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Modulation of the symbionts light environment *in hospite* in scleractinian corals

Claudia Tatiana Galindo-Martínez[1][*][†], Arelys Chaparro[2], Susana Enríquez[3] and Roberto Iglesias-Prieto[1][*]

[1]Mueller Lab, Department of Biology, The Pennsylvania State University, University Park, State College, PA, United States, [2]Center for Marine and Environmental Studies, University of the Virgin Islands, St. Thomas, VI, United States, [3]Laboratory of Photobiology, Unidad Académica de Sistemas Arrecifales Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de Mexico (UNAM), Puerto Morelos, Cancún, QR, Mexico

The upregulation of animal chromoproteins (CPs) during thermal stress produces "colorful" bleached corals that facilitate coral recovery after bleaching. *In situ* measurements indicate that animal CPs present in coral tissues reduce the elevated internal light environment of the remaining symbionts in bleached or low-pigmented stressed corals. However, there is still a lack of understanding regarding the extent to which animal CPs contribute to modifying the internal light environment of the symbionts *in hospite*. In this study, we evaluate the effect of three animal CPs on the optical properties of the coral tissue and their internal light environment using a numerical model. The model allows estimations of the absorbance spectra of corals as a function of changes in symbiont and animal pigmentation, as well as descriptions of the light environment *in hospite* of the symbionts. These descriptions were derived from the quantification of the contribution of each pigment component to light absorption, together with the contribution of the coral skeleton's reflectance. Simulations indicate that animal CPs upregulation modifies the spectral distribution and the intensity of the internal light field. Animal CPs can reduce up to 11% of the light intensity *in hospite* when present individually, and up to 24% when present in combination. Such reduction may play a critical role in preventing the full development of the bleached phenotype when irradiance rises to excessive levels at low coral pigmentation, facilitating coral recovery and symbiont tissue re-colonization after bleaching. Accordingly, coral's CPs components need to also be considered when selecting coral species for future restoration efforts.

KEYWORDS

coral bleaching, coral recovery, animal chromoproteins, light environment *in hospite*, $a*_{CP}$

1 Introduction

The light environment inside the tissue of scleractinian corals is mainly determined by the incident irradiance on the coral surface and the optical properties of the tissue (Salih et al., 2000; Enríquez et al., 2005; Wangpraseurt et al., 2014; Wangpraseurt et al., 2016) and the skeleton (Enríquez et al., 2005; Terán et al., 2010; Marcelino et al., 2013; Swain et al., 2016; Enríquez et al., 2017). In the tissue, the presence of animal chromoproteins (CPs) (Salih et al., 2000; Smith et al., 2013) and photosynthetic pigments from the symbiotic dinoflagellates (Enríquez et al., 2005; Scheufen et al., 2017b) increases the absorption capacity of the coral pigments. Meanwhile, multiple light scattering by the white skeleton produces diffuse light, reducing pigments' self-shading while enlarging the optical path, increasing the probability of light absorption by the pigments (Enríquez et al., 2005). However, the reduction of coral skeleton reflectivity due to the presence of endolithic organisms such as the chlorophyte *Ostreobium* spp. near the skeletal surface strongly affects pigment absorption and modifies the light environment of the symbionts inside the tissue, i.e., *in hospite* (Galindo-Martínez et al., 2022).

During thermal stress, reductions in the symbiotic dinoflagellate population within the coral tissue result in progressive increases in the light environment *in hospite* (Wangpraseurt et al., 2017). The remaining symbionts respond to these internal increases in the local illumination by reducing photosynthetic pigment content to photoacclimate to the new light environment (Iglesias-Prieto and Trench, 1994; Enríquez et al., 2005; Gómez-Campo et al., 2022). However, such typical algal response, which is intended to regulate the light dose absorbed by the symbionts, is not an appropriate response for organisms living inside one of the most efficient light collectors in nature (Enríquez et al., 2005; Scheufen et al., 2017b), as it exposes the symbionts *in hospite* to further increases in local irradiance, activating a positive feedback loop. Under these circumstances, dinoflagellates experience dramatic increases in photodamage that can compromise the symbiotic relationship when all other photoprotective mechanisms are overwhelmed, and the bleached phenotype is finally induced (Scheufen et al., 2017a; Scheufen et al., 2017b; Gómez-Campo et al., 2022). Hence the dramatic increases in the light environment of the symbionts *in hospite* due to the loss of coral pigmentation (i.e., loss of symbionts and reduction in symbiont pigmentation) is critical for understanding the limits of tolerance of this symbiotic association coral-Symbiodinacea. An important implication of this process is that coral recovery from bleaching remains a challenging task for the symbionts when the external stress is removed because internal light levels are still too high, even when the external irradiance remains constant (Swain et al., 2016; Wangpraseurt et al., 2017). However, corals can recover after bleaching, and populations have the capacity to restore their pigmentation and functionality, surviving the heat stress

event (Rodríguez-Román et al., 2006; Bollati et al., 2020; Galindo-Martínez et al., 2022).

The upregulation of animal chromoproteins (CPs) in the animal tissue, which is responsible for creating "colorful" bleached corals (Bollati et al., 2020; Bollati et al., 2022), has been proposed as one of the mechanisms for coral bleaching recovery. The most common group of animal CPs found in corals are the Green Fluorescent Proteins (GFP) (Matz et al., 1999; Salih et al., 2000; Alieva et al., 2008; Smith et al., 2013). They are primarily found in populations of shallow areas, exposed to high-light environments, and their upregulation can be promoted by blue light (Salih et al., 2000; D'Angelo et al., 2008), nutrient stress (Bollati et al., 2022), and exposure to mild heat stress (Bollati et al., 2020). Animal CPs generally accumulate in parts of the coral colony with low symbiont density composition, such as the areas with the highest growth rate, or parts that are particularly damaged (Smith et al., 2013; Bollati et al., 2020). Animal CPs' function in corals is not clear; however, it has been suggested that animal CPs can help in coral photoprotection to high levels of UVR or PAR (Salih et al., 2000; Smith et al., 2013; Gittins et al., 2015; Quick et al., 2018), antioxidant activity (Bou-Abdallah et al., 2006), and camouflage (Matz et al., 2006). They have also been proposed to amplify light scattering and increase the temperature within coral tissue (Lyndby et al., 2016). It also has been suggested that animal CPs could help corals attract symbionts (Aihara et al., 2019) and prey such as plankton (Ben-Zvi et al., 2022).

Due to their chemical composition, animal CPs can absorb light in the visible and UV range. Based on their optical properties, animal CPs can be classified as fluorescent proteins (FPs) and non-fluorescent chromoproteins (CPs) (Alieva et al., 2008). FPs can reemit light at particular wavelengths, a process known as photoconversion (Dove et al., 2001; D'Angelo et al., 2008; Smith et al., 2013; Bollati et al., 2022). Hence, it has been suggested that animal CPs could enhance algal photosynthesis in low light environments by modifying the light spectrum and intensity (Schlichter et al., 1994; Salih et al., 2000; Bollati et al., 2022). Nevertheless, considering that the number of photons generated through photoconversion is minimal compared to ambient light, its contribution to photosynthesis may be negligible (Ben-Zvi et al., 2021; Bollati et al., 2022). *In situ* spectral scalar irradiance in corals indicate that the presence of animal CPs reduces the light environment *in hospite* at particular wavelengths (Bollati et al., 2022) due to the CPs' light absorption capacity. However, there is still a limited understanding of the animal CPs' contribution to the modification of the light environment in the PAR range of the coral symbionts *in hospite*.

In this study, we analyzed the damping effect of three non-fluorescent animal CPs (asulCP562, amilCP580, and amilCP604) in the internal light environment of coral tissues using a numerical model for light transmission in corals. The model assumes light attenuation in the coral tissue due to light

absorption by symbiotic photosynthetic pigments and animal CPs, and the additional effect of skeleton light scattering. The portion of light reaching the skeleton is scattered back to the tissue in different ratios depending on the optical properties of the skeleton. Simulations indicate that upregulation of animal CPs in the coral tissue can reduce internal irradiance up to 24% when present in combination.
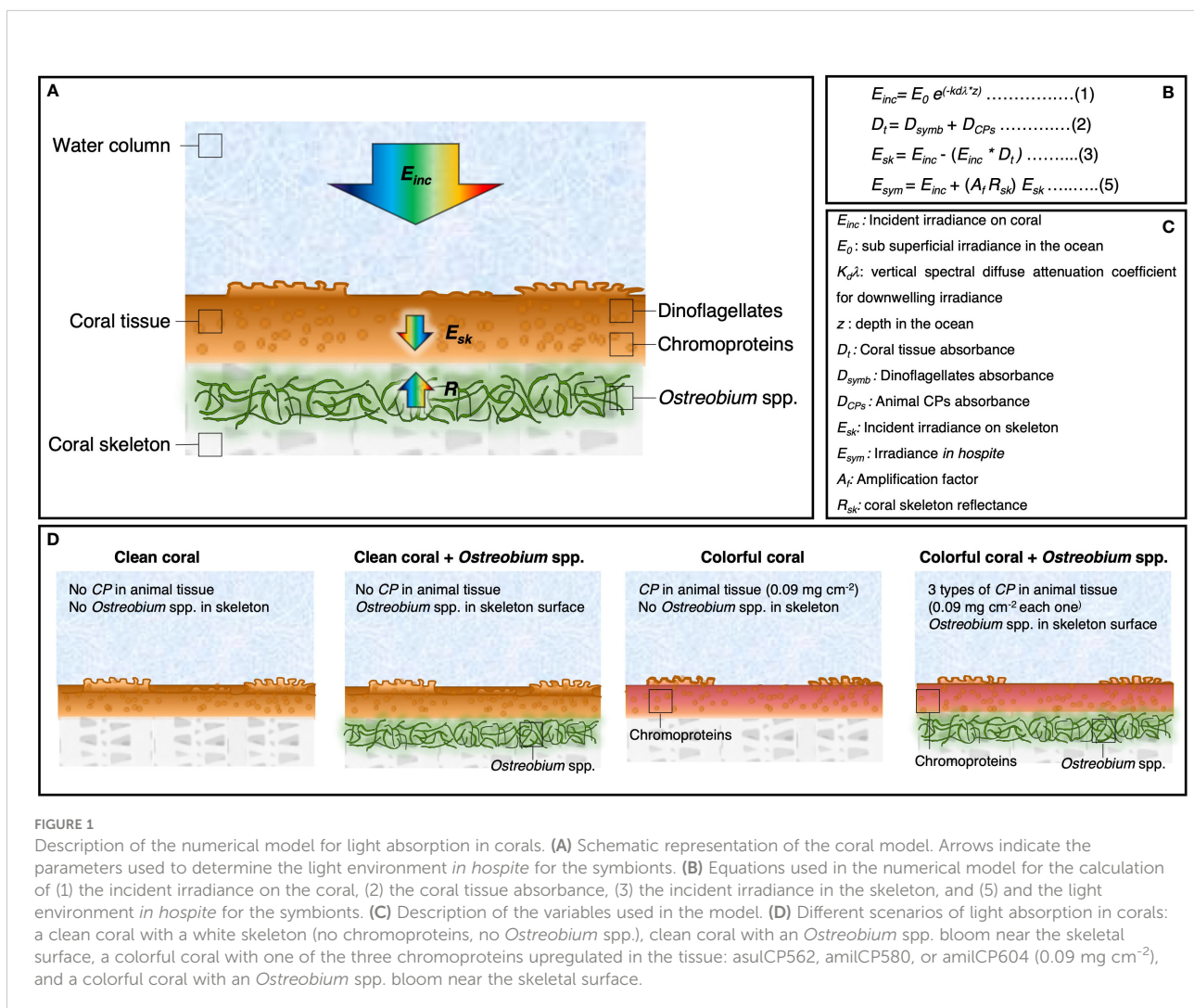
2 Materials and methods

2.1 Numerical model

The numerical model for light transmission in corals previously reported (Galindo-Martínez et al., 2022) was modified to further explore the effects of animal CPs in the internal light environment of coral tissue. Briefly, the model assumes a flat coral where polyps are retracted, and the transparent coral tissue, containing the spherical photosynthetic

symbionts, sits on top of the calcium carbonate skeleton. In the model, the skeleton reflectance can be modified due to the presence of the endolithic algae *Ostreobium* near the skeletal surface (Galindo-Martínez et al., 2022) (Figure 1A).

The model considers that 1) the incident light on the coral surface is attenuated inside the tissue by the photosynthetic pigments of the symbiotic dinoflagellates and by the animal CPs when present, and 2) that the light that is not attenuated and reaches the skeletal surface is scattered back to the coral tissue as a function of coral skeleton reflectance (R) (Figure 1A). By doing so, the model can predict the coral absorbance spectra and the light environment *in hospite* for the symbionts with 0.2 nm resolution in the PAR range (400 to 700 nm) as a function of the Chl*a* density due to the presence of the symbiotic dinoflagellates, the animal CP density when upregulated in the animal tissue, and the skeleton reflectance (Figures 1B, C). See detailed equations in supplementary materials.

To predict the light environment for the symbionts inside the coral tissue, the numerical model was designed in the

FIGURE 1
Description of the numerical model for light absorption in corals. **(A)** Schematic representation of the coral model. Arrows indicate the parameters used to determine the light environment *in hospite* for the symbionts. **(B)** Equations used in the numerical model for the calculation of (1) the incident irradiance on the coral, (2) the coral tissue absorbance, (3) the incident irradiance in the skeleton, and (5) and the light environment *in hospite* for the symbionts. **(C)** Description of the variables used in the model. **(D)** Different scenarios of light absorption in corals: a clean coral with a white skeleton (no chromoproteins, no *Ostreobium* spp.), clean coral with an *Ostreobium* spp. bloom near the skeletal surface, a colorful coral with one of the three chromoproteins upregulated in the tissue: asulCP562, amilCP580, or amilCP604 (0.09 mg cm^{-2}), and a colorful coral with an *Ostreobium* spp. bloom near the skeletal surface.

software Excel version 16.66.1 based on data previously reported: 1) the vertical spectral diffuse attenuation coefficient ($K_d\Lambda$) for downwelling irradiance in the ocean reported by López-Londoño et al. (2021), 2) the light absorption spectra of a coral measured in transmittance mode (Enríquez et al., 2005), 3) the *in vitro* absorption spectra of three animal CPs isolated from the coral tissue (asulCP562, amilCP580, and amilCP604) (Smith et al., 2013), 4) the light transmission properties of coral skeletons (Vásquez-Elizondo et al., 2017), and 5) the *in vivo* absorption spectra of *Ostreobium* spp. in coral skeletons (Galindo-Martínez et al., 2022). Transmission absorption spectra of coral tissues (Enríquez et al., 2005) and animal CPs (Smith et al., 2013) were digitized using the software PlotDigitizer (Version 2.6.9). Each animal CP considered for the model presents a particular absorption peak at 562, 580, and 604 nm for asulCP562, amilCP580, and amilCP604, respectively (Figure 2) (Smith et al., 2013).

For the model's components, equations were designed to predict absorption with 0.2 nm resolution in the PAR range (400 to 700 nm) (Figures 1B, C) (See Supplementary materials). The first component, $K_d\Lambda$ (López-Londoño et al., 2021), allows quantification of the incident irradiance in the coral (E_{inc}) as a function of depth (z). Where E_0 is the sub-superficial irradiance in the ocean

$$E_{inc} = E_0 e^{(-K_d\lambda \; \times \; z)} \qquad (1)$$

The second and third components enable the prediction of light absorption in the coral tissue (D_t) by adding the absorbance of the dinoflagellates (D_{sym}) and the animal chromoproteins (D_{CP}). These absorbance spectra were predicted using equations based on an exponential attenuation as a function of algal and animal pigment densities. D_t was later used for the calculation of the incident irradiance in the skeleton (E_{sk}).

$$D_t = D_{sym} + D_{CP} \qquad (2)$$

$$E_{sk} = E_{inc} - (E_{inc} \star D_t) \qquad (3)$$

The fourth and fifth components, coral skeleton transmittance (T_{sk}) and *Ostreobium* spp. absorption (D_{ost}), allow us to calculate the skeleton's reflectance (R_{skos}) considering the effects of the endolithic algae *Ostreobium* spp. when present in the skeleton. The absorbance spectrum of *Ostreobium* spp. was calculated using equations based on an exponential attenuation as a function of *Ostreobium* spp. density and its position in the skeleton (Galindo-Martínez et al., 2022).

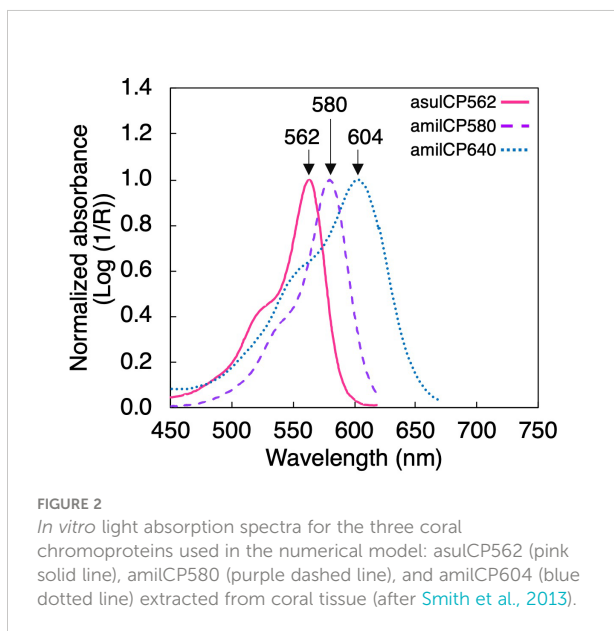$$R_{skos} \quad = \quad 1 - (1 - 10^{-T_{sk} \times D_{ost}}) \qquad (4)$$

Finally, using the previous parameters, the light environment *in hospite* for the symbionts (E_{sym}) was calculated as

$$E_{sym} \quad = \quad E_{inc} \quad + \quad (A_f \times R_{skos})E_{sk} \qquad (5)$$

In this expression, E_{inc} is the incident irradiance on the coral surface, A_f is the amplification factor for a flat surface as Chl*a* density changes (Enríquez et al., 2005), R_{skos} is the coral skeleton reflectance, and E_{sk} is the incident downwelling irradiance on the coral skeleton (Figure 1B). The amplification factor indicates the enhancement of the light absorption by the symbionts *in hospite* due to the presence of the coral skeleton in comparison with symbionts in suspension with the same amount of pigmentation (Enríquez et al., 2005).

2.2 Numerical model simulations

To quantify the damping effect of animal CPs in the light environment *in hospite*, simulations were run in the numerical model assuming different coral scenarios with different Chl*a* densities (100, 75, 50, 25, 12, and 6 mg Chl*a* m^{-2}) that correspond to variations in coral pigmentation from a well-pigmented coral (100 mg Chl*a* m^{-2}), to a bleached coral (less than 6 mg Chl*a* m^{-2}). The scenarios proposed represent corals with variations in the optical properties of the coral tissue and/or the coral skeleton, such as 1) a "clean" coral, representing a coral with no animal CPs in the tissue and with a white skeleton, 2) a "clean" coral with an *Ostreobium* spp. bloom located near the skeletal surface (less than 0.1 mm from the skeletal surface), 3-5) a "colorful" coral, representing a coral with one of the three animal CPs (asulCP562 (3), amilCP580 (4), and amilCP604 (5) (Smith et al., 2013)) upregulated in its tissue, assuming an animal CPs density of 0.09 mg cm^{-2} as reported by Smith et al., 2013, and with a white coral skeleton, and lastly, 6) a "colorful" coral with the three animal CP's (asulCP562, amilCP580 and, amilCP604) upregulated in its tissue and with

FIGURE 2
In vitro light absorption spectra for the three coral chromoproteins used in the numerical model: asulCP562 (pink solid line), amilCP580 (purple dashed line), and amilCP604 (blue dotted line) extracted from coral tissue (after Smith et al., 2013).

an *Ostreobium* spp. bloom located near the skeletal surface (Figures 1B–D). Simulations were run in the software Excel version 16.66.1. For each scenario, coral absorption spectra, percentage of light absorbed by each model component, and variation in the light environment *in hospite* were predicted.

2.3 Estimations of ACPs specific absorption coefficient

For the calculation of the specific absorption coefficient (Morel and Bricaud, 1981) of each animal CP (a*$_{CP562}$, a*$_{CP580,}$ and a*$_{CP604}$ for asulCP562, amilCP580, and amilCP604, respectively; m^2 Chl$a$ $^{-1}$), we used the predicted coral absorbance from the simulations run in the scenarios previously mentioned. In the simulations, the CPs' density was maintained constant (0.09 mg cm^{-2}) and only the Chl$a$ density in the coral was modified (100, 75, 50, 25, 12, and 6 mg Chl$a$ m^{-2}). For the calculation of the a*$_{CP}$ we used the equation:

$$a^*_{CP} = \left({}^D\!/_{\rho} \right) \ln 10 \qquad (6)$$

Where ρ is the Chl$a$ content per projected area in the coral (mg Chl$a$ m^{-2}) (Enríquez and Sand-Jensen, 2003; Enríquez et al., 2005) and D is the absorbance value predicted for the coral by the numerical model at 562 nm, 580 nm, and 604 nm, for a*$_{CP562}$, a*$_{CP580,}$ and a*$_{CP604}$ respectively. This parameter, a*$_{CPs}$, was calculated only for the absorbance value at the peak of absorption of each animal CPs. It can be considered a descriptor of the pigment light absorption efficiency of the animal CPs *in hospite*. An ANCOVA test was used to identify significant differences among animal chromoproteins. The statistical analysis was conducted using the software SPSS Statistics (Version 28).

3 Results

3.1 Light absorption

The numerical model indicates that the coral tissue of bleached/pale corals is able to absorb three times less incident light in the PAR range than pigmented corals (Figures 3A, G), allowing more incident light to reach the coral skeleton. The accumulation of chromoproteins in the coral tissue increases light absorption (Figures 3B-D). However, each chromoprotein contributes in a different proportion; asulCP562, amilCP604, and amilCP580 can absorb up to 13%, 15%, and 24%, respectively, of the incident light in a bleached/pale coral (3.3 mg Chl$a$ m^{-2}) (Figures 3B-D). On the contrary, a pigmented coral (100 mg Chl$a$ m^{-2}) can only absorb up to 5%, 6%, and 7%, respectively (Figures 3H-J). When *Ostreobium* spp. bloom in the skeletal surface, they can absorb up to 54% of the incident light

in a bleached/pale coral (Figure 3E, F), and only up to 10% in a pigmented organism (Figure 3K, L). However, if *Ostreobium* spp. is located near the skeletal surface of a "colorful" bleached coral, it can absorb only 14% of the incident light because the three animal CPs absorb up to 52% of the incident light (Figure 3F).

To quantify the variability in animal CPs' light absorption efficiency, differences in the specific absorption coefficient were estimated for each chromoprotein (a*$_{CP}$), as well as its variability as a function of Chl$a$ density for corals of different pigmentation. Model simulations indicate that a*$_{CP}$ increases with reductions in pigment density in the coral. However, they did not show significant differences between chromoproteins (ANCOVA, $f_{(15)}$ =0.015, p>0.05) (Figure 4). The a*$_{CP}$ varied from a minimum of 0.029 m^2 mg Chl$a$ $^{-1}$ for a pigmented coral (100 mg Chl$a$ m^{-2}) to a maximum of 0.284 m^2 mg Chl$a$ $^{-1}$ for a bleached coral (6 mg Chl$a$ m^{-2}) (Figure 4).

3.2 Light environment *in hospite*

Our simulations indicate that reductions in Chl$a$ density in the coral allow more incident light to reach the skeleton, producing dramatic increases in the light environment *in hospite* of the symbionts due to the extraordinary skeleton's capacity to scatter light (Figure 5). Under the "clean" coral scenario, the model estimated a 2.8-fold increase in light levels *in hospite* for bleached corals compared to a pigmented coral (Figures 5A, G). However, when chromoproteins were present in the tissue of "colorful" bleached corals, the *in hospite* light environment was amplified between 2.3 to 2.6 times (Figures 5B-D), relative to the amplification estimated for "colorful" pigmented corals (Figures 5H-J). Combining the presence of the three chromoproteins in the same bleached coral, a 2.1-fold increase in the light levels *in hospite* was estimated. Finally, for the last scenario, the combined presence of *Ostreobium* spp. and the three chromoproteins resulted in only a 1.3-fold increase in the light environment *in hospite* of the symbionts for "colorful" bleached corals (Figure 5F).

These simulations showed that the presence of optical dampers, such as animal CPs in coral tissues or *Ostreobium* spp. in the skeleton, reduces the light levels *in hospite* for the symbionts regardless of the variation in coral pigmentation (i.e., Chl$a$ density) (Figure 6). Nevertheless, corals with less Chl$a$ density showed more considerable reductions of the light environment *in hospite* for the symbionts when dampers were present, relative to regular pigmented corals. In bleached corals, the presence of animal CPs reduces between 11 to 24% of the light environment *in hospite* of the symbionts (Figures 5B-D; Figure 6) relative to tissues of "clean" bleached corals (Figure 5A; Figure 6). Meanwhile, in pigmented corals, the presence of animal CPs in the tissue leads to reductions of 2-6% (Figures 5H-J; Figure 6) in comparison to "clean" pigmented
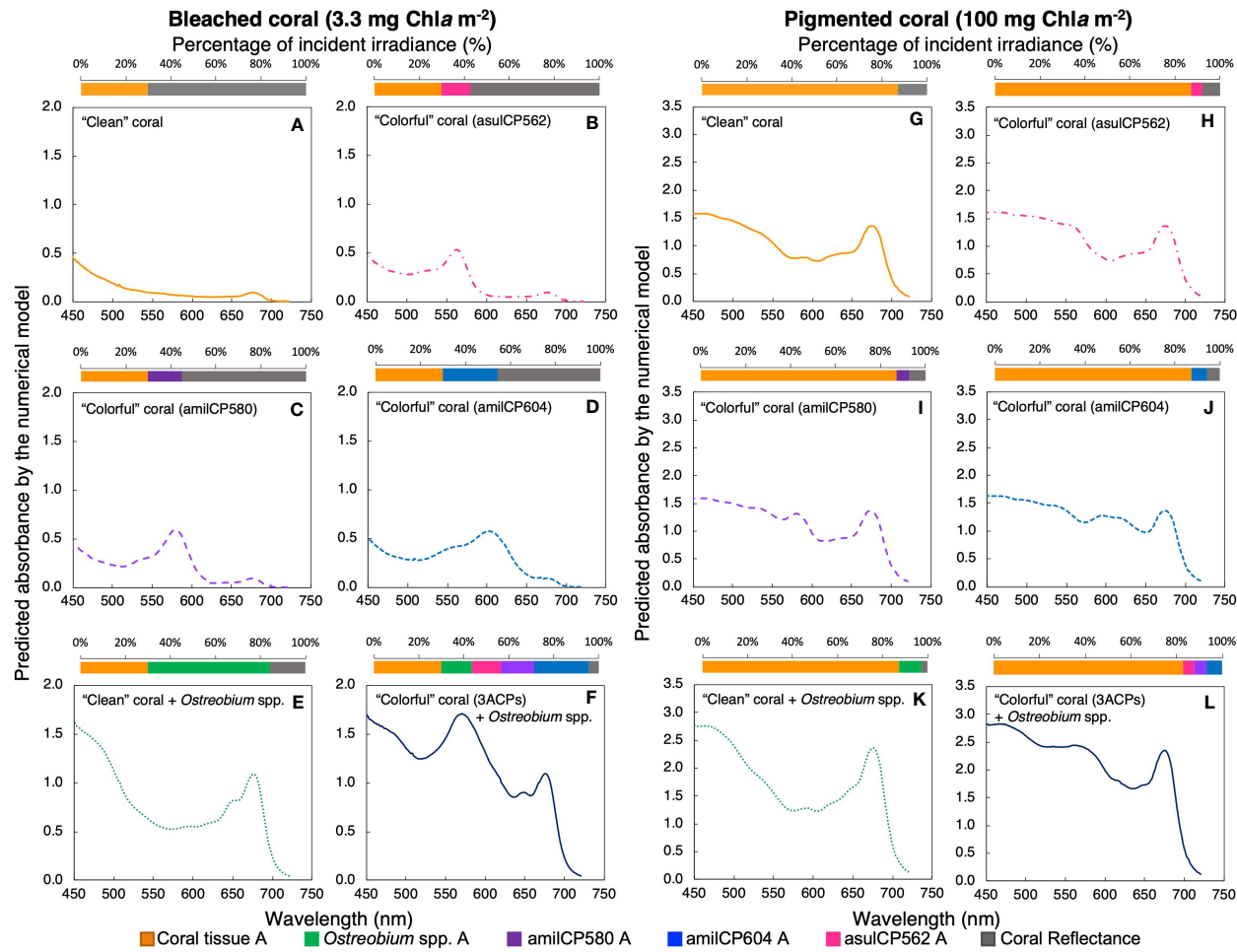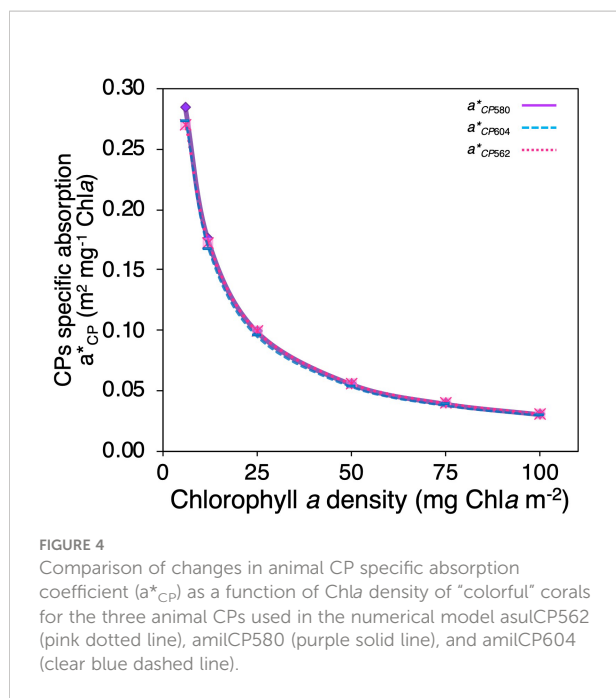
FIGURE 3

Predicted absorption spectra for a bleached (**A-F**, 3.3 mg Chl*a* m^{-2}) and a pigmented coral (**G-L**, 100 mg Chl*a* m^{-2}) under different scenarios: a coral with a white skeleton (yellow solid line, **A, G**), a coral with the chromoprotein asulCP562 upregulated in its tissue (pink dotted line, **B, H**), a coral with the chromoprotein amilCP580 upregulated in its tissue (purple dashed line, **C, I**), a coral with the chromoprotein amilCP604 upregulated in its tissue (clear blue dotted line, **D, J**), a coral with an *Ostreobium* bloom in the skeletal surface (green dotted line, **E, K**), and a coral with the three chromoproteins upregulated in its tissue and an *Ostreobium* bloom in the skeletal surface (navy blue solid line, **F, L**). Superior panels indicate the percentage of incident PAR utilized by each pigmented layer: coral tissue (yellow), chromoprotein asulCP562 (pink), chromoprotein amilCP580 (purple), chromoprotein amilCP604 (blue), *Ostreobium* spp. (green), and coral reflectance (gray).

FIGURE 4

Comparison of changes in animal CP specific absorption coefficient (a*$_{CP}$) as a function of Chl$a$ density of "colorful" corals for the three animal CPs used in the numerical model asulCP562 (pink dotted line), amilCP580 (purple solid line), and amilCP604 (clear blue dashed line).

corals (Figure 5G; Figure 6). In contrast, the presence of *Ostreobium* spp. near the skeletal surface can reduce up to 53% of the light environment *in hospite* of the symbionts (Figure 5E; Figure 6).
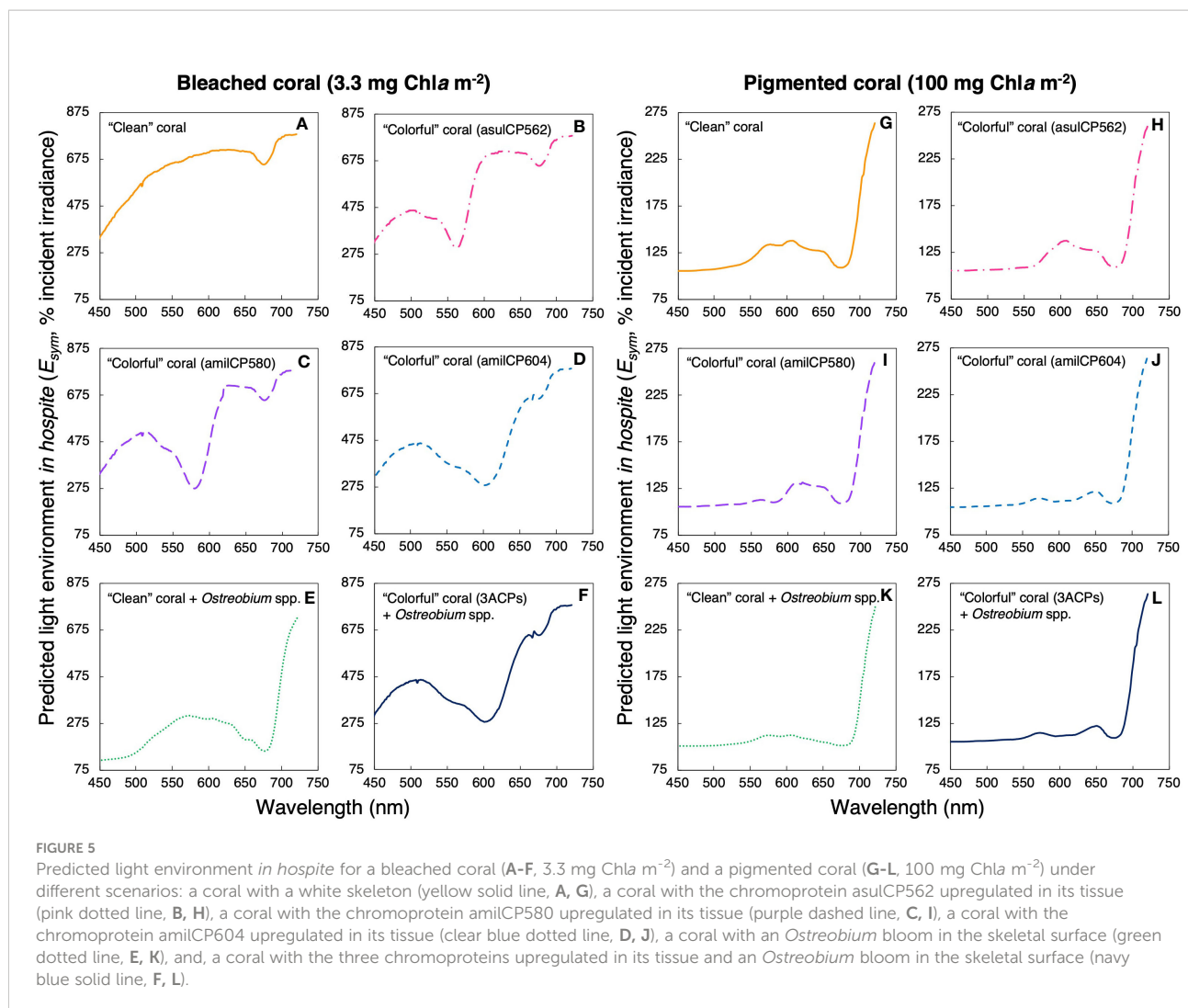
4 Discussion

The use of numerical models allows us to predict light absorbance spectra in corals (Figure 3) under different scenarios of pigment composition in their tissue and/or skeleton (Figure 1). Models determine the percentage of incident light absorbed by each component and variations in coral skeleton's reflectance, allowing estimation of potential changes in the light environment *in hospite* of the symbiotic dinoflagellates (Figures 5, 6). Our simulations indicated that reductions in light absorption in bleached corals, due to decreases in Chl$a$ density, may increase up to three times the internal light field of bleached corals, and that the main determinant is the presence of a highly reflective coral skeleton (Figures 5A, G). However, the presence of optical dampers in the tissue and/or the coral skeleton allows for significant reductions in the light environment *in hospite* (Figure 5). When corals upregulate the production of CPs in their tissue, the light environment *in hospite* of the symbionts reduces between 11- 24% in colorful bleached corals relative to "clean" bleached corals. (Figures 5B-D). Interestingly, when *Ostreobium* spp. increase in abundance near the skeletal surface, "colorful" bleached corals can reduce

up to 53% of the light environment *in hospite* of the symbionts (Figure 5F).

Measurements of *in vivo* scalar irradiances within tissues of bleached corals have documented 20% reductions in irradiances at the animal CP absorption peaks when they are present (Bollati et al., 2022). Our model predicts similar reductions for the CPs reported by Bollati et al. (2022). It also supports the critical contribution of animal CPs to the regulation of the spectral distribution and intensity of the light environment of the symbionts *in hospite* (Figure 6), according to their light absorption characteristics (Salih et al., 2000; Dove et al., 2001). Photoconversion has been suggested as another possible role of animal CPs (Wiedenmann et al., 2004; Bollati et al., 2022). This phenomenon denotes the capacity of a particular group of green fluorescent pigments (GFP), known as photoconvertibles RFPs (pcRFPs), to absorb light in the blue-green range and reemit it in the orange-red range (Wiedenmann et al., 2004; Bollati et al., 2022). However, considering that dinoflagellates have poor light absorption in the orange range, animal CPs photoconversion may not be as relevant in enhancing their photosynthetic activity (Ben-Zvi et al., 2021). Indeed, the number of photons generated through photoconversion is insignificant compared to those provided by ambient light (Bollati et al., 2022).

The effect of animal CPs on the light environment within coral tissues varies depending on the type and density of the CPs and symbiont pigment density (Figure 6). A combination of CPs has a more substantial effect damping the light environment within bleached corals than the presence of a single type of CPs (Figure 6). In this sense, the combination of animal CPs in addition with a bloom of the endolithic algae *Ostreobium* spp. near the skeletal surface, produce the largest light attenuation in our simulations (Figure 5; Figure 6) due to the synergistic effect of the increases in light absorption and reductions in skeleton light scattering. Moreover, model predictions indicate that the combination of the three animal CPs used in our simulations and coral pigmentation values above 50 mg Chl$a$ m^{-2} allow the coral to absorb most of the light available in the tissue (Figure 3L). This condition minimizes the amount of incident light reaching the skeleton, with the consequent control of *Ostreobium* spp. blooms. Therefore, the last scenario simulated in the model could only occur in low-pigmented corals (<40 mg Chl$a$ m^{-2}).

Multiple light scattering on coral skeleton together with reductions in Chl$a$ density during stressful conditions could affect both the animal CPs upregulation as well their efficiency of light absorption. As the upregulation of CPs in corals can be stimulated with light around 450 nm (D'Angelo et al., 2008; Bollati et al., 2020), the amplification of the light environment due to reductions in coral Chl$a$ density also involves higher levels of blue light within the coral tissue (Figure 5), and in consequence, facilitates animal CPs upregulation before the bleached phenotype

FIGURE 5
Predicted light environment *in hospite* for a bleached coral (**A-F**, 3.3 mg Chl*a* m⁻²) and a pigmented coral (**G-L**, 100 mg Chl*a* m⁻²) under different scenarios: a coral with a white skeleton (yellow solid line, **A, G**), a coral with the chromoprotein asulCP562 upregulated in its tissue (pink dotted line, **B, H**), a coral with the chromoprotein amilCP580 upregulated in its tissue (purple dashed line, **C, I**), a coral with the chromoprotein amilCP604 upregulated in its tissue (clear blue dotted line, **D, J**), a coral with an *Ostreobium* bloom in the skeletal surface (green dotted line, **E, K**), and, a coral with the three chromoproteins upregulated in its tissue and an *Ostreobium* bloom in the skeletal surface (navy blue solid line, **F, L**).

is expressed (Gómez-Campo et al., 2022). Accordingly, bleaching may not be necessary for inducing animal CPs upregulation (Bollati et al., 2020) as a small reduction in pigment density could be enough to enhance blue light levels within coral tissues. In addition, the amplification of the light environment enhances light availability in all wavelengths in the PAR range, increasing the probability of light absorption by both pigment types, symbiotic and animal. This effect can be quantified by each pigment's specific absorption coefficients (a*). Significant enhancement in light absorption efficiency of Chl*a* (a^*_{Chla}) at low pigmentation has already been documented (Enríquez et al., 2005; Scheufen et al., 2017a; Scheufen et al., 2017b), and our analysis estimated similar enhancements for animal CPs pigments (a^*_{CP}) in bleached/paled coral tissue (Figure 4). This finding supports the capacity of animal CPs to act as optical dampers, even at small concentrations.

The presence of animal CPs in the coral tissue could simply be considered as a mechanism that facilitates coral recovery after

bleaching (Bollati et al., 2020; Bollati et al., 2022). However, our results also support their utility in preventing the induction of the optical feedback loop that leads to the development of the bleached coral phenotype (Gómez-Campo et al., 2022). Contrary to CPs upregulation, *Ostreobium* spp. require a substantial reduction in Chl*a* density to bloom near the skeletal surface. Once *Ostreobium* spp. blooms, its presence near the skeletal surface can also modify the light environment *in hospite* of the symbionts (Galindo-Martínez et al., 2022). This coral condition facilitates coral recovery after bleaching and may help in future bleaching events. Consequently, the effect of the combination of both mechanisms (CPs upregulation and *Ostreobium* spp. blooms) on the optical properties of coral tissue and skeleton creates less efficient corals for light absorption but more robust under heat stress and with a higher capacity of recovery after bleaching.

Finally, the light absorption properties of each CP determine its specific characteristics as a light-damper. Consequently, differences in coral vulnerability to bleach under thermal stress
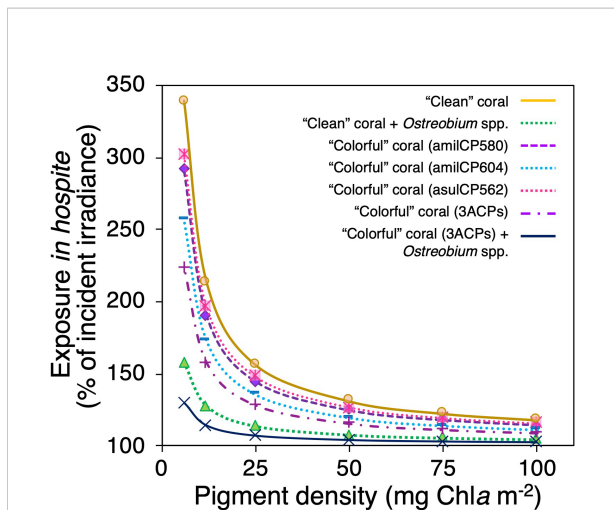
FIGURE 6

Modification of the light environment *in hospite* as a function of the pigment content for different coral scenarios, a "clean" coral with a white skeleton (yellow solid line), a coral with an *Ostreobium* bloom in the skeletal surface (green dotted line), a "colorful" coral with the chromoprotein asulCP562 upregulated in its tissue (pink dotted line), a "colorful" coral with the chromoprotein amilCP580 upregulated in its tissue (purple dashed line), a "colorful" coral with the chromoprotein amilCP604 upregulated in its tissue (clear blue dotted line), a "colorful" coral with the three chromoproteins upregulated in its tissue (purple dotted-dashed line), and a "colorful" coral with the three chromoproteins upregulated in its tissue and with an *Ostreobium* bloom in the skeletal surface (navy blue solid line).

or the coral's ability for recovery after bleaching may also be regulated by the coral's ability to maintain/enhance animal CPs production and/or the type of animal pigment upregulated. More research is still needed to understand further possible trade-offs in coral physiology associated with animal CPs production. However, their presence and variability in coral tissues could be an excellent criterion when considering species for coral restoration efforts.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

CG-M and RI-P designed the research; CG-M and AC participated in data collection; CG-M analyzed data and created the numerical model; CG-M performed numerical model simulations; CG-M, SE, and RI-P wrote the paper. All authors contributed to the article and approved the submitted version.

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.2022.1029201/full#supplementary-material

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