Is all seagrass habitat equal? Seasonal, spatial, and interspecific variation in productivity dynamics within Mediterranean seagrass habitat

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12 **Abstract**

13 Seagrass meadows' ability to capture carbon through actively sequestering autochthonous carbon via
14 photosynthesis means they represent a nature-based solution to rising carbon emissions. In
15 multispecies seagrass communities, and due to species introduction or predicted range shifts, it is
16 important to know which species deliver different carbon sequestration gains to inform conservation
17 actions. Large benthic chamber (volume = 288L) experiments assessed the seasonal and spatial
18 metabolism dynamics of the endemic and dominant Mediterranean seagrass *P. oceanica*, whilst small
19 benthic chamber (volume = 7L) experiments compared the dynamics between *P. oceanica*, the native
20 *C. nodosa* and non-native *H. stipulacea*. Within shallow *P. oceanica* edge habitat lower Net
21 Apparent Productivity (NAP) occurs in autumn ($\bar{x}$ = 1.4, SD ± 3.24 O_2 mmol m^{-2} d^{-1}) compared to
22 summer ($\bar{x}$ = 10.9, SD ± 3.03 O_2 mmol m^{-2} d^{-1}) corresponding with periods of light limiting and light
23 saturating conditions, but it remains overall autotrophic annually (2.6 C mol m^{-2} yr^{-1}). However,
24 spatial heterogeneity exists, core areas of *P. oceanica* were more productive ($\bar{x}$ =21.7, SD± 4.21 O_2
25 mmol m^{-2} d^{-1}) compared to edge habitat with spatial changes in productivity relating to plant surface
26 area (96%), shoot density (81%), blade length (72%) and seagrass percentage cover (64%). In fact,
27 patchy short *P. oceanica* has similar NAP ($\bar{x}$ = -3.6, SD ± 8.9 O_2 mmol m^{-2} d^{-1}) to the non-native
28 *H. stipulacea* ($\bar{x}$ = 2.1, SD ± 4.7 O_2 mmol m^{-2} d^{-1}). Yet *H. stipulacea* has a significant metabolic
29 advantage over *C. nodosa* (NAP $\bar{x}$ = 0.0004, SD ± 0.0011 O_2 mmol cm^{-2} d^{-1} vs $\bar{x}$ = -0.0012, SD ±
30 0.0007 O_2 mmol cm^{-2} d^{-1}). This study demonstrates that not all seagrass habitat is equal. If seagrass
31 meadows are to play a part in mitigating CO_2 emissions, variability in primary productivity within
32 seagrass meadows needs to be accounted for to produce comprehensive autochthonous carbon
33 sequestration estimates. This means seagrass meadow species composition, the condition of these
34 species and the potential interactions between seagrass species must be better understood.

35

1 Introduction

Seagrass meadows act as a major global carbon sink (Duarte et al., 2013), therefore restoration or expansion of seagrass beds represent a potential nature-based solution to rising carbon emissions. Seagrasses capture carbon through actively sequestering autochthonous carbon by photosynthesis and passively trapping allochthonous carbon within their architectural structure. Allochthonous carbon is typically considered more labile, therefore deposits of autochthonous carbon are those expected to lead to long-term stable carbon deposits (Mazarrasae et al., 2018). The metabolic rates of global seagrass communities favour net autotrophy, with temperate meadows typically favoured to have a higher net autotrophy than tropical meadows (Duarte et al., 2010), suggesting not all seagrass is equal in its ability to sequester carbon.

The temperate seagrass *Posidonia oceanica* forms vast monospecific meadows in the Mediterranean and is unique in its ability to form vertical mattes that can store sedimentary carbon for millennia (Mateo et al., 1997). It is perhaps why some herald these meadows to represent the global maximum in carbon sequestration among seagrasses (Lavery et al., 2013). Unlike terrestrial soils, *P. oceanica* sediments do not become saturated with carbon over time because they can accrete vertically. If the vertical accretion matches the rate of sea level rise, they potentially have a limitless capacity, which in part demonstrates their suitability for climate mitigation policy efforts (Howard et al., 2017). However, *P. oce*anica meadows have undergone severe regression in the last 50 years (34% loss), with only localised areas of persistence and growth (Telesca et al., 2015). The causes of decline for *P. oceanica* include water quality degradation, coastal modification, mechanical damage (i.e., bottom trawling, anchoring, mooring, culture farm occupation), extreme weather events and non-native macroalgae invasion (Santos et al., 2019).

At the Mediterranean scale, *P. oceanica* populations in the Western and Eastern basins maintain genetic differentiation due to present-day dispersal limits (Arnaud-Haond et al., 2007). There is a greater distribution of *P. oceanica* in the Eastern basin (713,992 ha) compared to the Western basin (510,715 ha) (Telesca et al., 2015). Despite the genetic variation between basins and larger coverage in the Eastern Mediterranean basin, the majority of *P. oce*anica metabolism estimates have come from the Western Mediterranean basin (Frankignoulle and Bouquegneau, 1987; Holmer et al., 2004; Gazeau et al., 2005; Barron and Duarte, 2009; Olive et al., 2015; Champenois and Borges, 2018). There is a single published study on *P. oceanica* metabolism in the Eastern Mediterranean basin, in the western region of the Aegean Sea (Apostolaki et al., 2010). Metabolism and carbon sequestration estimations for *P. oceanica* are considered one of the most well researched amongst seagrass species (Nordlund et al., 2018), yet there are distinct local knowledge gaps and spatial biases, particularly within the Eastern Mediterranean basin that need to be addressed. In the Eastern Mediterranean basin, the sea surface has warmed by 0.05 ± 0.009 °C yr^{-1} compared to just 0.03 ± 0.008 °C yr^{-1} in the Western Mediterranean basin from 1985 to 2006 (Nykjaer, 2009). Given the Eastern Mediterranean basin is warming faster than the Western Mediterranean basin understanding if the metabolism and drivers of productivity are different in Western Mediterranean seagrass is important.

Seagrass metabolism is influenced by multiple variables including light (Champenois and Borges, 2018), nutrient availability (Holmer et al., 2008; Apostolaki et al., 2010), temperature and ocean acidification (Berg et al., 2019); which leads to seasonal fluctuations in productivity. Seagrass depth distribution is determined by light availability, as under insufficient light conditions the plant does not meet the photosynthetic requirements needed to maintain positive metabolic and carbon balance (Ralph et al., 2007), moving away from a state of net autotrophy and net carbon storage. However, high light intensity also causes photodamage reducing the photosynthetic efficiency and causing

81   photoinhibition. Subsequently, maximum annual solar irradiance does not necessarily coincide with
82   annual maximum *P. oceanica* gross primary productivity (GPP) (Champenois and Borges, 2018).
83   The optimal thermal conditions for *P. oceanica* are between 17 - 20 °C (Champenois and Borges,
84   2018), therefore its metabolism both above and below these conditions, is not optimal for maximum
85   oxygen production and is more likely to become heterotrophic. Annual patterns of *P. oceanica*
86   metabolism therefore comprise periods that alternate from negative to positive carbon balance as
87   temperature and light availability change with seasons (Alcoverro et al., 2001). If metabolism
88   estimates were produced only during the summer months it would overestimate the meadow's net
89   carbon sequestration capacity (Champenois and Borges, 2012). Notably as stable carbon stocks rely
90   on autochthonous carbon deposits, we will also assess key environmental parameters that influence
91   photosynthesis in these different seasons: change in light and temperature.

92   Seagrass meadows are not always a uniform habitat and whilst *P. oceanica* meadows can form
93   continuous meadows, but patchy coverage across meadows is common. Patchy *P. oceanica* creates
94   complex seascapes, which are mosaics including habitats of sand, *P. oceanica* dead matte and live
95   *P. oceanica* (Borg et al., 2006; Abadie et al., 2015). This complexity also acts within a *P. oceanica*
96   meadow, because at the junction between the seagrass and adjacent habitats there are considerable
97   edge effects, resulting in distinct areas of central and edge *P. oceanica* habitat (Abadie et al., 2018).
98   Meadows that experience a wave exposure gradient from low to high energy develop patchier
99   dynamics (Folkard, 2005; Pace et al., 2016). Anthropogenic factors have also increased patchiness
100   including anchoring, impact from historic military activity, fishing practices and fish farming
101   (Montefalcone et al., 2009; Abadie et al., 2015). When a *P. oceanica* meadow is described as patchy
102   it has lower overall cover, more complex patch shapes and reduced within-patch architectural
103   complexity (Pace et al., 2016). This patchiness influences the available surface of photosynthetically
104   active plant material. It is therefore important that in this study we consider the spatial variation in
105   canopy architecture of *P. oceanica* when considering its carbon sequestration potential.

106   The Mediterranean temperate-tropical combination of seagrass species is considered a unique
107   bioregion of seagrass diversity (Short et al., 2007). Alongside the dominant endemic *P. oceanica*, the
108   next most prevalent species in the Aegean Sea is the native *Cymodocea nodosa*. The eastern region of
109   the Aegean Sea sits at a crossroad for alien species expansion (Pancucci-Papadopoulou et al., 2012),
110   including the non-native seagrass *Halophila stipulacea*, introduced to the Mediterranean and first
111   reported in 1894 off the Island of Rhodes in the south-eastern region of the Aegean Sea (Fritsch,
112   1895; also see *Halophila decipiens*, Gerakaris et al., 2019). *H. stipulacea* was listed amongst the '100
113   Worst Invasive Species' in the Mediterranean (Streftaris and Zenetos, 2006). However, there are
114   discrepancies in whether it should be considered 'invasive' or not as no ecological consequences of
115   its introduction and spread in the Mediterranean have been reported (Williams, 2007). Scarce
116   research has focused on its potential impact or contribution to ecosystem services within
117   Mediterranean coastal ecosystems, yet *H. stipulacea* habitat was recently suggested to support carbon
118   sequestration (Apostolaki et al., 2019; Wesselmann et al., 2021). Given *H. stipulacea* is one of the
119   longest monitored non-native species in the Mediterranean, there has been a clear lag from reporting
120   its presence and rate of expansion, to understanding its impact within the communities where it has
121   successfully established.

122   In the Mediterranean *H. stipulacea* can be found in single species meadows, multi-species meadows
123   with the native *Cymodocea nodosa*, in the free spaces between patches of *P. oceanica* or in habitats
124   previously devoid of seagrass (Boudouresque et al., 2009). Whilst there are reports of its 'invasive'
125   behaviour on sandy substrata when it exists in high abundances, no displacement of native species
126   has yet been reported (Tsiamis et al., 2010). Given that *H. stipulacea* has various contexts in which it

127   can be found in the Mediterranean its contribution to community productivity may be context
128   dependent. When *H. stipulacea* has colonised areas previously absent of seagrass its presence has
129   increased the distribution of seagrass habitat in the Mediterranean, this is one reason why it can be
130   considered a new potential blue carbon sink habitat (Apostolaki et al., 2019; Wesselmann et al.,
131   2021). The potential of *H. stipulacea* to also influence the net productivity of mixed seagrass
132   habitats, especially considering evidence it can colonise patchy areas of bare ground where
133   *P. oceanica* may have been present in the past (Telesca 2015), will be assessed in this study.

134   We will determine seasonal metabolism measurements for the dominant seagrass *P. oceanica* in the
135   eastern region of the Aegean Sea and the relative influence of seasonal changes in light, temperature,
136   and seagrass canopy height, on net productivity. The accumulative seasonal estimates will then
137   provide a conservative estimate of annual meadow carbon sequestration potential. Alongside this
138   spatial variation in productivity between edge and central *P. oceanica* habitat will be assessed,
139   together with the potential of various plant biometrics to describe spatial plant productivity. Finally,
140   species-specific metabolism from both native seagrass species *P. oceanica* and *C. nodosa* will be
141   placed in direct comparison to the non-native seagrass species *H. stipulacea*. Our results will
142   contribute to suitable Mediterranean scale carbon budgets and to begin to assess potential changes
143   that may take place in the future given current climate change predictions.

2   Methods

2.1   Study site

146   This study took place at Vroulia Bay (37.317460° N, 26.724704° E), Lipsi Island, which is part of
147   the Dodecanese Islands, in the eastern region of the Greek Aegean Sea. This island suited the
148   following study due the accessibility and distribution of the three seagrass species *P. oceanica*,
149   *C. nodosa* and *H. stipulacea*. Vroulia Bay is sheltered with minimal human presence. The bay
150   consists of a multispecies seagrass meadow, largely dominated by monospecific areas of *P. oc*eanica.
151   However, the bay also houses small monospecific patches of *C. nodosa* and *H. stipulacea*, as well as
152   areas where two or all three of the species form mixed meadows.

2.2   Experimental Design

154   This metabolism study exists in two parts. Firstly, and primarily, large benthic chamber experiments
155   focus on the seasonal and spatial metabolism dynamics of *P. oceanica*, these took place from autumn
156   2018 to summer 2019; seasonal *P. oceanica* sampling November 3rd – 9th, April 12th – 19th and July
157   2nd - 12th; spatial *P. oceanica* sampling July 2nd – August 12th. Secondly small benthic chamber
158   experiments focus on comparative metabolism dynamics between *P. oceanica*, *C. nodosa* and
159   *H. stipulacea*, collected 20th June – 17th July 2019.
160
2.2.1 Seasonal and spatial *P. oceanica* metabolism -large benthic chamber setup

162   The large dome shaped clear PVC benthic chambers (diameter = 1 m, height = 50 cm, benthic
163   surface area = 0.79 m^2, volume = 288 L) were deployed by free divers (Fig. 1) in the shallow areas of
164   Vroulia Bay 1.6 - 2 m depth amongst monospecific areas of *P. oceanica*. PME miniDOT® loggers
165   were fitted to the central (highest) part of the dome chamber, to record dissolved oxygen and
166   temperature in 10 minutes intervals. HOBO Pedant® loggers were placed within the chambers on the
167   seafloor to record relative irradiance in 5 minutes intervals. Benthic chambers were fitted with a
168   pump secured to the inside of the chamber roughly 30 cm from the seafloor. This pump circulated the
169   water within the dome at a flow rate of roughly 480 L hr^{-1} in 10 minute intervals (10 minutes on

170 followed by 10 minutes off), as such the overall flow rate within the chamber was considered to be
171 240 L hr^{-1}. A thin cable went from the pump, within the benthic chamber, to an external submersible
172 battery pack. Given the morphology and typically large aboveground biomass of *P. oceanica*, the
173 large benthic chambers combined with internal mixing support sufficient volume of water inside the
174 chamber relative to vegetative biomass to prevent oxygen saturation (Olive et al., 2015), and support
175 accurate measurement of oxygen by the sensors (Annex 1). The benthic chambers were held in place
176 by large chains and sank 5 cm into the sediment to create a seal. The benthic chambers were
177 deployed within the same 2 hour timeframe each morning (10:45 am -12:45 pm) then left *in situ* for
178 24 hour (autumn and summer) or 23 hour (spring) incubations.

179 The large *in situ* benthic chambers were deployed over edge habitat in autumn, spring and summer.
180 Patchy edge habitat is considered to be the edge of large *P. oceanica* areas (> 2m) or the edge and
181 centre of small *P. oceanica* patches (< 2m). Patches of *P. oceanica* < 2m in size are assumed to
182 consist entirely of edge habitat due to the proximity of the centre to the edge. Edge habitat creates a
183 good seal at the base of the large benthic chambers because of the high proportion of sand to low
184 proportion of rhizome. This avoids damage to the rhizome and roots from the chamber.
185 Simultaneously a large control benthic chamber was placed over the adjacent unvegetated sandy
186 control habitat. If it was not possible to simultaneously deploy the control chamber, they were
187 deployed at the next sampling opportunity the day after the first incubation is completed.

188 To achieve a comparison between more fragmented edge seagrass habitat and more continuous
189 central meadow habitat, in summer domes were placed over *P. oceanica* within the meadow centre in
190 addition to those deployed over edge habitat. Within dense areas of *P. oceanica* the rigid PVC
191 benthic chamber likely cut the rhizomes and roots, however the stress caused is generally considered
192 marginal (Champenois and Borges, 2012). Control chambers were not placed out simultaneously to
193 the central meadow measurements, as control measurements from the edge habitat studies (e.g., bare
194 sand, n = 4) were already available.

2.2.2 Species specific productivity -small benthic chamber setup

196 An area within Vroulia bay was chosen where all three species were in proximity, therefore
197 maintaining as much as possible similar *in situ* environmental conditions for each species (appx. 7m
198 depth). An area of patchy mixed meadow transitioned in areas from *P. oceanica* dominant to
199 *C. nodosa* dominant, with scarce intermittent presence of clumps of *H. stipulacea*, as such this was
200 chosen for the metabolism measurements focusing on *P. oceanica* and *C. nodosa.* Care was taken to
201 avoid placing benthic chambers over mixed species compositions and generally the benthic chambers
202 only encompassed the intended dominant species. Two of five *C. nodosa* chambers covered a small
203 amount of either *P. oceanica* or *H. stipulacea*. Nevertheless, in those instances *C. nodosa* represented
204 93% and 96% of the total seagrass plant surface area within the chamber and therefore these two
205 replicates were still considered representative of *C. nodosa* patches. One of six *P. oceanica*
206 chambers covered a small amount of *H. stipulacea* but *P. oceanica* represented 98% of the total plant
207 surface area within the chamber and therefore was also considered representative of *P. oceanica*.
208 Directly adjacent to the *P. oceanica* and *C. nodosa* was a monospecific area of *H. stipulacea*, which
209 was utilised for the metabolism measurements focused on this species.

210 Three smaller clear dome PVC benthic chambers (diameter = 30 cm, height = 15 cm, benthic surface
211 area = 0.071 m^2, volume = 7 L) were deployed by free divers, secured with a small chain and sank
212 into the sediment to create a seal (Fig. 2). The benthic incubations took place for each seagrass
213 species consecutively; *H. stipulacea* 20th June – 5th July (n = 6), *C nodosa* 10th – 14th July (n = 5) and
214 *P. ocea*nica 14th – 17th July (n = 6). An unvegetated control chamber was simultaneously deployed

215   every day. The same oxygen, light and temperature loggers and temporal sampling methods were
216   used as per the large domes described above. The benthic chambers were deployed within the same
217   half an hour timeframe each morning (11:00 - 11:30 am) and left *in situ* for ~ 23 hours. As
218   *H. stipulacea* and *C. nodosa* are smaller seagrass species with lower above ground biomass, the small
219   benthic chamber design should sufficiently provide a suitable volume of water to vegetative biomass
220   to prevent oxygen saturation. The *P. oceanica* within this area of the bay is naturally patchy and
221   short, which should also accommodate the smaller chamber size and volume (Fig. 2B).

222   ### 2.2.3 Quantifying seagrass canopy within the benthic chamber

223   The quantity of seagrass canopy enclosed within all benthic chambers was quantified; large benthic
224   chambers a representative sample was selected, measured *in situ* and scaled up to reflect the full
225   chamber; small chambers had all the leaf material collected and measured back at the lab.

226   For all large benthic chambers, several measurements were taken from the seagrass within the
227   benthic chambers; an estimate of *P. oceanica* cover (%); shoot density (Sht_{dens}) (m^{-2}) within three 20
228   x 20 cm quadrats randomly placed on *P. oceanica*; the number of blades (B_{Number}) (shoot^{-1}) from 5 - 6
229   randomly selected shoots; canopy blade length (B_{length}) and blade width (B_{width}) (cm) from 5 – 6
230   randomly selected blades.

231   Plant surface area (m^{-2}) for each chamber was calculated from the seagrass biometrics:

232
$$Shoot_{Surface\ Area} = 2\left(B_{length} \times B_{width}\right) \times B_{Number}$$

233
$$Plant\ surface\ Area = Shoot_{Surface\ Area} \times \left(Sht_{Dens} \times \frac{Cover}{100}\right)$$

234   For the small benthic chambers all leaf material from within the chambers was collected by cutting
235   the leaves leaving the rhizome and roots, this along with the small sample size within these
236   chambers' limits damage to the overall sampling area. The aboveground leaf material was
237   transported back to the lab where they were separated from any dead leaf litter and all individual
238   leaves were photographed using a Canon EOS 750D DSLR camera, on a white background. The
239   planar area of the seagrass leaves within corresponding benthic chambers were determined, by Image
240   J software, doubling to determine total leaf surface area (modified from, Schneider et al. 2012) and
241   converted into areal based estimate (cm^2 m^{-2}) using the chamber benthic surface area.

242   ### 2.3   Community metabolism calculations

243   There is no need to consider diffusive exchange with the atmosphere as benthic incubations were
244   carried out in closed systems. The record from the PME oxygen logger was used to calculate net
245   community productivity (NCP) for every 10-minute interval over each 24-hour period (modified
246   from Cole et al., 2000):

247
$$\Sigma\Delta DO = NCP_{Daily}$$

248   where DO is dissolved oxygen. This was applicable to the autumn and summer large benthic
249   chamber *P. oceanica* samples when 24-hour incubations were completed.

250   HOBO Pendant® light intensity data was used to distinguish the length of the night period. The total
251   hours of daylight (H_d) were determined as:

252
$$H_d = 24 - H_n$$

253   where H_n is the total hours of night-time darkness.

254   The spring *P. oceanica* and mixed species incubations were completed across 23-hour incubations
255   missing one hour of daylight incubation. $NCP_{Daytime}$ (Champenois and Borges, 2012; Rodriguez et al.,
256   2016) was calculated whereby t is the daylight incubation time:

257
$$NCP_{Daytime} = \left(\frac{\Sigma\Delta DO}{t}\right) \times H_d$$

258   During darkness GPP is 0, therefore the change in dissolved oxygen in any 10-minute interval is
259   assumed to be a result of community respiration. The change that occurred during the night-time dark
260   period were summed to calculate CR_{Night}:

261
$$\Sigma\Delta DO = CR_{Night}$$

262   The combination of the net community change during the daytime ($NCP_{Daytime}$) and night-time dark
263   period (CR_{Night}) determine NCP_{Daily} for 23-hour incubations made during Spring:

264
$$NCP_{Daily} = NCP_{Daytime} + CR_{Night}$$

265   Since the benthic chamber incubations do not acquire a direct measurement of CR_{Day}, we assume the
266   hourly value of CR_{Night} and CR_{Day} are equal (Cole et al., 2000):

267
$$CR_{Day} = \left(\frac{CR_{Night}}{H_n}\right) \times H_d$$

268   This allows daily community respiration (CR_{Daily}) to be found:

269
$$CR_{Daily} = CR_{Day} + CR_{Night}$$

270   NCP_{Daily} is then calculated as:

271
$$NCP_{Daily} = GPP_{Daily} - CR_{Daily}$$

272   All metabolism measurements (O_2 mg L^{-1} d^{-1}) are converted into areal based estimates (Olive et al.,
273   2015), whereby the volume (V) and area (A) is relative to the benthic chamber setup:

274
$$O_2 \; mmol \; m^{-2} \; d^{-1} = \frac{\left(\left(\frac{DO}{32}\right) \times V\right)}{A}$$

275   The corresponding GPP:CR ratios were calculated:

276
$$\frac{GPP}{CR}$$

277   The photosynthetic and respiratory quotient of 1 mol of O_2: 1 mol CO_2 is applied to terrestrial plants
278   that use starch and sugars as respiratory substrates, as observed in *P. oceanica* (Alcoverro et al.,

279 2001). The photosynthetic and respiratory quotient of 1 mol of O_2: 1 mol CO_2 is conservatively
280 applied to a wide number of seagrass species (Duarte et al., 2010) and therefore also used for
281 *H. stipulacea* and *C. nodosa*. Therefore, the metabolism values are interchangeable as units of
282 oxygen or carbon (O_2 mol m^{-2} d^{-1} and C mol m^{-2} d^{-1}).

2.4 Net Apparent Productivity calculations

284 The net apparent productivity (NAP) of the seagrass and epiphytes (modified from Murray and
285 Wetzel, 1987), was calculated as the difference between estimates for the NCP of the seagrass
286 benthic chambers and the average NCP of the sediment and plankton in the unvegetated control
287 chambers (Murray and Wetzel, 1987) from the same corresponding season. This calculation assumes
288 the only difference between the vegetated and unvegetated benthic chambers is the presence of the
289 seagrass and epiphytes.

290 The expected contribution of epiphyte productivity is deemed minimal due to the overall high
291 biomass of *P. oceanica* to that of the epiphytes (Cox et al., 2015), therefore the large benthic chamber
292 NAP primarily reflects the productivity of the *P. oceanica*. To account for seasonal changes in
293 seagrass canopy the seasonal NAP measurements were also presented separately standardised by the
294 canopy height with the large benthic chambers (O_2 mmol m^{-2} cm^{-1} d^{-1}).

295 To determine the NAP of the small benthic chambers the average NCP of the unvegetated control
296 chambers deployed at the same time as the corresponding seagrass species were used. Given each
297 seagrass species were deployed consecutively the corresponding unvegetated controls were grouped
298 thus; 20th June – 5th July (n = 6) corresponding to *H. stipulacea*, 10th – 14th July (n = 3) for
299 *C. nodosa* and 14th – 17th July (n = 3) for *P. oceanica*. These comparisons of species NAP were also
300 presented separately standardised by the respective plant surface area (O_2 mmol cm^{-2} d^{-1}), calculated
301 with the scaled-up plant surface area from within the small benthic chambers (cm^2 m^{-2}).

302 Accounting for the metabolism of the community within a seagrass meadow is important to
303 determine the net productivity at a community level, but as the autotrophy within the community is
304 largely attributed to the primary productivity of the seagrasses (Hemminga and Duarte, 2000),
305 distinguishing the NAP of the *P. oceanica* enables a clearer determination of the influences driving
306 this metabolic component of the community. Justifying the approach to distinguish between NCP
307 (proxy of community metabolism) and NAP (proxy of plant productivity) within the *P. oceanica*
308 meadow ecosystem, as seasonal community metabolism may partially mask the drivers in
309 *P. oceanica* productivity. However, NCP estimates are widely accepted for benthic chamber
310 metabolism studies within seagrass meadows (Duarte et al., 2010; Olive et al., 2015), because they
311 clearly quantify the extent to which the overall community is a carbon sink or source. Hence, we also
312 chose to present our results in NCP as it allows for closer comparisons to the existing *P. oceanica*
313 NCP estimates.

2.5 Data analysis

2.5.1 Seasonal *P. oceanica* NCP and NAP

316 The three samples from winter and spring and four samples in summer, meant finding an appropriate
317 data distribution to the seasonal *P. oceanica* benthic chamber data is challenging, but Shapiro-Wilk
318 tests confirmed that when grouped by Season the NCP and NAP does conform to normal distribution
319 (autumn $W = 0.9903741$, $P > 0.05$; spring $W = 0.8167365$, $P > 0.05$; summer $W = 0.9591216$, $P >$
320 0.05;) (ANNEX 2). Whilst Bartlett's test confirmed equal variances across the NCP and NAP data (K

321   = 0.00952, $P > 0.05$). Therefore, ANOVAs were applied to assess if there was a significant seasonal
322   difference in *P. oceanica* NCP, NAP and NAP when standardised by canopy height. Tukey post hoc
323   tests were used to test the differences between the seasons.

2.5.2 Influence of environmental conditions on *P. oceanica* NAP

325   The mean PME miniDOT water temperature was calculated across each incubation period. HOBO
326   logger irradiance (lux) were converted to PAR (photosynthetic active radiation), according to the
327   conversion factor appropriate to the light source 'daylight' (Thimijan and Heins, 1983). The
328   Instantaneous PAR with the unit $\mu mol \ s^{-1} \ m^{-2}$ is used to calculate Daily Light integral (DLI) given the
329   time interval in seconds (*t*) between each PAR reading over each 24-hour period:

330   $$DLI = \Sigma \Delta t \times PAR$$

331   The DLI is presented with the unit $mol \ m^{-2} \ d^{-1}$.

332   To examine the change in *P. oceanica* NAP relative to the changing light environment, the
333   photosynthesis-irradiance relationship was fit with a hyperbolic tangent function (Jassby and Platt,
334   1976), modified to account for respiration (Rheuban et al., 2014), as used for the seagrass species in
335   question (Koopmans et al., 2020). The model fitted was:

336   $$Flux = P_{max} tanh \frac{I}{I_k} - R_I$$

337   where P_{max} is the maximum photosynthetic rate, I_k is the saturation irradiance, and R_I is respiration.
338   The parameters were estimated by non-linear least squares approach (nls function, R version 3.5.1),
339   estimating approximate start values. The irradiance compensation point is the irradiance at which net
340   oxygen production equals zero.

341   As there was no significant interaction between temperature and seasonal NAP ($F_{1,4} = 0.189$, $P <$
342   0.05), or significant effect when temperature is assessed as a covariate for change in seasonal NAP
343   by ANCOVA ($F_{1,6} = 2.1154$, $P < 0.05$) (ANNEX 3). The maximal model to assess for significant
344   effect of temperature on NAP was by ANOVA.

2.5.3 Annual *P. oceanica* productivity

346   Annual NAP and NCP was estimated by scaling up the three average seasonal daily NAP and NCP
347   measurements; the November measurement was chosen to represent the period between October to
348   January (123 days), April represented the period from February to May (120 days) and July
349   represented June to September (122 days):

350   $$NAP_{Annual} = \left(NAP_{Daily(Nov)} \times 123\right) + \left(NAP_{Daily(Apr)} \times 120\right) + \left(NAP_{Daily(Jul)} \times 122\right)$$

351   $$NCP_{Annual} = \left(NCP_{Daily(Nov)} \times 123\right) + \left(NCP_{Daily(Apr)} \times 120\right) + \left(NCP_{Daily(Jul)} \times 122\right)$$

2.5.4 Influence of spatial dynamics on *P. oceanica* NAP

353   A Welch's t-test, to account for unequal sample size, is applied to determine if the NAP differs
354   between the central meadow area and the meadow edge. Then linear regressions are applied to the
355   summer NAP measurements to determine if the difference in central meadow and meadow edge
356   relate to changes in plant surface area, percentage cover, shoot density and blade length. Comparison

357   of the R^2 values provides an understanding of which seagrass biometric account for the variation in
358   NAP and are the best spatial predictor for *P. oceanica* NAP.

2.5.5 Species specific productivity comparison

360   The comparative species-specific NAP data conforms to normal distribution ($W_{1,7} = 0.922$, $P > 0.05$)
361   and an ANOVA applied to assess if there was a significant difference in NAP between seagrass
362   species during summer. The NAP standardised for plant surface area also confirmed to normal
363   distribution ($W_{1,7} = 0.968$, $P > 0.05$). An ANOVA was applied, and Tukey post hoc tests confirmed
364   any pairwise differences between species.

3   Results

3.1   Seasonal *P. oceanica* NCP and NAP

367   The *P. oceanica* meadow NCP is greater than the unvegetated control in every season (Fig. 3A). In
368   autumn, the *P. oceanica* community is overall heterotrophic, as CR is greater than GPP (GPP:CR
369   ratio < 1, Fig. 3 B). However, the oxygen deficit is greater in the community without seagrass (NCP
370    $\bar{x}$ = -3.4, SD ± 8.38 O_2 mmol m^{-2} d^{-1}), than in the *P. oceanica* community (NCP $\bar{x}$ = -2.0, SD ± 3.24
371   O_2 mmol m^{-2} d^{-1}) (Fig. 3A). There is a significant seasonal influence on *P. oceanica* NCP ($F_{2,7}$ =
372   10.924, $P < 0.05$). Pairwise post hoc comparisons show NCP is significantly higher in spring (NCP $\bar{x}$
373   = 8.3, SD ± 3.12 O_2 mmol m^{-2} d^{-1}) and summer (NCP $\bar{x}$ = 7.8, SD ± 2.03 O_2 mmol m^{-2} d^{-1}), compared
374   to autumn when it is heterotrophic (Tukey: $P < 0.05$). There is no significant difference in NCP
375   between the spring and summer.

376   During the transition from autumn to spring there is a large increase in GPP (GPP $\bar{x}$ = 20.2, SD ±
377   7.81 O_2 mmol m^{-2} d^{-1} to GPP $\bar{x}$ = 68.5, SD ± 47.85 O_2 mmol m^{-2} d^{-1}, Fig. 3C) and a simultaneous
378   increase in CR from autumn into spring (CR $\bar{x}$ = 22.2, SD ± 10.12 O_2 mmol m^{-2} d^{-1} to CR $\bar{x}$ = 60.2,
379   SD ± 44.80 O_2 mmol m^{-2} d^{-1}, Fig. 3D). However, the increase in GPP is greater than the increase in
380   CR transitioning the *P. oceanica* meadow from heterotrophic in autumn to autotrophic in spring
381   (GPP:CR ratio > 1, Fig. 3B). The *P. oceanica* meadow stays in an autotrophic state in the Summer
382   (GPP:CR ratio > 1, Fig. 3B) registering its highest GPP (GPP $\bar{x}$ = 94.1, SD ± 74.22 O_2 mmol m^{-2} d^{-1},
383   Fig. 3C), but also its highest CR (CR $\bar{x}$ = 86.4, SD ± 74.21 O_2 mmol m^{-2} d^{-1}, Fig. 3C). The increase in
384   GPP is not as great as the increase in CR, therefore the GPP to CR ratio and NCP is lower in summer
385   compared to spring (Fig. 3B). Further to this the organisms present within the unvegetated control
386   chambers have a higher metabolic rate in the summer (NCP $\bar{x}$ = -3.2, SD ± 0.81 O_2 mmol m^{-2} d^{-1})
387   compared to the spring (NCP $\bar{x}$ = -0.4, SD ± 0.71 O_2 mmol m^{-2} d^{-1}, Fig. 3A).

388   Whilst the *P. oceanica* NCP is highest in spring, *P. oceanica* NAP is highest in summer (NAP $\bar{x}$ =
389   10.9, SD ± 3.03 O_2 mmol m^{-2} d^{-1}) (Fig. 4A). There remains a significant seasonal difference in
390   *P. oceanica* NAP ($F_{2,7} = 8.3885$, $P < 0.05$). However, Tukey post hoc comparisons found NAP is
391   only significantly lower in autumn compared to summer (Tukey: $P < 0.05$). Although there is an
392   observational difference in NAP between the autumn (NAP $\bar{x}$ = 1.4, SD ± 3.24 O_2 mmol m^{-2} d^{-1}) and
393   spring (NAP $\bar{x}$ = 8.7, SD ± 3.12 O_2 mmol m^{-2} d^{-1}) the difference is not significant. There remains no
394   significant difference in NAP between the periods of highest productivity in spring and summer.

395   The canopy height within the edge *P. oceanica* habitat is lowest during autumn ($\bar{x}$ = 15.4, SD ± 2.84
396   cm), this increases into spring ($\bar{x}$ = 22.3, SD ± 4.77 cm) and peaks during summer ($\bar{x}$ = 25.1, SD ±
397   5.90 cm). When the *P. oceanica* NAP is standardised by the seagrass canopy height in the
398   corresponding season, autumn still maintains the lowest NAP, but it highlights that *P. oceanica* NAP

399   is more variable within autumn (NAP $\bar{x}$ = 0.07, SD ± 0.221 O_2 mmol m^{-2} cm^{-1} d^{-1}) (Fig. 4B). In
400   comparison *P. oceanica* NAP in Summer (NAP $\bar{x}$ = 0.43, SD ± 0.066 O_2 mmol m^{-2} cm^{-1} d^{-1}), is less
401   varied and similar to spring (NAP $\bar{x}$ = 0.40, SD ± 0.125 O_2 mmol m^{-2} cm^{-1} d^{-1}) (Fig. 4B). Thus, the
402   significant seasonal difference in NAP remains, between autumn and summer ($F_{2,7}$ = 6.3149 $P <$
403   0.05). There is no significant difference in NAP between autumn and spring or spring and summer.

3.2   Influence of environmental conditions on *P. oceanica* NAP

405   The daily light integral ranged from 4.7 mol photons m^{-2} d^{-1} during autumn to 25.2 mol photons m^{-2}
406   d^{-1} in the summer. Variation in environmental conditions within each season allowed for some
407   overlap in the irradiance encountered between seasons and the *P. oceanica* NAP resembled a
408   saturation curve when plotted as a function of irradiance (Fig. 5A), as did the curve for NAP
409   standardised by canopy height (Fig. 5B). The DLI conditions in autumn (Min = 4.7 mol photons m^{-2}
410   d^{-1}) sit near the predicted irradiance compensation point (IC= 4.6 mol photons m^{-2} d^{-1}) as such
411   within the autumnal DLI range there are conditions where the plant may only just or may not
412   maintain metabolic requirements due to low irradiance. In spring the seagrass transitions between
413   light limiting and light saturating levels. The light saturating conditions occur throughout summer,
414   when NAP (NAP $\bar{x}$ = 10.9, SD ± 3.03 O_2 mmol m^{-2} d^{-1} Fig. 4A) sits near the predicted maximum
415   (10.12 O_2 mmol m^{-2} d^{-1}, Fig. 5A). The period of summer light saturation corresponds to when NAP is
416   less varied whilst changes in canopy height across the year are also accounted for (Fig. 4B). The
417   changes in the DLI account for 71% of the variation in *P. oceanica* NAP.

418   The water temperature was lowest in spring ($\bar{x}$ = 17.7, SD ± 0.13 °C), increasing to a summer high ($\bar{x}$
419   = 23.6, SD ± 0.40 °C). The autumn temperatures encountered sat at a relative mid-point ($\bar{x}$ = 20.7, SD
420   ± 0.45 °C) between spring and summer, yet the NAP was lowest in autumn. Therefore, the change in
421   NAP was not relative to the change in water temperature and not a significant factor as main effects
422   (ANNEX 3), with season ($F_{1,6}$ = 2.1154, $P >$ 0.05) or without season (Temperature $F_{1,8}$ = 0.7265, $P >$
423   0.05).

3.3   Annual productivity of *P. oceanica* edge habitat

425   The annual NAP of the *P. oceanica* edge habitat in this meadow was estimated at 2.6 C mol m^{-2} yr^{-1}.
426   However, the organisms present within the *P. oceanica* meadow have their own metabolic
427   requirements (NCP without seagrass present -0.85 C mol m^{-2} yr^{-1}), as such the net carbon gain at the
428   community level for this *P. oceanica* meadow was less than the NAP produced annually by the
429   *P. oceanica* (NCP = 1.7 C mol m^{-2} yr^{-1}).

3.4   Influence of spatial dynamics on *P. oceanica* NAP

431   The *P. oceanica* NAP in summer is significantly different between the central areas of the meadow
432   and the meadow edge ($t_{(1,4)}$ = 3.7647, $P <$ 0.05). (Fig. 6). The *P. oceanica* NAP is highest in the
433   central areas of the meadow (NAP $\bar{x}$ =21.7, SD± 4.21 O_2 mmol m^{-2} d^{-1}) and approximately two-fold
434   that of the edge habitat (NAP $\bar{x}$ =10.9, SD± 3.03 O_2 mmol m^{-2} d^{-1}). The *P. oceanica* NAP increases
435   relative to the plant surface area of *P. oceanica* (LM: $F_{1,5}$= 132.5, $P <$ 0.01) (Fig. 6A). The plant
436   surface area was the best predictor of NAP and accounted for more than 96 % of the variation in
437   NAP. As standalone biometrics of seagrass meadow metabolism, shoot density (m^2), blade length
438   (cm) and seagrass cover (%), were all significant predictors of NAP (shoot density, LM: $F_{1,5}$= 21.13,
439   $P <$ 0.01; blade length, LM: $F_{1,5}$= 12.98, $P <$ 0.05; percentage cover, LM: $F_{1,5}$= 8.78, $P <$ 0.05) but
440   they only accounted for 81 %, 72 % and 64 % (Fig. 6B, C and D) of the variation in NAP of the
441   *P. oceanica*.

442   **3.5   Species specific productivity**

443   The seagrass benthic communities at 7m depth are all heterotrophic at the community level, ranging
444   from the least heterotrophic with *H. stipulacea* present (NCP $\bar{x}$ = -4.8, SD ± 4.7 O_2 mmol m^{-2} d^{-1}),
445   followed by the community with *P. oceanica* present (NCP $\bar{x}$ = -7.5, SD ± 8.9 O_2 mmol m^{-2} d^{-1}) and
446   finally the most heterotrophic the *C. nodosa* dominant community (NCP $\bar{x}$ = -10.5, SD ± 6.0 O_2
447   mmol m^{-2} d^{-1}) (Fig. 7A). The *H. stipulacea* NAP appears to be the highest comparatively and the only
448   seagrass species to on average maintain positive carbon balance (O_2 > 0). However, variation in NAP
449   for *H. stipulacea* (NAP $\bar{x}$ = 2.1, SD ± 4.7 O_2 mmol m^{-2} d^{-1}) and *P. oceanica* (NAP $\bar{x}$ = -3.6, SD ± 8.9
450   O_2 mmol m^{-2} d^{-1}) show both species fluctuate between positive and negative carbon balance within
451   this area of the bay in Summer (Fig. 7B). Whilst *C. nodosa* NAP is the lowest and consistently
452   negative (NAP $\bar{x}$ = -8.6, SD ± 6.0 O_2 mmol m^{-2} d^{-1}), however, there was no significant statistical
453   difference between species NAP (7B) ($F_{2,14}$ = 3.3806, P > 0.05).

454   The difference spatially in above ground vegetative material between species is demonstrated
455   through the increasing total plant surface between species from *H. stipulacea* ($\bar{x}$ = 5.1, SD ± 1.4 x10^{-3}
456   cm^2 m^{-2}), to *C. nodosa* ($\bar{x}$ = 10.6, SD ± 9.4 x10^{-3}cm^2 m^{-2}) and culminating in *P. oceanica* ($\bar{x}$ = 17.6,
457   SD ± 7.3 x10^{-3}cm^2 m^{-2}). However, the plant surface area is also more uniform for *H. stipulacea*
458   spatially across the habitat sampled, in comparison the plant surface area of both *C. nodosa* and *P.*
459   *oceanica* show higher variation between samples (Fig. 7C). Standardising the seagrass NAP for the
460   relative plant surface area within each sample, alters the relative differences between species NAP
461   (7B and D). The NAP standardised for plant surface area highlights a significant difference does
462   occur between species ($F_{2,14}$ = 4.1922, P < 0.05). Tukey post hoc comparisons show *C. nodosa* NAP
463   when standardised by plant surface area (NAP $\bar{x}$ = -0.0012, SD ± 0.0007 O_2 mmol cm^{-2} d^{-1}) to be
464   significantly lower than *H. stipulacea* (NAP $\bar{x}$ = 0.0004, SD ± 0.0011 O_2 mmol cm^{-2} d^{-1}) (Tukey: P <
465   0.05). But there was no significant difference between the native species *C. nodosa* and *P. oceanica*
466   NAP (NAP $\bar{x}$ = -0.0004, SD ± 0.0009 O_2 mmol cm^{-2} d^{-1}). There was also no significant difference
467   between *H. stipulacea* and *P. oceanica* NAP.

468   **4   Discussion**

469   **4.1   Seasonal *P. oceanica* NCP and NAP**

470   We found strong seasonality in *P. oceanica* productivity, at both the community (NCP Spring $\bar{x}$ =
471   8.3, SD ± 3.12; Autumn $\bar{x}$ = -2.0, SD ± 3.24 O_2 mmol m^{-2} d^{-1}) and plant level (NAP Summer $\bar{x}$ =
472   10.9, SD ± 3.03; Autumn $\bar{x}$ = 1.4, SD ± 3.24 O_2 mmol m^{-2} d^{-1}), which reinforces the need for seagrass
473   carbon sequestration studies to consider year-round dynamics, thereby ensuring carbon storage
474   estimates are not exaggerated by only reflecting summer peaks. Similar conclusions from studies of
475   net ecosystem productivity in freshwater lakes (Brentrup et al., 2020), and temperate saltmarshes
476   (Vazques Lule & Vargas 2021), suggest that this should now be the norm.

477   Multi-season approaches enable the assessment of seasonal drivers such as irradiance (Gazeau et al.,
478   2005; Champenois and Borges, 2012). During autumn, the overall irradiance reaching the plant is
479   lower as the daylight period is shorter, the likelihood of cloud cover increases, and increased
480   frequency of stormy conditions results in greater hydrodynamic activity reducing in-water visibility.
481   Subsequently autumnal photosynthetic activity occurs when conditions are light limiting, promoting
482   a greater variability in productivity. In contrast light saturating levels present throughout summer,
483   lead to a lower *P. oceanica* photosynthetic efficiency. Long-term exposure to saturating irradiance
484   decreases plant productivity and can lead to photoinhibition (Ralph and Burchett, 1995), though a
485   decline from photoinhibition is not considered in this study. The consecutive days of light saturating

486 irradiance which occur in summer represent an increasing likelihood that photoinhibition would
487 occur. However, shallow water *P. oceanica* have been demonstrated to adapt to high light conditions,
488 by specific photoacclimative and photoprotective responses; significant enrichment of up-regulated
489 transcripts associated with light-dependent reaction of photosynthesis (e.g., light-harvesting
490 proteins); and modifications in the structure of photosystems and tocopherol biosynthesis activation
491 in the summer (Dattolo et al., 2014). This is potentially why a strong negative photoinhibition
492 response was not observed in our seasonal metabolism measurements. The saturation response alone
493 has important considerations for modelling carbon sequestration capacity, re-emphasising the
494 importance of seasonality dependent on the concurrent irradiance levels. Physical disturbance to
495 seagrass meadows such as autumnal and winter storms will seasonally reduce the available
496 photosynthetically active plant material, i.e., as storms tear seagrass blades. Although we have
497 considered seasonal changes in seagrass metabolism and productivity, we have not directly measured
498 biomass export over winter, which can be vast enough seagrass exported onshore forms large
499 banquettes (Gomez-Pujol et al., 2013). This needs to be considered in future estimates.

500 Given *P. oceanica* meadows within the eastern region of the Aegean Sea have been noted to be
501 fragmented in response to elevated sea surface temperatures (Chefaoui et al., 2017), it is surprising
502 we found no statistically significant influence of temperature on the productivity of shallow water
503 *P. oceanica*. Other temperate seagrass species have been shown to transition to a negative carbon
504 balance when exposed to high Summer water temperatures (Marsh Jr. et al., 1986). Although our
505 highest average daily water temperature was above optimal thermal conditions (23.9 vs 17 - 20 ℃)
506 for *P. oceanica* (Champenois and Borges, 2018), this was well below *P. oceanica* critical
507 temperature limits (> 29 ℃). The *in-situ* nature of this study does not allow for the independent
508 control of water temperature or light intensity encountered at any time, and so they are often
509 correlated making it challenging to differentiate between them. Shallow water *P. oceanica* has a
510 greater tolerance to increased water temperatures than deeper *P. oceanica* (Marin-Guirao et al.,
511 2016). This heat acclimation in shallow *P. oceanica* emerges by stabilising respiration, thereby
512 establishing respiratory homeostasis (i.e., balanced photosynthetic carbon gains and respiratory
513 carbon losses; Marin-Guirao et al., 2016). This suggests that shallow *P. oceanica* may maintain net
514 productivity gains at higher water temperatures for longer periods. It is also possible that the
515 *P. oceanica* within the Eastern Mediterranean may have a greater acclimation to increased water
516 temperature, as the Eastern Mediterranean basin has been exposed to higher sea surface temperatures
517 for longer than the Western basin (since 1985) (Nykjaer, 2009). Ultimately any temperature effect on
518 *P. oceanica* metabolism in this study was confounded by the strong irradiance effect and thus could
519 not be disentangled.

520 **4.2   Annual *P. oceanica* NCP and NAP**

521 The annual net community productivity for *P. oceanica* meadows in our study was lower than
522 recorded for two *P. oceanica* meadows previously studied in the western region of the Aegean Sea,
523 even one negatively impacted by eutrophication (4.83 C mol m^{-2} yr^{-1}) (Apostolaki et al., 2010),
524 however this study used smaller chambers, which are more likely to cause oxygen saturation which
525 can overestimate productivity. The annual NCP in this study was conservative as it was obtained
526 from patchy *P. oceanica* edge habitat, this underestimates the meadows overall carbon sequestration
527 ability which consisted of both dense and patchy habitat. However, in shallow water meadows,
528 patchy edge habitat is a more prominent feature (Montefalcone et al., 2009), therefore it is an
529 appropriate conservative annual NCP estimate. Although we found meadow centre *P. oceanica*
530 productivity was two-fold that of the edge habitat, the overall meadow autochthonous carbon
531 sequestration potential lies between 1.7 - 3.4 C mol m^{-2} yr^{-2} which remains lower that other studies

532 have found. Despite a low annual NCP estimate our shallow water *P. oceanica* remained autotrophic
533 actively sequestering carbon, which if transitioned to an unvegetated state would result in it
534 becoming overall heterotrophic, a carbon source.

535 **4.3 Spatial dynamics of *P. oceanica* NAP**

536 Metabolism measurements are typically presented as an area-based unit (Apostolaki, et al., 2010;
537 Duarte et al., 2010; Olive et al., 2015). We have shown Net Apparent Productivity to be affected by
538 spatial variation in plant aboveground biomass, this would suggest that reported estimates may
539 benefit from additional information on canopy height and shoot density. Estimates should potentially
540 move away from denoting discrete areal measurements for meadows. Instead acquiring and mapping
541 large scale data on canopy height (shoot size) and shoot density to enable comprehensive habitat
542 wide autochthonous carbon sequestration estimates. Acquiring seagrass biometric data to support
543 productivity estimates requires greater effort than collating presence-absence or coverage data, but
544 simple plant biometrics of shoot density and leaf area index have been demonstrated as standalone
545 predictors of carbon sequestration and community composition (Samper-Villarreal et al., 2016;
546 Collier et al., 2021). High shoot density in shallow areas with a high degree of patchiness creates
547 very specific nest-like patterns, these have their highest shoot density in the centre and decrease in
548 density radially towards the edge of the patches (Zupo et al., 2005). Therefore, this distinction in
549 spatial productivity between edge and central areas of *P. oceanica* may be a specific characteristic to
550 consider for shallow meadows because overall shoot densities are highest in the shallow and decrease
551 with depth (Olesen et al., 2002; Zupo et al., 2005). More work would be needed to determine if the
552 same distinctions in shoot density and subsequent primary productivity exist between the edge and
553 central areas of *P. oceanica* meadows in deeper waters. The use of chambers with a larger benthic
554 surface area has a greater representation of community-scale metabolism, as trialled for heterogenic
555 coral reef habitats (Yates and Halley, 2003). The use of a larger benthic chamber for *P. oceanica*
556 metabolism measurements in this study (1m diameter) comprises community metabolism
557 measurements influenced by fine scale variation in shoot density, compared to previous studies using
558 smaller chambers (0.18m diameter), which house only a few shoots at similar densities within the
559 benthic chamber (Gazeau et al., 2005; Barron et al., 2006).

560 The carbon sequestration potential of seagrass meadows ultimately relates to how much of the
561 organic material produced by the seagrass, i.e. the productivity, accumulates as refractory material in
562 the seagrass meadow. Although the patchiness of shallow meadows may render them less effective at
563 attenuating currents and promoting settlement of organic and inorganic particles, they still actively
564 contribute to carbon acquisition within the carbon cycle. Given a total of 7139.92 km^2 of *P. oceanica*
565 is estimated to occur in the Eastern Mediterranean Basin (Telesca et al., 2015), and seagrass coverage
566 within Greek waters has been estimated at 2619 km^2 (Topouzelis et al., 2018), *P. oceanica* within
567 Greek waters represents around 36.7% of the total *P. oceanica* in the Eastern Mediterranean. The
568 quantity of *P. oceanica* habitat within the Aegean Sea and Eastern Mediterranean means it represents
569 a substantial blue carbon habitat irrespective of its fragmented nature (Chefoui et al., 2018). The
570 further loss of this habitat would risk climate current change targets therefore seagrass meadows need
571 distinct conservation management strategies given their proximity to current threats including
572 impacts from human infrastructure and coastal activities (Giakoumi et al., 2015).

573 **4.4 Species specific productivity**

574 We found *P. oceanica* meadow to be overall annually autotrophic, however *P. oceanica* at 7m depth
575 fluctuated between positive and negative carbon balance. Such heterogeneity over a small scale
576 within the same bay highlights that adjacent *P. oceanica* patches may simultaneously undergo growth

577   and loss. Given *P. oceanica* at 7m depth was particularly short (Plant surface area $\bar{x}$ = 17.6, SD $\pm$ 7.3
578   x10^{-3} cm^2 m^{-2}) relative to the other depths where the plant surface area was higher (Ranging from
579   37.6 – 293.0 x10^{-3} cm^2 m^{-2}) and given plant surface area acts as a predictor of productivity, lower
580   productivity is expected. It must also be considered that our results for this comparison are influenced
581   by differences in chamber area, volume, and incubation time.

582   Based on our productivity assessments alone, the non-native *H. stipulacea* was not competitive over
583   *P. oceanica*. This is akin to other studies which suggest a limited capacity to competitively displace
584   *P. oceanica* (Williams, 2007; Winters et al., 2020), although *H. stipulacea* can opportunistically
585   colonise space previously occupied by *P. oceanica*. With regression of *P. oceanica* meadows well
586   documented (Telesca et al., 2015), alongside *H. stipulacea* range expansion (Georgiou et al., 2016),
587   maintenance of Mediterranean seagrass meadow areal cover through replacement of current seagrass
588   species cover is likely. *H. stipulacea* productivity in this introduced range of the Mediterranean is
589   comparatively lower than its native range, given irradiance was the driving factor in *H. stipulacea*
590   productivity within its home range in the Gulf of Aquaba (Cardini et al. 2018). We found *H.*
591   *stipulacea* productivity to be comparable to patchy short *P. oceanica* (NAP $\bar{x}$ = 2.1, SD $\pm$ 4.7 vs -3.6,
592   SD $\pm$ 8.9 C mmol m^{-2} d^{-1}). The carbon sequestration capacity of *H. stipulacea* has been estimated to
593   be greater than *P. oceanica* in the Eastern Mediterranean (Wesselmann et al., 2021), but not greater
594   than *P. oceanica* carbon sequestration estimates in the Western Mediterranean (Mazarrasa et al.,
595   2017). Given its tropical origins, under future climate change predictions of a warming
596   Mediterranean *H. stipulacea* has potential to increase its productivity, whilst the same cannot be said
597   for *P. oceanica*.

598   Whilst *H. stipulacea* has persisted within the Mediterranean since 1984 and expanded its known
599   range (Fritsch, 1895; van der Velde and den Hartog, 1992; Gambi et al., 2009; Tsiamis et al., 2010;
600   Sghaier et al., 2011; Georgiou et al., 2016). *H. stipulacea* is known to disappear and recolonise as per
601   a metapopulation (Gambi et al., 2018), making the persistence of its sedimentary carbon stocks
602   questionable. While questions remain, it would appear the non-native *H. stipulacea* is already making
603   positive contributions to community blue carbon in the eastern Aegean.

604   The replacement of *P. oceanica* by *C. nodosa* is well documented (Montefalcone et al., 2006;
605   Montefalcone et al., 2007). This replacement is typically considered a result of *C. nodosa* being more
606   tolerant to varying environmental conditions. Compared against six dominant native Mediterranean
607   macrophytes *C. nodosa* presented the highest thermal optima (Savva et al., 2018). But the
608   substitution of *P. oceanica* for *C. nodosa* is not exclusive, replacement of *P. oceanica* dead matte to
609   algae dominated *Caulerpa spp.* habitats also occurs (Montefalcone et al., 2007). *C. nodosa* may not
610   always be the 'winner' following loss or fragmentation of *P. oceanica* meadows. We found when the
611   biomass of *H. stipulacea* and *C. nodosa* are comparable, *H. stipulacea* can hold a metabolic
612   advantage over *C. nodosa*. In the Southern Mediterranean replacement of *C. nodosa* by *H. stipulacea*
613   under warmer environmental conditions can occur (Sghaier et al., 2014). Very shallow water will be
614   readily heated by the sun, in the North Mediterranean this may provide warmer conditions closer to
615   the tropical native range of *H. stipulacea*. Within our study site, but at a shallower location (0.5m
616   depth), *H. stipulacea* was found mixed within dense *C. nodosa* beds and growing multiple paired
617   leaves off a vertical stem (Pers. obv., ANNEX 4). This is important given lateral growth is more
618   typical of this species (Posluszn and Tomlinson, 1990; Winters et al., 2020). Vertical growth would
619   give *H. stipulacea* the potential to increase its relative biomass and gain a competitive advantage over
620   *C. nodosa*. *C. nodosa* cover is predicted to reduce under future warming scenarios due to
621   environmental changes (circa -46.5%) (Chefaoui et al., 2018). As per the interactions with

622   *P oceanica*, a warming climate will lead to a faster and larger decline in *C. nodosa*, beyond the
623   current predictions that do not yet account for competition with *H. stipulacea*.

624   **4.5   Conclusions**

625   If natural ecosystems such as seagrass meadows are to play a part in mitigating increases in
626   anthropogenic CO_2 emissions spatio-temporal variability in primary productivity of seagrass
627   meadows needs to be accounted for. This study demonstrates that not all seagrass habitat is equal in
628   its potential to sequester autochthonous carbon, but the variability can in part be accounted for;
629   seasonally and spatially, using environmental predictors such as irradiance and plant biometrics such
630   as plant surface area. Alongside this the non-native *H. stipulacea* contributes to community Blue-
631   Carbon and has a metabolic advantage over *C. nodosa* under current conditions when both species
632   biomass are comparable. Under a warming Mediterranean this may promote direct competition
633   between the two species. Mediterranean seagrass meadow species composition, the condition of these
634   meadows and the potential interactions between seagrass species must be better understood for
635   accurate predictions of future seagrass community Blue Carbon productivity.

636   **5   Conflict of Interest**

637   The authors declare that the research was conducted in the absence of any commercial or financial
638   relationships that could be perceived as a potential conflict of interest.

639   **6   Author Contributions**

640   EW, TC, TW, CA, TT and AM contributed to the study conception and design. EW and CA led the
641   field-based studies, supported by TT and AM. TW led a preliminary pilot study integral to our final
642   experimental design. EW and TC led on data analysis and the manuscript first draft. All authors were
643   involved in the revision and final approval of this version of the manuscript.

644   **7   Funding**

648   **8   Acknowledgments**

654   **9   Supplementary Material**

655   The Supplementary Material are uploaded separately for submission.

656   **10   Data Availability Statement**

657   Datasets are available from the corresponding authors and will become available on the University of
658   Essex data repository.

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887 **12   Figure captions**

888 **Figure 1.** Large benthic chamber setup (**A**) Deployed in autumn over *P. oceanica* edge habitat (**B**)
889 Deployed in summer over dense central *P. oceanica* meadow. (**C**) Setup of the internal water pump
890 (foreground) within a benthic chamber over control unvegetated habitat. External submersible pump
891 battery pack in background. (**D**) Illustration of large benthic chamber set-up. Photographs © Emma A
892 Ward, Illustration © Tom Wade.

893 **Figure 2.** Small benthic chamber setup (**A**) Deployed over short patchy *P. oceanica* habitat (**B**)
894 Aerial view above patchy *P. oceanica* chambers deployed. Photographs; A and B © Jente van
895 Langerak.

896 **Figure 3.** (**A**) Net community productivity (NCP), (**B**) GPP:CR Ratio, (**C**) Gross primary
897 productivity (GPP) and (**D**) Community respiration (CR) for the *P. oceanica* meadow edge (grey)
898 and control chamber (White), autumn (November), spring (April) and summer (July). Error bars
899 represent standard deviation (autumn and spring n = 3, summer n = 4).

900 **Figure 4.** (**A**) The *P. oceanica* Net Apparent Productivity (NAP) given the season, (**B**) The
901 *P. oceanica* NAP when standardised by seagrass canopy height in the given season. Autumn and
902 spring n = 3, summer n = 4. Error bars represent standard deviation.

903 **Figure 5** (**A**) *P. oceanica* NAP (R^2 = 0.713) and (**B**) *P. oceanica* NAP standardised by canopy length
904 (R^2 = 0.711), as a function of PAR given as the Daily Light Integral. The irradiance compensation
905 point (I_C) was 4.6 mol photons $m^{-2} d^{-1}$. Replicate season denoted for visual reference autumn (●),
906 spring (●) and summer (●).

907 **Figure 6.** Net apparent productivity (NAP) of the *P. oceanica* in the central meadow (grey) and
908 meadow edge (Black) in relation to (**A**) *P. oceanica* blade surface area (**B**) *P. oceanica* shoot density
909 (m^{-2}) (**C**) *P. oceanica* blade length (cm) and (**D**) *P. oceanica* cover (%). Central meadow n = 3,
910 meadow edge n = 4. Significant linear regression from edge and central meadow combined * = $P <$
911 0.05, ** = $P < 0.01$. Grey bands reflect the 95% confidence level interval for predictions from a
912 linear model.

913 **Figure 7.** (**A**) Net community productivity (NCP), (**B**) Net apparent productivity (NAP), (**C**) Leaf
914 surface Area (**D**) NAP standardised by sampled plant surface area, for the three seagrass species
915 *H. stipulacea* (n = 6), *C. nodosa* (n = 5) and *P. oceanica* (n = 6). Error bars represent standard
916 deviation.