Title

Maintenance cost of photosynthesis sets key ecological constraints on zooxanthellate corals

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Abstract

Ecological models using light limitation to explain coral depth distribution have largely disregarded the energetic cost of sustaining photosynthetic activity. Here, we quantified photosystem II (PSII) turnover across a depth-simulated light gradient in a zooxanthellate coral, measuring PSII half-life, D1 protein abundance, and PSII-complex gene expression. Maximum photosynthetic capacity remained stable across irradiance levels while respiration rose and PSII turnover accelerated as a power law, imposing increasing ATP demand at the shallowest depths. Declining D1 protein abundance alongside stable transcript levels demonstrated that this escalating maintenance cost operates through post-transcriptional regulation. Consequently, a decreasing fraction of photosynthetic usable energy is available for translocation to the coral host at high irradiance, as the energy required for PSII repair increases. Integrating these physiological constraints into a bio-optical model revealed that the balance between photosynthetic capacity and its maintenance cost defines an optimal depth, the Photosynthetic Usable Energy Supply (*PUES*) maximum, where host energetic returns are maximized. This framework provides a mechanistic basis for understanding depth distributions in symbiotic corals and extends as a predictive tool for any photosynthetic organism operating under variable irradiance, including forecasting how environmental degradation contracts viable depth ranges.

MAIN TEXT

Introduction

Light supplies the energy that sustains coral reef ecosystems, but its role in shaping coral distribution cannot be explained by light availability alone. Variation in light quantity and spectral composition set physiological limits that structure community composition, species richness, and colony morphology across depth gradients (*1–6*). These ecological patterns emerge from fundamental biophysical constraints on how efficiently light energy is captured and converted into metabolic output. Corals are modular, sessile, mixotrophic organisms that host intracellular dinoflagellates in the family Symbiodiniaceae (*7*). Endosymbionts translocate a large fraction of their photosynthetically fixed carbon to the host, fueling basal metabolism and calcification (*8–10*). Light harvesting by the coral holobiont is determined by the emergent optical properties of symbionts, host tissue, and skeleton (*11*). Consequently, efficient photosynthesis requires coordinated adjustment across multiple levels of biological organization, from symbiont cell pigmentation and density, to host tissue optics, skeletal architecture, and whole colony morphology (*1*, *12–26*). These traits are integrated through photoacclimatory processes that optimize energy conversion under different light environments (*24*, *27–30*). Yet, the physiological limits through which photosynthesis constrains coral ecological niches across depth remain unresolved (*5*, *9*, *31*, *32*).

Depth gradients impose continuous selective pressures on coral–symbiont associations as sunlight simultaneously determines energy acquisition and physiological demands. If coral distribution were determined by solar energy alone, productivity and species richness would be expected to peak in shallow reefs and decline monotonically with depth as light attenuates. This pattern would reflect reduced growth rates and increased extinction risk under lower energy supply (*33*). However, for symbiotic corals, light availability by itself often fails to predict vertical patterns of biodiversity and performance (*3*). Instead, the amount of light that can be converted into biologically usable energy for the host better explains species richness and depth zonation in zooxanthellate corals (*5*). This distinction has relevant ecological implications. At intermediate depths, many corals maximize their net usable energy, expanding niche space and promoting greater species coexistence relative to both shallow and deep extremes. Under this framework, depth zonation cannot be simply considered a response to light attenuation with depth, but the outcome of selection on traits that determine how efficiently corals convert depth-specific available light into net energetic return. This is achieved through coordinated optimization of coral light capture, physiological adjustments of symbionts and host, and colony morphology. While lower depth limits are attributed to light limitation, upper depth limits are hypothesized to be constrained by the increasing energetic demands required to maintain performance under high irradiance.

Among the physiological processes that impose these energetic demands, protein damage and repair rank among the most energetically expensive cellular processes across living systems (*34–37*). However, their contribution to whole-organism energy budgets remains difficult to quantify. In photosynthetic organisms, this challenge is exemplified by the photosystem II (PSII) reaction center D1 protein, which undergoes rapid, light-dependent cycles of damage, degradation, and resynthesis (*38–43*). Replacement of photodamaged PSII reaction centers requires substantial ATP investment to support D1 synthesis, assembly, and regulation (*44–47*). In coral-associated Symbiodiniaceae, accelerated D1

turnover has been documented under both light- and thermal stress, consistent with a central role in sustaining photosynthetic function under stress conditions and maintaining the stability of the mutualism (*48–50*). Thus, empirical data on the energetic cost of sustaining this repair activity, and its consequences for energy partitioning within the symbiosis, are critical to determine energy utilization and delineate energetic boundaries in depth gradients.

We hypothesize that changes in PSII damage and repair across a light gradient affect the net energy that can be translocated from the symbiont to the coral host. Enhanced repair in high light environments sustains photosynthesis but requires more energy for ATP production and protein synthesis, reducing the fraction of photosynthetic energy available in support of host metabolism. Conversely, low light conditions limit energy production regardless of maintenance demands. These mechanisms predict a non-linear relationship between light availability and net autotrophic benefit to the coral host, providing an explanation for why abundant light in shallow reefs does not necessarily translate into enhanced coral growth or physiological performance (*5*).

To measure the effect of metabolic cost across high and low light conditions, we conducted a series of experiments to characterize coral photoacclimatory responses, quantify energetic demands of PSII damage-repair activity, and its impact on energy translocation to the coral host (**Fig. S1**). First, (1) we engineered a custom light system capable of simulating natural diurnal light cycles under controlled irradiance and spectral quality. This system minimized the confounding effects of ultra violet (UV) light (**Fig. S2**) and stabilized daily light integrals (DLI in mol quanta m^{-2} day^{-1}) against the variability caused by cloud cover (*51*, *52*). Second, (2) coral fragments from the depth generalist *Orbicella faveolata* were acclimated to DLI treatments for four weeks, followed by a detailed characterization of its optical, structural, and physiological light phenotypes, including PSII half-life and turnover dynamics. Third, (3) coral fragments were exposed to short-term shifts in DLI to evaluate repair capacity under light conditions that induce light limitation and light stress. Lastly, (4), we developed a bio-optical model integrating empirical results and theoretical considerations to predict shifts in photosynthetic usable energy available to the coral host across a depth gradient. This mechanistic framework provides a tool to predict the natural habitat and depth distribution of various coral taxa as well as quantify the impact of environmental changes and increase turbidity (diminished water quality) on the energetic cost to reef-building corals.

Results

Rapid photoacclimation across a realistic depth-dependent light gradient

Colonies in replicates were exposed to daily light integrals of 4 (DLI-4), 12 (DLI-12), 22 (DLI-22), and 32 (DLI-32) mol quanta m^{-2} day^{-1} (**Fig. 1A**, **Fig. S3A**), which simulates a depth gradient of 5–34 m (assuming a diffuse attenuation coefficient for downwelling irradiance, K_d, of 0.07 m^{-1}; typical for clear-water tropical reefs). PSII maximum photochemical efficiency (F_v/F_m) for experimental replicates (sample fragments) reached a steady state by day 10 (**Fig. S3B**), indicating that samples had acclimated to each of their respective daily doses of irradiance.

Diurnal photoprotection scaled with light exposure

Traits were treated as continuous functions of DLI rather than as discrete treatment means, characterizing phenotypic adjustments across the light gradient (**Fig. S4**). F_v/F_m was highest under DLI-4 and declined linearly with increasing light intensity (**Fig. 1B**). To quantify diurnal variation in PSII excitation pressure, we measured maximum pressure over PSII (*Qm*), which increased linearly corresponding to the transition from low to high irradiance (**Fig. S3C**). *Qm* was positively correlated with non-photochemical quenching (*NPQ*; $r^2 = 0.96$), consistent with increases in photoprotective energy dissipation capacity as excitation pressure increased.

PSII photochemical efficiencies, maximum (F_v/F_m) and effective ($\Delta F/F_m'$), measured every hour captured diurnal variation in PSII performance over the diurnal cycle. Differences in photochemical efficiency during the day were driven by light exposure, with a characteristic decline during the morning, a minimum at midday, and a reciprocal recovery in the afternoon (**Fig. 1C**). These diurnal dynamics reflected the balance among photoprotective mechanisms: induced dissipation as heat of the energy absorbed in excess (*NPQ*), induced PSII inactivation, and recovery (including *NPQ* relaxation) over the course of the day. The amplitude of diurnal oscillations increased proportionally with light exposure, reaching a maximum under the highest light treatment (DLI-32), which resulted in progressive increases in *NPQ* (**Fig. 1D**).

Optical reorganization reduces bulk light absorption under high irradiance

Coral tissue pigmentation darkened or lightened in response to the corresponding light treatment (**Fig. 2A**), resulting in systematic changes in tissue optical properties (**Fig. 2A–B, Fig. S3D**). From minimum to maximum exposure, Chlorophyll *a* (Chl*a*) content declined by ≈ 36% (113 ± 13 to 41 ± 7 mg Chl *a* m^{-2}), while intact tissue absorbance peak at 675 nm (De_{675}) decreased by ≈ 10%. This corresponded to a decline in average absorptance in the PAR range (A_{PAR}) of 6% from low to high light conditions. The reduction in bulk absorption resulted in a non-linear increase in chlorophyll-specific absorption (a^*_{Chla}) as Chl*a* declined with increasing light exposure (**Fig. 2B**).

Photosynthetic capacity is maintained despite increasing respiratory demands

164 Metabolic rates were quantified using photosynthesis–irradiance (P/E) curves fitted with a
165 hyperbolic tangent model, from which four photosynthetic parameters were extracted:
166 photosynthetic efficiency (α), maximum photosynthetic rate (P_{max}), saturation irradiance
167 (E_k), and compensation irradiance (E_c) (*53*). Photosynthetic efficiency (α) increased as
168 light exposure decreased, indicating enhanced efficiency under low irradiance conditions
169 (**Fig. 2C**). In contrast, maximum photosynthetic rate (P_{max}) remained stable across all light
170 treatments at approximately 12 ± 0.33 µmol O_2 m^{-2} s^{-1} (**Fig. 2D**), indicating that
171 photoacclimation preserved maximal photosynthetic capacity despite large differences in
172 light exposure and pigmentation.

173 P/E curves allowed estimation of dark respiration rates (*Rd*), which increased linearly with
174 light exposure (**Fig. 2E**), indicating a higher ATP demand in corals acclimated to higher
175 light conditions. The phototrophic contribution to host energy requirements also increased
176 with light exposure, as reflected by the higher daily integrated photosynthesis-to-
177 respiration ratios (*54*) (**Fig. S3E**). The minimum quantum requirements of oxygenic
178 photosynthesis ($\mathbf{\Phi}^{-1}_{O2}$) ranged from 10 to 17 quanta O_2^{-1} across treatments (**Fig. 2F**) and
179 the quantum efficiency of the photosynthetic process ($\mathbf{\Phi}_{O2}$) from 0.1 to 0.059 mol O_2
180 released per mol quanta absorbed. Both parameters revealed values close to the theoretical
181 minimum of 8 quanta O_2^{-1} for $\mathbf{\Phi}^{-1}_{O2}$ and the theoretical maximum of 0.125 for $\mathbf{\Phi}_{O2}$ (*55*,
182 *56*) for functional oxygenic photosynthesis.

183 **PSII functional half-life shortens sharply with increasing light exposure**

184 Having quantified how absorbed light energy is dissipated as excitation pressure increases,
185 and the resulting metabolic adjustments, we next examined processes regulating
186 maintenance of functional PSII reaction centers under contrasting light conditions. First, to
187 separate damage accumulation (before noon) from repair (before dusk), we inhibited *de*
188 *novo* protein synthesis using chloramphenicol (CAP) (**Fig. 3A**). In control corals (−CAP),
189 PSII activity declined through midday and recovered by the end of the light cycle as
190 expected, whereas CAP-treated corals (+CAP) showed sustained loss of PSII activity
191 consistent with inhibited repair.

192 This approach enabled estimation of PSII functional half-life (t½, h), defined as the
193 number of daylight hours required to inactivate 50% of functional PSII reaction centers
194 (**Fig. 3B**). PSII half-life declined exponentially from ~13 h under low light to ~3 h under
195 high light exposure (**Fig. 4A**). This resulted in PSII turnover rates (τ_{PSII} day^{-1}) increasing
196 significantly from low to high light exposure (**Fig. 4B**), revealing accelerated replacement
197 of photodamaged reaction centers under high irradiance.

198 To assess molecular regulation underlying these dynamics, we quantified transcriptional
199 and translational responses of major PSII reaction center proteins. Quantitative
200 immunoblotting revealed significant differences in D1 protein abundance across the light
201 conditions (**Fig. 4D–F**). D1 content declined sharply with increasing light exposure,
202 mirroring the exponential decrease in PSII half-life and supporting regulation at the
203 translational or post-translational level (**Fig. 4E**). Normalization of D1 content to
204 chlorophyll *a* content yielded the same pattern (**Fig. 4F)**. In contrast, transcript abundance
205 of the core components of the reaction center *psbA* (D1) and *psbD* (D2), and inner antenna
206 proteins (that flank the D1/D2 heterodimer) *psbB* (CP47) and *psbC* (CP43), showed no
207 systematic relationship with light treatment (**Fig. 4G**; **Fig. S5**).

208 **PSII half-life rapidly adjusts to acute changes in light exposure**

209 To quantify short-term adjustments in PSII half-life under acute light stress, corals
210 acclimated to a given DLI were transferred to the three alternative light conditions for a
211 day, following the same CAP protein synthesis inhibition protocol (**Fig. S6**). PSII half-life
212 responded rapidly to the new light environment and was independent of the prior
213 acclimatory state, indicating that short-term regulation was driven by the destination light
214 condition rather than the acclimation history (**Fig. 4H**).

215 To place these responses in the appropriate environmental context, we compared changes
216 in half-life of PSII activity under our experimental PAR, and under natural sunlight, which
217 also includes ultraviolet radiation (UV). In both cases, PSII half-life exhibited comparable
218 exponential declines as a function of the destination light condition (**Fig. 4H**). Corals
219 transferred from lower light treatments (DLI-4, DLI-12, DLI-22) to the highest light level
220 (DLI-32) converged on a PSII half-life of approximately 3 h, matching that of colonies
221 acclimated to DLI-32. These results demonstrate that PSII half-life can be rapidly adjusted
222 within a single day across a wide range of light environments.

223 Despite this rapid adjustment, short-term regulation was insufficient to prevent the
224 accumulation of PSII photodamage under high excitation pressure conditions. The
225 magnitude of light stress, conveyed as the balance between PSII damage and repair, and
226 quantified as *relative-*F_v/F_m changes (see methods) (*57*), declined with increasing excess
227 excitation energy (EEE) (**Fig. 4I**). This indicated an increase in the magnitude of
228 physiological light stress due to the rapid accumulation of damaged PSII.

229 **Energetic cost of photoacclimation constrains usable energy across depth**

230 The bio-optical model developed here integrates theoretical considerations, empirical
231 measurements, and equations describing phenotypic adjustments to predict the
232 photosynthetic energy available for the coral host in depth-dependent light gradients (see
233 methods). In a previous model implementation (*5*), community-averaged
234 photophysiological responses were represented using a lumped-parameter approach, with
235 photosynthetic and maintenance parameters optimized to reproduce observed biodiversity
236 patterns across depth. Here, we incorporated light-dependent photoacclimatory profiles to
237 explicitly predict photosynthetic energy allocation.

238 First, we computed DLI as a function of depth across a range of diffuse attenuation
239 coefficients (K_d = 0.04–0.40 m^{-1}), spanning from clear to turbid water conditions, to
240 account for variation in underwater light environments, (**Eq. 1–2; Fig. S7**). Then, for each
241 optical scenario, daily gross photosynthetic output ($DPg_{(z)}$) was estimated from
242 photosynthesis–irradiance curve parameters (**Eq. 3–4**), while depth-specific maintenance
243 cost ($ECMpt_{(z)}$) was derived from empirically constrained PSII turnover rates (**Eq. 5**).
244 These components were computed to predict the photosynthetic usable energy supply
245 (*PUES*) available to the coral host after accounting for symbiont metabolic demands (**Eq.
246 6**).

247 Across all optical scenarios, *PUES* exhibited a unimodal relationship with depth (**Fig. 5A**).
248 In shallow waters, high irradiance required elevated maintenance cost to sustain
249 photosynthetic rates. Consequently, an increasing fraction of photosynthetic energy was
250 allocated to symbiont maintenance rather than host translocation. At greater depths, light

limitation reduced carbon fixation, constraining energy availability despite lower PSII repair activity. Importantly, the depth at which *PUES* was maximized shifted systematically with K_d (**Fig. 5B**). Consequently, clearer waters supported deeper energetic optima, whereas increased turbidity compressed the energetic window for coral distribution toward shallower depths. These results define an optimal bio-optical state for coral performance that emerges from the balance between photosynthetic output and maintenance cost, and whose position and extent depend on water-column optical properties.

Discussion

This investigation provides a mechanistic basis for disentangling the apparent paradox between light availability, coral physiological performance, and vertical distribution of coral species by demonstrating that energetic constraints arise at both ends of the depth gradient. Clearly, carbon acquisition is limited by low irradiance. In shallow waters, however, abundant light increases the metabolic cost of maintaining photosynthetic rates. Across a realistic light gradient, maximum photosynthetic capacity remained stable despite rising excitation pressure, enhanced photoprotective capacity, and elevated respiration. This stability was sustained by accelerated PSII turnover and shortened reaction center half-lives, imposing increasing ATP demand under high irradiance levels. Consequently, greater light availability did not directly translate into greater net energetic benefit to the host. Instead, a growing fraction of photosynthetic usable energy was withheld by the symbiont for its cellular maintenance.

When these physiological dynamics were integrated into a depth-resolved bio-optical model, they predicted a unimodal relationship between light and usable energy supply, defining an optimal depth range bounded by shallow maintenance costs and deep carbon limitation. Photosynthetic Usable Energy Supply *(PUES)* was previously framed conceptually within species–energy theory (*33*) to explain patterns of coral biodiversity (*5*); here we provide the physiological basis for these distributions patterns by explicitly incorporating the metabolic cost of sustaining photosynthesis under a range of high to low light conditions. Classic carbon-budget studies show that zooxanthellae translocate the vast majority (more than 95%) of their net daily fixed carbon to the coral host, with the fraction of host respiratory demand this covers varying substantially with species, depth, and light regime, (*8*, *58*). Translocated products such as glycerol, glucose, and other metabolites that vary among Symbiodiniaceae lineages (*7*, *59–63*) support host metabolism, growth, and calcification, whereas only a small fraction is retained for algal growth (*58*, *64*). Our results demonstrated that this translocation is predictable. As irradiance increases, ATP-intensive photoprotective processes, particularly rapid PSII repair via D1 turnover, reduce the fraction of organic carbon available for host use.

The cost of maintaining cellular function is rarely included in photosynthesis or primary productivity models, which traditionally rely on photosynthesis:respiration ratios and/or chl*a* to identify conditions of positive carbon balance (*5*, *65–67*). By coupling depth-dependent photosynthetic output with associated maintenance cost, *PUES* reframes coral energetics as it centers in photosynthetic usable energy for the host. This bio-optical model emerges as a tool to scale physiological limits to the ecological potential of photosynthetic organisms, which in the case of zooxanthellate corals, involves colony growth and morphology as well as gamete production and the timing of reproduction. Additionally, it offers a framework for predicting how environmental stressors contract energetic boundaries by necessitating greater investment in metabolic maintenance.

The stability of P_{max} across the range of light exposure reveals the central energetic problem: photoacclimation in the coral holobiont preserves photosynthetic capacity without increasing it. Understanding why requires examining each component of the acclimatory response — photoprotection, optical adjustment, and reaction center maintenance — and what each reveal about the limits of metabolic flexibility.

The first and energetically cheapest line of defense against excess irradiance is thermal dissipation via *NPQ*. The tight coupling between Q_m and *NPQ* ($r^2 = 0.96$) reflects the dynamic photoprotective equilibrium, driven by xanthophyll cycling, that scales continuously with excitation pressure across diel cycles and light conditions (*1*, *16*, *68–71*), consistent with prior field and laboratory observations (*16*, *70*, *72–75*). Critically, however, *NPQ* alone cannot prevent photodamage when excitation pressure exceeds the capacity for thermal energy dissipation. The declining F_v/F_m with increasing irradiance marks precisely this transition, the point at which the *NPQ* buffer is insufficient and repair via D1 turnover becomes the dominant maintenance strategy, at escalating ATP cost.

The optical organization of the coral holobiont reflect similar acclimatory limits. The coral skeleton and tissue optics are engineered for light amplification (*11*, *24*). Despite a nearly threefold decline in Chl*a* content, overall absorptance remained effectively constant, with total energy absorbed by the holobiont preserved regardless of pigment reduction. Rather than lowering light absorption, pigment loss increased chlorophyll-specific (a^*_{Chla}) and symbiont-specific (a^*_{sym}) light absorption efficiency, driving the symbiosis toward the upper boundary of holobiont acclimatory capacity (*11*, *76*, *77*). This proximity to the optical maximum, constrains further pigment reduction under additional stressors such as thermal stress (*78*), explaining why bleaching thresholds are usually reached more rapidly in high light environments. Ecological implications are significant, as the same optical trait that enables colonization of light-limited deep reefs (*27*, *29*) simultaneously prevents meaningful reduction of absorbed energy through pigment adjustment at high irradiance. In shallow reef environments, when this optical limit is reached and repair capacity is overwhelmed, selection favors colony morphologies with structural self-shading, *i.e.* branching, foliose, and massive forms with strong within-colony light attenuation (*27*, *30*, *79*).

The stability of P_{max} across light treatments reflects a key constraint itself. It means that no additional irradiance above saturation serves to enhance carbon fixation rates, and thus, the absorbed energy above E_k can only be dissipated as heat, channeled into *NPQ*, or directed into PSII damage:repair. In our investigation, low light phenotypes approached the theoretical maxima for PSII photochemical efficiency in dinoflagellates *in hospite* ($F_v/F_m \approx 0.7$) and theoretical minimum quantum requirements for oxygen evolution (~10 quanta O_2^{-1}) (*55*, *56*), marking the lower boundary of photoacclimatory capacity (*1*, *54*). At the other extreme, high light phenotypes with higher light absorption efficiencies (a^*_{Chla}) were proportionally less efficient at converting absorbed energy into carbon fixation (lower α and Φ_{max}). The symbiosis therefore operates near the boundaries of its photosynthetic range at both ends of the depth gradient, saturated above and limited below, with maximum photosynthetic capacity as stable outcome.

Notably, the stability of maximum photosynthetic rates across treatments indicates that coral photoacclimation primarily operates through modulation of light absorption, energy dissipation and protein turnover, and not by regulating photosynthetic capacity. This decoupling suggests that photosynthetic rates *in hospite* are constrained by downstream

processes, such as inorganic carbon diffusion or alternative electron sinks within the symbiosome (*80–83*). Crucially, it demonstrates that maintaining photosynthetic performance under high light requires progressively greater metabolic support without proportional energetic return. The source of this increasing cost is PSII turnover and D1 protein dynamics.

By arresting protein synthesis, we decoupled PSII damage from repair and quantified changes in PSII half-life across experimental light conditions. PSII half-life declined exponentially with increasing irradiance and closely paralleled reductions in D1 protein abundance. Accordingly, corals acclimated to high light conditions maintained maximum photosynthetic capacity via faster replacement of photodamaged reaction centers and lower D1 pools. Similar relationships between D1 abundance, PSII half-life, and light history have been documented in higher plants, including how rapid D1 turnover accompanies elevated metabolic demand under high light exposure (*37*, *84–86*).

Protein turnover is among the most energetically expensive cellular processes (*34–37*). In higher plants, thylakoid protein turnover accounts for 13–38% of total ATP consumption, with D1 replacement representing a major fraction of this budget (*37*). Energy for this repair cycle is supplied through respiration, linking PSII maintenance directly to metabolic demand. The elevated dark respiration (R_d) found under high light conditions is therefore consistent with increased ATP requirements for D1 synthesis and PSII reassembly (*36*, *44*, *87*). ATP availability is known to constrain *de novo* D1 synthesis and full PSII repair (*47*, *88*, *89*), suggesting that ATP supply becomes the limiting currency sustaining photosynthetic function under light stress.

Under high irradiance, absorbed energy that exceeds photosynthetic capacity cannot be converted into additional carbon fixation and is instead partitioned between dissipation as heat through *NPQ* and investment in accelerated PSII repair. In this context, D1 turnover operates as a regulated sink for excess excitation, preventing over-reduction of the electron transport chain and protecting PSI under acceptor-side limitations (*45*, *86*). This hierarchy reflects structural cost optimization within the photosynthetic apparatus. Because antenna complexes are far more abundant (~7.6×10^6 cell^{-1}) and energetically more expensive than D1 protein (~1.0×10^5 cell^{-1}) (*90*), it makes selective turnover of PSII reaction centers a comparatively economical strategy. In fact, regulation of reactive oxygen species within the photosynthetic apparatus shows that while chlorophyll triplet states in antenna complexes are efficiently quenched by carotenoids, spatial constraints within the PSII reaction center prevent such protection, allowing singlet oxygen to target D1 directly and requiring rapid turnover as a controlled safeguard (*40*, *91*, *92*). D1 protein, then, becomes the unavoidable target of oxidative damage, making its rapid turnover a necessary mechanism to preserve photosynthetic integrity.

This bottleneck has direct ecological implications. Earlier work has primarily focused on how PSII repair impairment under thermal stress leads to coral bleaching. When repair fails to match damage rates, D1 protein abundance drops below the threshold needed to sustain photosynthetic activity, resulting in pigment loss, symbiont degradation, and ultimately, expulsion or symbiont digestion by the host (*48*, *93–96*). Even in the absence of heat stress, high light and even PAR alone shortened PSII half-life to approximately three hours and reduced D1 abundance, imposing substantial ATP demand. Thus, the upper tolerance limits of the coral holobiont are defined not solely by photodamage, but by the energetic capacity to sustain PSII repair. This constraint is always active in high

light conditions, revealing the high susceptibility of shallow water corals to any additional environmental stress. We confirmed the environmental regulation of this mechanism comparing PSII half-life under experimental PAR (400–700 nm) and natural sunlight (PAR + UV). No significant differences in PSII half-life were found, consistent with PAR being the primary driver of photoinactivation and daily damage accumulation. This result challenges the assumption that UV is the dominant driver of PSII photodamage in shallow-water corals (*83*, *97*).

Eco-evolutionary significance

We identified PSII repair as a fundamental energetic bottleneck that constrains coral holobiont performance at high irradiance. Sustaining photosynthesis under light stress requires continuous ATP investment in protein turnover, and thus diverting resources from growth, reproduction, and calcification. In this way, energetic maintenance cost of photosynthesis sets the upper boundaries of coral environmental tolerance.

In the bioenergetic framework, the *PUES* bio-optical model, specifically *PUES* optimum ($Depth_{opt}$) defines the depth at which photosynthetic supply and maintenance demand are optimally balanced, maximizing usable energy translocation while minimizing the cost of sustaining photosynthetic integrity. The $Depth_{opt}$ position and extent of coral colonization depend on water column optical properties. When exploring a range of light attenuation coefficients (K_d), spanning clear to turbid conditions, our analysis revealed that increased light attenuation shifts $Depth_{opt}$ toward shallower waters and compresses the energetic envelope. Therefore, environmental degradation that alters underwater light conditions, including progressive ocean darkening, reshapes the energetic landscape rather than simply reducing light availability.

This energetic landscape has further evolutionary consequences. Intermediate depths, where usable energy is maximized, represent zones of expanded energetic niche space capable of supporting multiple photophysiological strategies, species coexistence and diversification. In contrast, energetic extremes due to carbon limitation at depth or higher energetic demands of maintenance cost in shallow water, restrict viable trait combinations and narrow ecological opportunities through exclusion or specialization. Such patterns align with general species–energy theory and with emerging genomic evidence that closely related coral lineages repeatedly diverge across narrow depth gradients, with adaptation to distinct light conditions linked to environmental sensing and reproductive timing (*98–100*).

The bio-optical model developed here and focused on *PUES* provides a mechanistic scaling of coral bioenergetics to ecological patterns, with the power to delineate energetic boundaries of coral performance in the depth distribution of zooxanthellate corals. This allows predicting the fraction of photosynthetically derived energy that is available for supporting host metabolic requirements, including maintenance, growth, reproduction, and ecological interactions, hence, contributing to define fundamental ecological niches of the coral holobiont.

Materials and Methods

PAR LED Light System

We developed an experimental light system by engineering custom-made lamps and software able to simulate diurnal light cycles. Natural light in the tanks was absent throughout the experiments. The illumination system relied on 100W light-emitting diodes (LED)-lamps that enabled automation of the diurnal cycles (**Fig. S3A**). The four light treatments (Daily Light Integral, DLI) were: 4 mol quanta m^{-2} day^{-1} (DLI-4, peak of irradiance 200 µmol quanta m^{-2} s^{-1}); 12 mol quanta m^{-2} day^{-1} (DLI-12; peak of irradiance 450 µmol quanta m^{-2} s^{-1}); 22 mol quanta m^{-2} day^{-1} (DLI-22; peak of irradiance 750 µmol quanta m^{-2} s^{-1}); and 32 mol quanta m^{-2} day^{-1} (DLI-32; peak of irradiance 1100 µmol quanta m^{-2} s^{-1}).

Three parameters were prioritized for the control of each light condition: light intensity, light quality and time. We built each LED-lamp with a BC Series High CRI COB-LED-400L-100W- Unit (YujiLEDS®) which best covered the sunlight spectrum in the range of the Photosynthetic Active Radiation (PAR). LEDs were operated in continuous mode with a multifunction I/O card (USB-6001, National Instruments Corp., USA) to avoid potential artifacts on photosynthesis and fluorescence responses related to the "flashing effect" of commercial LEDs at different pulsating frequencies (*101*). Light intensity was controlled with a custom-made software in LabVIEW (Laboratory Virtual Instrument Engineering Workbench, National Instruments Corp., USA). To eliminate natural sunlight inside experimental tanks, we placed LED-lamps inside black boxes that fully covered each tank (**Fig. S1**).

Diurnal light exposure (mol quanta m^{-2} day^{-1}) was described by integrating the per second change in irradiance (µmol quanta m^{-2} s^{-1}) over a day as Daily Light Integral (DLI). Light exposure as an integral has proven to be a useful tool for assessing irradiance accumulated when the response of interest is growth or acclimation (*102*). DLIs conditions captured a wide range of coral vertical distribution in clear waters (5 to 35 m depth for a downwelling light attenuation coefficient, K_d, of 0.07 m^{-1}). Irradiance at depth depends on the optical properties of the water column given by the *Kd* at any reef location. Irradiance was calibrated and continuously monitored with the quantum sensor LI-1400 (LI-COR, USA).

Light spectra also play an important role in photosynthesis performance. The effective activation of the repair cycle of photodamaged PSII has its own action spectrum. Studies have shown that UV-radiation damages PSII more effectively than visible light (*97*), and that the reported action spectra are rather dissimilar in the range between 400 and 700 nm. We used a sun-like spectrum and UV was excluded by design (**Fig. S2**). We were able to effectively induce PSII damage repair cycles in the simulated DLIs treatments.

Acclimation to Daily Light Integrals

We sampled 64 fragments from 4 *Orbicella faveolata* colonies (each a different genet) between 4-5 m depth under similar light conditions in La Bocana, Puerto Morelos National Park. Experimental coral fragments (~5-9 cm^2) were set for a 2-week healing period after sampling by placing them on PVC-deployed structures located at 5 m depth near the sampling area. Corals were then transported to the National Autonomous

University of Mexico (UNAM) mesocosm facility, where each colony was equally distributed in four outdoor tanks (shaded natural sunlight to 16 ± 3 mol quanta m^2 day^{-1}) equipped with running natural seawater (n = 16 fragments per tank). Water temperature and flow were maintained at 28 ± 1°C and 1100 L h^{-1} using commercial aquaria chillers and heaters. Water temperature in the tanks was continuously monitored with Hobo data loggers (Onset Computer Corporation, MA, USA). Corals were acclimated to the mesocosm for two weeks before LED installation, followed by 4+ weeks under experimental DLI conditions before phenotyping.

We monitored daily PSII maximum photochemical efficiency (F_v/F_m) at dusk and effective photochemical efficiency ($\Delta F/F_m'$) at noon, with a pulse-amplitude modulated fluorometer (Diving-PAM; Heinz Walz, Effeltrich). Maximum excitation pressure over PSII (Q_m = 1 - [($\Delta F/F_m'$ at noon) / (F_v/F_m at dusk)]) was also estimated to monitor the moderate light stress induced during natural and daily photo-acclimation, and the adjustment to a stable photo-acclimatory condition (*1*).

Phenotyping in the range distribution of zooxanthellate corals

Following the 4+ weeks of acclimation to the experimental light gradient, we measured a suite of traits to characterize coral phenotypes (**Table 1**). Chl*a* fluorescence measurements were recorded as photochemical efficiency (F_v/F_m and $\Delta F/F_m'$), and non-photochemical quenching was calculated as $NPQ = [(F_m - F_{m'})/F_m]$.

To describe changes in coral pigmentation, we estimated Chl*a* and Chl*c* contents. Briefly, an air gun and filtered sea water (FSW) were used to obtain tissue slurries subsequently homogenized at low temperature (Tissue-Tearor Homogenizer BioSpec Inc, USA) and centrifuged. The resulting pellet was re-suspended in filtered seawater and preserved for pigment concentration (extracted with acetone/dimethyl sulfoxide 95:5 vol/vol) and Symbiodiniaceae cell density (counted in a haemocytometer after the addition of 200 µL of iodine preservation solution). Chl*a* and Chl*c* concentrations were estimated spectrophotometrically (3 reads per sample) with a modular spectrometer (Flame-T-UV-VIS, Ocean Optics Inc., USA) using the equations described by Jeffrey and Humphrey (*103*).

Light absorption spectra were determined on intact *in vivo* coral tissues from reflectance (*R*) measurements. *R* was used to estimate Absorbance (*De*) [$De = \log(1/R)$] and Absorptance (*A*), assuming that Transmittance through the coral skeleton was negligible (*104*). *A* was estimated for the PAR range (400 and 700 nm; $A_{PAR} = 1 - R_{PAR}$); and at the 675 peak of Chl*a* ($A_{675} = 1 - R_{675}$).

Specific-absorption coefficients (a*) were normalized to Chl*a* content (a^*_{Chla} ; m^{-2} mg $Pigm^{-1}$) as [$a^*_{Chla} = (De_{675}/\rho)\cdot\ln(10)$, where $De_{675} = \log(1/R_{675})$] (*11*, *77*, *105*). Likewise, a* was normalized to symbiont cell density (a^*_{Sym}; m^{-2} sym^{-1}) as [$a^*_{sym} = (De_{675}/\text{sym}\ \rho) \cdot \ln(10)$]. These descriptors estimate the holobiont efficiency to absorb light (a^*_{Chla}) and symbiont specific light absorption efficiency (a^*_{sym}) (*78*).

To describe changes in coral metabolic rates, we used photosynthesis / irradiance curves (P/E) fitted to a hyperbolic tangent model (**Fig. S4A**). Briefly, coral fragments were incubated using a laboratory-made water-jacketed respirometer (*76*) with filtered sea water at a constant temperature (28 °C) and constant water flow generated by continuous

520 agitation from magnetic stirrers, which ensure that the boundary layer around coral
521 surfaces is broken. One chamber was measured as a blank (no coral fragment) to correct
522 for background activity in the water. A LED-system was designed to enable automation of
523 light increments every 10 min. Oxygen evolution was measured continuously with a fiber-
524 optic oxygen meter system (FireSting, Pyroscience) to estimate the rate in the 10 min
525 range of: dark (pre-illumination), light (10 light increments), dark (post-illumination) for a
526 total period of the 2 h incubation. Photosynthetic efficiency (α), compensation irradiance
527 (E_c), saturation irradiance (E_k), respiration rates in the dark (R_D), light-enhanced
528 respiration (R_L), and maximum photosynthetic rates (P_{max}), were estimated from the PE
529 curves (*106*, *107*). Each curve reflects the photosynthetic potential of the light phenotype.
530 To estimate the energy absorbed in excess, we calculated the hours of light exposure
531 above E_k (number of hours in P_{max}; H_{sat} (*108*)) and the magnitude of energy absorbed
532 under these conditions (mol quanta m^{-2} day^{-1}).

533 Using absorptance values determined above [A = 1- R], we calculated the maximum
534 quantum yield of photosynthesis ($\mathbf{\Phi}_{O2}$; mol oxygen evolved per mol quanta $absorbed^{-1}$)
535 and its inverse, the minimum quantum requirements of photosynthesis [($\mathbf{\Phi}^{-1}_{O2}$; = 1/(α *
536 A_{PAR}); quanta required to release an O_2 $molecule^{-1}$)] (*106*, *107*). $\mathbf{\Phi}_{O2}$ was estimated from
537 α, the slope of the linear regression of photosynthesis in the sub-saturating region of the
538 P/E curve; corrected for the light absorbed (A) in our experimental setting [(photosynthetic
539 utilizable radiation (PUR) absorbed (A_{PUR})] (*76*, *106*, *107*). To estimate the integrative
540 index of the holobiont's metabolism, we calculated daily integrated photosynthesis-to-
541 respiration ratios [*Pg (E)* day^{-1}: *R (E)* day^{-1}].

542 **Algal symbiont identification**

543 *Orbicella faveolata* hosts distinct species of algal symbionts in this region (*e.g.*,
544 *Symbiodinium* sp. A3, *Breviolum faviinorum*, *Breviolum meandrinum*, *Cladocopium* sp.
545 C3, *Cladocopium* sp. C7, and *Durusdinium trenchii*), with the possibility of multiple
546 species simultaneously inhabiting a same colony (*109–111*). To account for this functional
547 diversity, symbiont identity was determined using two complementary approaches.

548 (1) One cm^2 coral fragments were used to extract genomic DNA using a modified
549 Promega Wizard protocol (Promega Madison, WI) (*112*, *113*). The large ribosomal
550 subunit (*LSU* rDNA) was amplified using *28S* forward (5'-
551 CCCGCTGAATTTAAGCATATAAGTAAGCGG-3') and *28S* reverse (5'-
552 GTTAGACTCCTTGGTCCGTGTTTCAAGA-3') (*114*) and an annealing temperature of
553 66 ºC. Amplifications were Sanger sequenced using the Big- Dye Terminator 3.1 Cycle
554 Sequencing Kit (ThermoFisher Scientific, Waltham, MA) and analyzed on the Applied
555 Biosciences Sequencer (Applied Biosciences, Foster City, CA) at the Penn State
556 University Genomics Core Facility. Sequences were checked and edited in Geneious
557 v11.0.5 (Biomatters Ltd, Auckland, NZ) and were queried against the NCBI nucleotide
558 database using BLASTn (National Center for Biotechnology Information).

559 (2) We separately aligned raw RNA-Seq reads (see below) from each sample against
560 reference transcriptomes using bwa v0.7.18 (*115*); mapping rates were determined using
561 SAMStat v2.2.3. The reference transcriptomes encompassed eight datasets from the most
562 closely related Symbiodiniaceae that *Orbicella* associates with: *Symbiodinium* sp. A3
563 (*116*), *Breviolum faviinorum* (*116*), *Breviolum* sp. B5 (*116*), *Cladocopium proliferum*
564 (*117*), *Cladocopium* sp. C1 MI (*118*), *Cladocopium* sp. C1 SM (*118*), and *Durusdinium*

565 *trenchii* (*117*, *118*). Symbionts present in each sample were determined by comparing
566 *LSU* rDNA and mapping results (**Fig. S5A**).

567 **PSII half-life and turnover rates under acclimatory conditions**

568 After the 4-week acclimation, the PSII damage and repair cycle was determined through
569 monitoring the variation of F_v/F_m and $\Delta F/Fm'$ in 12 h diurnal cycles. We tracked the
570 accumulation of photo-inactivated PSII and the accumulation of photo-repaired PSII. The
571 damage accumulation phase runs from dawn to midday, and repair from midday to dusk.

572 To quantify the effect of light acclimation on the photodamage and repair of the PSII
573 active pool, we inhibited the PSII repair process. In each acclimatory condition, fragments
574 were separated into two subgroups: control (n = 8, no inhibitor -CAP) and the inhibitory
575 treatment (n = 8, treated with D1 protein synthesis inhibitor chloramphenicol; +CAP).
576 Subgroups were placed separately in 1 L plastic containers with internal seawater
577 circulation (FSW) and positioned within tanks (water baths). Water was exchanged in the
578 containers every 2 h for both treatments (FSW+CAP) and controls (FSW-CAP). PSII
579 photochemical efficiency was measured every hour, and samples were snap frozen after
580 dusk for further analyses. This protocol was repeated for every light condition after 4+
581 weeks of acclimation. To estimate PSII half-life ($t_{1/2}$, h) photochemical efficiency
582 treatment-to-control ratios [+CAP / -CAP] were curve fitted using a logistic sigmoidal
583 function and expressed for each light condition as the number of hours required to
584 inactivate 50% of PSII ($t_{1/2}$, h).

585 **Abundance of PSII D1 protein**

586 Algal pellet assigned for protein analyses was flash frozen in liquid nitrogen and stored at
587 -80 °C. We quantified D1 protein content in algal symbionts isolated from three coral
588 fragments for each light regime. Each immunoblotting assay was performed multiple
589 times to load: (lane 1) a negative control, (lanes 2–6) 0.10-2.00 pmol *psbA*/D1 standard,
590 (lanes 7–10) one sample from each light regime to be normalized by total protein (µg
591 protein^{-1}), and (lanes 11–14) one sample from each light regime to be normalized by Chl *a*
592 (mg Chl a^{-1}). We performed quantitative immunoblotting following established protocols
593 (*93*, *94*, *96*, *119*, *120*). Briefly, proteins were extracted using protein extraction buffer PEB
594 (Agrisera AS08 300) supplemented with Pefabloc® SC (Sigma-Aldrich 11429868001) to
595 inhibit proteolysis. Samples were subjected to three cycles of sonication-to-liquid N_2 to
596 break cell wall and avoid over-heating. Protein concentrations were determined using The
597 Better Bradford assay with a standard curve. Equal amounts of total protein were mixed
598 with Bolt™ LDS sample buffer (Invitrogen B0007) and Bolt™ Sample Reducing Agent
599 (ThermoFisher B0004), denatured, and separated on NuPAGE™ 4–12% Bis-Tris gels
600 (Invitrogen NP0329BOX) alongside PageRuler™ Plus pre-stained protein ladder
601 (ThermoScientific 26619). Following electrophoresis, proteins were transferred to PVDF
602 membranes (Invitrogen LC2005) using Bolt™ transfer buffer (Invitrogen BT0006) and
603 blocked with ECL™ Advance Blocking Reagent (GE Healthcare GERPN418).
604 Membranes were probed with a rabbit polyclonal anti-PsbA (D1) antibody (Agrisera
605 AS05 084), followed by HRP-conjugated chicken anti-rabbit secondary antibody
606 (Agrisera AS10 833). Membranes were stained post-transfer with SimplyBlue™ SafeStain
607 (Invitrogen LC6060). D1 protein quantification was achieved by co-loading known
608 amounts of PsbA/D1 standard (Agrisera AS01 016S), imaging on a chemiluminescent
609 imager (ChemiDoc BIO-RAD), and pixel-quantifying in ImageJ.

610 **Expression of PSII-complex genes**

611 Expression of PSII genes from algal symbionts was assessed following an RNA-Seq
612 approach. Total RNA was extracted from 16 fragments, 4 untreated fragments (-CAP) per
613 light exposure. Each sample was homogenized in TRIzol reagent (Ambion, Life
614 Technology) before centrifugation with chloroform for 15 min at 12,000 *g* at 4 °C. The
615 aqueous phase was then isolated and cleaned using Qiagen RNeasy Mini kit (Qiagen), as
616 per the manufacturer's protocol with an additional on-column DNase treatment using
617 RNase-Free DNase Set (Qiagen). To maximize concentration of eluted RNA, the same
618 35 µL of RNAse-free water was twice passed through the spin column for the final
619 isolation step. Concentration and purity were pre-screened via Qubit spectrometer and
620 quality assessed (RNA integrity number; RIN > 7) with Agilent 2100 Bioanalyzer (Agilent
621 Technologies). Purified RNA was sent to Biomarker Technologies (BMK) GmbH where
622 concentration and purity were re-analyzed (Qubit® dsDNA BR Assay Kit on a Qubit®
623 2.0. Fluorometer). RNA libraries for 2 × 150 bp paired-end sequencing were non-stranded,
624 prepared using Hieff NGS Ultima Dual-mode mRNA Library Prep Kit for Illumina
625 (Yeasen) model:13533ES96. Samples were run in platform Illumina NovaSeq X.

626 Raw reads were assessed for quality using FastQC v0.12.1 (github.com/s-
627 andrews/FastQC) and results visualized using MultiQC v1.28 (*121*), followed by filtering
628 and trimming using Trimmomatic v0.39 (*122*). Pseudoalignments of the processed read
629 pairs and quantification of expression were done using the quant function of kallisto
630 v0.51.1 (*123*) in two manners: against all reference transcriptomes combined into a single
631 database and against separate transcriptomes according to the symbiont type identified per
632 sample. For the combined database, all reference transcriptomes were concatenated
633 removing redundant sequences using cd-hit-est v4.8.1 (*124*) at a sequence similarity
634 threshold of 0.99. The transcripts per million (TPM) output by kallisto were used as
635 measure of gene expression level. Genes of the core complex of PSII were identified by a
636 BLASTn v2.16.0 (*125*) search of Symbiodiniaceae GenBank records (JN557844 for *psbA*,
637 HG515018 for *psbB*, HG515019 for *psbC*, and HG515020 for *psbD*) as queries against the
638 reference transcriptomes with an e-value $\leq 10^{-5}$. The BLAST hit with the highest mean
639 expression across samples per genus was selected as the representative transcript for each
640 gene.

641 **PSII half-life under light-stress conditions**

642 To quantify the effect of light stress on the PSII photodamage and repair cycle, and the
643 variation of PSII half-life ($t_{1/2}$, h), we replicated the experimental protocol to inhibit the
644 PSII repair process. However, here the 4-weeks acclimated corals were switched (new
645 coral fragments for each experiment) to an alternative light exposure (*i.e.*, DLI-$4_{acclimated}$
646 switched to DLI-$12_{destination}$, DLI-$22_{destination}$ and DLI-$32_{destination}$) for one diurnal cycle. The
647 experimental protocol was repeated for each light exposure for a total of 12 experiments:
648 DLI-$12_{acclimated}$ switched to DLI-$4_{destination}$, DLI-$22_{destination}$ and DLI-$32_{destination}$; DLI-
649 $22_{acclimated}$ switched to DLI-$4_{destination}$, DLI-$12_{destination}$ and DLI-$32_{destination}$; and DLI-
650 $32_{acclimated}$ switched to DLI-$4_{destination}$, DLI-$12_{destination}$ and DLI-$22_{destination}$.

651 The severity of light stress was quantified with the metric Excess Excitation Energy *EEE*
652 (mol quanta m^{-2} day^{-1}) as follows (*57*): (1) Conditions where *EEE* = 0 (EEE_0) indicate that
653 corals are well acclimated (F_v/F_m is steady day-to-day), no net light stress is induced,
654 hence no photodamage is accumulated. (2) Conditions where *EEE* ≠ 0 ($EEE_{\neq 0}$) indicate

corals were switched to a different light condition and may experience light stress. *EEE* was quantified as the difference between DLI in the switched condition ($DLI_{destination}$) and DLI acclimated ($DLI_{acclimated}$). In the case that the switched condition resulted in lower light exposure, *EEE* shows negative values. The magnitude of the physiological stress was measured as the ratio between F_v/F_m in the switched condition and F_v/F_m acclimated, which results in the parameter *relative-*F_v/F_m.

PSII half-life ($t_{1/2}$, h) was estimated following the same protocol described above for PSII half-life under acclimatory conditions as the number of hours required to inactivate 50% of the active PSII pool.

Modeling the energetic cost of photo-acclimation

To estimate how the light environment shapes the energetic balance of the coral-algal symbiosis, we developed a bio-optical model that integrates theoretical light attenuation in the water column, gross photosynthetic output, and the energetic costs of PSII turnover. The analysis focused on the estimation of the potentially maximum photosynthetic output of the symbionts after subtracting the costs of maintenance of photosynthetic activity through PSII repair, which can be translocatable to the host. Other metabolic costs required by the maintenance and/or growth of algae and host were not considered into the model due to the difficulties of parameterization of the large diverse of biological processes potentially involved. Light availability at depth was expressed as daily light integrals (DLI) and computed from surface irradiance. Different light attenuation coefficients (K_d) were used. Depth-dependent photosynthetic output was then estimated using a photosynthesis-irradiance relationship parameterized with function-valued phenotyping derived from experimental profiles. To capture the costs of maintaining photosynthetic function under different light regimes, we incorporated PSII turnover dynamics by linking PSII lifetime ($t_{1/2}$, h) and its cost, maximum photochemical efficiency (F_v/F_m), and repair potential to DLI. The resulting framework yields the Photosynthetic Usable Energy Supply (*PUES*) by the symbionts to the host, a metric that represents the potentially maximum energy available for the coral host after subtracting the light-dependent costs of photosynthesis maintenance. Considerations and computations underlying the model proceeded as follows:

<u>Theoretical and empirical considerations</u>

As light is the primary factor that regulates primary production and the photoacclimatory response of photosynthetic organisms, we first estimated the amount of light available at a given depth (*126*):

1. Solar irradiance as a function of depth

The intensity of a parallel-beam radiation of a particular wavelength decreases along its path in pure water, obeying the Lambert Law. The general equation of light attenuation in seawater is (*126*):

$$E_{(z)} = E_0 * e^{-Kd*z} \qquad \text{(Eq. 1)}$$

Where $E_{(z)}$ is light intensity at depth z (here irradiance value for Photosynthetic Active Radiation, PAR, as UVR was not considered), E_0 is the PAR just beneath the water

surface (when $z = 0$) and Kd (m^{-1}) is the vertical attenuation coefficient of downwelling PAR irradiance.

2. Changes in daily light integral (DLI) with depth: Light exposure

Irradiance at any point on the Earth's surface is determined by solar elevation. This rises during the day from zero at dawn to its maximum value at noon, and then diminishes in a precisely symmetrical manner to zero at dusk under no cloud cover. Light exposure integrates the variation in irradiance per second and m^2 over time. The integrated quantum unit for light exposure at a certain depth and day is mol quanta m^{-2} day^{-1}, which describes the amount of quanta received by m^{-2} during a 24 h period (*126*):

$$DLI_{(z)} = \int_0^N E_0 * Sin\left(\frac{\pi t}{N}\right) * e^{(-Kdz)}\, dt \qquad \text{(Eq. 2)}$$

The parameter $DLI_{(z)}$ is then the daily light integral at depth, E_0 is the superficial irradiance at solar noon, N is the daylength (in seconds) and t is time along a day (seconds).

3. Photosynthesis as a function of DLI

The response of photosynthetic organisms to available light (from the light saturation curve), depends on two fundamental parameters in our model: the slope α at very low light availability (carbon fixed/oxygen evolved per unit of available light), and the asymptotic maximum production P_{max} (the rate of carbon fixation/oxygen evolved under saturating light) (*127*):

$$GPg_{(DLI)} = Pmax * \tanh\left(\alpha * \frac{DLI}{Pmax}\right) + R(DLI) \qquad \text{(Eq. 3)}$$

Where $GPg_{(DLI)}$ is the rate of gross photosynthesis measured at a given quantum irradiance, DLI; P_{max} is the maximal photosynthetic capacity; α is the is the photosynthetic efficiency; and $R_{(DLI)}$ is the light dependent variation of net coral respiration. As indicated previously, we used here the direct values of R_L and R_D measured for each coral phenotype, instead a single and general function for *Orbicella faveolata*, maintaining the same criteria: R_L was used for the period of the day at photosynthesis saturation (P_{max}), R_D in darkness or very low light levels, and the average for the sub-saturating region, according to each acclimatory condition.

4. Photosynthetic output as a function of depth

To estimate the photosynthetic output $\Delta Pg(z)$ at a given z, we needed to integrate daily photosynthesis at z (modified from (*127*)):

$$GPg_{(z)} = GPmax \int_0^N \tanh \frac{\alpha_{(z)} DLI_{(t)(z)}}{GPmax}\, dt \qquad \text{(Eq. 4)}$$

5. Photosynthetic usable energy for coral maintenance

We tracked the relationship between photosynthetic and maintenance at depth and incorporated the energy cost of photoacclimation $PUES(z)$ as the cost of protein turnover

rate at depth. Energetic cost of 1 turnover (0 if no energy cost is involved in protein turnover) (*37*, *54*):

$$ECMpt_{(z)} = Protein\ turnover_{(z)} * Energetic\ cost \qquad \text{(Eq. 5)}$$

Photosynthetic usable energy supply for coral at depth z was expressed by integrating equations 4 and 5:

$$PUES_{(z)} = DPg_{(z)} * (1 - ECMpt_{(z)}) \qquad \text{(Eq. 6)}$$

<u>Function-valued phenotyping included in the model, where *z* is depth and DLI daily light integral:</u>

1. *Photosynthetic parameters as a function of $DLI_{(z)}$:*
   a. Gross maximum photosynthetic rate *GPmax* = 15 µmol O_2 m^{-2} s^{-1}
   b. Saturation irradiance *Ek* as a function of $DLI_{(z)}$ (mol quanta m^{-2} day^{-1})

$$Ek_{(z,DLI)} = 9.50DLI_{(z)} + 300.32$$

   c. Photosynthetic efficiency α as a function of $DLI_{(z)}$

$$\alpha_{(z,DLI)} = -0.0005DLI_{(z)} + 0.0374$$

2. *Protein turnover rate as a function of $DLI_{(z)}$:*

   a. PSII-half-time (hours) as a function of *DLI* (mol quanta m^{-2} day^{-1}):

$$PSII1/2_{(z,DLI)} = \left[27.8374DLI_{(z)}{}^{-0.54723}\right]$$

   b. Relative maximum photochemical efficiency (*Fv/Fm*):

$$FvFm_{DLI} = -0.0044DLI + 0.698$$

$$Rel.FvFm_{(DLI)} = \left[\frac{FvFm_{(DLI)}}{maxFvFm}\right]$$

   c. Repair potential (dimensionless):

$$Repair\ potential_{(DLI)} = \left[\frac{12\ hours}{PSII1/2_{(DLI)}}\right]$$

   d. Protein turnover rate:

$$Protein\ turnover_{(z)} = Repair\ potential_{(z)} * Rel.FvFm_{(z)}$$

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Figures and Tables

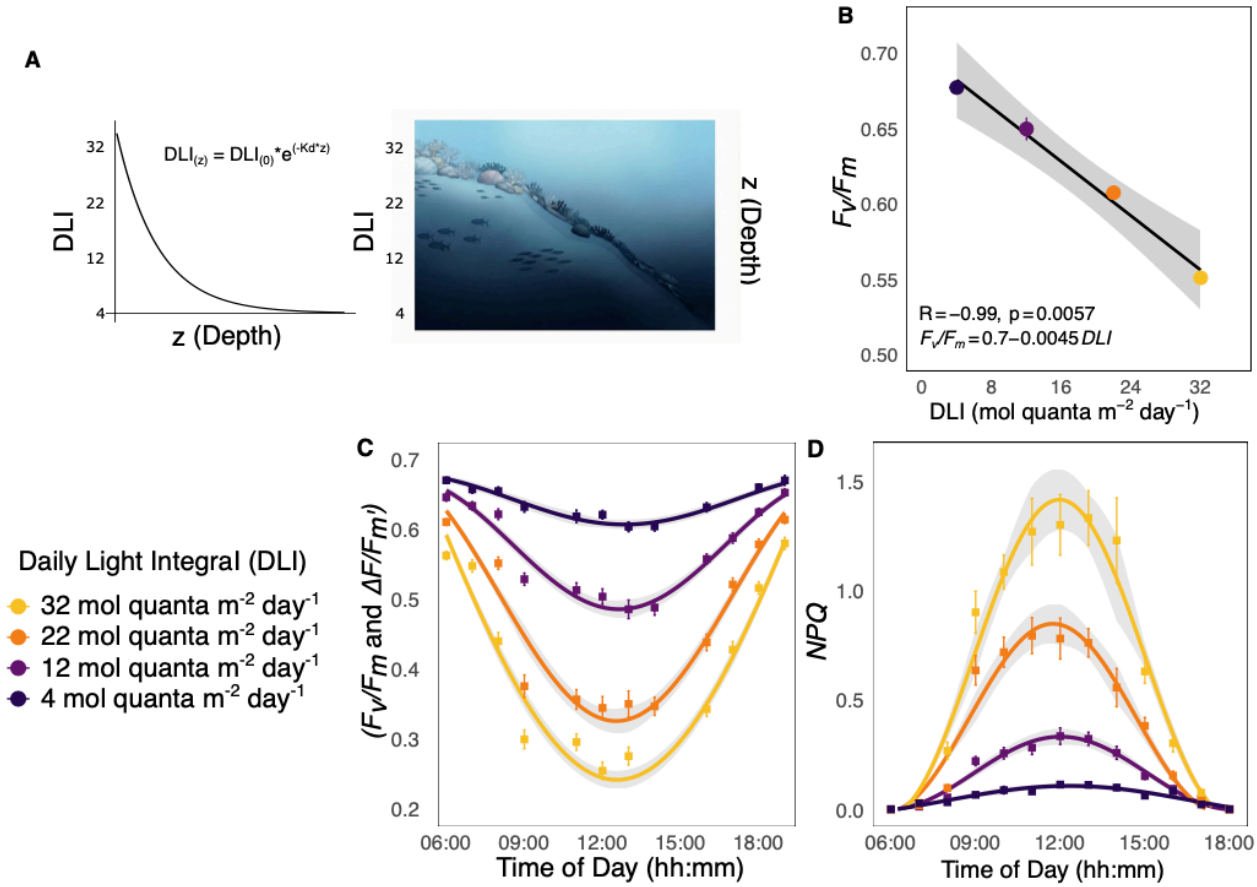

Fig. 1. Phenotyping after acclimation to light conditions. (**A**) The general equation of light attenuation in seawater ($DLI_{(z)} = DLI_{(o)} \times e^{(-Kd \times z)}$; Eq. 1) maps the four experimental DLI conditions to their corresponding depths (5–35 m, assuming K_d = 0.07 m^{-1}), illustrated alongside a depth gradient. (**B**) Maximum photochemical efficiency (F_v/F_m at dusk) as a function of DLI after 4+ weeks of acclimation illustrating a linear trend. Adjustments in photoprotection shown as (**C**) diurnal changes in photochemical efficiency (maximum F_v/F_m at dawn/dusk, and effective $\Delta F/F_m'$ during daylight) and (**D**) non-photochemical quenching (*NPQ*) measured hourly across light conditions. Symbols represent mean ± SE (n = 16). Shaded areas show bootstrapped 95% confidence intervals.

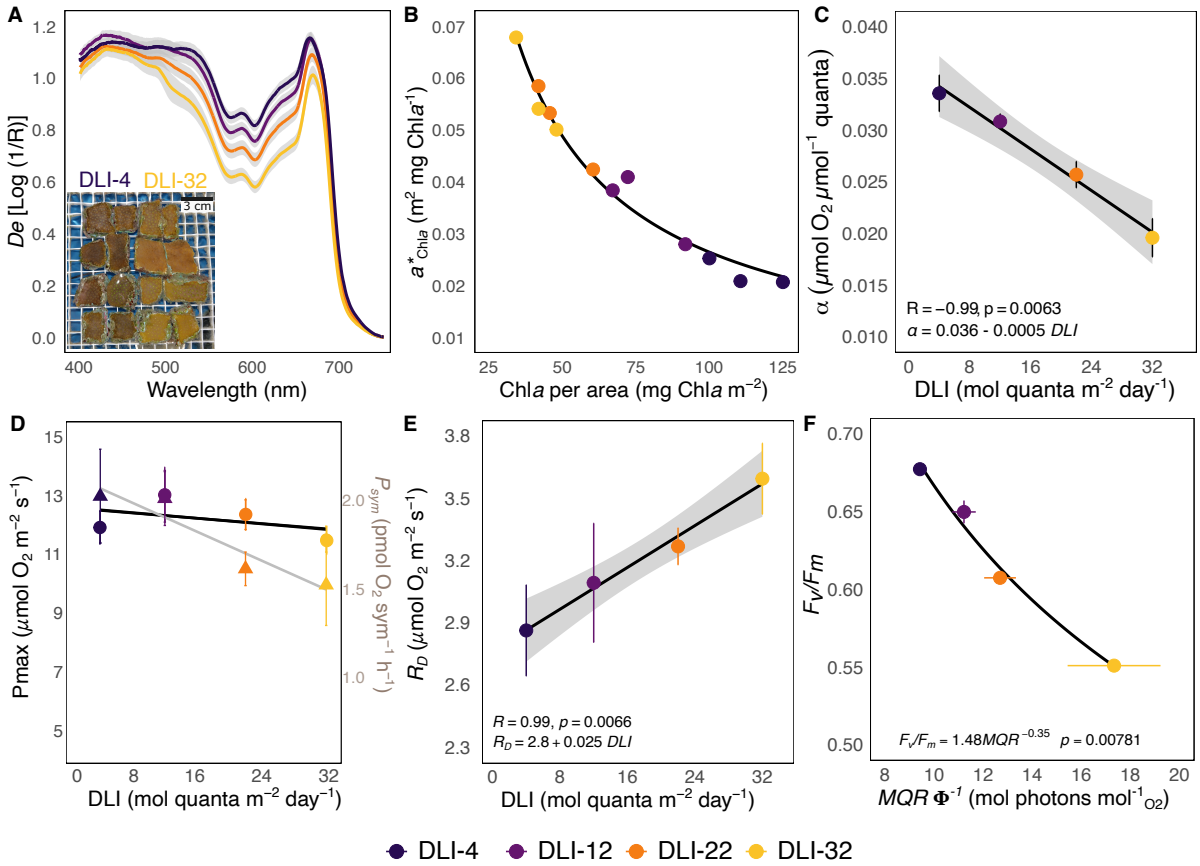

Fig. 2. Optical reorganization and metabolic rates for light harvesting across light conditions. (**A**) Estimated absorbance (*De*) from reflectance measurements indicating reduced absorption under high light (n = 16) and (photo) qualitative changes in tissue pigmentation. (**B**) Pigment-specific absorption coefficient (a^*_{Chla}) showing the non-linear increase in absorption efficiency in the coral tissue as pigment content declines, consistent with the package effect. (**C**) Photosynthetic efficiency (α), (**D**) maximum photosynthetic rate (P_{max} normalized to host area, and P_{sym} normalized to symbiont cell) showing no significant changes in P_{max} across light regimes (n = 8). (**E**) Dark respiration rates (R_D) (n = 8), and (**F**) maximum photochemical efficiency of PSII (F_v/F_m) as a function of the minimum quantum requirement for photosynthesis (MQR, Φ^{-1}; mol photons mol^{-1} O_2). Lower MQR values indicate higher photosynthetic efficiency or fewer photons required per molecule of O_2 evolved. DLI-4 corals achieved MQR values approaching the theoretical minimum (~8 quanta O_2^{-1}), indicating near-maximal photosynthetic efficiency and delineating the lower boundary of photoacclimatory capacity for the symbiosis. With increasing irradiance (toward DLI-32), both F_v/F_m and quantum efficiency declined, reflecting the increasing energetic cost of sustaining photosynthesis under high light. Shaded areas show bootstrapped 95% confidence intervals; symbols are means ± SE.

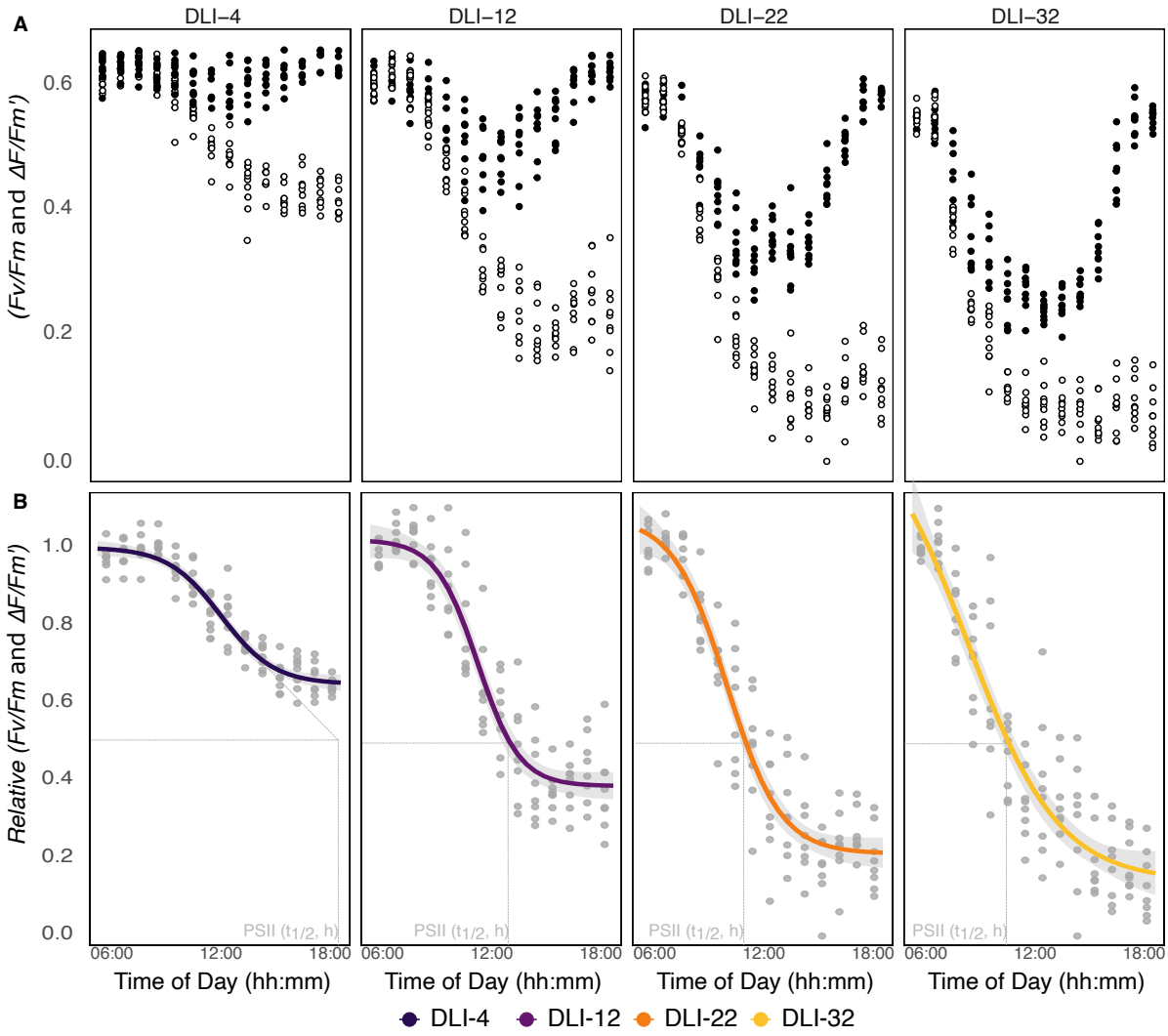

Fig. 3. Diurnal PSII activity and PSII half-life. (**A**) PSII photochemical efficiency measured hourly across a 12 h photoperiod in the presence (+CAP; empty circles) and absence (−CAP; filled circles) of the protein synthesis inhibitor chloramphenicol. Blocking *de novo* protein synthesis revealed net PSII damage accumulation, while control samples showed oscillations with characteristic daily photodamage and repair cycles. (**B**) Relative photochemical efficiency (+CAP/-CAP) decay showing proportional rate of photodamage with increased light intensity, reflecting the rate of PSII inactivation in the absence of repair. Dashed lines illustrate the time of day when 50% of PSII reaction centers are photo-inactivated. In DLI-4 PSII $t_{1/2}$ exceeded the 12 h photoperiod. Curves show four-parameter logistic fits (mean ± 95% CI).

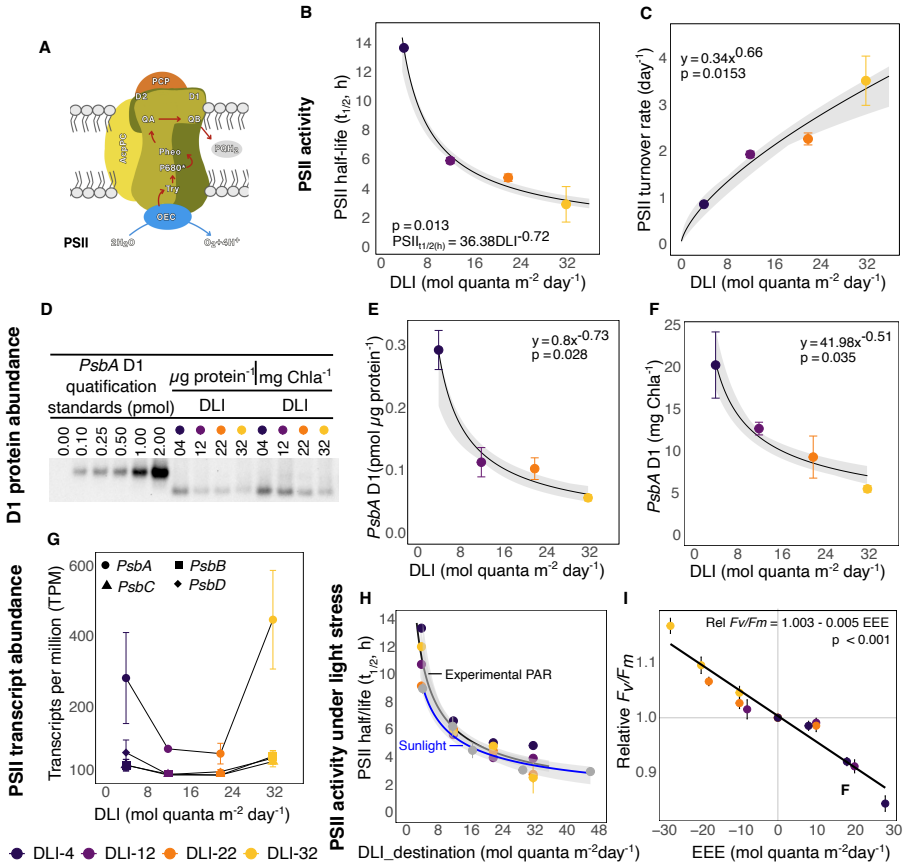

Fig. 4. PSII regulation in zooxanthellate corals across light conditions. (**A**) PSII large pigment–protein complex with its core reaction center D1 (encoded by *psbA* gene). D1 provides key ligands to the oxygen-evolving complex, harbors the QB plastoquinone binding site, and is the primary target of photodamage. (**B**) Power law decay of PSII half-life ($t_{1/2}$, h) with increasing DLI. (**C**) PSII turnover rate (day^{-1}) accelerated significantly under higher DLI. (**D**) Quantitative immunoblot of the D1 protein, showing patterns across light conditions. Lanes include a negative control (lane1, 0.00 pmol), quantification standards (lanes2–6, 0.10-2.00 pmol), and samples loaded by total protein (lanes7–10, total $protein^{-1}$) and Chl*a* content (11–14, mg $Chla^{-1}$). Quantification of D1 protein normalized to total protein (**E**; pmol D1 protein μg total $protein^{-1}$) and Chl*a* (**F**; pmol D1 protein mg $Chla^{-1}$), showing a similar power law decay with light exposure (n = 3 immunoblots). (**G**) Transcriptional abundance (transcripts per million; TPM) of PSII complex genes (*psbA, psbB, psbC, psbD*). Transcript levels showed no systematic relationship with DLI, in contrast to the exponential decline in D1 protein abundance shown in panels E and F, indicating post-transcriptional regulation. (**H**) PSII half-life ($t_{1/2}$, h) when acclimated corals (DLI) were changed to an alternative light condition (DLI-destination). Lines show a power law fit to experimental PAR (black line and colored circles; this study) and natural sunlight measurements (blue line and grey circles; data from (*5*)). Shaded areas show bootstrapped 95% confidence intervals; symbols are means ± SE. (**I**) Photodamage accumulation after the change in light condition. Results are shown as the relative change in F_v/F_m (*relative-*F_v/F_m = F_v/F_m-destination / F_v/F_m-acclimation) when coral fragments were exposed to *EEE* (*EEE* = DLI-destination - DLI-acclimation); the linear prediction is consistent with prior findings (*57*).

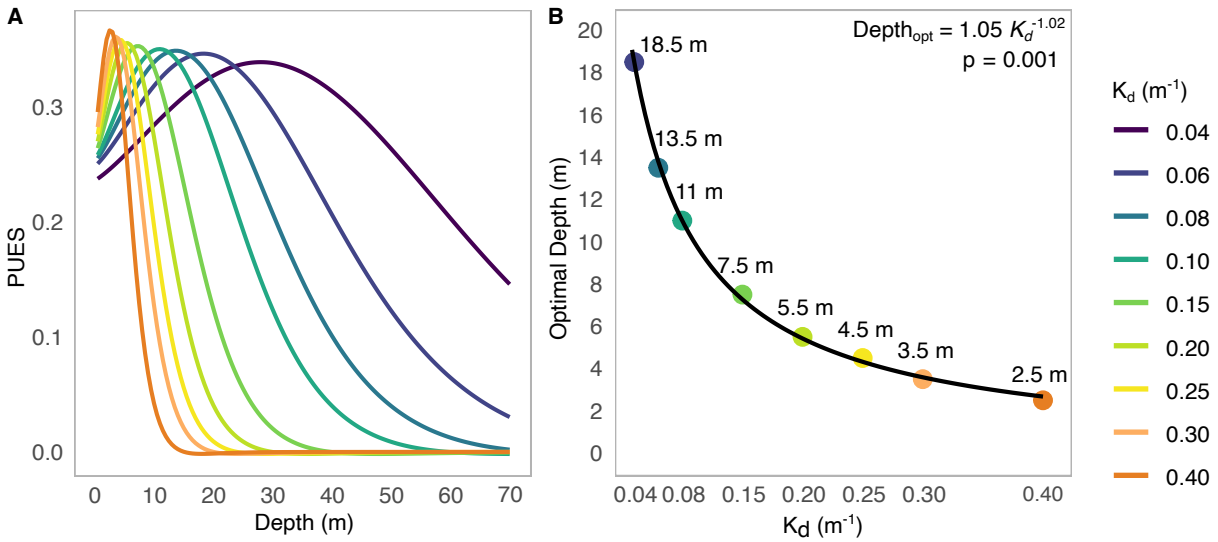

Fig. 5. Bio-optical model of *photosynthetic usable energy supply* (*PUES*). (**A**) Modeled profiles of *PUES* across depth for a range of vertical attenuation coefficients of downwelling irradiance (K_d = 0.04–0.40 m^{-1}), representing varying water column optical properties. *PUES* represents the photosynthetic energy available to the coral host after subtracting the depth-dependent energetic cost of PSII repair. Each curve represents a distinct K_d value, color-coded from clear to turbid conditions. (**B**) Optimal depth (*Depth$_{opt}$*) at which *PUES* is maximized, as a function of Kd. This bio-optical state represents the depth at which the balance between photosynthetic output and PSII repair cost is optimized, maximizing the energy potentially available for host metabolic demands.

1241
1242 **Table 1. Table of terms.** Parameters used to characterize coral holobiont phenotypes.
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Descriptors	Parameters and notations	Units
PSII	Maximum photochemical efficiency (F_v/F_m)	Dimensionless
	Effective photochemical efficiency ($\Delta F/Fm'$)	Dimensionless
	Maximum excitation pressure over PSII (Q_m)	Dimensionless
	PII half-life ($PSII_{1/2}$)	Hours
	PSII D1 protein abundance per protein	pmol D1 µg total protein^{-1}
	PSII D1 protein abundance per Chl*a*	pmol D1 µg Chla^{-1}
	PII-complex transcript abundance	Transcripts per million
Structural and optical traits	Chl*a* density per area	mg Chl*a* m^{-2}
	Chl*a* specific absorption coefficient (a^*_{Chla})	m^2 mg Chl*a*$^{-1}$
	Algal symbionts per area of host tissue	Cells cm^2
	Chl*a* per per cell (*Ci*)	Pg Chl*a* sym^{-1}
	Absorptance (*A*)	Dimensionless
	Absorbance (*De* 675 nm)	Dimensionless
	Chl*a* specific absorption coefficient (a^*_{Chla})	m^2 mg Chl*a*$^{-1}$
	Symbiont specific absorption coefficient (a^*_{Sym})	m^2 sym^{-1}
Metabolic rates and *P* efficiency	Photosynthetic efficiency ($\boldsymbol{\alpha}$)	mol O_2 mol incident quanta^{-1}
	Quantum yield of photosyntheis ($\boldsymbol{\Phi}_{O2}$)	mol O_2 mol absorbed quanta^{-1}
	Minimum Quantum Requirement ($1/\boldsymbol{\Phi}_{O2}$)	photons absorbed per O_2 evolved
	Maximum photosynthetic rate (*Pmax*)	µmol O_2 m^{-2} s^{-1}
	Saturation irradiance (E_k)	µmol quanta m^{-2} s^{-1}
	Compensation irradiance (E_c)	µmol quanta m^{-2} s^{-1}
	Dark respiration (R_D)	µmol O_2 m^{-2} s^{-1}
	Light-enhanced respiration (R_L)	µmol O_2 m^{-2} s^{-1}
	Photosynthetic rate per symb cell (*Psym*)	µmol O_2 m^{-2} s^{-1}

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