

From acoustics to biometrics for ecology of *Posidonia oceanica* in the Mediterranean Sea

Erhan Mutlu

emutlu@akdeniz.edu.tr

Akdeniz Üniversitesi: Akdeniz Üniversitesi <https://orcid.org/0000-0002-6825-3587>

Cansu Olguner

Bahçeşehir High School

Yaşar Özvarol

Akdeniz Üniversitesi: Akdeniz Üniversitesi

Mehmet Gökoğlu

Akdeniz Üniversitesi: Akdeniz Üniversitesi

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Abstract

Seagrasses, particularly *Posidonia oceanica*, are protected and endangered species in the Mediterranean Sea, where they function as both coastal engineers and interior ecosystem architects. These seagrass meadows provide essential ecological niches and ecosystem services, and their presence is widely regarded as an indicator of undisturbed marine environments. Therefore, the development of non-destructive methods to assess seagrass characteristics is of great importance. This study presents the first attempt to estimate fundamental ecological metrics, specifically, density-related variables (leaf biomass, shoot density, and leaf area index [LAI]) and a morphometric trait (leaf length) of a *P. oceanica* meadow using acoustic data collected in the Gulf of Antalya, Turkey, over a seven-month period spanning 2011–2012. Acoustically derived estimates of leaf biomass were converted into density-related variables based on empirical relationships established between biomass, shoot density, and LAI from SCUBA-based sampling. While leaf length showed significant differences, the density-related variables did not differ significantly across spatial (bottom depth) or temporal (monthly) gradients between the measured and acoustically estimated data. Ecological analyses including Generalized Linear/Additive Models and Redundancy Analysis revealed comparable spatiotemporal distribution patterns between the two datasets. Furthermore, similar collinearity patterns, effect sizes, and correlations between environmental variables (including water physical, chemical, and optical properties, as well as sediment composition) and seagrass metrics were observed. These findings suggest that integrating acoustic backscatter techniques with biometric estimations offers a promising, non-invasive approach for monitoring *P. oceanica* meadows and assessing key ecological indicators.

Introduction

Seagrasses are vulnerable species that play vital ecological roles (Den Hartog 1977; Boudouresque and Meinesz 1982; Edgar and Shaw 1995; Peirano et al. 2005; Pergent-Martini et al. 2005). *Posidonia oceanica* (Linnaeus) Delile, 1813 meadows are particularly important habitats within Mediterranean coastal ecosystems (Spalding et al. 2003; Foden and Brazier 2007). This species is protected under various international and national regulations and conservation frameworks (UNEP-MAP-RAC/SPA 2009; Boudouresque and Bianchi 2013; Comte et al. 2024).

A commonly used sampling method for *P. oceanica* involves SCUBA (Self-Contained Underwater Breathing Apparatus) diving, either to collect seagrass samples for onboard biometric analyses or to conduct in situ measurements underwater without removing plant material. However, due to ongoing environmental degradation (Ganteaume et al. 2005; Cossu et al. 2006; Deter et al. 2017; Pergent-Martini et al. 2022), this destructive approach has been increasingly restricted, limiting the number of meadow shoots that can be sampled (Pergent et al. 1995; Gobert et al. 2020; Mutlu et al. 2023a).

To assess seagrass area, canopy height, and spatial distribution, non-destructive remote sensing methods such as underwater video and cameras, satellite imagery, and acoustic technologies have been widely applied in the Mediterranean Sea (Prado et al. 2010; van Rein et al. 2011; Fakiris et al. 2018; Lee and Lin 2018; Dimas et al. 2022; Pergent-Martini et al. 2005; Bonacorsi et al. 2013; Montefalcone et al. 2013; Buchet 2015; Yücel-Gier et al. 2020). However, the effectiveness of these remote sensing systems can be constrained by atmospheric and sea surface conditions (McCarthy and Sabol 2000; Vis et al. 2003; Hossain and Hashim 2019), as well as by the need for sea-truthing and calibration between remote sensing outputs and submerged aquatic vegetation (SAV) biometrics (Pasqualini et al. 1998; Di Maida et al. 2011; Sánchez-Carnero et al. 2012). Since the launch of the Sentinel-2 satellite, satellite-based methods have become increasingly popular for seagrass monitoring, as they enable both large-scale mapping and ground-truthing opportunities (Dattola et al. 2018; Yücel-Gier et al. 2020). In contrast to acoustic methods, which use sound waves and can operate under turbid conditions, satellite imaging systems rely on atmospheric clarity and high water transparency to effectively penetrate the water column and detect seagrass meadows on the seafloor (McCarthy and Sabol 2000; Vis et al. 2003; Brown et al. 2011; Hossain and Hashim 2019).

From acoustics

Acoustics is a cost-effective and efficient method for measuring scattering patterns in both pelagic and benthic environments of aquatic systems (Sánchez-Carnero et al. 2023). A wide range of acoustic sampling platforms are available, including autonomous and towed bodies, platforms mounted on surface drones, and systems integrated into the sideboards or keels of research vessels (Greene and Wiebe 1990; Wiebe et al. 2002; Rende et al. 2020; Mutlu and Olguner 2023a). This diversity allows researchers to ensonify targets at various depths, depending on the penetration capacity of the acoustic frequencies used. Target detection spans a broad frequency range from 1 Hz to 38–420 kHz and up to 1–3 MHz using single- or multi-frequency transducers (Wiebe et al. 1990; Wiebe and Greene 1994). Different frequencies enable the detection of target sizes based on the relationship between sound wavelength and the size (length or diameter) of the target (Stanton et al. 1996; Mutlu 2003; Lavery et al. 2007; Mutlu and Olguner 2023a, b). For decades, ex situ and in situ studies have utilized various acoustic platforms to detect and calibrate organisms ranging in size from a few millimeters to several meters, particularly in marine environments (Elliott et al. 1996; George and Winfield 2000; McCarthy and Sabol 2000; Schneider et al. 2001; Sabol et al. 2002; Wanzenböck et al. 2003; Schmidt et al. 2005; Winfield et al. 2007; Sabol et al. 2009). These studies highlight the advantages of acoustic methods over other remote sensing approaches.

Initially, acoustic targets were mainly fish (e.g., SIMFAMI 2002), followed by zooplankton (Wiebe et al. 1990; Stanton et al. 1996; Mutlu 1996, 2003, 2006) and submerged aquatic vegetation (SAV). Acoustic techniques have been used not only for mapping the distribution of SAV (Pasqualini et al. 1998; Di Maida et al. 2011; van Rein et al. 2011; Lee and Lin 2018) but also for quantifying biometrics (Shao et al. 2019; Llorens-Esrich et al. 2021; Minami et al. 2021; Mutlu and Olguner 2023a, b), and for discriminating between seagrass species (Mutlu 2023; Mutlu and Olguner 2023c).

Vegetation acoustics has long been used to map seagrasses and eelgrass using side-scan sonar, multibeam systems, and echosounders (Pasqualini et al. 1998; Di Maida et al. 2011; van Rein et al. 2011; Lee and Lin 2018). However, acoustic data alone are inherently ambiguous regarding the identity of scatterers (Mutlu 2003, 2006). Direct identification of organisms was previously considered impractical due to the limitations of earlier acoustic methods. As a result, integrating acoustic scattering properties with biological characteristics of specific organisms is now considered one of the most promising strategies for species identification (Mutlu 2023; Mutlu and Olguner 2023a, b). Another approach involves using multi-frequency responses specific to the targets, evaluating their scattering in the Rayleigh, resonance, and geometric regions (SIMFAMI 2002; Lavery et al. 2007). Recent studies in vegetation acoustics have focused on calibrating the relationship between acoustic properties and plant biometrics (Shao et al. 2019; Llorens-Esrich et al. 2021; Minami et al. 2021). In this context, *P. oceanica* has been acoustically characterized and distinguished from *Cymodocea nodosa* (Ucria) Ascherson 1870 (Mutlu and Olguner 2023a, b), with successful species discrimination in the Mediterranean Sea (Mutlu and Olguner 2023c). These advances were supported by the development of "SheathFinder", an algorithm created by Mutlu and Balaban (2018), and "POSIBiom", a package of scripts developed by Mutlu (2023) to detect *P. oceanica* and estimate its leaf biomass and length.

Through biometrics

Biometric estimates of *Posidonia oceanica* vary among researchers, as different studies focus on different parameters. The most commonly measured biometric traits are shoot density (number of shoots per unit area) and leaf length, typically assessed by SCUBA divers during underwater surveys. In addition to these, biometric assessments can include elongation rates and lengths of horizontal and vertical rhizomes, internodal distances, leaf width, number of leaves per shoot, and the composition and abundance of epiphytes (Gobert et al. 2006; Mutlu et al. 2022a, 2023a, b). This information is valuable for ecologists, biologists, resource managers, and conservationists in developing appropriate management and conservation strategies (Marbà et al. 2002; Orth et al. 2006; Gobert et al. 2009; Mutlu et al. 2022b). Certain biometrics of *P. oceanica*, such as the leaf length-to-width ratio, rhizome characteristics, and reproductive traits, are influenced by environmental conditions and seasonal growth dynamics (Gobert et al. 2006; UNEP/MAP-RAC/SPA 2015; Mutlu et al. 2022a). In contrast, other traits like shoot density tend to remain stable under pristine conditions (UNEP/MAP-RAC/SPA 2015).

The growth dynamics of *P. oceanica* depend on the timing of leaf emergence, which typically occurs in autumn and early winter under undisturbed conditions (Gobert et al. 2006). These seasonal growth patterns may be slightly altered with increasing depth (Caye and Rossignol 1983). While *P. oceanica* exhibits marked seasonal and spatial dynamics under pristine conditions, its growth patterns become irregular under chronically disturbed environments (Marbà et al. 1996; Guidetti et al. 2002; Sghaier et al. 2006; Pagès et al. 2012; Montefalcone et al. 2016). Interannual variability in biomass can be substantial and is often linked to the availability of resources such as nutrients, carbon, or light (Alcoverro et al. 1997; Gobert et al. 2003). Recently, Mutlu et al. (2022a) applied, for the first time, biometric data to a seasonalized von Bertalanffy growth model to estimate key population dynamics parameters of *P. oceanica* in a pristine Mediterranean environment. These parameters included annual growth rate, theoretical maximum leaf length and width, age at germination, seasonal growth points (winter and summer), and the amplitude of growth oscillations.

To ecology

Pristine meadows of *Posidonia oceanica* and their associated epiphytes are key indicators of marine ecological status (Augier 1985; Pergent-Martini and Pergent 2000; Bhattacharya et al. 2003) and have long been used to monitor ecosystem health (Colantoni et al. 1982; Pal and Hogland 2022). *P. oceanica* responds rapidly to changes in marine environmental quality and is highly sensitive to both hydrographic and atmospheric variations (Gobert et al. 2006). It plays a foundational ecological role by shaping coastal zones, creating nearshore environments, and forming critical ecological niches (Koch 1994; Brun et al. 2009; Pergent et al. 2014; Chefaoui et al. 2016). These meadows are among the most important oxygen producers in marine ecosystems. They serve as habitat for numerous invertebrate and vertebrate species, spawning grounds for fish, refugia from predators, and competitors of invasive macrophytes. Additionally, they stabilize sediments, reduce coastal erosion (Boudouresque and Meinesz 1982; Peirano et al. 2005), and contribute significantly to blue carbon storage (Comte et al. 2024). *P. oceanica* is well adapted to oligotrophic (low-nutrient) conditions and forms extensive colonies in marine systems (Marbà et al. 1996; Walker 2000).

To thrive, *P. oceanica* requires adequate light intensity, low nitrogen concentrations (with temporary increases during flowering), and favorable seasonal and annual temperature and salinity regimes. It colonizes a range of substrates including rock, matte, sand, and mud depending on local conditions (Catucci and Scardi 2020; Gnisci et al. 2020; Mutlu et al. 2023b). Additionally, optimal pH, elevated carbonate levels in sediment and water, and suitable physical conditions such as wave exposure and wind stress are critical for its survival (Mutlu et al. 2023b). In high-energy environments (e.g., exposed to strong waves and winds), *P. oceanica* typically prefers hard substrates like rock and matte, whereas in sheltered areas it is more commonly found on soft substrates such as sand and mud. Healthy habitats typically exhibit consistent seasonal and annual patterns in biometric traits such as leaf length and width, number of leaves, and internodal distance which indicate stable and clean environmental conditions. However, *P. oceanica* is highly sensitive to the impacts of global warming and marine heatwaves (Gobert et al. 2006). Its abundance across depth gradients is one of the widely used biometrics for assessing the ecological status of marine environments.

In the present study, we conducted the first attempt to examine the ecological patterns of *P. oceanica* biometrics, specifically density-related variables (leaf biomass, leaf area index, and shoot density) and leaf length using acoustic estimations of leaf biomass calibrated against measured biometric data. This study was intentionally designed to avoid the use of destructive sampling methods, thereby respecting the ecological sensitivity and protected status of *P. oceanica*. Biometric estimates obtained from SCUBA-based sampling were compared with acoustically derived data in a study area where environmental parameters were concurrently measured.

Material and Methods

After calibrating the acoustic-biometric relationship for *Posidonia oceanica* (Mutlu and Olguner 2023a, b) and developing a software package called POSIBiom to estimate leaf biomass and length (Mutlu 2023), acoustic data were collected over seven different months: July 2011 (7), September 2011 (9), November/December 2011 (12), January 2012 (1), March 2012

(3), April/May 2012 (4), and August 2012 (8) (Fig. 1). These data were processed to estimate the primary density-related biometric parameters; leaf biomass (g/m^2), leaf area index (LAI, m^2/m^2), and shoot density (shoots/ m^2), as well as leaf length (m), for a pilot study area in the Gulf of Antalya, Eastern Mediterranean Sea (Fig. 1).

Due to a malfunction in the echosounder during September 2011, only the western half of the study area was acoustically surveyed at that time; the eastern half was subsequently surveyed in August 2012. SCUBA-based biometric and environmental sampling continued in September to complete the dataset.

Acoustic transects, spaced 420 m apart, were conducted across bottom depths ranging from 5 to 70 m (Fig. 1), using a 206 kHz scientific echosounder with a split-beam transducer (DT-X model, BioSonics Inc., USA). Transects were shifted 80 m eastward each month to achieve high horizontal resolution (final layout shown in Fig. 1). Before each survey, the echosounder was calibrated using a standard tungsten sphere (provided by BioSonics Inc.) at a pulse width of 0.4 ms. Data were collected at a pulse width of 0.1 ms, a ping rate of 5 pings/s, and with sound velocity and absorption coefficient settings adjusted monthly by the “Visual Acquisition” software according to in-situ measurements of water temperature, salinity, and pH. Each monthly cruise, conducted aboard the R/V *Akdeniz Su* at 2.6 m/s, was completed within 15 days.

In parallel, detailed SCUBA sampling was conducted at 80–100 stations along 14 transects (horizontal spacing of 3 nautical miles), each with five depth levels (5, 10, 15, 20, and 30 m) (Fig. 1), following the methods described in Mutlu et al. (2022a). Environmental parameters were measured at all stations (including at 40 m and 50 m depths): temperature, salinity, pH, oxygen, density, $\text{NO}_2^- + \text{NO}_3^-$, NH_4^+ , PO_4^{3-} , photosynthetically active radiation (PAR), PAR penetration depth (1%), Secchi disk depth, and sediment characteristics (gravel, sand, mud, total organic carbon, total carbonate, CaCO_3) (Mutlu et al. 2022a; Yalçın et al. 2023). Most parameters were measured onboard, while chemical and sediment samples were analyzed in the laboratory. Full environmental distributions are detailed in Mutlu et al. (2022a, 2023a) and Yalçın et al. (2023).

During the present study, *P. oceanica* was sampled at 8–21 stations per month (Table 1, Fig. 1c), keeping destructive sampling to a minimum in line with the species' protected status. At each SCUBA station, two divers collected entire seagrass samples within a 0.4×0.4 m quadrat, repeating the procedure three times. Leaf orientation was also recorded at each station as right (0), semi-right (1), or flat (2) (Table A1).

In the laboratory, acoustic data were processed using the POSIBiom algorithm (Mutlu 2023) to convert the relative area backscattering strength (S_a , dB/m^2) to absolute leaf biomass (g/m^2), based on conversion equations developed by Mutlu and Olguner (2023a). Bottom and habitat types were identified using *Visual Bottom Typer* software (BioSonics Inc., USA) (Fig. A1).

From the SCUBA surveys, spatiotemporal biometrics of *P. oceanica* were previously published (Mutlu et al. 2022a), including density variables (leaf biomass, shoot density, LAI, number of leaves per shoot, distance between shoots) and morphometric variables (vertical rhizome length, leaf length, and width). Each station's biometrics represent the average of three replicates.

For each sampling month in the present study, equations were developed to convert acoustically estimated leaf biomass to LAI and shoot density based on leaf biomass per leaf area (BLA) (Table 1). The orientation scores of leaves were averaged monthly to account for their effect on backscattered acoustic energy. Acoustic estimates of biomass and leaf length were then mapped using the “linear” gridding method in POSIBiom.

The conversion equations in Table 1 were evaluated for monthly variation using Analysis of Covariance (ANCOVA), and the statistical significance of correlations between variables was tested. A depthwise assessment of acoustic biometrics (biomass, LAI, shoot density, leaf length) was conducted at 5, 10, 15, 20, 25, and 30 m depths, averaged over $10 \text{ m} \times 10 \text{ m}$ areas to match the spatial resolution of SCUBA-based data. One-way ANOVA (by month and depth) and two-way ANOVA (month $\times$ depth) were applied to test for significant spatiotemporal differences. Least Significant Difference (LSD) post hoc tests were used to examine monthly and depth-wise variation. Paired-sample *t*-tests were conducted to compare estimated (acoustic) and measured (SCUBA) biometric values across months and depths.

To examine the influence of leaf orientation on acoustic estimates, Pearson correlation analyses were conducted between estimated biometrics and mean monthly orientation scores. For ecological modeling, environmental variables from the full depth range (5–50 m) were linked with acoustic biometrics using Generalized Linear Models (GLM) and Generalized Additive Models (GAM) to test collinearity and assess the predictive strength of environmental factors. All parametric statistical analyses were conducted using MATLAB (version 2021a, MathWorks Inc.).

Additionally, ecological relationships between $\log_{10}$ -transformed biometrics and raw environmental variables were analyzed using Redundancy Analysis (RDA). RDA was selected based on the results of detrended correspondence analysis, which showed that the length of the environmental gradient for the first four axes did not exceed 3 standard deviations (SDs), indicating suitability for linear ordination (Hill and Gauch 1980). The SD values were 0.751, 0.787, 1.029, and 0.000 for acoustic data, and 0.233, 0.132, 0.138, and 0.000 for SCUBA-based data (CANOCO 4.5).

Results

From Acoustics

Biomass-biometrics relation

Acoustically estimated leaf biomass was converted to other density-related variables using regression relationships between biomass, LAI, and shoot density (Table 1). The regression constants (a and b) and Pearson correlation coefficients (r) were statistically significant based on t -tests applied to each parameter ($p < 0.05$; Table 1). However, the correlation coefficients between biomass and shoot density were lower than those between biomass and LAI in both regression equations. With the exception of the biomass–LAI relationship, all other relationships presented in Table 1 showed significant differences among months, as determined by analysis of covariance (ANCOVA, $p < 0.05$).

Table 1

Equations established to convert leaf biomass based on leaf area (BLA in g/m², Equations 1) and leaf length (BL in g/m², Equations 2) to leaf area (LA in cm²/m²) and shoot density (SHT in shoots/m²) using the measured data. Pearson correlation coefficients (r_1 and r_2 for equations 1 and 2, respectively, and bold values denote significantly correlated at $p < 0.05$) and sample size (n) based on the number of sampling stations.

Months	Equation 1	Equation 2	r_1	r_2	n
January,1	LA = 61.539*BLA + 260.29	LA = 61.035*BL-101.59	0.9999	0.9971	13
	SHT = 0.7151*BLA + 153.52	SHT = 0.7259*BL + 143.17	0.7738	0.7898	
March,3	LA = 60.804*BLA + 579.17	LA = 59.256*BL + 1026	0.9996	0.9962	15
	SHT = 0.5408*BLA + 61.4458	SHT = 0.5294*BL + 63.917	0.9539	0.9548	
April,4	LA = 54.317*BLA + 937.78	LA = 54.46*BL-658.56	0.9998	0.9994	15
	SHT = 0.3449*BLA + 78.256	SHT = 0.348*BL + 66.082	0.9627	0.9683	
July,7	LA = 52.375*BLA + 1524.9	LA = 58.896*BL-2527	0.9996	0.9906	12
	SHT = 0.3286*BLA + 100.86	SHT = 0.3733*BL + 71.624	0.9437	0.9447	
August,8	LA = 52.754*BLA + 787.3	LA = 47.583*BL + 12001	0.9995	0.9912	21
	SHT = 0.0927*BLA + 74.264	SHT = 0.0839*BL + 92.796	0.7658	0.7625	
September,9	LA = 51.79*BLA + 671.79	LA = 53.715*BL-310.65	0.9991	0.9985	18
	SHT = 0.4687*BLA + 146.47	SHT = 0.4901*BL + 135.29	0.8609	0.8676	
December,12	LA = 56.826*BLA + 760.27	LA = 55.571*BL + 942.93	0.9998	0.9978	8
	SHT = 0.5714*BLA + 176.18	SHT = 0.5581*BL + 178.27	0.9199	0.9170	

Spatiotemporal distribution of the biometrics

In the Antalya Gulf study area, *Posidonia oceanica* was found exclusively on rocky substrates, despite the presence of sand and mud on the seafloor (Fig. 2; Fig. A1). The meadow was composed of three main large beds, with several smaller beds primarily located in the western half of the study area. Additionally, small patchy areas of *P. oceanica* were observed. The meadow began to appear mainly after the midpoint of the study area, moving eastward. Well-defined meadows were observed from April through late summer (August and September), and persisted into early winter (Fig. 2). Some small false-positive patches may be present in the distribution maps due to interpolation artifacts.

The lower depth limit of *P. oceanica* was observed at 28–31 meters, beyond which no meadows were found due to the absence of suitable rocky substrate (Figs. 1, 2, A1). Leaf biomass varied temporally (by month) and spatially (by depth). As reported in the literature (e.g., Sandoval-Gil et al. 2014), *P. oceanica* meadows are commonly classified into shallow and deep types. In this study, the transition zone occurred around 15 meters (occasionally 20 m), where biometric values fluctuated considerably throughout the year. Overall, this middle depth delineated two zones in the distribution of seagrass biometrics: the first, from the shallowest depth to 15 m, showed decreasing values with depth; the second, from 20 m to the maximum depth, showed increasing values (Figs. 1, 2).

Excluding very low values (< 1) averaged per ping, acoustic estimates of leaf biomass ranged from 93 g/m² (August) to 1829 g/m² (December). LAI varied from 1 m²/m² (January) to 10.26 m²/m² (December), shoot density from 64 shoots/m² (March) to 1199 shoots/m² (December), and leaf length from 0.05 m (observed in almost all months) to 0.714 m (December) (Table A1; Table 2). Paired-sample *t*-tests comparing estimated (acoustic) and measured (SCUBA) values indicated that only leaf length showed a statistically significant difference by month and bottom depth ($p < 0.05$). All other biometric variables were statistically similar between estimated and measured values (Table 2). Leaf orientation (Table A1) was not significantly correlated with any of the estimated mean variables ($p > 0.05$).

Table 2 Summary of estimates ($\bar{X} \pm SD$) of measured and estimated density variables (SHT, shoot density in shoots/m²; LAI, Leaf Area Index in m²/m²; BLA, leaf biomass in g/m², based on LA) and morphometric variable (LL, leaf length in cm) among the months and seafloor depths and their individual ANOVA test with “months/p” or “Bottom depths/p”. Post-hoc test for the pairwise difference in biometrics among months in red, and bottom depths in red. “All” denotes a significant difference in biometrics among each pair of all months or all bottom depths. “P for t-test” is significance level, p value estimated by paired- t test subjected between each of the measured and estimated biometrics along the month and bottom depth. The bold p values denote a significant difference at $p < 0.05$. Measured data in September include two averages of each variable; the first data were estimated for an area where the acoustic study was conducted (ceased because of malfunction of the echosounder), and the second data in parenthesis for the entire study area.

Factors/Variable	SHT		LAI		BLA		LL	
	Measured	Estimated	Measured	Estimated	Measured	Estimated	Measured	Estimated
Months/p	0.6899	0.000	1.78*10⁻⁴	0.000	4.13*10⁻¹³	0.000	0.000	0.000
January, 1	410±34	701±0.6	2.23±0.50	4.68±0.01	392.3±93.6	769.41±1.26	16.78±0.09	17.74±0.03
		all	M,Ap,J	all	M,Ap,J	All	M,Ap,J,Au,S,N	all
March, 3	406±32	181±0.5	3.93±0.47	1.41±0.01	713.3±87.2	221.95±1.03	25.46±0.11	16.76±0.03
		Ja,J,Au,S,N	Ja,J,N	all	Ja,J,N	All	Ja,Ap,J,Au,S,N	all
April, 4	391±32	186±0.4	5.02±0.47	1.81±0.01	941.1±87.2	336.55±0.86	35.30±0.11	18.97±0.02
		Ja,J,Au,S,N	Ja,Au,S,N	all	Ja,Au,S,N	All	Ja,M,J,Au,S,N	all
July, 7	450±36	360±0.6	5.72±0.52	4.30±0.01	1045.9±97.5	773.45±1.17	31.24±0.16	18.36±0.04
		all	Ja,M,Au,S,N	all	Ja,M,Au,S,N	All	Ja,M,Ap,Au,S,N	All
August, 8	364±27	131±0.7	3.18±0.40	3.42±0.01	565.7±75.5	466.71±1.53	24.01±0.11	14.42±0.05
		all	Ap,J	all	Ap,J	All	Ja,M,Ap,J,S,N	all
September, 9	346±67 (384±33)	508±2	2.31±1.06 (3.12±0.48)	4.05±0.01	417.8±196.8 (557.4±89.2)	760.55±2.77	21.37±0.38 (24.53±0.19)	15.75±0.09
		all	Ap,J	all	Ap,J	all	Ja,M,Ap,J,Au,N	all
December, 12	393±44	449±0.6	2.23±0.64	2.79±0.01	381.6±119.4	485.87±1.26	15.91±0.16	20.59±0.04
		all	M,Ap,J	all	M,Ap,J	all	Ja,M,Ap,J,Au,S	all
P for t-test	0.618		0.599		0.448		0.042	
Bottom depths (m)/p	1.47*10⁻¹⁷	0.000	7.04*10⁻⁸	0.000	2.23*10⁻⁷	0.000	0.000	3.75*10⁻²⁶
5	521±27	419±2	5.44±0.45	3.52±0.02	976.6±85.6	623.94±3.72	22.76±0.14	16.88±0.1
	15,20,30	all	15,20,30	all	10,15,20,30	all	10,15,20,30	all
10	469±25	346±1	4.49±0.42	2.79±0.01	812.1±78.4	477.03±2.01	27.89±0.11	17.74±0.05
	20,30	all	20,30	all	20,30	all	5,15,20,30	5,15,20,30
15	425±19	336±1	3.76±0.32	3.20±0.01	686.8±60.5	545.92±2.05	23.44±0.07	18.03±0.06
	5,20,30	all	5,20,30	all	5,20,30	all	5,10,20,30	5,10,20
20	305±21	319±2	2.53±0.35	2.90±0.01	459.1±66.8	499.89±2.31	21.96±0.13	18.56±0.06
	5,10,15,30	all	5,10,15	all	5,10,15	all	5,10,15,30	5,20,30
25		407±3		3.73±0.02		643.93±4.18		17.90±0.01
		all		all		all		5,30
30	87±44	606±4	1.02±0.74	5.93±0.03	177.1±138.3	1053.7±5.97	29.25±0.44	18.35±0.01
	5,10,15,20	all	5,10,15	all	5,10,15	all	5,10,15,20	5,10,25
P for t-test	0.735		0.868		0.941		0.007	

Two-way ANOVA revealed that the acoustically estimated biometric variables were significantly affected by month, depth, and their interaction ($p < 0.05$). In contrast, measured density variables showed no significant variation by month but did vary significantly by depth. Among the measured variables, leaf length showed significant differences by month, depth, and their interaction ($p < 0.05$) (Table 3).

Table 3

Significance level, p values of two-way ANOVA results for a difference of each estimated and measured biometrics among months, and bottom depth. Bold p value denotes a significant difference at $p < 0.05$.

Source	BLA		LAI		SHT		LL	
	Estimated	Measured	Estimated	Measured	Estimated	Measured	Estimated	Measured
Month	0	0.1165	0	0.1916	0	0.8961	3.5×10^{-74}	4.6×10^{-271}
Depth	4.9×10^{-146}	0.0067	7.8×10^{-141}	0.0063	1.1×10^{-190}	4.1×10^{-5}	1.8×10^{-37}	3.5×10^{-43}
Month*Depth	0	0.0051	0	0.0125	0	0.2155	7.1×10^{-201}	0

Through Biometrics

Among the density variables, shoot density (SHT) was notably underestimated in comparison to measured values during March, April, and August. A similar underestimation pattern was observed for LAI and leaf biomass (BLA), particularly during March and April. Leaf length (LL) also tended to be underestimated across most months, with the exception of December and January, when estimates were more consistent with measured values. In terms of depth-wise distribution, all density-related biometrics were generally overestimated at the 30 m depth compared to SCUBA-based measurements (Table 2; Figs. 3–6).

Leaf biomass (BLA)

The highest acoustically estimated leaf biomass occurred in January, July, and September, while the lowest biomass was recorded in March. Biomass tended to increase from its minimum in March to a maximum in July, followed by a sudden decrease in August, then a slight increase later in August, and a decline again in December (Table 2, Fig. 3).

The measured (SCUBA) biomass showed a similar monthly pattern, increasing from a minimum in January to a peak in July, then sharply decreasing in August, and returning to January levels by December, completing an annual cycle (Table 2, Fig. 3). Despite these seasonal patterns, no significant differences were found between measured and estimated biomass values across months ($p > 0.05$, paired samples t -test; Table 2).

When examining biomass by depth, the distributions of measured and estimated values appeared different (Fig. 3). However, statistical tests confirmed no significant differences between the two methods at any depth ($p > 0.05$; Table 2). The estimated biomass showed no clear pattern with depth: the minimum occurred at 10 m, followed by 20 m, while the maximum was observed at 30 m, followed by 5 m (Fig. 3). In contrast, the measured biomass exhibited a regular declining trend with depth, decreasing steadily from 5 m to 30 m (Fig. 3).

Leaf Area Index (LAI)

The distribution of LAI estimated acoustically closely resembled that of the measured LAI, both temporally (by month) and spatially (by depth) (Figs. 3, 4). The minimum monthly mean estimated LAI was 1.41 in March, while the maximum was 4.68 in January, followed by 4.30 in July (Table 2).

For the measured values, the lowest LAI was 2.23 observed in December and January, and the highest was 5.72 recorded in July (Fig. 4). Statistical analysis showed no significant difference between estimated and measured LAI values across months ($p > 0.05$, paired t -test; Table 2).

Regarding bottom depths, the highest estimated LAI was 5.93 at 30 m, whereas the highest measured LAI was 5.44 at 5 m. The minimum values were 2.79 at 10 m (estimated) and 1.02 at 30 m (measured), respectively (Table 2; Fig. 4). Again, no significant differences were detected between estimated and measured LAI across depths ($p > 0.05$, paired t -test; Table 2).

Shoot density (SHT)

The average measured SHT ranged from 364 shoots/m² in August to 450 shoots/m² in July, while the estimated SHT varied more widely, between 131 shoots/m² and 701 shoots/m² in January (Table 2, Fig. 5). Depth-wise, the minimum SHT was measured at 30 m (87 shoots/m²) and estimated at 20 m (319 shoots/m²). The maximum SHT differed between measured (521 shoots/m² at 5 m) and estimated (606 shoots/m² at 30 m) values (Table 2, Fig. 5).

Measured SHT exhibited a logarithmic decline from 5 m to 30 m, whereas estimated SHT decreased from 5 m to 10 m, then increased from 20 m to 30 m (Table 2, Fig. 5). Despite these differences in patterns, no significant differences were found between estimated and measured SHT across months and depths ($p > 0.05$, paired t -test; Table 2).

Leaf length (LL)

Mean measured LL varied between 15.91 cm (December) and 35.30 cm (April) across months, while estimated LL ranged from 15.75 cm (September) to 20.59 cm (December) (Table 2, Fig. 6). By bottom depth, estimated LL varied between 16.88 cm (5 m) and 18.56 cm (depth unspecified), whereas measured LL ranged from 21.96 cm (20 m) to 29.75 cm (30 m) (Table 2, Fig. 6). Overall, measured LL was consistently greater than estimated LL, with differences ranging from 5 to 11 cm. Unlike other biometric variables, LL showed a significant difference between estimated and measured values across both months and depths ($p < 0.05$, paired t -test; Table 2). Except for January and December, the monthly trends in estimated and measured LL were similar (Table 2, Fig. 6).

To Ecology

The GLM revealed significant co-linear relationships between biomass and environmental parameters, as well as between SHT and environmental parameters. However, no significant relationships were found between either LAI or LL and environmental parameters ($p > 0.05$; Table A2). Specifically, near-bottom water salinity, density, and PAR showed no significant slope (b) values in their relationships with leaf biomass, while Secchi depth, sea surface temperature, near-bottom oxygen content, PAR, and sediment total organic carbon content exhibited no significant b values in relation to SHT ($p > 0.05$; Table A2).

Using GAM, sea surface salinity was found to have a negative effect on density variables; biomass, LAI, and SHT while sea surface temperature negatively affected leaf length. Other negative influences on leaf length included sediment carbonate and silt content, sea surface phosphate, and PAR (Fig. 8). Conversely, positive effects on leaf biomass were associated with sea surface density, followed by Secchi depth and LAI (above-ground). SHT (below-ground) was positively influenced by Secchi depth, sea surface density, and near-bottom oxygen content. LL showed positive responses to increasing pH, Secchi depth, and nitrite plus nitrate concentrations in near-bottom water (Fig. 7).

Four main descriptive biometrics of *P. oceanica* showed significant spatiotemporal variation along the first redundancy analysis axis (RDA1) (Fig. 8). This discrimination was statistically significant at $p < 0.05$ based on the Monte Carlo test for both estimated ($F = 222.18$, $p = 0.0020$ for RDA1; $F = 9.39$, $p = 0.0020$ for all four RDA axes) and measured data ($F = 120.88$, $p = 0.0020$ for RDA1; $F = 5.038$, $p = 0.0020$ for all four RDA axes).

The estimated biometrics were primarily negatively correlated with bottom depth and sediment silt content, and to a lesser extent with water pH, despite *P. oceanica* inhabiting only rocky substrates in the study area. Conversely, biometrics were slightly positively correlated with sediment sand, gravel, and total carbonate content along RDA1 (Table A3, Fig. 8). Secondary environmental parameters influencing biometrics along RDA2 included water temperature (positive correlation) and near-bottom water density (negative correlation), while near-bottom oxygen showed a slight negative correlation. These results indicate that biometrics were mainly influenced by bottom depth, with seasonal effects being secondary (Fig. 8).

The effect of bottom depth accounted for 99.1% of the variance in the biometrics-environment relationship on RDA1, whereas seasonal variation explained only 0.09% of the variance (Table A3). Additionally, biometrics showed minor correlations with water pH and sediment total carbonate content over space and time (Table A3, Fig. 8).

Measured biometrics exhibited a very similar pattern of discrimination and environmental relationships as the estimated biometrics (Fig. 8). However, total carbonate content of the sediment was an even more influential parameter than bottom depth for the measured biometrics-environment relationship (Table A3, Fig. 8). Notably, RDA1 alone explained 100% of the total variance in the biometrics-environment relationship (Table A3).

Grab sampling and acoustic data confirmed that *P. oceanica* was absent below depths of 30 m, where only rocky substrates were present within the subtropical waters of the study area. This confirms why bottom depth emerged as the primary factor structuring meadow assemblages for both estimated and measured biometrics.

Discussion

This study represents the first attempt to estimate multiple biometrics and ecological characteristics of SAV, specifically seagrass, using acoustic methods. Unlike previous remote sensing studies that typically estimate only a single biometric variable, our approach estimates multiple biometric variables within the study area.

From acoustics

Regression equations relating measured biomass (SCUBA) to other density variables (LAI, and SHT) of *Posidonia oceanica* were significantly established to convert acoustically estimated leaf biomass into estimated LAI and SHT (Table 4) in a study conducted along the entire Turkish Mediterranean coast (Mutlu et al. 2023b). Therefore, leaf biomass and length estimated by the software package “POSIBiom” (Mutlu 2023) can be used to derive LAI and SHT without the need for SCUBA sampling of protected meadows, using these regression equations. SCUBA sampling of this vulnerable meadow is undesirable due to its destructive impact on below- and above-ground biomass. Because of its destructive nature, SCUBA sampling typically limits the number of shoots that can be collected (Pergent et al. 1995; Gobert et al. 2020; Mutlu et al. 2023a).

Table 4

Equations established to convert leaf biomass based on leaf area (BLA in g/m², Equations 1) and leaf length (BL in g/m², Equations 2) to leaf area (LA in cm²/m²) and shoot density (SHT in shoots/m²) using the measured data in another study conducted along the entire Turkish Mediterranean coast in 2018–2019 (Mutlu et al. 2023a, b). Pearson correlation coefficients (r_1 and r_2 for equations 1 and 2, respectively, and bold values denote significantly correlated at $p < 0.05$) and sample size (n) based on the number of sampling stations.

Months	Equation 1	Equation 2	r_1	r_2	n
December/January	LA = 57.893*BLA + 1661	LA = 55.032*BL + 7004.9	0.9978	0.9885	47
	SHT = 0.189*BLA + 60.606	SHT = 0.1878* BL + 64.191	0.8893	0.9213	
June/July	LA = 47.903*BLA + 3327.7	LA = 51.8*BL + 1404	0.9788	0.9957	100
	SHT = 0.3596*BLA + 107.4	SHT = 0.3667* BL + 105.66	0.8535	0.8188	

Acoustic methods are more effective than other techniques (e.g., SCUBA, video, satellite) for mapping, estimating, and assessing biometrics in marine environments, particularly vegetation. The acoustic reflectivity of aquatic vegetation whose acoustic impedance is close to that of seawater (1.026; Kruss et al. 2012), is well known, and acoustics have been successfully used to detect SAV as backscatterers (Maceina and Shireman 1980). Quantifying vegetation biometrics acoustically remains challenging, especially for vegetative organisms. While leaf weight has recently been linked to the target strength of some algae, extending acoustic estimates to other biometrics (e.g., LAI, SHT) crucial for assessing marine ecological status is still developing.

Posidonia oceanica is among the most important Mediterranean seagrasses and has attracted significant research interest. Recent ex situ and in situ acoustic studies have related seagrass biometrics to elementary distance sampling units (EDSU; Simmonds and MacLennan 2005). Examples include studies on *Cladophora* sp. (Depew et al. 2009), *P. oceanica* and *Zostera marina* (Monpert et al. 2012), *P. oceanica* (Llorens-Escrich et al. 2021), *Saccharina japonica* (Shao et al. 2019), and *Sargassum horneri* (Minami et al. 2021). Several studies have calibrated acoustic data with biometrics of *P. oceanica* and

Cymodocea nodosa (Mutlu and Balaban 2018; Olguner and Mutlu 2020; Mutlu and Olguner 2023a, b) and have distinguished these two seagrass species acoustically in the Mediterranean Sea (Mutlu and Olguner 2023c).

Both acoustic and other remote sensing techniques have estimated the spatio-temporal distribution and leaf length of seagrasses. In the present acoustic estimates, the spatial distribution of the meadow remained generally invariant among months, possibly due to the sampling strategy of shifting acoustic tracklines 80 m eastward monthly, as well as to the variable biometric detection sensitivity of the echosounder over time. The spatio-temporal distribution estimated by SCUBA and acoustics varied by month and bottom depth. Temporal distribution corresponded with the monthly growth of below- and above-ground meadow parts within the detection limits of the echosounder. Below-ground parts initiated growth until January in relation to gemmation or runner reproduction, followed by above-ground growth until foliage emergence in late summer or early fall (Mutlu et al. 2022a). Sexual reproduction was nearly absent along the Turkish coast, with only a single flower observed in both the study area and the entire Turkish Mediterranean coast (Mutlu et al. 2022a; 2023b).

Due to the seasonal growth patterns and biomass strength, temporal variation was more pronounced for leaf biomass, LAI, and leaf length than for shoot density. Old leaves were shed during August–September (Balestri and Cinelli 2003). Furthermore, Mutlu (2023) discussed temporal detection limits of vertical rhizome growth using echosounder data processed by “POSIBiom,” which relates to rhizome growth dynamics (Mutlu et al. 2022a, 2023b). Mutlu and Olguner (2023) also demonstrated acoustic differentiation of the dominant seagrasses *P. oceanica* and *C. nodosa* along the Turkish Mediterranean coast.

Unlike gas-bearing organisms such as fish, whose elongated swim bladders provide omnidirectional acoustic signatures, the orientation of seagrasses on the bottom (Table A1) was less effective in acoustic discrimination because a large proportion of the submerged seagrass meadow was acoustically measured in its entirety (Mutlu and Olguner 2023c).

Through biometrics

The spatiotemporal distribution of *P. oceanica* along the Turkish coast is shaped by a combination of hydrographic, atmospheric conditions, and substrate types. Among these, substrate type has been identified as a primary factor influencing meadow recolonization via vegetative fragments, due to the development of specific seedlings and root hairs adapted to each substrate (Alagna et al., 2019; Balestri et al., 2015; Pereda-Briones et al., 2018; Tomasello et al., 2018). Consequently, the lower depth limit of the meadow depends on the presence or absence of particular substrate types.

Previous studies in the western Mediterranean reported lower depth limits between 0.5–1 m and 33–43 m regardless of substrate type (Colantoni et al., 1982; Marbà et al., 2002), and similar depth limits were observed in the eastern Mediterranean (Mutlu et al., 2023b). Mutlu et al. (2023b) studied a large area exposed to diverse atmospheric and hydrographic conditions, including variable water velocities, which also influence the spatial and temporal limits of meadow expansion and bathymetric distribution (De Falco et al., 2008; Montefalcone et al., 2019). For example, *Zostera marina* prefers sandy bottoms with water velocities around 14 cm·s⁻¹, *P. oceanica* around 20 cm·s⁻¹, and *Cymodocea nodosa* around 21 cm·s⁻¹ (Pereda-Briones et al., 2018). Moreover, *P. oceanica* meadows reduce water velocity, sediment erosion, and the dispersion of biogenic materials and carbonate particles (De Falco et al., 2003, 2008; Pereda-Briones et al., 2018).

Calcium carbonate content in sediment is a key factor determining the presence or absence of *P. oceanica* in Antalya Bay. For instance, the Antalya Gulf, which hosts a large *P. oceanica* bed, has high carbonate content (70–90% with calcite rock), whereas Finike Gulf and Kekova Bay, where *P. oceanica* is absent, have lower carbonate levels (14–18% and 10–30%, respectively). Kaş Bay, with moderate carbonate content (45–60%), contains a smaller *P. oceanica* bed (Yalçın et al., 2023; Mutlu et al., 2023a, b). *P. oceanica* utilizes calcium carbonate and carbon for leaf and rhizome development (Milliman, 1993; Canals and Ballesteros, 1997).

Environmental variables strongly influence meadow biometrics in the Mediterranean. Shoot density, for example, varies mainly by geographic coordinates and seabed depth, followed by wind, bottom type, and gradient (Catucci and Scardi, 2020; Gnisci et al., 2020). Sandoval-Gil et al. (2014) categorized meadows into shallow (5–7 m) and deep (18–20 m) water types,

with biometrics showing high variability at intermediate depths (15–20 m) throughout the year (Mutlu et al., 2022a, 2023b). A depth of approximately 15 m marks an exceptional zone with lower photosynthetic activity compared to shallower (5 m) and deeper (30 m) zones, likely due to variations in solar irradiance and photosynthetically active radiation (PAR) (Mutlu et al., 2022a).

Among biometric variables, leaf biomass which has rarely been considered in prior studies provides valuable seasonal information for assessing the health of littoral marine zones beyond leaf quality metrics. Seasonal leaf growth typically follows an annual cycle in healthy, pristine environments, excluding reductions from grazing or natural leaf loss (Lal et al., 2010; Steele et al., 2014; Mutlu et al., 2022a). However, this cycle is disrupted in degraded environments (e.g., Marbà et al., 1996; Guidetti et al., 2002; Sghaier et al., 2006; Pagès et al., 2012; Montefalcone et al., 2016).

Consistent with the present findings, SHT and LAI show no significant temporal (monthly) variation in healthy meadows (Bay, 1984; Wittmann, 1984; Guidetti et al., 2002). While LAI reflects seasonal growth dynamics, shoot density remains relatively stable over the year. LAI typically decreases significantly with increasing bottom depth (Gobert et al., 2003), as observed in this study. Leaf biomass, LAI, and shoot density distinguish shallow (≤ 10 m) from deep (≥ 20 m) *P. oceanica* meadows, aligning with Sandoval-Gil et al.'s (2014) classification. This differentiation corresponds to depth-dependent changes in leaf pigment concentration, photosynthetic efficiency, and light absorption capacity (Sandoval-Gil et al., 2014).

LAI was found to be 42% lower on rock compared to sand and mat substrates (Maida et al., 2013). Leaf area is reduced on rock relative to sand and mat, likely due to the need for enhanced anchorage and lower nutrient availability on rocky substrates (Giovannetti et al., 2008; Touchette and Burkholder, 2000). Substrate or habitat type contributes substantially to seagrass biometric variability. Throughout the Mediterranean, *P. oceanica* occupies diverse substrates including rock, mat, sand, and mud, with meadow coverage differing by substrate: rock (> 75%), sand/fine sand (50–75%), and eroded mat (Sgorbini et al., 2002). In the current study area, the meadow occurred exclusively on rock, while along the entire Turkish Mediterranean coast, *P. oceanica* inhabited all four substrate types. Such differences in substrate may alter acoustic impedance and affect reflectivity, potentially explaining discrepancies between measured and acoustically estimated biometrics. Notably, except for leaf length, other biometric variables showed no significant differences between measured and estimated values in this study.

SHT varied by bottom depth, substrate type, and region, with densities on hard substrates approximately double those on soft bottoms (Colantoni et al., 1982; Vacchi et al., 2012; Catucci and Scardi, 2020). Bottom depth also significantly influenced SHT, with a logarithmic decrease observed in the Gulf of Antalya (Mutlu et al., 2022a). Consistent with our results, Sghaier et al. (2013) reported the highest shoot densities on rocky bottoms. Interestingly, SHT was inversely related to leaf area among substrates, being higher on rock than mat or sand (Giovannetti et al., 2008). This discrepancy is attributed to phenotypic plasticity: individual shoots tend to grow larger on rock compared to sand or mat (Perez et al., 1994; Marbà and Duarte, 1998). SHT exhibited high variability on rock and sand during winter, but on rigid substrates (rock and mat) during summer, paralleling observations by Gnisci et al. (2020).

LL showed less clear classification by substrate and depth. LL decreased spatially with increasing bottom depth and depth-related environmental factors over time. It temporarily increased from winter (15°C) to spring (21°C) at salinities below 39 PSU, then decreased slightly by July (27°C, 39 PSU), and further declined during August–September (28–29°C) at salinities near 40 PSU in Antalya Gulf (Mutlu et al., 2022a). High mortality at elevated salinities has been documented (Fernandez-Torquemada and Sanchez-Lizaso, 2005), with LL decline continuing until December (18°C) (Mutlu et al., 2022a), in agreement with Vasapollo and Gambi (2012).

Overall, LL growth varies with leaf type, substrate, depth, and timing relative to temperature changes (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 turtles and fish also influence LL and leaf width (LW) (Lal et al., 2010; Steele et al., 2014). Generally, LL seasonality depends on: (i) leaf type, (ii) substrate, and (iii) bottom depth, triggered primarily by water temperature (Zupo et al., 1997). Mature leaves fluctuate between 20 and 70 cm during growth, with new leaves appearing in fall and late spring

and reaching peak length in July (Caye and Rossignol, 1983). Juvenile leaves are shortest in winter, while intermediate and adult leaves peak in spring and summer, respectively (Guidetti et al., 2002; Koçak et al., 2011). Leaf length is generally shorter on rock than on sand or mat substrates (Maida et al., 2013). The longest leaf lengths occur at 10 m depth in June–July and at 30 m with a two-month delay (Bay, 1984; Via et al., 1998; Sghaier et al., 2006), likely due to reduced hydrodynamic forces at greater depths decreasing leaf shedding (Gambi et al., 1989).

To Ecology

The interannual dynamics of *P. oceanica* are influenced primarily by nutrient availability, carbon, and light conditions (Alcoverro et al., 1997; Gobert et al., 2003). Ecologically, spatial factors, particularly bottom depth, followed by temporal factors such as season (months) and associated water temperature, play key roles in shaping the biometrics-environment relationship for both measured and acoustically estimated data, as demonstrated by redundancy analysis (RDA).

Population and biometric dynamics are predominantly driven by bottom depth, with season exerting a secondary influence. This translates into distinct seasonal patterns within discrete depth zones: shallow waters (5–10 m), a transition zone (~ 15 m), and deeper waters (20–30 m). The effect of bottom depth on seagrass biometrics has been well documented, affecting variables such as SHT, LW, vertical rhizome length, and number of leaves (Mutlu et al., 2022a). Notably, samples from the transition zone were broadly scattered around the center of the RDA axes, indicating high dynamism and complexity in biometric variation linked to seasonal effects. Pirc (1986) previously identified 15 m as an exceptional depth with reduced photosynthetic activity compared to 5 m and 30 m, likely due to increased solar irradiance.

GAM analyses further clarified these relationships. When depth effects were excluded, salinity showed a negative influence on density biometrics (both above- and below-ground portions), whereas water density and optical depth (measured by Secchi depth, not PAR) positively influenced them. Additionally, below-ground components were positively affected by near-bottom oxygen concentrations.

LL was more sensitive to environmental parameters than density metrics. Negative effects on leaf length growth were associated with water temperature, sediment total carbonate (CaCO_3), sediment silt content, seawater phosphate, and PAR. Conversely, Secchi depth, nitrogen-based nutrients (excluding ammonium), and pH exerted positive effects. It is important to note that light reaching the leaves can be further reduced by shading from leaves and epiphyte canopies (Via et al., 1998), especially during summer and fall (May–August/October), when shading intensifies despite high growth rates (Ruiz and Romero, 2001).

P. oceanica utilizes calcium carbonate and carbon in the development of leaves and rhizomes (Milliman, 1993; Canals and Ballesteros, 1997). Nitrogen availability in seawater has differential effects: it negatively affects leaf width but positively influences the number of leaves per shoot. Nutrient deficiencies, more pronounced in fall, limit growth, with seasonal nutrient limitation particularly evident in late spring and summer (Alcoverro et al., 1997).

Inter-shoot distance was significantly correlated with water optical properties, many sea surface and near-bottom physical parameters, sea surface phosphate (PO_4), and near-bottom nitrite plus nitrate ($\text{NO}_2 + \text{NO}_3$) concentrations. Nitrogen uptake by roots occurs mainly during winter and early spring when nutrient concentrations are elevated (Lepoint et al., 2002), consistent with observations in the present study. Ammonium (NH_4) is a particularly important nitrogen source, being utilized by *P. oceanica* roots up to six times more efficiently than nitrate (NO_3) (Lepoint et al., 2002).

Temporal nutrient deficiencies in fall reduce meadow growth, with nutrient limitation more pronounced in late spring and summer (Alcoverro et al., 1997). Nodal (inter-shoot) distance is influenced by optical and physicochemical water parameters, primarily temperature, salinity, phosphate, and nitrite + nitrate (Mutlu et al., 2022a). The temporal pattern of nutrient usage by the meadow involves nitrogen uptake mainly via roots in winter and early spring, when water concentrations peak (Mutlu et al., 2022a).

GLMs revealed linear relationships between leaf biomass, shoot density, and environmental parameters, but not for leaf area index (LAI) or leaf length. This suggests environmental parameters exert a partially linear influence on biometrics up to certain quantitative thresholds annually, beyond which effects may reverse. Redundancy analysis supported these findings, except for CaCO_3 , which had a consistently positive effect on all biometrics. This positive effect was stronger in measured data compared to estimated data.

High leaf calcification occurs during May–August, coinciding with peak photosynthetic activity (Mateo et al., 1997; Enriquez and Schubert, 2004). Beyond its physiological role, CaCO_3 alters acoustic impedance and reflection coefficients due to differences in density and sound velocity between water and carbonate materials, making it a strong acoustic scatterer (Mavko et al., 1998; Merriam, 1999).

Regarding additional biometrics not addressed in the current study, physical parameters and nutrients, especially nitrogen, govern factors such as leaf number (Mutlu et al., 2022a). Optical water properties influence inter-shoot distance, while leaf width correlates with sediment total organic carbon (TOC). Sediment TOC also negatively affects temporal and seasonal dynamics of rhizome-related biometrics (Mutlu et al., 2022a). Leaf length correlates with water pH and nitrogen content; vertical rhizome length relates to water temperature and density, while shoot density correlates only with water density (Mutlu et al., 2022a).

Declarations

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CRediT authorship contribution statement

Erhan Mutlu: Conceptualization, Formal analysis, Funding acquisition, Methodology, Supervision, Software, Project administration, Validation, Writing – review & editing, Writing – original draft, Visualization. **Cansu Olguner:** Data curation, Resources, Investigation. **Yaşar Özvarol:** Data curation, Investigation, Resources. **Mehmet Gökoğlu:** Resources, Investigation, Data curation.

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Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

Consent to participate All authors declare their participation in the study and the development of the manuscript herein.

Data Availability

Data will be made available on request.

Competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Erhan Mutlu reports financial support was provided by the Scientific and Technical Research Council of Turkey (TUBITAK), Turkey.

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Figures

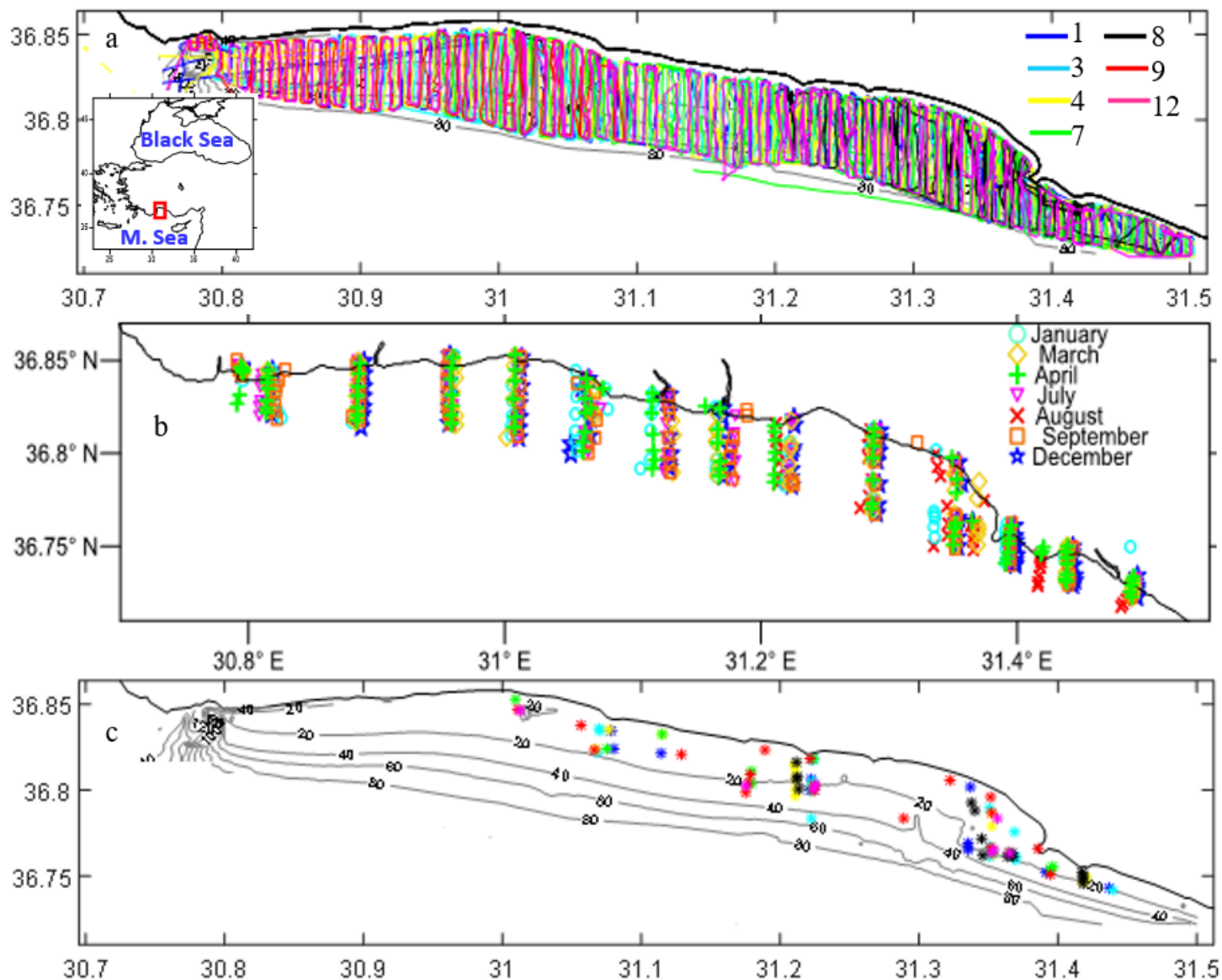


Figure 1

Monthly acoustical trackline (a), SCUBA sampling for the biometrics and enviromental variable measures (b), and SCUBA sampling stations where *Posidonia oceanica* was present and batimetrical contours of bottom depth measured by the acoustics (c).

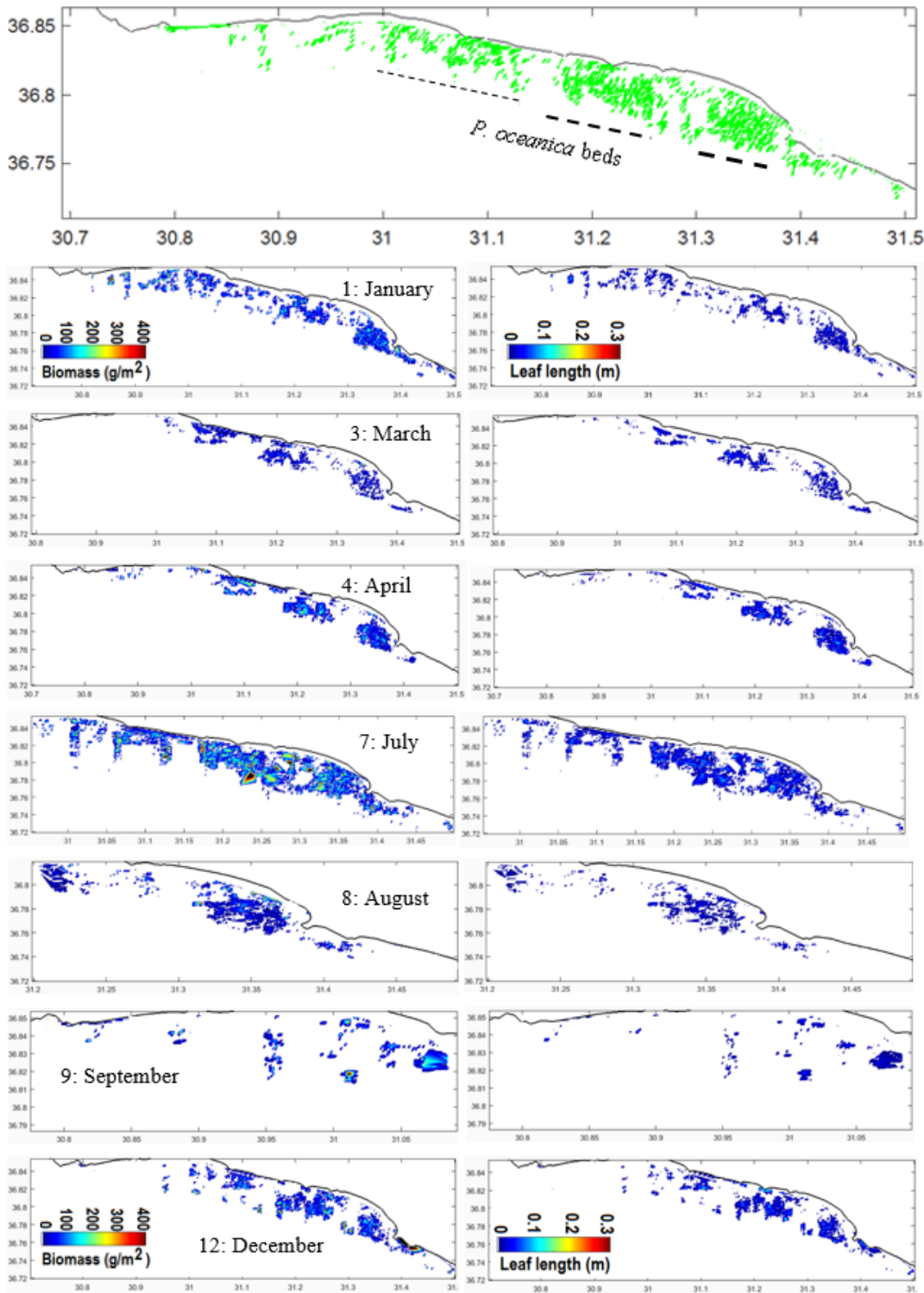


Figure 2

Distributional mapping (the thicker there is a dashed line present on the map the larger and denser *P. oceanica* covers a continuous area at the beds) estimated for *P. oceanica* using all monthly pooled acoustical data, monthly leaf biomass, and length estimates in the study area.

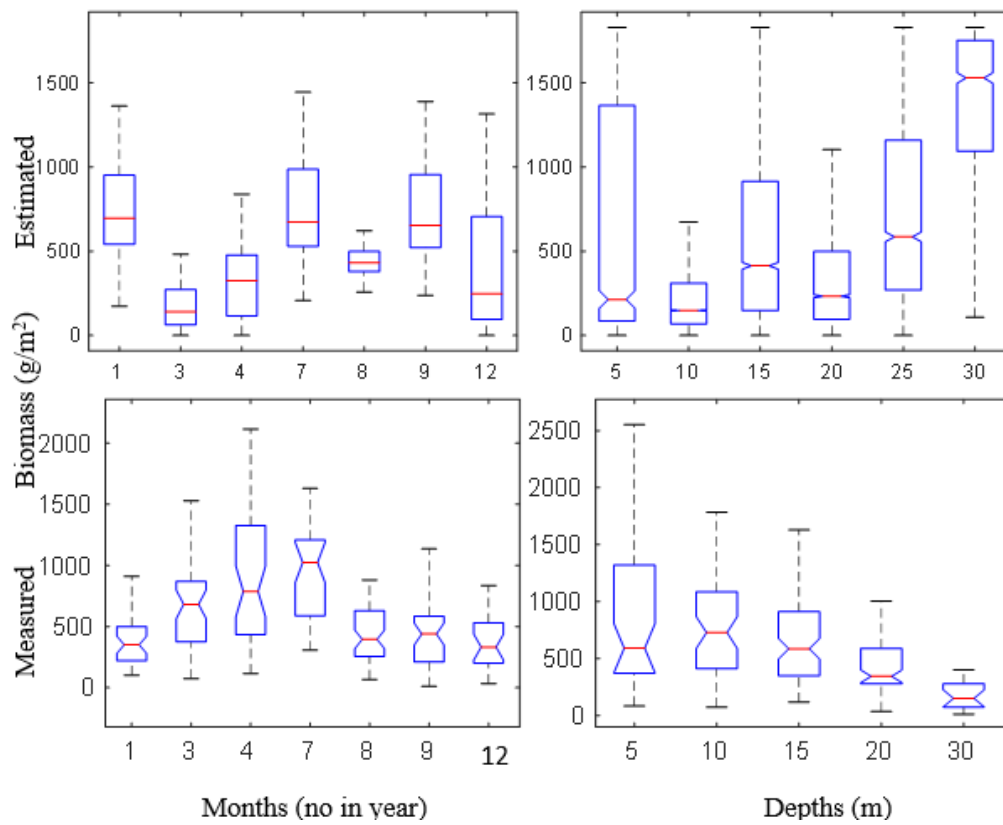


Figure 3

Box plots of estimated and measured leaf biomass by months and bottom depths where *P. oceanica* was present.

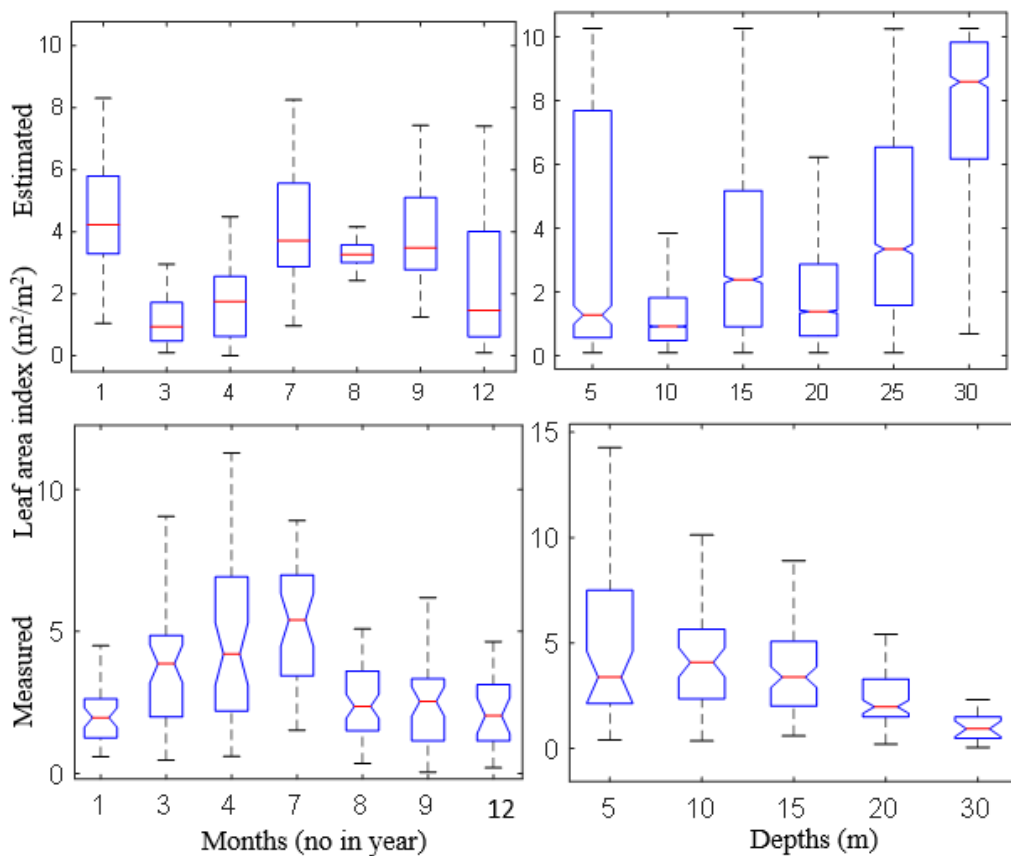


Figure 4

Box plots of estimated and measured leaf area index by months and bottom depths where *P. oceanica* was present.

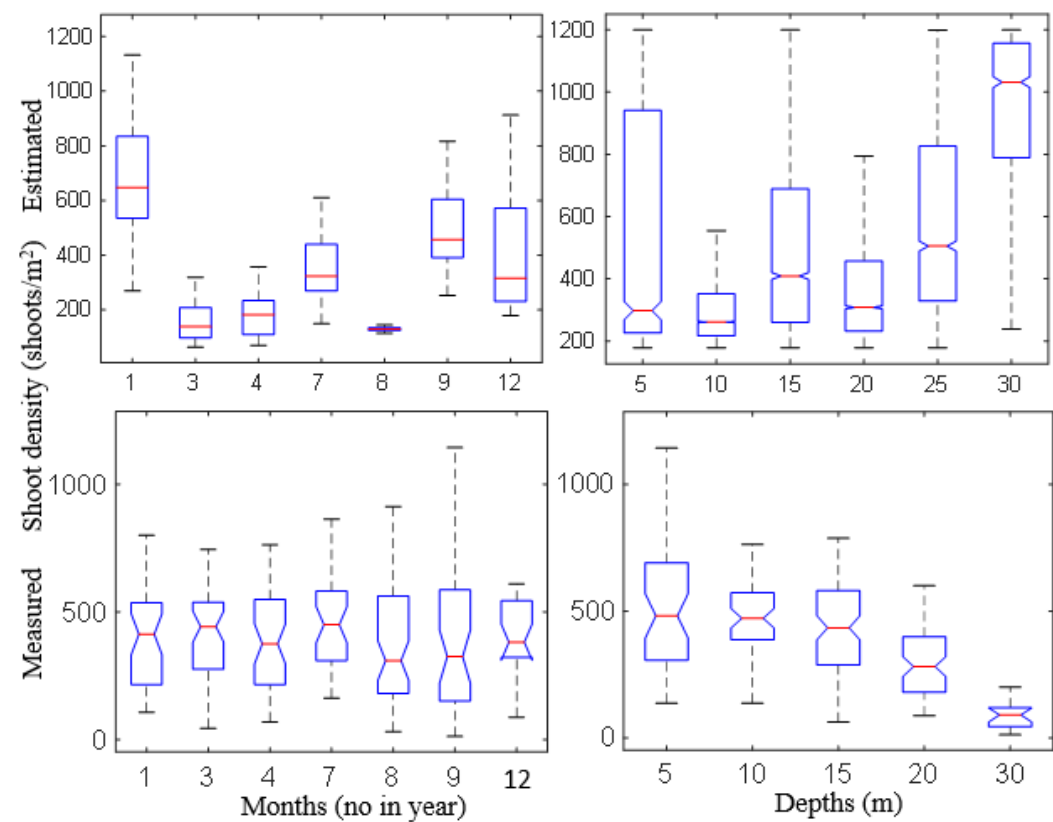


Figure 5

Box plots of estimated and measured shoot density by months and bottom depths where *P. oceanica* was present.



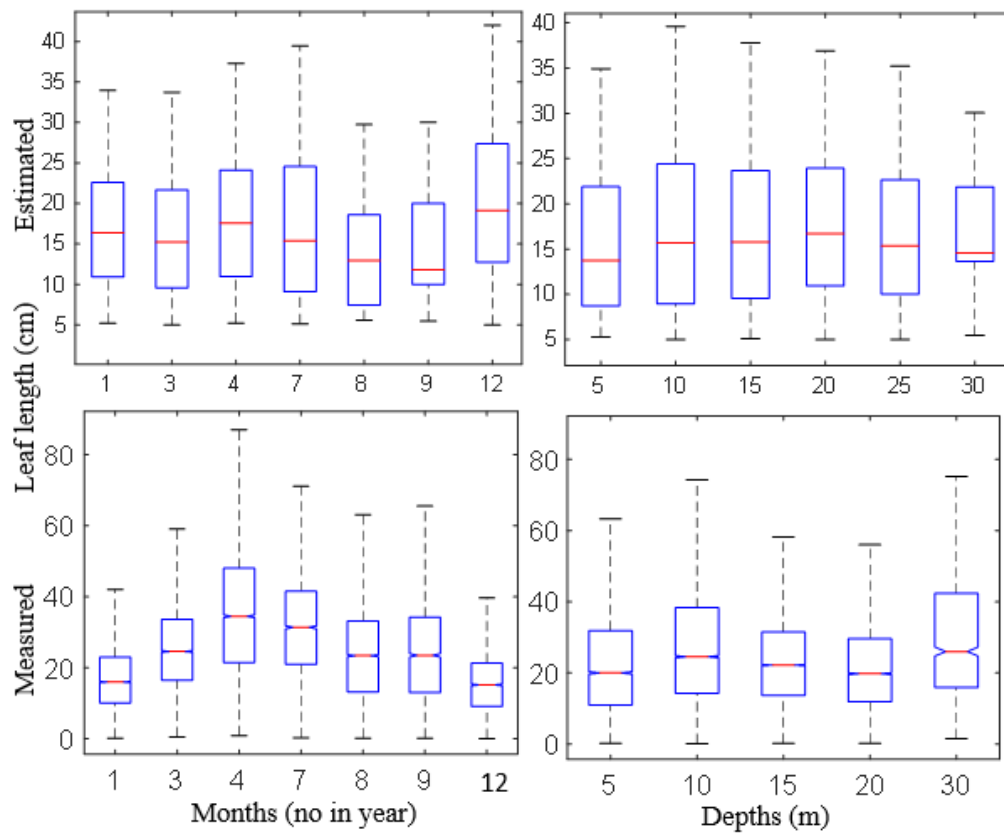


Figure 6

Box plots of estimated and measured leaf length by months and bottom depths where *P. oceanica* was present.

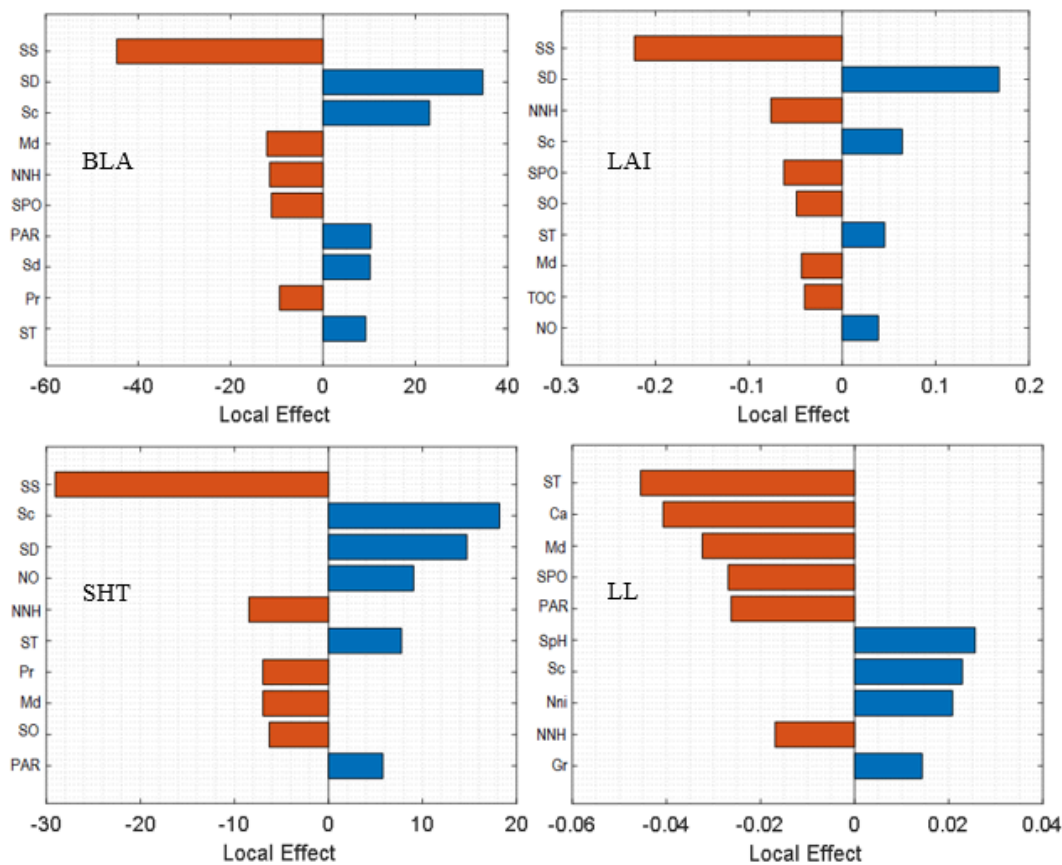


Figure 7

Generalized Additive Model solution to detect the effect of the environmental parameter (T; temperature, pH; pH, S; salinity, O; oxygen, D; density, ni; NO₂+NO₃, NH; NH₄, PO; PO₄ of the sea surface with a prefix of S, and near-bottom water with N, PAR; Photosynthetically Active Radiation, Pr: a depth where PAR value reached %1, Sc; Secchi disk depth of the water column, and Gr; gravel, Sd; sand, Md; mud, TOC; TOC, Ca; total carbonate, CaCO₃ of sediments) on the estimated biometrics (BLA: leaf biomass in g/m², LAI: leaf area index in m²/m², SHT: shoot density in shoot/m², and LL: leaf length in m).

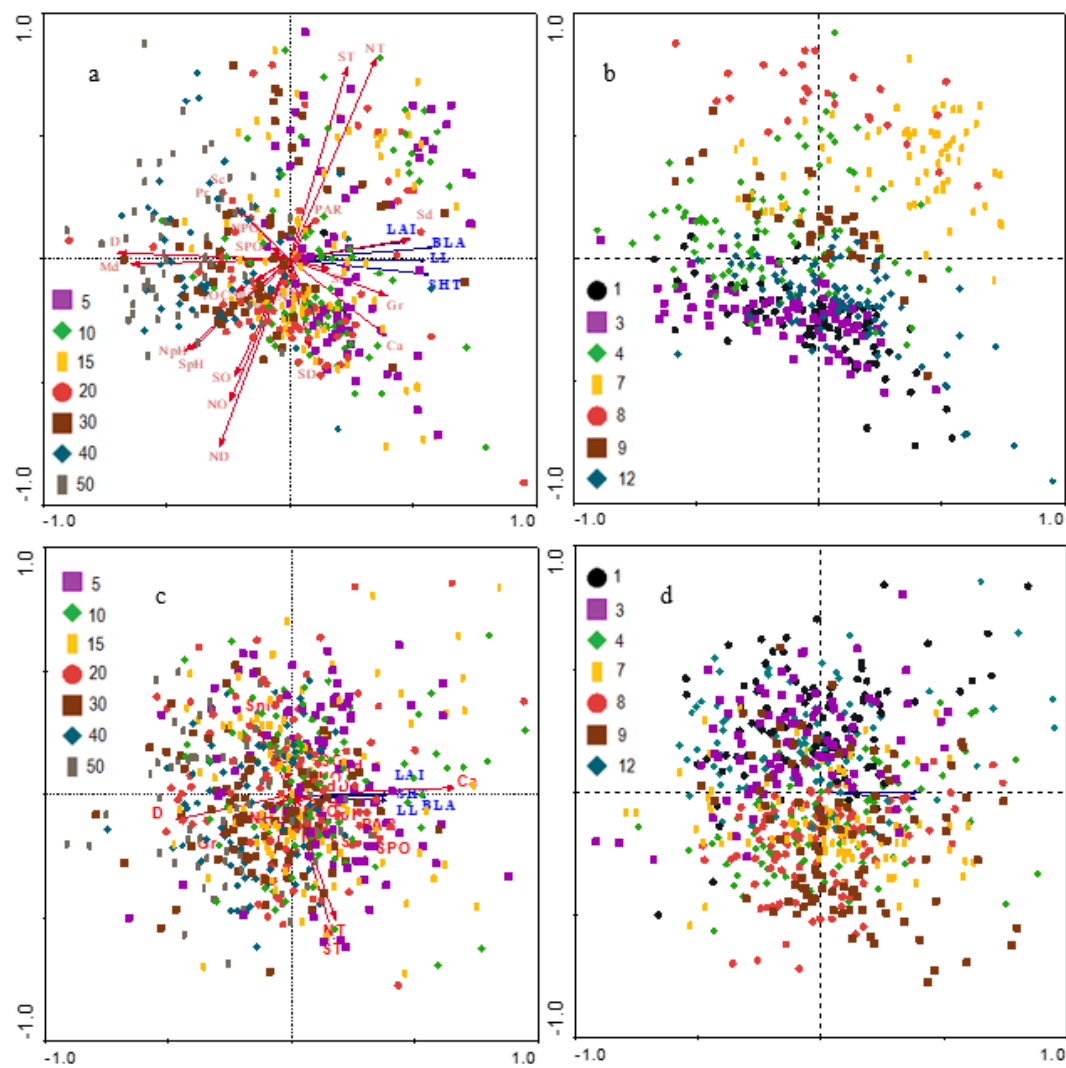


Figure 8

RDA triplot of stations classified by the bottom depths (a, c) and the months (b, d) with the environmental parameters (T; temperature, pH; pH, S; salinity, O; oxygen, D; density, ni; NO₂+NO₃, NH; NH₄, PO; PO₄ of sea surface with a prefix of S, and near-bottom water with N, PAR; Photosynthetically Active Radiation, Pr: a depth where PAR value reached %1, Sc; Secchi disk depth of the water column, and Gr; gravel, Sd; sand, Md; mud, TOC; TOC, Ca; total carbonate, CaCO₃ of sediments) in RDA solving the estimated (a, b) and measured (c, d) biometrical parameters (BLA: leaf biomass in g/m², LAI: leaf area index in m²/m², SHT: shoot density in shoot/m², and LL: leaf length in m) with the values on monthly average for each sampling station (Fig. 1b).

Supplementary Files

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