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Ecophysiological status of nine species of macroalgae and seagrasses in Moreton Bay, Queensland, Australia

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ABSTRACT

Macroalgae and seagrasses from subtropical Moreton Bay on the east Australian coast were measured *in situ* using a submersible pulse-amplitude modulated fluorometer (Diving-PAM). The measurements from these marine phototrophs growing in the relatively pristine waters of eastern Moreton Bay will provide useful baseline information for future comparable studies assessing anthropogenic-induced environmental stresses, like those that now exist in the western part of the Bay. Importantly, this study redresses the paucity of knowledge on macroalgae that currently exists in this region. The use of this chlorophyll-fluorescence technique was attractive because of its non-invasive, quantitative approach providing information on photosynthetic performance of both macroalgae and seagrasses without the need for transplanting or enclosures. ❑ *ecophysiology, photosynthesis, phototrophs, chlorophyll, fluorescence, seagrass, macroalgae*

Macroalgal and seagrass beds rank among the most productive communities in the biosphere (Mann 1973; Ziemann & Wetzel 1980; Charpy-Rouband & Sournia 1990; Duarte & Chiscano 1999). They maintain a number of ecosystem functions, such as providing carbon and nutrient (N and P) sinks, food and habitat for animals, oxygenation of the water column, and consolidation of marine sediments. These marine phototrophs act as an interface between the water column and the sediments, extending metabolically active surfaces into the water column (leaves and fronds) and into sediments and other marine substrata (holdfasts, stolons and roots). Pristine marine systems are usually characterised by species rich macroalgal communities and extensive seagrass beds (Shepherd *et al.* 1989; Duarte 1995: Eriksson *et al.* 1998). As such they are useful biological indicators of disturbance which is frequently a consequence of human activity.

The macroalgal and seagrass communities of Moreton Bay (Fig. 1) reflect the markedly different environmental conditions prevailing in the western and eastern sectors of the bay (Young & Kirkman 1975; Hyland *et al.* 1989). Western Moreton Bay is heavily impacted by suspended solids, high nutrient loads and low salinity water from sewage discharge, terrestrial and riverine runoff. Consequently, the seagrass communities along the mainland coast of the bay are both sparse and largely restricted to

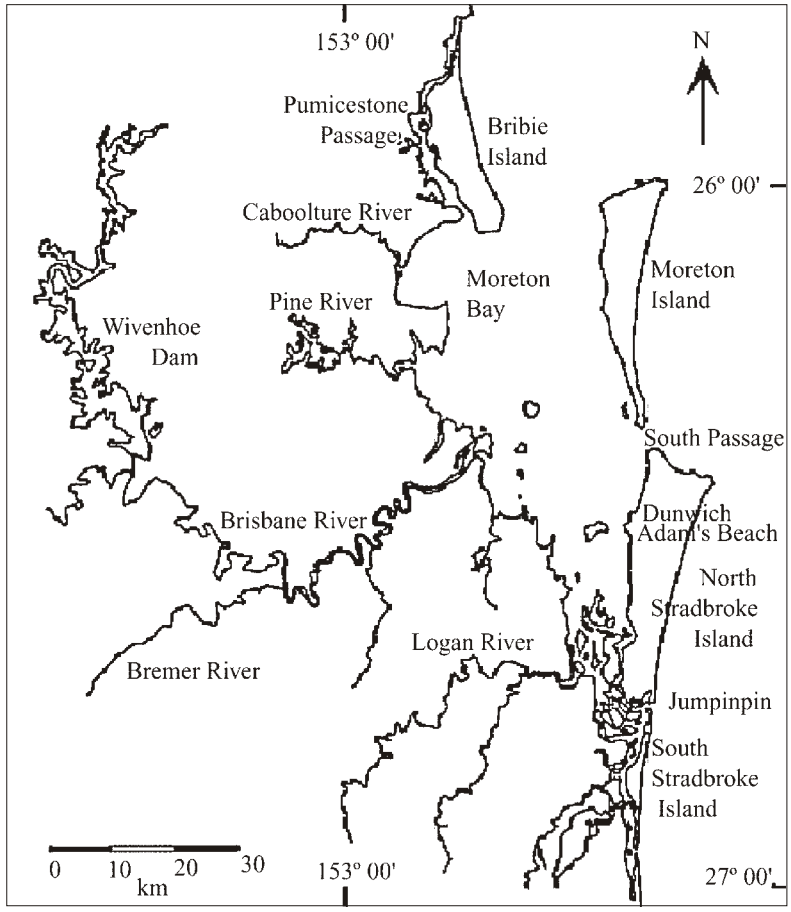

FIG. 1. Moreton Bay region of Southeast Queensland, Australia. Sampling sites were at Dunwich and Adam's Beaches on North Stradbroke Island.

depths <3 m. Macroalgal and cyanobacterial blooms, particularly of *Ulva* spp. and *Lyngbya majuscula*, are common in western Moreton Bay (Phillips pers. obs.). Increased nutrient loading favours the growth of opportunistic, stress-tolerant, bloom-forming macroalgal species that out-compete slower growing macroalgal and seagrass species for space and resources (Brown *et al.* 1990; Duarte 1995; Morand & Briand 1996; Hernandez *et al.* 1997; Raffaelli *et al.* 1998; McGlathery 2001; Taylor *et al.* 2001). Eastern Moreton Bay, on the other hand, undergoes constant flushing with oligotrophic oceanic waters. This relatively pristine environment supports dense and extensive seagrass meadows on the sandy substrata (Young & Kirkman 1975; Hyland *et al.* 1989).

In this study, chlorophyll fluorescence measurements were used to assess the physiological status of selected species of macroalgae and seagrasses growing in the relatively pristine waters of Eastern Moreton Bay (Fig. 1). The *in situ* photosynthetic capacity of these species (Table 1) was measured using a submersible pulse-amplitude modulated (PAM) fluorometer (Diving PAM). This measures efficiency of photochemistry from the fluorescence signal emitted by the phototrophs. The technique is non-destructive, rapid and adaptable to a range of aquatic photosynthetic organisms including benthic microalgae, seagrasses, macroalgae and corals. It is also a very sensitive indicator of perturbations in the photosynthetic process that may be due to changes in environmental

factors (Maxwell & Johnson 2000). The interpretation of the findings however, must be treated with care particularly when working with field samples that have an unknown nutrient history (Kruskopf & Flynn 2006; Raven & Beardall 2006). The quantum yield of photochemistry measured with PAM fluorometers has been used as a sensitive indicator of photosynthetic stress in seagrasses (Ralph 1999). Ralph & Burchett (1995) reported that fluorescence was more sensitive than oxygen electrode techniques for monitoring irradiance stress. PAM fluorescence has also been used to measure salinity stress (Kamermans *et al.* 1999), and carbon limitation (Schwarz *et al.* 2000) in seagrasses. Given these applications, measuring the photosynthetic health of marine phototrophs, growing in the clean waters of Eastern Moreton Bay, will provide valuable baseline information for future studies assessing anthropogenic induced stresses such as elevated nutrient levels, toxicants, turbidity effects and altered salinity levels that now exist in Western Moreton Bay.

MATERIALS AND METHODS

STUDY SITE

Moreton Bay (27ºS, 153ºE) is an important subtropical estuary in Southeast Queensland, Australia (Fig. 1). It is approximately 1400 km^2 with a maximum depth of 40 m in the north and 6 m in the south. Located adjacent to the City of Brisbane, the bay is separated from the South Pacific Ocean by Moreton, North and South Stradbroke Islands. Terrestrial runoff into the western side of the bay comes largely from four river catchments: Logan, Brisbane, Pine, and Caboolture (Fig. 1) while water exchange with the ocean (eastern side) occurs via the wide northern opening, between Bribie and Moreton Islands, South Passage situated between Moreton Island and North Stradbroke Island to the east, and Jumpinpin to the south. The study sites were located on the west coast of North Stradbroke Island (Fig. 1).

SAMPLE COLLECTION

Macroalgae and seagrasses (Table 1) were examined, *in situ,* at low tide (0–1 m) between 800 and 1100 hrs at Adam's and Dunwich Beaches on the eastern side of Moreton Bay (Fig. 1) during the period 7–25 February 2005 as part of the Thirteenth International Marine Biological Workshop on the Marine Fauna and Flora of Moreton Bay. These are soft sandy beaches with extensive macroalgal and seagrass communities. Plants were assessed immediately on site using a Diving-PAM (Pulse Amplitude Modulated) fluorometer (Walz, Germany) as described below. The green macroalgal species *Codium platyclados* and *Codium spongiosum* and the seagrass *Syringodium isoetifolium* were

Tab1e 1. List of marine plants investigated and their geographical distributions. Abbreviated code names (four letters) were used to label figures.

Plant	Higher Taxon	Code	Distribution
Macroalgae			
Caulerpa taxifolia (Vahl) C.Agardh	Chlorophyceae	*C tax*	pan tropical/subtropical
Codium platyclados R. Jones & Kraft	Chlorophyceae	*C pla*	east coast Australia
Codium spongiosum Harvey	Chlorophyceae	*C spo*	tropical Indopacific
Padina australis Hauck	Phaeophyceae	*P aus*	pan tropical/subtropical
Padina gymnospora (Kuetzing) Sonder	Phaeophyceae	*P gym*	pan tropical/subtropical
Seagrasses			
Zostera capricorni Ascherson	Zosteraceae	*Z cap*	endemic
Cymodocea serrulata (R. Brown) Ascherson & Magnus	Cymodoceaceae	*C ser*	tropical Indopacific
Halophila ovalis (R. Brown) Hooker f.	Hydrocharitaceae	*H ova*	pan tropical/subtropical
Syringodium isoetifolium Ascherson Dandy	Cymodoceaceae	*S iso*	tropical Indopacific

Table 2. List of parameters used, their abbreviations and units. Fluorescence definitions and equations were taken from Maxwell & Johnson (2000).

Parameter	Definition and equation	Units
PAM	pulse amplitude modulated fluorometer	
PAR	photosynthetically active radiation	mol photons m^{-2} s^{-1}
PSII	photosystem two	
F	background fluorescence	relative units
F_o	minimal fluorescence yield (in dark); all PSII reaction centres are open while the photosynthetic membrane is in the non-energised state; i. e., $q_P = 1$ and $q_N = 0$	relative units
F_m	maximum fluorescence yield (in dark); all PSII reaction centres are closed; all nonphotochemical quenching processes are at a minimum; i. e., $q_N = 0$	relative units
F_o'	minimum fluorescence yield subsequent to exposure to actinic and far-red light; all PSII reaction centres open in any light adapted state; i. e., $q_P = 1$ and nonphotochemical quenching 0	relative units
F_m'	maximum fluorescence yield (in light) obtained by a saturation pulse during exposure to actinic light; all PSII reaction centres closed in any light adapted state; i. e., $q_P = 0$ and nonphotochemical quenching 0	relative units
$\Delta F/F_m'$	effective quantum yield of photosynthetic energy conversion; Genty parameter. = $(F_m - F_o)/ F_m$	relative units
qP	photochemical quenching coefficient; varies between 0 and 1. = $(F_m - F)/(F_m - F_o)$	relative units
NPQ	nonradiative energy dissipation; varies between 0 and 10. = $(F_m - F_m)/F_m$	relative units
Rel. ETR	relative electron transport rate of PSII = $\Delta F/F'_m \times PAR \times 0.5 \times AF$	mol electrons m^{-2} s^{-1}
AF	absorptance factor; 0.84	relative units

collected from both Adam's and Dunwich Beaches. As there were no significant differences in fluorescence responses between locations, we grouped the data for each species.

PHYSICAL AND CHEMICAL PARAMETERS

Water quality parameters (salinity, pH and temperature) at collection sites were measured in the field using a Horiba Water Quality Checker (Model U-10, California, USA). Dissolved O_2 was measured with an YSI Environmental Oxygen Probe (John Morris Scientific Pty Ltd).

FLUORESCENCE MEASUREMENTS

We assessed the photosynthetic activity in a variety of macroalgae and seagrasses from Moreton Bay by measuring chlorophyll fluorescence signals from photosystem II (PSII) with a Diving-PAM (Walz, Germany). Fluorescence measurements were recorded from at least 2–3 separate blades/leaves from a minimum of three discrete plants of each species. *In situ* measurements were made on the actively-growing parts of the plant by positioning a fibreoptic-measuring head 10 mm from the plant tissue. To avoid effects associated with dessiccation and elevated temperature, the leaf/blade was kept immersed in seawater at its collection site and assayed within minutes of harvesting. The same measuring intensity and gain settings were used for all measurements and we were careful not to shade the plants being measured. Table 2 lists all fluorescence

parameters measured, their definitions, equations and units.

The Diving PAM allowed us to meaure fluorescence in ambient daylight and collect information on quenching coefficients. The effective quantum yield of photosynthetic energy conversion ($\Delta F/F'_m$) was calculated according to the relationship $(F'_m - F)/F'_m$ where F'_m is the maximum fluorescence yield of an illuminated sample and F is the background fluorescence for a given light state before a saturating light pulse. $\Delta F/F'_m$ is also referred to as the Yield or Genty-parameter (Genty *et al.* 1989).

Photosynthetic activity was estimated from the apparent relative electron transport rate of PSII (rel. ETR) which was determined using the relationship of Genty *et al.* (1989): relative ETR (mol electrons m^{-2} s^{-1}) = quantum yield ($\Delta F/F'_m$) × PAR × 0.5 × absorptance factor (AF). The PAR value is the instantaneous photosynthetic active irradiance (mol photons m^{-2} s^{-1}) directly measured close to the sample by the Diving PAM quantum sensor. The constant, 0.5, corrects for the fact that two quanta of light are required per electron as there are two coupled photosystems simultaneously absorbing light. The factor of 0.5 comes from the assumption (not always correct) that half the absorbed photons are used by PSII and half by photosystem I (PS I). The absorptance factor defines the fraction of incident light absorbed by the phototroph. As a best approximation we used the average light absorptance value of terrestial plant leaves AF = 0.84 (Björkman & Demmig 1987). There is however, a three-fold range of absorptances within seaweeds as a function of genotype and PAR environment (Table 4; Lüning 1990).

Table 3. Water quality parameters measured, between 8:00 and 11:00 hrs, at Adam's and Dunwich beaches during the study period. These parameters varied by less than 10% between sampling sites so the ranges over collection dates has been presented.

Parameter	Range
Salinity (ppt)	32–38
pH (rel units)	7.7–8.0
Water temperature (°C)	25–29
Dissolved O_2 (mg. L^{-1})	5.4–6.4
O_2 saturation (%)	82–96

The fluorescence quenching coefficients calculated by the instrument's subroutine program include photochemical quenching (qP) and nonradiative energy dissipation (NPQ), a type of nonphotochemical quenching. Photochemical quenching gives an indication of the proportion of PSII reaction centres that are open (photochemistry saturated) on a scale of zero to one. NPQ reflects heat-dissipation of excitation energy in the PSII antenna system so that it is a convenient indicator of excess light energy. The expression of nonphotochemical quenching (NPQ) used by the Diving PAM (Table 2) is based on the matrix model of antenna organisation and assumes the existence of nonphotochemical quenching traps (Schreiber *et al.* 1994). The sum of all the quenching processes is constant over wide variations in irradiance, indicating that they may be actively involved in the regulation and control of dissipation and utilisation of excitation energy in response to the current requirements of the photosynthetic apparatus (Maxwell & Johnson 2000).

RESULTS

Water quality parameters did not vary significantly between collection sites and collection dates (Table 3). Water temperature (27 ± 2°C), salinity (35 ± 3 ppt) and pH 7.85 (± 0.15 pH units) were typical for these sites at this time of the year. The water column was homogenously oxygenated with dissolved O_2 concentrations in the range 5.4–6.4 mg. L^{-1} (Table 3).

In situ chlorophyll *a* fluorescence measurements revealed a range of photosynthetic activity amongst the macroalgal and seagrass species examined (Figs 2–5). Yield values ranged from 0.48 ±0.09 for the seagrass *Cymodocea serrulata* to 0.85 ±0.05 for the brown alga *Padina gymnospora* (Fig. 2). The average $\Delta F/F_m'$ value for all plants measured in the present study was 0.72 ±0.06. This is similar to the Yield value typically reported in the literature for macroalgae and seagrasses from around the world (Table 4).

In general, macroalgae had lower rel. ETR values than the seagrasses (Fig. 3). The green algae, *Caulerpa taxifolia, Codium platyclados* and

Table 4. Literature values for various photosynthetic parameters measured with PAM fluorometers on seagrasses and **macroalgae**. In cases where parameters were measured but not reported, we used 'nr' to indicate 'not reported'. **Y** = Quantum yields; **Fv/Fm** = Photo-synthetic efficiency; **AF** = Measured absorption factor; **rel. ETR** = relative electron transport rate. Literature values for rel. ETR were calculated as described above in the methods section in most papers (§). However, some calculated rel. ETR without including AF (#) while others did not use AF or 0.5 (^).When errors were given as plus or minus standard deviations, we included them.

Species	Location	Y	Fv/Fm	AF	rel. ETR	Comments	Reference
terrestrial plant leaves			0.83	0.84			Björkman & Demmig (1987)
Zostera marina *Cymodocea nodosa*				0.44 ± 0.02 0.72			Beer *et al.* (1998)
Posidonia australis *P. sinuosa* *Amphibolis antartica* *A. griffithii* *Halophila ovalis*	Rottnest Island, Australia		ave = 0.68 ave = 0.70 ave = 0.63 ave = 0.55 ave = 0.58	0.84 §	max. 48 max. 27 max. 22 max. 30 max. 52	sampled between 5:00-19:00 hrs	Ralph *et al.* (1998)
Thalassia testudinum	Puerto Morelos, Mexico	nr	0.81	0.69	230	start of experiment (control)	Enríquez *et al.* (2001)
Ulva lactuca	Coobowie Australia	0.70–0.45		0.50	10 - 50	sampled between 900 & 1600 hrs	Longstaff *et al.* (2004)
Thalassia testudinum	Florida Bay, USA	0.78 ± 0.02	0.78 ± 0.03	0.67 ± 0.03	nr	youngest leaf measured	Durako & Kunzelman (2002)
Zostera marina	Chesapeake Bay,USA		0.75 – 0.80		20 – 45 ^	range given	Ralph *et al.* (2002)
Laminaria saccharina	Northern Brittany, France	0.15-0.73	0.74 ± 0.01		19 - 49 #	sampled between 1100 & 1800 hrs	Gévaert *et al.* (2003)
Posidonia australis	Jervis Bay, Australia	0.70 ± 0.06		0.68 ± 0.16	47 - 65	mean values	Runcie & Durako (2004)
Halimeda tuna	Florida Keys, USA				10 - 20	range given	Smith *et al.* (2004)
Thalassia hemprichii	Wanlitung, Taiwan			0.84 §	219 ± 20	sampled between 1000 & 1600 hrs	Liu *et al.* (2005)

Codium spongiosum had an average rel. ETR of 7.38 ±2.55 mol electrons m^{-2} s^{-1} which was not significantly different to that measured for the brown algae *Padina australis* and *Padina gymnospora* (7.43 ±1 mol electrons m^{-2} s^{-1}) (Fig. 3). While there is little overall variation in photosynthetic efficiency between the macroalgal genera, there is a great deal of variation between macroalgae and seagrasses (Fig. 3). On average, rel. ETR for the four seagrasses examined was 22 ±3 mol electrons m^{-2} s^{-1} (Fig. 3), about three times that measured for the macroalgae. The two seagrasses, *Halophila ovalis* and *Syringodium isoetifolium* were the most productive of all the plants measured (rel. ETR > 32 mol electrons m^{-2} s^{-1}; Fig. 3). Given that rel. ETR values can be used as a proxy for photosynthetic activity (gross), our findings (Fig. 3) reveal that the seagrasses in Moreton Bay are more productive (gross) than macroalgae.

Eighty percent of the PSII reaction centres in the plants (Fig. 4) were open at the time of measurement as indicated by the average qP for nine marine plants (0.8 ±0.09). All plants have qP values of 0.76 with the exception of *Cymodocea serrulata* which had a qP of 0.48. This seagrass also had a relatively low Yield of 0.48 (Fig. 2). The average NPQ for macroalgae (4.61) was similar to that for seagrasses (4.96) (Fig. 5). NPQ varied from 2.67 for *Padina australis* (Phaeophyta) to 8.41 for *Padina gymnospora* (Fig. 5). There were no evident trends in NPQ values between genera, taxa or families.

DISCUSSION

The measured fluorescence parameters provide a physiological summary of the photosynthetic performance of the nine marine plants examined under ambient environmental conditions. The phototrophs examined could be considered physiologically healthy based on their overall high Yields (Fig. 2), rel. ETR (Fig. 3), qP (Fig. 4) and NPQ (Fig. 5). Our findings for Yield and rel. ETR values are similar to those previously reported for plants growing in clean environments (Table 4). A photosystem's ability/efficiency to use light, expressed as rel. ETR, allows comparisons of photosynthetic efficiencies between different leaves and even between different plant species (Maxwell & Johnson 2000; Beer *et al*., 1998). Kevekordes *et al.* (2006) found that rel. ETR values varied 2-fold between eight species of *Caulerpa* ranging from 7–13 mol electrons m^{-2} s^{-1}. Interestingly, the broad form of the pan-tropical/subtropical green alga *Caulerpa taxifolia* (Phillips & Price 2002) we examined had an average rel. ETR of 7.3 mol electrons m^{-2} s^{-1} (Fig. 3). Changes in environmental conditions such as anthropogenic inputs (e.g. nutrients, toxicants, suspended solids) adversely affect the photosynthetic process. These impacts are detected by lowered reaction rates of the primary light reactions, thylakoid electron transport, darkenzymic stroma reactions and/or slow regulatory feedback processes to name a few. Yield and rel. ETR values, recorded for the phototrophs in this study, are indicative of a healthy environment.

The two most productive seagrasses (Fig. 3), *Halophila ovalis* and *Syringodium isoetifolium*, have leaf morphologies atypical for seagrasses resulting in lower overall leaf area. Leaves of *Halophila ovalis* are 1–4 cm long and petiolate, with laminae 0.5–2 cm in breadth while the narrow cylindrical leaves of *Syringodium isoetifolium* are 7–30 cm long and <2 mm wide. In eastern Moreton Bay, these species typically occur in either intertidal environments to depths of 5 m (*Halophila ovalis*) or just below low tide mark (*Syringodium isoetifolium*) where they still receive ample light for photosynthesis due to high water clarity (Young & Kirkman 1975). High rel. ETR (Fig. 3) with high photochemical activity (Fig. 2) have previously been reported for *Halophila ovalis* (Ralph *et al.* 1999), considered a colonising species. On the other hand, *Zostera capricorni* and *Cymodocea serrulata,* with more typical leaf morphology for seagrasses, had the lowest rel. ETR values (Fig. 3). These grow in either the intertidal zone to depths of 8 m (*Zostera capricorni*) or subtidally to depths of 3 m (*Cymodocea serrulata*) (Young and Kirkman 1975). These species have strap-like linear leaves which are 7–50 cm long and 2–5 mm broad (*Zostera capricorni*) or 6–15 cm long and 4–9 mm broad (*Cymodocea serrulata*) maximising absorption of more photosynthetically active radiation. Previous studies (summarised in Table 4) have also found larger seagrasses generally have lower photosynthetic activity (Figs 2 and 3).

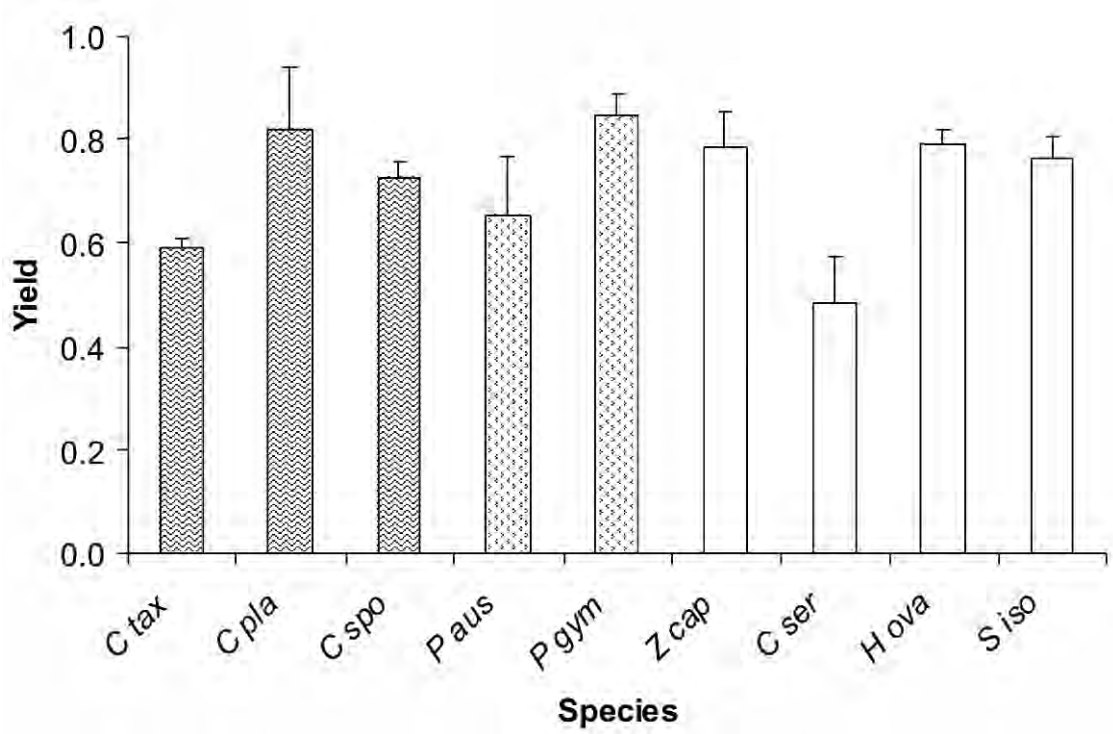

FIG. 2. Average Yield ($\Delta F/F_m'$) ± SE for the nine species of macroalgae (shaded bars) and seagrasses (non shaded bars) examined. High Yield values (>0.65) are an indicator of physiologically healthy plants. Abbreviations for macroalgae and seagrasses examined are listed in Table 1.

Unfortunately there are insufficient studies to make similar parallels for the macroalgae.

Diurnal rhythms of marine plants are known to influence *in situ* photosynthetic rate measurements. Beer & Björk (2000) observed that both F_v/F_m and rel. ETR decreased from early morning toward noontime in 2 seagrasses, *Halophila ovalis* and *Halodule wrightii*. Ralph *et al.* (1998) also observed significant diurnal variation in maximum ETR in three Australian seagrasses. Durako & Kunzelman (2002) found their Yield results were influenced by light intensity as well as by the selection of leaf tissue (age, health, etc.) and time of measurement. We endeavoured to make all our measurements on the actively growing sections of the marine plants and at approximately the same time of day (midmorning) to avoid these variables impacting on our results. While light intensity did vary with sampling time between 800 and 1100 hrs, we found no significant relationship ($p > 0.05$) between Yield values, species and the light intensity at the time measurements were made. The statistically similar results obtained for the three phototrophs (*Codium platyclados, Codium spongiosum* and *Syringodium isoetifolium*) collected from different beaches on different days confirms we were successful in avoiding spurious results due to sampling protocols.

The rel. ETR values, presented, should only be used as a proxy for primary productivity. To calculate absolute photosynthetic ETR using PAM fluorometry, the AF for each plant and the incident irradiance at the point of the fluorescence measurement need to be determined (Beer *et al.* 1998). Unfortunately we were unable to measure the AF of the plants. Hence, for ETR calculations, we used the standard AF for leaves of higher plants (0.84; Björkman & Demmig 1987) to give rel. ETR values. This is the value built into the instruments subroutine.

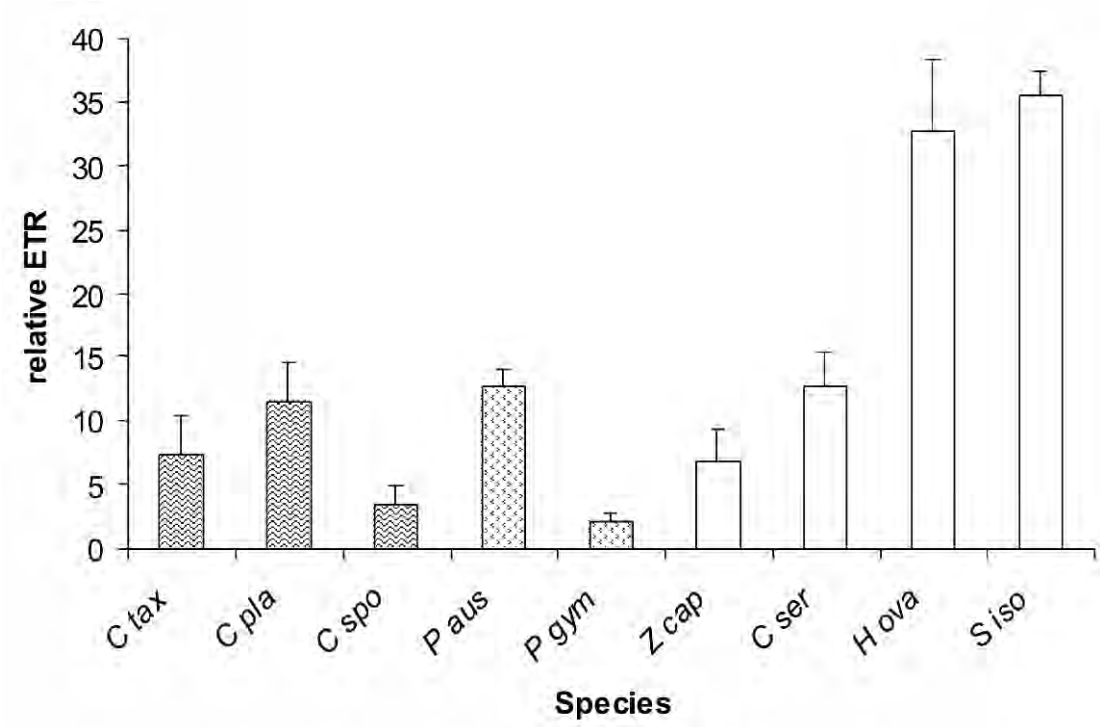

FIG. 3. Average rel. ETR (mol electrons m^{-2} s^{-1}) ±SE for the nine species of macroalgae (shaded bars) and seagrasses (non shaded bars) examined. The rel. electron transport rate can be used as a proxy for photosynthetic rate. Abbreviations for macroalgae and seagrasses examined are listed in Table 1.

A subsequent survey of the literature revealed AF values for macroalgae and seagrasses varies between 0.44 and 0.72 (Table 4). As these are all well below the AF for higher plants we have probably underestimated ETRs. Nonetheless, our rel. ETR were within the range of previously reported values when authors also used an AF of 0.84 (Table 4). Comparisons between plants and studies are reasonable as long as all the measuring parameters are clearly reported.

Assessment of overall photosynthetic performance has typically been made with the above parameters (Yield and rel. ETR) or their equivalents (F_v/F_m and primary productivity per unit of C or biomass). However, additional information on partial photochemical reactions can be obtained from analysis of induction kinetics which can reveal the complexity of the overall process. Saturation quench analysis, for example, allows us to distinguish between photochemical quenching coefficients. Fluorescence emission involves two fundamentally different types of competing de-excitation processes. First, photochemical energy conversion at the PSII centres and second, nonphotochemical loss of excitation energy at the antenna and reaction centre levels. Both mechanisms quench the maximal potential fluorescence yield according to the equations in Table 2. Because the Diving-PAM lacks an intrinsic far-red light source, the values presented here are only valid as first approximations.

An alternative expression for photochemical quenching (Table 2, Fig. 5) is 1-qP, the proportion of centres that are closed (Maxwell & Johnson 2000). This latter term is used as a measure of the excitation pressure on PSII. The macroalgae and seagrasses assessed in the present study had low amounts (0.2 ± 0.08) of excitation pressure on PSII (Fig. 4) indicating their photosynthetic apparatus coped with high photon fluxes which are typical of this region. Further, these measurements, along with the others undertaken in this study, show

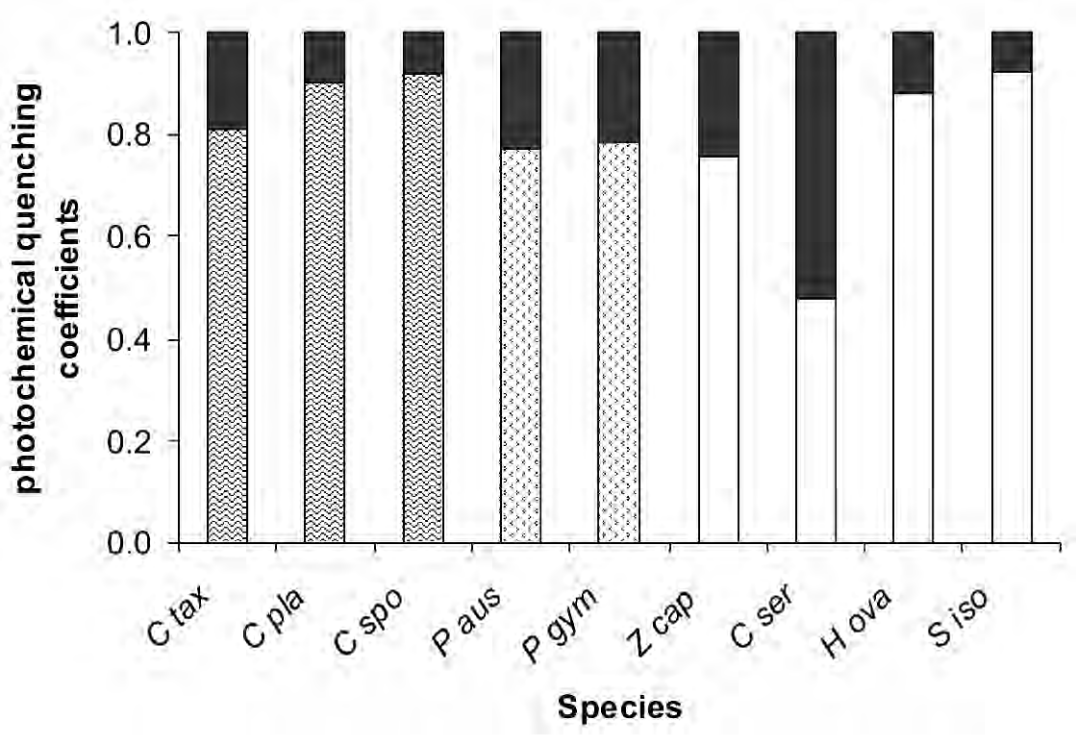

FIG. 4. The proportion of PSII reaction centres that are photochemically saturated (open) is defined on a scale of zero to one, and referred to as photochemical quenching (qP). On average, qP for macroalgal (shaded bars) and seagrasses (non shaded bars) was about 0.8. The average excitation pressure on PSII determined from the relationship 1-qP, was about 0.2 (filled bars for all species). Standard deviations were <20% of the means. Abbreviations for macroalgae and seagrasses examined are listed in Table 1.

that the plants were physiologically healthy. One exception was the seagrass *Cymodocea serrulata* which had a rather high 1-qP value of 0.52 (± 0.08) indicating that at least half of the open PSII reaction centres were suppressed by saturating light. This was consistent with the low Yield (Fig. 2) and rel. ETR (Fig. 3) measured for this species. There is no clear reason why this may be the case.

Non-photochemical quenching is due, in part, to heat-dissipation of excitation energy in the antenna system in the dark adapted state, or more simply, the amount of energy not used in photochemistry (Maxwell & Johnson 2000). Thus, NPQ is a useful indicator for 'excess light energy' and so is a good measure of photoprotection (Müller *et al.* 2001). Many of the macroalgae (the Chlorophyte *Codium platyclados*, the Phaeophyte *Padina gymnospora*) and the seagrasses (*Cymodocea serrulata*, *Halophila ovalis* and *Syringodium isoetifolium*) examined had high NPQ values (>4; Fig. 5). The remaining marine plants examined: *Caulerpa taxifolia* (Chlorophyta), *Codium spongiosum* (Chlorophyta), *Padina australis* (Phaeophyta) and *Zostera capricorni* (seagrass) had NPQ values in the range typically associated with higher plants (0.5 and 3.5; Maxwell & Johnson 2000) (Fig. 5). All these NPQ values are consistent with the plants being well adapted to their respective light environments and with plants having high Yield values (average of 0.72) (Fig. 2) and qP values (Fig. 4). Marine plants, growing in their natural environment, appear to keep energy dissipation pathways always engaged and ready to protect. Plants exposed to high light intensities and frequent sunflecks generally maintain elevated levels of zeaxanthin, antheraxanthin, and xanthophyll cycle pigments associated with photoprotective strategies (Demmig-Adams *et al.* 1999).

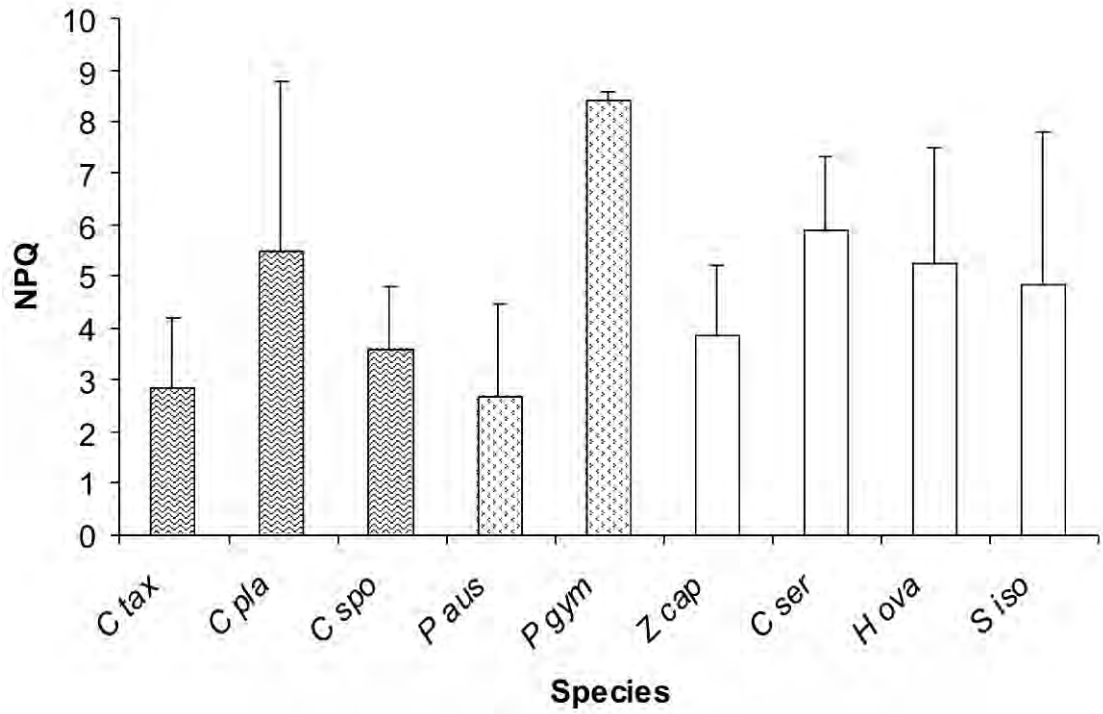

FIG. 5. Non photochemical quenching (NPQ) for the nine species of macroalgae (shaded bars) and seagrasses (non shaded bars) examined . The error bars are standard deviations of n > 5 plants. Abbreviations for macroalgae and seagrasses examined are listed in Table 1.

Future studies should focus on examination of seagrasses and macroalgae in other parts of Moreton Bay, particularly those growing on the western mainland coast that are exposed to stresses such as reduced light penetration from increased water turbidity, reduced salinity from increased freshwater inflows from the river systems and increased nutrient loading from sewage and agricultural runoff as well as other source and non source point pollutants. Macroalgal and seagrass communities are important primary producers which underpin many food webs in Moreton Bay. Understanding the productivity, physiology and stress responses of these plants will provide useful management tools for the conservation of these species and the protection of the Moreton Bay ecosystem.

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