

Effect of environmental light conditions on the growth of the coral *Orbicella faveolata* in the Mexican Caribbean

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ABSTRACT. Massive corals of the genus *Orbicella* are key organisms that help maintain the physical structure of Caribbean reefs. However, they are currently threatened by environmental changes, such as increased nutrient loads and pollution, which affect the optical properties of seawater and, consequently, limit reef development. Thus, analyzing the responses in the growth of coral species to changes in light environments can help us improve mitigation and conservation strategies for coral reefs. The objective of this study was to evaluate the effect of changes in environmental light conditions on the growth rate of *Orbicella faveolata* by comparing fragments transplanted from 9 m to 3 m depth and control fragments that were transplanted under the same light conditions (3 m). The fragments of both treatments showed similar growth (16–23%), as well as comparable extension and diameter values. The annual growth rate for the control fragments and transplantation treatment fragments was $1.04 \pm 0.18 \text{ cm} \cdot \text{y}^{-1}$ and $1.11 \pm 0.23 \text{ cm} \cdot \text{y}^{-1}$, respectively. The results of this study reveal that the coral *O. faveolata* can physiologically acclimate to new environmental light conditions after being transplanted from a deep environment to a shallow environment in the short-term (1–9 months). This suggests great potential for the use of *O. faveolata* in restoration strategies and management programs that aim to maintain the populations and structural framework of coral reefs in the Caribbean region.

Key words: coral fragments, coral reefs, coral transplantation, massive corals, skeletal growth.

INTRODUCTION

Coral reefs are among the most complex and diverse ecosystems on the planet. They are characterized as sites for feeding, reproduction, and shelter and host approximately 25% of all marine species (Sheppard et al. 2009, Veron 2010). Coral reefs are marine benthic formations formed by the accumulation of biogenic calcium carbonate (CaCO_3) secreted by calcifying organisms, such as hermatypic corals, mollusks, and coralline algae (Sheppard et al. 2009). As primary producers, hermatypic corals play a key role in forming these physical structures; under optimal conditions, they can generate up to $10 \text{ kg of CaCO}_3 \cdot \text{m}^3 \cdot \text{y}^{-1}$ (Chave et al. 1972,

Kleypas et al. 1999). In addition to increasing the three-dimensionality and complexity of habitats, hermatypic corals are fundamental to the balance of various biogeochemical cycles and ecosystem services (Perry and Alvarez-Filip 2018).

Hermatypic corals have the ability to form exoskeletons by precipitating CaCO_3 in the form of aragonite crystals. This process is controlled by intrinsic factors, such as genotypic variation, symbiotic community, morphology, and coral sex, as well as extrinsic factors, such as temperature, seawater chemistry, and light environment (Foster et al. 1979, Todd 2008, Allemand et al. 2011). Coral growth rates depend on carbonate calcification, which requires energy resources

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derived from photosynthesis, which are translocated by symbionts (Colombo-Pallota et al. 2010).

Both the symbiont and the host show outstanding phenotypic plasticity that allows them to develop in different light and hydrodynamic environments (Kaniewska et al. 2011). The skeletal architecture built by each polyp plays an important role in the internal light environment; optical (reflective) properties of the skeleton cause multiple light scattering, favoring photosynthesis in symbiont algae (Enríquez et al. 2017). Therefore, the role of the symbiotic community in the translocation of energy to the coral for the production of CaCO₃ and construction of its skeleton is highly relevant (Enríquez et al. 2005, 2017; Colombo-Pallotta et al. 2010, Scheufen et al. 2017). In this sense, the absorption and reflection properties of hermatypic coral skeletons depend on the structural arrangement that makes up their internal architecture, which modulates the dispersion of light, influencing the amount of energy available for the metabolic processes of the host (Enríquez et al. 2017). Therefore, depending on light conditions, corals can have different morphologies at the corallite level and at the colony level (Graus and Macintyre 1976, 1982; Klaus et al. 2007). In conditions of low light availability (>20 m), corals generally show plating morphologies to capture the greatest amount of light, whereas in conditions of greater light availability (1–5 m), corals have more complex morphologies (e.g., columnar or hemispherical), and colonies use self-shade to avoid excess light (Kramer et al. 2021).

Orbicella is one of the most important hermatypic coral genera in the Caribbean region and one of the most threatened by environmental changes, such as pollution or increased nutrients in seawater due to wastewater discharge (Rico-Ensenaro et al. 2023). Species of the genus *Orbicella* obtain energy from heterotrophic assimilation (15–35%) by feeding on zooplankton and from autotrophic assimilation (70–90%) through the translocation of nutrients from endosymbiotic algae (Houlbrèque and Ferrier-Pagès 2009, Yranzo et al. 2020). Symbiont photosynthetic products contribute the most to the energy balance needed for the survival and growth of *Orbicella* colonies (Teece et al. 2011). However, faced with changes in seawater quality (e.g., changes in optical or chemical properties), it is important to understand the effect that light environments have on the growth of corals and the phenotypic capacity of corals to acclimate to different environmental gradients (Merks et al. 2004).

Despite the important effect that light has on the morphology and phenotypic plasticity of corals, the information on the growth mechanisms associated with changes in light conditions is scarce (Todd 2008). In particular, how changes in light conditions affect coral growth has scarcely been explored. *Orbicella faveolata* is distributed over a wide depth gradient (1–50 m); thus, we believe it has great potential to acclimate physiologically to new light environments. Therefore, the objective of the present study was to evaluate the growth response of *O. faveolata* colonies transplanted

between different light habitats (i.e., deep to shallow) and assess their acclimation capacity and potential use in restoration interventions.

MATERIALS AND METHODS

Study area

The study was performed in the *Jardines* reef of the *Arrecife de Puerto Morelos* National Park (PNAPM, for its acronym in Spanish). This protected natural area was established in 1998 and is located in front of the town of Puerto Morelos in the state of Quintana Roo (21°00'00" to 20°48'33" N, 86°53'14.94" to 86°46'38.94" W; Fig. 1). The Puerto Morelos reef is a fringing coastal reef that forms an internal lagoon, with a depth of 3–5 m, characterized by calcareous sand stabilized by seagrass meadows (CONANP 2000). The area has a well-developed back reef and reef crest, a relatively flat fore reef with some massive coral sections, and several channels that gradually descend to 20–25 m toward an extensive sand platform (Rodríguez-Martínez et al. 2010). The reef zone is composed by 41 species of scleractinian corals and 32 gorgonian corals. The most abundant hermatypic coral species in the region are *O. faveolata*, *Orbicella annularis*, *Acropora palmata*, *Acropora cervicorni*, *Millepora complanata*, *Pseudodiploria strigosa*, *Montastraea cavernosa*, *Dichocoenia stokesii*, and *Agaricia tenuifolia* (Ruíz-Rentería et al. 1998, Alvarez-Filip et al. 2019, Caballero-Aragón 2020, Molina-Ramos 2020). However, in the last 5 years, live coral cover has decreased (>60%) due to the effects of thermal anomalies, hurricanes, and diseases that cause changes in species composition and dominance (Alvarez-Filip et al. 2022).

Obtaining growth parameters

For the transplantation treatment, 16 fragments of *O. faveolata* were obtained from 4 adult donor colonies of similar size (hemispherical, 40-cm height) that appeared healthy and were in the same light gradient (9 m). For the control treatment, the same procedure was done at a 3-m depth light gradient. All fragments (3 cm²) were extracted using a submersible hydraulic electric drill (Nemo Power Tools, Hong Kong, China). The fragments obtained at 9 m (transplantation treatment) were transplanted to the depth of the control fragments (3 m); all fragments were installed on 2 fiberglass beds. Each fragment was fixed to an acrylic plate using epoxy plasticine. After installation, the fragments were allowed to acclimate for 2 months to reduce the effect of handling stress (Fig. 2).

At the end of the acclimation period, during a period of 9 months, the following variables were measured monthly in each fragment: linear extension (cm), defined as the longitudinal distance from the base of the acrylic to the maximum height of the fragment, and the apical diameter (cm), defined as the maximum diameter from an aerial perspective. All

measurements were estimated from digital images (25 MP) obtained with a GoPro Hero 9 camera (San Mateo, USA) (in linear function) using a plastic vernier (accuracy 0.05 cm) as a reference scale. The images from each monthly sampling were processed for each fragment for both treatments using the ImageJ program (Schneider et al. 2012).

This study considered the environmental variables seawater temperature ($^{\circ}\text{C}$) and photosynthetically active radiation (PAR) to describe their influence on the growth of the massive coral *O. faveolata*. Daily values (May 2021 to February 2022) were obtained for both variables from the database of the *Sistema Académico de Monitoreo Meteorológico y Oceanográfico* (sammo.icmyl.unam.mx); these were averaged to obtain a monthly value for each variable.

Statistical analysis

Descriptive statistics were obtained for all monthly growth parameters (i.e., the average, standard deviation, ranges, and maximum and minimum values). The annual growth rate was obtained by extrapolating data from the 9 months of the study;

the average value of each month was used to avoid overestimating the growth. A general monthly value was obtained, which was added to each of the 3 missing months to complete the annual period. After testing the normality and homoscedasticity of the data, various one-way analyses of variance (ANOVA) were performed, using generalized linear models (GLM), to evaluate the differences in growth parameters at the treatment and time level (monthly), including their interaction. Finally, simple linear regression models (r^2) were used to evaluate the relationship between growth characteristics and environmental factors (temperature and PAR). All statistical analyses were performed in the SigmaPlot program v. 11 (Graffiti LLC, Palo Alto, USA), using a 95% confidence interval ($\alpha = 0.05$).

RESULTS

Linear extension

At the end of the experimental period, no signs of bleaching, loss, or death of tissue were observed in any of

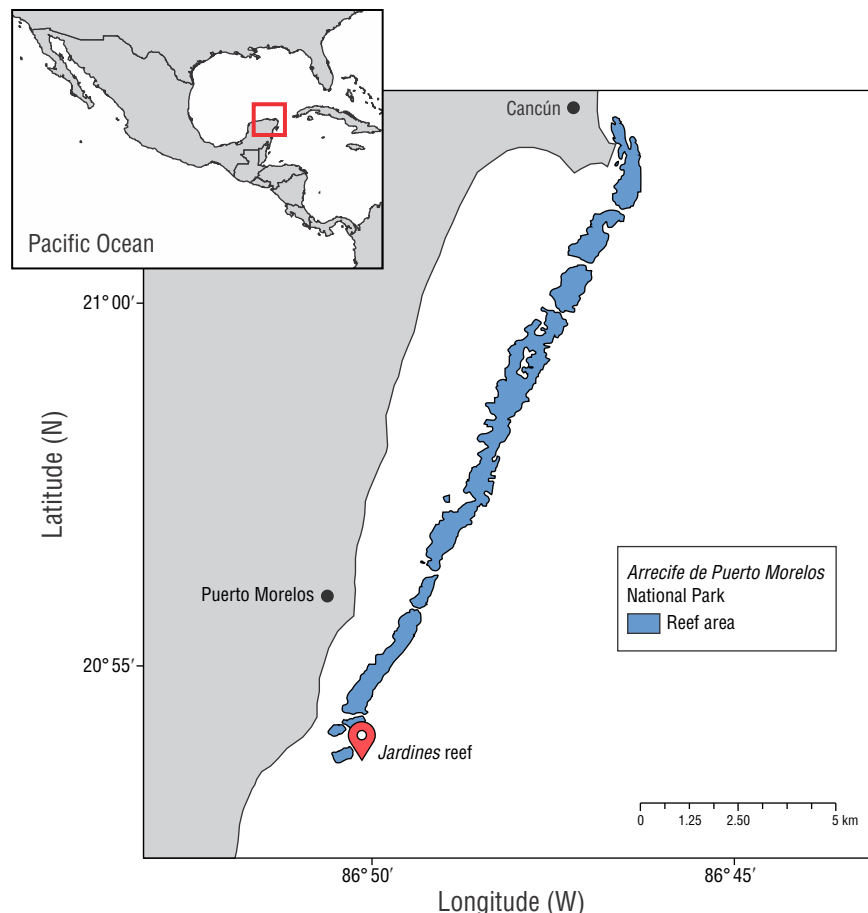


Figure 1. Map of Arrecife de Puerto Morelos National Park (APMNP), Mexico. The marker indicates the study site.

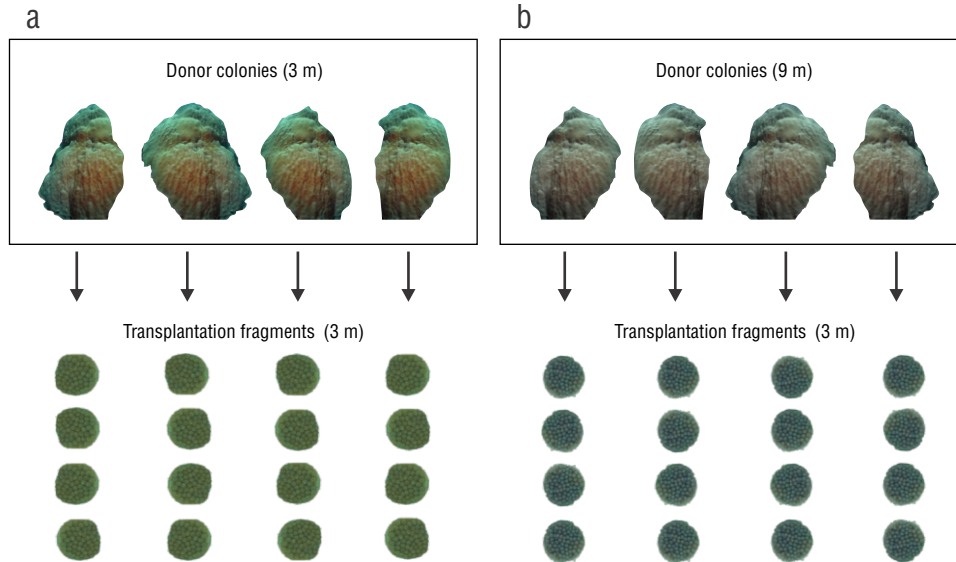


Figure 2. Experimental design. Donor coral fragments were collected at 2 depths: (a) 3 m (control treatment) and (b) 9 m (transplantation treatment). Four fragments were obtained from each donor colony, which were transplanted to a depth of 3 m.

the fragments in the 2 treatments. Growth in linear extension showed a cumulative increase of 0.74 cm for the control treatment after a 9-month period, showing a monthly growth of 0.09 ± 0.02 cm (range: 0.04–0.26) (Table 1). The transplantation treatment showed a total accumulated growth of 0.70 cm, with a monthly average of 0.08 ± 0.01 cm (range: 0.06–0.64). The annual growth of the linear extension was 1.04 ± 0.18 $\text{cm}\cdot\text{y}^{-1}$ and 1.11 ± 0.23 $\text{cm}\cdot\text{y}^{-1}$ for the control treatment and the transplanted fragments, respectively. The results obtained for the linear extension showed no significant differences between treatments ($F_{1,69} = 0.050$, $P > 0.823$), over time (months; $F_{6,69} = 2.154$, $P > 0.061$), or in interactions between both variables ($F_{6,69} = 0.745$, $P > 0.616$) (Fig. 3). The relative growth of the linear extension showed a similar increase (control: 16%; transplant: 15%) (Table 2).

Apical diameter

The total cumulative apical diameter growth for the control treatment after the study period was 0.96 cm, with a monthly average of 0.12 ± 0.02 cm (range: 0.06–0.17) (Table 1). The total cumulative growth of the transplantation treatment was 1.03 cm, with a monthly average of 0.13 ± 0.03 cm (range: 0.09–0.22). The annual growth of the apical diameter was 1.45 ± 0.67 $\text{cm}\cdot\text{y}^{-1}$ for the control treatment and 1.54 ± 0.40 $\text{cm}\cdot\text{y}^{-1}$ for the transplantation treatment.

The results of the apical diameter showed no significant differences between treatments ($F_{1,69} = 0.0641$, $P > 0.801$), over time (months; $F_{6,69} = 0.365$, $P > 0.898$), or in the interaction between variables ($F_{6,69} = 0.599$, $P > 0.730$) (Fig. 4). Apical diameter growth increased 23% for the

control treatment and 24% for the transplantation treatment (Table 2).

Environmental variables

The monthly average of the sea surface temperature for PNAPM during the study period was 28.62 °C (25.95 – 30.56 °C) (Table 1), with the highest values during the months of August and September (~ 30.32 °C) and the lowest values in January and February (~ 26.21 °C). Irradiance remained at an average of $52,286$ $\mu\text{mol}\cdot\text{quanta}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, with the lowest values in November ($42,145$ $\mu\text{mol}\cdot\text{quanta}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) and maximum values in August ($60,112$ $\mu\text{mol}\cdot\text{quanta}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) (Table 1). August showed the highest values for temperature and light incidence; however, the results of the linear regression models showed no deterministic relationship (r^2) between the environmental variables, or with the linear extension ($P > 0.05$), or with the apical diameter ($P > 0.05$).

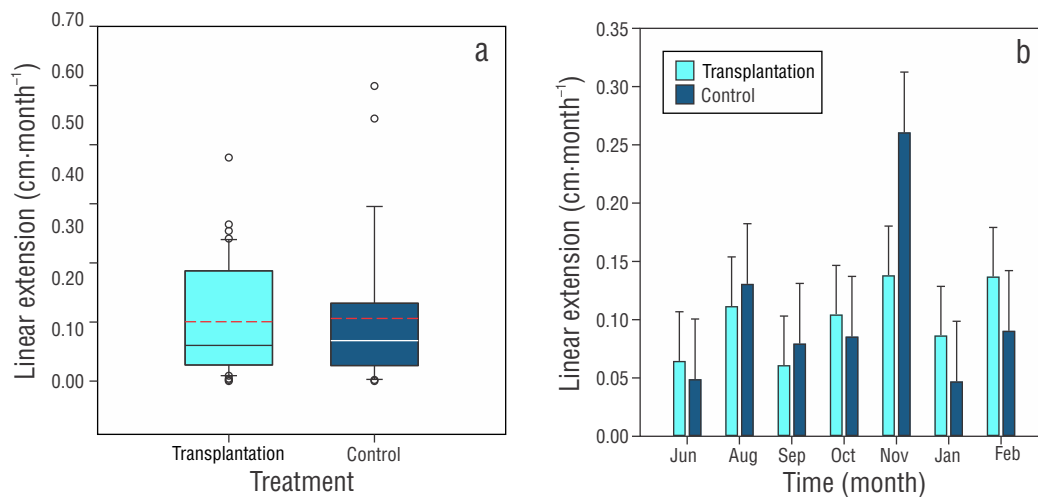
DISCUSSION

In corals, skeletal growth is controlled by various factors, such as salinity, nutrients, exposure to waves, sedimentation, aragonite saturation state, temperature, and light; the last 2 factors have the most influence (Nybakken 2001, Sheppard et al. 2009, Veron 2010, Calderón-Aguilera et al. 2017). In the case of light, it has been proposed that the average calcification rate and extension rate decrease proportionally as irradiance decreases with increasing depth (Dustan 1975, Bosscher 1993). Conversely, in shallow waters, irradiance can reach excessive energy levels and

Table 1. Growth variables ($\text{cm} \cdot \text{month}^{-1}$) measured in *Orbicella faveolata* fragments for the transplantation and control treatments at 3-m depth and environmental variables measured in the *Arrecife de Puerto Morelos* National Park (PNANP, for its acronym in Spanish).

Month	Transplantation		Control		Temperature (°C)	PAR ($\mu\text{mol} \cdot \text{quanta} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$)
	Linear extension (cm)	Apical diameter (cm)	Linear extension (cm)	Apical diameter (cm)		
June	0.64 ± 0.67	0.15 ± 0.15	0.04 ± 0.05	0.06 ± 0.11	29.61 ± 1.09	$52,539 \pm 39,084$
August	0.11 ± 0.09	0.18 ± 0.16	0.13 ± 0.10	0.12 ± 0.17	30.56 ± 1.10	$60,112 \pm 40,072$
September	0.06 ± 0.07	0.09 ± 0.07	0.07 ± 0.05	0.17 ± 0.18	30.09 ± 0.97	$54,275 \pm 38,510$
October	0.10 ± 0.07	0.17 ± 0.08	0.08 ± 0.07	0.14 ± 0.12	29.94 ± 0.88	$54,513 \pm 34,755$
November	0.13 ± 0.14	0.09 ± 0.04	0.26 ± 0.24	0.14 ± 0.11	27.21 ± 0.87	$42,145 \pm 28,672$
January	0.08 ± 0.10	0.10 ± 0.06	0.04 ± 0.01	0.16 ± 0.21	25.95 ± 1.15	$42,612 \pm 30,077$
February	0.13 ± 0.09	0.22 ± 0.19	0.09 ± 0.06	0.15 ± 0.21	26.48 ± 1.10	$52,144 \pm 34,325$

PAR: photosynthetically active radiation

**Figure 3.** Boxplots of the average monthly growth of the linear extension (\pm SD) of *Orbicella faveolata* at 3-m depth over 9 months by (a) treatment (the black line represents the median, and the dashed red line denotes the mean) and (b) over time (months).

cause photodamage due to oxidative stress (increase in reactive oxygen species) that reduces the photosynthetic capacity of the symbiont algae (Todd et al. 2004, Rodríguez-Troncoso et al. 2014).

Previous studies focused on the relationship between coral morphology and light show that colonies modify their morphology to flatter shapes with increasing depth to increase their ability to capture light (Graus and Macintyre 1982, Willis 1987, Gutiérrez-Estrada 2017, Prada et al. 2022). Ow and Todd (2010) suggested that these morphological changes provide a long-term solution that requires less energy investment compared to the energy required for physiological adjustments.

The effect of light intensity on the characteristics and morphology of skeletal growth in hermatypic corals has been studied previously (Graus and Macintyre 1982, Hubbard and Scature 1985, Carricart-Ganivet et al. 2007, Todd 2008, Gutiérrez-Estrada 2017, Mallon et al. 2022). However, the effect of coral transplantation between depths with different environmental light conditions has been unexplored. This study shows a rapid response in the skeletal growth of the coral *O. faveolata* and its short-term physiological plasticity (1–9 months), which could be a mechanism to compensate the effects of transplantation between sites with different light gradients. Therefore, the coral *O. faveolata* shows physiological plasticity in the short-term that possibly entails

morphotypic modification in the long-term (>1 year), which allows it to acclimate to new light environments.

Reports indicate that, in the Caribbean Sea, corals of the genus *Orbicella* are physiologically capable of living in shallow and deep habitats for at least 6 months after being transplanted (transplantation from shallow habitat to deep habitat and from deep habitat to shallow habitat) (Prada et al. 2022). This finding coincides with the results obtained in this study; *O. faveolata* showed physiological plasticity (in terms of growth) in response to changes in light and depth conditions. This could show that corals of the genus *Orbicella* have adapted to different light environments through an energy balance via autotrophy and heterotrophy in relation to light availability (Prada et al. 2022).

Our results demonstrated that the transplanted colonies quickly reached the growth rate of the control colonies and showed similar monthly growth during the 9-month period of the study. At 3 m depth, the annual linear extension for the control treatment and the transplantation treatment was $1.04 \text{ cm}\cdot\text{y}^{-1}$ and $1.11 \text{ cm}\cdot\text{y}^{-1}$, respectively. These results contrast with the extension rate ($0.80 \text{ cm}\cdot\text{y}^{-1}$) reported for *O. faveolata* at 9 m depth in the Mexican Caribbean (Gutiérrez-Estrada 2017). A similar pattern has been reported in Florida (USA), where the linear extension of colonies in the shallow zone was higher than that of colonies in the deep zone (>6 m) during the same time period (Manzello et al. 2015). Gutiérrez-Estrada (2017) suggested that this could be due to the fact that skeletal extension depends on the number

Table 2. Increase in monthly growth percentage (%) for the linear extension and apical diameter variables in *Orbicella faveolata* fragments for the control and transplantation treatments at 3-m depth.

Month	Trasplantation		Control	
	Linear extension (cm)	Apical diameter (cm)	Linear extension (cm)	Apical diameter (cm)
June	1.37 ± 1.34	3.92 ± 3.92	1.38 ± 1.88	1.67 ± 2.84
August	2.44 ± 2.44	4.78 ± 4.70	3.50 ± 3.70	3.05 ± 4.36
September	1.16 ± 1.32	2.03 ± 1.82	1.78 ± 1.56	4.11 ± 4.33
October	2.34 ± 2.05	3.86 ± 1.90	2.08 ± 2.23	3.55 ± 3.62
November	2.54 ± 2.69	1.96 ± 0.99	4.70 ± 4.36	3.27 ± 2.72
January	2.08 ± 3.14	2.31 ± 1.60	0.88 ± 0.21	3.70 ± 5.07
February	3.07 ± 2.70	4.83 ± 4.38	1.81 ± 1.31	3.15 ± 4.23

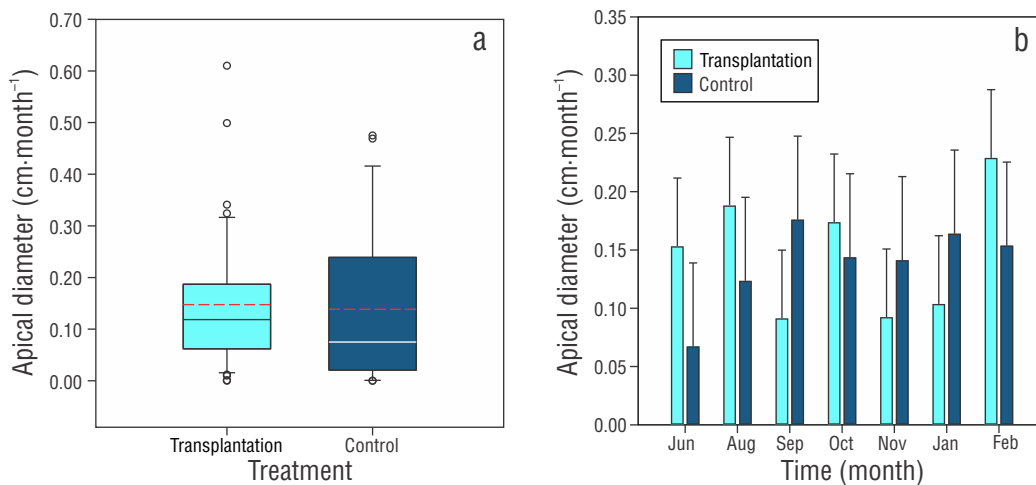


Figure 4. Boxplots of the average monthly growth of the apical diameter (\pm SD) of *Orbicella faveolata* at 3-m depth over 9 months by (a) treatment (the black line represents the median, and the dashed red line represents the mean) and (b) over time (months).

of exothecal dissepiments deposited per year, whereas density depends on their thickness, which are directly influenced by blue (lunar) light and conditions detected by corals at relatively shallow depths.

In light environments that facilitate optimal growth, massive colonies of *Porites* have been observed to exhibit higher growth in linear extension in contrast to colonies located in environments with high turbidity (Lough et al. 1999). Furthermore, reports indicate that colonies transplanted to shallower environments show increased lateral extension (diameter), which coincides with the results of the present study (Table 1). This could be explained by the size of the coral fragments (3–3.5 cm²), because, when a sexually mature colony fragments, the coral resources are allocated to growth and calcification processes instead of gametogenesis (Forsman et al. 2015). In this context, the transplant site and genotype of origin can influence calcification rates, resulting in an interaction effect between environmental and parental factors on the skeletal characteristics of massive corals (Smith et al. 2007). This could suggest that colony morphology varies depending on habitat, which results in high phenotypic plasticity in the skeletal characteristics of corals (Smith et al. 2007).

Previous reports with similar methodologies have found that coral species, such as *Turbinaria mesenterina*, found at depths of 1 m (shallow) and 4 m (deep) were able to adapt to the environmental conditions of both depths after transplantation; nevertheless, their growth was lower in the deep zone (Willis 1987). Other species of massive corals have shown similar patterns when transplanted to different environments. For example, Ow and Todd (2010) found higher growth in *Goniastrea pectinata* colonies transplanted to a depth of 7 m in contrast to the growth of colonies transplanted to a depth of 3 m after a short period (163 days). This could be explained by the high phenotypic plasticity and photo adaptive response to light irradiance of some genera of massive corals, such as *Porites* and *Orbicella*, which allow them to distribute over a depth light gradient (Smith et al. 2007, Todd 2008).

CONCLUSIONS

The results indicate that there were no significant differences in the linear extension or apical diameter between treatments and time periods (months). Therefore, the coral *O. faveolata* has the potential to acclimate to new environmental light conditions after being transplanted from a deep environment to a shallow environment in a short period of time. Furthermore, we suggest that transplanted colonies can achieve growth rates similar to those of control colonies relatively fast (1–9 months), which demonstrates phenotypic plasticity to changes in their light environment. Focusing on the lateral extension of the colonies, we observed a higher increase in diameter compared to the linear extension in both treatments; therefore, we can conclude that the colonies of

both treatments used the available resources to repair the periphery damage caused by fragmentation.

However, the study period was relatively short to determine if the short-term response will be beneficial in the long term or if the survival and health of the colony will be compromised in the future. Therefore, we suggest conducting similar studies that consider long-term time periods (>9 months). The information from this study reveals that *O. faveolata* colonies transplanted from a deep to a shallow environment have the potential to acclimate to new light conditions in a short period of time.

English translation by Claudia Michel-Villalobos.

DECLARATIONS

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

Conceptualization: GGE, JJATL, and JPCG; Data curation: JLJ; Formal analysis: JJATL and JLJ; Funding acquisition: JPCG; Methodology: GGE, JJATL; Software: JLJ and JJATL; Supervision: JJATL and JPCG; Validation: GGE, JJATL, and JPCG; Visualization: JLJ and JJATL; Writing—original draft: JLJ and JJATL; Writing—review and editing: JLJ, JJATL, GGE, and JPCG.

Data availability

The data for this study are available from the corresponding author upon reasonable request.

Use of AI tools

The authors did not use any artificial intelligence tools for this work.

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