



Iron Deficiency in Seagrasses and Macroalgae in the Red Sea Is Unrelated to Latitude and Physiological Performance

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Iron can limit primary production in shallow marine systems, especially in tropical waters characterized by carbonated sediments, where iron is largely trapped in a non-available form. The Red Sea, an oligotrophic ecosystem characterized by a strong N-S latitudinal nutrient gradient, is a suitable setting to explore patterns *in situ* of iron limitation in macrophytes and their physiological performance under different iron regimes. We assessed the interactions between environmental gradients and physiological parameters of poorly-studied Red Sea macrophytes. Iron concentration, chlorophyll *a* concentration, blade thickness, and productivity of 17 species of macrophytes, including seven species of seagrasses and 10 species of macroalgae, were measured at 21 locations, spanning 10 latitude degrees, along the Saudi Arabian coast. Almost 90% of macrophyte species had iron concentrations below the levels indicative of iron sufficiency and more than 40% had critically low iron concentrations, suggesting that iron is a limiting factor of primary production throughout the Red Sea. We did not identify relationships between tissue iron concentration, chlorophyll *a* concentration and physiological performance of the 17 species of seagrass and macroalgae. There was also no latitudinal pattern in any of the parameters studied, indicating that the South to North oligotrophication of the Red Sea is not reflected in iron concentration, chlorophyll *a* concentration or productivity of Red Sea macrophytes.

Keywords: coral reefs, fluorescence, latitudinal gradient, macroalgae, oligotrophic, primary production, seagrass, seaweed

INTRODUCTION

Iron (Fe) is an essential nutrient that can act as a limiting factor controlling primary production in freshwater and marine systems (Coale et al., 1996; Sterner et al., 2004). In particular, iron limits phytoplankton production across vast spans of the open ocean (Martin et al., 1994; Welch and Shuman, 1995). Iron can also limit primary production in shallow marine systems, especially in

carbonated sediments characterized by very low iron pools (Pestana et al., 2003). Observations and field experiments provide evidence of iron deficiency in seagrasses growing on carbonate sediments (Marbà et al., 2008), where iron addition to sediments stimulates seagrass growth in the Yucatan Peninsula (Duarte et al., 1995), Southern Florida (Chambers et al., 2001), and the Balearic Islands (Marbà et al., 2007). Field observations on coral reefs, which are also carbonate-rich habitats, also suggest potential iron limitation in the growth of macroalgae, as indicated by higher growth rates of these macrophytes near ship wrecks, which leak iron in micronutrient-poor islands in the Central Pacific (Kelly et al., 2012).

Iron limits the growth of primary producers because it is required for the synthesis of photosynthetic pigments and the functioning of the key enzyme in photosynthesis, Rubisco (Winder and Nishio, 1995). As such, iron concentration has been positively linked to pigment concentration across many groups

of primary producers (Geider et al., 1993; Abadía, 2008). In marine benthic habitats, experimental iron additions in plots of seagrasses growing on coralline carbonate sediments in the Caribbean increased the chlorophyll *a* (Chl *a*) concentration in seagrass leaves and enhanced seagrass growth (Duarte et al., 1995). Moreover, iron addition experiments show that the survival of seedlings and growth of young plants of the seagrass *Zostera marina* can be limited by iron availability (Wang et al., 2017). However, there is a paucity of studies *in situ* across a broad range of iron inputs to assess effects on primary production in marine benthic ecosystems (Marbà et al., 2008).

The Red Sea is a suitable location to describe patterns of primary production under different iron regimes. The Red Sea is an oligotrophic ecosystem characterized by a strong nutrient gradient, including potentially trace metals like iron, driven by the depletion of nutrients as the water entering the southern Red Sea from the Gulf of Aden flows north (Raitsoos et al., 2015).

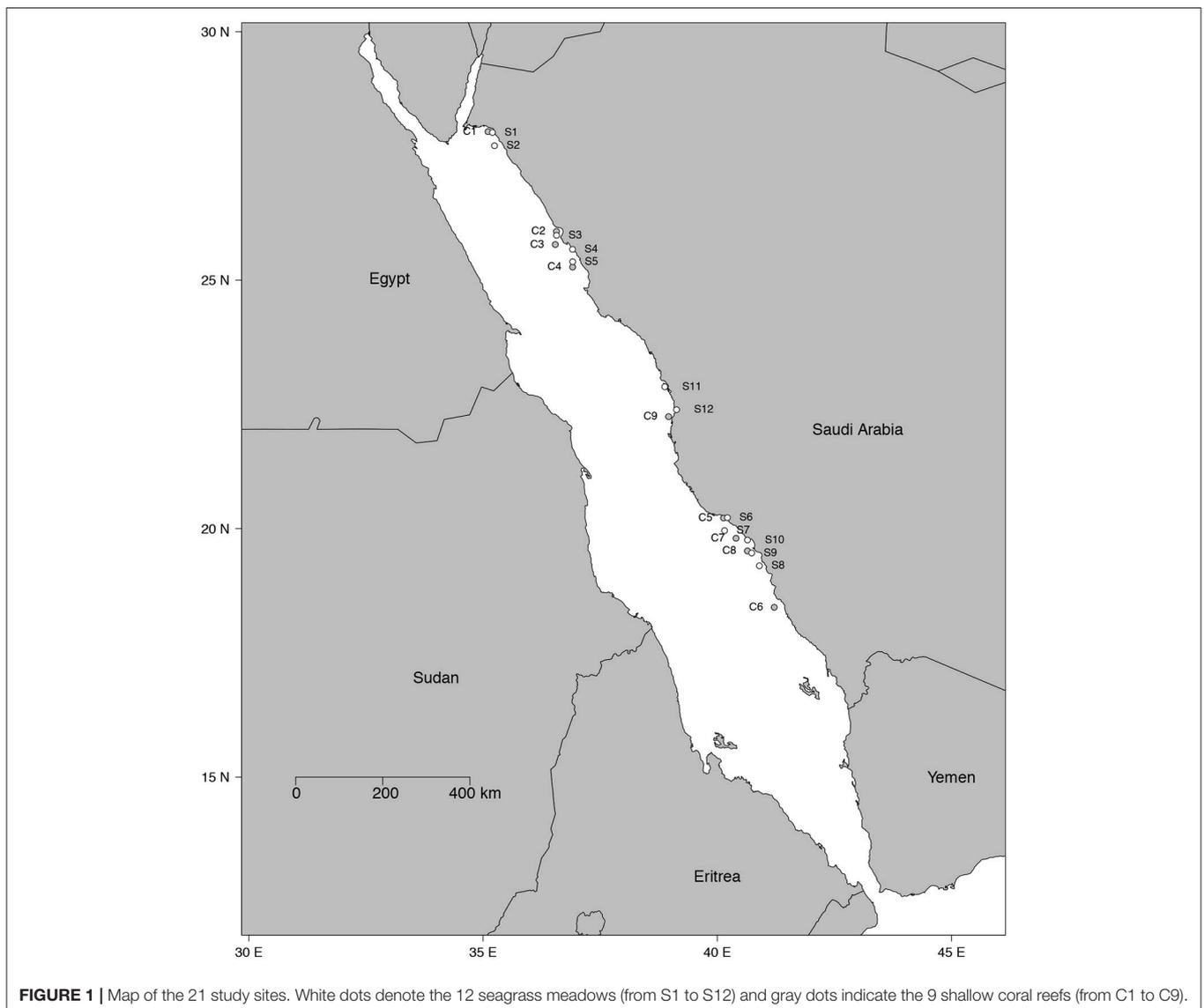


FIGURE 1 | Map of the 21 study sites. White dots denote the 12 seagrass meadows (from S1 to S12) and gray dots indicate the 9 shallow coral reefs (from C1 to C9).

This nutrient gradient is associated with a gradual decrease of Chl *a* concentration in phytoplankton from south to north of the Red Sea (Raitos et al., 2013; Kürten et al., 2015). This gradient is especially prominent during the summer months and more diffuse during the winter, when wind-driven water-mixing replenishes the nutrients in the sea surface in the northern Red Sea (Sofianos and Johns, 2003). This gradient also affects primary production in the ubiquitous coral *Pocillopora verrucosa* (Sawall et al., 2015) and to a certain extent phytoplankton growth (Qurban et al., 2017). Thus, the Red Sea presents a unique environment to study the effect of iron concentration regimes *in situ*. Indeed, Almahasheer et al. (2016a) reported the dominant mangrove species *Avicennia marina* to be iron-limited in the Central Red Sea.

The Red Sea, with the exception of the Gulf of Aqaba, is grossly understudied when compared to other vast coral reef regions such as the Great Barrier Reef, the Coral Reef Triangle, the Caribbean Basin or the Hawaiian Archipelago. With a few exceptions (Almahasheer et al., 2016a,b,c), corals and phytoplankton are the main focus of research on primary producers in the Red Sea (Cantin et al., 2010; Ziegler et al., 2014; Kürten et al., 2015; Sawall et al., 2015; Roik et al., 2016; Qurban et al., 2017, among others). However, other important and

uncharismatic habitat-forming macrophytes, such as seagrasses and macroalgae within coral reefs (Duarte et al., 2008), are common but poorly studied in the Red Sea.

Here we assessed patterns of iron concentration in macrophyte tissue and its association with macrophyte productivity, as a proxy of iron availability, along a latitudinal gradient in the Saudi Arabian Red Sea. Specifically, we sampled macrophytes from 12 seagrass meadows and 9 shallow coral reefs spanning nearly 10 latitudinal degrees (Figure 1). Our first goal was to describe tissue iron concentration, Chl *a* concentration, blade thickness, and physiological performance of seagrass and macroalgae species in the Red Sea and identify potential relationships between these variables. Our second goal was to test for a latitudinal pattern of physiological parameters in the Red Sea associated with tissue iron concentration regimes in macrophytes in general and, in particular, for two ubiquitous species, the seagrass *Halophila stipulacea* and the macroalgae *Turbinaria ornata*. We tested whether productivity was related with the blade thickness and Chl *a* concentration of the photosynthetic tissues, as has been reported for marine plants in general (Enriquez et al., 1995; Enriquez et al., 1996), and whether such potential relationships depended on iron concentration.

TABLE 1 | Study site information and the species surveyed on each site.

Site	Lat.	Long.	D (m)	T (°C)	S (ppt)	Species collected
CORAL REEF SITES						
C1	27.989	35.106	3	23.22	40.53	<i>Dictyosphaeria cavernosa</i> , <i>Turbinaria ornata</i>
C2	25.704	36.568	4	23.87	40.53	<i>Dictyosphaeria cavernosa</i>
C3	25.717	36.542	6	24.13	40.12	<i>Turbinaria ornata</i>
C4	25.363	36.912	6	23.35	40.21	<i>Caulerpa serrulata</i> , <i>Halimeda tuna</i> , <i>Tydemania expeditionis</i>
C5	19.963	40.135	2	27.31	38.71	<i>Turbinaria ornata</i>
C6	18.416	41.216	3	29.1	38.82	<i>Caulerpa racemosa</i> , <i>Halimeda tuna</i> , <i>Halymeria</i> sp., <i>Sargassum ilicifolium</i>
C7	19.505	40.753	3	28.79	38.91	<i>Sargassum ilicifolium</i> , <i>Turbinaria ornata</i>
C8	19.611	40.644	5	28.79	38.91	<i>Halimeda tuna</i> , <i>Udotea flabellum</i>
C9	22.253	38.961	2	27.77	38.73	<i>Halimeda tuna</i> , <i>Turbinaria ornata</i>
SEAGRASS MEADOW SITES						
S1	27.969	35.201	8	22.55	40.65	<i>Halophila stipulacea</i>
S2	27.955	35.245	2	23.32	40.59	<i>Thalassia hemprichii</i> , <i>Thalassodendron ciliatum</i>
S3	25.702	36.569	4	23.87	40.53	<i>Halophila decipiens</i> , <i>Halophila ovalis</i> , <i>Halophila stipulacea</i>
S4	25.362	36.911	1	22.85	40.36	<i>Halodule uninervis</i> , <i>Halophila decipiens</i> , <i>Halophila ovalis</i>
S5	25.371	36.914	1	22.85	40.36	<i>Halodule uninervis</i> , <i>Padina pavonica</i>
S6	20.159	40.217	0.5	26.23	40.58	<i>Halophila decipiens</i> , <i>Halimeda tuna</i> , <i>Halodule uninervis</i> , <i>Padina pavonica</i> , <i>Thalassia hemprichii</i>
S7	19.959	40.155	0.5	29.53	38.68	<i>Halophila stipulacea</i> , <i>Halodule uninervis</i> , <i>Thalassia hemprichii</i>
S8	19.27	40.899	0.5	29.01	38.89	<i>Caulerpa racemosa</i> , <i>Halophila decipiens</i> , <i>Thalassia hemprichii</i>
S9	19.509	40.735	1	29.06	37.45	<i>Thalassia hemprichii</i>
S10	19.682	40.645	0.5	29.47	38.86	<i>Halophila ovalis</i> , <i>Halophila stipulacea</i> , <i>Halodule uninervis</i> , <i>Thalassia hemprichii</i> , <i>Udotea flabellum</i>
S11	22.934	38.88	1.5	27.9	41.3	<i>Halophila stipulacea</i>
S12	22.393	39.131	1.5	29.44	41.43	<i>Enhalus acoroides</i>

Lat, Long, D, T, and S indicate latitude, longitude, depth, temperature, and salinity, respectively. Number of replicates indicated in Table 2.

TABLE 2 | Number of replicates collected on each study site per species.

Site	Species	n1	n2
C1	<i>D. cavernosa</i>	3	0
C1	<i>T. ornata</i>	3	3
C2	<i>D. cavernosa</i>	5	2
C3	<i>T. ornata</i>	5	4
C4	<i>C. serrulata</i>	3	2
C4	<i>H. tuna</i>	4	0
C4	<i>T. expeditionis</i>	6	2
C5	<i>T. ornata</i>	6	4
C6	<i>C. racemosa</i>	6	2
C6	<i>H. tuna</i>	0	2
C6	<i>Halymenia</i> sp.	2	2
C6	<i>S. ilicifolium</i>	0	2
C7	<i>S. ilicifolium</i>	5	2
C7	<i>T. ornata</i>	5	4
C8	<i>H. tuna</i>	3	2
C8	<i>U. flabellum</i>	2	2
C9	<i>H. tuna</i>	0	2
C9	<i>T. ornata</i>	3	4
S1	<i>H. stipulacea</i>	9	4
S2	<i>T. hemprichii</i>	6	2
S2	<i>T. ciliatum</i>	6	2
S3	<i>H. decipiens</i>	0	2
S3	<i>H. ovalis</i>	3	1
S3	<i>H. stipulacea</i>	10	4
S4	<i>H. uninervis</i>	2	0
S4	<i>H. decipiens</i>	5	2
S4	<i>H. ovalis</i>	6	2
S5	<i>H. uninervis</i>	6	2
S5	<i>P. pavonica</i>	2	2
S6	<i>H. decipiens</i>	0	2
S6	<i>H. tuna</i>	0	2
S6	<i>H. uninervis</i>	9	1
S6	<i>P. pavonica</i>	0	2
S6	<i>T. hemprichii</i>	6	1
S7	<i>H. stipulacea</i>	8	4
S7	<i>H. uninervis</i>	0	2
S7	<i>T. hemprichii</i>	3	2
S8	<i>C. racemosa</i>	6	2
S8	<i>H. decipiens</i>	0	2
S8	<i>T. hemprichii</i>	8	1
S9	<i>T. hemprichii</i>	3	2
S10	<i>H. ovalis</i>	6	1
S10	<i>H. stipulacea</i>	8	4
S10	<i>H. uninervis</i>	0	2
S10	<i>T. hemprichii</i>	8	2
S10	<i>U. flabellum</i>	0	2
S11	<i>H. stipulacea</i>	6	4
S12	<i>E. acoroides</i>	6	2

n1 indicates number of replicates of ETR_{max} ($\mu\text{mol electrons m}^{-2} \text{s}^{-1}$), Chl *a* (mg g^{-1} DW), and thickness (mm) and n2 indicates number of replicates of iron concentration (mg kg^{-1} DW). For full names of species see **Table 1**.

MATERIALS AND METHODS

Study Sites and Species Information

Twenty-one study sites were surveyed along the Saudi Arabian coast of the Red Sea (**Figure 1**) between February 19th and April 10th 2016 from 18.4 to 27.9° latitude, covering a large range of environmental conditions. *In situ* temperature ranged from 22.6 to 29.5°C and salinity varied from 37.5 to 41.4 ppt (**Table 1**). Sites included 9 shallow coral reefs and 12 seagrass meadows growing at depths ranging between 1 and 8 m (**Table 1**). Specimens of the most common conspicuous species of macroalgae and seagrasses were collected at each study site snorkeling or diving. In total, we evaluated 10 species of macroalgae in coral reefs and seagrass meadows (*Caulerpa racemosa*, *Caulerpa serrulata*, *Dictyosphaeria cavernosa*, *Halimeda tuna*, *Halymenia* sp., *Padina pavonica*, *Sargassum ilicifolium*, *Tydemania expeditionis*, *T. ornata*, and *Udotea flabellum*) and seven species of seagrasses (*Enhalus acoroides*, *Halodule uninervis*, *Halophila decipiens*, *Halophila ovalis*, *H. stipulacea*, *Thalassodendron ciliatum*, and *Thalassia hemprichii*). Chl *a* concentration, thickness, and the maximum electron transport rate of photosystem II, ETR_{max}, a proxy of productivity, were assessed for most of the specimens collected (see **Table 2** for specific number of replicates), after carefully rinsing them with seawater and removing the epiphytes. Thickness was measured on the blades of seagrasses and macroalgae using a Fisherbrand Traceable digital caliper. For irregular macroalgae, blade thickness was assessed on the photosynthetic unit (e.g., the diameter of the spheroids on *C. racemosa* or the height of the pyraminoid blades on *T. ornata*), as reported previously (Agusti et al., 1994). Iron concentration was measured in the tissues of the macrophytes (see **Table 2** for specific number of replicates). Additional measurements of iron concentration were performed for *T. ornata* and *H. stipulacea* at five sites (C1, C3, C5, C7, C9, and S1, S3, S7, S10, S11 for *T. ornata* and *H. stipulacea* respectively, see **Tables 1, 2**) to perform more robust species-specific latitudinal analyses.

Chl *a* and Iron Concentration of Macrophytes

Chl *a* content and iron concentration of seagrass and macroalgae blades were quantified in the fragment of macrophyte where

TABLE 3 | Results of the Kruskal–Wallis rank test comparing ETR_{max} measurements *in situ* in the field and in aquaria.

Species	Study site	n in situ	n in aquaria	X ² -value	p-value
<i>Halophila stipulacea</i>	S1	6	3	0.6	0.438
<i>Halophila stipulacea</i>	S3	6	4	0.3	0.584
<i>Halophila stipulacea</i>	S7	4	4	0.5	0.456
<i>Halophila stipulacea</i>	S10	6	2	0.5	0.456
<i>Halodule uninervis</i>	S6	3	6	1	0.317
<i>Thalassia hemprichii</i>	S8	2	6	2.7	0.095
<i>Thalassia hemprichii</i>	S10	3	5	0	1

n indicates the number of replicates.

the ETR_{max} of photosystem II activity was performed (see Physiological Performance section below). Chl *a* concentration was obtained from a known amount of frozen tissue using a QIAGEN TissueLyser II and extracted overnight in 10 ml of acetone 80%. Pigment concentration was assessed spectrophotometrically by measuring absorbance at 646, 663, and 710 nm. First, absorbance (A) at each wavelength was subtracted from A of the blank following Wellburn (1994):

$$A_{646} = A_{\text{sample}}[646] - A_{\text{blank}}[646]$$

$$A_{663} = A_{\text{sample}}[663] - A_{\text{blank}}[663]$$

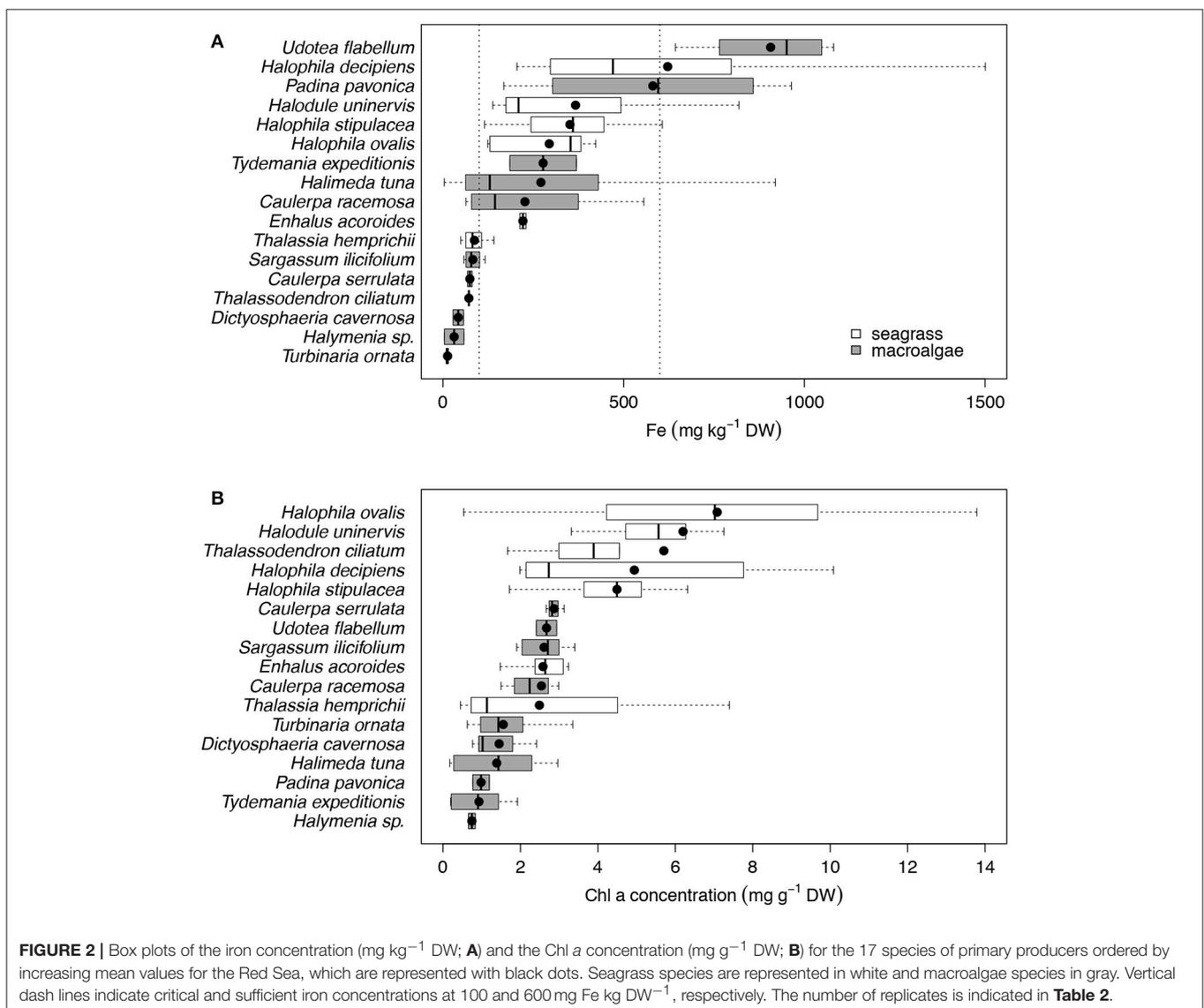
$$A_{710} = A_{\text{sample}}[710] - A_{\text{blank}}[710]$$

Then, the concentration of the Chl *a* was determined as follows (Wellburn, 1994):

$$\text{Chl}a = 12.21 \times (A_{663} - A_{710}) - 2.81 \times (A_{646} - A_{710})$$

We analyzed the iron concentration on the blades of seagrass and macroalgae to assess potential iron limitation in macrophytes since iron content is a robust indicator of the trace metal status of seagrasses (Duarte et al., 1995; Chambers et al., 2001). For small species of seagrasses (*H. uninervis*, *H. decipiens*, *H. ovalis*, and *H. stipulacea*) we collected four shoots per replicate and for large species (*E. acoroides*, *T. ciliatum*, and *T. hemprichii*) we collected the second-youngest leaf of four shoots for each replicate. Iron concentration in macroalgae was analyzed within a piece of blade.

Leaves and blades were dried at 60°C and ground using an agate mortar and pestle until powdered. Iron concentrations were determined after digesting 50–100 mg of the powdered tissue material with 5 ml of HNO₃ (69%) and 1 ml of H₂O₂ (30%), using a 2 step temperature microwave heating protocol for 5 min and 10 min at 180°C. The samples were allowed to cool, then diluted with Milli-Q water and analyzed by Inductively



Coupled Plasma-Optical Emission Spectrometry (Varian Inc. model 720-ES).

Physiological Performance

The measurement of the Chl *a* fluorescence is a powerful method of assessing the properties of the photosynthetic apparatus (Ralph and Gademann, 2005) and has been shown to be a good proxy for the productivity of macrophytes (Beer, 1998; Beer and Björk, 2000; Silva et al., 2005). Chl *a* fluorescence was assessed using an underwater Pulse Amplitude Modulated (PAM) shutter fluorometer (Aquation, Australia). Fluorescence measurements were performed *in situ* and soon after collection in intact specimens of macroalgae and seagrasses that were transferred to flow-through aquaria (122 × 50 × 40 cm) filled with water from the nearby study site and therefore kept at *in situ* salinity and temperature and under natural light conditions. The majority of the fluorescence measurements were performed in the aquaria (140 out of 196), due to time constraints in the field, and the rest (56 out of 196) were performed *in situ*. Statistical analyses (see Statistical Analysis section below) indicated no significant differences between the fluorescence measurements performed in the field and at the aquariums for several species of seagrasses at 6 locations (Table 3). For large seagrass species (*E. acoroides*, *T. ciliatum*, and *T. hemprichii*) all measurements took place above the meristem of the second leaf to reduce the effect of variability within leaves. Rapid light curves (RLCs; Ralph and Gademann, 2005) were quantified by applying a saturating pulse to specimens after dark-adaptation for 5 min. Samples were illuminated with a series of 12 increasing actinic light intensities

(from 0 to 990 μmol photons m⁻² s⁻¹) at intervals of 10 s. At the end of each interval a saturating light pulse was applied (~2,800 μmol photons m⁻² s⁻¹) and the effective yield recorded. The absorbance (AF) of each species was measured by placing specimens in front of a PAR sensor and recording the percentage of light absorbed by the sample (Beer, 1998). Irradiance through 1 to 4 layers of leaves or blades was recorded in 3–5 replicates for each species and the *ln* of the recorded irradiance was then plotted against the number of layers. Using a linear correlation, the slope (α) of the resulting line was determined and AF calculated as 1-exp(-α).

The relative Electron Transport Rates (ETR_r; μmol electrons m⁻² s⁻¹) from each RLC was calculated following Beer et al. (2001):

$$ETR_r = yield * irradiance * 0.5 * AF$$

The maximum ETR_r (ETR_{max}) was derived by fitting the RLCs to the equations defined by Eilers and Peeters (1988).

Statistical Analyses

We performed a Kruskal–Wallis rank test to determine differences between the fluorescence measures performed *in situ* in the field and in the aquaria, because sample sizes were unbalanced (Table 3). Because no significant differences were detected within species and locations (Table 3), we used indistinctly the ETR_{max} measurements from the field and the aquaria.

The relationships between ETR_{max} and iron concentration, Chl *a* concentration and blade thickness were tested using

TABLE 4 | Mean and SD of iron concentration (mg kg⁻¹ DW), Chl *a* concentration (mg g⁻¹ DW), ETR_{max} (μmol electrons m⁻² s⁻¹), and blade thickness (mm) by species.

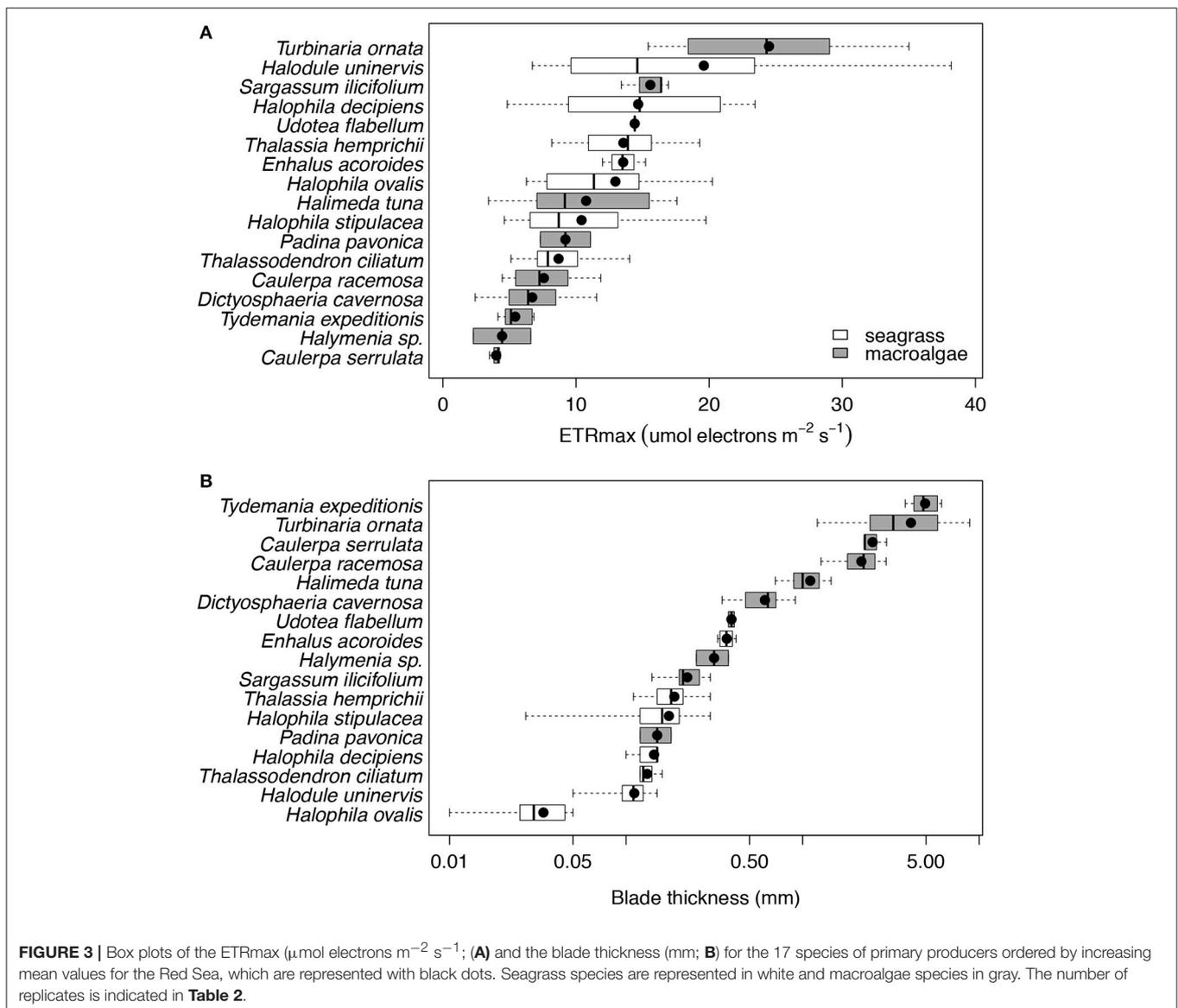
	Iron mean	Iron SD	Chl <i>a</i> mean	Chl <i>a</i> SD	ETR _{max} mean	ETR _{max} SD	Thickness mean	Thickness SD
Macroalgae species	204.8	314.5	1.8	1.0	13.6	9.0	2.44	2.11
<i>C. racemosa</i>	226.7	226.1	2.5	1.1	7.6	2.3	2.15	0.57
<i>C. serrulata</i>	74.4	9.2	2.9	0.2	4.0	0.4	2.49	0.43
<i>D. cavernosa</i>	42.2	20.5	1.5	0.9	6.7	2.9	0.61	0.18
<i>H. tuna</i>	270.9	338.2	1.4	1.2	10.8	5.4	1.10	0.37
<i>Halymenia</i> sp.	30.9	38.3	0.7	0.1	4.4	3.1	0.32	0.09
<i>P. pavonica</i>	580.8	349.7	1.0	0.3	9.2	2.7	0.15	0.04
<i>S. ilicifolium</i>	82.6	25.5	2.6	0.6	15.6	1.5	0.22	0.06
<i>T. ornata</i>	12.7	7.0	1.6	0.7	24.5	6.1	4.10	2.21
<i>T. expeditionis</i>	277.0	130.3	0.9	0.7	5.4	1.1	4.94	0.92
<i>U. flabellum</i>	906.6	193.1	2.7	0.4	14.4	0.1	0.40	0.02
Seagrass species	335.0	275.6	4.5	3.0	13.0	7.1	0.16	0.09
<i>E. acoroides</i>	221.2	12.0	2.6	0.6	13.5	1.2	0.37	0.03
<i>H. uninervis</i>	366.8	264.1	6.2	2.6	19.6	13.4	0.11	0.03
<i>H. decipiens</i>	621.7	428.9	4.9	3.7	14.7	7.7	0.14	0.04
<i>H. ovalis</i>	294.0	132.0	7.1	3.8	13.0	8.0	0.03	0.01
<i>H. stipulacea</i>	351.2	157.6	4.5	1.5	10.4	4.8	0.17	0.08
<i>T. hemprichii</i>	87.1	29.7	2.5	2.1	13.6	3.0	0.19	0.05
<i>T. ciliatum</i>	71.6	2.4	5.7	5.7	8.7	3.1	0.13	0.02

Number of replicates indicated in Table 2. For full names of species see Table 1.

linear regression analysis for all species of seagrasses and macroalgae separately, using the mean of each species per site for the three variables. To assess the relationship between iron concentration and Chl *a* concentration in the macrophyte tissue, exponential regressions and linear regressions were fitted to describe the relationship between Chl *a* and blade thickness. We also performed linear regressions to describe the relationships between latitude and iron concentration, Chl *a* concentration and ETRmax for seagrasses or macroalgae species separately. The latitudinal patterns of *H. stipulacea* and *T. ornata* were analyzed using mixed-effects models with *site* as random factor using the *nlme* R package (Pinheiro et al., 2015), on which the information for each specimen at each location was included to strengthen the power of the analysis. All calculations, graphs and statistical analyses were performed using RStudio 0.99.491 (1.0.143) (©RStudio, Inc.).

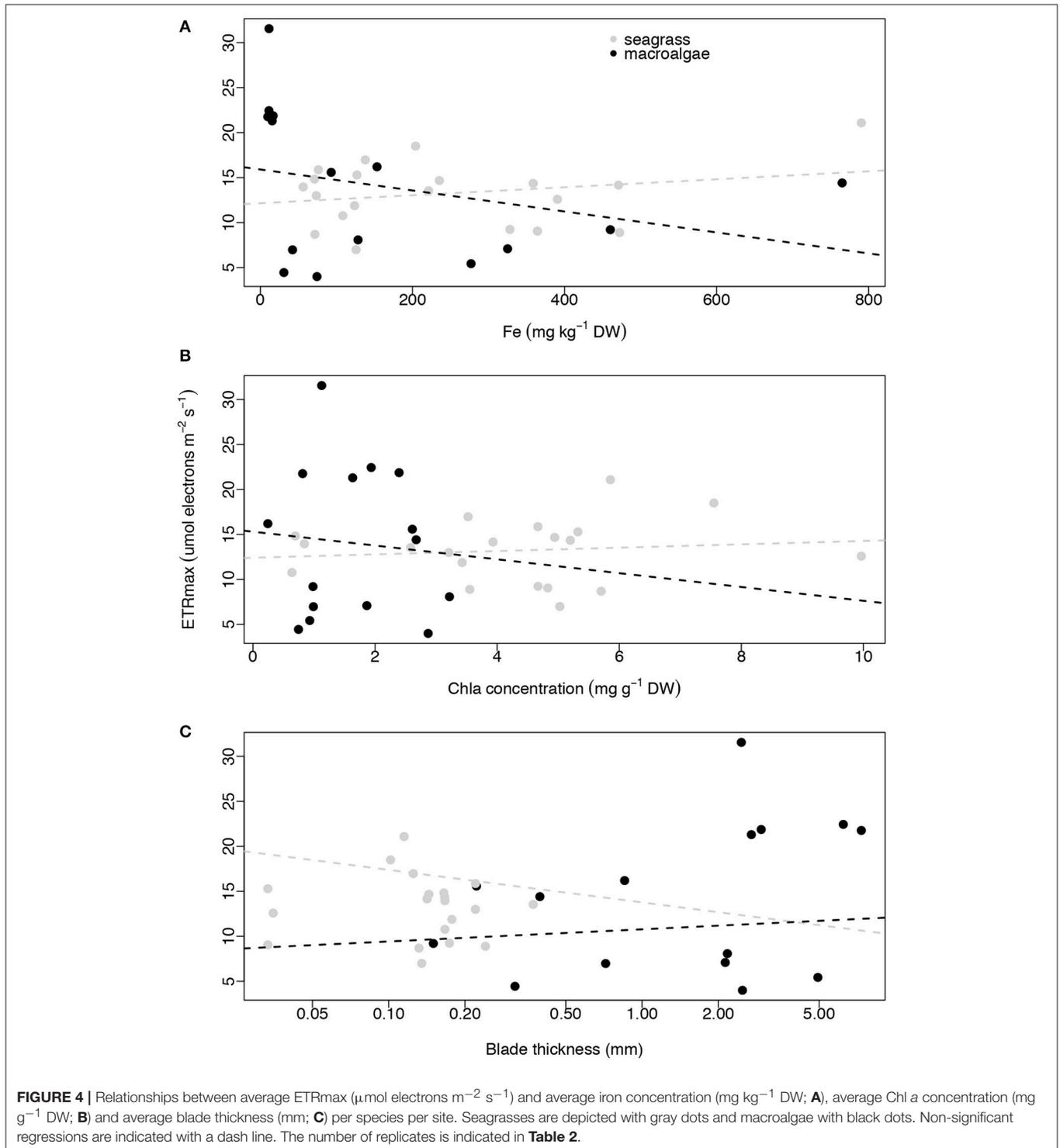
RESULTS

We found that seven species of macrophytes in the Red Sea, two seagrasses (*T. hemprichii* and *T. ciliatum*) and five macroalgae (*C. serrulata*, *D. cavernosa*, *Halymenia* sp. *S. ilicifolium*, and *T. ornata*), had average iron concentrations below 100 mg Fe kg DW⁻¹ (Figure 2A, Table 4), considered to be the critical iron concentration for marine macrophytes (Duarte et al., 1995). Additionally, eight species in the Red Sea, including four seagrasses (*E. acoroides*, *H. uninervis*, *H. ovalis*, and *H. stipulacea*) and four macroalgae (*C. racemosa*, *H. tuna*, *P. pavonica*, and *T. expeditionis*), had average iron concentrations below 600 mg Fe kg DW⁻¹ (Figure 2A, Table 4), which is still below iron sufficiency (Duarte et al., 1995). Only two species of macrophytes, the seagrass *H. decipiens* and the macroalgae *U. flabellum*, were iron sufficient with an average concentration of 621 and 906 mg



Fe kg DW^{-1} , respectively (Figure 2A, Table 4). In general, Chl *a* content was relatively homogeneous within different macrophyte taxa (Figure 2B), with seagrasses having consistently higher concentration of Chl *a* than macroalgae. Five species of seagrasses, *H. decipiens*, *H. ovalis*, *H. stipulacea*, *H. uninervis*, and *T. ciliatum*, had the highest Chl *a* concentrations while six

species of macroalgae, *C. racemosa*, *D. cavernosa*, *Halymenia* sp., *P. pavonica*, *T. ornata*, and *T. expeditionis*, had the lowest Chl *a* concentrations (Figure 2B). ETRmax, a proxy for productivity, was intermediate for seagrasses, while the photophilic species of brown macroalgae (*S. ilicifolium* and *T. ornata*) exhibited high levels of ETRmax and the species of macroalgae that



inhabit crevices (e.g., *T. expeditionis* and *Halymenia* sp.) had low ETRmax values (Figure 3A). Macrophyte thickness is also an important plant trait and we found it was primarily associated to taxonomic affiliation: Seagrass leaves were thinner than macroalgal blades with two species exceptions (e.g., *P. pavonica* and *E. acoroides*; Figure 3B).

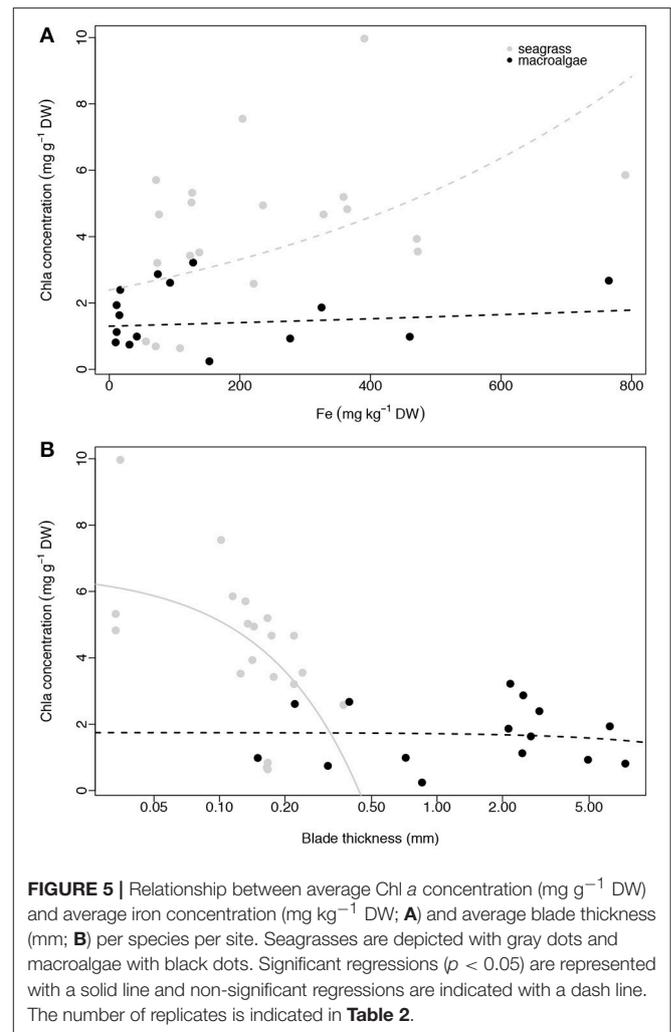
None of the three plant traits examined, iron concentration, Chl *a* abundance and blade thickness, were related to macrophyte productivity (ETRmax) for seagrasses (linear regressions, $p = 0.316$, $R^2 = 0.056$, $p = 0.624$, $R^2 = 0.014$, $p = 0.742$, $R^2 = 0.006$, respectively; Figure 4) or macroalgae (linear regressions, $p = 0.286$, $R^2 = 0.086$, $p = 0.765$, $R^2 = 0.007$, $p = 0.189$, $R^2 = 0.128$, respectively; Figure 4). The concentration of iron in the photosynthetic tissues of the seagrass and macroalgae blades was unrelated to the concentration of Chl *a* when compared across all species (exponential regressions, $p = 0.070$, $R^2 = 0.170$ for seagrasses, and $p = 0.663$, $R^2 = 0.015$ for macroalgae; Figures 5A,B). The thickness of the seagrass leaves was negatively associated with the concentration of Chl *a* (linear regression, $p = 0.017$, $R^2 = 0.277$; Figure 5B), but this relationship was not found in macroalgae blades (linear regression, $p = 0.777$, $R^2 = 0.006$; Figure 5B).

Contrary to our expectations, we found no relationship between latitude and iron concentration in the leaves of the seagrasses and macroalgae (linear regression, $p = 0.958$, $R^2 \leq 0.001$, and $p = 0.627$, $R^2 = 0.018$, respectively; Figure 6A). Similar results were found for Chl *a* concentration and ETRmax for seagrasses and macroalgae along the latitudinal gradient (linear regression, $p = 0.520$, $R^2 = 0.023$, and $p = 0.387$, $R^2 = 0.041$ for seagrasses and $p = 0.882$, $R^2 = 0.002$, and $p = 0.856$, $R^2 = 0.002$ for macroalgae; Figures 6B,C).

We performed additional latitudinal analyses for the two most common species of macrophytes, the seagrass *H. stipulacea* and the macroalgae *T. ornata*. For both species we found no relationship between latitude and leaf iron concentration (linear regressions with *site* as random factor, $p = 0.224$ and $p = 0.243$, respectively, for the seagrass and macroalgae; Figures 7A,B), between latitude and leaf Chl *a* concentration (linear regressions with *site* as random factor, $p = 0.114$ and $p = 0.296$, respectively, for the seagrass and macroalgae; Figures 7C,D), or between latitude and ETRmax (linear regressions with *site* as random factor, $p = 0.536$ and $p = 0.283$ respectively for the seagrass and macroalgae; Figures 7E,F).

DISCUSSION

Benthic macrophytes in the oligotrophic Red Sea were characterized by low iron concentration, with 86% of our seven species of seagrasses and 90% of our ten species of macroalgae having iron concentration below the levels indicative of iron sufficiency (600 mg Fe kg DW⁻¹, Duarte et al., 1995) in their blades (Figure 2, Table 4). Furthermore, Fe levels indicated that iron limitation was critical for more than 40% of the species of macrophytes, as indicated by Fe concentrations in the blades below 100 mg Fe kg DW⁻¹ (Duarte et al., 1995). For instance, the iron concentration for two species of macroalgae, *T. ornata*



and *S. ilicifolium* was 12.7 and 82.6 mg Fe kg DW⁻¹ respectively, which is 69 and 10 times lower than the concentrations reported for two *T. ornata* and *Sargassum mangarevense* on coral reefs in the island of Tahiti (Zubia et al., 2003), illustrating severe iron limitation. Overall, the seagrasses and macroalgae sampled along the Red Sea had average Fe concentrations of 335 (± 275 SD) and 204 (± 314 SD) mg Fe kg DW⁻¹, respectively, which are well below the average global values reported for seagrasses (412 mg Fe kg DW⁻¹) and macroalgae (426 mg Fe kg DW⁻¹; Sánchez-Quiles et al., 2017). Iron limitation was recently reported for the mangrove species *A. marina* in the Central Red Sea (Almahasheer et al., 2016a) but, to our knowledge, this is the first documentation of iron depletion down to limiting levels in seagrasses and macroalgae in the Red Sea, which suggests a potential generalized iron limitation for growth and productivity of benthic macrophytes at the basin level. Trace metal concentration in macrophytes in the Red Sea has only previously been assessed in the Gulf of Aqaba (Sánchez-Quiles et al., 2017), the northern most region in the Red Sea, where Fe concentrations in macrophyte blades are orders of magnitude higher than those in our study (e.g., 10,689 and 7,872 mg Fe kg

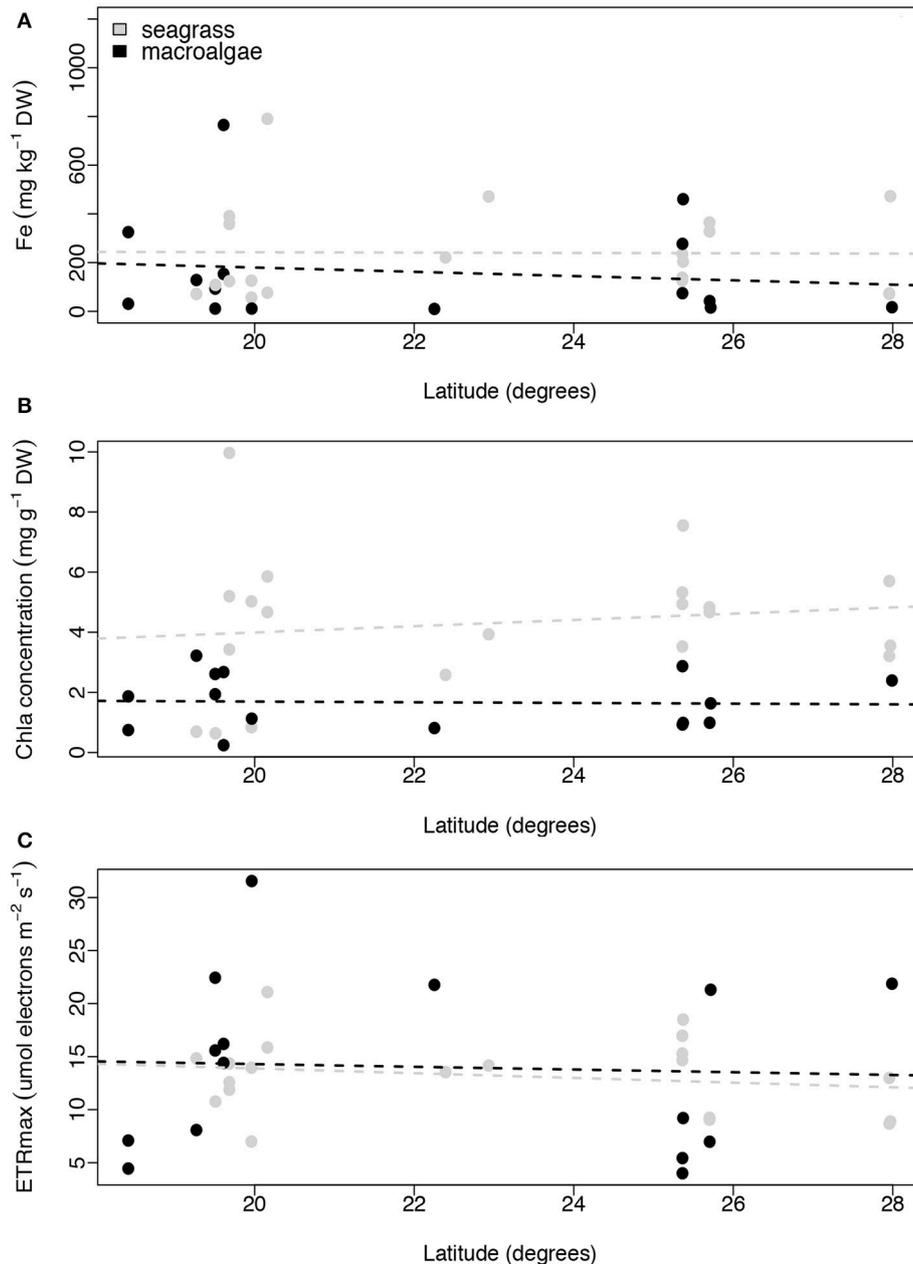
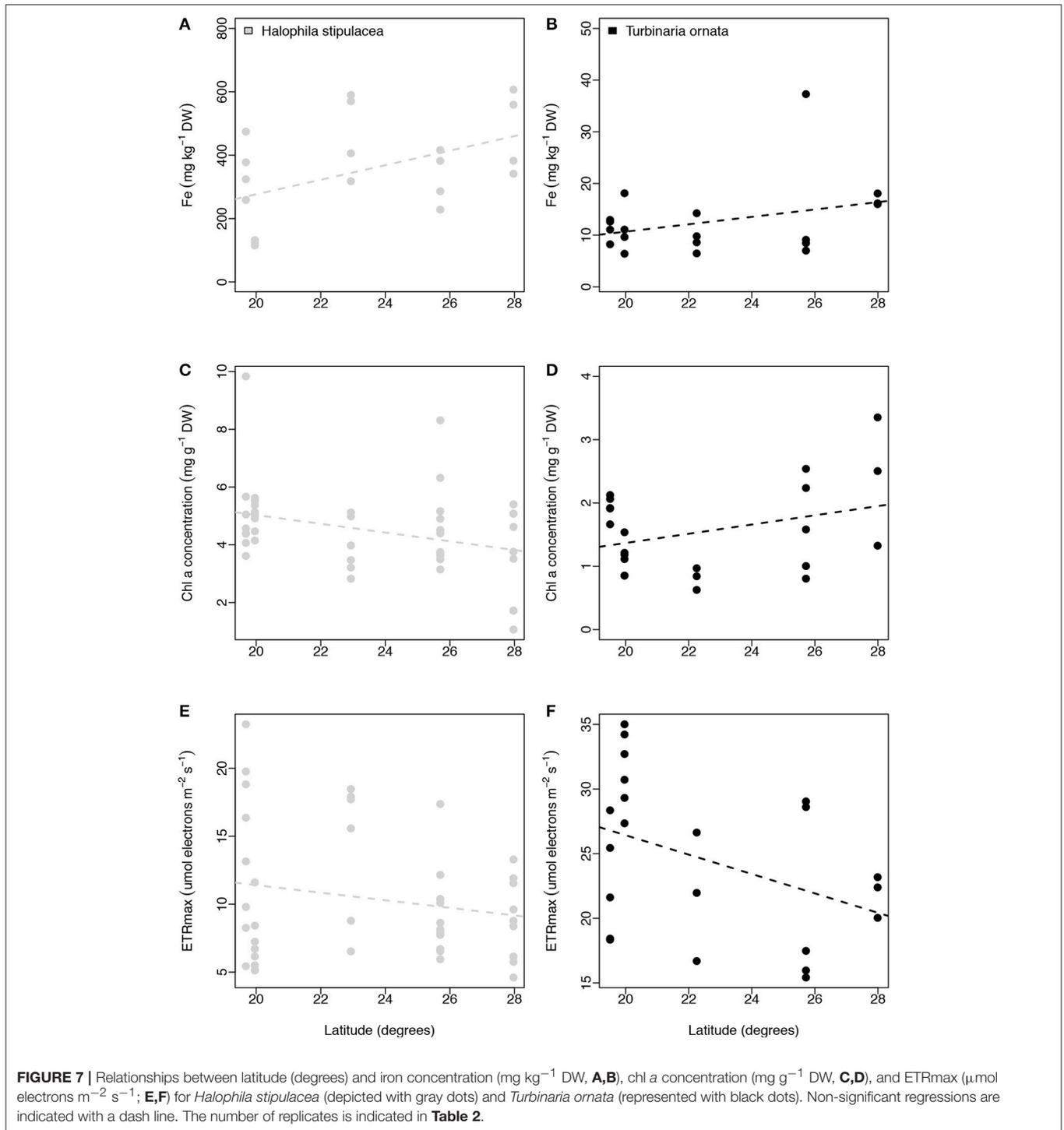


FIGURE 6 | Relationships between latitude (degrees) and average iron concentration (mg kg⁻¹ DW; **A**), average Chl a concentration (mg g⁻¹ DW, **B**), and average ETRmax (μmol electrons m⁻² s⁻¹; **C**) per species per site. Non-significant regressions are indicated with a dash line. The number of replicates is indicated in **Table 2**.

DW⁻¹ for *H. stipulacea* and *H. uninervis* respectively; Wahbeh, 1984; Abu-Kharma, 2006). The Gulf of Aqaba has undergone massive commercial and industrial development in the past five decades (Al-Rousan et al., 2007) compared to the main body of the Red Sea. This development has been reported to lead to the pollution of sediments, corals, and fishes of the Gulf with heavy metals (Abu-Hilal, 1987; Al-Rousan et al., 2007, 2012; Abu-Hilal and Ismail, 2008), likely explaining the elevated concentrations of Fe in Gulf of Aqaba macrophytes as well.

We found no correlation between the iron concentration in the blades of macrophytes and their productivity, as measured by ETRmax (**Figure 4A**). These results are surprising for seagrasses, since it has been shown that Fe inputs can stimulate seagrass growth in iron-deficient carbonate systems in tropical and temperate regions (Duarte et al., 1995; Chambers et al., 2001; Marbà et al., 2007, 2008). Little is known about iron-limitation and growth of macroalgae on coral reefs, with few observations in the Line Islands (Kelly et al., 2012) and Guam (Kuffner and Paul, 2001) indicating contrasting results. Kelly et al. (2012) found



that iron concentrations in macroalgae tissue from coral reefs near shipwrecks (which release iron) were six times higher than in macroalgae collected from reference sites. Kuffner and Paul (2001), on the other hand, reported a lack of iron-limitation in the growth of three species of macroalgae (*Padina tenuis*, *Dictyota bartayresiana*, and *Halimeda incrassata*) in experimental mesocosms in the Cocos Lagoon in Guam. Our results show a lack of relationship between Fe concentration in the tissue of

macroalgae and the associated ETRmax, which could indicate a generalized iron limitation for the growth of macroalgae in the main body of the Red Sea. Nonetheless, ETRmax provides a measure of the capacity of the photosystems to utilize the absorbed light energy (Marshall et al., 2000) but this does not necessarily translate into plant growth (e.g., Seboek et al., 2017), and further experimental investigation manipulating Fe inputs while assessing gross primary production is necessary.

We did not find a relationship between Fe concentration and Chl *a* abundance in seagrasses leaves (**Figure 5A**). This was unexpected since iron deficiency of angiosperms, including seagrasses, is often diagnosed from a deficiency of Chl *a* (Duarte et al., 1995; Belkhdja et al., 1998). Similarly, increasing Chl *a* in seagrasses was not related to increasing productivity, as denoted by the ETR_{max} values (**Figure 4B**). These results indicate that seagrasses may adjust their photosynthetic efficiency (e.g., α) based on the amount of light-harvesting pigments (Chl *a*), resulting in similar productivity rates across a gradient of Chl *a* abundance. We found no relationship between Fe and Chl *a* concentrations in the blades of ten species of macroalgae in the Red Sea (**Figure 5A**), with Chl *a* concentration being independent of productivity (**Figure 4B**). Our Chl *a* concentrations in the blades of macroalgae were low when compared to values reported in the literature: For instance, 1.4 mg Chl *a* g DW⁻¹ were reported for *H. tuna* in this study (**Table 4**) vs. 2.36 mg Chl *a* g DW⁻¹ reported by Beach et al. (2003) in the Florida Keys (we used a conversion factor of 8.18 from fresh weight to dry weight for *H. tuna*), which could indicate low Chl *a* concentration levels in macroalgae throughout the Red Sea. Plants have developed a remarkably uniform strategy for harvesting light using mainly Chl *a* and Chl *b*, while macroalgae have evolved a greater diversity of pigments for capturing light, including, for instance, Chl *c* and carotenoid fucoxanthin (Larkum and Barrett, 1983). Hence, the absence of a relationship between Chl *a* concentration and Fe concentration or productivity of macroalgae might be also due to a limitation in our study to assess of the abundance of all light-harvesting pigments, rather than an actual lack of a relationship with Fe concentration and productivity.

In photosynthetic organisms, the amount of Chl *a* per unit of tissue weight decreases with leaf thickness (Agusti et al., 1994). Our results on seven species of seagrasses in the Red Sea support this general trend, but we did not find such correlation for the 10 species of macroalgae studied here (**Figure 5B**). Similarly, we did not find a correlation between leaf blade thickness and productivity (**Figure 4C**), suggesting that this morphological trait might be unrelated to photosynthetic performance in these two types of Red Sea benthic macrophytes.

Our results showed a lack of latitudinal gradients in all studied parameters. We did not find evidence of the expected North to South gradients for Fe concentration, Chl *a* concentration or productivity when looking at all species of seagrasses or macroalgae together (**Figure 6**). The same was true for the two species that were collected throughout the Red Sea, the seagrass *H. stipulacea* and the macroalgae *T. ornata* (**Figure 7**), since we did not find a latitudinal gradient of Fe concentration or Chl *a* concentration in either of the two species (**Figure 7**). A similar pattern was described for the photocollecting-pigments in the zooxanthellae of the ubiquitous coral *P. verrucosa*, which do not increase toward southern latitudes (Sawall et al., 2014, 2015). Productivity, as indicated by ETR_{max}, did not show a latitudinal pattern neither when all species of seagrasses or macroalgae were grouped together (**Figure 6C**) nor for *H. stipulacea* or *T. ornata* alone (**Figures 7E,F**, respectively).

This lack of a gradient in productivity for macrophytes contrasts with the results reported for other species found on coral reefs in the Red Sea, such as the coral *P. verrucosa* (Sawall et al., 2015), which productivity decreased from South to North. On the other hand, the lack of a latitudinal pattern described here for seagrasses and macroalgae aligns with the results for productivity of phytoplankton obtained in several research cruises in the Red Sea (Qurban et al., 2017), which showed no clear latitudinal patterns. Hence, whereas the South to North oligotrophication of the Red Sea affects some species of benthic invertebrates on corals reefs (Sawall et al., 2015; Al-Aidaros et al., 2016) and to a certain extent pelagic phytoplankton Chl *a* concentrations (Raitsos et al., 2013; Kürten et al., 2015), it is not reflected in iron concentration, Chl *a* concentration or physiological performance of Red Sea macrophytes.

The Red Sea is characterized by scarce rainfall and an absence of rivers. Similar to our results, the seagrasses *Syringodium filiforme* and *Thalassia testudinum* were described to be iron-limited in a karstic region in the Mexican Caribbean also lacking riverine inputs (Duarte et al., 1995). In the Red Sea Basin inputs of iron are likely coming from three sources: The Indian Ocean via the Strait of Bab al Mandab, wind-induced upwelling of deep water (Triantafyllou et al., 2014; Al-Aidaros et al., 2016), and dust deposition from the Sahara and Arabian Deserts (Jish Prakash et al., 2015). Although the quantitative sources and inputs of Fe in the Red Sea are barely known (Jish Prakash et al., 2015), our results on Fe concentration in the tissue of 17 species of macrophytes suggest that Fe is scarce and limiting in most benthic shallow ecosystems in the Arabian Red Sea, regardless of their latitudinal location. This is characteristic of carbonate rich sediments, such as those in the Red Sea, where iron is often bound in unavailable forms (e.g., Ruiz-Halpern et al., 2008). In addition, the other two potential sources of iron, dust deposition and upwelling, may play a role at homogenizing iron inputs throughout the Red Sea.

Understanding what factors limit benthic macrophytes is important given their role sequestering carbon both within blue carbon habitats and in the deep ocean (Fourqurean et al., 2012; Krause-Jensen and Duarte, 2016; Duarte and Krause-Jensen, 2017), as well as their role in supporting food webs (Antón et al., 2011). The results reported in this study contribute to unravel the complex interactions between environmental gradients and poorly-studied Red Sea macrophytes at large spatial scales. The next step forward in this research would be to experimentally investigate potential iron limitation in benthic macrophytes and evaluate more complex interactions using factorial studies examining possible synergistic effects of temperature, nitrate, phosphate, and iron.

AUTHOR CONTRIBUTIONS

AA and CD: Conceived the project; AA, IH, NM, and DK-J: Collected the samples; AA: Performed the research and processed the samples; AA: Analyzed the data and wrote the first draft of the paper; all authors interpreted the data, made a substantial

contribution to final drafts of the paper, and approved it for publication.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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