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Ocean Acidification: Understanding Coral Acclimatization through Phenotypic Plasticity

Biology * Environment * Climate Change

1. Introduction: The Ocean Acidification Crisis and the Plasticity Imperative

The Anthropocene epoch has ushered in a period of rapid environmental alteration, unparalleled in the recent geological history of the planet. Among the most insidious of these changes is the fundamental shift in the chemical composition of the Earth's oceans, a phenomenon known as ocean acidification (OA). As the global ocean absorbs approximately one-third of the anthropogenic carbon dioxide (CO₂) emitted into the atmosphere, a series of chemical reactions ensues, lowering seawater pH and reducing the saturation state of calcium carbonate minerals.[1] For marine calcifiers, and specifically for the scleractinian corals that engineer the biodiverse citadels of the tropical seas, this chemical shift represents an existential threat. The reduction in carbonate ions increases the thermodynamic cost of building the aragonite skeletons that form the reef framework, challenging the very physiological basis of coral existence.

The scientific consensus, forged through decades of laboratory experiments and field observations, predicts a decline in surface ocean pH of 0.3 to 0.4 units by the end of the 21st century under high-emission scenarios.[2] However, the biological response to this chemical trajectory is far from linear. Corals are not passive rocks eroding in acid; they are dynamic, living holobionts -- complex associations of a cnidarian host, photosynthetic dinoflagellates (Symbiodiniaceae), and a diverse microbiome.[3] They possess biological agency, the capacity to regulate their internal environment, and the potential to adjust their physiology in real-time. This capacity for adjustment within a single generation is known as phenotypic plasticity.[4]

The central question facing coral reef ecology today is whether this plasticity is sufficient to bridge the gap between the rapid rate of environmental change and the slower pace of evolutionary adaptation. Can corals "acclimatize" their way through the acidification crisis? The answer lies in a complex matrix of physiological trade-offs, energetic calculations, and molecular adjustments. This report provides a comprehensive deep-dive into the mechanisms of coral acclimatization, exploring the limits of physiological plasticity, the hidden costs of survival, and the potential for transgenerational resilience. By synthesizing data from genomic studies, energetic models, and natural "time machine" laboratories at volcanic CO₂ seeps, we evaluate whether the biological ingenuity of corals can outpace the relentless chemistry of a high-CO₂ world.

1.1 The Nature of the Threat: Carbonate Chemistry and Calcification

To understand the magnitude of the challenge, one must first appreciate the chemical

battlefield. When CO₂ dissolves in seawater, it forms carbonic acid, which rapidly dissociates into hydrogen ions (H⁺) and bicarbonate ions. The increase in hydrogen ions lowers the pH, making the water more acidic. Crucially, these hydrogen ions react with available carbonate ions to form more bicarbonate, thereby reducing the pool of carbonate ions available for calcification.[1]

Calcification, the process by which corals build their skeletons, relies on the precipitation of calcium carbonate crystals (aragonite). This precipitation is favored when the saturation state of aragonite (Ω_{arag}) is high -- typically greater than 3.0 in healthy tropical waters. As ocean acidification progresses and Ω_{arag} falls, the thermodynamic favorability of precipitation declines. Current models predict that by the year 2100, tropical surface oceans may have an Ω_{arag} of ~2.5, a level that historic data suggests is marginal for reef accretion.[5]

However, corals do not calcify directly in seawater. They create a specialized, biologically controlled compartment known as the extracellular calcifying fluid (ECF), located between the calcicoblastic epithelium and the existing skeleton. It is within this microscopic space that the battle for acclimatization is fought.

1.2 Defining the Terms: Acclimatization vs. Adaptation

It is vital to distinguish between the two primary biological responses to environmental stress:

* **Acclimatization (Phenotypic Plasticity):** This refers to the adjustments an individual organism makes during its lifetime to cope with environmental changes. These adjustments can be morphological (changing shape), physiological (altering metabolic rates), or biochemical (producing different enzymes).[4] Plasticity does not involve a change in the underlying DNA sequence but rather a change in how that DNA is expressed.

* **Adaptation (Evolutionary Rescue):** This refers to the change in the genetic makeup of a population over generations, driven by natural selection. Individuals with beneficial traits (genotypes) survive and reproduce more successfully, passing those traits to the next generation.[6]

While adaptation is the ultimate mechanism of species persistence, it is a slow process, constrained by generation times and genetic standing stock. The velocity of current ocean acidification -- occurring at a rate 10 to 100 times faster than past geological acidification events like the Paleocene-Eocene Thermal Maximum -- suggests that evolutionary rescue may arrive too late for many species.[7] Therefore, the immediate persistence of coral reefs in the coming decades depends heavily on the capacity for phenotypic plasticity.

2. The Cellular Machinery of Resistance: Regulating the Internal Milieu

The primary mechanism of coral acclimatization to acidification is the active upregulation of pH at the site of calcification. Corals are not conformers; they are regulators. To build skeletons in chemically hostile waters, they must manipulate the chemistry of their ECF to create conditions favorable for mineral precipitation, regardless of the external seawater pH.

2.1 The Proton Pump Mechanism

Recent advances in geochemical proxies, specifically the use of boron isotopes (^{11}B) to reconstruct internal pH, have revealed that corals elevate the pH of their calcifying fluid (pH_{cf}) significantly above ambient levels. In resilient genera such as *Porites* and *Montipora*, the pH_{cf} can be elevated by 0.4 to 0.7 units relative to the surrounding seawater.[8] This elevation shifts the carbonate equilibrium in favor of carbonate ions (CO_3^{2-}), raising the saturation state (Ω_{cf}) and facilitating the precipitation of aragonite crystals.[10]

This regulation is achieved through active ion transport across the calcicoblastic membrane. The central player is the Calcium-ATPase enzyme (Ca^{2+} -ATPase), which functions as an antiporter. This molecular pump actively transports calcium ions (Ca^{2+}) into the calcifying space while simultaneously removing two protons (H^+) for every calcium ion imported.[11] By pumping protons out of the ECF, the coral reduces acidity and drives the conversion of bicarbonate into carbonate, the essential building block of the skeleton.

2.2 The "Proton Flux Limitation" Model

While effective, this mechanism is constrained by thermodynamics. The "proton flux limitation model" posits that the efficiency of this pumping is determined by the gradient between the internal and external environments. As the external seawater becomes more acidic (higher concentration of H^+), the gradient against which the coral must pump protons steepens.[12]

Imagine a pump trying to push water uphill. As the hill gets steeper (lower external pH), the pump must work harder and consume more energy to move the same amount of water. In biological terms, this means that maintaining a high pH_{cf} in acidified seawater requires a greater expenditure of metabolic energy (ATP). If the gradient becomes too steep, the pump may simply be unable to overcome the thermodynamic barrier, leading to a collapse of the internal regulatory system and a cessation of calcification.[12]

2.3 Taxon-Specific Regulatory Capacities

Not all corals possess the same capacity for this physiological juggling act. The variability in regulatory control largely defines the "winners" and "losers" of the acidification era.

* The Stress-Tolerators (*Porites* spp.): Massive *Porites* corals are the paragons of pH regulation. Studies indicate that species like *Porites cylindrica* can maintain a near-constant pH_{cf} of ~8.4-8.6, independent of large external fluctuations or chronic acidification.[8] This powerful homeostasis allows them to continue calcifying even when seawater pH drops to levels that dissolve other organisms. However, this stability is not absolute; it is maintained only as long as the coral has sufficient energy reserves.

* The Weedier Calcifiers (*Acropora* spp.): Branching *Acropora* species, which provide much of the three-dimensional complexity on healthy reefs, often operate with lower regulatory overhead but higher baseline calcification rates. They are "fast growers" rather than "strong regulators." Under acidification stress, *Acropora* species

frequently show a sharper decline in calcification performance compared to Porites, likely because their rapid growth demands an energy budget that cannot sustain the increased costs of pH upregulation.[13]

* The Deep-Water Specialists (*Desmophyllum pertusum*): Cold-water corals, which lack photosynthetic symbionts, face a stricter energetic bottleneck. Their ability to upregulate pH_{cf} is entirely dependent on heterotrophic energy input. Unlike their tropical cousins, which can potentially divert photosynthetic energy to the proton pumps, *Desmophyllum* must eat to calcify. Consequently, their resilience is tightly coupled to food availability, making them highly vulnerable in nutrient-poor waters.[14]

2.4 The Role of Proteomic Plasticity

Beyond ion transport, acclimatization involves a restructuring of the cellular proteome. Proteomic analyses of corals exposed to high CO₂ reveal complex adjustments in the abundance of proteins related to metabolism, structure, and stress response.

A fascinating, and somewhat counterintuitive, finding is the downregulation of molecular chaperones (such as heat shock proteins) in some acclimatized populations.[15] Typically, stress induces the expression of these proteins to repair damaged cellular components. However, in *Acropora millepora* populations naturally acclimatized to high CO₂ at volcanic seeps, these chaperones are constitutively downregulated. This may represent a metabolic trade-off: by suppressing the costly "emergency response" system, the coral conserves energy for the relentless demand of proton pumping.[15] This strategy, often termed "front-loading" or "metabolic depression," allows for survival in chronic stress but may leave the coral dangerously exposed to novel acute stressors, such as heat waves.

Other proteomic studies have highlighted the upregulation of proteins associated with the extracellular matrix (ECM). ECM proteins, such as collagen-like molecules, play a critical role in nucleation -- the seeding of crystals. Under acidification stress, some corals modify the composition of their organic matrix to facilitate crystal formation even in less favorable chemical conditions.[17] This suggests that plasticity is not just about pumping ions, but also about engineering the organic scaffold upon which the skeleton is built.

3. The Energetic Calculus: Costs and Trade-offs

Acclimatization is never free. The overarching theme of coral responses to OA is the concept of trade-offs. The laws of thermodynamics dictate that energy used to power proton pumps or repair cellular damage must be diverted from other biological functions. This reallocation of resources shapes the phenotype of the acclimatized coral.

3.1 The Energy Cost of Calcification

Historically, the energetic cost of precipitation was thought to be relatively low. However, refined estimates incorporating the cost of active ion transport suggest that calcification may account for up to 30% of a coral's total metabolic

budget.[18] Under OA conditions, this cost rises. To maintain the same rate of calcification in lower pH water, a coral must burn more ATP.

If the coral cannot increase its energy intake (via enhanced photosynthesis or feeding), it faces a deficit. This deficit manifests in several critical trade-offs:

- * Skeletal Density vs. Linear Extension: The "Coralporosis" effect.
- * Reproduction vs. Somatic Maintenance: The generational debt.
- * Immunity vs. Regulation: The health compromise.

3.2 "Coralporosis": The Structural Trade-off

One of the most insidious effects of OA is the decoupling of linear extension from skeletal density. For decades, coral growth was measured primarily by how fast the branches lengthened (linear extension). However, recent high-resolution CT scanning studies have revealed a disturbing trend: corals often maintain their linear extension rates under acidification but produce significantly more porous skeletons.[2]

This phenomenon, termed "coralporosis," represents a strategic trade-off. For a coral, maintaining height is crucial for competing with algae and other corals for light and water flow. Therefore, the organism prioritizes extension, spreading its limited calcification budget over a larger volume.[20]

* Mechanism: The coral continues to build the scaffold of the skeleton but reduces the infilling of the micro-architecture. This results in a skeleton that is visually normal but structurally compromised.

* Consequences: Low-density skeletons are brittle and fragile. They are more susceptible to breakage during storms and less resistant to bioeroding organisms like sponges and worms.[2] While the reef may appear to be growing, its functional integrity is eroding from the inside out. This "osteoporosis of the reef" undermines the ecosystem service of coastal protection, as fragile reefs cannot effectively dissipate wave energy.[21]

3.3 Reproductive Trade-offs

Energy diverted to pH regulation is often stolen from the reproductive budget. Gametogenesis (the production of eggs and sperm) is an energy-intensive process, particularly the production of lipid-rich eggs.

* Gamete Quality: In Acropora species exposed to high CO₂, researchers have observed reductions in egg size and sperm motility.[22] Smaller eggs have fewer lipid reserves, which translates to lower survival rates for the resulting larvae.

* Recruitment Failure: If larvae start life with a depleted energy pack, their ability to survive the planktonic phase, settle, and metamorphose is compromised. This creates a "demographic debt" -- adult corals may survive and acclimatize, but they fail to replenish the population, leading to a slow-motion collapse.[23]

3.4 The Heterotrophy Rescue Hypothesis

Can corals eat their way out of the acidification crisis? The "heterotrophy rescue

hypothesis" suggests that enhanced feeding on zooplankton could provide the surplus energy needed to fuel the proton pumps without compromising other functions.[24]

Evidence from the Mediterranean coral *Cladocora caespitosa* supports this view. Colonies at CO₂ vent sites in Ischia were found to maintain their calcification rates by significantly increasing their feeding rates and biomass compared to conspecifics in ambient water.[25] This suggests a physiological plasticity where the coral shifts from a reliance on symbiont-derived sugars to heterotrophic protein and lipid intake.

However, this rescue mechanism is contingent on food availability. In the oligotrophic (nutrient-poor) waters of many tropical reefs, zooplankton concentrations may be insufficient to support this increased demand. Furthermore, stress can sometimes impair the polyp's feeding behavior, reducing capture efficiency and rendering the rescue mechanism ineffective.[14] Thus, while heterotrophy offers a pathway for resilience, it is not a universal panacea.

4. The Holobiont Response: Microbial and Symbiotic Shifts

The coral is not an individual; it is a consortium. The response to OA involves the entire holobiont, including the Symbiodiniaceae and the bacterial microbiome.

4.1 Symbiodiniaceae: Shuffling for Survival?

Corals host various genera of Symbiodiniaceae (e.g., *Cladocopium*, *Durusdinium*), which differ in their thermal tolerance and nutritional contributions. The "adaptive bleaching hypothesis" suggests that corals can shuffle these communities to favor more tolerant strains under stress.

While well-documented for thermal stress, the response to acidification is more ambiguous. In *Pocillopora damicornis*, transgenerational exposure to high CO₂ did not trigger a significant shift in the dominant symbiont communities, suggesting that pH alone may not be a strong driver of symbiont shuffling compared to temperature.[27] However, other studies suggest that the stability of the symbiosis is crucial. Disruption of the symbiosis (bleaching) immediately halts the energy supply to the proton pumps, making calcification impossible.[14] Therefore, the maintenance of a robust symbiont community is a prerequisite for the energetic support of acclimatization.

4.2 The Microbiome: A Sentinel of Health

The bacterial component of the holobiont is highly sensitive to pH changes. A healthy coral microbiome is often dominated by specific beneficial associates, such as bacteria from the genus *Endozoicomonas*. These bacteria are thought to play roles in nutrient cycling and the production of antimicrobial compounds.

Research at natural CO₂ seeps has revealed a concerning trend: acidification often leads to the loss of these beneficial microbes and a rise in opportunistic pathogens.

* The *Endozoicomonas* Decline: In sensitive species like *Pocillopora* at the Maug CO₂ seeps, the abundance of *Endozoicomonas* plummeted as pH decreased. This loss was correlated with a destabilization of the microbiome and signs of host stress.[28]

* Microbial Homogenization: Under high CO₂ conditions, the distinct microbiomes of different coral species tend to converge, becoming more similar to the microbial communities of the surrounding water and sediment. This "homogenization" suggests a breakdown in the host's ability to regulate its specific microbial partners, potentially opening the door to disease.[29]

* Resilience via Stability: In contrast, resilient *Porites* corals at the same seeps maintained stable *Endozoicomonas* populations even at low pH.[28] This suggests that the ability to maintain microbiome homeostasis is a key trait of OA-tolerant phenotypes.

5. Transgenerational Acclimatization: Hope or Hype?

If plasticity within a single lifetime has limits, can the experience of the parents prime the offspring for success? Transgenerational acclimatization (TGA) refers to non-genetic inheritance where parental exposure to an environmental cue alters the phenotype of the offspring to be better suited to that environment.[30]

5.1 Mechanisms of Soft Inheritance

TGA is mediated by epigenetic mechanisms such as DNA methylation, histone modification, and the transmission of maternal factors (proteins, mRNA, nutrients) in the egg.

* DNA Methylation: Research on *Pocillopora damicornis* has shown that individuals exposed to low pH exhibit distinct DNA methylation patterns compared to controls. These epigenetic marks can modify gene expression without changing the DNA sequence, potentially allowing for rapid functional adjustments.[31] Interestingly, "environmentally sensitive" species often show more dramatic methylation changes than resistant ones, suggesting that epigenetics serves as a rapid response system for those lacking robust constitutive defenses.[31]

5.2 Evidence for TGA

The evidence for adaptive TGA in corals is compelling but mixed.

* The Positive Case: In a landmark study, *Pocillopora damicornis* parents were exposed to high CO₂ and temperature during the brooding period. Their larvae, when reared in the same high-CO₂ conditions, exhibited improved metabolic rates and survival compared to larvae from naïve parents.[33] This suggests that the parents were able to "condition" their offspring, possibly through epigenetic tagging or metabolic provisioning, to handle the stress.

* The Negative Carryover: However, TGA is not always beneficial. In some cases, the stress experienced by the parents results in "negative carryover effects." For example, in the gastropod *Hexaplex trunculus*, parental exposure to low pH significantly delayed larval development and reduced the likelihood of hatching.[35] Similarly, in the Pacific oyster *Crassostrea gigas*, maternal exposure to low pH resulted in significantly fewer larvae, indicating that the energetic cost of stress on the mother compromised her reproductive output.[36]

5.3 The Limits of Parental Provisioning

The success of TGA likely depends on the severity of the stress and the energetic status of the parent. If the parent is mildly stressed but energetically intact, it may invest in epigenetic programming or high-quality eggs (a "predictive adaptive response"). However, if the stress is severe enough to deplete the parent's energy reserves, the offspring will suffer from poor provisioning (smaller eggs, fewer lipids), leading to reduced fitness regardless of any epigenetic benefits. Thus, TGA may "buy time" for one or two generations, but it is unlikely to sustain a population indefinitely if the environmental pressure remains chronic and severe.[37]

6. Windows to the Future: Lessons from Natural CO₂ Seeps

To understand the long-term ecological consequences of acclimatization (or the lack thereof), scientists turn to natural "time machines": volcanic CO₂ seeps. Sites in Papua New Guinea (PNG), Japan, and Ischia (Italy) release pure CO₂ into the water column, creating localized gradients of acidification that have persisted for decades or centuries. These sites allow us to observe the outcome of long-term exposure, filtering out short-term shock responses.

6.1 The "Winners" and "Losers"

The community shifts observed at these seeps provide a sobering preview of future reefs. The response is characterized by a dramatic simplification of the ecosystem.

- * The Loss of Complexity: Branching corals, particularly the fast-growing *Acropora* and *Seriatopora* species that provide the complex thickets for fish nurseries, are the first to disappear. They are the "losers" of the acidification lottery, unable to sustain their high calcification demands.[38]

- * The Rise of the Boulders: The "winners" are almost invariably massive *Porites* species. These corals come to dominate the high-CO₂ zones, forming large, monolithic boulder fields. As discussed, their success is attributed to their superior ability to upregulate pH_{cf} and their thick tissue layers which may protect the skeleton from external dissolution.[38]

- * The Phase Shift: In temperate systems like Ischia, the shift is even more profound. Calcifying organisms (corals, coralline algae) are largely replaced by non-calcifying fleshy algae and seagrasses (*Posidonia*). The reef ecosystem effectively transitions from a hard-bottom carbonate system to a soft-bottom algal system.[41]

6.2 The Hidden Costs of Winning

Even the "winners" at these seeps are not unscathed. While massive *Porites* persist, detailed analysis reveals that their skeletal density is often reduced by up to 20% compared to conspecifics at control sites.[2] They are growing, but they are osteoporotic. Furthermore, these corals often show higher rates of bioerosion and susceptibility to storm damage.

This observation is critical: it implies that even after generations of exposure, full acclimatization -- where the organism functions entirely normally -- is rarely

achieved. The physiological stress persists, imposing a chronic tax on the coral's energy budget that manifests in subtle but structurally significant ways.

6.3 Ecological Cascades

The simplification of the coral community has cascading effects on the wider ecosystem. The loss of branching corals removes the architectural complexity of the reef. Studies at PNG seeps show a decline in the diversity and abundance of reef fish, particularly small habitat-specialists that rely on coral branches for protection.[43] The "flattening" of the reef reduces the available niche space, leading to a functional collapse of the ecosystem's biodiversity even if coral cover (in the form of boulders) remains relatively high.

7. The Synergy Trap: Warming Meets Acidification

Perhaps the most daunting aspect of the coral crisis is that ocean acidification does not occur in isolation. It is the "evil twin" of ocean warming. The interaction between these two stressors is often synergistic -- the combined lethality is greater than the sum of the parts.

7.1 The Bleaching-Acidification Feedback

Thermal stress causes coral bleaching -- the expulsion of the symbiotic algae. This event is catastrophic for acclimatization to acidification.

- * Energy Cutoff: The proton pumps required to fight OA are powered by ATP derived from algal photosynthesis. When a coral bleaches, this energy source is cut off.
- * Regulatory Collapse: Without energy, the proton pumps fail. The pH_{cf} drops, and calcification ceases. In many cases, the skeleton begins to dissolve.
- * Narrowed Tolerance: Conversely, the metabolic strain of fighting OA leaves the coral with fewer resources to produce the heat shock proteins and antioxidants needed to resist thermal stress. This "narrowing of thermal tolerance" means that corals in acidified waters may bleach at lower temperatures than they would in normal waters.[16]

7.2 Modeling the Limits of Evolutionary Rescue

Can evolution rescue corals from this synergistic trap? Eco-evolutionary models that incorporate both symbiont shuffling and host evolution offer a glimmer of hope, but with severe caveats.

- * The Lag: Evolution requires time. Models suggest that while adaptive processes can delay extinction, there is a significant "lag" phase where populations decline precipitously before adapted genotypes can proliferate.[45]
- * The Bottleneck: Frequent marine heatwaves act as a blunt instrument, killing adults indiscriminately. This reduces the effective population size, creating a genetic bottleneck that strips away the diversity required for natural selection to operate efficiently. Under high-emission scenarios (RCP 8.5), the rate of warming and acidification simply outpaces the biological maximum for evolutionary adaptation.[6]

Table 1: Comparative Acclimatization Strategies and Outcomes

Coral Group	Key Mechanism	Physiological Cost	Ecological Outcome (Seeps)
Massive Porites	Strong pH _{cf} upregulation (ion pumps)	Reduced skeletal density ("coralporosis")	Winner: Dominates high CO ₂ zones; forms boulder fields.
Branching Acropora	Rapid calcification; limited regulation	High ATP demand; metabolic burnout	Loser: Rare or absent; susceptible to dissolution.
Pocillopora	Epigenetic plasticity; TGA potential	Reproductive trade-offs; microbiome instability	Variable: Persistence depends on local context and TGA.
Cladocora (Temperate)	Heterotrophy rescue (increased feeding)	Dependent on plankton availability	Resilient: Maintains calcification if food is abundant.
Astroides (Asymbiotic)	Heterotrophy only	No photosynthetic subsidy; metabolic cost	Vulnerable: Shows decline in calcification/abundance.

8. Conclusion: The Limits of Resilience

The comprehensive body of evidence from cellular biology to ecosystem ecology points to a nuanced but sobering conclusion. Corals possess a remarkable capacity for phenotypic plasticity. Through the upregulation of ion pumps, the restructuring of proteomes, the shuffling of symbionts, and epigenetic adjustments, many species can maintain calcification and survival in acidified waters that would have been thought lethal a decade ago.

However, this acclimatization is not a magic bullet. It is a biological negotiation with strict thermodynamic limits.

- * Acclimatization creates trade-offs: The maintenance of growth comes at the cost of skeletal density ("coralporosis") and reproductive output.
- * Acclimatization has a ceiling: Even the most resilient "super-corals" at natural seeps show signs of chronic stress and structural weakness.
- * Acclimatization is vulnerable to synergy: The energy-dependent mechanisms of acid resistance are easily toppled by the energy-depriving effects of thermal bleaching.

Can acclimatization outpace ocean acidification? In the short term, and for specific "weedy" or stress-tolerant species like Porites, the answer is a qualified yes. These corals will likely persist, creating a new type of reef ecosystem. But for the complex, diverse, three-dimensional coral reefs that humanity values for fisheries, tourism, and coastal protection, the answer appears to be no. The velocity of chemical change, particularly when coupled with warming, exceeds the physiological bandwidth of the majority of reef-building taxa.

The future of coral reefs will likely define a "new normal" -- a simplified, flatter, and less diverse ecosystem. While plasticity and epigenetics provide a crucial buffer -- a way to buy time -- they cannot indefinitely compensate for the rapid chemical alteration of the global ocean. The ultimate survival of these ecosystems depends not on the unlimited flexibility of coral biology, but on the

mitigation of the global carbon emissions driving the change.

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