1 Reviews and Syntheses: Spatial and temporal patterns in seagrass

2 metabolic fluxes

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- 19 Abstract: Seagrass meadow metabolism has been measured for decades to gain insight into

20 ecosystem energy and biomass production and food web dynamics, and more recently, to inform

- 21 its potential in ameliorating ocean acidification (OA). This extensive body of literature can be
- 22 used to infer trends and drivers of seagrass meadow metabolism. Here, we synthesize the results
- 23 from 62 studies reporting *in situ* rates of seagrass gross primary productivity, respiration, and/or

24 net community productivity to highlight spatial and temporal variability in oxygen (O_2) fluxes. 25 We illustrate that daytime net community production (NCP) is positive overall, and similar 26 across seasons and geographies. Full-day NCP rates, which illustrate the potential cumulative 27 effect of seagrass beds on seawater biogeochemistry integrated over day and night, were also 28 positive overall, but were higher in summer months in both tropical and temperate ecosystems. 29 Although our analyses suggest seagrass meadows are generally autotrophic, the effects on 30 seawater oxygen are relatively small in magnitude. We also find positive correlations between 31 gross primary production and temperature, although this effect may vary between temperate and 32 tropical geographies and may change under future climate scenarios if seagrasses approach 33 thermal tolerance thresholds. In addition, we illustrate that periods when full-day NCP is highest 34 could be associated with lower nighttime O_2 and increased diurnal variability in seawater O_2 . 35 These results can serve as first order estimates of when and where OA amelioration by 36 seagrasses may be likely. However, improved understanding of variations in NCP_{DIC}:NCP₀₂ 37 ratios and increased work directly measuring metabolically-driven alterations in seawater pH 38 will further inform the potential for seagrass meadows to serve in this context.

39

40 **1 Introduction**

Seagrasses are productive marine macrophytes, lauded for numerous ecosystem functions
including habitat formation for diverse species assemblages, stabilization of marine sediments,
storm surge buffering, and many others. Seagrass meadow productivity has been studied for
decades, with community metabolism work published as early as 1956 (Odum, 1956).
Foundational work assessed the role of seagrass community metabolism in local food web
dynamics and ecosystem energy exchanges (e.g., Odum and Hoskin 1958, Murray and Wetzel,

47 1987). In recent decades, seagrass metabolism has been highlighted for its potential role in
48 reducing aqueous CO₂ concentrations thereby locally mitigating ocean acidification (OA) (e.g.,
49 Hendriks et al. 2014, Ricart et al. 2021) – an ecosystem function that has led to renewed interest
50 in metabolism research.

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52 At the global scale, seagrass meadows are considered net autotrophic (Duarte et al. 2010), 53 suggesting that gross primary production (GPP, defined here as the rate of oxygen production) 54 should exceed respiration (R, defined here as the rate of oxygen consumption, determined using 55 incubations or measurements in the dark) on average. Past research has suggested that net 56 autotrophic systems (or positive NCP, defined here as the GPP-R, when both photosynthesis and 57 respiration are accounted for) are likely to export biomass or energy (e.g., Duarte and Cebrián 58 1996), or may serve to mitigate OA through the resulting water chemistry modifications (e.g., 59 Unsworth et al. 2012, Ricart et al. 2021). However, periods of net autotrophy in seagrass 60 meadows can be intermittent or transient in time. In particular, metabolic variability can be 61 expected on several different temporal scales, resulting in subsequent variability in ambient 62 water chemistry including dissolved oxygen and carbonate chemistry parameters. First, daytime 63 and nighttime patterns in photosynthesis and respiration can cause substantial diurnal variability 64 on ambient seawater chemistry. Moreover, tidal cycles and local hydrodynamics may alter the 65 chemical impact of these processes on hourly timescales as well (Cyronak et al. 2018, Koweek et 66 al. 2018). Local hydrodynamics significantly influence the time that a water mass experiences 67 chemical alteration by a seagrass meadow, as well as the water depth through which light must 68 penetrate to reach the seagrass canopy and the volume of water that must be modified, and 69 therefore the magnitude of the change. On a longer timescale, seasonal patterns in temperature

70 and light can also cause substantial seasonal variability in the biomass and productivity of 71 submerged aquatic vegetation (Maher and Eyre 2011, Clavier et al. 2014, Ricart et al. 2021). 72 Spatial metabolic variation may also interact with temporal variation, further complicating 73 resulting meadow metabolism. For example, diurnal variability in O₂ fluxes and seawater 74 chemistry could be more pronounced in geographies that support higher daytime GPP and 75 nighttime R (Duarte et al. 2010). In addition, seasonal variability in NCP could be more 76 pronounced in locations where there are larger fluctuations in light and other environmental 77 drivers, such as high latitude or temperate ecosystems.

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79 Because local OA mitigation will depend on the community metabolism of the vegetation, 80 accounting for spatial and temporal variability in metabolism is especially important for 81 managers considering local OA mitigation strategies. Specifically, understanding whether GPP, 82 R, and NCP vary predictably across time and in different geographies can provide important, 83 first order information about when and where local OA mitigation approaches might be effective. 84 It can further inform whether potential OA mitigation aligns with windows of vulnerability for 85 sensitive living resources or how variability is integrated through time by important species. 86 Although potential local OA mitigation is caused by changes in the dissolved inorganic carbon 87 (DIC) in seawater, which can be influenced by several other important biological and physical 88 factors (Koweek et al. 2018, James et al. 2020), the relationship between O₂ fluxes associated 89 with seagrass metabolism and seawater DIC is roughly proportional (i.e., if O₂ production goes 90 up, DIC in seawater will go down). Variability in these proportions can be introduced by other 91 environmental processes such as calcification and aerobic metabolism (Barrón et al. 2006; Van 92 Dam et al. 2019). However, empirical studies of changes in seawater DIC are currently limited,

and the comprehensive literature on seagrass community metabolism on O₂ fluxes can provide
important spatial and temporal context for managers interested in seagrass metabolism and its
potential for local OA mitigation.

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97 Here, we synthesize published studies of seagrass metabolism to characterize the variability in 98 O₂ fluxes associated with GPP, R, and NCP across seasons and geographies. In recognition of 99 the substantial temporal diel variability in O₂ fluxes associated with daytime NCP and nighttime 100 respiration, as well as the uncertainty in our understanding of how this temporal variability 101 translates to pH variability and is integrated by vulnerable marine organisms associated with 102 seagrass beds, we focus on both hourly rates of NCP taken during peak daylight hours and full-103 day NCP. Hourly measurements of NCP collected during peak daylight hours can provide insight 104 into the maximum elevation of seawater O_2 . Similarly, hourly measurements of respiration 105 provide insight into the potential maximum depression of nighttime O_2 . In contrast, 106 measurements of NCP taken over longer time periods or that incorporate the full 24-hour cycle 107 (full-day NCP) provide insight into the cumulative effect of seagrass on seawater chemistry. In 108 particular, we tested: (1) If seasonal variability is present in daytime and full-day O₂ fluxes, (2) If 109 the temporal variation in O_2 fluxes varies among tropical and temperate geographies, and (3) 110 How much of the residual variation in O_2 fluxes not accounted for by seasons or geography can 111 be attributed to variation in temperature and aboveground biomass of the seagrass assemblage. 112

113 2 Methods

114 We conducted a literature search for *in situ* measurements of seagrass community metabolism

using the Web of Science. Search terms included [seagrass OR eelgrass OR submerged aquatic

116 vegetation] AND [metabol* OR carbon/oxygen fluxes OR community prod* community resp* 117 OR benthic incubation chambers OR primary prod* OR carbon* chemistry OR pH]. For each 118 paper, we then searched the literature cited for more applicable studies, as well as any papers 119 listed in the Web of Science that cited the study in question. In addition, we searched the datasets 120 used by Duarte et al. (2010) and Unsworth et al. (2012). Studies were included when O₂ fluxes of 121 a seagrass-associated community were measured in situ. While the study initially aimed to 122 include both O_2 and carbon fluxes, this analysis is limited to seagrass community metabolism 123 studies directly measuring O₂ due to the relative paucity of carbon flux studies and their 124 methodological differences. This included studies using a variety of methods, including 125 incubation chambers, eddy correlation techniques, mass balance estimates, and isotope 126 enrichment, among others. Studies were included that were published prior to January 1, 2020. 127

128 Within a single study, regardless of the methods used, each deployment/set of measurements was 129 included as a data point in the synthesis when deployments/measurements were repeated across 130 different locations, months, or species. We collected measurements of GPP, R or NCP from each 131 study using data reported in the text, tables, or graphs using software (Graph Click or Data 132 Thief), or provided by the authors by request. In addition, we recorded information other 133 metadata associated with the study (e.g., species, location, temperature, month the study was 134 conducted, etc.). We classified each study as either tropical or temperate based on the 135 designation in the primary study and then classified the metabolic measurements as either (a) 136 hourly rates or (b) daily rates. This classification was defined by the reporting within the studies 137 (i.e., the primary authors either reported hourly or daily rates), but the difference in reporting was 138 ostensibly due to differences in the length of the deployment used to measure metabolism (e.g.,

139<4 hour deployment = an hourly rate, ~12-24 hour deployment = a daily rate). The shorter</td>140"hourly" deployments were usually taken during peak daylight hours, which we used to infer the141potential for any daytime local O_2 elevation. In contrast, we use the daily rates to infer the142cumulative, full-day local O_2 fluxes – indicative of NCP. It is important to note that positive143daily NCP can still encompass marked diel or diurnal variability in O_2 fluxes and carbonate144chemistry. This variability could still prove deleterious to seagrass associated species during145transient periods of low O_2 or pH.

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147 Positive NCP values represent net autotrophy and O₂ fluxes to the water column from the 148 seagrass tissue, and negative NCP values represent net heterotrophy and O₂ fluxes from the 149 seagrass tissue to the water column. For chamber based-studies, incubation chambers were all 150 placed on the benthos (no mid-water column chambers) and had volumes ranging from 1.1 to 151 350 L. We interpret that these measurements captured seagrass community metabolism (benthos, 152 seagrass, and water column), and could be compared with other community based approached. 153 Nonetheless, we recognize variation could be introduced by methodological differences and 154 differences in chamber volume. To assess differences in estimates based on the methods used to 155 measure metabolism, we plotted the O_2 fluxes as a function of study type. Based on these plots 156 (Fig. S1), we decided to perform separate analyses for studies that used the "mass balance" 157 approach (Odum 1956) versus other methods (e.g., incubations, eddy correlations). The studies 158 using the mass balance approach may overrepresent water column productivity over benthic 159 productivity compared to other methods, and as such, displayed a much higher range and 160 magnitude of responses than those measured by other methods (see Methodological Analyses in 161 Results below).

163 To assess the drivers of variability in O₂ fluxes (hourly and daily rates of GPP, R and NCP), we 164 first assessed the collinearity in the primary drivers of interest: seawater temperature and 165 aboveground biomass for those studies reporting both variables. Because temperature and 166 above ground biomass are correlated (temperature \times geography: P = 0.011, Fig S2), we decided 167 to focus first on the effect of season, using *month* as a predictor variable, which ostensibly 168 encompasses some of the variability in both temperature and aboveground biomass (Figs S3 and 169 S4). Furthermore, the use of month as a predictor variable allowed us to include the maximum 170 number of studies in the analysis, since not all studies reported temperature and aboveground 171 biomass. To standardize months to seasons across the hemispheres, we used the numerical 172 notation for months in the northern hemisphere (i.e., January = 1, etc.). For the southern 173 hemisphere, we subtracted 6 from the numerical notation and used the absolute value. In 174 addition, we tested for differences between seagrass communities in temperate and tropical 175 geographies based on the hypothesis that seagrass meadows in temperate geographies have 176 greater seasonality in light, temperature, and aboveground biomass, and thus, should have a more 177 pronounced seasonal fluctuation (Fig S3 and S4).

178

We then tested for effects of temperature and aboveground biomass on the residual variation of the monthly models. Specifically, we first fit mixed-effects models of both hourly and daily rates of GPP, R, and NCP using maximum likelihood with *geography* as a categorical factor (tropical vs. temperate) and a linear and quadratic term for *month* as fixed effects, as well as the two-way interactions between *geography* and each term for *month*. We also included *replicate* nested in *study* as a random effect to account for non-independence arising from the inclusion of repeated

measures from the same sites over time and measurements from multiple sites within a singlestudy:

- 187 188

 $\begin{array}{l} metabolism \sim month \ + \ month^2 \ + \ geography \ + \ month \ \times \ geography \\ \ + \ month^2 \ \ \times \ geography \ + \ 1|study(replicate) \end{array}$

190	We then used backwards model selection to determine the significance of fixed effects based on
191	likelihood ratio tests. Final models were fit using restricted maximum likelihood to calculate
192	model estimates. We then performed two separate analyses using (1) environmental temperature
193	and (2) aboveground biomass to assess any remaining variability in the residuals from the
194	seasonal models. First, using just the subset of studies that either reported temperature or
195	biomass, we fit the final seasonal models again using restricted maximum likelihood to obtain
196	the conditioned residuals. Then, using these residuals, we fit linear models with geography as a
197	categorical factor, plus a linear term for either temperature or aboveground biomass as well as
198	the interaction between geography and temperature/biomass as fixed effects. We used
199	backwards model selection, comparing nested models with a series of ANOVAs. Finally, we
200	tested for net autotrophy (NCP>0) using a one-tailed t-test. All analyses were performed in R
201	(version 3.6.2) (R Core Team 2019) with the following packages as needed: nlme (version
202	3.1.145) (Pinheiro et al. 2020), broom (version 0.7.3) (Robinson et al. 2020), and broom.mixed
203	(version 0.2.6) (Bolker and Robinson 2020).
204	

- 205 **3 Results**
- 206 *3.1 Description of the database*
- 207 Using our search criteria, we identified 62 published papers (spanning 1956 to 2020) that
- 208 reported *in situ* rates of seagrass community metabolism (Table S1). The complete set of studies

209 spanned temperate and tropical ecosystems. The inclusion of 36 temperate studies and an 210 additional 15 tropical studies significantly expanded the scope of inference beyond previous 211 reviews (Duarte et al. 2010; Unsworth et al. 2012). Many studies occurred in the Western 212 Atlantic and Mediterranean (Fig. 1), and there were no studies from the North Pacific. Most 213 studies measured seagrass metabolism during the spring and summer months, while fewer 214 studies measured the metabolism in fall and winter conditions (Fig. 1). Environmental 215 temperature was highest during late summer/early fall months and was higher overall in tropical 216 biomes (Fig S3). Aboveground biomass was highest during summer months and higher in the 217 temperate geographies (Fig S4).





Sampling Season

- ⊖ Winter
- C Spring
- Summer
- 🔘 🖓 Fall
- Multiple Seasons





226 3.2 Methodological analyses

227 Our results illustrate greater variability in the ranges of response observed using the "mass 228 balance" method, which extend in magnitude beyond those observed using other methods for 229 measuring both GPP and R (Fig. S1 a-f). This greater variability does not appear to be driven by 230 timing of the measurements as the "mass balance" method produced metabolic measurements of 231 higher variability or magnitude across seasons (Fig S1 g-l). Measurements taken using 232 incubations, eddy correlation methods, and water column measurements of pH using in situ 233 sensors and an acoustic doppler velocimeter (or other instrument capable of measuring flow) are 234 generally of similar magnitude and variation.

235

236 *3.3 Spatial and temporal patterns in oxygen fluxes*

237 3.3.1. Daytime oxygen fluxes

238 Measurements of hourly O₂ fluxes (N=83 for NCP), typically obtained from shorter duration 239 deployments conducted during peak sunlight hours, reveal differences in seasonal patterns of 240 GPP and respiration. Both GPP and R peak during summer months across both ecosystems (Fig. 241 2a-b). Despite higher biomass in temperate systems during summer months (Fig S4), we do not 242 detect a statistical difference in the seasonal patterns among GPP in temperate and tropical 243 ecosystems (Table 1). This result is highly influenced by two studies in tropical geographies 244 (Morgan and Kitting 1984, Herbert and Fourgurean 2008); when these studies are not included, 245 summertime GPP is higher in temperate geographies than in tropical geographies (Fig S5). 246 Similarly, R peaks in summer months in both temperate and tropical ecosystems, and we detect a 247 sharper increase and a higher seasonal peak in R in temperate ecosystems (Fig 2b; Table 1). The 248 seasonal peaks in GPP and R effectively cancel each other out, resulting in no statistically

detectable difference in hourly NCP rates across seasons (Fig 2c). Although the net hourly O_2 flux associated with NCP does not vary seasonally, the mean net hourly O_2 flux from the seagrass to the seawater is positive (mean hourly NCP = 5.48 +/- 5.87 SD mmol O_2/m^2 /hour), indicating a net production of O_2 during peak daylight hours regardless of geography (one-tailed t-test: $t_{82} = 8.50$, P<0.001). Ninety-two percent of the 83 measurements were net autotrophic.



Figure 2. Hourly rates for O₂ fluxes (mmol⁻¹m²⁻¹hour⁻¹) associated with seagrass communities as a function of time, with GPP measurements taken during peak sunlight hours (~ 10 am to 2) pm local time). Studies performed in temperate versus tropical ecosystems are illustrated by color (blue = temperate, red = tropical), and significance (p < 0.05) is denoted by a fit line with a quadratic term and 95% CI. The colors of the lines denote significant differences between tropical and temperate systems in GPP and R, while a black line denotes a significant relationship but no difference between temperate and tropical geographies.

Table 1. Statistics for linear mixed effects models of hourly rates of O₂ fluxes. Terms in grey

were removed from the final model using backward model selection.

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	Outliers				
Response	removed	Fixed effect	df	L-ratio	p-value
GPP (mmol O ₂ /m ² /hr)	0	month			
		month ²	5	6.48809	0.01086
		geography	6	0.28685	0.59224
		month \times geography	8	0.29199	0.58895
		$month^2 \times geography$	7	0.02472	0.87501
	4	month			
		month ²	7	13.6797	0.00022
		geography			
		month × geography	8	4.30634	0.03797
		$month^2 \times geography$	8	3.32282	0.06832
R (mmol O ₂ /m²/hr)	0	month			
		month ²			
		geography			
		month × geography	8	5.11054	0.02378
		month ² × geography	8	4.85086	0.02763
	1	month			
		month ²			
		geography			
		month × geography	8	8.37289	0.00381
		month ² × geography	8	7.93239	0.00486
NCP (mmol O ₂ /m ² /hr)	0	month	4	0.02961	0.86337
		month ²	5	2.52439	0.1121
		geography	6	0.09330	0.76002
		month × geography	7	3.42526	0.06421
		month ² × geography	8	1.12950	0.28788

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277 3.3.2 Full-day oxygen fluxes

278 We found 164 measurements/deployments that reported full-day NCP using methods that span a

279 wider range of photoperiods and environmental conditions, and thus provide insight into the

280 potential for full-day net metabolic status, and possible local OA mitigation potential. Based on

281 the accompanying daily rates of GPP and R, there is evidence of a seasonal cycle in O₂ fluxes to 282 and from the water column associated with seagrass metabolism (Fig. 3a-b). The seasonal 283 fluctuation differed statistically between temperate and tropical geographies, with a sharper slope 284 in the seasonal fluctuation among the tropical studies (Fig 2a). We did not detect a difference in 285 R between geographies. In general, the seasonal fluctuation in GPP exceeds the seasonal 286 fluctuation in respiration in both geographies, resulting in higher daily net O₂ flux from the 287 seawater to the seagrass associated with NCP in summer months (Fig. 3c). The seasonal 288 fluctuation in NCP was greater among the tropical studies than the temperate studies (Table 2). 289 The mean NCP for tropical geographies was 62.5 (+/- 62.4 SD) mmol $O_2/m^2/day$, with 84% of 290 the 77 total reported measurements being autotrophic. The mean NCP for temperate geographies was 29.0 (+/- 79.1) mmol $O_2/m^2/day$, with 68% of the 187 total reported measurements being 291 292 autotrophic. Overall, the seagrass meadows in both geographies were net autotrophic (one-tailed 293 *t-test:* tropical t_{76} =8.78, P<0.001; temperate t_{186} = 5.02, P<0.001). Despite these overall trends, 294 there are several individual studies that reported net heterotrophy and net O₂ fluxes from the 295 water column, even during summer months.



Figure 3. Daily rates for O_2 fluxes (mmol⁻¹m²⁻¹day⁻¹) associated with seagrass communities as a function of time. Studies performed in temperate versus tropical ecosystems are illustrated by color (blue = temperate, red = tropical), and significance (p<0.05) is denoted by a fit line with a

300 quadratic term and 95% CI. The colors of the lines denote significant differences between

301 tropical and temperate systems.

- **Table 2.** Statistics for linear mixed effects models of daily rates of O₂ fluxes. Terms in grey were
- 305 removed from the final model using backward model selection.

	Response	Fixed effect	df	L-ratio	p-value
	GPP (mmol O2/m2/day)	month			
		month ²	7	54.8757	<0.0001
		geography			
		month × geography	7	4.27394	0.03870
		month ² × geography	8	0.06117	0.80465
	R (mmol O ₂ /m²/day)	month			
		month ²	5	40.7951	<0.0001
		geography	6	2.70137	0.10026
		month × geography	7	2.21684	0.13651
		month ² × geography	8	2.09202	0.14807
	NCP (mmol O ₂ /m ² /day)	month			
		month ²			
		geography			
		month × geography	8	7.81735	0.00517
207		month ² × geography	8	6.7597	0.00932
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3.4 Drivers of chemical variability

318	Within seasons, there is still marked variation in GPP and respiration (Fig. 2-3). Using the subset
319	of studies that report environmental temperature ($N = 28$), we found that temperature did not
320	explain the residual variability in any metric besides hourly GPP (Fig. 4; Table 3), suggesting the
321	seasonal models may generally account for hypothesized temperature effects. As noted,
322	temperature explained some of the residual variability from the seasonal models of hourly GPP,
323	with the effect differing among tropical and temperate geographies (Fig S6; Hourly GPP
324	<i>Geography x Temperature</i> : $F_{42} = 8.67$, P = 0.005). Among studies reporting aboveground
325	biomass (N=23), biomass explains some of the residual variability in daily NCP, although the
326	effect depends on geography as well (Fig 5; Table 3). Aboveground biomass also explains some
327	of the residual variability in the seasonal models of hourly GPP, respiration, and NCP, and the
328	effect of biomass on hourly GPP also depended on the geography (Fig. S7; Table 3).



Figure 4. Conditioned residuals of the daily rates of O_2 fluxes (mmol⁻¹m²⁻¹day⁻¹) from a seasonal model as a function of temperature. Studies performed in temperate versus tropical ecosystems are illustrated by color (blue = temperate, red = tropical). None of the relationships are statistically significant.



Figure 5. Conditioned residuals of the daily rates for seagrass O_2 fluxes (mmol⁻¹m²⁻¹day⁻¹) from a seasonal model as a function of aboveground biomass measured in the field during metabolism measurements. Studies performed in temperate versus tropical ecosystems are illustrated by color (blue = temperate, red = tropical). Significance is denoted by a fit line and 95% CI.

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- 342

343 Table 3. Statistics for mixed effects models of the residuals of the hourly metabolic rates as a

344 function of biomass or temperature and geography and the interactions.

Response	Fixed effect	df _{res}	SS _{res}	SS	F	p-value
GPP (mmol O ₂ /m ² /hr)	biomass					
	geography					
	biomass × geography	33	3122.0	-1157.5	18.855	0.0001
R (mmol O ₂ /m²/hr)	biomass	31	176.06	-13.997	2.5910	0.1179
	geography	30	162.06	-6.6773	1.2462	0.2734
	biomass × geography	29	155.39	-1.5157	0.2758	0.6036
NCP (mmol O ₂ /m ² /hr)	biomass	38	1616.5	-159.55	4.0517	0.0514
	geography	39	1822.5	-206.00	4.8425	0.0339
	biomass × geography	37	1457.0	-110.28	2.9480	0.0945
GPP (mmol O ₂ /m ² /hr)	temp					
	geography					
	temp × geography	42	398.71	-69.600	8.6708	0.0053
R (mmol O ₂ /m ² /hr)	temp	61	240.03	-1.0118	0.2540	0.6161
	geography	60	239.02	-0.1130	-0.0279	0.8679
	temp × geography	59	238.91	-0.0020	0.0005	0.9826
NCP (mmol O ₂ /m ² /hr)	temp	46	1453.0	-41.82	1.334	0.254
	geography	47	2141.0	-688.0	21.78	<0.0001
	temp × geography	45	1416.1	-13.603	0.4268	0.5170

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346

347 4 Discussion

348 4.1 Spatial and temporal variability in seagrass metabolism

349 Here, we report that the NCP of seagrass beds during daylight hours is positive and similar

across seasons and geographies (Fig 2C). This is ostensibly due to GPP generally exceeding R

- during daylight and the seasonal fluctuations in hourly rates of GPP and R balancing each other
- 352 out. Our results suggest that metabolically driven alterations in seawater chemistry during
- 353 daylight hours is similar across time and ecosystems, but small in magnitude.

355 We also demonstrate that seagrass beds are generally net autotrophic over the length of the day 356 (based on daily NCP), and the magnitude of this full-day NCP is more pronounced during 357 summer months and in tropical geographies (Fig 3C). However, underlying the summertime 358 peak in full-day NCP is the potential for marked diurnal variability in O_2 . In particular, the 359 demonstrated summertime peak in hourly respiration rates could drive more pronounced 360 nighttime lows in O_2 during the most pronounced windows for net autotrophy (i.e., summer 361 months with the highest daily NCP). However, diurnal fluctuations in seawater chemistry 362 associated with seagrass metabolism will also be influenced by hydrodynamics that are not 363 captured in our synthesis (Koweek et al. 2018), and recent field studies of estuarine eelgrass by 364 Ricart et al. (2021) demonstrated that sustained elevations in pH associated with seagrass 365 meadows were not restricted to daylight hours.

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367 Given the positive correlations between GPP and temperature, we assume that most of these 368 measurements were taken when the environmental temperatures were not physiologically 369 stressful to the seagrass community. Thus, the positive relationship between environmental 370 temperature and GPP should not necessarily be viewed through the lens of temperature 371 exposures associated with future warming driven by climate change. Continued warming 372 associated with climate change could cause photosynthesis and respiration to decline at stressful 373 temperatures. The probability that the relationship between temperature and metabolic responses 374 will change with future warming is likely to differ geographically based on how close a 375 community is to its thermal limit and the scope for acclimation or adaptation. This may partially 376 explain the differences in the relationships between temperature and the residuals of the seasonal

377 model between geographies, with increasing temperature negatively related to the residuals from 378 tropical geographies and positively related to the residuals from temperate geographies. Many 379 tropical seagrass species are growing close to their photosynthetic and physiological optima (Lee 380 et al. 2007, Koch et al. 2012), and elevated temperatures in these geographies may be 381 detrimental, causing metabolism (in this case hourly GPP) to be less than expected based on 382 seasonal patterns. In contrast, the positive relationship between the residuals from the seasonal 383 model and temperature in temperate geographies indicate that there may be a stimulatory effect 384 before a thermal tolerance threshold is crossed and metabolism decreases.

385

386 The significant relationships between above ground biomass and the residual variation in hourly 387 GPP and NCP indicate that aboveground biomass also plays an important role in O₂ fluxes 388 beyond that which is already captured by any seasonal fluctuations in biomass. Although the 389 relationships between aboveground biomass and the residual variation in hourly GPP are 390 generally what would be expected (higher biomass = higher metabolic rates than expected based 391 on the seasonal model), the negative relationship between aboveground biomass and the residual 392 variation in hourly NCP is somewhat surprising. This relationship suggests that 393 deployments/measurements in seagrass beds with higher aboveground biomass generally had 394 lower hourly NCP than what is predicted by the seasonal model. This negative relationship may 395 be explained by self-shading in dense meadows, or it could be due to other organisms that 396 contribute to daytime respiration (e.g., heterotrophs) that are associated with the higher biomass 397 meadows due to its structural complexity or other habitat features, but are not accounted for in 398 the aboveground biomass measurements. Dedicated experiments may be able to determine the 399 mechanism for these findings; however, the positive relationships between aboveground biomass and the residual variation in daily NCP suggests that, overall, higher aboveground biomassgenerally increases production relative to respiration.

402

403 *4.2 Implications for local OA mitigation and management*

404 If O₂ fluxes translate proportionally to community drawdown of CO₂, our results can yield 405 insights regarding local OA mitigation potential. Specifically, as with oxygen production, 406 maximum pH elevations likely also occur during daylight hours and are similar across time and 407 ecosystems, but small in magnitude. OA mitigation potential may be similarly influenced by the 408 factors identified by model outputs, including biomass, geography, and temperature. However, 409 we recognize that additional sources of variability may alter the ratio of NCP based on carbon 410 fixed and oxygen evolved, making conclusions regarding OA mitigation potential from oxygen 411 metabolism difficult. Although the ratio between O₂ produced and carbon fixed by an individual 412 seagrass is generally assumed to be balanced (i.e., 1:1), the other processes that occur in a 413 seagrass meadow, including respiration from organisms living within the seagrass and carbonate 414 production and dissolution, also influence the dissolved inorganic carbon (DIC) concentration in 415 the seawater. Current empirical measurements of NCP_{DIC}:NCP_{O2} in seagrass meadows range 416 from 0.3 to 6.8 (Ziegler and Benner 1998, Barrón et al. 2006), suggesting the effect of seagrass 417 NCP on seawater pH could be substantially more or less pronounced than illustrated here. 418 Because of this variability in the relationship between O₂ and DIC, care must be taken when 419 drawing OA mitigation conclusions from these data. A better understanding of the 420 NCP_{DIC}:NCP_{O2} in particular meadows will better inform how the demonstrated seasonal 421 variability and the potential diurnal variability in oxygen translates to carbonate chemistry 422 variability and potential for OA mitigation. It will be additionally important to understand how

this variability is integrated over time by organisms, especially under conditions projected for
coastal habitats in the future. Finally, the utility of seagrass as a climate mitigation tool will
depend on the goal of the management, and in most cases, will require more research. For
example, if the goal of management is to prevent negative effects of ocean acidification on oyster
growth, then studies that quantify the sensitivity of oyster growth to the variability in pH
observed here are still required.

429

430 5 Conclusions

431 Few conservation or restoration efforts currently take into account the potential chemical 432 ecosystem services of seagrasses and other submerged aquatic vegetation. Here, we demonstrate 433 that daytime O_2 fluxes associated with seagrass metabolism are likely to be similar across 434 seasons and geography, while the full-day O_2 fluxes peak during summer months in both tropical 435 and temperate geographies. Integrating across seasons, seagrass meadows are net autotrophic. 436 However, our simplified model results suggest the daytime O₂ fluxes reported across the global 437 ocean may translate to small changes in surrounding seawater chemistry. These seasonal patterns 438 largely capture the present-day effects of variability in temperature and aboveground biomass on 439 seagrass metabolism, but likely do not adequately model the effects of future warming as it 440 becomes physiologically stressful.

441

These results highlight challenges, as well as gaps in our understanding, that may be relevant to the use of seagrasses for sustained local OA mitigation and need to be addressed by the scientific community. In particular, we demonstrate that while peak daytime O₂ fluxes are similar across seasons and geographies, nighttime respiration is highest during summer months. Thus, although

446 seagrass beds are generally net autotrophic, nighttime respiration could reduce seawater O_2 447 during periods of greatest autotrophy. This work also elucidated that certain geographies, such as 448 the North Pacific, are currently underrepresented in our dataset. Thus, continued study of 449 seagrass metabolism and its effects on seawater carbonate chemistry are needed to expand our area of inference. In addition, studies are needed to constrain the relationship between dissolved 450 451 oxygen fluxes and DIC, and this relationship may be important to elucidate at local scales to 452 truly understand the potential for OA mitigation at a given location. Finally, more information is 453 needed to understand how vulnerable organisms respond to the chemical variability highlighted 454 in our study (Gimenez et al. 2018, Lowe et al. 2018), and in particular, how this variability is 455 integrated through time. Despite the considerations of geographic and temporal variability in O₂ 456 fluxes illustrated here, we recognize that seagrass conservation and restoration may be important 457 strategies for climate adaptation for numerous other reasons, including carbon sequestration and 458 habitat provisioning.

459

460 **6 Code Availability:** Code is available at

461 <u>https://github.com/tyekindinger/SeagrassCommunityMetabolism</u>

462

7 Data Availability: All data used in this analysis is publicly available via the published studies.

465 8 Author Contributions: Ward: investigation, writing – review & editing; Kroeker:

466 conceptualization, funding acquisition, investigation, methodology, writing – original draft

467 preparation; Kindinger: formal analysis, visualization, writing – review & editing; Hirsh:

468 investigation, visualization, writing – review & editing; Hill: conceptualization, funding

469	acquisition, writing – review & editing; Jellison, Koweek, Lummis, Rivest, Waldbusser:
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472	
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474	
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