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Biogeosciences
Discussions

Reviews and Syntheses: Spatial and temporal patterns in metabolic fluxes inform potential for seagrass to locally mitigate ocean acidification

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Abstract: As global change continues to progress, there is a growing interest in assessing any local levers that could be used to manage the social and ecological impacts of rising CO_2 concentrations. While habitat conservation and restoration have been widely recognized for their role in carbon storage and sequestration at a global scale, the potential for managers to use vegetated habitats to mitigate CO_2 concentrations at local scales in marine ecosystems facing the accelerating threat of ocean acidification (OA) has only recently garnered attention. Early studies have shown that submerged aquatic vegetation, such as seagrass beds, can locally draw down CO_2 and raise seawater pH in the water column through photosynthesis, but empirical studies of local OA mitigation are still quite limited. Here, we leverage the extensive body of literature on seagrass community metabolism to highlight key considerations for local OA management through seagrass conservation or restoration. In particular, we synthesize the results from 62 studies reporting *in situ* rates of seagrass gross primary productivity, respiration, and/or net community productivity to highlight spatial and temporal variability in carbon fluxes. We illustrate that daytime net community production is positive overall, and similar across seasons and geographies. Full-day net community production rates, which illustrate the potential cumulative effect of seagrass beds on seawater biogeochemistry integrated over day and night, were also positive overall, but were higher in summer months in both tropical and temperate ecosystems. Although our analyses suggest seagrass meadows are generally autotrophic, the modeled effects on seawater pH are relatively small in magnitude. In addition, we illustrate that periods when full-day net community production is highest could be associated with lower nighttime pH and increased diurnal variability in seawater pCO_2/pH. Finally, we highlight important areas for future research to inform the next steps for assessing the utility of this approach for management.

1 Introduction

As carbon dioxide (CO_2) emissions continue to rise, there is an intense interest among managers and decision makers in developing local strategies to minimize the social and ecological costs of global change. While habitat restoration or conservation has been recognized for its utility in carbon storage and sequestration at a global scale in both terrestrial and aquatic systems (Canadell and Raupach 2008, Duarte et al. 2010, Agrawal et al. 2011, Mcleod et al. 2011, Nahlik and Fennessy 2016), the potential for using vegetated habitat to mitigate CO_2 concentrations in the surrounding environment at very local scales has received far less attention. In marine ecosystems, however, increasing CO_2 concentrations cause ocean acidification (OA), which poses a threat to species and ecosystems worldwide (Kroeker et al. 2010; 2013). Submerged aquatic vegetation can reduce CO_2 concentrations in the water column through photosynthesis at a local scale (hereafter termed *local OA mitigation*) (Hendriks et al. 2014). Thus, conservation, restoration, and purposeful culturing of submerged aquatic vegetation have emerged as some of the few potential strategies for local OA mitigation for managers, providing possible benefits to other vulnerable species associated with these habitats (Washington State Blue Ribbon Panel on Ocean Acidification 2012, Chan et al. 2016, Nielsen et al. 2018).

Because both carbon sequestration and local OA mitigation will depend on the productivity of the vegetation, temporal variability in productivity may be especially important for managers considering local OA mitigation strategies. Carbon storage and sequestration in marine ecosystems is largely considered to be a cumulative process, whereas photosynthesis-based, local OA mitigation in the water column will necessarily be more intermittent or transient in time. In particular, variability in potential local OA mitigation can be expected on several different temporal scales. First, daytime and nighttime patterns in photosynthesis and respiration can cause substantial diurnal variability in seawater pH and saturation state (Hendriks et al. 2014, Pacella et al. 2018), such that potential local OA mitigation will vary on hourly timescales with daylight. Moreover, tidal cycles and local hydrodynamics may alter the impact these processes have on ambient water chemistry on hourly timescales as well (Cyronak et al. 2018, Koweek et al. 2018). Local hydrodynamics could significantly influence the time that a water mass experiences chemical alteration by a seagrass meadow, as well as the water depth through which light must penetrate to reach the seagrass canopy and the volume of water that must be modified, and therefore the magnitude of the change. On a longer timescale, seasonal patterns in temperature and light can also cause substantial seasonal variability in the biomass and productivity of submerged aquatic vegetation (Maher and Eyre 2011, Clavier et al. 2014, Ricart et al. 2021). Thus, the degree of any potential local OA mitigation may vary on seasonal or monthly timescales as well (Manzello et al. 2011, Unsworth et al. 2012, Cryonak et al. 2018, Saderne et al. 2019). This potential for temporal variability in photosynthesis-based, local OA mitigation has important implications for how the strategy might be used by managers, particularly with respect to whether potential OA mitigation aligns with windows of vulnerability for sensitive living resources or how variability is integrated through time by important species.

Seagrasses are productive marine macrophytes that are considered net autotrophic at the global scale (Duarte et al. 2010), suggesting that gross primary production (GPP, defined here as the rate of oxygen production) should exceed respiration (R, defined here as the rate of oxygen consumption, determined using incubations or measurements in the dark) on average. Assessing the utility of seagrass meadows for local OA mitigation, however, requires a better understanding of the spatial and temporal variability in GPP, R, and net community production (NCP, defined here as the GPP-R, or the net carbon flux, when both photosynthesis and respiration are accounted for). For example, diurnal variability in seawater carbonate chemistry could be more pronounced in geographies that support higher daytime GPP and nighttime R (Duarte et al. 2010). In addition, seasonal variability in NCP could be more pronounced in locations where there are larger fluctuations in light and other environmental drivers, such as high latitude or temperate ecosystems.

Scientists have been quantifying NCP in seagrass meadows for decades (Odum 1956), and insight regarding the potential for temporal and spatial variability in carbon fluxes can be gained using this literature. In particular, understanding whether GPP, R, and NCP vary predictably across time and in different geographies can provide important, first order information about when and where local OA mitigation approaches might be effective, as well as insight into challenges that could arise in particular localities. Although potential local OA mitigation is caused by changes in the dissolved inorganic carbon (DIC) in seawater, which can be influenced by several other important biological and physical factors (Koweek et al. 2018, James et al. 2020), the relationship between O_2 fluxes associated with seagrass metabolism and seawater DIC is roughly proportional (i.e., if O_2 production goes up, DIC in seawater will go down). While empirical studies of changes in seawater DIC are currently limited, the comprehensive literature on seagrass community metabolism on O_2 fluxes can provide important spatial and temporal context for managers interested in carbon fluxes and the potential for local OA mitigation.

Here, we synthesize published studies of seagrass metabolism to characterize the variability in carbon fluxes associated with GPP, R, and NCP across seasons and geographies. In recognition of the substantial temporal diel variability in carbon fluxes associated with daytime NCP and nighttime respiration, as well as the uncertainty in our understanding of how this temporal variability is integrated by vulnerable marine organisms associated with seagrass beds, we focus on both hourly rates of NCP taken during peak daylight hours and full-day NCP. Hourly measurements of NCP collected during peak daylight hours can provide insight into the maximum elevation of seawater pH. Similarly, hourly measurements of respiration provide insight into the potential maximum depression of nighttime pH. In contrast, measurements of NCP taken over longer time periods or that incorporate the full 24 hour cycle (full-day NCP) provide insight into the cumulative effect of seagrass on seawater chemistry. In particular, we tested: (1) If seasonal variability is present in daytime and full-day carbon fluxes, (2) If the temporal variation in carbon fluxes varies among tropical and temperate geographies, and (3) How much of the residual variation in carbon fluxes not accounted for by seasons or geography can be attributed to variation in temperature and aboveground biomass of the seagrass assemblage. To connect the metabolic measurements to seawater chemistry, we model potential changes in bulk seawater pH based on the estimated carbon fluxes given variation in seawater residence time and water depth.

2 Methods

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 vegetation]* AND [*metabol** OR *carbon/oxygen fluxes* OR *community prod* community resp** OR *benthic incubation chambers* OR *primary prod** OR *carbon* chemistry* OR *pH]*. For each paper, we then searched the literature cited for more applicable studies, as well as any papers listed in the Web of Science that cited the study in question. In addition, we searched the datasets used by Duarte et al. (2010) and Unsworth et al. (2012). Studies were included when either O_2 or carbon fluxes of a seagrass-associated community were measured *in situ.* This included studies using a variety of methods, including incubation chambers, eddy correlation techniques, mass balance estimates, and isotope enrichment, among others. Studies were included that were published prior to January 1, 2020.

Within a single study, regardless of the methods used, each deployment/set of measurements was included as a data point in the synthesis when deployments/measurements were repeated across different locations, months, or species. We collected measurements of GPP, R or NCP from each study using data reported in the text, tables, or graphs using software (Graph Click or Data Thief), or provided by the authors by request. In addition, we recorded information on the photosynthetic quotient (PQ) and respiratory quotient (RQ) values used to convert from O_2 to carbon, as well as other metadata associated with the study (e.g., species, location, temperature, month the study was conducted, etc.). We classified each study as either tropical or temperate based on the designation in the primary study and then classified the metabolic measurements as either (a) hourly rates or (b) daily rates. This classification was defined by the reporting within the studies (i.e., the primary authors either reported hourly or daily rates), but the difference in

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reporting was ostensibly due to differences in the length of the deployment used to measure metabolism (e.g., <4 hour deployment = an hourly rate, ~12-24 hour deployment = a daily rate). The shorter "hourly" deployments were usually taken during peak daylight hours, which we used to infer the potential for any daytime local OA mitigation. In contrast, we use the daily rates to infer the cumulative, full-day local OA mitigation potential of seagrass. It is important to note that positive daily NCP (used to infer the full-day local OA mitigation potential) can still encompass marked diel or diurnal variability in carbon fluxes that could prove deleterious to seagrass associated species during transient periods of low pH.

Although no studies included here measured changes in seawater DIC directly, several studies (N = 17) converted metabolism measurements based on oxygen consumption and production to units of carbon. For studies that only reported metabolism in units of oxygen, we converted the reported GPP, R, and NCP measurements to carbon using a PQ or RQ of 1 (Duarte et al. 2010). We then converted all measurements to the same scale: either *mmol* $C/m^2/hour$ or *mmol* $C/m^2/day$. Positive NCP values represent net autotrophy and carbon fluxes *from* the water column *to* the seagrass tissue, and negative NCP values represent net heterotrophy and carbon fluxes *from* the seagrass tissue *to* the water column.

To assess differences in estimates based on the methods used to measure metabolism, we plotted the carbon fluxes as a function of study type. Based on these plots (Fig. S1), we decided to perform separate analyses for studies that used the "mass balance" approach (Odum 1956) versus other methods (e.g., incubations, eddy correlations). The studies using the mass balance approach often do not differentiate between water column and benthic productivity, and as such, displayed a much higher range and magnitude of responses than those measured by other methods (see *Methodological Analyses* in *Results* below).

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

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 single study:

$$\text{metabolism} \sim \text{month} + \text{month}^2 + \text{geography} + \text{month} \times \text{geography} + \text{month}^2 \times \text{geography} + 1|\text{study}(\text{replicate})$$

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

To illustrate how water depth and residence time may mediate the effects of the carbon fluxes associated with seagrass communities on bulk seawater pH for potential local OA mitigation, we applied the range of hourly net carbon fluxes (NCP) covered in our synthesis to a simplified, steady state box model developed by Koweek et al. (2018). We use the hourly rate rather than the full-day rate because we recognize that the effects of seagrass on seawater carbonate chemistry will be intermittent and fluctuate over the daylight hours. We modeled the change in dissolved inorganic carbon as a function of NCP as

$$\Delta DIC = \frac{L}{\bar{u}\rho h} \times \mathrm{NCP}$$

where L = the box length (m), $\bar{u}$ = mean water velocity (m s^{-1}), ρ = is the seawater density (kg m^3), and h = water depth (m),. Because of the familiarity among managers and decision makers with seawater pH, we then converted the delta DIC to pH, assuming a relevant, temperate coastal ocean condition (e.g., total alkalinity = 2300 μmol/kg, temperature = 15°C, and salinity = 35 ppm). We then plotted the change in pH as a function of hourly daytime carbon fluxes (i.e., hourly NCP) for two different water depths (0.5 and 2m) and three different water residence times ($L/\underline{u}$ = 15 minutes, 60 minutes, and 4 hours) at each water depth. We selected four hours as the maximum duration for the model for two reasons: seagrass beds are rarely extensive enough for water to remain over seagrass for more than a few hours, and longer residence times would tend to overlap with lower-light conditions when the hourly NCP does not apply.

3 Results

3.1 Description of the database

Using our search criteria, we identified 62 published papers (spanning 1956 to 2020) that reported *in situ* rates of seagrass community metabolism (Table S1). None of the studies directly measured changes in DIC, but 17 of the 62 studies reported metabolic measurements in units of carbon. The complete set of studies spanned temperate and tropical ecosystems. The inclusion of 36 temperate studies and an additional 15 tropical studies significantly expanded the scope of inference beyond previous reviews (Duarte et al. 2010; Unsworth et al. 2012). Many studies occurred in the Western Atlantic and Mediterranean (Fig. 1), and there were no studies from the North Pacific. Most studies measured seagrass metabolism during the spring and summer months, while fewer studies measured the metabolism in fall and winter conditions (Fig. 1). Environmental temperature was highest during late summer/early fall months and was higher overall in tropical biomes (Fig S3). Aboveground biomass was highest during summer months and higher in the temperate geographies (Fig S4).

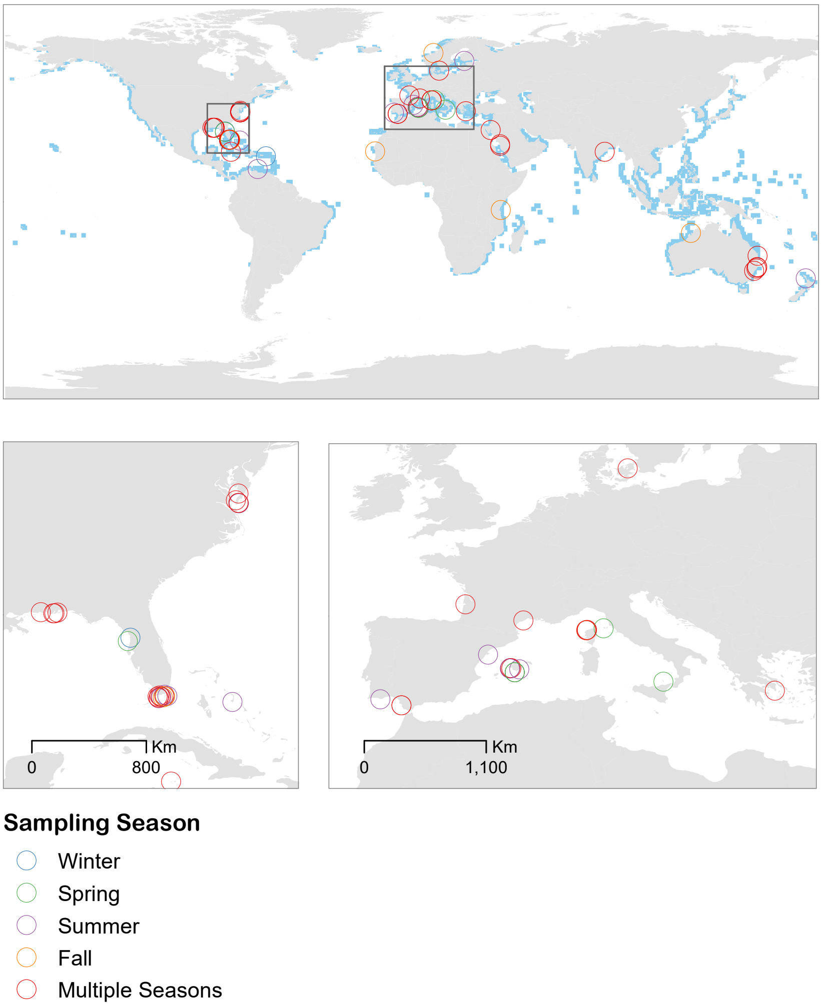

Figure 1. Studies included in the analyses span temperate to tropical ecosystems, with many studies occurring in the Western Atlantic and Mediterranean. Most studies measured seagrass metabolism during the spring and summer months, while fewer studies measured the metabolism in fall and winter conditions. Blue pixels represent the distribution of seagrasses from UNEP-WCMC and Short (2018).

3.2 Methodological analyses

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

3.3 Spatial and temporal patterns in carbon fluxes

3.3.1. Daytime carbon fluxes

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

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detectable difference in hourly NCP rates across seasons (Fig 2c). Although the net hourly carbon flux associated with NCP does not vary seasonally, the mean net hourly carbon flux from the seawater to the seagrass is positive (mean hourly NCP = 5.32 +/- 5.93 SD mmol C/m^2/hour), indicating a net draw down of seawater DIC during peak daylight hours regardless of geography (one-tailed t-test: t_{82} = 8.18, P<0.001). Ninety-three percent of the 83 measurements were net autotrophic.

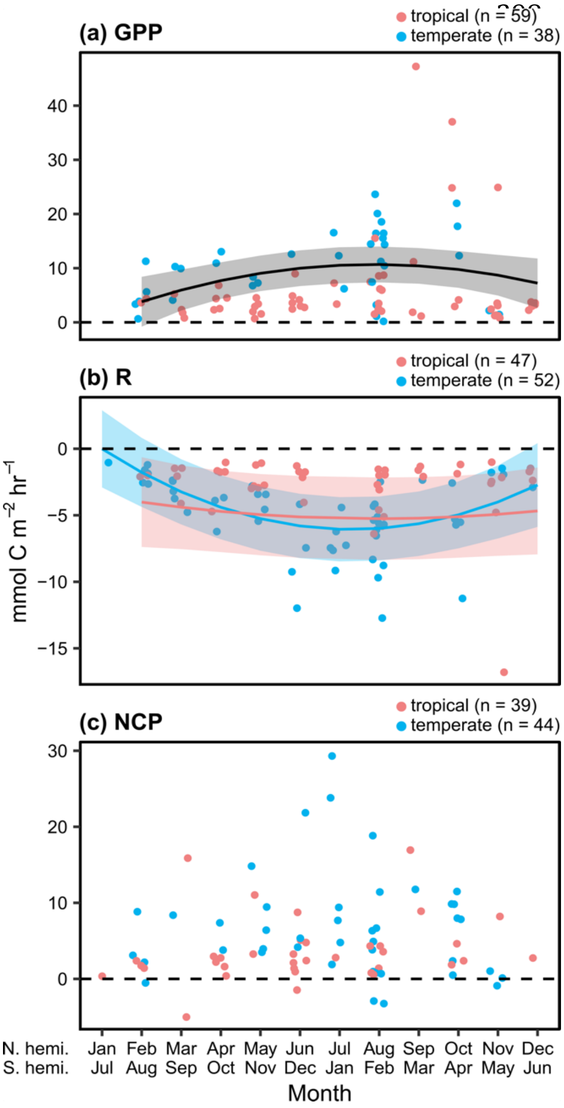

Figure 2. Hourly rates for C fluxes (mmol^{-1}m$^{2-1}$hour^{-1}) associated with seagrass communities as a function of time, with GPP measurements taken during peak sunlight hours (~10 am to 2 pm local time). Studies performed in temperate versus tropical ecosystems are illustrated by color (blue = 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.

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Table 1. Statistics for linear mixed effects models of hourly rates of carbon fluxes. Terms in grey were removed from the final model using backward model selection.

Response	Outliers removed	Fixed effect	df	L-ratio	p-value
GPP (mmol C/m^2/hr)	0	month			
		month^2	5	6.76905	**0.0093**
		geography	6	0.73356	0.3917
		month × geography	7	0.00066	0.9795
		month^2 × geography	8	0.32073	0.5712
	4	month			
		month^2	7	13.7499	**0.0002**
		geography			
		month × geography	8	4.60594	**0.0319**
		month^2 × geography	8	3.5689	0.0589
R (mmol C/m^2/hr)	0	month			
		month^2			
		geography			
		month × geography	8	5.98346	**0.0144**
		month^2 × geography	8	5.72857	**0.0167**
	1	month			
		month^2			
		geography			
		month × geography	8	9.23633	**0.0024**
		month^2 × geography	8	8.73371	**0.0031**
NCP (mmol C/m^2/hr)	0	month	4	0.04176	0.8381
		month^2	5	2.65064	0.1035
		geography	6	0.04703	0.8283
		month × geography	7	3.41018	0.0648
		month^2 × geography	8	1.09949	0.2944

3.3.2 Full-day carbon fluxes

We found 164 measurements/deployments that reported full-day NCP using methods that span a wider range of photoperiods and environmental conditions, and thus provide insight into the potential for full-day local OA mitigation. Based on the accompanying daily rates of GPP and R, there is evidence of a seasonal cycle in carbon fluxes to and from the water column associated with seagrass metabolism (Fig. 3a-b). The seasonal fluctuation differed statistically between temperate and tropical geographies, with a sharper slope in the seasonal fluctuation among the tropical studies (Fig 2a). We did not detect a difference in R between geographies. In general, the seasonal fluctuation in GPP exceeds the seasonal fluctuation in respiration in both geographies, resulting in higher daily net carbon flux from the seawater to the seagrass associated with NCP in summer months (Fig. 3c). The seasonal fluctuation in NCP was greater among the tropical studies than the temperate studies (Table 2). The mean NCP for tropical geographies was 62.5 (+/- 62.4 SD) mmol C/m^2/day, with 84% of the 77 total reported measurements being autotrophic. The mean NCP for temperate geographies was 28.8 (+/- 79.0) mmol C/m^2/day, with 68% of the 187 total reported measurements being autotrophic. Overall, the seagrass meadows in both geographies were net autotrophic (*one-tailed t-test:* tropical t_{76}=8.78, P<0.001; temperate t_{186} = 4.98, P<0.001). Despite these overall trends, there are several individual studies that reported net heterotrophy and net carbon fluxes to the water column, even during summer months.

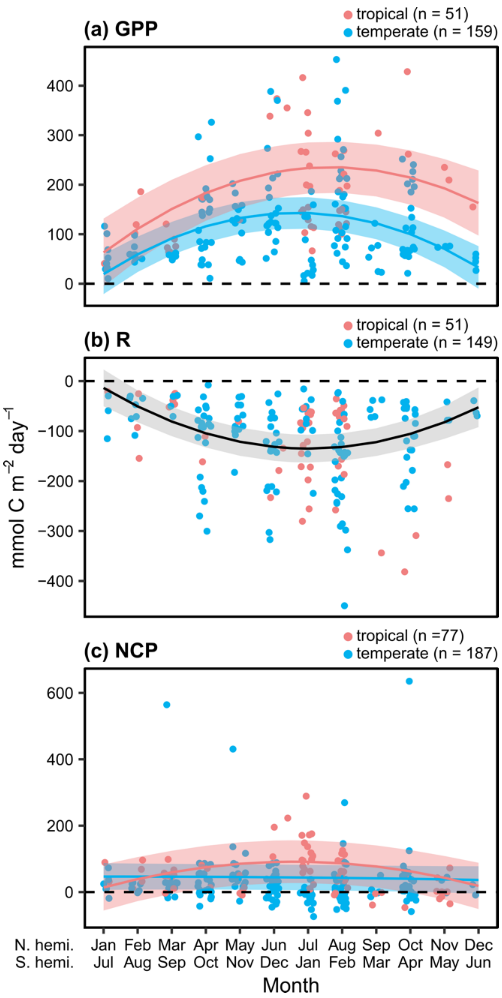

Figure 3. Daily rates for C fluxes (mmol^{-1}m$^{2-1}$day^{-1}) associated with seagrass communities as a function of time. Studies performed in temperate versus tropical ecosystems are illustrated by color (blue = temperate, red = tropical), and significance ($p<0.05$) is denoted by a fit line with a quadratic term and 95%CI. The colors of the lines denote significant differences between tropical and temperate systems.

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

Response	Fixed effect	df	L-ratio	p-value
GPP (mmol C/m^2/day)	month			
	month^2	7	54.5932	**<0.0001**
	geography			
	month × geography	7	4.28394	**0.0385**
	month^2 × geography	8	0.05199	0.8196
R (mmol C/m^2/day)	month			
	month^2	5	40.5399	**<0.0001**
	geography	6	2.7621	0.0965
	month × geography	7	2.2282	0.1355
	month^2 × geography	8	2.04071	0.1531
NCP (mmol C/m^2/day)	month			
	month^2			
	geography			
	month × geography	8	16.9111	**<0.0001**
	month^2 × geography	8	15.1501	**<0.0001**

3.4 Drivers of chemical variability

Within seasons, there is still marked variation in GPP and respiration (Fig. 2-3). Using the subset of studies that report environmental temperature (N = 28), we found that temperature did not explain the residual variability in any metric besides hourly GPP (Fig. 4; Table 3), suggesting the seasonal models may generally account for hypothesized temperature effects. As noted, temperature explained some of the residual variability from the seasonal models of hourly GPP, with the effect differing among tropical and temperate geographies (Fig S6; Hourly GPP *Geography x Temperature*: F_{42} = 10.83, P = 0.001). Among studies reporting aboveground biomass (N=23), biomass explains some of the residual variability in daily NCP, although the effect depends on geography as well (Fig 5; Table 3). Aboveground biomass also explains some of the residual variability in the seasonal models of hourly GPP, respiration, and NCP, and the effect of biomass on hourly GPP also depended on the geography (Fig. S7; Table 3).

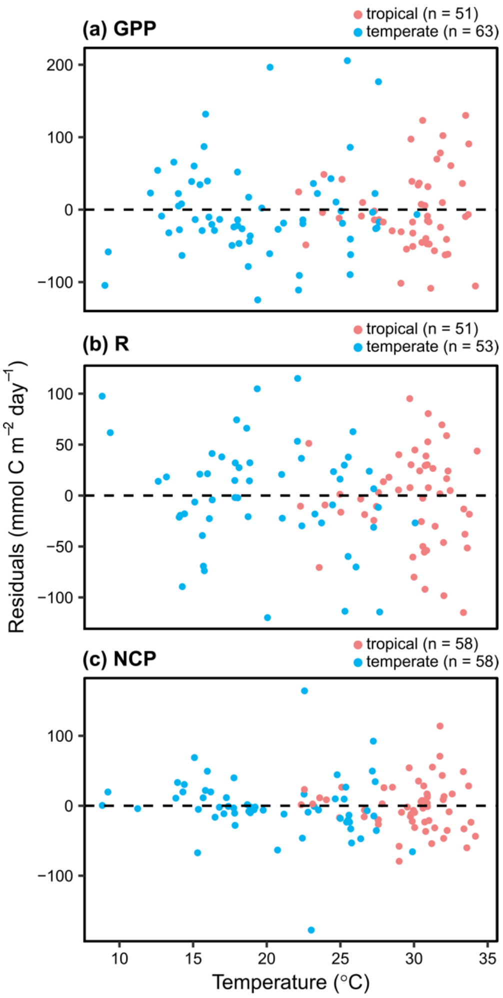

Figure 4. Conditioned residuals of the daily rates of C fluxes (mmol^{-1}m$^{2-1}$day^{-1}) from a seasonal model as a function of temperature. Studies performed in temperate versus tropical ecosystems are illustrated by color (blue = temperate, red = tropical). None of the relationships are statistically significant.

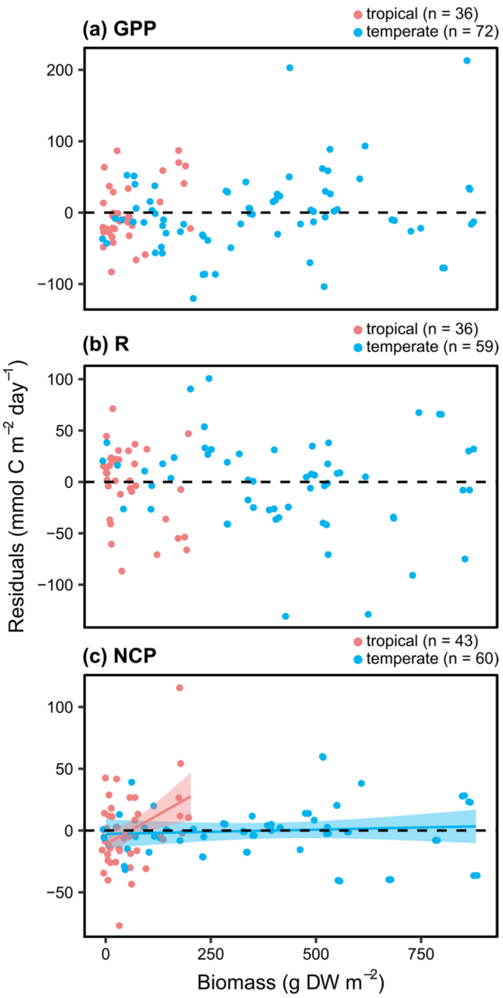

Figure 5. Conditioned residuals of the daily rates for seagrass C fluxes (mmol^{-1}m$^{2-1}$day^{-1}) from a seasonal model as a function of aboveground biomass measured in the field during metabolism measurements. Studies performed in temperate versus tropical ecosystems are illustrated by color (blue = temperate, red = tropical). Significance is denoted by a fit line and 95% CI.

Table 3. Statistics for mixed effects models of the residuals of the hourly metabolic rates as a function of biomass or temperature and geography and the interactions.

Response	Fixed effect	df_{res}	SS_{res}	SS	F	p-value
GPP (mmol C/m^2/hr)	biomass					
	geography					
	biomass × geography	33	2806.1	-1081.7	20.074	**<0.0001**
R (mmol C/m^2/hr)	biomass	30	175.9	-20.68	3.864	0.059
	geography	30	161.9	-6.681	1.248	0.273
	biomass × geography	29	155.3	-1.505	0.274	0.605
NCP (mmol C/m^2/hr)	**biomass**	38	1640.2	-186.1	4.736	**0.036**
	geography	38	1721.4	-267.4	6.803	**0.013**
	biomass × geography	37	1454.1	-140.3	3.844	0.058
GPP (mmol C/m^2/hr)	temp					
	geography					
	temp × geography	42	375.4	-71.84	9.704	**0.003**
R (mmol C/m^2/hr)	temp	61	221.7	-0.930	0.253	0.617
	geography	60	220.8	-0.104	0.028	0.868
	temp × geography	59	220.7	-0.004	0.001	0.976
NCP (mmol C/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	1411.2	-12.30	0.387	0.537

3.5 Potential OA amelioration

The steady state box model illustrates that the largest potential change in seawater pH occurs when NCP is highest and the water depth and residence time are lowest (Fig. 6). Using the mean hourly NCP from our analysis (~5.32 mmol C/m^2/hour; Fig. 2C), the potential change in seawater pH in a seagrass meadow that meets the assumptions of the box model (e.g., ΔO_2:ΔDIC = 1) in a low flow environment at low tide (i.e., 0.5m water depth) ranges from 0.006 – 0.085 pH units for a residence time from 15 minutes to 4 hours. At the modeled higher tide (i.e., 2m water depth), the potential changes in seawater pH for the same NCP range from 0.001-0.022 pH units for the same residence times (15 minutes to 4 hours).

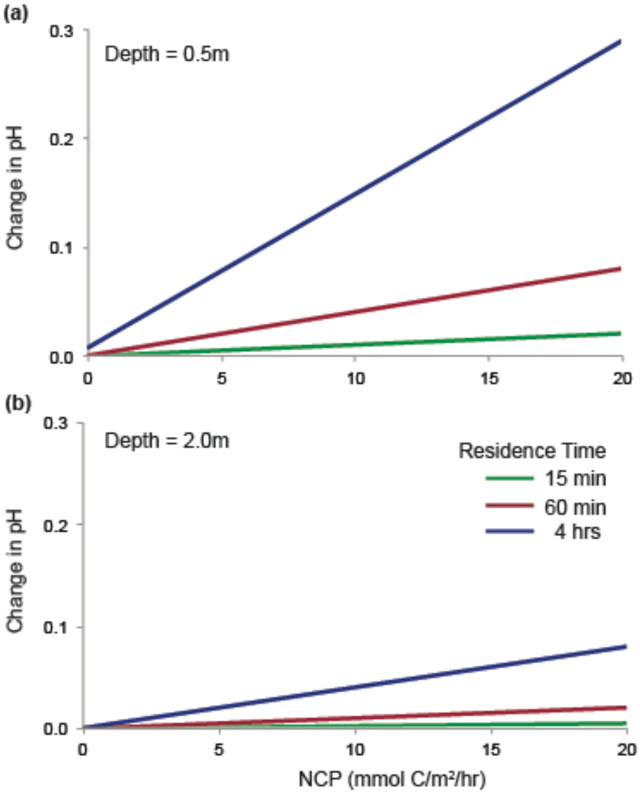

Figure 6. Results from a steady state box model illustrating the change in seawater pH as a function of NCP at (A) 0.5 m water depth and (B) 2 m water depth. The change in seawater pH is illustrated for a series of different residence times (L/u). Both panels are modeled at the same temperature (15°C), total alkalinity (2300 µmol/kg), and salinity (35 ppm), with an incoming DIC of 2100 µmol/kg.

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4 Discussion

4.1 Spatial and temporal variability in seagrass metabolism

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 out. If O_2 fluxes translate proportionally to community drawdowns in CO_2, the assumption underlying our box model, our results suggest that the maximum potential local OA mitigation due to seagrass metabolism during daylight hours is similar across time and ecosystems, but small in magnitude.

We also demonstrate that seagrass beds are generally net autotrophic over the length of the day (based on daily NCP), and the magnitude of this full-day NCP is more pronounced during summer months and in tropical geographies (Fig 3C). However, underlying the summertime peak in full-day NCP is the potential for marked diurnal variability in pH. In particular, the demonstrated summertime peak in hourly respiration rates could drive more pronounced nighttime lows in pH/saturation state during the most pronounced windows for net autotrophy (i.e., summer months with the highest daily NCP). However, diurnal fluctuations in seawater pH associated with seagrass metabolism will also be influenced by hydrodynamics that are not captured in our synthesis (Koweek et al. 2018), and recent field studies of estuarine eelgrass by Ricart et al. (2021) demonstrated that sustained elevations in pH associated with seagrass meadows were not restricted to daylight hours. Regardless, a critical next step for understanding the utility of seagrass beds for climate adaptation is to determine how the demonstrated seasonal

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variability and the potential diurnal variability in carbonate chemistry are integrated over time by organisms, especially under conditions projected for coastal habitats in the future.

Given the positive correlations between GPP and temperature, we assume that most of these measurements were taken when the environmental temperatures were not physiologically stressful to the seagrass community. Thus, the positive relationship between environmental temperature and GPP should not necessarily be viewed through the lens of temperature exposures associated with future warming driven by climate change. Continued warming associated with climate change could cause photosynthesis and respiration to decline at stressful temperatures. The probability that the relationship between temperature and metabolic responses will change with future warming is likely to differ geographically based on how close a community is to its thermal limit and the scope for acclimation or adaptation. This may partially explain the differences in the relationships between temperature and the residuals of the seasonal model between geographies, with increasing temperature negatively related to the residuals from tropical geographies and positively related to the residuals from temperate geographies. Many tropical seagrass species are growing close to their photosynthetic and physiological optima (Lee et al. 2007, Koch et al. 2012), and elevated temperatures in these geographies may be detrimental, causing metabolism (in this case hourly GPP) to be less than expected based on seasonal patterns. In contrast, the positive relationship between the residuals from the seasonal model and temperature in temperate geographies indicate that there may be a stimulatory effect before a thermal tolerance threshold is crossed and metabolism decreases.

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

4.2 Implications for local OA mitigation and management

The results of our steady state box model analyses illustrate the potential scope for seagrass NCP to influence seawater pH on an hourly basis (Fig. 6), with the change in pH being proportional to NCP during daylight hours and R during nighttime hours. While the box model is useful in making coarse estimates on what particular NCP values might correspond to in seawater pH, it is important to note that it only represents a first step in translating the seagrass community metabolism estimates to seawater biogeochemistry. This is in part because the ratio of NCP based on carbon fixed and oxygen evolved in seagrass communities is likely to be quite variable. Although the ratio between O_2 produced and carbon fixed by an individual seagrass is generally assumed to be balanced (i.e., 1:1), the other processes that occur in a seagrass meadow, including respiration from organisms living within the seagrass and carbonate production and dissolution, also influence the dissolved inorganic carbon (DIC) concentration in the seawater. Current empirical measurements of NCP_{DIC}:NCP_{O2} in seagrass meadows range from 0.3 to 6.8 (Ziegler and Benner 1998, Barrón et al. 2006), suggesting the effect of seagrass NCP on seawater pH could be substantially more or less pronounced than illustrated here. Because of this variability in the relationship between O_2 and DIC, care must be taken when interpreting the results from the box model. A better understanding of the NCP_{DIC}:NCP_{O2} in particular meadows will better inform their potential for local OA mitigation. 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.

5 Conclusions

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

These results highlight challenges, as well as gaps in our understanding, that may impede the use of seagrasses for sustained local OA mitigation. In particular, we demonstrate that while peak daytime carbon fluxes are similar across seasons and geographies, nighttime respiration is highest during summer months. Thus, although seagrass beds are generally net autotrophic, nighttime respiration could reduce seawater pH during periods of greatest autotrophy. We provide examples of how water depth and residence time can influence the effect of seagrass on seawater pH, and we demonstrate that the overall magnitude of the effect is likely quite small.

This work has elucidated several gaps that need to be addressed by the scientific community. For example, certain geographies, such as the North Pacific, are currently underrepresented in our dataset. Thus, continued study of 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 oxygen fluxes and DIC, and this relationship may be important to elucidate at local scales to truly understand the potential for OA mitigation at a given location. Perhaps most importantly, more information is needed to understand how vulnerable organisms respond to the chemical variability highlighted in our study (Gimenez et al. 2018, Lowe et al. 2018), and in particular, how this variability is integrated through time. Despite the considerations of geographic and temporal variability in carbon fluxes illustrated here, we recognize that seagrass conservation and restoration may be important strategies for climate adaptation for numerous other reasons, including carbon sequestration and habitat provisioning.

6 Code Availability: Code is available at https://github.com/tyekindinger/SeagrassCommunityMetabolism

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

8 Author Contributions: Kroeker: conceptualization, funding acquisition, investigation, methodology, writing – original draft preparation; Kindinger: formal analysis, visualization, writing – review & editing; Hirsh: investigation, visualization, writing – review & editing; Ward: investigation, writing – review & editing; Hill: conceptualization, funding acquisition, writing – review & editing; Jellison, Koweek, Lummis, Rivest, Waldbusser: conceptualization, writing – review & editing; Gaylord: conceptualization, funding acquisition, methodology, writing – review & editing.

9 Competing Interests: The authors declare no competing interests

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11 References

Agrawal, A., D. Nepstad, and A. Chhatre. Reducing emissions from deforestation and forest degradation. Ann. Rev. Environ. Resour. **36**:373-396, 2011.

Barrón, C., C. M. Duarte, M. Frankignoulle, and A. V. Borges. Organic carbon metabolism and carbonate dynamics in a Mediterranean seagrass (*Posidonia oceanica*) meadow. Estuaries and Coasts **29**:417-426, 2006.

Bolker, B,. and D. Robinson. broom.mixed: Tidying Methods for Mixed Models. R package version 0.2.6. https://CRAN.R-project.org/package=broom.mixed, 2020.

Canadell, J. G., and M. R. Raupach. Managing forests for climate change mitigation. Science **320**:1456-1457, 2008.

Chan, F., A. B. Boehm, J. A. Barth, E. A. Chornesky, A. G. Dickson, R. A. Feely, B. Hales, T. M. Hill, G. Hofmann, D. Ianson, T. Klinger, J. Largier, J. Newton, T. F. Pedersen, G. N. Somero, M. Sutula, W. W. Wakefield, G. G. Waldbusser, S. B. Weisberg, and E. A. Whiteman. The West Coast Ocean Acidification and Hypoxia Science Panel: Major Findings, Recommendations, and Actions. Oakland, CA, USA, 2016.

Clavier, J., L. Chauvaud, E. Amice, P. Lazure, M. v. d. Geest, P. Labrosse, A. Diagne, A. Carlier, and S. Chauvaud. Benthic metabolism in shallow coastal ecosystems of the Banc d'Arguin, Mauritania. Marine Ecology Progress Series **501**:11-23, 2014.

Cyronak, T., A. J. Andersson, S. D'Angelo, P. Bresnahan, C. Davidson, A. Griffin, T. Kindeberg, J. Pennise, Y. Takeshita, and M. White. Short-term spatial and temporal carbonate chemistry variability in two contrasting seagrass meadows: implications for pH buffering capacities. Estuaries and Coasts **41**:1282-1296, 2018.

Duarte, C. M., and C. L. Chiscano. Seagrass biomass and production: a reassessment. Aquatic Botany **65**:159-174, 1999.

Duarte, C. M., N. Marbà, E. Gacia, J. W. Fourqurean, J. Beggins, C. Barrón, and E. T. Apostolaki. Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. Global Biogeochemical Cycles **24**:GB4032, 2010.

Gattuso, J. P., D. Allemand, and M. Frankignoulle. Photosynthesis and calcification at cellular, organismal, and community levels in coral reefs: A review on interactions and control by carbonate chemistry. Amer. Zool. **39**:160-183, 1999.

Gimenez, I., G. G. Waldbusser, and B. Hales. Ocean acidification stress index for shellfish (OASIS): Linking Pacific oyster larval survival and exposure to variable carbonate chemistry regimes. Elem Sci Anth **6**, 2018.

Hendriks, I. E., Y. S. Olsen, L. Ramajo, L. Basso, A. Steckbauer, T. S. Moore, J. Howard, and C. M. Duarte. Photosynthetic activity buffers ocean acidification in seagrass meadows. BIOGEOSCIENCES **11**:333-346, 2014.

Herbert, D.A. and J.W. Fourqurean. 2008. Ecosystem structure and function still altered two decades after short-term fertilization of a seagrass meadow. Ecosystems **11**: 688-700.

James, R. K., M. M. van Katwijk, B. I. van Tussenbroek, T. van der Heide, H. A. Dijkstra, R. M. van Westen, J. D. Pietrzak, A. S. Candy, R. Klees, R. E. M. Riva, C. D. Slobbe, C. A. Katsman, P. M. J. Herman, and T. J. Bouma. Water motion and vegetation control the pH dynamics in seagrass-dominated bays. Limnology and Oceanography **65**: 349-362, 2020.

Koch, M., G. Bowes, C. Ross, and X.-H. Zhang. Marine macro-autotrophs and climate change. Global Change Biology **19**:103-132, 2012.

Koweek, D. A., R. C. Zimmerman, K. M. Hewett, B. Gaylord, S. N. Giddings, K. J. Nickols, J. L. Ruesink, J. J. Stachowicz, Y. Takeshita, and K. Caldeira. Expected limits on the ocean acidification buffering potential of a temperate seagrass meadow. Ecological Applications **28**:1694-1714, 2018.

Kroeker, K. J., R. L. Kordas, R. N. Crim, and G. G. Singh. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecology Letters **13**:1419-1434, 2010.

Lowe, A. T., J. Kobelt, M. Horwith, and J. Ruesink. Ability of eelgrass to alter oyster growth and physiology is spatially limited and offset by increasing predation risk. Estuaries and Coasts **42:**743–754, 2019.

Maher, D., and B. D. Eyre. Benthic carbon metabolism in southeast Australian estuaries: habitat importance, driving forces, and application of artificial neural network models. Marine Ecology Progress Series **439**:97-115, 2011.

Manzello, D. P., I. C. Enochs, N. Melo, D. K. Gledhill, and E. M. Johns. Ocean acidification refugia of the Florida Reef Tract. PloS one **7**:e41715., 2011.

Mcleod, E., G. L. Chmura, S. Bouillon, R. Salm, M. Björk, C. M. Duarte, C. E. Lovelock, W. H. Schlesinger, and B. R. Silliman. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Frontiers in Ecology and the Environment **9**:552-560, 2011.

Nahlik, A. M., and M. S. Fennessy. Carbon storage in US wetlands. Nature Communications **7**:13835, 2016.

Nielsen, K., J. Stachowicz, H. Carter, K. Boyer, M. Bracken, F. Chan, F. Chavez, K. Hovel, M. Kent, K. Nickols, J. Ruesink, J. Tyburczy, and S. Wheeler. Emerging understanding of the potential role of seagrass and kelp as an ocean acidification management tool in California. Oakland, California, USA, 2018.

Odum, E. Primary production in flowing waters. Limnology and Oceanography **1**:102-117, 1956.

Odum, H. T., P. R. Burkholder, and J. Rivero. Measurements of productivity of turtle grass flats, reefs, and the Bahia fosforenscente of southern Puerto Rico. Publ. Inst. Mar. Sci **6**:159-170, 1959.

Pacella, S. R., C. A. Brown, G. G. Waldbusser, R. G. Labiosa, and B. Hales. Seagrass habitat metabolism increases short-term extremes and long-term offset of CO_2 under future ocean acidification. Proc. Natl. Acad Sci USA **115**:3870-3875, 2018.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-145, https://CRAN.R-project.org/package=nlme, 2020.

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/, 2019.

Rheuban, J. E., P. Berg, and K. J. McGlathery. Multiple timescale processes drive ecosystem metabolism in eelgrass (*Zostera marina*) meadows. Marine Ecology Progress Series **507**:1-13, 2014.

Ricart, A. M., M. Ward, T. M. Hill, E. Sanford, K. J. Kroeker, Y. Takeshita, S. Merolla, P. Shukla, A. Ninokawa, K. Elsmore and B.P. Gaylord. Coast-wide evidence of low pH amelioration by seagrass ecosystems. Global Change Biology, 27: 2580-2591, 2021.

Robinson, D., A. Hayes, and S. Couch. broom: Convert Statistical Objects into Tidy Tibbles. R package version 0.7.3. https://CRAN.R-project.org/package=broom, 2020.

UNEP-WCMC and F. T. Short. Global distribution of seagrasses (version 6.0). Sixth update to the data layer used in Green and Short (2003). Cambridge (UK): UN Environment World Conservation Monitoring Centre. URL: http://data.unep-wcmc.org/datasets/7, 2018.

Unsworth, R. K. F., C. J. Collier, G. M. Henderson, and L. J. McKenzie. Tropical seagrass meadows modify seawater carbon chemistry: implications for coral reefs impacted by ocean acidification. Environ. Res. Lett. **7**:024026, 2012.

Washington State Blue Ribbon Panel on Ocean Acidification. Ocean Acidification: From Knowledge to Action, Washington State's Strategic Response. Publication no. 12-01-015., Olympia, Washington, 2012.

Ziegler, S., and R. Benner. Ecosystem metabolism in a subtropical, seagrass-dominated meadow. Marine Ecology Progress Series **173**:1-12, 1998.