Sánchez *et al. Discover Conservation* (2025) 2:23
https://doi.org/10.1007/s44353-025-00044-0

Discover Conservation

REVIEW
Open Access

Tropical reefs in the aftermath of climate change

Juan Armando Sánchez[1*], Amalia Murgueitio[1], Catalina Rivera-Forero[1], Dairo H. Marín-Casas[1,2] and Carlos E. Gómez[1]

*Correspondence:
Juan Armando Sánchez
juansanc@uniandes.edu.co
[1] Laboratorio de Biología Molecular Marina (BIOMMAR), Departamento de Ciencias Biológicas, Facultad de Ciencias, Universidad de Los Andes, Bogotá, Colombia
[2] Grupo de investigación Biología Evolutiva, Departamento de Biología y Química, Facultad de Educación y Ciencias, Universidad de Sucre, Sincelejo, Colombia

Abstract
As an era of significant environmental and societal transformations, forecasting the future entails considerable uncertainty. This article gives a perspective on calcifying organisms capable of adapting to a warmer and more acidic ocean, which may also contribute to future reef construction. While it is challenging to conceive, we cannot rule out a transformation of reef ecosystems, possibly characterized by increase in octocorals, a greater presence of giant clams, and a greater ecological prominence of coralline algae along with their rhodoliths. In the Caribbean Sea, reefs will possibly no longer be dominated by the extensive *Acropora* communities that characterized their preindustrial zenith. Instead, there may be a shift towards ecosystems composed of dense octocoral communities and mesophotic assemblages where scleractinian corals with symbionts adapted to low-light environments are more likely to persist. Rehabilitation in shallow waters can take advantage of coralline algae and coastal reef systems close to seagrass and mangrove ecosystems can improve coral health. Although these changes may seem unsatisfactory, essential ecological services could persist, including habitat provision for many species, spaces for human recreation, and, significantly, a notable contribution to global carbonate cycles. It is crucial to highlight that any human effort to prevent biodiversity loss is both praiseworthy and equitable, as the decline in biodiversity due to climate change is a collective obligation of humanity.

Keywords Reef-building shifts, Future reefs, Octocorals, Calcifying bacteria, Endolithic algae (*Ostreobium*), Mesophotic reefs, Crustose coralline algae

1 Introduction

Coral reefs are among the world's most biodiverse ecosystems and are vital to human well-being, providing ecosystem services such as food security, coastal protection, bioactive compounds, and support tourism [1–4]. Aesthetically, coral reefs are unparalleled in the marine environment (Fig. 1). Unfortunately, they face multi-dimensional anthropogenic threats from both local and global pressures. Local threats may originate on land (e.g., declining water quality due to nutrient inputs, pollutants, plastic debris and sediment accumulation) or from the sea (e.g., habitat destruction, overexploitation, and the introduction of potentially invasive species); they may arise from the spread of infectious diseases, or they may be associated with global environmental change, such as

Fig. 1 Reef-building corals (Scleractinia: Anthozoa: Cnidaria) comprising various species of *Acropora*, along the coast of Dahab, Egypt, Red Sea (Image: Juan A. Sánchez)

ocean warming, acidification, rising sea levels, increased stratification and altered circulation patterns [4–7]. Collectively, these threats paint an alarming picture of how these irreplaceable ecosystems may change over the course of the century [2, 8].

Currently, atmospheric carbon dioxide (CO_2) levels and global temperatures exceed those recorded over the past 420,000 years [8]. As of February 2025, atmospheric CO_2 concentrations have reached approximately 427 ppm, surpassing levels from the last 800,000 years and increasing at an unprecedented rate [9–11]. Likewise, carbonate ion concentrations (~ 210 µmol kg^{-1}) are now at their lowest levels in 420,000 years. Since the beginning of the industrial era, seawater has also become more acidic (-0.1 pH units) and sea temperature has risen (0.7 °C), accompanied by an increase in the frequency and intensity of marine heatwaves over the past century [8, 12–14]. Under these novel circumstances, population-level shifts are occurring in marine ecosystems due to physiological intolerance to new environmental conditions. Additionally, altered dispersal patterns and interactions among species are being documented globally, leading to major shifts in community structure and diversity [15, 16].

Given the magnitude of the coral reef crisis, researchers have increasingly sought to predict the future of these ecosystems. Changes in community composition are anticipated, potentially favoring thermally resilient species or those with high recruitment rates [17–21]. The possibility of species shifting poleward, leading to a bimodal distribution in species richness around the equator, has also been discussed [22, 23]. However, reefs in regions with favorable environmental conditions or high inherent resilience —termed coral reef refugia— may respond differently [21, 24–26]. Reefs that naturally experience extreme physicochemical conditions have been identified as key systems for improving ecosystem-scale predictions of future reef dynamics [27]. Additionally, various stressors, including the loss of herbivores and eutrophication, may trigger coral-algal phase shifts in benthic dominance [28]. Shifts in community composition may also diverge from the typical coral-macroalgae transitions, resulting in alternative benthic communities dominated by sponges, corallimorpharians, or soft corals [29–31].

Who will build tropical reefs in the aftermath of climate change and ocean acidification? This review investigates the potential repercussions of coral reefs undergoing significant alterations due to the decline of stony corals while remain as ecosystems. As scleractinian-dominated reefs face mounting threats, this review explores the potential of alternative calcifiers that may emerge as key architects of future tropical reefs. As researchers from the Global South, drawing primarily from our experience in the Southern Caribbean and Tropical Eastern Pacific, we emphasize the critical importance of incorporating alternative perspectives to develop a more comprehensive understanding of the coral reef crisis. Here, we offer a perspective shaped by geographic and ecological contexts distinct from the predominant reef models in most studies, which we hope will contribute to a more diverse understanding of coral reef futures.

2 What is the extent of the crisis?

Coral reefs are among the most endangered environments on the planet. The immediate impacts of elevated temperatures on corals have been well-documented since the 1980s [2]. The structural integrity of coral reef ecosystems relies on the deposition of calcium carbonate ($CaCO_3$) by corals (Fig. 1), a process facilitated by their mutualistic endosymbionts —photosynthetic dinoflagellates from the family *Symbiodiniaceae*, previously known as zooxanthellae— [32]. Coral bleaching occurs when disruptions in the symbiont's photosynthesis lead to the production of reactive oxygen species (ROS), triggering the expulsion of dinoflagellates. This process often causes cellular damage in both the host and the symbiont. A temperature increase of just 1 °C above the maximum average can induce bleaching [8, 33]. However, bleaching can also be triggered by factors other than temperature, such as an increase of radiation, resulting from diminished cloud cover or a calm sea surface [34]. Coral bleaching may occasionally correlate with dysbiosis —a disruption in the composition or function of microbial communities—, which can alter coral health and resilience. Additionally, some bleaching events have been linked to microbial infections targeting Symbiodiniaceae algae [35, 36]. At the colony level, moderate bleaching is a form of stress that reduces growth rate, while intense and prolonged bleaching may lead to coral death. A higher susceptibility of corals to disease may also be associated with bleaching events [36]. The combination of bleaching and disease may have devastating effects on living corals at a large spatial scale [37]. Since the 1980s, four global bleaching events have been recorded, all linked to thermal stress [38]. The fourth global bleaching event has been the most destructive to date. This event began in the Caribbean during the boreal summer and extended into the austral summer of 2023–2024, with severe bleaching and mortality reported across Latin America, the Caribbean, and certain Pacific Islands [39–41].

The ability of corals to build massive complex structures is vulnerable to mild shifts in pH and temperature [7, 42]. For corals and other calcifying organisms, ocean acidification makes the process of secreting and maintaining a skeleton more difficult [13]. Current massive losses of coral cover indicate corals will be particularly vulnerable to future ocean warming and acidification [6]. Also, acidifying waters jeopardize the ability of young recruits to achieve the levels of calcifying fluid supersaturation needed to support rapid growth [43] and for adults, growth rates might be reduced, and coral skeletons may become less dense, increasing the likeliness of damage during storms [7].

Populations of several reef-building species are expected to decline [7]. This in turn will have a negative impact in fish assemblages, including declines of diversity and abundance [44]. In fact, it has been suggested that fish biodiversity is threatened by reef degradation associated with climate change and the creation marine reserves is not enough to secure their survival [45]. Invertebrates will also be threatened by the loss of coral cover. Since coral traits are related to the diversity of reef-associated invertebrates, progressive decline of coral habitat is expected to lead to losses in invertebrate diversity [46].

The degradation of coral reef habitats compromises important ecosystem services for coastal communities including fisheries provision. The decline in fish populations directly threatens the livelihoods of millions of people who already depend on reef fishing highlighting the socioeconomic consequences of coral loss [47, 48]. Low-income countries highly dependent on tourism might face severe consequences with a shift away from coral-dominated reefs since this will alter the perceived attractiveness of these ecosystems for tourists [49]. Even in high income countries such as Australia and the United States, coral reef degradation will impact the tourism industry [50]. Coastal protection provided by barrier reefs will also be in jeopardy, leaving coastal communities and ecosystems such as mangroves, saltmarshes and seagrass meadows more vulnerable to the impact of storms and hurricanes [51]. This is especially worrying under a scenario of increasingly severe hurricanes and cyclones in the tropics [52]. The combined effect of sea level rise, the loss of beach sand attributed to storms and hurricanes together with the loss of sand production linked to coral reefs will lead to less stable beach ecosystems. This will likely have an important impact on the subsistence of coastal communities, fishing activities and tourism [8, 50]. Thus, the ecosystem services we receive from coral reefs are rapidly declining, threatening the sustainability of millions of people who directly benefit from these fragile ecosystems [53].

Addressing the coral reef crisis, characterized by substantial decline since the 1950s, requires a major undertaking. This damage makes it unlikely that reefs will return to their pristine state, as documented initially by coral reef scientists [54]. Numerous coral reefs currently exhibit diminished ecosystem integrity, since major predators, like groupers and sharks, have vanished from their habitats [47]. Moreover, herbivorous fish, including parrotfish, have been substantially depleted, primarily as a result of overfishing in recent decades [55]. In the absence of parrotfish, the main herbivores on the reef, rapidly proliferating algae directly compete with corals [47]. The accumulation of sediments and nutrients, such as nitrogen and phosphorus, from rivers in coastal areas facilitates macroalgal proliferation, which monopolizes the space vacated by corals as they gradually perish following coral bleaching events [56]. The transformation of the ecosystem is evidenced by a nutrient imbalance, characterized by an accumulation of phosphorus, now sequestered by algae, and an overabundance of labile dissolved organic carbon, abundant in polysaccharides [57].

3 What if scleractinian corals are unable to endure?

First, we must consider that within the vast diversity of scleractinian corals, some species may not be able to cope with the accelerating rise in temperature and ocean acidification. One-third of zooxanthellate reef-building corals are classified as being at high risk of extinction [58]. Among the species listed on the International Union for Conservation of Nature (IUCN) Red List, the acroporids *Acropora cervicornis* and *A. palmata* were once major reef builders in the Caribbean. However, drastic population declines have left them critically endangered, rendering them unable to fulfill their historical ecological role. In the Rosario Islands (Cartagena, Colombia), an eleven-kilometer fringing reef once featured a broad expanse of these corals near the reef front [59]. In recent years, brain corals from the family Meandrinidae, including notable species such as the cathedral coral (*Dendrogyra cylindrus*), have been particularly vulnerable to stony coral tissue loss disease (SCTLD). This disease originated in the Florida Keys and has progressively spread throughout the Caribbean [60]. *D. cylindrus* has already vanished from the Florida coral tract, and its current status remains uncertain. Given these trends, the extinction of some hard coral species in the coming years would not be unexpected.

3.1 Could certain scleractinian corals flourish on future Caribbean reefs?

Identifying resilient corals capable of enduring fluctuating conditions can be achieved by observing them in ecologically stressed environments [27]. Coral reefs in the Colombian Caribbean are exposed to effluents from major rivers, such the Magdalena, Sinú, and Atrato [61]. While excessive sedimentation and increased nutrient levels typically considered limiting factors for coral growth, robust coral reefs exist in these conditions [62]. The genus *Agaricia* (formerly *Undaria*) comprises brooding scleractinian corals present in ten ecoregions from the Caribbean and the Atlantic [63]). With seven species, it stands out amongst the limited scleractinian diversity of the Caribbean Sea. The lettuce coral *Agaricia tenuifolia* appears to thrive in reefs with significant continental influence, adapting to sedimentation by developing a honeycomb structure with vertical ridges that help mitigate sediment suffocation [64]. The distribution of *A. tenuifolia* is erratic within the Caribbean, ranging from Colombia to Belize, but being absent in the Antilles, Bahamas, and Florida. Scientists working in Belize and Panama previously noted its substantial proliferation, proposing that it was a “weed-like” opportunistic coral that expanded rapidly following *Acropora* mortality [65]. However, while its environmental preferences overlap somewhat with those of Caribbean *Acropora* species, they do not completely coincide. In regions where elkhorn corals cannot persist, the lettuce coral is among the few that thrive. Moreover, numerous animals and algae are associated with the microhabitats created by their skeletons [66]. While the resilience of this coral may make it a potential “winner” in future Caribbean reefs, it is important to note that widespread bleaching in this species has been noted, as it primarily inhabits shallow reef zones (0–10 m), where bleaching is often severe [36, 67]. In the future, the most persistent agariciids may be those found in mesophotic environments.

Another aspect of the remarkable ecological flexibility of *Agaricia* is the ability of some of its species to colonize the mesophotic zone [68]. Commonly referred to as the twilight zone, or mesophotic coral ecosystems, this region receives less than 1% of the solar radiation that penetrates the ocean surface and harbors certain reef-building corals at depths ranging from 40 to 150 m. This reef ecosystem has garnered our interest because to the significant environmental alterations in the water column—such as light, nutrients, phytoplankton, and water density—that facilitate species diversification, although it remains largely underexplored [69]. Additionally, the limited light exposure and relatively cooler temperatures compared to the surface provide a sanctuary from drastic environmental fluctuations [67, 70]. Similarly, if we seek ancient adaptations that appear outmoded, this relatively pristine location serves as a great setting for such exploration. There, we discovered another species of *Agaricia*, the mushroom coral *A. undata*, a mesophotic specialist characterized by dark blotches extending from the base to the periphery of the coral [71]. These blotches are also seen in *A. fragilis*, a species that extends well down to 60 m.

3.2 Do corals possess a concealed repertoire of photosymbionts that are more adaptable to climate change?

Agaricid corals often exhibit dark blotches caused by endolithic algae of the genus *Ostreobium*, which belongs to the siphonous green algal order Bryopsidales [72–75]. While considered a monophyletic group, molecular evidence suggests that the diversity of this genus is currently underestimated [73, 74, 76–79]. *Ostreobium* spp. chemically penetrate coral skeletons to establish their habitat; they are formally referred to as euendolithic, as they must reside within mineral substrates. *Ostreobium* is a widespread coral symbiont reported in 85% of coral species across a geographic and bathymetric range [77]. These endolithic algae often create a high-density green band underneath the coral tissue [80, 81]. Photosynthesis in *Ostreobium* is quite particular, displaying a set of adaptations that allow them to inhabit low-light environments like the limestone skeleton of a coral or deep-water habitat where light penetration can be less than 0.01% [82]. For instance, *Ostreobium* can absorb green light using xanthophyll pigments, is able to alter its chlorophyll b: chlorophyll a ratio according to water depth, and can absorb light in the red and far-red wavelengths [81, 83–86].

From an ecological perspective, endolithic algae are proposed to have a dual role as coral symbionts, exhibiting both mutualistic and parasitic characteristics [72, 77, 82, 87, 88]. Metabolic interactions between endolithic algae and coral hosts suggest there is a mutualistic ectosymbiosis, where the algae help cycle and store nutrients, contributing to the high productivity of tropical and subtropical reef ecosystems [83]. Studies have recorded the transfer of photoassimilates, including carbon [89, 90] and nitrogen [89] from *Ostreobium* spp. to the coral host. During bleaching events, increased photosynthetically active radiation stimulates blooms of endolithic algae and photoassimilate production, enhancing translocation to the host. For example, transfer of 14 C-labelled carbon from endolithic algae to the coral Mediterranean *Oculina patagonica* was significantly higher in bleached individuals than in non-bleached ones, suggesting that endolithic algae may help the host survive bleaching events [91]. Similarly, a photobiology study in the Caribbean species *Montastrea faveolata* found that endolithic blooms during bleaching periods could aid coral recovery by reducing skeleton reflectance [92].This energy source may be insufficient for costly processes such as reproduction, likely only supporting survival and recovery from stress [93, 94]. Conversely, endolithic algae also act as agents of microbioerosion, dissolving $CaCO_3$ in dead skeletons and increasing the microporosity of live skeletons [95]. This bioerosion activity can destabilize coral reef structures, increasing the susceptibility to abrasion and further dissolution, thus impacting reef topology [83, 87]. Additionally, endolithic algae contribute to the trophic chain by serving as a food source for macrobioeroders, such as sea urchins and parrotfishes [87].

The depth-generalist coral *Agaricia undata*, which colonizes mesophotic reefs as deep as 100 m, exhibits a greater diversity of *Ostreobium* (12 clades) compared to *Symbiodinium* (7 clades) [71, 79]. No genetic structuring was found for either the host or *Symbiodinium* across depths in *A. undata*. The high diversity and bathymetric structuring of *Ostreobium* clades associated with this species, coupled with the lack of partitioning for hosts and *Symbiodinium*, suggest a potential role for endolithic algae in the coral's ability to colonize mesophotic ecosystems. In the genus *Agaricia*, symbiosis with *Ostreobium* is common across all seven species (Murgueitio & Sánchez, in preparation), including those inhabiting mesophotic environments such as *A. undata* and *A. grahamae*, which thrive at depths of 60–100 m, as well as species like *A. humilis* and *A. agaricites*, typically found in shallower waters [96, 97].

To establish endolithic algae as a resource comparable to Symbiodiniaceae algae, several criteria must be met for a close coral-endosymbiont relationship. First, evidence of interaction between these algae and coral tissue is essential. While previous data of translocation of photoassimilates was reported in Mediterranean trials during bleaching events, further evidence was needed to demonstrate interactions under normal conditions [91]. The black blotches on *Agaricia* mushroom corals provided such evidence. Studies on *A. undata* and *A. fragilis* revealed a close association between the algae and the darkened area of the coral skeleton [79] (Fig. 2). Algal filaments not only inhabit the shaded region but also protruded through pores on the surface of the skeleton, specifically within the calcification matrix. Remarkably, the algae formed tubes penetrating the coral tissue lamellae, making direct contact with the living polyp tissue [98]. In *A. fragilis* the algae also make flat junction between coral costae never seen before (Fig. 2C, D). These findings suggest that endolithic algae might fulfill fundamental criteria to be regarded as a resource different from Symbiodiniaceae algae in the context of a close coral-endosymbiont relationship.

Reviewing samples from our *Agaricia* collection (ANDES-IM) and following the methods in [79], we found pipeline-like structures across the costae of corals in 11% of the specimens of *A. fragilis* but absent in *A. grahamae*, *A. lamarcki*, *A. humilis* or *A. agaricites*. These pipelines, which varied in shape and calcification, were observed in samples both with and without dense endolithic algae coverage. However, where comparisons were possible, pipeline density appeared higher in samples with dense *Ostreobium* coverage. EDS analyses revealed differences in composition between the pipeline and the coral skeleton. While coral skeleton is primarily composed of carbon (C), calcium (Ca) and oxygen (O), pipelines additionally contain sulphur (S) (often in high proportions), magnesium (Mg) and barium (Ba). This phenomenon, so far only seen in *Agaricia*, deserves further research to assess the potential mutualistic role of *Ostreobium* spp. in low-light environments. In *Porites* corals, old cavities created by *Ostreobium* and other bioeroders seem to be filled through a secondary mineralization process [99]. Interestingly, *Sidereastrea radians*, a shallow-water coral (intertidal to 3 m), associated with seagrass beds, also exhibits dense perforation of *Ostreobium* spp. deep within the skeleton apparently from a very thin type of the algae (Fig. 3). This provides information about the coral's resilience to bleaching occurrences in the research area (Rosario islands, Cartagena, Colombia).

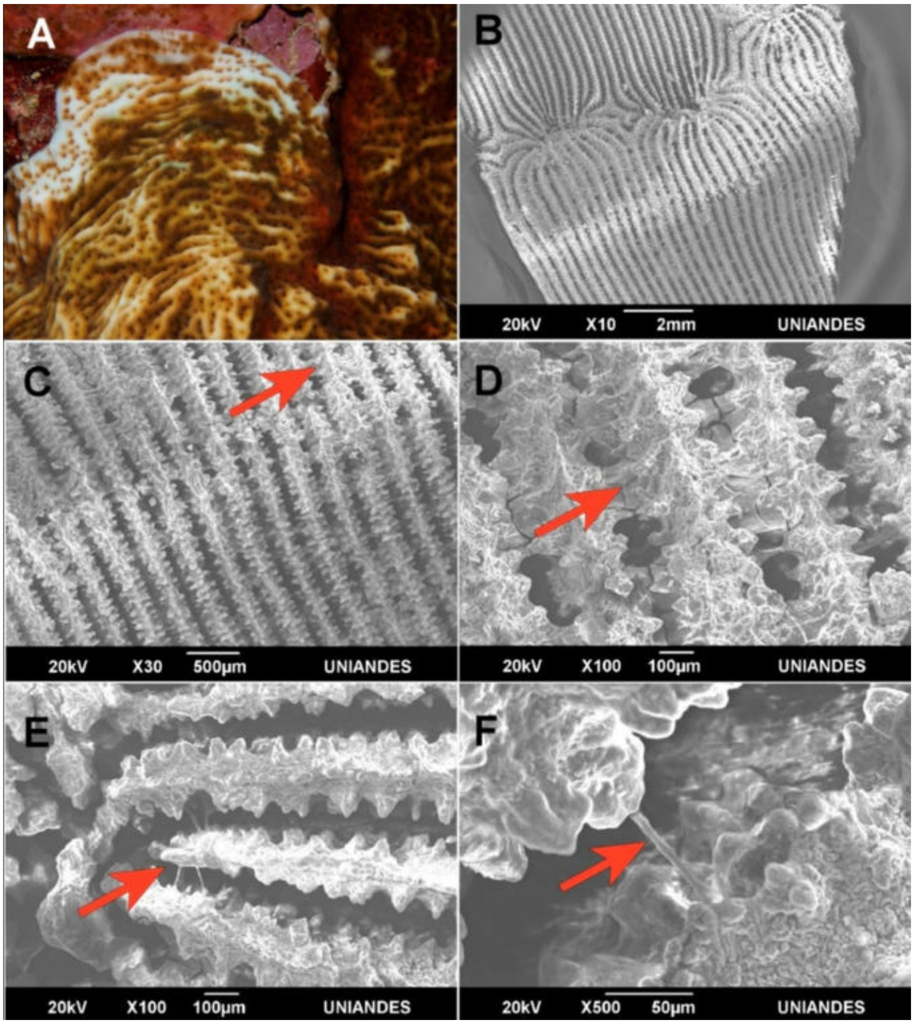

Fig. 2 Mesophotic coral *Agaricia fragilis* at depth of 60 m in Bajo Trompadas (Barú, Cartagena, Colombia). A. Underwater Photo by Juan A. Sánchez. B-F) Several *Ostreobium* structures visible at coral surface from sample ANDES-IM 4199, a specimen with macroscopic dense coverage of endolithic algae noted as dense green. B-C) Flat junctions between coral costae. E-F) Pipelines between coral costae (From Amalia Murgueitio honors thesis at Universidad de los Andes)

4 Coral reefs: a collection of reef-building life

Renowned marine paleontologist George Stanley, after examining fossil coral reefs throughout his career, concluded that contemporary coral reefs function as an “obsolescence museum” still including all past reef-building types [100]. It is as if, in a metropolis such as New York, every transportation system that has ever existed—horse-drawn carriages, steam trains, streetcars, subways, buses, and automobiles—remained in operation. While the subway serves as the primary mode of horizontal transportation for most individuals, various alternatives persist, much like coral reefs. Similarly, while stony corals (Anthozoa) are currently the dominant reef-builders, coral reefs also support other calcifying organisms, albeit in lesser abundance today, including fire corals (Hydrozoa), octocorals (Anthozoa), giant clams (Gastropoda), and coralline algae (Rhodophyta). Additionally, stromatolites, which thrived several billion years ago, can still be found in regions such as the Bahamas. All these organisms rely on photosynthesis, either directly or via symbiosis with microalgae, to sustain high growth rates. Although they

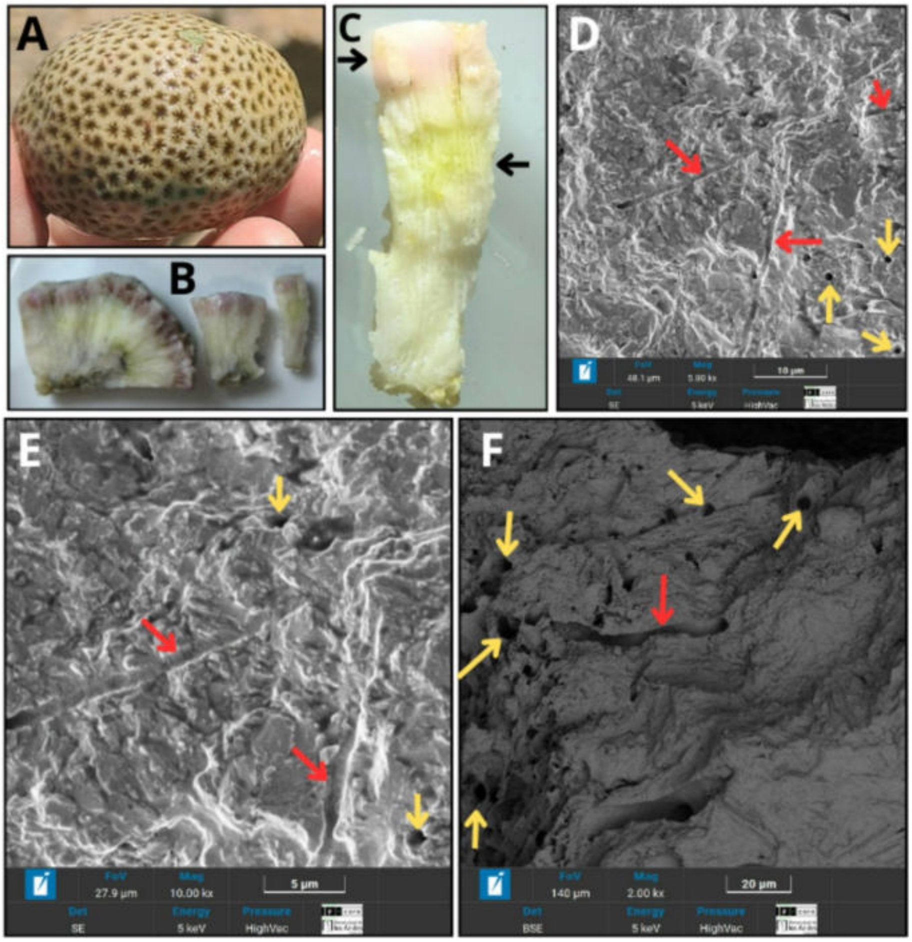

Fig. 3 Macrostructural and microstructural views of the coral *Siderastrea radians*. (A) Macroscopic view of the coral *Siderastrea radians*, showing its semispherical structure and the corallites on the surface. (B) Transverse sections of different sizes from the core to the surface of the coral. (C) Transverse section of the coral's calcareous skeleton, indicating distinct pigmentation areas (upper black arrow: live coral tissue; lower black arrow: zone with *Ostreobium*). (D) SEM image (5,800X) of the internal surface of the calcareous skeleton (zone with *Ostreobium*), showing microbioerosion of the skeleton caused by *Ostreobium*, (grooves in red arrows, holes in yellow arrows). (E) SEM image (10,000X) highlighting the microbioerosion grooves and holes. (F) SEM image (2000X) revealing dense and porous zones in the calcareous matrix, with internal microbioerosion indicated by the arrows

are not currently the primary reef architects, they could claim that role in the future. Over 100 million years ago, rudists, a form of clam, were the reef-builders. Their extinction—likely due to the same catastrophe that eradicated the dinosaurs—left an ecological niche vacant, allowing scleractinian corals to dominate to the present day [101].

4.1 Is it possible for climate change to induce a phase shift in reef construction?

It is important to note that, while shifts in reef-building organisms are well-documented in the geological record, such changes in the near future could have severe consequences for coastal communities. The increase in atmospheric CO_2, depletes carbonate ions needed for $CaCO_3$ deposition and lowers ocean pH, reducing aragonite (Ω_{arag}) and calcite ($\Omega_{ca.}$) saturation states [102]. Initially, it impacts species that crystallize $CaCO_3$ as aragonite, but organisms that deposit calcite are comparatively less affected ($\Omega_{ca.}$), indicating their greater resilience to ocean acidification. The fossil record indicates the depletion of aragonite saturation, permitting calcite-dominant species to prevail among reef builders [66]. The ocean's acidifying periods posed significant challenges for marine animals, yet they served as evolutionary pressure, leading to the emergence of many skeletal types, some integrated with corneal proteins, in octocorals over a hundred million years ago [103].

Numerous evolutionary innovations for $CaCO_3$ deposition persist among octocoral species in coral reefs. While they are not primary reef builders like scleractinian corals, octocorals play an important role by contributing to structural complexity [104] and in certain areas, they are significant contributors of $CaCO_3$ to sediments [105]. The octocorals of the soft coral variety, prevalent in the Indo-Pacific, deposit spiculite—a conglomerate of granular calcite skeletons—at their bases. In several Indo-Pacific locations, spiculite deposits form towers that rival the rock produced by stony corals [106]. Observations from southern Japan, where naturally acidified waters from CO_2 vents have led to a transition from hard coral-dominated to octocoral-dominated reefs, provide insights into alternative scenarios [29]. Are these reefs in Japan a glimpse into the future of coral reefs? It is encouraging to consider that, despite the reduction of stony corals, the ecosystem itself may persist. In the Caribbean Sea, gorgonian corals —a group of octocorals— are prevalent; they are primarily soft with a proteinaceous endoskeleton but deposit $CaCO_3$ at their bases, similar to small stony corals [107] (Fig. 4). Gorgonians have shown a notable increase in recent decades, contrasting with the swift decline of hard corals [70, 108, 109]. Mesocosm experiments simulating ocean acidification conditions, have revealed the remarkable resilience of gorgonians in acidic environments, maintaining growth and calcification of their granular skeletons even at very low $\Omega_{ca.}$ and Ω_{ara} saturation [110]. Despite their deposits being smaller than those of spiculite, the substantial populations of gorgonians could potentially mitigate this effect. A similar trend might be observed in other organisms involving fire corals or giant clams in

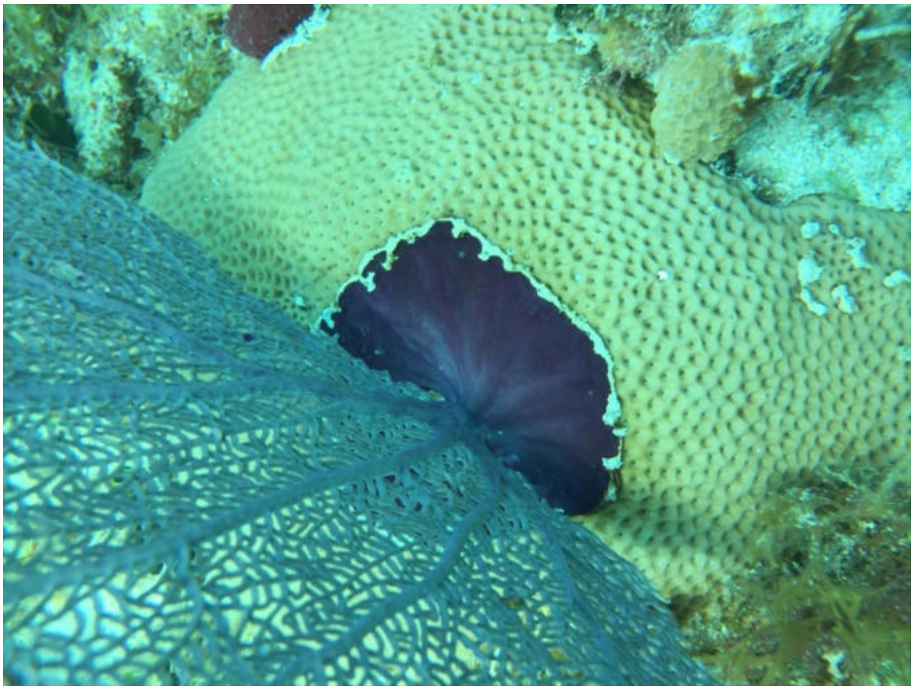

Fig. 4 The octocoral seafan *Gorgonia ventalina*, growing on top of a colony of *Siderastrea siderea* in the Florida keys, Low key reef 5 m (Photo: Juan A. Sánchez)

a different region. While the specific ecosystem services provided by coral reefs may change or be lost, as shown by the historical fossil record, the ecosystem itself may persist in an alternate form.

5 Bacteria-Mediated calcification

Another process that may gain ecological relevance in future reefs is bacteria-mediated calcification, also known as microbially induced $CaCO_3$ precipitation (MICP). This process plays a key role in the formation of $CaCO_3$ deposits in aquatic ecosystems and is fundamental for marine biogeochemistry and global carbon cycling [111, 112]. Through MICP, bacteria modify their surrounding chemical environment via metabolic processes, leading to $CaCO_3$ precipitation. In marine ecosystems, this mineralization is closely associated microbialite formation, such as stromatolites, and other biogenic carbonate structures, significantly contributing to sedimentation and carbon accumulation [113–115]. This process is distinct from biologically controlled mineralization, where cellular activity specifically directs the mineral's nucleation, morphology, and final location, as seen in calcifying organisms like algae, echinoderms, and mollusks [115, 116].

5.1 Geological records and ecological implications of bacterially mediated calcification: could bacteria replace corals?

The formation of stromatolites and other carbonate microbial structures in marine environments represents one of the oldest records of bacterially induced biomineralization. Stromatolites, laminated structures formed by the accumulation of $CaCO_3$, date back to the Precambrian and were created through the cyclic growth of microbial communities that precipitated or trapped mineral particles in their environment. This mineralization process was crucial in primitive oceans, where microbial mats dominated the seascape and regulated water chemistry by consuming CO_2 and producing oxygen, thus transforming Earth's early atmosphere [113, 115].

In present-day marine environments, microbial mats play an important role in $CaCO_3$ precipitation, particularly in hypersaline areas where high alkalinity and light levels support the photosynthetic activity of cyanobacteria. Photosynthesis in these organisms consumes CO_2, increasing local alkalinity and promoting carbonate precipitation [117]. Sites like Shark Bay, Australia, the Bahamas, and Laguna Vermelha, Brazil, exhibit the accumulation and fossilization of carbonate deposits within microbial mats, providing record of microbial activity [118, 119]. These mats also alter the balance of reduced and oxidized forms of carbon, influencing $CaCO_3$ precipitation by altering pH and alkalinity [115]. While some metabolic activities generate alkalinity and facilitate carbonate precipitation, others produce dissolved inorganic carbon or organic acids, potentially reducing pH and leading to carbonate dissolution. This balance between precipitation and dissolution ultimately contributes to the lithification of microbial mats, reflecting the interaction of various microbial processes [115, 120].

Throughout the Phanerozoic, carbonate platforms have been predominantly composed of metazoan and algal skeletons, with benthic microbial carbonates playing a relatively minor role in marine environments. This stands in stark contrast to the Proterozoic, where deposits formed through bacteria-mediated calcification were dominant. The diversification of metazoans near the end of the Proterozoic marked the beginning of a decline in microbial carbonates, a trend that has persisted throughout the Phanerozoic [121–123].

The primary drivers of this decline are thought to include competition with eukaryotes and changes in substrate conditions [123–125]. Consequently, some authors argue that since metazoan competition was the principal factor limiting the abundance of microbial carbonates, a temporary reduction in metazoan activity could lead to a resurgence of microbial carbonate deposition [123].

Historically, during periods following mass extinction events of metazoans, microbial carbonates partially regained the abundance they had prior to the emergence of these organisms [126]. This is evidenced by the record of stromatolites in the Late Devonian and Early Triassic, where they acted as opportunistic generalists that proliferated in the aftermath of these extinction events [123, 127, 128]. However, there is no direct evidence to confirm that competitive exclusion due to the rise of metazoans was the primary cause of the decline in microbial carbonates. Furthermore, there remains disagreement within the scientific community regarding the precise timing of the origin of metazoans [123].

In contrast, there is consensus on the diversification of algae, which is estimated to have occurred approximately 1,500 million years ago, after which they likely became integrated into microbialite communities [123]. This is of great significance, as it has been proposed that two key components of the tissue-like structure of thrombolites in tropical regions are calcified filaments of the green algae genus *Ostreobium* spp. and structures formed from spores of *Acetabularia* spp [129]. In shallow reefs of regions such as Tahiti, microbialites experienced widespread development during the last deglaciation, a period marked by rising sea levels and environmental degradation [130]. These microbialites formed during a late stage of encrustation on dead coral colonies or related encrusting organisms, such as red algae. This succession reflects an increase in nutrient availability in the environment, as one of the essential prerequisites for microbialite development is the presence of nutrients supplied by surface runoff from adjacent rivers [130–132]. The massive input and subsequent concentration of nutrients in the environment not only hinder coral reef formation but also promote the growth of algal turf and, in turn, the development of microbialites [130–133].

The exopolymeric matrix (EPS) secreted by bacteria around microbial cells serves as a barrier between the cell and its metabolic substrates, playing a key role in marine biogeochemical processes [134–136]. This matrix is where carbonate minerals nucleate and grow, influencing both the morphology and mineralogy of the resulting precipitates during organomineralization [136]. The acidity and functional groups within the EPS matrix are critical for its metal-binding potential and susceptibility to biotic and abiotic degradation, both essential for $CaCO_3$ precipitation [137]. Beyond its role in mineral formation, EPS also supports sediment stability by resisting erosion, retains critical nutrients within the microbial community, facilitates cell-to-cell communication, and traps viruses [138]. These processes are not only fundamental to microbialite formation but also contribute to their broader ecological functions in coastal ecosystems. For instance, microbialites act as buffers against nutrient pollution, as the primary producer communities associated with them absorb nitrogen and phosphorus [139, 140]. Furthermore, through photosynthetic processes, microbialites accumulate CO_2, fixing it into inorganic layers as carbonate and sequestering carbon over the long term. This mechanism is like that observed in other habitats formed by calcifying organisms, such as coral reefs. The net primary production of microbialites ranges from 2.17 to 14.49 Mg C ha^{-1} yr^{-1}, a rate comparable to that recorded in South African mangroves [139, 140].

5.2 Symbiotic interactions and calcification in marine organisms

Bacteria-mediated calcification is also observed in symbiotic interactions with marine organisms, such as sponges and crustaceans [141, 142] and possible in octocorals. In sponges, endosymbiotic bacteria produce calcitic spherulites that strengthen the host structure, against pathogen and physical abrasion. Sponge cells, similar to archaeocytes, engulf these bacteria, which then thrive and proliferate within internal vacuoles, contributing to $CaCO_3$ precipitation and forming an additional skeleton [143]. Similarly, in terrestrial crustaceans such as the isopod *Titanethes albus*, symbiotic bacteria generate calcium deposits within specialized organs, creating an acidic polysaccharide matrix that facilitates carbonate mineral nucleation [144]. Many octocorals deposit $CaCO_3$ at their holdfasts [107]. In the case of Caribbean gorgonian corals, the deposits only occur in very large colonies regardless of the species and in the two main families, Gorgoniidae and Plexauridae. It is possible that these deposits are related to their symbiotic bacteria.

5.3 Bacterial adaptations to extreme environments and their contribution to biomineralization

Bacteria involved in biogenic calcification often inhabit extreme environments, where metabolic adaptations enable them to induce carbonate precipitation under adverse conditions. For example, *Planococcus halocryophilus*, found in psychrophilic environments, upregulates carbonic anhydrase expression, a key enzyme in $CaCO_3$ mineralization, allowing carbonate deposition within cell envelopes. This adaptation is crucial for survival in cold environments and offers insights into low-temperature biomineralization [145]. In hypersaline lakes and anaerobic conditions, bacteria, including sulfate-reducing bacteria, manipulate pH and alkalinity to enhance $CaCO_3$ precipitation even in the absence of oxygen [137]. These extreme environments provide valuable insights into how bacteria modify their surroundings to promote carbonate formation and reveal how these processes have persisted and evolved over time [146].

The study of bacterially induced biomineralization has broad implications, for carbon cycling, fossil preservation and adaptation to extreme conditions [119]. Calcifying bacteria influence carbonate deposit formation on the seafloor and in lake sediments, impacting coastal ecosystems stability geological structure durability. Furthermore, bacterial biomineralization has potential applications in ecosystem restoration, historical monument conservation, and building material sustainability [147].

6 From corals to coralline algae: carbon capture pathways in a changing ocean

Although bacteria in reef systems could be a hidden source of calcification, coralline algae could be the elephant in the room of future calcifiers in coral reefs. In terms of calcification, Crustose Coralline Algae (CCA) have relevant advantages over corals. For instance, Table 1 presents a summary of calcification rates in corals and CCA. Carbonate production exhibits a distinct latitudinal gradient, with significantly higher rates observed in tropical ecosystems, such as the Great Barrier Reef (Australia), Florida, and the Caribbean, compared to temperate and polar environments, including Ireland, Norway, and Wales. This pattern reflects the influence of warmer temperatures and elevated metabolic activity, which enhance calcification in tropical reef-building organisms. However, certain cold-water calcifying algae, such as *Lithothamnion glaciale* in Norway, exhibit carbonate production rates comparable to those of tropical reefs. This finding suggests that, despite the generally lower growth rates characteristic of high-latitude environments, their contribution to global carbonate cycles remains significant. The coralligenous assemblages from the Mediterranean sea host one most diverse ecosystems in temperate regions [148]. The presence of highly productive calcifying species in cold waters underscores the need for further research into their ecological roles and potential responses to climate change. Moreover, crustose coralline algae (CCA) generally exhibit higher calcification rates than corals across multiple locations. Studies conducted in Colombia, Tobago and Barbados indicate that CCA are the primary contributors to carbonate production. Additionally, massive corals such as *Orbicella faveolata* and *Porites astreoides* display higher calcification rates compared to branching corals like *Acropora cervicornis*, suggesting that differences in biomineralization may be influenced by morphological traits. These variations highlight the complexity of carbonate production across different reef structures and emphasize the importance of understanding species-specific contributions to reef accretion in the context of environmental change (Table 1). For most calcifying phototrophs, calcification and photosynthesis occur simultaneously under light conditions [149, 150]. This interaction can act as an important "recycling" pathway for carbon substrates [151]. Recent advancements have improved our understanding and measurement of carbon dynamics [152]. The balance between photosynthesis, respiration, calcification, and $CaCO_3$ dissolution can significantly alter seawater carbonate chemistry in reef ecosystems over daily and seasonal cycles [153]. Both photosynthesis and calcification contribute to a reduction of dissolved inorganic carbon (DIC) in seawater, whereas respiration and $CaCO_3$ dissolution result in an increase in DIC. Photosynthesis raises pH by reducing the concentration of hydrogen ions, whereas respiration lowers pH by increasing it. These $[H^+]$ shifts can alter the relative concentrations of CO_3^{2-}, HCO_3^-, and CO_2, which in turn influence calcification [154]. This balance is crucial for understanding of the carbonate chemistry process [155, 156].

Photoautotrophic marine ecosystems are recognized as major reef-building facies due to their biomass and associated sediments over geological timescales [183]. These ecosystems, located at the boundary between land-sea and across the continental shelf, play a crucial role in global carbon cycle [152, 184, 185]. This has become a growing conservation priority due to its potential in mitigating climate change impacts [152, 183]. Due to their current significance in carbon capture through both organic and inorganic pathways, coral reefs could be considered an important net carbon sink ecosystems [186].

Crustose coralline algae (CCA), together with other organisms like *Halimeda* spp., foraminifera, mollusks, contributes to the construction of reef frameworks. CCA is a significant but frequently underestimated source of framework carbonate [187–189]. Recent studies have indicated that corals and CCA may play a significant role in carbon sequestration by absorbing and storing atmospheric CO_2 [190, 191]. CCA also contributes to reef structure to a comparable extent [191]. Despite higher abundances of primary producers can have negative repercussions for reefscapes, in the case of coralline algae they also have the potential to positively influence the physicochemical environment and help mitigate the adverse effects of problems as ocean acidification (OA) [192]. The

Table 1 Calcification rates across several coral and free-living crustose coralline algae (CCA) species by country and methodological approach; e: estimated calcification from caco$_3$ µmol cm^{-2} hr^{-1} original values; c: calculated from caco$_3$ g cm^{-2} yr^{-1}, g m^{-2} yr^{-1} or Mg cm^{-2} d^{-1} original values; GBR: great barrier reef; CCA: when the Article does not mention the species; NA: not applicable

Species	Depth (m)	Original calcification data				kg CaCO$_3$ m^{-2} yr^{-1}	Method	Reference	Net/gross	Location	Country	Observations
		µmol cm^{-2} hr^{-1}	mg cm^{-2} d^{-1}	g m^{-2} yr^{-1}	g cm^{-2} yr^{-1}							
Siderastrea radians	2	0.052				0.455^{e}	Total alkalinity	Marin et al. (in review)	Net	Isla Grande, Southern Caribbean	Colombia	Higher calcification in CCA than in corals
CCA	3	0.254				2.23^{e}						
Acropora cervicornis	NA	0.27				2.37^{e}	Total alkalinity	[157]	Net	Florida	USA	A better understanding of light-driven reef metabolism is needed for predicting global change impacts
CCA1		0.18				1.58^{e}						
CCA2		0.26				2.28^{e}						
Orbicella faveolata		0.58				5.09^{e}						
Porites astreoides		0.72				6.31^{e}						
Siderastrea siderea		0.49				4.30^{e}						
Acropora intermedia	5–8					4.84–5.78	Buoyant weight	[158]	Net	Heron Reef, GBR	Australia	Provides a reef-scale carbonate budget and insights into carbonate dynamics
Porites lobata	5–8					3.42–7.29						
CCA	4.7 – 6.5		0.48			1.75^{c}	Buoyant weight	[159]	Net	Heron Island, southern GBR	Australia	Description of the benefits and costs of each material and/or orientation used for monitoring CCA
CCA	10			3.8–105.3		0.0038 ^{c} – 0.105^{c}	Weight	[160]	Net	Northern Coast	Tobago	CCA had the highest CaCO$_3$ production among studied organisms
Porolithon sp.	10			2378		2.378^{c}	Extension + density	[161]	NA	West Coast	Barbados	Corals and CCA fix ~ 163 metric tons of CaCO$_3$ annually
Neogoniolithon sp.	10			1225		1.225^{c}						
Lithophyllum sp.	10			1355		1.355^{c}						
Mesophyllum sp.	10			167		0.167^{c}						
CCA	4–6		0.13			0.475^{c}	Buoyant weight	[162]	Net	Florida Keys	USA	Coral-calcification rates were higher than those of CCA
Siderastrea siderea	4–6		2.7			9.855^{c}						

Table 1 (continued)

Species	Depth (m)	Original calcification data				kg $CaCO_3$ m^{-2} yr^{-1}	Method	Reference	Net/gross	Location	Country	Observations
		µmol cm^{-2} hr^{-1}	mg cm^{-2} d^{-1}	g m^{-2} yr^{-1}	g cm^{-2} yr^{-1}							
Hydrolithon onkodes	0					3.31	Total alkalinity	[163]	Net	Lizard Island, Northern GBR	Australia	These estimates predict annual deposition rates, assuming measurements are taken between late summer and midwinter
Hydrolithon onkodes	2					0.82						
Hydrolithon reinboldii	3					0.91						
Hydrolithon reinboldii	6					1.24						
Neogoniolithon brassica-florida	0					2.07						
Neogoniolithon brassica-florida	3					2.55						
Neogoniolithon brassica-florida	6					1.20						
Neogoniolithon conicum	0					1.55						
Neogoniolithon conicum	6					0.99						
Neogoniolithon conicum	18					0.30						
Rhodolith	8			163.33		0.163[c]	Extension + density	[164]	NA	Northern Coastline	Brazil	High growth rates and significant structural roles are not necessarily linked to dense rhodolith assemblages
Lithophyllum sp.	8.5–10.5			55–136.3		0.055–0.136[c]	Extension + weight of nodules	[165]	Net	Arvoredo Island	Brazil	Carbonate production aligns with rates in other temperate regions
Fosliella sp.	NA			30–300		0.03–0.30[c]	Total alkalinity	[166]	Net	Shark Bay	Australia	NA
Lithothamnion sp.	10–20			81.09		0.081[c]	Extension + weight of nodules	[167]	NA	Gulf of Chiriquí	Panama	Coralline carbonate production rates in the Gulf of Chiriquí are slightly higher than in the Gulf of Panama
Lithothamnion sp.	10–20			23.38		0.023 [c]				Gulf of Panama		

Table 1 (continued)

Species	Depth (m)	Original calcification data				kg $CaCO_3$ m^{-2} yr^{-1}	Method	Reference	Net/gross	Location	Country	Observations
		μmol cm^{-2} hr^{-1}	mg cm^{-2} d^{-1}	g m^{-2} yr^{-1}	g cm^{-2} yr^{-1}							
Lithothamnion corallioides	1–16			29–164		0.029–0.164^{c}	Growth rates to calcification rates	[168]	Net	Mannin Bay	Ireland	The calcium carbonate production rates are comparable to those in tropical non-reef environments.
Phymatolithon Lithothamnion calcareum	1–16			79–422		0.79–0.422^{c}						
Lithoghainnion glaciale	7			895–1432		0.895–1.432^{c}	Extension + weight of thalli	[169]	Net	Troms	Norway	The annual carbonate production rate matches subtropical-tropical counterparts
Lithoghainnion glaciale	18			420–630		0.420–0.630^{c}			Net			
Lithophyllum incrustuns	NA			379		0.379^{c}	Extension + density	[170]	Net	Pembroke, south-west	Wales	The growth rates are comparable to other Arctic and temperate encrusting red algae but significantly lower than those in the tropics.
Lithothamnion corallioides	0–10			876		0.876^{c}	Buoyant weight	[171]	Gross	Bay of Brest, Brittany	France	A rate lower than tropical reef coralline algae but higher than temperate European reef-builders
Lithothamnion corallioides	20–30			212–1197		0.212–1.197^{c}	Extension + weight of thalli	[172]	Net	Mannin Bay	Ireland	These rates align with the lower range observed in tropical coral reefs
Lithothamnion corallioides	1–8			300–3000		0.3–3^{c}	Total alkalinity	[173]	Net	Bay of Brest	France	These results align with the reported carbonate productivity in tropical coralline algae
Lithothamnion corallioides	0–3			487		0.487^{c}	Total alkalinity	[174]	Net	Bay of Brest	France	NA
Rhodoliths	20–45					0.3–2.7	Extension + density	[175]	Net	Abrolhos Shelf	Brazil	There were no differences in $CaCO_3$ production according to depth
Rhodoliths	15–30			858		0.858^{c}	Extension + density	[176]	NA	Queimada Grande Island	Brazil	$CaCO_3$ production by coralline algae and bryozoans helps counterbalance large-scale reef erosion

Table 1 (continued)

Species	Depth (m)	Original calcification data				kg $CaCO_3$ m^{-2} yr^{-1}	Method	Reference	Net/gross	Location	Country	Observations
		µmol cm^{-2} hr^{-1}	mg cm^{-2} d^{-1}	g m^{-2} yr^{-1}	g cm^{-2} yr^{-1}							
Porolithon antillarum	5–10				0.75	7.5^{c}	Crust growth method	[177]	Net	Gayraca Bay, Tayrona Park	Colombia	*Porolithon antillarum* contributes more to overall CCA calcification than the branching forms of *Lithophyllum cf. kaiseri.*
Lithophyllum cf. kaiseri	5–10				0.68	4.7^{c}						
Porolithon antillarum	5–10				1.49	14.9^{c}	Buoyant weight					
Lithophyllum cf. kaiseri	5–10				0.52	5.2^{c}						
Porolithon cf. onkodes	1–14				0.51	5.1^{c}	Buoyant weight	[178]	Net	Moorea Island	French Polynesia	CCA growth and calcification is species-specific and spatially and temporally variable
Neogoniolithon cf. megalocystum	1–14				0.16	1.6^{c}						
Lithophyllum sp.	1–14				0.03	0.3^{c}						
Lithothamnion corallioides	47			90.8		0.091^{c}	Extension + weight	[179]	NA	Cilento Shelf	Italy	These results align with prior studies
Maërl beds	40–85			210		0.210^{c}	Dry weight, decalcification and reweighing	[180]	NA	Mallorca-Menorca	Spain	The results provide a minimum estimate of total carbonate production considering only the phytobenthos
Lithothamnion glaciale	45			200.3		0.200^{c}	Extension + weight of thalli	[181]	Net	Floskjeret, Svalbard	Norway	Light is the primary physical parameter influencing the rhodolith communities
Lithothamnion glaciale	41–50			169.8–181.5		0.169–0.181^{c}				Krossfjorden, Svalbard		
Lithothamnion glaciale	44			119.8		0.119^{c}				Mosselbukta, Svalbard		
Lithothamnion glaciale	27–45			100.9–157.7		0.1–0.157^{c}				Nordkappbukta, Svalbard		
Lithothamnion glaciale	15–17			196		0.196^{c}	Weight change	[182]	Net	Newfoundland	Canada	$CaCO_3$ production rates align with those of other rhodolith beds in polar and subpolar regions
Lithothamnion glaciale	15–17			326		0.326^{c}	Extension + biomass	[182]	Net			

remarkable productivity and substantial carbonate deposits of CCA further underscore their role as critical contributors to the present and future of tropical reefs, highlighting the need for further research to better understand the dynamics, stability, and long-term carbon sequestration capacity of coralline algal beds [190, 193].

7 Rehabilitating the coral reef ecosystem

Tropical marine ecosystems are biodiversity hotspots with significant interconnection between estuaries, mangroves, seagrasses, and coral reefs. Understanding and preserving these ecosystems requires knowledge of the energy fluxes, interconnections and interdependencies. The global coral reef crisis, driven by climate change, overfishing, particularly of herbivorous species, and nutrient pollution, highlight the importance of adjacent ecosystems like seagrass beds. The excess of nutrients benefits its competing algae, and significantly alters the water and marine sediment microbiota leading to coral disease [194, 195]. Despite progress in coral propagation within nurseries over the last decade [196, 197], some transplanted corals exhibit disease primarily due to environmental factors, especially alterations in water microbes [194]. Effective coral reef restoration needs novel ecosystem-based approaches that prioritize water quality and create optimal conditions for coral health.

The remedies to halt the deterioration of coral reefs are evident. Yet, their execution necessitates a fundamental shift in the prevailing paradigm of human development. The mitigation of climate change effects is essential to prevent coral bleaching. However, even with an immediate energy transformation, measures must be implemented to remove excess greenhouse gases currently present, and achieving pre-industrial levels will require decades [198]. Local degradation factors, such as overfishing and nutrient surplus, may be more manageable in the short to medium term. Nevertheless, while coral reefs are predominantly located in the Global South nations such as Colombia, it lacks initiatives to manage their waters and mitigate the nutrient load released by their cities and rivers [199]. Overfishing results from societal inequality and exemplifies a predicted tragedy of the commons [59]. Moreover, the symbiosis between corals and Symbiodinaceae has two major weaknesses in the face of climate change: their optimal temperature is not far from the threshold at which coral bleaching occurs, and the symbiont have few resources to photoacclimate due to the lack of chlorophyll b and having type II Rubisco, a rarity among photoautotrophs with oxygenic photosynthesis, which is less efficient compared to type I present in green algae and plants [200].

In the last decade, scientists have been divided on what the approach should be to prevent the loss of corals and coral reefs. Many have mobilized to support the restoration processes of coral populations through coral nursery techniques [201]. There exists the adequate understanding regarding the settings that facilitate the restoration of coral reefs amidst various environmental stressors. Most common techniques include coral gardening based on asexual propagation [202]. For example, coral micro-fragmentation uses small fragments of coral that are cloned and allowed to grow in a structure away from the reef, where algae and other threats are manually removed to prevent them from coming into contact with the coral sprouts [196, 203]. While a few projects have successfully used coral larvae, most rely on fragments from surviving corals on the reef. After one or two years, when the coral fragments have reached an adequate size, they are replanted onto the reef [202]. The growth of fragments in nurseries is very successful compared to the often modest survival of transplanted fragments. Some research efforts aim to develop genetically modify coral strains and Symbiodiniaceae algae better equipped to survive in the face of climate change potentially offering a critical tool for reef restoration in the future [204–206].

The likelihood that coral nurseries can effectively restore the coral reefs, which have been in steady decline over the past three decades, is low. All initiatives to mitigate coral reef degradation are legitimate, but a community-shift perspective may yield accurate forecasts and management strategies for this vital ecosystem. A 'One Health' approach to coral reef restoration recognizes the interconnectedness of human and coral health with proximity to seagrass beds reducing disease-causing bacteria in the water that induce both human and coral illnesses by 50% [207]. Corals adjacent to seagrass beds are typically healthier than those located distantly from the meadow or reefs without connection with this ecosystem [207]. The presence of mangroves and seagrasses reduces pollutant influx, while simultaneously offering a nursery habitat for diverse invertebrates and herbivorous fish that maintain low algal biomass, thereby reducing competition with corals and promoting a healthier water microbiota with reduced coral pathogens [208, 209]. The stoplight parrotfish, *Sparisoma viride*, exhibits diverse trophic preferences and facilitates live Symbiodiniaceae algae dispersal through its feces, which potentially could act as inoculum for newly settled or bleached corals [210]. Crustose coralline algae enhance coral health by contributing to reef construction, forming and cementing rhodoliths and coral fragments, providing a substrate for coral larvae recruitment, and exhibiting resistance to ocean acidification [20, 211].

We earnestly hope that coral restoration methods will ultimately succeed in rehabilitating scleractinian coral populations and halting the degradation of coral reefs. However, this idea emphasizes the restoration of modified reef ecosystems and the establishment of new reef patches by integrating elements that promote coral vitality, including mangroves, seagrasses and coralline algae. Reef rehabilitation acknowledges the difficulties in conserving and managing coastal natural resources amid a changing environment, while emphasizing the urgent necessity to address alterations in ecosystem functionality to restore resilience and enhance water conditions conducive to coral development.

8 Conclusions: who will be responsible for depositing the limestone in the future?

As we enter the onset of climate change, characterized by fast environmental and societal transformations, forecasting the future entails significant uncertainty. A potential effect is a gradual transition in the distribution of coral reefs from tropical regions to temperate zones, where scleractinian corals may encounter colder temperatures, as observed in recent years at their extreme tolerances [27]. However, ocean acidification, lower light regimes at higher latitudes and relatively slow growth and reproduction may constrain their success. The fossil record indicates that limestone, the matrix of tropical reefs, can exist as either aragonite or calcite, depending on environmental conditions. Aragonite (Ω_{arag}) formation is favored by high aragonite saturation states similar to pre-industrial conditions. On the other hand, calcite ($\Omega_{ca.}$) becomes more likely under conditions of ocean acidification, akin to our current scenario. In this last scenario, however challenging to envision, we cannot dismiss the possibility of a transformation in the reef ecosystem, characterized by an increase in octocorals, potentially huge clams [212]—albeit absent in the Atlantic—and possibly an abundance of coralline algae and their rhodoliths.

Regardless, certain scleractinian corals may continue to be relevant reef-builders. The close association of corals with the potentially adversarial microbioerosion algae *Ostreobium* instills optimism for the continued construction of coral reefs by hard corals at least in the mesophotic zone. In regions such as the Caribbean, these reefs may not be like the *Acropora*-dominated reefs of their preindustrial peak, but rather reefs resembling mesophotic coral ecosystems, with abundant coralline algae in shallow reefs like those subjected to sedimentation in the southern Caribbean around Cartagena. Even in an altered state, these reefs may continue to provide essential ecosystem services, including habitat provision for various species, including those for human use, recreational spaces, and, crucially, a large contribution to global carbonate cycles. It is essential to emphasize that any human attempt to prevent a species from extinction is both commendable and just, as the loss of biodiversity resulting from climate change is a shared responsibility of humanity. Coral nurseries have galvanized society in the fight against coral extinction more effectively than any previous initiative. They only have our admiration for their commitment and integrity. Coral reef rehabilitation procedures may be enhanced by identifying alternative calcifying species and creatures, developing new technologies, while mitigating external stressors that undermine coral resilience, including overfishing and nutrient influx.

Acknowledgements To Minciencias (Colombia) and the Faculty of Sciences (Uniandes) for the financial support and administration of the program “Observatory of Microbioerosion, Ocean Acidification, and Dissolution in Coral Reefs” (contract 80740-489-2020, code 1204-852-70251). Finally, we would like to express our gratitude for the support, technical and scientific efforts provided by the MicroCore Microscopy Center, which is funded by the Vice-Rectorate for Research and Creation of the University of Los Andes. Comments and recommendations from two anonymous reviewers greatly improved the manuscript.

Author contributions

J.A.S. conceptualization, J.A.S., A.M., C.R., D.H.M-C. and C.E.G. did the research and wrote the main manuscript text. J.A.S., A.M. and D.H.M-C. prepared figures. All authors reviewed the manuscript.

Data availability

No datasets were generated or analysed during the current study.

Declarations

Competing interests

The authors declare no competing interests.

Received: 1 December 2024 / Accepted: 16 June 2025

Literature cited

1. Moberg F, Folke C. Ecological goods and services of coral reef ecosystems. Ecol Econ. 1999;29:215–33. https://doi.org/10.1016/S0921-8009(99)00009-9.
2. Hughes TP, Barnes ML, Bellwood DR, et al. Coral reefs in the anthropocene. Nature. 2017;546:82–90. https://doi.org/10.1038/nature22901.
3. Lamb JB, Willis BL, Fiorenza EA, et al. Plastic waste associated with disease on coral reefs. Science. 2018;359:460–2. https://doi.org/10.1126/science.aar3320.
4. Weijerman M, Gove JM, Williams ID, et al. Evaluating management strategies to optimise coral reef ecosystem services. J Appl Ecol. 2018;55:1823–33. https://doi.org/10.1111/1365-2664.13105.

5. Harvell CD. Climate warming and disease risks for terrestrial and marine biota. Science. 2002;296:2158–62. https://doi.org/10.1126/science.1063699.
6. Jackson JBC. The future of the oceans past. Philos Trans R Soc B Biol Sci. 2010;365:3765–78. https://doi.org/10.1098/rstb.2010.0278.
7. Doney SC, Ruckelshaus M, Emmett Duffy J, et al. Climate change impacts on marine ecosystems. Annu Rev Mar Sci. 2012;4:11–37. https://doi.org/10.1146/annurev-marine-041911-111611.
8. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, et al. Coral reefs under rapid climate change and ocean acidification. Science. 2007;318:1737–42. https://doi.org/10.1126/science.1152509.
9. Lüthi D, Le Floch M, Bereiter B, et al. High-resolution carbon dioxide concentration record 650,000–800,000 years before present. Nature. 2008;453:379–82. https://doi.org/10.1038/nature06949.
10. NOAA. (2019) ESRL Global Monitoring Division - Global Greenhouse Gas Reference Network. https://www.esrl.noaa.gov/gmd/ccgg/trends/. Accessed 1 Aug 2019.
11. NOAA Trends in CO2 - NOAA Global Monitoring Laboratory. https://gml.noaa.gov/ccgg/trends/mlo.html. Accessed 18 Mar 2025.
12. Petit JR, Jouzel J, Raynaud D, et al. Climate and atmospheric history of the past 420,000 years from the Vostok ice core. Antarctica Nat. 1999;399:429–36. https://doi.org/10.1038/20859.
13. Salvat B, Allemand D, Levin PS, Harvey CJ. 2009. Quantitative evaluation of marine ecosystem indicator performance using food web models. Ecosystems 12:1283–98.
14. Oliver ECJ, Donat MG, Burrows MT, et al. Longer and more frequent marine heatwaves over the past century. Nat Commun. 2018;9:1324. https://doi.org/10.1038/s41467-018-03732-9.
15. Cooley S, Schoeman D, Bopp L et al. (2022) Chap. 3: Oceans and Coastal Ecosystems and their Services. In: IPCC AR6 WGII. https://www.ipcc.ch/report/ar6/wg2/downloads/report/IPCC_AR6_WGII_FinalDraft_Chapter03.pdf. Accessed 9 Aug 2024.
16. Kubicek A, Breckling B, Hoegh-Guldberg O, Reuter H. Climate change drives trait-shifts in coral reef communities. Sci Rep. 2019;9:3721. https://doi.org/10.1038/s41598-019-38962-4.
17. Loya Y, Sakai K, Yamazato K, et al. Coral bleaching: the winners and the losers. Ecol Lett. 2001;4:122–31.
18. Wooldridge SA. Differential thermal bleaching susceptibilities amongst coral taxa: re-posing the role of the host. Coral Reefs. 2014;33:15–27. https://doi.org/10.1007/s00338-013-1111-4.
19. Ritson-Williams R, Arnold SN, Paul VJ. Patterns of larval settlement preferences and post–settlement survival for seven Caribbean corals. Mar Ecol Prog Ser. 2016;548:127–38. https://doi.org/10.3354/meps11688.
20. Jury CP, Bahr KD, Cros A, et al. Experimental coral reef communities transform yet persist under mitigated future ocean warming and acidification. Proc Natl Acad Sci. 2024;121:e2407112121. https://doi.org/10.1073/pnas.2407112121.
21. Lachs L, Donner SD, Mumby PJ, et al. Emergent increase in coral thermal tolerance reduces mass bleaching under climate change. Nat Commun. 2023;14:4939. https://doi.org/10.1038/s41467-023-40601-6.
22. Chaudhary C, Richardson AJ, Schoeman DS, Costello MJ. Global warming is causing a more pronounced dip in marine species richness around the equator. Proc Natl Acad Sci. 2021;118:e2015094118. https://doi.org/10.1073/pnas.2015094118.
23. Fuchs YH, Edgar GJ, Bates AE, et al. Limited net Poleward movement of reef species over a decade of climate extremes. Nat Clim Change. 2024;14:1087–92. https://doi.org/10.1038/s41558-024-02116-w.
24. Fine M, Gildor H, Genin A. A coral reef refuge in the red sea. Glob Change Biol. 2013;19:3640–7. https://doi.org/10.1111/gcb.12356.
25. Kavousi J, Keppel G. Clarifying the concept of climate change refugia for coral reefs. ICES J Mar Sci. 2018;75:43–9. https://doi.org/10.1093/icesjms/fsx124.
26. McClanahan TR, Darling ES, Beger M, et al. Diversification of refugia types needed to secure the future of coral reefs subject to climate change. Conserv Biol. 2024;38:e14108. https://doi.org/10.1111/cobi.14108.
27. Camp EF, Schoepf V, Mumby PJ, et al. The future of coral reefs subject to rapid climate change: lessons from natural extreme environments. Front Mar Sci. 2018;5. https://doi.org/10.3389/fmars.2018.00004.
28. Nyström M, Folke C, Moberg F, et al. Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol Evol. 2000;15:413–7. https://doi.org/10.1016/S0169-5347(00)01948-0.
29. Inoue S, Kayanne H, Yamamoto S, Kurihara H. Spatial community shift from hard to soft corals in acidified water. Nat Clim Change. 2013;3:683–7. https://doi.org/10.1038/nclimate1855.
30. Norström A, Nyström M, Lokrantz J, Folke C. Alternative States on coral reefs: beyond coral–macroalgal phase shifts. Mar Ecol Prog Ser. 2009;376:295–306. https://doi.org/10.3354/meps07815.
31. Lalas JAA, Jamodiong EA, Reimer JD. Spatial patterns of soft coral (Octocorallia) assemblages in the shallow coral reefs of Okinawa island, Ryukyu archipelago, japan: dominance on highly disturbed reefs. Reg Stud Mar Sci. 2024;71:103405. https://doi.org/10.1016/j.rsma.2024.103405.
32. LaJeunesse TC, Parkinson JE, Gabrielson PW, et al. Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr Biol. 2018;28:2570–e25806. https://doi.org/10.1016/j.cub.2018.07.008.
33. van Woesik R, Shlesinger T, Grottoli AG, et al. Coral-bleaching responses to climate change across biological scales. Glob Change Biol. 2022;28:4229–50. https://doi.org/10.1111/gcb.16192.
34. Ainsworth TD, Heron SF, Ortiz JC, et al. Climate change disables coral bleaching protection on the great barrier reef. Science. 2016;352:338–42.
35. Miller AW, Richardson LL. Emerging coral diseases: a temperature-driven process? Mar Ecol. 2015;36:278–91. https://doi.org/10.1111/maec.12142.
36. Boilard A, Dubé CE, Gruet C, et al. Defining coral bleaching as a microbial dysbiosis within the coral holobiont. Microorganisms. 2020;8:1682. https://doi.org/10.3390/microorganisms8111682.
37. Miller J, Muller E, Rogers C, et al. Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. Coral Reefs. 2009;28:925. https://doi.org/10.1007/s00338-009-0531-7.
38. Hughes TP, Kerry JT, Álvarez-Noriega M, et al. Global warming and recurrent mass bleaching of corals. Nature. 2017;543:373–7. https://doi.org/10.1038/nature21707.

39. Reimer JD, Peixoto RS, Davies SW, et al. The fourth global coral bleaching event: where do we go from here? Coral Reefs. 2024;43:1121–5. https://doi.org/10.1007/s00338-024-02504-w.
40. Goreau TJF, Hayes RL. 2023 record marine heat waves: coral reef bleaching hotspot maps reveal global sea surface temperature extremes, coral mortality, and ocean circulation changes. Oxf Open Clim Change. 2024;4:kgae005. https://doi.org/10.1093/oxfclm/kgae005.
41. Hoegh-Guldberg O, Skirving W, Dove SG, et al. Coral reefs in peril in a record-breaking year. Science. 2023;382:1238–40. https://doi.org/10.1126/science.adk4532.
42. Kleypas JA, Feely RA, Fabry VJ et al. (2006) Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research. Research, report of a workshop held 18–20 April 2005, St. Petersburg, FL, sponsored by NSF, NOAA, and the US Geological Survey. Clim Change Surf Ocean Acidif.
43. Cohen AL, McCorkle DC, de Putron S, et al. Morphological and compositional changes in the skeletons of new coral recruits reared in acidified seawater: insights into the biomineralization response to ocean acidification. Geochem Geophys Geosyst. 2009;10. https://doi.org/10.1029/2009GC002411.
44. Pratchett MS, Hoey AS, Wilson SK, et al. Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. Diversity. 2011;3:424–52. https://doi.org/10.3390/d3030424.
45. Jones GP, McCormick MI, Srinivasan M, Eagle JV. Coral decline threatens fish biodiversity in marine reserves. Proc Natl Acad Sci. 2004;101:8251–3. https://doi.org/10.1073/pnas.0401277101.
46. Idjadi J, Edmunds P. Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. Mar Ecol Prog Ser. 2006;319:117–27. https://doi.org/10.3354/meps319117.
47. Mumby PJ. Fishing, trophic cascades, and the process of grazing on coral reefs. Science. 2006;311:98–101. https://doi.org/10.1126/science.1121129.
48. Mumby PJ. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. Coral Reefs. 2009;28:761–73. https://doi.org/10.1007/s00338-009-0506-8.
49. Bryant D, Burke L, McManus J, Spalding M. Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resour Inst Wash DC; 1998.
50. Hoegh-Guldberg O. Coral reef ecosystems and anthropogenic climate change. Reg Environ Change. 2011;11:215–27. https://doi.org/10.1007/s10113-010-0189-2.
51. Barbier EB. Valuing the storm protection service of estuarine and coastal ecosystems. Ecosyst Serv. 2015;11:32–8. https://doi.org/10.1016/j.ecoser.2014.06.010.
52. Webster PJ, Holland GJ, Curry JA, Chang H-R. Changes in tropical cyclone number, duration, and intensity in a warming environment. Science. 2005;309:1844–6. https://doi.org/10.1126/science.1116448.
53. Hughes TP, Kerry JT, Baird AH, et al. Global warming impairs stock–recruitment dynamics of corals. Nature. 2019;568:387–90. https://doi.org/10.1038/s41586-019-1081-y.
54. Gardner TA, Cote IM, Gill JA, et al. Long-term region-wide declines in Caribbean corals. Science. 2003;301:958–61.
55. López-Angarita J, Moreno-Sánchez R, Maldonado JH, Sánchez JA. Evaluating linked Social-Ecological systems in marine protected areas. Conserv Lett. 2014;7:241–52. https://doi.org/10.1111/conl.12063.
56. Restrepo JD, Park E, Aquino S, Latrubesse EM. Coral reefs chronically exposed to river sediment plumes in the Southwestern caribbean: Rosario islands, Colombia. Sci Total Environ. 2016;553:316–29. https://doi.org/10.1016/j.scitotenv.2016.02.140.
57. Lapointe BE, Brewton RA, Herren LW, et al. Nitrogen enrichment, altered stoichiometry, and coral reef decline at Looe key, Florida keys, USA: a 3-decade study. Mar Biol. 2019;166:108. https://doi.org/10.1007/s00227-019-3538-9.
58. Carpenter KE, Abrar M, Aeby G, et al. One-Third of Reef-Building corals face elevated extinction risk from climate change and local impacts. Science. 2008;321:560–3. https://doi.org/10.1126/science.1159196.
59. Camargo C, Maldonado JH, Alvarado E, et al. Community involvement in management for maintaining coral reef resilience and biodiversity in Southern Caribbean marine protected areas. Biodivers Conserv. 2009;18:935–56.
60. Alvarez-Filip L, González-Barrios FJ, Pérez-Cervantes E, et al. Stony coral tissue loss disease decimated Caribbean coral populations and reshaped reef functionality. Commun Biol. 2022;5:1–10. https://doi.org/10.1038/s42003-022-03398-6.
61. Restrepo J, Zapata P, Diaz J, et al. Fluvial fluxes into the Caribbean sea and their impact on coastal ecosystems: the Magdalena river, Colombia. Glob Planet Change. 2006;50:33–49. https://doi.org/10.1016/j.gloplacha.2005.09.002.
62. Rodríguez L, Acosta A, González-Zapata FL, et al. Conservation at the edge: connectivity and opportunities from non-protected coral reefs close to a National park in the Colombian Caribbean. Biodivers Conserv. 2023;32:1493–522.
63. Veron JEN, Stafford-Smith MG, Turak E, Devantier LM. (2019) Corals of the World. http://www.coralsoftheworld.org/coral_geographic/interactive_map/results/result_lists?resultType=ecoregions. Accessed 1 Aug 2019.
64. Cáceres SM, Sánchez JA. Growth strategies of an abundant reef-building coral in the Southern Caribbean (*Undaria tenuifolia*). Rev Acad Colomb Cienc Exactas Físicas Nat. 2015;39:348. https://doi.org/10.18257/raccefyn.195.
65. Aronson RB, Precht WF, Macintyre IG. Extrinsic control of species replacement on a holocene reef in belize: the role of coral disease. Coral Reefs. 1998;17:223–30.
66. Quattrini AM, Rodríguez E, Faircloth BC, et al. Palaeoclimate ocean conditions shaped the evolution of corals and their skeletons through deep time. Nat Ecol Evol. 2020;4:1531–8. https://doi.org/10.1038/s41559-020-01291-1.
67. Bellworthy J, Fine M. Beyond peak summer temperatures, branching corals in the Gulf of Aqaba are resilient to thermal stress but sensitive to high light. Coral Reefs. 2017;36:1071–82. https://doi.org/10.1007/s00338-017-1598-1.
68. Prata KE, Riginos C, Gutenkunst RN, et al. Deep connections: divergence histories with gene flow in mesophotic Agaricia corals. Mol Ecol. 2022;31:2511–27. https://doi.org/10.1111/mec.16391.
69. Sánchez JA, González-Zapata FL, Prada C, Dueñas LF. Mesophotic Gorgonian corals evolved multiple times and faster than deep and shallow lineages. Diversity. 2021;13:650. https://doi.org/10.3390/d13120650.
70. Sánchez JA, Dueñas LF, Rowley SJ, et al. Gorgonian corals (39). In: Loya, et al. editors. Mesophotic coral ecosystems. Springer Nature Switzerland AG; 2019. pp. 727–45.
71. Gonzalez-Zapata FL, Bongaerts P, Ramírez-Portilla C, et al. Holobiont diversity in a Reef-Building coral over its entire depth range in the mesophotic zone. Front Mar Sci. 2018;5. https://doi.org/10.3389/fmars.2018.00029.

72. del Campo J, Pombert J-F, Šlapeta J, et al. The 'other'coral symbiont: *Ostreobium* diversity and distribution. ISME J. 2017;11:296–9.
73. Verbruggen H, Ashworth M, LoDuca ST, et al. A multi-locus time-calibrated phylogeny of the siphonous green algae. Mol Phylogenet Evol. 2009;50:642–53. https://doi.org/10.1016/j.ympev.2008.12.018.
74. Verbruggen H, Marcelino VR, Guiry MD, et al. Phylogenetic position of the coral symbiont *Ostreobium* (Ulvophyceae) inferred from Chloroplast genome data. J Phycol. 2017;53:790–803. https://doi.org/10.1111/jpy.12540.
75. Marcelino VR, Verbruggen H. Multi-marker metabarcoding of coral skeletons reveals a rich Microbiome and diverse evolutionary origins of endolithic algae. Sci Rep. 2016;6. https://doi.org/10.1038/srep31508.
76. Tandon K, Hu J, Pasella MM, et al. Coral skeleton dwelling endolithic algae: Ostreobium and its biology. In: Peixoto RS, Voolstra CR, editors. Coral reef Microbiome. Cham: Springer Nature Switzerland; 2025. pp. 41–6.
77. Gutner-Hoch E, Fine M. Genotypic diversity and distribution of Ostreobium quekettii within scleractinian corals. Coral Reefs. 2011;30:643–50.
78. del Campo J, Pombert J-F, Šlapeta J, et al. The 'other' coral symbiont: *Ostreobium* diversity and distribution. ISME J. 2017;11:296–9. https://doi.org/10.1038/ismej.2016.101.
79. Gonzalez-Zapata FL, Gómez-Osorio S, Sánchez JA. Conspicuous endolithic algal associations in a mesophotic reef-building coral. Coral Reefs. 2018;37:705–9.
80. Highsmith RC. Lime-boring algae in hermatypic coral skeletons. J Exp Mar Biol Ecol. 1981;55:267–81. https://doi.org/10.1016/0022-0981(81)90117-9.
81. Magnusson SH, Fine M, Kühl M. Light microclimate of endolithic phototrophs in the scleractinian corals *Montipora monasteriata* and *Porites cylindrica*. Mar Ecol Prog Ser. 2007;332:119–28. https://doi.org/10.3354/meps332119.
82. Verbruggen H, Tribollet A. Boring algae. Curr Biol. 2011;21:R876–7. https://doi.org/10.1016/j.cub.2011.09.014.
83. Schlichter D, Kampmann H, Conrady S. Trophic potential and photoecology of endolithic algae living within coral skeletons. Mar Ecol. 1997;18:299–317. https://doi.org/10.1111/j.1439-0485.1997.tb00444.x.
84. Fork DC, Larkum AWD. Light harvesting in the green Alga *Ostreobium* sp., a coral symbiont adapted to extreme shade. Mar Biol. 1989;103:381–5. https://doi.org/10.1007/BF00397273.
85. Koehne B, Elli G, Jennings RC, et al. Spectroscopic and molecular characterization of a long wavelength absorbing antenna of *Ostreobium* Sp. Biochim Biophys Acta BBA-Bioenerg. 1999;1412:94–107.
86. Shashar N, Stambler N. Endolithic algae within corals life in an extreme environment. J Exp Mar Biol Ecol. 1992;163:277–86. https://doi.org/10.1016/0022-0981(92)90055-F.
87. Verbruggen H, Tribollet A. Boring algae. Curr Biol. 2011;21:R876–7.
88. Tribollet A. Dissolution of dead corals by euendolithic microorganisms across the Northern great barrier reef (Australia). Microb Ecol. 2008;55:569–80. https://doi.org/10.1007/s00248-007-9302-6.
89. Sangsawang L, Casareto BE, Ohba H, et al.) ^{13} C and ^{15} N assimilation and organic matter translocation by the endolithic community in the massive coral *Porites lutea*. R Soc Open Sci. 2017;4:171201. https://doi.org/10.1098/rsos.171201.
90. Schlichter D, Zscharnack B, Krisch H. Transfer of photoassimilates from endolithic algae to coral tissue. Naturwissenschaften. 1995;82:561–4. https://doi.org/10.1007/BF01140246.
91. Fine M, Loya Y. Endolithic algae: an alternative source of photoassimilates during coral bleaching. Proc R Soc B Biol Sci. 2002;269:1205–10. https://doi.org/10.1098/rspb.2002.1983.
92. Galindo-Martínez CT, Weber M, Avila-Magaña V, et al. The role of the endolithic Alga Ostreobium spp. During coral bleaching recovery. Sci Rep. 2022;12:2977. https://doi.org/10.1038/s41598-022-07017-6.
93. Tribollet A. The boring microflora in modern coral reef ecosystems: a review of its roles. In: Wisshak M, Tapanila L, editors. Current developments in bioerosion. Berlin, Heidelberg: Springer Berlin Heidelberg; 2008. pp. 67–94.
94. Fine M, Loya Y, Zibrowius H. *Oculina patagonica*: a non-lessepsian scleractinian coral invading the mediterranean sea. Mar Biol. 2001;138:1195–203. https://doi.org/10.1007/s002270100539.
95. Tribollet A, Golubic S. Reef bioerosion: agents and processes. In: Dubinsky Z, Stambler N, editors. Coral reefs: an ecosystem in transition. Dordrecht: Springer Netherlands; 2011. pp. 435–49.
96. Bongaerts P, Frade PR, Ogier JJ, et al. Sharing the slope: depth partitioning of agariciid corals and associated *Symbiodinium* across shallow and mesophotic habitats (2–60 m) on a Caribbean reef. BMC Evol Biol. 2013;13:205. https://doi.org/10.1186/1471-2148-13-205.
97. Hoeksema BW, Bongaerts P, Baldwin CC. High coral cover at lower mesophotic depths: a dense *Agaricia* community at the Leeward side of curaçao, Dutch Caribbean. Mar Biodivers. 2017;47:67–70. https://doi.org/10.1007/s12526-015-0431-8.
98. Massé A, Dormart-Coulon I, Golubic S, Tribollet A. Early skeletal colonization of the coral holobiont by the microboring Ulvophyceae *Ostreobium* Sp. | Sci Rep Sci Rep. 2018;8:2293.
99. Uribe ES, Murgueitio A, Gómez CE et al. (2025) Endolithic algae influence the skeletal microstructure and porosity of reef-building corals. Sci Rep.
100. Stanley GD. The evolution of modern corals and their early history. Earth-Sci Rev. 2003;60:195–225. https://doi.org/10.1016/S0012-8252(02)00104-6.
101. Pandolfi JM, Kiessling W. Gaining insights from past reefs to inform Understanding of coral reef response to global climate change. Curr Opin Environ Sustain. 2014;7:52–8. https://doi.org/10.1016/j.cosust.2013.11.020.
102. Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S. Coral reef ecosystems under climate change and ocean acidification. Front Mar Sci. 2017;4. https://doi.org/10.3389/fmars.2017.00158.
103. Quattrini AM, Rodríguez E, Faircloth BC, et al. Palaeoclimate ocean conditions shaped the evolution of corals and their skeletons through deep time. Nat Ecol Evol. 2020;4:1531–8.
104. Sánchez JA, Díaz JM, Zea S. Octocoral and black coral distribution patterns on the barrier reef-complex of Providencia island, Southwestern Caribbean. Caribb J Sci. 1998;34:250–64.
105. Velimirov B, Böhm EL. Calcium and magnesium carbonate concentrations in different growth regions of gorgonians. Mar Biol. 1976;35:269–75. https://doi.org/10.1007/BF00396874.
106. Schuhmacher H. (1997) Soft corals as reef builders,. In: In: H.A. Lessios and I.G. Macintyre, editors Proceedings of the 8th International Coral Reef Symposium Vol. 1. Smithsonian Tropical Research Institute, Panama. pp 99–502.

107. Kocurko MJ, Kocurko DJ. Fossil Octocorallia of the red bluff formation, lower oligocene, Mississippi. J Paleontol. 1992;66:594–602.
108. Edmunds PJ, Tsounis G, Lasker HR. Differential distribution of octocorals and scleractinians around st. John and st. Thomas, US Virgin Islands. Hydrobiologia. 2016;767:347–60.
109. Sánchez JA. Diversity and evolution of octocoral animal forests at both sides of tropical America. Marine animal forests: the ecology of benthic biodiversity hotspots. Springer International Publishing; 2017. pp. 111–43.
110. Gómez CE, Paul VJ, Ritson-Williams R, et al. Responses of the tropical Gorgonian coral *Eunicea fusca* to ocean acidification conditions. Coral Reefs. 2015;34:451–60.
111. Castro-Alonso MJ, Montañez-Hernandez LE, Sanchez-Muñoz MA, et al. Microbially induced calcium carbonate precipitation (MICP) and its potential in bioconcrete: Microbiological and molecular concepts. Front Mater. 2019;6:126. https://doi.org/10.3389/fmats.2019.00126.
112. Golovkina DA, Zhurishkina EV, Ivanova LA, et al. Calcifying Bacteria flexibility in induction of CaCO3 mineralization. Life. 2020;10:317. https://doi.org/10.3390/life10120317.
113. Semikhatov MA, Gebelein CD, Cloud P, et al. Stromatolite morphogenesis—progress and problems. Can J Earth Sci. 1979;16:992–1015.
114. Burne RV, Moore LS. Microbialites: organosedimentary deposits of benthic microbial communities. Palaios. 1987;2:241–54. https://doi.org/10.2307/3514674.
115. Dupraz C, Reid RP, Braissant O, et al. Processes of carbonate precipitation in modern microbial Mats. Earth-Sci Rev. 2009;96:141–62. https://doi.org/10.1016/j.earscirev.2008.10.005.
116. Lowenstam HA, Weiner S. On biomineralization. USA: Oxford University Press; 1989.
117. Visscher PT, Reid RP, Bebout BM. Microscale observations of sulfate reduction: correlation of microbial activity with lithified micritic laminae in modern marine stromatolites. Geology. 2000;28:919–22. https://doi.org/10.1130/0091-7613(2000)28<919:MOOSRC>2.0.CO;2.
118. Burns BP, Goh F, Allen M, Neilan BA. Microbial diversity of extant stromatolites in the hypersaline marine environment of shark bay, Australia. Environ Microbiol. 2004;6:1096–101. https://doi.org/10.1111/j.1462-2920.2004.00651.x.
119. Vasconcelos C, Warthmann R, McKenzie JA, et al. Lithifying microbial Mats in Lagoa vermelha, brazil: modern precambrian relics? Sediment Geol. 2006;185:175–83. https://doi.org/10.1016/j.sedgeo.2005.12.022.
120. Visscher PT, Stolz JF. Microbial Mats as bioreactors: populations, processes, and products. In: Noffke N, editor. Geobiology: objectives, concepts, perspectives. Amsterdam: Elsevier; 2005. pp. 87–100.
121. Nogueira ACR, Santos RFD, Romero GR, et al. Ediacaran-Cambrian microbialites of the Southern Amazon craton: relation with the metazoan rise, sea-level changes, and global tectonics. Braz J Geol. 2022;52:e20210065. https://doi.org/10.1590/2317-4889202220210065.
122. Pratt BR. Stromatolite decline—A reconsideration. Geology. 1982;10:512. https://doi.org/10.1130/0091-7613(1982)10<512:SDR>2.0.CO;2.
123. Riding R. Microbial carbonate abundance compared with fluctuations in metazoan diversity over geological time. Sediment Geol. 2006;185:229–38. https://doi.org/10.1016/j.sedgeo.2005.12.015.
124. Awramik SM. The history and significance of stromatolites. In: Schidlowski M, Golubic S, Kimberley MM, et al. editors. Early organic evolution. Berlin, Heidelberg: Springer Berlin Heidelberg; 1992. pp. 435–49.
125. Reid RP, Suosaari EP, Oehlert AM, et al. Microbialite accretion and growth: lessons from shark Bay and the Bahamas. Annu Rev Mar Sci. 2024;16:487–511. https://doi.org/10.1146/annurev-marine-021423-124637.
126. Riding R. Temporal variation in calcification in marine cyanobacteria. J Geol Soc. 1992;149:979–89. https://doi.org/10.1144/gsjgs.149.6.0979.
127. Schubert JK, Bottjer DJ. Aftermath of the Permian-Triassic mass extinction event: paleoecology of lower triassic carbonates in the Western USA. Palaeogeogr Palaeoclimatol Palaeoecol. 1995;116:1–39. https://doi.org/10.1016/0031-0182(94)00093-N.
128. Guido A, Rosso A, Sanfilippo R, et al. Skeletal vs microbialite Geobiological role in bioconstructions of confined marine environments. Palaeogeogr Palaeoclimatol Palaeoecol. 2022;593:110920. https://doi.org/10.1016/j.palaeo.2022.110920.
129. Planavsky N, Ginsburg RN. Taphonomy of modern marine Bahamian microbialites. Palaios. 2009;24:5–17. https://doi.org/10.2110/palo.2008.p08-001r.
130. Camoin G, Cabioch G, Eisenhauer A, et al. Environmental significance of microbialites in reef environments during the last deglaciation. Sediment Geol. 2006;185:277–95. https://doi.org/10.1016/j.sedgeo.2005.12.018.
131. Camoin GF, Gautret P, Montaggioni LF, Cabioch G. Nature and environmental significance of microbialites in quaternary reefs: the Tahiti paradox. Sediment Geol. 1999;126:271–304. https://doi.org/10.1016/S0037-0738(99)00045-7.
132. Li Y, Wang F, Liu Z, et al. The formation of biogenic reef stone: from coral skeleton to reef rubble. J Oceanogr. 2022;78:135–49. https://doi.org/10.1007/s10872-022-00636-7.
133. Mutti M, Hallock P. Carbonate systems along nutrient and temperature gradients: some sedimentological and geochemical constraints. Int J Earth Sci. 2003;92:465–75. https://doi.org/10.1007/s00531-003-0350-y.
134. Costerton DE, Lewandowski Z, Caldwell DE, et al. Microbial biofilms. Annu Rev Microbiol. 1995;45:711.
135. Bhaskar PV, Bhosle NB. Microbial extracellular polymeric substances in marine biogeochemical processes. Curr Sci. 2005;88:45–53.
136. Braissant O, Cailleau G, Dupraz C, Verrecchia EP. Bacterially induced mineralization of calcium carbonate in terrestrial environments: the role of exopolysaccharides and amino acids. J Sediment Res. 2003;73:485–90. https://doi.org/10.1306/111302730485.
137. Dupraz C, Visscher PT. Microbial lithification in marine stromatolites and hypersaline Mats. Trends Microbiol. 2005;13:429–38. https://doi.org/10.1016/j.tim.2005.07.008.
138. Bonacolta AM, Visscher PT, Del Campo J, White Iii RA. The eukaryome of modern microbialites reveals distinct colonization across aquatic ecosystems. Npj Biofilms Microbiomes. 2024;10:78. https://doi.org/10.1038/s41522-024-00547-z.
139. Rishworth GM, Dodd C, Perissinotto R, et al. Modern supratidal microbialites fed by groundwater: functional drivers, value and trajectories. Earth-Sci Rev. 2020;210:103364. https://doi.org/10.1016/j.earscirev.2020.103364.

140. Du Plooy SJ, Rishworth GM, Perissinotto R, Dodd C. Nutrient uptake and primary production in lithifying peritidal Tufa stromatolites. J Exp Mar Biol Ecol. 2020;525:151314. https://doi.org/10.1016/j.jembe.2020.151314.
141. Ehrlich H, Shaala LA, Youssef DTA, et al. Discovery of Chitin in skeletons of non-verongiid red sea demosponges. PLoS ONE. 2018;13:e0195803. https://doi.org/10.1371/journal.pone.0195803.
142. Qin W, Wang C, Ma Y, et al. Microbe-Mediated extracellular and intracellular mineralization: environmental, industrial, and biotechnological applications. Adv Mater. 2022;34:2109924. https://doi.org/10.1002/adma.202109924.
143. Uriz MJ, Agell G, Blanquer A, et al. Endosymbiotic calcifying bacteria: a new cue to the origin of calcification in metazoa?? Evolution. 2012;66:2993–9. https://doi.org/10.1111/j.1558-5646.2012.01676.x.
144. Vittori M, Kostanjšek R, Žnidaršič N, et al. Calcium bodies of *Titanethes albus* (Crustacea: Isopoda): Molt-related structural dynamics and calcified matrix-associated bacteria. J Struct Biol. 2012;180:216–25. https://doi.org/10.1016/j.jsb.2012.05.014.
145. Mykytczuk NCS, Lawrence JR, Omelon CR, et al. Microscopic characterization of the bacterial cell envelope of *Planococcus halocryophilus* Or1 during subzero growth at – 15°C. Polar Biol. 2016;39:701–12. https://doi.org/10.1007/s00300-015-1826-5.
146. Ehrlich H. Marine biological materials of invertebrate origin. Cham: Springer International Publishing; 2019.
147. Dhami NK, Reddy MS, Mukherjee A. Application of calcifying bacteria for remediation of stones and cultural heritages. Front Microbiol. 2014;5. https://doi.org/10.3389/fmicb.2014.00304.
148. Ballesteros E. Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanography and marine biology. 0 ed. CRC; 2006. pp. 135–208.
149. Gattuso JP, Alemand D, Frankignoulle M. Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. Am Zool. 1999;39:160–83. https://doi.org/10.1093/icb/39.1.160.
150. Krieger EC, Nelson WA, Grand J, et al. The role of irradiance in controlling coralline algal calcification. Limnol Oceanogr. 2023;68:1269–84. https://doi.org/10.1002/lno.12345.
151. Mao J, Burdett H, Kamenos N. Efficient carbon recycling between calcification and photosynthesis in red coralline algae. Biol Lett. 2024;20:20230598. https://doi.org/10.1098/rsbl.2023.0598.
152. Macreadie PI, Anton A, Raven JA, et al. The future of blue carbon science. Nat Commun. 2019;10:3998. https://doi.org/10.1038/s41467-019-11693-w.
153. Cyronak T, Andersson AJ, Langdon C, et al. Taking the metabolic pulse of the world's coral reefs. PLoS ONE. 2018;13:e0190872. https://doi.org/10.1371/journal.pone.0190872.
154. Jokiel PL, Jury CP, Rodgers KS. Coral-algae metabolism and diurnal changes in the CO2-carbonate system of bulk sea water. PeerJ. 2014;2:e378. https://doi.org/10.7717/peerj.378.
155. Van Dam BR, Zeller MA, Lopes C, et al. Calcification-driven CO2 emissions exceed blue carbon sequestration in a carbonate seagrass meadow. Sci Adv. 2021;7:eabj1372. https://doi.org/10.1126/sciadv.abj1372.
156. Saderne V, Fusi M, Thomson T, et al. Total alkalinity production in a Mangrove ecosystem reveals an overlooked blue carbon component. Limnol Oceanogr Lett. 2021;6:61–7. https://doi.org/10.1002/lol2.10170.
157. Mallon J, Cyronak T, Hall ER, et al. Light-driven dynamics between calcification and production in functionally diverse coral reef calcifiers. Limnol Oceanogr. 2022;67:434–49. https://doi.org/10.1002/lno.12002.
158. Brown KT, Bender-Champ D, Achlatis M, et al. Habitat-specific biogenic production and erosion influences net framework and sediment coral reef carbonate budgets. Limnol Oceanogr. 2021;66:349–65. https://doi.org/10.1002/lno.11609.
159. Kennedy EV, Ordoñez A, Lewis BE, Diaz-Pulido G. Comparison of recruitment tile materials for monitoring coralline algae responses to a changing climate. Mar Ecol Prog Ser. 2017;569:129–44. https://doi.org/10.3354/meps12076.
160. Mallela J. Calcification by Reef-Building sclerobionts. PLoS ONE. 2013;8:e60010. https://doi.org/10.1371/journal.pone.0060010.
161. Stearn CW, Scoffin TP, Martindale W. Calcium carbonate budget of a fringing reef on the West Coast of BarbadosPart I—Zonation and productivity. Bull Mar Sci. 1977;27:479–510.
162. Kuffner IB, Hickey TD, Morrison JM. Calcification rates of the massive coral Siderastrea siderea and crustose coralline algae along the Florida keys (USA) outer-reef tract. Coral Reefs. 2013;32:987–97. https://doi.org/10.1007/s00338-013-1047-8.
163. Chisholm JRM. Calcification by crustose coralline algae on the Northern great barrier reef, Australia. Limnol Oceanogr. 2000;45:1476–84. https://doi.org/10.4319/lo.2000.45.7.1476.
164. Carneiro PB, de Lima M, de Bandeira JP ÊVP, et al. Structure, growth and CaCO3 production in a shallow rhodolith bed from a highly energetic siliciclastic-carbonate Coast in the Equatorial SW Atlantic ocean. Mar Environ Res. 2021;166:105280. https://doi.org/10.1016/j.marenvres.2021.105280.
165. Gherardi DFM. Community structure and carbonate production of a temperate rhodolith bank from Arvoredo island, Southern Brazil. Braz J Oceanogr. 2004;52:207–24.
166. Walker D, Walkerling W. (1988) (PDF) quantitative study of sediment contribution by epiphytic coralline red algae in seagrass meadows in shark bay, Western Australia. ResearchGate. https://doi.org/10.3354/meps043071
167. Schäfer P, Fortunato H, Bader B, et al. Growth rates and carbonate production by coralline red algae in upwelling and non-upwelling settings along the Pacific Coast of Panama. Palaios. 2011;26:420–32. https://doi.org/10.2110/palo.2010.p10-138r.
168. Bosence DWJ. Sedimentary facies, production rates and facies models for recent coralline algal gravels, co. Galway, Ireland. Geol J. 1980;15:91–111. https://doi.org/10.1002/gj.3350150203.
169. Freiwald A, Henrich R. Reefal coralline algal build-ups within the Arctic circle: morphology and sedimentary dynamics under extreme environmental seasonality. Sedimentology. 1994;41:963–84. https://doi.org/10.1111/j.1365-3091.1994.tb01435.x.
170. Edyvean RGJ, Ford H. Growth rates of *Lithophyllum incrustans* (Corallinales, Rhodophyta) from South West Wales. Br Phycol J. 1987;22:139–46. https://doi.org/10.1080/00071618700650161.
171. Potin P, Floc'h JY, Augris C, Cabioch J. (1990) Annual growth rate of the calcareous red alga *Lithothamnion corallioides* (Corallinales, Rhodophyta) in the Bay of Brest, France. In: Lindstrom SC, Gabrielson PW, editors Thirteenth International Seaweed Symposium. Springer Netherlands, Dordrecht, pp 263–267.
172. Bosence D, Wilson J. Maerl growth, carbonate production rates and accumulation rates in the Ne Atlantic. Aquat Conserv Mar Freshw Ecosyst. 2003;13:S21–31. https://doi.org/10.1002/aqc.565.

173. Martin S, Castets M-D, Clavier J. Primary production, respiration and calcification of the temperate free-living coralline Alga *Lithothamnion corallioides*. Aquat Bot. 2006;85:121–8. https://doi.org/10.1016/j.aquabot.2006.02.005.
174. Martin S, Clavier J, Chauvaud L, Thouzeau G. Community metabolism in temperate Maerl beds. I. Carbon and carbonate fluxes. Mar Ecol Prog Ser. 2007;335:19–29. https://doi.org/10.3354/meps335019.
175. Amado-Filho GM, Moura RL, Bastos AC, et al. Rhodolith beds are major CaCO3 Bio-Factories in the tropical South West Atlantic. PLoS ONE. 2012;7:e35171. https://doi.org/10.1371/journal.pone.0035171.
176. Randi CB, Becker AC, Willemes MJ, et al. Calcium carbonate production in the southernmost subtropical Atlantic coral reef. Mar Environ Res. 2021;172:105490. https://doi.org/10.1016/j.marenvres.2021.105490.
177. Pulecio-Plaza L, Diaz-Pulido G, García-Urueña R. Seasonal upwelling conditions promote growth and calcification in reef-building coralline algae. J Phycol. 2023;59:908–25. https://doi.org/10.1111/jpy.13370.
178. Vizon C, Lagourgue L, Payri CE, Nugues MM. Seasonal growth and calcification of three species of crustose coralline algae in moorea, French Polynesia. Mar Ecol Prog Ser. 2024;739:31–48. https://doi.org/10.3354/meps14626.
179. Savini A, Basso D, Bracchi VA, et al. Maerl-bed mapping and carbonate quantification on submerged terraces offshore the Cilento Peninsula (Tyrrhenian sea, Italy). Geodiversitas. 2012;34:77–98. https://doi.org/10.5252/g2012n1a5.
180. Canals M, Ballesteros E. Production of carbonate particles by phytobenthic communities on the Mallorca-Menorca shelf, Northwestern mediterranean sea. Deep Sea Res Part II Top Stud Oceanogr. 1997;44:611–29. https://doi.org/10.1016/S0967-0645(96)00095-1.
181. Teichert S, Freiwald A. Polar coralline algal $CaCO_3$-production rates correspond to intensity and duration of the solar radiation. Biogeosciences. 2014;11:833–42. https://doi.org/10.5194/bg-11-833-2014.
182. Teed L, Bélanger D, Gagnon P, Edinger E. Calcium carbonate (CaCO3) production of a subpolar rhodolith bed: methods of estimation, effect of bioturbators, and global comparisons. Estuar Coast Shelf Sci. 2020;242:106822. https://doi.org/10.1016/j.ecss.2020.106822.
183. James K, Macreadie PI, Burdett HL, et al. It's time to broaden what we consider a 'blue carbon ecosystem'. Glob Change Biol. 2024;30:e17261. https://doi.org/10.1111/gcb.17261.
184. Mao J, Burdett HL, McGill RAR, et al. Carbon burial over the last four millennia is regulated by both Climatic and land use change. Glob Change Biol. 2020;26:2496–504. https://doi.org/10.1111/gcb.15021.
185. Moritsch MM, Young M, Carnell P, et al. Estimating blue carbon sequestration under coastal management scenarios. Sci Total Environ. 2021;777:145962. https://doi.org/10.1016/j.scitotenv.2021.145962.
186. Frankignoulle M, Gattuso J-P. Air-Sea CO2 exchange in coastal ecosystems. In: Wollast R, Mackenzie FT, Chou L, editors. Interactions of C, N, P and S biogeochemical cycles and global change. Berlin, Heidelberg: Springer; 1993. pp. 233–48.
187. Wolfe K, Anthony K, Babcock R et al. (2020) Priority species to support the functional integrity of coral reefs. pp 179–318.
188. Montaggioni L, Braithwaite C. (2009) Quaternary Coral Reef Systems: History, Development Processes and Controlling Factors. 5.
189. Castro-Sanguino C, Bozec Y-M, Mumby PJ. Dynamics of carbonate sediment production by halimeda: implications for reef carbonate budgets. Mar Ecol Prog Ser. 2020;639:91–106. https://doi.org/10.3354/meps13265.
190. Schubert N, Tuya F, Peña V, et al. Pink power—the importance of coralline algal beds in the oceanic carbon cycle. Nat Commun. 2024;15:8282. https://doi.org/10.1038/s41467-024-52697-5.
191. Cornwall CE, Carlot J, Branson O, et al. Crustose coralline algae can contribute more than corals to coral reef carbonate production. Commun Earth Environ. 2023;4:1–12. https://doi.org/10.1038/s43247-023-00766-w.
192. Isaak AL, Ho M, Dhillon MS, et al. Macroalgal presence decreases coral calcification rates more than ocean acidification. Coral Reefs. 2024;43:1133–7. https://doi.org/10.1007/s00338-024-02515-7.
193. van der Heijden LH, Kamenos NA. Reviews and syntheses: calculating the global contribution of coralline algae to total carbon burial. Biogeosciences. 2015;12:6429–41. https://doi.org/10.5194/bg-12-6429-2015.
194. Moriarty T, Leggat W, Huggett MJ, Ainsworth TD. Coral disease causes, consequences, and risk within coral restoration. Trends Microbiol. 2020;28:793–807. https://doi.org/10.1016/j.tim.2020.06.002.
195. Thurber RLV, Silva D, Speare L et al. (2024) Coral Disease: Direct and Indirect Agents, Mechanisms of Disease, and Innovations for Increasing Resistance and Resilience. https://doi.org/10.1146/annurev-marine-011123-102337
196. Rinkevich B. Rebuilding coral reefs: does active reef restoration lead to sustainable reefs? Curr Opin Environ Sustain. 2014;7:28–36.
197. Rinkevich B. Augmenting coral adaptation to climate change via coral gardening (the nursery phase). J Environ Manage. 2021;291:112727. https://doi.org/10.1016/j.jenvman.2021.112727.
198. Legg S. IPCC, 2021: climate change 2021-the physical science basis. Interaction. 2021;49:44–5.
199. Velásquez J, López-Angarita J, Sánchez JA. Evaluation of the FORAM index in a case of conservation. Biodivers Conserv. 2011;20:3591–603. https://doi.org/10.1007/s10531-011-0152-7.
200. Leggat W, Whitney S, Yellowlees D. (2004) Is coral bleaching due to the instability of the zooxanthellae dark reactions? Symbiosis.
201. Young C, Schopmeyer S, Lirman D. A review of reef restoration and coral propagation using the threatened genus *Acropora* in the Caribbean and Western Atlantic. Bull Mar Sci. 2012;88:1075–98. https://doi.org/10.5343/bms.2011.1143.
202. Bayraktarov E, Banaszak AT, Maya PM, et al. Coral reef restoration efforts in Latin American countries and territories. PLoS ONE. 2020;15:e0228477. https://doi.org/10.1371/journal.pone.0228477.
203. Page CA, Muller EM, Vaughan DE. Microfragmenting for the successful restoration of slow growing massive corals. Ecol Eng. 2018;123:86–94. https://doi.org/10.1016/j.ecoleng.2018.08.017.
204. van Oppen MJH, Blackall LL. Coral Microbiome dynamics, functions and design in a changing world. Nat Rev Microbiol. 2019;17:557–67. https://doi.org/10.1038/s41579-019-0223-4.
205. Boström-Einarsson L, Babcock RC, Bayraktarov E, et al. Coral restoration – A systematic review of current methods, successes, failures and future directions. PLoS ONE. 2020;15:e0226631. https://doi.org/10.1371/journal.pone.0226631.
206. Burdett HL, Albright R, Foster GL, et al. Including environmental and Climatic considerations for sustainable coral reef restoration. PLOS Biol. 2024;22:e3002542. https://doi.org/10.1371/journal.pbio.3002542.
207. Lamb JB, van de Water JAJM, Bourne DG, et al. Seagrass ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates. Science. 2017;355:731–3. https://doi.org/10.1126/science.aal1956.

208. Shaver EC, Silliman BR. Time to cash in on positive interactions for coral restoration. PeerJ. 2017;5:e3499. https://doi.org/10.7717/peerj.3499.
209. Peixoto RS, Voolstra CR, Sweet M, et al. Harnessing the Microbiome to prevent global biodiversity loss. Nat Microbiol. 2022;7:1726–35. https://doi.org/10.1038/s41564-022-01173-1.
210. Castro-Sanguino C, Sánchez JA. Dispersal of *Symbiodinium* by the stoplight Parrotfish *Sparisoma viride*. Biol Lett. 2012;8:282–6.
211. Kamenos NA, Perna G, Gambi MC, et al. Coralline algae in a naturally acidified ecosystem persist by maintaining control of skeletal mineralogy and size. Proc R Soc B. 2016;283:20161159. https://doi.org/10.1098/rspb.2016.1159.
212. Neo ML, Eckman W, Vicentuan K, et al. The ecological significance of giant clams in coral reef ecosystems. Biol Conserv. 2015;181:111–23. https://doi.org/10.1016/j.biocon.2014.11.004.

Publisher's note