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Research Article

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Spatial and depth-related variation in the less-mobile vagile crustacean associates of *Posidonia oceanica* (L.) Delile in seagrass meadows on the Turkish coast of the Aegean Sea

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ABSTRACT

We conducted quantitative and qualitative sampling of the less-mobile (vagile) crustaceans associated with *Posidonia oceanica* (L.) Delile in seagrass meadows in the Turkish Aegean Sea. We sampled 29 stations that revealed more than 35,000 individuals of 199 species belonging to seven orders, 73 families, and 119 genera of crustaceans including eight species recorded for the first time on the Turkish Aegean coast. Two introduced species, *Ampithoe bizseli* Özaydinli & Coleman, 2012 (Amphipoda) and *Processa macrodactyla* Holthuis, 1952 (Caridea), and one wood-boring species of *Limnoria* Leach, 1814 (Isopoda) were collected. Amphipods, isopods and decapods were the most dominant groups at all depth ranges. Amphipods were the most abundant group at 0–5 m, tanaids at 6–15 m, with *Chondrochelia savignyi* (Kroyer, 1842) the most common species. Multivariate analyses detected significant regional structuring, with four main station clusters emerging characterized by a few widespread amphipod taxa. No significant correlations were observed between physicochemical variables and community descriptors. Results demonstrate high crustacean diversity, clear spatial structuring, and emerging ecological pressures, emphasizing the need for targeted monitoring and proactive conservation to safeguard the ecological integrity of *P. oceanica* meadows.

KEYWORDS: Amphipoda, biodiversity, community composition, Crustacea, introduced species, Isopoda, spatial structure, Tanaidacea

INTRODUCTION

Posidonia oceanica (Linnaeus) Delile, a seagrass native to the Mediterranean Sea, plays a crucial role in coastal ecosystems and is protected under the 1976 Convention for the Protection of the Mediterranean Sea Against Pollution (Barcelona Convention). The species thrives along coasts to depths of 48 m (Augier & Boudouresque, 1979; Boudouresque *et al.*, 2012). It is recognized as an 'ecosystem engineer' because of its vital contributions to ecological functions. The dense patches it forms provide essential habitats for numerous marine animals, serving as nursery grounds, feeding areas, shelters, and reproduction sites. Seagrasses function as primary producers, supporting marine food web and contributing to oxygen production through photosynthesis. Their extensive root systems also play a crucial role in preventing underwater erosion and stabilizing nutrient levels within the surrounding environment (Boudouresque *et al.*, 2012).

Crustaceans are integral inhabitants of *P. oceanica* meadows and play key roles in nutrient cycling and trophic interactions. Their activities, which include detritivory, herbivory, and predation, contribute to organic matter decomposition, nutrient recycling, and energy transfer within the ecosystem (Mazzella *et al.*, 1992). Various amphipods and isopods break down plant material, including seagrass detritus, accelerate mineralization, and allow primary producers to take up nutrients more efficiently. Higher trophic-level crustaceans, particularly decapods, serve as prey for fishes and other marine predators, linking benthic and pelagic food webs (Gambi *et al.*, 1992; Mazzella *et al.*, 1992).

Numerous studies have documented the crustacean fauna living in *P. oceanica* meadows, particularly along the western Mediterranean (Mazzella *et al.*, 1989; García Raso, 1990; Gambi *et al.*, 1992; García Raso *et al.*, 1996; Sánchez-Jerez & Ramos Esplá, 1996; Sánchez-Jerez *et al.*, 1999; Como *et al.*, 2008; Terlizzi *et al.*, 2010; Zakhama-Sraieb *et al.*, 2011; Bedini *et al.*, 2011, 2015; Belgacem *et al.*, 2011; Michel *et al.*, 2015; Sturaro *et al.*, 2015; Bellisario *et al.*, 2016; Mateo-Ramírez *et al.*, 2016; Camisa *et al.*, 2017). The distribution of crustaceans in these meadows is well documented, whereas studies in the eastern Mediterranean, particularly along the Turkish coasts, remain limited. The first such study (Holthius, 1961) identified 27 decapod species at 0–1 m depth. Subsequent investigations recorded 40 amphipod species

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at depths of 2–5 m (Katağan *et al.*, 2001) and 69 decapod species at depths of 5–38 m (Ateş *et al.*, 2004a) on the Turkish Aegean coast.

Our study aimed to address this knowledge gap by analyzing the spatial and depth-related variations in the less mobile crustacean communities within *P. oceanica* meadows in the eastern Mediterranean. Multi-dimensional community analyses (e.g. PERMANOVA, clustering, and SIMPER) were employed to uncover underlying ecological patterns and assess the effects of environmental gradients on species composition and distribution.

MATERIAL AND METHODS

Study area and sampling

The study was conducted from May to August 2016 at 29 stations along the Turkish Aegean coast, from Ibrice Harbor (Enez) in the north to Turunç (Marmaris) in the south (Fig. 1). We collected samples at 0–5 m and 6–15 m, depending on local conditions. We recorded coordinates using global positioning system (GPS) to ensure spatial accuracy. Most stations were sampled at both depth ranges; however, some locations (Geyikli, Babakale, and Mordoğan) were restricted to a single depth range because of environmental constraints (Supplementary material Table S1).

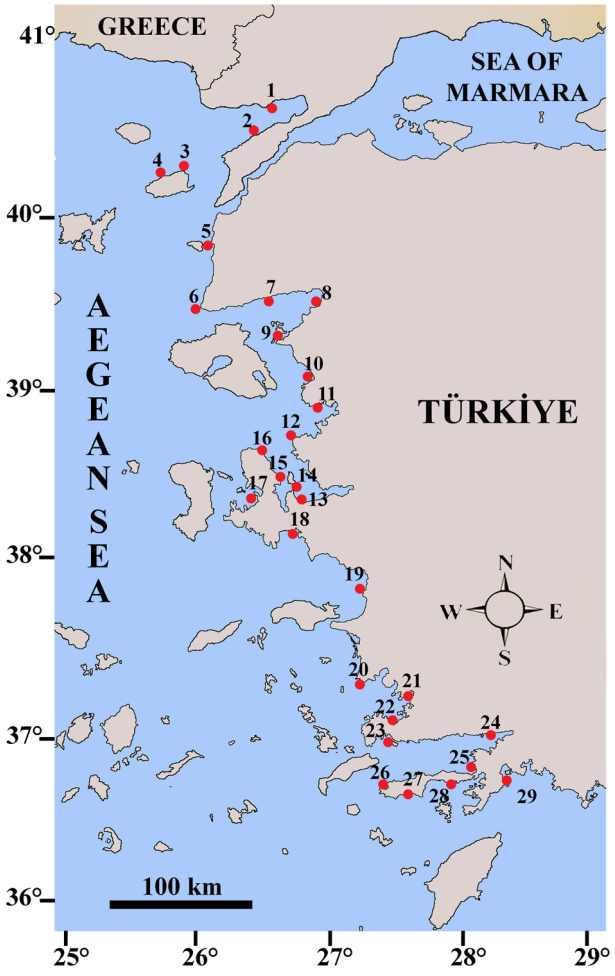


Figure 1. Study area along the Aegean coast of Turkey. The numbered red dots represent the 29 sampling stations.

The Turkish Aegean coast is a transitional marine region influenced by the Black Sea and the Levantine Sea, the easternmost portion of the Mediterranean, as well as by the outflow of the Black Sea through the Dardanelles Strait. These hydrographic interactions create a north-south physicochemical gradient, characterized by progressive changes in temperature and salinity (Eronat & Sayin, 2014), which are known to shape benthic community composition and species distribution (Okoro *et al.*, 2024; Feng *et al.*, 2025).

To evaluate how these environmental transitions affect the composition of benthic assemblages, the coastline was divided *a priori* into five regions (A–E) (Supplementary material Table S1) before data analysis. This division was based on the positions of major gulfs, regional hydrodynamic patterns, and coastal population density, providing a geographically and ecologically meaningful framework for comparison. Accordingly, the five regions (A–E) encompass distinct environmental settings from north to south, reflecting variability in hydrographic conditions and potential anthropogenic pressures: Region A (Saros Bay), influenced by colder, less saline inputs from the Black Sea; Region B (Edremit Bay), moderately affected by Black Sea water; Region C (Izmir Bay), subject to heavy ship traffic and high population density; Region D (Kuşadası to Bodrum), intensive tourism area; Region E (Gökova Bay). influenced by warmer, saltier Levantine water.

We sampled *P. oceanica* meadows by scuba diving at predefined regions and depth intervals. For qualitative sampling, we randomly collected *P. oceanica* shoots from different patches within each station to represent habitat composition and structural variability. This sampling design aimed to capture the natural heterogeneity of the *P. oceanica* meadows, ensuring that the collected samples were representative of each habitat.

For quantitative sampling, we used a 20 × 20 cm quadrat with three replicates per station. We used a spatula to scrape the material, which consisted of seagrass leaves, rhizomes, and roots but did not include sediment. This sampling strategy was primarily designed to characterize less mobile crustacean fauna, such as amphipods, isopods, and tanaids. Highly mobile epifaunal crustaceans (e.g. caridean and penaeoid shrimps, stomatopods, and swimming crabs), however, may have escaped during sampling and are therefore likely underrepresented in the dataset. We placed the collected material into cloth bags and immediately preserved all samples in a 4% seawater-formalin solution in the field before transporting them to the laboratory.

Physicochemical variables were parameterized from the surface water at all stations to analyze water quality. We measured temperature, salinity, and conductivity using a YSI Model 30 SCT Meter (YSI, Yellow Springs, OH, USA), dissolved oxygen and pH with a YSI Model 55 oxygen meter and a YSI Model 100 pH meter, respectively.

The samples were rinsed in the laboratory with fresh water through a 0.5 mm mesh sieve. We sorted specimens into taxonomic groups, identified them, and counted them using stereoscopes and compound microscopes. We preserved all specimens

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in 70% ethanol and deposited them at the Institute of Marine Science and Technology, Dokuz Eylul University.

Statistical analysis

Occurrence of crustaceans was analyzed using Soyer's frequency index (Fi%) (Soyer, 1970), species dominance via the quantitative dominance index (D%) (Bellan-Santini, 1969). The frequency index was calculated as Fi% = (m/M) × 100, where m represents the number of samples containing a given species and M the total number of samples. According to Soyer's classification, species with Fi% ≥ 50 are considered constant, 50 > Fi% ≥ 25 are common, and Fi% < 25 are rare. Dominance was expressed as D% = (a/A) × 100, where a is the total number of individuals of a given species and A the total number of individuals of all species across stations. We evaluated species diversity and evenness using the Shannon-Weaver diversity index (H′) and Pielou's evenness index (J′) (Clarke *et al.*, 2014; Clarke & Gorley, 2015). We square-root transformed species-by-sample abundance data to down-weight dominant taxa. We then computed a Bray-Curtis resemblance matrix from the transformed data and used this same matrix for all multivariate tests and ordinations to ensure methodological consistency.

We analyzed the effects of region, depth, and their interaction using PERMANOVA (Anderson, 2001). We performed the analysis using Type III (partial) sums of squares and permuted residuals under a reduced model, with a total of 999 permutations. We treated depth ranges (0–5 m and 6–15 m) as a fixed factor and the sampling regions (A–E) as random factors. We further examined significant terms through pairwise PERMANOVA using the same data matrix.

We visualized the results of the PERMANOVA pairwise comparisons using an interactive heatmap created on the Flourish Studio platform (https://app.flourish.studio/). Each cell in the matrix represents a pairwise comparison between regions, with colors indicating significance levels ($P < 0.05$* and $P < 0.01$**). This visualization highlighted patterns of community dissimilarity detected by the PERMANOVA tests and facilitated the interpretation of spatial trends in crustacean assemblages.

We analyzed group dispersions for homogeneity using PERMDISP (Anderson, 2006) to differentiate between location (centroid) and dispersion effects. We calculated Bray-Curtis distances and projected them using principal coordinates analysis (PCoA) to determine group centroids and mean distances to the centroid.

We conducted ordination of the multivariate dataset through two-dimensional non-metric multidimensional scaling (nMDS) based on the Bray-Curtis similarity matrix (Kruskal, 1964) to visualize patterns of similarity among samples and to illustrate the results of the PERMANOVA tests. We considered stress values < 0.2 as acceptable representations of two-dimensional configurations.

To further explore community patterns, we performed hierarchical cluster analysis using group-average linkage on the same Bray-Curtis similarity matrix to group stations with similar community structures (Bray & Curtis, 1957). We subsequently applied the similarity percentage analysis (SIMPER) routine to identify the species contributing most to within-group similarity and between-group dissimilarity.

We tested relationships between physicochemical variables (temperature, salinity, dissolved oxygen, conductivity, and pH) and community descriptors (the number of species the number of individuals H′, and J′) using Spearman's rank correlation coefficient (Gaddis & Gaddis, 1990).

We performed all multivariate statistical analyses using PRIMER v6 with PERMANOVA+ add-on and STATISTICA 7 (Clarke *et al.*, 2014; Clarke & Gorley, 2015).

RESULTS

Faunistic analysis

We collected less-mobile crustacean samples from the 29 stations revealing 199 species from 119 genera, 73 families, and seven orders, comprising 35,811 individuals (Supplementary material Table S2). Most specimens were identified to the species level, but some could only be identified to the genus level due to damage or incompleteness.

We recorded four species of amphipods (*Gammaropsis crenulata* Krapp-Schickel & Myers, 1979; *Iphimedia gibbula* Ruffo & Schiecke, 1979; *Neoischyrocerus inexpectatus* (Ruffo, 1959); *Microprotopus maculatus* Norman, 1867), three isopods (*Gnathia dentata* (Sars, 1872); *Idotea pelagica* Leach, 1816; *Stenosoma lancifer* (Miers, 1881), and one caridean shrimp (*Processa robusta* Nouvel & Holthuis, 1957) as new records for the Turkish Aegean coast. The amphipods *G. crenulata*, *I. gibbula*, *N. inexpectatus*, and *M. maculatus* were found within the 0–5 m depth range, whereas the isopod *G. dentata* occurred in both depth ranges. The isopods *I. pelagica* and *S. lancifer* were only found in the qualitative samples collected from both depth ranges (Supplementary material Table S2). *Processa robusta* was found at northern stations (5 and 8) in both quantitative and qualitative samples, and at stations 1 (0–5 m) and 19 (6–15 m).

We identified two introduced species, the amphipod *Ampithoe bizseli* Özaydinli & Coleman, 2012 and the caridean shrimp *Processa macrodactyla* Holthuis, 1952, as rare based on their Fi%. *Ampithoe bizseli* was absent from Site A but occurred at all the other sites, with D% of one, whereas *P. macrodactyla* (0.1 D%) was found at all sites except Site B.

An unidentified species of *Limnoria*, a wood-boring isopod, was found within the sheaths of *P. oceanica* leaves, where it formed branching tunnels. It was present in qualitative and quantitative samples across all the sites except for stations 20, 21, and 27. We also found the isopod *Janira maculosa* Leach, 1814, which was not previously reported as a wood-boring crustacean, within the cavities formed in the leaf sheaths.

Qualitative analysis

We identified 160 crustacean species belonging to seven orders, 66 families, and 100 genera from qualitative sampling, comprising 14,778 individuals collected from 28 stations (Supplementary material Table S2) as no qualitative sampling was conducted at the Ildır station. We recorded the highest number of species within the 0–5 m depth range at station 18 (48 species) and in Region D (82 species), in the 6–15 m depth range, the highest diversity was at station 19 (52 species) and in Region A (74 species) (Supplementary material Table S2).

Based on Fi%, we classified 18 species as constant, 23 as common, and 97 as rare in the 0–5 m depth range, 20 as constant, 22 as

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common, and 82 as rare in the 6–15 m depth range (Supplementary material Table S2).

Quantitative analysis

From the quantitative samples, we identified 174 crustacean species belonging to seven orders, 71 families, and 111 genera, comprising 21,033 individuals collected from 24 stations (Supplementary material Table S1) as no quantitative sampling was conducted at 2, 10, 13, 15 and 25 stations. Amphipods, decapods, and isopods were the most dominant groups in both depth ranges, respectively. Amphipods constituted the most abundant group in the 0–5 m depth range (50.5%), followed by tanaids (27.3%) and isopods (14.2%), but, a shift to tanaids (36.9%), amphipods (33.1%), and isopods (18.1%) in 6–15 m (Fig. 2).

According to Fi%, 25 species were classified as constant in the 0–5 m depth range, and 29 in 6–15 m, 28 in 0–5 m, and 24 in 6–15 m. The rare category included 91 species in the 0–5 m depth range and 81 in 6–15 m (Supplementary material Table S2). The tanaid *Chondrochelia savignyi* was the most dominant species in both depth ranges.

We observed variation in the mean values of the community descriptors across the five regions and two depth ranges. We recorded the highest mean number of species (28.4) and individuals (66.6) in Region D at the 6–15 m depth range. The highest diversity ($H' = 4.93$) and evenness ($J' = 0.98$) in Region A at the 6–15 m depth range (Fig. 3).

PERMANOVA detected a significant regional effect on the number of species (Pseudo-F = 3.927, $P = 0.004$), whereas Depth and the Region × Depth interaction were not significant ($P = 0.121$ and $P = 0.082$) (Table 1). Pairwise tests showed that the regional signal was driven mainly by contrasts involving Region E, with D–E and B–E significant ($P < 0.01$) and A–E and C–E marginal ($P \approx 0.06$); all other pairs were non-significant (Fig. 4; Supplementary material Table S3). The PERMDISP indicated unequal within-region dispersion ($P < 0.05$). We found the highest dispersion in Region A (mean distance to centroid 9.42) and the lowest in Region B (3.31). Pairwise PERMDISP confirmed that B differed in dispersion from A, C, D, and E ($P \leq 0.014$), while D and E exhibit similar dispersion ($P = 0.606$).

We attribute the strong D–E separation in PERMANOVA primarily to centroid (location) differences, whereas the B–E separation likely reflects both location and dispersion effects. Consistent with these results, the nMDS ordination (2-D stress = 0.01) shows Region E displaced relative to the other regions, Region B forming a compact cluster, and Region A appearing more heterogeneous with a few outlying samples (Fig. 5). These results reveal clear regional structuring of the number of species, dominated by contrasts with Region E, with dispersion heterogeneity, particularly the compactness of B and the variability of A, modulating some pairwise outcomes.

PERMANOVA indicated a strong regional effect on the number of individuals (Pseudo-F = 6.333, $P < 0.01$), whereas Depth and the Region × Depth interaction were not significant ($P = 0.066$ and $P = 0.127$, respectively) (Table 1). Pairwise contrasts revealed significant differences for D–E ($P < 0.01$) and B–D ($P < 0.01$), with additional separations for A–D, B–E, C–D, and C–E

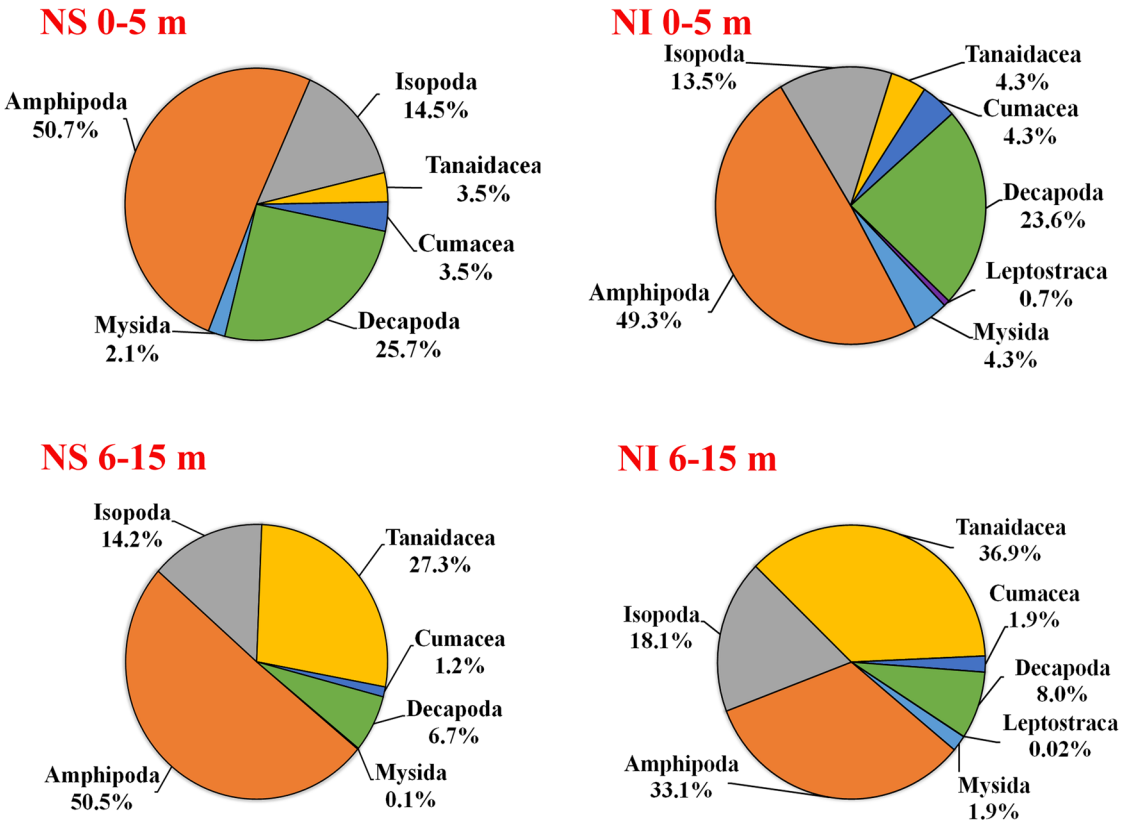


Figure 2. Relative dominance of crustaceans associated with *Posidonia oceanica* meadows by order based on the number of species (NS) and individuals (NI) at two depth ranges (0–5 m and 6–15 m).

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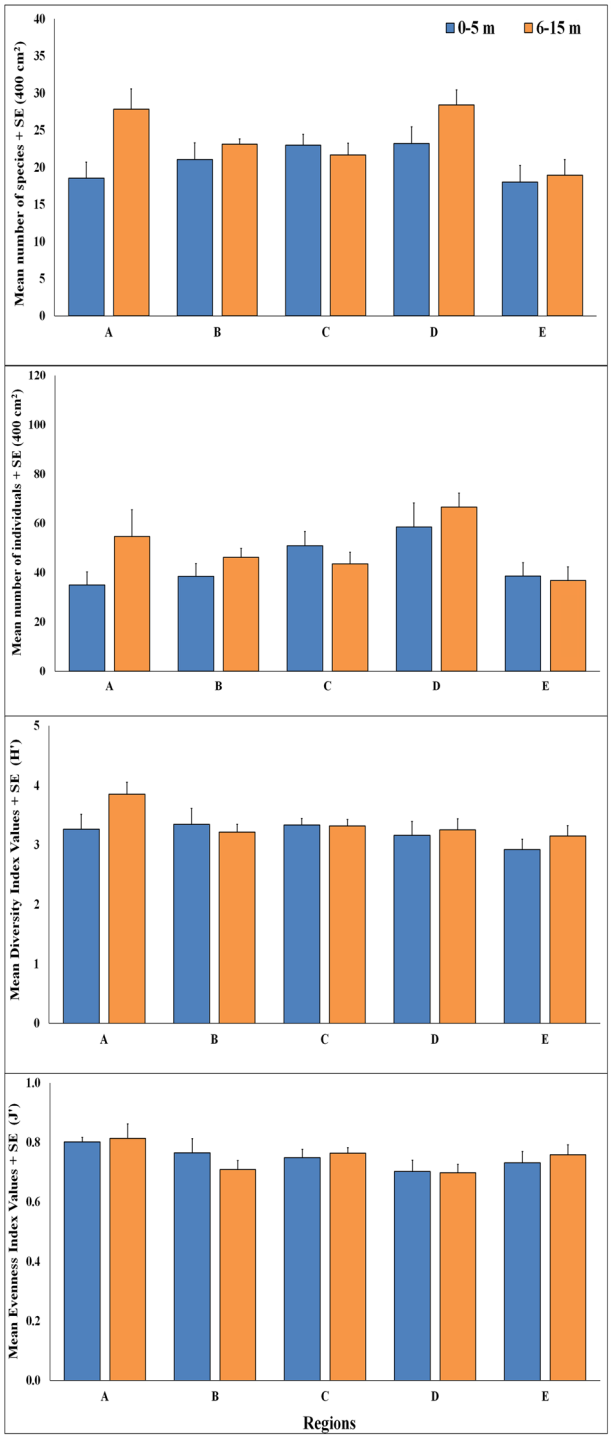


Figure 3. The mean number of crustacean species and individuals associated with *Posidonia oceanica* meadows and the diversity and evenness indices at the regions according to depth ranges. The line above each bar represents the + standard error.

($P < 0.05$); all other pairs were non-significant (Fig. 4; Supplementary material Table S3).

The PERMDISP based on the number of individuals was not significant overall ($F = 2.63$, $P = 0.093$), indicating that the regional effect mainly reflects centroid (location) differences. Pairwise PERMDISP suggested larger dispersion in Region E relative to Regions B ($P = 0.021$) and C ($P = 0.047$), whereas other comparisons were non-significant; we interpreted these differences cautiously given the non-significant omnibus test. The nMDS ordination (Stress = 0.01) supports these results, showing Region D (and part of E) displaced relative to the remaining regions, with B and C forming comparatively compact clusters (Fig. 6).

PERMANOVA detected no significant effects of Region (Pseudo-F = 1.831, $P = 0.113$), Depth (Pseudo-F = 1.614, $P = 0.273$), or their interaction (Pseudo-F = 1.182, $P = 0.296$) on the diversity index (Table 1). Given the absence of significant main effects and interaction, we did not perform pairwise PERMANOVA contrasts or nMDS for this descriptor to avoid inferring unsupported patterns.

PERMANOVA detected a significant regional effect on the evenness index (Pseudo-F = 2.768, $P < 0.05$), whereas Depth and the Region × Depth interaction were not significant ($P = 0.895$ and $P = 0.696$, respectively) (Table 1). Pairwise contrasts indicated that differences were confined to comparisons involving Region A (A–D $P < 0.01$; A–B, A–C, A–E $P < 0.05$), with all other pairs being non-significant (Fig. 4; Supplementary material Table S3).

The PERMDISP based on the evenness index revealed significant heterogeneity among regions ($F = 5.223$, $P = 0.010$): we found the highest mean distances to centroid in regions D (4.04) and E (3.81), intermediate values in B (2.68), and the lowest in A (1.77) and C (1.67). Pairwise PERMDISP indicated larger dispersion in D and E relative to A and C (A–D $P = 0.010$; A–E $P = 0.028$; C–D $P = 0.005$; C–E $P = 0.023$), whereas D and E did not differ ($P = 0.822$).

We interpreted the regional signal in evenness with caution: contrasts such as A–D and A–E likely reflect a combination of centroid and dispersion effects, whereas A–B and A–C are more consistent with centroid differences alone. The nMDS ordination (Stress = 0.01) supports these patterns, showing broader scatter for D and E and more compact groupings for A and C, without a strong segregation into distinct clusters (Fig. 7).

PERMANOVA detected no effect of Depth or the Depth × Region interaction on the community descriptors. We therefore pooled samples from the two depth ranges by station and evaluated among station structure using a hierarchical cluster dendrogram based on the same square-root-transformed Bray-Curtis matrix. Most stations aggregated into a broad main cluster, whereas a small number formed separate branches, consistent with the nMDS pattern of a compact core plus a few outliers (Fig. 8).

We identified four groups with similarity values exceeding 48%: Group 1 in Gökova Bay; Group 2 comprising the Kıyıkışlacık, Torba, and Bodrum stations; Group 3 in Saros, Edremit, and Izmir Bays; and Group 4 including the Geyikli and Burhaniye stations at the Dardanelles exit (Fig. 8). The four groups showed moderate within-group cohesion (G1 52.9%; G2 62.8%; G3 51.4%; G4 53.4%). Among-group separation was strongest between G2 and G4 (69.4%) and between G1 and G4 (63.5%), with the remaining pairs ranging from approximately 54% to 60%.

The SIMPER results indicate that a limited set of common species underpins both the internal cohesion of the station clusters

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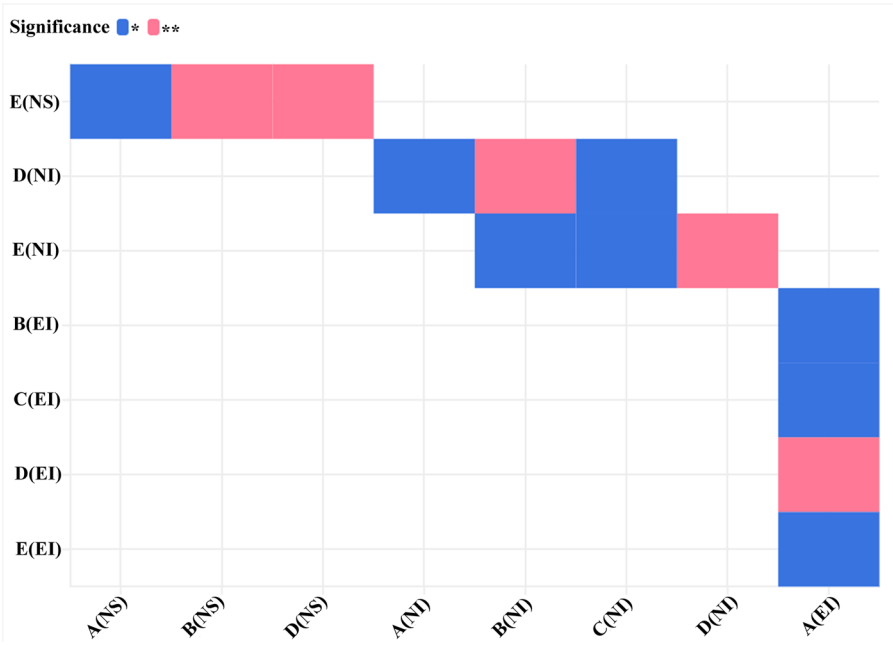


Figure 4. Heatmap of significant pairwise PERMANOVA contrasts among regions for three community descriptors in the present study from the meadows of *Posidonia oceanica*. NS, number of species; NI, number of individuals; EI, evenness index. Filled cells indicate significant contrasts (blue = $P < 0.05$, pink = $P < 0.01$); blank cells are non-significant.

Table 1. Results of PERMANOVA applied to the community descriptors with regard to depth range (0–5 m and 6–15 m) and region (A–E).

Source	Degree of freedom	Sum of square	Mean of square	Pseudo–F	*P* (Perm)	Perms
Number of species						
Region	4	1114.6	278.65	3.927	**	999
Depth	1	432.69	432.69	3.0251	0.121	997
Depth × Region	4	581.23	145.31	2.0478	0.082	999
Residue	115	8160	70.956			
Total	124	10220				
Number of individuals						
Region	4	2860.4	715.11	6.333	**	997
Depth	1	337.76	337.76	2.9913	0.066	999
Depth × Region	4	816.16	204.04	1.807	0.127	997
Residue	115	12985	112.92			
Total	124	17058				
Diversity index						
Region	4	192.96	48.24	1.8313	0.113	999
Depth	1	50.035	50.035	1.614	0.273	999
Depth × Region	4	124.59	31.147	1.1824	0.296	999
Residue	115	3029.3	26.342			
Total	124	3347.6				
Evenness index						
Region	4	179.57	44.891	2.7683	*	999
Depth	1	0.6225	0.6225	0.0071	0.895	997
Depth × Region	4	33.741	8.4353	0.5202	0.696	999
Residue	115	1864.9	16.216			
Total	124	2081.2				

Asterisks denote significance levels:
*$P < 0.05$;
**$P < 0.01$.

and their pairwise dissimilarities. A single widespread taxon, *C. savignyi*, accounted for the largest share of within-group similarity across all groups (~13–17%) and contributed substantially to between-group dissimilarities (~4–10%). Additional consistent contributors to within-group similarity included the amphipod *Ericthonius argenteus* Krapp-Schickel, 1993 (~4–7%) and the isopods *Gnathia vorax* (Lucas, 1849) (~7–8%) and *Limnoria* spp. (~7–8%) (Supplementary material Table S4).

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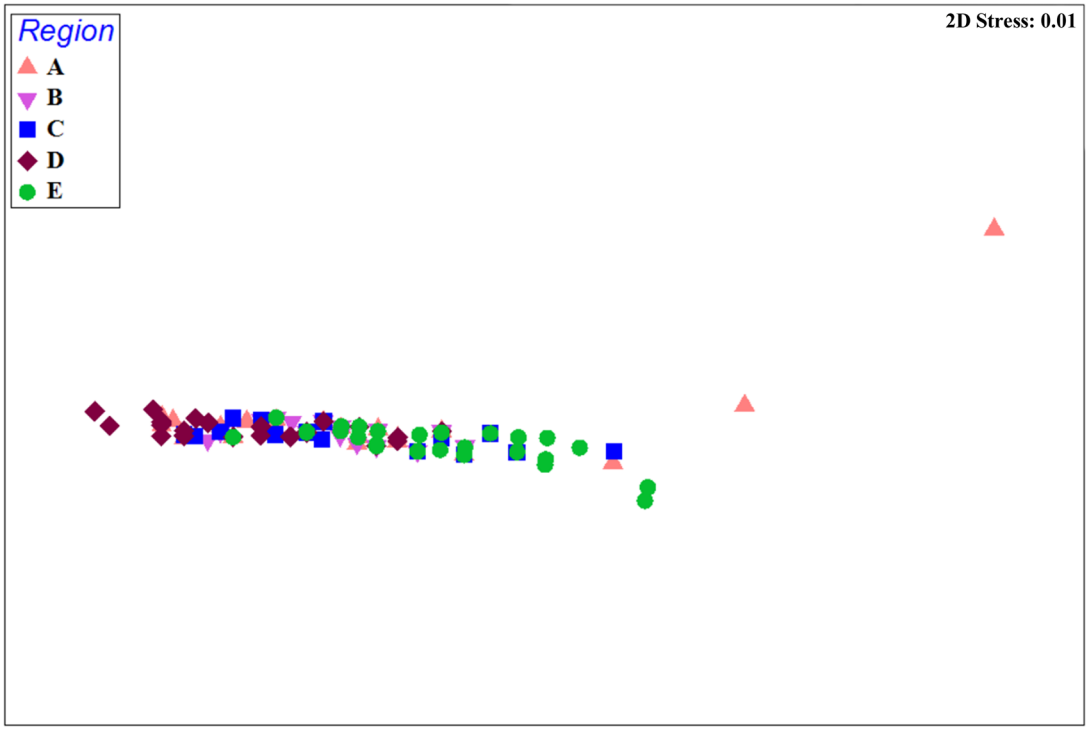


Figure 5. nMDS ordination based on square-root transformed the number of species associated with *Posidonia oceanica* meadows.

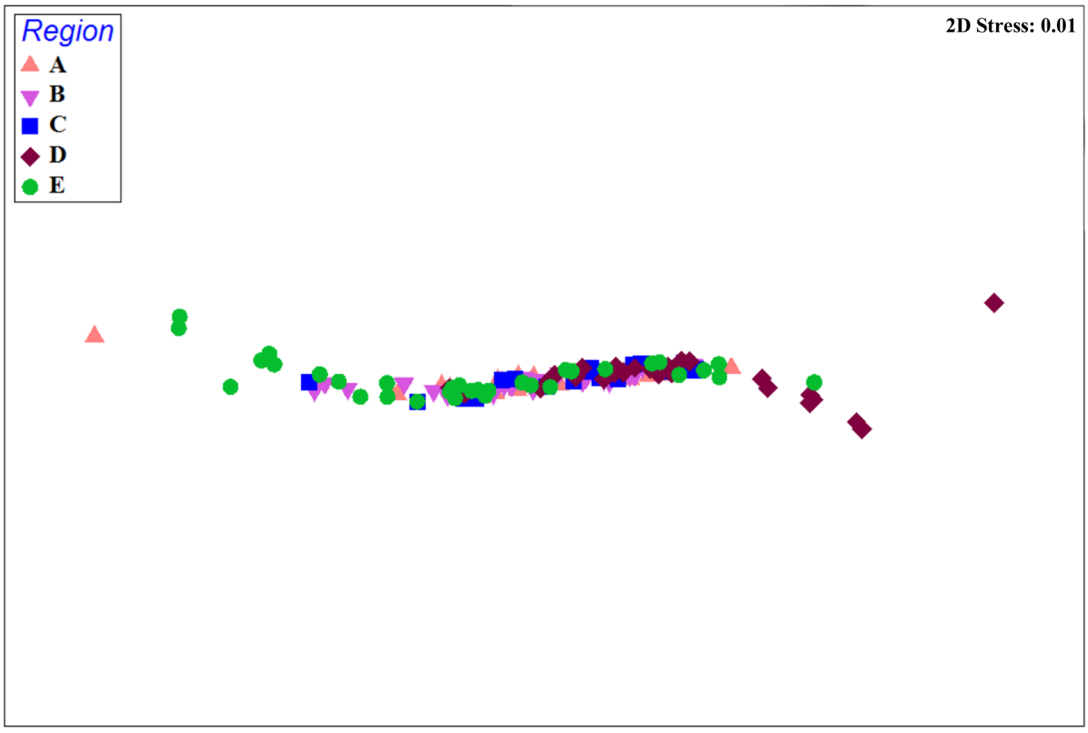


Figure 6. nMDS based on square-root transformed the number of individuals associated with *Posidonia oceanica* meadows.

Group-specific signatures were most evident in G2, where the caprellid amphipods *Caprella acanthifera* Leach, 1814, *Phtisica marina* Slabber, 1769, togetherwith the amphipod *Dexamine spinosa* (Montagu, 1813) and the cumacean *Cumella* (*Cumella*) *limicola* Sars, 1879 featured prominently. These taxa jointly structured the pronounced G2–G4 and G1–G4 separations (Supplementary material Table S4).

We did not detect any statistically significant relationships between physicochemical variables in the shallow layer (0–5 m) and community parameters using Spearman's rank correlation ($P \geq 0.05$)

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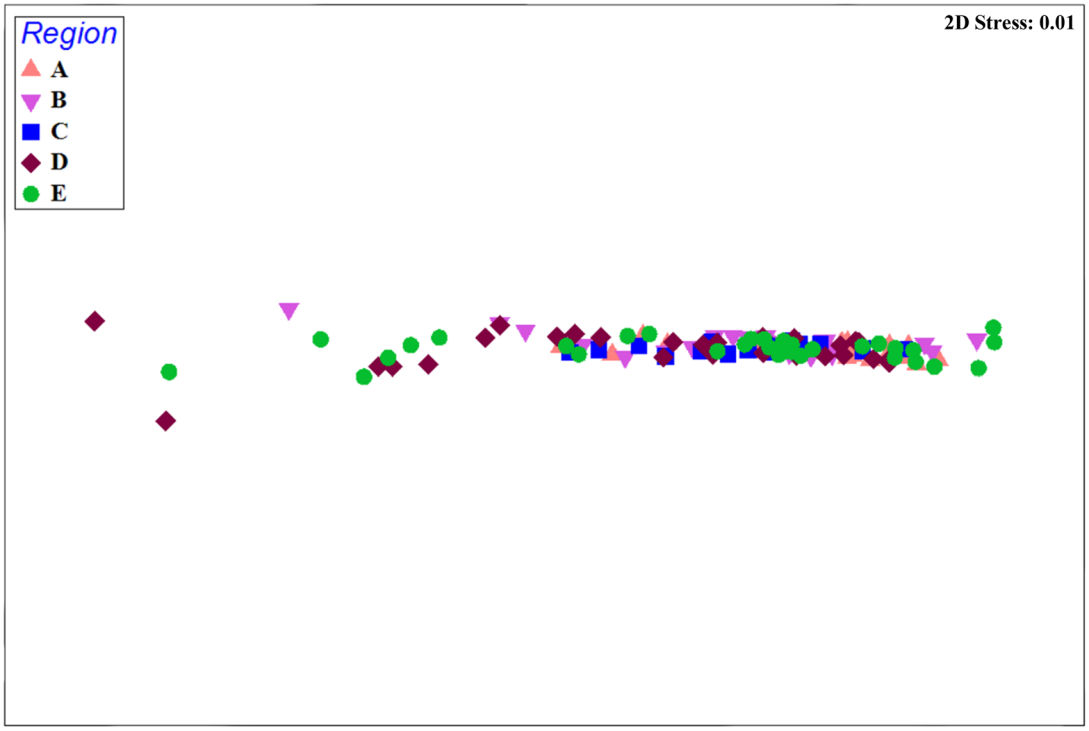


Figure 7. nMDS based on square-root transformed the evenness index associated with *Posidonia oceanica* meadows.

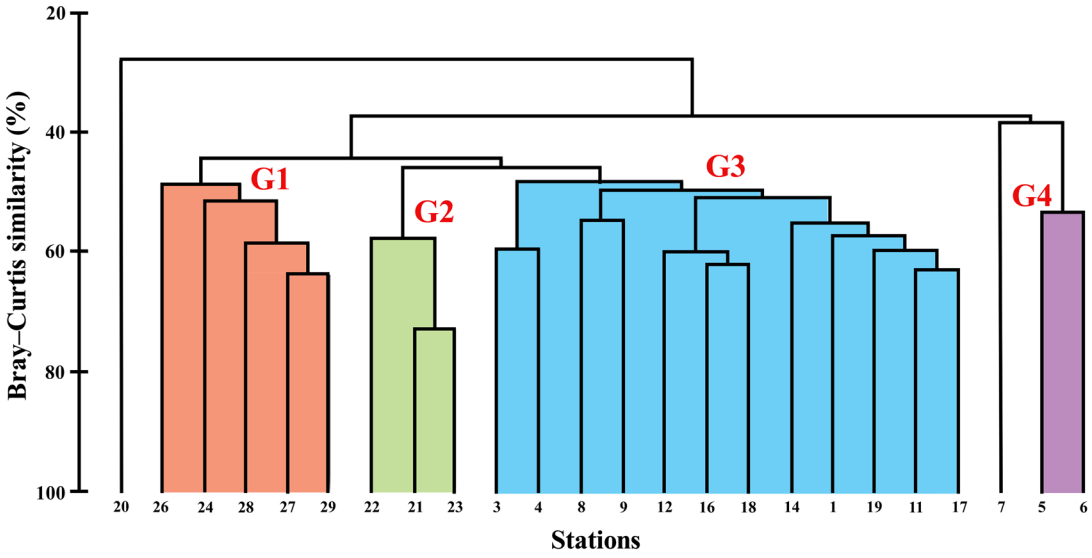


Figure 8. Analysis of Bray-Curtis similarity at sampling stations within the 0–15 m depth range (G1, Group 1; G2, Group 2; G3, Group 3; G4, Group 4).

(Table 2). Temperature and dissolved oxygen showed a negative trend, whereas conductivity and salinity were positively associated. The number of species and H′, and H′ and J′ tended to be positively correlated, but J′ and the number of individuals exhibited a negative trend (Table 2).

DISCUSSION

Our results provide significant insights into the biodiversity and ecological functions of less-mobile crustacean communities associated with *P. oceanica* meadows. The identification of 199 species, including eight new records, highlights the substantial faunal diversity within the seagrass ecosystems. Recent studies on the crustacean fauna in marine and brackish waters documented 1,788 species along the Turkish coasts, with 1,285 species recorded in the Aegean Sea (Bakır *et al.*, 2024). Our study increased the known biodiversity to 1,293 species.

The Indo-West Pacific *A. bizseli* (Amphipoda), first recorded in the Mediterranean near Çeşme, Turkey, is believed to have been introduced by shipping (Özaydinli & Coleman, 2012). We found

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Table 2. Spearman's rank correlations between surface physicochemical variables and crustacean community descriptors in the shallow water (0–5 m). Significant correlations ($P < 0.05$) are in bold. Sal, salinity; Tem, temperature; DO, dissolved oxygen; Con, conductivity; NS, number of species; NS, number of individuals; J′, evenness index; H′, diversity index.

Variables	Sal	Tem	DO	pH	Con	NS	NI	J′
Tem	0.012							
DO	0.096	**–0.923**						
pH	–0.162	–0.426	0.347					
Con	**0.834**	0.467	–0.317	–0.263				
NS	0.086	–0.414	0.459	0.116	–0.162			
NI	0.216	–0.018	0.131	0.008	0.091	**0.491**		
J′	–0.211	0.049	–0.157	0.172	–0.067	–0.290	**–0.864**	
H′	–0.127	–0.265	0.222	0.240	–0.183	**0.495**	–0.430	**0.671**

the species at seven stations at depths of 0–10 m. Also introduced by shipping is the tropical eastern Atlantic caridean shrimp *P. macrodactyla*, first reported from the Turkish coast by Ateş *et al.* (2004b) on sandy, muddy substrates and among *P. oceanica* meadows. We recorded *P. macrodactyla* at 12 stations in the 0–10 m depth range. Although classified as 'rare,' *A. bizseli* and *P. macrodactyla* illustrate the ongoing influence of biogeographical shifts that are likely driven by climate change and human-mediated dispersal. Their establishment on the Aegean raises urgent concerns regarding potential long-term ecological impacts, particularly if they outcompete and displace native species. Such shifts could lead to changes in species composition that might disrupt ecological balances and result in loss of biodiversity. The presence of the two species underscores the need for monitoring and effective conservation strategies (Giangrande *et al.*, 2020).

The wood-boring species of *Limnoria*, which inhabit the sheaths of *P. oceanica*, gain protection from predators while also deriving nutrition through endogenous enzymes that digest lignocellulose (Daniel *et al.*, 1991). The isopod can negatively impact the growth of *P. oceanica* by degrading the sheath tissue and increasing microbial activity in the surrounding environment (Menzies, 1957; King *et al.*, 2010). Guidetti *et al.* (1997) identified species of *Limnoria* as characteristic wood-boring organisms inhabiting *P. oceanica* meadows on the Adriatic and Sardinian coast of Italy.

We also found *J. maculosa* within the leaf sheaths of *P. oceanica*. This isopod has a broad distribution in the Mediterranean, particularly in the Iberian Peninsula, where it primarily feeds on detritus and frequently associates with polychaete tubes, algal beds, and sponges (Castelló & Carballo, 2001). It has not traditionally been classified as a wood-boring species; however, the cavities of *P. oceanica* leaf sheaths we found raises questions on its ecological role and potential interactions. It remains unclear whether *J. maculosa* actively bores into these sheaths or opportunistically utilizes pre-existing cavities created by other species, such as *Limnoria* spp., for shelter or nesting.

The dominant groups that we found in terms of species richness were consistent with those in previous studies, but the dominant groups varied across different studies (Mazzella *et al.*, 1989; Gambi *et al.*, 1992; Sánchez-Jerez & Ramos Esplá, 1996; Como *et al.*, 2008; Terlizzi *et al.*, 2010; Bedini *et al.*, 2011, 2015; Belgacem *et al.*, 2011; Sturaro *et al.*, 2015).

In previous studies conducted in *P. oceanica* meadows and our study, *Nebalia bipes* (Fabricius, 1780) was the only reported species of cumacean (Leptostraca) (Gallmetzer *et al.*, 2005; Bedini *et al.*, 2011). Various species of mysids have been reported in the Mediterranean, with some species dominating in particular regions (Chessa *et al.*, 1989; Mazzella *et al.*, 1989; Sánchez-Jerez & Ramos Esplá, 1996; Bedini *et al.*, 2015). Among these, *Siriella clausii* Sars, 1877 has been consistently recorded from *P. oceanica* e. Its regular occurrence highlights its ecological importance and stable association with seagrass meadows, suggesting a key role.

Amphipods are also widely represented in *P. oceanica* meadows, though the dominant species can vary across different studies. Species of *Ampelisca* Krøyer, 1842, *Ericthonius* H. Milne Edwards, 1830, *Ampithoe* Leach, 1814, *Dexamine* Leach, 1814, *Apherusa* Walker, 1891, *Aora* Krøyer, 1845, *Caprella* Lamarck, 1801, *Phtisica* Slabber, 1769, and *Apolochus* Hoover & Bousfield, 2001 have been consistently reported (Mazzella *et al.*, 1989; Gambi *et al.*, 1992; Sánchez-Jerez & Ramos Esplá, 1996; Sánchez-Jerez *et al.*, 1999; Katağan *et al.*, 2001; Gallmetzer *et al.*, 2005; Zakhama-Sraieb *et al.*, 2011; Bedini *et al.*, 2015; Michel *et al.*, 2015; Sturaro *et al.*, 2015; Bellisario *et al.*, 2016; Camisa *et al.*, 2017).

Isopods exhibit significant regional variation across the Mediterranean. Studies in Spain (Sánchez-Jerez & Ramos Esplá, 1996), Corsican (Gallmetzer *et al.*, 2005), and Italy (Mazzella *et al.*, 1989; Gambi *et al.*, 1992; Bedini *et al.*, 2011) identified particular dominant species, probably reflecting the influence of local environmental conditions.

Species of Tanaidacea, particularly *C. savignyi*, have been commonly recorded in the Mediterranean (Gambi *et al.*, 1992; Como *et al.*, 2008; Bedini *et al.*, 2011). Several species of Cumacea have also been documented in Italy, with many of them also recorded in our study, highlighting both similarities and slight regional differences in species composition (Mazzella *et al.*, 1989; Como *et al.*, 2008).

The distribution of decapods associated with *P. oceanica* meadows varies considerably across the Mediterranean region. Holthuis (1961) and Ateş *et al.* (2004a) reported a few common species, but later investigations identified additional dominant species, perhaps reflecting changes in community composition over time. Similar studies conducted in Spain, France, Italy, and Tunisia have also reported region-specific decapod species. Our study aligns with findings from Italy. Comparable studies conducted along other Mediterranean coasts (Spain: García Raso, 1990; García Raso *et al.*, 1996; Sánchez Jerez & Ramos Esplá, 1996; Mateo-Ramírez *et al.*, 2016; France: Gallmetzer *et al.*, 2005; Italy:

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Mazzella *et al.*, 1989; Gambi *et al.*, 1992; Como *et al.*, 2008; Bedini *et al.*, 2011, 2015; Tunisia: Belgacem *et al.*, 2011) further emphasize the region-specific nature of decapod inhabiting *P. oceanica* meadows.

In summary, *w*hile genus-level similarities are evident across regions, species-level differences suggest that *P. oceanica* meadows host unique crustacean communities, reflecting local ecological conditions and broader Mediterranean biodiversity patterns. The results of the PERMANOVA analysis indicated that region-specific factors significantly affect crustacean community structures in *P. oceanica* meadows. Northern Aegean sites, which are characterized by colder and nutrient-rich waters influenced by the Black Sea, displayed higher species diversity compared to the warmer, oligotrophic southern sites. Similarly, Bedini *et al.* (2015) and Bellisario *et al.* (2016) reported that crustacean species inhabiting *P. oceanica* meadows in Italy did not vary significantly with depth; instead, they showed regional differences. The significant regional variations underscore the importance of local ecological factors, including salinity and temperature gradients. These findings underscore the need for tailored conservation strategies, as crustacean communities play crucial roles in nutrient cycling, organic matter decomposition, and food web dynamics within seagrass ecosystems. Understanding these variations is crucial for mitigating potential anthropogenic impacts, such as those from coastal tourism and marine traffic.

The absence of depth effects is consistent with both range lying within the well-lit shallow zone where light availability governs seagrass performance and depth limits; within 0–15 m many Aegean meadows occupy optimal conditions for *P. oceanica* (Boudouresque *et al.*, 2012; Panayotidis *et al.*, 2022). Regional differences are therefore plausibly linked to variability in meadow architecture (shoot density, leaf morphology) and hydrography/sediments (exposure, currents, fine-sediment size), which are known to influence seagrass-associated fauna (Chessa *et al.*, 1989; Bedini *et al.*, 2011; Boudouresque *et al.*, 2012).

SIMPER linked multivariate structure to taxa: a small set of widespread species accounted for most within-group similarity. In our shallow (0–5 m) dataset, Spearman's tests did not yield statistically significant bivariate correlations between surface physicochemical variables and the community descriptors (Table 2). Evidence from *P. oceanica* systems indicates that oxygen availability and hydrographic regime can structure crustacean assemblages. In Tunisia, species richness increased with dissolved oxygen and decreased with temperature, and diversity rose with oxygen (Belgacem *et al.*, 2011). Distributions of amphipods in the Bizerte Lagoon (Tunisia) were primarily influenced by temperature and salinity (Zaabar *et al.*, 2015), and salinity has been identified as a principal driver of benthic zonation elsewhere (Cacabelos *et al.*, 2010). Taken together, these studies suggest that oxygen and salinity/temperature may be important drivers, even though such effects were not detectable at the bivariate level in our shallow-layer data. Future work with concurrent, station-level environmental measurements and multivariate linking approaches (e.g. BIO-ENV/DistLM) is warranted to resolve these relationships.

The limitations of this study include the lack of concurrent environmental covariates that could mechanistically explain regional differences (e.g. *in situ* light/attenuation, meadow morphometry, sediment texture), the unbalanced design that may affect power for specific contrasts, and the absence of temporal replication. Region-focused monitoring coupled with seasonal resampling and station-level environmental measurements within a model-based multivariate framework (e.g. DistLM) is recommended.

Our sampling design was deliberately focused on less mobile crustaceans, particularly peracarids, whereas highly mobile taxa such as caridean and penaeoidean shrimps were not specifically targeted and may therefore be underrepresented. This methodological bias does not reduce the value of the study, as it provides novel insights into the less mobile fraction of the seagrass-associated fauna. Nevertheless, alternative methods such as hand-towed net (Ledoyer, 1962; Russo *et al.*, 1985; Mazzella *et al.*, 1989; Gambi *et al.*, 1992; Russo & Terlizzi, 1997; Buia *et al.*, 2004; Bedini *et al.*, 2011), air-lift (De Metrio *et al.*, 1978, Russo *et al.*, 1986; Russo & Terlizzi, 1997; Buia *et al.*, 2004), small epibenthic trawls (Kerneis, 1960; Buia *et al.*, 2004), and pushnet sampling (Manning, 1975; Bauer, 1985a, b) are known to be highly effective in capturing mobile epifauna. These were beyond the scope of the present research; however, future studies that combine quadrat-based sampling with complementary techniques could provide a more comprehensive understanding of seagrass-associated crustacean communities.

By employing multi-dimensional community analyses, our study provides new insights into the ecological patterns of crustacean assemblages in *P. oceanica* meadows. The observed spatial variations underline the influence of natural environmental factors and human-induced changes. Our findings not only expand the current knowledge on marine biodiversity in the eastern Mediterranean region but also offer practical guidance for conservation efforts, particularly in areas facing ecological pressure due to human activities. Continued research focusing on the long-term monitoring of these communities is essential for sustainable management of seagrass-associated biodiversity.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Table. Sampling stations.

S2 Table. List of crustacean species collected.

S3 Table. Pairwise PERMANOVA comparisons among regions.

S4 Table. Species contributing most to similarity and dissimilarity between associations.

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