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Photosynthetic responses of subtidal seagrasses to a daily light cycle in Torres Strait: a comparative study

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Abstract

In this study we examined the photosynthetic responses of five common seagrass species from a typical mixed meadow in Torres Strait at a depth of 5-7m using Pulse Amplitude Modulated (PAM) fluorometry. The photosynthetic response of each species was measured every 2 hours throughout a single daily light cycle from dawn (6am) to dusk (6pm). PAM fluorometry was used to generate rapid light curves from which measures of electron transport rate (ETR_{max}), photosynthetic efficiency (α), saturating irradiance (E_k) and light adapted quantum yield ($\Delta F/F_m^{'}$) were derived for each species. The amount of light absorbed by leaves (absorption factor) was also determined for each species. Similar diurnal patterns were recorded among species with 3-4 fold increases in maximal electron rate from dawn to midday and a maintenance of ETR_{max} in the afternoon that would allow an optimal use of low light by all species. Differences in photosynthetic responses to changes in the daily light regime were also evident with *Syringodium isoetifolium* showing the highest photosynthetic rates and saturating irradiances suggesting a competitive advantage over other species under conditions of high light. In contrast *Halophila ovalis, Halophila decipiens and Halophila spinulosa* were characterised by comparatively low photosynthetic rates and minimum light requirements (i.e. low E_k) typical of shade adaptation. The structural makeup of each species may explain the observed differences with large, structurally complex species such as *Syringodium isoetifolium* and *Cymodocea serrulata* showing high photosynthetic effciciencies (α) and therefore high light adapted traits (e.g. high ETR_{max}, and E_k) compared with the smaller *Halophila* species positioned lower in the canopy. For the smaller *Halophila* species these shade adapted traits are features that optimise their survival during low light conditions. Knowledge of these

characteristics and responses improves our understanding of the underlying causes of changes in seagrass biomass, growth and survival that occur when modifications in light quantity and quality arise from anthropogenic and climatic disturbances that commonly occur in Torres Strait.

Keywords: Fluorescence, Rapid Light Curves, photosynthesis, seagrass, photon flux, PAM, multi-species stands[but169 1]

Regional Index: Torres Strait, Queensland, Australia

1. Introduction

Seagrass meadows in northern Australia provide large tracts of nearshore marine benthic habitat, are highly productive and support many key faunal food chains (Walker, 1989; Duarte et al., 1997; Waycott et al., 2005). For seagrass ecosystems light is one of the most important factors controlling their productivity, distribution and survival (Longstaff et al., 1999; Carruthers et al., 2002; Biber et al., 2005). Excessive loadings of sediments and nutrients into marine systems from terrestrial sources can reduce available light and inhibit physiological processes such as photosynthesis, causing seagrass die-off (Short and Wyllie-Echeverria, 1996). In northern Australia turbidity-related light stress has been identified as a major driver of seagrass habitat structure (Long and Poiner, 1997; Carruthers et al., 2002). However our knowledge of the photosynthetic responses of different seagrass species to changes in light in this region have received relatively little research attention (Longstaff and Dennison, 1999; Longstaff et al., 1999) and our knowledge is limited.

The northern region of Australia in Torres Strait possesses some of the most extensive shallow and deep water seagrass communities in Australia, which provide critical habitat and food for demersal and pelagic fisheries (Long and Poiner, 1997), the green turtle and dugong (Long and Poiner, 1997; Andre et al., 2005). The standing biomass and distribution of these meadows has been well described with extensive areas of seagrass growing from intertidal to depths greater than 40 m in Torres Strait (Long and Poiner, 1997). The systems are highly dynamic and respond to a complex suite of physical environmental factors including tides, currents and turbidity that affect the quality and quantity of light reaching seagrass communities. Recent large scale die back of seagrass in north-western Torres Strait has been attributed to reductions in light availability due to the movement and deposition of sediments and increased turbidity that result from climatic events (e.g. storms, monsoons) (Pitcher et al., 2004).

Pulse Amplitude Modulated (PAM) fluorometry is a common tool that has been used to rapidly measure real-time changes in the photosynthetic activity and photo-adaptation of seagrasses in response to changes in light availability from diurnal fluctuations (Ralph et al., 1998; Silva and Santos, 2003), depth gradients (Schwarz and Hellblom, 2002; Durako et al., 2003) and turbidity (Campbell et al., 2003). Rapid light curves measure the photosynthetic efficiency in light adapted plants or the effective quantum yield as a function of irradiance and provide a reliable assessment of photosynthetic activity and integration of a leafs short-term light history (Ralph and Gademann, 2005). The technique can reliably be used to compare responses among species to changes in light and provide insight into these responses under known light regimes that may occur in different habitat types (e.g. shallow water vs deep water habitats) (Campbell et al., 2007). Because processes operating at small scales of metres are often most important in structuring seagrass assemblages (Long and Poiner, 1997), the photosynthetic response of individual seagrass species to predictable and constant changes in light, that occur throughout a daily cycle, is likely to have a strong influence on seagrass growth, and is fundamental to the development of predictive models that explain the dynamics of these ecosystems.

In this study we employed PAM fluorometry to measure the photosynthetic responses of five common seagrass species, at a depth of 5-7m, from a typical mixed meadow in Torres Strait. We were interested in comparing responses of these subtidal species throughout a single daily light cycle from dawn to dusk to provide insight into the photosynthetic strategies that enable species to adapt to changing and at times limiting light environments.

2. Methods

2.1 Study site

The photosynthetic performance of seven species of seagrass was examined on 28 March 2004, at a site at 5-7m depth at Turnagain Island, Torres Strait, Queensland, Australia (Fig. 1). The site represents a typical subtidal seagrass meadow consisting of a mix of species including *Syringodium isoetifolium*, *Cymodocea serrulata*, *Halophila spinulosa*, *Halophila ovalis* and *Halophila decipiens*. The photosynthetic performance of all five species was examined using PAM (Walz GmbH,Effeltrich, Germany) fluorometry.

2.2 Light adapted rapid light curves (RLC's)

RLC's are a useful tool to evaluate a plant's photosynthetic response to varying light conditions based on the background light that they have been acclimated to. All plants in this study were collected from the same area so were exposed to the same light conditions and inter-species comparisons of photo-biology are therefore possible (Ralph and Gademann, 2005). Seagrasses were collected as whole seagrass plants including sediments, maintained in shaded conditions in seawater on the boat. At each site, *ex situ* measures of rapid light curves (RLC's) were made on the midpoint of 5 replicate attached leaves from separate plants for each species at 2 h intervals between 6am and 6pm. Leaves were measured for RLC's within 5 minutes of collection using an external power source. Rapid light curves (RLC's) were generated automatically with a diving PAM using an incremental sequence of actinic illumination periods, with light intensities increasing in 8 steps from 0 to 1760 µmol photons m^{-2} s^{-1} according to methods outlined by Ralph and

Gademann (2005). Each illumination period lasted 10s, at the end of which time, fluorescence (F), and following a saturating pulse of white light (800 ms of 8000 µmol quanta m^{-2} s^{-1} PPFD), maximum fluorescence (F_m'), was measured.

Apparent photosynthetic electron transport rates (ETR) were calculated from the fluorescence measures taken at the end of each illumination period, as the product of effective quantum yield ($\Phi_{PSII} = F- F_m' / F_m' = \Delta F / F_m'$; where F is initial fluorescence, F_m' is maximum fluorescence and ΔF is variable fluorescence), the actinic illumination irradiance (I) (Ralph and Gademann, 2005) and the absorbance factor (AF), i.e. the fraction of light absorbed by the leaf (Beer et al., 2001). This product was further multiplied by 0.5 because it is assumed that half the photons required for the movement of electrons along the photosystem pathways are absorbed by Photosystem II (PSII) (Schreibers et al., 1995). The first of 7 actinic illuminations (i.e 50, 150, 340, 580, 850, 1150 and 1760) were used to calculate RLC's, the actinic width or illumination period was 0.15 s and gain was set at 4.

AF values for all species were derived by measuring the proportion of light absorbed by single leaves according to the method described by Beer et al. (2001). The maximal rate of ETR (ETR_{max}) and photosynthetic efficiency (α) were calculated by fitting the RLC data to an exponential function; $ETR = ETR_{max} * (1-\exp[-\alpha(I)/ETR_{max}])$ modified from Jassby and Platt (1976); where ETR = Electron transport rate and I = Irradiance. For the most part ETR values plateaued at the highest light intensities and therefore no photo-inhibition term was used in the exponential function fitted to data and used to derive ETR_{max} and α. The onset of light saturation (E_k) was calculated as ETR_{max}/α. Light adapted effective quantum yields

($\Phi_{PSII} = F\text{-}\ F_m{}^{'} / F_m{}^{'} = \Delta F / F_m{}^{'}$) used for analysis were chosen from the first yield measured of the RLC when PPFD = 0 µmol photons m^{-2} s^{-1}, i.e. just prior to applying the increasing irradiances.

2.3 Photosynthetic photon flux density

Underwater photosynthetic photon flux density (PPFD) (µmol photons m^{-2} s^{-1}) was measured using the optical light sensor of the PAM fluorometer (Waltz, Germany) calibrated with a Li-Cor (USA) quantum sensor. Measures of PPFD were made at the start and end of each set of rapid light curves for each species at a given time interval. The mean value of all measures is given as the integrated PPFD for a given time interval. Means are only shown as variation in PPFD was low due to relatively constant light levels and water quality conditions during sampling.

2.4 Data analysis

To examine the influence of species and time on photosynthetic variables we tested for significant difference in means among times for each variable (ETR_{max}, α, E_k, $\Delta F / F_m{}^{'}$) (n=10) using 2 way ANOVA. ETR_{max} and E_k data were $\log_e$ transformed prior to analysis to meet assumptions of normality and homogeneity of variances. Post-hoc tests (Bonferroni) were performed to explain significant differences in the photosynthetic parameters for factors including species, time and species x time.

All analyses were performed using SYSTAT ver. 10.2.

3. Results

Mean absorbance factors ranged from 0.52 to 0.68 among the 5 species. Means (±SE) were lowest for *Halophila ovalis* (0.522±0.009) and *Halophila decipiens* (0.527±0.009), intermediate for *Halophila spinulosa* (0.627±0.022) and *Syringodium isoetifolium* (0.624±0.028) and highest for *Cymodocea serrulata* (0.682±0.056).

Most variation in the 4 photosynthetic traits ($\mathrm{ETR}_{\mathrm{max}}$, E_{k}, α, $\Delta F/F_m^{'}$) was due to the effects of time and species (ie high F ratios) and not interactive effects (Table 1). For $\mathrm{ETR}_{\mathrm{max}}$ the effect of species was due to higher $\mathrm{ETR}_{\mathrm{max}}$ of *Syringodium isoetifolium* compared with *Cymodocea serrulata*, *Halophila ovalis* and *H. spinulosa* which were all higher than *H. decipiens* (Table 1). For E_{k} the effect of species was due to higher values for *Syringodium isoetifolium* compared with all other species. For photosynthetic efficiency (α) *Syringodium isoetifolium* was also higher than all species while *Cymodocea serrulata* was higher compared with the 3 *Halophila* species and lowest values were found in *Halophila decipiens*. Significant effect of species on effective quantum yield ($\Delta F/F_m^{'}$) was due to higher values *Syringodium isoetifolium* than all species and higher values for *Cymodocea serrulata* and *Halophila ovalis* than *H. spinulosa* and *H. decipiens* (Table 1).

Significant interactions between time and species were found for all variables except effective quantum yield ($\Delta F/F_m^{'}$) (Table 1). Post-hoc tests revealed that significant interactions between time and species for $\mathrm{ETR}_{\mathrm{max}}$ and saturating irradiance (E_{k}) were generally due to lower values at 6am compared with 8am–4pm for all species, while all species except *Halophila decipiens* and *Halophila spinulosa* had lower values at 6pm compared with measures at 12pm–4pm (Fig. 2). For α, the significant interaction between time and species was because values remained relatively constant from 8am to 4pm in *Halophila ovalis* and *Halophila decipiens* whereas for *Syringodium isoetifolium*, *Cymodocea serrulata* and *Halophila spinulosa* a decline in α occurred at 12pm before a recovery at 2pm (Fig. 2). For $\Delta F/F_m{}'$ all species showed a similar pattern over the diurnal cycle with highest values recorded at low photon fluxes at 6am and 6pm (Fig. 2).

Rapid light curves at 8am, 12pm and 4pm show that *Syringodium isoetifolium* had the highest ETR and *Halophila decipiens* had the lowest ETR compared with all other species. At 8am and 4pm *Cymodocea serrulata* had higher ETR compared with the 3 *Halophila* species, while *H. ovalis* and *H. spinulosa* had similar ETR values. In contrast, at 12pm *Halophila ovalis* had a higher ETR than both *Cymodocea serrulata* and *Halophila spinulosa* (Fig. 3).

4. Discussion

This study was limited to a subtidal habitat in Torres Strait over a single day, yet provided insight into the comparative photosynthetic traits of several dominant seagrass species in the region. Key findings were that all species maintained relatively high rates of photosynthesis from 12pm until 4pm, despite declining light availability. This maintenance of ETR_{max} and E_k would serve to optimise photosynthetic output and assist growth during fluctuating and limiting light conditions in subtidal waters. Differences among species were also apparent with the photosynthetic responses of structurally complex seagrass species adapted to both high and low light conditions while smaller species showed photosynthetic traits well suited to shaded and deep water habitats.

Of all species *Syringodium isoetifolium* had the highest photosynthetic rates and saturating irradiances suggesting it has competitive advantage during high light conditions. In contrast the low minimum light requirements (i.e. low E_k) of *Halophila spinulosa*, *Cymodocea serrulata*, *H. ovalis* and *H. decipiens* may infer a competitive ability under extreme low light conditions as found in depths greater than 10 metres. The abundance of *H. ovalis* and *H. decipiens* in deep water environments greater than 10 metres (Lee Long 1996 et al., 1996; Campbell et al., 2007) and the paucity of *Halophila spinulosa* and *Cymodocea serrulata* at these depths is almost certainly due to their low biomass and hence low respiratory demand enabling maximal productivity at low light climates. Although *Halophila spinulosa* and *Cymodocea serrulata* also showed low E_k values capable of utilising low light, their greater biomass would confer a high respiratory demand which would impede the maintenance of productivity and biomass in very deep habitats. Similar findings have been found for temperate species of *H. ovalis* (Ralph et al., 1998) and other tropical *Halophila* species (Schwarz and Hellblom, 2002; Durako et al., 2003), and these features may explain the survival of these species in deep waters greater than 30m (Lee Long et al., 1996; Long and Poiner, 1997).

For all species except *Syringodium isoetifolium* saturating irradiances throughout the day were generally below *in situ* photon fluxes between 8am and 4pm, suggesting that plants were light saturated for about 8-10h a day. Persistent low saturating irradiances from 6am till 10am for all species, except *Syringodium isoetifolium*, would allow these plants to optimise available light and take advantage of low photon fluxes during the morning and afternoon. In contrast the relatively high E_k values recorded for *Syringodium isoetifolium* meant that it was light limited during morning and afternoon and light saturated for only 6h each day. The high photosynthetic efficiency and performance reported here is consistent with relatively high E_k values recorded for *Syringodium filiforme* (Touchette and Burkholder, 2000) and its previously reported high productivity and colonising ability (Rollon et al., 1998; Duarte and Chiscano, 1999; Rasheed, 2004).

The diurnal pattern in ETR_{max} and E_k, was characterised by low morning values between 6 and 8pm and a 1-3 fold increase in values between 8am and 4pm before a decline occurred at 6pm. The pattern differs somewhat to that shown for intertidal and shallow water species (Silva and Santos, 2003; Campbell et al., 2003; Durako et al., 2003) where a downturn in maximal ETR corresponds with reduced photon flux in the afternoon and midday reductions in photosynthetic efficiency (α) and light adapted effective quantum yield help regulate photosynthetic rates under changing light conditions. Interestingly, in the present study reductions in photosynthetic efficiency (α) occurred in the larger species well adapted to high light, but not in the small leafed species *Halophila ovalis* and *H. decipiens.* These *Halophila* species are positioned lowest in the canopy and subject to severe light limitation and the lack of reduction in α at midday implies an inability to regulate photosynthesis or take advantage of increased light fluxes. Most interesting though was that both *Halophila ovalis* and *H. spinulosa* maintained ETR_{max} from midday to 4pm, a trait that would help adaptation to low light climates and optimise photosynthetic output. Similarly, ETR_{max} for both *Syringodium isoetifolium* and *Cymodocea serrulata* were highest in the afternoon, suggesting that these species were also able to regulate and maintain photosynthetic output as afternoon photon fluxes waned. Overall the results demonstrate an optimal use of low light characteristics in this suite of subtidal species which differs from that found for shallow water species (Campbell et al., 2003; Durako et al., 2003; Silva and Santos 2003).

The morphological and structural makeup may to some extent explain the differences in photosynthetic characteristics of the species examined. *Cymodocea serrulata* is a larger, more structurally complex species with slower growth rates compared with *Halophila* species and *Syringodium isoetifolium* (Brouns, 1987; Rollon et al., 1998). Its high absorbance values which may reflect high pigment content (Beer et al., 2000, Silva and Santos, 2003) would permit a more efficient capture of photon fluxes. This may optimise its metabolic and growth rates through a more efficient use of carbon reserves during periods of limiting light conditions (Alcoverro et al., 1999). An interesting finding was also the lowering of photosynthetic efficiency during midday for *Cymodocea serrulata*, *Syringodium isoetifolium* and *Halophila spinulosa* but not for *Halophila ovalis* and *Halophila decipiens*. The former three species are all structurally more complex than the two small *Halophila* species and the lowering of photosynthetic efficiency was due to their relatively small increase in photosynthetic rates from 10am till 12pm compared with the *Halophila* species. For the structurally less complex and smaller *Halophila decipiens* these shade adapted characteristics (i.e. low ETR_{max}, α, E_k) likely reflect its position in the canopy, lying flat on or partially covered by sediments and often shaded by the more structurally complex larger species. In comparison, although both *Halophila spinulosa* and *Halophila ovalis* are also likely to be shaded, their higher photosynthetic performance over the daily cycle may reflect their ability to grow "higher" in the canopy and even colonise open spaces in the canopy (S. Campbell, pers. obs.). Of all the species *Halophila decipiens* showed most sensitivity to high light fluxes evidenced by a depression in quantum yield during maximal photon flux. Such down regulation of photosynthesis as measured by changes in $\Delta F/F_m{}'$ suggests photo-inhibition and has been reported for shallow water species stressed during high light conditions (Ralph et al., 1998; Campbell et al., 2003; Durako et al., 2003).

The light adapted photosynthetic responses described above pertain to how these species have adapted to variable light conditions in a low light environment at a depth of 7 metres. Although we have shown that differences exist between structurally complex species, which are possibly more likely to be advantaged by high light conditions, and less structurally species possibly more competitive in low light conditions, it must be stressed that these features may change and different patterns emerge if the plants were acclimated to a different light environment such as described for shallow water species (Ralph, 1998; Campbell et al., 2003; Silva and Santos, 2003).

Both *Syringodium isoetifolium* and *Cymodocea serrulata* are the dominant seagrasses in terms of biomass and percentage cover in Torres Strait (Long and Poiner, 1997). Although they provide habitat for fish and other marine fauna they represent relatively low nutritional value for grazing by large herbivores (J. Sheppard, pers. comm.). More nutritious (i.e. high starch and nitrogen) and less fibrous species such as *Halophila ovalis* and *Halodule uninervis* are more preferred by marine herbivores such as dugong and turtle (Sheppard et al. 2007). The shade adapted characteristics of these species, coupled with their capacity to rapidly colonise areas following disturbance (Preen et al., 1995), are features that will optimise their survival during reductions in light availability from climatic events or when shading by larger seagrass occurs. Although commonly found in deep waters greater than 10m both *Halophila ovalis* and *Halophila decipiens* also have wide depth distributions and geographic ranges in Torres Strait (Long and Poiner, 1997) that possibly make them the most important seagrass species for marine herbivore foraging.

4.1 Conclusion

We found both similarities and differences in the photosynthetic responses of subtidal seagrasses examined. Similar diurnal patterns were recorded among species with 3-4 fold increases in maximal electron rate from dawn to midday and a maintenance of ETR_{max} in the afternoon as photon flux declined. This sustained ETR_{max} into the afternoon was characteristic of all the subtidal species examined and contrasts with reports on shallow water species acclimated to high photon flux, where ETR_{max} drops with declining photon flux in the afternoon. Such a strategy may enable optimal use of fluctuating and low light climates. Differences were also evident with highly structured species such as *Syringodium* *isoetifolium* and *Cymodocea serrulata* showing photosynthetic traits well adapted to high light conditions while *Halophila ovalis* and *H. decipiens* were best suited to low light. These differences may reflect the position of species in this multi-sepcies canopy with larger species more able to capture incident light than those smaller species in the understorey. The higher respiratory demand of larger species also means they are unable to maintain biomass and survive in very low light conditions while small species can. Our improved knowledge of these characteristics and responses increase our understanding of the underlying causes of changes in seagrass biomass, growth and survival that occur when modifications in light quantity and quality arise from anthropogenic and climatic disturbance. However, more studies are required to examine responses to short-term perturbations in PPFD at different times and depths in order to evaluate the full range of photosynthetic performance and resilience of these species to changes in photon flux.

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Figure captions

Figure 1. Map showing survey location (black arrow) near Turnagain Island, Torres Strait.

Figure 2. Diurnal changes in a) ETR_{max}, b) saturating irradiance (E_k), c) photosynthetic efficiency (α) and d) effective quantum yield ($\Delta F/F_m^{'}$), at 5-7 m depth for 5 seagrass species: Hs = *Halophila spinulosa*, Hd = *Halophila decipiens*, Cs = *Cymodocea serrulata*, Si = *Syringodium isoetifolium*, Ho = *Halophila ovalis*, PPFD = photon flux density (µmol photon m^{-2} s^{-1}) (n=5).

Figure 3. Mean (±SE) (n=5) ETR (µmol e^{-} m^{-2} s^{-1}) versus photosynthetic photon flux density (PPFD) for 5 seagrass species: Hs = *Halophila spinulosa*, Hd = *Halophila decipiens*, Cs = *Cymodocea serrulata*, Si = *Syringodium isoetifolium*, Ho = *Halophila ovalis* at a) 8am, b) 12pm and c) 4pm.

Figure 1.

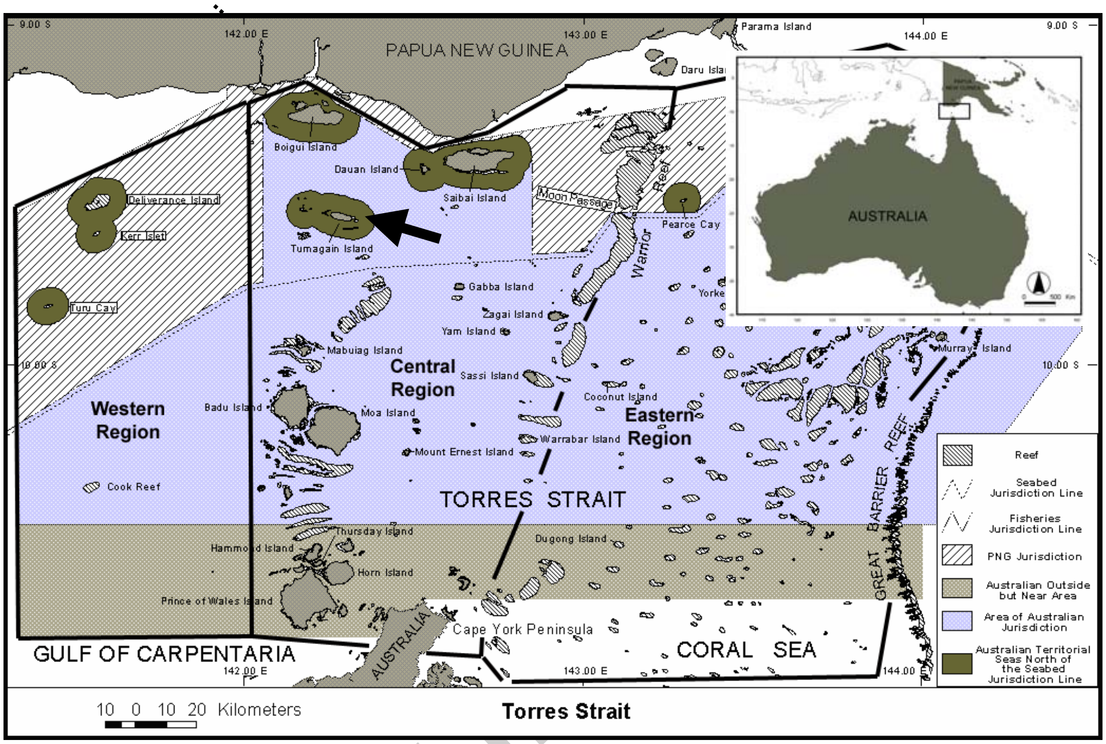
9.00 S
142.00 E
143.00 E
144.00 E
PAPUA NEW GUINEA
Parama Island
Daru Isla
Boigui Island
Dauan Island
Saibai Island
Moon Passage
Warrior Reef
Pearce Cay
Deliverance Island
Kerr Islet
Turu Cay
Tumagain Island
Gabba Island
Yorke
Zagai Island
Yam Island
Mabuiag Island
Central Region
Sassi Island
Murray Island
10.00 S
Western Region
Badu Island
Moa Island
Coconut Island
Eastern Region
Warrabar Island
Mount Ernest Island
Cook Reef
TORRES STRAIT
Thursday Island
Dugong Island
Hammond Island
Horn Island
Prince of Wales Island
GREAT BARRIER REEF
Cape York Peninsula
AUSTRALIA
GULF OF CARPENTARIA
CORAL SEA
AUSTRALIA
PAPUA NEW GUINEA
500 Km
Reef
Seabed Jurisdiction Line
Fisheries Jurisdiction Line
PNG Jurisdiction
Australian Outside but Near Area
Area of Australian Jurisdiction
Australian Territorial Seas North of the Seabed Jurisdiction Line
10 0 10 20 Kilometers
Torres Strait

Figure 2

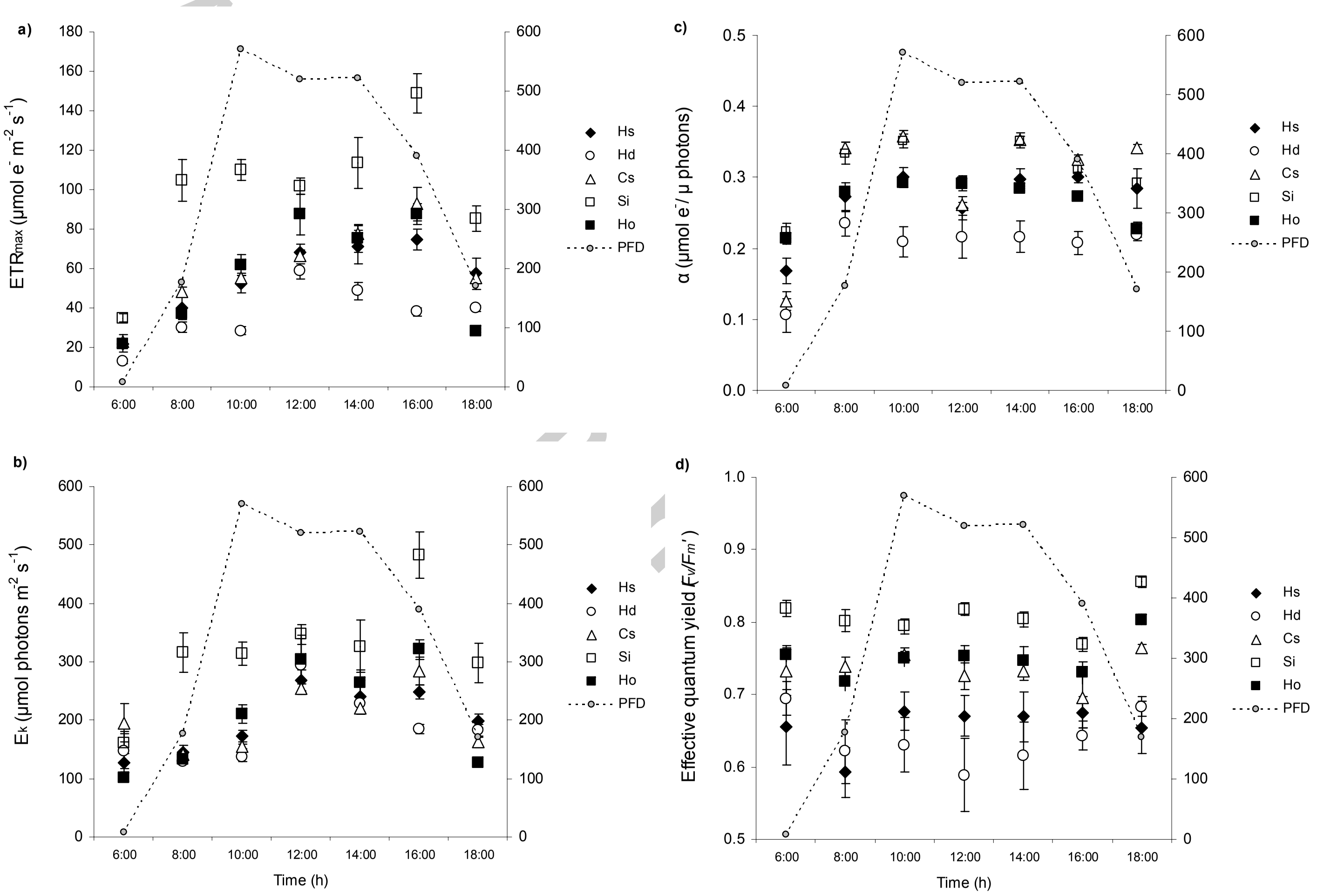
a)
ETRmax (μmol e⁻ m⁻² s⁻¹)
180
160
140
120
100
80
60
40
20
0
600
500
400
300
200
100
0
6:00
8:00
10:00
12:00
14:00
16:00
18:00
◆ Hs
○ Hd
△ Cs
□ Si
■ Ho
PFD
c)
α (μmol e⁻/ μ photons)
0.5
0.4
0.3
0.2
0.1
0.0
600
500
400
300
200
100
0
6:00
8:00
10:00
12:00
14:00
16:00
18:00
◆ Hs
○ Hd
△ Cs
□ Si
■ Ho
PFD
b)
Ek (μmol photons m⁻² s⁻¹)
600
500
400
300
200
100
0
600
500
400
300
200
100
0
6:00
8:00
10:00
12:00
14:00
16:00
18:00
Time (h)
◆ Hs
○ Hd
△ Cs
□ Si
■ Ho
PFD
d)
Effective quantum yield (Fv/Fm')
1.0
0.9
0.8
0.7
0.6
0.5
600
500
400
300
200
100
0
6:00
8:00
10:00
12:00
14:00
16:00
18:00
Time (h)
◆ Hs
○ Hd
△ Cs
□ Si
■ Ho
PFD

Figure 3

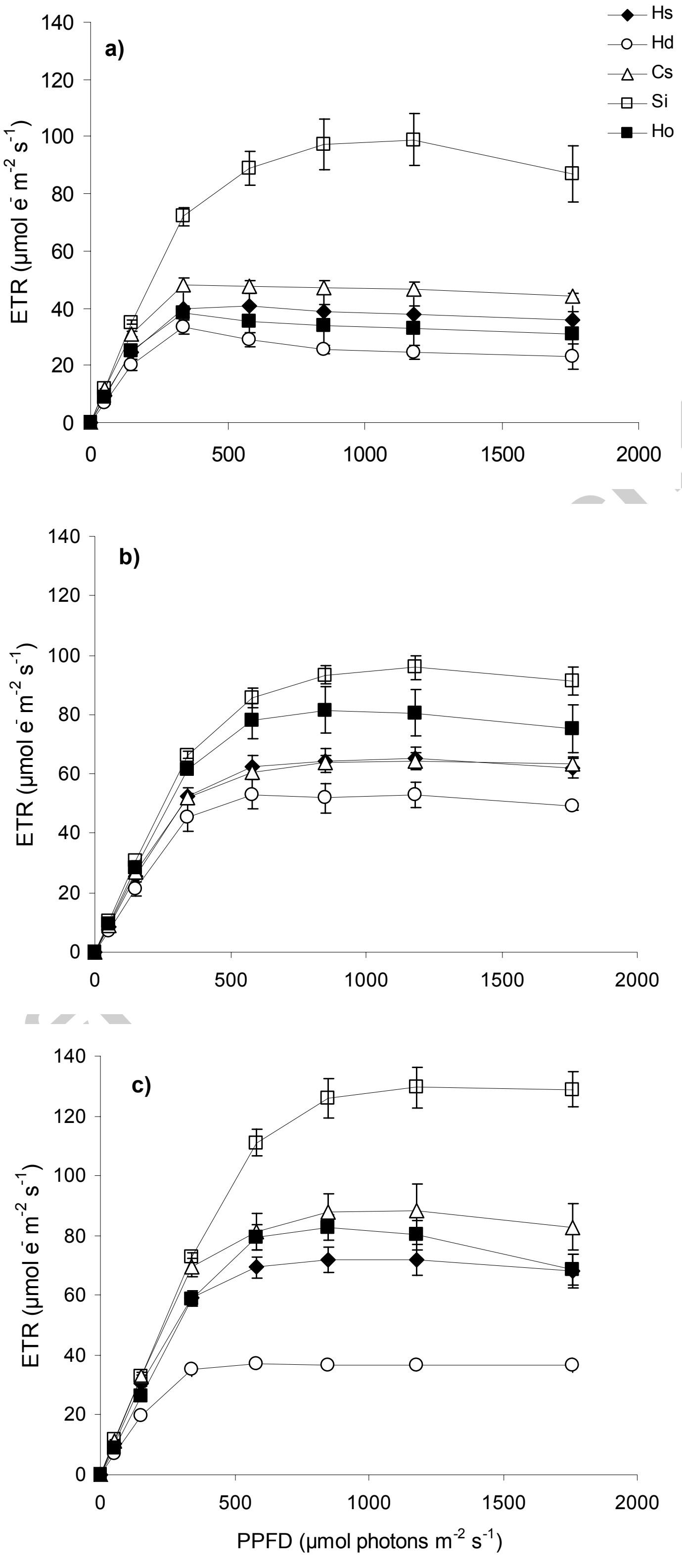
a)
b)
c)
Hs
Hd
Cs
Si
Ho
ETR (µmol e⁻ m⁻² s⁻¹)
PPFD (µmol photons m⁻² s⁻¹)
0
20
40
60
80
100
120
140
0
500
1000
1500
2000

Table 1. Two-way nested ANOVA of the effects of time and species on ETR_{max}, photosynthetic efficiency (α), saturating irradiance (E_k), and effective quantum yield ($\Delta F/F_m{}'$) for 5 seagrass species from Turnagain Island, Torres Strait. %Variance values are based on the % contribution of *F* values. Bonferoni post-hoc tests show significance among times (numbers shown are times from 6am to 6pm given in 24h format) and species (species codes same as in Fig 3).

Source	df	MS	*F* value	*P* value	%Var	*Post hoc tests*
ETR_{max}						
Time	6	5.177	136.70	< 0.001	51.88	6<8,10<12,14,16>18, 6<18
Species	4	4.626	122.13	< 0.001	46.35	SI>CS, HO, HS>HD
Time*Species	24	0.177	4.68	< 0.001	1.78	
Error	140	0.038				
α						
Time	6	0.055	53.80	< 0.001	45.21	6<8,10,12,14,16,18
Species	4	0.062	61.39	< 0.001	51.58	SI>CS>HO,HS>HD
Time*Species	24	0.004	3.82	< 0.001	3.21	
Error	140	0.001				
E_k						
Time	6	2.102	52.38	< 0.001	53.30	6<8,10<12,14,16>18, 6<18
Species	4	1.665	41.49	< 0.001	42.22	SI>CS,HD,HO,HS
Time*Species	24	0.176	4.40	< 0.001	4.48	
Error	140	0.040				
$\Delta F/F_m{}'$						
Time	6	0.089	2.77	0.014	5.02	no sig. differences
Species	4	0.651	51.47	< 0.001	93.36	SI>CS,HO>HD,HS
Time*Species	24	0.016	0.89	0.611	1.62	
Error	140					