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REPORT

Fitted F_v/F_m temperature response curves: applying lessons from plant ecophysiology to acute thermal stress experiments in coral holobionts

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Abstract Maximum photochemical efficiency, F_v/F_m, is the preferred metric for quantifying the loss of photosystem II (PSII) function in photosynthetic algal symbionts (Symbiodiniaceae) of reef-building corals exposed to heat stress, particularly at the early stages of coral bleaching. Loss of PSII function can be quantified as the temperature at which a holobiont loses 50% of maximum photochemical efficiency (50% effective dose, or ED50) when exposed to a range of experimental temperatures. Here, we demonstrate that dose–response curves can be substantially more informative about a coral's stress response by including ED5 (5% effective dose), ED95 (95% effective dose), and decline width (ED95–ED5) values in summary statistics. These parameters are commonly used in plant ecophysiology and can be extracted from fitted F_v/F_m temperature response curves. This suite of metrics provides a broader understanding of the loss of PSII function in acute thermal stress experiments in corals and could enhance comparability among coral and plant studies.

Keywords Coral bleaching · Dose–response curves · ED50 · Maximum photochemical efficiency · Acute thermal stress

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Coral bleaching

Coral reefs are one of the ecosystems most vulnerable to climate change (IPCC 2023; Reimer et al. 2024). For instance, rapidly warming oceans cause mass coral bleaching and therefore, significant declines of Scleractinian corals that are responsible for engineering tropical reefs. Coral bleaching appears to be initiated by the temperature-dependent loss of photosystem II (PSII) function in their algal mutualists (Iglesias-Prieto et al. 1992; Jones et al. 1998, 2000; Warner et al. 1999; Ragni et al. 2010), often tracked by measuring the maximum quantum yield of PSII or the maximum photochemical efficiency (F_v/F_m). The ratio of F_v/F_m has been used extensively in coral research with changes in F_v/F_m being strongly linked to coral bleaching severity (Warner et al. 1996, 1999) and differences in thermotolerance among Symbiodiniaceae species (Kemp et al. 2014). However, measuring F_v/F_m and accurately interpreting the results can be challenging. Here, we provide a brief perspective on the value of measuring F_v/F_m and present summary statistics of photochemical performance in response to acute thermal stress experiments, aiming to advance coral bleaching research.

During thermal bleaching, the coral animal and its algal symbionts (the holobiont) experience a severe reduction in pigmentation (Chlorophyll *a*, Chl*a*), in the number of algal cells, and a suppression of photosynthesis. The loss of PSII function in the zooxanthellate algae due to elevated temperatures may result from incomplete repair of the D1 protein in PSII reaction centers (Iglesias-Prieto et al. 1992; Warner et al. 1996, 1999; Iglesias-Prieto and Trench 1997; Takahashi et al. 2004, 2008; Hill and Ralph 2007; McGinley et al. 2012; Hill and Takahashi 2014), impaired Calvin–Benson cycle activity (Jones et al. 1998; Smith et al. 2005), and/or damaged thylakoid membranes (Tchernov et al. 2004).

These processes lead to excess excitation energy and the production of reactive oxygen species (Weis 2008; Szabó et al. 2020). During heat stress events outside the limits of acclimation, corals enter a positive feedback loop where the loss of algal cells increases the local irradiance within the tissue, leading to further algal cell loss. Increases in the magnitude of environmental stress accelerate this symbiont loss (Swain et al. 2016). This is additionally accompanied by a nutritional imbalance between host and algae, which culminates in a "bleached phenotype" (Hillyer et al. 2016; Scheufen et al. 2017; Gómez-Campo et al. 2022; Krämer et al. 2022) (Fig. 1).

Coral holobionts respond to similar temperature stress in a variety of ways, and since there is a predicted rapid increase in thermally stressful conditions, heat-resilient populations, species, and host/symbiont combinations are of immense interest for research and restoration applications (Baums et al. 2019; Morikawa and Palumbi 2019). It is thus beneficial to experimentally expose coral holobionts to a range of temperatures up to and outside the acclimation range. Moreover, the strongest thermal tolerance comparisons across species and locations are made when the experimental heat exposure is standardized (McLachlan et al. 2020; Voolstra et al. 2020; Grottoli et al. 2021), which allow further comparisons among populations (Barshis et al. 2013; Fine et al. 2013; Palumbi et al. 2014; Osman et al. 2018; Voolstra et al. 2020; Evensen et al. 2022) and coral genets (Baums et al. 2013; Palumbi et al. 2014; Dixon et al. 2015; Parkinson et al. 2015; Hoadley et al. 2024). However, despite the many methodological advances in coral bleaching research, the phenotypes routinely quantified during heat stress challenges remain limited.

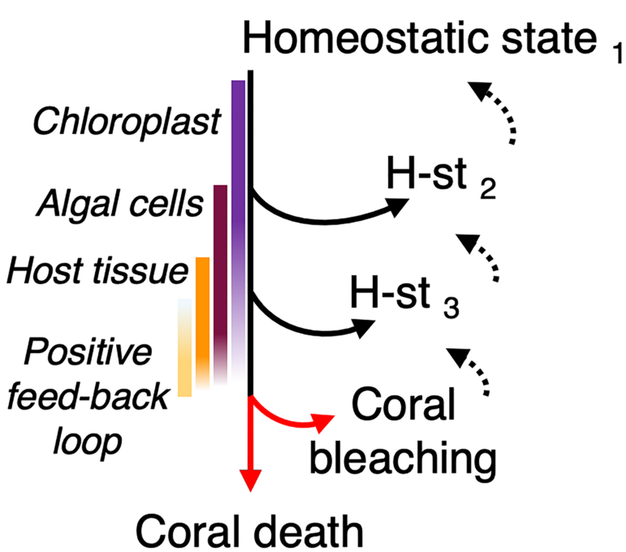

Fig. 1 Multiple homeostatic states lead to coral bleaching. Corals acclimated under certain environmental condition (Homeostatic state 1) experience time-dependent adjustments that take place in different cellular compartments: in the chloroplast (Photosystem II [PSII], H-st 2), zooxanthellate algal cells (Chlorophyll *a*, Chl*a*), and host cells (zooxanthellae loss by exocytosis, autophagy, and Programed Cell Death, H-st 3). When heat stress exceeds the upper limits of tolerance, the (putative) net accumulation of oxidative damage triggers the significant loss of coral pigmentation and algal cells, culminating in coral bleaching (modified from (Gómez-Campo et al. 2022). Homeostatic states, including coral bleaching, are reversible when environmental conditions improve, and the holobiont may return to previous homeostatic states

Assessing thermal stress with pulse amplitude modulated fluorometry

Pulse amplitude modulated (PAM) fluorometry (Schreiber et al. 1986) is a widely used noninvasive technique for assessing several aspects of oxygenic photosynthesis. By measuring chlorophyll fluorescence, it has the potential to disentangle primary photophysical events (excitation energy transfer, charge separation), and secondary reactions (electron transport). While the F_v/F_m ratio is commonly used to assess PSII efficiency under dark-acclimated conditions, the PAM technique can also evaluate the electron transport rate (ETR) and non-photochemical quenching (NPQ), which provide insights into energy conversion and photoprotective mechanisms, respectively (Papageorgiou and Govindjee 2004; Suggett et al. 2010; Gorbunov and Falkowski 2022). It is important to note that ETR curves are not equivalent to conventional photosynthetic response to irradiance (P vs. E), and, that the use of relative descriptors (relETR) overlooks light absorption regulation in the absence of absorptance measurements (González-Guerrero et al. 2021). Advanced techniques like fast repetition rate fluorometry (FRRf) and fast chlorophyll a fluorescence induction (OJIP) kinetics further extend these capabilities by capturing more detailed fluorescence transients and dynamic changes in electron transfer (*e.g.*, functional absorption cross section of PSII, and energy transfer between PSII units) making them remarkably valuable for characterizing energy conversion (Kolber et al. 1998; Suggett et al. 2010; Gorbunov and Falkowski 2022). Here, we focused on the F_v/F_m ratio, one of the most used parameter to fit temperature response curves (Díaz-Almeyda et al. 2011; Mansour et al. 2018; Voolstra et al. 2020; Evensen et al. 2021, 2022, 2023).

F_v/F_m is the maximum quantum yield of a stable charge separation for the dark-adapted state. This is derived by calculating the ratio F_v/F_m [$(F_m–F_0)/F_m$, where F_m and F_0 represent the maximum and minimum fluorescence intensities of dark-adapted samples]. In corals, maximum quantum yield is a widely accepted measure of Photosystem II (PSII) efficiency, interpreted as a descriptor of photodamage accumulation at the level of the photosynthetic membrane (Skirving et al. 2018), and a valuable tool for studying responses to environmental stress in photosynthetic organisms such as (vascular) plants, microalgae, and cyanobacteria (Suggett et al. 2010). In physiological and ecological studies, dose–response curves are commonly used to understand how an organism responds to varying degrees of heat stress. These curves typically plot a physiological response, such as F_v/F_m, against a gradient of temperature stress, similar to what is done in plant heat stress experiments (Slot et al. 2019; Araújo et al. 2021; Tiwari et al. 2021). The sigmoidal fit of the curve allows for the extraction of key parameters that describe the loss of PSII function in different ways. In plants and corals, 50% effective dose (ED50) has been extracted from fitted F_v/F_m temperature response curves (effective dose model of the dose–response curves package in R) (Ritz et al. 2015), which determines the temperature at which F_v/F_m decreases by 50% of its baseline temperature. The baseline temperature is typically based on the local climatology summarized as the monthly maximum mean (MMM) (Voolstra et al. 2020; Evensen et al. 2021, 2022, 2023). In plant studies, several parameters, in addition to the ED50 metric, are further calculated. For example, effective dose 5 (ED5) is the temperature at which F_v/F_m declines by 5% of its maximum value, a breakpoint temperature associated with the onset of the temperature-induced decline in F_v/F_m. In addition, effective dose 95 (ED95) is the temperature at which F_v/F_m declines by 95% of its maximum, where PSII functions are effectively lost. Furthermore, decline width (DW) provides a measure of the temperature range over which the plant experiences a decline in photochemical efficiency due to thermal stress and is calculated as the difference between ED95 and ED5. DW also describes how rapid or gradual the F_v/Fm decline rate is. Introducing these extended parameters into coral studies offers a novel and nuanced approach to comparing thermal stress responses. By integrating ED5, ED95, and DW into our analyses, we can capture the full spectrum of F_v/F_m decline in temperature response curves from coral symbionts, providing a richer, more detailed assessment of coral exposed to acute thermal stress experiments.

To explore ED5, ED95, and DW metrics, a dataset of *Stylophora pistillata, Acropora hemprichii*, and *Pocillopora verrucosa* corals exposed to acute thermal stress assays (Coral Bleaching Automated Stress System, CBASS) (Evensen et al. 2022) was retrieved to showcase that the extended parameters mentioned above can be additionally extracted from coral temperature response curves (Fig. 2). In this study, several locations were compared, including Eilat (Northern Red Sea) with a local MMM of 27.56 °C, and Al Fahal (Central Red Sea) with a local MMM of 30.87 °C. In the Red Sea, *S. pistillata* displayed a North to South gradient of increasing ED50 thermal thresholds, with lower values in Eilat (34.72 °C ± 0.21; mean ± S.E.M., n = 7) than Al Fahal (37.22 °C ± 0.11). The breakpoint temperature, ED5, averaged 31.08 °C ± 0.31 in Eliat and 35.31 °C ± 0.2 in Al Fahal. The photochemical efficiency, F_v/Fm, maintained a high breakpoint temperature (ED5) followed by a rapid decline in *S. pistillata* in Al Fahal (Fig. 2b) and by *A. hemprichii* in Eilat (Fig. 2d). These measurements resulted in a “narrow” shaped response curve which shows similarity to some plant species (Slot et al. 2019; Araújo et al. 2021; Tiwari et al. 2021). Depending on the conditions, plant species may also show a low ED5 breakpoint temperature, like. *S. pistillata* (Fig. 2a) and *P. verrucosa* in Eilat (Fig. 2c), resulting in a “wide” shaped temperature response curve due the gradual loss of PSII function.

The differences in coral holobiont response curves, narrow or wide, could be associated with tolerant or sensitive phenotypes as suggested in plants (Slot et al. 2019; Araújo et al. 2021; Tiwari et al. 2021). In coral holobionts, several photoprotective pathways, including enhanced capabilities for alternative photosynthetic electron transport (Reynolds et al. 2008), non-photochemical quenching (Hoegh-Guldberg and Jones 1999; Gorbunov et al. 2001), regulation of light-harvesting antenna (Takahashi et al. 2008), regulation of xanthophyll cycling (Brown et al. 1999), and increased PSII D1-synthesis-mediated activity (Takahashi et al. 2004; Hill and Takahashi 2014; Schrameyer et al. 2016), could explain the shape of the F_v/F_m response curve. Especially valuable would be comparative temperature response curve experiments on Symbiodiniaceae in culture and *in hospite* that directly quantify these photoprotective pathways (Brown et al. 1999; Dove 2004; Hill et al. 2005; Erickson et al. 2015). For example, plant species with wide response curves were thought to have early onset of PSII protective mechanisms (such as heat shock proteins) and switch from non-cyclic to cyclic electron transport around Photosystem I (Tiwari et al. 2021). Variability in functional traits of coral hosts and algae represent diverse strategies of regulation and photoprotection to avoid, minimize, and repair photooxidative damage in stress conditions. While the exact mechanisms that underpin the thermal stability of photosynthesis in reef-building corals have not been fully characterized, complementary approaches to dose–response experiments could test specific hypotheses related to the cascade of cellular events.

Limitations of F_v/F_m in coral bleaching research

Using the maximum quantum yield of PSII (F_v/F_m) as a sole phenotype for coral bleaching has limitations. For example, one factor that significantly influences the explanatory power of F_v/F_m as a metric for bleached phenotypes is the reduction in F_v/F_m resulting solely from increased light exposure within the tissue. The loss of pigmentation induces a synergistic effect of light stress and heat stress, which impacts

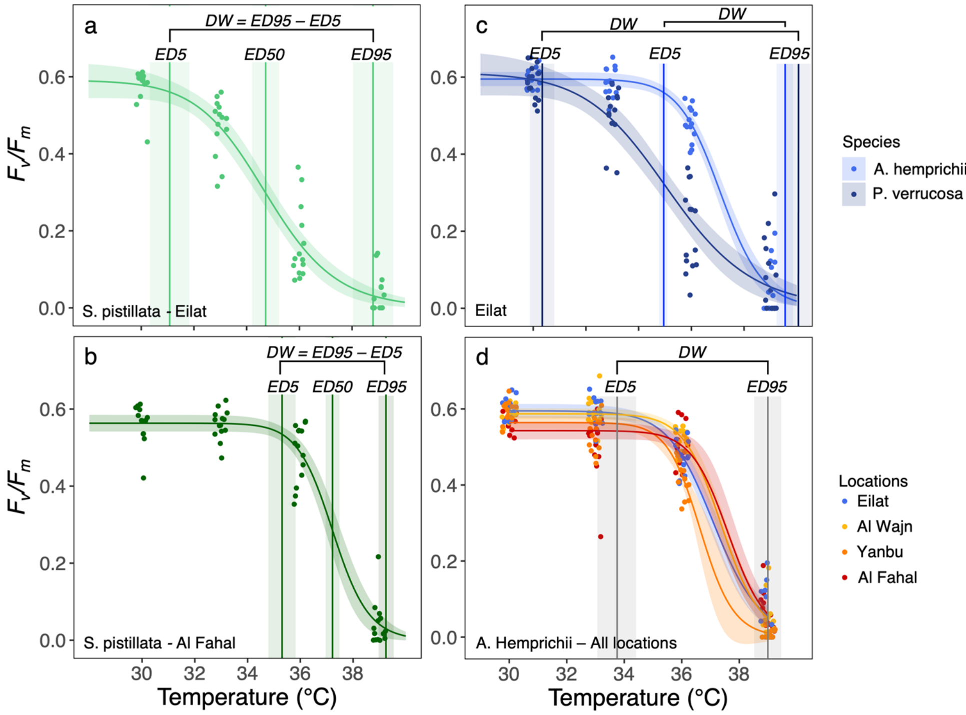

Fig. 2 Key parameters describing the loss of photosystem II function can be extracted from temperature response curves in acute thermal stress experiments. F_v/F_m curves were fitted to an 18 h short-term heat stress in the Coral Bleaching Automated Stress System (CBASS) (data retrieved from (Evensen et al. 2022)). Parameters extracted from the fit are temperatures at which F_v/F_m declines by 5, 50, and 95% of its maximum F_v/F_m (baseline temperature, MMM °C) expressed as ED5, ED50, and ED95, respectively. Decline width (DW) expressed as ED95–ED5 describes the shape of the curve (wide or narrow). **a** and **b** *Stylophora pistillata* maximum photochemical efficiency (F_v/F_m) in relation to temperature in two locations with different maximum monthly mean (MMM), the Northern Red Sea (Eilat, MMM 27.01 °C, blue), and Central Red Sea (Al Fahal, MMM 31.56 °C, red). **c** *Pocillopora verrucosa* and *Acropora hemprichii* temperature response in Eilat and **d** *Acropora hemprichii* across four locations in the Red Sea showing curves with similar shapes across the region

F_v/F_m measurements. Consequently, in some cases, the rapid accumulation of photodamage and the extent of F_v/F_m declines do not accurately reflect the loss of photosynthetic performance or the degree of pigment or symbiont loss.

Furthermore, measuring F_v/F_m requires a well-defined reference state due to its dependency on numerous factors such as sampling (environmental conditions, season, depth-dependent light condition, intracolonial light condition, local climatology), experimental light conditions, experimental temperature conditions (ramp-up and ramp-down), duration of heat stress (heat-hold), duration of the experiment (acute, moderate, long-term), water flow rate, and F_v/F_m measurement (dark-adapt samples prior measurement ensuring PSII are in an "open state" and photochemical quenching is minimized), which are also essential for cross-study comparisons (McLachlan et al. 2020; Grottoli et al. 2021). Discrepancies in instrumentation, even between instruments of the same brand and model, can lead to varying results and natural variability in fluorescence across temporal and spatial scales must also be considered (Suggett et al. 2010). The value of F_v/F_m measurements is thus tightly linked to strict experimental standardization. Although chlorophyll fluorescence is often regarded as an important indicator of the relative "health" of reef-building corals, it is critical to recognize that it primarily reflects the photochemical activity of symbionts *in hospite*, rather than providing a complete picture of the holobiont's overall health, which poses a potential limitation.

Additional, noninvasive techniques to F_v/F_m for coral bleaching research

Noninvasive techniques other than the maximum quantum yield of PSII, such as absorption measurements, are crucial for assessing the physiological condition of corals under heat stress that results in coral bleaching. For instance, corals exhibit photoprotective mechanisms like tissue retraction, the production of fluorescent proteins, and endolithic algae in the skeleton, which are not detected by F_v/F_m measurements alone and change with increasing heat stress (Salih et al. 2000; Brown et al. 2002; Dove 2004; Dizon et al. 2021;

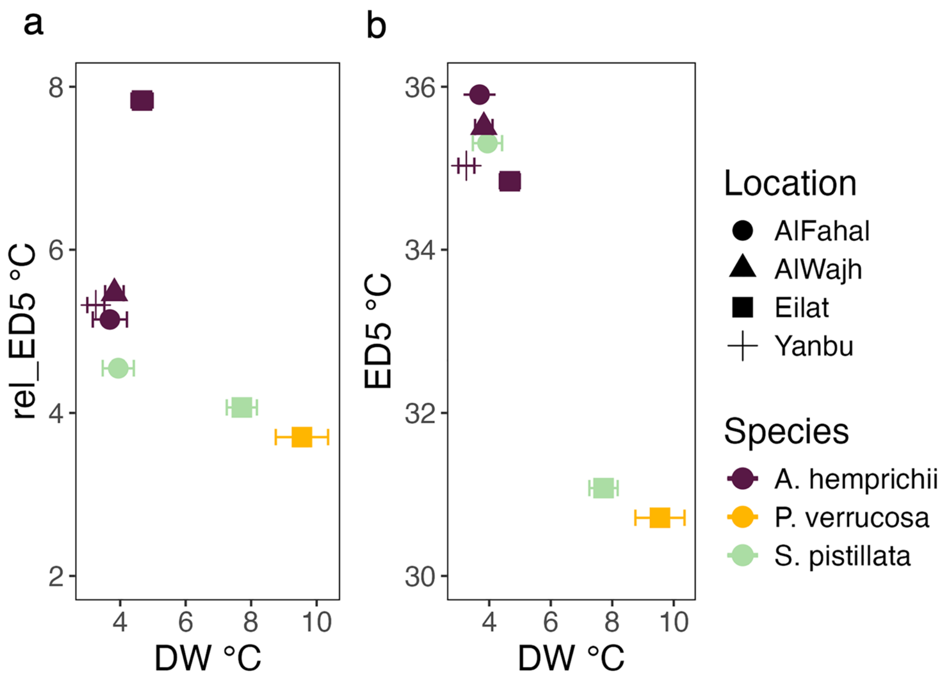

Fig. 3 Putative relationships between the breakpoint temperature (ED5), and decline width (DW). This type of visualization segregates species and locations by gradual changes in F_v/F_m over treatment temperatures and therefore wide DWs (*P. verrucosa* and *S. pistillata* in Eilat) or narrow DWs that indicate rapid (*A. hemprichii*) declines in F_v/F_m. Moreover, species with high breakpoint temperatures tend to display narrow DWs. **a** Relative ED5 (rel_ED5 °C = ED5 °C–MMM °C) and **b** absolute ED5 °C are shown for comparison

Satoh et al. 2021; Bollati et al. 2022; Galindo-Martínez et al. 2022b, 2022a). Absorptance (A), estimated from reflectance (R) measurements, describes the relative amount of solar energy/incident light that can potentially be used in photosynthesis for organic carbon fixation. Comparisons of pigment-specific absorptance (A) and absorbance (*De*) peaks, for example Chl*a* at 675 nm (A_{675}, De_{675}), are also informative of the change in functional optical properties of the holobiont tissue (i.e., a proxy of Chl*a* content, considering that at 675 nm the interference of accessory algal and animal pigments are minimized) (Enríquez et al. 2005; Rodríguez-Román et al. 2006; Scheufen et al. 2017; Hoadley et al. 2024). Together, these noninvasive descriptors provide a more comprehensive picture of the holobiont's overall physiological condition, allowing for better insight into coral thermal stress responses than solely using the maximum quantum yield of PSII.

Conclusion

This perspective provides a structured approach to incorporating plant biology metrics into coral thermal tolerance studies, offering a comprehensive framework for future research and conservation efforts. The effective dose (ED) metrics—ED5, ED50, and ED95—alongside the decline width (DW) have proved to be useful tools in plant photobiology, offering complementary quantifications of temperature-dependent PSII functionality. These metrics enable researchers to determine the temperature at which photosynthetic efficiency begins to decline, reaches a critical midpoint, and ultimately fails. By extending these concepts to coral photophysiology, we can potentially unlock new insights into PSII loss of function in well-standardized experimental approaches (Fig. 3).

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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