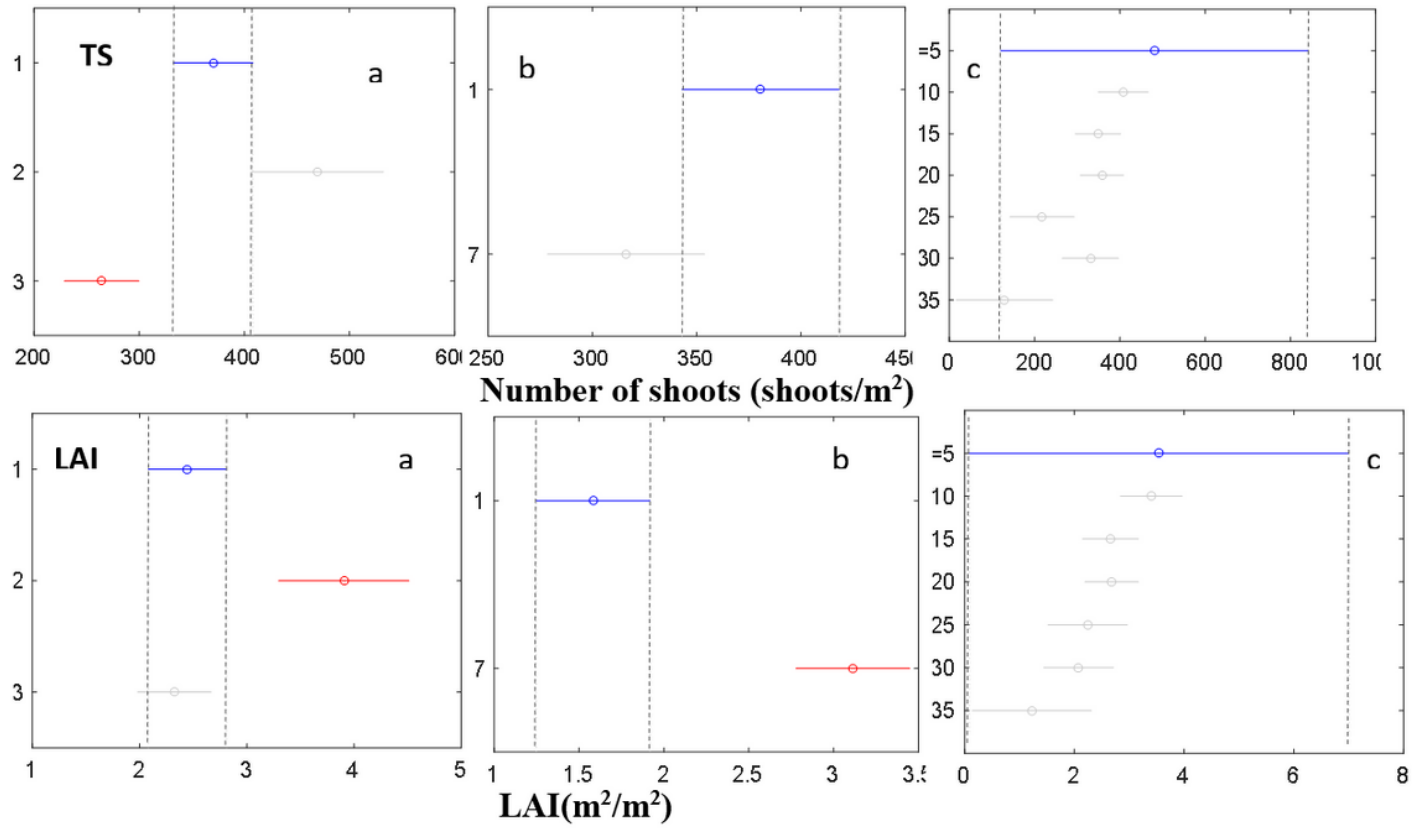

Figure 5

Post-hoc test (least significant difference, LSD) of the shoot density (TS) and LAI of *P. oceanica* among the regions (a; 1: Antalya, 2: Mersin, 3: Muğla on Y axis), seasons (b, 1: winter, 2: summer on Y axis), and bottom depths (c, meter on Y axis), respectively. (blue mark; to be tested among the months or depths, red: significantly different, grey: significantly not different between vertical discrete grey lines)

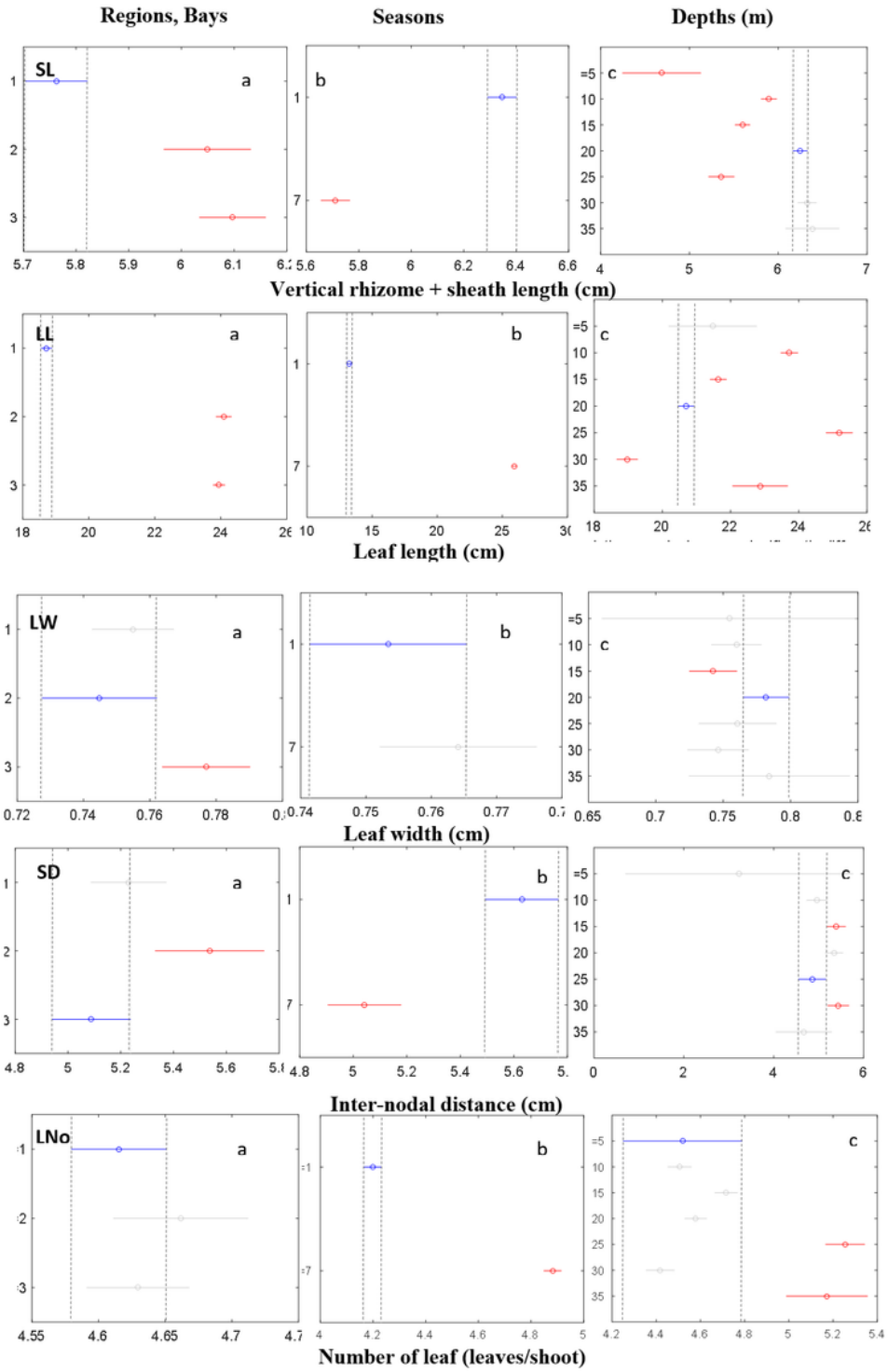

Figure 6

Post-hoc test (least significant difference, LSD) of the morphometrical variables; vertical rhizome + sheath (SL), leaf length (LL), leaf width (LW), inter-nodal (shoot) distance (SD), and number of leaves per shoot (LNo) of *P. oceanica*among the regions (a; 1: Antalya, 2: Mersin, 3: Muğla on the Y axis), seasons (b, 1: winter, 2: summer on the Y axis), and bottom depths (c, meter on Y axis), respectively. (blue mark: to

be tested among the months or depths, red: significantly different, grey: significantly not different between vertical discrete grey lines)

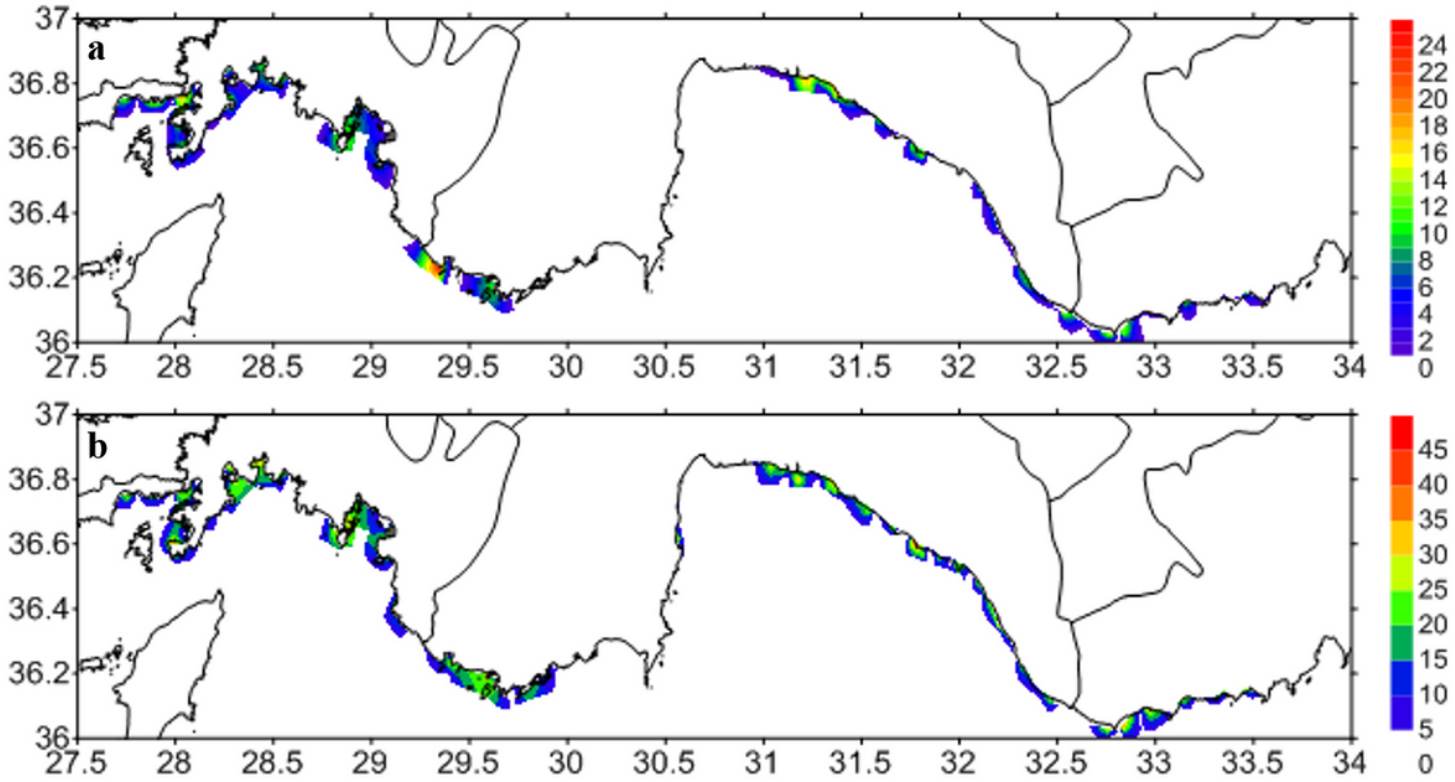

Figure 7

Distribution of the leaf length (cm on the color bar) along the Turkish coast in winter (a) and summer (b).

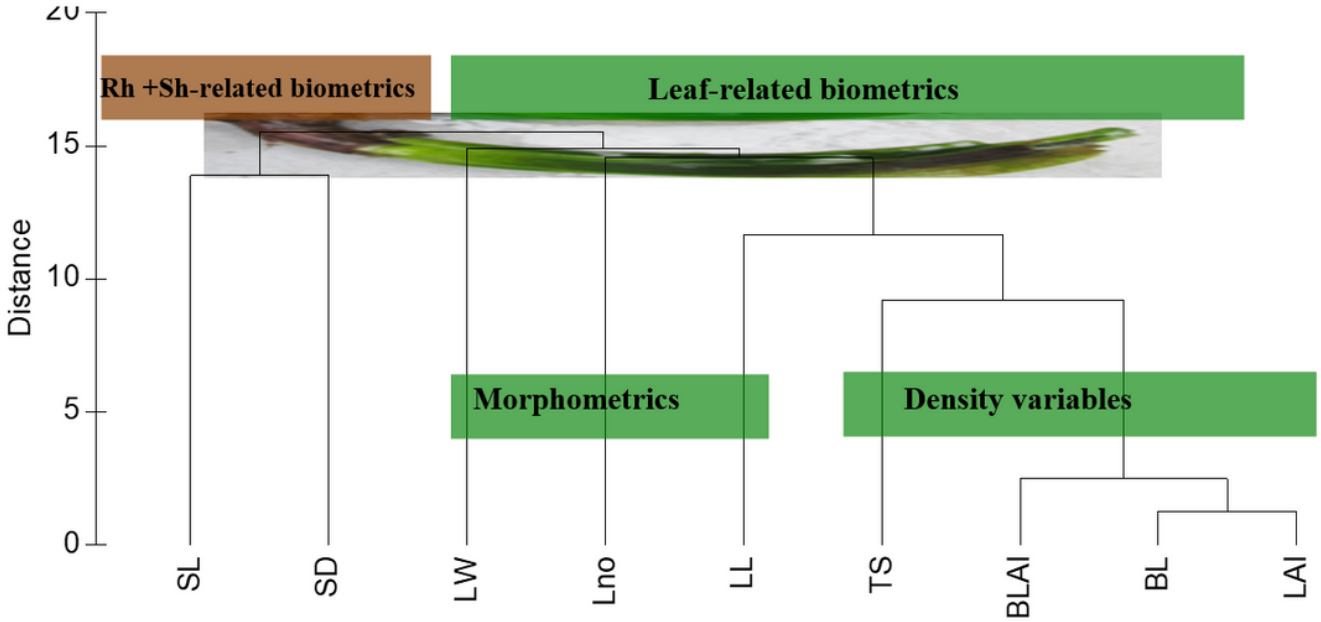

Figure 8

Interrelation of the biometrics of *P. oceanica* using the Cluster analysis discriminating below-grounded (Rh: vertical rhizome, Sh: sheath) and above-grounded parts of the specimens in a year.

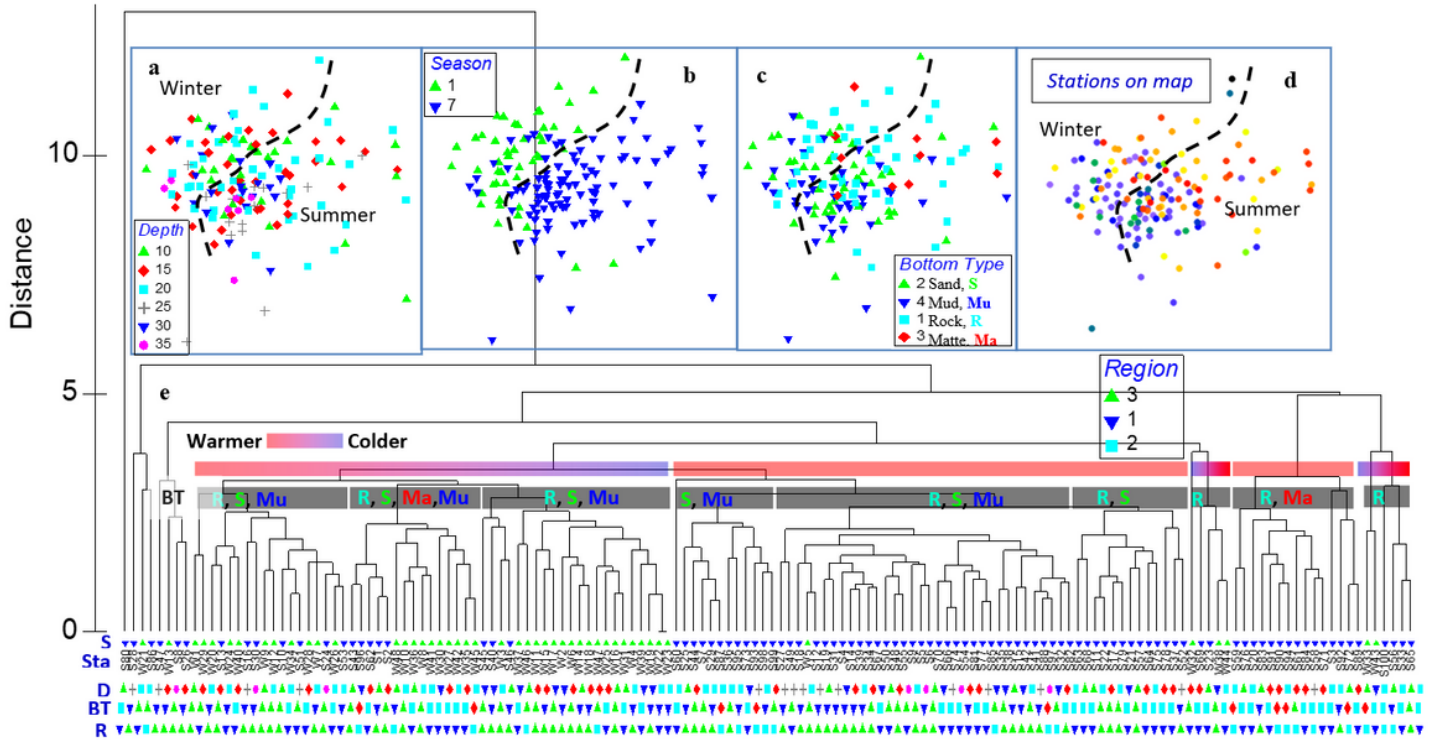

Figure 9

nMDS (a-d) and Cluster (e; S: season, Sta: station code in Fig. 3a, D: bottom depth, BT: bottom type, R; region) of the biometrics of *P. oceanica* in both winter and summer at the stations classified by bottom depths (a), season (b; 1: winter and 7: summer), bottom type (c), and location (d) on map in Fig. 1e. A dashed line separated summer and winter on nMDS.

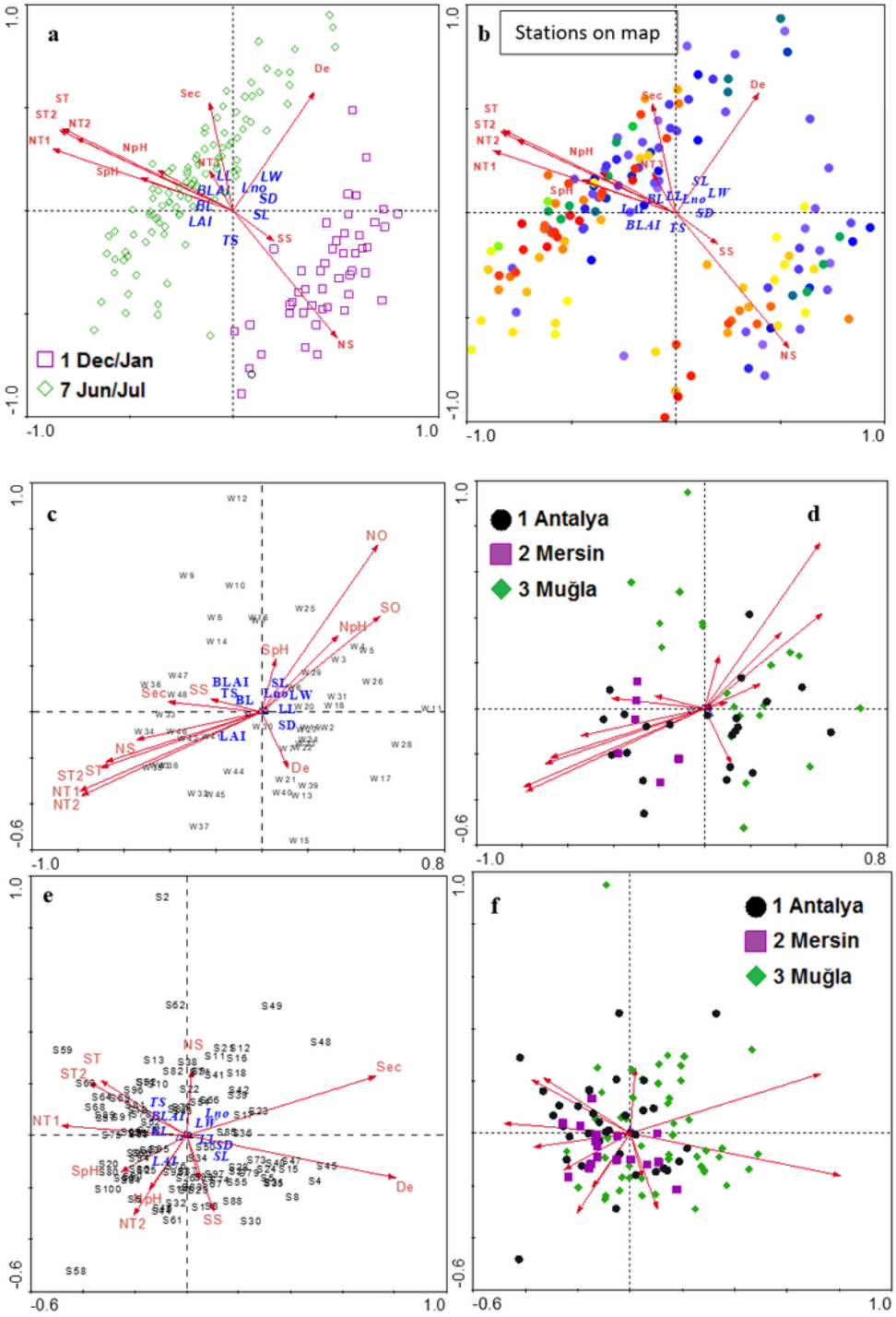

Figure 10

CCA analysis for the biometrics (in blue color, see Online Resource 4 for the abbreviations of the biometrics)-physical environment (in red color, see Online Resource 2 for the abbreviations of the environmental parameters) relationship in both winter and summer together (a-b) at the stations classified by season (a; 1: winter, 7: summer) and location on map (b) (see Fig. 1e for the location of the

stations), only in winter at the stations (c) labeled by station name (Fig. 1), and region (d), and only in summer at the stations (e) labeled by station name (Fig. 1), and region (f).

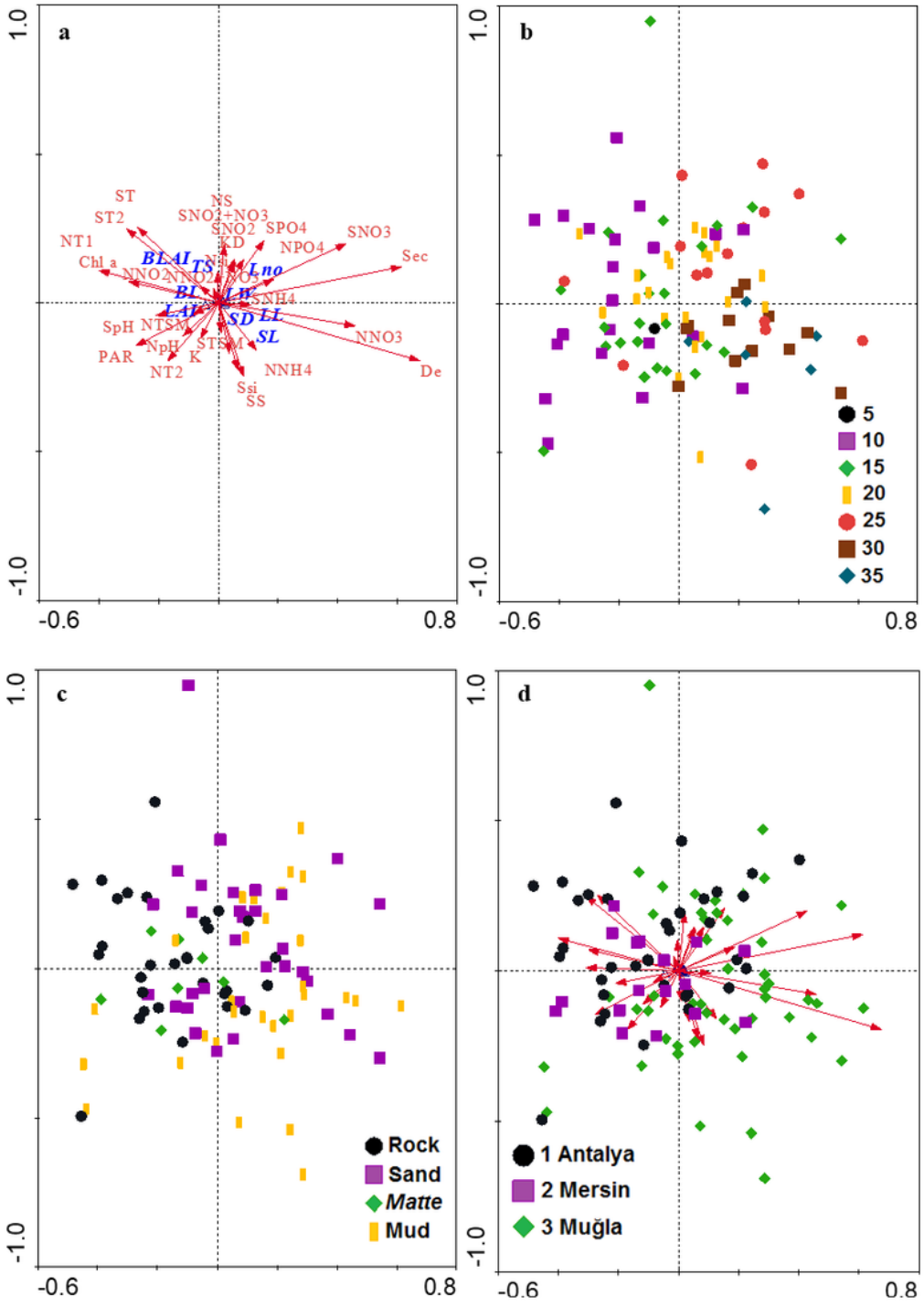

Figure 11

CCA analysis for the biometrics (in blue color, see Online Resource 4 for the abbreviations of the biometrics)-physicochemical and optical environment (in red color, see Online Resource 2 for the

abbreviations of the environmental parameters) relationship in summer (a) at the stations classified by bottom depth (b), bottom type (c), and region (d).

Supplementary Files

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- PosidoniaDistributionSupllR1.docx