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Meiofauna is an important, yet often overlooked, component of biodiversity in the ecosystem formed by *Posidonia oceanica*

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Abstract

The ecosystem formed by the marine flowering plant *Posidonia oceanica* is a biodiversity reservoir and provides many ecosystem services in coastal Mediterranean regions. Marine meiofauna is also a major component of that biodiversity, and its study can be useful in addressing both theoretical and applied questions in ecology, evolution, and conservation. We review the meiofaunal diversity in the meadow ecosystem of *P. oceanica* by combining a literature review and a case study. First, we gathered records of 672 species from 71 published studies, as well as unpublished sources, highlighting 4 species exclusive to this ecosystem. Eighteen of those studies quantified the spatial and temporal changes in species composition, highlighting habitat-specific assemblages that fluctuate following the annual changes experienced by these meadows. Hydrodynamics, habitat complexity, and food availability, all three inherently linked to the seagrass phenology, are recognized in the literature as the main factors shaping the complex distribution patterns of meiofauna in the meadows. These drivers have been identified mainly in studies of Copepoda and Nematoda, and their effect may depend ultimately on species-specific preferences. Second, we tested the generality of these observations using marine mites as a model group, showing that similar ecological preferences might be found in other less abundant meiofaunal groups. Overall, our study highlights the high diversity of meiofauna in meadows of *P. oceanica* compared with algae and sessile macrofauna associated with this seagrass and shows the complexity of the interactions and habitat use by meiofauna associated with the seagrass.

KEYWORDS
Acari, Copepoda, habitat sorting, microscopic animals, Nematoda

1 | INTRODUCTION

Named after the Greek god Poseidon, the marine flowering plant *Posidonia oceanica* (Linnaeus) Delile 1813 constitutes an iconic Mediterranean endemic organism that forms extensive lush meadows, imprinting shallow Mediterranean bays and beaches with a unique character. Beyond the ethnographic importance, the meadows of *P. oceanica* foster an outstanding diversity of organisms and provide many ecosystem services. The leaves act as a major carbon sink filtering and oxygenating the seawater (Mateo et al., 1997; Terrados & Duarte, 2000), and they create a local hydrodynamic regime that favors sedimentation (e.g., Gacia & Duarte, 2001; Manca et al., 2012). Underneath the leaves, a monumental formation of rhizomes, roots, and detritus, typically termed "matte" (Boudouresque & Jeudy de Grissac, 1983), stabilizes the sediment and entraps particles of organic matter (Mateo et al., 1997; Pergent et al., 2012). Leaves and matte together prevent erosion in the littoral zone, support food webs, and enrich the surrounding bare sand with organic matter and nutrients (González-Ortiz et al., 2014; Jørgensen et al., 1981), thus forming an oasis for local species. The adjacent sandy areas form corridors and wide spaces among seagrass patches, constituting a habitat where certain species settle (e.g., the Mediterranean fan mussel; Coppa et al., 2010), seek refuge (e.g., sea urchins; Pinna et al., 2013), and feed (e.g., mysids; Sánchez-Jerez et al., 1999b). Furthermore, exported materials from the meadows accumulate and constitute other habitats, mostly on nearby sandy areas (Cresson et al., 2012; Dimech et al., 2006), but also further down to deep waters or into caves and pits (Picard, 1965), where they boost local food webs (Mateo et al., 2003; Simeone & De Falco, 2013). Detritus from meadows of *P. oceanica* washes up throughout the year and forms "banquettes," which extend along vast sections of shoreline and vary in complex dynamics throughout the year (Boudouresque & Meinesz, 1982). These banquettes not only protect beaches from erosion, stabilize sand dunes, and enrich underlying sediments with nitrogen but also harbor various aquatic and terrestrial organisms (Boudouresque et al., 2016). Because of such significant modification of the environment, *P. oceanica* is considered an ecosystem engineer (Unsworth & Cullen-Unsworth, 2017), which forms a complex system composed of living seagrass and its exported detritus, as well as the rich community of organisms associated with its different habitats (Boström et al., 2006; Mazzella et al., 1989).

Over the last decades, scientists have described the taxonomic diversity and functioning of the ecosystem formed by *P. oceanica*, along with the local dynamics of the mosaic of habitats associated with them. Initial research focused on the phenological annual changes of the individual plants of *P. oceanica* themselves (e.g., Ott, 1980), followed by detailed characterizations of the diversity and structure of their associated communities. Indeed, many studies have addressed the dynamics of meadows of *P. oceanica*, highlighting the economic and ecological importance of their inhabitants (e.g., Como et al., 2008; Dimech et al., 2002; Duffy et al., 2003; Honkoop et al., 2008; Kalogirou et al., 2010; Whippo et al., 2018). For instance, the leaves foster nurseries of fish and cephalopods that often represent important resources for local fisheries (Cetinić et al., 1999, 2011), whereas the assemblages of gastropods and bivalves associated with the plant include several emblematic, often endemic, Mediterranean species (Urra et al., 2013). In the matte, many species of infaunal crustaceans, molluscs, annelids, and brachiopods thrive (Albano & Stockinger, 2019; Borg et al., 2006), contributing to the overall recycling of the entrapped organic matter (Vizzini et al., 2002). Even beyond the plant, the phytal detritus drifting away from the meadows on the adjacent sandy areas host diverse macrofaunal communities (Gallmetzer et al., 2005; Guidetti, 2000; Sánchez-Jerez et al., 1999a). However, the epiphytic organisms growing on the plant structure constitute the communities that have received most attention, partially because of their high number of species (∼660 species, after Piazzi et al., 2016), but also because they have been used as bioindicators of the health of the meadows (Giovannetti et al., 2010; Martínez-Crego et al., 2010; Mateu-Vicens et al., 2014). Interestingly, such research on epiphytic organisms has shown that the distribution of these species is heterogeneous within the seagrass: Some epiphytes dominate the older but more exposed leaf tips, whereas others prefer their sheltered middle or basal parts, and a few even select the shaded rhizomes (Gambi et al., 1995; Piazzi et al., 2016).

In contrast with macrofaunal communities, information is much more scattered for the meiofaunal animals inhabiting the ecosystem formed by *P. oceanica*. Meiofauna include the heterogeneous subset of organisms ranging 63–500 μm in size, largely dominated by microscopic animals, but also including larger forms with elongated morphologies or contractible bodies (Giere, 2009; Schmidt-Rhaesa, 2020). Meiofauna play a fundamental role in many processes in the seafloor (Schratzberger & Ingels, 2018) and represent a numerically important, yet often neglected, component of the diversity of many regions (Curini-Galletti et al., 2012, 2020; Martínez et al., 2019). Furthermore, the study of meiofauna can address both theoretical and applied eco-evolutionary questions (e.g., Fontaneto, 2011; Fontaneto et al., 2007; Gansfort et al., 2020; Laumer et al., 2015; Martín-Durán et al., 2021; Martínez et al., 2020), because these organisms belong to virtually every animal phylum, thus alleviating the confounding effect of potential phylogenetic bias during inductive hypothesis tests (Giere, 2009; Rundell & Leander, 2010). Moreover, meiofauna critically support marine food webs by transferring the energy from decomposer and primary producer microorganisms to higher trophic levels (Danovaro, 1996; Danovaro et al., 2007). In fact, detritivore and herbivore meiofaunal species contribute actively to the energy transfer in local food webs throughout the degradation of detritus exported from living meadows (François et al., 2018; Mascart, Lepoint, et al., 2015; Pusceddu et al., 2016). Although scattered in the literature, numerous records indicate that many meiofaunal species inhabit the ecosystem of *P. oceanica*, and these organisms crawl on leaves or across the matte labyrinths, gliding in the interstices of the adjacent sediments, or even drifting within the detritus over the sea bottom. Several studies addressed the composition and community dynamics of some meiofaunal groups associated with *P. oceanica*, revealing that the biotic (e.g., species interactions or food sources) and abiotic conditions (e.g., physical stressors) of the meadow shape the distribution of meiofaunal species (e.g., Mascart et al., 2013; Mascart, Lepoint, et al., 2015; Novak, 1982, 1989; Pusceddu et al., 2016). However, besides these few comprehensive ecological studies, mainly focusing on copepods and nematodes, most of this research involves occasional taxonomic descriptions from punctual samples. Unfortunately, the lack of a comprehensive updated review of literature obscures our understanding of the overall diversity and ecology of meiofauna in this iconic Mediterranean ecosystem.

The aim of this study is two-fold. First, we reviewed the taxonomic diversity and ecology of meiofauna associated with *P. oceanica* through a literature survey, completed with unpublished data provided by our colleagues. The main aim of this review was exploratory, for which we gathered, to our knowledge, all the available information about meiofauna found in the habitats associated with *P. oceanica*. We describe the patterns of meiofaunal taxonomic diversity reported in the existing literature. Based on the information available for macroscopic organisms, we expected that taxonomic composition of meiofaunal assemblages (i.e., species richness and abundance) differ among the habitats of *P. oceanica*, and that these communities change following the annual phenological cycle of the meadows. Although our initial intention was to perform a formal meta-analysis, our work here was limited to a more narrative review because of the scarcity of studies focusing on the ecology of meiofauna associated with *P. oceanica*, and the heterogeneity of the questions, methods, and metrics used in the available studies. Second, we performed a case study using halacarid marine mites as model organisms to further explore the spatial and temporal variation as found for other groups in the literature. Specifically, we expected that different halacarid species would prefer different habitats within an individual of *P. oceanica*. Marine mites are common inhabitants of seagrasses such as *P. oceanica* (Durucan, 2018, 2021; Durucan et al., 2019; Durucan & Boyacı, 2018; Mari & Morselli, 1990; Zupo, 1993), yet the habitat preferences of the species associated with *P. oceanica* have never been explicitly investigated. We expected that this case study would provide evidence of such preferences to complement information available in the literature from the better studied copepods and nematodes (Mascart et al., 2013; Novak, 1989). Despite the limitations above, our review, in conjunction with the present case study, shows that meiofauna living in the habitats provided by meadows of *P. oceanica* can serve as ecological models, and we hope this will encourage further research in this iconic ecosystem.

2 | METHODS

2.1 | Literature review

2.1.1 | Selection of references

We systematically screened Google Scholar for all published literature containing records of vagile meiofaunal species within habitats of *Posidonia oceanica*. The search, performed in December 2020, consisted of the word "Meiofauna" or the name of a target animal group (i.e., "Acari," "Annelida," "Cephalocarida," "Copepoda," "Gastrotricha," "Gnathostomulida," "Kinorhyncha," "Loricifera," "Mystacocarida," "Nematoda," "Platyhelminthes," "Rotifera," or "Tardigrada") followed by the term "Posidonia" (e.g., "Copepoda" AND "Posidonia"). After carefully screening the abstract and cross-references (e.g., supporting information) of the compiled references, we included those studies that either reported meiofaunal species in any of the habitats associated with *P. oceanica* or contained ecological information about any meiofaunal group inhabiting the latter habitats. To maximize the completeness of our database, the references cited in all downloaded papers were checked for additional sources.

2.1.2 | Compilation of the species inventory

First, to evaluate the known diversity of meiofaunal species in the ecosystem formed by *P. oceanica*, we carefully screened each selected paper to compile all available records. Each entry included the taxon name, locality, WGS84 geographic coordinates (extracted directly or calculated after the description of each locality), depth, collection method, and the habitat within the seagrass ecosystem, when these data were available (see Supporting Information Table S1). We considered four types of habitats: (1) seagrass, consisting of the structure created by the plant; (2) adjacent sediments, including the bare sediments and interstitial habitats next to seagrass patches; (3) macrophyte detritus, the wandering vegetal debris from individuals of *P. oceanica* accumulated on sediments (termed "macrophytodetritus accumulations" in Mascart, Lepoint, et al., 2015); and (4) banquette, the detritus deposited on the shore after leaves of *P. oceanica* detach (Boudouresque & Meinesz, 1982; Mateo & Romero, 1997). When this information was provided, we further divided the seagrass habitat into its two discrete compartments, the leaves and the matte (i.e., the underlying ensemble of living rhizomes, plant debris, and roots). This information was subsequently used to describe the potential habitat preferences of the meiofaunal species living in the ecosystem formed by *P. oceanica* (see below). Furthermore, to maximize the number of provided records, we consulted different specialists, who kindly shared their unpublished records for this study. Finally, the names of the species compiled here were checked and validated through the World Register of Marine Species (WoRMS Editorial Board, 2022).

2.1.3 | Review of ecological questions

Complementary to the inventory of species, all papers with an ecological scope in our database were further screened for relevant hypotheses and findings regarding the preferences of meiofaunal species within the habitats of *P. oceanica*. The information contained in these papers was organized in a table (Table S2), comprising the aim of the study, the targeted meiofaunal groups, and the diversity metrics implemented. For each study we further provided a concise summary of the findings as to whether they found differences in the biodiversity metrics or abundance between (a) habitats, (b) between samples within the same habitat from a given locality (i.e., local scale), (c) between localities (i.e., regional scale), or (d) over time. Last, the table included the future research questions proposed by each study.

2.2 | Case study: halacarids associated with *P. oceanica*

2.2.1 | Study site and sampling design

In addition to our literature survey, we investigated the habitat specificity in the community of halacarids inhabiting a meadow of

P. oceanica in Cala del Cuartel (Alicante, SE Spain; WGS84 coordinates 38.210, −0.505), located in a region where animal communities associated with these meadows have been well documented (Martínez et al., 2021; Sánchez-Jerez et al., 1999a; Sánchez-Jerez et al., 1999b; Villora-Moreno, 1997; Villora-Moreno et al., 1991). Sampling was carried out during four campaigns in December 2015 and March, April, and August 2016, each coinciding with a different season according to the classification for the Mediterranean area (i.e., autumn, winter, spring, and summer, respectively; see Alpert et al., 2004). During each campaign, SCUBA divers sampled 6 randomly selected patches of *P. oceanica*, totaling 24 patches for the whole study. We used 20 × 20 cm quadrats to sample the leaves, matte, and adjacent sediments, so that the surface of each sample was standardized to 400 cm^2 (e.g., Novak, 1989; Pusceddu et al., 2016; Sánchez-Jerez et al., 1999b; but see Bell et al., 1984). The leaves were first cut at the ligule level and collected carefully in a hermetic bag; then, the underlying matte was shoveled into another hermetic bag (following Cvitković et al., 2017; Novak, 1982, 1989). A surface of 400 cm^2 of the sediments adjacent to each sampled patch was collected into separate jars using identical quadrats.

Halacarid mites were extracted combining magnesium chloride and “bubble and blot” techniques (Higgins & Thiel, 1988; Sørensen & Pardos, 2008), filtered through a 63-μm mesh (which has been showed to be optimal for collection of all mite developmental stages; see Bartsch, 2006), and fixed in 7% formaldehyde. Fixed halacarids were then sorted using a MOTIC® SMZ-168 stereoscope and whole-mounted on slides in a modified Hoyer's medium (Mitchell & Cook, 1952). Whole-mounted specimens were examined using an Olympus DP70 camera mounted on a light microscope equipped with differential interference contrast microscopy (DIC). We followed André (1946), Green and MacQuitty (1987), and specific taxonomic literature (Bartsch, 1986, 2001, 2006; Morselli, 1980) for species identification. Adult and juvenile specimens were distinguished following Bartsch (2015). Nomenclature followed the World Register of Marine Species (WoRMS Editorial Board, 2022).

2.2.2 | Data analysis

All statistical analyses were performed using the R software version 3.6.1 (R Core Team, 2019). We investigated the variation in species richness (i.e., number of species), abundance (i.e., number of individuals), and evenness (i.e., Pielou's J) within the leaves and the matte, because no mites were found in the sediments adjacent to the seagrass. First, we investigated differences in species richness, abundance ($\log_{10}$-transformed, to cope with stark differences in numbers between samples), and evenness between leaves and matte samples collected from the same sampling point, using a paired-samples t-test (paired t-test) through the function t.test in R. Pielou's J was calculated for each sample using the function diversity in the R package vegan v. 2.2–1 (Oksanen et al., 2013) to first obtain the

Shannon index and then dividing it by the logarithm of the number of species. For one sample in the matte, Pielou's J was not calculated because only one species was observed. Second, we tested whether richness or abundance changed with food availability and habitat complexity, as well as over time. We used the length of the leaves and the organic carbon content of the sediment as a proxy for food availability in the leaves and the matte, respectively. The length of the leaves was measured as the average distance in centimeters from the ligule to the apical end of all the complete leaves found in each sample, which is known to correlate positively with the abundance of epiphytic microorganisms (Mabrouk et al., 2011) that may serve as food for many halacarid species (Bartsch, 1989). Likewise, the percentage of organic carbon in the sediment was calculated using the Walkley–Black method (Walkley & Black, 1934), indicating the amount of accumulated organic matter in the matte, which represented available food for mites. Habitat complexity was inferred through the density of leaves or matte, calculated as the dry weight of the leaves or the matte divided by the total volume of the habitat, which varied in the leaves (average leaf length × 20 cm × 20 cm) and was constant in the matte (2 cm × 20 cm × 20 cm). We performed generalized linear models using function glm to examine the effect on richness, abundance (as $\log_{10}$), and evenness of the environmental variables within each habitat: the length and density of the leaves within the leaves and the percentage of organic matter and density of the matte. We accounted for the temporal variation in the seagrass over the period of study by including the sampling date in all models. We performed generalized linear models because these allow the use of a Poisson distribution for richness (count of species) and a Gaussian distribution for log-abundance and evenness (continuous decimal data). The significance of each independent variable was summarized as a Type II ANOVA table, using the function Anova in the R package *car* v. 3.0.9 (Fox et al., 2013). The assumptions of the linear models were controlled visually by checking the normality of model residuals, the plots of residual versus fitted values, and normal Q-Q plots (Crawley, 2013).

To further investigate whether halacarids preferred a certain habitat, we performed two additional analyses. First, because different ecological preferences have been reported between life stages in halacarids (Bartsch, 2004; Somerfield & Jeal, 1995, 1996), we tested for differences in percentage of juveniles (i.e., number of non-adult individuals/total individuals of each sample, expressed as a percentage) between the matte and the leaves within sampling points. Second, we tested for differences in abundance between habitats of the dominant species found in each habitat, for which data were sufficient to perform the analyses. Again, we performed paired t-tests for both differences in percentage of juveniles and abundance of the dominant species between habitat samples within sampling points. Paired samples were removed from the analyses when no individuals were found in a sampling point. For all paired t-tests, we used Shapiro–Wilk tests in the function shapiro.test in R to check the normality of the differences between paired samples.

Last, we examined the differences in species composition between communities occurring in different habitats, including their nestedness and turnover components, through the Jaccard abundance-based index (Legendre, 2014) in the function beta in the R

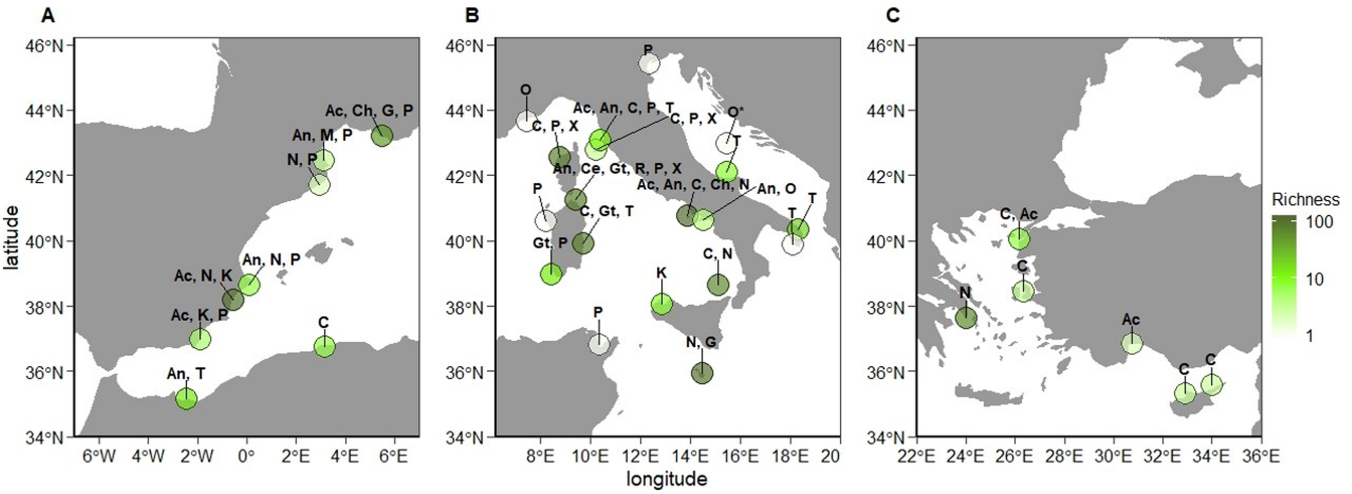

FIGURE 1 Distribution of the meiofauna recorded in association with *Posidonia oceanica* in the western (A), central (B), and eastern (C) Mediterranean Sea, colored according to the number of species (see Table S1 for coordinates). *, unspecified location in the Adriatic Sea; Ac, Acari; An, Annelida, C, Copepoda; Ce, Cephalocarida; Ch, Chaetognatha; G, Gastropoda, Gt, Gastrotricha, K, Kinorhyncha; M, Mystacocarida; N, Nematoda; O, Ostracoda; P, Platyhelminthes; R, Rotifera; T, Tardigrada; X, Xenacoelomorpha

package *BAT* v. 1.5.5 (Cardoso et al., 2015). For both species- and community-level tests, the abundances were again $\log_{10}$-transformed (abundance + 1) to cope with stark differences in abundance between samples, as well as for 0 values. We then assessed the percentage of variability in community composition observed across samples through a permutational analysis of variance (PERMANOVA) using distance matrices in the function adonis included in the R package *vegan*. Again, we explicitly included the sampling date as an independent variable to account for the temporal variation in the seagrass in structuring differences in species assemblage.

3 | RESULTS

3.1 | Review of meiofauna associated with *P. oceanica*

We reviewed a total of 71 relevant studies: 53 of them consisted of taxonomic papers, species inventories exclusively, or unpublished data, and 18 comprised ecological studies (see Supporting Information Tables S1 and S2). Together with the data published within the present study, we compiled 1079 records for 672 species (Table S1). Reports of Nematoda, Copepoda, and Acari accounted for 78% of the records; Tardigrada, Platyhelminthes, Gastrotricha, and Annelida accounted for 18%; Kinorhyncha, Xenacoelomorpha, Ostracoda, Gastropoda, Chaetognatha, Mystacocarida, and Rotifera accounted for the remaining 4% of the dataset. No records were found for Gnathostomulida and Loricifera. The majority of sampling sites were concentrated in the central Mediterranean Sea, particularly in Corsica, Sardinia, and the Gulf of Naples (Figure 1). Although the number of species recorded per meiofaunal group followed the number of studies dedicated to those groups, this correlation was rather weak (Pearson's correlation, $R = 0.55$, $p = 0.035$; Figure S1A), likely due to the substantial differences in sampling effort among studies.

Most of the species have been recorded within the seagrass (365 species), mostly in the matte (313 species), as well as in the sediments adjacent to the meadows (273 species) (Figure 2A), which coincides with the most studied habitats (~80% of the total studies). Interestingly, ~85% of the species recorded in the adjacent sediments and within the seagrass have been exclusively found in these habitats. Copepoda, Platyhelminthes, Gastrotricha, Annelida, Tardigrada, and Xenacoelomorpha were mainly found in the sediments, whereas Nematoda and Acari were observed principally within the seagrass (Figure 2D), with records for Nematoda particularly abundant in the matte. Most studies relied on samples collected by hand (565 species), generally by SCUBA divers (Figure 2B), which recovered generally different species from the studies that relied on boat-operated collections (Figure 2E). Most species and meiofaunal groups were reported from shallow waters (477 species; 0–20 m), and these numbers decreased with increasing depth (Figure 2C,F). Finally, only in Copepoda, Nematoda, Tardigrada, and Acari were there species that occurred in more than one habitat (Figure 3).

We sorted 18 ecological studies (Table S2) that addressed the variation in taxonomic richness, species composition, and abundance of meiofaunal communities at regional (i.e., between localities, generally kilometers away; 9 studies) and local spatial scales (i.e., between samples within the same habitat in a given locality; 13 studies). Only three of these studies incorporated functional metrics (Guilini et al., 2017; Mirto et al., 2014; Novak, 1989), and a single paper investigated diet preferences (Mascart et al., 2018). Nematodes and copepods were the preferred groups (seven studies at specific level), whereas other groups were often recorded at the taxonomic rank of

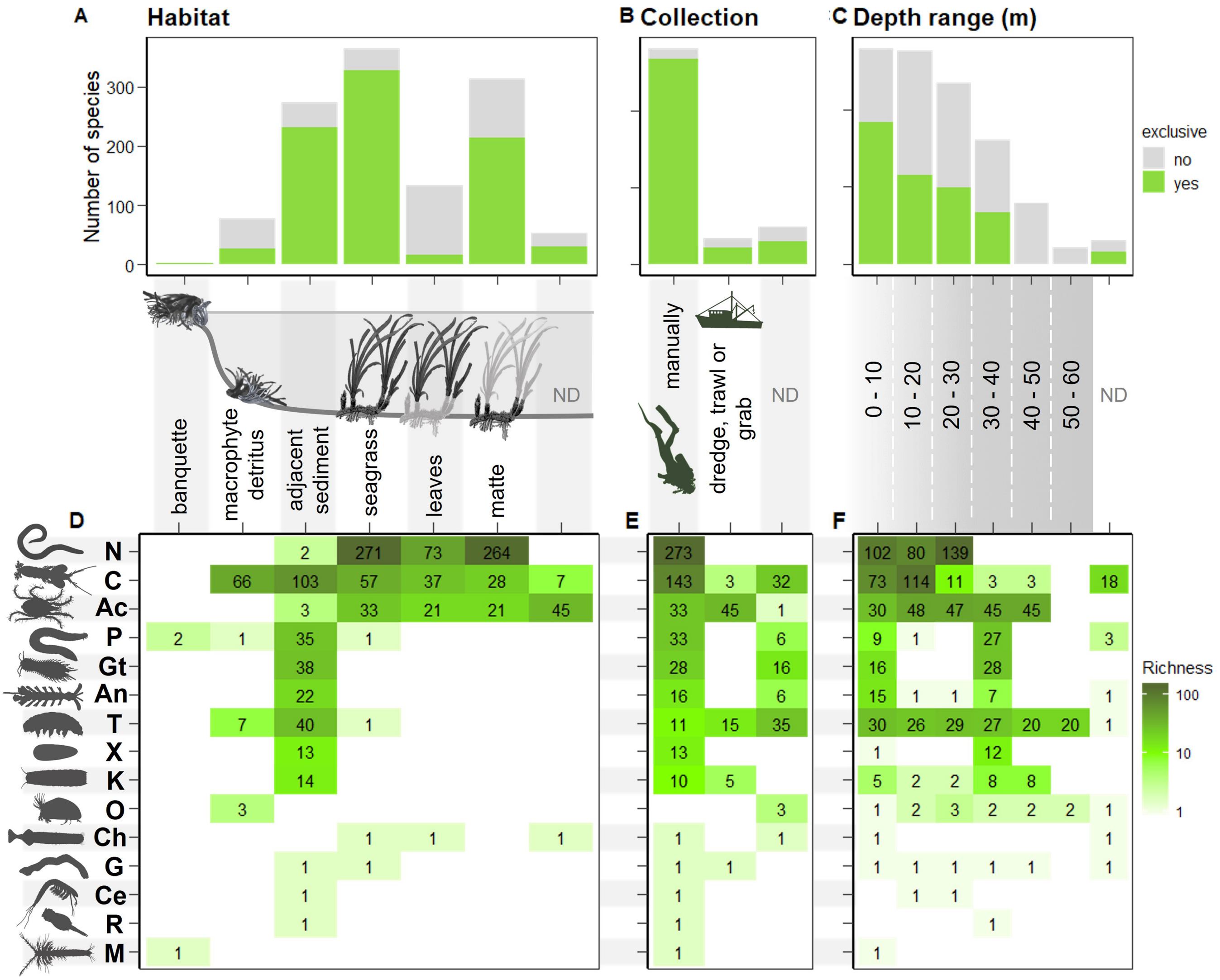

FIGURE 2 Meiofauna associated with *Posidonia oceanica*, with number of species per meiofaunal group categorized by habitat, collection method, and depth range. In the top panels (A–C), green bars indicate number of species observed exclusively in one category, and grey bars indicate the number found in more than one category. Bottom panels (D–F) show the number of species per meiofaunal group, with color range from light (least species rich) to dark green (most species rich). In A and D, the seagrass habitat was further divided into the leaves and the matte. Abbreviations as in Figure 1; ND, no data

phylum or class. Moreover, 16 studies searched for the ecological factors influencing the presence of meiofauna in different habitats of the meadows, stressing the importance of hydrodynamics (in 5 studies), habitat complexity (6 studies), and food availability (11 studies). Even when no direct measurements were taken, many of the latter 16 papers noticed the relevance of these three factors and their combination in shaping species assemblages during the studied period and mentioned the importance of addressing these factors in future research (e.g., see Novak, 1982, 1989). Finally, 10 of the studies highlighted temporal variation as another major driver of meiofaunal communities, mainly affecting abundances. The low number of available studies, as well as the heterogeneity of methodologies and metrics used in these papers, prevented us from performing further analyses through explicit statistical tests.

3.2 | Case study on halacarid mites

We counted 1730 individuals belonging to 21 species and 9 genera (Table 1). Of these, 1 species was restricted to the leaves and 5 to the matte, whereas 15 species co-occurred in both habitats. No halacarids were found in the sediments. The genus *Copidognathus* was represented by seven species, followed by the genera *Agauopsis* and *Agaue* (three species each), and *Rhombognathus* (two species). The genera *Arhodeoporus*, *Halacarus*, *Lohmannella*, *Pelacarus*, *Plegadognathus*, and *Simognathus* were each represented by one species.

There were no significant differences in species richness between habitats (Figure 4A; paired t-test: t = 0.78, p = 0.44), although abundances were significantly higher in the leaves than in the matte (Figure 4B; paired t-test: t = −5.77, p < 0.001), with 82% of the

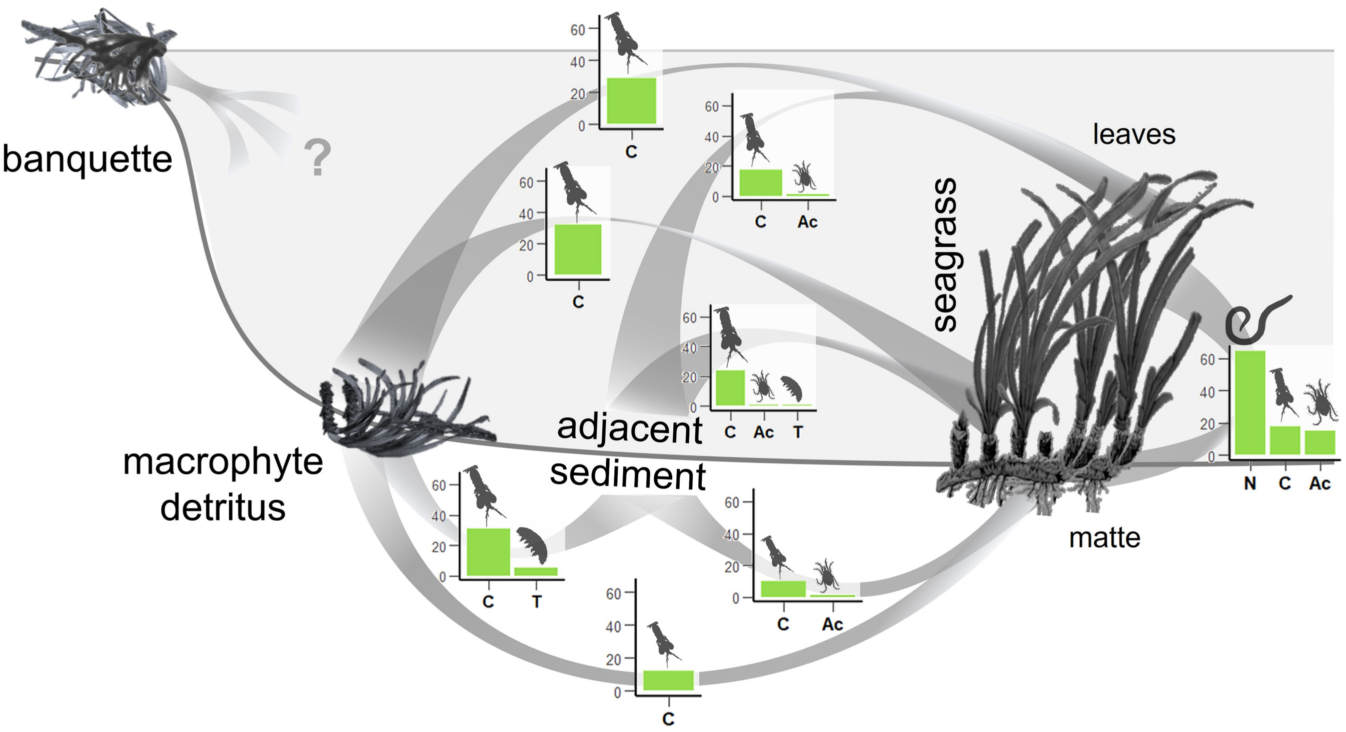

FIGURE 3 Meiofauna found in different habitats (banquette, macrophyte detritus, adjacent sediment, seagrass, leaves, matte) of the ecosystem associated with *Posidonia oceanica*. Bar graphs indicate the number of species per meiofaunal group shared between different habitats of the ecosystem (i.e., species which occur in both habitats). The grey bands between habitats indicate pair-wise comparisons of the species in each habitat (see Table S1 for further details). Note that no shared species have been recorded yet between the banquette and any of the rest of habitats. Ac, Acari; C, Copepoda; N, Nematoda; T, Tardigrada

individuals found in the leaves. Species evenness, however, was significantly higher in the matte than in the leaves (Figure 4C; paired t-test: $t = 7.63$, $p < 0.001$). *Rhombognathus praegracilis* Viets 1939 was the dominant (58% of total mites found) and most frequent (96% of total samples) species in the meadow, occurring predominantly in the leaves; after *R. praegracilis*, *Copidognathus lamelloides* Bartsch 2000 was numerically dominant in the matte, yet was much sparser in the meadow (4% of total mites). These two species together with *Copidognathus magnipalpus* (Police 1909) accounted for 85% of the total mite abundance and occurred in more than 50% of the samples. In contrast, the eight species that ranked next in abundance represented only 11% of the total mite abundance, with the remaining species representing only 1%. Three of these rare species were represented by one individual.

Halacarid abundances (as $\log_{10}$) changed significantly over time in both habitats, reaching the highest abundance in summer in the leaves and in autumn in the matte, but no temporal change was found in species richness or evenness (Figure 4G–I; Table S3). Within the leaves, we found no effect of length or density of the leaves on species richness nor abundance, whereas evenness was negatively affected by the length of the leaves; however, this effect changed over time (Table S3). Within the matte, the density of matte positively affected halacarid abundance, as well as evenness, when accounting for the temporal variation (Table S3). No effect of any of the environmental variables in this habitat was found on species richness (Table S3).

Juvenile mites were relatively more abundant in the matte than in the leaves (Figure 4D; paired t-test: $t = 2.66$, $p = 0.01$). Likewise, we found significant differences in abundance between habitats for the numerically dominant species in the leaves, *Rhombognathus praegracilis* (Figure 4E; paired t-test: $t = -7.53$, $p < 0.001$), as well as for the second dominant species of the matte, *Copidognathus lamelloides* (Figure 4F; paired t-test: $t = 3.29$, $p = 0.005$). Last, we found that species composition accounting for abundance of mites varied between leaves and matte, through different sampling events in time, as well as with the interaction term between habitat and time (Table 2, Figure 4J). This suggests that the composition of halacarid species not only differed between habitats, but also shifted within each habitat over the studied period. In addition, most of the overall differences in species composition were caused by species replacement between habitats (69%), although such replacement was higher in the autumn and winter samplings (92% and 95%, respectively) than in the spring and summer samplings (54% and 49%).

4 | DISCUSSION

4.1 | Meiofaunal diversity associated with *P. oceanica*

Overall, we gathered evidence of 672 meiofaunal species occurring in the different habitats provided by the seagrass *P. oceanica* (Table S1).

TABLE 1 Halacarid species found in this study and their abundances (i.e., number of individuals) and occurrences (i.e., percentage of samples in which each species was observed) within the leaves and the matte of the meadow of *Posidonia oceanica*

	Abundance		Occurrence (%)	
Species	**Leaves**	**Matte**	**Leaves**	**Matte**
Agaue adriatica Viets 1940	2	1	4.17	4.17
Agaue cf. *A. abyssorum* (Trouessart 1896)	0	1	0.00	4.17
Agaue panopae (Lohmann 1893)	15	5	41.67	12.50
Agauopsis brevipalpus (Trouessart 1889)	3	8	12.50	29.17
Agauopsis microrhyncha (Trouessart 1889)	12	8	45.83	25.00
Agauopsis minor (Trouessart 1894)	13	8	33.33	29.17
Arhodeoporus gracilipes (Trouessart 1889)	6	17	25.00	54.17
Copidognathus lamelloides Bartsch 2000	22	52	41.67	66.67
Copidognathus latisetus Viets 1940	6	20	12.50	45.83
Copidognathus magnipalpus (Police 1909)	360	23	66.67	45.83
Copidognathus oculatus (Hodge 1863)	49	9	79.17	20.83
Copidognathus quadricostatus (Trouessart 1894)	0	3	0.00	8.33
Copidognathus remipes (Trouessart 1894)	7	21	12.50	54.17
Copidognathus reticulatus (Trouessart 1893)	6	0	8.33	0.00
Halacarus actenos Trouessart 1889	0	1	0.00	4.17
Lohmannella falcata (Hodge 1863)	7	6	20.83	16.67
Pelacarus aculeatus (Trouessart 1896)	1	3	4.17	12.50
Plegadognathus labronicus Morselli 1981	0	4	0.00	12.50
Rhombognathus cf. *R. procerus* Bartsch 1975	0	1	0.00	4.17
Rhombognathus praegracilis Viets 1939	901	109	100.00	91.67
Simognathus minutus (Hodge 1863)	4	16	12.50	37.50

Interestingly, 264 of these 672 species were reported by the authors as doubtful or unclear identification (e.g., reporting either "sp." or "cf." in the specific name; see Figure S1B). Because most of these reports were done by internationally acknowledged specialists in taxonomy (e.g., Curini-Galletti et al., 2012; Guilini et al., 2017; Novak, 1989), this uncertainty suggests that they may correspond to undescribed, new species to science, or belong to poorly investigated groups meriting further attention. Moreover, most meiofaunal groups are barely known in *P. oceanica*, because the research effort has focused on few taxa (~80% studies on five groups), whereas some groups remain unattended (e.g., Gnathostomulida and Loricifera). This scenario increases the value of the ecosystem formed by *P. oceanica* as a biodiversity reservoir, not only for macrofaunal species as previously indicated, but also for meiofaunal groups. In fact, the high diversity of meiofaunal species found here is greater than the diversity recorded for other groups in terms of species richness. In a similar review, Piazzi et al. (2016) compiled records for 307 species of algae and 353 species of sessile macrofauna associated with *P. oceanica*, whereas field-based studies report generally lower diversity for other groups in this seagrass, such as 68 species of diatoms from a meadow in the Adriatic Sea (Kanjer et al., 2019), 171 species of molluscs in the Alborán Sea (Urra et al., 2013), and 42 species of fish in Hellenic waters (Kalogirou et al., 2010). In Mediterranean marine caves, another iconic ecosystem for which a seminal review was conducted recently (Gerovasileiou et al., 2016; Gerovasileiou & Bianchi, 2021), the diversity of most meiofaunal groups was lower than that found among the habitats associated with *P. oceanica*. For example, in Nematoda, 37 species were found in caves versus 273 species in seagrass; in Copepoda, 113 species in caves versus 162 species in seagrass; in Acari, 5 species in caves versus 60 species in seagrass; in Tardigrada, 31 species in caves versus 42 species in seagrass; and in Kinorhyncha, 1 species in caves versus 14 species in seagrass.

Interestingly, meiofaunal species were not reported evenly across the different habitats associated with *P. oceanica*. Whereas most of the reports correspond to the seagrass habitat (i.e., leaves and matte; 559 records) and the adjacent sediments (343 records), the meiofaunal communities in the macrophyte accumulations (112 records; see also Mascart et al., 2013; Mascart, Lepoint, et al., 2015) and the banquette (6 records; Jansson, 1966; Casu & Curini-Galleti, 2006) remain neglected, despite the fact that the banquette is a vast inshore habitat that extends from the water line up to several meters inland (Boudouresque et al., 2017; Mateo et al., 2003). This bias suggests that the actual meiofaunal diversity associated with *P. oceanica* might be much greater than currently reported, especially in those poorly studied habitats. The lack of information on meiofaunal diversity is not unique to these meadows; meiofauna are often ignored in most biodiversity reports, despite being major components of diversity in marine ecosystems (Schratzberger &

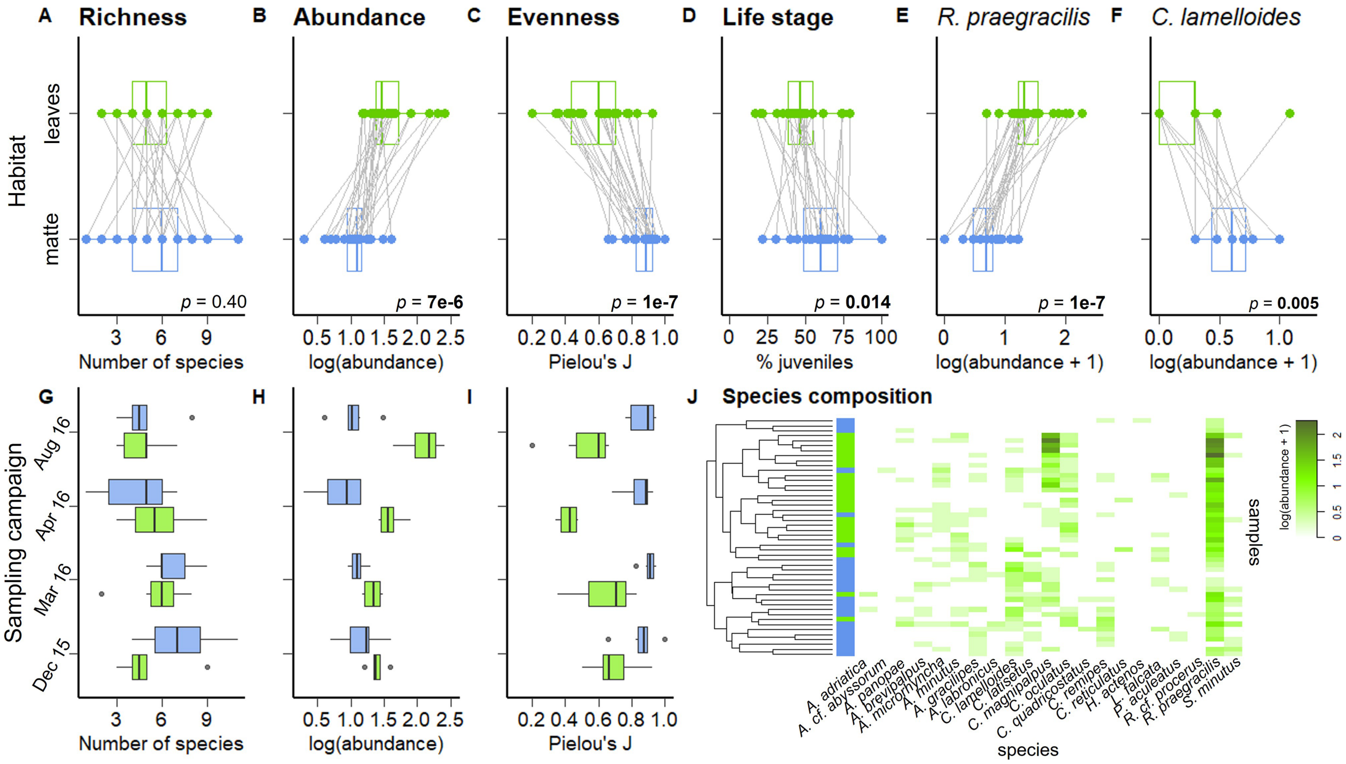

FIGURE 4 Main findings of the case study on halacarids in a meadow of *Posidonia oceanica* (see text for details). Colors differentiate between samples from the leaves (green) and the matte (blue). (A–F) Paired t-tests and p-values for the species richness, abundance ($\log_{10}$), evenness, the percentage of juveniles, and the abundances ($\log_{10}+1$) of the two dominant species per 400 cm^2 samples, comparing between the leaves and the matte. Samples collected from the same sampling point are connected by lines. (G–I) Boxplots of the variation in richness, abundance ($\log_{10}$), and evenness in the leaves and the matte through the four sampling campaigns of this study. Error bars indicate 10th and 90th percentiles, box boundaries indicate 25th and 75th percentiles, and the solid line within each box marks the median. (J) Abundance ($\log_{10}+1$) of each species per sample, colored from light to dark green. Rows indicate the samples of leaves or matte, whereas columns denote the species; the dendrogram was built using the method complete in the function hclust in R (R Core Team, 2019)

TABLE 2 PERMANOVA results based on Jaccard dissimilarities using the abundance ($\log_{10}+1$) for the differences in composition of halacarid species between habitats (leaves vs. matte) and through sampling campaigns; *p* values are based on 999 permutations.

Factors	*df*	pseudo-*F*	R^2	*p*
Habitat	1	9.958	0.164	0.001
Sampling campaign	3	1.755	0.087	0.008
Habitat × Sampling campaign	3	1.793	0.089	0.004
Residuals	40		0.660	

Ingels, 2018). Nematodes and copepods are the most recorded groups (418 and 317 records, respectively), especially in the seagrass, although they seem to show opposite preferences between the two habitats within the seagrass (Figure 2D). Whereas nematodes thrive in the sheltered matte (Novak, 1989), copepods are predominantly found in the leaves, where adaptations such as prehensile grasping legs and flattened bodies allow attachment to withstand stronger currents (Mascart et al., 2013). Last, some of the species recorded in the literature are putatively exclusive of the ecosystem formed by *P. oceanica*, including evolutionarily interesting species such as the cephalocarid *Lightiella magdalenina* Carcupino, Floris, Addis, Castelli & Curini-Galletti 2006, and annelids such as *Psammodrilus curinigallettii* Worsaae, Kvindebjerg & Martínez 2015 and *P. didomenicoi* Worsaae & Martínez 2018 in Worsaae et al. 2018, as well as a single record of *Lobatocerebrum*, possibly corresponding to a new, undescribed species (Kerbl et al., 2015; Sanna et al., 2014; Worsaae et al., 2018, 2015).

A similar meiofaunal diversity might occur in meadows dominated by different seagrass species (Cvitković et al., 2017; Sánchez-Jerez et al., 1999b). For example, surveys conducted in meadows of *Cymodocea nodosa* (Ucria) Asch. in the Canary Islands have revealed a large diversity of Gnathostomulida (Riera, 2012; Sterrer, 1997), Chaetognatha (Hernández et al., 2009), Kinorhyncha (Martínez, pers. obs.), and Annelida (Brito et al., 2001, 2005), including the description of new species only known from *Cymodocea nodosa* so far (Brito &

Núñez, 2003). These results collectively warrant future comprehensive investigations in other geographical areas and seagrass species.

4.2 | Habitat preferences of species associated with *P. oceanica*

Meiofauna showed differences in habitat occupation in almost all analyzed ecological studies (>90%), regardless of the taxonomic ranks of the units that were analyzed. Overall, these studies highlighted hydrodynamics, habitat complexity, and food availability as the major drivers for these differences. These drivers not only act at different spatial scales, but also vary through time. Indeed, the same drivers seem to affect the structure of meiofaunal assemblages in other seagrass ecosystems (mainly copepods and nematodes; see Bell et al., 1984; Decho et al., 1985; Hicks, 1989; De Troch et al., 2003, 2001, 2006, 2005).

At a regional scale, shore hydrodynamics exert a relatively homogeneous physical pressure on the entire ecosystem formed by *P. oceanica* (Vacchi et al., 2017). However, the great structural heterogeneity of this ecosystem—consisting of a mosaic of living plants, macrophyte accumulations, and sandy patches—provides areas sheltered from currents within the meadow (see Abadie et al., 2018). More specifically, patches of high habitat complexity protect the meiofaunal communities from the local hydrodynamics within the ecosystem formed by *P. oceanica* (Mascart, Lepoint, et al., 2015), as has been commonly observed for animal groups associated with other seagrasses (e.g., Hall & Bell, 1988; Heck & Orth, 1980; Moore & Hovel, 2010; Stoner & Lewis, 1985). Such sheltering effect is stronger in the matte, which also shows a higher diversity than that in the leaves, both in meiofaunal (Novak, 1982, 1989; Guilini et al., 2017; see Figure 2A,D) and macrofaunal species (Borg et al., 2006; Gambi et al., 1995; Piazzi et al., 2016). Food availability within each habitat, finally, drives the presence of different species not only depending on the amount of food (Castejón-Silvo, 2011; Cvitković et al., 2017; Losi et al., 2012; Mascart et al., 2013; Mirto et al., 2014, 2010; Polese et al., 2018) but also upon the presence of specific food sources. In fact, it has been shown that even closely related meiofaunal species may prefer different food sources (Mascart et al., 2018).

Temporally, hydrodynamics, habitat complexity, and food availability are inherently linked to the annual cycle of *P. oceanica*, in which long, old leaves fall at the end of the summer and are replaced by short, young leaves (Larkum et al., 2006). These drastic annual changes in the plant structure affect how the hydrodynamic forces impact individuals of *P. oceanica*, since the habitats become increasingly complex and sheltered as the meadow develops (Folkard, 2005), creating diverse and protected spaces to be occupied by meiofaunal organisms. At the same time, longer leaves foster more epiphytes, offering new and more abundant food sources to the meiofauna (Velimirov & Walenta-Simon, 1993; Mascart et al., 2018; but see Lebreton et al., 2012 on *Zostera noltii*). Indeed, all studies addressing temporal variation in *P. oceanica* found substantial differences in the meiofaunal assemblages over time, not only in taxa composition and abundance (Cvitković et al., 2017; Losi et al., 2012; Mascart, Lepoint, et al., 2015; Novak, 1989; Polese et al., 2018; Villora-Moreno et al., 1991), but also in species' dietary preferences (Mascart et al., 2018). These studies collectively showed that abundances of most meiofaunal taxa peaked between spring and summer (Cvitković et al., 2017; Losi et al., 2012; Mascart, Lepoint, et al., 2015; Novak, 1982, 1989; Polese et al., 2018; Sánchez-Jerez et al., 1999b; Villora-Moreno et al., 1991), at the same time as the peak of vegetation density in meadows of *P. oceanica*. This synchronic temporal variation indicates that the life cycle and reproduction of meiofaunal species living in these habitats are closely related to cycles of *P. oceanica*. Similar trends are found in other groups, such as epiphytic forams, diatoms, and dinoflagellates (Piazzi et al., 2016), as well as in macrofauna (e.g., Bedini et al., 2011; Gambi et al., 1995, 1992; Urra et al., 2013).

An assessment of migration between adjacent habitats is also important to understand the distribution of meiofauna in the meadow (Mascart, Agusto, et al., 2015; Mascart et al., 2013; Sánchez-Jerez et al., 1999a; Villora-Moreno et al., 1991; Figure 3). Meiofaunal migration occurs among the different habitats in a meadow and depends on the dispersal ability of the different taxa (Mascart, Agusto, et al., 2015; but see Commito & Tita, 2002; De Troch et al., 2005). These movements may take place seasonally (e.g., nematodes migrating from the matte to the leaves in summer; Novak, 1989), or in shorter time frames (e.g., day–night cycles of vertical migration in copepods; Sánchez-Jerez et al., 1999b). In similar seagrasses, some meiobenthic copepods migrate over their life spans between the sediment and the vegetated canopy (Bell & Hicks, 1991; Walters, 1988), even within the same day (Hicks, 1986), emerging into the water column at night (Bell et al., 1988). Of special importance is the colonization of the exported macrophyte detritus of *P. oceanica* from nearby habitats, particularly that of herbivore and detritivore meiofaunal species, as these species play an important role in the detritus degradation, contributing to the energy transfer in local food webs (François et al., 2018; Mascart, Lepoint, et al., 2015; Pusceddu et al., 2016). Although the colonization of this drifting seagrass detritus habitat has been studied in copepods (Mascart et al., 2013; Mascart, Agusto, et al., 2015; Figure 3), the process of colonization by other meiofaunal groups remains unknown. Moreover, whether some species are present throughout the entire journey of this detritus until it finally reaches the shoreline and forms the banquette is still unexplored.

In summary, the hydrodynamic stress, habitat complexity, and food availability are recognized in the literature as the main drivers shaping the meiofaunal distribution across the habitats formed by *P. oceanica*. These three drivers are inherently linked to phenology of *P. oceanica*, because its annual cycle includes a major change in the meadow structure, biomass, and food sources, altogether leading to changes in the composition and abundance of meiofaunal assemblages. Last, although meiofaunal species show specific habitat preferences, migration between nearby habitats define ultimately the spatial and temporal variation in their distribution, especially in actively swimming species.

4.3 | Halacarid assemblages in the meadow

In congruence with published studies on copepods and nematodes (Mascart, Lepoint, et al., 2015; Novak, 1989), we found that halacarid communities in the leaves consisted mainly of few very abundant species, whereas in the matte there was more evenness in abundance of mite species (Figure 4A–C). We speculate that such difference might be explained by the higher exposure of the leaves to both hydrodynamics (Borg et al., 2006; but see Pugh & King, 1985, in halacarids) and predation (Hovel et al., 2002; Hovel & Fonseca, 2005), which may filter and select for those species that withstand the water currents and avoid predation (Martínez et al., 2021). In effect, the exposure of the halacarids in the leaves to these stressors might explain that neither the species richness nor abundance was affected by seasonal changes in this habitat (e.g., increase in leaf length and, correspondingly, its epiphytic load; Mabrouk et al., 2011). Yet, fewer species were present in patches with longer leaves, where only a few species can withstand the currents and thrive. In contrast, halacarids are protected from predators and water currents in the matte, and we found more individuals in more complex patches of this habitat. However, unlike other detritivorous groups, such as copepods, annelids, and nematodes (Cvitković et al., 2017; Mirto et al., 2014; Vizzini et al., 2002), there was no relationship between halacarid abundance and the amount of organic carbon in the matte. Whether this is due to different dietary preferences in halacarids (Bartsch, 1989; Pugh & King, 1986) will warrant future research.

The findings of our case study supported partially the habitat preferences shown by the literature survey for meiofaunal species associated with *P. oceanica* (Figure 2A,D). Indeed, 15 of the 21 halacarid species recorded here co-occurred in both the leaves and the matte. Nonetheless, when accounting for abundances, the species composition of halacarid assemblages differed between the leaves and the matte (Table 2). These differences were mainly due to turnover, indicating a certain habitat sorting between the leaves and matte, yet the strength of this sorting may change over time. Such habitat sorting is evident in the dominant species *Rhombognathus praegracilis* and *Copidognathus lamelloides*, which prefer the leaves and the matte, respectively (Figure 4E,F). Indeed, *Rhombognathus praegracilis* belongs to the phytophagous subfamily Rhombognathinae, which possess morphological adaptations such as complex and thick claws and serrate setae for an epiphytic phytophagous lifestyle that includes both grazing on the rich algal communities of the leaves and withstanding the currents (Bartsch, 2006; Martínez et al., 2021; Pugh et al., 1987). In contrast, we found that individuals of *Copidognathus lamelloides* thrive in the matte and are infaunal, as has been reported from studies of other sheltered habitats (Bartsch, 2009; Riesgo et al., 2010; Somerfield & Jeal, 1995). In addition, juvenile halacarids were significantly rarer than adults in the leaves (Figure 4D). Noticeably, adult structures such as claws, an additional pair of legs, and more leg segments are lacking or still developing in juveniles (Bartsch, 2015). These structures enhance the adult's grip to the substrate, and so, their absence might relegate the juveniles to the matte, which is considerably more protected from currents than the leaves. Overall, our results suggest that, as in nematodes and copepods (Mascart, Agusto, et al., 2015; Novak, 1989), migration between leaves and matte is frequent in halacarids (Figure 3), yet only certain species thrive in each of those habitats.

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CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

AUTHOR CONTRIBUTIONS

GGG and AM surveyed the literature and compiled the datasets for the review. GGG, AGH, NS, AM, and FP planned the sampling design of the case study. GGG, AGH, NS, and AIM collected the samples; GGG, AGH, and NS sorted the latter samples for animals of interest and measured the environmental variables, whereas GGG identified the animals. GGG, AM, and DF planned the statistical approach and performed analyses. FP provided facilities and support. GGG, AM, and DF wrote the first draft. All authors contributed to the writing to additions and comments to the text.

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