Assessment of coral reef resilience patterns in response to local stressors and climate change at Gorgona Island, Colombia.

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Department of Marine Ecology, Faculty of Biology and Chemistry
University of Bremen

Submitted by

Ana Lucia Castrillón-Cifuentes

Supervised by

Prof. Dr. Christian Wild
University of Bremen, Germany

Prof. Dr. Fernando Zapata
Universidad del Valle, Colombia

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Dissertation Committee members

Chairperson
Prof. Dr. Juliane Filser (University of Bremen)
General and Theoretical Ecology
Center for Environmental Research and Sustainable Technology

Co-Examiners
Prof. Dr. Christian Wild
Marine Ecology Department, Faculty of Biology and Chemistry
University of Bremen
Germany

Prof. Dr. Fernando Zapata
Coral Reef Ecology, Faculty of Natural Sciences
Universidad del Valle
Colombia

Dr. Ana Palacio
National Oceanic and Atmospheric Administration, NOAA
National Research Council Miami
USA

Other non-voting members of the dissertation committee
Bianca Thobor
PhD candidate, Marine Ecology Department
Faculty of Biology and Chemistry
University of Bremen

Inae Kim-Frommherz
MSc. Ecology Coordinator
Faculty of Biology and Chemistry
University of Bremen

Summary

Scleractinian corals and coral reefs have traditionally been classified as steno-tolerant due to their preference for warm, clear, shallow, and fully saline waters. However, it can also exist outside this range, inhabiting conditions where abiotic factors reach extreme values, or their fluctuations are wide. Such coral reefs can be categorized as extreme or marginal. It has been proposed that at extreme and marginal environments, corals can adapt to climate change. The Eastern Tropical Pacific region is recognized as an extreme and marginal environment for coral reef development due to its atypical oceanographic conditions, small size of reefs, and low coral diversity. The largest coral reefs in the Colombian Pacific occur at Gorgona Island, and these reefs have shown remarkable recovery from past El Niño events (1982-83 and 1997-98), and they have not experienced significant bleaching in recent warming events.

To provide insights into the resilience capacity of coral reefs on Gorgona Island, this research aims to identify the physiological mechanisms in *Pocillopora* corals when they face local and global stressors. Through laboratory and field experiments, coupled with environmental monitoring and a literature review of studies carried out on the island, some traits in the corals and environmental conditions were identified that aided in explaining the resilience of pocilloporid reefs on the island to different stressors. The first study in this research assessed the effect of deoxygenation (a global stressor) on *Pocillopora capitata* and the coral reefs of Gorgona Island. The second study evaluated the physiological changes that occur in *Pocillopora* when they face cool temperatures and hypoxia, conditions that occur during upwelling events (a regional stressor). The last study evaluated the resistance and resilience capacity of *Pocillopora damicornis* to local stressors (low salinity and sediments) using a reciprocal transplant experiment between two neighboring reefs, that differ in their distance from shore.

Ocean deoxygenation was evidenced as a real threat for *Pocillopora* corals at Gorgona Island because the hypoxic threshold of these corals coincides with the mean oxygen concentration reported during the upwelling season, and even lower dissolved oxygen conditions occur at the deepest parts of the reefs, which possibly sets a bathymetric restriction for reef development. Hence, if hypoxic conditions increase because of stronger upwelling events or eutrophication, *Pocillopora* corals will be severely impacted in their aerobic metabolic processes. Additionally, although upwelling is a natural event that regularly exposes coral to extreme ambient conditions,

the occurrence of cool temperatures and hypoxia was evidenced that reduced *Pocillopora* growth, respiration, and translocation of glycerol from the Symbiodiniaceae. Also, it was identified that if warm conditions occur for a short period, *Pocillopora* corals experienced an increase in growth and a decrease in hypoxia susceptibility, hence the physiological negative effects of upwelling were ameliorated, which may help to explain the resilience of corals during moderate El Niño events at upwelling localities.

Regarding the coral response to local stressors (runoff), this research found a resistance capacity in *Pocillopora* corals that used to inhabit conditions of high salinity, low sediments, currents, and 0.2°C cooler conditions, because when moved to a less suitable environment (back reef), they could tolerate low salinity and sediments. Furthermore, resilience capacity was observed in corals from inshore areas exposed to runoff because, although these corals regularly experience adverse conditions, when the ambient conditions were improved (moved to reef areas far from shore), their physiological performance was enhanced. The existence of both resistance and resiliency capacity in *Pocillopora* corals reveals favorable attributes for the persistence of coral reefs at Gorgona Island. In general, corals from Gorgona Island exemplify that, in the absence of additional human-related stressors, corals and coral reefs can thrive in an atypical and dynamic environment; however, the result of this research evidenced that *Pocillopora* corals are currently living in a delicate balance to resist the effects of stress factors, particularly the effects of local stressors; hence, controlling the sources of runoff is a priority task for the management of coral reefs on Gorgona island.

Zusammenfassung

Skleraktinische Korallen und Korallenriffe wurden traditionell als steno-tolerant eingestuft, aufgrund ihrer Vorliebe für warmes, klares, flaches und vollständig salziges Wasser. Jedoch können sie auch außerhalb dieses Bereichs existieren und Bedingungen bewohnen, in denen abiotische faktoren extreme Werte erreichen oder starke Schwankungen aufweisen. Solche Korallenriffe können als extrem oder randständig kategorisiert werden. Die region des Östlichen Tropischen Pazifiks wird aufgrund ihrer untypischen ozeanografischen bedingungen, der geringen größe der Riffe und der geringen vielfalt an korallen als extrem und randständig für die Entwicklung von Korallenriffen anerkannt. Es wurde vorgeschlagen, dass sich Korallen in extremen und randständigen Umgebungen an den Klimawandel anpassen. Die größten korallenriffe im Kolumbianischen Pazifik befinden sich auf der Insel Gorgona, und diese Riffe haben sich von vergangenen El Niño-Ereignissen (1982-83 und 1997-98) beeindruckend erholt und keine signifikante bleichung bei jüngsten erwärmungsereignissen erfahren.

Um Einblicke in die Widerstandsfähigkeit der Korallenriffe auf der Insel Gorgona zu gewinnen, zielt diese Forschung darauf ab, die physiologischen Mechanismen bei *Pocillopora*-Korallen zu identifizieren, wenn sie lokalen und globalen Belastungen ausgesetzt sind. Durch Labor- und Feldexperimente, Umweltüberwachung und eine Literaturübersicht über Studien, die auf der Insel durchgeführt wurden, wurden einige Eigenschaften der Korallen und Umweltbedingungen identifiziert, die zur Erklärung der Widerstandsfähigkeit der *Pocillopora*-Riffe auf der Insel gegenüber verschiedenen Belastungen beitragen. Die erste Studie in dieser Forschung untersuchte die Auswirkungen von Sauerstoffmangel (einem globalen Stressor) auf *Pocillopora capitata* und die Korallenriffe von Gorgona Island. Die zweite Studie bewertete die physiologischen Veränderungen, die bei *Pocillopora* auftreten, wenn sie kühlen Temperaturen und Hypoxie ausgesetzt sind, Bedingungen, die während Auftriebsereignissen auftreten. Die letzte Studie bewertete die Widerstands- und Widerstandsfähigkeit von *Pocillopora damicornis* gegenüber lokalen Stressoren (geringe Salinität und Sedimente) mittels eines transplantierten Experimentes zwischen zwei benachbarten Riffen, die sich in ihrer Entfernung von der Küste unterscheiden.

Ozeanische Sauerstoffmangel aufgrund des Klimawandels wurde als eine reale Bedrohung für *Pocillopora*-Korallen auf Gorgona Island nachgewiesen, da ihr hypoxischer Schwellenwert mit der durchschnittlichen Sauerstoffkonzentration während der Auftriebssaison zusammenfällt und sogar

niedrigere gelöste Sauerstoffbedingungen in den tiefsten Teilen der Riffe auftreten, was möglicherweise eine bathymetrische Beschränkung für die Riffentwicklung darstellt. Daher würden Pocillopora-Korallen bei zunehmenden hypoxischen Bedingungen aufgrund stärkerer Auftriebsevents oder Eutrophierung stark beeinträchtigt werden in ihren aeroben Stoffwechselprozessen. Zusätzlich reduzierten kühle Temperaturen und Hypoxie das Wachstum, die Atmung und die Glycerinübertragung von den Symbiodiniaceae bei *Pocillopora*, obwohl Auftrieb ein natürlicher Vorgang ist, der Korallen regelmäßig extremen Umgebungsbedingungen aussetzt. Wenn warme Bedingungen für einen kurzen Zeitraum auftreten und das Wachstum steigern und die Hypoxie-Anfälligkeit von *Pocillopora* verringern, werden die negativen physiologischen Effekte des Auftriebs gemildert, was die Widerstandsfähigkeit der Korallen während mäßiger El Niño-Ereignisse an Auftriebsorten erklären könnte.

In Bezug auf die Reaktion auf lokale Stressoren (Abfluss) wurde eine Widerstandsfähigkeit bei *Pocillopora*-Korallen festgestellt, die in Bedingungen hoher Salinität, geringem Sedimentgehalt, Strömungen und 0,2°C kühler lebten, da sie, wenn sie in eine weniger geeignete Umgebung (hinteres Riff) versetzt wurden, eine niedrige Salinität und Sedimente tolerieren konnten. Darüber hinaus wurde bei Korallen aus küstennahen Gebieten, die dem Abfluss ausgesetzt waren, eine Fähigkeit zur Widerstandsfähigkeit beobachtet, da ihre physiologische Leistung verbessert wurde, als sich die Umgebungsbedingungen verbesserten (wenn sie in Riffgebiete weit weg von der Küste verlegt wurden). Das Vorhandensein sowohl einer Widerstands- als auch einer Resilienzfähigkeit bei *Pocillopora*-Korallen zeigt günstige Merkmale für das Überleben der Korallenriffe auf Gorgona Island auf. Im Allgemeinen zeigen die Korallen von Gorgona Island, dass sie in Abwesenheit zusätzlicher durch den Menschen verursachter Stressfaktoren in einer untypischen und dynamischen Umgebung gedeihen können. Die Ergebnisse dieser Forschung belegen jedoch, dass die *Pocillopora*-Korallen derzeit in einer empfindlichen Balance leben, um den Auswirkungen von Stressfaktoren, insbesondere den Auswirkungen lokaler Stressoren, zu widerstehen. Daher ist die Kontrolle der Quellen von Abfluss eine prioritäre Aufgabe für das Management der Korallenriffe auf dieser Insel.

Resumen

Los corales escleractinios y los arrecifes de coral se han clasificado tradicionalmente como estenotolerantes debido a su preferencia por aguas cálidas, claras, poco profundas y totalmente salinas. Sin embargo, también pueden existir fuera de este rango, habitando condiciones en las que los factores abióticos alcanzan valores extremos o sus fluctuaciones son amplias. Tales arrecifes coralinos pueden clasificarse como extremos o marginales. Se ha propuesto que en los entornos extremos y marginales los corales se adaptan al cambio climático. La región del Pacífico Oriental Tropical está reconocida como un entorno extremo y marginal para el desarrollo de los arrecifes coralinos debido a sus condiciones oceanográficas atípicas, el tamaño reducido de los arrecifes y la escasa diversidad de corales. Los arrecifes de coral más desarrollados del Pacífico Colombiano se encuentran en la isla Gorgona, y estos arrecifes han mostrado una notable recuperación tras los pasados episodios de El Niño (1982-83 y 1997-98), y no han experimentado un blanqueamiento significativo en los recientes episodios de calentamiento.

Para proporcionar información sobre la capacidad de resiliencia de los arrecifes de coral en la isla Gorgona, esta investigación tuvo como objetivo identificar los mecanismos fisiológicos en *Pocillopora* cuando se enfrentan a factores de estrés locales y globales. A través de experimentos de laboratorio y de campo, junto con el monitoreo de las condiciones ambientales y una revisión bibliográfica de los estudios realizados en la isla, se identificaron algunos rasgos en los corales y condiciones ambientales que ayudaron a explicar la resiliencia de los arrecifes pocilloporidos de la isla frente a diferentes factores de estrés. El primer estudio de esta investigación evaluó el efecto de la desoxigenación (un estresor global) sobre *Pocillopora capitata* y los arrecifes de coral de la isla de Gorgona. El segundo estudio evaluó los cambios fisiológicos que se producen en *Pocillopora* cuando se enfrentan a temperaturas bajas e hipoxia, condiciones que se dan durante los eventos de surgencia. El último estudio evaluó la capacidad de resistencia y resiliencia de *Pocillopora damicornis* frente a factores de estrés locales (baja salinidad y sedimentos) mediante un experimento de trasplante recíproco entre dos arrecifes vecinos, que difieren en la distancia a la costa.

La desoxigenación del océano se identificó como una amenaza real para los corales del género *Pocillopora* de isla Gorgona, ya que su umbral de hipoxia coincide con la concentración promedio de oxígeno registrada durante la época de surgencia, y en las partes más profundas de los

arrecifes se dan condiciones de oxígeno disuelto aún más bajas, lo que posiblemente la disponibilidad de oxígeno disuelto establece una restricción batimétrica para el desarrollo de los arrecifes de coral. Por lo tanto, si condiciones de hipoxia aumentan debido a la intensificación de los eventos de surgencia o a la eutrofización, *Pocillopora* se verán gravemente afectada en sus procesos metabólicos aeróbicos. Además, aunque la surgencia es un fenómeno natural que expone regularmente a los corales a condiciones ambientales extremas, se identificó que las temperaturas frías y la hipoxia disminuyen el crecimiento, la respiración y la translocación de glicerol desde las algas Symbiodiniaceae al coral. Sin embargo, si se producen condiciones cálidas durante un breve período, en los corales *Pocillopora* aumenta el crecimiento y disminuyen su susceptibilidad a la hipoxia, siendo aliviados los efectos fisiológicos negativos de la surgencia, lo que puede explicar la resiliencia de los corales durante los episodios moderados de El Niño en las localidades donde se produce la surgencia.

En cuanto a la respuesta a los factores locales de estrés (escorrentía), se observó la existencia de una capacidad de resistencia en los corales *Pocillopora* que habitaban condiciones de alta salinidad, bajos sedimentos, corrientes y 0.2°C más frío, ya que al ser trasladados a un entorno menos adecuado (arrecife trasero), podían tolerar la baja salinidad y los sedimentos. Además, se observó capacidad de resistencia en los corales de zonas cercanas a la costa y expuestas a la escorrentía porque, aunque estos corales experimentan regularmente condiciones adversas, cuando se mejoraban las condiciones ambientales (trasladados a zonas de arrecife alejadas de la costa), mejoraba su rendimiento fisiológico. La existencia de capacidad tanto de resistencia como de resiliencia en los corales del género *Pocillopora* revela atributos favorables para la persistencia de los arrecifes de coral en isla Gorgona. En general, los corales de la isla Gorgona ejemplifican que, en ausencia de factores estresantes adicionales relacionados con los humanos, los corales y los arrecifes de coral pueden prosperar en un entorno atípico y dinámico; sin embargo, esta investigación también evidenció que las *Pocilloporas* viven actualmente en un delicado equilibrio para resistir los efectos de los factores de estrés, en particular los efectos de los factores de estrés locales; por lo tanto, el control de las fuentes de escorrentía es una tarea prioritaria para la gestión de los arrecifes de coral en esta isla.

Contribution of the candidate to multi-author articles and manuscript included in the thesis

Chapter 2: **Castrillón-Cifuentes AL**, Zapata FA, Giraldo A, Wild C. 2023. Spatiotemporal variability of oxygen concentration in coral reefs of Gorgona Island (Eastern Tropical Pacific) and its effect on the coral *Pocillopora capitata*. PeerJ 11: e14586. Doi:10.7717/peerj.14586.

Experimental concept and design	90%
Experimental work and/or acquisition of (experimental) data	90%
Data analysis and interpretation	90%
Preparation of figures and tables	100%
Writing of the first and last version of the manuscript	100%

Chapter 3: **Castrillón-Cifuentes AL**, Zapata FA, Wild C. 2023. Physiological responses of *Pocillopora* corals to upwelling events in the Eastern Tropical Pacific. Front. Mar. Sci. 10: 1212717. Doi: 10.3389/fmars.2023.1212717

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Preparation of figures and tables	100%
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Por su amor incondicional,

y siempre estar presentes a pesar de las adversidades,

la distancia y el tiempo que estuve lejos de casa.

Una gota puede romper la roca.

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Chapter 1: **General Introduction**

Factors controlling coral reef development

The interaction of organisms with biotic and abiotic factors helps to define their population's distribution and abundance, and the extent of these interactions is determined by the physiological tolerance of organisms, also its physiological responses can have consequences for community and ecosystem functioning (Carscadden et al., 2020). This idea is particularly applicable to -engineer species, such as scleractinian corals, which have the ability to modify their surroundings and create biogenic structures that provide shelter for other organisms (Burkepile and Hay, 2008). In general, organisms can be categorized based on their degree of physiological tolerance, as eury-tolerant, meaning they have high tolerance limits towards changes in ambient conditions, or steno-tolerant, representing populations adapted to stable environments with low tolerance limits towards environmental change (Kültz, 2003). Scleractinian corals (henceforth corals) and coral reefs have traditionally been classified as steno-tolerant due to their preference for warm, clear, shallow, and fully saline waters (Kleypas et al., 1999).

Optimal conditions for coral reef development are typically found in the intertropical zone (Martin-Garin and Montaggioni, 2023), where annual mean temperature ranges from 21.7 °C to 29.6 °C, annual mean salinity between 28.7 and 40.4 psu, nitrate concentrations above 4.51 µmol L^{-1}, phosphate levels reaching the threshold of 0.63 µmol L^{-1}, aragonite saturation state (Ω_{arag}) threshold of 2.82 (below which coral reefs disappear), and a minimum light intensity of 450 µmol photons m^{-2} s^{-1} (Guan et al., 2015). However, coral reefs can also exist out of this range, and can inhabit atypical conditions such as areas with low or variable pH, high temperatures, tide pools, high-latitude environments with wide temperature fluctuations, turbid sites, mesophotic depths with limited light availability, or at zones where multiple stressors co-occur, such as mangroves, shallow in-shore reefs, macrotidal environments, and upwelling centers (Camp et al., 2019). Coral reefs found under these challenging conditions can be categorized as extreme reefs if they exhibit significant deviations from optimal abiotic conditions, or as marginal reefs if they display altered coral cover, community composition, and ecosystem functioning (Schoepf et al., 2023).

Climate change is causing ocean acidification, warming in the upper mass water, and reduced oxygen solubility due to a warmer and more stratified seas (Allen et al., 2018). These environmental changes are having severe consequences on marine ecosystems, altering the way species inhabit their environments (Gibbin et al., 2017). Among the most endangered ecosystems are tropical coral reefs, with estimates indicating that approximately 50 % of global coral cover has been lost over the past four decades (Torda et al., 2017; Tebbett et al., 2023). The global decline of coral reefs has prompted increased research and management efforts in environments where corals persist at the edge of their tolerance (Chapron et al., 2022; Schoepf et al., 2023). It has been proposed that at extreme and marginal environments occur adapted corals to climate change effects; hence, this sites can offer valuable insights into how corals and coral reefs may survive in a changing ocean (Kleypas et al., 1999; Camp et al., 2019).

Resistance and resilience capacity to stressors

Organisms and ecosystems have a variable ability to withstand the impacts of stressors through their resilience and resistance capacity. Resilience refers to an ecosystem's ability to recover from the negative effects of a disturbance and return to its previous level of organization (Holling, 1973), an alternative definition include the speed at which a system can return to an initial state following a disturbance (Lirman and Manzello, 2009). On the other hand, resistance represents the ability to persist under stressful conditions, which can be influenced by intrinsic tolerance or extrinsic factors that provide some level of protection (West and Salm, 2003). Both concepts are valid at various scales, ranging from coral physiology to the coral reef ecosystem (Donovan et al., 2023). The applicability of these concepts depends on the indicators employed to evaluate the pre- and post-disturbance states of the system. Examples of such indicators include growth rates, bleaching percentage, lipid content, reproductive output, recruitment, herbivory rates, associated fauna, dominance of coral communities, and even socio-economic services (Bachtiar et al., 2019; Thompson et al., 2020; Fisher, 2022).

Higher latitude reefs have been suggested as thermal refuge from ocean warming because some evidence indicates that these reefs experience lower rates of bleaching and mortality, and display faster recovery from bleaching events compared to coral reefs at lower latitudes (Mies et al., 2020). However, this assumption is under debate, since exists high variability in bleaching responses, and corals are experiencing longer recovery times from bleaching events as climate change intensify

(Moriarty et al., 2023). In line, evidence from marginal patch reefs demonstrates deteriorating conditions caused by both local and global anthropogenic pressures, resulting in reduced reef resilience (De et al., 2023).

Response of coral reefs from the Eastern Tropical Pacific to stress factors

The Eastern Tropical Pacific (ETP) region is recognized as an extreme and marginal environment for coral reef development due to its atypical oceanographic conditions, small size of reefs, and low coral diversity (Veron et al., 2015; Glynn et al., 2017). Coral reefs in the ETP are exposed to various challenges, including upwelling events, El Niño Southern Oscillation (ENSO), sub-aerial exposure during extreme low tides, low salinity, and sediment input from rivers; the occurrence of upwelling and ENSO events subject corals to extreme temperatures, acidification, and hypoxia, which are the effects of climate change in the ocean (Fiedler and Lavín, 2017). Despite the limited development of coral reefs in the ETP, they provide habitat for endemic organisms, serve as corridors for fish, sea birds, turtles, and marine mammals to migrate through the region (Enright et al., 2021), support thriving fisheries (Martin et al., 2016), and contribute to the economic development of coastal communities through tourism (Cupul-Magaña and Rodríguez-Troncoso, 2017; Villalobos-cubero et al., 2023).

The response of corals and coral reefs of the ETP to warming events is species-specific and influenced by the local conditions. For instance, *Pocillopora*, the main reef-building coral of the region, exhibits high tolerance to El Niño in Colombia, with increased growth rates in response to temperature rises (Vargas-Ángel et al., 2001); at Isla Marietas (Mexico), La Niña events reduce growth rate (Tortolero-Langarica et al., 2017). In the Gulf of Chiriqui (GC; Panama), *Pocillopora* shows greater tolerance to warming compared to corals from the Gulf of Panama (GP) (D'Croz and Maté, 2004). However, this genus appears to be more susceptible compared to massive corals that also occurs in reefs of the ETP but at lower abundances (Hueerkamp et al., 2001).

In terms of coral reef response, El Niño events have caused a decline in live coral cover at sites without environmental management, while marine protected areas have shown better protection against such declines (Guzman and Cortés, 2007; Alvarado et al., 2020). The negative effects of El Niño is intensified by upwelling events, resulting in fewer coral species decline in the GC where upwelling has no influence compared to the GP where upwelling occurs (Gomez et al., 2017). Similarly, the northern Galapagos Islands have exhibited benthic recovery and no loss of coral species, in contrast to the southern islands that are influenced by upwelling events (Glynn et al., 2015). Overall, the ETP has experienced temporary reductions in coral cover during El Niño events, with the severity being greater in 1982-83 compared to 1997-98; however, reefs have shown high resilience, with no net reductions observed across the entire region (Romero-Torres et al., 2020). Nevertheless, past ENSO events and changes in the Inter-Tropical Convergence Zone (ITCZ; which modulates upwelling events) have led to reef collapse during the Holocene, raising concerns about similar consequences under current climate change (Toth et al., 2012).

Regarding acidification, it is reducing *Pocillopora* growth at a rate of 0.9 % per year (Manzello, 2010). Although corals can tolerate thermal stress or acidification to some extent, the combination of these stressors can lead to the complete loss of reef framework structures, as demonstrated in the southern Galápagos Islands during the 1982-83 El Niño event. In this region, Ω_{arag} had levels comparable to those projected for the rest of the tropics under a scenario of doubling current CO_2 emissions; and the simultaneous occurrence of acidification and a 2-3 °C warm thermal anomaly over two consecutive months proved lethal for corals there (Manzello et al., 2017). In the ETP, coral reef degradation is further exacerbated by bioerosion. The activity of sea urchins, boring bivalves, and excavating sponges is expected to increase in response to warming and acidification (Carballo et al., 2013; Manzello et al., 2017; Rodriguez-Ruano et al., 2023).

Coral reefs of Gorgona Island; the study case

The largest coral reefs in the Colombian Pacific occur at Gorgona Island. These reefs have shown remarkable recovery, regaining coral cover to pre-El Niño 1982-83 levels in less than a decade, and they have not experienced significant bleaching or mortality in recent warming events (Zapata and Vargas-Angel, 2003; Navas-Camacho et al., 2010; Zapata et al., 2010; Zapata, 2017). Until the 16th century, Gorgona Island was exclusively utilized by natives for fishing; subsequently, Europeans used the island as shelter for their ships, and introduced agricultural activities (Casas-Dupuy, 1990). In 1960, the Colombian government build there a maximum-security prison, resulting in the clearance of 70 % of the forest, overfishing, and coral extraction for souvenirs (Murillo-García and Bedoya-Durán, 2014).

Because Gorgona Island is one of Colombia's rainiest areas, the loss of forest led to runoff and degradation of marine environments (Blanco, 2009; Giraldo et al., 2014; Vásquez-Vélez, 2014). The ecological crisis was exacerbated by El Niño 1982-83, that coincides with spring low tide events, resulting in mass bleaching and a significant loss of live coral cover (85 %) (Vargas-Ángel et al., 2001). As a consequence of the ecological crisis and human rights violations (Suares-Porras, 2016), the jail was closed and the island declared a marine protected area on November 25th, 1983. Then, natural recovery was allowed, and human activities were regulated; by 1989, live coral cover reached 50 % (Guzman and Lopez, 1991), and by 1996, it had increased to 73 % (Vargas-Ángel et al., 2001). At present, live coral coverage can range from 50 % on reef flat to 100 % on reef slope (Zapata, 2017).

At a regional scale, coral reefs of Gorgona Island maintain the connectivity among the equatorial ETP, an seems to contributes to the restoration of neighboring reefs after El Niño events (Lequeux et al., 2018). Despite Gorgona Island possesses one of the most comprehensive historical records of benthic coverage in the ETP (Garzón-Ferreira and Rodríguez-Ramírez, 2010; Zapata, 2017; Romero-Torres et al., 2020), most research has focused on ecological processes, mainly a consequence of the remoteness and limited facilities at the island, which pose restrictions for non-observational studies. Hence, exist gaps about the physiological mechanisms behind the resistance and resilience capacity of corals there. Table 1 provides a summary of the known responses of corals from Gorgona Island to different stressors. Given that corals exhibit some tolerance to El Niño, sediments, and extreme low tides, and the fact that the ETP is recognized as an extreme and marginal environment that can act as a thermal refuge from climate change, corals from this island present an appropriate model to study the interactive effects of local and global stressors on their resilience capacity.

Table 1. Coral's response to stressors at Gorgona Island. The coral response was classified as tolerant if the stressor has no effect on a particular biological process; resilient if a biological process was initially affected, but after the stressor stops the biological process return to the initial state; or susceptible if the stress causes a negative impact on a biological process and corals do not recuperate to the original state or even dead.

Stress factor	Specie	Effect on coral	Coral response	Reference
Sediments	*P. damicornis*	not effects on growth or reproduction.	Tolerant	Zambrano-Franco, 2016
Salinity	*P. damicornis*	Seasonal variation induces gamete development.	Not assessed	Castrillón-Cifuentes et al., 2015
Extreme low tides	*P. damicornis*	decreased fecundity, bleaching, and even mortality	Resilient	Castrillón-Cifuentes et al., 2017
Temperature	*Pocillopora*	El Niño: bleaching (but even enhanced growth rate), and mortality.	from susceptible to resilient	Vargas-Ángel et al., 2001
		Seasonal variation induces gamete development. No gamete development on partially bleached colonies.		Castrillón-Cifuentes et al., 2015
	Psammocora	El Niño: bleaching, low growth rate, mortality.	Susceptible	Vargas-Ángel et al., 2001
Alga overgrowth	*P. damicornis*	no gamete development.	Susceptible	Castrillón-Cifuentes et al., 2015
Corallivory	*Pocillopora*	Reduces linear extension, but increases branch thick	Tolerant	Palacios et al., 2014

Knowledge gaps and contribution of the thesis

Of the three primary global stressors resulting from climate change in the ocean (warming, acidification, and deoxygenation), the effect of deoxygenation on corals and reefs of the ETP have not been assessed, despite of the well-known trend of oxygen loss in this region (49 mmol m^2 yr^{-1}) (Stramma et al., 2008). In ETP localities where upwelling occurs (like at Gorgona Island), the negative effects of climate change can be intensified; although these sites have been suggested as thermal refuges (Randall et al., 2020), evidence from fish and sea urchins suggests that the cool, acidic, and oxygen-deficient waters that rise to shallow depths can lead to habitat compression and reduction in organism performance and survival (Clarke et al., 2021; Lucey et al., 2021); but no evidence is available for corals. Furthermore, the presence of other stressors such as runoff, low salinity, and sedimentation can exacerbate the negative impacts of climate change, particularly at sites where pluviosity is high. Therefore, it is expected that the co-occurrence of global and local stressors at the marginal and extreme reefs of the ETP can deteriorate the environmental conditions for corals and their resilience capacity. The main objective of this research is to identify the physiological mechanisms in *Pocillopora* corals from Gorgona Island that confer resistance to local and global stressors. Filling this gap also helps to provide insights of the resilience capacity of coral reefs during past warming events, and their future persistence to climate change effects.

Thesis structure

This thesis is composed by a General introduction (Chapter 1, this chapter), three core chapters, and a General discussion (Chapter 5). The core chapters consist of two published articles and one manuscript intended for publication; the chapters were arranged to show the effects of global, regional, and local stressors on the physiological performance of *Pocillopora* corals from Gorgona Island. The research question(s), hypothesis, and specific objectives for each chapter were listed in Table 2.

In chapter 2 the effect of deoxygenation (a global stressor) on *Pocillopora* and coral reefs of Gorgona island were assessed by combining a long-term seasonal monitoring of dissolved oxygen conditions and measuring (in the laboratory) the hypoxic threshold of corals. This approach helps to address when hypoxic conditions occur, how tolerant corals are, and the restrictions that poses dissolved oxygen availability for reef development.

In chapter 3, through laboratory tests and field measurements, was evaluated the physiological changes that suffer *Pocillopora* when face cool temperatures and hypoxia, conditions that occurs during upwelling events (a regional stressors). Results revealed that upwelling pushes *Pocillopora* corals toward their physiological limit, information that contributes to understand the resilience of reefs to ENSO events, a phenomenon that occurs in the Pacific Ocean and that modulate upwelling intensity in the ETP.

In chapter 4, the tolerance of *Pocillopora* to local stressors (low salinity and sediments) was evaluated using a reciprocal transplant experiment between two neighboring reefs, that differ in the distance from shore (82 and 674 m); and was evidenced that the historical micro-ambient conditions where corals growth modulate the response to stressors: resilient capacity was observed in corals from the inshore reef, while resistance capacity in corals from the offshore reef. In chapter 5, the main results of the three previous chapter were summarized and discussed in terms of how the physiological effects that suffer *Pocillopora* when face local and global stressors influence the resistance and resilience capacity of coral reefs on Gorgona island.

Table 2. Research question, hypothesis, and objectives for each chapter.

	Chapter 2	Chapter 3	Chapter 4
Research question (s)	Do occur hypoxic events at coral reefs of Gorgona Island? If occurs, which levels of low oxygen can tolerate Pocillopora corals?	Which physiological effects has thermal and oxygen stress during upwelling events?	Do local stressors influence coral reefs of Gorgona Island in the same level? How corals respond to changes in the micro-ambient conditions?
Hypothesis	Hypoxic events do not occur at coral reefs of Gorgona island, as mortality related to this ambient condition is not reported for the island. As in other corals the hypoxic threshold will be close to the lower DO recorded at reefs of Gorgona.	Exposure to cool thermal stress and hypoxic conditions during upwelling events will significantly affect the physiology of Pocillopora on a seasonal basis.	Micro-ambient conditions modulate the physiological performance of Pocillopora corals at Gorgona Island
Objectives	To characterize the spatial and temporal variability of DO concentration in reefs around Gorgona Island. To identify the DO concentration that represents a hypoxic condition for Pocillopora capitata corals.	To characterize the interannual changes in temperature and DO on coral reefs of Gorgona Island. To determine the average and extreme thermal and oxygen conditions that corals face during upwelling events. To assess the physiological response of Pocillopora to changes in temperature and oxygen conditions that can occur during upwelling events.	To evaluate the effect of micro-ambient conditions on the physiology of Pocillopora corals. To test the tolerance of Pocillopora to local stressors when face changes ambient conditions.

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Chapter 2: Spatiotemporal variability of oxygen concentration in coral reefs of Gorgona Island (Eastern Tropical Pacific) and its effect on the coral *Pocillopora capitata*

Ana Lucia Castrillón-Cifuentes [1,2,*], Fernando A. Zapata [2], Alan Giraldo [3], Christian Wild [1]

1 Marine Ecology Department, Faculty of Biology & Chemistry, University of Bremen, Bremen, Germany

2 Grupo de Investigación en Ecología de Arrecifes Coralinos, Universidad del Valle, Cali, Colombia

3 Grupo de Investigación en Ciencias Oceanográficas, Universidad del Valle, Cali, Colombia

*Corresponding Author: castrillon.ana@correounivalle.edu.co, analucia@uni-bremen.de

Abstract

Dissolved oxygen concentration (DO) is one of the main factors limiting benthic species distribution. Due to ocean warming and eutrophication, the ocean is deoxygenating. In the Eastern Tropical Pacific (ETP), deep waters with low DO (< 1 mg L^{-1}) may reach coral reefs, because upwelling will likely intensify due to climate change. To understand oxygen variability and its effects on corals, we characterize the Spatio-temporal changes of DO in coral reefs of Gorgona island and calculate the critical oxygen tension (P_{crit}) to identify the DO concentration that could represent a hypoxic condition for *Pocillopora capitata*, one of the main reef-building species in the ETP. The mean (± SD) DO concentration in the coral reefs of Gorgona island was 4.6 ± 0.89 mg L^{-1}. Low DO conditions were due to upwelling, but hypoxia (< 3.71 mg L^{-1}, defined as a DO value 1 SD lower than the Mean) down to 3.0 mg O_2 L^{-1} sporadically occurred at 10 m depth. The P_{crit} of *P. capitata* was 3.7 mg L^{-1} and lies close to the hypoxic condition recorded on coral reefs during the upwelling season at 10 m depth. At Gorgona Island oxygen conditions lower than 2.3 mg L^{-1} occur at > 20 m depth and coincide with the deepest bathymetric distribution of scattered colonies of *Pocillopora*. Because DO concentrations in coral reefs of Gorgona island were comparably low to other coral reefs in the Eastern Tropical Pacific, and the hypoxic threshold of *P. capitata* was close to the minimum DO record on reefs, hypoxic events could represent a threat if conditions that promote eutrophication (and consequently hypoxia) increase.

Keywords: Dissolved oxygen, Hypoxia, Respiration rate, Upwelling, Scleractinian coral

Introduction

Oxygen (O_2) concentration is one of the main environmental factors limiting the occurrence of species in nature (Dodds et al., 2007). This is because, through metabolism the ingested food, and stored reserves are converted into energy to fuel any function in organisms (Claireaux & Chabot, 2016). In particular, O_2 works as the terminal electron acceptor in aerobic energy (ATP) production (Wang et al., 2014). The term normoxia refers to a range of dissolved oxygen (DO) concentrations mostly observed in nature, while hypoxia to a level below the normoxic range that can trigger negative effects on organisms (Welker et al., 2013). The Metabolic rate (MO_2) is one of the most common metrics used to assess the physiological performance of an organism under a particular ambient condition, and respirometry is a cost-effective way to measure it (Harianto et al., 2019). Also, together with quantifying hypoxia tolerance, it is possible to make predictions about species' response and resilience to ocean deoxygenation (Negrete & Esbaugh, 2019; Siebel et al., 2021). Identifying the hypoxic threshold in aquatic organisms is a widely employed tool that helps to define the DO concentration from which organisms cannot sustain their physiological functions normally (Hughes et al., 2020). This oxygen limit is highly variable and depends on the taxa, life stage, exposure time, temperature, and previous O_2 history (Vaquer-Sunyer & Duarte, 2008; Hughes et al., 2020).

Classically, organisms are assigned to one out of two mechanisms for the regulation of their MO_2 when face changes in O_2 conditions. To define the mechanism, MO_2 is plotted as a function of the environmental oxygen levels (PO_2); in a classic conformer, MO_2 declines in direct proportion to declining PO_2, and for an oxyregulator, the MO_2 remains constant down to a PO_2 level (called the critical oxygen tension), from which the MO_2 conforms to the environmental O_2 condition, but with an energetic cost for the organism (Regan et al., 2019, Claireaux & Chabot, 2016; Cobbs & Alexander Jr, 2018; Negrete & Esbaugh, 2019).

However, organism rarely performs as strict oxyregulators, and instead, a spectrum of responses has been observed; the regulatory ability and regulatory index are similar metrics that quantify an animal's ability to regulate MO_2 under changes in O_2 conditions (Cobbs & Alexander Jr 2018, Muller & Seymour 2011). Other common methods to assess hypoxia tolerance include measuring the time to loss of equilibrium, which is the amount of time an animal can survive when forced to rely on anaerobic metabolism (Negrete & Esbaugh 2019), and determining the critical oxygen tension (P_{crit}).

Effects of hypoxia on scleractinian corals

Hypoxia has been shown to promote bleaching in *Acropora nobilis* and *Alveopora verrilliana* (Baohua et al., 2004). *Montipora peltiformis* was able to tolerate anoxia (absence of O_2) for up to 4 days, but its co-occurrence with acidification becomes lethal in 24 h (Weber et al., 2012). Additional to bleaching, hypoxia (< 4 mg L^{-1}) has been shown to lead to tissue lost, increased respiration rate, and reduced photosynthetic O_2 production in *Acropora yongei* (Hass et al., 2014). *Acropora cervicornis* has been observed to experienced tissue lost after one day exposure to 1.0 mg L^{-1} of O_2, and mortality after five days; however, in *Orbicella faveolata* the same conditions had no effect after a week (Johnson et al., 2021). Gravinese et al. (2021) found that *O. faveolata* significantly reduced their respiration rate (34.2 % and 62.8 %) when exposed (1 h) to hypoxia (0.77 mg L^{-1}) or hypoxia and warming (31.4 °C). *Pocillopora*, *Acropora* and *Motipora* corals suffered mass (71 %) mortality (as evidenced by tissue peeling without decoloration) when DO was 1.4 - 2.0 mg L^{-1} due to a micro-algal bloom (Raj et al., 2020).

Compared to pH conditions, O_2 also has a great effect on calcification. In healthy *Montastraea faveolota*, an increase in DO (from 5.4 to 7.8 mg L^{-1}) promotes dark calcification, but in bleached corals, both glycerol and well-oxygen conditions were required to continue calcification (Collombo-Pallota et al., 2010). The optimal O_2 condition for calcification in *Galaxea fascicularis* was stated at 7.3 mg L^{-1}, while 3.3 mg L^{-1} (under light or dark conditions) reduced calcification even in fed corals (Wijgerde et al., 2012). Likewise, 1.9 mg L^{-1} of O_2 at night decrease (51%) calcification in *Acropora millepora* regardles of the pH condition (Wijgerde et al., 2014).

In *Symbiodinium microadriaticum*, hypoxia (6 % O_2 saturation) reduces the activity of Superoxide dismutase, Catalase, and Ascorbate peroxidase (Matta & trench, 1991). Isolated zooxanthellae from *Dichocoenia stokensii* reduced their photosynthesis and respiration rates due to 50 % O_2 saturation (Gardella & Edmunds, 1999), and 0% air saturation reduced the photochemical efficiency of PSII in zooxanthellae extracted from *Pocillopora damicornis* (Ulstrup et al., 2005).

However, hypoxia (20 % O_2 saturation) has no effects on zooxanthellae of *Galaxea fascicularis* (Osinga et al., 2017).

Anaerobic metabolism was the fast response in *Montipora capitata* to hypoxia during diel changes in O_2 (hyperoxia during the day, due to photosynthesis, and hypoxia at night, result of respiration); however, this response was inefficient for survival under prolonged hypoxia (5 days) (Murphy & Richmond, 2016). The Hypoxia Inducible Factor (HIF-1) was responsible for maintaining O_2 homeostasis in *Stylophora pistillata* and *Acropora tenuis* (Zoccola et al., 2017; Alderdice et al., 2020). In *Acropora yongei*, metabolic enzymes are expressed constantly throughout the diel cycle, and only Strombine (a fermentation end-product) peaking at the onset of hypoxia and hyperoxia (Linsmayer et al., 2020). Larvae of *Acropora selago*, when exposed to 12 h of hypoxia at night, and 12 h of oxygenation during the day, experienced negative effects on pathways related to Homeobox genes, mitochondrial activity, and lipid metabolism (Alderdice et al., 2021). In *Acropora* spp, hypoxia (1.75 mg L^{-1}) during the night causes oxidative stress and damage of DNA, without activation of the antioxidant defense (Deleja et al., 2022).

Ocean deoxygenation

Ocean warming and acidification are considered leading contributors to live coral cover decline on coral reefs around the world (Hoegh-Guldberg et al., 2017; Heron et al., 2017; Hughes et al., 2018). However, growing evidence indicates that ocean deoxygenation (due to low solubility of O_2 in a warmer ocean, and eutrophication) is another immediate threat to corals' survival (Altieri et al., 2017; Nelson & Altieri, 2019; Hughes et al., 2020). In the last 50 years, the ocean has lost 2 % of its O_2 (Schmidtko et al., 2017), and this loss is expected to climb to 5% by 2100 under the Representative Concentration Pathway (RCP) 8.5 (Keeling et al., 2010), a high green-house gases emission ("business as usual") scenario, or a Shared Socio-economic Pathways, SSP5, (Ho et al., 2019).

Currently, 13 % of tropical coral reefs are at risk of hypoxia (Altieri et al., 2017). A meta-analysis by Sampaio et al. (2021) demonstrates that hypoxia has more negative effects on marine animals (including corals) than ocean warming and acidification. During the End-Permian period, ocean warming and deoxygenation, rather than ocean warming and acidification, triggered the mass extinction of ancient reefs (Penn et al., 2018).

In the Eastern Tropical Pacific region (ETP) the oxygen minimum zones (< 1 mg L^{-1}) are expanding vertically, and there is a trend of oxygen loss of 49 mmol m^2 $year^{-1}$ (Stramma et al., 2008). Additionally, climate change will cause increased stratification and upwelling of hypoxic waters onto the surface layer, leading to adverse effects for benthic organisms, including coral reefs (Fiedler & Lavín, 2017). Coastal coral reefs can also experience hypoxic conditions when water quality decreases because of land-based runoff (Altieri et al., 2017; Kealoha et al., 2020). The ETP region is recognized for hosting a few species of scleractinian corals that live under extreme environmental conditions (high pCO_2, low aragonite saturation, high nutrients, fluctuating temperatures, and intense bioerosion, Glynn et al., 2017). Hence, additional stress from climate change, including particularly low DO, imposes a serious threat to the coral reefs in this region.

As expected from the environmental conditions in the ETP, coral reefs of Gorgona Island (Colombian Pacific) develop under particularly limiting conditions: they occur in waters with one of the lowest salinities for reef development in the world (Kleypas et al., 1999; Blanco 2009; Guan et al., 2015), and the water temperature varies widely from as low as 16 °C during upwelling events to up to 32 °C during ENSO events (Vargas-Ángel et al., 2001; Giraldo et al., 2008; Zapata, 2017). However, despite the low diversity (24 species, Glynn et al., 2017), corals grow vigorously, particularly those in the genus *Pocillopora* (mean linear extension from 1.89 to 4.08 cm $year^{-1}$; Lizcano-Sandoval et al., 2018; Céspedes-Rodríguez & Londoño-Cruz, 2021) and reefs exhibit relatively high live coral cover (50.7 ± 5.7 %, mean ± SE; Zapata, 2017). Here, coral reefs seem to be quite resilient because they fully recovered in less than a decade from the 1982-83 El Niño mass bleaching and mortality event, have not been significantly affected by more recent El Niño events, and have recovered in a relatively short time from significantly detrimental sub-aerial exposure events (Vargas-Ángel et al., 2001; Navas-Camacho et al., 2010; Zapata et al., 2010; Glynn et al., 2017; Zapata, 2017).

Coral reefs at Gorgona Island (and in the ETP in general) have been studied for longer than three decades, but information about corals' physiological thresholds in response to stressors is scarce.

Furthermore, there are limited descriptions of the micro-environment (i.e, at each reef, < 1 km) with which corals cope. Given the effect of global climate change and local stressors on DO availability and its effects on the survivorship of scleractinian corals, this research aims to, first, characterize the spatial (reefs and depths) and temporal (seasons, and years) variability of DO concentration in areas where scleractinian corals abound around Gorgona Island and, second, to identify the DO concentration that represents a hypoxic condition for *Pocillopora capitata* corals, one of the main reef-building corals in the ETP region.

Materials and Methods

Characterization of dissolved oxygen concentrations in coral reefs of Gorgona Island

Gorgona (2º58’10” N - 78º11’05” W, Fig. 1) is a continental island in the Colombian Pacific, 9.3 km long and 2.6 km wide, located 30 km off from the nearest point on the continent (Giraldo et al., 2008; Muñoz et al., 2018), and in front of the Sanquianga National Natural Park where high sediment discharge from the Patia River occurs (Restrepo & Cantera, 2013). This island is a natural national park and hosts several well-developed (~ 1 km long, 8 m thick) coral reefs, incipient and relict reefs, and several coral communities (Glynn, Prahl & Guhl, 1982; Zapata & Vargas-Angel, 2003).

To determine the oxygen conditions in which corals cope at reefs, DO concentration (in mg L^{-1}) data were extracted from the technical reports of the environmental monitoring program of Gorgona Island (a list of the reports is in SM1) implemented by the Oceanographic Sciences research group from Universidad del Valle (Cali, Colombia). Since 2005 the program assessed marine environmental conditions during a week in the first and the second semester of each year (March or April, for the upwelling season, and September, October, or November, for the non-upwelling season), and in 5 monitoring stations around the island, that are close to coral reefs (Fig. 1). At each monitor station, and during daylight hours, a water sample was collected (at 1 and 10 m depth) with a Niskin bottle (5 L). And a YSI-85 (YSI Inc) was employed to measure DO.

The YSI-85 is a handheld multiparameter sensor (polarographic), that measures DO, conductivity, salinity, and temperature. Before each oceanographic campaign, the membrane and the 0 O_2

electrolyte solution of the sensor were replaced. Then, the sensor was calibrated according to the manufacturer's instructions. In short, three to six drops of clean water were added to a sponge located in an internal chamber of the sensor; this creates a 100 % water-saturated air environment for dissolved oxygen calibration. The calibration of the sensor was checked in a 0 and 100% air satured solution. Also, measurements were calibrated according to the altitude of the sampling sites (0 msl, 760 mmHg). The oxygen sensor exhibited a range of measurements from 0 to 20 mg L^{-1}, a resolution of 0.01 mg L^{-1}, and accuracy of ± 0.3 mg L^{-1}. The measurement of DO was done inside the Niskin bottle once it arrives on board. When the bottle was opened, the probe was introduced (making slow circular movements) and the DO data was recorded when a DO value was stabilized.

The monitor stations (Fig. 1C) correspond to La Ventana reef, Playa Blanca reef, El Remanso reef, La Camaronera reef, and El Planchon (an artificial reef). The available data included the years 2005, 2006, 2008, 2009, 2012 - 2014, and 2016 - 2019. The full data set was highly imbalanced since it did not include complete data for both seasons or depths in most years. Hence, to rigorously examine the effects of temporal and spatial factors on DO variability, we used the data from the years 2013, 2017, and 2019, which were complete for all levels of the four factors.

A factorial nested ANOVA was performed using the General Linear Models module of Statistica software (Statsoft®) to establish the effects on DO of the categorical factors Reef (5 levels) and Depth (2 levels, nested within Reef) crossed with Year (3 levels) and Season (2 levels, nested within Year). Assumptions of homogeneity of variances and normal distribution of residuals were examined with a Levene's Test ($F = 1.18$, $df = 9,50$, $p = 0.32$) and a Kolmogorov-Smirnov test with Lilliefors correction ($D = 0.113$, $p = 0.06$), respectively.

We follow the definition of Welker et al. (2013) to establish the normoxic and hypoxic conditions at Gorgona's reefs. Here we defined normoxia (and the normoxic range) according to the DO concentration values within the Mean ± 1 SD, while hypoxia as any value of DO below the Mean minus 1 SD.

Aiming to describe DO conditions, particularly at different depths, at La Azufrada reef (where coral samples were collected for the determination of the coral hypoxic threshold), additional DO measurements were done with a YSI-85 on March 2 and 5, 2022 on the reef or its immediate vicinity offshore. Eighteen water samples were taken at the surface (1 m) and seven water samples were taken at 10 m depth. Mean DO values for each depth were compared with a two-sample *t* -test with separate variance estimates due to significant variance heterogeneity (Levene's test, F = 8.27, Df = 23, p = 0.008).

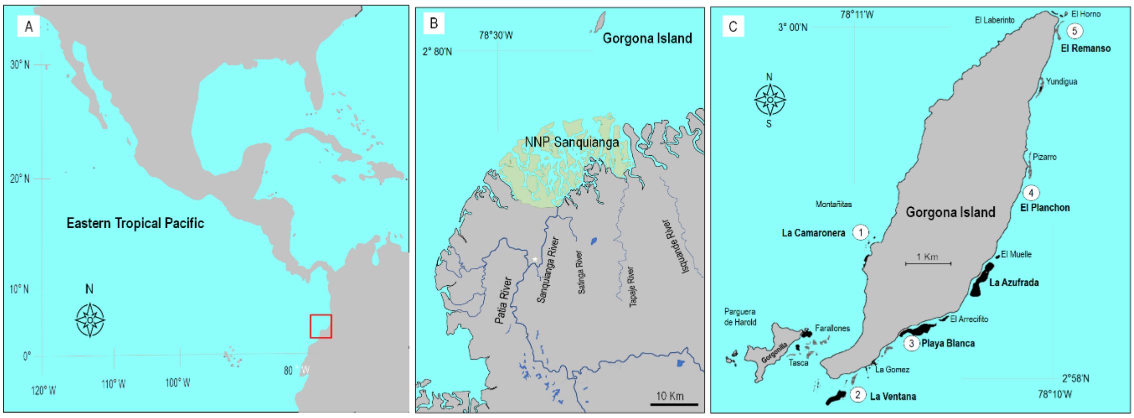

Figure 1. Location of Gorgona Island. (A) The red square indicates the location of Gorgona Island in the Eastern Tropical Pacific. (B) Position of Gorgona Island in front of the mangrove ecosystem at the National Natural Park (NNP) Sanquianga (green area), where sediments from the Patia River are discharged into the ocean. The white star indicates the position of a constructed channel that connects the Sanquianga and Patia rivers. (C) Numbers (from 1 to 5) indicate the location of coral reefs where dissolved oxygen was monitored.

Identification of the hypoxic threshold

Coral reefs of Gorgona Island (and in general in the ETP) are dominated by *Pocillopora* corals (Glynn et al., 2017). However, the morphological and molecular characteristics within genus in the region do not yet allow to clearly delimit species (Pinzon et al., 2013). For this study, we select colonies that follow the morphological features of *Pocillopora capitata* (Veron, 2000), one of the most common in Gorgona Island.

In November 2021, seven coral colonies of *P. capitata* were selected from the outer reef slope (~7 m depth) of La Azufrada reef. A fragment of each one was collected and transported to the wet lab facility of the Henry von Prahl Research Station of Gorgona Island (located 1.1 km from La Azufrada reef, at 0 msl, 760 mmHg). Coral fragments were kept in a 70 L tank (filled with water collected from the reef), in which water movement was generated by a submersible pump. Coral fragments were maintained in dark conditions for 2 h before the experiment.

To describe the relationship between the respiration rate of *P. capitata* and the environmental oxygen availability, we incubated coral fragments in sealed respiration chambers to allow DO depletion due to respiration by the corals. The resultant recordings of DO inside the chamber were then used to calculate the corals' MO_2 and relate it with a gradient of environmental oxygen saturation to identify the P_{crit}.

The experimental setup (Fig. 2) consisted of eight hermetically sealed respiration chambers (with internal movement of water generated by a peristaltic pump), seven containing a coral fragment, and one without coral (363 mL of water) to measure microbial respiration. All chambers were filled with seawater collected from the reef (30 PSU, 28°C), and with an initial DO concentration of 6.7 mg L^{-1} due to water movement with a submersible pump.

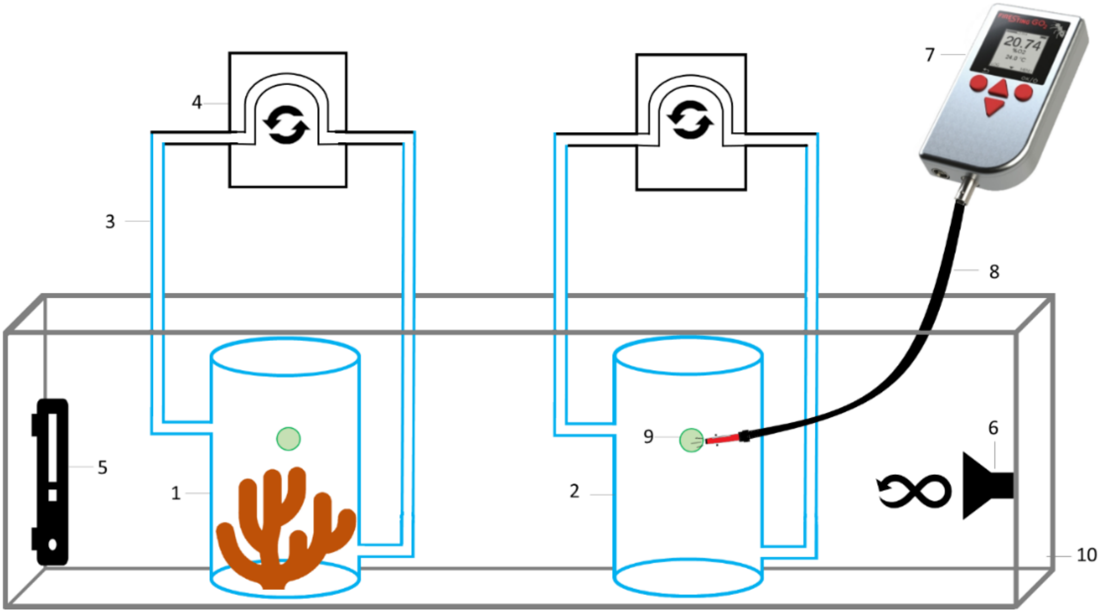

Figure 2. Schematic representation of the experimental setup to measure oxygen consumption by *Pocillopora capitata*. (1) Respiration chamber with a coral fragment, (2) control respiration chamber for microbial respiration, (3) hoses for water movement, (4) peristaltic pump, (5) thermostat, (6) submersible water pump, (7) hand-held oxygen meter connected to an (8) optical fiber, to measure dissolved oxygen on each respiration chamber by placing it on the (9) oxygen sensor spot, (10) water bath at 28°C.

In the inner wall of the chambers, an oxygen sensor spot (OXSP5, PyroScience GmbH) was glued. DO inside each chamber was recorded every ~20 min over the course of 5 h by manually locating an optical fiber (SPFIB-LNS, PyroScience GmbH) on the sensor spot (on the external side of the chamber). The optical fiber was connected to an oxygen meter that recorded the DO concentration adjusted to salinity, temperature, and atmospheric pressure (Firesting-GO2, PyroScience GmbH).

Following the oxygen meter manufacturer´s instructions, oxygen-free water, and 100% O_2-saturated water were used to calibrate the oxygen sensors. Oxygen-free water was prepared using 1.5 g of sodium sulfite (Na_2SO_3) powder dissolved in 50 mL of deionized water while stirring. For the 100 % O_2-saturated water, air was pumped into 50 mL of water while stirring using an aquarium air pump. After 20 min, the air pump was switched off and the solution was stirred for another 10 min.

Data recording for oxygen consumption started at 6.7 mg L^{-1} (101 % air saturation), approximately 1 h after closing the chambers to allow acclimation of corals to the closed system. Measurements were done at 30 PSU, 28 ± 0.3 °C (mean ± SD) and in the dark, by placing all respiration chambers in a water bath (within an aquarium) containing a thermostat and a submersible water pump to maintain a constant temperature throughout the aquarium and all chambers incubated there. As stated previously, data recording stops after 5 h, at that point the DO inside the respiration chambers was < 2.0 mg L^{-1}, a value considered as hypoxic (Vaquer-Sunyer & Duarte, 2008), and lower than the recorded at coral reefs of Gorgona Island (see results).

We selected the critical oxygen tension (P_{crit}) metric to identify the DO concentration that represents a hypoxic condition for *P. capitata* corals. P_{crit} was defined by Regan et al. (2019) as "the lower bound of the oxygen partial pressure (PO_2) spectrum over which an animal supports its MO_2 predominantly using aerobic metabolism, albeit with a diminishing aerobic scope for activity as PO_2 approaches P_{crit}". From this point, the MO_2 conforms to the environmental O_2 condition, but with a cost for the organism, or until PO_2 conditions became lethal (Claireaux & Chabot, 2016; Cobbs & Alexander Jr, 2018; Negrete & Esbaugh, 2019). From the P_{crit} the organism is exposed to severe hypoxia (Grieshaber et al., 1994). P_{crit} is considered the most appropriate benchmark when measured in fasted and resting animals (the standard MO_2) because it is truly ‘critical’ for the animal’s survival (Ultsch & Regan, 2019).

P_{crit} is considered a powerful tool to assess hypoxia tolerance, as a lower value is consistent with more tolerance (Negrete & Esbaugh, 2019). Because the P_{crit} is strongly correlated with the environmental O_2 level that organisms face, it is therefore ecologically relevant and allows to identify the detrimental O_2 ambient conditions (Regan et al., 2019).

We used the packages respR (http://cran.r-project.org/package=respR) and respirometry (http://cran.r-project.org/package=respirometry) to calculate corals’ respiration rate and P_{crit} (Harianto et al., 2019; Siebel et al., 2021). The respR package used the time *versus* oxygen data to calculate whole organism MO_2 and P_{crit} (methods: Broken-Stick regression, and Segmented regression, and we set width to 0.1 and 0.2 for its calculus:). The respirometry package used the time versus oxygen data to calculate MO_2; to calculated P_{crit} use MO_2 versus PO_2 as input, and three methods for its quantification: α-Pcrit, Broken-stick regression, and nonlinear regression (NLR). Differences in the resulting P_{crit} values were assessed between packages and methods (and widths).

The Broken-stick method depends on a relatively constant MO_2 as PO_2 declines, and a discontinuity in MO_2 must be taken as P_{crit} (Yeager & Ultsch, 1989). The Segmented method estimates the P_{crit} by iteratively fitting two intersecting models and selecting the value that minimizes the difference between the fitted lines (Muggeo, 2003). For the Nonlinear regression (NLR) the P_{crit} is an inflection point in the data after being fit to different functions, and the best function was selected according to the smallest Akaike’s Information Criterium (Muggeo, 2003). The Physiological oxygen supply capacity (α) is the maximum amount of oxygen that can be supplied per unit of time and oxygen pressure, and α-P_{crit} is the PO_2 at which physiological oxygen supply mechanisms are operating at maximum capacity. α is a species- and temperature specific constant that describes the linear dependency of P_{crit} on MO_2 (Siebel et al., 2021).

The MO_2 (mg O_2 h^{-1}) was standardized by the weight (g) of coral tissue (mg O_2 h^{-1} g^{-1}), estimated by the difference between wet weight (31.2 ± 10.6 g) and ash-free dry weight (28.0 ± 9.5 g) of coral fragments. The environmental authority of Parques Nacionales Naturales de Colombia endorsed all aims and methods of this research (PIR NO.014.19, Agreement 239; December 20, 2019).

Results

Temporal and spatial variability of dissolved oxygen concentration

The mean DO concentration on reefs range from 4.3 to 4.9 mg L^{-1} (Fig. 3A). DO at surface was 4.5 ± 0.7 mg L^{-1} (mean ± SD), and at 10 m was 4.6 ± 1.0 mg L^{-1} (Fig. 3B). According to the Nested Anova (Table 1), there were no differences in DO concentration between reefs or depths at each reef, but the factors Year (Fig. 3C) and season (Fig. 3D) had a significant effect on DO variability. In 2019, DO concentration was significantly high and more variable (5.3 ± 1.0 mg L^{-1}) than in 2017 (4.3 ± 0.3 mg L^{-1}) or 2013 (4.1 ± 0.6 mg L^{-1}). During the upwelling season DO concentration was lower than during the non-upwelling season, and marked differences were recorded in 2013 and 2017 (Table 1). Regarding the interaction between depth and season on DO concentration (Fig. 3E), significant low values (4.0 ± 0.9 mg L^{-1}) occurred during the upwelling season at 10 m depth (Fig. 3E. Two-way Anova: $F = 5.1$, $p = 0.02$; Tukey HSD = 0.6, $df = 56$, $p < 0.04$).

Table 1. Statistical analysis to examine differences in Dissolved oxygen concentration at coral reefs of Gorgona Island.

Test	Factor	SS	*df*	MS	F	*p*
Nested Anova	Reef	3.22	4	0.80	1.94	0.11
	Depth (in Reef)	0.44	5	0.08	0.21	0.95
	Year	15.44	2	7.72	18.64	0.000001
	Season (in Year)	9.16	3	3.05	7.37	0.0004
	Error	18.63	45	0.41		
Factorial Anova	Depth	0.16	1	0.16	0.26	0.61
	Season	7.01	1	7.01	10.81	0.001
	Depth x Season	3.37	1	3.37	5.19	0.02
	Error	36.35	56	0.64		

Normoxic range and hypoxic conditions

The range of normoxic conditions on coral reefs of Gorgona Island was stablished based on the average value of DO: 4.6 ± 0.89 mg L^{-1}, and values below 3.71 mg L^{-1} (DO < mean – SD) should be considered hypoxic. Such conditions, with values between 3.70 and 3.0 mg L^{-1} (lowest DO reported), were recorded in 2013 and 2017 during the upwelling season at 10 m depth, and represented 16 % of all data points.

DO concentration at La Azufrada reef

There were significant differences in DO concentrations, during March 2022, between the surface and 10 m water depth (Student's t test = 5.7, Df = 7.17, p = 0.0006). In the surface water layer, the mean DO concentration was 7.3 ± 0.5 mg L^{-1}, and minimum and maximum values were 6.0 mg L^{-1} and 8.4 mg L^{-1}. At 10 m depth, the mean DO was 4.8 ± 1.1 mg L^{-1}, and minimum (3.1 mg L^{-1}) and maximum (5.8 mg L^{-1}) values were lower than at the surface (Fig. 3F).

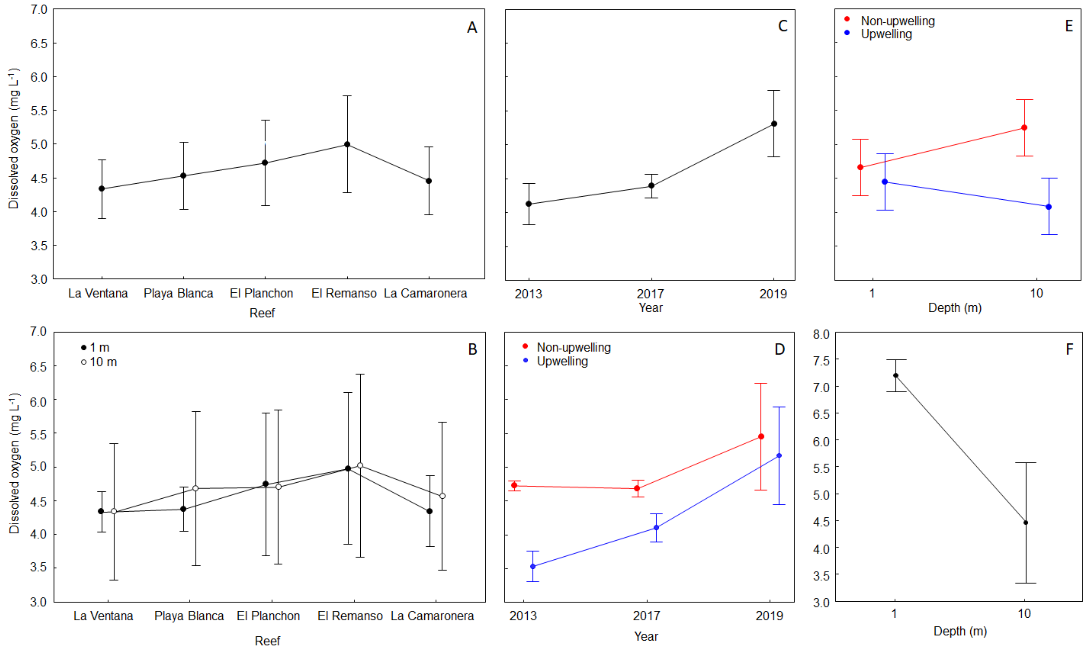

Figure 3. Effect of temporal and spatial factors on dissolved oxygen concentration (DO) at reefs of Gorgona Island. (A) DO concentration in reefs of Gorgona Island. (B) DO concentration at 1 and 10 m depth in reefs of Gorgona Island. (C) Interannual variation in DO. (D) Seasonal variation of DO between years, red corresponds to the non-upwelling season and blue to the upwelling season. (E) DO concentration at 1 and 10 m depth between seasons. (F) DO concentration at 1 and 10 m depth in La Azufrada reef during the upwelling season of 2022. In all panels: mean (●), and 0.95 confidence intervals (⌶).

Hypoxic threshold of *Pocillopora capitata*

The mean (± SD) MO_2 of *Pocillopora capitata* coral fragments at 28 °C was 0.26 ± 0.02 mg O_2 h^{-1}, and there were no differences in the results obtained from the two packages employed to calculate it (Table 2, Student's t test in Supplementary material 2).

Table 2. Metabolic rate (MO_2) of *Pocillopora capitata*.

Coral	respR			respirometry		
	MO_2 (mg O_2 h^{-1})	MO_2 (mg O_2 h^{-1} g^{-1})	R2	MO_2 (mg O_2 h^{-1})	MO_2 (mg O_2 h^{-1} g^{-1})	R2
A	0.256	0.071	0.88	0.266	0.074	0.88
B	0.223	0.046	0.86	0.233	0.048	0.85
C	0.287	0.137	0.97	0.297	0.142	0.97
D	0.259	0.069	0.86	0.269	0.071	0.86
E	0.287	0.105	0.91	0.297	0.108	0.90
F	0.257	0.064	0.70	0.267	0.066	0.69
G	0.249	0.146	0.98	0.256	0.151	0.98
Mean ± SD	0.260 ± 0.02	0.091 ± 0.03	0.88 ± 0.09	0.269 ± 0.02	0.094 ± 0.03	0.88 ± 0.10

The mean P_{crit} calculated with the respR package was 3.5 ± 0.9 mg O_2 L^{-1} (Fig. 4, Table 3), and according to a nested Anova, there were no statistical differences if a particular method was selected or if the width value was set to 0.1 or 0.2 (Supplementary material 3).

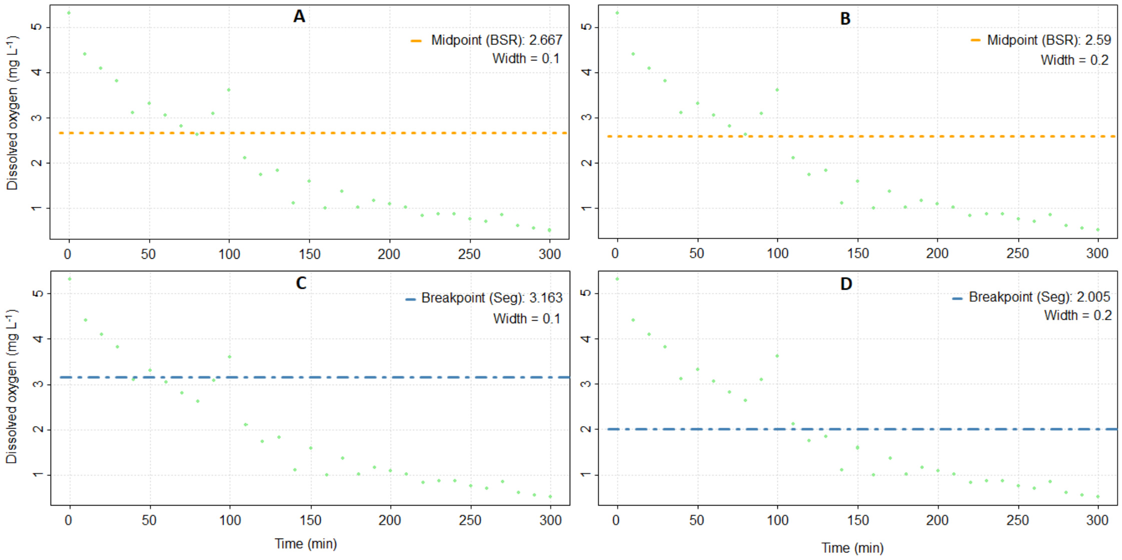

Figure 4. Critical oxygen tension (P_{crit}) of *Pocillopora capitata* calculated with the respR package. P_{crit} (mg O_2 L^{-1}) of a fragment of *Pocillopora capitata* (incubated at 28°C, 30 PSU, and dark conditions) was calculated using the respR package (Harianto et. al., 2019). The panels show the P_{cri}t from the broken stick method with the width set at 0.1 (A) and 0.2 (B), and the Pcrit from the segmented method with width at 0.1 (C) and 0.2 (D).

However, different P_{crit} values were obtained when the respirometry package was employed (One-way Anova, Sum of square = 23.5, df = 2, F = 9.4, p =0.001. Assumptions: homogeneity of variance [Cochran test, C = 0.5, df = 2, p = 0.3]; normal distribution of residuals [D = 0.14, p > 0.2]). Both the Broken-stick regression (BSR) and NLR methods produce similar results (Fig, 5, Table 3), but the α-Pcrit method produces significantly low values (Tukey HSD test = 1.2, df = 18, p < 0.004). This is because this method describes the oxygen limit for the MO_2 (Siebel et al. 2021).

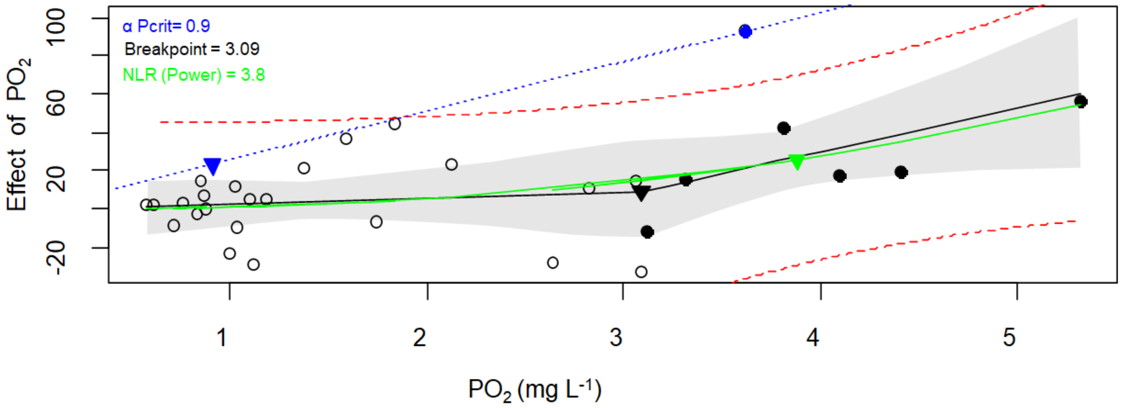

Figure 5. Critical oxygen tension (P_{crit}) of *Pocillopora capitata* calculated with the respirometry package. P_{crit} (mg O_2 L^{-1}) of a fragment of *Pocillopora capitata* (incubated at 28 °C, 30 PSU, and dark conditions) was calculated using the respirometry package (Seibel et al., 2021). Three P_{crit} metrics were plotted: the broken stick regression (black line, Pcrit (▼) = 3.09), the nonlinear regression metric (green line, Pcrit (▼) = 3.8), and the α-based Pcrit method (blue dash line, α-Pcrit (▼) = 0.9). Black circles represent oxyregulating observations, while empty circles represent the oxyconforming observations. For the Broken stick regression (BSR), the dashed red curves is the 95% prediction interval. The NLR curve was fitted to the Power function (selected for its smallest AIC from the Michaelis-Menten, Hyperbola, Pareto, and Weibull functions). The blue line represents _ (the animal's oxygen supply capacity, Seibel et al., 2021). The gray bands represent the 95% confidence interval.

Table 3. Critical oxygen tension (P_{crit}) of *Pocillopora capitata*.

	respR				**respirometry**			
	BSR		Segmented					
coral	*0.1*	*0.2*	*0.1*	*0.2*	α-Pcrit and α		BSR	NLR
A	3.6	3.2	4.0	2.8	1.4	23.87	4.3	4.2
B	3.3	3.3	3.6	2.8	2.9	15.83	4.3	4.9
C	5.4	3.7	4.9	5.1	2.4	6.24	5.0	4.1
D	2.6	2.5	3.1	2.0	0.9	25.56	3.0	3.8
E	2.7	2.9	4.2	3.7	1.1	18.88	4.4	0.7
F	3.7	3.1	3.90	2.8	1.4	33.00	3.1	4.7
G	5.0	4.6	5.37	2.3	0.8	8.76	2.1	4.5
Mean ± SD	3.8 ± 1.0	3.3 ± 0.6	4.1 ± 0.7	3.1 ± 1.0	1.5 ± 0.8	18.8 ± 9.4	3.7 ± 1.0	3.8 ± 1.4

When both packages and their methods were compared (Table 3), only the α-Pcrit method from the respirometry package produce significantly different lower values (Nested Anova, Supplementary material 5). Hence, a DO of 3.7 ± 1.0 (average from all methods except α-Pcrit) could represent the lower bound PO_2 over which *Pocillopora capitata* corals can regulate their MO_2, and ambient DO values below this value could expose this coral to hypoxia. However, the limit to maintain an aerobic metabolism (independent if the animal is resting or at maximum activity) is at 1.6 mg O_2 L^{-1}, the α-Pcrit.

Discussion

Oxygen conditions on reefs of Gorgona island

Low dissolved oxygen (DO) concentration in coral reefs of Gorgona Island occurred during the upwelling season, and even hypoxic values (< 3.7 mg L^{-1}) were recorded at 10 m depth. Additionally, DO varied significantly over years. Low DO concentrations during 2013 and 2022 coincided with the onset and full development (respectively) of La Niña conditions (NOAA, 2022), when winds and upwelling intensify (Fiedler & Lavín, 2017), while high DO concentration in 2016 and 2019 (Fig. 3) coincided with El Niño events (Canchala et al., 2020; NOAA, 2022) when the winds and upwelling are relaxed (Ledesma et al., 2022). These findings coincide with what has been previously described for the Colombian Pacific basin during different phases of ENSO events, with high DO conditions during an El Niño year (1998, 6.8 mg L^{-1}) and low DO conditions during a La Niña year (1999, 4.5 mg L^{-1}; Devis-morales et al., 2002).

As we observed at Gorgona Island, at Matapalo reef (Gulf of Papagayo, Costa Rica) low DO (4.5 mg L^{-1}) occurs during extreme upwelling events at 3 m depth, but the water in this area is on average well oxygenated (7.2 ± 0.01 mg L^{-1} mean ± SE, 100 – 120% saturation; Rixen et al., 2012; Stuhldreier et al., 2015). Likewise, in reefs at San Agustin Bay (Gulf of Tehuantepec, Mexico) and Taboguilla Island (Gulf of Panama) DO was lower during the upwelling season than during the non-upwelling season (Gulf of Tehuantepec: 3.3 vs 5.2 mg L^{-1}, Gulf of Panama: 3.6 vs 6.3 mg L^{-1}, Ramírez-Gutiérrez et al., 2007; Lucey et al., 2021). However, none of these studies state if oxygen conditions in the Gulfs of Tehuantepec and Panama were statistically lower during the upwelling than the non-upwelling seasons.

The average DO conditions in coral reefs of Gorgona Island during the non-upwelling season (4.9 mg L^{-1}) are among the lowest in the ETP region and resemble the sporadically low oxygen conditions in the Gulf of Papagayo during the upwelling season. The lowest mean DO values in coral reefs of the ETP occur in the Gulf of Tehuantepec (3.3 mg L^{-1}), where upwelling events last longer (D'Croz & O'Dea, 2007; O'Dea et al., 2012). DO on coral reefs typically ranges from 3.4 to 13.6 mg L^{-1} at 27°C or 50 % up to 200 % air saturation (Nelson & Altieri, 2019), and hypoxic environments at 2.8 mg L^{-1} or < 41% air saturation (Vaquer-Sunyer & Duarte, 2008), which is in line with the normoxic (4.6 ± 0.89 mg L^{-1}) and the hypoxic values that we reported for Gorgona (3.0 – 3.7 mg L^{-1}, Table 4).

Table 4. Dissolved oxygen concentration in different coral reefs of the world.

Site	Dissolved oxygen (mg L^{-1})	Reference
Eastern Tropical Pacific		
Non-Upwelling sites		
Gulf of Chiriqui, Panama	6.5	Camilli, 2007
Coco Island, Costa Rica	5.3	Esquivel-Garrote et al., 2020
Bahia de Navidad, Mexico	7.2	Godínez-Domínguez et al., 2000
Upwelling sites		
Gulf of Tehuantepec, Mexico	3.5 – 5.2	Ramírez-Gutiérrez et al., 2007
Gulf of Papagayo, Costa Rica	7.1 – 7.7	Stuhldreier et al., 2015
Gulf of Panama, Panama	3.6 – 6.3	Lucey et al., 2021
Gorgona Island, Colombia	4.2 – 4.9	This study
Caribbean		
Non-Upwelling sites		
Rosario Island, Colombia	6	Severiche et al., 2017
Bermuda. UK	7.5	Ziegler et al., 2021
Florida keys, USA	6.5	Ziegler et al., 2021
Puerto Rico	6.4	Ziegler et al., 2021
Cayo coral, Panama	5.4	Johnson et al., 2021
Upwelling sites		
Tayrona, Colombia	6.3	Bayraktarov et al., 2014
Indopacific		
Non-Upwelling sites		
Cocos Islands, Australia	4.5	Hobbs & Mcdonald, 2010
Bouraké, New Caledonia	5.5	Maggioni et al., 2021
Hawaii, USA	6.8	Ziegler et al., 2021
Upwelling sites		
Nanwan Bay, Taiwan	3.5-7.4	Meng et al., 2008
Red Sea		
Aqaba, Jordan	5.1 -10.3	Wild et al., 2010
Gulf of Oman	8.3	Bauman et al., 2010
Mean DO	4.5 - 6.6 mg L^{-1}	

Low oxygen water layers (from anoxia to <1 mg L^{-1}), between 50 m and 500 m water depth, and known as oxygen minimum zones, occur south of the equator (below the Peru Current) and off the coast of southern Mexico (below the Eastern Pacific warm pool), and during upwelling events reach sub-surface (20-50 m water depth) layers (Fiedler & Talley, 2006). During the past 50 years, the oxygen minimum zones have expanded vertically, from a thickness of 370 m in 1960 to 690 m in

2006, and in the ETP there is a trend of oxygen loss of 49 mmol m^2 $year^{-1}$ (Stramma et al., 2008). It is likely that this tendency will continue, adding another potential threat to coral reef communities of the ETP (Fiedler & Lavín, 2017). Although the arrival of oxygen-poor subsurface water occurred only during the upwelling season at Gorgona Island, upwelling of hypoxic waters might become more common in the future due to the expansion of the oxygen minimum zone and a strengthening of the trade winds system (and its associated upwelling) due to climate change (Rixen et al., 2012; Bakun et al., 2015; Sydeman et al., 2014; Xiu et al., 2018).

Fluctuations in DO are related to variation in the amount of organic matter, and the activity of aerobic organisms that decompose it (Testa et al., 2014). Oxygen minimum zones are the result of high phytoplanktonic production at the surface, a sharp permanent pycnocline that prevents local ventilation of subsurface waters, and a slow deep-water circulation (Gooday et al., 2010). We propose that the low DO concentration at Gorgona during the non-upwelling seasons, is due to high productivity that could increase the biological oxygen demand.

In the ETP high concentration of chlorophyll-a (Cl-a) occurs during the upwelling season. In the Gulf of Tehuantepec Cl-a concentration was 2.8 mg m^{-3} during the upwelling season and 0.1 mg m^{-3} during the non-upwelling season (Coria-Monter et al., 2019). In the Gulf of Papagayo, Cl-a concentration was 1.2 mg m^{-3} during the upwelling season, and 0.59 mg m^{-3} during the non-upwelling season (Stuhldreier et al., 2015). In the Gulf of Panama Cl-a was 1.4 and 0.2 mg m^{-3} during the upwelling and non-upwelling seasons, respectively (D'Croz & O'Dea, 2007). At Gorgona Island Cl-a mean value on coral reefs was 5.0 mg m^{-3} during the upwelling season, and 3.5 mg m^{-3} during the non-upwelling season (A. Giraldo, unpublished data). Values of Cl-a concentrations at Gorgona Island are like those in Peru (5 - 2 mg m^{-3}, Echevin et al., 2008). Two factors lead to a high concentration of Cl-a throughout the year along the Colombian Pacific coast: first, upwelling throughout most of Panama Bight at the beginning of the year, and second, high pluviosity and numerous rivers on the region that supply large amounts of nutrients through runoff (Corredor-Acosta et al., 2020). Of local importance, Gorgona Island is 29 km offshore of the Sanquianga National Natural Park (NNP), where high sediment discharge from the Patia River occurs.

The Patia river (Fig. 1) has the largest delta on the western coast of South America (23700 km^2), and its plume reaches Gorgona Island during La Niña events (Restrepo & Kettner, 2012). In 1972 a 3 km long channel was constructed to connect the Patia and Sanquianga rivers. After that, more than 90% of the Patia River discharge started to flow northward through the Sanquianga River, leading to the degradation of the mangrove ecosystem in NNP Sanquianga (Restrepo, 2012; Restrepo & Cantera, 2013).

The actual sediment yield into the Pacific Ocean through the Sanquianga river is 1500 t km^2 yr^{-1} (Restrepo & Kettner, 2012), and there is concern about the effects of sediment runoff on coral reefs of Gorgona because deforestation on the Colombian Pacific coast is increasing dramatically (Belokurov et al., 2016). Despite the importance of the Colombian Pacific forests in terms of carbon storage and as a biodiversity hot spot (Canchala et al., 2020), forest loss has been exacerbated in the region by illicit crops and alluvial mining to finance Colombia's armed conflict. Between 2001 and 2018, 2324 km^2 of the Colombian Pacific Forest were deforested (Anaya et al., 2020), causing a 25.7% increase in deforestation of the mangrove at PNN Sanquianga (Clerici et al., 2020).

Eutrophication is considered a factor that induces hypoxia (Diaz & Breitburg, 2009). Nutrient excess from runoff increases the dominance of algae, which deplete oxygen during the night, smother coral by overgrowth, and in the longer term reduce coral cover and reef calcification (Fabricius, 2005). For example, runoff during floods results in massive mortality of coral reef organisms, after phytoplankton blooms deplete oxygen, together with extremely low salinity and high nutrient concentration (Jokiel et al., 1993; Lapointe & Matzie 1996; Le Hénaff et al., 2019). Examining the interactive effects of low salinity, high sediments, and low oxygen levels on scleractinian corals and establishing their tolerance is another important step to understand coral reef resilience at Gorgona Island.

Hypoxic threshold of *Pocillopora capitata*

At 28°C, the minimum level of O_2 required to sustain a constant MO_2 (0.26 ± 0.02 mg O_2 h^{-1}) of *Pocillopora capitata* was 3.7 mg L^{-1} (56 % air saturation). It is likely that below this DO, the aerobic metabolism of corals decrease, and could be exposed to hypoxia and undergo metabolic depression (Reemeyer & Rees, 2019). Protruded polyps, observed in *P. capitata* at the end of the experiment, is a behavior that might facilitate oxygen uptake (by increasing the surface in contact with the environment) during hypoxia (Dodds et al. 2007; Henry & Torres, 2013). Mucus production during the incubation could fuel microbial respiration, who also deplete O_2 (Wild et al. 2010). At Gorgona Island oxygen depletion due to mucus production could occurs at reef flat during spring low tides (Castrillon-Cifuentes et al., 2017). Hence shallow corals could exhibit similar tolerance to hypoxic conditions to the ones studied here.

The hypoxic threshold of *P. capitata* (P_{crit} 3.7 mg L^{-1}) and the low DO concentration recorded at La Azufrada reef (3.1 mg L^{-1}) and other coral reef sites of Gorgona Island (3.0 – 3.7 mg L^{-1}) evidenced that although these corals inhabit well-oxygenated waters (mean DO 4.6 ± 0.89 mg L^{-1}), they are close to the limit of hypoxic conditions, hence, when DO decreases from 3.7 mg L^{-1} corals could face metabolic constraints depending on the duration of hypoxic conditions. Assessing the molecular responses to diel and seasonal changes in DO will help to understand the resilience of *Pocillopora* corals to deoxygenation (as proposed by Murphy & Richmond, 2016; Zoccola et al., 2017; Alderdice et al., 2020; Alderdice et al., 2021; Deleja et al., 2022).

A similar value between the P_{crit} and the lower DO conditions at reefs were also found for 14 tropical scleractinian corals and the cold-water coral *Lophelia pertusa*. The P_{crit} (at 26 °C, and 35 PSU) for the tropical corals range from 2 to 4 mg O_2 L^{-1}, and the lower ambient DO was 2 mg O_2 L^{-1} (Hughes et al., 2022). The P_{crit} (at 9°C, and 35 PSU) for the cold-water coral was 3.9 - 4.3 mg O_2 L^{-1}, and the lower ambient DO 3.2 mL L^{-1} (Dodds et al., 2007). Although there is a discussion around the use and way to calculate this metric (Wood, 2018; Regan et al., 2019), the similarity between P_{crit} and DO ambient conditions highlight its ecological relevance, and in our case similar values of P_{crit} were obtained from different methods.

Two *Pocilloporids* were included on Hughes et al. (2022) research, *Pocillopora acuta* (P_{crit} 1.3 mg O_2 L^{-1}) and *Pocillopora damicornis* (P_{crit} 1.2 mg O_2 L^{-1}). These congeners had P_{crit} lower than the P_{crit} of *P. capitata*, and it could be due to taxa, or a response to local changes in temperature and O_2 conditions (Vaquer-Sunyer & Duarte, 2008). However, P_{crit} in *P. acuta* and *P. damicornis* were like the α-Pcrit of *P. capitata* (1.6 mg O_2 L^{-1}), which is the oxygen limit to maintain the aerobic metabolism (Siebel et al. 2021).

We suspect that different Pocilloporids of the ETP could have different tolerance to hypoxic conditions, and due to thermal dependence of P_{crit} (Siebel et al., 2021), even a seasonal response could occur in *Pocillopora*, especially for corals that inhabit sites were upwelling develops (Table 4). Hence, we encourage researchers to assess the hypoxic tolerance of corals from the ETP, due to predictions of deoxygenation that the region will face (Fiedler & Lavín, 2017). However, trying to identify a species-specific response could be hampered due to taxonomic gaps for *Pocillopora* in the region.

At Gorgona Island DO values lower than 2.1 mg L^{-1} occur at 30 m depth during the upwelling season (Giraldo et al., 2014). DO < 2 mg L^{-1} is considered a hypoxic condition because it is lethal for many aquatic organisms (Levin et al., 2009), but the lethal oxygen thresholds for aquatic animals are species-specific because they can range from 0.28 to 4 mg L^{-1} (Vaquer-Sunyer & Duarte, 2008; Welker et al., 2013). The low DO values recorded in this study (3.0 mg L^{-1}) and by Giraldo et al. (2014) open the possibility that some benthic organisms (that occur deeper than 10 m) may be occasionally exposed to hypoxic conditions.

Because water samples to describe DO conditions were collected during daylight hours and were not regularly monitored, it is possible that even lower DO concentrations may occur at reefs of Gorgona Island. A study in the Red Sea found strong diurnal variation in O_2 concentrations (5.1 to 9.3 mg L^{-1}) in algae-dominated reefs compared to coral-dominated ones (6.6 to 8.5 mg L^{-1}), with the lowest DO values during dusk and before dawn, and highest values around midday (Wild et al., 2010). During the day, photosynthesis by zooxanthellae and benthic algae produce oxygen that exceeds the respiratory demands of reef aerobic organisms, but during the night photosynthetic processes stop and respiration of organisms depletes oxygen to levels at which severe hypoxic conditions (down to 0.7 mg L^{-1}) can occur (Nelson & Altieri, 2019).

We propose that the occurrence of hypoxic waters during the upwelling season at 20-30 m depth and even at 10 m depth during intense upwelling events, impose a bathymetric restriction for *Pocillopora* corals. In fact, the deepest distribution of scattered *Pocillopora* colonies at Gorgona Island is 20 m (Muñoz et al., 2018) and for coral reefs is ~8 m (Vargas-Ángel, 2003). Untangling which abiotic factor(s) that reach extreme levels during upwelling events (e.g., temperature, salinity, nutrients, pH or oxygen) limits the depth distribution of corals and coral reefs at Gorgona Island could be a potentially important line of research at this marine protected area. Most of the literature attributes the restriction of ETP coral reefs to shallow areas to low temperatures and low light conditions (Glynn et al., 2017). However, oxygen conditions play a major role in the success of benthic organisms, including calcification processes, a physiological function with key ecological consequences for reef accretion (Wijgerde et al., 2012; Wijgerde et., al 2014; Nelson & Altieri, 2019; Hughes et al., 2020; Sampaio et al., 2021).

When hypoxia is not lethal, it reduces growth, reproduction, photosynthesis, or immune responses due to low energy production in organisms, while the remaining energy is invested in survival (Diaz et al., 2012; Dupont-Prinet et al., 2013; Wooldridge, 2014; Nelson & Altieri 2019; Hughes et al., 2020). Testing whether hypoxia induces trade-offs in *Pocillopora* corals (reducing vital functions like gamete production) to balance aerobic metabolism deprivation during upwelling events, could help to understand why *Pocillopora* in the ETP have low sexual reproduction (Glynn et al., 1991). A trade-off between growth and sexual reproduction has already been observed in *P. damicornis* at Gorgona Island after stress due to aerial exposure during extreme low tides (Castrillón-Cifuentes et al., 2017). Other trade-offs can also occur. For instance, the sea pen *Veretillum cynomorium* experiences oxygen deprivation in internal tissues during air exposure, but they display a costly enzymatic protective response to prevent tissue oxidation (Teixeira et al., 2013).

Other factors (independent of upwelling events) that potentially can induce hypoxia at coral reefs of the ETP are algal overgrowth, eutrophication, sedimentation (Fabricius, 2005; Diaz & Breitburg, 2009; Murphy & Richmond, 2016; Nelson & Altieri, 2019). For the ETP there are only two reports of *Pocillopora* mortality (at Caño Island, Costa Rica, and Utria, Colombia) apparently due to oxygen deprivation after a dinoflagellate bloom of *Chlodinium catenatum* and *Gonyaulax monilata* (Guzmán et al., 1990; Vargas-Ángel, 1996).

Conclusions

In conclusion, we found well-oxygenated water conditions in coral reefs of Gorgona Island, but noticed the occurrence of hypoxic waters reaching the deepest parts of reefs (< 3.7 mg O_2 L^{-1} at 10 m depth) during upwelling events. We found that the hypoxic threshold (P_{crit}) of *Pocillopora capitata* (3.7 mg O_2 L^{-1}) was similar to the low DO concentration recorded on coral reefs of Gorgona Island during the upwelling season at 10 m depth. Hence, if hypoxic events intensify because of climate change, or if local hypoxic inducing circumstances increase (e.g., eutrophication from Patía

River), this could represent a real threat to *Pocillopora* corals, the main reef-builder scleractinian coral at Gorgona Island. Preventing nutrient enrichment (that decreases water quality) and sediment input from the Patía River is an important task for the reef management at Gorgona Island. Further questions to solve are how long do hypoxic conditions persist at reefs of Gorgona, what is the frequency of occurrence of hypoxic events, how long can corals tolerate hypoxic conditions, the role of oxygen conditions on the bathymetric distribution of corals (especially in the calcification process), and what are the long-term effects of hypoxia on the physiology (the molecular response) of corals, including other branching and massive coral species different from *P. capitata* that inhabit Gorgona Island.

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Chapter 3: Physiological responses of *Pocillopora* corals to upwelling events in the Eastern Tropical Pacific

Ana Lucia Castrillón-Cifuentes1,2*, Fernando A. Zapata 2†, Christian Wild 1†

1Marine Ecology Department, University of Bremen, Bremen, Germany
2Coral Reef Ecology Research Group, Universidad del Valle, Cali, Colombia

†These authors share senior authorship

* Corresponding Author: analucia@uni-bremen.de, castrillon.ana@correounivalle.edu.co

Abstract

Upwelling events can change the sea water conditions within few hours during several months on a seasonal regimen. These events are predicted to intensify due to climate change, exposing shallow benthic organisms to hypoxia and thermal stress, among other extreme conditions. Some coral reefs in the Eastern Tropical Pacific (ETP) recurrently experience upwelling events. Coral reefs off Gorgona Island, Colombia, are exposed to lower oxygen concentrations (3.0 - 3.7 mg O_2 L^{-1}) and lower temperatures (17 - 24 °C) from mid-January to mid-April, when upwelling develops, compared to the rest of the year (4.9 ± 0.7 mg O_2 L^{-1}, 28.4 ± 0.3 °C, mean ± SD). While no visible signs of stress have been reported for corals during upwelling, it can be hypothesized that corals would be negatively affected by these changes. Therefore, the objectives of this study were to (1) identify the effects of temperature and hypoxia on the metabolic rate (MO_2) of *Pocillopora* corals under lab conditions, and (2) to examine the changes in skeletal growth and Symbiodiniaceae density of *Pocillopora* in the field between upwelling and non-upwelling seasons. Findings revealed that MO2 was significantly reduced by 20% at 24°C and significantly increased by 10% at 32°C compared to 28°C. During the upwelling season, *Pocillopora* corals exhibited a 52% increase in Symbiodiniaceae density, but the growth rate decreased by 50% compared to the non-upwelling season. Fast changes in water conditions during the upwelling strongly affects the metabolism of *Pocillopora* corals. Although conditions during upwelling were not lethal, they compromised the energy of the coral for their vital functions, indicating that upwelling pushes them toward their physiological limit. Consequently, predicted increases in upwelling events in combination with ocean warming and deoxygenation may be particularly critical for upwelling-exposed corals and the reefs they build in the Eastern Tropical Pacific.

Keywords: thermal stress, metabolic rate, growth rate, zooxanthellae density, hypoxic threshold.

Introduction

Upwelling is a process where cool deep waters are transported to shallow depths due to the displacement of a surface water mass by winds. This phenomenon can occur in the open ocean and along coastlines, and is characterized by a series of circulation cells that cause changes in pH, oxygen levels, and nutrient concentrations (Spring and Williams, 2023). Coastal upwelling in the Eastern Tropical Pacific (ETP) is initiated when wind jets exceed 10 m s^{-1} and pass from the Caribbean and Gulf of Mexico to the Pacific through topographic depressions at the gulfs of Tehuantepec (Mexico), Papagayo (Costa Rica), and Panama (D'Croz and O'Dea, 2007; Coria-Monter et al., 2019). The temperature decrease associated with upwelling occurs rapidly, typically within 1 hour, and is characterized by pulses that can last several hours during the first quarter of the year (Rixen et al., 2012; Stuhldreier et al., 2015).

In the Gulf of Panama seasonal upwelling is primarily driven by the migration of the Intertropical Convergence Zone (ITCZ) from 10° N to 3° N during the dry season (December to April). During this time, the northeast trade winds intensify and cross the isthmus of Panama, causing the 20°C thermocline to reach its shallowest position (< 20 m depth) (Poveda et al., 2006; D'Croz and O'Dea, 2007; Alexander et al., 2012). During the upwelling season the temperature, pH and aragonite saturation decrease in the sub-surface water column (4 – 20 m depth), while salinity, nutrients and some carbonate parameters increase, promoting phytoplankton growth near the surface (D'Croz and O'Dea, 2007; Manzello, 2010b). Also, hypoxic conditions (0.1 mg L^{-1}) from the oxygen minimum zone (OMZ) reach the 10 m depth (Lucey et al., 2021). However, this pattern may be modified by El Niño Southern Oscillation (ENSO) events (Wang et al., 2017).

Despite seasonal abrupt changes in water conditions associated with upwelling, several coral reefs are present in the ETP region (Glynn et al., 2017a). However, at upwelling sites reef development is limited to protected areas shielded from direct oceanic influence, reef frameworks are thinner compared to those at non-upwelling sites, and *Pocillopora* corals exhibit low growth rates. These reef characteristics are thought to result from the low temperature, low pH, and high nutrient availability during upwelling events (Glynn and Stewart, 1973; Medellín-Maldonado et al., 2016; Tortolero-Langarica et al., 2017). Nonetheless, the rates of long-term reef accretion are similar throughout the ETP region (Toth et al., 2012, 2015, 2017).

Upwelling has been suggested to reduce warm thermal stress during El Niño events and provide a thermal refuge from ocean warming (Randall et al., 2020), and warming associated with El Niño can counteract the negative effects of low temperature on coral growth during upwelling (Vargas-Ángel et al., 2001; Jiménez and Cortés, 2003a). However, some discrepancy exists regarding trends in bioerosion and future persistence of reefs at upwelling sites (Manzello et al., 2008; Manzello, 2010a; Enochs et al., 2021; Rodriguez-Ruano et al., 2023). It has been proposed that to effectively reduce thermal stress during warming events, upwelling must occur simultaneously and provide sufficient cooling, phosphate levels must increase to alleviate nutrient starvation of Symbiodiniaceae, or corals must actively feed during plankton blooms (Chollett et al., 2010; Riegl et al., 2019). However, upwelling can also lead to the growth of benthic algae that compete with corals for space, and higher abundance of suspension-feeding macroboring fauna (Smith, 2006; Riegl et al., 2019; Palmer et al., 2022; Rodriguez-Ruano et al., 2023).

At present, climate change is causing vertical expansion of the OMZ and ocean deoxygenation (Clarke et al., 2021). The rate of ocean deoxygenation in the ETP is 49 mmol m^{-2} yr^{-1} (Stramma et al., 2008). For the near future it is predicted that upwelling events will increase in frequency and strength (Rixen et al., 2012; Sydeman et al., 2014; Bakun et al., 2015; Fiedler and Lavín, 2017). Additionally, the current low pH conditions at upwelling centers highlights the susceptibility of Pocillopora corals to ocean acidification (Manzello et al., 2008). However, predictions on the effect of future trends of ENSO and its influence on upwelling are uncertain (García-Reyes et al., 2015; Wang et al., 2017; Bograd et al., 2023).

Temperature and oxygen (O_2) conditions regulate many metabolic processes, and imbalances at the organismal level can impact ecological processes, particularly for habitat-forming taxa such as scleractinian corals. Metabolic impairments occur because enzyme activity is temperature-dependent, with maximum kinetics occurring within a specific range; below or above this range, enzymes become inactivated or denatured (Fitt et al., 2001; Daniel et al., 2010; Sawall et al., 2022). Additionally, the energy for enzymatic processes depends on ATP production, which requires O_2 as the terminal electron acceptor during aerobic synthesis (Salin et al., 2015). Mitochondrial activity is particularly reduced under low temperature and hypoxia (Gnaiger, 2001; Fangue et al., 2009), which occurs at dissolved O_2 concentrations (DO) < 2 mg L^{-1}, or any DO insufficient to maintain metabolic functions (Vaquer-Sunyer and Duarte, 2008; Welker et al., 2013; Hughes et al., 2020).

Thermal stress (cool or warm temperatures) induces the collapse of the symbiosis between the corals and the endosymbiotic algae (Symbiodiniaceae), leading to coral bleaching. When bleaching is not lethal, such stress increases susceptibility to diseases, and reduces growth and reproductive output (Baird et al., 2009; Kemp et al., 2011; Miller and Richardson, 2015; McLachlan et al., 2020). Even if thermal stress does not cause bleaching, at low temperatures the membrane permeability of cells is reduced, restricting the movement of glycerol from the symbiotic algae to the coral (Mayfield and Gates, 2007; Rodríguez-Troncoso et al., 2014), and the respiration rate of corals increases faster than the photosynthetic rate of the algae with increasing temperature (Coles and Jokiel, 1977; Castillo and Helmuth, 2005), both of which result in a deficiency of autotrophic energy for the corals' needs.

Hypoxia also has multiple negative impact on corals; when it is no lethal, it causes bleaching, partial tissue detachment from the skeleton, affects the activity of calcifying cells, homeobox genes, and lipid metabolism; and it produces oxidative stress, and DNA damage (Baohua et al., 2004; Weber et al., 2012; Wijgerde et al., 2012; Haas et al., 2014; Raj et al., 2020; Alderdice et al., 2021; Johnson et al., 2021; Deleja et al., 2022; Gravinese et al., 2022). The co-occurrence of hypoxia and warming reduce the respiration rate and energy for vital functions of corals (Gravinese et al., 2022), and although corals may switch to anaerobic metabolism, this is inefficient for survival under prolonged stress (Murphy and Richmond, 2016; Linsmayer et al., 2020).

In Symbiodiniaceae, hypoxia can reduce the activity of antioxidant enzymes, the respiration rate, and the photochemical efficiency of PSII (Matta and Trench, 1991; Gardella and Edmunds, 1999; Ulstrup et al., 2005). However, hypoxia may also have no effects on the endosymbiotic algae (Osinga et al., 2017). The bleaching response is associated with the activation of the Hypoxia-Inducible Factor, a gene important for the mitigation of hypoxic stress (Alderdice et al., 2022). However, Symbiodiniaceae community association and hypoxia tolerance could be species and site-specific; for example, the bleaching resistant *Acropora tenuis* associates with a different *Cladocopium* community than the bleaching sensible *A. selago* (Alderdice et al., 2020); *Pocillopora* acuta host mainly *Durusdinium* in hypoxic environments (mangroves), while *Cladocopium* at normoxic sites (reef); but transplantation evidenced stable symbiont association (Haydon et al., 2021).

Despite the well-known negative effects of hypoxia and cool stress on scleractinian corals, and the occurrence of both conditions in the ETP during upwelling events, there is lack of research comparing the effects of hypoxia vs those of thermal stress (Rodríguez-Troncoso et al., 2014, 2016; Glynn et al., 2017b; Tortolero-Langarica et al., 2017). To our knowledge, two reports have linked bleaching and mass mortality of *Pocillopora* corals with hypoxia after dinoflagellate blooms at Caño Island (Costa Rica) and Ensenada de Utría (Colombia) (Guzman et al., 1990; Vargas-Angel, 1996), and our previous work showed that the hypoxic threshold of *Pocillopora capitata* (Critical oxygen tension or Pcrit = 3.7 mg L^{-1}) from Gorgona Island lies within the lower DO conditions reported on reefs in this island (3.0 - 3.7 mg L^{-1}) (Castrillón-Cifuentes et al., 2023). The Pcrit, a metric for assessing the minimum DO level that maintains the metabolic rate (Negrete Jr and Esbaugh, 2019; Regan et al., 2019), has been found to be closer to the lower DO levels recorded in the environment of different scleractinian corals, indicating their sensitivity to drops in DO below the ambient typical range (Dodds et al., 2007; Hughes et al., 2022). Therefore, our objective was to assess the physiological response of *Pocillopora* (the main reef builder in the ETP) to rapid changes in temperature and O_2 conditions that can occur during upwelling events, with particular interest on the effect of the interaction of low temperatures and hypoxia.

We hypothesized that exposure to cool thermal stress and hypoxic conditions during upwelling events would significantly affect the physiology of *Pocillopora*. This is because these corals naturally experience pronounced changes in temperature and O_2 conditions on a seasonal basis. To test this hypothesis, our first step was to characterize the interannual changes in temperature and DO on coral reefs of Gorgona Island, Colombia, in order to determine the average and extreme conditions that corals face during upwelling. Subsequently, we assessed the physiological response of Pocillopora corals to these conditions using a combination of field and laboratory measurements. We have already characterized the spatio-temporal changes in DO on coral reefs of Gorgona Island (data available in Castrillón-Cifuentes et al., 2023). Therefore, this research complements our previous publication and expands our knowledge of coral responses to multifactorial changes in the environment.

Materials and Methods

Study area

Gorgona Island (2°58'10" N - 78°11'05" W, Fig. 1a,b) is a National Natural Park located 30 km off the nearest point on the Colombian Pacific coast. Despite its tropical position, there is marked climatic seasonality, primarily driven by the seasonal latitudinal displacement of the ITCZ, which affects most of Panama Bight (Rodriguez-Rubio and Stuardo, 2002; Corredor-Acosta et al., 2020). From January to April, there is low precipitation (350 mm month^{-1}) and the thermocline is at its shallowest position (7.5 m), allowing for the lifting of cool, high-salinity, nutrient rich, and low-oxygen deep waters (25°C, 30.8 PSU, 0.6 mg L^{-1} of Chl-a, 4.0 mg O_2 L^{-1}). For the rest of the year, precipitation increases (587 mm month^{-1}), and the thermocline deepens (47 m), allowing for warmer and more oxygenated waters to occurs, but with lower salinity and chlorophyll-a conditions (27 °C, 4.9 mg O_2 L^{-1}, 29.8 PSU, 0.1 mg L^{-1} of Chl-a) (Giraldo et al., 2008, 2014; Blanco, 2009; Sampson and Giraldo, 2014; Zapata, 2017; Castrillón-Cifuentes et al., 2023). Changes in pH did not reveal a temporal pattern (Ramírez-Martínez et al., 2022).

Interannual variability in oceanographic conditions occurs due to ENSO events. During El Niño, sea surface temperatures can increase by more than 1.7°C above the mean for several months and high oxygen conditions occur (5.1 mg O_2 L^{-1}) due to less intense upwelling events (Ledesma et al., 2022; Castrillón-Cifuentes et al., 2023). In contrast, cool temperatures as low as 18°C and hypoxic conditions (< 3.7 mg O_2 L^{-1}) have been registered on the reef slope during La Niña events, when upwelling intensifies (Vargas-Ángel et al., 2001; Mora and Ospina, 2002; Castrillón-Cifuentes et al., 2023).

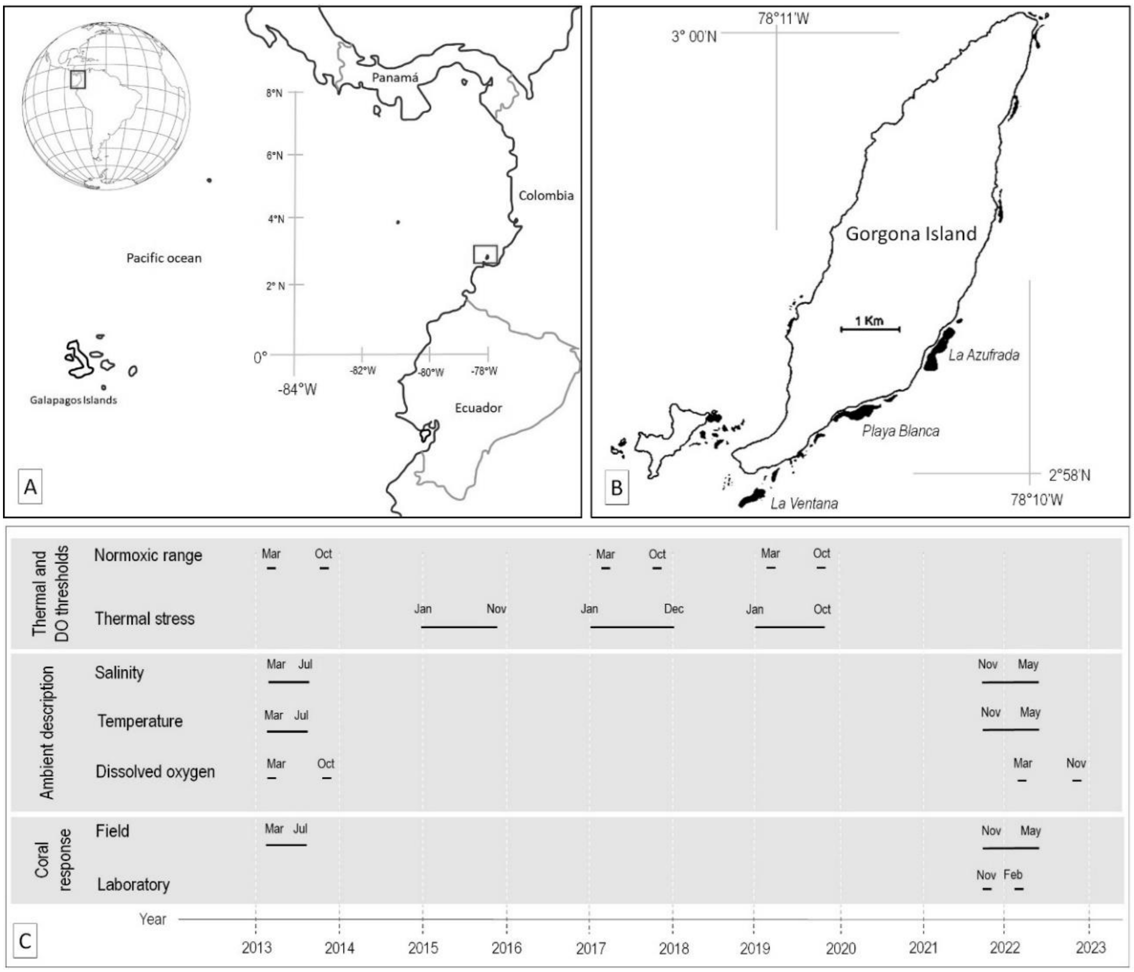

Figure 1. (A) Location of Gorgona Island in the Colombian Pacific. (B) Black areas denote the coral reefs of Gorgona Island where colonies of *Pocillopora* were collected for experiments. (C) Timeline for the data collection to stablish the normoxic and hypoxic conditions, and the cool and warm thermal stress that face corals at Gorgona Island; also, to show when was assessed the coral response to upwelling events in the field (growth rate and Symbiodiniaceae density) and laboratory (hypoxic threshold and respiration rate).

Environmental conditions on coral reefs of Gorgona Island during field measurements of growth and Symbiodiniaceae density of *Pocillopora*

In 2013, temperature and salinity were recorded with a datalogger at La Azufrada (LA) reef between March 1 and July 31. During March temperature was 24.8 ± 1.5 °C (mean ± SD), and salinity 34.8 ± 2.0 PSU. The rest of the time (April – July), temperature was 27.6 ± 0.6 °C, and salinity 34.1 ± 0.9 PSU (Supplementary Information file 1). All reefs of the island exhibited the same trend of lower DO during the upwelling season (3.5 ± 0.3 mg O_2 L^{-1}) than during the non-upwelling season (4.7 ± 0.1 mg O_2 L^{-1}) (Castrillón-Cifuentes et al., 2023). Chlorophyll-a concentration (a proxy for nutrient conditions) was higher (although not statistically significantly so) during March (1.23 ± 0.056 µg L^{-1}) than during October (1.04 ± 0.056 µg L^{-1}) (Cuellar-Chacon, 2017). pH was 7.4 in March (Giraldo and Valencia, 2013), and 8.6 in October (Vivas-Aguas et al., 2014), but values were collected by different devices and researchers. Nevertheless, no statistical differences in pH conditions at La Azufrada reef were detected between seasons in a study that was carried out from October 2010 to November 2011 (Ramírez-Martínez et al., 2022).

From November 14, 2021, to May 22, 2022, temperature was recorded with a datalogger at La Ventana (LV) and Playa Blanca (PB) reefs (Supplementary Information file 1). Salinity was recorded for the same period at PB, but only until the end of February at LV due to a device failure. Upwelling occurred from February 25 to March 31, 2022. During this period mean (± SD) temperature was 25.9 ± 1.0 °C and 26.1 ± 1.1 °C at LV and PB, respectively, and salinity was 32.1± 0.5 PSU at PB reef. Previous to the upwelling event (November 14, 2021 to February 24, 2022) the temperature was 27.0 ± 0.3 °C at both reefs, and salinity 30.9 ± 0.3 PSU at PB and 33.5 ± 0.4 PSU at LV. After the upwelling (April to May 2022) the temperature was 28.3 ± 0.2 °C at LV and 28.5 ± 0.3°C at PB, and salinity 31.2 ± 0.2 PSU at PB. Dissolved oxygen conditions at LA reef during March 2022 were 4.8 ± 1.0 mg O_2 L^{-1} (Castrillón-Cifuentes et al., 2023), and during November 2022 they were 6.7 ± 0.7 mg O_2 L^{-1}, measured with a Firesting-GO2 (PyroScience GmbH).

Field measurements of growth and Symbiodiniaceae density of *Pocillopora*

Study organism

Species delimitation of *Pocillopora* corals in the ETP has not been fully resolved, particularly if based on morphological characteristics. According to molecular analyses there are three types of Pocillopora within this region: type 1 is widespread throughout the ETP; type 2 is restricted to the Clipperton Atoll, and type 3 inhabits Panama and Galapagos Islands (Pinzón and Lajeunesse, 2011; Pinzón et al., 2013). Also, *Pocillopora* colonies from the ETP can switch morphology (Paz-García et al., 2015), but morphospecies did not exhibit differences in growth rates (Tortolero-Langarica et al., 2017). In this text we refer to the study organism simply as *Pocillopora*. The colonies selected for this study had morphological features (Supplementary Information file 1) of *Pocillopora damicornis* (Veron et al., 2022), although Schmidt-Roach et al. (2014) state that this species is absent from the ETP.

Growth rate

To identify seasonal changes in *Pocillopora* growth at Gorgona Island, during 2013, 27 colonies from LA reef were monitored from March to July. Each colony was photographed with a size reference in March 13, May 3, and July 4, and the diameter of the colonies was calculated using the ImageJ software (National Institute of Health, USA). The growth rate of the colonies was then calculated for two periods: March to May, corresponding to the effects of upwelling season, and May to July, corresponding to the non-upwelling season. Statistical differences in growth between seasons were examined with a paired t-test after checking for the normality of the distribution of differences between paired observations (Shapiro-Wilk's W = 0.979, p = 0.842).

From November 2021 to May 2022, the growth rate of coral fragments from LV and PB reefs were monitored (10 fragments per reef, each one from a different colony). The fragments were cemented with marine epoxy to ceramic tiles in April 2021 and allowed to grow at their respective reefs, and photographed with a size reference on November 14, 2021, and February 25 and May 22, 2022. The linear extension based on the height of the fragments was measured using the ImageJ software. The growth rate of the fragments was then calculated for two periods: November 2021 to February 2022 for the upwelling season, and February to May 2022 for the non-upwelling season. Differences in growth between seasons and reefs were compared using a Repeated Measures ANOVA, with season as a within-subject factor and reef as a between-subject factor. The normality of residuals assumption was satisfied for both seasons (Shapiro-Wilk's W = 0.909 and 0.951, p = 0.063 and 0.384, respectively), and variances were homogeneous between reefs in November-February and in February-May (Levene's test, F = 1.566 and 4.323, p = 0.226 and 0.052, respectively).

Symbiodiniaceae density

To identify seasonal changes on the Symbiodiniaceae density of *Pocillopora* corals at Gorgona Island, the density of algae from the 27 colonies monitored at LA reef was measured on March 13, 2013 (upwelling) and July 4, 2013 (non-upwelling). Once during each month, a 3 cm fragment was collected. The soft tissue from the fragments was fixed in Zenker's solution, decalcified in HCL (4 %), preserved in 70 % ethanol, and stained with Toluidine blue. Histological slides were cut at a thickness of 5 µm. On each slide, 15 polyps were randomly selected, and all endosymbiotic algae cells within each polyp were counted. The area of the polyps in the histological slide was calculated after measuring their diameter with a micrometer scale. The density of Symbiodiniaceae was established for the polyp area (μm^2) and extrapolated to cm^2. No taxonomic identification of the symbionts was made.

The luminosity (amount of white) in the color of the 27 colonies monitored at LA reef was determined in the photos used to measure the growth. Luminosity is related to the density of Symbiodiniaceae in corals, and lighter colors (or high luminosity) in the coral correspond to low algal density (Siebeck et al., 2006). Differences between the upwelling and non-upwelling seasons for the density of Symbiodiniaceae and the luminosity in the color of corals were compared using a paired t-test. Both Symbiodiniaceae density and luminosity satisfied the normality of paired differences assumption (Shapiro-Wilk's $W = 0.937$ and 0.930, $p = 0.101$ and 0.071, respectively).

Assuming that coral tissue luminosity is an indicator of Symbiodiniaceae density (Siebeck et al., 2006), the luminosity in the color of coral fragments from LV and PB reefs was measured in photos taken during February and May of 2022 (upwelling and non-upwelling, respectively). Differences in the luminosity of coral fragments at each reef were assessed between seasons using a repeated measures ANOVA. These data met the assumption of normality of residuals in both February (Shapiro-Wilk's $W = 0.973$, $p = 0.828$) and May (Shapiro-Wilk's $W = 0.964$, $p = 0.646$) as well as the assumption of homogeneity of variances between reefs both in February (Levene's test $F = 0.020$, $p = 0.888$) and in May ($F = 0.024$, $p = 0.879$).

Definition of thermal conditions to evaluate the metabolic response of *Pocillopora*

Temperature data loggers (Onset Hobo) were located at 1 and 5 m depths on LA reef during 2015, 2017, and 2019. Data were retrieved to account for the thermal variability that may occur on coral reefs of Gorgona Island. Data loggers recorded every 30 minutes for the entire year or until battery depletion. The annual average temperature (27.5 ± 1.5, mean ± SD) was calculated between January 1 and the last record of each year: November 15, 2015, December 31, 2017, and October 9, 2019 (Fig 1C). The upwelling season was described using the data between January 19 and April 15, time at which temperatures < 26 °C (annual mean – SD) begin to occur, while data after April 16 were used for characterizing the non-upwelling season (Table 1).

A normal thermal condition was 27.5 ± 1.5 °C, which corresponds to the mean annual temperature. Cool stress conditions, which occur during the upwelling season, were defined as any temperature < the mean – SD (24.0 °C). Warm stress conditions were temperatures > the annual mean + SD (29.0 °C). Cool events (< 24 °C) were more intense during 2019. Warm events (> 29 °C) occurred through all year, but were more intense between May and July, and in specially during 2015 (Supplementary Information file 1).

Table 1. Descriptive statistics for the thermal variation (°C) recorded by data loggers at La Azufrada reef, at 1 and 5 m depth, and during the years 2015, 2017, and 2019.

Depth	year	Annual	Upwelling season			Non-upwelling season		
		mean ± SD	mean ± SD	Min	Max	mean ± SD	Min	Max
1 m	2015	28.1 ± 1.0	26.8 ± 0.8	23.0	29.3	28.7 ± 0.4	26.4	30.4
	2017	27.4 ± 1.4	25.9 ± 2.0	18.8	29.5	28.0 ± 0.5	25.7	30.3
	2019	27.3 ± 1.4	25.6 ± 1.3	21.2	30.6	28.1 ± 0.5	24.5	30.9
	mean	27.6 ± 1.4	26.1 ± 1.6	21.0	29.8	27.4 ± 1.9	25.5	30.5
5 m	2015	27.9 ± 1.1	26.4 ± 1.0	22.1	29.0	28.6 ± 0.4	26.1	29.8
	2017	27.1 ± 1.8	25.1 ± 2.5	17.2	29.1	27.9 ± 0.5	25.6	30.0
	2019	27.0 ± 1.8	24.8 ± 1.7	18.4	29.5	28.0± 0.5	24.6	31.3
	mean	27.4 ± 1.7	25.5 ± 2.0	19.3	29.2	27.0 ± 2.4	25.5	30.4

Metabolic response of *Pocillopora* to changes in temperature and dissolved oxygen

On November 12, 2021, seven fragments from different colonies of *Pocillopora* were collected at LA reef and transported to the laboratory on the island. There, the fragments were incubated in hermetically sealed respiration chambers filled with seawater from the reef (6.2 mg O_2 L^{-1}, 30 PSU). The respiration chambers were kept at 28 ± 0.7 °C (mean ± SD, a normal thermal condition), in the dark for 6 hours, including 1 hour of acclimation and 5 hours for DO measurements.

To maintain a stable temperature, all respiration chambers were incubated in a water bath equipped with a thermostat and submersible water pump to circulate the water and homogenize the temperature. A total of eight respiration chambers were used, seven containing coral fragments and one serving as a control, containing 363 ml of water and no coral to measure background or microbial respiration. All respiration chambers had internal water movement generated by peristaltic pumps. Changes in DO (mg L^{-1}) were recorded every 20 minutes with a Firesting-GO2 (PyroScience GmbH); the sensor was calibrated according to the manufacturer's instructions.

The process was repeated on November 17, 2021, with different colonies than those employed for the normal thermal conditions, and with a water bath at 32.0 ± 0.3 °C (Warm stress), which exceeds by ~1 °C the maximum temperature recorded by the loggers, and is a temperature that occurred during a previous El Niño event (Vargas-Ángel et al., 2001). On February 27, 2022, the experiment was repeated (using again different colonies) with a water bath at 24.0 ± 1.1 °C (Cool stress). To maintain this low temperature, frozen gel packages were added to the water bath, and coral fragments were left in the respiration chambers for 7 h, with 1 h for acclimation and 6 h for DO measurements. This time encompassed the time required to deplete DO to hypoxic levels, which occurs during the upwelling season. All incubations ended when DO fell to ≤ 2.0 mg L^{-1} in at least four respiration chambers, which was after 6 h in the 28 °C and 32 °C incubations, and 7 h in the 24 °C incubation.

The metabolic or respiration rate (MO_2) was calculated using the calc_MO2 function of the Respirometry package in R (Seibel et al., 2021). We set the bin_width to 0 which computes a MO_2 value from one PO_2 observation to the next along the incubation period. Then the Pcrit of each coral fragment at the given temperature was calculated using the calc_pcrit function with the paired PO_2 and MO_2 values obtained after applying the calc_MO2 function and established according to the broken stick regression (Yeager and Ultsch, 1989). Scripts and data are presented in Supplementary Information file 2. The Pcrit of each coral fragment at the given temperature was statistically compared using a one-way ANOVA. The data met the assumptions of homoscedasticity (Cochran's test C = 0.53, df = 2, p = 0.36) and normality of residuals (K-S d = 0.13, p > 0.20).

The MO_2 values recorded on each coral from one PO_2 observation to the next were grouped according to whether they were below or above the Pcrit, which corresponds to hypoxic and normoxic conditions, respectively. Then, the mean MO_2 at normoxic and hypoxic conditions for each coral fragment at their respective temperature were compared statistically using a Repeated Measures ANOVA. Raw data met the assumptions of homogeneity of variances and covariances (Box's M test= 9.2, df= 6, p= 0.2). MO_2 data were standardized as the amount of O_2 consumed per mass of coral tissue per minute (mg O_2 g^{-1} min^{-1}). The weight of coral tissue was determined by the difference between the wet and dry (ash-free) weights of the coral fragments.

Results

Field measurements of growth and Symbiodiniaceae density of *Pocillopora*

The growth rate of *Pocillopora* colonies during 2013 and at La Azufrada reef during the upwelling season was 43.3% lower than during the non-upwelling season (t-test: -2.1, df = 26, p = 0.04). The mean (± SD) growth rate during upwelling was 0.017 ± 0.01 cm day^{-1} vs. 0.030 ± 0.02 during non-upwelling. The same seasonal pattern was evidenced in coral fragments monitored from November 2021 to May 2022 at Playa Blanca and La Ventana reefs: during the upwelling season growth rate was reduced by 68% (Table 2). However, during both seasons, coral fragments at Playa Blanca reef exhibited a lower growth rate (-0.001 vs. 0.0003 cm day^{-1} during upwelling and non-upwelling season, respectively) compared to fragments at La Ventana reef (0.004 vs. 0.008 cm day^{-1} during the upwelling and non-upwelling season, respectively).

Symbiodiniaceae density was significantly higher in March than in July 2013, a reduction of symbiotic algae populations from the upwelling to the non-upwelling seasons of 53% (Table 2). As expected, the luminosity of colonies was significantly lower in March than in July 2013, indicating that colonies had darker colors, and likely a higher density of Symbiodiniaceae, during the upwelling season (Fig 2). The same seasonal pattern of low luminosity during the upwelling season was found for the coral fragments at La Ventana and Playa Blanca reefs during 2022, but no statistical differences between reefs were observed (Table 2).

Table 2. Statistical analysis to identify the effects of upwelling and non-upwelling seasons on the physiology of *Pocillopora* from Gorgona Island.

Physiological feature	Reef	Year	Season	Mean (± SD)	Statistical test	*P* value
Growth rate (cm day^{-1})	La Azufrada	2013	Upwelling	0.017 (0.01)	t-test: -2.1, df= 26	0.04
			Non-upwelling	0.030 (0.02)		
	Playa Blanca and La Ventana	2022	Upwelling	0.001 (0.005)	Repeated measures ANOVA: Reef (F: 18.0, df: 1). Season (F: 4.9, df: 1) Reef x Season (F: 0.7, df: 1)	Reef: 0.0004 Season: 0.03 Reef x Season: 0.4
			Non-upwelling	0.004 (0.006)		
Symbiodiniaceae density (x 10^{2} cells cm^{2})	La Azufrada	2013	Upwelling	784.7 (185.8)	t-test: 4.9, df: 26	0.00004
			Non-upwelling	513.1 (181.7)		
Luminosity	La Azufrada	2013	Upwelling	63.4 (9.4)	t-test: -10.2, df: 26	< 0.0000001
			Non-upwelling	101.6 (16.9)		
	Playa Blanca and La Ventana	2022	Upwelling	121.5 (25.1)	Repeated measures ANOVA: Reef (F: 1.5, df: 1). Season (F: 10.4, df: 1) Reef x Season (F: 0.10, df: 1)	Reef: 0.2 Season: 0.004 Reef x Season: 0.7

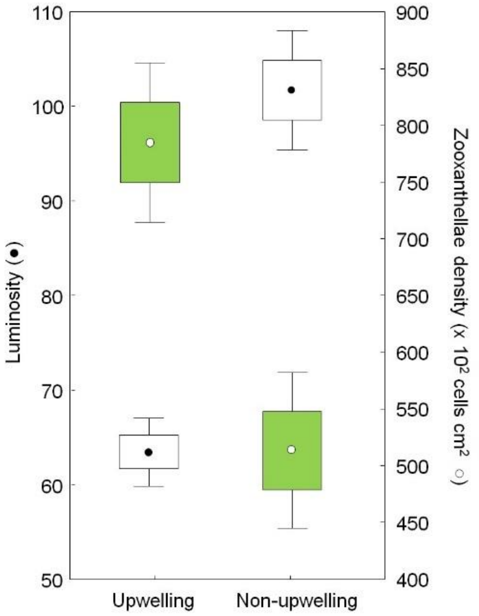

Figure 2. Seasonal changes of zooxanthellae density (green) and luminosity (white) of *Pocillopora* from La Azufrada reef during 2013.

Metabolic response of *Pocillopora* to changes in temperature and dissolved oxygen

The critical oxygen tension of *Pocillopora* was significantly influenced by temperature (one-way ANOVA, F = 7.9, df = 2, p = 0.003); specifically, Pcrit decreased as temperature increased. At 24 °C the Pcrit was 4.2 ± 1.2 mg O_2 L^{-1}, at 28 °C it was 3.7 ± 1.0 mg O_2 L^{-1} and at 32 °C the Pcrit was 1.9 ± 0.7 mg O_2 L^{-1}.

Temperature also had a significant effect on the MO_2 (Repeated measures ANOVA, F = 4.31, df = 2, p = 0.02), such that oxygen consumption increased as temperature increased. At 24°C the MO2 was 0.46 ± 0.18 mg O_2 g^{-1} min^{-1}, at 28 °C it was 0.74 ± 0.33 mg O_2 g^{-1} min^{-1}, and at 32 °C it was 0.74 ± 0.55 mg O_2 g^{-1} min^{-1}. When corals were first exposed to normoxic conditions and then to hypoxic conditions, as expected, the MO_2 decreased significantly from 0.85 ± 0.47 mg O_2 g^{-1} min^{-1} to 0.45 ± 0.15 mg O_2 g^{-1} min^{-1} (F = 18.0, df = 1, p = 0.0004).

There was a significant interaction between temperature and O_2 conditions (i.e., normoxia and hypoxia) on the MO_2 (F = 5.42, df = 2, p = 0.01). Under normoxic conditions the rate of oxygen consumption increased with temperature, and as expected the MO_2 was different between the extreme temperatures, also between 24°C and 28°C, but not between 28°C and 32°C (Fig 3, Table 3). In contrast, under hypoxic conditions the MO2 tented to increase from 24°C to 28°C, but tended to decrease from 28°C to 32°C. Both at cool and warm temperatures MO_2 was lower respect the normal condition (28°C). However, none of the latter differences were significant. In short, temperature had the expected effect under normoxia but not under hypoxia (Fig 3, Table 3).

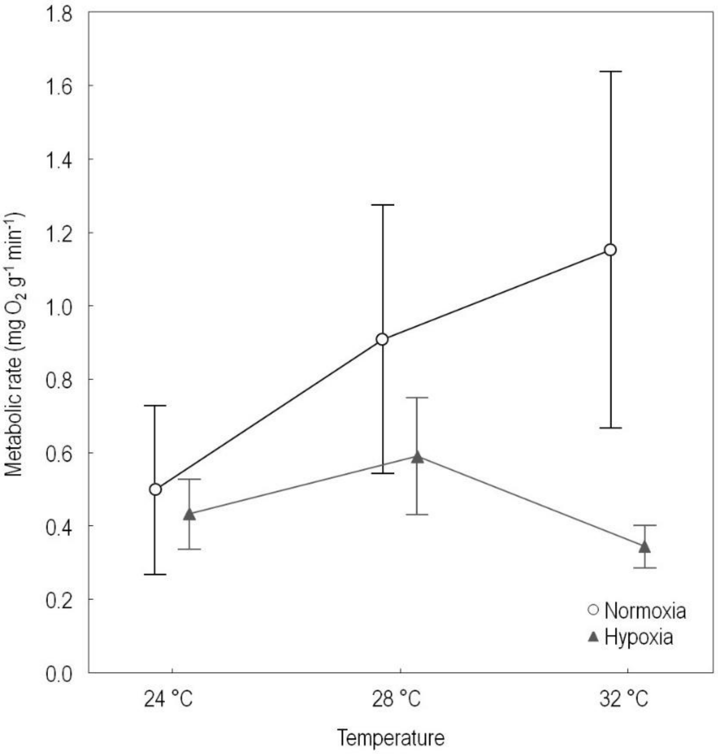

Figure 3. Effect of temperature and oxygen conditions (normoxia and hypoxia) on the metabolic rate of *Pocillopora.*

Table 3. Multiple comparison test (Fisher LSD) to determine the probability of significant differences in the metabolic rate at different temperatures (24, 28 and 32 °C) and oxygen conditions (Nor: normoxia, Hyp: hypoxia).

	24 °C - Nor	24 °C - Hyp	28 °C - Nor	28 °C - Hyp	32 °C - Nor	32 °C - Hyp
24 °C - Nor	-					
24 °C - Hyp	0.690	-				
28 °C - Nor	0.014	0.005	-			
28 °C - Hyp	0.569	0.331	0.065	-		
32 °C - Nor	0.0002	0.00006	0.135	0.001	-	
32 °C - Hyp	0.340	0.582	0.001	0.132	0.0001	-

Discussion

Many corals exhibit seasonal modulation of their physiology, with lower symbiont densities and tissue biomass during the warmer months than during cooler months, because warm conditions affect the symbiosis between the coral and the Symbiodiniaceae leading to energy deficits (Fagoonee et al., 1999; Fitt et al., 2001; Kemp et al., 2011, 2016; Gantt et al., 2023). Our study provides evidence of plasticity in the physiology of *Pocillopora* in response to seasonal changes in environmental conditions. However, the pattern of reduced coral biomass during warm months due to the sensibility of Symbiodiniaceae does not hold true for corals that are influenced seasonally by upwelling, such as those at Gorgona Island, where abrupt changes in ambient conditions (mainly low temperature and dissolved oxygen conditions) significantly affect coral performance.

Growth rate

Our study reveals that both colonies and fragments of *Pocillopora* exhibit reduced growth rates during the upwelling season compared to the non-upwelling season. We observed a 43.3% reduction in growth rate for colonies and a 68% reduction for fragments. Our findings are consistent with the results of Glynn and Stewart (1973) in the Gulf of Panama, who described seasonal variation in the growth of *Pocillopora* fragments due to changes in temperature, with a drop in growth rate of approximately 80% during the upwelling season (February and March: < 0.5 mm month^{-1}) compared to the growth rate before upwelling (2 – 3 mm month^{-1}), and growth cessation occurring at temperatures below 20°C.

Although different methods were applied in our work and the work of Glynn and Stewart (1973), the growth rate of our fragments (Upwelling: 0.4 mm month^{-1}; Non-upwelling: 1.3 mm month^{-1}) was similar to the growth rate reported by these authors. Interestingly, they did not find differences between measuring the growth rate with photographic records (as we did) or staining corals with alizarin red. Previous growth rates of *Pocillopora* fragments reported for Gorgona Island during the non-upwelling season were between 1.9 and 4.8 cm year^{-1} (Lizcano-Sandoval et al., 2018; Ishida-Castañeda et al., 2020), and the growth rate of our fragments during the non-upwelling season was close to that range (1.6 cm year^{-1}).

Additionally, as reported by Céspedes-Rodríguez and Londoño-Cruz (2021), we found low growth rates at Playa Blanca reef, where higher sediment loads may account for depressed coral growth (Zapata, 2001). However, we discard the possibility that the low growth rate at Playa Blanca was the result of differences in temperature or DO between reefs, as both abiotic conditions respond to seasonal changes and there is no between-reef variability in such parameters (SM1; Castrillón-Cifuentes et al. 2023). Although salinity was lower at Playa Blanca than at La Ventana during the non-upwelling season, conclusions cannot be made due to a lack of data for La Ventana during the upwelling season.

The negative effect of upwelling on the growth rate of *Pocillopora* in the ETP can also be observed when comparing localities influenced or not by these events (Manzello, 2010a; Medellín-Maldonado et al., 2016; Randall et al., 2020), as well as during ENSO events that modulate upwelling intensity. During La Niña events, upwelling intensifies and causes low growth rates in *Pocillopora* (Tortolero-Langarica et al., 2017), and at upwelling localities *Pocillopora* experiences increases in growth rates during moderate El Niño events (Vargas-Ángel et al., 2001; Jiménez and Cortés, 2003b). Additionally, tissue recovery after thermal stress has been found to be greater in response to warm stress rather to cool stress events (Glynn and Fong, 2006).

We propose that the low growth rate of *Pocillopora* during the upwelling season could be the result of reduced metabolic activity, particularly in the calcifying cells, due to low DO and temperature conditions. At upwelling localities, low temperatures coincide with low DO conditions (Rixen et al., 2012), and the coral reefs of Gorgona Island are no exception (Castrillón-Cifuentes et al., 2023). As a result of this stressful environment, metabolic constraints occur due to reduced ATP production under hypoxia and reduced enzymatic activity at low temperatures (Fitt et al., 2001; Gnaiger, 2001; Fangue et al., 2009; Salin et al., 2015; Sawall et al., 2022). Additionally, we suspect that negative effects of low DO in the environment could be worsened due to the development of hypoxia within coral tissues, which might result from the night respiration of Symbiodiniaceae (Altieri et al., 2017), whose population was observed to increases during the upwelling season (Table 2).

Acidifying conditions, which characterizes the ETP, also contributes to depress growth rate (Manzello, 2010a), but its seasonal variation was not evident on coral reefs at Gorgona Island (Ramírez-Martínez et al., 2022). Although there is a consensus that the decreased production of cement components in *Pocillopora* reefs at upwelling localities of the ETP is the result of low Ω_{arag} (Manzello et al., 2008), we propose that O_2 limitation may also play a vital role in this process. Low DO in the environment reduces ATP production by the calicoblastic mitochondria, which is required to pump calcium ions and protons for coral skeleton construction. Therefore, under conditions of low temperature, low glycerol, and low O_2, it is expected that the calicoblastic mitochondria will not be able to produce skeletal components (Colombo-Pallotta et al., 2010). In fact, well-oxygenated conditions (80 – 100% oxygen saturation) are required for optimum calcification rate in *Galaxea fascicularis*, and neither feeding nor light conditions mitigate the negative effects of hypoxia on calcification (Wijgerde et al., 2012). In *Acropora millepora*, DO rather than pH controls coral growth (Wijgerde et al., 2014).

To explain how corals survive stressful conditions, like those that occurs during the upwelling in the ETP, Wooldridge (2014) has highlighted a series of counterintuitive trade-offs between linear extension rate and other traits such as skeletal density, lipid storage, immune response, and reproductive capacity. This may be the case for *Pocillopora* at Gorgona Island, as ambient conditions during the upwelling season depress their metabolism, but corals can survive even worsen conditions: the co-occurrence of sub-aerial exposure during spring tides that also happens during the upwelling season. To survive sub-aerial exposure, *Pocillopora* corals at Gorgona Island seem to maintain their growth rate while reducing reproductive output (Castrillón-Cifuentes et al., 2017). As consequence of low sexual reproduction, populations are primarily maintained through fragmentation (Muñoz et al., 2018). Hence, high growth rates during the non-upwelling season (Lizcano-Sandoval et al., 2018; Ishida-Castañeda et al., 2020; Céspedes-Rodríguez and Londoño-Cruz, 2021) is advantageous for asexual reproduction.

Symbiodiniaceae density

Symbiodiniaceae density (or luminosity as its proxy) in *Pocillopora* corals at Gorgona Island varied seasonally, with a 53% higher density during the upwelling season compared to the non-upwelling season. Mayfield and Gates (2007) propose that corals under stress disrupt the symbiosis, because the cell's ability to transport molecules (mainly Glycerol and free amino acids) across membranes is affected creating osmotic stress, which in turns results in reactive oxygens species (ROS) formation, photoinhibition, apoptosis and exocytosis of Symbiodiniaceae, and host cell detachment. Most records of bleaching events (loss of Symbiodiniaceae or their pigments) are attributed to thermal stress, mainly due to warm temperatures (Hughes et al., 2017, 2018); however, other physical factors (light, depth, currents) that modulates temperature (Van Oppen and Lough, 2009), as well low salinity (Kerswell and Jones, 2003; Kongjandtre et al., 2021) also contributes to bleaching.

Under no stress conditions corals also constantly expel Symbiodiniaceae (1% of the population per day; Davy et al. 2012), and the density of Symbiodiniaceae varies temporally in response to environmental conditions. In *P. damicornis* and *Pocillopora verrucosa* from Hawaii and the Red Sea, an increase in Symbiodiniaceae density during winter is promoted by an increase in nutrients rather than by changes in temperature (Stimson, 1997; Al-Sofyani and Floos, 2013; Sawall et al., 2014). Similarly, *Acropora formosa* has more symbiotic algae during the autumn-winter than during the spring-summer, and the temporal pattern is explained by a combination of temperature, solar radiation, nitrate, and oxygen concentration (Jones and Yellowlees, 1997). The effect of oxygen on Symbiodiniaceae was explained as hyperoxia inducing the accumulation of ROS (Fagoonee et al., 1999). However, ROS can form during both hypoxia and hyperoxia and can inhibit photosynthesis among other metabolic processes (Ulstrup et al., 2005; Welker et al., 2013; Deleja et al., 2022).

In the ETP only one study reported temporal variation of Symbiodiniaceae density, and found a positive correlation between Symbiodiniaceae density and increased nitrate and phosphate concentrations (Martínez-Castillo et al., 2020). The effect of thermal stress is well documented through experiments and field measurements during El Niño events; temperatures above 30°C resulted in a decrease in symbiont density in *Pocillopora capitata, P. verrucosa, P. damicornis, Pocillopora elegans,* and *Porites lobata* (Glynn and D'croz, 1990; Glynn et al., 2001; Hueerkamp et al., 2001; D'Croz and Maté, 2004; Flores-Ramírez and Liñán-Cabello, 2007; Rodríguez-Troncoso et al., 2016). Conversely, low temperatures (19°C) increased the Symbiodiniaceae density in *P. verrucosa* by 27% (Rodríguez-Troncoso et al., 2014).

Overall, the high density of Symbiodiniaceae in *Pocillopora* corals during the upwelling season at Gorgona Island could be a result of the combined effects of high nutrient concentrations that enhance algae population growth, low dissolved oxygen levels (but not at hypoxic levels) that reduce the possibility of oxidative stress, and the thermo-tolerance of the symbionts (Cunning et al., 2013; Baker et al., 2017; Palacio-Castro et al., 2022). However, further research is needed to understand the specific contributions of these environmental factors to the population dynamics of Symbiodiniaceae, including the molecular identification of symbionts and the quantification of the translocated fixed carbon from the algae to the host under upwelling conditions (thermal stress and hypoxia).

We also suspect that increases in Symbiodiniaceae density during the upwelling affect the growth rate of corals, because under low temperatures the movement of glycerol might be restricted causing osmotic stress, low temperatures can cause metabolic depression in coral's cells, and low oxygen in the environment and inside corals tissue (due to increased Symbiodiniaceae number and its night respiration) limits the calcification process (Colombo-Pallotta et al., 2010). In fact Rodríguez-Troncoso et al. (2014) evidenced that during low temperatures Symbiodiniaceae increase but corals lipids (glycerol) decrease.

Additionally, during the upwelling season, Symbiodiniaceae are likely to reduce their photosynthetic capacity due to self-shading resulting from the increased number of algae and less availability of CO_2 from the coral metabolism to start up photosynthesis (Hoogenboom et al., 2010). Moreover, if corals host thermo-tolerant Symbiodiniaceae like *Durusdinium* (formerly known as clade D; LaJeunesse et al. 2018), this might account for reduced growth rates. It is known that symbiosis with this algae reduces coral growth rates but allows higher survivorship under thermal stress (Little et al., 2004; Manzello, 2010a; Cunning et al., 2015; LaJeunesse et al., 2018). Further research is needed to understand the specific contributions of these factors to the growth rates of corals during the upwelling season.

Critical oxygen tension

Temperature had a significant effect on the Pcrit of *Pocillopora* corals at Gorgona Island. These parameters were negatively related, as increases in temperature caused a decrease in the Pcrit. Species with a lower Pcrit are likely more tolerant to hypoxic conditions, as they possess a greater capacity to extract O_2 from a hypoxic environment and might delay the initiation of anaerobic metabolism (McArley et al., 2019). If an organism is able to do so, it can avoid the accumulation of lactic acid or other by-products of anaerobic metabolism, which cause a decrease in pH within the tissue (Grieshaber et al., 1988). Scleractinian corals activate anaerobic metabolism during hypoxic exposure, but they employ opine dehydrogenases rather than lactate dehydrogenase (Murphy and Richmond, 2016; Linsmayer et al., 2020). However, anaerobic metabolism seems to be inefficient for survival under multifactorial stress conditions or under prolonged periods (Weber et al., 2012).

During the non-upwelling season, it is likely that *Pocillopora* corals face well-oxygenated conditions, as the Pcrit of coral fragments incubated at 28 °C (ambient temperature) was similar to the lower edge of dissolved oxygen (DO) conditions on the reefs of Gorgona Island (Pcrit: 3.7 mg L^{-1}; Environmental DO range: 3.7 – 6.5 mg L^{-1}, mean: 4.9 mg L^{-1}). During the upwelling season, *Pocillopora* might face hypoxia, as the Pcrit of corals incubated at 24 °C falls within the range of DO that the reefs experienced during that season (Pcrit: 4.2 mg L^{-1}; Environmental DO range: 3.0 – 6.6 mg L^{-1}, mean: 4.2 mg L^{-1}). Corals incubated at warm conditions (32 °C) had an enhanced ability to extract O_2 from the environment (at least up to 6 h, incubation time) and maintain their MO_2 over a broad range of DO conditions (Pcrit = 1.9 mg L^{-1}). This suggests that atypical warm episodes during the upwelling season (SM1) could ameliorate the effect of deoxygenation.

To the best of our knowledge, this is the first time that the Pcrit of a tropical scleractinian coral has been tested under different thermal conditions. Only one study assessed the Pcmax (an analogous value to Pcrit) of different coral species, but at their mean ambient temperature (Hughes et al., 2022). In the cold-water coral *Lophelia pertusa*, the Pcrit was lower at a cooler temperature (6.5°C, Pcrit = 5-6 Kpa) than at normal (9°C) or warm (11°C) conditions (Pcrit = 9-10 Kpa) (Dodds et al., 2007). In *Crassostrea gigas*, the Pcrit increases with temperature, and this positive relation was assumed to be an effect of the low solubility of oxygen in warm waters (Moullac et al., 2007).

As the Pcrit is an effective way to measure tolerance to hypoxic condition, it has been intensively assessed in fish. Within species, high temperatures result in a higher Pcrit (Rogers et al., 2016), but variation in this pattern occurs among species; for example, various *Etheostoma* species had a low Pcrit at warm temperatures, possibly because they had a mechanism to increase O_2 transport at higher temperatures (Ultsch et al., 1978). Because cnidarians lack of ventilation or circulatory systems, we propose that the mechanism that operates in *Pocillopora* to increase O_2 transport at warm conditions is related with the Diffusive Boundary Layer (DBL).

The DBL is the water layer adjacent to the surface of all coral polyps, where diffusion is the main method of transport for oxygen (and other substances) from the environment to the corals' cells. In this transport process the cilia of polyps aid in generating vortices to move O_2 within this layer (Shapiro et al., 2014; Pacherres et al., 2020, 2022). We speculate that low temperatures can lead to decreased ciliary activity (Muscatine et al., 1991), and because the viscosity of water increases at cooler temperatures (Bolton and Havenhand, 2005), the O_2 diffusion through the DBL is reduced, resulting in a high Pcrit of *Pocillopora* at 24°C, and in an efficient oxygen transport at warm conditions (28 and 32 °C), as result of low water viscosity and normal activity of cilia.

Metabolic rate

The MO_2 is a sensitive indicator of an organism's response to environmental changes, as it integrates numerous energy-requiring processes, such as growth, reproduction, and tissue repair (Edmunds, 2005). We found that temperature and DO conditions significantly affect the rate of oxygen consumption (MO_2), as expected, since enzymes involved in respiration are temperature- and oxygen-dependent in order to successfully produce ATP (Sawall et al., 2022).

Under normoxic conditions, MO_2 increases with temperature. This pattern has been observed in all stony corals examined (Coles and Jokiel, 1977; Castillo and Helmuth, 2005; Dodds et al., 2007; Paradis et al., 2019; Gravinese et al., 2022). However, this correlation is only positive within a specific range, known as the optimum temperature range. Beyond this range, the temperature becomes lethal at either low or high critical values (Sokolova and Pörtner, 2003). While the high and low temperatures tested in this study had statistically significant effects on *Pocillopora* metabolism, the duration of the incubations should not be considered indicative of a critical range. Therefore, further tests are needed to identify long-term thermal tolerance.

An indicator of compensatory acclimation to temperature should display an inverse correlation between MO_2 and temperature (Ulbricht, 1973). According to Al-Sofyani and Floos (2013), if acclimation is complete, the MO_2 of corals should be identical during the summer and winter, as is the case for *P. verrucosa* in the Red Sea; this, however, is not the case for *Pocillopora* at Gorgona Island. Therefore, our corals were not acclimated to the cool stress conditions that occur during the upwelling season, as MO_2 at 24°C was statistically different from that at 28°C. However, corals in warm conditions might have been acclimated, as differences in MO_2 between 28°C and 32°C were not significant (Table 3). It is important to mention that incubations at 24°C were conducted during the upwelling season, when the corals were naturally subjected to upwelling. Incubations at 28°C and 32°C were conducted during the non-upwelling season.

The low MO_2 of *Pocillopora* at cool temperatures validates the reduced growth rate during the upwelling season reported by this and previous studies, as well as the limited reef development during La Niña events and at upwelling centers (Glynn et al., 2017a). The similar MO_2 at normal and warm temperatures supports the idea that moderate El Niño events can ameliorate the negative effect of upwelling, which reduces metabolism and, in particular, skeletal growth (Vargas-Ángel et al., 2001; Jiménez and Cortés, 2003a).

A decrease in MO_2 occurs under hypoxic conditions at any temperature, but it is more marked at extreme temperatures (Fig 3, Table 3). In *Orbicella faveolata*, combined exposure to warm and hypoxic conditions reduces the respiration rate by 62.8%, which is associated with a gradual shift to anaerobic respiration (Gravinese et al., 2022). Testing whether anaerobic metabolism is activated in *Pocillopora* during extreme upwelling conditions requires further research. However, the fact that corals are less efficient in terms of growth opens up this possibility as a costly way to survive stressful conditions.

Conclusion

Our results demonstrated that the environmental variability that occurs during upwelling events at Gorgona Island has negative effects on the physiology of *Pocillopora* (Fig 4); specifically, cool thermal stress and hypoxia that develop during upwelling result in significant changes in the growth rate, respiration rate, and Symbiodiniaceae density of corals. It is possible that *Pocillopora* corals on the reefs of Gorgona Island have reached their physiological limits and rely on trade-offs to survive the stressful upwelling conditions, as the aforementioned physiological traits did not appear to contribute to mortality. Therefore, the occurrence of additional stressors or the intensification of upwelling could be detrimental to this island's primary reef constructors.

In contrast, coral metabolism increased when exposed to elevated temperatures and abundant oxygen. This may explain why *Pocillopora* in upwelling regions thrive more during El Niño events, as warm conditions appear to alleviate the metabolic constraints that occur during upwelling. However, we do not suggest that El Niño events are advantageous for *Pocillopora*, as our experiments evaluated coral responses to brief periods of exposure to stressors and not responses to long-term warming. However, the postulated oxygen extraction efficiency under warm conditions could account for the observed tolerance of *Pocillopora* corals and the resilience of reefs to El Niño events in the ETP.

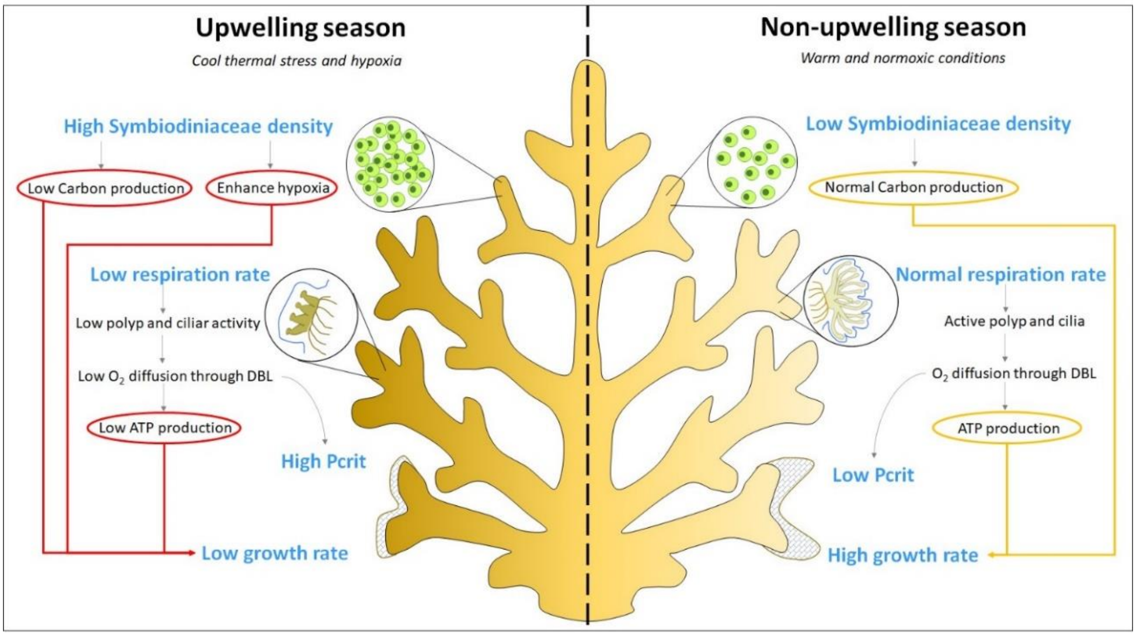

Figure 4. Response of *Pocillopora* to cool and hypoxic conditions that occur during upwelling events. The observed response of corals during the upwelling and non-upwelling season is presented in blue font. Factors that promote (yellow lines) or depress (red lines) coral growth rate are denoted inside circles. During the upwelling season, the high density of Symbiodiniaceae results in low photosynthesized carbon and enhanced hypoxia within coral tissue. The cool and hypoxic ambient conditions lead to a low respiration rate, resulting in less available energy (ATP) for polyp activity. This reduction in polyp activity, in turn, decreases the diffusion of oxygen (O_2) through the Diffusive Boundary Layer (DBL), resulting in a high Pcrit value. A high Pcrit value indicates that corals are less tolerant to hypoxic conditions. Finally, due to low ATP, cool stress, and hypoxia, corals have a reduced growth rate.

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Chapter 4: Micro-environmental conditions modulate the tolerance of *Pocillopora* corals to local stressors at Gorgona Island

Ana Lucia Castrillón-Cifuentes[1, 2, *], Christian Wild[1], Fernando A. Zapata[2]

1. Marine Ecology Department. Faculty of Biology and Chemistry. University of Bremen, Germany.
2. Coral Reef Ecology Research Group, Universidad del Valle. Colombia.

* Corresponding author: analucia@uni-bremen.de, castrillon.ana@correounivalle.edu.co

Abstract

Coral reef degradation has increased worldwide because local stress factors amplify the negative effects of climate change. At the Eastern Tropical Pacific (ETP), Pocilloporid reefs are naturally exposed to thermal stress, hypoxia, and acidification due to upwelling and El Niño events; and the intensity of these events and conditions are expected to intensify due to climate change. Moreover, land use and sedimentation put coral reefs in the ETP region at risk. To assess the tolerance of *Pocillopora* (the main reef-builder at the ETP) to local stressors at Gorgona Island (Colombian Pacific), a reciprocal transplant experiment was performed between two neighboring reefs: Playa Blanca (PB) and La Ventana (LV); and changes in growth, calcification, and photosynthesis of corals were recorded after 19 months. PB and LV reefs differ in the degree of influence of low salinity and sediments, as they are 82 and 674 m from shore, respectively. Results evidenced that low salinity and high sediment conditions at PB depress *Pocillopora* performance. Control corals from PB had 71, 67, and 78% lower growth, calcification, and photosynthesis rates (respectively) compared to control corals from LV. However, transplanted corals from LV exhibited some resistance capacity to local stress conditions of PB, as they had similar growth (0.72 vs. 0.57 cm year^{-1}) and calcification (1.35 vs. 1.33 g cm^{-2} year^{-1}) compared to the control corals of PB; a particular host-zooxanthellae association could confer this resistance capacity, by providing efficiency in photosynthesis. Corals from PB had (at some degree) resilient capacity, when they were move to a better ambient condition (to LV), their physiological performance was enhanced, and they had similar growth (2.33 vs. 1.97 cm year^{-1}) and calcification (5.50 vs. 4.07 g cm^{-2} year^{-1}) than the control corals of LV. Nevertheless, our data reveal the urgent need to reduce run-off and sedimentation at Gorgona Island by assisting the natural recuperation of the tropical rain forest.

Keywords: Hyposalinity, Sediments, Calcification, Survival, Photosynthesis, Resistance, Resilience, Eastern Tropical Pacific.

Introduction

Coral reefs typically occur at warm, clear, shallow, and fully saline waters (Kleypas et al., 1999). However, some coral reefs can occur out of this range; these reefs are known as marginal and extreme coral reefs, and there is evidence indicating that on these reefs exist corals adapted to climate change (Camp et al., 2018; Schoepf et al., 2023). One of the aims of adaptive management strategies is to restore reefs with stress-tolerant corals, coupled with improving ambient conditions; however, it require intensive research to evaluate how scleractinian corals respond to stress factors (Mcleod et al., 2019), and to identify corals that retain beneficial traits following transplantation to new ambient conditions and their integration into the population (Barott et al., 2021).

The physiological adjustments to new or changing environmental conditions could occur if organisms are resistant or resilient to stressors. In corals, a resistance response is the ability to persist under stress conditions and depends on intrinsic species (or colony)-specific physiological tolerance or on environmental factors that offer some protection (West and Salm, 2003). Resilience is the ability to speed-up a return to an initial state after a disturbance (Lirman and Manzello, 2009). And as ecosystem engineer species, the resistance and resilience of scleractinian corals scale the ecosystem level.

The Eastern Tropical Pacific (ETP) is recognized as a marginal and extreme environment for coral reef development, as it is one of the most isolated regions of the world, and it is separated from the Central Pacific by 5000 km of open ocean, which results in low trans-Pacific gene flow (Combosch et al., 2008); also, this region is characterized by atypical oceanographic conditions like extreme temperatures, acidification, high nutrients, and low dissolved oxygen availability, which drive to low diverse coral reef assemblages to develop there (Glynn et al., 2017a). Approximately 24 marine protected areas (MPAs) manage the natural resources in the ETP (Alvarado et al., 2017), which benefit over 3.5 million people and their local economies (Price, 2022). For the Colombian Pacific, the Natural National Park Gorgona is the locality where occur the major and best-developed coral reefs, and is one of the most well-preserved coral reef areas in the ETP (Zapata and Vargas-Angel, 2003). This island was traditionally used as an artisanal fishing site, and its biodiversity is key for different social, cultural, economic, and scientific processes in Colombia (Giraldo et al., 2014a).

It is broadly known that coral reefs worldwide have been continuously declining due to local and global stressors, but local stress factors are expected to amplify the negative effects of climate change (Hoegh-Guldberg et al., 2017; van Oppen et al., 2017; Camp et al., 2018; Hughes et al., 2018; Tebbett et al., 2023). However, site-specific management strategies have a significant effect on how coral reefs respond (Guzman and Cortés, 2007; Ateweberhan et al., 2013; Alvarado et al., 2020). Local stress factors for coral reefs in the ETP are divided into those from natural sources and induced by humans. The first group includes upwelling events, sub-aerial exposure during extreme low tides, low salinity, and sediments from rivers. The second category includes overfishing, nutrient enrichment, sedimentation, pollution, coral harvesting for souvenirs, and mechanical fragmentation from divers and boats. However, the difference between natural and human induced local stressors is not always clear for some factors like sedimentation, and nutrient enrichment (Cortés and Reyes-Bonilla, 2017).

Upwelling and El Niño conditions make that corals in the ETP experience extreme temperatures, acidification, and hypoxia, which are the expected effects of climate change; and despite corals has some resistance and resilience capacity to those stressors acting alone, their combination is likely to result in the elimination of the reef framework (Glynn et al., 2017b; Manzello et al., 2017). Additionally, land use has contributed to increase coral mortality (Nava and Ramírez-Herrera, 2012). Notwithstanding, eutrophication has been observed to cause no negative effects in some *Pocillopora* corals (Martínez-Castillo et al., 2020).

Aiming to contribute to understand the response of corals against local stressors at Gorgona Island, a locality that potentially could host adapted corals to climate change, this research evaluated the effect of micro-ambient conditions on the physiology of *Pocillopora* corals (the main reef-builder at the ETP) to assess their resistance and resilience capacity. We used a reciprocal transplant experiment between two neighboring coral reefs, which differ in their distance from shore, and hence the influence on runoff. The results of this research evidenced that coral exhibited different response despite the short distance between the coral reefs; specifically, conditions on the inshore reef depress corals' performance but corals resist at some degree those stressors, and as expected moving corals to a reef less impacted by sediment enhances key physiological traits for reef persistence (i.e., linear extension, calcification, and photosynthesis).

Materials and methods

Study area

The Natural National Park (NNP) Gorgona (2°57'40.5" N, 78°11'12.1" W) is located 30 km off the nearest point from the Colombian Pacific coast. This tropical island has marked climatic seasonality due to the latitudinal displacement of the Intertropical Convergence Zone (Rodriguez-Rubio and Stuardo, 2002; Rodríguez-Rubio et al., 2003; Corredor-Acosta et al., 2020). During the dry season (January to April; precipitation: 350 mm month^{-1}) upwelling develops, hence the 20°C thermocline is shallow (7.5 m), and cool, high-salinity, nutrient rich, and hypoxic deep waters reach the surface water column; during the wet season (May to August; precipitation: 587 mm month^{-1}) the thermocline deepens (47 m), allowing for warmer and more oxygenated waters to occurs, but with lower salinity and chlorophyll-a conditions (Giraldo et al., 2008, 2014b; Blanco, 2009; Sampson and Giraldo, 2014; Zapata, 2017; Castrillón-Cifuentes et al., 2023).

Although ambient conditions in the Colombian Pacific are considered not suitable for coral reef development (compared to the Caribbean or Indo-Pacific; Kleypas et al., 1999), the largest coral reefs of this region occur at Gorgona Island, and although they cover small areas (like other coral reefs in the ETP) they are among the best developed within the ETP and resilient to El Niño 1982-83, because live coral cover was recovered in less than a decade, and no further massive bleaching or mortality has been observed there (Zapata and Vargas-Angel, 2003; Zapata, 2017).

Reefs selection for the transplant experiment

The reefs selected for this study were Playa Blanca and La Ventana (Fig 1). Live coral coverage accounts 61% at Playa Blanca and 73 % at La Ventana, and *Pocillopora* is the main reef builder scleractinian coral; massive corals account to less than 1 % of the benthic cover (Palacios and Zapata, 2014; Céspedes-Rodríguez and Londoño-Cruz, 2021). On each reef, the transplant experiment was located on the western sides of the reef flats and on topographic depressions that protect corals from aerial exposure during extreme low tides (especially at Playa Blanca). The experimental sites were 82 m and 674 m far from shore, for Playa Blanca and La Ventana, respectively.

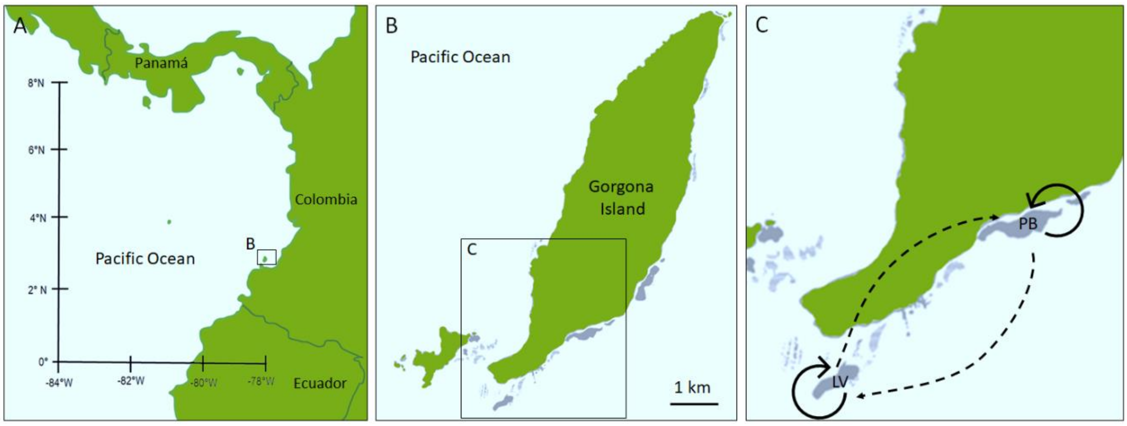

Fig 1. (A) Location of Gorgona Island on the Colombian Pacific coast. (B) Coral reefs (gray areas) around Gorgona Island. (C) Reefs for the reciprocal transplantation experiment, La Ventana (LV) and Playa Blanca (PB) reefs. Solid arrows represent the control treatment, while dashed arrows the transplant treatment.

Species selection

Colonies with the morphological features of *Pocillopora damicornis* (Veron et al., 2022) were selected, although was proposed that this species do not occur at the ETP (Schmidt-Roach et al., 2014). It is important to highlight that species delimitation within this genus at the ETP is not yet possible, because morphological and molecular characteristics do not match (Pinzón and Lajeunesse, 2011; Pinzón et al., 2013). Also, colonies can switch morphology (Paz-García et al., 2015), but evidence also indicates that growth rates did not differ within morphospecies (Tortolero-Langarica et al., 2017).

Transplant experiment

On April 2021, 10 colonies of *P. damicornis* were collected at each reef. From each colony, six fragments were extracted (3 - 5 cm long). A reciprocal transplantation of coral fragments was done between Playa Blanca and La Ventana reefs. From each colony, four fragments were maintained at their home reef (Control treatment), and two fragments were moved to the neighboring reef (Transplant treatment). Coral fragments were underwater cemented (with epoxy putty) to ceramic tiles to avoid air exposure stress.

Coral response assessment

Survival, growth rate, skeletal density, calcification rate, respiration rate, and photosynthesis were measured in fragments as the physiological response after the transplant experiment. Survival was reported as the percentage of fragments alive for each colony and per treatment (control or transplant). Growth rate was established according to the change in the linear extension (height) of fragments over time. Each fragment was photographed with a size reference on July 7, 2021, and November 17, 2022, and the height was measured using the ImageJ software (National Institute of Health, USA). Growth rate per colony was established as the average for fragments alive at control or transplant treatment.

Between November 17 and 21, 2022 coral fragments were removed from the reefs and transported to a lab on the island for measuring oxygen consumption and production. There, the fragments were incubated at 26.9 ± 0.4 °C (mean ± SD) in hermetically sealed respiration chambers filled with seawater from the reefs. To maintain a stable temperature, respiration chambers were submerged in a water bath equipped with a thermostat and a submersible water pump to homogenize the temperature. Also, the respiration chambers had internal water movement generated by peristaltic pumps.

Changes in oxygen were recorded every 5 s, over the course of 1 h using the Firesting-GO2 (PyroScience GmbH), previously calibrated according to the manufacturer’s instructions. Coral fragments were under dark conditions during the first half hour, the next half hour was under light conditions (4000 lux; the average light for both reefs), generated with a LED lamp, and light conditions confirmed with a temperature/light sensor (MX2200, Onset). During the hour of measurements, corals were exposed to normoxic conditions (95 - 100 % air saturation).

Oxygen consumption and production were calculated using the respR R package (Harianto et al., 2019). The data from the second 400 to the second 1500 was employed to establish the respiration rate, and the data from the second 2500 to the second 3600 for net photosynthesis. Background oxygen fluxes were measured and subtracted from coral measurements. Respiration rate and gross photosynthesis were standardized as the amount of O_2 consumed or produced per mass of coral tissue per hour (mg O_2 g^{-1} h^{-1}). The weight of coral tissue was determined by the difference between the wet and dry weights of coral fragments.

The clean and dry coral fragments from the oxygen fluxes measurements were employed to assess skeletal density, following the methods described by Manzello 2010 (Manzello, 2010). The calcification rate was established as the product of linear extension and skeletal density.

A factorial ANOVA was employed to establish the interactive effect of the home reef (2 levels: Playa Blanca and La Ventana) and treatment (2 levels: control and transplant) on the coral response: survival, growth rate (linear extension), skeletal density, calcification rate, respiration rate, and photosynthesis. The survival and growth rate data of satisfied the assumptions for homogeneity of variances and normality of residuals. However, to meet those assumptions, skeletal density was Log10 transformed, and the Box-cox transformation (SM2) was applied for respiration rate and photosynthesis.

Characterization of micro-environmental conditions

On July 10, 2021, one data logger for salinity/temperature (U24-002-C, Onset) and one for light/temperature (UA-002-64, Onset) were attached to a stainless-steel rod at each reef and located next to coral fragments. Loggers were programmed to record every hour until November 18, 2022. Light/temperature loggers were cleaned on November 21, 2021, February 27, 2022, and May 23, 2022. The first 22 days after cleaning were suitable for analysis, as fouling organisms start to growth and cover the sensor after that time. Temperature, light, and salinity were described in terms of the reef and seasonal differences. Precipitation for Gorgona Island was retrieved from POWER Data Access Viewer (https://power.larc.nasa.gov/data-access-viewer/), for the period between July 10, 2021, and November 18, 2022, and at daily intervals. Because temperature, salinity, and light were constantly monitored over time at the same location, a Repeated measurements Anova was employed to assess the differences between reefs over time.

The benthic components of each reef (i.e., crustose coralline algae (CCA), turf algae, and sediments) were monitored on 29 ceramic tiles (where the coral fragments grow) and on July 7, and November 14, 2021, and February 25, May 22, and November 17, 2022. Ceramic tiles were photographed with a size reference, and using the ImageJ software, an area of 26 cm^2 was selected from each ceramic tile, and 25 points were randomly distributed within this area. The benthic component observed below each point was noted. Benthic cover on ceramic tiles was expressed as a percentage, and reef differences over time were analyzed with a Repeated measurements Anova (raw data satisfies the assumption of Sphericity). A Principal Components Analysis was employed to discuss the relation between the abundance of crustose coralline algae and turf algae with abiotic conditions (temperature, salinity, light, and sediments) at each reef.

Results

Coral response

The survival of coral fragments was similar between reefs if the effect of the treatment was not taken into consideration (Table 1), coral survival (mean ± SD) at La Ventana reef was 60 ± 31.8 %, and 50 ± 38.0 % at Playa Blanca. However, the treatment had significant effects on survival (Table 1), control corals had similar survival at both reefs, but lower survival occurred for coral fragments transplanted from Playa Blanca to La Ventana (Fig 2A, Table 1).

The growth rate of coral fragments was similar between reefs (Table 1), coral fragments from La Ventana grow on average 1.38 ± 1.22 cm year^{-1}, and those from Playa Blanca 1.23 ± 1.20 cm year^{-1}. However, the effect of the treatment was significant (Table 1): in the control treatment coral fragments on La Ventana reef had a higher growth rate than corals on Playa Blanca reef, and regarding the transplanted corals, when coral fragments from La Ventana were transplanted to Playa Blanca their growth rate was reduced by 63.4 % compared to control fragments, and exhibited similar growth rates as the control fragments of Playa Blanca; conversely, coral fragments from Playa Blanca transplanted to La Ventana increased their growth rate by 75.5 % compared to control fragments, and had similar values as the control fragments of La Ventana (Fig 2B).

Skeletal density was similar between reefs (La Ventana: 2.13 ± 0.62 g cm^{-3}, Playa Blanca: 1.89 ± 0.21 g cm^{-3}), and the transplant treatment had no statistical effects (Table 1; Fig 2C). As expected, the calcification rate follow the same pattern as growth rate, it was similar between Playa Blanca and La Ventana reefs without taking into consideration the treatments; however, the interactive effect of treatment and reef had a significant effect: control corals on La Ventana reef had a higher calcification rate than control corals on Playa Blanca reef (Table 1), and the calcification rate was reduced by 66.8 % when coral fragments from La Ventana were transplanted to Playa Blanca and was similar to the control corals of Playa Blanca, while the calcification rate increased by 75.8 % in coral fragments from Playa Blanca transplanted to La Ventana (Fig 2D).

The dark respiration rate of coral fragments was similar between reefs (La Ventana: 0.54 ± 1.05 mg O_2 h^{-1} g^{-1}, Playa Blanca: 0.14 ± 0.16 mg O_2 h^{-1} g^{-1}; F = 2.69, df = 1, p = 0.11), and although the treatments had no statistical effects (F = 1.77, df = 1, p = 0.19), coral fragments increased their respiration rate when transplanted from La Ventana to Playa Blanca (Fig 2E). Gross photosynthesis in coral fragments from La Ventana was statistically high compared to corals from Playa Blanca (La Ventana: 1.20 ± 1.26 mg O_2 h^{-1} g^{-1}, Playa Blanca: 0.20 ± 0.21 mg O_2 h^{-1} g^{-1}) but the treatments has no effect: the movement of coral fragments to the neighboring reef did not affect photosynthesis (Table 1; Fig 2F).

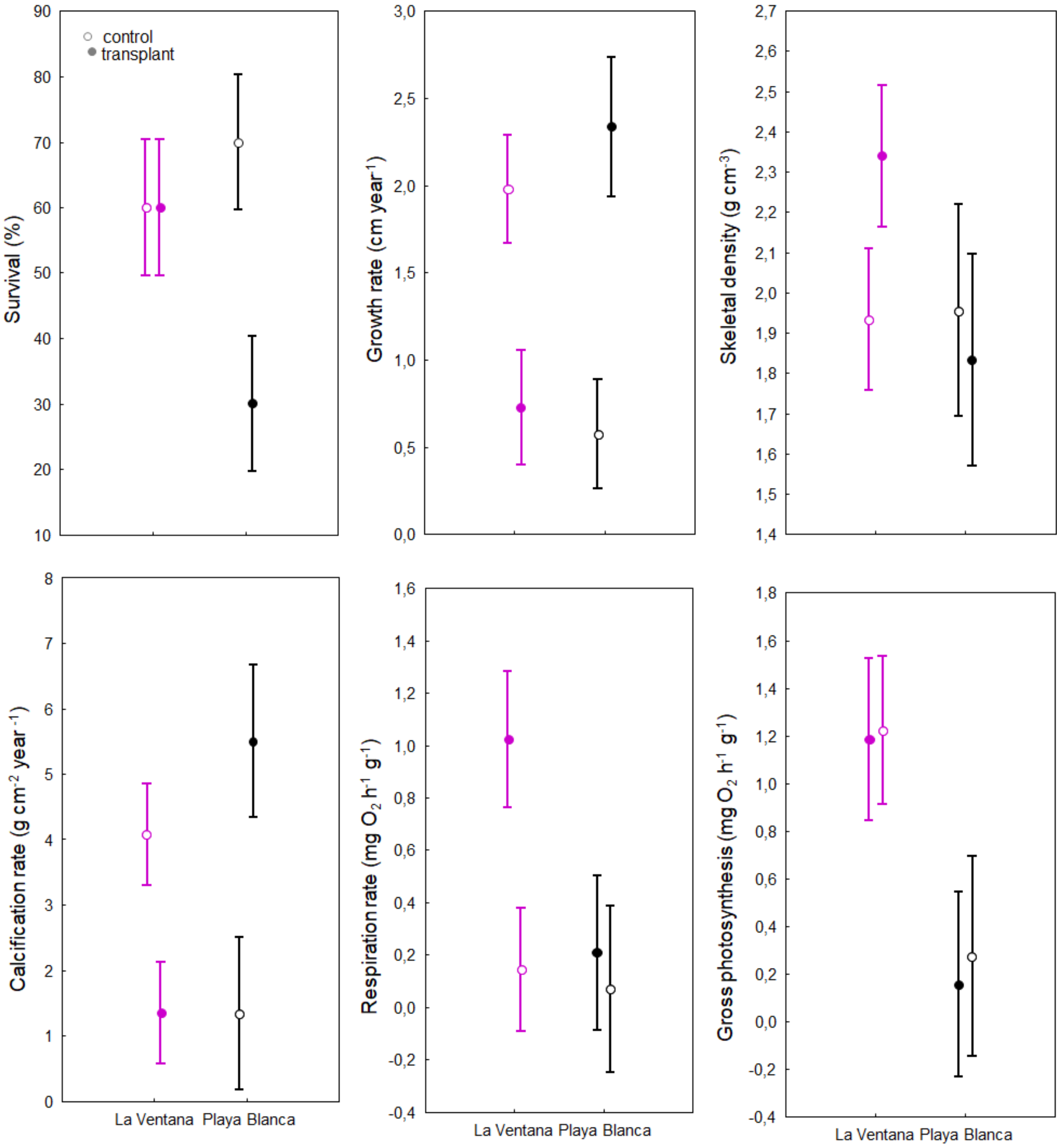

Figure 2. (A) Coral survival, (B) growth rate, (C) skeletal density, (D) calcification rate, (E) respiration rate, and (F) photosynthesis of *Pocillopora* coral fragments after a reciprocal transplant experiment between La Ventana (violet) and Playa Blanca (black) reefs. Empty circles corresponds to the response of control fragments, and filled circles for the transplanted fragments. In all panels the circles correspond to the mean, and whiskers to the standard error.

Table 1. Factorial Anova to assess the physiological differences (survival, growth rate, calcification rate, and gross photosynthesis) between *Pocillopora* fragments from La Ventana and Playa Blanca reefs (Home reefs), and the effect of the transplantation of corals between both reefs (Treatment). Also, the probability for statistical differences (Fisher LSD test) on the physiological for the combination of factors. Reef and treatment names were abbreviated by: 1) La Ventana control, 2) La Ventana transplant, 3) Playa Blanca control, and 4) Playa Blanca transplant.

			Survival		**Growth rate**		**Calcification rate**		**Gross photosynthesis**	
	Factor	**Df**	**F**	**p**	**F**	**P**	**F**	**p**	**F**	**p**
Factorial Anova	Home reef (HR)	1	0.92	0.34	0.09	0.76	0.51	0.48	6.43	0.01
	Treatment (T)	1	3.71	0.034	0.56	0.45	0.53	0.47	0.15	0.69
	HR x T	1	7.71	0.06	19.59	0.001	12.16	0.002	0.20	0.65

		Survival				**Growth rate**				**Calcification rate**				**Gross photosynthesis**			
		1	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Fisher LSD test	**1**	-				-				-				-			
	2	1.00	-			0.009	-			0.02	-			0.96	-		
	3	0.49	0.49	-		0.003	0.73	-		0.06	0.99	-		0.15	0.15	-	
	4	0.04	0.04	0.009	-	0.48	0.004	0.001	-	0.31	0.007	0.01	-	0.03	0.04	0.58	-

Micro-environmental conditions

Thermal variation follows the same seasonal trends on both coral reefs (Fig 3A). The mean temperature at La Ventana was 27.58 ± 0.69 °C and at Playa Blanca was 27.70 ± 0.72 °C, a differences that was statistically significant (F(1, 6)= 28.49, p= 0.001). Temperatures below the annual mean – SD (cool season) occurred from December 2021 to March 2022, but upwelling events occurred only in March 2022, with a minimum temperature of 23.8 °C. Temperatures above the annual mean + SD (warm season) occurred from April to September (SM3).

The mean light condition at Playa Blanca (4188.58 ± 5041.14 lux) was statistically higher (F (1, 526) = 17.17, p=0.00004) than at La Ventana (3652.85 ± 4443.46 lux). As expected for a tropical location, maximal light conditions occur at noon for both reefs (7993.87 ± 6779.65 lux; Hourly differences: F (11, 526) = 40.79, p= 0.00001; Hour x Reef: F (11, 526) = 0.86, p= 0.57). Light conditions at La Ventana reef were similar over the study period, but were particularly high at Playa Blanca reef during March 2022 (Month x Reef x Hour: F (33, 1578) = 2.08, p= 0.0003. Fig 3B).

Salinity was on average lower at Playa Blanca reef (26.85 ± 0.80 PSU) than at La Ventana reef (28.73 ± 0.84 PSU), a difference that was statistically significant (F (1, 6) = 325.79, p=0.000001). An increase in salinity was evident at La Ventana reef from December 2021 to February 2022 (the dry season). At Playa Blanca the increase in salinity occurs from February to March 2022, also the dry season, but when upwelling occurs. Low salinity conditions were observed from April 2022 and for both reefs due to La Niña conditions (Fig 3C). Precipitation was low from July 2021 to March 2022 (2.51 – 7.86 mm day^{-1}) and increased from April to June 2022 (36.02– 35.33 mm day^{-1}), then started to decrease from 25.34 ± 16.07 mm day^{-1} in July to 9.84 ± 11.26 mm day^{-1} in November 2022 (Fig 3D).

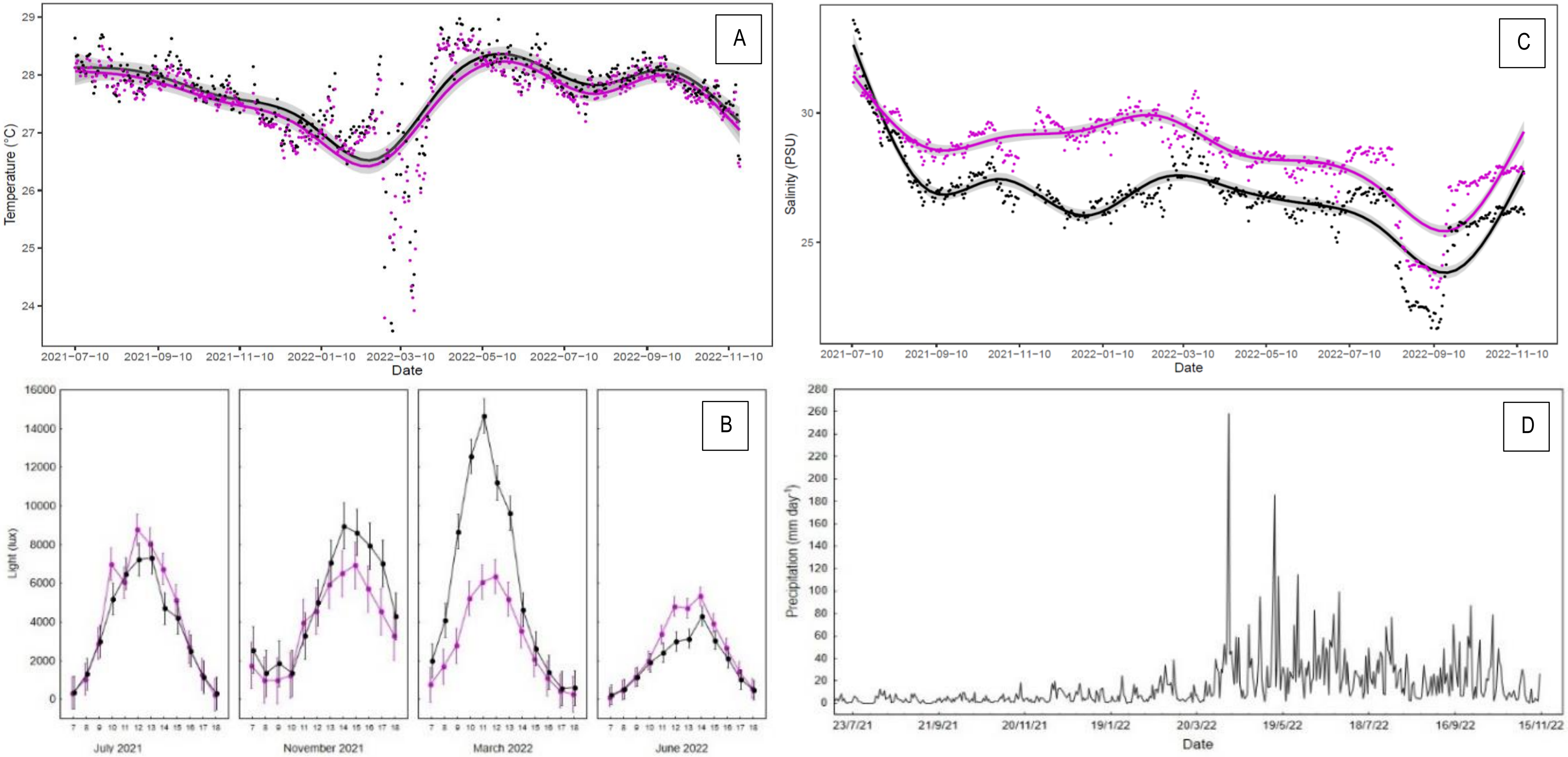

Figure 3. Temperature(A), light (B), and salinity (C) at La Ventana (purple) and Playa Blanca reefs (black), and precipitation at Gorgona Island (D). In A and C, the points correspond to the mean daily temperature, while the gray bands the 95 % confidence intervals of the tendency (GAM as the smoothing method). In B points corresponds to mean (± SE) light conditions at each hour for the given month.

Benthic coverage

The dominant component on ceramic tiles from La Ventana reef was CCA, while sediments predominated on Playa Blanca reef. The second most abundant component for both reefs was turf algae (Fig 4). At La Ventana reef CCA covered 57.84 ± 22.63 % of the ceramic tiles, and 5.84 ± 8.37 % of the ceramic tiles from Playa Blanca reef; May 2022 was the month with the lower record of CCA coverage (25.79 ± 27.63 %). Also, there was no statistical effect for the interaction of reef and months on changes of CCA coverage (Table 2).

The turf algae coverage on ceramic tiles was similar between reefs (La Ventana: 28.63 ± 22.42 %, Playa Blanca: 25.95 ± 28.34 %). The highest record of turf algae coverage occurred during May 2022 (39.37 ± 27.80 %); and as determined for the CCA, there was no statistical effect of the interaction of the reef and month factors on the changes in turf algae cover (Table 2).

The presence of sediments on ceramic tiles was significantly different between reefs, influenced by months, and their interaction (Table 2). Ceramic tiles at Playa Blanca had the highest coverage by sediments (53.46 ± 29.51 %) compared to ceramic tiles at La Ventana (5.04 ± 14.81 %). May 2022 was the month with the lower record of sediments (23.24 ± 31.31 %). Sediments were more abundant during February 2022 at La Ventana reef (17.65 ± 21.04 %), and during November 2022 at Playa Blanca (64.00 ± 29.91 %).

Table 2. Repeated measures Anova to assess the statistical effect of the reef and temporal variation on the benthic components that cover the ceramic tiles at La Ventana and Playa Blanca reef from July 2021 to November 2022.

Source		**Crustose coralline algae**		**Turf algae**		**Sediments**	
	DF	*F*	*p*	*F*	*p*	*F*	*p*
Reef	1	1435.19	< 0.000001	0.63	0.42	242.63	< 0.000001
Month	4	3.52	0.008	6.95	0.0001	2.54	0.040
Reef x Month	4	2.01	0.09	2.39	0.051	4.20	0.002

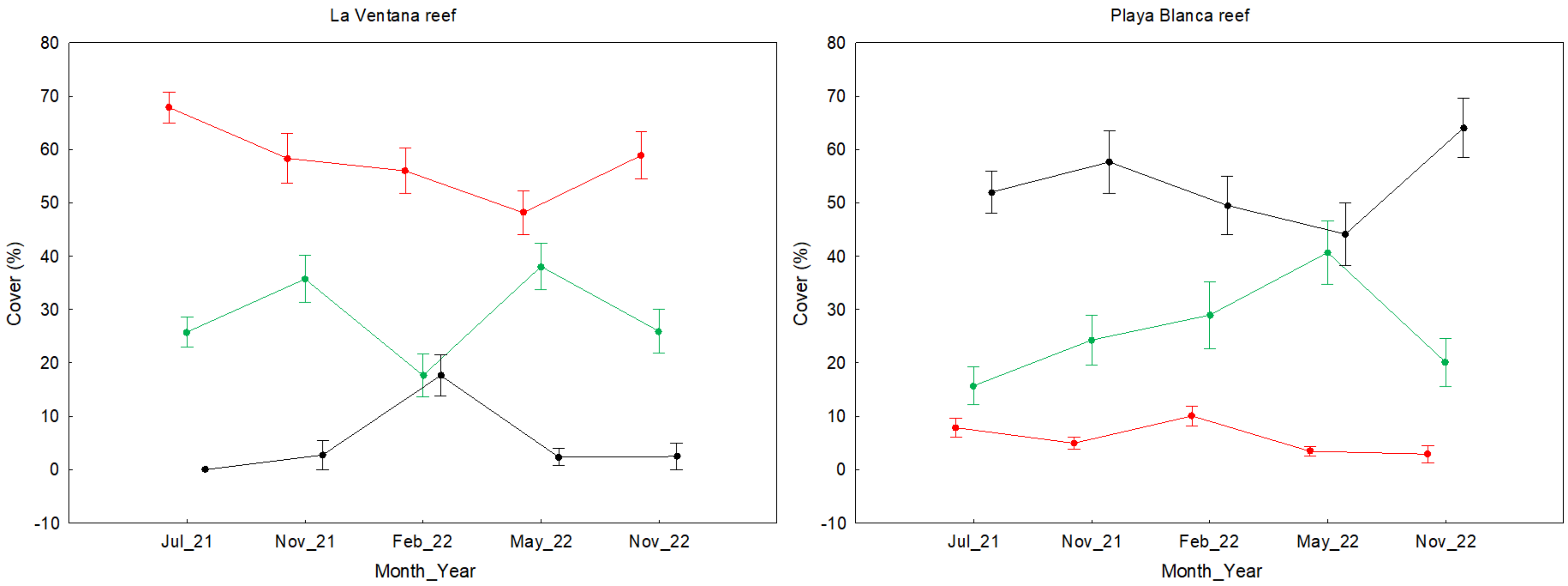

Figure 4. Benthic coverage of ceramic tiles at La Ventana and Playa Blanca reefs. Data shows the mean (●) and standard deviation (⌶), and in red the crustose coralline algae, green for turf algae, and black for sediments.

Discussion

This study pursued to explore how micro-environmental conditions impact the response capacity of Pocillopora damicornis corals, one of the key reef-builder morpho-species of the Eastern Tropical Pacific. Run-off could potentially drive how corals respond, as these local stress factor affects reefs of Gorgona island at different levels. Also, the observed differences in survival, growth rate, calcification, and photosynthesis between colonies at the two sites during the reciprocal transplant could potentially indicate genetic-based coral resilience.

Factors that promote adverse ambient conditions on reefs of Gorgona island

Salinity and sediments were the abiotic factors that most differentiated between reefs (Fig 3C, 4, 5). Playa Blanca reef has the direct influence of run-off from streams due to its short distance from shore. The south end of the Playa Blanca back reef (where the experimental site was located) is close to a permanent stream, El Roble, with a flow of 75 m^3 s^{-1}, and that can provide 3.000 mg s^{-1} of dissolved organic carbon and 46 mg s^{-1} of phosphorus (Blanco et al., 2009). Hence, the low salinity and high sediment conditions at Playa Blanca reef (compared to La Ventana reef), and particularly during the wet season, were attributed to El Roble stream. Sediments at Playa Blanca reef (Fig 4) were generally constant but increased at the end of the study period (November 2022), likely due to the intensification of La Niña conditions that increase precipitation (NOAA, 2022). It has already been established that erosional processes increase during the wet season at Gorgona Island (Gómez-García et al., 2014), a process that speeds up during La Niña events.

Another factor that potentially promotes that sediments perdure longer on Playa Blanca reef is low current velocity. Current velocity tends to be low all year on the near-shore and wind protected west site of Gorgona Island (Guerrero-Gallego et al., 2012), where Playa Blanca reef is located, while intense on the east side of the island due to the direct oceanic influence (Giraldo et al., 2008; Guerrero-Gallego et al., 2012). As consequence of the movement of ITCZ at the beginning of the year, wind velocity and currents intensify; hence currents could also explain why sediments increase on ceramic tiles at La Ventana during February 2022, as more material could be transported as a result t of increased water movement at this reef that is not well protected from winds force.

Temperature was similar between reefs, and although slightly lower (0.12°C) at La Ventana reef, both reefs experienced extreme low temperatures during upwelling events in March 2022 (Fig 3A). Likewise, light conditions were similar between the reefs, except during March 2022 when light conditions were particularly higher between 10:00 and 14:00 hrs at Playa Blanca reef (Fig 3B); this could be the result of low cloud cover during the dry season (Corredor-Acosta et al., 2020), and a reduced water column during extreme low tides, and not due to reduced run-off, as sediment conditions were similar from July 2021 to May 2022 (the study period), a lapse that includes wet and dry seasons.

According to the PCA (Fig 5), high salinity conditions were positive associated with high coverage of CCA at La Ventana Reef, while low salinity and high sediment conditions were correlated to low CCA cover at Playa Blanca reef. Turf algae was positively associated with temperature, which suggests that the difference of 0.12 °C between reefs, makes that the slightly warm waters at Playa Blanca promote turf algae abundance. High temperature combined with nutrient-rich conditions from sediments, and the tolerance of algae to low salinity conditions could make it a superior space competitor under low water quality conditions at Playa Blanca (Fabricius, 2011; Mueller et al., 2016; Anton et al., 2020).

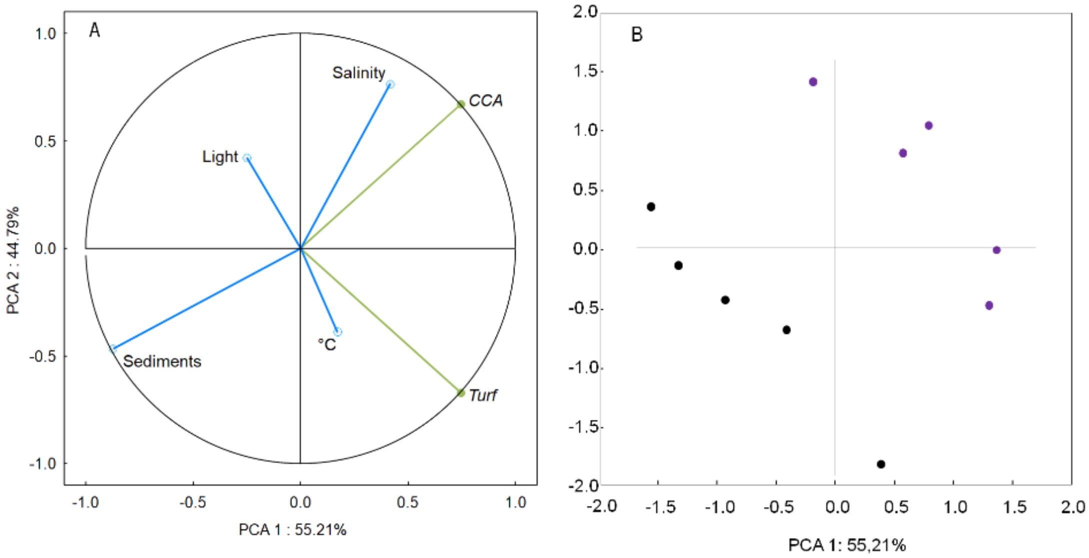

Figure 5. Principal Component Analysis applied to state the correlations between the coverage (%) of crustose coralline algae (CCA) and turf algae (Turf) with temperature (°C), Salinity, Light, and Sediment conditions (A), recorded at La Ventana (●) and Playa Blanca (●) reefs (B).

Response of *Pocillopora* to changes in ambient conditions

The effects of low salinity and sediments on corals' physiology has been well documented. Low salinity destroys gametes, decreases fertilization, reduces larval settlement, increases larvae abnormalities, and retards the metamorphosis of planula (Hédouin et al., 2015; Chui et al., 2016; Chui and Ang, 2017). Low salinity on adult corals reduces growth rate, tissue regeneration, and respiration rate, it also increases mortality, particularly when combined with warm conditions (Mayfield and Gates, 2007; Kuanui et al., 2015; Dias et al., 2019; Kongjandtre et al., 2021). High salinity can also confer some thermo-tolerance (Gegner et al., 2017; Ochsenkühn et al., 2017). Like the effects of low salinity, sediments reduce gamete fertilization, and planula settlement (Perez et al., 2014; Jones et al., 2015; Humanes et al., 2017). On adult corals, sediments reduce photosynthesis (P) and increase respiration rate (R), hence, the P:R ratio declines and the energy for growth, reproduction, immunity, and survival declines (Anthony and Fabricius, 2000; Junjie et al., 2014; Browne et al., 2015).

As expected from improved ambient conditions on offshore reefs (high salinity and low sediments), *Pocillopora* corals on La Ventana reef had enhanced physiological performance; there corals had a higher growth rate, calcification rate, and photosynthesis (Fig 2); crucial traits for the persistence of the reef framework (Fisher, 2022). The transplant experiment also corroborates the positive effect of the ambient conditions on La Ventana reef in enhancing growth and calcification rates in corals that were transplanted from Playa Blanca reef, and the depressing effect on the same physiological traits in corals moved from La Ventana to Playa Blanca reef.

Regarding survival, the fact that moving corals from Playa Blanca to La Ventana resulted in a low percentage of survival, could be the effect of: (1) the time that corals need to acclimatize to a 0.12 °C cool ambient, (2) cool conditions had more negative effects than warm conditions at upwelling localities (Castrillon-Cifuentes et al, previous chapter), and (3) there is some capacity of corals from upwelling conditions to tolerate warming (Vargas-Ángel et al., 2001; Jiménez and Cortés, 2003; Glynn and Fong, 2006; Romero-Torres et al., 2020). In fact, the lower survival occurred during the upwelling season (SM6), and corals at playa Blanca were exposed during less time to cool temperatures than corals at La Ventana (SM3).

Photosynthesis in corals is stimulated by high flow (Osinga et al., 2017), and reduced by low salinity and sediments (Anthony and Fabricius, 2000; Mayfield and Gates, 2007), the contrasting ambient conditions between La Ventana and Playa Blanca reefs, which explains higher photosynthesis at La Ventana than at Playa Blanca. However, the fact that the transplant experiment has no effect on photosynthesis (transplanted corals from Playa Blanca did not increase photosynthesis, nor transplanted corals from La Ventana decrease it), makes us speculate that some intrinsic factor enables the zooxanthellae to not alter photosynthesis processes under different ambient conditions; likely a particular symbiont association (Palacio-Castro et al., 2022; Ravindran et al., 2022). Another possibility is that zooxanthellae acclimated to the new environment, and after a certain time, the photosynthesis rate returned to normal values (Poquita-Du et al., 2020; Oakley et al., 2022). Also, high salinity conditions confer thermo-tolerance in some coral-symbiont associations (Gegner et al., 2017). The former hypothesis requires identifying Symbiodiniacea diversity and measuring its photosynthetic efficiency over time in a transplant experiment that simulates our contrasting ambient conditions.

Although there were no statistical differences in the respiration rate of corals between reefs, nor an effect of the transplant experiment; an increase in the respiration rate was observed for corals from La Ventana transplanted to Playa Blanca reef. This could be the effect of increased ciliary activity to remove sediments from their tissue, a process that is energy-demanding (Browne et al., 2015; Humanes et al., 2017), and the low currents at Playa Blanca reef do not aid in removing deposits of sediment within the coral branches' bases (Fabricius, 2011).

Corals at Playa Blanca had thin branches, this morphological feature may prevent sediments from settling onto the tissue (Fig 6). Although transplanted corals from La Ventana to Playa Blanca also resulted in thin branches, the arborescent structure of those colonies seems to be more compacted than the native corals of Playa Blanca, which allow sediments to still deposit on the bases of branches. Wide branches at la Ventana could be the result of increased currents.

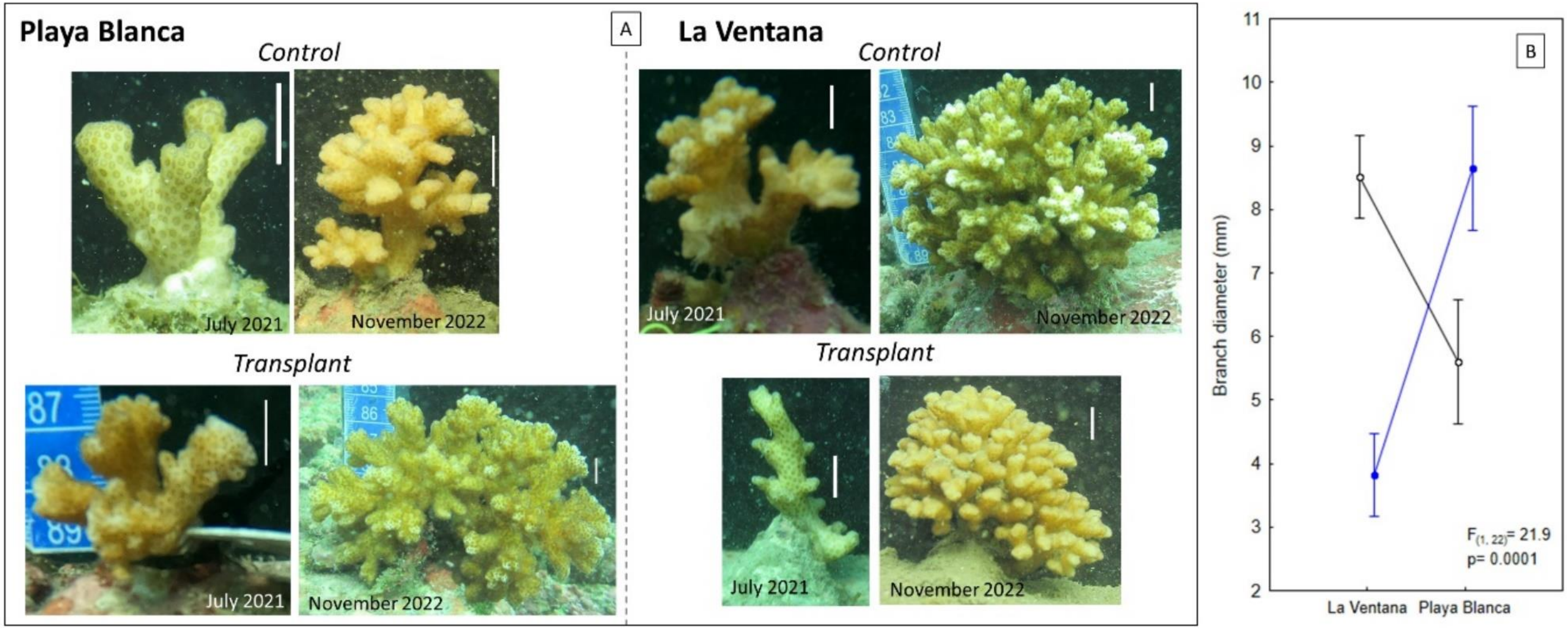

Figure 6. (A) Changes in the morphology of *Pocillopora* fragments from Playa Blanca and La Ventana that were reciprocal transplanted. (B) differences on branch diameter of fragments observed at the end of the experiment, black correspond to control fragment, while blue to transplanted fragments; whiskers denote mean ± SD.

Local and global stressors that potentially increase adverse ambient conditions for corals at Gorgona Island

Because Gorgona Island is part of the Chocó biogeographic province, characterized as one of the rainiest regions in the world, the island is covered by a tropical rainforest, which is considered a value of conservation interest (VOC) for the environmental authority (Vásquez-Vélez, 2014). Despite the fact that 70% of the native forest of Gorgona was deforested due to the operation of a high-security prison, the vegetation coverage has recovered (since the prison was closed), establishing a successional gradient (Murillo-García and Bedoya-Durán, 2014). However, the forest at Gorgona Island is in an undesirable ecological state and requires efficient management actions for its maintenance, as failure to follow up runs the risk of losing the VOC (Giraldo et al., 2014a). The instability of the successional vegetation, plus the steep slopes (50-75%) that characterizes the island, implies that during the rainy season the discharge of sediments into the sea intensifies through the numerous streams surrounding the island (Blanco et al., 2009).

Approximately 30 km separate Gorgona Island and the NNP Sanquianga, a mangrove forest where degradation start since 1972, due to excess in sediment yields (1500 t km2 yr-1) after the construction of a channel that connected the Sanquianga and Patia rives, whose plume reached Gorgona island during La Niña events (Restrepo A, 2012; Restrepo and Kettner, 2012; Restrepo and Cantera, 2013). There is increasing concern about the effects of sediment from the Patia river on the coral reefs of Gorgona island consequence of a 25.7% increase in the deforestation of the mangrove at PNN Sanquianga due to illicit crops and alluvial mining (Anaya et al., 2020; Clerici et al., 2020).

Global warming is leading to greater evaporation and water holding capacity of air, which in turn leads to increased water vapor in the atmosphere, and more intense precipitation events, hence, wet areas will become wetter; additionally in the tropics and subtropics precipitation patterns are dominated by shifts in sea surface temperatures, like warming due to El Niño events (Trenberth, 2011). An increase in precipitation around the area of influence of Gorgona island could result in lower salinity conditions and increase in sediments at coral reefs. A similar scenario is already registered on the Pacific coast of Panama (Valiela et al., 2012).

Conclusion

Our results corroborate the importance of high salinity and low sediment conditions for *Pocillopora* corals to maintain growth, calcification, and photosynthesis rates. These are key physiological features of colonies that have an impact at the ecosystem level (reef accretion). Also, the speculated intensification of upwelling events due to climate change (Chollett et al., 2010; Bakun et al., 2015; Bograd et al., 2023) could be detrimental for in-shore corals of Gorgona Island that regularly deal with local stress factors (low salinity and run-off), as low survival was observed in corals from Playa Blanca when face cooler ambient conditions when transplanted to La Ventana reef.

Our data evidenced a resistance capacity in *Pocillopora damicornis* corals from La Ventana, because when moved to lest suitable environment (Playa Blanca reef) they tolerate the local stressors (low salinity and sediments). Furthermore, some degree of resilience capacity was observed in corals from Playa Blanca reef, although these corals regularly experience adverse conditions, when the ambient conditions were improved (high salinity and low sediments at La Ventana, except for the longer cool periods), their physiological performance were improved.

The existence of both resistance and resiliency capacity in *Pocillopora damicornis*, is an insight into beneficial innate traits for the restoration process of coral reefs at Gorgona Island. However, our data also reveals the urgent need to actively reduce local stressors by managing the forest. Although diving and fishing activities are prohibited on the reefs where the study was carried out, and no forest harvesting occurred since 1983, when the island was declared a MPA; the tropical rain forest of Gorgona is an undesirable condition, hence, these results highlight that conservation actions to protect the coral reefs of Gorgona island must consider ecosystem interactions and even socio-ecologic aspects, not only the reefs as isolated systems.

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Chapter 5: **General discussion**

The central goal of this research was to identify the physiological mechanisms in *Pocillopora* corals from Gorgona Island (Colombian Pacific) that confer resistance to local and global stressors. Through laboratory and field experiments, coupled with environmental monitoring and a literature review of studies carried out on the island, it was possible to identify some traits in the corals and environmental conditions that aided in explaining the resilience of Pocilloporid reefs from Gorgona to different stressors. Corals from Gorgona Island exemplify that, in the absence of additional human-related stressors, corals and coral reefs can thrive in an atypical and dynamic environment; however, the result of this research evidenced that *Pocillopora* corals are currently living in a delicate balance to resist the effects of stress factors, particularly the effects of local stressors.

Hence, additional pressures from climate change (ocean warming, acidification, and deoxygenation) and the intensification of local stressors put their future persistence under debate. The obtained data represent a baseline of knowledge for the general understanding of *Pocillopora*'s physiological response to changes in temperature, oxygen, salinity, and sediments, which are some of the most remarkable factors that will be altered due to climate change and that affect corals in synergy with local stressors.

Effects of thermal stress, acidification, and deoxygenation on *Pocillopora*

Thermal stress, and particularly bleaching after the impact of El Niño events, is generally the most studied stress factor in the ETP (Wang et al., 2017). Bleaching has been proposed as an opportunity to alter the Symbiodiniacea community within *Pocillopora* colonies, a process suspected to provide resistance (increased survival) to future warming stress events, but at the cost of reduced growth rate (Baker, 2001, 2003; Cunning et al., 2013, 2015). Interestingly, over the last two decades, El Niño events have not led to massive bleaching or coral mortality on Gorgona Island (Zapata, 2017; Romero-Torres et al., 2020). Nevertheless, as expected, El Niño 1997-1998 caused bleaching without resulting in significant mortality, and surprisingly, bleached *Pocillopora* corals exhibited enhanced growth rates (Vargas-Ángel et al., 2001). However, there is evidence indicating that bleached *Pocillopora* corals do not produce gametes (Castrillón-Cifuentes et al., 2015).

Another natural phenomenon that can expose corals to heat stress is extreme low tides. These events can be lethal if corals remain out of water for more than 45 minutes (Castrillón-Cifuentes et al., 2017), especially when ambient conditions promote desiccation due to high solar radiation and winds, as seen during El Niño 1982-1983 (Vargas-Ángel, 2003; Zapata, 2017). However, *Pocillopora* corals from Gorgona Island can tolerate these stressful events to some extent, although they experience certain consequences in their reproductive output. During extreme low tide events, despite corals producing a foam-like substance that protects the base of their branches, they still suffer partial tissue loss at the branch tips, bleaching, and reduced gamete production. Nevertheless, their growth rate remains stable (Castrillón-Cifuentes et al., 2017).

Growth rate is a crucial feature for reef persistence, as it directly affects reef integrity (Fisher, 2022). Notably, skeletal extension does not appear to be compromised during warming stress events at Gorgona Island (Vargas-Ángel et al., 2001; Castrillón-Cifuentes et al., 2017). In contrast, during cool stress events, which occur annually during upwelling events and intensify during La Niña conditions, a different pattern emerges; it was observed that the ambient conditions during upwelling events contribute to depressing the host metabolism, leading to significantly lower growth rates despite an increase in Symbiodiniacea density (Castrillon-cifuentes et al., 2023). It remains uncertain whether *Pocillopora* populations can sustain reef integrity in the long term solely through coral growth, which is a fundamental trait for reef accretion and fragmentation for asexual reproduction at Gorgona (Muñoz et al., 2018). Sexual reproduction appears to be suppressed to maintain energetic balance under the challenging environmental conditions present at Gorgona. However, alternative sources of genetic variability can still occur in corals, such as somatic mutations (van Oppen et al., 2011; Rinkevich et al., 2016).

Acidification also plays a critical role in reef persistence, and in the ETP the co-occurrence of low pH conditions and El Niño events can be detrimental for reef stability (Manzello, 2010a, 2010b). However, at Gorgona Island, there is currently insufficient evidence to consider pH variability a significant threat to corals. An analysis of oceanographic data shows a decrease of 0.3 in pH during March (the upwelling season, pH 8.7) compared to September (non-upwelling season, pH 8.4). However, there is evidence that these seasonal changes in pH are not statistically different (Ramírez-Martínez et al., 2022). Conducting a more detailed analysis of pH variability on hourly, daily, and interannual scales is crucial, as bioeroders' detrimental effects may intensify under acidifying, warm, and nutrient-rich conditions. Some rates of bioerosion on Gorgona Island's reefs are 0.8, 0.08, and 0.06 kg m^2 $year^{-1}$ of CaCO3, contributed solely by *Arothron meleagris*, *Diadema mexicanum*, and *Lithophaga* spp, respectively (Palacios et al., 2014; Londoño-cruz et al., 2016; Mendoza-Arcos and Londoño-Cruz, 2017).

Maintaining normal growth function in *Pocillopora* is also crucial for reef stability and carbonate balance because this genus contributes 93.1% of the total carbonate production, which amounts to 3 kg m^2 $year^{-1}$ of CaCO3; in contrast, other calcifying organisms, including crustose coralline algae, make a minor contribution of only 6.9% to the overall carbonate production on the reefs (Céspedes-Rodríguez and Londoño-Cruz, 2021). Understanding the complex interactions between pH variability (among other environmental factors), bioeroders, and carbonate production is vital for assessing their potential impacts on the long-term stability and health of Gorgona's coral reefs, as bioeroders activity is predicted to intensify under warm and nutrient rich conditions (Enochs et al., 2021; Rodriguez-Ruano et al., 2023).

Reefs that develop in areas where upwelling occurs have been proposed as thermal refuges from ocean warming (Riegl et al., 2019; Randall et al., 2020). However, upwelling is a multifactorial event or stressor in this context. Even if there is synchrony between El Niño and upwelling to decrease warm stress (Chollett et al., 2010), this research evidenced that during upwelling, Pocillopora metabolism was depressed due to hypoxia and cool temperatures, pushing them to their physiological limits (Castrillon-cifuentes et al., 2023). Furthermore, upwelling events are reduced during El Niño conditions as wind intensity decreases, which is the leading force of upwelling; additionally, upwelling events occur in pulses for one month, whereas El Niño is a sustained warm condition lasting several months (Alexander et al., 2012; Stuhldreier et al., 2015; Toth et al., 2015; Wang et al., 2017). On the other hand, while El Niño might ameliorate the negative effects of upwelling (Vargas-Ángel, 2003; Castrillon-cifuentes et al., 2023), the prolonged warm temperatures could be detrimental for corals, depending on their duration and intensity. Moreover, it is well established that at upwelling centers, bioerosion poses a significant threat, and under projected scenarios of climate change, reef stability will be impacted (Enochs et al., 2021; Rodriguez-Ruano et al., 2023).

Different climate models indicate that there has been an increase in the deoxygenation rate during the twentieth century, and they predict its acceleration during the twenty-first century for all greenhouse gas emission scenarios (Oschlies et al., 2018). This situation is particularly relevant for the corals and reefs of Gorgona Island, as well as for the ETP in general, because in this region, the OMZ is shallow and expanding vertically (Stramma et al., 2008, 2010; Schmidtko et al., 2017). As a result, hypoxic waters can reach coral reefs more frequently (Levin and Breitburg, 2015; Lucey et al., 2021). Moreover, *Pocillopora* at Gorgona Island is highly sensitive to hypoxic conditions (Castrillón-Cifuentes et al., 2023), especially when temperatures are low (Castrillon-cifuentes et al., 2023). Consequently, the lifting of hypoxic waters during upwelling events poses an imminent threat to the persistence of the reefs. Given these projections, monitoring the effects of deoxygenation on coral ecosystems in the ETP, including Gorgona Island, is of importance for effective reef conservation and management in the face of ongoing climate change.

Response of *Pocillopora* to local stressors at Gorgona Island

While global stressors alone affect 11% of coral reefs worldwide, the impact on coral reefs is doubled (22%) when local stressors come into play, and among the local stressors, land-use change and terrestrial runoff emerge as the primary responsible factors for reef degradation, leading to heightened sedimentation and eutrophication on coral reefs near the shore (Good and Bahr, 2021). The positive fact is that local stressors can be directly manipulated and managed through local efforts. In contrast, addressing global stressors necessitates international political will and cooperation to have a meaningful impact on coral reef conservation and protection. By focusing on managing local stressors, such as controlling land-use changes and minimizing terrestrial runoff, there is a greater potential to enhance the resilience and sustainability of the coral reefs on Gorgona island.

At Gorgona Island, the impact of run-off on *Pocillopora* varies depending on the distance from the stressor source, particularly the distance from the mouth of creeks. Salinity, as an independent factor, plays a crucial role in coral reproduction, restricting this process in *Pocillopora damicornis* to high salinity periods (> 30 PSU) (Castrillón-Cifuentes et al., 2015). When low salinity and sediment occur due to run-off, *Pocillopora* corals inhabiting the reef back exhibit reduced growth, calcification, and photosynthesis rates (Castrillón-cifuentes et al., 2023). Although there is no negative effect of runoff on survival (Castrillón-cifuentes et al., 2023), corals invest in mucus production and polyp activity to remove the sediments (Zambrano-Franco, 2011), and in cases of burial, *Pocillopora* colonies can tolerate up to 8 hours, beyond which time burial becomes lethal (Zambrano-Franco, 2016). Consequently, local stress factors significantly impact key traits for the persistence of *Pocillopora* corals at Gorgona, such as coral growth and photosynthesis, which is the primary nutritional source for any biological function (Stimson, 1997; Kopp et al., 2015). Understanding and managing the effects of run-off is essential for the long-term health and resilience of coral reefs on Gorgona Island.

The environmental conditions around Gorgona Island are largely influenced by the movement of the ITCZ (Giraldo et al., 2008), hence, changes in salinity and sediment levels are closely related to the rainfall patterns, which in turn, are modulated by ENSO events. Although, there is no consensus on how ENSO will respond to climate change, the projected changes in extreme ENSO events include significant increases in precipitation over the eastern equatorial Pacific, eastward propagation of warm sea surface temperature (SST) anomalies that characterize extreme El Niño events, and strong SST cooling over the central Pacific associated with extreme La Niña events (Cai et al., 2015, 2018). These changes in ENSO dynamics could have significant implications for the rainfall patterns, salinity, and sediment levels around Gorgona Island, ultimately affecting the local environmental conditions and potentially impacting the coral reef ecosystems in the area.

Under a scenario of increased precipitation and run-off, coupled with increased thermal stress and deoxygenation, it becomes crucial to take relevant actions for protecting the forest, particularly around the basins of the Patia and Sanquianga rivers. During La Niña events, the sediments from these rivers form a plume that reaches Gorgona Island and decreases water quality (Restrepo and D., 2003; Restrepo and Kettner, 2012; Restrepo and Cantera, 2013). Also, preserving the forest of Gorgona and mitigating sediment run-off can help to maintain the delicate balance of the marine ecosystem, supporting the health and resilience of the coral reefs surrounding the island (Fig 1).

Factors that contribute to *Pocillopora* reef resilience at Gorgona island

In Table 1, different environmental factors and biological aspects of *Pocillopora* corals are summarized according to their potential to affect the resistance of corals and influence the resilience of coral reefs on Gorgona island. As the reefs are exposed to different degrees of stressors, being greater from shore for the case of run-off, while increasing with depth for upwelling, contrary to the effect of extreme low tides, the identification of coral reef areas with low exposure and high resistance and resilience is a high management priority, such as the case of La Ventana reef, which is far from shore, not too shallow to be air-exposed during extreme low tides, or with great differences in depth between the reef flat and fore reef to suffer the influence of upwelling at the deepest parts of the reef (see Gómez-García et al., 2014 for the bathymetry of the coastal area adjacent to Gorgona island).

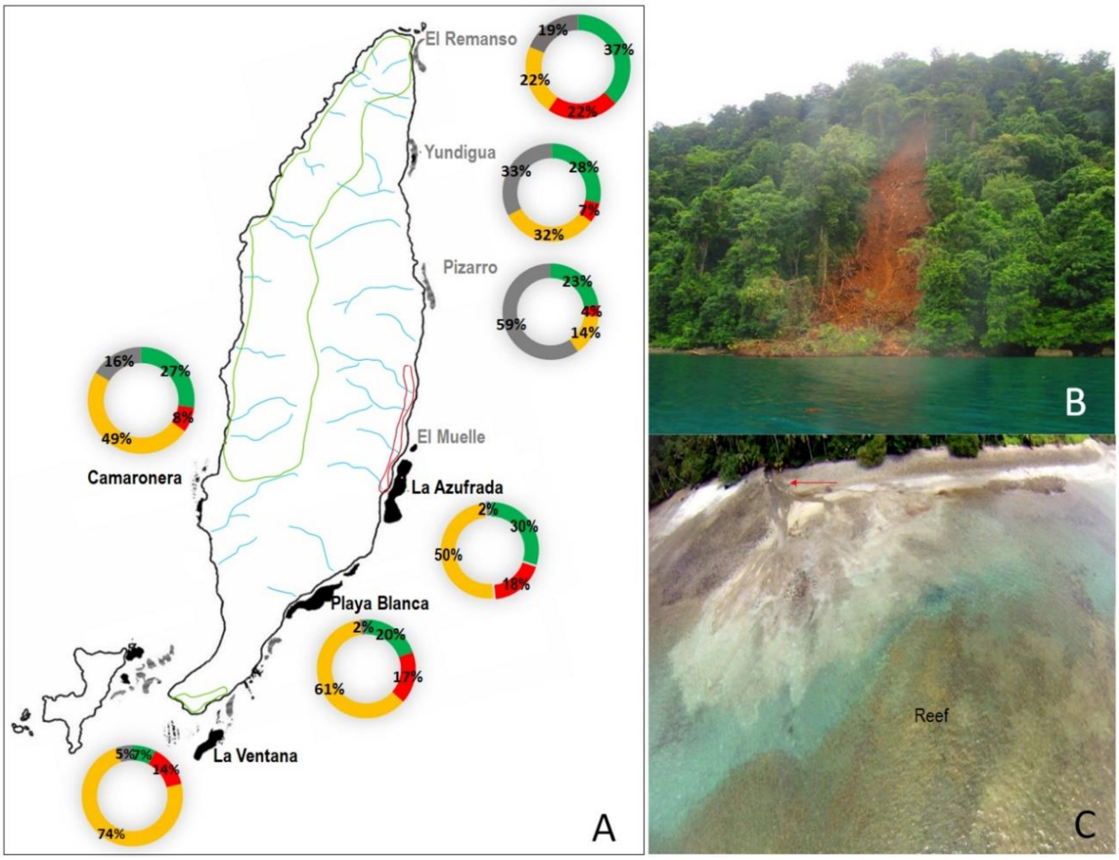

Figure 1. (A) Black areas denote the location of coral reefs (black font) and coral communities (gray font) around Gorgona island, blue lines shows to the location of permanent creeks, green areas the pristine forest, the red area denotes the zone commonly used by the inhabitants of the island, and the pie charts represent the percentage of benthic cover: in green turf algae, red for calcareous algae, yellow for scleractinian corals, and gray for inert substrate. Data for El Remanso, Yundigua and Pizarro where collected in July 2021 (photo quadrants), data of La Ventana and La Camaronera retrieved from Palacios and Zapata (2014), and La Azufrada from Zapata (2017). (B) landslides that occurs after heavy rains, and its sediments affects reefs. (C) aerial view of the influence of creeks (red arrow) on coral reefs (Photo taken by Carlos Muñoz-Bernal).

Table 1. Environmental and physiological factors that contribute (positive or negative) to coral resistance and reef resilience at Gorgona island.

Factor	Positive effect	Negative effect
Distance from creeks	-	The closer downstream a coral reef is to a creek, the greater is its exposure to sediments and low salinity.
Bathymetry	Shallow reef areas are less affected by turbidity than are at deep areas, where light becomes limiting factor for photosynthesis.	Low tides affect more the shallow reef areas. Deep reef areas are more exposed to upwelling.
Currents	Mid to high current velocity reduce the deposition of sediments on corals and enhance ventilation of coral polyps, which helps to increase photosynthesis.	High current velocity can break thin branches of corals and dislodge colonies from the substrate.
Clouds	Cloud cover can reduce the UV effects on shallow reef zones.	-
Turbidity	Turbidity at shallow reef zones protect corals from UV radiation.	Turbidity reduces light penetration at deep reef zones.
Upwelling	Cool, low oxygenated and nutrient rich conditions increase Symbiodiniacea density.	Cool conditions reduce the capacity of corals to tolerates hypoxia. Cool conditions reduce the translocation of glycerol from the Symbiodiniacea to the coral.
El Niño	During El Niño pluviosity is reduced, hence the negative effects of run-off on corals is reduced too.	Extreme temperatures during El Niño events can cause massive mortality of corals.
La Niña	-	Rain and wind intensification potentially decrease the performance of corals, due to increased run-off and upwelling events.
High salinity	Increase gamete production of corals	-
Warm conditions	Enhance metabolism of corals. Reduce the susceptibility to hypoxia of corals. Regulate Symbiodiniacea density within corals.	Extreme warm events produce bleaching and mortality.
Symbiodiniacea density	Is the main source of carbon for the metabolic functions of corals	Given that Pocillopora depends mainly on photosynthesis from de endosymbiotic algae, bleaching conduces to starvation, while increased density reduces algae photosynthetic efficiency.
Coral growth	the preference to maintain the colony structural integrity instead of investing on sexual reproduction favors fragmentation, hence coral coverage can fast recover after a disturbance, rather than if the process depends on sexual recruitment.	Reduced sexual reproduction could decrease the genetic diversity of the population, hence the resilience of the quasi mono-genera reefs could be compromised.

Conclusion

Through this research was intended to answer if environmental conditions were similar along coral reefs of Gorgona Island, and if so, how corals cope with ambient variability. There was also interest in clarify if corals that were frequently exposed to extreme natural conditions (like those of Gorgona island) were able to tolerate the effects of climate change, with special interest to know the effect of deoxygenation and thermal stress, conditions that regularly occurs during upwelling and ENSO events, and expected to intensify due to climate change. Moreover, to understand the effects of local stressors to modify micro-ambient conditions and how it influence the resistance and resilience capacity of corals and reefs. In Figure 2 was represented the major local and global stressors that influence the resistance and resilience response of corals and coral reefs of Gorgona island.

The results of this research evidenced that abiotic conditions on coral reefs of Gorgona island exhibited similar temporal variation, in which seasonality was influenced by the ITCZ and upwelling; however, some factors like temperature and salinity differ among reefs and had significant effect on coral physiology. For example, salinity was greater at reef zones and reefs far from shore, while temperature decrease with depth. Other factors such as dissolved oxygen concentration decrease during the upwelling and at the deepest zone for all reefs of the island. The major local stressor was run-off, and its effect variates according to the raining season and ENSO events and had a greater effect for corals on the back reef zone.

As the hypoxic threshold of *Pocillopora* corals coincides with the mean oxygen concentration reported during the upwelling season, ocean deoxygenation due to climate change was evidenced as a real threat for *Pocillopora* corals at Gorgona island. Also, if hypoxic events intensify because of eutrophication, *Pocillopora* corals will be severely impacted in their physiology, particularly depressing growth process. Preventing nutrient enrichment from run-off and sediment input from the Patía River is an important task for the reef management at Gorgona island. Future research should focus to understand how long corals can tolerate hypoxic conditions and it’s the long-term effects on the corals physiology, including other massive coral species.

Upwelling, although a natural event that expose coral to extreme ambient conditions, had negative effects on the physiology of *Pocillopora*, specifically the co-occurrence of cool thermal stress and hypoxia result in significant changes of coral growth, respiration, and Symbiodiniaceae density. It is possible that *Pocillopora* corals of Gorgona island rely on trade-offs to survive the stressful conditions during upwelling. Therefore, the occurrence of additional stressors or the intensification of upwelling due to climate change could be detrimental to this island's primary reef constructors.

Under warm conditions *Pocillopora* metabolism increase (increase growth and decrease hypoxia susceptibility), hence the physiological negative effects of upwelling were ameliorated, this may explain the resilience of corals during moderate El Niño events. Future research should assess for how long warming conditions are beneficial for corals, given that more intense El Niño events are predicted to occur as consequence of climate change.

Regarding micro-ambient conditions, exist a resistance capacity in *Pocillopora* corals that inhabit conditions not exposed to run-off (reef areas far from shore), because when moved to lest suitable environment (back reef) they can tolerate low salinity and sediments. Furthermore, resilience capacity was observed in corals from in-shore areas, because although these corals regularly experience adverse conditions, when the ambient conditions were improved (moved to reef areas far from shore) their physiological performance were improved. The existence of both resistance and resiliency capacity in *Pocillopora* corals reveals favorable attributes for the persistence of coral reefs at Gorgona Island.

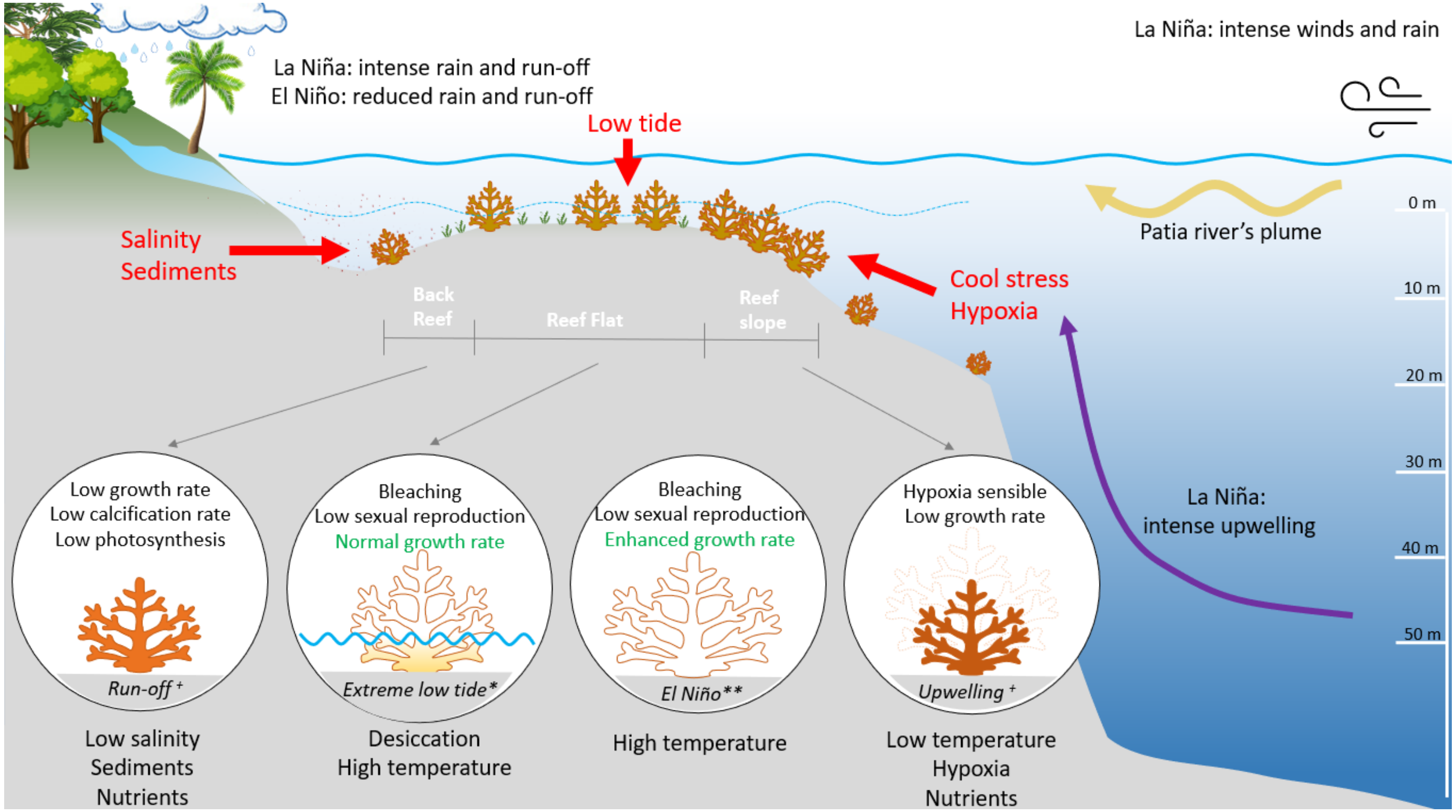

Figure 2. Schematic representation of the major stressors that influence the resistance and resilience response of corals and coral reefs of Gorgona island. The abundance of *Pocillopora* corals at each reef zone (Back reef, Reef flat, and reef slope) was illustrated with a variable quantity of branching corals, being scattered at the back reef, and down to 20 m (their deepest distribution). Red fonts and arrows indicate the factors that negatively affect each reef zone: low salinity and sediments on the back reef, low tide on reef flat, and cool stress and hypoxia during upwelling on the reef slope. The physiological response of *Pocillopora* corals to each stressor (run-off, extreme low tide, El Niño, and Upwelling) was indicated within circles, in black font are denoted the negative physiological effects, while in green positive physiological effects that aid reef resilience. Below each circle were described the specific abiotic factors that account for the stress conditions. Information was taken from: (+) this research, (*) Castrillón-Cifuentes et al., 2017, (**) Vargas-Ángel et al., 2001; and Castrillón-Cifuentes et al., 2015.

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Appendix

Supplementary material chapter 2

1. List of the technical reports assessed to extract dissolved oxygen conditions in reef of Gorgona island, Colombian Pacific.

Giraldo, A., B. Valencia, D. Ramírez, J. Jaramillo, D. Lozano. 2008. Condiciones oceanográficas durante noviembre 2008 en el PNN Gorgona. Informe técnico. Grupo de Investigación en Ecología de Arrecifes Coralinos. Facultad de Ciencias, Universidad del Valle.

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Giraldo, A. & Valencia B. 2013. Plancton y condiciones oceanográficas en el PNN Gorgona, Informe técnico de las campañas oceanográficas: septiembre de 2011, marzo de 2012 y septiembre de 2012. Grupo de Investigación en Ciencias Oceanográficas, Departamento de Biología, Facultad de Ciencias Naturales y Exactas, Universidad del Valle. A.A. 25360, Cali - Colombia. 18p.

Giraldo, A. & Valencia, B. 2013. Monitoreo del ambiente pelágico del PNN Gorgona: marzo 2013. Informe Técnico producto No. 8 del proyecto de investigación "Monitoreo de los valores objeto de conservación priorizados para las áreas protegidas Gorgona y Utría adscritas a la Dirección Territorial Pacífico". Universidad del Valle, Facultad de Ciencias Naturales y Exactas, Departamento de Biología. Grupo de Investigación en Ciencias Oceanográficas. Cali, Colombia. 15 p.

Valencia, B. & A. Giraldo. 2015. Condiciones oceanográficas en Isla Gorgona: relación entre los indicadores biológicos del ambiente pelágico (biomasa del zooplancton y larvas de peces) y las condiciones físico-quimicas de la columna de agua. Informe técnico. Grupo de Investigación en Ciencias Oceanográficas, Departamento de Biología, Facultad de Ciencias Naturales y Exactas, Universidad del Valle. Cali, Colombia. 37 p.

Rivera Gómez, M & A. Giraldo.2016. Monitoreo oceanográfico en el ecosistema pelágico del Parque Nacional Natural Gorgona, durante 2016 (Marzo y Septiembre). Universidad del Valle Facultad de Ciencias Departamento de Biología, Grupo de Investigación en Ciencias Oceanográficas. 10p

Rivera Gómez, M & A. Giraldo. 2018. Condiciones oceanográficas en el Parque Nacional Natural Gorgona, durante marzo y septiembre de 2017. Informe final Fundación Calima – Parque Nacional Natural Gorgona. 82p

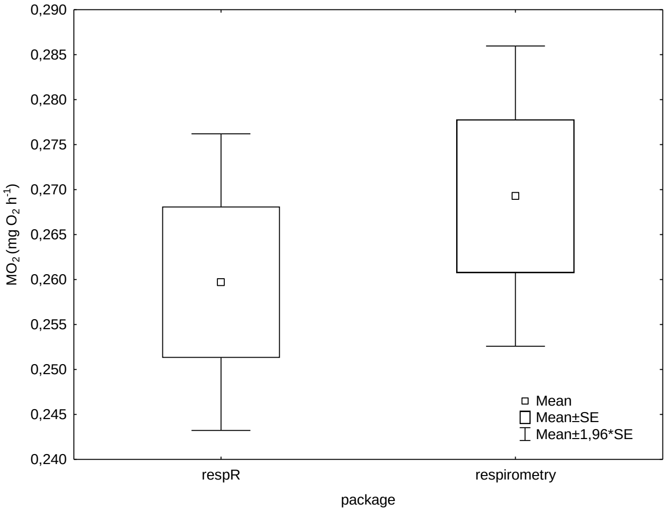
Giraldo, A., W. Bolívar-García y M. Rivera-Gómez. 2018. Resultado de monitoreo de ambiente pelágico, anfibios – reptiles y mamíferos en el PNN Gorgona durante 2018. Informe técnico final del Convenio de asociación no. 004 de 2018 suscrito entre Parques Nacionales Naturales De Colombia (Direccion Territorial Pacifico) y Fndación para la Investigación de la Biodiversidad y Conservación en el Trópico. Cali. 63p

Giraldo, A. & W. Bolívar-García. 2019. Resultado de monitoreo de ambiente pelágico y anfibios – reptiles en el PNN Gorgona durante 2019. Informe técnico final del Convenio de asociación no. 003 de 2018 suscrito entre Parques Nacionales Naturales De Colombia (Direccion Territorial Pacifico) y Fndación para la Investigación de la Biodiversidad y Conservación en el Trópico. Cali. 44 p.

2. Statistical analysis to set the differences in results obtained from the R packages respR and respirometry to calculate metabolic rate (MO$_2$) of *Pocillopora capitata*.

	N	*mean*	*SD*	t-value	*df*	*p*
respR	*7*	0.25	*0.02*	-0.79	*12*	*0.43*
Respirometry	*7*	0.26	*0.02*			

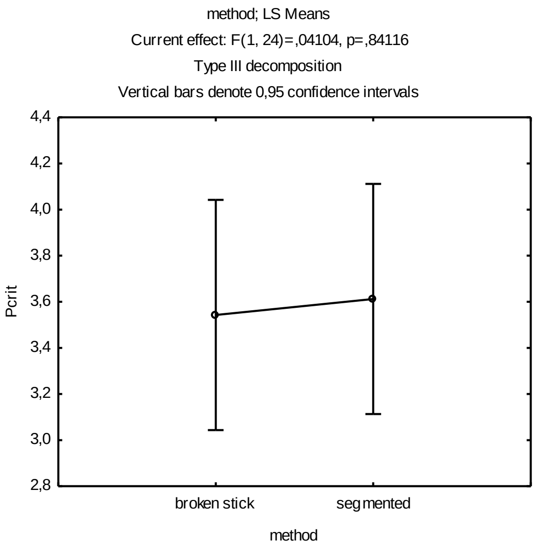
Normality of residuals: Kolmogorov-Smirnov test with Lilliefors correction, *D* = 0.21, *p* = 0.1

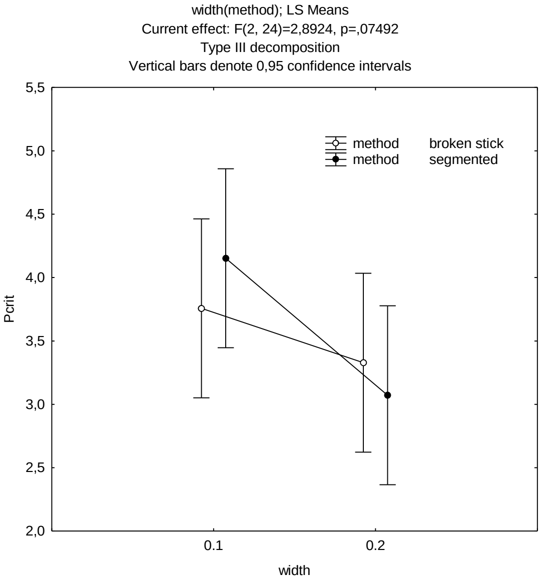


3. Statistical analysis (Nested Anova) to set the differences in results obtained from the respR package to calculate the critical oxygen tension (Pcrit) of *Pocillopora capitata*.

Effect	SS	df	MS	F	p
method	0.03	1	0.03	0.04	0.84
width(method)	4.73	2	2.36	2.89	0.07
Error	19.64	24	0.81		

Assumptions: homogeneity of variance [Cochran test, C = 0.3, *df* = 3, *p* = 0.6], normal distribution of residual [Kolmogorov-Smirnov test with Lilliefors correction, *D* = 1.19, *p* < 0.2]).





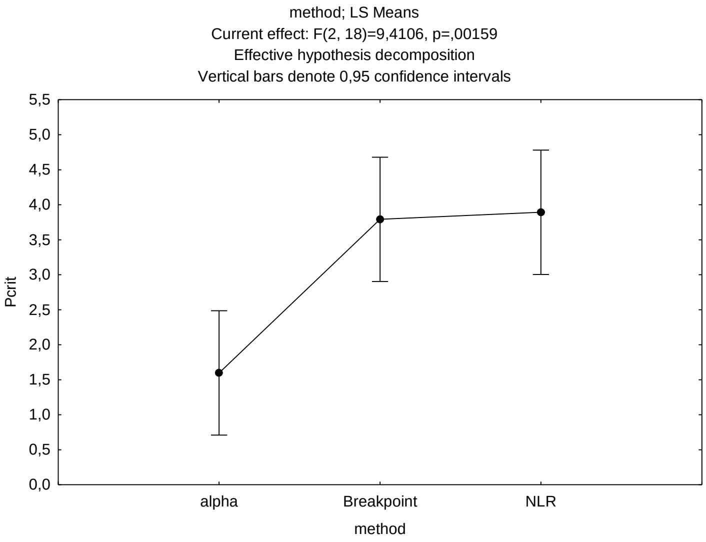
4. Statistical analysis (One-way Anova) to set the differences in results obtained from the respirometry package to calculate the critical oxygen tension (Pcrit) of *Pocillopora capitata*.

Effect	SS	df	MS	F	p
Intercept	201.02	1	201.0258	160.7783	0.000
method	23.53	2	11.7663	9.4106	0.001
Error	22.50	18	1.2503		

Assumptions: homogeneity of variance [Cochran test, C = 0.5, *df* = 2, *p* = 0.3]; normal distribution of residuals [*D* = 0.14, *p* > 0.2]

Cell No	method	1	2	3
1	alpha	-		
2	Breakpoint	0.004	-	
3	NLR	0.003	0.984	-

Tukey HSD test; Between MS = 1.25, df = 18

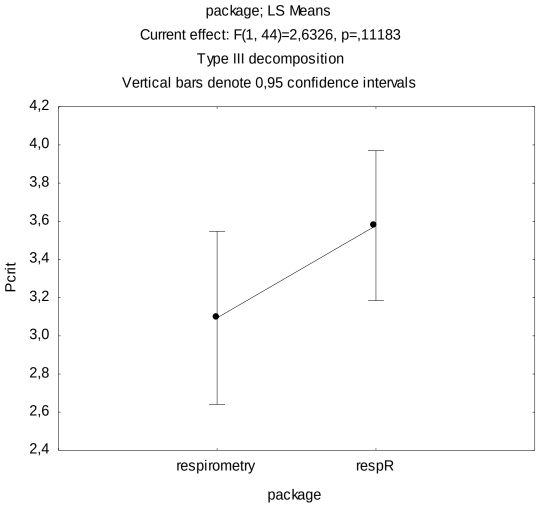


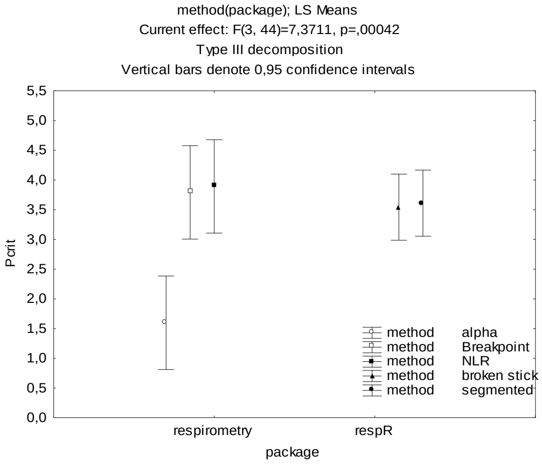
5. Statistical analysis (nested Anova) to set the differences in results obtained from the respirometry and respR packages (and the respective methods that each one employs) to calculate the critical oxygen tension (Pcrit) of *Pocillopora capitata*.

Effect	SS	df	MS	F	p
package	2.80	1	2.80	2.63	0.1118
method(package)	23.56	3	7.85	7.37	0.0004
Error	46.89	44	1.06		

Cell No	package	method	1	2	3	4	5
1	respirometry	alpha	-				
2	respirometry	Breakpoint	0.002	-			
3	respirometry	NLR	0.001	0.99	-		
4	respR	broken stick	0.001	0.98	0.94	-	
5	respR	segmented	0.001	0.99	0.97	0,99	

Tukey HSD test; Between MSE = 1.06, df = 44





5. Chlorophyll-a in reefs of Gorgona island during the upwelling and non-upwelling seasons.

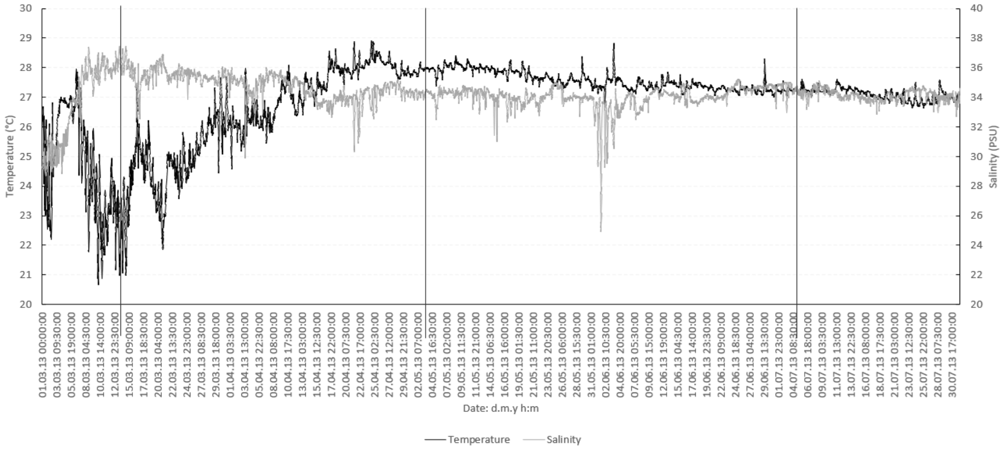
Reef	Chlorophyll a ($mg\ m^3$)	year	season	Technical report (supplementary material 1)
ventana	0.06	2009	Non-Upwelling	Giraldo 2010
playa blanca	0.12	2009	Non-Upwelling	Giraldo 2010
planchon	0.06	2009	Non-Upwelling	Giraldo 2010
remanso	0.18	2009	Non-Upwelling	Giraldo 2010
camaronera	0.06	2009	Non-Upwelling	Giraldo 2010
ventana	5	2012	Upwelling	Giraldo y Valencia 2013
playa blanca	3	2012	Upwelling	Giraldo y Valencia 2013
planchon	5	2012	Upwelling	Giraldo y Valencia 2013
remanso	4	2012	Upwelling	Giraldo y Valencia 2013
camaronera	3	2012	Upwelling	Giraldo y Valencia 2013
ventana	5	2012	Upwelling	Giraldo y Valencia 2013

playa blanca	4.5	2012	Upwelling	Giraldo y Valencia 2013
planchon	6	2012	Upwelling	Giraldo y Valencia 2013
remanso	5	2012	Upwelling	Giraldo y Valencia 2013
camaronera	5	2012	Upwelling	Giraldo y Valencia 2013
ventana	2	2012	Non-Upwelling	Giraldo y Valencia 2013
playa blanca	2	2012	Non-Upwelling	Giraldo y Valencia 2013
planchon	2	2012	Non-Upwelling	Giraldo y Valencia 2013
remanso	2	2012	Non-Upwelling	Giraldo y Valencia 2013
camaronera	3.5	2012	Non-Upwelling	Giraldo y Valencia 2013
ventana	2	2012	Non-Upwelling	Giraldo y Valencia 2013
playa blanca	2	2012	Non-Upwelling	Giraldo y Valencia 2013
planchon	2	2012	Non-Upwelling	Giraldo y Valencia 2013
remanso	3	2012	Non-Upwelling	Giraldo y Valencia 2013
camaronera	2	2012	Non-Upwelling	Giraldo y Valencia 2013
ventana	4.5	2017	Upwelling	Rivera-Gomez & Giraldo 2018
playa blanca	6.5	2017	Upwelling	Rivera-Gomez & Giraldo 2018
planchon	6.5	2017	Upwelling	Rivera-Gomez & Giraldo 2018
remanso	6.5	2017	Upwelling	Rivera-Gomez & Giraldo 2018
camaronera	4.5	2017	Upwelling	Rivera-Gomez & Giraldo 2018
ventana	6.5	2017	Upwelling	Rivera-Gomez & Giraldo 2018
playa blanca	7.5	2017	Upwelling	Rivera-Gomez & Giraldo 2018
planchon	6.5	2017	Upwelling	Rivera-Gomez & Giraldo 2018
remanso	6.5	2017	Upwelling	Rivera-Gomez & Giraldo 2018
camaronera	7.5	2017	Upwelling	Rivera-Gomez & Giraldo 2018
ventana	4.5	2017	Non-Upwelling	Rivera-Gomez & Giraldo 2018
playa blanca	4.5	2017	Non-Upwelling	Rivera-Gomez & Giraldo 2018
planchon	4.5	2017	Non-Upwelling	Rivera-Gomez & Giraldo 2018
remanso	6.5	2017	Non-Upwelling	Rivera-Gomez & Giraldo 2018
camaronera	6.5	2017	Non-Upwelling	Rivera-Gomez & Giraldo 2018
ventana	5.3	2017	Non-Upwelling	Rivera-Gomez & Giraldo 2018
playa blanca	5.3	2017	Non-Upwelling	Rivera-Gomez & Giraldo 2018
planchon	5.3	2017	Non-Upwelling	Rivera-Gomez & Giraldo 2018
remanso	5.3	2017	Non-Upwelling	Rivera-Gomez & Giraldo 2018
camaronera	5.3	2017	Non-Upwelling	Rivera-Gomez & Giraldo 2018
ventana	4.9	2018	Upwelling	Giraldo et al 2018
playa blanca	7.7	2018	Upwelling	Giraldo et al 2018
planchon	7.7	2018	Upwelling	Giraldo et al 2018
remanso	6.1	2018	Upwelling	Giraldo et al 2018
camaronera	3.7	2018	Upwelling	Giraldo et al 2018
ventana	5.7	2018	Upwelling	Giraldo et al 2018
playa blanca	7.7	2018	Upwelling	Giraldo et al 2018
planchon	7.7	2018	Upwelling	Giraldo et al 2018
remanso	7.7	2018	Upwelling	Giraldo et al 2018
camaronera	5.7	2018	Upwelling	Giraldo et al 2018
ventana	3.7	2018	Non-Upwelling	Giraldo et al 2018
playa blanca	2.5	2018	Non-Upwelling	Giraldo et al 2018

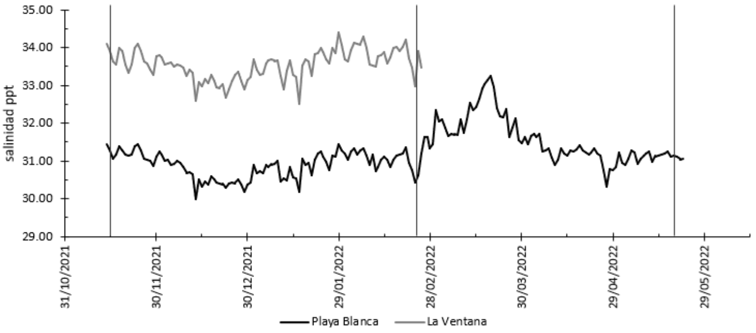
planchon	3.7	2018	Non-Upwelling	Giraldo et al 2018
remanso	3.7	2018	Non-Upwelling	Giraldo et al 2018
camaronera	3.7	2018	Non-Upwelling	Giraldo et al 2018
camaronera	3.7	2018	Non-Upwelling	Giraldo et al 2018
ventana	4.9	2018	Non-Upwelling	Giraldo et al 2018
playa blanca	3.7	2018	Non-Upwelling	Giraldo et al 2018
planchon	4.9	2018	Non-Upwelling	Giraldo et al 2018
remanso	3.7	2018	Non-Upwelling	Giraldo et al 2018

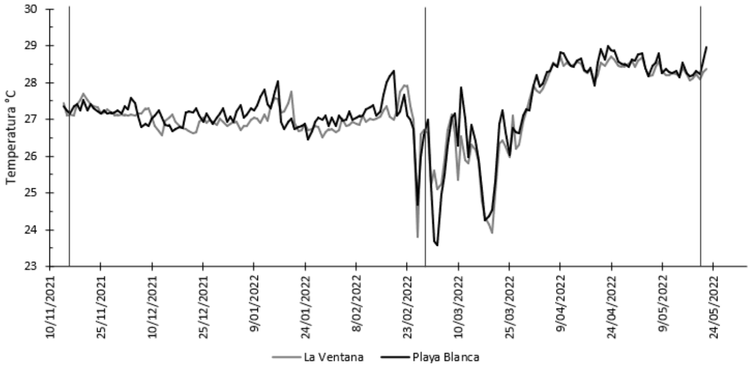
Supplementary material chapter 3

1.Temperature and salinity at La Azufrada reef between March 1 and July 31, 2013. The vertical lines denote the time at which tissue (for zooxanthellae density) and photos (for growth and luminosity) were taken from *Pocillopora* colonies.

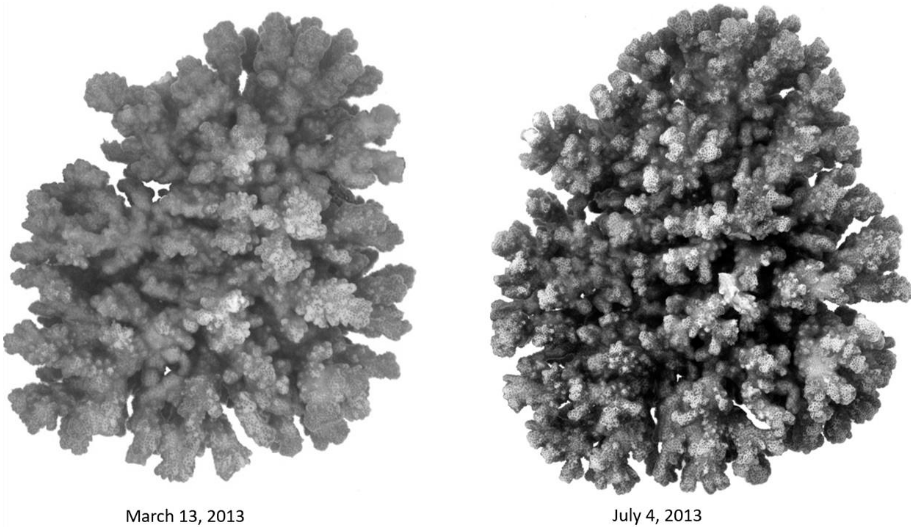


2. Temperature and salinity were recorded with dataloggers at Playa Blanca and La Ventana reefs between November 14, 2021, and May 22, 2022. The vertical lines denote the time at which photos (for growth and luminosity) were taken for *Pocillopora* coral fragments.



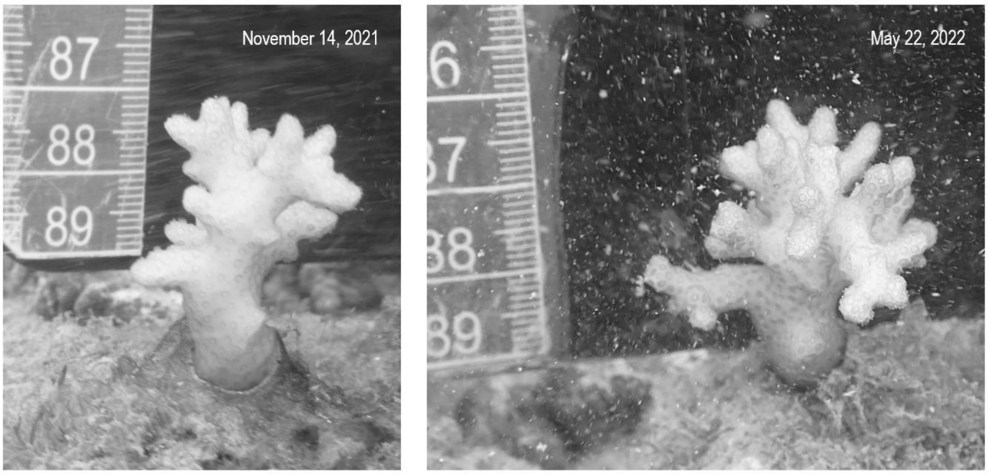


3.1. *Pocillopora* colony from La Azufrada, employed for growing measurements.

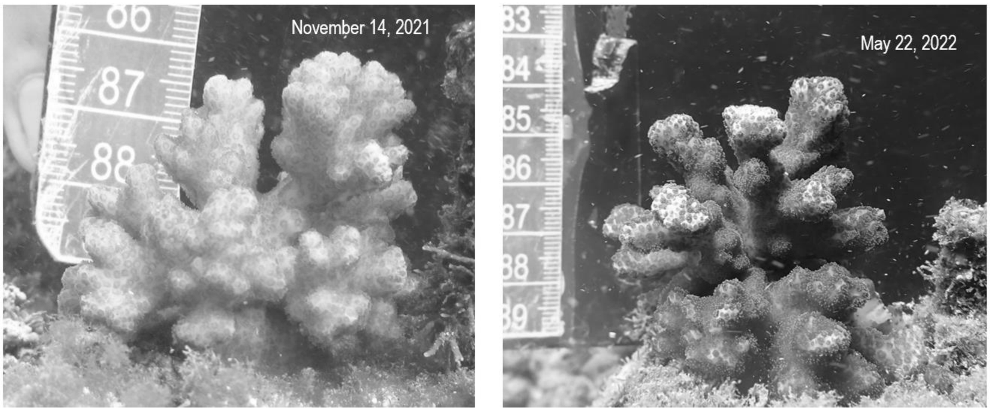

March 13, 2013

July 4, 2013

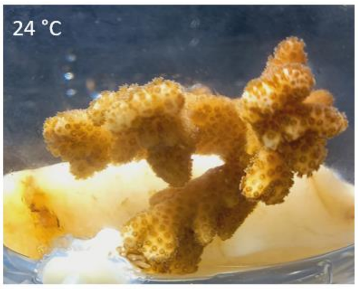
3.2. Pocillopora fragment from Playa Blanca reef, employed for growing measurements.

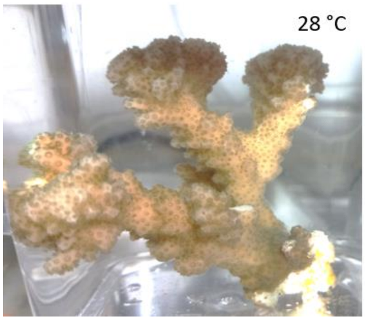


3.3. Pocillopora fragment from La Ventana reef, employed for growing measurements



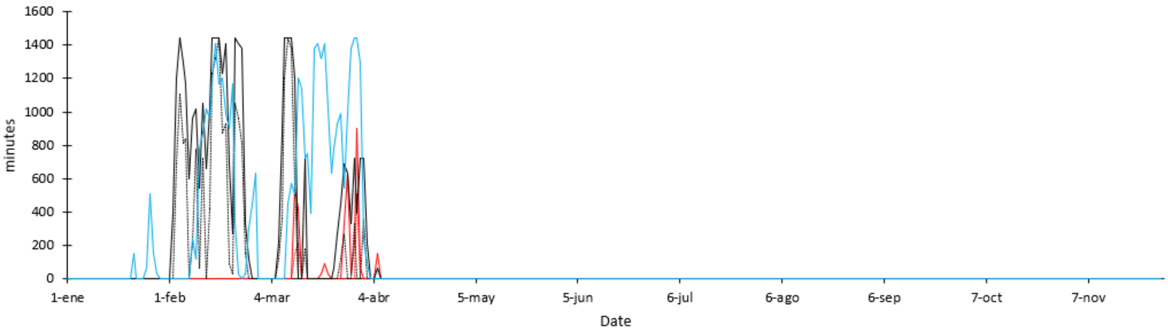
3.4. *Pocillopora* fragments from La Azufrada reef, employed for metabolic measurements



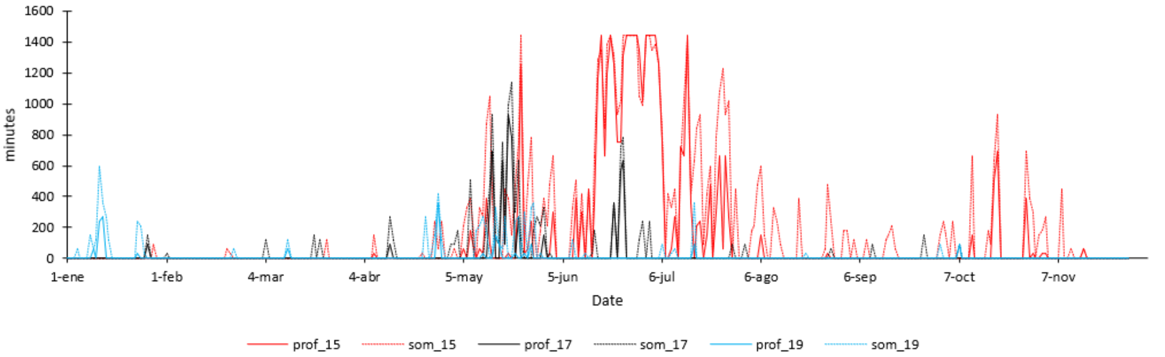


4. Occurrence of *Cool* (A) and *Warm* (B) thermal stress on La Azufrada coral reef (Gorgona Island, Colombian Pacific). The red lines correspond to data from 2015, black to 2017, and blue to 2919. Solid lines represent data collected at 1 m depth, and dashed lines at 5 m depth

(A) Cool events (°C < 24)



(B) Warm events (°C > 29)



Supplementary material chapter 4

1. Tests for homogeneity of variances and normality of residuals for the physiological variables measured in Pocillopora, and the environmental factors measured at Playa Blanca and La Ventana reefs

Factor	**Test for homogeneity of variances**	**Test for normality residuals**
Survival	Levene's test: F = 0.39, p = 0.75	Shapiro-Wilk's test: w = 0.94, p = 0.06
Growth rate	Levene's test: F = 2. 41, p = 0.08	Shapiro-Wilk's test: w = 0.94, p = 0.06
Skeletal density	Levene's test: F = 0.68, p = 0.57	Kolmogorov-Smirnov's test: d = 0.17, p > 0.20
Calcification	Levene's test: F = 1.17, p = 0.34	Shapiro-Wilk's test: w = 0.96, p = 0.50
Respiration rate	Levene's test: F = 0.23, p = 0.62	Kolmogorov-Smirnov's test: d = 0.16, p > 0.20
Gross photosynthesis	Levene's test: F = 1.13, p = 0.35	Kolmogorov-Smirnov's test: d = 0.15, p > 0.20
Crustose coralline algae	Mauchley sphericity test: W = 0.74, p = 0.07	
Turf algae	Mauchley sphericity test: W = 0.88, p = 0.64	
Sediments	Mauchley sphericity test: W = 0.90, p = 0.78	

2. Formula applied during the Box-cox transformation: the following equation was applied to standardize and normalize respiration rate and gross photosynthesis data.

$$\frac{(x^{0.08}) - 1}{0.08}$$

3. Abiotic conditions at Playa Blanca and La Ventana reefs

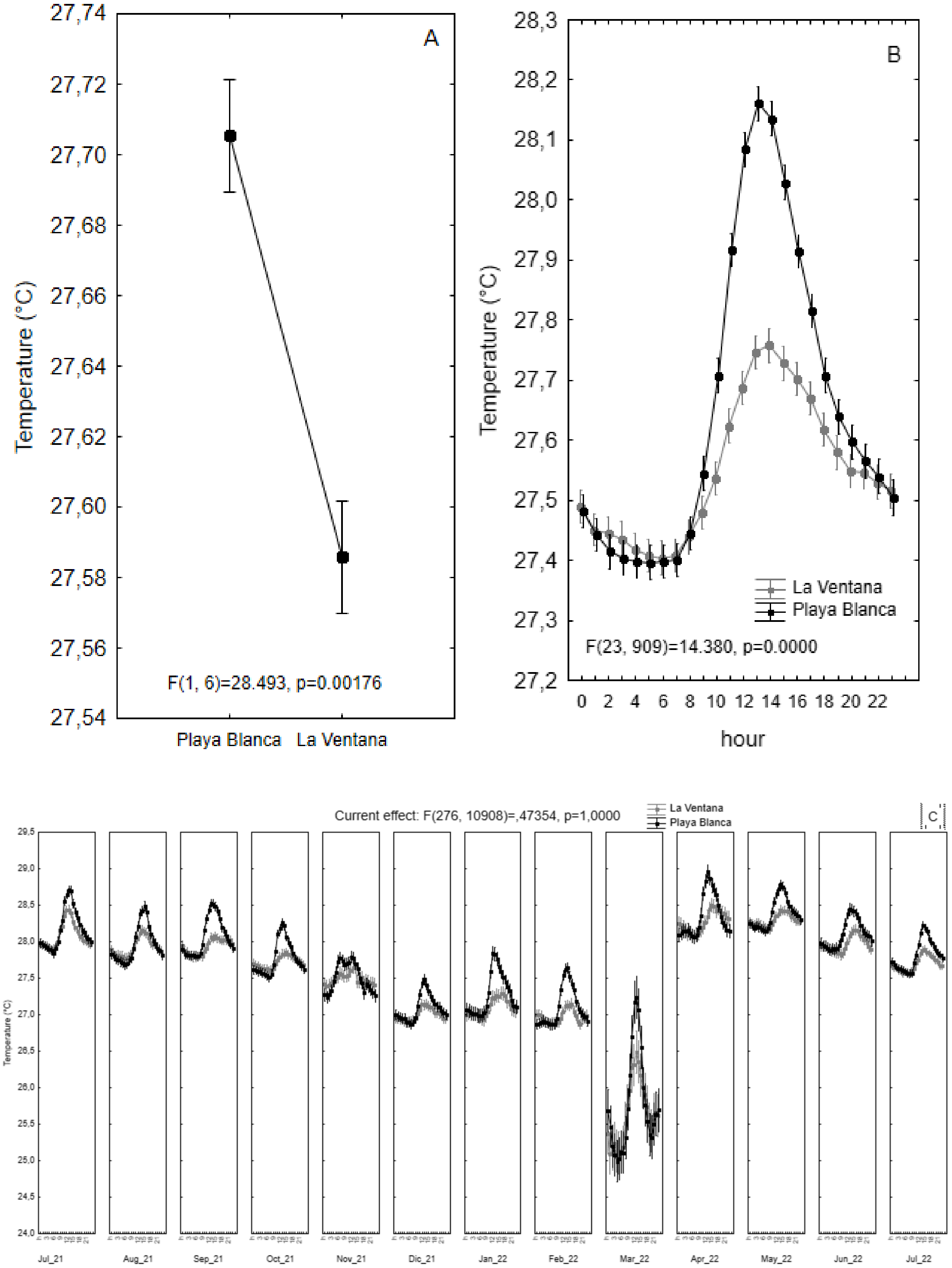


Fig 1. Variability of temperature (Mean ± SD). (A) Differences between reefs. (B) hourly differences in temperature by reef. (C) hourly differences in temperature by reef from July 2021 to July 2022. Colors represent data from Playa Blanca (●) and La Ventana coral reefs (●).

Table 1. Number of days per month that corals face cool and warm conditions at Playa Blanca and La Ventana coral reef. Cool conditions were defined as the occurrence of temperatures < annual mean - 1SD. Similarly warm conditions were defined as any temperature > annual mean + 1SD. The annual temperature at Playa Blanca reef was 27.70 ± 0.72 °C, and at La Ventana was 27.58 ± 0.69 °C.

	Cool		Warm	
Date	Playa Blanca	La Ventana	Playa Blanca	La Ventana
Jul-21	0	0	5	3
Aug-21	0	0	1	1
Sep-21	0	0	1	0
Oct-21	0	0	0	0
Nov-21	0	0	0	0
Dec-21	10	10	0	0
Jan-22	13	13	0	0
Feb-22	7	9	0	0
Mar-22	22	26	0	0
Apr-22	0	0	20	22
May-22	0	0	11	12
Jun-22	0	0	6	1
Jul-22	0	0	0	0
Aug-22	0	0	0	0
Sep-22	0	0	0	2
Oct-22	0	0	0	0
Nov-22	2	2	0	0
Total days	54	61	44	41

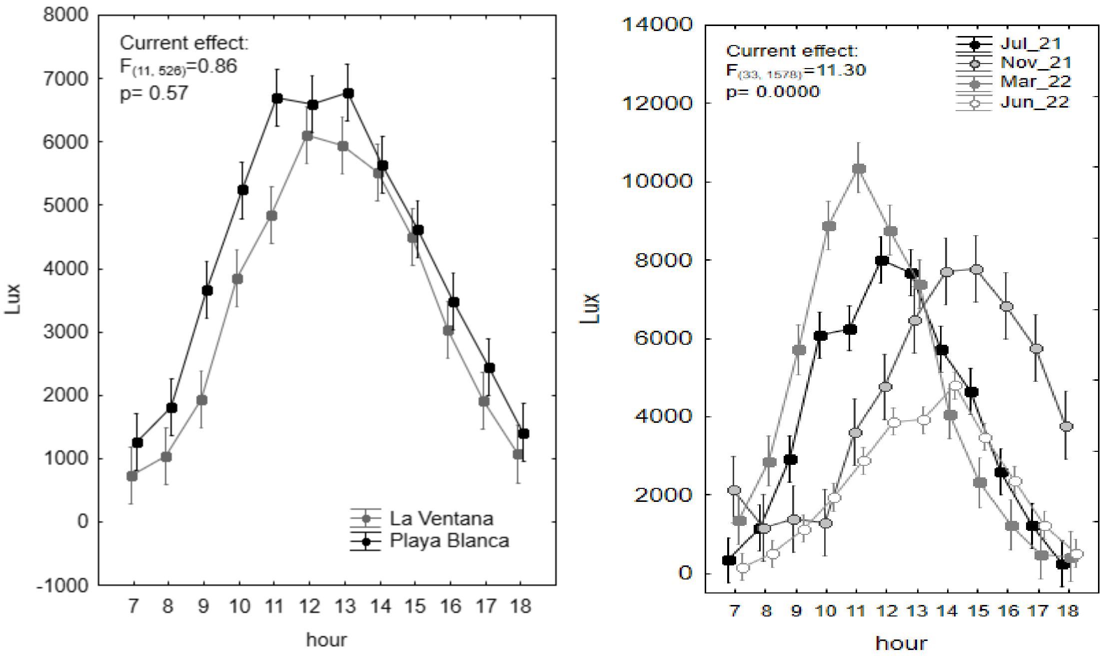


Fig 2. (left) Dial variation of light conditions (lux; mean ± SE) at Playa Blanca (●) and La Ventana coral reefs (●). (Right) Monthly variation of light conditions (lux; mean ± SE).

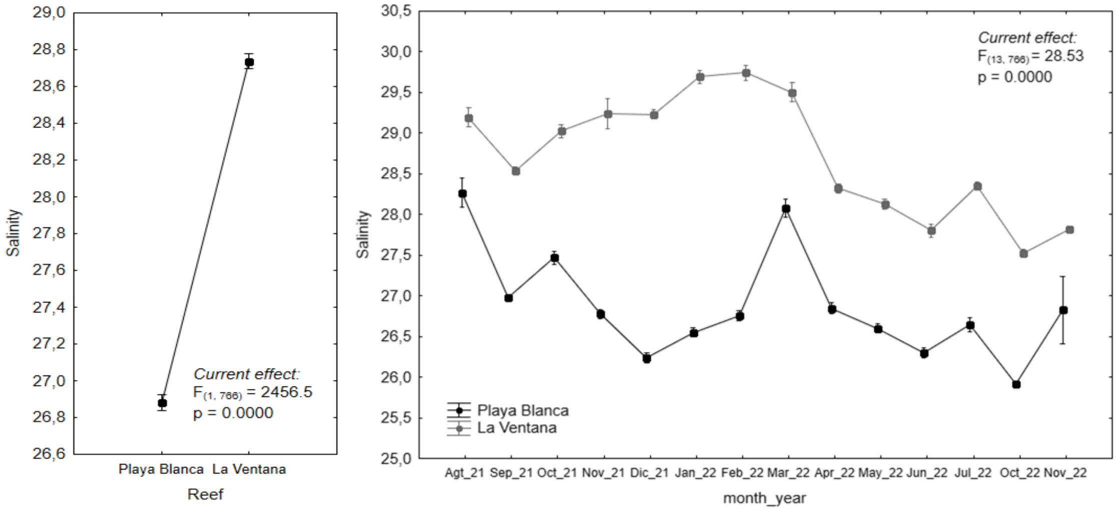
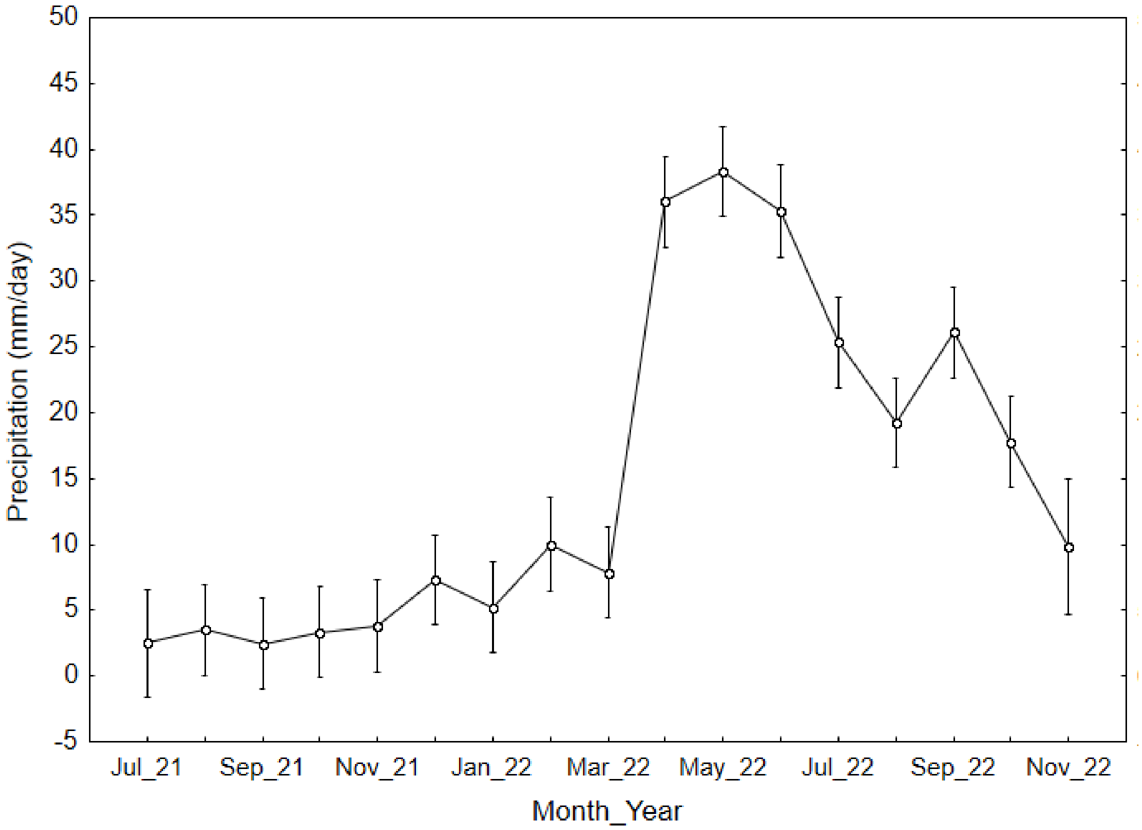


Fig 3. (left) Reef differences in salinity conditions (psu; mean ± SD), and its monthly variations discriminated by reef: Playa Blanca (●), La Ventana coral reefs (●).

4. Monthly precipitation (mean ± SD) at Gorgona Island (mm day^{-1})



5. Principal Components Analysis to relate algae coverage (Crustose Coralline Algae and Turf algae) and abiotic conditions at La Ventana and Playa Blanca reefs.

Table 1. Eigenvalues of the correlation matrix

	Eigenvalue	% Total variance	Cumulative Eigenvalue	Cumulative %
PCA 1	1,10	55,21	1,10	55,21
PCA 2	0,89	44,78	2,00	100,00

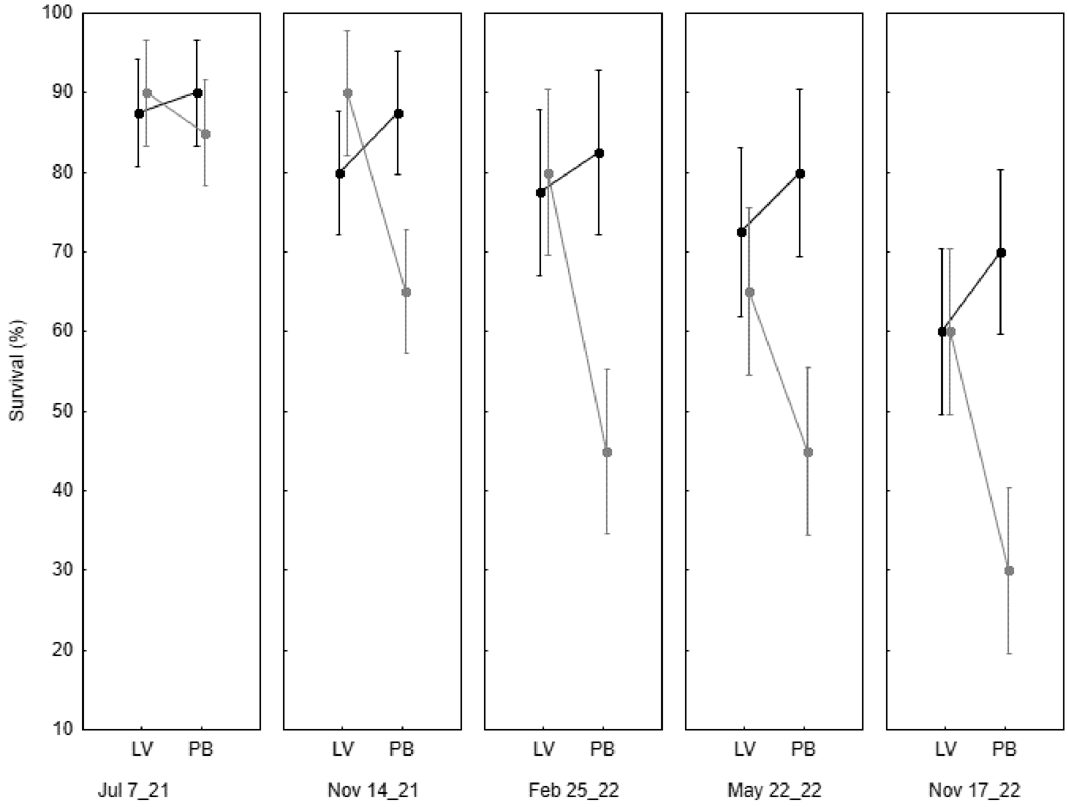
Table 2. Principal Components, based on correlations for Active (Act) and Supplementary (Sup) variables.

Variable		PCA 1	PCA 2
Act	CCA	0,74	0,66
Act	Turf algae	0,74	-0,66
Sup	Temperature	0,16	-0,38
Sup	Salinity	0,41	0,76
Sup	Light	-0,24	0,41
Sup	Sediments	-0,87	-0,46

Table 3. Correlations between Active and Supplementary variables

	CCA	Turf algae	Temperature	Salinity	Light	Sediments
CCA						
Turf algae	0,10					
Temperature	-0,13	0,38				
Salinity	0,82	-0,20	-0,10			
Light	0,09	-0,46	-0,43	-0,007		
Sediments	-0,96	-0,33	-0,04	-0,72	0,02	

6. Survival over time of the transplanted and control corals between Playa Blanca (PB) and La Ventana (LV) reefs. Data shows the mean ± SD. In black control corals, and in gray the transplanted corals.



Versicherung an Eides Statt

Ich, Ana Lucia Castrillon Cifuentes, San Andres Island Colombia, matrikelnummer 6171503

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San Andres Island, August 28 2023

Ort, Datum

Unterschrift

AFFIDAVIT (Translation)

I, the undersigned Ana Lucia Castrillon Cifuentes, San Andres Island Colombia, student number 6171503

hereby affirm in lieu of oath that the present dissertation is my own work and that I have duly referenced all passages cited from publications, either literally or in content, and that I have not used any literature or aides other than those referenced.

I hereby affirm that to the best of my knowledge and belief, all the information I have supplied is true and that I have not failed to disclose any relevant facts

.

I am aware that making false statements in lieu of oath is an offense that, in the event of intention, pursuant to § 156 StGB may be punished by fine or up to three years' imprisonment and, if committed by negligence, pursuant to § 161 Abs. 1 StGB by fine or up to one year's imprisonment.

(Signature of applicant)