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Imaging PAM fluorometry reveals stable photosynthetic efficiency in multibiont symbioses on coral reefs

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Many cryptic invertebrates residing within the coral reef matrix exhibit symbiotic relationships with scleractinian hosts. Despite their contribution to reef biodiversity, these host-symbiont associations and their potential impact on coral fitness and survival remain poorly understood. Additionally, the presence of symbiotic Symbiodiniaceae within coral tissue further enhances the complexity of these multibiont relationships. This study focuses on coral-dwelling gall crabs (Cryptochiridae) that structurally modify their host's skeleton. By using Imaging Pulse-Amplitude-Modulated (PAM) fluorometry, which provides a spatial assessment of maximum quantum yields of PSII fluorescence (F_v/F_m values), we investigated the impact of cryptochirids on the photosynthetic performance of the corals' symbiotic algae in eight coral-crab associations, encompassing six coral species from the central Red Sea. Visual output of F_v/F_m values at coral fragment scale showed no distinct effects of cryptochirid presence on Symbiodiniaceae in uninhabited areas. However, F_v/F_m measurements near the crabs' dwellings (<3 mm) showed significant increases (3–6%) in three colonies and significant decreases (4–12%) in two colonies. Although the exact cause of the increased photosynthetic efficiency in two associations remains speculative, the presence of filamentous algae and trapped sediment near the dwelling likely accounts for the reduced values observed in one of the *Echinopora* associations. Considering that the photosynthetic efficiency of Symbiodiniaceae in most studied corals was not affected by the crabs, we suggest that their presence has no widespread negative impact on these multisymbiotic relationships. This study highlights the need for additional research to better understand the ecological function of multibiont assemblages on coral reefs.

KEYWORDS

coral photobiology, Decapoda, photosynthesis, pulse-amplitude-modulated (PAM) fluorometry, symbiosis, Cryptochiridae, coral-associated fauna

Introduction

A significant proportion of the high biodiversity found on coral reefs is represented by invertebrates (Stella et al., 2011; Hoeksema et al., 2012; Pearman et al., 2018; van der Schoot and Hoeksema, 2024). Often grouped under the broad term ‘cryptic fauna’, many of these taxa exhibit a secluded lifestyle within the structural framework provided by corals (Paulay, 1997; Glynn and Enochs, 2011; Goldberg, 2013). Although estimates predict that 10–25% of these invertebrates depend to some extent on corals for food, habitat and/or settlement cues, at least 900 species have been recorded to live in close association with corals (Stella et al., 2011). Approximately half of these species exhibit strictly obligate relationships with their coral hosts, meaning they rely on their host for survival (Castro, 1988; Stella et al., 2011; Hoeksema et al., 2012). Despite growing evidence that coral-associated fauna can have a significant influence on their hosts’ fitness and survival, the nature of these associations and their overall impact on coral reef ecosystems is often poorly understood (Gates and Ainsworth, 2011; Montano et al., 2017).

Symbiotic relationships can take different forms and should ultimately be regarded as a broad continuum including heterospecific associations of various types and degrees of interactions (Parmentier and Michel, 2013; Castro, 2015). The most frequently used concept to evaluate the nature of a symbiotic relationship is based on the costs and benefits that both partners are experiencing (e.g. mutualism, commensalism, parasitism), but these boundaries are not well defined (Roughgarden, 1975; Parmentier and Michel, 2013). Quantifiable parameters such as reproductive success, growth, longevity or host use are often used to evaluate the nature of the association, but this type of data is lacking or incomplete for many invertebrate-coral associations (Stella et al., 2011; Castro, 2015). Moreover, the role of symbiotic dinoflagellates (Symbiodiniaceae Fensome, Taylor, Norris, Sarjeant, Wharton and Williams, 1993; commonly known as zooxanthellae) as a third taxon in this multisymbiotic relationship is often overlooked in studies on coral-associated fauna (Barneah et al., 2007; Barneah and Brickner, 2010; Gates and Ainsworth, 2011), as is the wider coral microbiome (Bourne et al., 2016; van Oppen and Blackall, 2019). While these communities significantly influence the fitness and resilience of the coral holobiont the interactions between the coral host, its microbiome, algal symbionts and associated invertebrates remain understudied (Peixoto et al., 2017).

A limited number of studies have explored the interactions of invertebrate and algal coral symbionts beyond symbiont-host dynamics. For instance, there is evidence that the excretion of ammonium by symbiotic crustaceans and polychaete worms can function as fertilizer in oligotrophic waters, enhancing zooxanthellae proliferation and growth of blue-green algae (Simon-Blecher et al., 1996; Wielgus and Levy, 2006). The extraordinary complexity of coral-invertebrate-zooxanthellae associations, and the difficulties in accurately defining the true nature of these symbioses, have led to knowledge gaps on the relative energetic contribution of each party in this multisymbiotic system (Barneah et al., 2007).

Coral-dwelling gall crabs (Cryptochiridae) represent a prime example of coral-associated invertebrates that exhibit obligate

relationships with their scleractinian host. On average, 20% of available coral hosts are inhabited, and notable aggregations of up to 200 specimens per m² have been observed (Hoeksema and van der Meij, 2013; van Tienderen and van der Meij, 2016). These minute crabs reside in gall, pits or dwellings (skeletal modifications of their coral hosts) that serve as sheltered habitats (Potts, 1915; van der Meij and Hoeksema, 2013). Since their first description over 150 years ago (Stimpson, 1859), gall crabs have been categorized with the neutral term symbionts but also as commensals and parasites. These classifications are primarily based on their proposed feeding modes (e.g. mucus ingestion, filter/deposit feeding) or the impact of dwelling formation on their coral hosts. Moreover, with only a few notable exceptions (Simon-Blecher et al., 1996; Terrana et al., 2016; Bravo et al., 2024), most studies exploring the nature of their relationship are primarily observational, and interactions with their coral hosts are generally overlooked. This oversight leads to knowledge gaps concerning the overall impact of their presence on the coral or lack thereof. Additionally, their specific influence on the photosynthetic endosymbionts within the coral tissue and our understanding of their role in this multisymbiotic relationship remains unclear.

A single study investigated chlorophyll *a* (*chl a*) content and Symbiodiniaceae density around the pits of cryptochirid crabs (Simon-Blecher et al., 1996), reporting higher *chl a* concentrations in close proximity to the crabs’ dwellings possibly linked to increased Symbiodiniaceae densities. Their findings, based on fluorescence spectral imaging, were limited to assessing the quantity of algal symbionts in the host tissue, leaving the impact of the crab’s presence on the photobiology of the Symbiodiniaceae-coral symbiosis unknown. In coral research, Pulse-Amplitude-Modulated (PAM) fluorometers have become a state-of-the-art tool to investigate the photobiology of coral-algae associations by estimating the photochemical efficiency of Symbiodiniaceae through *chl a* fluorescence (Bhagooli et al., 2021). PAM fluorometers are commonly used to study the primary mechanisms of coral bleaching by assessing the influence of abiotic stressors on coral photobiology (Warner and Suggett, 2016). Despite their widespread use, PAM fluorometers are seldom utilized to examine how biotic interactions such as coral diseases, symbiotic relationships or competition with other benthic organisms impact the photosynthetic performance of Symbiodiniaceae (Roff et al., 2008; Rasher and Hay, 2010). The advancement of standard PAM fluorometers with fluorescent imaging technology may help to bridge this gap by enabling the capture of photochemical parameters over a large area rather than probing a single coral polyp, revealing the topography of damage in regions not directly exposed to a potential stressor (Murchie and Lawson, 2013). For instance, in terrestrial plants, Imaging PAM fluorometry has effectively demonstrated the adverse effects of arthropod herbivory and oviposition, detecting photosynthetic impairment even at a distance from directly injured tissue that would otherwise remain unseen (Aldea et al., 2006; Velikova et al., 2010). These findings make this technique a promising method to study whether the presence of gall crabs or their dwellings might compromise the photosynthetic efficiency of Symbiodiniaceae, thus having adverse effects on their host corals invisible to the naked eye.

Here, we apply Imaging PAM fluorometry to the cryptochirid coral symbiosis with two aims. First, to provide a fine-scale visual output of the spatial distribution of photochemical efficiency (F_v/F_m) on colony fragment scale, including the skeletal modifications induced by the crabs. Unlike studies that rely on handheld PAM fluorometers focusing on single polyp measurements, this approach enables the assessment of sample heterogeneity at a broader scale and the detection of potential concealed effects of cryptochirid presence. Second, to measure F_v/F_m within a narrow band (approx. 0.3 cm) of coral tissue directly adjacent to the crab's dwelling. These measurements are compared with uninhabited regions of the colony, further divided into ridges and valleys, to account for the inherent spatial heterogeneity of coral photochemical parameters. With this approach, we test the hypothesis that factors associated with cryptochirid presence could negatively impact the coral-algae symbiosis. These factors include mucus ingestion or the formation of their dwellings, which may result in alterations of the microenvironment on the coral surface or host tissue being overgrown by algae. By establishing a framework for applying Imaging PAM fluorometry to invertebrate-coral symbioses, this study offers a promising tool to explore complex multisymbiotic relationships on coral reefs and enhances our understanding of the role of coral-associated invertebrates in reef health and ecosystem functioning.

Materials and methods

Sample collection

Eight partial coral colonies with inhabited cryptochirid dwellings were photographed and sampled by scuba diving on 11 June 2023 at Rose Reef (N 22.186095, E 38.531884) near Thuwal in the central Saudi Arabian Red Sea. Colonies were retrieved between 7 - 11 m depth. We targeted the host genera *Goniastrea* Milne Edwards and Haime 1848, *Echinopora* Lamarck, 1816, *Platygyra* Ehrenberg, 1834 and *Dipsastraea* Blainville, 1830, with crabs inhabiting cylindrical pits, as well as *Pavona* Lamarck, 1801, with crabs inhabiting canopy tunnels with a crescent-shaped opening (Wei et al., 2013). We selected these coral genera because they are among the most commonly inhabited genera on Red Sea reefs. Coral fragments (diameter of 10 - 20 cm) were collected with a hammer and chisel, placed in individual ZIP-lock bags (39 x 34 cm) filled with seawater, and transported back to the laboratory within an hour in a shaded container (30 L) with additional seawater. Corals were identified to the lowest taxonomic level based on the original species descriptions and comparison with type material (Table 1). Gall crabs were extracted from the corals and identified morphologically, and subsequently, a partial COI sequence was obtained following the protocol in Bähr et al. (2021).

Imaging PAM fluorometry measurements

In the laboratory, corals were placed in an aquarium filled with seawater, equipped with an air bubbling system, and the

temperature was set to 29°C, matching the ambient water temperature at the time and location of sampling. The total time from sampling to the start of measurements was approximately 2 hours, including a dark-acclimation period of 60 minutes to avoid non-photochemical processes of dissipation of PSII. Subsequently, the Symbiodiniaceae's initial fluorescence (F_0), maximum fluorescence (F_m) and the maximum quantum yield of PSII photochemistry were measured with a Maxi Imaging-PAM *M-series* (Heinz Walz GmbH, Effeltrich, Germany), equipped with an IMAG-K4 camera and an IMAG-MAX/F filter. Here, variable fluorescence (F_v) is calculated as $F_v = F_m - F_0$, making F_v/F_m a measure of photosynthetic efficiency. The measurements were conducted using: measuring light intensity 6-7, F_t of 0.14, Gain 2, Damping 2, Aperture 4-2.8 and Frequency 1. Factory standard settings were used for the remaining parameters. Area of Interest (AOI) diameter was 15 pixels, which corresponds to a measured area of 11.9 mm². The Imaging-PAM was operated, and measurements were taken using the ImagingWin V2.41a (Heinz Walz GmbH, Effeltrich, Germany) software.

A narrow band (approx. 0.3 cm) of coral tissue adjacent to the crab dwelling was measured, with five points distributed evenly around the edge for an averaged value (Figure 1A, B). To ensure methodological consistency, this band was placed uniformly across all samples, even when localized variations caused AOIs to include algae or trapped sediments. These features were interpreted as part of the crab's ecological impact on the dwelling area, reflecting their influence on the microenvironment. Reference measurements were taken from uninhabited areas of the coral colony, capturing the spatial heterogeneity of photochemical parameters by sampling five points each on ridges (elevated features) and valleys (depressed features) (Figure 1C). Additional AOI examples are provided in Supplementary Figure 1.

Statistical analysis

All statistical analyses were carried out in R Statistical Software (v4.3.1; R Core Team, 2023) using the packages 'car' (Fox and Weisberg, 2019), 'multcomp' (Hothorn et al., 2008) and 'ggplot2' (Wickham, 2016). A Shapiro-Wilk test was used to verify if the data was normally distributed, and a Levene test was applied to test for homogeneity of variance. A one-way ANOVA was conducted to test for differences in F_0 , F_m and F_v/F_m between the valleys, ridges and the dwellings of the coral colonies. When significant, a Tukey HSD *post hoc* test was used to test for differences in means between the groups.

Results

Visual assessment of coral-crab associations

Five gall crab species, belonging to three genera, were identified in the sampled corals (Table 1). *Pavona* cf. *varians* (Verrill, 1864)

TABLE 1 Overview of the corals and cryptochirid symbionts included in this study with identification to the lowest taxonomic level.

Coral species	Colony ID	Depth	Gall crab species
<i>Pavona</i> cf. <i>varians</i>	SAD233H	11.4m	<i>Opecarcinus</i> SET 13
<i>Platygyra crosslandi</i>	SAD227H	9.1m	<i>Cryptochirus coralliodytes</i>
<i>Platygyra lamellina</i>	SAD230H	11.1m	<i>Cryptochirus coralliodytes</i>
<i>Echinopora gemmacea</i>	SAD231H	8.2m	<i>Lithoscaptus</i> cf. <i>tri</i>
<i>Echinopora gemmacea</i>	SAD235H	6.5m	<i>Lithoscaptus</i> cf. <i>tri</i>
<i>Goniastrea pectinata</i>	SAD232H	10.3m	<i>Lithoscaptus</i> sp. K
<i>Goniastrea pectinata</i>	SAD234H	10.2m	<i>Lithoscaptus</i> sp. K
<i>Dipsastraea</i> cf. <i>favus</i>	SAD236H	9.6m	<i>Lithoscaptus</i> sp. A

Species placeholder names based on unpublished data (SETvdM).

(SAD233H), *Platygyra lamellina* (Ehrenberg, 1834) (SAD230H) and *Goniastrea pectinata* (Ehrenberg, 1834) (SAD232H) were inhabited by a single cryptochirid, whereas both *Echinopora gemmacea* (Lamarck, 1816) colonies (SAD231H and SAD235H) and *Dipsastraea* cf. *favus* (Forsk., 1775) (SAD236H) harbored two crabs. *Platygyra crosslandi* (Matthai, 1928) (SAD227H) and the remaining *G. pectinata* colony (SAD234H) had three inhabited dwellings, respectively. Photographs show no to little visible alterations of the coral tissue surrounding the gall crab dwellings in *Pl. crosslandi* (Figures 2B1, B2), *G. pectinata* (SAD234H) (Figures 2G1, G2) and *D. cf. favus* (Figures 2H1, H2). In *Pl. lamellina* (Figures 2C1, C2), the tissue close to the dwelling was of a lighter color in contrast to the rest of the colony, whereas in *G. pectinata* (SAD232H) (Figures 2F1, F2), the bordering tissue is a darker shade than the tissue further away. The dwellings of *Pa. cf. varians* (Figures 2A1, A2) and both *E. gemmacea* colonies (Figures 2D/E1-D/E2) seem to have a larger visible effect on their immediate surroundings, with noticeable growth of algae and a darker appearance of the surrounding host tissue. Furthermore, the larger pit in *E. gemmacea* (SAD231H) is delimited from the remaining colony by a border of sand and particulate matter trapped by what appears to be red filamentous algae (Figures 2D1, D2).

Chlorophyll a fluorescence measurements

The photographs and measurements of photochemical parameters (F_0 , F_m and F_v/F_m) obtained with the Imaging PAM indicate spatial heterogeneity in these parameters on all coral colonies (Figures 2A3–H3, F_0 , F_m provided in the Supplementary Table 1). This observation is strengthened by the statistical comparison of F_0 , F_m and F_v/F_m values measured around the crab dwelling with the coral surface ridges and valleys (Supplementary Table 2). Only *G. pectinata* (SAD234H) expressed a homogenous photosynthetic efficiency pattern (F_v/F_m values) without significant differences between ridges and depressions on the coral surface (Figure 3, Supplementary Table 2). F_v/F_m values ranged between 0.46 and 0.56, with *G. pectinata* (SAD234H) showing the lowest

values across all colonies (Figure 3, Supplementary Table 2). In contrast, the valleys of *Pa. cf. varians*, *Pl. crosslandi* and *Pl. lamellina* exhibited the highest photosynthetic efficiency (Supplementary Tables 1, 2). Lastly, overall valleys showed higher F_v/F_m values than ridges (Figure 3, Supplementary Tables 1, 2). Based on these results, the photosynthetic efficiency of ridges was selected as the reference for comparison with the dwelling region.

Five sampled colonies showed significant differences in photosynthetic efficiency between the dwelling region and the ridges (Figure 3). In *Pa. cf. varians*, *Pl. crosslandi*, and *D. cf. favus*, the tissue adjacent to the crabs' dwellings showed an increase in F_v/F_m values of 3% for *Pavona* and 6% for the other two colonies (Figure 3). In contrast, *E. gemmacea* (SAD231H) exhibited a 12% decrease in photosynthetic efficiency, which may have been influenced by the presence of filamentous algae and trapped sediment over the coral tissue. A similar but smaller decrease (4%) was observed in *G. pectinata* (SAD232H) (Figure 3). No significant differences between tissue around the pits and the ridges could be discerned for the remaining three colonies: *Pl. lamellina*, *G. pectinata* SAD234H) and *E. gemmacea* (SAD235H) (Figure 3).

Discussion

Photosynthetic performance of collected coral fragments

We determined the maximum quantum yields of PSII fluorescence (F_v/F_m values) of six scleractinian coral species from the central Red Sea to assess the photosynthetic performance of their zooxanthellae symbionts and the potential impact of coral-dwelling crabs on this performance. The coral species in this study are not frequently targeted in photobiological studies, and data for the central Red Sea is entirely lacking, hampering the comparison with values reported in the literature. Our F_v/F_m values ranged from 0.47 to 0.56, which is below the commonly cited threshold of 0.6 for healthy corals (Warner and Suggett, 2016, and references therein). However, the sampled corals showed no signs of paling, bleaching, or disease (Figure 2), and the water temperature of 29°C was typical for this time of year (NOAA Coral Reef Watch, 2024). Moreover, scleractinian corals are well-known to show diel variations in their *chl a* fluorescence patterns characterized by a daily mid-day decline in the photochemical activity of PSII resulting in lower F_v/F_m values (Jones and Hoegh-Guldberg, 2001; Warner et al., 2010). The mid-day measurements might provide an explanation for the observed low F_v/F_m values in this study, suggesting that the *in situ* photosynthetic efficiencies of the colonies has not been compromised. However, to fully confirm this interpretation, future research should incorporate measurements at multiple time points, enabling clearer differentiation between daily photoinhibition cycles and localized stress responses. Lastly, we observed a pronounced spatial variation between the valleys and ridges of the colonies, which aligns with findings in literature (Ralph et al., 2002).

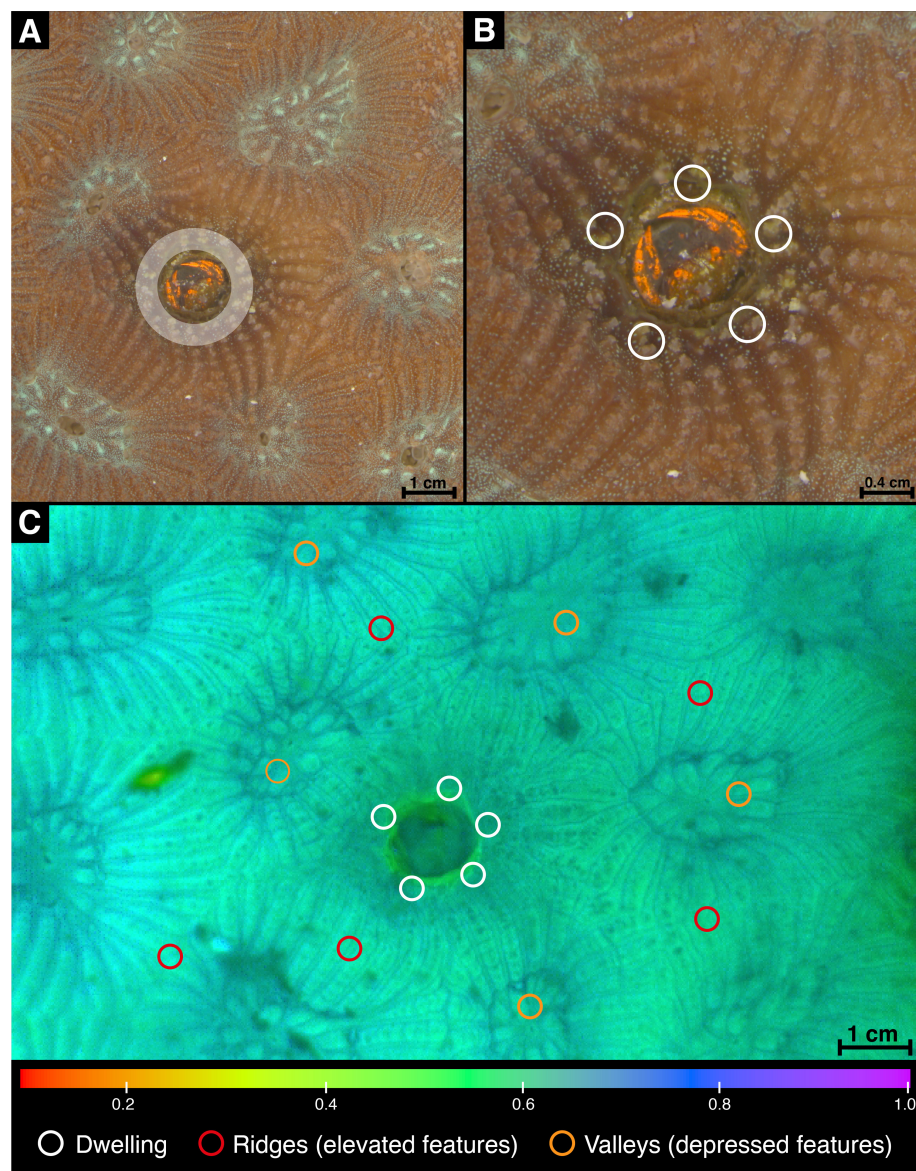


FIGURE 1

Imaging setup and area selection for photochemical measurements in the *Goniastrea pectinata* (SAD232H) gall crab association. (A) Stereo microscope image showing the gall crab within its dwelling; the shaded white area represents the narrow band of coral tissue directly adjacent to the crabs dwelling, which was consistently selected for measurement. (B) Enlarged view of the same dwelling with five example AOIs (Areas of Interest) placed within this adjacent tissue band to measure photochemical parameters. (C) *chl a* fluorescence image of the maximum quantum yield (F_v/F_m), representing photochemical efficiency, as output from the Imaging PAM system. Example AOI placements are shown for the three distinct features: white = dwelling, red = ridges (elevated features), orange = valleys (depressed features).

Gall crab presence and coral host photobiology

To evaluate whether gall crabs influence the photosynthetic efficiency of their coral hosts, we used Imaging PAM fluorometry to capture spatial variation of F_v/F_m values at coral fragment scale. While this approach has successfully detected concealed effects of biotic interactions in other systems, such as plant-herbivore interactions (Aldea et al., 2006; Velikova et al., 2010), we found no widespread reductions in F_v/F_m values across the colony surface. Instead, changes in photosynthetic efficiency were primarily confined to the immediate

vicinity of the crab dwellings, as indicated by our F_v/F_m measurements. The presence of cryptochirid crabs did not lead to a general decline in photosynthetic efficiency across most scleractinian colonies examined, as F_v/F_m values around the crab dwellings were not found to be significantly lower than those of the coral ridges. In fact, in a few cases (SAD227H, SAD232H and SAD236H), their presence even led to a significant efficiency increase (Figure 3, Supplementary Table 2). In the association of the *Opecarcinus* Kropp and Manning, 1987 crab and *Pavona* coral a possible explanation for this slight increase could be the presence of endolithic algae (e.g. *Ostreobium* Bornet and Flahault, 1889) within the coral skeleton, as indicated by the notable darker color

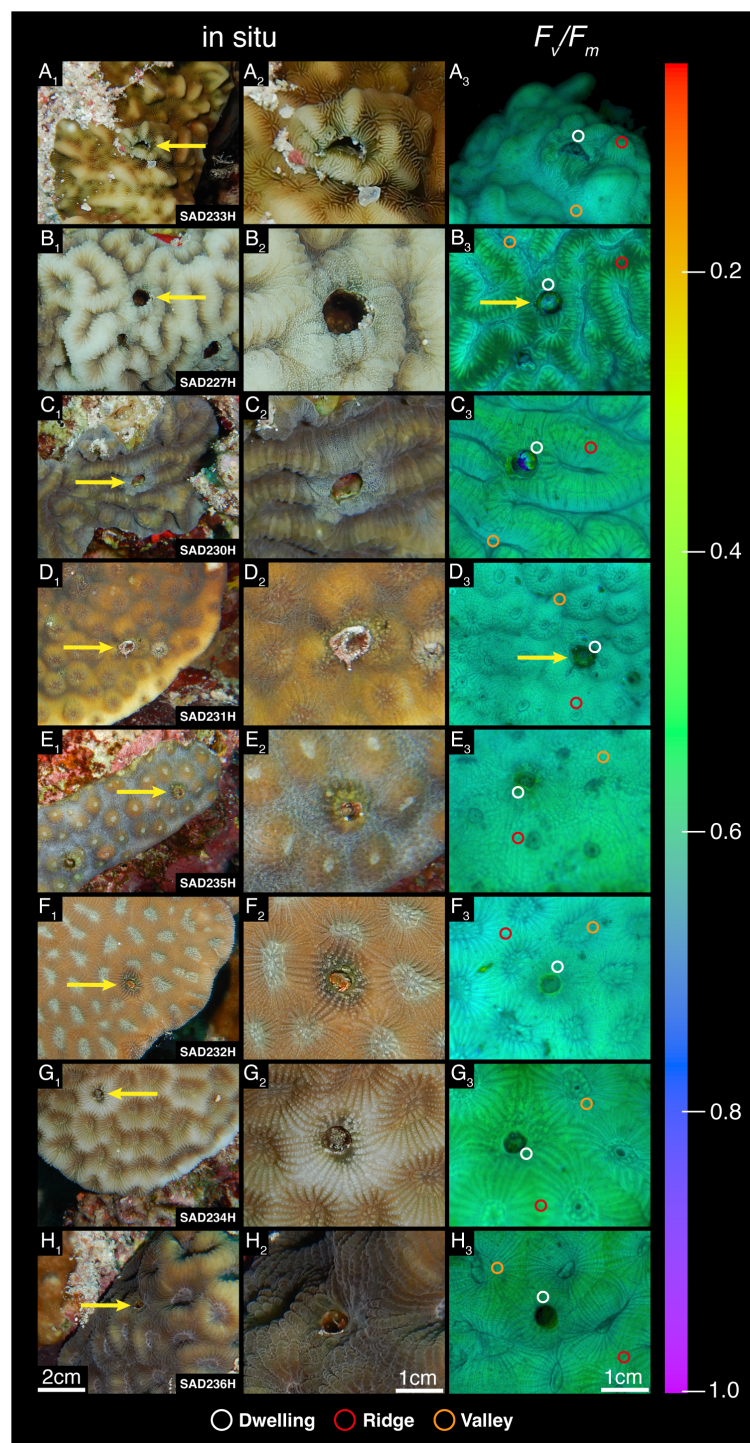


FIGURE 2

Gall crab-coral associations sampled in this study. (A1–H1): *In situ* photographs of coral colonies with crab dwellings (specimen code at the bottom right corner of each image; host identity in Table 1). Yellow arrows indicate the dwelling measured for this study. (A2–H2): Enlarged *in situ* photographs of the crab dwellings where photochemical parameters were measured. (A3–H3): *chl a* fluorescence images of the maximum quantum yield (F_v/F_m), representing photochemical efficiency, acquired with Imaging PAM. Identical false color scale displays fluorescence parameter values from 0 to 1. Circles represent examples of the measured features on the coral colony (white = dwelling, red = ridges, orange = valleys).

near the dwelling opening. *Ostreobium* is known to contribute to the overall photosynthetic activity of corals (Fine et al., 2004; Tandon et al., 2025). Additionally, there is evidence that coral-associated invertebrates, such as Lithophaginae boring bivalves, may foster a

mutualistic relationship with endolithic algae through metabolic exchange. This in turn influences the coral holobiont by promoting bioerosion and weakening of the skeleton (Fordyce et al., 2020), which could also affect the overall F_v/F_m . Similarly, nutrient-rich excretions

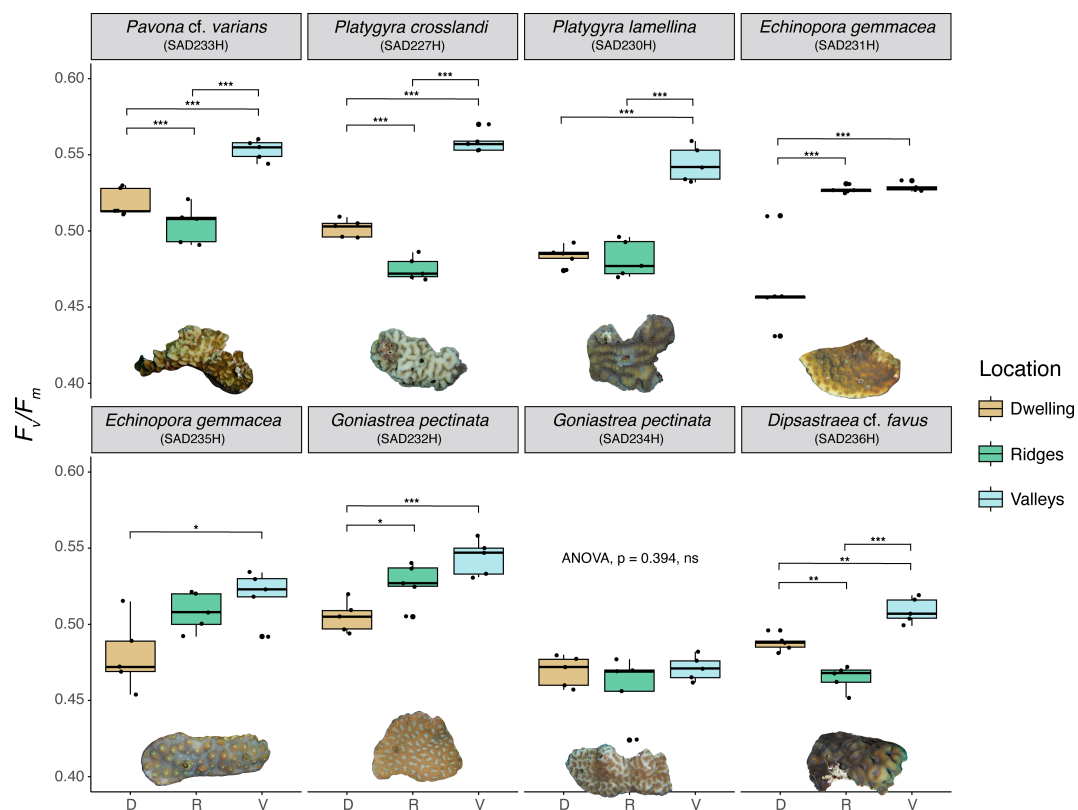


FIGURE 3

Boxplots showing differences in maximum quantum yield (F_v/F_m) values among crab dwelling regions (tan), coral ridges (green) and coral valleys (light blue) of every colony subsample (depicted as image below the boxplots). Results of ANOVA are displayed with asterisks indicating Tukey *post-hoc* test comparison: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. For cases where the ANOVA was not significant, no *post hoc* comparisons were conducted, and the corresponding p -value is reported.

from gall crabs could stimulate growth of endolithic algae around the dwelling, as they have been observed to excrete directly into their pits, potentially leading to a comparable mutualistic interaction (Simon-Blecher et al., 1996). Future studies should test this hypothesis by measuring ammonium excretion rates of gall crabs, using methods established for other coral-associated invertebrates (Mokady et al., 1998). The only other dwelling with clearly visible signs of algae growth was the one in *E. gemmacea* (SAD231H). Here, we also observed an accumulation of red-filamentous algae, sand and particulate matter forming a clear border with the surrounding coral tissue (Figure 2D1). For *Lithoscaptus* sp. (incorrectly identified as *Cryptochirus coralliodytes* Heller, 1860: unpublished data SETvdm) growth of blue-green algae of the family Oscillatoriaceae Engler, 1898 around the dwelling has previously been described by Simon-Blecher et al. (1999). Furthermore, filamentous algae of the genera *Dichothrix* Zanardini ex Bornet and Flahault, 1886 and *Lyngbya* C. Agardh ex Gomont, 1892 were hypothesized to form “pruned gardens” around the dwellings of the Atlantic gall crab *Troglocarcinus corallicola* Verrill, 1908 serving as food source (Carricart-Ganivet et al., 2004). Whether algal growth around dwellings negatively affects the dwelling’s surrounding zooxanthellae is unknown. Notably, the *Echinopora* (SAD231H) colony affected by algal growth exhibited the most significant decline in photosynthetic efficiency. Because our

measurements consistently included the first 3 mm around the dwelling, it is possible that algae and trapped sediment influenced the results, meaning the decline may not accurately represent the photosynthetic efficiency of the zooxanthellae in the host tissue. However, the algal band was narrow (<2 mm) (Figure 1D4), suggesting that any adverse effects of cryptochirid presence were confined to the immediate dwelling opening and can thus be considered minimal. Additionally, the visual output of photochemical efficiency indicates no widespread adverse effects across the remaining coral surface. Lastly, it is crucial to note that visible algae growth around the cylindrical pits was observed only in this specific pit. The factors facilitating algae growth around specific gall crab dwellings, as opposed to others, remain unclear and warrant further investigation.

We observed a small but significant decline in photosynthetic efficiency (4%) around the dwelling of *G. pectinata* (SAD232H), with the surrounding area visibly darker compared to the remaining colony surface (Figure 1, Figures 2F1–F3). Determining why the presence of this crab has a detrimental effect on its host is speculative. One potential explanation could be the crab’s diet that includes the ingestion of tissue/mucus produced by its host (Simon-Blecher et al., 1999), however, the metabolic drain of the crab’s presence on the coral is likely minimal (Kropp, 1986; Bravo et al., 2024). Additionally, the impact of mucus consumption on the

Symbiodiniaceae within the coral tissue is unknown. Considering that all the here examined cryptochirid genera have previously been proposed to feed on coral tissue/mucus (Simon-Blecher and Achituv, 1997; Bravo et al., 2024), our results suggest that the crab's diet does not seem to adversely affect the photochemical efficiency of the zooxanthellae in the adjacent coral tissue.

There is evidence that the complex morphology of corals, in combination with incident irradiance and water flow, results in distinct microenvironments on the coral surface (Murthy et al., 2023). This spatial heterogeneity may influence the distribution of photosynthetic efficiency on colonies significantly (Carpenter and Patterson, 2007; Finelli et al., 2007). Moreover, Abelson et al. (1991) found a vortical flow above and within gall crab dwellings. This flow may impact thickness and shape of coral surface boundary layers, subsequently influencing the distribution of photosynthetic efficiency and potentially explaining part of the observed variation in this study. However, similar flows might also occur around pronounced 'hills' and 'ridges' naturally present on certain hillcocky or frondose coral species (e.g. *Pavona cactus*), but this has not been studied. Future research employing novel approaches, including 3D modelling of the radiative, thermal, and chemical microenvironments based on microsensor measurements (Murthy et al., 2023), could significantly enhance our understanding of altered hydrodynamic conditions and their influence on boundary-layer dynamics and photosynthetic efficiency at the colony scale.

Although we studied the impact of gall crabs on coral colonies with only a few individuals, cryptochirids can be present in much larger numbers on their hosts, (Terrana et al., 2016) or in dense aggregations on reefs (Hoeksema and van der Meij, 2013). To assess whether higher densities of gall crabs negatively impact coral hosts, we recommend expanding the focus beyond individual specimens to explore the collective influence of multiple crabs within their host. Further investigations should incorporate additional host species, coral and dwelling morphologies (e.g., branching corals with enclosed galls) and expand geographically to reefs in other biogeographic regions to better evaluate the ecological relevance of these findings.

Imaging PAM fluorometry as means to investigate coral-dwelling associates

PAM fluorometry is a powerful tool to study mechanisms of coral bleaching and is most frequently applied to investigate the photoinactivation of Symbiodiniaceae as response to thermal stress (Warner et al., 1996). In addition, PAM fluorometry has been used to determine the impact of other abiotic stressors, such as salinity, turbidity, herbicides, toxins, plastic pollution, and oxygen conditions on the photosynthetic performance of Symbiodiniaceae within their hosts (Jones et al., 1999; Jones and Kerswell, 2003; Philipp and Fabricius, 2003; Finelli et al., 2006; Marzonie et al., 2021; Mendrik et al., 2021). So far, few studies have focused on the impact of heterogeneous/symbiotic biotic interactions on the photosynthetic efficiency of coral symbionts. Examples include only interactions with diseases or seaweeds (Roff et al., 2008;

Rasher and Hay, 2010), despite growing evidence that coral-associated invertebrates can significantly alter the abiotic environment around their hosts, which in turn likely affects coral photobiology. Worm snails (Vermetidae) have been shown to alter physical and chemical conditions of coral-macro algae interactions (Brown and Osenberg, 2018), and while the authors speculate about the impact on the photosynthetic performance of Symbiodiniaceae, they regrettably did not apply any active fluorescence-based method to test their assumptions.

To date, invertebrate-coral associations have only been investigated using other fluorescence-based techniques, allowing authors to draw conclusions about chlorophyll content or zooxanthellae density but not photosynthetic performance. For instance, Wielgus and Levy (2006) applied *in situ* fast repetition fluorometry to investigate the Symbiodiniaceae housed in *Astreopora myriophthalma* (Lamarck, 1816) infested by spionid polychaetes. The infested areas showed elevated σ PSII values, reflecting an increase in the functional absorption cross-section of Photosystem II, leading to the hypothesis that this is an effect of zooxanthellae proliferation, potentially linked to fertilization of the surrounding waters by the polychaetes. Fluorescence spectral imaging did not reveal significant differences in chlorophyll concentration in the coral tissue surrounding the boring mussel *Leiosolenus lessepsianus* (Vaillant, 1865) (as *Lithophaga lessepsiana*) and the barnacle *Savignium milleporum* (Darwin, 1854). However, enhanced growth of blue-green algae led to increased chlorophyll content around the dwelling of *Lithoscaptus* sp. (Simon-Blecher et al., 1996). Our results show that algae growth can result in different photosynthetic performances of the coral, with a slight increase for the proposed association between, *Pa. cf. varians* (SAD233H) and *Ostreobium* spp. and a decrease observed in *E. gemmacea* (SAD231H). In the latter case, the observed decline in photosynthetic efficiency was likely due to confounding effects of the algae and trapped sediment over the coral tissue, rather than a direct impact of the crab on the photochemical efficiency of the Symbiodiniaceae. While the extent to which this algal growth drains the coral's resources remains unknown, the small size of the affected area suggests that its overall impact is probably minimal.

In this study, we applied Imaging PAM fluorometry to investigate the influence of gall crab dwellings on the photosynthetic efficiency of the Symbiodiniaceae within host coral tissue across various coral-crab associations. This marks the first application of this method to study an invertebrate-coral-symbiont relationship. We observed that in the majority of samples, the presence of cryptochirid crabs had either no impact or a slight positive effect on photosynthetic efficiency, indicating that they take a neutral position towards the coral's algal symbionts in this multisymbiotic relationship. The observed variation in photosynthetic efficiency between samples highlights how crab presence can alter the microenvironment of the coral, resulting in small-scale changes in photosynthetic efficiency. In two of our samples, we saw increased algal growth in and around the dwellings, perhaps related to gall crab excretion. The role of small cryptobenthic invertebrate fauna on coral reefs remains poorly understood, particularly in terms of their interactions with coral

hosts and their influence on the overall coral holobiont. Considering the remarkable diversity of coral-associated invertebrates, and the limited knowledge about how they may affect coral photobiology, we recommend applying Imaging PAM fluorometry or similar techniques to investigate a broader range of symbionts. This approach could help to reveal the impact of coral-dwelling communities on host photosynthetic efficiency, deepening our understanding of these complex multisymbiotic reef relationships.

Data availability statement

Sequences are deposited to GenBank (<https://www.ncbi.nlm.nih.gov/genbank>) under accession numbers PP356663-PP356670.

Ethics statement

The animal study was approved by KAUST Institutional Bioethics and Biosafety Committee Protocol N: 23IBEC009. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

SB: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. SvdM: Supervision, Validation, Writing – review & editing. ES: Investigation, Software, Writing – review & editing. FB: Funding acquisition, Resources, Supervision, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research 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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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2025.1568287/full#supplementary-material>

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