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Photophysiological performance of zooxanthellate endosymbionts (*Symbiodiniaceae*) in the golden jellyfish *Mastigias papua* across a natural environmental gradient in marine lakes of Palau (Micronesia)

Philippe Pondaven[1]*, Herwig Stibor[2]*, Jessica Yu-Tung Huang[2], Maria Stockenreiter[2], Stephan Behl[2], Thomas C. Stieglitz[3,4], Sharon Patris[5] and Gerda Ucharm[5]

[1]Université de Bretagne Occidentale, UBO, Institut Universitaire Européen de la Mer, IUEM, LEMAR UMR 6539, Univ Brest, CNRS, IRD, Ifremer, Plouzané, France, [2]Department Biologie, Aquatische Ökologie, Ludwig-Maximilians-Universität München, Planegg, Germany, [3]Aix Marseille University, CNRS, IRD, INRA(E), Coll France, CEREGE, Aix-en-Provence, France, [4]Centre for Tropical Water and Aquatic Ecosystem Research TropWATER, James Cook University, Townsville, QLD, Australia, [5]Coral Reef Research Foundation, Koror, Palau

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EDITED BY
Caroline Eve Dubé,
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REVIEWED BY
Todd LaJeunesse,
The Pennsylvania State University (PSU),
United States
Ruben X. G. Silva,
University of Aveiro, Portugal

*CORRESPONDENCE
Philippe Pondaven,
✉ philippe.pondaven@univ-brest.fr
Herwig Stibor,
✉ stibor@zi.biologie.uni-muenchen.de

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Introduction: Understanding how organisms adapt to complex and variable environments requires *in situ* analysis of ecological performance in different environments.
Methods: In this multi-year study, we investigate the photophysiological performance of dinoflagellate endosymbionts (Symbiodiniaceae) of the golden jellyfish *Mastigias papua* across a natural environmental gradient of marine lakes and semienclosed coves in the Palau Archipelago (Western Caroline Islands, Pacific Ocean).
Results: These sites vary in terms of age, distance from the nearby ocean (lagoon) and underwater light conditions, all of which influence the ecology of the host and that of its symbionts. Jellyfish endosymbionts from isolated lakes - remote from the ocean and characterized by more turbid conditions – were found to exhibit significantly lower photosynthetic performance (quantum yield and PSII performance index) than endosymbionts from sites more connected to the nearby ocean and with clearer waters. The pigment composition of endosymbionts varied little between those collected from inland lakes and ocean-connected coves, and showed little sign of adaptation to light spectra dominated by reddish wavelengths.
Discussion: This suggests a mismatch between the optical characteristics of waters in more turbid lake environments and those of pigments that appear to remain optimized for blue light use in marine dinoflagellates. While published studies show evidence of morphological and behavioral adaptations in *Mastigias* jellyfish living in Palau's marine lakes, this study suggests that their symbionts are limited by reduced pigment plasticity and lower photosynthetic performance. These results highlight the importance of symbiont characteristics and

physiological compatibility in driving host adaptation, and the potential for evolutionary mismatch in tightly integrated symbioses, under novel environmental conditions.

KEYWORDS

endosymbiotic dinoflagellates, environmental gradient analysis, marine lakes, Mastigias papua, Palau

1 Introduction

In recent years, important progresses have been made in understanding the molecular biology of cells, mapping genomes and identifying gene functions (Goodwin et al., 2016; Lewin et al., 2018; Eriksson et al., 2025). However, a substantial gap remains in translating molecular-level knowledges into an understanding of large-scale ecological and evolutionary processes, such as for example how organisms living in ecosystems adapt to complex and changing environments (Feder and Mitchell-Olds, 2003; Savolainen et al., 2013; Page and Lawley, 2022). While molecular biology tools allow to make important functional predictions based on gene content and functions, these predictions are often confounded by several factors. Notably, the flexibility of organismal behavior and physiology introduces significant variability, and many genes still remain poorly characterized or have an unknown function (West-Eberhard, 2003; Rodríguez Del Río et al., 2023). This may partly limit the predictive power of purely genomic approaches, when it comes to studying adaptation directly at ecosystem level. In this context, empirical field studies remain invaluable. It is by studying phenotypes *in situ*, in a wide range of environmental contexts, that hypotheses concerning organism's adaptation can be tested and refined (Stinchcombe and Hoekstra, 2008). Such fieldwork remains crucial for a better understanding of how molecular and genetic mechanisms scale up to influence organism's fitness, population dynamics, or interactions under contrasted natural environmental conditions. Importantly, organisms do not adapt in isolation. All life forms interact with other co-occurring species - through predation, competition, mutualism, etc., - and these biotic interactions are critical components of their adaptive landscapes (McFall-Ngai et al., 2013). For example, many species depend on obligate symbioses with species-specific microbial symbionts for their energy and nutrients requirements (Selosse et al., 2017). A typical example is animals that harbor photosynthetic endosymbionts, such as cyanobacteria or algae, which provide their hosts with photosynthetically fixed carbon and other metabolic benefits (Venn et al., 2008; Muscatine, 1990). These symbioses add a layer of complexity to adaptation, because the evolutionary rates of hosts and their symbionts may differ significantly. Species with short generation times, such as unicellular algae or bacteria, can evolve and adapt rapidly. In contrast, their multicellular hosts, which often have much longer life cycles, may adapt over far longer timescales. This mismatch raises questions about how such symbiotic association respond to environmental changes: Do for example the faster-evolving symbionts buffer the host against environmental stress? Or does this disparity introduce instability into the interaction? As Kristensen et al. (2018) pointed out, adaptation in interacting organisms may occur on different timescales, with implications for their co-evolutionary dynamics.

The phylum Cnidaria offers several examples of such tightly integrated symbiotic associations. While reef-building corals are perhaps the best-known cnidarian hosts of photosynthetic symbionts, many jellyfish species also depend on endosymbiotic algae, commonly dinoflagellates of the family Symbiodiniaceae, often referred to as zooxanthellae (Venn et al., 2008). These symbioses are central to the biology and ecology of the hosts. One of the examples is found in the golden jellyfish *Mastigias papua*, which form stable holobionts with their dinoflagellate endosymbionts (Dawson and Hamner, 2005). These jellyfish are widely distributed across tropical Pacific marine environments but are especially well-known for forming large and isolated populations in Palau's marine lakes (Dawson and Hamner, 2003; 2005). In the archipelago of Palau, located in the western Pacific Ocean, ~70 marine lakes–small and saline water masses within the karstic limestone topography of the islands–have been described (Colin, 2009). These lakes are partially isolated from the nearby ocean, with more or less important connections via tunnels and/or narrow subterranean fissures. As a result, the exchange of water - and thus of marine organisms and nutrients - is partly limited. Over thousands of years, these geographic barriers have allowed each lake to evolve as unique ecosystems, with distinct physicochemical properties and biological communities (Dawson and Hamner, 2005). The most famous of these lakes is Jellyfish Lake (Ongeim'l Tketau), which is inhabited by a population of the golden jellyfish *Mastigias papua* that undertake daily horizontal migrations in response to sunlight (Dawson and Hamner, 2003). However, this lake is just one among many in Palau Islands hosting populations of different subspecies of *M. papua* (Dawson and Hamner, 2005; Colin, 2009). These lakes are characterized by a gradient of environmental conditions, ranging from semi-enclosed coves, closely connected to the neighboring ocean lagoon, to fully land-locked lakes. This environmental gradient provides a set of natural laboratories for studying how isolation, water biogeochemistry, and light availability influence the ecological and evolutionary processes of marine organisms. These marine lakes were formed approximately 12,000 years ago, at the end of the last ice age, when rising sea levels filled several low-lying basins in the limestone islands (Colin, 2009). The timing and extent of lake formation varied depending on their location and depth. Deeper basins filled earlier, while shallower basins filled later on (Colin, 2009). Each population of *M. papua* shows evidences of variation in morphology, behavior, and genetic markers, despite being derived from a common ancestor (Dawson and Hamner, 2003; Dawson and Hamner, 2005). Remarkably, all populations continue to rely on the same genus of photosynthetic endosymbionts (Dinophyceae, Suessiales, Symbiodiniaceae). It is likely even the same clade, based on current phylogenetic evidence (Dawson and Hamner, 2003), which was recently named *Cladocopium* (LaJeunesse et al., 2018). However, the environmental conditions to which these holobionts are subjected

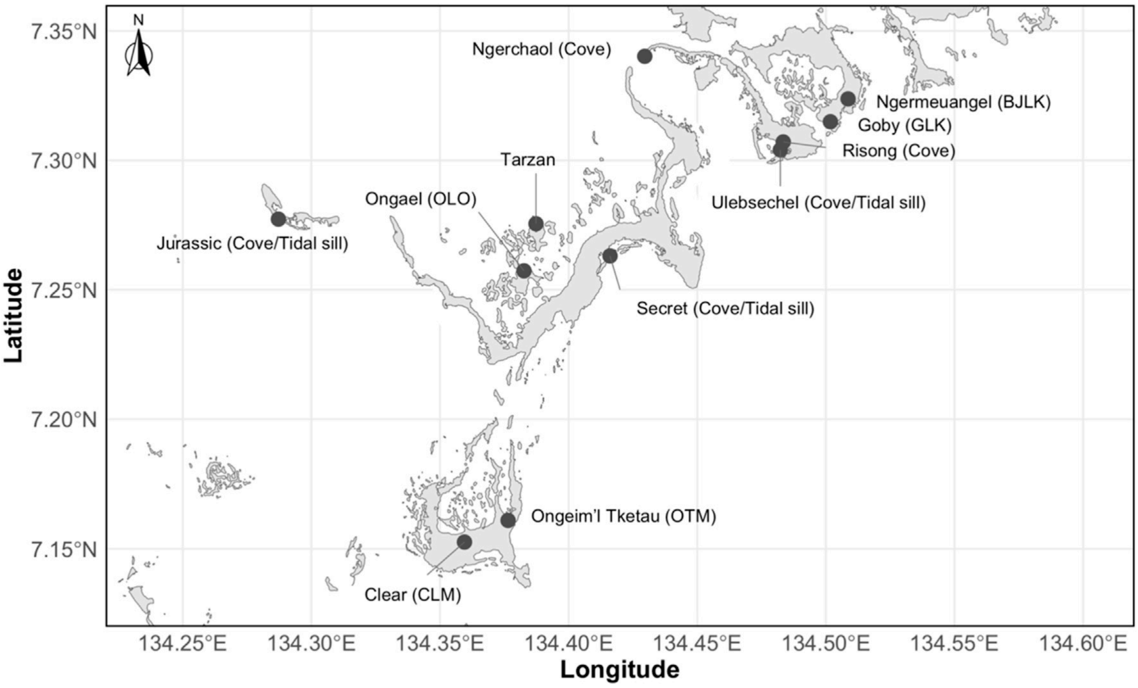

FIGURE 1
Location of sampling sites. Map background: shapefile data from NCCOS: https://products.coastalscience.noaa.gov/collections/benthic/e102palau/.

differ from site to site, particularly in terms of depth, nutrient content, light availability, and trophic status (oligotrophic, mesotrophic, eutrophic). In this respect, light is an essential resource for endosymbionts. Coastal coves and lakes with strong connections to the nearby ocean are generally oligotrophic, with clearer waters and light regimes similar to those found in open marine environments. By contrast, lakes further inland from the lagoon often receive humic substances and organic matter from the surrounding tropical forests, via surface runoff. These inputs of dissolved organic matter, combined with the development of phytoplankton, result in the browning and opacification of surface waters, and a concomitant reduction in light penetration and spectral quality (Matthews et al., 2023). These significant differences in luminosity between lakes and coves are then likely to influence the physiology of endosymbionts, possibly leading to plastic and evolutionary responses. To explore these dynamics, we used the natural variations between Palau's marine lakes mentioned above to study the interaction between environmental conditions and the photosynthetic characteristics and performance of symbionts. Specifically, we addressed the following questions:

1. Does the pigment composition of endosymbiotic algae vary in response to different light environments between open and closed marine systems?
2. Do endosymbiotic algae exhibit different photosynthetic performance between open marine systems and closed marine lakes along a shore distance gradient?
3. Are there specific photo physiological characteristics that suggest adaptation in endosymbiotic algae living in different lacustrine environments?

By examining these questions, using samples of jellyfish collected over several years in these different marine lake environments, we aim to shed light on the mechanisms underlying host-symbiont interactions and their ability to adapt - or acclimatize - to environmental change.

2 Materials and methods

2.1 Study area and sample collection

Field surveys were conducted in the Palau Archipelago, Micronesia (7°–8° N, 133°–135° E), during multiple expeditions between 2010 and 2015 (Figure 1; Table 1). Sampling sites included coastal marine lakes and coves inhabited by symbiotic jellyfish of the genera *Mastigias* (Cnidaria: Scyphozoa: Rhizostomeae; Dawson and Hamner, 2005; Arai et al., 2017).

Individual medusae were collected on site by snorkeling and transported in containers filled with ambient seawater to the Coral Reef Research Foundation (CRRF, Koror, Palau). During transport from the sampling site to CRRF (travel time of ≤1 h), individual jellyfish were kept in the dark in their containers. Once at CRRF, animals were maintained in clean, aerated seawater for 2–3 h in darkness prior to processing. Bell diameter and wet weight were measured using a graduated ruler (±0.1 cm) and a laboratory bench balance (±0.1 g) (data not shown here). For bell diameter measurements, individuals were gently placed on a laboratory dissecting pan (PVC). They were then weighed after being placed in a pre-tared weighing dish. Subsequently, fragments of oral arms were excised from

TABLE 1 Summary of site characteristics and jellyfish sampling information from 2010 to 2015.

Site name$^{(a)}$	Habitat type	Jellyfish sampling			Geography			BGC	Optical properties	
		Years (i)$^{(b)}$	$n_i^{(j)}$	$n_{tot}^{(j)}$	SD (m)	$M_D^{(c)}$ (m)	Age $^{(d)}$ (years)	TP$^{(e)}$ (μg L^{-1})	$K_{PAR}^{(f)}$ (m^{-1})	Secchi depth$^{(g)}$ (m)
Clear (CLM)	Lake	2013, 2015	3, 5	8	244	34	?	37.74	0.34	8.7 (1.0)
Goby (GLK)	Lake	2010, 2011, 2015	$9^{(5)}$, $10^{(5)}$, 5	$24^{(10)}$	89	15	9,000	68.21	0.42	5.5 (0.3)
Ngermeuangel (BJLK)	Lake	2010, 2011, 2013	$16^{(5)}$, $5^{(5)}$, 2	$23^{(10)}$	184	38	15,000	28.66	0.10	12.7 (0.4)
Ongael (OLO)	Lake	2010, 2013	$5^{(5)}$, 3	$8^{(5)}$	119	4	6,000	39.99	0.66	3.2-Bottom
Ongeim'1 tketau (OTM)	Lake	2010, 2011, 2015	$8^{(6)}$, $5^{(5)}$, 5	$18^{(11)}$	96	33	10,000	29.32	0.39	8.4 (0.2)
Tarzan	Lake	2015	5	5	36	~5–10	?	3.40	$(0.03)^{(e)}$	n.d
Jurassic (ulong island)	Cove/Tidal sill	2010	$10^{(5)}$	$10^{(5)}$	23	~5–10	?	9.98	$(0.09)^{(e)}$	Bottom
Secret	Cove/Tidal sill	2015	3	3	18	>10	?	14.72	$(0.14)^{(e)}$	n.d
Ulebsechel (RCA, Risong bay)	Cove/Tidal sill	2015	3	3	15	20	?	24.09	0.17	10.8 (0.3)
Unnamed (ngerchaol island)	Cove	2011	$3^{(3)}$	$3^{(3)}$	0	~5–10	?	22.34	$(0.21)^{(e)}$	n.d
Unnamed (Risong bay, site2)	Cove	2015	3	3	0	~5–10	?	n.d	n.d	n.d
			Total =	$108^{(44)}$						

Sampling dates were: 2010 (19 August–09 September), 2011 (27 July–09 August), 2013 (06–27 August), and 2015 (18 April–09 May). Columns indicate site name, habitat type, and sampling year (*i*); with total number of individuals collected per year, $n_i^{(j)}$, and total number of individuals sampled per site, $n_{tot}^{(j)}$, with (*j*) the number of individuals subsampled for photosynthetic pigment analysis. Reported parameters include geographical and biogeochemical (BGC) characteristics—shore distance (SD), maximum depth (M_D), lake age (Age) and total phosphorus (TP) — and optical properties: mean extinction coefficient (K_{PAR}; PAR: photosynthetically active radiation from 400 to 700 nm), and Secchi depth.

[a] Site names as recorded in Colin (2009).

[b] Underlined Years: years (2010 and 2011) for which photosynthetic pigment samples were able to be sampled. For example, in Goby Lake, a total of 9 jellyfish individuals were collected in 2010. Among these 9, $j = 5$ individuals were subsampled for subsequent analysis of photosynthetic pigments.

[c] Adapted from from Colin (2009). For Tarzan, Jurassic, Secret, Ngerchaol, and Risong bay (site 2) M_D, is not known precisely.

[d] Based on Hamner and Hamner (1998), and Colin (2009).

[e] From Wollrab et al. (2021).

[f] K_{PAR} values in parentheses: Estimations based on the established relationship between TP and K_{PAR} including all other sites (without jellyfish) for which TP and K_{PAR} data were both available (from Wollrab et al., 2021, for TP), with: $\ln(K_{PAR}) = 1.10$ (SE: ±0.20) × ln (TP) − 4.95(SE: ±0.69) ($p < 0.0001$) (Supplementary Material S1).

[g] Mean Secchi depth (± standard error) calculated from the monitoring program for CLM (n = 7), GLK (n = 30), BJLK (n = 30), OLO (n = 8), OTM (n = 48), RCA (n = 48), and Jurassic (n = 1). For Lake OLO, the Secchi depth reached the bottom (4 m) 5 times out of 8. See Supplementary Material S2.

each specimen for (i) photophysiological measurements (2010, 2011, 2013, and 2015) and (ii) pigment composition analyses (2010 and 2011).

2.2 Environmental parameters

2.2.1 Distance from the seashore, maximum depth, site age, and total phosphorus concentrations

The shortest distance from each site to the seashore (SD, m) was estimated using satellite imagery from Google Earth. The maximum depth was initially sourced from Colin (2009), and updated, if possible, during the field surveys. Bathymetry data were recorded at 2-s intervals using a Furuno single-beam echosounder paired with a Garmin GPS. The resulting bathymetric data were then analyzed, interpolated, and gridded in RStudio. The maximum depth (M_D) for each site was then extracted from the gridded bathymetry model. For some other sites, M_D is not precisely known, and only approximate estimates are reported in Table 1. Site ages were available for some sites as well (based on Hamner and Hamner, 1998). Total phosphorus (TP) concentrations were sourced from Wollrab et al. (2021).

2.2.2 Irradiance

Vertical profiles of spectral irradiance (320–950 nm, $\Delta\lambda = 3$ nm) were measured using a RAMSES ACC-VIS hyperspectral radiometer (TriOS, Germany), from the surface to 10 m depth at 0.5–1 m intervals. Photosynthetically available radiation (PAR, 400–700 nm) was then calculated, and the extinction coefficient (K_{PAR}, m^{-1}) was estimated from the exponential decay of light intensity with depth, using the equation $PAR_{(z)} = PAR_{(z=0)} \times \exp^{(-K_{PAR} \times Z)}$, with Z = depth (m). In instances where the RAMSES ACC-VIS hyperspectral radiometer was unavailable (for specific years or sites), the diffuse attenuation coefficient for photosynthetic active radiation (K_{PAR}) was estimated using the empirical relationship between total phosphorus (TP) and K_{PAR}.

This relationship was derived from data collected at all other sites where both TP and K_{PAR} measurements were available, regardless of jellyfish presence. The relationship is described by the equation: $\ln(K_{PAR}) = 1.10\ (\pm 0.20) \times \ln(TP) - 4.95\ (\pm 0.69)$ ($p_{value} < 0.0001$; see Supplementary Material S1 for details). In addition, Secchi depth (m) is recorded as part of a monitoring program established by the CRRF (Palau) for 7 of the 11 sites studied here (Table 1, Supplementary Material S2).

2.3 Jellyfish

2.3.1 Photosynthetic pigment analysis

Jellyfish samples were collected for chlorophyll a and accessory pigments analysis in 2010 and 2011 (for a total of n = 44 jellyfish individual samples, Table 1). Tissue samples from the oral arm of jellyfish were rinsed in clean seawater, weighed, and stored at −20 °C in cryogenic tubes. For both years, photosynthetic pigment samples were processed and analyzed immediately upon return from the field expedition. Pigments were extracted in 3 mL of 95% ethanol at −20 °C for 24 h and quantified by HPLC (Agilent 1200) following Van Heukelem and Thomas (2001), using certified pigment standards (DHI, Denmark).

2.3.2 Photosynthetic efficiency of endosymbionts

Photophysiological measurements of symbiotic dinoflagellates (Symbiodiniaceae, genus: *Cladocopium*) were performed on a total of 108 individuals in 2010, 2011, 2013 and 2015 (Table 1), using customized AquaPen-C AP-C 100 fluorometers (Photon Systems Instruments, Czech Republic). Jellyfish oral arm fragments were dark-adapted for ~30 min, and chlorophyll *a* fluorescence transients were recorded using LEDs at 455, 470, 505, 530, 590, 620, or 630 nm and actinic light intensity of 60 µmol photons $m^{-2}\ s^{-1}$. A white-light-equipped fluorometer (400–700 nm) was used to normalize across sensors.

Fluorescence parameters were extracted from chlorophyll fluorescence induction curves (OJIP transients), where each letter - O, J, I, and P - corresponds to a distinct step associated with the redox states of photosystems II. The OJIP transient curve included the following parameters (see Strasser et al., 2000):

- F_0: Minimum fluorescence intensity at 50 µs; measured after dark adaptation
- F_m: Maximum fluorescence intensity
- F_v/F_m: Maximum quantum yield of PSII photochemistry (ϕ_{po}), calculated as

$$F_v/F_m = (F_m - F_0)\,/\,F_m$$

- ψ_0: defined as $1 - (F_j - F_0)/(F_m - F_0)$, with F_j = fluorescence intensity at J-step (at 2 ms)
- PI_{abs}: Performance index on absorption basis, calculated as:

$$PI_{abs} = (RC\,/\,ABS) \times \left[\phi_{po}\,/\,\left(1 - \phi_{po}\right)\right] \times \left[\psi_0\,/\,\left(1 - \psi_0\right)\right]$$

where RC is the flux trapped by reaction centers and ABS is the flux of photons absorbed by antenna pigments. PI_{abs} is a well-established photosynthetic index that provides a more sensitive indicator of environmental stress conditions on PS II than quantum yield alone (Ceusters et al., 2019; Zuo et al., 2025). More details are supplied in Supplementary Material S3.

For each jellyfish sample, baseline fluorescence measurements at different illumination wavelengths, $F_0(\lambda)$, were normalized by the maximum fluorescence value, F_0^{max}, observed at λ = 455 or 470 nm. The normalized fluorescence, $F_0^{n}(\lambda)$, was calculated as:

- $F_0^{n}(\lambda) = F_0(\lambda)/F_0^{max}$

This normalization step was applied prior to any comparative or statistical analysis to account for potential biases arising from variations in jellyfish sub-sample sizes or year-to-year changes in instrument gain of the AquaPen-C AP-C 100 fluorometers.

2.4 Statistical analysis

All statistical analyses and figures were generated using RStudio (version 2025.05.1). Non-metric multidimensional scaling (NMDS) analysis was employed to investigate differences in photosynthetic pigment composition among jellyfish from different lakes and coves. Relationships between photosynthetic performance and shore distance were assessed using linear correlations, and non-parametric Pearson correlation coefficients.

3 Results

3.1 Environmental parameters

3.1.1 Distance from the shore, maximum depth and site age

In total, 11 sites were analyzed from 2010 to 2015 (Table 1); including six lakes, two open coves directly connected to the lagoon, and three semi-enclosed coves partially separated from the lagoon by a tidal sill. The minimum distance (SD) separating each site from the lagoon ranges from 0 m (Ngerchaol and Risong coves) to a maximum of 244 m (Clear Lake, CLM). Maximum depths (m) range from a minimum of ~5–10 m (in coves) to a maximum of 38 m (Ngermeuangel, BJLK). Estimated lake ages reported in the literature range from ~6,000 years for Lake Ongael (OLO) to ~15,000 years for Lake Ngermeuangel (BJLK) (Table 1), and deeper lakes are presumed to have filled earlier, during the last deglaciation (Hamner and Hamner, 1998). Thus, an approximate age estimate can be derived from the Age–Maximum Depth relationship - using GLK, BJLK, OLO and OTM Age and M_D data–and expressed as: Age (years) ~ 5000(SE: ±2000) + 200(SE: ±70) × M_D (R^2adj = 0.74, p = 0.092). Based on this relationship, Clear Lake (CLM; max depth: 34 m) filled ~12,000 years ago, with shallower coves filling less than ~5,000–10,000 years ago. These estimates, however, remain speculative owing to the age-depth model's limited robustness.

3.1.2 Optical site characteristics and biogeochemical context

The extinction coefficients (K_{PAR}, m^{-1}) and mean Secchi depth (m), are given in Table 1. We used an established relationship

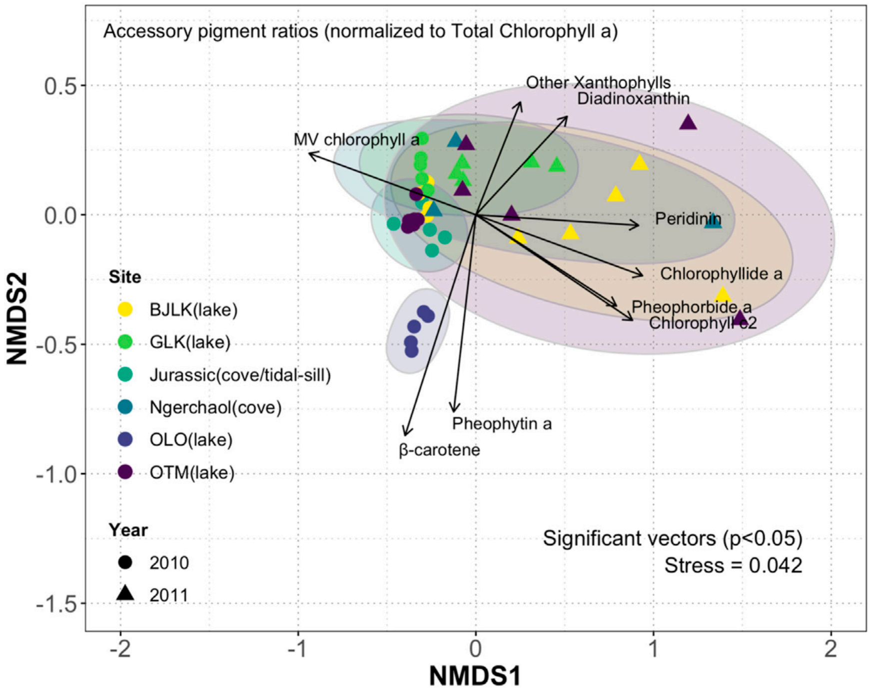

FIGURE 2
NMDS ordination plot of the relative mass concentrations of accessory photosynthetic pigments "i" — P^{i}_{ratio} = [Biomass of accessory pigment "i" (μg L^{-1})] ÷ [Biomass of chlorophyll a (μg L^{-1})] — measured in *Mastigias* jellyfish samples collected from lakes and coves in the Palau Islands over two consecutive years (2010 and 2011) (for a total of n = 44 individuals sampled). Lakes include Uet era Ngermeuangel (BJLK), Goby (GLK), Ongael (OLO), and Ongeim'l Tketau (OTM); coves within the lagoon are Jurassic (with a tidal sill) and Ngerchaol.

between total phosphorus concentration (TP, μg·L^{-1}) and K_{PAR}–from data collected across all sites surveyed from 2010 to 2015 (irrespective of jellyfish presence) (Supplementary Material S1) - to estimate K_{PAR} for sites lacking RAMSES ACC-VIS hyperspectral radiometer deployments (Table 1):

$$\ln(K_{PAR}) = 1.10\ (\pm\ 0.20) \times \ln(TP) - 4.95\ (\pm\ 0.69)\ (\pm\ SE;\ p < 0.0001)$$

Given this approach, in lakes and coves inhabited by *Mastigias* jellyfish, photosynthetically active radiation (PAR) extinction coefficients (K_{PAR}) exhibit variations ranging from 0.03 m^{-1} in Tarzan Lake, to 0.66 m^{-1} in Ongael Lake (OLO). As expected, mean Secchi depth and K_{PAR} are correlated (Pearson correlation coefficient, r = −0.95, p-value = 0.0133), with Secchi depth ranging from a minimum of ~3–4 m in the more turbid waters of Ongael Lake (OLO), to a maximum of ~12–13 m in the clearer waters of Ngermeuangel Lake (BJLK). Regular monitoring of Secchi depth - conducted as part of the monitoring program established by CRRF (Palau) - revealed consistent year-to-year differences between sites (Supplementary Material S2). However, intra-site interannual variability is also observed, depending in particular on tidal and weather conditions. For example, in Goby Lake (GLK), Secchi depth readings dropped to 1.0–2.5 m in May–June 2015, following a lake overturning event in April–May 2015 (Supplementary Material S2).

3.1.3 Jellyfish photosynthetic pigment content

Irrespective of sites (lakes or coves) and sampling year (2010 and 2011), endosymbionts contained a common pool of accessory pigments. A total of 10 photosynthetic pigments were detected by HPLC (on n = 44 individual samples, Table 1). For each jellyfish sample, the relative photosynthetic accessory pigment composition of endosymbiotic zooxanthellae was expressed using a ratio calculated as follow:

$$P^{i}_{ratio}\ (\pm\ SE) = [\text{accessory pigment "}i\text{" } (\mu g/L)]/ \times [\text{Total chlorphyll a } (\mu g/L)]$$

The most abundant pigments were, in descending order of relative mass concentrations, peridin (P^{i}_{ratio} = 2.71 ± 0.92), chlorophyll c2 (P^{i}_{ratio} = 1.58 ± 0.45), monovinyl (MV) chlorophyll a (P^{i}_{ratio} = 0.82 ± 0.07), diadinoxanthin (P^{i}_{ratio} = 0.33 ± 0.05), chlorophyllide a (P^{i}_{ratio} = 0.18 ± 0.07), and pheophytin a (P^{i}_{ratio} = 0.15 ± 0.09). β-carotene, and the sum of other xanthophylls (zeaxanthin, diatoxanthin, and violaxanthin) were also detected, but in smaller quantities (P^{i}_{ratio} < 0.03).

Alongside this common pool of accessory pigments, NMDS (Non-metric MultiDimensional Scaling) analysis revealed differences in P^{i}_{ratios}, both between years, and within and between sites (Figure 2; NMDS stress = 0.042). Axis 1 of the NMDS shows lower MV chlorophyll a P^{i}_{ratios}, and higher peridinin, chlorophyllide a, chlrophyll c2, and pheoporbide P^{i}_{ratios}, in some of the individuals sampled in 2011, compared to those sampled in 2010, in lake OTM, lake BJLK, and Ngelchaol Cove. Similarly, NMDS axis 2 shows that some individuals collected in 2011 in lake GLK and OTM had higher diadinoxanthin, and other xanthophylls P^{i}_{ratios}. Conversely,

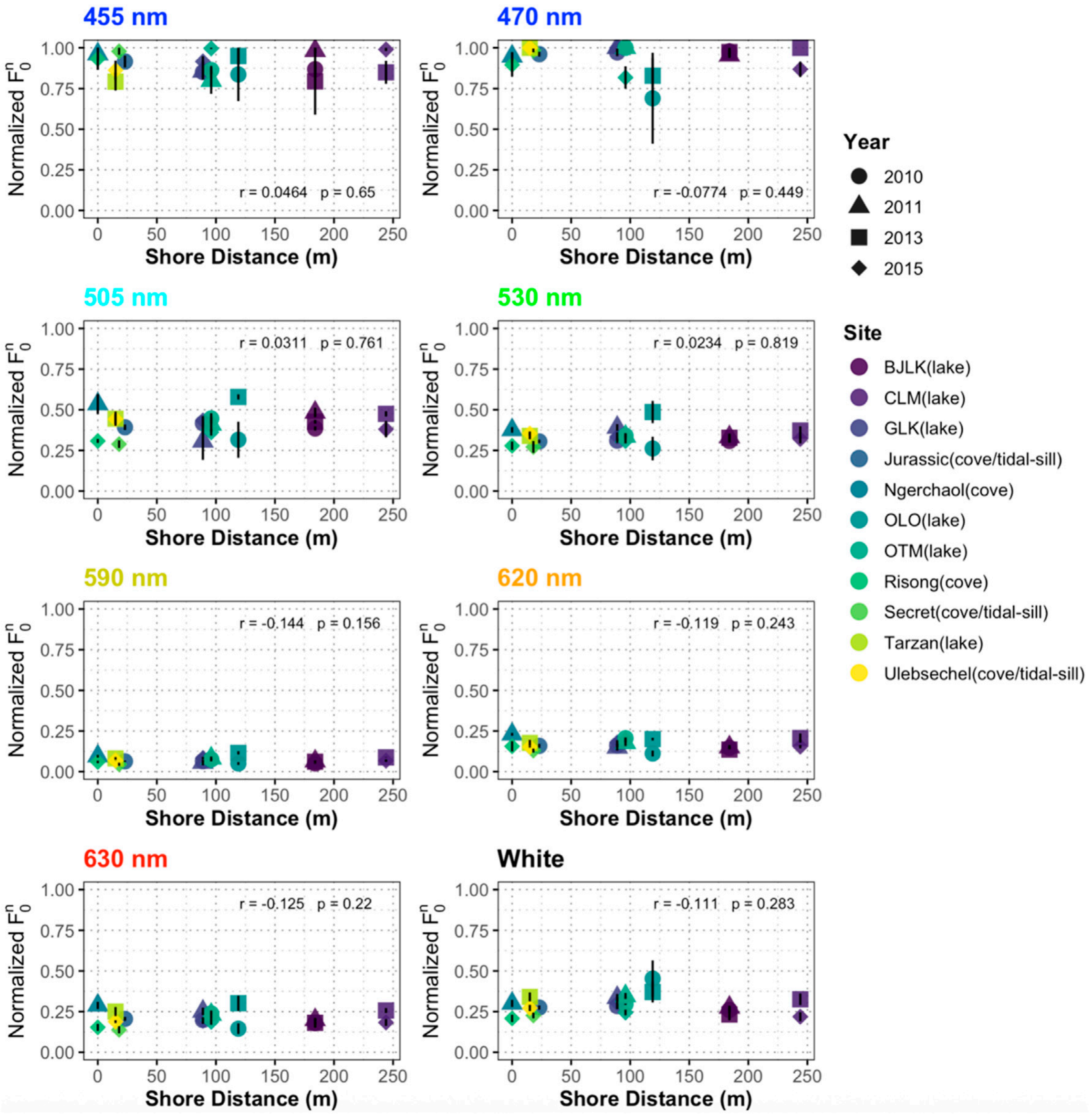

FIGURE 3
Relationships between Normalized fluorescence (F_0^n) and shore distance (m) under different wavelength illuminations. Symbols represent means ± standard error (vertical bars). Pearson correlation coefficients were calculated using all combined samples. Lake names follow Colin (2009). Lake Ongeim'l Tketau (OTM), Clear (CLM), Goby (GLK), Ngermeuangel (BJLK), and Ongael (OLO).

individuals collected from lake OLO in 2010 had higher β-carotene and pheophytin a P^i_{ratios}.

3.1.4 Photosynthetic dynamics of the photosystem II (PSII)

Normalized baseline fluorescence (F_0^n) in all jellyfish samples exhibited peak values at λ = 455 nm and 470 nm, then declined along the wavelength gradient to a minimum at λ = 590 nm (Figure 3). Additionally, when data from all years were pooled, F_0^n at all wavelengths exhibited no significant variation along the shore distance gradient for individuals sampled in lakes and coves (Figure 3).

Conversely, both the quantum yield (F_v/F_m) and the photosynthetic performance index (PI_{abs}) were negatively correlated with increasing shore distance across all wavelength bands, except at 590 nm (yellow) and 620 nm (orange) (Figures 4, 5).

Plotting the residuals from the regressions of F_V/F_m and PI_{abs} versus shore distance (Figures 4, 5) against Maximum depth (a proxy of lake age) revealed no significant relationship (Figure 6; Pearson correlation coefficient, $p > 0.05$).

4 Discussion

Many marine organisms form endosymbiosis with autotrophic dinoflagellates, so called zooxanthellae. Zooxanthella could be important for supporting nutrition but also for life cycle dynamics such as for example facilitating strobilation in some

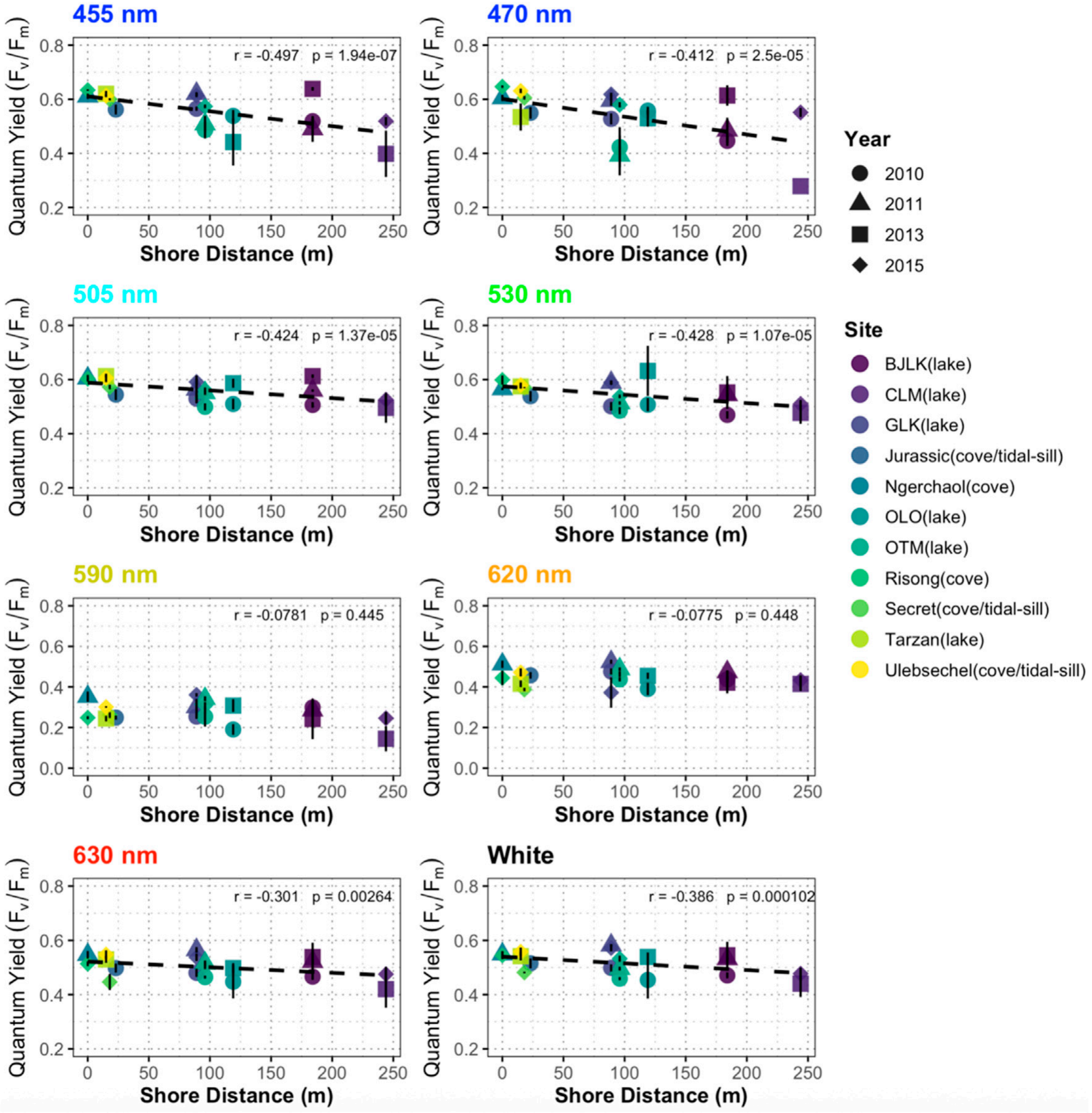

FIGURE 4
Relationships between maximum quantum yield (F_V/F_m) and shore distance (m) under different wavelength illuminations. Symbols represent means ± standard error (vertical bars). Pearson correlation coefficients were calculated across all samples. Only significant correlations are highlighted with a dotted line (fitted to the data using the "geom_smooth ()" function from the R ggplot2 package). Lake names follow Colin (2009): Ongeim'l Tketau (OTM), Clear (CLM), Goby (GLK), Ngermeuangel (BJLK), and Ongael (OLO).

jellyfish species (Djeghri et al., 2019). The family Symbiodiniaceae is a well-known complex of dinoflagellate endosymbionts of different species from the Cnidaria phylum (LaJeunesse et al., 2018). Most famously is its symbiosis with corals, which evolved in the early Mesozoic, approximately 200–180 million years ago (Stanley and Van De Schootbrugge, 2009; LaJeunesse et al., 2018). Symbiodiniaceae comprise a wide range of genera most commonly found in marine Cnidarians (Baker, 2003; Goodson et al., 2001) and most likely well adapted to marine light environments (Falkowski et al., 2004). Marine light environments are usually characterized by high visibility and a large proportion of blue wavelength within the PAR (Stomp et al., 2007). Therefore, it is not surprising that marine Symbiodiniaceae produce pigments allowing for high absorption of blue wavelengths. In contrast, freshwater systems have lower visibility and more turbid water, shifting the PAR spectrum towards a higher proportion of red wavelength. In such light environments, algae that are efficient in using the red PAR spectrum are favored, such as green algae. Therefore, most endosymbionts in animals in freshwaters harbor green algae, so called zoochlorella, for example *Chlorella spp*. (Summerer et al., 2008; Stomp et al., 2007).

Pertaining to marine lakes, their underwater light environment is more similar to typical freshwater lakes than to open marine sites. Hence, it seems that for the jellyfish living in marine lakes the pigments in the endosymbionts and the underwater light climate in the lakes do not match as well as for jellyfish living in lagoons or open ocean areas. Our multi-annual measurements of the photosynthetic index, or the photosynthetic performance of PSII,

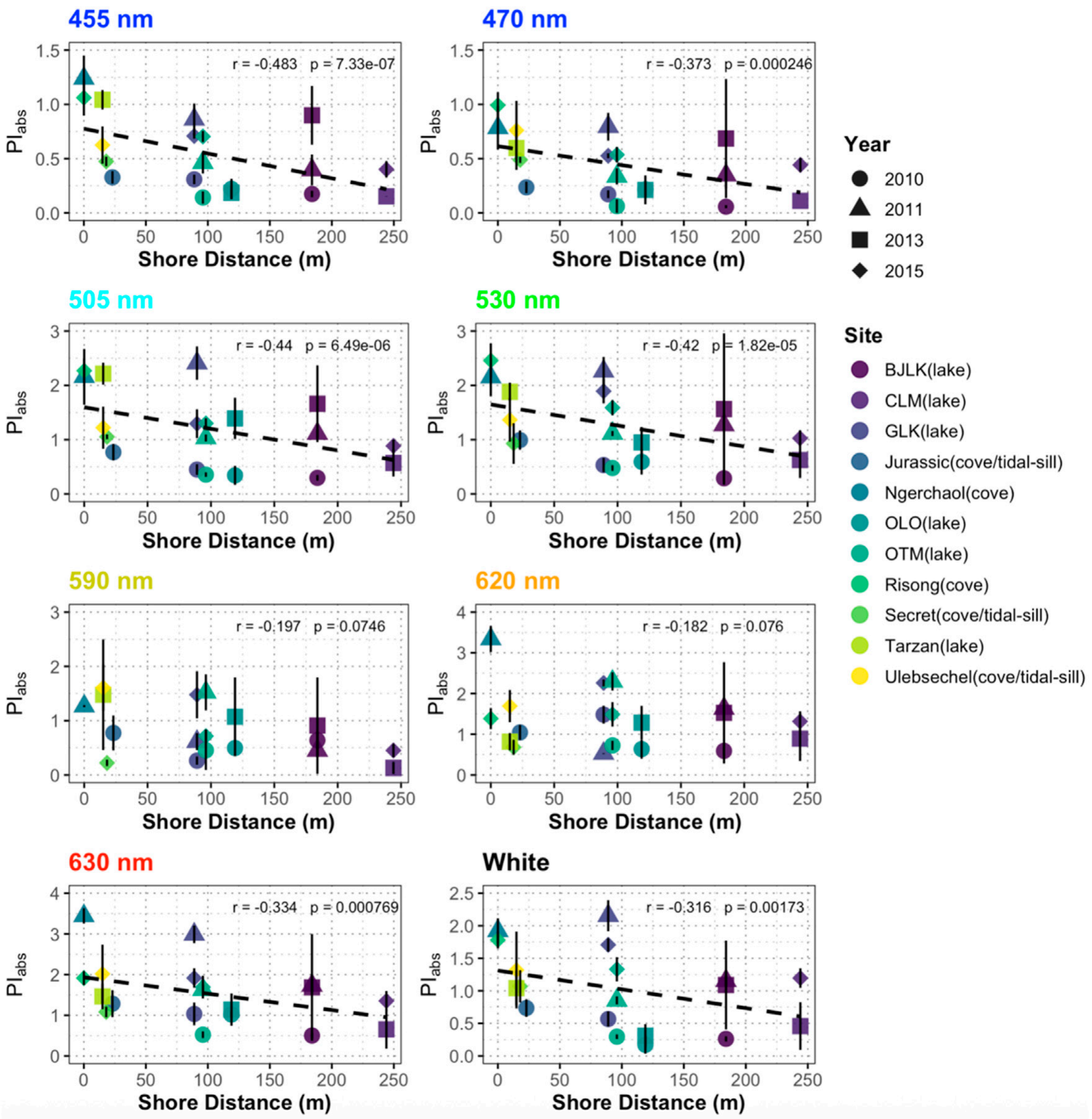

FIGURE 5
Relationships between the relative performance index on an absorption basis (PI_{abs}) and shore distance (m) under different wavelength illuminations. Symbols represent means ± SE (vertical bars). Pearson correlation coefficients were calculated across all samples. Only significant correlations are highlighted with a dotted line (fitted to the data using the “geom_smooth ()” function from the R ggplot2 package). Lake names follow Colin (2009): Ongeim’l Tketau (OTM), Clear (CLM), Goby (GLK), Ngermeuangel (BJLK), and Ongael (OLO).

of jellyfish endosymbionts supports this mismatch. The photosynthetic performance of *Mastigias* in the lakes was negatively correlated with the distance from the surrounding lagoon. One would expect a larger input of humic substances affecting light climate towards a higher contribution of red wavelengths with larger terrestrial catchment areas indicated by larger distance from the lagoon.

While *Mastigias* evolved differently in lakes towards smaller sizes, smaller tentacles, and complex behaviors such as diel vertical migration (Dawson and Hamner, 2005) - which are all beneficial in this type of environment - the endosymbionts are still showing best photosynthetic performances in the lagoon environment. Because Maximum depth (M_D, used as a proxy of sites’ Age) and distance from the shore are slightly correlated in marine lakes (Table 1; Pearson correlation r = 0.670, p = 0.048; for Maximum depth, M_D ~5–10 m we used M_D = 7.5 m, and for M_D >10 m we used M_D = 12 m), we additionally analyzed the residuals of the regression of photosynthetic performance vs. distance from shore as a function of M_D of the lakes. We could not find any indication that jellyfish in deeper (older) lakes (having more time to adapt) showed a better photosynthetic performance than in shallower (younger) lakes, even if taken distance into account. A simple reason for this might be that potential endosymbiotic algae that would be well adapted to such light conditions are not present in marine lakes. Additionally, whereas most algae can shift pigment ratios to a certain amount, they most often cannot completely change their pigment pattern or develop new pigments (Falkowski and

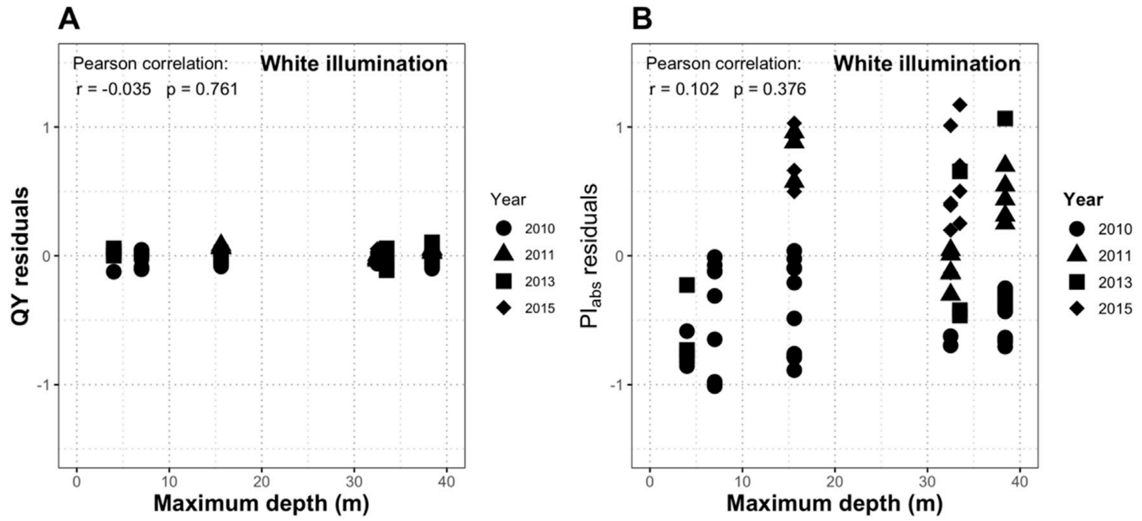

FIGURE 6
Relationships between the residuals of **(A)** the maximum quantum yield (F_V/F_m), and **(B)** the relative performance index on an absorption basis (Plabs)—both calculated from the regression of F_V/F_m or Plabs against shore distance (m) under white light illumination (see Figures 4, 5)—and maximum depth (m). Sites with unknown maximum depth (Tarzan, Jurassic, Secret, and two unnamed coves: Ngerchaol and Risong Bay, site 2; see Table 1) were excluded from this analysis.

LaRoche, 1991). This is also shown in our pigment analyses which gave no evidence for large pigment flexibility in the endosymbionts from different lakes.

This mismatch between the spectral qualities of light in marine lakes and the pigment composition of *Cladocopium* sp. may have far-reaching consequences for the energy budgets and overall fitness of *Mastigias* inhabiting these environments. Reduced photosynthetic efficiency, as demonstrated by the lower PSII performance in lake-dwelling jellyfish, implies lower net carbon fixation by the symbionts, which in turn may reduce the autotrophic contribution to the host's metabolic demands. This metabolic shortfall might necessitate compensatory strategies such as increased heterotrophic feeding, a behavior observed in several mixotrophic cnidarians (Davy et al., 2012). However, food availability in marine lakes can be seasonally limited and spatially heterogeneous, potentially placing further constraints on the energetics and growth potential of the host organism (Dawson and Hamner, 2005). Additionally, also population densities of jellyfish have a large impact on the allocation of autotroph and heterotroph pathways on total carbon uptake (Djeghri et al., 2020).

Interestingly, the ecological flexibility of the host appears to exceed that of its symbiont. As noted, *Mastigias* in marine lakes have evolved substantial morphological and behavioral adaptations to cope with their isolated and often stratified habitats (Dawson and Hamner, 2005). These adaptations may include diel vertical migration not only for predator avoidance or prey acquisition but also as a mechanism to optimize light exposure for photosynthesis in symbionts (Hamner et al., 1982). However, this behavioral buffering may not fully compensate for the fundamental incompatibility between the spectral absorption properties of endosymbiont pigments and the red-shifted light regime of turbid lake waters (Stomp et al., 2007).

One might also consider whether the persistence of *Cladocopium* spp. in marine lake jellyfish is a consequence of historical constraints rather than present-day optimality. Given the isolated nature of marine lakes, opportunities for acquiring novel endosymbionts may be limited. Horizontal transmission of symbionts is common in *Mastigias* spp. (Sugiura, 1964) and the endosymbiont community in the jellyfish hence originates from a free-living community in the environment. The free-living community is assembled from different dispersal processes, including the release of endosymbionts by jellyfish after mortality such as by predation (Vega de Luna et al., 2019). However, *Cladocopium* spp. originating from other sources, for example corals, might constantly dilute potentially adapted *Cladocopium* algal strains from jellyfish. The genus *Cladocopium* common in *Mastigias* (Ferreira et al., 2022) is generally a very abundant endosymbiont and is present in a large variety of marine organisms, including corals (Armstrong et al., 2024), which are common in the connected lagoon environment. Moreover, the absence of alternative symbionts in the local lake environment, as suggested, further reduces the potential for symbiont switching or replacement.

Interestingly a recent study found evidence for significant adaptive differentiation in *Cladocopium* associated with corals across reef environments in Palau (Armstrong et al., 2024). In contrast to the variable light regimes of marine lakes, reef environments exhibit relatively uniform underwater light conditions that are likely well aligned with the pigment composition of *Cladocopium* and its associated light requirements. Future research might focus on the possibility of local diversification within *Cladocopium* lineages that could eventually yield strains with pigment profiles better matched to red-light-dominated habitats. Indeed, recent molecular work has revealed a high level of cryptic diversity within the former *Symbodinium* complex with different clades exhibiting variable environmental tolerances and pigment compositions (LaJeunesse et al., 2018). *Mastigias* across marine environments in Palau seems to harbor *Cladocopium*, this has been also found in *Mastigias* jellyfish from marine lakes in Indonesia and Vietnam (Ferreira et al., 2022). The presence of specialized lake-adapted strains of this genus—if any exist—could provide key insights into the potential for adaptive symbiosis in atypical environments such as marine lakes.

In summary, the reduced photosynthetic performance of jellyfish endosymbionts in marine lakes likely reflects a fundamental ecological mismatch driven by the light environment. While *Mastigias papua* spp. have adapted morphologically and behaviorally to these habitats, their dinoflagellate endosymbionts appear to face significant physiological constraints. This highlights the critical role of symbiont availability and compatibility in shaping host success and opens avenues for exploring co-evolution, symbiont plasticity, and the ecological limits of mutualistic associations in novel environments.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

PP: Writing – original draft, Conceptualization, Formal Analysis, Investigation, Supervision, Validation, Data curation, Funding acquisition, Project administration, Resources, Visualization, Writing – review and editing. HS: Writing – original draft, Conceptualization, Formal Analysis, Funding acquisition, Investigation, Project administration, Supervision, Validation, Data curation, Resources, Visualization, Writing – review and editing. JY-TH: Writing – original draft, Conceptualization, Formal Analysis, Investigation, Validation, Data curation, Visualization. MS: Writing – original draft, Conceptualization, Formal Analysis, Investigation, Validation, Data curation, Project administration, Resources, Supervision, Visualization, Writing – review and editing. SB: Writing – original draft, Conceptualization, Formal Analysis, Investigation, Validation, Data curation, Visualization. TS: Writing – original draft, Formal Analysis, Investigation, Methodology, Data curation, Visualization. SP: Writing – original draft, Investigation. GU: Writing – original draft, Investigation.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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