



Thermal dependence of seagrass ecosystem metabolism in the Red Sea

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ABSTRACT: The Red Sea is one of the warmest seas with shallow seagrass ecosystems exposed to extreme temperatures, in excess of 35°C, during the summer months. Seagrass meadows are net autotrophic ecosystems, but respiration increases faster than primary production with temperature. This may lead to a shift from an autotrophic to a heterotrophic system at the highest temperatures. Although tropical seagrasses are adapted to high temperatures, the metabolic rates of Red Sea seagrasses have not yet been reported. Here we assessed the community metabolism of 2 seagrass ecosystems, an *Enhalus acoroides* monospecific meadow and a *Cymodocea serrulata* and *Halodule uninervis* mixed meadow, located in the central Red Sea. We measured *in situ* net community production (NCP), community respiration (*R*), gross primary production (GPP), activation energy and community production–irradiance curves along their natural temperature gradient over 1 yr by measuring diel fluctuations in dissolved oxygen. The results were species-specific; while the monospecific meadow was autotrophic throughout the year (annual weighted average NCP: 64.63 ± 11.89 mmol O₂ m⁻² d⁻¹, GPP:*R* ratio: 1.42 ± 0.06), the mixed meadow was heterotrophic during the summer months (annual weighted average NCP: -4.15 ± 9.39 mmol O₂ m⁻² d⁻¹, GPP:*R*: 1.04 ± 0.05). In both seagrass meadows, *R* and GPP increased with increasing temperature, but differences in activation energies indicated that the mixed meadow is more sensitive to increasing seawater temperatures. These findings suggest contrasting responses in tropical seagrass species to rising temperature, pointing out the potential vulnerability of seagrasses to ocean warming in the Red Sea.

KEY WORDS: Seagrass ecosystems · Community metabolism · Thermal dependence · Activation energy · PI curves · Red Sea

1. INTRODUCTION

Seagrass ecosystems rank among the most productive (Duarte & Chiscano 1999) and economically valuable ecosystems in the world (Costanza et al. 1997), offering important ecosystem services such as nurseries, food and shelter for commercially important fisheries, coastal stabilization, carbon sequestration, removal of nutrients (Orth et al. 2006, Ruiz-Frau et al. 2017) and bacterial pathogens (Lamb et al. 2017) and protection of archaeological heritage (Krause-Jensen et al. 2019). Seagrass ecosystems can

be found worldwide, except for Antarctica (Green & Short 2003), and inhabit a broad thermal range (Lee et al. 2007, Pedersen et al. 2016). However, warming can lead to the loss of seagrass meadows and the services they provide, with warming-derived loss of seagrass reported for the western Mediterranean (Díaz-Almela et al. 2009, Marbà & Duarte 2010), Western Australia (Arias-Ortiz et al. 2018), Florida Bay (Carlson et al. 2018) and Chesapeake Bay (Moore & Jarvis 2008, Moore et al. 2014).

Due to climate change, the global mean surface temperature has increased since pre-industrial

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times and is predicted to increase by 0.3–1.7°C, under a mitigation scenario (Intergovernmental Panel on Climate Change representative concentration pathway [RCP] 2.6), to 2.6–4.8°C, under a business-as-usual scenario (RCP 8.5), by the end of the 21st century (Collins et al. 2013). Yet, some seagrass species already live close to or even exceed their thermal limit (York et al. 2013, Pedersen et al. 2016, Collier et al. 2017). Increasing temperatures can negatively affect the productivity of seagrasses (Marsh et al. 1986) and their ecosystem services (Pedersen et al. 2011) as well as their mortality rate (Marbà & Duarte 2010, Collier & Waycott 2014). However, these effects vary with different species, their thermal optima and geographical ranges as well as local acclimation and adaptation (Short & Neckles 1999).

Warming can also have varying effects on the different metabolic rates within a seagrass meadow. Net community production (NCP) and the photosynthesis:respiration ($P:R$) ratio define the metabolic state of an ecosystem, where a net autotrophic ecosystem is characterized by $NCP > 0$ and $P:R > 1$, while a system with $NCP < 0$ and $P:R < 1$ is defined as heterotrophic (Duarte et al. 2011). Rising temperatures are known to increase photosynthesis at lower rates than respiration (Harris et al. 2006) up to the system's thermal optimum and to decrease photosynthesis past the optimum temperature (Marsh et al. 1986), potentially leading to a shift from an autotrophic to a heterotrophic system. In a heterotrophic system, the photosynthetically fixed carbon cannot meet the requirements of community respiration, leading to an imbalance between these metabolic rates that requires allochthonous subsidies of organic carbon and leads to these communities acting as CO_2 sources and O_2 sinks (Duarte et al. 2011).

Globally, seagrass ecosystems tend to be autotrophic systems, with average NCP rates of 27.2 ± 5.8 mmol O_2 m^{-2} d^{-1} (Duarte et al. 2010). Tropical seagrass ecosystems, despite the warmer temperature regimes they experience, also tend to be net autotrophic systems although with lower NCP rates than temperate seagrasses (23.7 ± 7.8 and 33.5 ± 8.0 mmol O_2 m^{-2} d^{-1} , respectively, Duarte et al. 2010). Nevertheless, tropical seagrasses are adapted to high temperatures as evidenced by higher optimum temperature (T_{opt}) for photosynthesis (35°C in *Cymodocea serrulata* and *Halodule uninervis*: Adams et al. 2017, Collier et al. 2017; and 32–33°C in *Thalassia hemprichii* and *Enhalus acoroides*: Pedersen et al. 2016) compared to the T_{opt} found in tem-

perate seagrasses (25°C in *Zostera marina*: Marsh et al. 1986; and 18–23°C in *Posidonia sinuosa*: Masini et al. 1995). However, these studies only display T_{opt} of single species using leaf pieces or shoots and do not necessarily reflect how temperature affects the entire community or ecosystem. A community might experience different effects, as many organisms (e.g. epiphytes, algae, microbes, plankton), besides the foundation seagrass species, contribute to the community metabolism of a seagrass ecosystem. *In situ* community measurements can therefore contribute to previous single-species studies, as we can assess the effects on a community level taking into account not only the present seagrass species but also the whole community. Studies on ecosystem metabolism are limited, and the metabolic rates of seagrass ecosystems are especially lacking for the Red Sea.

The Red Sea is a semi-enclosed sea basin supporting high sea surface temperatures (up to 36°C) and rapid warming (Belkin 2009, Chaidez et al. 2017). Thus, seagrass ecosystems in the Red Sea encounter the warmest thermal regimes globally and are likely to be near their upper natural thermal thresholds. The Red Sea therefore provides a unique study site to evaluate the ecological dynamics of tropical seagrasses to better understand how climate change will affect seagrass ecosystems and their performance. Measuring seagrass community production, community respiration and community primary production rates along their annual *in situ* thermal range will help assess their thermal dependence as well as predict how these ecosystems will cope with future warming. Additionally, the photosynthetic performance of seagrasses is closely related to temperature, temperature changes and irradiance (Bulthuis 1987, Lee et al. 2007) and typically varies between species and seasons, with higher rates at higher temperature (Lee et al. 2007). Community metabolism–irradiance curves can help evaluate seagrass productivity by identifying changes with changing light levels, increasing temperatures, and between species.

In this study, we assessed the net community production, gross primary production, community respiration and community metabolism–irradiance curves of 2 tropical seagrass meadows in the central Red Sea by measuring diel fluctuations in dissolved oxygen using *in situ* incubation chambers over 1 yr. In addition, we assessed the temperature dependence of seagrass ecosystem metabolism under its natural thermal range in the warm Red Sea.

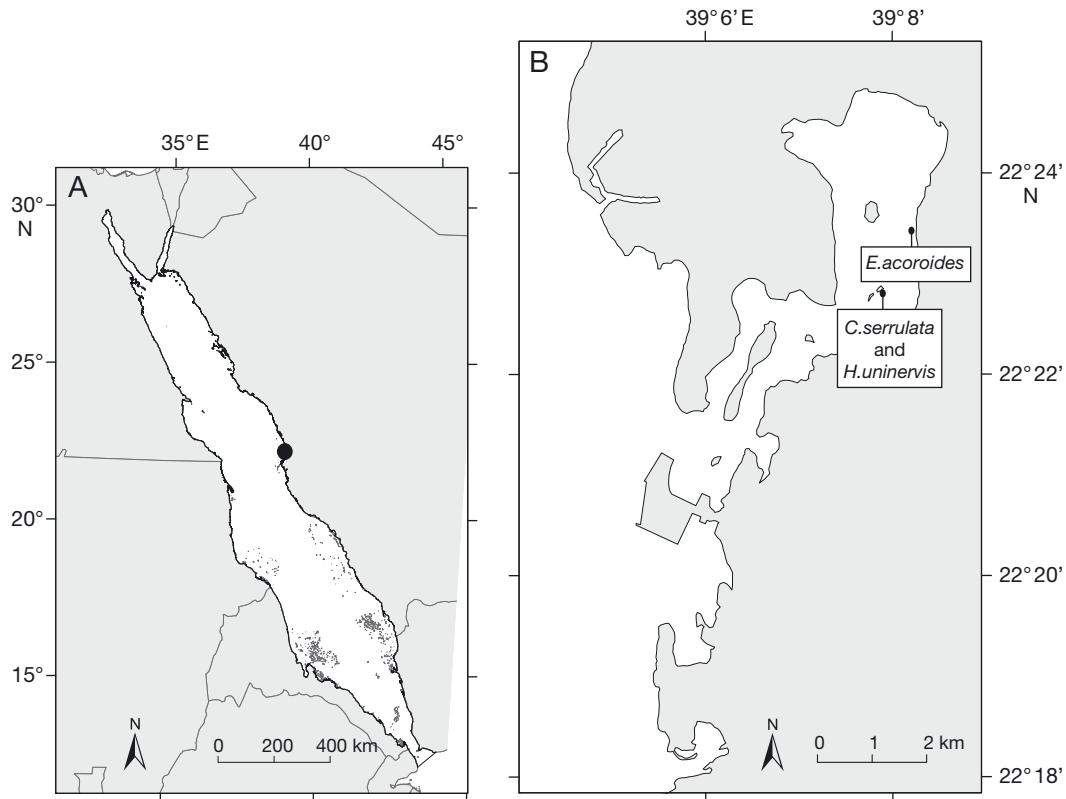


Fig. 1. (A) Location of the study sites in the Red Sea and (B) a closer view of the locations of the monospecific (*Enhalus acoroides*) and mixed (*Cymodocea serrulata* and *Halodule uninervis*) meadows

2. MATERIALS AND METHODS

2.1. Study site

The study was conducted in a shallow, enclosed coastal lagoon located in the central Red Sea (Fig. 1). We sampled 2 seagrass meadows: a *Cymodocea serrulata* and *Halodule uninervis* mixed meadow at 0.7 m depth (22° 22' 50.40" N, 39° 7' 54.50" E) and an *Enhalus acoroides* monospecific meadow at 2.0 m depth (22° 23' 23.2" N, 39° 08' 08.0" E). Hereafter, we refer to these 2 meadows as mixed and monospecific meadows, respectively, acknowledging that we studied the whole community response, taking into account the metabolism of many other organisms present in this community besides the foundation seagrass species. We estimated *in situ* metabolic rates of the seagrass community in both sites from June 2016 to April 2017. We conducted 9 and 6 samplings (covering 7 and 6 mo) in the mixed meadow and the monospecific meadow, respectively. During summer, we increased the sampling effort to capture the warmest period, especially in the shallow mixed meadow. Each sampling consisted of 2 consecutive

days of fieldwork during which we deployed incubation chambers.

2.2. Field setup

At each sampling, we randomly deployed 4 replicate incubation chambers containing sediment and seagrass shoots in both meadows. The incubation chambers consisted of a plastic cylindrical core (mixed meadow: 26 cm length and 9.5 cm diameter, monospecific meadow: 40 cm length and 9.5 cm diameter) that was carefully pushed into the sediment and a plastic bag (mixed meadow: 40 cm length, monospecific meadow: 80 cm length) that was firmly attached to the plastic core with rubber bands and plastic ties. The plastic bag was built with a transparent coextruded multilayer film highly impermeable to oxygen (Multifol GVA 180, Südpack). The flexibility of the plastic film allowed the movement of the plastic bag with wave and tidal movements. Because of the enclosed nature of the lagoon (Fig. 1B), tidal currents were strong in the 2 locations and provided, in interacting with the flexible walls, mixing of the seawater enclosed in the

chamber. After deployment, the length of the core and bag above the ground were recorded to calculate the total volume of each chamber. Inside each chamber, we deployed a dissolved oxygen and temperature logger (miniDOT, Precision Measurements Engineering) recording every 10 min for 24 h. The miniDOT loggers were attached to a stainless steel bar that was previously fixed in the center of the plastic core, preventing damage to seagrass rhizomes and roots. In each meadow, we also deployed an Odyssey logger (Dataflow Systems) within the canopy to record photosynthetically active radiation (PAR) in 1 of the 4 replicate chambers. In addition, we monitored and recorded the seawater temperature, dissolved oxygen and PAR outside the chambers for the same 24 h periods by deploying another dissolved oxygen and temperature logger (miniDOT, Precision Measurements Engineering), an EXO1 multiparameter sonde (Xylem) and an Odyssey PAR logger (Dataflow Systems) within the seagrass meadow but outside the chambers. Annual (mean \pm SE) minimum oxygen values were 3.7 ± 0.5 and 5.9 ± 0.2 mg O₂ l⁻¹ inside the incubation chambers and 5.0 ± 0.2 and 3.2 ± 0.8 mg O₂ l⁻¹ outside the chambers in the mixed and monospecific meadows, respectively. Annual (mean \pm SE) maximum oxygen values were 10.7 ± 0.3 and 11.0 ± 0.4 mg O₂ l⁻¹ inside the incubation chambers and 6.6 ± 0.2 and 7.6 ± 0.5 mg O₂ l⁻¹ outside the incubation chambers in the mixed and monospecific meadows, respectively.

At the end of the 24 h incubations, the chambers were opened by detaching the plastic bags but keeping the plastic core at the base. Then, the sediment and seagrass shoots were collected using the same cylindrical plastic core by carefully pulling the core up to avoid disruption of the sediment structure. The cores were then transported to the laboratory, where the shoots and rhizomes were dried at 60°C to a constant dry weight (DW) to record the plant biomass in each core.

2.3. Net community production, respiration and gross primary production

NCP was calculated by the difference between the initial and final dissolved oxygen concentration in the 24 h incubations. The community respiration (R) rate was calculated from the slope of the linear decrease in dissolved oxygen concentration during night, when PAR = 0 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and then converted into daily rates. The community gross primary production (GPP) was estimated according to Duarte et al. (2010) as follows:

$$\text{GPP} = \text{NCP} - R \quad (1)$$

The rates were converted to an aerial base taking into account the core surface area and the total volume of the incubation chamber and standardized by seagrass biomass taking into account the plant biomass (DW) in each chamber.

2.4. Activation energy

We assessed the thermal dependence of seagrass community GPP and R rates by fitting the Arrhenius function. We estimated the activation energy, derived from the relationship between the natural logarithm of GPP and R rates and the inverse temperature multiplied by the Boltzmann constant. The activation energy is the slope of the Boltzmann factor or the Arrhenius equation (Brown et al. 2004, Dell et al. 2011, Marbà et al. 2015):

$$\ln(V) = C + \left[E \times \left(\frac{1}{kT} \right) \right] \quad (2)$$

where V is the value of the metabolic rate, C is the intercept of the fitted regression equation, E is the activation energy, k is the Boltzmann constant and T is the temperature (in K). The activation energy provides useful ecological information on the thermal dependence of a given metabolic process (Dell et al. 2011).

2.5. Community production–irradiance curves

Community production–irradiance (PI) curves were estimated for both meadows and each sampled month. The net community production rate was calculated hourly from the change in the dissolved oxygen concentration. The respiration rate was calculated from the linear decrease in dissolved oxygen concentration when PAR = 0 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. The hourly mean PAR and the hourly mean seawater temperature were calculated as well. For each month and site, we adjusted a community PI curve to our hourly rates from all replicate chambers by fitting the Jassby and Platt model (Jassby & Platt 1976) in R software 1.1.442 (R Core Team 2017) together with the phytotools package (Silsbe & Malkin 2015). We extracted the following parameters from the adjusted curves: efficiency of community production (α) as the slope of the initial curve where irradiance is limited, light saturation point of the community (I_k) and community respiration (R) as the y intercept when PAR = 0 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Then, we calculated the maximum community production (P_{max}) as:

$$P_{\max} = (\alpha \times I_k) - R \quad (3)$$

while the community compensation irradiance (I_c) was calculated as:

$$I_c = \frac{(y - R)}{\alpha} \quad (4)$$

when $y = 0$.

2.6. Data analysis

The normality of all response variables was analyzed using the Shapiro-Wilk test. One-way ANOVA and post hoc Tukey's HSD tests were conducted to test for significant differences in NCP, R , GPP and GPP: R ratio between sites and sampling months. Because of the uneven sampling frequency, we calculated the annual weighted average of all our response variables. Moreover, we tested if the annual weighted average NCP and GPP: R ratio for each site were significantly different from a theoretical value of 0 and 1, respectively, using t -tests to formally assess the autotrophy of both meadows. In addition, we tested the effect of seawater temperature (our continuous explanatory variable) and site (our categorical explanatory variable with 2 levels: monospecific meadow and mixed meadow), as well as their interaction, on NCP, R , GPP and GPP: R (our continuous response variables) by linear model (lm, standard least squares) when variables met the assumptions of normal distribution, or by generalized linear model (GLM) when variables were not normally distributed. Differences in α , I_k , I_c , P_{\max} and R between sites were analyzed with and without matching sampling months by using the Wilcoxon signed rank test and the Mann-Whitney test, respectively. The reported values are standardized by area unless stated otherwise. All statistical analyses were conducted in JMP Pro 13.1.0 (SAS Institute) and PRISM (GraphPad Software) statistical software.

3. RESULTS

3.1. *In situ* seawater temperature, irradiance and biomass

The range of *in situ* daily mean seawater temperature was similar in both meadows. The mean *in situ* seawater temperature varied from 22.8°C in February to 33.9°C in August in the *Cymodocea serrulata* and *Halodule uninervis* mixed meadow and from 22.4°C in February to 33.4°C in July in the *Enhalus*

acoroides monospecific meadow (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m614p079_supp.pdf). While both meadows showed a similar thermal regime, the mixed meadow was exposed to warmer seawater temperatures (>32°C) over a longer period than the monospecific meadow was. The *C. serrulata* and *H. uninervis* meadow experienced the highest daily mean temperature 1 mo later (August) than the *E. acoroides* meadow, which was already 2°C colder by then. Maximum daily PAR values ranged from 499 to 877.5 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in the mixed meadow, while the monospecific meadow reached maximum daily PAR values of 314.2 to 498 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Mean above-ground biomass was $839.34 \pm 49.03 \text{ g DW m}^{-2}$ in the monospecific meadow and $269.11 \pm 16.97 \text{ g DW m}^{-2}$ in the mixed meadow.

3.2. Net community production

The NCP of the *E. acoroides* monospecific meadow was significantly higher than the NCP of the *C. serrulata* and *H. uninervis* mixed meadow over the year, except for February (Table S1 in the Supplement). While the monospecific meadow was net autotrophic during the entire year, the mixed meadow was heterotrophic in September and October (Table 1, Fig. 2). In the monospecific meadow, the highest NCP was detected in July and was significantly higher than the NCP during the winter months (November–April; Fig. 2A). Specifically, the mean NCP in the monospecific meadow ranged from $34.58 \pm 10.59 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in February to $139.15 \pm 9.67 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in July. The NCP of the mixed meadow was significantly lower in October compared to February–August (Fig. 2B), with the mean NCP ranging from $-44.23 \pm 7.75 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in October to $16.1 \pm 13.93 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in April. The monospecific meadow was autotrophic during the year, with an annual weighted average NCP ($64.63 \pm 11.89 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) significantly higher than 0 (t -test, $p < 0.05$). On the other hand, the annual weighted average NCP of the mixed meadow ($-4.15 \pm 9.39 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) was not significantly different from 0 (t -test, $p > 0.05$).

Temperature and site had a significant effect on NCP (lm; site \times temperature $F_{1,58} = 16.28$, $p < 0.001$) with a different response depending on the site (Fig. 3A). While the NCP of the monospecific meadow significantly increased with increasing temperature ($p < 0.0001$), the NCP of the mixed meadow tended to

Table 1. Mean (\pm SE) net community production (NCP), respiration (R), gross primary production (GPP) and GPP:R ratio over the year and the annual weighted average (\pm SE) for each parameter in the *Enhalus acoroides* monospecific and the *Cymodocea serrulata* and *Halodule uninervis* mixed meadows. Blank cells indicate data not available

Sampling month	NCP (mmol O ₂ m ⁻² d ⁻¹)		R (mmol O ₂ m ⁻² d ⁻¹)		GPP (mmol O ₂ m ⁻² d ⁻¹)		GPP:R	
	<i>E. acoroides</i>	<i>C. serrulata</i> and <i>H. uninervis</i>	<i>E. acoroides</i>	<i>C. serrulata</i> and <i>H. uninervis</i>	<i>E. acoroides</i>	<i>C. serrulata</i> and <i>H. uninervis</i>	<i>E. acoroides</i>	<i>C. serrulata</i> and <i>H. uninervis</i>
June	108.89 \pm 7.75		-231.39 \pm 33.37		340.28 \pm 39.63		1.49 \pm 0.05	
July	139.15 \pm 11.16	13.18 \pm 7.71	-278.83 \pm 24.85	-254.15 \pm 5.99	417.97 \pm 35.61	267.33 \pm 9.40	1.50 \pm 0.01	1.05 \pm 0.03
August	95.45 \pm 16.27	14.47 \pm 16.21	-168.46 \pm 29.60	-256.20 \pm 21.04	263.91 \pm 45.51	270.67 \pm 34.26	1.57 \pm 0.03	1.04 \pm 0.06
September		-36.55 \pm 16.83		-342.17 \pm 53.97		305.62 \pm 61.21		0.88 \pm 0.07
October		-44.23 \pm 7.75		-307.48 \pm 19.51		263.26 \pm 19.93		0.85 \pm 0.03
November	45.48 \pm 8.63	3.22 \pm 4.53	-165.56 \pm 21.23	-233.47 \pm 36.01	211.04 \pm 28.46	236.69 \pm 38.53	1.27 \pm 0.04	1.01 \pm 0.02
February	34.58 \pm 12.23	12.17 \pm 9.97	-152.97 \pm 21.71	-91.30 \pm 20.38	187.55 \pm 27.86	103.47 \pm 10.44	1.24 \pm 0.10	1.22 \pm 0.13
April	73.69 \pm 17.66	16.10 \pm 13.93	-109.40 \pm 11.00	-159.81 \pm 33.14	183.09 \pm 27.94	175.90 \pm 22.02	1.65 \pm 0.10	1.15 \pm 0.09
Annual weighted average	64.63 \pm 11.89	-4.15 \pm 9.39	-152.12 \pm 17.73	-217.72 \pm 27.98	216.75 \pm 25.34	213.58 \pm 23.04	1.42 \pm 0.06	1.04 \pm 0.05

slightly decrease, although the slope was not statistically different from 0 ($p > 0.05$). In contrast, site and temperature did not have an effect on NPC when standardized by plant biomass. However, the same trend was detected: the NCP of the mixed meadow slightly decreased with increasing temperature ($y = 0.006x + 0.16$, $R^2 = 0.03$), and the NCP of the monospecific meadow increased with temperature (GLM; temperature $\chi^2_{1,22} = 10.86$, $p < 0.001$, $y = 0.009x - 0.16$, $R^2 = 0.37$).

3.3. Respiration

In the monospecific meadow, respiration rates peaked in July (-278.83 ± 24.85 mmol O₂ m⁻² d⁻¹) and were more than 2-fold higher than respiration rates in the winter months (November–April), reaching the lowest value in April (-109.4 ± 10.1 mmol O₂ m⁻² d⁻¹; Table 1, Fig. 2A). Respiration rates of the mixed meadow peaked in September (-342.17 ± 53.97 mmol O₂ m⁻² d⁻¹), 2 mo later than in the monospecific meadow, and were almost 4-fold higher than the lowest value detected in February (-91.3 ± 20.38 mmol O₂ m⁻² d⁻¹; Fig. 2B). In August, respiration was significantly higher in the mixed meadow compared to the monospecific meadow (Table S1). The annual weighted average respiration was higher in the mixed meadow with -217.72 ± 27.98 mmol O₂ m⁻² d⁻¹ compared to -152.12 ± 17.73 mmol O₂ m⁻² d⁻¹ in the monospecific meadow.

Temperature and site had a significant effect on respiration (lm; temperature $F_{1,58} = 28.95$, $p < 0.0001$; site $F_{1,58} = 4.1$, $p < 0.05$). The magnitude of respiration rates increased linearly with increasing temperature in the monospecific ($p < 0.05$) and mixed ($p < 0.0001$) meadows (Fig. 3B). The same effect was seen when respiration rates were standardized by plant biomass (GLM; temperature $\chi^2_{1,56} = 5.0$, $p < 0.05$; site $\chi^2_{1,56} = 34.28$, $p < 0.0001$, monospecific meadow: $y = -0.03x + 0.42$, $R^2 = 0.22$, mixed meadow: $y = -0.03x + 0.05$, $R^2 = 0.13$). The associated activation energies of community respiration were 0.32 ± 0.17 and 0.87 ± 0.12 eV for the monospecific and mixed meadows, respectively (Fig. 4A).

3.4. Gross primary production

The highest GPP in the monospecific meadow was detected in July (417.97 ± 35.61 mmol O₂ m⁻² d⁻¹) and was significantly higher than the GPP measured

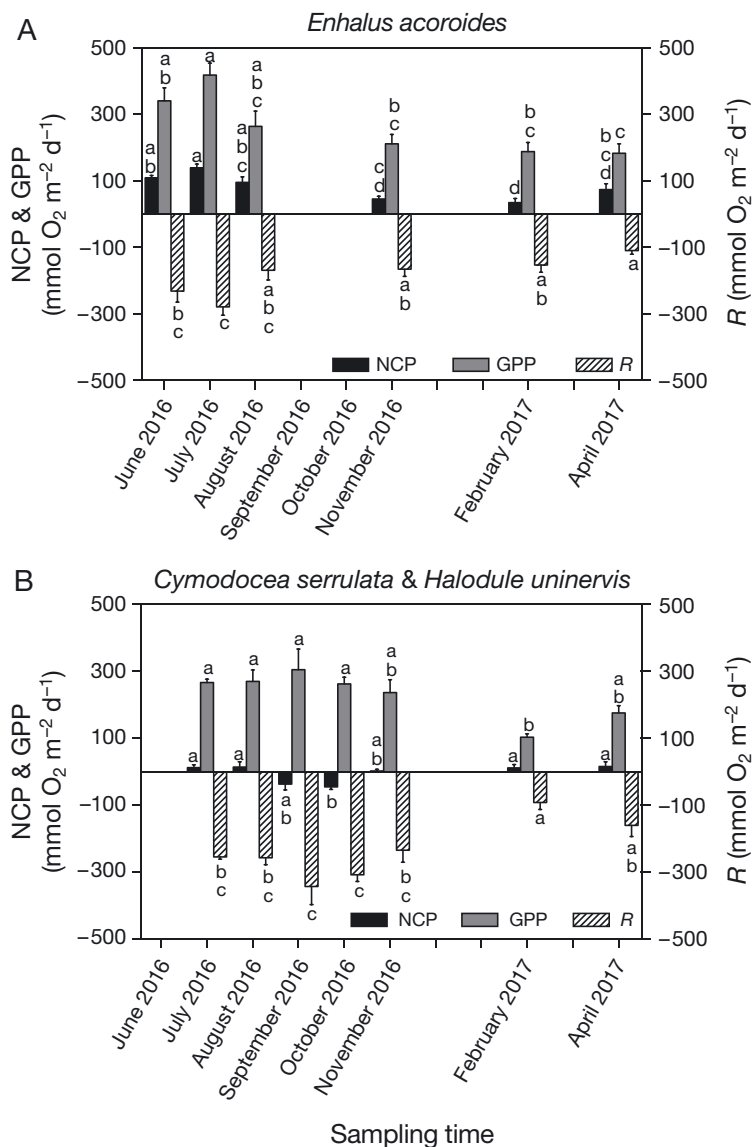


Fig. 2. Mean (\pm SE) net community production (NCP, black), gross primary production (GPP, gray) and respiration (R , striped) over the year in the (A) monospecific and (B) mixed meadows. Letters indicate differences among sampling months (ANOVA test)

during the winter months (November–April, Table 1, Fig. 2A). The highest GPP in the mixed meadow was detected in September (305.62 ± 61.21 mmol O₂ m⁻² d⁻¹) and was 3-fold higher than the lowest GPP, which was detected in February (103.47 ± 10.44 mmol O₂ m⁻² d⁻¹; Fig. 2B). The GPP of the monospecific meadow was significantly higher than the GPP of the mixed meadow in July and February (Table S1). The annual weighted average GPPs were very similar in both sites: 213.58 ± 23.04 and 216.75 ± 25.34 mmol O₂ m⁻² d⁻¹ in the mixed and the monospecific meadows, respectively.

Temperature and site had a significant effect on GPP (lm; temperature $F_{1,58} = 37.33$, $p < 0.0001$; site $F_{1,58} = 7.31$, $p < 0.01$). GPP increased linearly with increasing temperature in the monospecific ($p < 0.001$) and mixed ($p < 0.0001$) meadows (Fig. 3C). The same trend was seen when GPP was standardized by plant biomass (GLM; temperature $\chi^2_{1,56} = 4.96$, $p < 0.05$; site $\chi^2_{1,56} = 24.74$, $p < 0.0001$, monospecific meadow: $y = 0.04x - 0.4$, $R^2 = 0.34$, mixed meadow: $y = 0.04x - 0.1$, $R^2 = 0.09$). The associated activation energies of the community GPP were 0.49 ± 0.15 and 0.72 ± 0.11 eV for the monospecific and mixed meadows, respectively (Fig. 4B).

3.5. GPP:R ratio

The GPP:R ratio was significantly higher in the monospecific meadow than in the mixed meadow, except for February (Table S1), and it was higher than 1 throughout the year in the monospecific meadow with an annual weighted average ratio of 1.42 ± 0.06 (Table 1). The mixed meadow, on the other hand, showed a GPP:R ratio of < 1 in September and October and had an annual weighted average ratio of 1.04 ± 0.05 (Table 1). While the annual weighted average GPP:R ratio in the monospecific meadow was significantly higher than 1 (t -test, $p < 0.05$), GPP:R in the mixed meadow was not significantly higher than 1 (t -test, $p > 0.05$). There was an effect of temperature and site on GPP:R (GLM; site \times temperature $\chi^2_{1,55} = 16.4$, $p < 0.0001$). While GPP:R increased linearly with increasing temperature in the monospecific meadow (GLM; $\chi^2_{1,22} = 9.41$, $p < 0.01$), it decreased in the mixed meadow (GLM; $\chi^2_{1,33} = 6.91$, $p < 0.01$) (Fig. 3D).

3.6. Community PI curves

The community production efficiency (α) extracted from the community PI curves (Fig. S2 in the Supplement) ranged from 0.42 ± 0.17 to 0.02 ± 0.01 mmol O₂ h⁻¹ (μ mol photons s⁻¹)⁻¹ in September and February, respectively (Table 2). The annual weighted average α was 0.06 ± 0.03 and 0.09 ± 0.04 mmol O₂ h⁻¹ (μ mol photons s⁻¹)⁻¹ in the monospecific and mixed meadows, respectively, with no significant differences be-

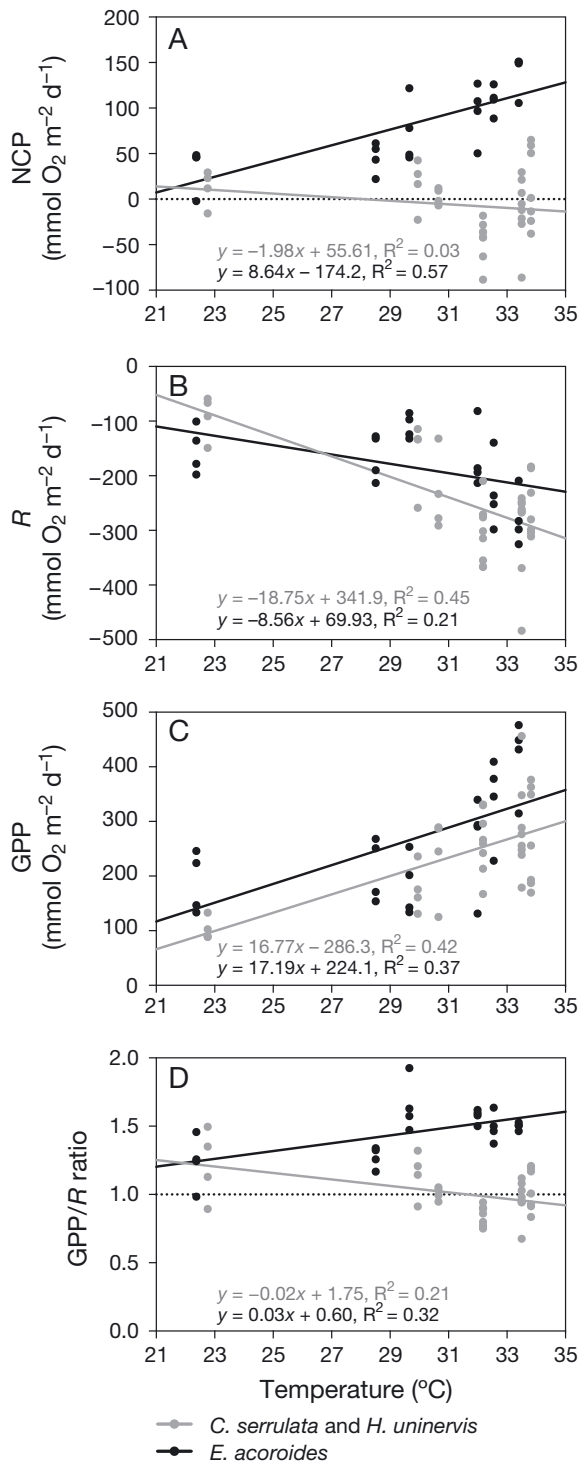


Fig. 3. Relationship of temperature with (A) net community production (NCP), (B) respiration (R), (C) gross primary production (GPP) and (D) GPP:R ratio in the monospecific (*Enhalus acoroides*, black dots) and mixed (*Cymodocea serrulata* and *Halodule uninervis*, gray dots) meadows. Solid lines indicate the linear regression for the monospecific meadow (black) and the mixed meadow (gray). Dashed lines in (A) and (D) indicate the threshold from autotrophic to heterotrophic communities

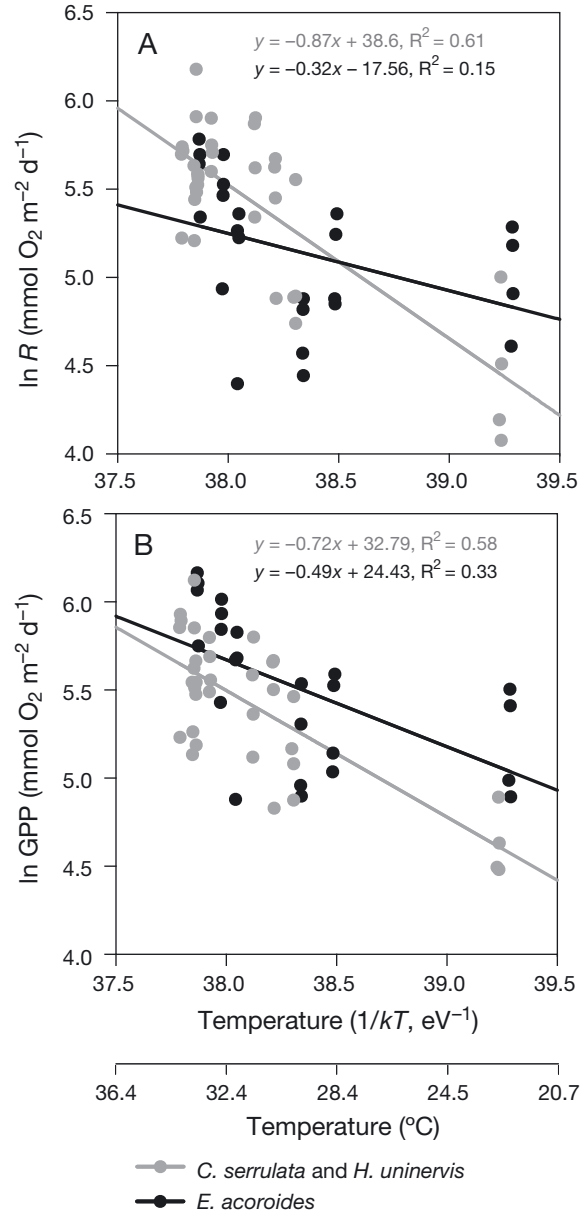


Fig. 4. Arrhenius plots showing the relationship between the inverted temperature multiplied by the Boltzmann constant (1/kT) and the natural logarithm of (A) respiration (R) and (B) gross primary production (GPP) for the monospecific (black dots) and mixed (gray dots) meadows. Solid lines indicate the linear regression for the monospecific meadow (black) and the mixed meadow (gray). Corresponding temperatures (in °C) are shown in the lower x-axis

tween meadows (Wilcoxon matched-pairs test, $p > 0.05$; Mann-Whitney test, $p > 0.05$; Table 2).

The highest P_{max} in the mixed meadow (4.62 mmol O₂ m⁻² h⁻¹) was reached in August coinciding with the highest temperature, while in the monospecific meadow, the highest P_{max} (8.17 mmol O₂ m⁻² h⁻¹) was detected in February at the lowest temperature

Table 2. Results from community production–irradiance curves for both sites per sampling month and the annual weighted average (\pm SE) for each parameter. Community production efficiency (α), light saturation point (I_k) and community respiration (R) were derived from the model (mean \pm SE), while maximum community production (P_{\max}) and community compensation irradiance (I_c) were calculated from the model equation (mean). Blank cells indicate data not available

Sampling month	<i>Enhalus acoroides</i>					<i>Cymodocea serrulata</i> and <i>Halodule uninervis</i>				
	α (mmol O ₂ h ⁻¹ [μmol photons s ⁻¹ J ⁻¹])	I_c (μmol photons m ⁻² s ⁻¹)	I_k (μmol photons m ⁻² s ⁻¹)	P_{\max} (mmol O ₂ m ⁻² h ⁻¹)	R (mmol O ₂ m ⁻² h ⁻¹)	α (mmol O ₂ h ⁻¹ [μmol photons s ⁻¹ J ⁻¹])	I_c (μmol photons m ⁻² s ⁻¹)	I_k (μmol photons m ⁻² s ⁻¹)	P_{\max} (mmol O ₂ m ⁻² h ⁻¹)	R (mmol O ₂ m ⁻² h ⁻¹)
June	0.15 \pm 0.03	32.08	64.42 \pm 11.44	4.86	-4.82 \pm 0.58	0.09 \pm 0.02	59.90	96.46 \pm 18.01	3.10	-5.08 \pm 0.59
July	0.07 \pm 0.02	62.21	149.02 \pm 32.02	6.24	-4.47 \pm 0.64	0.03 \pm 0.01	124.08	298.26 \pm 73.23	4.62	-3.29 \pm 0.57
August	0.02 \pm 0.01	123.55			-2.58 \pm 0.49	0.42 \pm 0.17	24.62	30.45 \pm 10.41	2.42	-10.21 \pm 1.27
September						0.16 \pm 0.03	48.43	64.75 \pm 11.54	2.60	-7.72 \pm 0.63
October	0.18 \pm 0.09	22.44	35.95 \pm 15.28	2.48	-4.13 \pm 0.75	0.07 \pm 0.02	69.40	110.65 \pm 30.01	2.94	-4.95 \pm 0.66
November	0.02 \pm 0.01	129.56	532.96 \pm 701.30	8.17	-2.62 \pm 0.50	0.02 \pm 0.01	114.02	217.93 \pm 47.89	2.11	-2.32 \pm 0.31
February	0.02 \pm 0.01	77.88	218.47 \pm 59.28	3.14	-1.74 \pm 0.38	0.03 \pm 0.01	128.50	201.59 \pm 48.59	1.99	-3.49 \pm 0.46
April						0.09 \pm 0.04	92.22 \pm 14.0	159.40 \pm 29.28	2.53 \pm 0.27	-4.71 \pm 0.93
Annual weighted average	0.06 \pm 0.03	83.89 \pm 16.16	243.06 \pm 88.29	4.39 \pm 1.21	-2.78 \pm 0.42					

(Table 2, Fig. S2). The annual weighted average P_{\max} was significantly higher in the monospecific meadow than in the mixed meadow (4.39 ± 1.21 and 2.53 ± 0.27 mmol O₂ m⁻² h⁻¹, respectively, Mann-Whitney test, $p < 0.05$).

In the monospecific meadow, both I_k (532.96 ± 701.3 μmol photons m⁻² s⁻¹) and I_c (129.56 μmol photons m⁻² s⁻¹) were highest in February, while the mixed meadow experienced its highest I_k (298.26 ± 73.23 μmol photons m⁻² s⁻¹) in August and its highest I_c (128.5 μmol photons m⁻² s⁻¹) in April (Table 2, Fig. S2). The I_k estimate for the monospecific meadow involves considerable error, as indicated by its high standard error, even if an O₂ saturation point was clearly reached. The annual weighted average I_k was 243.06 ± 88.29 and 159.4 ± 29.28 μmol photons m⁻² s⁻¹ in the monospecific and mixed meadows, respectively, with no significant differences between sites (Wilcoxon matched-pairs test, $p > 0.05$; Mann-Whitney test, $p > 0.05$). The annual weighted average I_c was similar in both sites, with 83.86 ± 16.16 μmol photons m⁻² s⁻¹ in the monospecific meadow and 92.22 ± 14.0 μmol photons m⁻² s⁻¹ in the mixed meadow, with no significant differences (paired t -test, $p > 0.05$; unpaired t -test, $p > 0.05$).

The monospecific meadow experienced the highest respiration rate in June (-4.82 ± 0.58 mmol O₂ m⁻² h⁻¹) and the lowest in April (-1.74 ± 0.42 mmol O₂ m⁻² h⁻¹). In the mixed meadow, the lowest R (-2.32 ± 0.31 mmol O₂ m⁻² h⁻¹) was detected in February, while the highest R (-10.21 ± 1.27 mmol O₂ m⁻² h⁻¹) was detected in September (Table 2, Fig. S2). Annual weighted average R values were -2.78 ± 0.42 and -4.71 ± 0.93 mmol O₂ m⁻² h⁻¹ in the monospecific and mixed meadows, respectively, with no significant differences between sites (paired t -test, $p > 0.05$; unpaired t -test, $p > 0.05$).

4. DISCUSSION

Here we present, for the first time, the metabolic rates and thermal dependence of 2 seagrass ecosystems in the Red Sea, with species-specific results. While the *Enhalus acoroides* meadow was clearly autotrophic throughout the year, the mixed *Cymodocea serrulata* and *Halodule uninervis* meadow was heterotrophic during the summer months. This trend was also confirmed by the mixed meadow having activation energies for both GPP and R twice as high as those of the monospecific meadow, indicating its higher thermal sensitivity compared to the monospecific meadow. These differences in community meta-

bolism between the 2 meadows can be attributed to multiple factors, such as seagrass biomass density, infauna biomass, epiphyte loads and sediment characteristics, besides the foundation seagrass species. The results presented here were therefore not the sole response of a single seagrass species but represent potential differences in the community composition, including microbial and metazoan components as well as epiphytic algae, of the 2 seagrass meadows studied.

The annual weighted average NCP of the *E. acoroides* meadow in the Red Sea was almost 3-fold greater than the global average rate of $23.7 \pm 7.8 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for tropical seagrass meadows (Duarte et al. 2010). A similar trend was stated by Duarte et al. (2010), who noted that the only available record of *E. acoroides* was 5-fold higher than the global average NCP for all seagrass meadows ($27.2 \pm 5.8 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$). In contrast, the annual weighted average NCP of the *C. serrulata* and *H. uninervis* meadow in the Red Sea was considerably lower than the global average. The annual weighted average respiration in the mixed meadow was remarkably similar to the reported global average of tropical seagrass meadows ($-217.48 \pm 13.9 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, Duarte et al. 2010), while the annual weighted average respiration was lower in the monospecific meadow. The annual weighted average GPP in both meadows was very similar, yet both rates were slightly lower than the global average of tropical seagrass meadows ($252.30 \pm 14.47 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, Duarte et al. 2010). The difference in respiration was also reflected in the GPP:R ratio, as the mixed meadow, with its higher respiration, consequently had a lower GPP:R ratio, indicating a more balanced state of the ecosystem, while the monospecific meadow was clearly autotrophic. However, the global P:R ratio of tropical seagrass meadows (1.61 ± 0.19 ; Duarte et al. 2010) was somewhat higher than the ratios reported in this study, particularly for the mixed meadow.

As expected, increasing temperature had significant effects on all metabolic rates, with both R and GPP increasing with warming in both meadows. In contrast, opposite responses were seen in NCP measurements, with NCP increasing with increasing temperature in the *E. acoroides* meadow and decreasing with increasing temperature in the mixed meadow. Even though these species have shown to be capable of withstanding higher temperatures (Collier et al. 2011, 2017, Adams et al. 2017), our results confirmed that the mixed meadow experienced thermal stress at higher temperatures. However, on a community

level, we not only see the response of the foundation seagrass species but can also account for the changes in the metabolism of other primary producers present in the community. We can therefore assume that the *C. serrulata* and *H. uninervis* community had already exceeded its thermal optimum in the Red Sea. When seagrass communities become heterotrophic, they act as O_2 sinks, which would favor sulfide production and likely lead to a risk of seagrass mortality (Calleja et al. 2007, Garcias-Bonet et al. 2008). The mixed meadow was exposed to higher temperatures ($>32^\circ\text{C}$) for an extended period of time, while the temperature in the monospecific meadow was already 2°C lower. A negative effect of extended exposure times was also reported for *C. serrulata* and *H. uninervis* (Collier et al. 2018) and for *Zostera marina* (Beca-Carretero et al. 2018). *E. acoroides* did not seem to be negatively affected during the warmer summer months, suggesting that *E. acoroides* in the Red Sea had a higher optimal temperature than previously reported, possibly due to local adaptations and acclimation to the conditions in this exceptionally warm sea (Berry & Bjorkman 1980). Additionally, its large shoot size and the density of the meadow make it more prone to self-shading, which may play a protective role against warm temperatures by reducing exposure to saturating light levels at which photosynthesis is particularly impacted by high temperature (Pedersen et al. 2013). While we saw mixed responses, Egea et al. (2019) reported a positive effect of increased seawater temperature on a *C. nodosa* meadow in southern Spain, indicating that this community was still well below its thermal optimum. They reported the meadow to be more autotrophic when exposed to short-term heatwaves, highlighting a potential positive effect of elevated temperatures on healthy seagrass meadows below their thermal limit (Egea et al. 2019).

The thermal dependence of these 2 meadows confirmed the overall trend in this study. Generally, the monospecific meadow had lower activation energies, indicating that the metabolism of the mixed meadow was more sensitive to temperature. The monospecific meadow had a higher activation energy for GPP than for R. Beca-Carretero et al. (2018) reported a similar trend in *Z. marina*, with activation energies of leaf respiration (0.27–0.46 eV) and rhizome respiration (0.53–0.67 eV) lower than their results for P_{max} (0.77–0.99 eV). In contrast, the mixed meadow had a higher activation energy for R compared to GPP, albeit none of these differences were statistically significant, explaining the lower GPP:R ratio at higher temperatures in summer and the overall lower GPP:R ratio

compared to the monospecific meadow (Regaudie-De-Gioux & Duarte 2012). Our results therefore confirmed that the mixed meadow was more sensitive to higher temperatures and was more likely to shift to a heterotrophic state with warming.

Contrary to our expectations and previous results, the monospecific meadow did not show PI curve characteristics of a shade-adapted species. Shade-adapted species compensate for lower light availability by exhibiting lower I_k values (Campbell et al. 2007). Even though *E. acoroides* is more likely to be shade-adapted because of its size and the density of the meadow, neither the higher I_k nor the lower photosynthetic efficiency compared to the mixed meadow indicated an adaptation at the community level (Larkum et al. 2006). However, the highest α coincided with the lowest I_k and the lowest I_c in both meadows, confirming a photoadaptive response of both meadows to being more efficient at low light levels (Campbell et al. 2007). Georgiou et al. (2016) reported an increasing photosynthetic efficiency with increasing temperature for *Halophila stipulacea* in the Mediterranean, while Pollard & Greenway (2013) found the same trend for *C. serrulata* in Australia. However, this trend could not be confirmed in our study, as we saw mixed responses throughout the year.

Both P_{\max} and R were generally higher during the warmer summer months, confirming the expectation that both parameters increase with increasing temperature (Georgiou et al. 2016), with high P_{\max} values at higher temperatures indicating a response mechanism to compensate for higher respiration rates caused by higher temperatures (Pollard & Greenway 2013). While R was highest in summer in both meadows, the elevated response was higher in the mixed meadow (5-fold) compared to the monospecific meadow (3-fold), confirming the general trend that it is more sensitive to temperature (Pollard & Greenway 2013).

In summary, our results suggest a species-specific response of seagrass meadows to increasing seawater temperatures in the Red Sea. On the one hand, the monospecific *E. acoroides* meadow did not show signs of thermal stress, seemed to be well below its thermal optimum and showed relatively low activation energy for community metabolism. On the other hand, in the mixed *C. serrulata* and *H. uninervis* meadow, the community metabolism increased steeply with increasing temperature and shifted to a heterotrophic state at higher temperatures, turning the meadow into a carbon source rather than a carbon sink. It can therefore be implied that some seagrass

species in the Red Sea, even though they are expected to be adapted to higher temperatures, grow close to or already exceed their thermal optima during the warmest period of the year. The steep warming that the Red Sea is experiencing is likely to pose serious challenges to the more vulnerable species, such as those in the mixed seagrass meadow studied here. These results confirm that some seagrasses in the Red Sea are thermally stressed, which may have important implications for the future of the essential ecosystem functions and services seagrass ecosystems perform in the Red Sea.

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