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SHORT COMMUNICATION

Physical contact stress can trigger larval release in the brooding coral *Siderastrea stellata*

Ana Carolina Grillo[1,2] · **Guilherme Ortigara Longo**[1]

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Abstract

Abiotic and biotic stressors are known to trigger reproductive activities in several aquatic organisms. In reef environments, physical contact as a response to competition for space on the benthos is a common stressor among sessile organisms, often leading to severe tissue damage and even mortality due to biological and chemical mechanisms. However, the effect of physical stress on coral reproduction has received less attention. In this study, we observed colonies of the scleractinian coral *Siderastrea stellata* releasing larvae in response to physical contact with the zoantharian *Palythoa caribaeorum*. Organisms were collected from reefs in Brazil and taken to the laboratory, where competition through physical contact was simulated in tanks by placing the two species in direct contact for 72 h. During this period, seven out of eight corals that were in physical contact with the zoantharian released larvae, showing tissue discoloration and a marked decrease in photosynthetic efficiency. Only one of the other eight colonies held as a control with no physical contact released larvae, indicating that physical contact may have been the trigger for larval release. This is, to our knowledge, the first report of physical contact-induced larval release in a scleractinian species, providing grounds for further investigating the potential mechanisms involved in this phenomenon.

Keywords Coral reproduction · Coral spawning · Ecological interactions · Spatial competition · *Palythoa caribaeorum*

Introduction

Environmental and biological cues are widely known to induce reproductive activities in aquatic organisms, including water temperature, pheromones that synchronize fish spawning (Kobayashi et al. 2002; Vine et al. 2019), and solar and lunar cycles that trigger spawning in corals (Boch et al. 2011; Lin et al. 2021). Spawning events in marine invertebrates have also been associated with short-term acute stress. For example, heat shock is commonly used to stimulate spawning in sea cucumbers, oysters, and giant clams in aquaculture (Morgan 2000; Battaglene et al. 2002; Mies and Sumida 2012); light shocks stimulate spawning in bryozoans and ascidians (Marshall and Keough 2004); and sea urchins often spawn when handled and transported in dry environments (James and Evensen 2022). In hard corals, larval release has been documented following changes in pH and oil pollution (Loya and Rinkevich 1979; Petersen and Van Moorsel 2005), and soft corals can propagate after mechanical damage (Henry et al. 2003), pointing to stress as a common factor triggering reproductive activities in these organisms.

In sessile benthic invertebrates, competition for space through physical contact is a common source of stress given an often limited space availability for settlement and growth (Chadwick and Morrow 2011). Sessile benthic organisms can preempt space using physical means to harm neighboring organisms, by overgrowing, overtopping, or abrading them, but also using chemicals, by releasing harmful secondary metabolites (McCook et al. 2001; Chadwick and Morrow 2011). Moreover, the modular construction in colonial invertebrates allows them to allocate different energetic resources according to the requirements of their specific polyps (Hughes 2005). This trade-off allows colonial sessile organisms to

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Ana Carolina Grillo
a.grillomonteiro@gmail.com

1 Marine Ecology Laboratory, Department of Oceanography and Limnology, Universidade Federal Do Rio Grande Do Norte, Natal, RN, Brazil

2 College of Science and Engineering, James Cook University, Townsville, QLD, Australia

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display different responses to competitive or environmental stress within the same colony and might represent an adaptative strategy to escape from detrimental situations (Sammarco 1982; Dias et al. 2008).

The zoantharian *Palythoa caribaeorum* Duchassaing & Michelotti, 1860 (Cnidaria: Anthozoa: Zoantharia: Sphenopidae), commonly found in shallow reefs of the Western Atlantic, is a strong competitor and has been recorded overgrowing and killing several sessile organisms, including sponges, gorgonians, scleractinian corals, and hydrocorals (Suchanek and Green 1981). Regardless of the mechanisms employed by this zoantharian, physical contact is mostly detrimental to corals, causing tissue discoloration, reduction in photosynthetic efficiency, and necrosis (Lonzetti et al. 2022; Grillo et al. 2024). Furthermore, changes in both sexual and asexual reproductive strategies following environmental and competitive stress have been recorded for other invertebrates (Hughes et al. 2003; Dias et al. 2008). It is unclear, however, if stress following physical contact with a competitor may affect spawning in corals. Here, we document an unexpected larval release response of the scleractinian coral *Siderastrea stellata* Verrill, 1868, following a simulated contact interaction with *P. caribaeorum* in laboratory conditions.

Materials and methods

The organisms were collected in shallow coastal reefs of Northeastern Brazil (APARC – Coral Reefs Marine Protected Area; 5° 12′ 34.4″S, 35° 21′ 46.4″W) in December 2021. We collected 16 healthy colonies of the scleractinian coral *S. stellata* (~5 cm diameter) and 8 fragments of the zoantharian *P. caribaeorum* (~10 cm^2 area). Specimens were transported to the laboratory, 70 km from the collection site, and left to acclimatize for 5 days under ambient conditions in separate tanks (27.7 °C, salinity 37 psu, pH 8.2). This study was initially delineated as a pilot experiment for a wider research looking into competition between corals, macroalgae, and zoantharians (Grillo et al. 2024).

We used two different recirculating systems, each divided in four 30-L connected tanks, and we placed two coral colonies in each tank ($n = 16$): one physically contacting the zoantharian and another placed ~5 cm away from the contacting pair as a control (totalizing eight interacting groups). The interactions lasted 72 h. Because of the massive morphology of the corals, the zoantharian fragments were carefully attached to the colonies with cable ties to simulate competition through physical contact and with the polyps of both organisms facing each other to guarantee a contacted area in the corals (refer to Supplementary Information in Grillo et al. (2024) for the manipulation setup). Although in the field this interaction mainly occurs through the edges of the colonies, another study has obtained similar results to field interactions using this approach and different responses from corals when using an inert mimic (Lonzetti et al. 2022).

Every 24 h, during 3 days, the zoantharian was carefully detached to analyze the photosynthetic efficiency of corals (effective quantum yield; *Y*) using a pulse-amplitude modulated (PAM) fluorometer (Diving-PAM underwater fluorometer; Walz, Germany), after which the contact was reestablished.

We conducted a Fisher's exact test to confirm the influence of physical interactions (contact and non-contact coral colonies) on the spawning activity of corals (categorical variables) and a Kruskal–Wallis test to investigate differences in the photosynthetic efficiency (response variable) between contact and non-contact areas within coral colonies (independent variable). Statistical tests were run using R in RStudio (R Core Team, v.4.2.3).

Results and discussion

Before the end of the interaction period (after 24–48 h of interaction), seven out of the eight contacted corals released larvae, while only one control colony out of eight had a similar response ($p < 0.05$, Fisher's exact test). We could not observe if the larvae were fully developed nor if they were able to settle upon release, but they were motile (Supplementary Material 1). Among the contacted colonies, only the polyps that were in direct physical contact with the zoantharian released larvae (Fig. 1). These polyps further suffered local discoloration and reduction of photosynthetic efficiency, which was not observed in the rest of the colonies (average *Y* of contacted area: 0.136 ± 0.007 SE; average *Y* of adjacent area not contacted: 0.822 ± 0.016 SE; $p < 0.01$, Kruskal–Wallis test; Fig. 1).

In corals, environmental factors are considered cues for spawning events in nature, like lunar and solar light (Boch et al. 2011), solar insolation (Van Woesik et al. 2006), and rapid increases in sea surface temperature (Keith et al. 2016). Reproductive activity has also been observed following other conditions considered stressful, including rapid increases in pH (Petersen and Van Moorsel 2005), chemical pollution in the water by oil and alcohol (Loya and Rinkevich 1979), and mechanical disturbance (Henry et al. 2003), although these could later negatively affect the survival of larvae and colonies (Loya and Rinkevich 1979; Henry et al. 2003). Our experiment did not involve changes in overall environmental parameters in the aquariums, but the interacting corals underwent physical stress by contacting the zoantharian that triggered spawning. This is further enforced by the differences observed

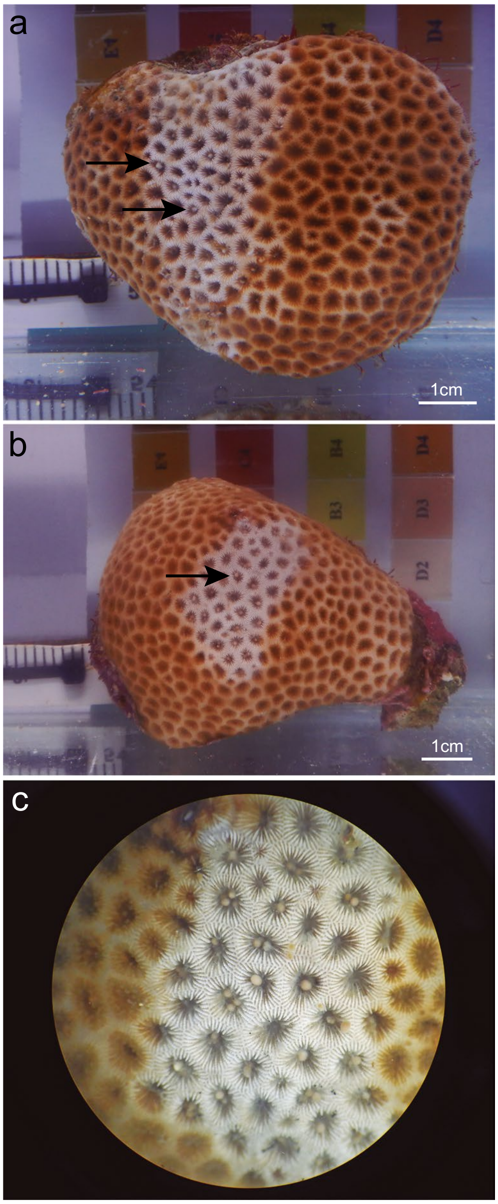

Fig. 1 **a**, **b** Tissue damage in the brooding coral *Siderastrea stellata* when in physical contact with the zoantharian *Palythoa caribaeorum* (white band). Arrows point to larvae that are being released by polyps that were previously interacting with the zoantharian. **c** Close-up of polyps releasing larvae, seen at the microscope

between contacted and non-contacted areas of the same colonies.

The zoantharian *P. caribaeorum* is known to outcompete corals using biological mechanisms that allow it to quickly overgrow coral colonies (Suchanek and Green 1981; Bastidas and Bone 1996) and release chemical toxic compounds that can damage corals' tissue upon contact (Suchanek and Green 1981; Lonzetti et al. 2022). The interaction in our experiment lasted a few days, which allowed us to observe a short-term response of the corals following a likely stressful interaction with the zoantharian. A caveat of our experiment is that we did not control for the chemical or biological effects of *P. caribaeorum* and, therefore, we cannot exclude the possibility of other stressful conditions, indirectly caused by contacts with the zoantharian, that could trigger spawning in corals like shading. This could have altered the conditions at a micro-environmental scale. Experiments conducted between corals and algae have shown that contact and close proximity led to local hypoxia and shifts in microbial communities in the interacting zones of corals, which could be highly detrimental to them and a source of stress (Smith et al. 2006; Barott et al. 2009; Haas et al. 2013a, 2013b). Therefore, it remains to be tested whether the reproductive activity of corals triggered by stress was directly or indirectly influenced by contacts with the competitor.

Colonial invertebrates can allocate different resources and invest in distinct reproductive mechanisms depending on specific needs and phases of their modules or polyps (Hughes 2005). Central older polyps can require more energy if they are in sexual reproductive activity, while peripheral polyps would invest more on colony growth (Burgess et al. 2017). Also, it has been reported that hermaphrodite bryozoans and ascidians can increase the proportion of male polyps or reduce the number of female polyps in response to stress conditions like competition for space, since less energy is needed for male gonad production (Hughes et al. 2003; Dias et al. 2008). In our experiment, we report a differential investment in sexual reproductive activity within the same colony, highlighting possible energetic trade-offs. Under stressful conditions imposed in a specific area of the colonies, the release of larvae could represent a strategy to reduce the energy lost by the colony, where the polyps could be highly damaged after contacting the zoantharian. Moreover, this strategy could be an adaptative response to escape from stress and ensure reproduction within the species (Sammarco 1982).

To our knowledge, this is the first coral spawning observation induced by contact interactions with a sessile competitor. We were unable to analyze the viability of the larvae and the specific mechanisms involved in this phenomenon, but this record can provide grounds for further investigation. The zoantharian *P. caribaeorum* is considered a strong sessile competitor on reefs and triggered larval release in coral colonies by either biological, chemical, or physical means. This also possibly led to distinct energy investments among the colonies, where spawning occurred in polyps that were contacted by the zoantharian. Our observation adds information on the reproduction behavior of scleractinian corals under stressful conditions and can generate insights on the potential consequences of negative ecological interactions.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval No animal testing was performed during this study.

Sampling and field studies All necessary permits for sampling have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements.

Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Author contribution ACG and GOL conceived the study; ACG collected samples in the field, performed the experiment, and drafted the manuscript; and both authors contributed to the final version of this manuscript.

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