LIMNOLOGY and OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 68, 2023, 2529–2543

doi: 10.1002/lno.12439

Photoacclimation dynamics in coral holobionts responding to thermal and irradiance changes correlate with photon pressure per symbiont

Robert A. B. Mason [1*,a], **William J. Skirving** [2], **Sophie G. Dove** [1]

[1]School of Biological Sciences and ARC Centre of Excellence for Coral Reef Studies, University of Queensland, St. Lucia, Queensland, Australia

[2]NOAA Coral Reef Watch and ReefSense Pty. Ltd., Townsville, Queensland, Australia

Abstract

Photoacclimation is a key homeostatic process that enables photosymbiotic reef corals to flourish within highly variable light environments. However, the temporal dynamics of photoacclimation remain poorly characterized. We studied photoacclimation at several time points over 24 d in two scleractinian coral taxa (mounding *Porites* spp. and branching *Acropora muricata*). Coral specimens preacclimated at 24°C and 171 μmol quanta m^{-2} s^{-1} were exposed to three light levels (−32%, +27%, and +65% relative to that of the acclimation period) at two temperatures (control, 24°C; mildly stressful, 29°C). Intra-tissue light environment—specifically, photon pressure per symbiont—increased dramatically with each additional light dose and again with increasing temperature in *Porites* spp.; net photosynthesis (P^{net}) rates continued to change for at least 2 weeks following light increase but not light reduction, and vice versa for symbiont densities. Intra-tissue light environments were substantially dimmer and more homogeneous among all light treatments in *A. muricata*, which continued to increase its light-use efficiency and P^{net} through time in most or all treatments. Consequently, prolonged change in F_v/F_m at elevated temperature in *Porites* spp. but not *A. muricata* may have been caused by differing photodamage loads. Moderation of light levels by conditions within the coral tissue seems to affect the temporal dynamics of the photoacclimation response, and this finding emphasizes new avenues for photoacclimation research.

Extremes of light intensity can lead to photosystem damage (at high light) or to carbon fixation rates below metabolic requirements (at low light). Due to changes in water clarity, surface conditions, cloud cover and season, the surface ocean possesses a highly variable light environment, and marine photosynthesizers are equipped with a range of mechanisms to physiologically adjust (photoacclimate) to light fluctuations. In single-celled marine photosynthesizers these mechanisms occur within the chloroplast and include alterations in the number of photosynthetic units and the size of the photosynthetic units (Prézelin 1987; Mauzerall and Greenbaum 1989), changes in quantity of xanthophyll cycle pigments (Iglesias-Prieto and Trench 1997), islands of heat-dissipating PSII reaction centers (Matsubara and Chow 2004), photochemical quenching through alternative electron transport pathways (Reynolds et al. 2008) and upregulation of rates of repair of photodamage (Jeans et al. 2013).

In symbiotic partnerships between animal hosts and single-celled photosynthesizers (symbionts), the residence of the symbionts within the host tissue provides further options for photoacclimation, including regulation of the symbiont population size (Titlyanov et al. 2001), or production of photoprotective substances by the host (Roth et al. 2010). Changes in symbiont population size alter the photon pressure (amount of light) per symbiont residing in the host tissue (Enríquez et al. 2005). Symbiont density changes may thus exert further pressure on the remaining symbionts to induce their own photoacclimative mechanisms, or alternatively, may return the photon pressure

*Correspondence: r.mason4@uq.edu.au

Additional Supporting Information may be found in the online version of this article.

[a]Present address: CSIRO Environment, Queensland Bioscience Precinct, St. Lucia, Queensland, Australia

Author Contribution Statement: R.A.B.M. involved in conceptualization, methodology, formal analysis, funding acquisition, software, investigation, data curation, writing-original draft, visualization, and project administration. W.J.S. involved in conceptualization, methodology, resources, supervision, funding acquisition, writing-review and editing, project administration. S.G.D. involved in conceptualization, methodology, resources, supervision, funding acquisition, writing-review and editing, project administration.

to the level that the symbionts were exposed to prior to a change in incident light, thereby negating the need for some other photoacclimative mechanisms (Scheufen et al. 2017). The speed of photoacclimation following a change in incident light level determines the amount of time that the holobiont (the host and symbiont acting as one organism) remains maladjusted to the new light intensity.

Scleractinian corals and their intracellular dinoflagellates form one of the most economically important photosynthetic symbioses in the ocean. Important practical applications of research on coral holobiont photoacclimation are emerging in the remote monitoring and modeling of coral reefs. Satellite methods for predicting coral bleaching use sea-surface temperature, but have recently undergone further development to take into account sea-surface light levels (Eakin et al. 2010). One approach (Skirving et al. 2018) uses summer sea surface temperature anomaly (°C above the maximum monthly mean) and excess excitation energy (in moles of quanta per m^2 per day), approximated as photosynthetically active radiation (PAR) today minus PAR in previous days adjusted for photoacclimation that has occurred, to produce an index of coral photophysiology that is correlated with bleaching. The photoacclimation rate (i.e., 1 divided by the number of days required for photochemical parameters to stabilize following a change in light) moderates the capacity of excess excitation energy to cause photodamage, and thereby bleaching (Skirving et al. 2018). Recent models of coral photophysiological dysfunction, developed alongside the eReefs Great Barrier Reef system model, require photoacclimation rate parameters (Baird et al. 2018). Improvement to the scant data available on coral photoacclimation rates will thus contribute to better bleaching prediction and modeling.

The mechanisms of photoacclimation have been widely studied in corals, however, temporal aspects, including photoacclimation rate, have been determined in only two coral species. Temporal characterization involves repeatedly sampling one or more photobiological parameters (typically light-use efficiency, subsaturation irradiance or the maximum rate of photosynthesis) after a change in light intensity, to identify the period of time required for the variable(s) to stabilize. Using this method, photoacclimation was measured to completion within 10 d in *Turbinaria mesenterina* (Anthony and Hoegh-Guldberg 2003). Photoacclimation was faster after movement from low to high light compared to movement in the opposite direction, in *Stylophora pistillata* (Falkowski and Dubinsky 1981). However, another study of *S. pistillata* found the opposite, i.e., that adaptation to high light was slower than adaptation to low light (Gattuso and Jaubert 1984). Falkowski and Dubinsky (1981) suggested, based on evidence from a diatom (Hitchcock 1980*a*,*b*), that such differences may be due to the water temperature rather than the direction of light change. An elevation in temperature could, hypothetically, increase the photoacclimation rate by increasing the kinetic rate of reactions in the biochemical pathways involved (Sheridan et al. 2012). However, in the ensuing decades (to our knowledge), the effect of temperature on photoacclimation rate in corals has not yet been tested.

The effect of direction of light change on photoacclimation rate also remains to be clarified. Anthony and Hoegh-Guldberg (2003) found no statistically significant effect of an increase vs. a decrease in light, nor of large vs. small changes in light, on photoacclimation rate. However, modeling of the photoacclimation rates required to maintain observed patterns of photophysiology over an annual cycle of seasons suggests that photoacclimation to a decrease in light should be faster than photoacclimation to an increase in light (Skirving et al. 2018). Furthermore, a trend for photoacclimation time to be shorter in response to a larger magnitude change in light was present in Anthony and Hoegh-Guldberg's (2003) study, and thus the effect of the size of the change in light level on photoacclimation rate also remains to be resolved. We suggest that photoacclimation rate could be more rapid following a change to a substantially different light level because the risk of negative effects of the new light level on a non-acclimated photosystem may be more pronounced, or because the physiological induction of acclimation may be more effective when a larger external signal is present. For instance, in green algae a highly reduced state of the plastoquinone pool triggers the repression of the transcription of light-harvesting complex apoproteins associated with photosystem II, hinting at a direct link between light intensity and the speed of photoacclimative changes to the light harvesting complex (Escoubas et al. 1995). An oxidized plastoquinone pool can also act as a direct quencher of chlorophyll *a* minimum fluorescence (Hohmann-Marriott et al. 2010).

To investigate the influence of temperature, direction of light change and magnitude of light change on photoacclimation rate, this article describes a laboratory-based time-course investigation of photoacclimation in response to a long-term (24 d) change in light intensity, under two temperature levels. This study focuses on two taxa that are dominant on reefs in eastern Australia and elsewhere in the Indo-Pacific, *Acropora muricata* and mounding *Porites* species (Veron and Wallace 1984; Forsman et al. 2009). These taxa are juxtaposed in their response to adverse conditions, e.g., mounding *Porites* spp. appear to be more resilient to bleaching-induced mortality, and occur at a wider range of turbidity, and light and temperature variability, than the genus *Acropora* (Marshall and Baird 2000; Hennige et al. 2010). We made measurements of photobiological parameters at several time points following a change in light level and inferred that photoacclimation of a parameter was complete when that parameter had ceased to change. Existing evidence suggests that the bulk of photoacclimatory changes likely occur within the first 10 days following a change in light level (Anthony and Hoegh-Guldberg 2003). Therefore, any extension of the time required to photoacclimate beyond this period may incur physiological costs due to the extended time spent in a state of ill-adjustment to

the environmental conditions. Hence, we focused our measurements on the period beyond the first 10 d.

Methods

Overview

To measure the photoacclimation rate, we made measurements of several chloroplast-level photoacclimation parameters (light-use efficiency (α) and maximum photochemical yield of photosystem II (F_v/F_m)), a holobiont-level parameter (symbiont population size) and a parameter reflecting processes at both levels (net photosynthesis (P^{net}) per cm^2 of coral surface area at ambient light levels). P^{net} was chosen instead of gross photosynthesis (P^{gross}) as (1) it better ties photoacclimative processes to the net energy balance of the holobiont, and (2) it is difficult to measure P^{gross} directly, and estimation using the proxy of (dark respiration + P^{net}) may be inaccurate (Schrameyer et al. 2014). Here, α was determined using relative electron transport rate (rETR) which has a linear relationship to gross photosynthesis in corals within the low rETR range at which α is calculated (see fig. 5 in Rodolfo-Metalpa et al. 2008). Physiological markers were sampled and resampled at ~ 15 and ~ 24 d following the movement of corals to changed light conditions.

We hypothesized that, where an extended photoacclimation period (a lack of stabilization between days 15 and 24) is seen at one level of an independent variable but not the other(s), that level will be of the following:

1. The control temperature (24°C) as opposed to elevated temperature (29°C).
2. An increase in light as opposed to a decrease in light.
3. A smaller-magnitude change in light (e.g., from 171 to 218 μmol quanta m^{-2} s^{-1}) as opposed to a larger-magnitude change in light (e.g., from 171 to 282 μmol quanta m^{-2} s^{-1}).

To investigate the knock-on effects of changes in symbiont population size on the within-tissue light environment, we measured photon pressure per symbiont towards the end of the experiment.

Experimental setup

Mounding *Porites* spp. (4 cm diameter cores, $n = 192$) and *A. muricata* branch tips (3–5 cm, $n = 180$) were collected at a depth of 5–9 m, near Heron Island, Queensland (23°26′S, 151°54′E). At the collection location, *A. muricata* associates with Symbiodiniaceae phylotype C3 (Tonk et al. 2013), and C15 predominates in *Porites* (LaJeunesse et al. 2003, 2004; Fisher et al. 2012). Samples were left to heal for 3 months at 9 m below datum, under Austral Spring field conditions of 24°C and 171 μmol quanta m^{-2} s^{-1} (averaged over a 13 h 46 min daylength of the final 2 weeks in situ). Samples were recovered, divided among treatments (four aquaria per treatment and seven to eight samples per aquarium). The treatments were three light levels supplied by metal halide lamps (low, 117 μmol quanta m^{-2} s^{-1}; medium, 218 μmol quanta m^{-2} s^{-1}; and high, 282 μmol quanta m^{-2} s^{-1}) at a 13 h daylength, crossed with two water temperatures: 24.25°C (± 0.0032 SEM, $n = 36{,}573$), and 28.57°C (± 0.0036 SEM, $n = 36{,}573$). The former is within the normal springtime seawater temperature range at the study site, while the latter is 1.45°C above the maximum monthly mean for the region (NOAA Coral Reef Watch 2017), a thermal anomaly of a magnitude that is considered to be physiologically stressful to corals (Goreau and Hayes 1994). Additional details on experimental setup are provided in the Supporting Information, "Detailed methods".

Response variables

F_v/F_m was measured every evening with a Diving PAM (Walz, Effeltrich, Germany) 1.5–2.5 h after lights-out. Light-use efficiency, α, was measured during daylight hours using rETR vs. irradiance curves performed with a Diving PAM at two time points (days 15–16 and 22–23). Dissolved-oxygen measurements of photosynthesis were made in the evening or early morning (pre-dawn) hours, at two time points (days 15–16 and 22–23 [*A. muricata*]; days 16–17 and 23–24 [mounding *Porites* spp.]). Each sample was sealed into a transparent, stirred Perspex chamber; dissolved oxygen in chamber water was measured with an Oxy-10 optode (PreSens, Regensburg, Germany) during 20 min of light exposure at the treatment light and temperature level. Corals were then liquid N_2-frozen, and coral tissue was later removed by airbrushing. Symbiont cell counts were performed via flow cytometry, and surface area determined using wax dipping. Photon pressure per symbiont was calculated at days 19–21 through first measuring coral sample reflectance (S2000 spectrometer, Ocean Optics, Dunedin, USA), which was then multiplied by treatment photosynthetic photon flux density and divided by treatment mean areal symbiont density. Additional details on analytical procedures are provided in the Supporting Information, "Detailed methods", and Supporting Information Figs. S1, S2.

Statistical analysis

Differences between aquaria ("tank effects") were dealt with by averaging the coral replicates from within each aquarium within each treatment, providing $n = 4$ averaged values per variable per treatment at each time point. We analyzed the F_v/F_m time-series, α, P^{net}, symbiont cell density and photon pressure per symbiont using generalized least squares (GLS) models that accounted for heteroskedasticity. Models were factorial and fully crossed: the fixed-effects model structures were temperature × light × day (repeated measures) for F_v/F_m, temperature × light for photon pressure per symbiont, and temperature × light × sampling time point for all other variables. ANOVA assumptions were checked with quantile–quantile and residuals vs. fitted values plots, and least-square means with Tukey's test were used for post hoc tests.

Time-series analysis was performed on F_v/F_m time-series of (1) the median of the aquarium median per treatment and (2) the mean of the aquarium median per treatment. To identify the correlation type for repeated measures analysis of the time-series (Enders 2010), we used time-series diagnostics that included visual inspection of the time-series plots, plots of the autocorrelation function (ACF) and plots of the partial autocorrelation function (PACF). The ACF and PACF plots were created using the astsa package in R version 3.3.1 (R Core Team 2016). Missing F_v/F_m values on days 15 and 16 were filled in by taking, respectively, the median or mean (as appropriate) F_v/F_m of days 11–19 (excluding 15–16), and the median or mean F_v/F_m of days 12–20 (excluding 15–16). A repeated measures ANOVA for days 1–14 was performed by modeling the data with a GLS model, under the following four correlation types: a compound symmetry model, an autoregressive model of order 1, a moving average model of order 1, and a combined autoregressive and moving average model (of order 1). We allowed all models to permit heteroskedastic variances. The model with the most efficacious correlation type was identified by comparing the Akaike Information Criterion and Bayesian Information Criterion of each model.

Porites spp. specimens were analyzed together as one taxon, as identification to species while alive is impractical (requiring microskeletal analysis; Forsman et al. 2009), and thus targeted collection of one species, or sufficient collection to ensure adequate sample numbers to analyze multiple species individually, was not possible. This approach is consistent with previous physiological experiments on massive *Porites* species (Krief et al. 2010; Edmunds 2012). Later analysis of skeletal markers identified that the specimens were a mixture of *P. lobata*, *P. lutea*, *P. australiensis*, *P. myrmidonensis*, *P.* cf. *murrayensis*, *P.* cf. *lutea*, and several identifiable only to genus.

Results

Light-use efficiency

Mounding *Porites* spp. and *A. muricata* displayed very different patterns in light-use efficiency (α). Treatment means of α ranged from 0.30 to 0.32 (*A. muricata*) and 0.18 to 0.26 (mounding *Porites* spp.). In *A. muricata*, α was lower with statistical significance at 29°C vs. 24°C and a main effect of time was present, with α being higher with statistical significance at the second time point (Table 1; Fig. 1a,e). Therefore, α did not achieve stabilization between days 15 and 24 in all treatments for *A. muricata*.

Light level had a non-significant effect on α in *A. muricata* (Table 1), but a slight downward trend in α with increasing light was seen (Fig. 1c). This may have been an indication that the rate of change in α through time had varied among the light treatments. In mounding *Porites* spp., α decreased with increasing light level (Tukey's test: low > medium > high; Fig. 1d), while increasing temperature and time point had no effect (Fig. 1b,f), though after adjustment to take into account coral absorptance, α declined with increasing temperature (Supporting Information, "Impact of absorptance on light-use

Table 1. ANOVA table for light-use efficiency (α), net photosynthesis (P^{net} cm^{-2}), symbiont cell density and F_v/F_m.

	α	P^{net} cm^{-2}	Cells cm^{-2}	F_v/F_m
A. muricata				
Temp.	$p <$ **0.01** $F_{1,36} = 10.59$	$p <$ **0.01** $F_{1,36} = 24.8$	$p <$ **0.01** $F_{1,24} = 45.4$	$p <$ **0.01** $F_{1,252} = 141$
Light	$p = 0.18$ $F_{2,36} = 1.81$	$p <$ **0.01** $F_{2,36} = 150$	$p <$ **0.01** $F_{1,24} = 20.9$	$p <$ **0.01** $F_{2,252} = 1922$
Time point	$p <$ **0.01** $F_{1,36} = 12.34$	$p <$ **0.01** $F_{1,36} = 28$	$p = 0.6$ $F_{1,24} = 0.29$	$p <$ **0.01** $F_{13,252} = 47$
Temp. × light	$p = 0.21$ $F_{2,36} = 1.63$	$p <$ **0.01** $F_{2,36} = 8.12$	$p <$ **0.05** $F_{1,24} = 4.48$	$p <$ **0.01** $F_{2,252} = 79$
Temp. × time point	$p = 0.27$ $F_{1,36} = 1.26$	$p = 0.27$ $F_{1,36} = 1.25$	$p = 0.72$ $F_{1,24} = 0.13$	$p < 0.01$ $F_{13,252} = 4$
Light × time point	$p = 0.35$ $F_{2,36} = 1.07$	$p = 0.58$ $F_{2,36} = 0.55$	$p = 0.39$ $F_{1,24} = 0.75$	$p = 0.21$ $F_{26,252} = 1$
Temp. × light × time point	$p = 0.68$ $F_{2,36} = 0.38$	$p = 0.29$ $F_{2,36} = 1.27$	$p = 0.62$ $F_{1,24} = 0.26$	$p = 0.27$ $F_{26,252} = 1$
Porites spp.				
Temp.	$p = 0.28$ $F_{1,36} = 1.21$	$p <$ **0.01** $F_{1,36} = 68.6$	$p <$ **0.01** $F_{1,24} = 24.3$	$p <$ **0.01** $F_{1,252} = 89.5$
Light	$p <$ **0.01** $F_{2,36} = 76.35$	$p <$ **0.01** $F_{2,36} = 29.1$	$p <$ **0.01** $F_{1,24} = 37.5$	$p <$ **0.01** $F_{2,252} = 1298$
Time point	$p = 0.25$ $F_{1,36} = 1.36$	$p <$ **0.01** $F_{1,36} = 18.23$	$p = 0.8$ $F_{1,24} = 0.063$	$p <$ **0.01** $F_{13,252} = 25.7$
Temp. × light	$p = 0.89$ $F_{2,36} = 0.12$	$p = 0.12$ $F_{2,36} = 2.22$	$p = 0.18$ $F_{1,24} = 1.87$	$p <$ **0.01** $F_{2,252} = 6.74$
Temp. × time point	$p = 0.75$ $F_{1,36} = 0.11$	$p = 0.72$ $F_{1,36} = 0.13$	$p =$ **0.04** $F_{1,24} = 4.53$	$p <$ **0.01** $F_{13,252} = 2.54$
Light × time point	$p = 0.36$ $F_{2,36} = 1.05$	$p <$ **0.01** $F_{2,36} = 9.98$	$p = 0.61$ $F_{1,24} = 0.27$	$p <$ **0.01** $F_{26,252} = 4.60$
Temp. × light × time point	$p = 0.59$ $F_{2,36} = 0.53$	$p =$ **0.04** $F_{2,36} = 3.41$	$p <$ **0.05** $F_{1,24} = 4.47$	$p = 0.22$ $F_{26,252} = 1.22$

Temp., temperature.
For symbiont cells cm^{-2}, the high light level (282 μmol quanta m^{-2} s^{-1}) was not included for *A. muricata* and the medium light level (218 μmol quanta m^{-2} s^{-1}) was not included for mounding *Porites* spp. due to missing light × temperature treatments. The ANOVA of F_v/F_m was performed on a GLS autoregressive moving average model of order 1 allowing for heteroskedasticity. For α, P^{net} cm^{-2} and cells cm^{-2}, "Time point" refers to measurements made at two time points of the experiment. For F_v/F_m, "Time point" refers to daily measurements. The intercept had a probability value of $p < 0.0001$ for all ANOVAs. Probability values that are < 0.05 are highlighted in bold.

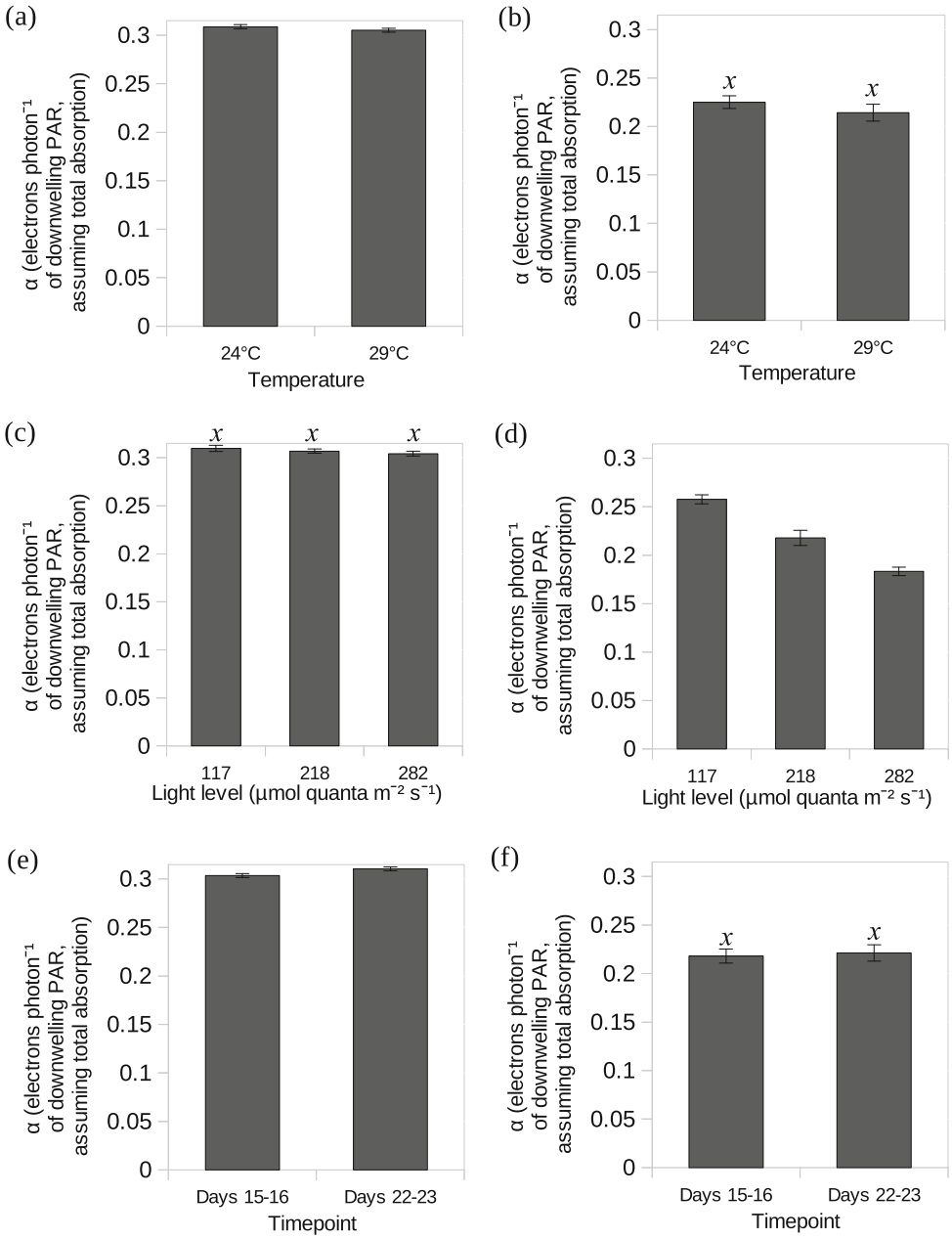

Fig. 1. Light use efficiency: the slope, α, of the light-limited part of an rETR vs. irradiance curve in *A. muricata* (**a**, **c**, **e**) and mounding Porites spp. (**b**, **d**, **f**). All data points are the means (± SEM) over the mean value per aquarium ($n = 4$ aquaria per treatment). Treatments sharing an alphabetic character were not significantly different from one another ($p > 0.05$). The value at each level of a factor is averaged over all the levels of the other factors.

efficiency measurements", Supporting Information Table S1; Supporting Information Fig. S3). Therefore, α was stable between days 15 and 24 in all treatments for mounding *Porites*. For α in both species, there were no two- or three-way interactions among any of temperature, light and time point.

Net photosynthesis

In both taxa, under the main effect of each factor, P^{net} was significantly greater at 29°C vs. 24°C, significantly lower at low light (Tukey's test: low < medium = high) and significantly lower at the first compared to second time point (Table 1; Fig. 2a,b).

P^{net} in the two taxa differed with regard to the interactions of time point with either or both of temperature and light. There was no interaction of time point with temperature or with light, nor a three-way interaction of all three factors, in *A. muricata* (Table 1). In other words, P^{net} failed to stabilize between day 15 and 24 across all treatments in *A. muricata*. In

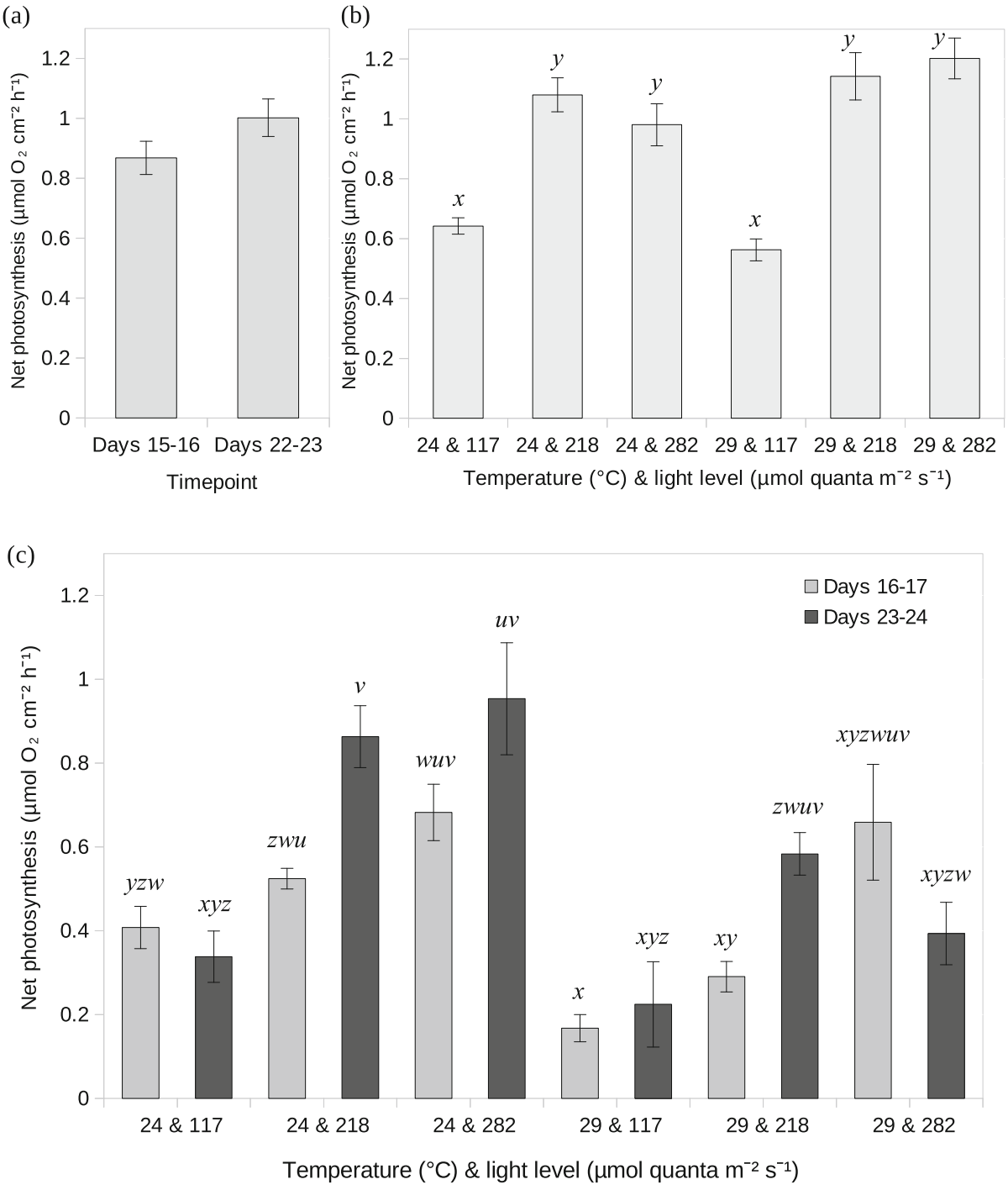

Fig. 2. Net photosynthesis measured via net oxygen production per unit of surface area (P^{net} cm^{-2}) in (**a**) *A. muricata*, at both time points averaged across all treatments; (**b**) *A. muricata*, in all treatments averaged across both time points; (**c**) mounding Porites. All data points are the means (± SEM) over the mean value per aquarium ($n = 4$ aquaria per treatment). Treatments sharing at least one alphabetic character were not significantly different from one another ($p > 0.05$) in post hoc tests.

mounding *Porites* spp., there was a two-way interaction of time point with light (Table 1) and a three-way interaction of temperature, light and time point (letters in Fig. 2c). This was because high light displayed an increase with increasing time at 24°C and a decrease with increasing time at 29°C (at high light, 24°C was not significantly different from 29°C at the first time point, however at the second time point, 24°C significantly exceeded 29°C, $p = 0.0326$, t ratio = 3.66, df = 36).

For both temperatures, there was no difference between time points at low light, and a significant increase through time at medium light (24°C: $p = 0.0055$, t ratio $= -4.33$, df $= 36$; 29°C: $p = 0.002$, t ratio $= -4.69$, df $= 36$). Thus, in mounding *Porites* spp., P^{net} displayed stability between day 15 and day 24 at low light, but changed between day 15 and 24 at medium and high light.

Areal symbiont densities

Areal symbiont densities within *A. muricata* (at low and medium light) and within mounding *Porites* spp. (at low and high light) statistically differed with temperature (24°C > 29°C) and light (*A. muricata*: low < medium; mounding *Porites* spp.: low > high). There was a statistically significant interaction of light with temperature in *A. muricata* (Tukey's test: 29°C at low light < 24°C at low light = 24°C at medium light = 29°C at medium light). There was no effect of time point or interaction of time point with temperature or with light in *A. muricata* (Table 1). Thus, areal symbiont densities were apparently stable between day 15 and day 24 in all treatments in *A. muricata*. Time point had a significant three-way interaction with temperature and light in mounding *Porites*. At high light, areal symbiont densities showed no significant difference between the two time points at both temperature levels and at low light, 24°C and 29°C did not significantly differ at the first time point. However, at the second time point, 24°C significantly exceeded 29°C ($p = 0.0198$, t ratio $= 3.73$, df $= 24$; Table 1). Effectively, areal symbiont densities were stable between day 15 and 24 at high light, but changed between day 15 and 24 at low light, increasing through time at 24°C and decreasing through time at 29°C (Fig. 3). Time point also had a significant two-way interaction with temperature in mounding *Porites* spp. (Table 1) but we chose not to interpret this due to the three-way interaction.

Photon pressure per symbiont

Measurements of photon pressure (approximated as the amount of reflected and scattered light) per symbiont remaining in the host tissue were made over days 19–21. In *A. muricata*, the photon pressure per symbiont on the corallite undersides was affected by significant main effects of temperature (24°C < 29°C) and light (medium > low) (Fig. 4a). In *A. muricata*, light level had a significant main effect on the photon pressure per symbiont on the corallite tops (Table 2) (medium > low). A statistically significant effect of temperature on corallite tops was absent.

For mounding *Porites* spp. (corallite tops), there was a significant temperature × light interaction (Table 2); all treatments were significantly different from one another by Tukey's post hoc tests (Fig. 4b). The difference in reflected photon pressure per symbiont was much higher among treatments as light and temperature increased in mounding *Porites*

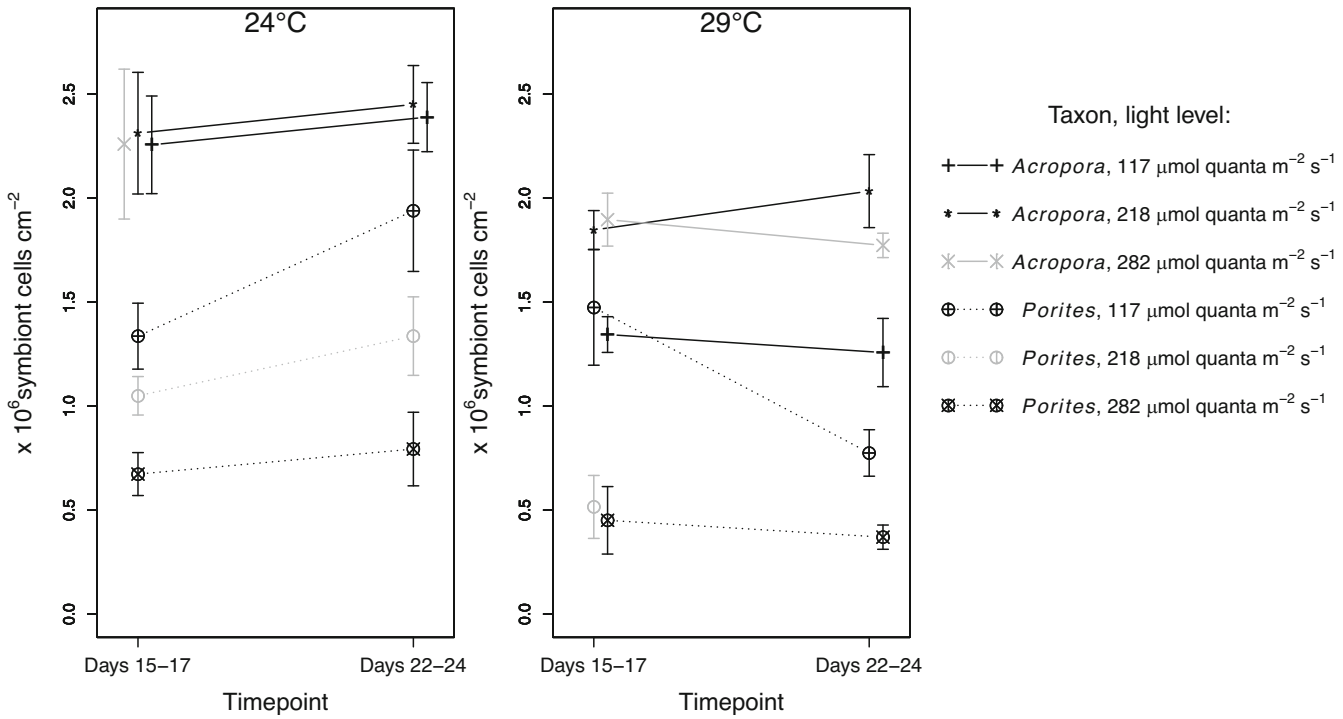

Fig. 3. Areal densities of symbiont cells. All data points are the means (± SEM) over the mean value per aquarium ($n = 4$ aquaria per treatment). Treatments shaded in gray were not included in the statistical testing to prevent unbalancing of tests. Horizontal positions of some data points have been slightly offset to avoid overlap.

spp. vs. *A. muricata*: for instance, the high light 29°C treatment was ~ 20 fold higher than the low light 24°C treatment in mounding *Porites* spp., compared to ~ 4 fold higher for the same comparison in *A. muricata*.

Maximum photochemical yield

For both taxa, the best fit to the F_v/F_m repeated-measures data was a combined autoregressive and moving average model with both components of order 1 (ARMA(1)) allowing for heteroskedastic variances (based on an interpretation of the ACF and PACF plots, Table S2). This was corroborated by evidence that a repeated-measures GLS model with ARMA(1) correlation type had the best AIC values out of all correlation types tested (Table S3).

Increases in light level caused decreases in F_v/F_m in both species (Tukey's test: low > medium > high), except from medium to high light at 29°C in *A. muricata* (Tukey's test $p > 0.05$). Increased temperature caused differences in F_v/F_m in *A. muricata* at low and medium light (Tukey's test: 24°C > 29°C), but not high light (Tukey's test $p > 0.05$).

Water temperature caused a significant difference in average F_v/F_m in mounding *Porites* spp. (24°C > 29°C). An interactive effect of temperature with light was observed (Table 1), but post hoc tests found no significant difference in the pairwise comparisons of 24°C low light with 29°C low light, 24°C medium light with 29°C medium light, and 24°C high light with 29°C high light. There was a significant interaction of temperature with time point in mounding *Porites* spp. (Table 1), with its F_v/F_m time-series (Fig. 5a,b) indicating a downward trend between days 6 and 14 at 29°C but not 24°C.

Because of high F_v/F_m variation from day to day in some treatments, it was not feasible to choose particular days as

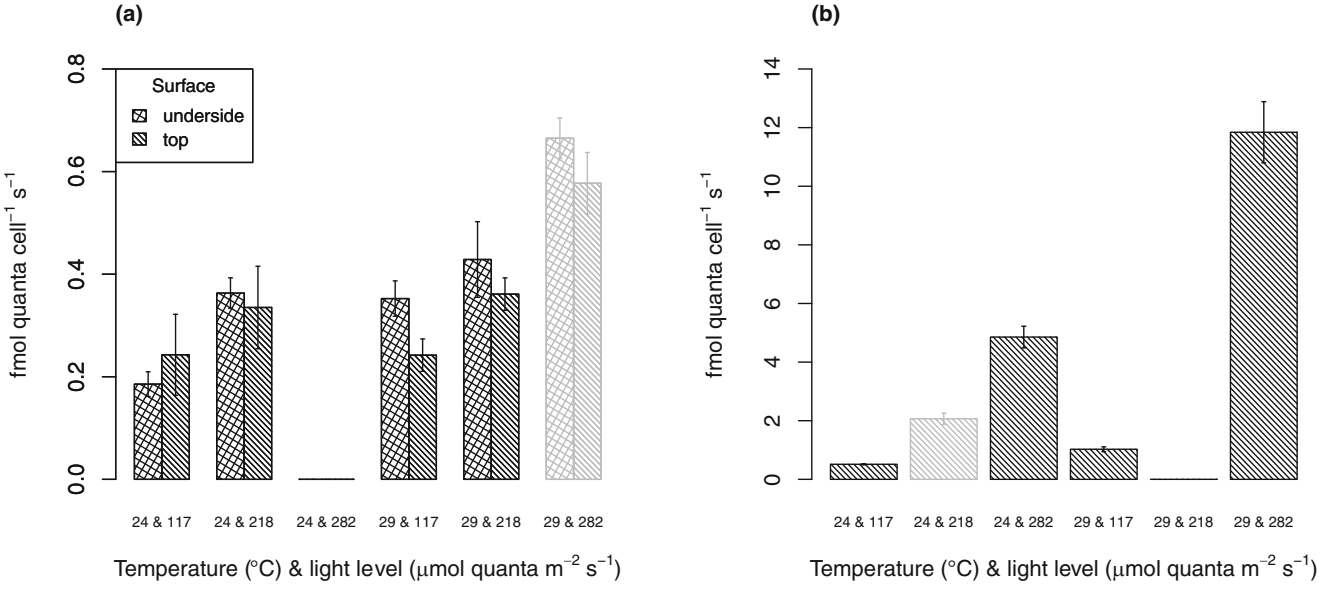

Fig. 4. Estimated photon pressure per symbiont cell within each treatment on days 19–21 for (**a**) *A. muricata* (no significant interaction of light and temperature) and (**b**) mounding *Porites* spp. (a significant interaction of light and temperature was present). All data points are the means (± SEM) over the mean value per aquarium ($n = 4$ aquaria per treatment). For *A. muricata* corallite undersides, light and temperature each had a significant main effect. For *A. muricata* corallite tops, light had a significant main effect while temperature did not. For mounding *Porites* spp., light and temperature each had a significant main effect but the significant interactive effect between these factors makes the main effect hard to interpret. In each graph, columns in gray were not included in the statistical testing to prevent unbalancing of tests.

Table 2. ANOVA table for measurements of photon pressure per symbiont cell.

	A. muricata		*Porites* spp.
	Corallite undersides	**Corallite tops**	**Corallite tops**
Temp.	$p = \mathbf{0.01}$ $F_{1,12} = 9.21$	$p = 0.83$ $F_{1,12} = 0.05$	$p < \mathbf{0.01}$ $F_{1,12} = 45.3$
Light	$p < \mathbf{0.01}$ $F_{1,12} = 21.1$	$p = \mathbf{0.02}$ $F_{1,12} = 7.72$	$p < \mathbf{0.01}$ $F_{1,12} = 211$
Temp. × light	$p = 0.28$ $F_{1,12} = 1.27$	$p = 0.83$ $F_{1,12} = 0.05$	$p < \mathbf{0.01}$ $F_{1,12} = 34$

Temp., temperature.
Probability values that are <0.05 are highlighted in bold.

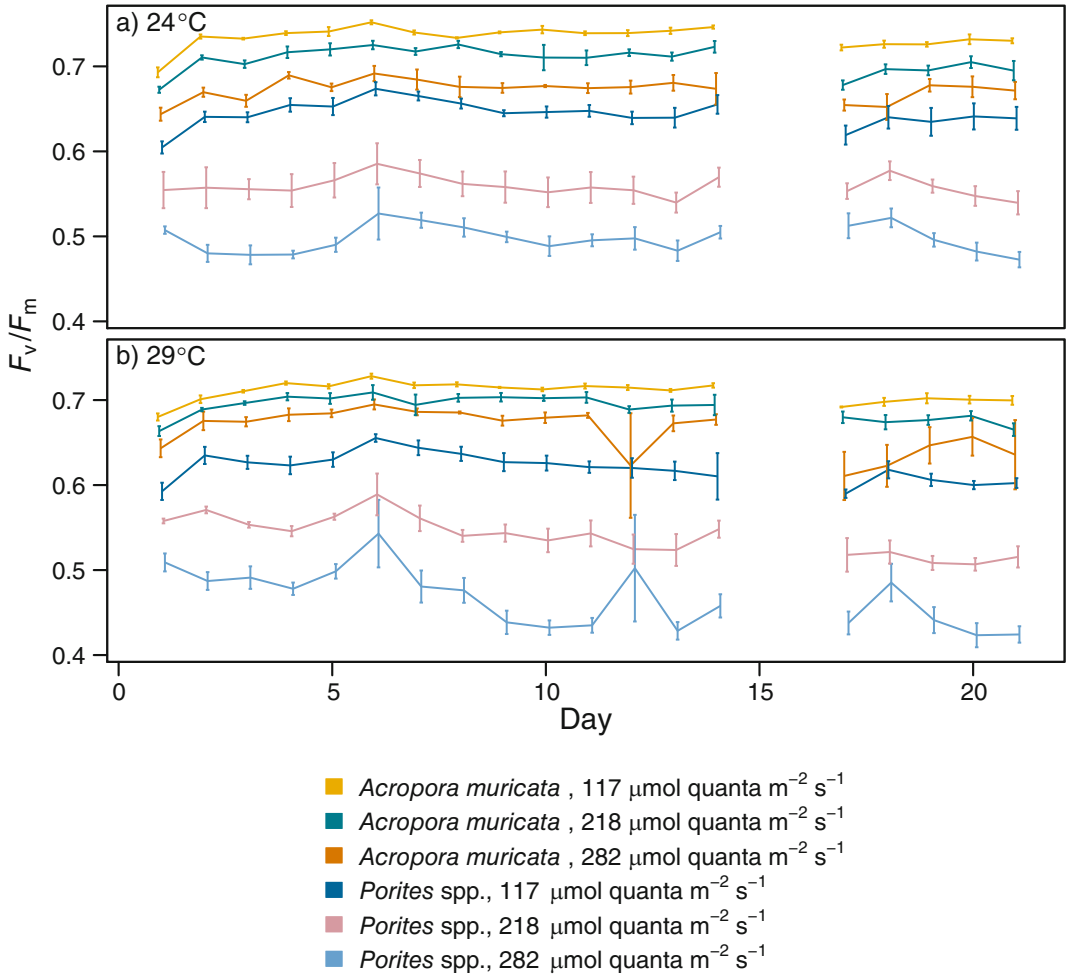

Fig. 5. Times series of the dark-adapted yield of photosystem II (F_v/F_m), at (**a**) 24°C and (**b**) 29°C. All data points are the means (± SEM) of the median value per aquarium ($n = 4$ aquaria per treatment). Horizontal positions of data points have been very slightly offset to avoid the complete overlap of some error bars.

"midpoints" and "endpoints" to determine whether F_v/F_m had stabilized within each treatment by the end of the experiment. This could have resulted in these comparisons being driven by high inter-day variation rather than being driven by the overall tendency of F_v/F_m through time. Instead, we determined whether samples had stabilized by the end of the experiment by pooling the F_v/F_m data into a midpoint group (days 10–14) and an endpoint group (days 17–21), and testing for a difference between the two groups with a mixed-effects model with heteroskedastic variances, with the model structure of temperature × light × group as fixed effects and "day of experiment" as a nested random effect. A significant main effect of mid/endpoint in *A. muricata* ($p < 0.0001$, $F_{1,8} = 74.4$; not reported in Table 1) revealed a significant decrease in F_v/F_m towards the end of the experiment, though graphs suggest that this may have been sudden and not a continuation of a trend through time (Fig. 5a,b). A significant interaction of temperature with mid/endpoint in mounding *Porites* spp. ($p = 0.0274$, $F_{1,219} = 4.93$; not reported in Table 1) was found, and while post hoc tests did not yield any significant differences between midpoint and endpoint at either temperature (Tukey's test: $p > 0.05$), the graph of the time series suggests that the downward trend may have continued beyond day 15 (Fig. 5a,b).

Discussion

This study exposed two coral taxa to three changes in light level, combined with two temperature levels, to investigate whether photoacclimation rate is influenced by temperature, direction of light change, or magnitude of light change. The variables used in this study reflect different physiological processes that may change as a part of a photoacclimation response. Light-use efficiency, α, is a measurement of the efficiency with which the downwelling light is absorbed and then utilized to drive the electron transport chain (Falkowski and Raven 2007). It is therefore an estimate of the efficiency with which incident light is utilized to power photochemical

processes that can include carbon fixation (Harland and Davies 1994). This efficiency can be enhanced by increasing the number of photon-trapping pigments contributing to each photosynthetic unit (Herron and Mauzerall 1972; Falkowski and Owens 1980; Falkowski and Dubinsky 1981). If the light level is above saturation, P^{net} cm^{-2} can be physiologically optimized to ambient light levels by changing one or more of the turnover time of PSII, the number of photosynthetic units per symbiont cell (Falkowski and Raven 2007), and the number of symbiont cells (Cunning et al. 2015). If the light level is below saturation, P^{net} cm^{-2} can be physiologically optimized by changing the aforementioned factors *and* α. F_v/F_m can reveal photoacclimatory changes in the processes that repair or manufacture PSII. Decoupled PSII (delinked due to photodamage or photoprotection) will fluoresce and dissipate some energy as heat, but cannot engage in photochemical quenching, and hence F_v/F_m will decrease during the day. However, if repair mechanisms can keep up, F_v/F_m will recover to its previous maximum level during the evening (Vass et al. 1992). Finally, symbiont population densities may alter due to host regulation or self-regulation of symbiont populations (Davy et al. 2012; Weston et al. 2015). As photoacclimation can occur through one or more of a number of mechanisms, it stands to reason that the ecological and organismal consequences of a particular photoacclimation rate may depend on the mechanism(s) involved.

Impacts of temperature

Our results suggested that factors such as rate of repair of photosystem II, or photoprotective mechanisms, could be a greater influence on F_v/F_m stabilization than any advantage bestowed by increased kinetic rates. Full stabilization of F_v/F_m in mounding *Porites* spp. appeared to be reached sooner (by days 6–14) at the lower temperature rather than the elevated temperature, running contrary to part 1 of our hypothesis that thermal increase of kinetic rates would drive photoacclimation rates.

No other response variables in either species displayed differences in the time of stabilization between the two temperatures, though we may have missed potential effect(s) as the high-resolution time series used for F_v/F_m was not possible for the other variables. Some response variables continued to change through to the end of the experiment in both temperature treatments, e.g., α and P^{net} in *A. muricata*, P^{net} at medium and high light and symbiont densities at low light in mounding *Porites*. A comparable result has been found in *S. pistillata*, where K_m (the irradiance at which $P^{net} = P^{net}{}_{max}/2$) did not stabilize until 45 d or longer after the incident light intensity was permanently changed (Gattuso and Jaubert 1984). For these variables, the sampling regime would not have detected evidence of differences in photoacclimation rate between temperatures that manifested following the end of the experiment.

F_v/F_m is known to be a very temperature sensitive variable. This may be because the quantum efficiency of PSII is affected by several heat-sensitive processes, such as the rate of repair of photodamage to the psbA protein of the reaction center in PSII (Takahashi et al. 2004). Some photoprotective processes that are enacted at elevated temperature, including dissipation of light as heat due to "inactive PSII" delinked from the electron transport chain, also cause a decrease in F_v/F_m (Warner et al. 1996). Thus, assuming that one or both processes are capable of operating in the symbionts of mounding *Porites* spp., the fact that F_v/F_m takes longer to photoacclimate in mounding *Porites* spp. at elevated temperature is mechanistically understandable. The fact that F_v/F_m does not take longer to photoacclimate in *A. muricata* at elevated temperature raises the possibility that in this species, psbA damage and/or "inactive PSII" did not differ substantially between 24°C and 29°C. This is likely because experimental light levels were too low to induce substantial psbA damage and/or photoprotection in *A. muricata* (see below).

Magnitude of light change

Because of the greater signal provided by a larger abiotic change, or more negative ramifications of delayed photoacclimation for the organism under such a change, larger magnitude changes in light may induce faster photoacclimation rates than smaller magnitude changes in light (referred to in part 3 of our hypothesis). The level of 218 μmol quanta m^{-2} s^{-1} represents a smaller magnitude light change (of + 47 μmol quanta m^{-2} s^{-1} compared to pre-experiment levels) while 282 μmol quanta m^{-2} s^{-1} represents a larger magnitude light change (of + 111 μmol quanta m^{-2} s^{-1}). However, between these light treatments, neither species displayed any difference in stabilization rate for any parameter, providing no confirmation nor rebuttal of this hypothesis.

Direction of light change

Modeling evidence suggests that corals exposed to a decrease in incident light will take less time to photoacclimate than those exposed to an increase in incident light (Skirving et al. 2018). This study did not confirm this result in *A. muricata*, nor for any variables except P^{net} cm^{-2} in mounding *Porites* spp., though the results in the latter species are more nuanced. In *A. muricata*, symbiont densities exhibited no significant change between day 15 and 24, suggesting that either change in this variable had been completed within 14 d in all treatments, or that no photoacclimatory changes occurred. α and P^{net} cm^{-2} in *A. muricata* continued to photoacclimate between day 15 and day 24 in all treatments. In mounding *Porites* spp., α had stabilized within 14 d in all treatments. For the other response variables in mounding *Porites* spp., the primary influence of the direction of light change was to elicit the stabilization within 14 d of symbiont cell densities in the "light increase" treatments,

which contributed to P^{net} cm^{-2} stabilizing within 14 d in the "light decrease" treatment.

Increased time for stabilization of P^{net} cm^{-2} at medium and high light in mounding *Porites* spp. is paralleled by changes in the amount of photon pressure per symbiont cell in this taxon. Treatments that increased their P^{net} cm^{-2} with time—medium light at both temperatures and high light at 24°C—experienced elevated photon pressure per symbiont cell (Fig. 4b) compared to those treatments—low light at both temperatures—that experienced stable P^{net} cm^{-2} through time. High light (282 μmol quanta m^{-2} s^{-1}) at 29°C, which saw a decrease in P^{net} cm^{-2} with time, experienced extremely high photon pressure per symbiont cell compared to all other treatments (Fig. 4b). This suggests that photoinhibition was reducing P^{net} cm^{-2} through time in this treatment, while treatments experiencing moderate levels of available light per symbiont cell upregulated their areal rate of photosynthesis through time.

In contrast, P^{net} cm^{-2}, light-use efficiency and photon pressure per symbiont cell in *A. muricata* seemed to indicate an ability to acclimate to light levels under all experimental conditions. The increase of α through time in *A. muricata* implies that the efficiency of photochemical quenching at PSII per unit of light increased through time in most or all treatments. Such an increase in efficiency of light utilization is an expected response in corals acclimating to low light (Falkowski and Dubinsky 1981). A main effect of increase in P^{net} cm^{-2} through time was also observed (Fig. 2a), suggesting that *A. muricata* was becoming more efficient at using incident light, regardless of its treatment light level. While *A. muricata* nubbins were exposed to the same light levels as mounding *Porites* spp., photon pressure per *A. muricata* symbiont cell in all light treatments (ca. 0.2–0.7 fmol quanta cell^{-1} s^{-1}) was of the same order of magnitude as that at low light in mounding *Porites* spp. (ca. 0.5–1 fmol quanta cell^{-1} s^{-1}) (Fig. 4a,b). Thus, the local light micro-environment of *A. muricata* symbionts in all light treatments could have been one at which photodamage was not a concern, perhaps explaining why differences in stabilization rate between light-increase and -decrease treatments were not observed.

We did not directly measure E_K—the light level at which the photosystem turnover rate is balanced by photon capture (Falkowski and Raven 2007)—nor the maximal rate of photosynthesis (P^{net}_{max}). These parameters define the shape of the photosynthesis vs. irradiance curve, and the completion of photoacclimation can be inferred from the stabilization of both parameters (Falkowski and Dubinsky 1981). However, P^{net} is directly related to both parameters as $P^{net} = P^{net}_{max} \tanh(E/E_K)$, where E is the ambient irradiance (Anthony and Hoegh-Guldberg 2003), and therefore stabilization of P^{net} under the treatment irradiance allows the inference that E_K and P^{net}_{max} have likely both stabilized. If measured on corals in situ prior to retrieval for experimentation (e.g., via Dellisanti et al. 2020), E_K and P^{net}_{max} may be useful to relate the acclimation state in experimental treatments to that in the field. As laboratory-simulated light conditions may qualitatively differ from field conditions, we highlight field vs. lab E_K and P^{net}_{max} comparisons as a future avenue to validate that treatments are generating physiologically- and ecologically-relevant light input to coral photosystems.

As a consequence of the respective photon pressures experienced by symbionts, areal symbiont densities could have been driven by photoinhibition in mounding *Porites* spp., but by other factors in *A. muricata*. In mounding *Porites* spp., cell loss with increasing light levels under non-stressful temperature suggests that the cause of cell loss is photoinhibition. In accord with the photoinhibition model of bleaching (Iglesias-Prieto 1995; Hoegh-Guldberg 1999), there was a trend for cell loss in mounding *Porites* spp. to be aggravated by increased temperature (Table 1; Fig. 3). While symbiont cell densities in *A. muricata* also decreased with elevated temperature (Fig. 3), a much greater decrease in symbiont density at high temperature occurred for low light than medium or high light, suggesting that an additional mechanism rather than only photoinhibition was driving this change. To our knowledge, this is the first factorial light × temperature experiment on corals that, at an elevated temperature, has found a greater decline in symbiont density at low light intensity compared to a higher intensity. Elevated temperature causes an increase in the kinetic rate of biochemical reactions (Sheridan et al. 2012) and therefore increases the metabolic rate of each symbiotic partner (Gillooly et al. 2001). Symbiodiniaceae are known to be mixotrophic, capable of deriving nutrition from both the host and from photosynthesis (Steen 1987; Banaszak et al. 2013). One hypothesis for the decline in symbiont density in *A. muricata* at 29°C and low light is that the symbiont population may have been reduced to mitigate against the symbiont population becoming parasitic due to photosynthesis failing to keep up with a rising respiratory demand of the holobiont (Fig. 2b, trend only) (Knowlton and Rohwer 2003; Baker et al. 2018). A second hypothesis is that the symbiont population may have been thinned to reduce self-shading, increasing the photosynthetic performance of the remaining symbiont cells. Other hypotheses are that the combination of low light and elevated temperature induced symbiont apoptosis (Dunn et al. 2004), or induced some host cell apoptosis or necrosis that involved degradation of symbiont cells (Dunn et al. 2002*a*,*b*).

The increased areal P^{net} at medium and high light at both temperatures in *A. muricata* also suggests that photoinhibition at high temperature was a low risk in this species. This concurs with past experiments on a taxonomically diverse group of other coral species that showed that those that *do not* experience a high increase in photon-pressure per symbiont with increasing temperature (like *A. muricata*: Fig. 4a) experience reduced photophysiological dysfunction compared to those that *do* (like mounding *Porites* spp.: Fig. 4b) (Swain et al. 2016).

While we did not explore what physiological mechanisms might be responsible for the substantially reduced photon pressure per symbiont in *A. muricata* compared to mounding *Porites*, these could include increases in pigment levels within symbionts, host tissue thickness or host pigmentation. Larger areal symbiont densities in *A. muricata* almost certainly contributed, through increased self-shading of symbionts. The planar orientation of *Porites* specimens vs. the vertical orientation of *Acropora* specimens, which approximates both species' orientations in nature, may have resulted in *Porites* receiving a higher daily light dose, possibly contributing to reduced symbiont densities. Skeletal light scattering may also play a role (Enríquez et al. 2005); however, it is plausible that this characteristic may impact photobiology differently in aquaria vs. the wild, due to differences in direct vs. diffuse lighting between these environments. We acknowledge that the use of *treatment-averaged* symbiont cell density and photon flux density to calculate photon pressure per symbiont created a risk that important variation could have been missed, e.g., due to an association of very high symbiont densities with very high absorptance, and vice versa. On the other hand, the order of magnitude difference in photon pressure per symbiont between the two species suggests that the conclusions drawn about the role of this variable in explaining interspecific photoacclimation patterns are, nevertheless, probably robust.

Porites spp. on the southern Great Barrier Reef, as well as in many other reef areas of the world, predominantly harbor the C15 Symbiodiniaceae type (LaJeunesse et al. 2003, 2004; Fisher et al. 2012). However, in *P. rus* and *P. cylindrica* in Palau (examples of encrusting and branching *Porites*), C15 splits into different sub-types distinguished on the basis of DNA sequence differences in the psbA non-coding region. Different C15 sub-types associate with different host species and sub-reef-scale habitats, and demonstrated different photophysiological responses to thermal stress (Hoadley et al. 2021). We highlight that due to a mixture of mounding *Porites* species having been used, there is the possibility of a mixture of C15 sub-types in our experimental population, though it is still unknown whether C15 partitions into different subtypes among mounding *Porites* species from within one reef habitat (as our specimens were).

Differences in photoacclimation responses due to differences in host physiology, if they exist, might introduce confounding effects into our mounding *Porites* spp. cohort. There have been relatively few comparative studies of host or holobiont physiology between mounding *Porites* species to date. Resource partitioning studied with stable isotopes in *P. lobata* and *P. solida* suggested that both species occupied similar ecological niches, and employed similar metabolic strategies (Plass-Johnson et al. 2015). Forsman et al. (2020) found no differences in bleaching susceptibility between different genetic groups within the *P. lobata* species complex in the Hawaiian Islands. In the same reef region, *P. lobata* and *P. evermanni* displayed similar responses to environmental parameters and low intra-species dispersion in physiological profiles compared to species of other genera. However, *P. evermanni* displayed a positive correlation between lipid reserves and flow (measured as significant wave height) that was not detected in *P. lobata* (McLachlan et al. 2021). Taken together, these initial results suggest that *Porites* congeners with mounding morphology have similar host and/or holobiont physiology, though the final example shows that we cannot rule out the existence of some physiological differences that might impact on photoacclimation.

Conclusions

Exploration of photobiology through time following light change, with knowledge of photon pressure per symbiont within coral tissue, has revealed that this parameter appears to play a major role in photoacclimation rates. This builds on previous work that has shown that mechanisms of photoacclimation appear to be influenced by the within-tissue light environment. Ziegler et al. (2015) showed that the same symbiont type had substantially different photoacclimation states in different coral species, likely indicating a strong effect of the coral host. Earlier, Hennige et al. (2008) showed that coral species with an increased absorptance of the host tissue fraction (= possible lower internal light environment) promoted greater absorptance in symbionts (= possibly greater light-use efficiency) than a species in which host fraction absorptance was mildly less. Our results draw a link between a higher internal light field as experienced by symbionts and within-species differences in photoacclimation rate under different directions of light change and water temperature. In contrast, a low internal light level as experienced by symbionts was associated with an apparent lack of effect of light change direction and water temperature on photoacclimation rate, at least over the experimental period. Whether these impacts are due to inherent species-specific differences in internal light fields and/or other inherent species differences, or are broader effects that will occur at low and high internal light levels in any species in which this parameter is plastic, is a potentially fruitful avenue for coral photobiology research.

Data availability statement

Data and code used in study are available at https://doi.org/10.5281/zenodo.8216867.

References

Anthony, K. R. N., and O. Hoegh-Guldberg. 2003. Kinetics of photoacclimation in corals. Oecologia **134**: 23–31. doi:10.1007/s00442-002-1095-1

Baird, M. E., M. Mongin, F. Rizwi, L. K. Bay, N. E. Cantin, M. Soja-Woźniak, and J. Skerratt. 2018. A mechanistic model of coral bleaching due to temperature-mediated light-driven reactive oxygen build-up in zooxanthellae. Ecol. Model. **386**: 20–37. doi:10.1016/j.ecolmodel.2018.07.013

Baker, D. M., C. J. Freeman, J. C. Y. Wong, M. L. Fogel, and N. Knowlton. 2018. Climate change promotes parasitism in a coral symbiosis. ISME J. **12**: 921–930. doi:10.1038/s41396-018-0046-8

Banaszak, A. T., M. García Ramos, and T. L. Goulet. 2013. The symbiosis between the gastropod *Strombus gigas* and the dinoflagellate *Symbiodinium*: An ontogenic journey from mutualism to parasitism. J. Exp. Mar. Biol. Ecol. **449**: 358–365. doi:10.1016/j.jembe.2013.10.027

Cunning, R., N. Vaughan, P. Gillette, T. R. Capo, J. L. Maté, and A. C. Baker. 2015. Dynamic regulation of partner abundance mediates response of reef coral symbioses to environmental change. Ecology **96**: 1411–1420. doi:10.1890/14-0449.1

Davy, S. K., D. Allemand, and V. M. Weis. 2012. Cell biology of cnidarian-dinoflagellate symbiosis. Microbiol. Mol. Biol. Rev. **76**: 229–261. doi:10.1128/MMBR.05014-11

Dellisanti, W., R. H. L. Tsang, P. Ang, J. Wu, M. L. Wells, and L. L. Chan. 2020. A diver-portable respirometry system for in-situ short-term measurements of coral metabolic health and rates of calcification. Front. Mar. Sci. **7**: 571451.

Dunn, S. R., J. C. Bythell, M. D. A. Le Tissier, W. J. Burnett, and J. C. Thomason. 2002*a*. Programmed cell death and cell necrosis activity during hyperthermic stress-induced bleaching of the symbiotic sea anemone *Aiptasia* sp. J. Exp. Mar. Biol. Ecol. **272**: 29–53. doi:10.1016/s0022-0981(02)00036-9

Dunn, S. R., J. C. Thomason, M. D. A. Le Tissier, and J. C. Bythell. 2002*b*. Detection of cell death activity during experimentally induced bleaching of the symbiotic sea anemone *Aiptasia* sp., p. 145–153. *In* Proceedings of the Ninth International Coral Reef Symposium, Bali. 23-27 Oct. 2000. International Society for Reef Studies.

Dunn, S. R., J. C. Thomason, M. D. A. Le Tissier, and J. C. Bythell. 2004. Heat stress induces different forms of cell death in sea anemones and their endosymbiotic algae depending on temperature and duration. Cell Death Differ. **11**: 1213–1222.

Eakin, C. M., and others. 2010. Monitoring coral reefs from space. Oceanography **23**: 118–133.

Edmunds, P. 2012. Effect of pCO_2 on the growth, respiration, and photophysiology of massive *Porites* spp. in Moorea, French Polynesia. Mar. Biol **159**: 2149–2160. doi:10.1007/s00227-012-2001-y

Enders, W. 2010. Applied econometric time series, 3rd ed. John Wiley & Sons, Inc.

Enríquez, S., E. R. Méndez, and R. Iglesias-Prieto. 2005. Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. Limnol. Oceanogr. **50**: 1025–1032. doi:10.4319/lo.2005.50.4.1025

Escoubas, J. M., M. Lomas, J. LaRoche, and P. G. Falkowski. 1995. Light intensity regulation of *cab* gene transcription is signaled by the redox state of the plastoquinone pool. Proc. Natl. Acad. Sci. USA **92**: 10237–10241.

Falkowski, P. G., and T. G. Owens. 1980. Light—Shade adaptation: Two strategies in marine phytoplankton. Plant Physiol. **66**: 592–595. doi:10.1104/pp.66.4.592

Falkowski, P. G., and Z. Dubinsky. 1981. Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. Nature **289**: 172–174. doi:10.1038/289172a0

Falkowski, P. G., and J. A. Raven. 2007. Aquatic photosynthesis. Princeton University Press.

Fisher, P. L., M. K. Malme, and S. Dove. 2012. The effect of temperature stress on coral–*Symbiodinium* associations containing distinct symbiont types. Coral Reefs **31**: 473–485. doi:10.1007/s00338-011-0853-0

Forsman, Z. H., D. J. Barshis, C. L. Hunter, and R. J. Toonen. 2009. Shape-shifting corals: Molecular markers show morphology is evolutionarily plastic in *Porites*. BMC Evol. Biol. **9**: 45.

Forsman, Z. H., R. Ritson-Williams, K. H. Tisthammer, I. S. S. Knapp, and R. J. Toonen. 2020. Host-symbiont coevolution, cryptic structure, and bleaching susceptibility, in a coral species complex (Scleractinia; Poritidae). Sci. Rep. **10**: 16995. doi:10.1038/s41598-020-73501-6

Gattuso, J.-P., and J. Jaubert. 1984. Premières données concernant l'action de la lumière sur le métabolisme, la croissance et la calcification in situ du Sclèractinaire hermatypique *Stylophora pistillata*. Compt. Rendus Acad. Sci. III Sci. Vie **299**: 585–590.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of size and temperature on metabolic rate. Science **293**: 2248–2251. doi:10.1126/science.1061967

Goreau, T. J., and R. L. Hayes. 1994. Coral bleaching and ocean "hot spots". Ambio **23**: 176–180. doi:10.2307/4314195

Harland, A. D., and P. S. Davies. 1994. Time-course of photoadaptation in the symbiotic sea anemone *Anemonia viridis*. Mar. Biol. **119**: 45–51. doi:10.1007/BF00350105

Hennige, S. J., D. J. Suggett, M. E. Warner, K. McDougall, and D. J. Smith. 2008. Unravelling coral photoacclimation: *Symbiodinium* strategy and host modification, p. 128–132. *In* Proceedings of the 11th international coral reef symposium, Fort Lauderdale, Florida. International Society for Reef Studies.

Hennige, S. J., D. J. Smith, S.-J. Walsh, M. P. McGinley, M. E. Warner, and D. J. Suggett. 2010. Acclimation and adaptation of scleractinian coral communities along environmental gradients within an Indonesian reef system. J. Exp. Mar. Biol. Ecol. **391**: 143–152. doi:10.1016/j.jembe.2010.06.019

Herron, H. A., and D. Mauzerall. 1972. The development of photosynthesis in a greening mutant of *Chlorella* and an analysis of the light saturation curve. Plant Physiol. **50**: 141–148.

Hitchcock, G. L. 1980*a*. Influence of temperature on the growth rate of *Skeletonema costatum* in response to variations in daily light intensity. Mar. Biol. **57**: 261–269. doi:10.1007/BF00387569

Hitchcock, G. L. 1980*b*. Diel variation in chlorophyll *a*, carbohydrate and protein content of the marine diatom *Skeletonema costatum*. Mar. Biol. **57**: 271–278. doi:10.1007/BF00387570

Hoadley, K. D., and others. 2021. Different functional traits among closely related algal symbionts dictate stress endurance for vital indo-Pacific reef-building corals. Glob. Chang. Biol. **27**: 5295–5309. doi:10.1111/gcb.15799

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar. Freshwat. Res. **50**: 839–866.

Hohmann-Marriott, M. F., K. Takizawa, J. J. Eaton-Rye, L. Mets, and J. Minagawa. 2010. The redox state of the plastoquinone pool directly modulates minimum chlorophyll fluorescence yield in *Chlamydomonas reinhardtii*. FEBS Lett. **584**: 1021–1026. doi:10.1016/j.febslet.2010.01.052

Iglesias-Prieto, R. 1995. The effects of elevated temperature on the photosynthetic responses of symbiotic dinoflagellates, p. 793–796. *In* P. Mathis [ed.], Photosynthesis: From light to biosphere. Kluwer Academic Publishers.

Iglesias-Prieto, R., and R. K. Trench. 1997. Acclimation and adaptation to irradiance in symbiotic dinoflagellates. II. Response of chlorophyll–protein complexes to different photon-flux densities. Mar. Biol. **130**: 23–33. doi:10.1007/s002270050221

Jeans, J., D. A. Campbell, and M. O. Hoogenboom. 2013. Increased reliance upon photosystem II repair following acclimation to high-light by coral-dinoflagellate symbioses. Photosynth. Res. **118**: 219–229. doi:10.1007/s11120-013-9918-y

Knowlton, N., and F. Rohwer. 2003. Multispecies microbial mutualisms on coral reefs: The host as a habitat. Am. Nat. **162**: S51–S62. doi:10.1086/378684

Krief, S., E. J. Hendy, M. Fine, R. Yam, A. Meibom, G. L. Foster, and A. Shemesh. 2010. Physiological and isotopic responses of scleractinian corals to ocean acidification. Geochim. Cosmochim. Acta **74**: 4988–5001. doi:10.1016/j.gca.2010.05.023

LaJeunesse, T., R. Bhagooli, M. Hidaka, L. DeVantier, T. Done, G. Schmidt, W. Fitt, and O. Hoegh-Guldberg. 2004. Closely related *Symbiodinium* spp. differ in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients. Mar. Ecol. Prog. Ser. **284**: 147–161. doi:10.3354/meps284147

LaJeunesse, T. C., W. K. W. Loh, R. van Woesik, O. Hoegh-Guldberg, G. W. Schmidt, and W. K. Fitt. 2003. Low symbiont diversity in southern Great Barrier Reef corals, relative to those of the Caribbean. Limnol. Oceanogr. **48**: 2046–2054. doi:10.4319/lo.2003.48.5.2046

Marshall, P. A., and A. H. Baird. 2000. Bleaching of corals on the great barrier reef: Differential susceptibilities among taxa. Coral Reefs **19**: 155–163. doi:10.1007/s003380000086

Matsubara, S., and W. S. Chow. 2004. Populations of photoinactivated photosystem II reaction centers characterized by chlorophyll *a* fluorescence lifetime in vivo. Proc. Natl. Acad. Sci. USA **101**: 18234–18239. doi:10.1073/pnas.0403857102

Mauzerall, D., and N. L. Greenbaum. 1989. The absolute size of a photosynthetic unit. Biochim. Biophys. Acta Bioenerg. **974**: 119–140. doi:10.1016/S0005-2728(89)80365-2

McLachlan, R. H., J. T. Price, A. Muñoz-Garcia, N. L. Weisleder, C. P. Jury, R. J. Toonen, and A. G. Grottoli. 2021. Environmental gradients drive physiological variation in Hawaiian corals. Coral Reefs **40**: 1505–1523. doi:10.1007/s00338-021-02140-8

NOAA Coral Reef Watch. 2017. NOAA coral reef watch daily global 5-km satellite climatology data for Heron Island. [Accessed 2017 October 16]. Available from ftp://ftp.star.nesdis.noaa.gov/pub/sod/mecb/crw/data/5km/v3/climatology/data/

Plass-Johnson, J. G., C. D. McQuaid, J. M. Hill, J. G. Plass-Johnson, C. D. McQuaid, and J. M. Hill. 2015. Morphologically similar, coexisting hard corals (*Porites lobata* and *P. solida*) display similar trophic isotopic ratios across reefs and depths. Mar. Freshwat. Res. **67**: 671–676. doi:10.1071/MF14248

Prézelin, B. B. 1987. Photosynthetic physiology of dinoflagellates, p. 174–223. *In* F. J. R. Taylor [ed.], The biology of dinoflagellates. Blackwell Scientific Publishers.

Reynolds, J. M., B. U. Bruns, W. K. Fitt, and G. W. Schmidt. 2008. Enhanced photoprotection pathways in symbiotic dinoflagellates of shallow-water corals and other cnidarians. Proc. Natl. Acad. Sci. USA **105**: 13674–13678.

Rodolfo-Metalpa, R., Y. Huot, and C. Ferrier-Pagès. 2008. Photosynthetic response of the Mediterranean zooxanthellate coral *Cladocora caespitosa* to the natural range of light and temperature. J. Exp. Biol. **211**: 1579–1586. doi:10.1242/jeb.016345

Roth, M. S., M. I. Latz, R. Goericke, and D. D. Deheyn. 2010. Green fluorescent protein regulation in the coral *Acropora yongei* during photoacclimation. J. Exp. Biol. **213**: 3644–3655. doi:10.1242/jeb.040881

Scheufen, T., R. Iglesias-Prieto, and S. Enríquez. 2017. Changes in the number of symbionts and symbiodinium cell pigmentation modulate differentially coral light absorption and photosynthetic performance. Front. Mar. Sci. **4**: 309.

Schrameyer, V., D. Wangpraseurt, R. Hill, M. Kühl, A. W. D. Larkum, and P. J. Ralph. 2014. Light respiratory processes and gross photosynthesis in two Scleractinian corals. PloS One **9**: e110814. doi:10.1371/journal.pone.0110814

Sheridan, C., J. Petersen, and J. Rohwer. 2012. On modifying the Arrhenius equation to compensate for temperature changes for reactions within biological systems. Water SA **38**: 149–151.

Skirving, W., and others. 2018. Remote sensing of coral bleaching using temperature and light: Progress towards an operational algorithm. Rem. Sens. **10**: 18. doi:10.3390/rs10010018

Steen, R. G. 1987. Evidence for facultative heterotrophy in cultured zooxanthellae. Mar. Biol. **95**: 15–23. doi:10.1007/BF00447480

Swain, T. D., and others. 2016. Skeletal light-scattering accelerates bleaching response in reef-building corals. BMC Ecol. **16**: 10. doi:10.1186/s12898-016-0061-4

Takahashi, S., T. Nakamura, M. Sakamizu, R. van Woesik, and H. Yamasaki. 2004. Repair machinery of symbiotic

photosynthesis as the primary target of heat stress for reef-building corals. Plant Cell Physiol. **45**: 251–255.

Titlyanov, E. A., T. V. Titlyanova, and K. Yamazato. 2001. Formation, growth and photo-acclimation of colonies of the hermatypic coral *Galaxea fascicularis* under different light conditions. Symbiosis **30**: 257–274.

Tonk, L., P. Bongaerts, E. Sampayo, and O. Hoegh-Guldberg. 2013. SymbioGBR: A web-based database of *Symbiodinium* associated with cnidarian hosts on the great barrier reef. BMC Ecol. **13**: 7.

Vass, I., S. Styring, T. Hundal, A. Koivuniemi, E. Aro, and B. Andersson. 1992. Reversible and irreversible intermediates during photoinhibition of photosystem II: Stable reduced Q_A species promote chlorophyll triplet formation. Proc. Natl. Acad. Sci. USA **89**: 1408–1412.

Veron, J. E. N., and C. C. Wallace. 1984. Scleractinia of eastern Australia. Part V. Family Acroporidae. Australian Institute of Marine Science in association with Australian National Univ. Press.

Warner, M. E., W. K. Fitt, and G. W. Schmidt. 1996. The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral: A novel approach. Plant Cell Environ. **19**: 291–299. doi:10.1111/j.1365-3040.1996.tb00251.x

Weston, A. J., W. C. Dunlap, V. H. Beltran, A. Starcevic, D. Hranueli, M. Ward, and P. F. Long. 2015. Proteomics links the redox state to calcium signaling during bleaching of the Scleractinian coral *Acropora microphthalma* on exposure to high solar irradiance and thermal stress. Mol. Cell. Proteomics **14**: 585–595. doi:10.1074/mcp.M114.043125

Ziegler, M., C. M. Roder, C. Büchel, and C. R. Voolstra. 2015. Mesophotic coral depth acclimatization is a function of host-specific symbiont physiology. Front. Mar. Sci. **2**: 4. doi:10.3389/fmars.2015.00004

Acknowledgments

This research was supported by an Australian Government Research Training Program Scholarship. Financial support for this research was received from the Australian Research Council (ARC) Linkage Grant LP 110200874 with the partner NOAA, as well as from ARC funding (CE140100020) of the ARC Centre of Excellence for Coral Reef Studies. Coral Reef Watch/ReefSense staff were fully supported, and this study was partially supported, by NOAA grant NA19NES4320002 (Cooperative Institute for Satellite Earth System Studies) at the University of Maryland/ESSIC. Funding for Coral Reef Watch is provided by NOAA's Coral Reef Conservation Program. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the authors and do not necessarily reflect the views of NOAA or the US Department of Commerce. Financial support was also received from a University Grants Award (Australian Wildlife Society). The coral specimens were collected under permit number G11/34549.1 issued by the Great Barrier Reef Marine Park Authority. K. Hay and M. Mello Athayde are thanked for assisting with diving. A. Chai and G. Bernal Carillo are thanked for technical advice on aspects aquatic husbandry and equipment. Heron Island Research Station staff are thanked for scientific, field and boating assistance. R. Allen and P. Uehling are thanked for extensive assistance in running the experiment. R. Borrego-Acevedo is thanked for lamp spectrum measurement. M. Pichon is thanked for the taxonomic identifications of the *Porites* specimens. D. Cameron is thanked for manufacture of respirometry chambers. The study was developed along the lines of an initial suggestion provided by R. Iglesias-Prieto. This article formed a part of the PhD thesis of R.A.B. M. Open access publishing facilitated by The University of Queensland, as part of the Wiley - The University of Queensland agreement via the Council of Australian University Librarians.

Conflict of Interest

None declared.

Submitted 19 March 2023
Revised 07 August 2023
Accepted 23 September 2023

Associate editor: Christopher Cornwall