Meiofauna is an important, yet neglected, component of biodiversity of *Posidonia oceanica*

GUILLERMO GARCÍA-GÓMEZ[1,2,3]*, ÁLVARO GARCÍA-HERRERO[1,2], NURIA SÁNCHEZ[1], FERNANDO PARDOS[1], ANDRÉS IZQUIERDO-MUÑOZ[4], DIEGO FONTANETO[2], ALEJANDRO MARTÍNEZ[2]

[1]*Department of Biodiversity, Ecology and Evolution, Department of Biology, Universidad Complutense de Madrid, C/José Antonio Novais 2, 28040, Madrid, Spain.*

[2]*Molecular Ecology Group (MEG), Water Research Institute (IRSA), National Research Council of Italy (CNR), Largo Tonolli 50, 28922, Verbania, Italy.*

[3]*Department of Earth, Oceans and Ecological Sciences, School of Environmental Sciences, University of Liverpool, 4 Brownlow Street, L69 3GP, Liverpool, United Kingdom.*

[4]*Marine Biology Laboratory in Santa Pola (CIMAR), Marine Research Center of Santa Pola, University of Alicante, Aptdo. 99, 03080, Alicante, Spain.*

*Corresponding author: guillegar.gz@gmail.com Telephone: +34 619 245 191

Meiofauna in *Posidonia oceanica*

1   **ABSTRACT**

2   *Posidonia oceanica* meadows are biodiversity reservoirs and provide many ecosystem services in

3   coastal Mediterranean regions. Marine meiofauna, on the other hand, not only represents a major

4   component of regional marine biodiversity, but also a useful tool to address both theoretical and

5   applied questions in ecology, evolution, and conservation. We review the meiofaunal diversity in the *P.*

6   *oceanica* ecosystem combining a literature review and a case study. First, we gathered records of 664

7   species from 69 published studies as well as unpublished sources, including few species exclusive from

8   this ecosystem. Eighteen of those studies quantified the spatial and temporal changes of species

9   composition, highlighting habitat-specific assemblages that fluctuate following the annual changes

10   experienced by *P. oceanica*. Hydrodynamics, habitat complexity, and food availability, all three

11   inherently linked to the seagrass phenology, are recognised as the main factors at shaping the complex

12   distribution patterns of meiofauna in the meadows. These drivers have been identified mainly from

13   Copepoda and Nematoda, and depend ultimately on species-specific preferences. Second, we tested the

14   generality of these observations using marine mites as a model group, showing that the same processes

15   might be in place also for other less abundant meiofaunal groups. Overall, our study highlights an

16   outstanding diversity of meiofauna in *P. oceanica* and shows its potential for future research, not only

17   focused on exploring and describing new species of neglected meiofaunal organisms, but also

18   providing a more complete understanding on the functioning of the iconic Mediterranean ecosystem

19   created by *P. oceanica*.

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21   **KEYWORDS:** Acari; Biodiversity; Copepoda; Habitat sorting; Nematoda

1. INTRODUCTION

Named after the Greek God Poseidon, the marine flowering plant *Posidonia oceanica* (L.) 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, meadows of *P. oceanica* also provide many ecosystem services. The leaves, which may extend around one meter beyond the seafloor, act as a major carbon sink filtering and oxygenating the seawater (Bay, 1984; Pirc, 1985; Mateo et al., 1997; Terrados & Duarte, 2000), and shelter the local hydrodynamics favouring sedimentation (e.g., Gacia & Duarte, 2001; Folkard, 2005; Manca et al., 2012). Underneath the leaves, a monumental formation of rhizomes, roots, and detritus, typically termed as "matte" (Boudouresque & Jeudy de Grissac, 1983), stabilises 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 (Jørgensen et al., 1981; Simeone & De Falco, 2013; González-Ortiz et al., 2014; Connolly & Waltham, 2015). The adjacent sandy areas form corridors and wide spaces among seagrass patches, constituting an ideal zone at the meadow's edges, where certain species settle (Coppa et al., 2010), seek refuge (Pinna et al., 2013), and feed (Sánchez-Jerez et al., 1999a). Furthermore, exported materials from the meadows accumulate and constitute other habitats, mostly on nearby sandy areas (Dimech et al., 2006; Cresson et al., 2012), but also further down to deep-waters or into caves and pits (Picard, 1965), where they boost local food webs as an additional source of allochthonous nutrients (Romero et al., 1992; Mateo et al., 2003; Guala et al., 2006; Simeone et al., 2013). Even when washed-up on the seashore, *P. oceanica* detritus cover vast extensions with complex dynamics throughout the year, called "banquettes" (Boudouresque & Meinesz, 1982). Banquettes are fundamental in protecting beaches from erosion, stabilising the sand dune, and enriching underlying sediments with nitrogen (Boudouresque et al., 2016). Due to such significant and multifaceted modification of the environment, *P. oceanica* is considered as an ecological engineer (Unsworth & Cullen-Unsworth, 2017), which forms a complex ecosystem composed of living seagrass and its exported detritus, as well as the rich community of organisms associated to its different habitats (Mazzella et al., 1989; Boström et al., 2006).

50   Over the last decades, scientists have described the diversity and functioning of the *P. oceanica*
51   ecosystem, along with the local dynamics of the mosaic of habitats associated with them. Initial
52   research focused on the phenological annual changes of the *P. oceanica* plants themselves (e.g., Ott,
53   1980; Bay, 1984), followed by detailed characterizations of the diversity and structure of their
54   associated communities. Indeed, many studies have addressed the dynamics of *P. oceanica* meadows
55   highlighting the economic and ecological importance of their inhabitants (e.g., Dimech et al., 2002;
56   Duffy et al., 2003; Como et al., 2008; Honkoop et al., 2008; Kalogirou et al., 2010; Whippo et al.,
57   2018). For instance, the leaves foster nurseries of fish and cephalopods that often represent important
58   resources for local fisheries (Cetinić et al., 1999, 2011), whereas the assemblages of gastropods and
59   bivalves associated to the plant include several emblematic, often endemic, Mediterranean species
60   (Urra et al., 2013). In the matte, many species of infaunal crustaceans, molluscs, and annelids thrive
61   (Borg et al., 2006), contributing to the overall recycling of the entrapped organic matter (Vizzini et al.,
62   2005). Even beyond the plant, the phytal detritus drifting away from the meadows on the adjacent
63   sandy areas host diverse macrofaunal communities (Sánchez-Jerez et al., 1999b; Guidetti, 2000;
64   Gallmetzer et al., 2005). However, the epiphytic organisms growing throughout the plant structure
65   constitute the communities that have received most attention, partially due to their high species
66   diversity (ca. 660 species, after Piazzi et al., 2016), but also because they have been used as
67   bioindicators of the health of the meadows (Martínez-Crego et al., 2010; Giovannetti et al., 2010;
68   Mateu-Vicens et al., 2014). Interestingly, such research on epiphytic organisms has shown that the
69   distribution of these species is not uniform within the seagrass, but rather the opposite: some epiphytes
70   dominate the older but more exposed leaf tips, others prefer their sheltered middle or basal parts, and
71   few even select the shaded rhizomes (Gambi et al., 1995; Piazzi et al., 2016).

72   In contrast with macrofaunal communities, information is much more scattered for the
73   meiofaunal animals inhabiting the *P. oceanica* ecosystem. Meiofauna includes a heterogeneous subset
74   of organisms that are retained between a tandem of meshes with 500 µm and 63 µm size, largely
75   dominated by microscopic animals, but also including larger forms with elongated morphologies or
76   contractible bodies (Giere, 2009; Schmidt-Rhaesa, 2020). Meiofauna plays a fundamental role in many
77   processes in the seafloor (Schratzberger & Ingels, 2018) and represent a numerically important, yet
78   often neglected, component of the diversity of many regions (Curini-Galletti et al., 2012, 2020;

79   Martínez et al., 2019). Furthermore, meiofauna represents an invaluable tool to address both theoretical

80   and applied eco-evolutionary questions (e.g., Fontaneto et al. 2007; Fontaneto 2011; Gansfort, ;

81   Laumer et al. 2015; Martínez et al., 2020; Fontaneto & Zhai, 2020; Martin-Duran et al., 2021), as these

82   organisms belong to virtually every animal phylum, thus alleviating the confounding effect of potential

83   phylogenetic bias during inductive hypothesis tests (Giere, 2009; Rundell & Leander, 2011). Moreover,

84   meiofauna critically supports marine food webs by transferring the energy from decomposer and

85   primary producer microorganisms to higher trophic levels (Danovaro, 1996; Danovaro et al. 2007).

86   Although scattered in the literature, numerous records indicate that many meiofaunal species inhabit

87   the *P. oceanica* ecosystem, whether crawling on the leaves or across the matte labyrinths, gliding in the

88   interstices of the adjacent sediments, or even drifting within the detritus over the sea bottom. Several

89   studies addressed the composition and community dynamics of some meiofaunal groups in *P.*

90   *oceanica*, revealing that the biotic and abiotic conditions of the meadow shape the distribution of

91   meiofaunal species (e.g., Novak, 1982, 1989; Mascart et al., 2013; Mascart, Lepoint, et al., 2015;

92   Pusceddu et al., 2016). However, besides these few comprehensive ecological studies, mainly focusing

93   on copepods and nematodes, most of this research involves occasional taxonomic descriptions from

94   punctual samples. Unfortunately, the lack of a comprehensive updated review of all this literature

95   obscures our understanding of the overall diversity and role of meiofauna in this iconic Mediterranean

96   ecosystem.

97   The aim of this study is two-folded. First, we reviewed the diversity (i.e., species richness) and

98   ecology of meiofauna in *P. oceanica* through a literature survey, completed with unpublished data

99   provided by our colleagues. Despite our aim is mainly exploratory (Yanai & Lercher, 2020), we depart

100   from the assumption that the patterns in meiofaunal diversity in *P. oceanica* resembles those described

101   for larger organisms. We expect that meiofaunal species do not occur homogeneously in the *P.*

102   *oceanica* ecosystem, but they segregate spatially and temporally across its different habitats following

103   the annual phenological cycle of the meadows. Second, we selected a case study to test explicitly the

104   latter assumption. We used halacarid marine mites as model organisms because they are common in

105   seagrasses such as *P. oceanica* (Mari & Morselli, 1990; Zupo, 1993; Durucan, 2018; Durucan &

106   Boyacı, 2018; Durucan & Levent, 2019), yet the habitat preferences of the species associated with this

107 plant have never been explicitly investigated. This case study, therefore, provides a point of

108 comparison with the better studied copepods and nematodes (Novak, 1989; Mascart et al., 2013)

109

110 **2. MATERIALS AND METHODS**

111 2.1 Literature review

112 2.1.1 Selection of references

113   We systematically screened Google Scholar for all published literature containing records of

114 vagile meiofaunal species within *Posidonia oceanica* habitats. The search, performed in December

115 2020, consisted of the word 'Meiofauna' or the name of a target animal group (i.e., 'Acari', 'Annelida',

116 'Cephalocarida', 'Copepoda', 'Gastrotricha', 'Gnathostomulida', 'Kinorhyncha', 'Loricifera',

117 'Mystacocarida', 'Nematoda', 'Platyhelminthes', 'Rotifera', 'Tardigrada') followed by the term

118 'Posidonia' (e.g., 'Copepoda' AND 'Posidonia'). After screening the abstract of all the compiled

119 references, all papers including relevant information were downloaded. To maximize the completeness

120 of our database, the references cited in all downloaded papers were checked for additional sources.

121 2.1.2 Compilation of the species inventory

122   First, to evaluate the known diversity of meiofaunal species in the *P. oceanica* ecosystem, we

123 carefully screened each selected paper to compile all available records. Each entry included the taxon

124 name, locality, WGS84 geographic coordinates (extracted directly or calculated after the description of

125 each locality), depth, collection method, and the habitat within the *Posidonia oceanica* ecosystem,

126 when these data were available (see Supplementary Information Table S1). We considered four types

127 of habitats: (1) seagrass, consisting of the structure created by the plant; (2) adjacent sediments,

128 including the bare sediments and interstitial habitats next to seagrass patches; (3) macrophyte detritus,

129 the wandering vegetal debris from *P. oceanica* seagrass accumulated on sediments (termed as

130 'macrophytodetritus accumulations' in Mascart, Lepoint, et al., 2015); and (4) banquette, the detritus

131 deposited on the shore after the falling of the *P. oceanica* leaves (Boudouresque & Meinesz, 1982).

132 When this information was provided, we further divided the seagrass habitat in its two discrete

133 compartments: the leaves and the matte, i.e., the underlying ensemble of living rhizomes, plant debris,

134 and roots (see Figure 2). This information was subsequently used to evaluate the habitat preferences of

135   the meiofaunal species living in the *P. oceanica* ecosystem (see below). Furthermore, to maximize the

136   number of provided records, we consulted different specialists, who kindly shared their unpublished

137   records to this study.

138   2.1.3 Review of ecological questions

139   Complementary to the inventory of species, all papers with an ecological scope in our database

140   were further screened for relevant hypotheses and findings regarding the preferences of meiofaunal

141   species within the habitats of *P. oceanica*. The information contained in these papers was organised in

142   a table (Table S2), comprising the aim of the study, the targeted meiofaunal groups, and the diversity

143   metrics implemented. For each study we further provided a concise summary of the findings, on

144   whether they found differences in the biodiversity metrics or abundance between (i) habitats, (ii)

145   between samples within the same habitat from a given locality (i.e., local scale), (iii) between localities

146   (i.e., regional scale), and (iv) over time. Last, the table included the future research questions proposed

147   by each study.

148   2.2 Case study: halacarids in *P. oceanica*

149   2.2.1 Study site and sampling design

150   In addition to our literature survey, we investigated the habitat specificity in the community of

151   halacarids inhabiting a *Posidonia oceanica* meadow in Cala del Cuartel (Alicante, SE Spain; WGS84

152   coordinates 38° 12' 34.04" N, 0° 30' 19.12" W), located in a region where animal communities

153   associated to these meadows have been well documented (Villora-Moreno et al., 1991, 1997; Sánchez-

154   Jerez et al., 1999a, 1999b; Martínez, García-Gómez, in press). Sampling was carried out during four

155   campaigns in December 2015, and March, April and August 2016, each coinciding with a different

156   season. During each campaign, SCUBA divers sampled six randomly selected patches of *P. oceanica,*

157   totalling 24 patches for the whole study. Samples of (1) leaves, (2) matte, and (3) adjacent sediments

158   were collected at each patch and standardised through 400 cm^2-quadrats (20 x 20 cm) (e.g., Novak,

159   1989; Sánchez-Jerez et al., 1999a; Pusceddu et al., 2016; but see Bell et al., 1984). The leaves were

160   first cut at the ligula level and collected carefully with a hermetic bag; then, the underlying matte was

161   shovelled into another hermetic bag (following Novak, 1982, 1989; Cvitković et al., 2017). Identical

162   samples of the adjacent sediments to each sampled seagrass patch were collected using jars.

163   Halacarid mites were extracted combining magnesium chloride and "bubble and blot"
164   techniques (Higgins & Thiel 1988, Sørensen & Pardos 2008), filtered through a 63 μm mesh, and fixed
165   in 7% formaldehyde. Fixed halacarids were then sorted using a MOTIC® SMZ-168 stereoscope and
166   whole-mounted on slides in a modified Hoyer's medium (Mitchell & Cook 1952). Whole-mounted
167   specimens were examined using an Olympus DP70 camera mounted on a light microscope equipped
168   with differential interference contrast microscopy (DIC). We followed André (1946), Green &
169   MacQuitty (1987), and specific taxonomic literature (Morselli, 1980; Bartsch, 1986, 2001, 2006) for
170   species identification. Adult and juvenile specimens were distinguished following Bartsch (2015).
171   Nomenclature followed the World Register of Marine Species (WoRMS Editorial Board 2021).

172   2.2.2 Data analysis

173   All statistical analyses were performed using the *R* software version 3.6.1 (R Core Team 2019).
174   We investigated the variation in species richness (i.e., number of species), abundance (i.e., number of
175   individuals) and evenness (i.e., Pielou's J) within the leaves and the matte, because no mites were
176   found in the sediments adjacent to the seagrass. First, we investigated differences in species richness,
177   abundance (as $\log_{10}$ to cope with stark differences between samples), and evenness between leaves and
178   matte samples collected from the same sampling point, using a paired-samples t-test (paired t-test)
179   through the function 't.test'. Pielou's J was calculated for each sample using function 'diversity' in the
180   R package *vegan* v. 2.2-1 (Oksanen et al., 2015) to obtain first the Shannon index and then dividing it
181   by the natural logarithm of the number of species. For one sample in the matte, Pielou's J was not
182   calculated as only one species was observed. Second, we tested whether richness or abundance changed
183   with food availability and habitat complexity, as well as over time. We used the length of the leaves
184   and the organic carbon content of the sediment as a proxy for food availability in the leaves and the
185   matte, respectively. The length of the leaves was measured as the average distance in centimetres from
186   the ligula to the apical end of all the complete leaves found in each sample, which is known to correlate
187   positively with the abundance of epiphytic microorganisms (Mabrouk et al., 2010) that may serve as
188   food for many halacarid species (Bartsch, 1989). Likewise, the percentage of organic carbon of the
189   sediment was calculated using the Walkley-Black method (Walkley & Black, 1934), indicating the
190   amount of accumulated organic matter in the matte, representing available food for mites. Habitat
191   complexity was inferred through the density of leaves or matte, calculated as the dry weight of the

192   leaves or the matte divided by the total volume of the habitat, which varied in the leaves (Average

193   leave length * 20 cm x 20 cm) and was constant in the matte (2 cm x 20 cm x 20 cm). We performed

194   linear models using function 'lm' to examine the effect on richness, abundance (as $\log_{10}$), and evenness

195   of the environmental variables within each habitat: the length and density of the leaves within the

196   leaves, and the percentage of organic matter and density of the matte within the matte. We accounted

197   for the temporal variation in the seagrass over the period of study by including the sampling date in all

198   models. The significance of each independent variable was summarized as a Type II ANOVA table,

199   using the function 'Anova' in the R package *car* version 3.0.9 (Fox et al., 2012). The assumptions of

200   the linear models were controlled visually by checking the normality of model residuals, the plots of

201   residual versus fitted values, and normal Q-Q plots (Crawley, 2013).

202   To further investigate whether halacarids preferred a certain habitat, we performed two

203   additional analyses. First, since different ecological preferences have been reported between life stages

204   in halacarids (Somerfield & Jeal, 1995, 1996; Bartsch, 2004), we tested for differences in percentage of

205   juveniles (i.e., number of non-adult individuals / total individuals of each sample; in %) between the

206   matte and the leaves within sampling points. Second, we tested for differences in abundance between

207   habitats of the dominant species found within each habitat, for which data were sufficient to perform

208   the analyses. Again, we performed paired t-tests for both differences in percentage of juveniles and

209   abundance of the dominant species between habitat samples within sampling points. Paired samples

210   were removed from the analyses when no individuals were found in a sampling point. For all paired t-

211   tests, we first checked the normality of the differences between paired samples by Shapiro-Wilk tests

212   using the function 'shapiro.test'.

213   Last, we examined the differences in species composition between communities occurring in

214   different habitats including their nestedness and turnover components, through the Jaccard abundance-

215   based index (Legendre, 2014), using the function 'beta' in the R package *BAT* v. 1.5.5 (Cardoso et al.,

216   2015). For both species- and community-level tests, the abundances were again transformed to $\log_{10}$

217   (abundance + 1) to cope with stark differences in abundance between samples as well as with 0 values.

218   We then assessed the percentage of variability in community composition observed across samples

219   through a permutational analysis of variance (PERMANOVA) using distance matrices with the

220   function 'adonis' included in the R package *vegan*. Again, we explicitly included the sampling date as

221   an independent variable, to account for the temporal variation in the seagrass in structuring differences

222   of species assemblage.

223

224   **3. RESULTS**

225   3.1 Review of meiofauna in *P. oceanica*

226   We reviewed a total of 69 relevant studies: 51 of them consisting of taxonomic papers or

227   species inventories and 18 comprising ecological studies (see Supplementary Information). Together

228   with the data published within the present study, we compiled 1045 records for 664 species (Table S1).

229   Nematoda, Copepoda, and Acari accumulated 73% of the records; Tardigrada, Platyhelminthes,

230   Gastrotricha, and Annelida 21%; Kinorhyncha, Xenacoelomorpha, Ostracoda, Gastropoda,

231   Chaetognatha, Mystacocarida, and Rotifera accounted for the remaining 6% of the dataset. No records

232   were found for Gnathostomulida and Loricifera. The majority of sampling sites were concentrated in

233   the Central Mediterranean Sea, particularly in Corsica, Sardinia, and the Gulf of Naples (Figure 1).

234   Most of the species have been recorded within the seagrass (346 species), mostly in the matte (292

235   species), as well as in the sediments adjacent to the meadows (275 species) (Figure 2A). Interestingly,

236   ca. 85% of the species recorded in the adjacent sediments and within the seagrass have been

237   exclusively found in these habitats. Copepoda, Platyhelminthes, Gastrotricha, Annelida, Tardigrada,

238   and Xenacoelomorpha were mainly found in the sediments, whereas Nematoda and Acari were

239   observed principally within the seagrass (Figure 2D), being records for Nematoda particularly abundant

240   in the matte. Most studies relied on samples collected by hand (562 species), generally by SCUBA

241   divers (Figure 2B), which recovered generally different species from the studies that relied on boat-

242   operated collections (Figure 2E). Most species and meiofaunal groups were reported from shallow

243   waters (476 species; between 0–20 m), and these numbers decreased with increasing depth (Figure 2C

244   and 2F).

245   We sorted 18 ecological studies (Table S2) that addressed the variation in taxonomic richness,

246   species composition, and abundance of meiofaunal communities at regional (i.e., between localities,

247   generally kilometres away; in nine studies) and local spatial scales (i.e., between samples within the

248   same habitat in a given locality; in 13 studies). Only three of these studies incorporated functional

249 metrics (Novak, 1989; Mirto et al., 2014; Guilini et al., 2017), and a single paper investigated diet

250 preferences (Mascart et al., 2018). Nematodes and copepods were the preferred groups (six studies at

251 specific level), whereas other groups were often recorded at the taxonomic rank of phylum or class.

252 Moreover, 16 studies searched for the ecological factors influencing the presence of meiofauna in

253 different habitats of the meadows, stressing the importance of hydrodynamics, habitat complexity, and

254 food availability. Last, 10 of the studies highlighted temporal variation as another major driver of

255 meiofaunal communities, mainly affecting abundances.

256 3.2 Case study on halacarid mites

257 We counted 1730 individuals belonging to 21 species and 9 genera (Table 1). One species was

258 restricted to the leaves and four to the matte, whereas 16 species co-occurred in both habitats. No

259 halacarids were found in the sediments. The genus *Copidognathus* was represented by 7 species,

260 followed by the genera *Agauopsis* and *Agaue* (3 species each), and *Rhombognathus* and *Arhodeoporus*

261 (2 species each). The genera *Halacarus*, *Lohmanella*, *Pelacarus,* and *Simognathus* were represented by

262 one species.

263 Species richness showed no significant differences between habitats (Figure 3A; paired t-test: t

264 = -0.78, *p* = 0.44), though abundances were significantly higher in the leaves than in the matte (Figure

265 3B; paired t-test: t = 5.77, *p* < 0.001), with 82% of the individuals found in the leaves. Species

266 evenness, however, was significantly higher in the matte than in the leaves (Figure 3C; paired t-test: t =

267 7.63, *p* < 0.001). *Rhombognathus praegracilis* Viets, 1939 was the dominant (58% of total mites

268 found) and most frequent (96% of total samples) species in the meadow, occurring predominantly in

269 the leaves; after *R. praegracilis*, *Copidognathus lamelloides* Bartsch, 2000 dominated the matte, yet

270 being much sparser in the meadow (4% of total mites). These two species together with *Copidognathus*

271 *magnipalpus* (Police, 1909) accounted for 85% of the total mite abundance and occurred in more than

272 50% of the samples. In contrast, the following 8 species ranked by abundance represented only 11% of

273 the total mite abundance, with the remaining species representing only 1%. Three of these rare species

274 were represented by one individual.

275 Halacarid abundances changed significantly over time only in the leaves, reaching the highest

276 abundance in summer, but no temporal change was found in species richness or evenness (Figure 3G-I;

11

277   Table S3). However, we found no effect of length or density of the leaves on species richness,

278   abundance, or evenness (Table S3). Within the matte, by contrast, halacarid abundance was positively

279   affected by the density of matte (Table S3). No temporal differences (Figure 3G-I) and no effect of any

280   of the environmental variables in this habitat was found on species richness or evenness (Table S3).

281   Juvenile mites were relatively more abundant in the matte than in the leaves (Figure 3D; paired

282   t-test: t = 2.67, p = 0.01). Likewise, we found significant differences in abundance between habitats for

283   the dominant species of the leaves, *Rhombognathus praegracilis*, which preferred the leaves (Figure

284   3E; paired t-test: t = -7.53, p < 0.001), as well as for the second dominant species of the matte,

285   *Copidognathus lamelloides*, which preferred the matte (Figure 3F; paired t-test: t = 3.29, p = 0.005).

286   Last, we found that species composition accounting for abundance of mites varied between leaves and

287   matte, through different sampling events in time, as well as with the interaction term between habitat

288   and time (Table 2 and Figure 3J). This suggests that the composition of halacarid species not only

289   differed between habitats, but also shifted within each habitat over the studied period. In addition, most

290   of the differences in species composition were caused by species replacement between habitats (69%).

291

292   **4. DISCUSSION**

293   The main findings of the present paper are straightforward: (1) the diversity of meiofauna in *P.*

294   *oceanica* is not only comparable, but even higher than that reported for other groups of organisms

295   associated with this plant (i.e., epiphytes and macrofauna); (2) most species show specific habitat

296   preferences, which vary from regional to local scales, depending mainly on hydrodynamics, habitat

297   complexity, and food availability. The latter has been shown mainly by copepods and nematodes in the

298   literature, and by marine mites in the presented case study.

299   4.1 Meiofaunal diversity in *P. oceanica*

300   Overall, we gathered evidence of 664 meiofaunal species occurring in the different habitats

301   provided by the *P. oceanica* (Table S1). Interestingly, 258 of these 664 species were reported by the

302   authors as doubtful or unclear identification (e.g., reporting either 'sp.' or 'cf.' in the specific name).

303   Since most of these reports were done by internationally acknowledged taxonomical specialists (e.g.,

12

304 Novak, 1989; Curini-Galletti et al., 2012; Guilini et al., 2017), this uncertainty suggests that they may

305 correspond to undescribed, new species to science, or belong to poorly investigated groups meriting

306 further attention. This scenario increases the value of the *P. oceanica* ecosystem as a biodiversity

307 reservoir, not only for macrofaunal species as previously indicated, but also for meiofaunal groups. In

308 fact, the outstanding diversity of meiofaunal species found here largely overcomes the diversity

309 recorded for other groups in species richness. In a similar review, Piazzi et al. (2016) compiled records

310 for 307 species of algae and 353 species of sessile macrofauna in *P. oceanica*, whereas field-based

311 research reports generally lower diversity for other groups. For instance, 68 species of diatoms were

312 reported in a meadow from the Adriatic Sea (Kanjer et al., 2019), 171 species of molluscs in the

313 Alborán Sea (Urra et al., 2013), and 42 species of fish in Hellenic waters (Kalogirou et al., 2010).

314 Interestingly, meiofaunal species were not reported evenly across the different habitats within

315 the *P. oceanica* ecosystem. While most of the reports correspond to the seagrass habitat (i.e., leaves

316 and matte; 525 records), and the adjacent sediments (341 records),the meiofaunal communities in the

317 macrophyte accumulations (114 records; see also Mascart et al., 2013; Mascart, Lepoint, et al., 2015),

318 and the banquette (6 records; Jansson, 1966; Casu & Curini-Galletti, 2006) remain neglected, despite

319 the latter provides a vast inshore habitat that extends from the water line up to several meters inland

320 (Mateo et al., 2003; Boudouresque et al., 2017). This bias suggests that the actual meiofaunal diversity

321 associated with *P. oceanica* might be much greater than currently reported. This is not a unique feature

322 of these meadows, since meiofauna is often ignored in most biodiversity reports, despite it has been

323 acknowledged as one the major components of diversity in marine ecosystems (Schatzberger et al.

324 2018). Moreover, many of the species recorded in the literature are putatively exclusive from the *P.*

325 *oceanica* ecosystem, including evolutionarily interesting species such as the cephalocarid *Lightiella*

326 *magdalenina* Carcupino et al. 2006, and annelids such as *Psammodrilus curinigallettii* Worsaae,

327 Kvindebjerg & Martínez, 2015 and *P. didomenicoi* Worsaae & Martínez 2018, as well as a single

328 record of *Lobatocerebrum*, possibly corresponding to a new undescribed species (Sanna et al., 2014;

329 Kerbl et al., 2015; Worsaae et al., 2015; 2018).

330 A similar meiofaunal diversity might occur in meadows dominated by different seagrass species

331 (Sánchez-Jerez et al., 1999a; Cvitković et al., 2017). For example, surveys conducted in meadows of

332 *Cymodocea nodosa* (Ucria) Ascherson, 1870 in the Canary Islands have revealed a large diversity of

333 Gnathostomulida (Sterrer, 1997; Riera, 2012), Chaetognatha (Hernández et al., 2009), Kinorhyncha
334 (Martínez, pers. obs.), and Annelida (Brito et al., 2001, Brito et al., 2005), including the description of
335 new species only known from *Cymodocea* so far (Brito & Nuñez, 2003). These results collectively
336 warrant future comprehensive investigations in other geographical areas and seagrass species.

337 4.2 Habitat preferences in *P. oceanica*

338 Meiofauna showed differences in habitat occupation in almost all analysed ecological studies
339 (>90%), regardless of the taxonomic ranks of their operational units. Overall, these studies highlighted
340 hydrodynamics, habitat complexity, and food availability as the major drivers for these differences.
341 These drivers not only act hierarchically nested at different spatial scales, but also vary through time.
342 Indeed, the same drivers seem to affect the structure of meiofaunal assemblages in other seagrass
343 ecosystems (mainly copepods and nematodes; see Bell et al., 1984; Decho et al., 1985; Hicks, 1989; De
344 Troch et al., 2001, 2003, 2005, 2006).

345 At a regional scale, shore hydrodynamics exerts a relatively homogeneous physical pressure on
346 the entire *P. oceanica* ecosystem (Vacchi et al., 2017). However, the great structural heterogeneity of
347 *P. oceanica*—consisting of a mosaic of living plants, macrophyte accumulations, and sandy patches—
348 shelters certain areas within a meadow from the currents (see Abadie et al., 2018). More specifically,
349 patches of high habitat complexity protect the meiofaunal communities from the local hydrodynamics
350 in *P. oceanica* (Mascart, Lepoint, et al., 2015), as commonly observed in seagrasses for other animal
351 groups (e.g., Heck & Orth., 1980; Stoner & Lewis, 1985; Hall & Bell, 1988; Moore & Hovel, 2010).
352 Such sheltering effect is stronger in the matte, which also shows a higher diversity than that in the
353 leaves, both in meiofaunal (Novak, 1982, 1989; Guilini et al., 2017; see Figure 2A and 2D) and
354 macrofaunal species (Gambi et al., 1995; Borg et al. 2006; Piazzi et al. 2016). Food availability within
355 each habitat, finally, drives the presence of different species not only depending on the amount of food
356 (Mirto et al., 2010, 2014; Castejón Silvo, 2011; Losi et al., 2012; Mascart et al., 2013; Cvitković et al.,
357 2017; Polese et al., 2018) but also upon the presence of specific food sources. In fact, it has been shown
358 that even closely related meiofaunal species may prefer different food sources (Mascart et al., 2018).

359 Temporally, hydrodynamics, habitat complexity, and food availability are inherently linked to
360 the annual cycle of *P. oceanica*, in which long old leaves fall at the end of the summer, being replaced

361 by short young leaves (Larkum et al., 2006). These drastic annual changes in the plant structure affect

362 how the hydrodynamic forces impact *P. oceanica*, since the habitats become increasingly complex and

363 sheltered as the meadow develops (Folkard, 2005). At the same time, densely aggregated leaves foster

364 many epiphytes, offering new and more abundant food sources to the meiofauna (Velimirov &

365 Walenta-Simon, 1993; Mascart et al., 2018; but see Lebreton et al., 2012 on *Zostera noltii*). Indeed, all

366 studies addressing temporal variation in *P. oceanica* found substantial differences over time, not only

367 in taxa composition and abundance (Novak, 1989; Villora-Moreno et al., 1991; Losi et al., 2012;

368 Mascart, Lepoint, et al., 2015; Cvitković et al., 2017; Polese et al., 2018), but also in species' dietary

369 preferences (Mascart et al., 2018). These studies collectively showed that abundances of most

370 meiofaunal taxa peaked between spring and summer (Novak, 1982, 1989; Villora-Moreno et al. 1991;

371 Sánchez-Jerez et al. 1999a; Losi et al., 2012; Mascart, Lepoint, et al., 2015; Cvitković et al., 2017;

372 Polese et al., 2018), in accordance with the apogee of *P. oceanica*. Similar trends are found in other

373 groups, such as epiphytic forams, diatoms, and dinoflagellates (Piazzi et al., 2016), as well as

374 macrofauna (e.g., Gambi et al., 1992, 1995; Bedini et al., 2011; Urra et al., 2013).

375 Migration between adjacent habitats is also important to understand the distribution of

376 meiofauna in the meadow (Villora-Moreno et al., 1991; Sánchez-Jerez et al., 1999b; Mascart et al.,

377 2013; Mascart, Agusto, et al., 2015). Meiofaunal migration occurs amongst the different habitats in a

378 meadow and depends on the dispersal ability of the different taxa (Mascart, Agusto, et al., 2015; but

379 see Commito & Tita, 2002; De Troch et al., 2005). These movements may take place seasonally (e.g.,

380 nematodes migrating from the matte to the leaves in summer; Novak, 1989), or in shorter time frames

381 (e.g., day-night cycles of vertical migration in copepods; Sánchez-Jerez et al., 1999a). In similar

382 seagrasses, some meiobenthic copepods migrate between the sediment and the vegetated canopy over

383 their life spans (Walters, 1988; Bell & Hicks, 1991), and even within the same day (Hicks, 1986),

384 emerging into the water column at night-time (Bell et al., 1988).

385 4.3 Halacarid assemblages in the meadow

386 In congruence with published studies on copepods and nematodes (Novak, 1989; Mascart,

387 Lepoint, et al., 2015), we found that halacarid communities in the leaves consisted mainly of few very

388 abundant species, whereas in the matte, mite abundances were more even between species (Figure 3A-

389   C). We speculate that such difference might be explained by the higher exposure of the leaves to both

390   hydrodynamics (Borg et al., 2006; but see Pugh & King, 1985, in halacarids) and predation (Hovel et

391   al., 2002; Hovel & Fonseca, 2005), which may filter and select for those species that withstand the

392   water currents and avoid predation. In effect, the exposure of the halacarids in the leaves to these

393   stressors might explain that neither their species richness nor abundances were affected by the changes

394   in this habitat (e.g., increase of leaf length and so its epiphytic load; Mabrouk et al., 2010). In contrast,

395   halacarids are protected from predators and water currents in the matte since more individuals occurred

396   in patches of greater habitat complexity. However, unlike other detritivorous groups, such as copepods,

397   annelids, and nematodes (Vizzini et al., 2002; Mirto et al., 2014; Cvitković et al., 2017), halacarids

398   showed no relationship with the organic carbon in the matte. Whether this is due to different dietary

399   preferences in halacarids (Pugh & King, 1986; Bartsch, 1989) will warrant future research.

400   The findings of our case study supported partially the habitat preferences shown by the

401   literature survey for *P. oceanica* meiofaunal species (Figure 2A and 2D). Indeed, 16 of the 21 halacarid

402   species recorded here co-occurred in both the leaves and the matte. Nevertheless, when accounting for

403   abundances, the species composition of halacarid assemblages differed between the leaves and the

404   matte (Table 2). These differences were mainly due to turnover rather than to differences in species

405   nestedness, indicating a certain habitat sorting between the leaves and matte. Such habitat sorting is

406   evident amongst the dominant species *Rhombognathus praegracilis* and *Copidognathus lamelloides*,

407   preferring the leaves and the matte, respectively (Figure 3E and 3F). Indeed, *Rhombognathus*

408   *praegracilis* belongs to the phytal-specialist subfamily Rhombognathinae, which possesses

409   morphological adaptations for an epiphytic phytophagous lifestyle, such as complex and thick claws

410   and serrate setae, useful to graze on the rich algal communities of the leaves and withstand the currents

411   (Pugh et al., 1987; Bartsch, 2006; Martínez, García-Gómez, in press). In contrast, *Copidognathus*

412   *lamelloides,* which thrive in the matte, is attributed with an infaunal lifestyle, as it has been usually

413   reported from sheltered habitats (Somerfield & Jeal, 1995; Barstch, 2009; Riesgo et al., 2010). In

414   addition, juvenile halacarids were significantly rarer than adults in the leaves (Figure 3D). Noticeably,

415   juveniles have developing structures, such as claws, an additional pair of legs, and more leg segments

416   (Bartsch, 2015). These structures enhance the adult's grip to the substrate, and so, their absence might

417   relegate the juveniles to the matte, which is considerably more protected from currents than the leaves.

418   Overall, our results suggest that, as in nematodes and copepods (Novak, 1989; Mascart, Agusto, et al.,
419   2015), migration between leaves and matte is frequent in halacarids, yet only certain species thrive in
420   each of those habitats.

421

434   **Ethical approval:** All applicable international, national, and/or institutional guidelines for the care and
435   use of animals were followed (Directive 2010/63/EU).

436   **AUTHOR CONTRIBUTION STATEMENTS**

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

443   .

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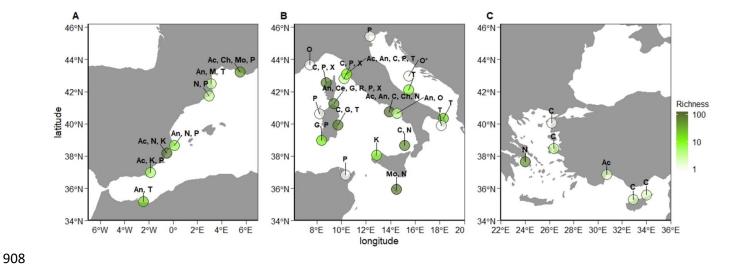905　　　*oceanica* ecosystem. *Coenoses*, *8*, 85-95.

906

FIGURES

Figure 1. Distribution of the meiofauna recorded in *Posidonia oceanica* in the West (A), Central (B), and East (C) Mediterranean Sea, coloured according to the number of species (see Table S1 for coordinates). Abbreviations: Ac, Acari; An, Annelida, C, Copepoda; Ce, Cephalocarida; Ch, Chaetognatha; G, Gastrotricha; K, Kinorhyncha; M, Mystacocarida; Mo, Mollusca; N, Nematoda; O, Ostracoda; P, Platyhelminthes; R, Rotifera; T, Tardigrada; X, Xenacoelomorpha. *Unspecified location in the Adriatic Sea.
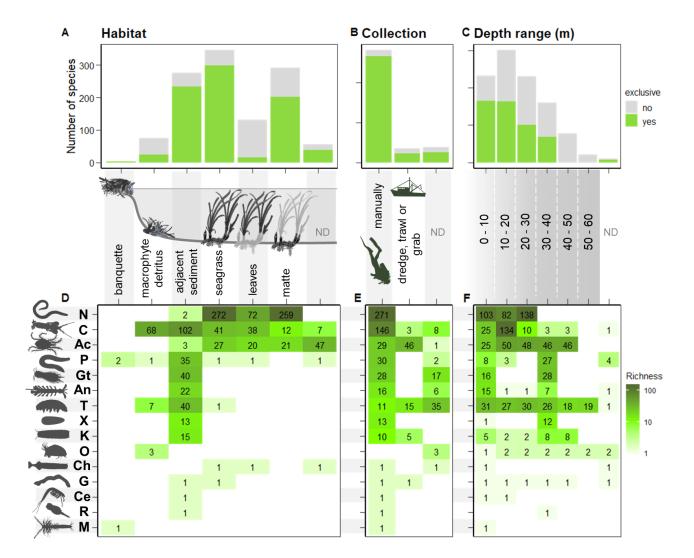
Figure 2. Number of species per meiofaunal group categorized by habitat, collection method, and depth range. Top panels (A-C) indicate the species exclusively observed in one category in green, and those found in more than one category in grey. Bottom panels (D-F) show the number of species per meiofaunal group from light to dark green. In A and D, the seagrass habitat was further divided into the leaves and the matte. Abbreviations as in Figure 1; ND, no data.
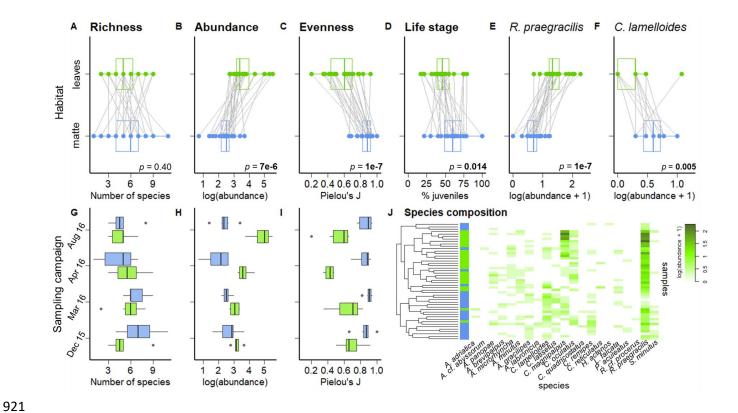
Figure 3. Main findings of the case study on halacarids in a *P. oceanica* meadow (see text for details). Colours differentiate between samples from the leaves (green) and the matte (blue). Top panels (A-F) show paired-t tests and *p*-values for the metrics in this study comparing the leaves and the matte. Panels G-I are boxplots of the variation in species richness, abundance, and evenness in the leaves and the matte through the four sampling campaigns of this study. Panel J show the abundance (as $\log_{10}+1$) of each species per sample, coloured from light to dark green. In A-F, samples collected from the same sampling point are connected by lines. In G-I, the error bars indicate the 10th and 90th percentiles of the data, the box's boundaries indicate the 25th and 75th percentiles, and the solid line within each box marks the median. In J, rows indicate the samples of leaves or matte, whereas columns denote the species; the dendrogram was built using method 'complete' by function 'hclust'. Abbreviations: Dec 15, December 2015; Mar 16, March 2016; Apr 16, April 2016; Aug 16; August 2016.

934 **TABLES**

935 Table 1. Halacarid species found in this study and their abundances (i.e., number of individuals) and

936 occurrences (i.e., % of samples in which each species was observed) within the leaves and the matte of

937 the *Posidonia oceanica* meadow.

Species	Abundance		Occurrence	
	Leaves	**Matte**	**Leaves**	**Matte**
Agaue adriatica Viets, 1940	2	1	4.17	4.17
Agaue cf. 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
Arhodeoporus labronicus (Morselli, 1981)	0	4	0.00	12.50
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
Rhombognathus cf. 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

938

939 Table 2. PERMANOVA results based on Jaccard dissimilarities using the abundance (as $\log_{10}+1$) for

940 the differences in composition of halacarid species between habitats (leaves vs. matte) and through

941 sampling campaigns. *P* values are based on 999 permutations. Abbreviation: Df, Degrees of freedom.

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	

942

943

944 **SUPPORTING INFORMATION**

945 Table S1. Records of meiofaunal species in *Posidonia oceanica* habitats compiled during our review,

946 both collected from the literature as well as directly from the specialists' unpublished records.

947

Meiofauna in *Posidonia oceanica*

948   Table S2. Summary of the ecological research on meiofauna in *Posidonia oceanica*.

949

950 Table S3. Results of the linear models for richness (i.e., number of species), abundance (log_{10}-
951 transformed) and evenness (Pielou's J), and the environmental factors measured in each habitat,
952 reported as type-II analysis-of-variance tables. Abbreviation: Df, Degrees of freedom.

Habitat	Response variable	Environmental predictors	Df	F	*p*
Leaves	Richness	length of leaves	1	0.104	0.751
		density of leaves	1	0.000	0.993
		sampling campaign	3	0.194	0.899
		residuals	18		
	Abundance	length of leaves	1	0.900	0.355
		density of leaves	1	2.481	0.133
		sampling campaign	3	9.874	**0.005**
		residuals	18		
	Evenness	length of leaves	1	0.006	0.941
		density of leaves	1	3.593	0.074
		sampling campaign	3	1.487	0.252
		residuals	18		
Matte	Richness	density of matte	1	4.052	0.059
		organic matter	1	0.063	0.805
		sampling campaign	3	3.103	0.053
		residuals	18		
	Abundance	density of matte	1	9.232	**0.007**
		organic matter	1	0.254	0.620
		sampling campaign	3	3.153	0.050
		residuals	18		
	Evenness	length of leaves	1	0.207	0.655
		density of leaves	1	0.810	0.381
		sampling campaign	3	0.006	0.999
		residuals	17		

953