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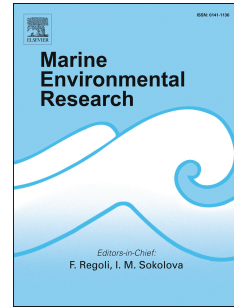
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1 Seagrass recovery after fish farm relocation in the eastern Mediterranean

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9 ABSTRACT

10 Finfish aquaculture has damaged seagrass meadows worldwide as wastes from the farms
11 can kill these habitat-forming plants. In Cyprus, the Mediterranean endemic *Posidonia oceanica* is
12 at its upper thermal limits yet forms extensive meadows all around the island. Understanding this
13 under-studied isolated population may be important for the long-term survival of the species given
14 that the region is warming rapidly. When fish farming began around Cyprus in the 90s, cages
15 were moored above seagrass beds, but as production expanded they were moved into deeper water
16 further away from the meadows. Here, we monitored the deepest edge of meadows near fish farms
17 that had been moved into deeper waters as well as at a decommissioned farm site. Four *P.*
18 *oceanica* monitoring systems were set up using methods developed by the Posidonia Monitoring
19 Network. Seagrass % coverage, shoot density, % of plagiotropic rhizomes, shoot exposure, leaf
20 morphometry, and sediment organic matter content and grain size were monitored at 11 fixed
21 plots within each system, in 2012-2014 and in 2017. Expansion at the lower depth limit of
22 seagrass meadows was recorded at all monitoring sites. Most other *P. oceanica* descriptors either
23 did not change significantly or declined. Declines were most pronounced at a site that was far
24 from mariculture activities but close to other anthropogenic pressures. The most important
25 predictor affecting *P. oceanica* was depth. Monitoring using fixed plots allowed direct
26 comparisons of descriptors over time, removes patchiness and intra-meadow variability increasing
27 our understanding of seagrass dynamics and ecosystem integrity. It seems that moving fish farms
28 away from *P. oceanica* has helped ensure meadow recovery at the deepest margins of their
29 distribution, an important success story given that these meadows are at the upper thermal limits
30 of the species.

31
32 **Keywords:** aquaculture; bioindicators; Cyprus; ecological monitoring; ecosystem change; eastern
33 Mediterranean; seagrass.

34

35

36 1. INTRODUCTION

37 Seagrasses are major contributors to human well-being and the economies of coastal
38 countries (Barbier et al., 2011; Campagne et al., 2015; Dewsbury et al., 2016). Their meadows are
39 among the most productive ecosystems on Earth but are declining at unprecedented rates
40 (Waycott et al., 2009; Costanza et al., 2014). They provide: coastal protection from erosion, by
41 attenuating waves and stabilising sediments; water purification by assimilating nutrients and
42 pollutants; transfer of matter and energy up trophic levels and sustaining fisheries; carbon
43 sequestration to help mitigate climate change; and provision of complex habitat for enhanced
44 biodiversity, which boosts tourism, recreation, education and research (Barbier et al., 2011;
45 Campagne et al., 2015). However, there are multiple mounting pressures, including: sediment and
46 nutrient runoff, physical disturbance, invasive species, disease, commercial fishing practices,
47 aquaculture, overgrazing, algal blooms and global warming, which have caused major declines in
48 seagrasses, raising awareness of the need to protect, monitor, manage and restore these habitats
49 (Orth et al., 2006; Barbier et al., 2011).

50 The endemic seagrass *Posidonia oceanica* (Linnaeus) Delile, 1813, forms one of the most
51 important coastal ecosystems in the Mediterranean Sea. Its rhizomes propagate vertically as well
52 as horizontally, producing reefs called “matte” that can extend many meters down into the
53 sediment and persist for millennia, resulting in the largest documented stores of organic carbon
54 among seagrasses (Buia et al., 2004; Lo Iacono et al., 2008; Fourqurean et al., 2012; Lavery et al.,
55 2013). The seagrass forms meadows that can extend up to 15 km wide and clone for thousands,
56 possibly tens of thousands of years (Arnaud-Haond et al., 2012). The structurally complex
57 meadows are the climax stage of many upper subtidal bottoms extending from the surface down to
58 depths of 40-45 m in oligotrophic clear waters; supporting hundreds of associated species (Piazzi
59 et al., 2016). An estimated 34% of *P. oceanica* meadows died in the last half century, classifying
60 the *P. oceanica* habitat as an ‘endangered’ ecosystem (Telesca et al., 2015).

61 The Mediterranean coast is home to about 250 million people and supports about one third
62 of all global tourism, which is anticipated to reach 0.5 billion arrivals per year by 2030 (Randone
63 et al., 2017). Residents and tourists place a high demand on seafood. In the last two decades, there
64 has been a dramatic growth in the Mediterranean aquaculture production expanding
65 approximately 5% annually (Massa et al., 2017). The development of fish aquaculture along the
66 Mediterranean coasts has caused localised losses of *P. oceanica* (Delgado et al., 1997; Pergent et

67 al., 1999; Ruiz et al., 2001; Cancemi et al., 2003; Pergent Martini et al., 2006; Diaz-Almela et al.,
68 2008; Holmer et al., 2008; Pérez et al., 2008; Apostolaki et al., 2009). Several factors cause this
69 damage including reduction of light under the cages (Ruiz et al., 2001), an increase in particulate
70 matter and nutrient concentrations in the water, which can cause an increase in epiphyte biomass
71 (Delgado *et al.* 1997), enhanced herbivory (Holmer et al., 2003), expansion of competitive
72 opportunistic seaweed (Holmer et al., 2009), sulphide invasion into the roots (Frederiksen et al.,
73 2007), and high input of organic matter into the sediments (Cancemi et al., 2003; Apostolaki et al.,
74 2007; Diaz-Almela et al., 2008). Organic enrichment may be the most important factor as this can
75 lead to anoxic and toxic benthic conditions causing high *P. oceanica* mortality (Pérez et al., 2008).
76 Seagrass loss can continue even after several years of fish farming cessation as the mat itself
77 begins to rot (Delgado et al., 1999; Apostolaki et al., 2010). *Posidonia oceanica* losses are
78 considered irreversible over human time-scales, because it grows slowly (only 3-4 cm per year)
79 and has extremely low natural colonization rates (Boudouresque et al., 2012). Although sexual
80 reproduction rates are speeded up by warming, seedlings usually settle at the shallow boundaries
81 of seagrass meadows (Balestri et al., 2017). Hence, the deep and exposed seagrass meadows near
82 fish farms have the lowest recruitment rates limited to vegetative propagation and horizontal
83 growth under low light conditions.

84 Today, fish farm cages are moored 1-3 km off Cyprus in water depths of 22-75 m,
85 cultivating mainly gilthead seabream (*Sparus aurata* Linnaeus, 1758) and European seabass
86 (*Dicentrarchus labrax* Linnaeus, 1758). National mariculture production expanded from 210
87 tonnes in 1994 to 6625 tonnes in 2016, now exceeding 80% of the total fisheries production (data
88 from Department of Fisheries and Marine Research, Cyprus). The number of licenced units has
89 remained the same for many years and the production increase is due to existing units that have
90 expanded production, especially during the last decade. Most fish farms are within the Vasiliko-
91 Moni area in south Cyprus. Fish farming in the area started in the mid-1990s with small
92 production units (100-300 tonnes per year), using floating cages starting at 22-28 m depth and
93 over seagrass meadows. One of these units ceased operations soon after, the rest of the farms
94 expanded and are now each licenced to produce 1000-1800 tonnes per year. A prerequisite to
95 receive expansion permits by the national authorities was to relocate cages in deeper water and
96 further away from the *P. oceanica* meadows. Currently, the shallowest cages in Vasiliko-Moni
97 area are found at the depth of about 37 m, but seagrass meadows still exist within the impact zone
98 (<400 m) of aquaculture effluents (Holmer et al., 2008).

99 Despite the temporal and spatial scale of this development, no studies have been
100 conducted to evaluate the effects of the fish farm units to the adjacent *P. oceanica* meadows. In

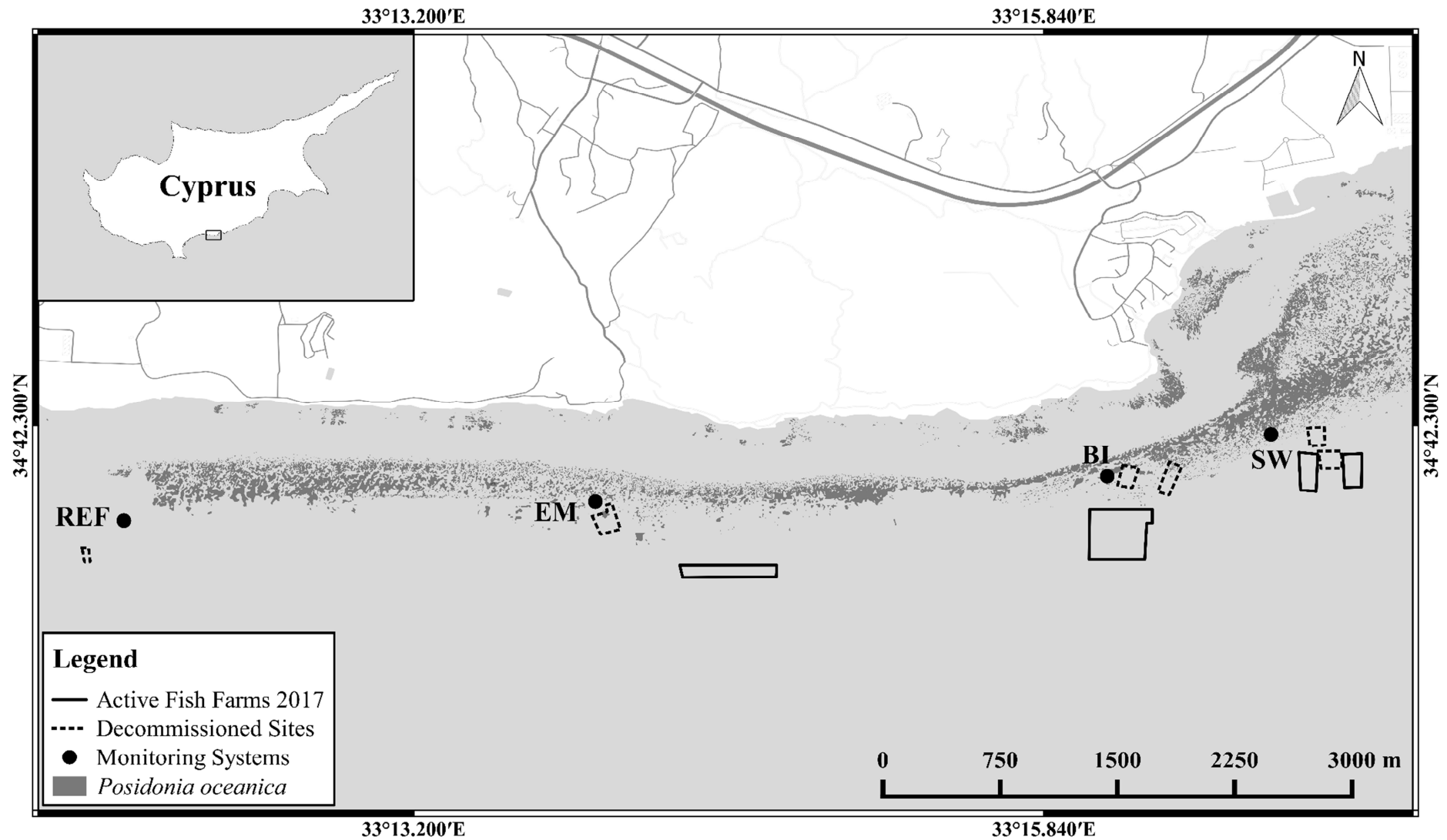
101 this study, four *P. oceanica* observatory systems were established near major fish farms that have
102 just relocated and expanded deeper and at a reference (decommissioned fish farm) site in the
103 Vasiliko-Moni area. The aims were: to assess progression or regression of *P. oceanica* meadow's
104 edge, evaluate the changes in *P. oceanica* and sediment descriptors between the two sampling
105 periods for each monitoring system and examine whether fish farm or environmental drivers are
106 affecting these descriptors. Our study shows how fish farm impacts to seagrass beds can be
107 monitored effectively, assisting integrated coastal management decisions.

108 2. MATERIALS AND METHODS

109 2.1 Study area

110 Four *P. oceanica* monitoring systems were set up using standardised methods developed
111 by the Posidonia Monitoring Network (PMN) (Boudouresque et al., 2000; Pergent, 2007) at the
112 warmest and easternmost geographic limits of *P. oceanica*. Three systems were deployed at the
113 regressive lower limits of seagrass meadows near active fish farm sites (SW, BI, EM) that recently
114 relocated and expanded production to deeper nearby waters (Figure 1, Table 1). During the first
115 data collection, the three farms had a total production *ca* 2.5 kt yr⁻¹ and operated shallow cages
116 near the seagrass meadows investigated (EM) or had just relocated to deeper water as they
117 expanded (SW and BI). At the second data collection three to five years later, the three farms had
118 a total production larger than 4 kt yr⁻¹ (Figure 1, Table 1). The fourth monitoring system (REF)
119 was set up *ca* 300 m far from a licensed small (*ca* 100 t yr⁻¹) production unit, which operated for a
120 few years in the nineties and ceased operations about 15 years ago. This monitoring system was
121 set at stable lower limits of the seagrass meadow, over 3.5 km from the nearest fish farms and
122 resembles the natural deeper boundaries of *P. oceanica* meadows in the coastal area studied
123 (Table 1).

124



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Figure 1. Locations of *P. oceanica* monitoring systems and coastal areas occupied by decommissioned and active fish farms. The surrounding meadows of *P. oceanica* are also shown.

129 **Table 1.** Details of *Posidonia oceanica* monitoring systems set up near farms operating in south Cyprus.

<i>Posidonia oceanica</i> Monitoring System – Fish farm information	Distance from the fish farm, depth and time of data collection.	Added Value
<p><u>SW</u> Established in 1995 with licenced annual production 300 t yr⁻¹. Licenced production increased to 450 t yr⁻¹ in 2008, 750 t yr⁻¹ in 2010, 1000 t yr⁻¹ in 2013, 1250 t yr⁻¹ in 2014 and to 1500 t yr⁻¹ after 2016. Shallow cages relocated in deeper water in 2011. # of finfish cages in 2017: 36</p>	<p>About 275 m northwest of the existing finfish cages and 240 m west of the previous position of cages, which were relocated deeper in 2011. The monitoring system was set up at regressive lower limits, at 25-26 m depth, in the summer of 2012. First set of data were collected the same period. Second set of data were collected in early autumn 2017.</p>	<p>Future monitoring and comparison with the data presented in this study, will be able to detect whether the relocation but expansion of the fish farm in deeper waters had any impacts on the adjacent <i>P. oceanica</i> meadows.</p>
<p><u>BI</u> Established in 1993 with licenced annual production 300 t yr⁻¹. Licenced production increased to 500 t yr⁻¹ in 2004, 900 t yr⁻¹ in 2007, 1300 t yr⁻¹ in 2009, 1500 t yr⁻¹ in 2014 and to 1800 t yr⁻¹ in 2017. Shallow cages relocated in deeper water in 2011. # of finfish cages in 2017: 66</p>	<p>About 250 m north of the existing finfish cages and less than 100 m west of the previous position of the cages, which were relocated deeper in 2011. The monitoring system was established at regressive lower limits, at 22-23 m depth, in the autumn of 2012. First set of data were collected two years later in autumn of 2014. Second set of data were collected in autumn 2017.</p>	<p>Future monitoring and comparison with the data presented in this study, will be able to detect whether the relocation but expansion of the fish farm in deeper waters had any impacts on the adjacent <i>P. oceanica</i> meadows.</p>
<p><u>EM</u> Established in 1993 with a licence to produce 100 t yr⁻¹. In 2011 it received permit to produce 1000 t yr⁻¹ at a new, deeper (50 m depth) site over 600 m further offshore. The old shallow mooring system was gradually decommissioned and went from 10 cages in 2012, to 6 in 2013 to 2 in 2014 to 1 in 2015. # of finfish cages in 2017: 0 in old and 22 in new mooring.</p>	<p>About 100 m north/northwest of the shallow mooring, which ceased operations gradually. Operations moved and expanded deeper about 750 m southeast from the monitoring system. The monitoring system was established at regressive lower limits, at 21-23 m depth, in the summer / autumn of 2012. First set of data were collected the same period. Second set of data were collected in autumn 2017.</p>	<p>Future monitoring and comparison with the data presented in this study will provide vital information about the recovery rates of the <i>P. oceanica</i> meadow following the cessation of mariculture operations in the near vicinity.</p>
<p><u>REF</u> Farming started in mid-nineties and lasted about a decade (production <i>ca</i> 100 t yr⁻¹). It has remained inactive for <i>ca</i> fifteen years.</p>	<p>About 300 m northeast from a small production unit, which terminated operations a long time ago. The monitoring system was established at stable lower limits, at 28-29 m depth, in the summer of 2013. First set of data were collected the same period. Second set of data were collected in early autumn 2017.</p>	<p>Future monitoring and comparison with the data presented in this study will provide a point of reference for other monitoring systems and if fish farming initiates near this system it will provide baseline data and vital information about the direct effects of the fish farm on the adjacent <i>P. oceanica</i> meadows.</p>

130 2.2 Dispersal of fish farm effluents

131 To predict the dispersal of fish farm effluents and sedimentation, we simulated the dispersion
 132 MERAMOD model developed for gilthead sea bream *S. aurata* and European sea bass *D.*
 133 *labrax* farming (Cromey et al., 2012). The simulation occurred in 2012, just after the relocation
 134 of BI and SW, and before the relocation of EM fish farm. Historical daily current data (2005-
 135 2010) of the surface waters and the 10 m depth zone in the study area were extrapolated using
 136 3-D interpolations of the Cyprus Coastal Ocean Forecasting and Observing System
 137 (CYCOFOS); a validated hydrodynamic flow model covering the Levantine region (Zodiatis
 138 et. al., 2003; 2008). Two scenarios were applied that included the coldest-water period
 139 (February) and the warmest-water period (August). The latter accounts for the worst-case
 140 scenario since maximum biomass/feed input were used. Data incorporated into the
 141 MERAMOD model included: daily average current speed and direction for the months of
 142 August and February obtained from the CYCOFOS, bathymetric data at each site and a range
 143 of husbandry data collated from the managers of the three fish farms (Table 2).

144

145 **Table 2.** Husbandry data (year 2012) used in MERAMOD for each of the two scenarios.

Data	Scenario 1 (Winter)			Scenario 2 (Summer)		
	SW	BI	EM	SW	BI	EM
Feed input (kg d ⁻¹)	3665	7500	2200	7500	11000	1200
Feed input (kg cage ⁻¹ d ⁻¹)	136	221	183	278	324	200
Max biomass (t)	580	1194	300	600	861	150
Cage diameter (m)	19	22	22	19	22	22
Cage surface area (m ²)	286	390	390	286	390	390
Cage volume (m ³)	4011	5459	5459	4011	5459	5459
No of cages	27	34	12	27	34	6
Feed input per day per unit cage surface area (kg d ⁻¹ m ⁻²)	0.47	0.57	0.47	0.97	0.83	0.51

146

147 Waste feed and faeces were assigned a random starting position in the cage volume. An
 148 average settling velocity of feed pellets representing 1 to 5 mm pellets and settling velocity of
 149 faecal particles for bream and bass (Magill et al., 2006) were assigned to cages according to the
 150 percentage of bream and bass being farmed at each site. For particles between sea surface and 5
 151 m depth, surface current speed and direction were used for advection, whereas 10 m current
 152 speed and direction were used for particles from 5 m to the sea bed. Predicted flux was scaled
 153 to standard units of g m⁻² yr⁻¹ of total dry solids. Numerous default data were used consistently
 154 across sites (Table 3), so that differences between predicted impact were primarily driven by

155 differences between the sites in terms of depth, hydrography, feed input and husbandry data in
 156 general.

157

158 **Table 3.** MERAMOD default data applied across all scenarios.

Model default parameter	Value
Feed wasted, digestibility, water content	5%, 85%, 9%
Wild fish consumption of waste pellets	50 % of wasted pellets are consumed by wild fish and do not contribute to flux
Horizontal dispersion coefficients: k_x, k_y ($m^2 s^{-1}$)	0.4, 0.1
Vertical dispersion coefficient: k_z ($m^2 s^{-1}$)	0.001
Particle trajectory time step (seconds)	60
Feed settling velocity ($cm s^{-1}$)	Mean = 8.4, standard deviation = 4.3
Faecal settling velocity: Sea Bream ($cm s^{-1}$)	0.4 $cm s^{-1}$ (24%), 1.5 (45%), 2.5 (18%), 3.0 (13%)
Faecal settling velocity: Sea Bass ($cm s^{-1}$)	0.4 $cm s^{-1}$ (6%), 1.4 (9%), 2.5 (20%), 3.6 (38%), 4.6 (27%)

159

160 2.3 Monitoring systems and data collection

161 The four monitoring systems were set up according to the ‘Protocol for the setting up of
 162 *Posidonia* meadows monitoring systems «MedPosidonia» Programme’ (Pergent, 2007). In
 163 each monitoring system, 11 numbered cement markers were positioned at 5 m intervals and
 164 anchored with 12 mm diameter iron stakes, at the edge of the meadow (total 50 m length).
 165 Additionally, 16 mm diameter iron “photostakes”, from where photographs were taken, were
 166 hammered 50 cm into the sediment and sticking out 1 m, across each marker and the meadow’s
 167 edge.

168 At every marker, the following variables were recorded by scuba divers: depth and
 169 angle to other markers, % seagrass cover in a 0.36 m^2 quadrat, shoot density and % of
 170 plagiotropic (horizontally oriented) rhizomes in three fixed quadrats (0.04 m^2), and shoot
 171 exposure or burial of orthotropic (vertically oriented) shoots (three replicates taken at both the
 172 edge and another three at the inner side of the meadow). Surface sediment samples were
 173 collected from each marker by a diver and granulometry was conducted using an Endecotts
 174 Octagon sieve shaker after first drying the samples at 100 °C until constant weight. The
 175 granulometry data were processed with the GRADISTAT particle size analysis software. Fine
 176 sediment passing through the 212 μm sieve was homogenised, three replicates of 1.5 g from
 177 each marker were combusted at 550 °C and the organic carbon was determined as % weight
 178 loss following ignition. In addition, about 20 randomly selected orthotropic shoots from each
 179 monitoring system were removed and leaf morphometric analyses were carried out using the
 180 technique of Giraud (1977), including estimating the foliar surface per shoot, which was later
 181 used to estimate the Leaf Area Index (LAI). The past annual *P. oceanica* leaf production rate

182 was calculated following a standardised procedure, known as lepidochronology, which uses the
183 thickness of the scales (previous leaf petioles that remain attached on the rhizome) to determine
184 annual cycles (Pergent, 1990; Pergent and Pergent-Martini, 1991). The lepidochronological
185 analysis involves carefully removing the scales from the rhizomes and ordering them from the
186 older (near the rhizome base) to the more recent (near the living leaves). A cross section was
187 made 10-12 mm above the base of each scale, viewed and photographed under an Olympus
188 CX41 microscope attached to a camera. The thickness (μm) of the central/wider portion of the
189 scale was measured with Image Pro Plus software.

190 About half a decade following deployment, the monitoring systems were revisited.
191 Initially an inspection was carried out to record any missing cement markers, labels, or
192 photostakes. Progression or regression of the edge was measured using a measuring tape from
193 the marker's inner side to the rhizome that was furthest from the marker in progression or
194 closest in regression. Data collection from each monitoring system was repeated (except for
195 lepidochronology) using the same methods. At each of the 44 markers, the measurements of
196 shoot densities and % of plagiotropic rhizomes were repeated from the same fixed quadrats.

197 **2.4 Statistical analysis**

198 To evaluate changes between the two sampling periods for each fish farm, a paired t-
199 test was computed for variables taken from fixed quadrats (i.e. shoot density, plagiotropic
200 rhizomes % and coverage %), following Elzinga et al. (1998). Variables derived from
201 randomly selected shoots (i.e. number of leaves, foliar surface, shoot exposure) within the
202 meadow were compared with a 2-sample t-test (Elzinga et al., 1998). The assumptions for
203 normality and homogeneity of variances were verified using a Shapiro-Wilk and F test,
204 respectively and if assumptions were violated, \log_{10} or square root transformations were
205 conducted. To calculate the rate of annual leaf production of *P. oceanica* acquired from the
206 lepidochronological analysis and examine the patterns of change over the years (increase,
207 decrease or none), a simple linear regression was performed. When assumptions were not met,
208 the analysis proceeded with the non-parametric Wilcoxon signed rank test for data collected
209 from the fixed quadrats, non-parametric Mann-Whitney U test for data collected from random
210 shoots and non-parametric regression Kendall–Theil Sen Siegel for the lepidochronological
211 data. Shoot progression was compared between the different monitoring sites using the non-
212 parametric Kruskal-Wallis test.

213 In order to identify the predictors that affect the *P. oceanica* and sediment descriptors, a
214 multiple regression analysis was applied, where all the descriptors were categorised into two

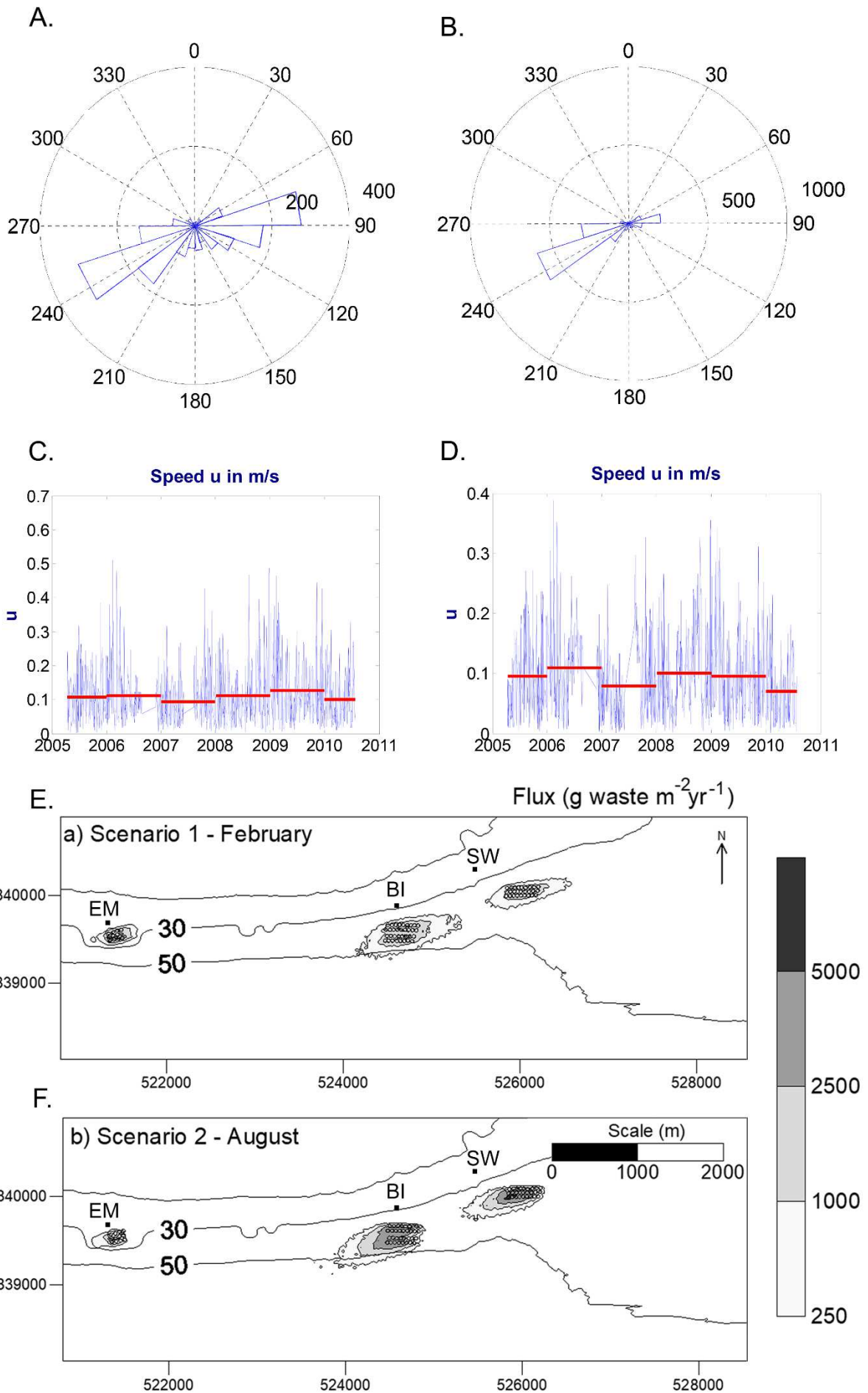
215 environmental predictors (depth and time) and three fish farm associated predictors (distance of
216 a monitoring system to the nearest fish farm, direction of a monitoring system to the nearest
217 fish farm, and the size of production of the nearest fish farm in tonnes). The assumptions for
218 normality and heteroscedasticity were verified via Shapiro-Wilk test and Breusch-Pagan test on
219 either untransformed or cox box transformed data. The multiple regression analysis was further
220 complemented with the relative importance analysis, which aims to identify the factor with the
221 highest controlling effect on the descriptor (Tonidandel and LeBreton, 2011). This was based
222 on the calculation of lmg , the relative contribution of each predictor to the R^2 , averaged over
223 the orderings among predictors (Grömping, 2006).

224 For all the statistical analyses the significance level α was adjusted to 0.05, computation
225 was carried out by R-studio (v 1.0.153) and all the graphic material was generated via the
226 package `ggplot2` (Wickham, 2009). The relative importance analysis was conducted via the
227 package `relaimpo` (Grömping, 2006).

228 3. RESULTS

229 3.1 Fish farm effluents

230 The scalar and vector averages for the entire period considered indicated that there is
231 alternation of surface currents towards the east and west respectively, but the prevailing
232 average direction of the currents at 10 m depth is west – southwest (Figure 2). The predominant
233 direction of the currents during the two scenarios simulated in the MERAMOD, February and
234 August, were towards east and southwest respectively. For all farms, there were virtually no
235 areas predicted to have deposition greater than $5000 \text{ g m}^{-2} \text{ yr}^{-1}$; areas of 2500 to $5000 \text{ g m}^{-2} \text{ yr}^{-1}$
236 were evident for farms BI and SW but not for the small EM farm (before relocation) (Figure 2).
237 The extent of the deposition footprints was high as a result of the reasonably high current and
238 depth. According to the model and driven by the currents direction, the main dispersal of the
239 effluents was not in the direction of the *P. oceanica* monitoring systems.



241 **Figure 2.** *Top panel:* Angle histogram in degrees (rose diagram) showing the frequency of current
 242 direction for the whole period 2005-2010 at surface (A) and at 10 m depth (B), estimated with
 243 CYCOFOS; *Middle panel:* Sea surface current speed data and annual averages at surface (C) and at 10
 244 m depth (D), estimated with CYCOFOS; *Bottom panel:* MERAMOD predicted waste flux ($\text{g m}^{-2} \text{yr}^{-1}$)
 245 under winter (E) and summer (F) scenarios.
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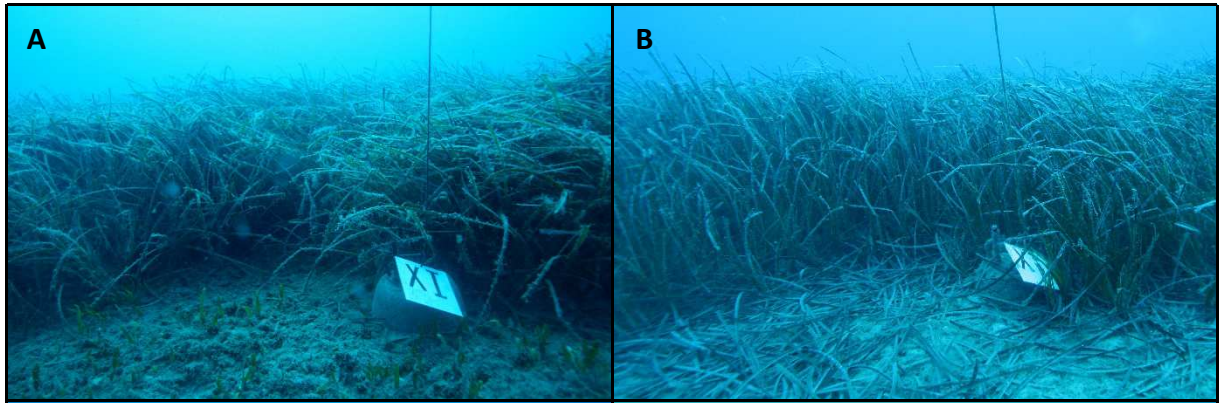
247 3.2 Field Observations and Sediments

248 When the monitoring systems were set up in 2012-13, epiphytes and fine particulate
 249 matter were covering the leaves of *P. oceanica* (Figure 3). The lower limits investigated were
 250 sharp at the edge with high *P. oceanica* cover, surrounded by dead matte covered
 251 predominantly by *Caulerpa prolifera* (Forsskål) J.V.Lamouroux. Four to five years following
 252 the initial deployment, all 44 markers and 132 iron stakes were still in place. Only one
 253 photostake and two labels from the initial 44 were missing. Visually, the ecological condition
 254 seemed to be improved in 2017 compared to the first surveys. The fine particulates and the
 255 epiphytes covering the seagrass leaves were less pronounced, some calcareous organisms
 256 (bryozoans and rhodophytes) were found within the rhizomes under the canopy and *C.*
 257 *prolifera* had almost disappeared from the surface of the dead matte (Figure 4). Improvement
 258 of the ecological condition was also reflected in sediment variables. Overall, the organic matter
 259 in the sediment was reduced by about 15% and the mean grain size enlarged overall by almost
 260 90%, from very fine sand to sand (Folk and Ward method) (Table 4).

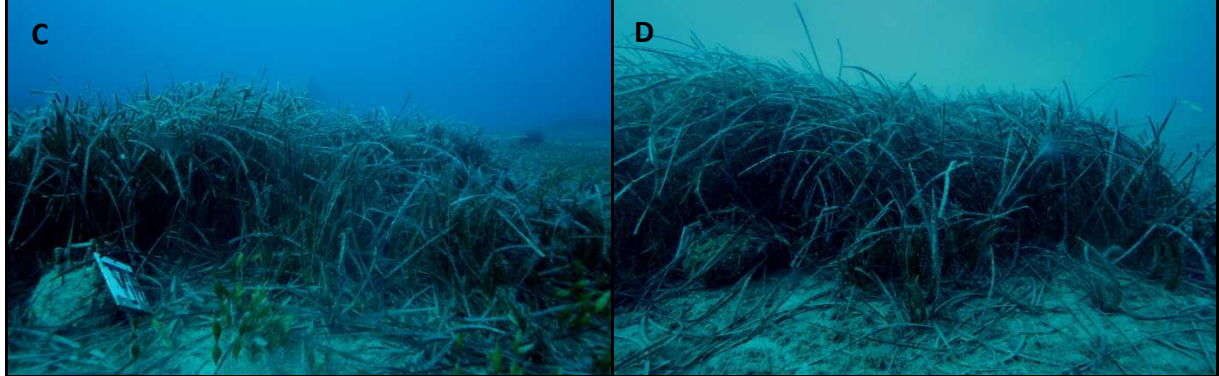


261
 262 **Figure 3.** Seagrass meadows near fish farms (SW left, BI right), covered in fine particles and epiphytes
 263 during first data collection.

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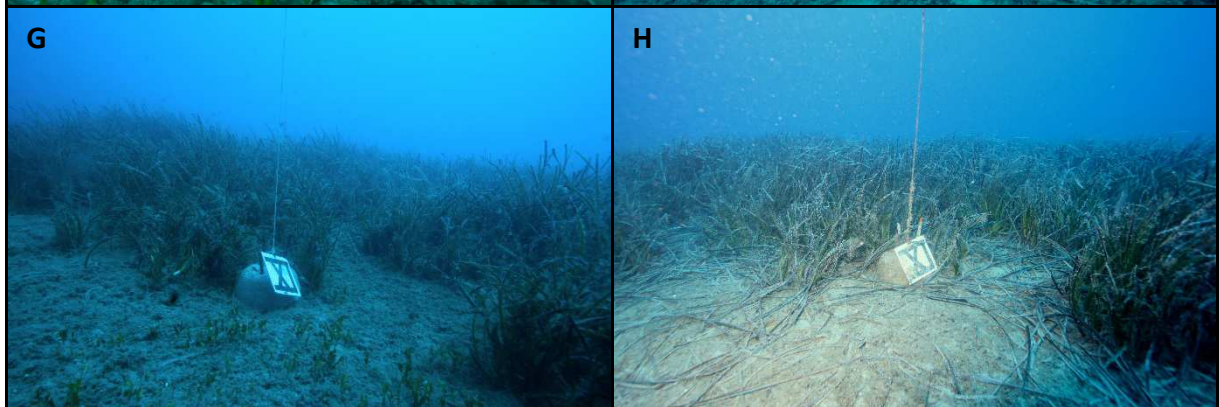
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268 **Figure 4.** Photographs taken from fixed positions during the first data collection (left) and the follow-up
 269 monitoring (right) from: i) SW monitoring system - Marker 11 in 2012 (A) and 2017 (B), ii) BI
 270 monitoring system - Marker 8 in 2014 (C) and 2017 (D), iii) EM monitoring system - Marker 9 in 2012
 271 (E) and 2017 (F) and iv) REF monitoring system - Marker 11 in 2013 (G) and 2017 (H).

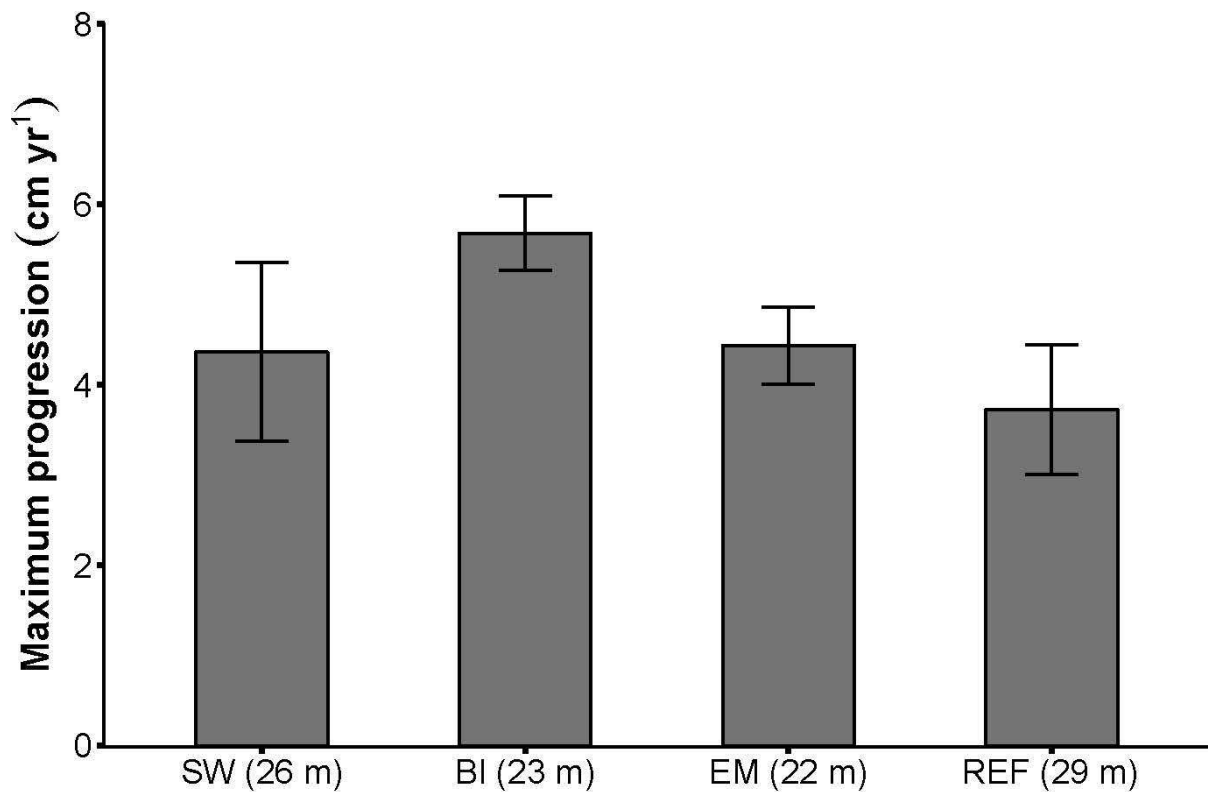
272 **Table 4.** Coordinates, depth, relative abundance of sand, silt and clay, and the % organic carbon for
 273 each of the four monitoring systems at both times of sampling.

Monitoring System	Latitude Longitude	Mean depth (m)	Year of sampling	Sand (%)	Silt (%)	Clay (%)	Organic carbon (%)
SW	34°42.262'N	25.9	2012	71.54	23.72	4.74	9.41 ± 0.47
	33°16.791'E		2017	76.97	19.19	3.84	8.23 ± 0.17
BI	34°42.086'N	22.7	2014	76.01	19.99	4.00	8.73 ± 0.29
	33°16.105'E		2017	78.85	17.63	3.53	7.87 ± 0.17
EM	34°41.979'N	22.2	2012	68.09	26.59	5.32	8.35 ± 0.19
	33°13.961'E		2017	80.64	16.13	3.23	7.26 ± 0.22
REF	34°41.901'N	28.8	2013	66.49	27.92	5.58	10.43 ± 0.22
	33°11.986'E		2017	80.28	16.43	3.29	7.74 ± 0.19

274 .

275 3.3 *Posidonia oceanica* metrics

276 The seagrass limit had not regressed between sample dates; on the contrary, it had
 277 progressed at all markers (range 1.2 - 9 cm per year). The slowest progression was recorded at
 278 the REF monitoring system, which was the deepest and with no farm in its vicinity (mean
 279 progression 14.9 cm in 4 years; Figure 5). Progression was higher at the other monitoring
 280 systems, but despite varying distances from the cages and different depths among the stations,
 281 the shoot progression was not statistically different (Kruskal-Wallis, $\chi^2 = 4.43$, $df = 3$, $p >$
 282 0.05).



283 **Figure 5.** Mean maximum progression (\pm standard error) of *P. oceanica* measured from all markers at
 284 each monitoring system.
 285
 286

287 The monitoring system REF, which had no fish farm in the near vicinity but was closer
 288 to the city of Limassol, appeared the most impacted, exhibiting significant decline in almost all
 289 the descriptors measured, including: seagrass % coverage, % of plagiotropic rhizomes, number
 290 of leaves per shoot, foliar surface area and shoot exposure. Shoot density from fixed quadrats
 291 was not significantly different between the two samplings (Figure 6, Table 5).

292 The EM monitoring system, which was approximately 100 m north from a small fish
 293 farm that gradually relocated and expanded about 750 m southeast from the monitoring system,
 294 had no significant change in seagrass coverage, foliar surface area and number of leaves per
 295 shoot. However, a significant increase in shoot exposure and a significant decline in shoot
 296 density was apparent, as well as in % of plagiotropic rhizomes, which was around half in 2017
 297 compared to the first values in 2013 (Figure 6, Table 5).

298 SW monitoring system, that was at a distance between 240-275 m northeast from a
 299 major fish farm in both sampling periods, appeared to be unaffected over time, with no
 300 significant change in any descriptor being detected. Similar results were found at the BI
 301 monitoring system, which is located 250 m north from the largest fish farm (previous distance

302 was 80 m west from the decommissioned mooring). In this case, however, while there was no
 303 significant change in seagrass coverage, shoot density, % plagiotropic shoots and foliar surface
 304 area, the shoot exposure increased and the number of leaves per shoot decreased (Figure 6,
 305 Table 5).

306 **Table 5.** Changes of *P. oceanica* and sediment descriptors at each monitoring system between first data
 307 collection (2012 for SW and EM, 2013 for REF and 2014 for BI) and follow-up monitoring from the
 308 same fixed points (2017). Arrows indicate significant change, – indicates no significant change.

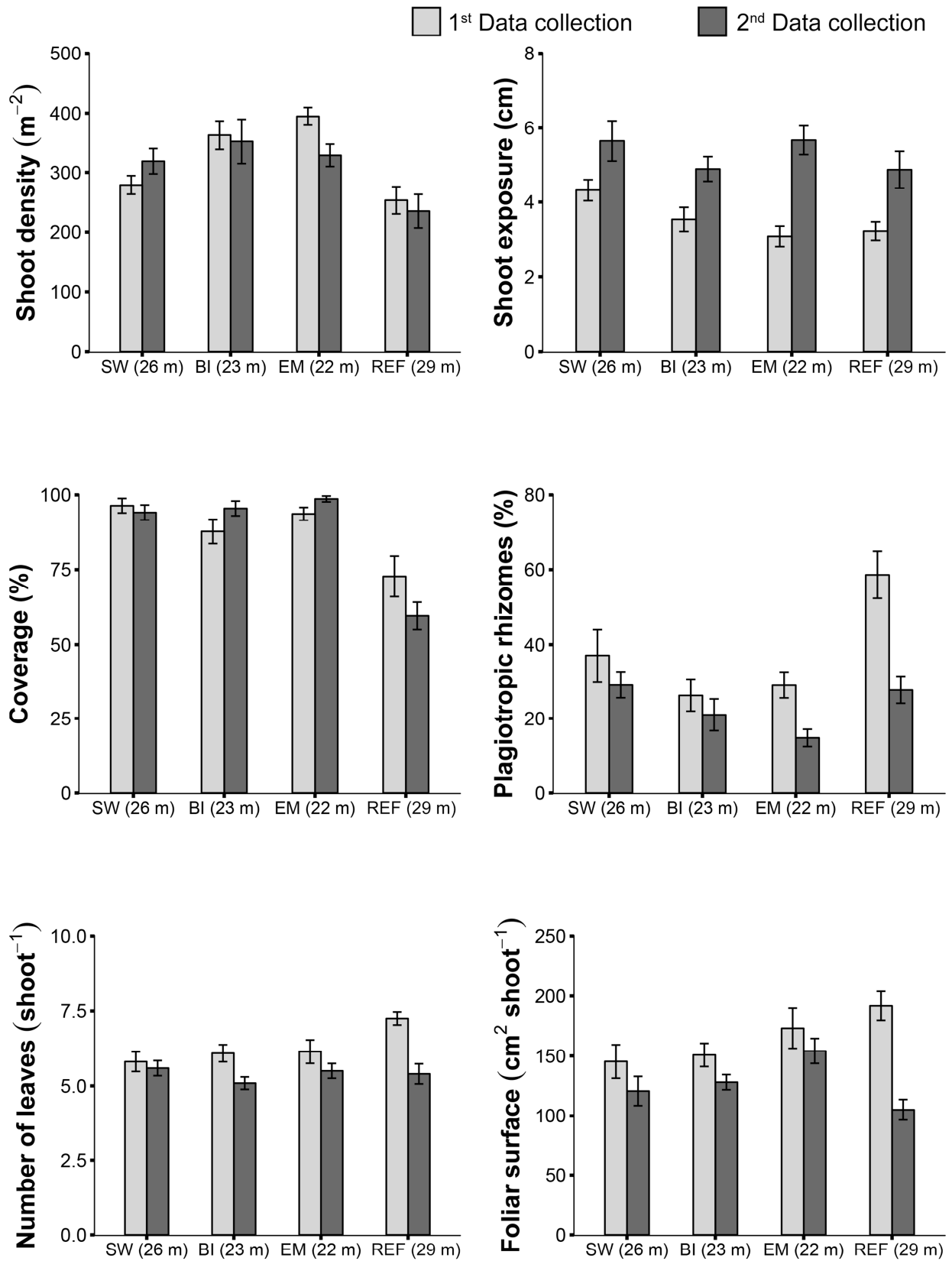
Descriptors	Monitoring Systems			
	SW	BI	EM	REF
	-	-	-	↓
Coverage (%)	Wilcoxon signed rank test, $V = 14$, $p > 0.05$	Wilcoxon signed rank test, $V = 6$, $p > 0.05$	Wilcoxon signed rank test, $V = 4$, $p > 0.05$	Paired t-test, $df = 10$, $t = -10.09$, $p < 0.05$
	-	-	↓	-
Shoot Density (m^{-2})	Paired t-test, $df = 10$, $t = -1.77$, $p > 0.05$	Wilcoxon signed rank test, $V = 40$, $p > 0.05$	Paired t-test, $df = 10$, $t = 4.25$, $p < 0.05$	Paired t-test, $df = 10$, $t = 0.79$, $p > 0.05$
	-	-	↓	↓
Plagiotropic rhizomes (%)	Paired t-test, $df = 10$, $t = 0.87$, $p > 0.05$	Paired t-test, $df = 10$, $t = 0.95$, $p > 0.05$	Paired t-test, $df = 10$, $t = 6.46$, $p < 0.05$	Paired t-test, $df = 10$, $t = 6.81$, $p < 0.05$
	-	↓	-	↓
Leaf Number (shoot ⁻¹)	2-sample t-test, $df = 46$, $t = 0.51$, $p > 0.05$	Mann-Whitney U test, $W = 353$, $p < 0.05$	Mann-Whitney U test, $W = 246$, $p > 0.05$	Mann-Whitney U test, $W = 339$, $p < 0.05$
	-	-	-	↓
Foliar Surface (cm^2 shoot ⁻¹)	2-sample t-test, $df = 46$, $t = 1.40$, $p > 0.05$	2-sample t-test, $df = 42$, $t = 1.96$, $p > 0.05$	Mann-Whitney U test, $W = 242$, $p > 0.05$	2-sample t-test, $df = 38$, $t = 5.86$, $p < 0.05$
	-	↑	↑	↑
Shoot Exposure (cm)	2-sample t-test, $df = 20$, $t = -1.97$, $p > 0.05$	2-sample t-test, $df = 19$, $t = -2.83$, $p < 0.05$	2-sample t-test, $df = 20$, $t = -5.44$, $p < 0.05$	2-sample t-test, $df = 20$, $t = -2.92$, $p < 0.05$
	-	↓	↓	↓
Organic Matter (%)	Paired t-test, $df = 10$, $t = 2.17$, $p > 0.05$	Paired t-test, $df = 10$, $t = 4.38$, $p < 0.05$	Paired t-test, $df = 10$, $t = 3.38$, $p < 0.05$	Paired t-test, $df = 10$, $t = 11.07$, $p < 0.05$
	-	↑	↑	↑
Grain size (μm)	Wilcoxon rank sum	Paired t-test,	Wilcoxon rank sum	Wilcoxon rank

test, $V = 11$,
 $p > 0.05$

$df = 10$, $t = -2.74$,
 $p < 0.05$

test, $V = 0$,
 $p < 0.05$

sum test, $V = 0$,
 $p < 0.05$



310 **Figure 6.** *P. oceanica* descriptors determined from fixed positions in the summer-autumn period, firstly
 311 in 2012 for SW and EM, 2013 for REF and 2014 for BI (in light grey), and follow-up monitoring in
 312 2017 at all the monitoring systems (in dark grey). Mean \pm standard error.

313 The lepidochronological analysis carried out during the first data collection at each of
 314 the monitoring systems showed no significant change in leaf production over the years that
 315 preceded sampling and when farms operated shallow moorings nearer to *P. oceanica* meadows
 316 (Table 6).

317 The LAI decreased between the two sampling periods across all monitoring systems.
 318 The smallest decrease was recorded at SW monitoring system (from 4.06 to 3.85 m² of canopy
 319 per m²), while the largest decrease was recorded at the deepest REF monitoring system (from
 320 4.85 to 2.47 m² of canopy per m²). At both times of data collection, the EM monitoring system,
 321 which is also the shallowest site, had the highest LAI values (6.84 m² of canopy per m² in 2012
 322 and 5.07 m² of canopy per m² in 2017) compared to all other systems.

323 **Table 6.** Mean number of leaves per shoot \pm SE, during lepidochronological years determined from 15-
 324 20 orthotropic shoots collected in 2012-14 from each monitoring system.

Lepidochronological year	Monitoring System			
	SW	BI	EM	REF
2012	5.6 \pm 0.3	6.9 \pm 0.2	7.6 \pm 0.4	6.9 \pm 0.4
2011	5.7 \pm 0.4	6.9 \pm 0.4	6.2 \pm 0.4	7.2 \pm 0.4
2010	5.8 \pm 0.4	6.6 \pm 0.5	6.6 \pm 0.5	7.1 \pm 0.4
2009	4.7 \pm 0.5	6.4 \pm 1.0	6.1 \pm 0.3	7.0 \pm 0.4
2008	-	-	6.3 \pm 0.3	6.5 \pm 0.6
2007	-	-	6.1 \pm 0.4	6.3 \pm 0.5
Rate of change \pm SE	0.22 \pm 0.17	0.24 \pm 0.14	0.06 \pm 0.06	0.03 \pm 0.08
R²	0.03	0.04	0.006	0.001
df	50	57	155	84
p	> 0.05	> 0.05	> 0.05	> 0.05
Statistical analysis	Simple linear regression	Simple linear regression	Kendall–Theil Sen Siegel	Kendall–Theil Sen Siegel

325 3.4 Underlying predictors

326 Out of the five predictors that were investigated, time and depth had the greatest effect
 327 on the descriptors studied, but all the predictors considered seemed to play a key role in
 328 explaining most of the descriptors and had similar weight in their contribution (Table 7). The
 329 shoot density was the only descriptor that was not affected over time. Depth, distance and
 330 direction from the cages were significant predictors of shoot density and had the largest
 331 contribution in relative importance (Table 7).

332 **Table 7.** The source of variation and the relative importance of two environmental and three fish farm
 333 related predictors on seven measured descriptors, acquired from the multiple regression analysis. Note:
 334 The source of variation in the model takes in account all the predictors, whereas % lmg takes in account
 335 the average relative importance of each predictor without and with all the possible combinations with
 336 the rest of the predictors.

Variable	Source of variation					Relative Importance
	Predictor	Df	Sum of squares	<i>F</i>	Prob. > <i>F</i>	% lmg
Shoot density	Depth	1	2321	6.83	< 0.05	35.9
	Distance	1	1380	4.06	< 0.05	21.7
	Tonnes	1	192	0.56	ns	16.2
	Direction	2	9184	13.52	< 0.001	22.9
	Time	1	248	0.73	ns	3.2
Plagiotropic rhizomes	Depth	1	2.10	6.80	< 0.05	21.3
	Distance	1	1.56	9.65	< 0.05	16.9
	Tonnes	1	0.46	1.48	ns	11.7
	Direction	2	5.96	5.04	< 0.001	24.8
	Time	1	5.70	18.46	< 0.001	25.3
Number of Leaves	Depth	1	0.00	0.17	ns	3.2
	Distance	1	0.00	0.11	ns	16.2
	Tonnes	1	0.00	3.94	< 0.05	20.1
	Direction	2	0.00	0.91	ns	15.4
	Time	1	0.00	6.55	< 0.05	45.1
Foliar Surface	Depth	1	0.23	7.75	< 0.01	21.5
	Distance	1	0.00	0.29	ns	9.7
	Tonnes	1	0.04	1.52	ns	8.9
	Direction	2	0.00	0.02	ns	11.5
	Time	1	0.50	16.80	< 0.001	48.4
Shoot exposure	Depth	1	15.05	15.04	< 0.01	14.7
	Distance	1	3.11	1.48	ns	16
	Tonnes	1	9.10	9.09	< 0.05	9.5
	Direction	2	14.64	3.48	< 0.05	32.1
	Time	1	19.54	9.29	< 0.01	27.8
Grain size	Depth	1	0.00	0.80	ns	3.7
	Distance	1	0.00	12.66	< 0.001	18.9
	Tonnes	1	0.00	100.73	< 0.001	8.7
	Direction	2	0.00	29.17	< 0.001	19.6
	Time	1	0.00	10.04	< 0.05	49.0
Organic matter	Depth	1	0.00	21.67	< 0.001	14.5
	Distance	1	0.01	52.62	< 0.001	15.7
	Tonnes	1	0.00	5.60	< 0.05	9.2
	Direction	2	0.00	2.06	ns	16.6
	Time	1	0.00	12.06	< 0.001	44.0

337

338 **4. DISCUSSION**

339 In Cyprus, mariculture activities are concentrated in an area between the cities of
340 Limassol and Larnaca. Small scale production started here in the mid-nineties in shallow water
341 (< 30 m) over *P. oceanica* meadows and this may have contributed to degradation and
342 regression of the lower limits of the meadows. Thereafter, managers followed a precautionary
343 approach (Pergent-Martini et al., 2006) and only allowed new production units to be placed in
344 deeper water while asked for the relocation of the shallow cages when existing farms requested
345 expansion of their production. Our study has shown that this management intervention may
346 have been effective in preventing further declines in the lower limits of the meadows studied. It
347 proves the point that local impacts on *P. oceanica* can be managed at the local level (Guillén et
348 al., 2013).

349 Our permanent *P. oceanica* monitoring systems are the first in Cyprus and the
350 easternmost seagrass PMN systems in the Mediterranean. Setting up monitoring systems using
351 permanent cement markers is a durable and effective method to monitor the edge of seagrass
352 meadows from fixed positions over medium to long timeframes (Pergent et al., 2015) and is
353 substantially more robust than random plots for monitoring seagrasses (Schultz et al., 2015).
354 About five years following deployment, all cement markers were still in place, despite some
355 major storms. Our results indicate that *P. oceanica* has not regressed during this time and
356 although an overall lower performance was recorded in some *P. oceanica* structural
357 descriptors, this was not detected near fish farms.

358 Contrary to expectations, *P. oceanica* meadows had progressed at all monitoring
359 stations and although differences among the monitoring systems were not statistically
360 significant, the largest observed progression was recorded near the largest fish farm. There is
361 hope, therefore, that despite major losses of *P. oceanica* from fixed PMN markers at deep
362 meadows in the north-western Mediterranean (Boudouresque et al., 2000, 2012; Pergent et al.,
363 2015), a decline has not been detected in impacted deep meadow limits in the eastern
364 Mediterranean. This is despite the fact that water temperatures are close to the reported upper
365 limit of the species (Celebi et al., 2006). The seagrass horizontal growth rates reported in this
366 study may be overestimated as there was a selection bias for the furthest rhizome from the
367 marker; however the values obtained are consistent with previous estimations but lower than
368 recolonization rates measured along labelled fixed pegs at shallower healthy patches in the

369 western Mediterranean (Gobert et al., 2016). In other studies, *P. oceanica* meadows could
370 survive close to fish farm cages, even though effects on *P. oceanica* descriptors were detected
371 at large distances from the fish cages (Borg et al., 2006; Marbà et al., 2006; Holmer et al.,
372 2008; Rountos et al., 2012). In this study, *P. oceanica* descriptors did not clearly detect impacts
373 of the fish farm operations.

374 The impacts of mariculture on *P. oceanica* meadows are site-specific and dependant on
375 variables, such as the size of the farm and the intensity of feeding, depth and hydrodynamics.
376 In Cyprus, it seems that the decision to relocate the fish farms deeper (southern), in an area
377 dominated by west and east currents, has been successful in mitigating impacts to the *P.*
378 *oceanica* meadows that stretch northwards. The model simulations presented in this study,
379 showed that the main dispersal of particulate matter is not in the direction of the seagrass
380 meadows investigated. However, only two months were considered and resuspension, which
381 would tend to increase dispersion of waste particles, was not considered in the model.
382 Furthermore, with the estimated velocity of currents, farm effluents can disperse over a
383 distance covering several kilometres (Sarà et al., 2006) and affect *P. oceanica* meadows even
384 *ca* 3 km away, in ways that are not always reflected by alterations in structural descriptors
385 (Ruiz et al., 2010).

386 At the sites monitored, improvement was also recorded in sediment variables: the
387 organic matter content decreased, and the mean grain size increased in all monitoring systems,
388 except at SW where the changes were not significant. This, together with the increase in *P.*
389 *oceanica* shoot exposure measured during the follow-up monitoring, may indicate less
390 sedimentation of suspended fine particulates or resuspension of silty sediments during storms
391 that preceded the second sampling. It is also noteworthy that *C. prolifera*, a highly nitrophilous
392 green seaweed, was very abundant during the first data collection but rare during follow up
393 monitoring, which is another indication of improved water quality condition (Holmer et al.,
394 2009).

395 Across the four monitoring systems assessed, the lowest rates of progression and the
396 highest reduction in the performance of *P. oceanica* descriptors were recorded at the REF
397 monitoring system, which lies far from any aquaculture operations. At both times of sampling,
398 lower seagrass coverage and shoot densities were measured at this monitoring system
399 compared to its shallower counterparts, although the values of shoot densities measured still
400 indicate high ecological condition of the meadows (Pergent et al., 1995) and progression of the

401 meadow was still recorded despite a strong dynamic regression at other PMN lower limit
402 reference sites in the Mediterranean (Pergent et al., 2015). The deeper water, and consequently
403 the reduced light availability and water circulation, may be the most important limiting factor
404 of the *P. oceanica* descriptors (Martínez-Crego et al., 2008). Furthermore, this site was closer
405 to the anthropogenic footprint of Limassol city, which may be affecting the *P. oceanica*
406 meadow. For example, about 1.4 km to the northeast there is a sewage outlet releasing
407 processed effluents generated from Limassol. This monitoring system can provide valuable
408 baseline data if fish farming begins nearby.

409 The variation in descriptors considered in this study was explained by the cumulative
410 effects of environmental and farm predictors. The variables having the most cumulative effect
411 on *P. oceanica* descriptors, were: water depth followed by direction, and then distance to the
412 nearest fish farm or production tonnage. The multiple regression analysis to identify main
413 predictors was purely suggestive. The creation of more PMN systems at different directions
414 from the fish farms can enable better discrimination of the factors contributing to the changes
415 in structural and demographic *P. oceanica* descriptors.

416 The PMN protocol allows microscale detection of regression/progression of seagrass
417 lower limits using structural and morphological *P. oceanica* descriptors that are widely applied
418 in generic ecosystem monitoring. Most of the structural indicators considered exhibit marked
419 seasonality and/or strong bathymetric dependence (Marbà et al., 2013). This bottleneck of
420 inherent patchiness and differences of these indicators across the meadow was removed by
421 sampling around the same time of year (summer - autumn period) and from the same fixed
422 plots (same depth). However, data should be interpreted based on the validity of the structural
423 indicators used to reflect stress. The diversity of *P. oceanica* indicators is striking; structural
424 descriptors of *P. oceanica* used in this study such as coverage and shoot density are widely
425 used in monitoring programmes (e.g. EU Water Framework Directive) as they are linked
426 directly to ecosystem integrity and can detect generalized degradation responses (Martínez-
427 Crego et al., 2008; Marbà et al., 2013). A recent global review of seagrass indicators identified
428 structural indicators such as density, coverage and depth limit among the best suited indicators
429 for generic ecosystem monitoring, stress screening and ecological assessment (Roca et al.,
430 2016).

431 Lower shoot size, shoot density and coverage are commonly reported responses for *P.*
432 *oceanica* meadows exposed to fish farm effluents (Pergent-Martini et al., 2006), though this

433 was not detected in our study. The number of leaves per shoot are responding consistently to
434 light stress in seagrasses making them a robust bioindicator of degraded water quality
435 (McMahon et al., 2013). Lepidochronological analysis showed that before our study and
436 relocation of farms, the number of leaves per shoot at each monitoring station was stable and
437 not very different across stations. Between the two sampling periods, the leaf number
438 decreased in two stations but declines of this descriptor near aquaculture are not always
439 consistent (Pergent-Martini et al., 2006). The percentage of plagiotropic rhizomes is correlated
440 with water quality (Gobert et al., 2009). On the other hand, the plagiotropic rhizomes remain
441 plagiotropic when surrounding substrate space is sufficient to allow lateral expansion and
442 revert to orthotropic in dense meadows where space is inadequate for colonization (Molenaar et
443 al., 2000). This makes any comparisons using this descriptor difficult. Plagiotropic rhizomes
444 are the most common rhizome on edges of meadows, while orthotropics are predominant in
445 continuous meadow (Lapeyra, 2016). Hence the lower plagiotropic rhizome measured from the
446 fixed positions of decommissioned sites (REF and EM) in the follow-up monitoring may be
447 partly explained by the fact that the edge has progressed a little and what used to be the edge of
448 the meadow is now a little further inside.

449 Structural descriptors are responsive to degradation but are not effective in reflecting
450 early improvements and recoveries because they respond slowly and detect impacts much too
451 late for effective management action to be taken (Roca et al., 2015, 2016). Environmental
452 change is first reflected in plant physiology, which modifies seagrass growth and morphology,
453 which induce changes in meadow structure (Collier et al., 2012). Thus, physiological indicators
454 present more stressor-specific responses and can detect degradation responses much faster
455 (Roca et al., 2015, 2016). To the highest level of cellular response, altered gene expression of
456 stress-related genes are the faster predictors of an imminent seagrass collapse (Ceccherelli et
457 al., 2018). One drawback of the PMN protocol is that it only includes structural variables and
458 once a decline in these parameters is sufficiently large to be detected in *P. oceanica* meadows,
459 there is a considerable risk that the seagrass meadow has already degraded irreversibly. The
460 PMN protocol applied in this study can benefit from incorporating early-warning indicators
461 together with the structural *P. oceanica* descriptors considered. The response of the
462 physiological indicators is highly stress-specific so the choice depends on the objectives of the
463 management strategy (Roca et al., 2016).

464 Despite national and international protection, large declines of *P. oceanica* meadows
465 have been documented since the second half of the 20th century, especially near urban areas of

466 the western Mediterranean (Marbà et al., 2014; Telesca et al., 2015). The loss of *P. oceanica*
467 meadows may result in the erosion and rapid remineralisation of the carbon-rich matte,
468 accelerating climate change (Pergent et al., 2014). Efforts to conserve *P. oceanica* lie mostly in
469 the establishment of marine protected areas, which seem to be insufficient to guarantee the
470 protection of *P. oceanica* meadows (Montefalcone et al., 2009). Across the Mediterranean Sea,
471 seagrass monitoring is extensive, but the adoption of different sampling designs and methods
472 may result in erroneous comparisons (Lopez y Royo et al., 2010). Recently, the PMN has
473 refined a standardised methodology for setting up *P. oceanica* monitoring systems, which has
474 been applied in the Euro-Mediterranean region. Comparable temporal monitoring along the
475 edge of the meadow is possible through photography and measurements of vitality parameters
476 from fixed positions. Slow growing seagrasses such as *P. oceanica* are especially suited to
477 fixed-plot monitoring (Schultz et al., 2015) as small-spatial scale progression or regression of
478 the meadow can be monitored effectively.

479 The *P. oceanica* monitoring systems set up and monitored in this study are valuable
480 tools for researchers, managers and decision makers and their application should be promoted.
481 Set up at the deepest boundaries of the meadows, near the compensation depth where the plants
482 are most sensitive to changes in water quality, they form an important indicator of ecological
483 integrity and allow for detection of small losses, which is critical for slow growing *P. oceanica*
484 (Holmer et al., 2003; Buia et al., 2004). Future comparisons will guide responsible
485 management and increase our understanding regarding the mariculture impacts on *P. oceanica*
486 in the eastern Mediterranean. They can also be compared with other PMN systems set up in
487 other places across the Mediterranean Sea to assess the *P. oceanica* population dynamics in
488 different regions. The use of fixed plot methods using cement markers, like the PMN method
489 applied in the Mediterranean or using quadrats placed over transects like the SeagrassNet
490 method applied globally (www.SeagrassNet.org), allow reliable and effective microscale
491 monitoring of seagrass descriptors from the same positions using standardised methodologies,
492 have high statistical power, and their use should be encouraged and widely adopted in generic
493 ecosystem monitoring (Schultz et al., 2015). The disadvantage with the used *P. oceanica*
494 descriptors is that they respond late to generalised pressures. If the management strategy aims
495 to achieve effective early detection of stress imposed on *P. oceanica* by specific anthropogenic
496 activities (e.g. burial, metal pollution, eutrophication, organic enrichment, shading), it is
497 recommended to incorporate stress-specific biochemical and genetic indicators in the
498 monitoring program.

499

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Highlights

- Around Cyprus, fish farming initially operated shallow cages over seagrass meadows. The farms expanded rapidly but cages moved away from the seagrass beds to mitigate impacts.
- Four seagrass monitoring systems were set up near fish farms and decommissioned sites.
- Data collection was repeated from the same fixed-plots about five years later.
- Progression of previously impacted seagrass beds was noted and present-day farms, located in deep water, are not preventing nearby seagrass meadow growth.