



Innate resistance of PSII efficiency to sunlight stress is not an advantage for cyanobacteria compared to eukaryotic phytoplankton

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Abstract The effects of acute solar radiation stress on photosynthetic efficiency in freshwater unialgal cultures representing three phytoplankton pigment groups were measured by pulse amplitude modulated fluorometry (Walz Phyto-PAM) and compared to previous observations on field populations. Ultraviolet radiation (UVR) (UV-B and UV-A) induced a loss of photochemical quantum efficiency (F_v/F_m) in all 13 taxa examined in culture, while effects of photosynthetically active radiation (PAR) were smaller and often insignificant. Cyanobacteria were the most sensitive to PAR and UVR stress, chlorophytes the least and chromophytes intermediate but variable. The kinetics of maximal (F_m) and minimal (F_0) fluorescence responses suggested uncoupling of antenna

pigments from reaction centers (decreased F_m) persistent after dark adaptation was a common response, in particular for chromophytes, while the extent of impairment from damaged reaction centers (increased F_0) was more variable. Changes in F_v/F_m with irradiance exposure were well described by the Kok model of photoinhibition and indicated that damage, rather than recovery, processes were predictive of acute cumulative inhibition. Field populations of cyanobacteria and chromophytes tended to greater tolerance and lower damage rates than laboratory strains. The results for cultures under standardized conditions supported field results in showing cyanobacteria more sensitive to acute UVR exposure than eukaryotic algae, and thus lacking any innate resistance of photosystem II to sunlight stress that might help explain their success in surface bloom formation.

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List of symbols

F_0	Minimal fluorescence
F_v	Variable fluorescence
F_m	Maximal fluorescence
F_v/F_m	Maximum quantum yield of photochemistry

Abbreviations

Chl <i>a, b, c</i>	Chlorophyll <i>a, b</i> and <i>c</i> , respectively
NPQ	Non-photochemical quenching
P	PAR-only experimental light treatment
PA	PAR + UV-A experimental light treatment
PAB	PAR + UV-A + UV-B experimental light treatment
PAR	Photosynthetically active radiation
PAM	Pulse amplitude modulation
PC	Phycocyanin
PE	Phycocerythrin
PSII	Photosystem II
ROS	Reactive oxygen species
UVR	Ultraviolet radiation

Introduction

Exposure of phytoplankton to ultraviolet radiation (UVR) and strong blue light can cause primary photodamage to photosystem II (PSII) at the oxygen-evolving complex, often manifesting as photoinhibition (Heraud and Beardall 2000; Bouchard et al. 2006; Nishiyama et al. 2006). Consequent impairment of photosynthetic carbon fixation and growth rates (e.g., (Litchman and Neale 2005) makes photoinhibition a significant factor in natural community dynamics (Xenopoulos et al. 2000, 2009), more so because phytoplankton may experience increased potential for photoinhibition due to elevated atmospheric UVR transmission and climate-driven changes in stratification (Häder et al. 2011; Williamson et al. 2014). In addition to temperature and nutrients, different susceptibilities to photoinhibition among taxa may play a role in the success of harmful algal blooms (Paerl and Paul 2012; Sommaruga et al. 2009; Wulff et al. 2007), yet the number of controlled comparisons among multiple algal groups remains small, and some of the currently held tenets on the role of light in competitive dominance have not been robustly tested. We address this knowledge gap by measuring the sensitivity of three major phytoplankton groups to stressful levels of photosynthetically active radiation (PAR) and UVR. Using multi-wavelength, PAM fluorometry allowed us to examine both individual laboratory strains and field populations from a local lake. A major goal was to evaluate the common impression that many cyanobacteria are resistant to potentially inhibitory levels of

solar radiation, enabling their dominance as near-surface blooms in eutrophic systems.

Phytoplankton exhibits a range in light preferences and tolerances, with different strategies of light utilization and photoprotective mechanisms. These responses decrease light-induced damage to phytoplankton cells and reaction centers by decreasing photodamage, increasing repair or a combination of both. Short-term photoprotective mechanisms include alternate electron flow pathways, de novo protein synthesis and photorepair, non-photochemical quenching (NPQ), state transitions, antioxidant activity and vertical migration for motile and buoyant taxa. Regular exposure to high irradiance can lead to photoacclimation, including upregulation of the above-mentioned processes, production of photoprotective carotenoids and UVR-absorbing compounds, and adjustment of cell pigment concentrations (MacIntyre et al. 2002; Moore et al. 2006; Brunet et al. 2011; Qin et al. 2015).

Photoinhibition is measured by decreases in carbon fixation or oxygen evolution, but can also be conveniently assessed with instruments such as Phyto-PAM by measuring variable chlorophyll *a* (Chl *a*) parameters, such as the maximum quantum yield of photochemistry in PSII (F_v/F_m). F_v/F_m is determined from the difference of PSII Chl *a* fluorescence before and after a saturating light pulse, termed variable fluorescence (F_v) = $F_m - F_0$ (Genty et al. 1989; Falkowski and Raven 2007). Minimum fluorescence (F_0) is the fluorescence of dark-adapted cells when all PSII reaction centers are oxidized; maximum fluorescence (F_m) is the fluorescence measured after a saturating pulse reduces (closes) all reaction centers. Variations in F_0 and F_m under irradiance stress can provide insight into photoinhibition and photoacclimation. Reaction center impairment via photodamage can cause increases in F_0 and decreases in F_m (Demers et al. 1991; Herrmann et al. 1996; Maxwell and Johnson 2000; Brunet et al. 2011). Losses in reaction center excitation via de-coupling of antenna pigments can cause decreases in both F_0 and F_m , as well as potential increases in background fluorescence (F_0) from the pigment bed, for example via state transitions in cyanobacteria and green algae (Acuña et al. 2016; Kirilovsky 2015). The contribution of such acclimation and damage processes to changes in photosynthetic yield metrics (i.e., carbon fixation, oxygen evolution, F_v/F_m) during irradiance exposure can be

elucidated using models such as the Kok model of photoinhibition, which treats the inhibition kinetics of F_v/F_m (or other photosynthesis metrics) as a dynamic balance between damage and repair processes (Kok and Businger 1956; Heraud and Beardall 2000; Shelly et al. 2002; Lesser et al. 1994; Guan et al. 2011).

Phytoplankton contain different accessory pigments that can transfer excitation energy to the photosynthetic reaction centers and/or provide photo-protection (Brunet et al. 2011; MacIntyre et al. 2002; Kirk 1994; Kirilovsky 2015). Accessory pigments exhibit similarities within taxonomic groups and are used to differentiate algal groups based on excitation and/or emission spectra (Yentsch and Yentsch 1979; Phinney and Yentsch 1985), using a variety of equipment and mathematical procedures (Richardson et al. 2010; MacIntyre et al. 2010; Jakob et al. 2005). The Phyto-PAM fluorometer (Heinz Walz GmbH 2003) uses pulse amplitude modulation (PAM) and four wavebands of excitation light to distinguish three major pigment groups: greens (chlorophytes), blues (cyanobacteria) and browns (chromophytes) (Kolbowski and Schreiber 1995; Schreiber 1998).

In theory, instruments like Phyto-PAM enable assessments of phytoplankton pigment groups in natural communities (Jakob et al. 2005; Schmitt-Jansen and Altenburger 2008; Zhang et al. 2008; Beecraft et al. 2017), with a potential for insights into their photosynthetic physiology and light utilization under dynamic in situ conditions. Laboratory studies are nonetheless still necessary to obtain controlled comparisons of traits among taxa and pigment groups. Many algal traits are maintained over time under controlled culture conditions (Xiong et al. 1999; Stamenkovic and Hanelt 2011), but they cannot be extrapolated uncritically to nature, as responses apparent in situ may arise from a variety of environmental influences not occurring in culture, as well as taxon-specific traits. Application of the Phyto-PAM in a meso-eutrophic embayment suggested that natural populations of large colonial cyanobacteria were more sensitive to solar UVR than co-occurring eukaryotic taxa (Beecraft et al. 2017), contrary to previously reported observations (Sommaruga et al. 2009; Xenopoulos et al. 2009; Wu et al. 2011; Paerl and Paul 2012). Experiments under controlled conditions would help determine whether such results truly depict characteristic group differences or reflect unrecognized environmental influences in nature, or even

instrument uncertainty in application to mixed communities.

The objectives of this study were to (1) determine how the tolerance to stressful PAR and UVR varies within and among phytoplankton pigment groups that can be resolved by instruments such as Phyto-PAM (based on the response of maximum quantum yield of photochemistry, F_v/F_m), (2) test whether differences of tolerance among groups observed in unialgal cultures are predictive of differences observed in natural communities, and (3) determine whether variations of tolerance are predictable from metrics thought to reflect varying degrees of non-photochemical quenching, PSII damage and repair processes. We hypothesized that all taxa would exhibit photoinhibition when exposed to UVR, but that chlorophytes would show the most tolerance, while chromophyte and cyanobacterial taxa would show variable sensitivity. We also hypothesized that field populations, with a history of exposure to full-spectrum sunlight at periodically high intensities, would be better-acclimated and more tolerant than laboratory cultures, but would show a similar ranking of tolerance among groups. Finally, we proposed that the kinetics of F_v/F_m , F_0 and F_m would reveal group-specific differences in the contribution of acclimation, repair and damage processes to the variations of stress tolerance among groups and taxa.

Methods

Culture conditions

Clonal non-axenic microalgal and cyanobacterial cultures (Table 1) were obtained from the Canadian Phycological Culture Center (CPCC, University of Waterloo, Waterloo ON) and the Canadian Center for Inland Waters (CCIW, Burlington ON), Environment and Climate Change Canada. Representative taxa were chosen to capture some of the variation within the three algal groups classified by the Phyto-PAM, and because of their common occurrence in a wide variety of freshwater environments. Batch monocultures were grown in 1-L flasks of nutrient-replete WC media, modified by S.B. Watson from (Guillard and Lorenzen 1972) adjusted to pH 8.2–8.4 (Watson 1999). Cultures were incubated at 19 ± 2 °C at an illumination intensity of ca. 48 ± 4 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ from

Table 1 Phytoplankton taxa used in irradiance exposure experiments

Taxon	Phyto-PAM group	Algal phylum
<i>Anabaena oscillarioides</i> ^a	Bl	Cyanophyta
<i>Dolichospermum</i> ^b <i>lemmermannii</i> LO08-01	Bl	Cyanophyta
<i>Microcystis aeruginosa</i> Kutz.em. Elenkin CPCC 299	Bl	Cyanophyta
<i>Synechococcus</i> sp. ^a	Bl	Cyanophyta
<i>Synechococcus rhodobaktron</i> NIVA 8	Br ^c	Cyanophyta
<i>Coelastrum cambricum</i> HH001-05	Gr	Chlorophyta
<i>Pediastrum simplex</i> Meyen CPCC 431	Gr	Chlorophyta
<i>Scenedesmus obliquus</i> EC-SW1	Gr	Chlorophyta
<i>Asterionella formosa</i> Hass CPCC 605	Br	Ochrophyta
<i>Fragilaria crotonensis</i> Kitton CPCC 269	Br	Ochrophyta
<i>Cryptomonas</i> sp. CPCC 336	Br	Cryptophyta
<i>Synura petersenii</i> Korshikov CPCC 495	Br	Ochrophyta
<i>Peridinium inconspicuum</i> UTEX LB 2255	Br	Dinophyta

^aStrain number not known

^bFormerly named *Anabaena*

^c*Synechococcus rhodobaktron* is a phycoerythrin-rich cyanobacterium included as a member of the ‘blue’ group taxonomically; however, it is recognized as predominantly ‘brown’ by the Phyto-PAM when using typical ‘blue’ reference spectra species. It is included with the cyanobacteria/blue group throughout the present study

cool white fluorescent bulbs on a 16:8-h light/dark cycle, and mixed manually each day.

Growth was monitored by daily measurements of fluorescence and F_v/F_m using a Phyto-PAM (S/N: PPAA0220, Walz GmbH, Effeltrich, Germany), supplemented by less frequent microscopic cell counts, to estimate growth phase. Irradiance exposure experiments were performed on samples from exponential phase cultures acclimated to the described growth conditions, and diluted approximately one hour prior to experiments with fresh media to reach cell densities for manufacturer-suggested gain settings when creating new reference spectra.

Irradiance exposure experiments

Acute irradiance exposures were completed in a solar simulator containing a Xenon arc lamp (1 kW, Oriol Instruments, Irvine, CA) and optical glass cutoff filters (Schott optical filters) with nominal 50% transmission at 305, 340 and 420 nm to produce three spectral treatments: PAR only (> 420 nm); PAR + UV-A (> 340 nm); and PAR + UV-A + UV-B (> 305 nm), hereafter referred to as P, PA and PAB, respectively. The incident spectral irradiance was measured using an LT-

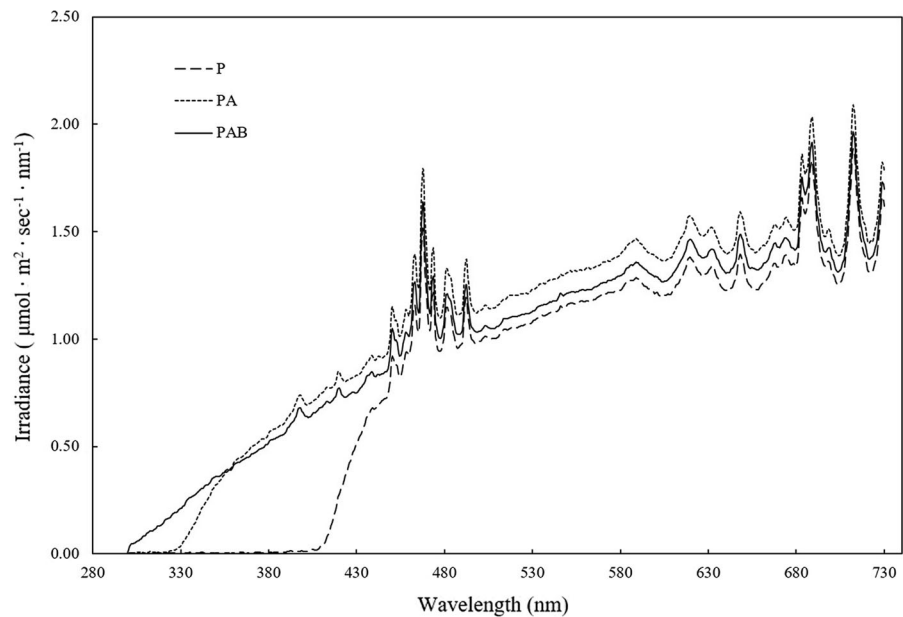
14 spectrometer (S/N: 09121132, Stellarnet Inc., Tampa, FL) (Table 2, Fig. 1). These filters produce a PAB treatment that adds both UV-B and more short-wavelength UV-A exposure relative to the PA treatment. The slight amounts of UVR irradiance indicated for the P treatment and UV-B for the PA treatment are likely artifacts of the radiometer, and too small to exert appreciable effect. PAR was monitored using a LI-COR (Q15458) photometer (Li-COR Biosciences, Lincoln, NE) throughout experiments to maintain consistent irradiance levels. Temperature was maintained at 19 ± 1 °C by a water circulation system.

Subsamples (ca. 50 mL) of experimental batch cultures were transferred to 400-mL Pyrex beakers under dim light and placed in the incubation chambers. Samples were illuminated from above and exposures were 75 min, with 3 mL aliquots removed after mixing from each treatment at 11 time points (pre-exposure/time zero samples taken from experimental batches at the start of exposures). Suspensions were diluted and started at a maximum of 1.5 cm in depth, such that attenuation and self-shading effects would be negligible. Subsamples were dark-acclimated at ambient temperature for ca. 30 min, to allow for relaxation of NPQ, before measurement of Chl *a* fluorescence

Table 2 Broadband photon flux density (PFD) for UV-B, UV-A and PAR in the three experimental spectral treatments

Spectral treatment	UV-B: 300–315 nm ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	UV-A: 315–400 nm ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	PAR: 400–700 nm ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
P (> 420 nm)	0.06	0.46	319.04
PA (> 340 nm)	0.12	29.80	384.11
PAB (> 305 nm)	1.70	32.23	356.01

Fig. 1 Spectral irradiance of experimental treatments P—PAR only (dashed line), PA—PAR + UV-A (dotted line) and PAB—PAR + UV-A + UV-B (solid line). For complete spectral irradiance data, refer to Table S1 in Supplementary Materials



using the Phyto-PAM. Low-intensity measuring light was used to measure F_0 , and then, a saturating pulse (0.2 s up to $2600 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ at 655 nm) was applied to produce F_m . The dark-adapted F_v/F_m of cyanobacteria is characteristically lower compared to eukaryotic microalgae, due to the fluorescence contributions of phycobilisomes (PBS), photosystem I (PSI) Chl *a*, and a partially reduced electron transport chain in the dark (Campbell et al. 1998; Schuurmans et al. 2015; Acuña et al. 2016). In the current study, we were not comparing absolute variable fluorescence among taxa or treatments but rather the relative changes under experimental treatments, and our consistent use of dark adaptation was suitable to that purpose. Corrections for background dissolved fluorescence were made with 0.2- μm -filtered culture media. For each species, triplicate irradiance exposure experiments were performed on subsamples taken from the same batch culture.

The Phyto-PAM gives fluorescence-derived parameters for four excitation wavelengths (470, 520, 645 and 665 nm) and up to three algal groups: blues (most cyanobacteria), greens (chlorophytes) and browns (diatoms, dinoflagellates, chrysophytes, cryptophytes and some cyanobacteria). Algal group values are determined by deconvolution of the four diode signals using linear un-mixing and one reference spectrum for each of the three pigment groups. While cryptophytes are not typically classified as brown/chromophyte taxa, they are categorized as such by Phyto-PAM due to their high phycoerythrin (PE) content, excited by the 520-nm diode, as are PE-rich cyanobacteria. For laboratory experiments, only the reference spectrum corresponding to the measured taxon was used, and Phyto-PAM was forced to assign all measured signal to the correct algal group. Field experiments used multiple reference spectra and the group discrimination abilities of the Phyto-PAM (Beecraft et al. 2017).

Statistical analysis

The dynamics of F_0 and F_m were analyzed via polynomial regression, using a step function based on the Akaike information criterion (AIC) to select the regression model (first, second and third order) that best described each time series. The fitted models were compared among spectral treatments, taxa and pigment groups. For each taxon and spectral treatment, the relative F_v/F_m over time was fitted to the Kok model of photoinhibition (1956) using nonlinear regression analysis and least-squares error minimization:

$$\frac{P}{P_i} = \frac{r}{(r+k)} + \frac{k}{(k+r)} * e^{-(k+r)t} \quad (1)$$

where t is the time, P_i is the initial F_v/F_m at time zero (prior to irradiance exposure), P is the F_v/F_m at time t and k and r are rate constants for damage and repair processes, respectively (Lesser et al. 1994; Heraud and Beardall 2000).

The laboratory culture results were compared with those from similar irradiance exposure experiments (Beecraft et al. 2017) performed on samples collected from a depth of 1 m from April to September in Hamilton Harbour, a meso-eutrophic embayment of Lake Ontario, Canada. Damage rate estimates for PA and PAB spectral treatments (those for treatment P could not be measured reliably) were scaled for comparison with laboratory culture results by assuming damage rates would be directly proportional to the applied irradiance in otherwise identical experiments: k multiplied by 0.45, for exposures of 450 vs 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The scaled damage rates were then used to calculate the post-exposure F_v/F_m that would be expected under the lower irradiance of the culture experiments. Comparisons with culture results were made using two sample t tests for the blue and brown groups only, as greens were rarely abundant enough in the natural community to provide reliable metrics. Statistical analyses used Systat 10 (Systat Software, Inc., Chicago, IL) and R (R Core Team 2015).

Results

Cumulative inhibition of F_v/F_m in acute exposure experiments

F_v/F_m decreased in all spectral treatments, except for the chlorophytes *Coelastrum cambricum* and *Scenedesmus obliquus* under the PAR-only (P) treatment (Table 3). The full-spectrum (PAB) treatment produced the greatest reductions in F_v/F_m , while P elicited the smallest. The average relative sensitivity of the three algal groups was consistent across spectral treatments, with the blue group having the highest sensitivity to UVR, greens the least and browns showing an intermediate, but variable response (Table 3, Figure S1). Two-way analysis of variance (ANOVA) showed significant differences in post-exposure relative F_v/F_m among spectral treatments and algal groups, but no interactive effect between the two. Based on post hoc tests using Tukey's honestly significant difference (HSD) for multiple comparisons, the blue group was significantly different from the brown and green groups ($p < 0.05$), while the latter two were not significantly different from each other. P and PAB treatment effects differed ($p < 0.05$) for all three algal groups, but PA and PAB effects differed only at $p < 0.10$ for the greens and browns. PAR intensity varied by up to 20% among spectral treatments (Table 2), but given that the relatively minor effect of PAR such differences was unlikely to affect the measured responses to UVR.

The three chlorophytes (green group) showed the greatest resistance to photoinhibition and the most within-group consistency in F_v/F_m response (Table 3). In contrast, the five taxa from the brown group exhibited a broad range in response. The synurophyte *Synura petersenii* was the most sensitive brown taxon, while the cryptoflagellate *Cryptomonas* sp. and diatom *Fragilaria crotonensis* were more tolerant, with post-exposure F_v/F_m values similar to those of the chlorophytes. The five cyanobacteria showed the highest overall sensitivity to photoinhibition, with similar responses for *Microcystis aeruginosa*, *Dolichospermum lemmermannii* and *Synechococcus* sp. and larger reductions in F_v/F_m for *Anabaena oscillarioides* and *Synechococcus rhodobaktron* (Table 3).

Table 3 Group-specific initial F_v/F_m and post-exposure relative F_v/F_m (normalized to initial) of phytoplankton taxa for spectral treatments P (PAR only), PA (PAR + U/A), and PAB(PAR + UV-A + UV-B). Values are mean (\pm standard deviation). Algal group refers to Phyto-PAM designated groups (Bl—blues, Gr—greens, Br—browns)

Taxon	Algal group	Initial F_v/F_m (no exposure)	Post-exposure relative F_v/F_m		
			P	PA	PAB
<i>A. oscillarioides</i>	Bl	0.44 (\pm 0.03)	0.57 (\pm 0.06)	0.3 (\pm 0.02)	0.07 (\pm 0.01)
<i>D. lemmermannii</i>	Bl	0.39 (\pm 0.03)	0.85 (\pm 0.04)	0.67 (\pm 0.1)	0.31 (\pm 0.1)
<i>M. aeruginosa</i>	Bl	0.42 (\pm 0.01)	0.87 (\pm 0.01)	0.63 (\pm 0.04)	0.49 (\pm 0.04)
<i>Synechococcus</i> sp.	Bl	0.32 (\pm 0.01)	0.76 (\pm 0.03)	0.51 (\pm 0.08)	0.3 (\pm 0.05)
<i>S. rhodobaktron</i>	Bl	0.3 (\pm 0.01)	0.32 (\pm 0.06)	0.07 (\pm 0)	0.05 (\pm 0.02)
<i>C. cambricum</i>	Gr	0.69 (\pm 0.01)	1.01 (\pm 0.02)	0.9 (\pm 0.01)	0.83 (\pm 0.02)
<i>P. simplex</i>	Gr	0.59 (\pm 0.01)	0.94 (\pm 0.01)	0.82 (\pm 0.04)	0.65 (\pm 0.01)
<i>S. obliquus</i>	Gr	0.63 (\pm 0.03)	0.99 (\pm 0.04)	0.92 (\pm 0.03)	0.66 (\pm 0.06)
<i>A. formosa</i>	Br	0.56 (\pm 0.03)	0.82 (\pm 0.03)	0.62 (\pm 0.02)	0.55 (\pm 0.05)
<i>F. crotonensis</i>	Br	0.6 (\pm 0.02)	0.96 (\pm 0.02)	0.85 (\pm 0.04)	0.71 (\pm 0.05)
<i>Cryptomonas</i> sp.	Br	0.67 (\pm 0)	0.95 (\pm 0.01)	0.87 (\pm 0.03)	0.68 (\pm 0.02)
<i>S. petersenii</i>	Br	0.62 (\pm 0.01)	0.91 (\pm 0.02)	0.46 (\pm 0.15)	0.25 (\pm 0.05)
<i>P. inconspicuum</i>	Br	0.48 (\pm 0.02)	0.89 (\pm 0.05)	0.66 (\pm 0.04)	0.49 (\pm 0.02)

Dynamics of F_0 and F_m

The changes in minimum (F_0) and maximum (F_m) fluorescence over time (e.g., Fig. 2) varied among taxa and spectral treatments, with polynomial regression revealing significant relationships (first, second or third order, $p < 0.05$) for 71 out of 78 cases (Table S2). The model of best fit was most often third order (third order = 48, second order = 15, first order = 13), with no apparent pattern in the polynomial order or incidence of significant versus non-significant relationships for either F_0 or F_m among pigment groups or spectral treatments. The percent change of post-exposure (75 min endpoint) fluorescence relative to initial (Table 4) was typically greater for F_m than F_0 , except for *S. rhodobaktron* (Fig. 2, Table S2), which showed large changes in F_0 and skewed the mean for the blue group. F_0 responses were variable with spectral treatment and across algal groups: The largest decreases generally occurred in the P treatment, followed by the PA and PAB treatments (Table 4), though only the brown group had reductions in F_0 across all taxa. *S. rhodobaktron* showed a unique response, with a large and sustained increase in both F_0 and F_m following irradiance exposure (Fig. 2a, b). The majority of taxa across all three pigment groups showed a decrease in F_m from

initial values under all spectral treatments (i.e., negative values in Table 4, Fig. 2d, f).

Modeling kinetics and estimating repair and damage rates

In one case, the Kok model could not converge on an estimate (*C. cambricum*, P treatment), and in several other cases involving green or brown taxa, the estimates of kinetic constants, usually for repair, were not significantly different from zero (16 of 78 cases; Table S3). In these cases, there was little change in F_v/F_m , and thus little variance for the model to describe. The Kok model does not encompass the possibility of processes that would generate negative rate constants under continued radiation exposure. Thus, where negative rate constant estimates were obtained, they were reported as zero, as they could not be interpreted in the context of the model. The model fits well for the majority of taxa and spectral treatments that displayed appreciable photoinhibition, capturing 80–100% of the variation in F_v/F_m for the PAB treatment (Table 5, Fig. 3). The range in estimates, in particular for treatment P, produced large variations around average algal group and spectral treatment effects (Tables 5, 6, S3).

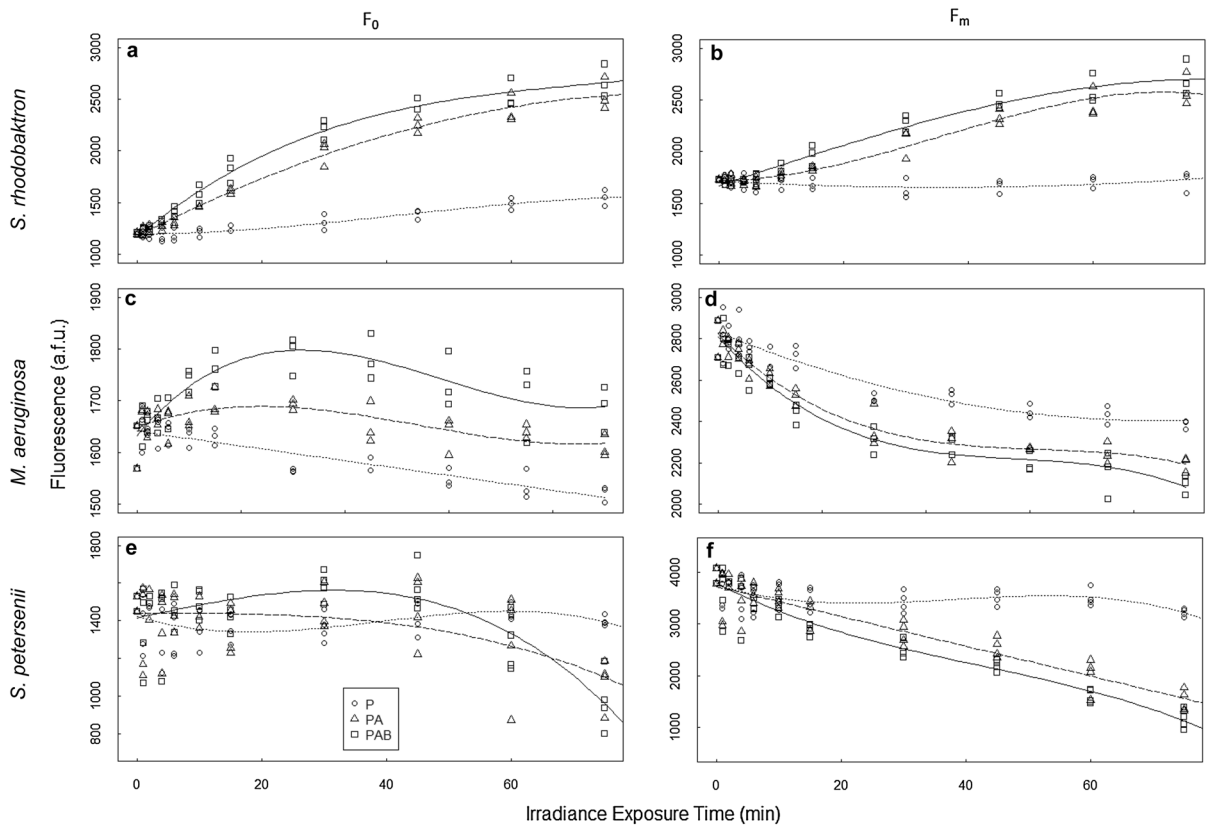


Fig. 2 Minimal (F_0) and maximal (F_m) fluorescence over time for *Synechococcus rhodobaktron* (a F_0 , b F_m), *Microcystis aeruginosa* (c F_0 , d F_m) and *Synura petersenii*. (e F_0 , f F_m) with

fitted polynomial regressions for each spectral treatment (P—dotted line, PA—dashed line, PAB—solid line)

Table 4 Percent change in minimal fluorescence (F_0) and maximal fluorescence (F_m) (endpoint relative to initial) during experimental irradiance exposures (P—PAR only, PA—PAR + UV-A, PAB—PAR + UV-A + UV-B) for each algal group, calculated using fitted polynomial regressions

	F_0			F_m		
	P	PA	PAB	P	PA	PAB
<i>Blue</i>						
Mean	2.0	28.1	22.9	- 11.4	- 3.6	- 12.1
Median	- 3.7	1.2	3.9	- 12.3	- 17.4	- 24.9
<i>Green</i>						
Mean	- 30.8	- 9.3	3.4	- 33.4	- 28.2	- 29.4
Median	- 20.2	0.0	14.6	- 23.5	- 17.5	- 23.9
<i>Brown</i>						
Mean	- 23.1	- 28.3	- 19.4	- 31.5	- 48.6	- 47.7
Median	- 15.4	- 23.5	- 15.0	- 23.6	- 44.3	- 40.7

Visual examination of residual plots was used to further assess the applicability of the Kok model to the exposure response data (sample from each algal group and spectral treatment in Figure S2). There were a few cases where residuals suggested systematic lack of fit.

In the most extreme example, F_v/F_m of *D. lemmermannii* decreased faster than the Kok model estimates, reached a plateau and then increased slightly, suggesting some recovery that was not accounted for by the model (Fig. 3a, Figure S2B). For other taxa, there

Table 5 Kok model damage and repair rate constants of relative F_v/F_m exposure response kinetics for the PAB (PAR + UV-A + UV-B) treatment (complete results in Table S3)

Taxon	Algal group	Mean corrected r^2	Repair rate (min^{-1})	Damage rate (min^{-1})
<i>A. oscillarioides</i>	Bl	0.931	0.02	0.109
<i>D. lemmermannii</i>	Bl	0.939	0.027	0.072
<i>M. aeruginosa</i>	Bl	0.983	0.03	0.033
<i>Synechococcus</i> sp.	Bl	0.984	0.027	0.061
<i>S. rhodobaktron</i>	Bl	0.992	0.004	0.084
<i>C. cambricum</i>	Gr	0.888	0.007	0.004
<i>P. simplex</i>	Gr	0.929	0.015	0.01
<i>S. obliquus</i>	Gr	0.946	0.012	0.008
<i>A. formosa</i>	Br	0.973	0.043	0.037
<i>F. crotonensis</i>	Br	0.826	0	0.004
<i>Cryptomonas</i> sp.	Br	0.976	0.03	0.015
<i>S. petersenii</i>	Br	0.981	0	0.015
<i>P. inconspicuum</i>	Br	0.931	0.019	0.022

was little to no indication of lack of fit, and the model appeared to capture the dynamics without bias.

Damage rate constants (k) were generally lowest for the green taxa (0.004–0.01 min^{-1} under PAB), intermediate for the brown taxa (0.004–0.037 min^{-1}) and highest for the blue taxa (0.033–0.109 min^{-1}) (Table 5). Damage rates increased with short-wavelength exposure ($P < PA < PAB$) for the blue and brown groups and were higher for the blue group than the greens and browns for all three spectral treatments (Table 6, Table S3). The range of repair rate estimates (r) overlapped among taxa and pigment groups (Table 5), and average repair rates were highest under the PAR-only (P) treatment for all pigment groups (Table 6). Two-way ANOVA for each rate coefficient (factors: algal group and spectral treatment) indicated significant effects of algal group ($p \ll 0.05$) when comparing k , near significant effects of spectral treatment when comparing r ($p = 0.086$), and no interaction effects for r or k . Regression analyses indicated significant inverse relationships between damage rate constants and post-exposure F_v/F_m for the PA and PAB spectral treatments, but none between repair rate constants and post-exposure F_v/F_m (Fig. 4).

Comparisons between laboratory and natural populations

Experiments on field populations from Hamilton Harbour revealed small changes of F_v/F_m in response to treatment P and larger decreases from PA and PAB, similar to laboratory cultures (Table 7). Despite the approximately 2.2 times higher experimental irradiance in the field population experiments, post-exposure relative F_v/F_m and damage rates in PA and PAB were similar to those for culture experiments. Average repair rates showed little systematic difference between field and laboratory populations. When scaled for the difference in exposure irradiance, field populations had lower damage rates and higher post-exposure relative F_v/F_m than laboratory cultures, with the exception of greens (Table 7). Under PA and PAB, both culture and field populations of greens showed low damage rate constants and high resistance. The differences of scaled damage rate constants and post-exposure F_v/F_m between cultures and field populations were not statistically significant ($p > 0.05$) possibly due to the small sample numbers and large within-group variance, although damage rate constants for the blue group (PA) and post-exposure F_v/F_m for the brown group (PAB) differed at $p < 0.10$. Cultures and field populations showed the same

Fig. 3 Kinetics of relative F_v/F_m for **a** *Dolichospermum lemmermannii* (blue), **b** *Scenedesmus obliquus* (green) and **c** *Peridinium inconspicuum* (brown) with fitted values from the Kok model for each spectral treatment (P—PAR only, PA—PAR + UV-A and PAB—PAR + UV-A + UV-B)

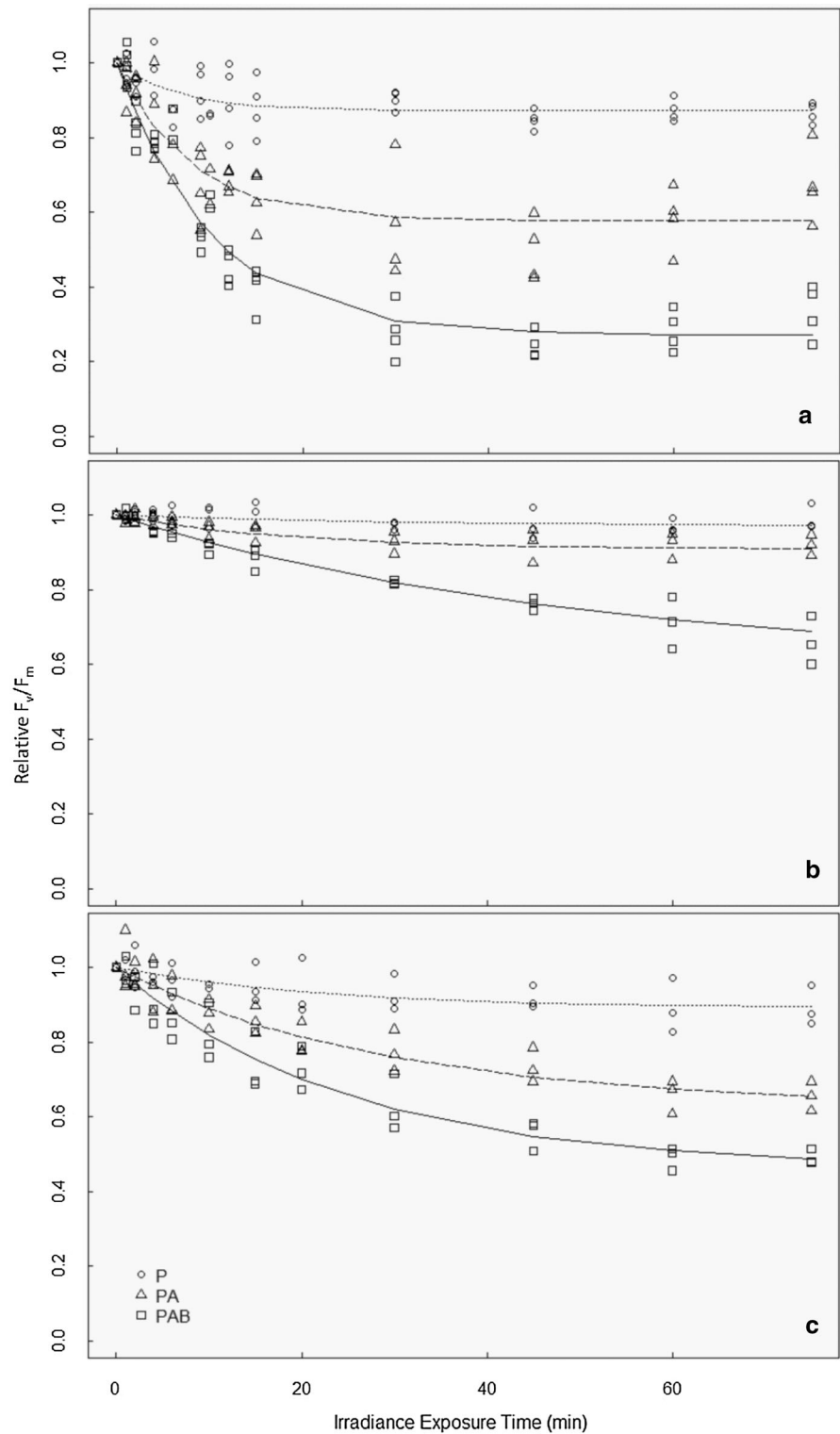


Table 6 Average rate constants of damage and repair (\pm SD) for each spectral treatment and pigment group

Algal group	Spectral treatment	Repair rate (min^{-1})	Damage rate (min^{-1})
Blue	P	0.089 (\pm 0.099)	0.032 (\pm 0.046)
	PA	0.036 (\pm 0.026)	0.049 (\pm 0.02)
	PAB	0.022 (\pm 0.011)	0.072 (\pm 0.028)
Green	P	0.16 (\pm 0.181)	0.011 (\pm 0.013)
	PA	0.03 (\pm 0.026)	0.005 (\pm 0.004)
	PAB	0.011 (\pm 0.004)	0.007 (\pm 0.003)
Brown	P	0.172 (\pm 0.335)	0.006 (\pm 0.007)
	PA	0.034 (\pm 0.031)	0.012 (\pm 0.008)
	PAB	0.018 (\pm 0.019)	0.019 (\pm 0.012)

rankings of group sensitivity based on damage rates and degree of inhibition (blues > browns > greens).

Discussion

The results presented here provide a comparison of PSII sensitivity to sunlight stress in a large number of taxa from multiple pigment groups, with outcomes that both support and contradict existing generalizations about group characteristics. The expectation that acute irradiance exposure effects would increase with the addition of shorter wavelength radiation, and that the green group (i.e., chlorophytes) would be especially tolerant of sunlight stress, was supported, while the possibility that at least some cyanobacteria might also be highly tolerant was not. By designing the study to address groups that can be distinguished by current Chl *a* fluorescence methods, it was possible to show that group differences evident in culture were also displayed in nature.

The green taxa showed minimal sensitivity of the quantum yield of PSII (F_v/F_m) to the acute irradiance stress that we applied in our experiments. F_v/F_m decreased by only 17–35% even under the full-spectrum treatment (PAB). By comparison, there is a range of UVR and/or PAR tolerance reported for other chlorophyte strains and species (Xiong et al. 1999). Some marine picoplanktonic chlorophytes are sensitive to UVR (Six et al. 2009; Sobrino et al. 2005), while other marine species from the Chlorophyceae (and related groups, i.e., Prasinophyceae) appear relatively resistant to UV-B (Herrmann et al. 1996; Montero et al. 2002a; Andreasson and Wängberg 2006). Despite such variability, the prevailing view is that chlorophytes, at least of the freshwater and larger

(non-picoplanktonic) variety, are typically well adapted to high light environments (Schwaderer et al. 2011; Deblois et al. 2013) and this view is supported by the present results.

Considering the phylogenetic and ecological diversity within the brown pigment group, a wide range of sunlight stress tolerance in laboratory and field populations was expected and was observed. The diatom *F. crotonensis* and the cryptophyte *Cryptomonas* sp. were relatively tolerant (29–32% reduction in F_v/F_m under PAB), but the diatom *A. formosa* (45%) and the dinoflagellate *P. inconspicuum* (51%) had less tolerance, and the synurophyte *S. petersenii* (75%) was highly sensitive. Diatoms are commonly associated with variable PAR environments, such as vertically mixed water columns, and many can maintain high photosynthetic efficiency at low light levels while responding rapidly to high irradiance (Schwaderer et al. 2011; Wagner et al. 2006), often utilizing NPQ via the xanthophyll cycle (Laurion and Roy 2009; Dimier et al. 2007). Even within the diatoms, however, the sensitivity to PAR and UVR can be variable, as exemplified here and in previous studies (Montero et al. 2002b; Dimier et al. 2007; Fouqueray et al. 2007). The present results also support previous evidence from culture (*Ochromonas danica*, (Herrmann et al. 1996)) and studies of lake communities (Xenopoulos and Frost 2003; Doyle et al. 2005) that chrysophycean flagellates such as our *S. petersenii* are often highly sensitive to PAR and UVR.

The cryptomonads and dinoflagellates have shown variable sensitivities to PAR and UVR in previous studies and can be found in a range of light environments. F_v/F_m of a marine *Cryptomonas* sp. was more resistant to UVR than in the marine dinoflagellate *Amphidinium* sp. (Montero et al. 2002b), consistent

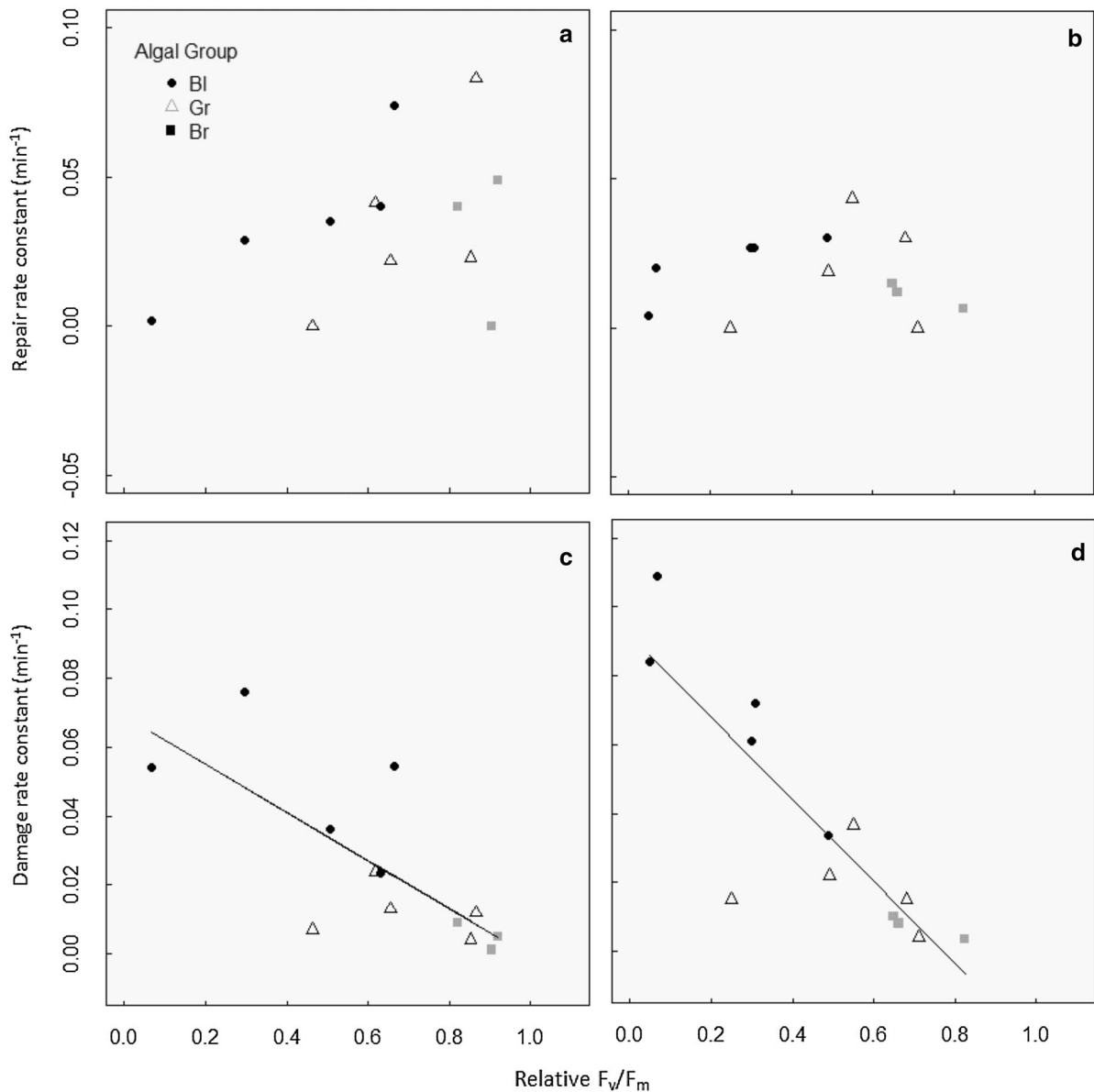


Fig. 4 Repair (upper panel) and damage (lower panel) rate constants compared to post-exposure relative F_v/F_m for PA (A,C) and PAB (B,D) spectral treatments for each algal group (BI—blues, Gr—greens, Br—browns). Linear regression analyses yielded significant relationships between damage rate and

relative F_v/F_m for PA and PAB (PA $r^2 = 0.561$, $p = 0.003$, dashed line; PAB $r^2 = 0.748$, $p < 0.003$, solid line). Relationships between repair rate and relative F_v/F_m were nonsignificant ($p > 0.2$)

with the relative sensitivity of *Cryptomonas* sp. and *P. inconspicuum* seen here. In contrast, other studies demonstrated higher UVR sensitivity in *Cryptomonas* and *Rhodomonas* compared to marine taxa from different groups (Litchman and Neale 2005; Montero et al. 2002a). Dinoflagellates also vary in UVR sensitivity (Demers et al. 1991; Laurion and Roy

2009), with some showing high sensitivity to photoinhibition, and others a measure of UVR tolerance afforded by the capacity to synthesize UV-absorbing compounds and xanthophyll cycle pigments (Demers et al. 1991; Marcoval et al. 2007; Litchman et al. 2002).

Table 7 Comparison of irradiance response metrics (F_v/F_m and Kok model coefficients) across spectral treatments (P—PAR only, PA—PAR + UV-A and PAB—PAR + UV-A + UV-B) between laboratory monocultures (“Culture”), Hamilton Harbour field assemblages (“Field”^a) and field results adjusted for comparison with the lower-irradiance laboratory experiments (“Adjusted field,” see Methods). Values are pigment-group averages (95% confidence interval)

Parameter	Spectral treatment	Culture	Field ^a	Adjusted field
<i>Blue</i>				
Pre-exposure F_v/F_m		0.376 (0.302–0.45)	0.483 (0.37–0.596)	
Post-exposure relative F_v/F_m	P	0.674 (0.388–0.961)	0.864 (0.8–0.929)	
	PA	0.434 (0.124–0.744)	0.521 (0.358–0.684)	0.635 (0.542–0.727) ^b
	PAB	0.242 (0.013–0.472)	0.302 (0.035–0.569)	0.378 (0.262–0.495) ^b
Repair rate constant (min ⁻¹)	PA	0.036 (0.004–0.068)	0.031 (0.03–0.032) ^b	
	PAB	0.022 (0.009–0.035)	0.026 (0.018–1.143) ^b	
Damage rate constant (min ⁻¹)	PA	0.049 (0.024–0.074)	0.043 (0.028–0.058) ^b	0.019 (0.013–0.026) ^b
	PAB	0.072 (0.037–0.107)	0.097 (0.078–0.115) ^b	0.043 (0.035–0.052) ^b
<i>Green</i>				
Pre-exposure F_v/F_m		0.637 (0.516–0.758)	0.623 (0.591–0.655) ^b	
Post-exposure relative F_v/F_m	P	0.982 (0.885–1.078)	0.88 (0.768–0.992) ^b	
	PA	0.881 (0.749–1.013)	0.718 (0.52–0.915) ^b	0.725 (n/a)
	PAB	0.712 (0.468–0.956)	0.407 (0.315–0.499) ^b	0.667 (0.557–0.777) ^b
Repair rate constant (min ⁻¹)	PA	0.03 (– 0.035–0.094)	0.02 (n/a)	
	PAB	0.011 (0.001–0.022)	0.019 (0.017–0.021) ^b	
Damage rate constant (min ⁻¹)	PA	0.005 (– 0.005–0.015)	0.02 (n/a)	0.009 (n/a)
	PAB	0.007 (– 0.001–0.015)	0.028 (0.014–0.041) ^b	0.012 (0.006–0.018) ^b
<i>Brown</i>				
Pre-exposure F_v/F_m		0.585 (0.497–0.673)	0.642 (0.571–0.712)	
Post-exposure relative F_v/F_m	P	0.907 (0.836–0.978)	0.961 (0.897–1.025)	
	PA	0.691 (0.481–0.901)	0.78 (0.607–0.953)	0.867 (0.802–0.932)
	PAB	0.537 (0.308–0.765)	0.499 (0.323–0.674)	0.586 (0.449–0.724)
Repair rate constant (min ⁻¹)	PA	0.034 (– 0.005–0.073)	0.049 (– 0.015–0.113)	
	PAB	0.018 (– 0.005–0.042)	0.017 (0.011–0.022)	
Damage rate constant (min ⁻¹)	PA	0.012 (0.003–0.021)	0.017 (– 0.005–0.039)	0.008 (– 0.002–0.018)
	PAB	0.019 (0.004–0.033)	0.033 (– 0.003–0.068)	0.015 (– 0.001–0.031)

^a Results from Beecraft et al. (2017)

^b Range in cases where $n = 2$ (rather than 95% confidence interval)

All five cyanobacteria had large decreases in F_v/F_m under each spectral treatment, but two (*A. oscillarioides* and *S. rhodobaktron*) showed especially large responses (93–95%). A diversity of sensitivity has been reported previously. Marine picocyanobacteria had a greater sensitivity to PAR and UVR and lower photoacclimation potential compared to eukaryotic picoplankton (Neale et al. 2014; Kulk et al. 2011), but sensitivity to UVR varies among strains and taxa in culture (Zeeshan and Prasad 2009; Fragoso et al. 2014; Giordanino et al. 2011). The differences in tolerance

among the cyanobacteria studied here may reflect adaptation to different habitats. The three more tolerant taxa (*M. aeruginosa*, *D. lemmermannii*, and *Synechococcus* sp.) are members of the pelagic and surface mixed layer phytoplankton (Fragoso et al. 2014; Callieri et al. 2014), with *Microcystis* notorious for its surface blooms (Wu et al. 2011; Qin et al. 2015). *Microcystis* and other surface bloom-forming taxa contain photoprotective carotenoids, such as zeaxanthin (Qin et al. 2015; Sommaruga et al. 2009) that mitigate light stress. *Synechococcus* is a polyphyletic

genus with numerous strains having varying habitat preferences and irradiance sensitivities (Willame et al. 2006; Lohscheider et al. 2011; Neale et al. 2014). Studies using PC-rich cyanobacteria strains (of which our *Synechococcus* sp. is an example) have demonstrated UVR sensitivity, but also effective repair capacity via synthesis of the D1 protein (Fragoso et al. 2014).

Specific habitat information is limited for the two more sensitive cyanobacteria in this study, but taxa similar to *A. oscillarioides* tend to be benthic (Willame et al. 2006). PE-rich cyanobacteria (e.g., *S. rhodobaktron*) are also commonly located deeper in the water column and exhibit greater sensitivity and limited ability to photoacclimate to high PAR and UVR compared to PC-rich strains (Lohscheider et al. 2011; Selmezy et al. 2016), consistent with the response of *S. rhodobaktron* seen here. Despite variability among taxa, our results agree with the view that cyanobacteria are characteristically adapted to low light environments, as evidenced by their high efficiency of light utilization and susceptibility to photoinhibition (Schwaderer et al. 2011; Deblois et al. 2013).

Cell size can influence sensitivity to PAR and UVR stress due to intracellular shading and package effects, as well limiting the effectiveness of sunscreen pigments in particles of small dimension (Garcia-Pichel 1994). Larger cells and colonies (microplankton) may be expected to be most tolerant of light stress and picoplankton least (Garcia-Pichel 1994; Fouqueray et al. 2007; Key et al. 2010). While microplanktonic chlorophytes used in the present study were more tolerant than picoplanktonic cyanobacteria, cell size was not a consistent indicator of UVR sensitivity among the taxa examined. For example, the two diatoms (microplankton) showed high (*F. crotonensis*) and low (*A. formosa*) tolerance, while the two filamentous cyanobacteria had very different sensitivities (*D. lemmermannii* vs. *A. oscillarioides*), as did the two picoplanktonic *Synechococcus* species. UVR sensitivity is influenced by a variety of factors, and while cell size may contribute, in particular among species within the same taxonomic group (Key et al. 2010), it is not a clear predictor of sunlight sensitivity (Montero et al. 2002a; Laurion and Vincent 1998).

Responses of F_0 and F_m induced by sunlight stress may help elucidate the relative contributions of reaction center impairment and loss of excitation (antenna de-coupling) to changes in F_v/F_m . Previous

studies have observed decreasing F_m in diatoms (Fouqueray et al. 2007), a chlorophyte (*Dunaliella salina*) and a chrysophyte (*Ochromonas danica*) (Herrmann et al. 1996), and increasing F_0 attributed to photoinhibitory damage. Under the full-spectrum treatment, we observed the chromophytes to have the largest proportional decreases in F_m and F_0 (based on median group responses), with larger decreases in F_m compared to F_0 . This could imply that there was extensive de-coupling of antenna pigments persisting through the dark adaptation period, as well as reaction center impairment. The cyanobacteria exhibited decreases in F_m , while F_0 remained similar or even increased, suggesting large effects of reaction center damage and fluorescence contributions from antenna pigments (PBS). Similar to the cyanobacteria, the chlorophytes exhibited decreases in F_m and increases in F_0 , which could indicate persistent de-coupling of antenna pigments from reaction centers, as well as background fluorescence contributions from those antennas. The higher-order kinetics observed in the majority of cases suggested not only the extent but also the nature of acclimative and damage responses changed during the exposures. F_0 and F_m did not always show unidirectional changes over time, although the departures from unidirectional behavior were not extreme and the endpoint values appeared to capture the dominant patterns of change. However, the F_0 and F_m dynamics were not obviously predictive of the variations of sunlight sensitivity of F_v/F_m among taxa or groups.

Previous studies have applied the Kok model to photosynthetic metrics under inhibitory light exposures and have reported damage and repair rate constants in a similar range to those found in the current study (Harrison and Smith 2011a; Shelly et al. 2002; Heraud et al. 2005). The modeled responses for the taxa examined suggested that differences in acute photoinhibition among pigment groups were driven primarily by differences in damage processes, while repair rate constants were not significantly different among algal groups and were not predictive of endpoint sensitivity. Damage processes are largely similar across species, while photoacclimation can vary widely in mechanism and response time (Brunet et al. 2011; Dimier et al. 2007; Laurion and Roy 2009), which may explain why damage rates were more predictive of observed sensitivity here. With the exceptions of *F. crotonensis* and *P. simplex*, damage

rates increased with the addition of shorter wavelength radiation, consistent with earlier studies (Heraud and Beardall 2000; Harrison and Smith 2011b; Wong et al. 2015; Guan et al. 2011). The blue group had the highest average damage rates in each spectral treatment, and greens the lowest.

Prediction of solar radiation effects in nature from laboratory studies is complicated by environmental factors (e.g., temperature and nutrients) and photoacclimation processes, which can alter susceptibility to photoinhibition on a species-specific basis (Halac et al. 2013; Marcoval et al. 2007; Halac et al. 2014; Doyle et al. 2005). Acclimation to PAR has been widely demonstrated and acclimation to UVR has also been documented, though less extensively (Ragni et al. 2008; Harrison and Smith 2011a; Moore et al. 2006). The present results provided evidence that field populations with histories of exposure to full-spectrum sunlight are more resistant to UVR than laboratory populations with low irradiance (and zero UVR) histories. However, the relative UVR sensitivity of the groups was the same for cultures and field populations. PSII efficiency of cyanobacterial-dominated populations in the harbor samples showed the highest sensitivity to UVR, while chlorophyte populations showed the least, and chromophyte populations were intermediate. The high sensitivity of the natural and culture populations of cyanobacteria studied here differs markedly from the high PAR and UVR tolerance often attributed to this group (Paerl and Kellar 1979; Paerl and Paul 2012; Xenopoulos et al. 2000, 2009; van Donk et al. 2001; Sommaruga et al. 2009; Wulff et al. 2007), and is not an artifact of the culture conditions or taxon selection. Tolerance to sunlight stress may still be an important attribute of some bloom-forming cyanobacteria, but is not mediated by an innate PSII resistance to acute irradiance stress.

Future studies should aim to further understand how changes in the quantum yield of photochemistry correspond to photosynthetic income (carbon fixation) and growth, and how those outcomes compare among the pigment groups. Changes in F_v/F_m under acute stress are in part measures of photoprotection mechanisms and not necessarily predictive of negative outcomes for cellular or population dynamics on longer timescales. Beecraft et al. (2017) did find that both carbon fixation and F_v/F_m were impaired in the field populations, suggesting the current results do

indicate a sensitivity of both PSII efficiency and photosynthesis in commonly occurring cyanobacteria to photoinhibition. However, that study had limited success in discriminating carbon fixation to the group level, and further efforts to establish the relationships among variable fluorescence parameters and other photosynthetic metrics (oxygen evolution, carbon assimilation, growth rate) in natural populations and recently isolated phytoplankton strains would be valuable. Experiments to elucidate longer-term responses, and integrate them with behavioral responses (notably vertical migration), would also be helpful in resolving the apparent paradox of high sunlight sensitivity in PSII with the ability of many species of cyanobacteria to form near-surface blooms.

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