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REVIEW ARTICLE

Microfragmentation as a Coral Reef Restoration Tool: The Role of Genetics, Microbiomes, and Climate Challenges

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ABSTRACT: Coral reefs, vital elements of marine ecosystems, are facing unprecedented challenges posed by the detrimental effects of climate change. Microfragmentation, a newly developed restoration technique that uses controlled coral specimen fragmentation and reattachment to accelerate coral growth, promises to boost reef rehabilitation efforts. This review collates the current knowledge about the effect of holobiont interactions, genetic diversity, and evolutionary processes on coral survival under environmental stress before and after microfragmentation. While investigating the role of microbiome-mediated mechanisms such as stress reduction and nutrient cycling in coral regeneration, the study elucidates the mechanisms by which genetic variety improves coral resilience and adaptability. The interdependence between holobiont dynamics and coral genetics emphasizes the need for all-encompassing restoration approaches that incorporate biological and environmental elements. Despite the fact that microfragmentation is effective in encouraging rapid coral growth, its effectiveness is currently limited by issues such as predation vulnerability and a lack of long-term field studies. This review contributes to the growing body of knowledge on coral reef conservation by providing evidence-based strategies for improving reef resilience in a marine environment prone to the deleterious effects of rapid global warming.

KEYWORDS: Coral Reef Restoration, Microfragmentation, Evolutionary Genetics.

Introduction

Coral reef ecosystems are critical marine habitats that contribute immensely to biodiversity. However, these extensive and ecologically noteworthy benthic structures are facing unprecedented anthropogenic threats that jeopardize their long-term viability. These intricate biogenic structures comprise innumerable limestone-secreting organisms known as polyps, belonging to the phylum[1] Cnidaria, interconnected via 'coenosarc', a connective tissue. Corals have crucial symbiotic relationships with various algal species, most notably zooxanthellae. These algae photosynthesize within the safety of the coral bodies and produce essential nutrients like carbohydrates and oxygen, pivotal to the nourishment of the corals.[2] Zooxanthallae also facilitate the removal of metabolic waste products, thus helping the corals to thrive.

In addition to their ecological importance, coral reefs contribute significantly to the protection of coastlines from powerful tidal waves, thereby preventing erosion and mitigating the impact of storms.[3] Coral systems are sensitive and are significantly impacted by changes in environmental conditions such as ocean acidification, temperature fluctuations, and increased water toxicity, which threaten coral growth and development. These stressors result in coral bleaching, a process in which the symbiotic algal species are expelled from the coral bodies, severely compromising coral health and making the coral vulnerable to disease and mortality.[4]

Additionally, the weakening ozone layer causes excessive quantities of ultraviolet light to penetrate oceans, further contributing to coral bleaching due to the formation of toxic active oxygen species.[5] Furthermore, accelerated urbanization resulting in coastal development and pollution smothers corals with fine sediments, impeding photosynthesis and triggering harmful algal blooms. Such intense changes have the potential to wipe out entire coral colonies, disrupting the harmony of marine life. The impact of the environmental stressors on the delicate nature of the ocean ecosystem also goes beyond the coral reefs and has a detrimental effect on several marine species, such as clownfish and sea anemones, that rely on the coral reefs for their survival.

Corals are largely dependent on coral microbiomes for resilience in the face of stressors and for their ability to adapt for survival under hostile conditions. However, beneficial microbial associations are often severed due to the disrupted marine ecosystem, resulting in the proliferation of pathogenic microbial colonization, tipping the scales against the survival of healthy coral ecosystems.[6,7] The widespread decline of coral reefs worldwide has prompted scientists and conservationists to investigate the multifaceted interactions between evolutionary processes, environmental stressors, and novel conservation strategies.

Clonality is a hallmark characteristic of corals. They can entire colonies from a single polyp through asexual budding. This inherent ability to clone themselves makes them great candidates for the implementation of fragmentation techniques. Coral fragments that break off due to storms or physical damage reattach to substrates and continue growing, forming new colonies that are genetically identical to the parent coral. Microfragmentation is a unique coral restoration technique in which coral polyps are severed into 4-5-inch-thick fragments and attached to artificial surfaces to promote logarithmic growth. This technique leverages the clonality of corals to achieve the restoration of corals.

However, this process is influenced by the genomic configuration, the coral species, and other biotic factors such as enzyme and hormone biokinetics. Adding to the hurdles faced in ensuring successful microfragmentation is the pivotal role that microbiomes associated with the corals play in their resilience and health. Therefore, altered microbiome species caused by differences from the marine environment also affect the success rate of coral microfragmentation.[7,8]

Our review aims to explore the complex relationships between evolutionary mechanisms, environmental stressors, and the process of coral microfragmentation. We searched peer-reviewed literature using the key search terms 'microfragmentation', 'coral restoration', 'coral microbiome', 'coral clonality', and 'coral genetic diversity' in Google Scholar and PubMed. Although we have included some relevant older literature, studies published 2015 onwards were prioritized. References were shortlisted based on their direct relevance to research related to microfragmentation techniques, coral clonality, genetic diversity in corals, coral resilience in the face of climate challenges, and the coral microbiome. Our study investigates the effect of the changes in coral genomes and their associated microbiomes, resulting from evolutionary mechanisms and environmental stressors, on microfragmentation processes. Knowledge of these interactions will better inform conservation strategies and potentially improve the effectiveness of coral restoration techniques in the face of ongoing environmental challenges.

Discussion

Microfragmentation: Hope or Hindrance?

The deterioration of reef systems worldwide caused by ecological stressors warrants their immediate restoration to prevent severe damage to marine ecosystems and the diverse organisms that depend on them for survival. Scientists are now implementing microfragmentation techniques to revive corals previously considered irreversibly bleached. This innovative process aims to stimulate exponential growth in growth-impaired corals and rejuvenate dead corals by reskinning.

Coral fragments with a surface area of approximately 5 cm^2 demonstrate double the growth rate of those with a surface area of 1 cm^2. Based on this, measured coral fragments are secured to frames or ceramic disks using cyanoacrylate adhesive and replanted in the ocean. The fragmented and replanted corals are monitored biweekly for growth indicators for nine weeks. The fragmented corals regrow and fuse with neighboring fragments, establishing large colonies at an accelerated rate compared to natural growth. Once these colonies reach sufficient size, they regain sexual maturity and are capable of reproduction.[9]

While microfragmentation shows promise, several factors influence its success rate and post-fragmentation reef health. Lack of genetic diversity in the coral populations resulting from microfragmentation may result in the proliferation of genetically uniform corals rather than resilient populations. Additionally, the rapid growth induced by microfragmentation may compromise coral immune systems by diverting resources and energy from the development of defense mechanisms to microfragmentation-induced rapid growth. Through natural selection, coral populations with diverse genetic expressions demonstrate enhanced resistance to disease outbreaks, ocean acidification, and other environmental stressors. This supports survival in suboptimal conditions, potentially leading to higher success rates of the microfragmentation process and improved reef restoration outcomes. Sexual reproduction promotes more genetic diversity than asexual reproduction in fragmented corals, increasing coral abundance and inheritance of beneficial properties, contributing to long-term reef recovery and survival.[10] Differences in growth rates exhibited by different coral genera and species make universal standardization and implementation add to the challenges associated with the microfragmentation technique.[11]

The composition of the coral-associated microbiome plays a significant role in improving coral health post-fragmentation. The addition of a beneficial microbial consortium enhances certain important physiological processes, particularly calcification rates. Accelerated calcification reduces coral vulnerability by creating a protective coating, which is crucial during and after restoration. Corals treated with certain beneficial bacteria, such as ones from the *Yangia* and *Salinicola* genera, demonstrate a 33% higher rate of calcium deposition and increased protein concentrations. These enhancements facilitate rapid regrowth in coral fragments, reducing their susceptibility to infection and improving nutrient recycling efficiency.[12]

Coral genetic diversity and resilience

Corals reproduce via broadcast spawning, a unique process of sexual reproduction that involves the release of the male and female gametes into the water column, followed by fertilization in the presence of favorable conditions, resulting in the formation of the larval stage of corals known as planulae. Initially, the planulae are extremely sensitive to sunlight, exhibit positive phototaxis, and swim in the surrounding waters, eventually settling at the bottom of the ocean and transmuting into coral polyps.[13] Broadcast spawning facilitates the transfer of genetic material between different coral species, resulting in the production of offspring with inherited genes that are a unique combination of the parental traits. The offspring are thus genetically diverse and have enhanced abilities to adapt to disease and various environmental stressors such as changes in pH, temperature, and pollution.[14,15] However, increasing environmental stressors negatively impact the success rate of sexual reproduction in corals. Decreasing coral populations, in addition to elevated temperatures and increased exposure to UV radiation, induce oxidative stress in coral tissues, which may cause the next generation to have limited genetic variability, causing offspring to be depauperate and be compromised in their ability to adapt to environmental stressors.[16]

Environmental stressors, particularly elevated temperatures and increased UV radiation, induce oxidative stress in corals, potentially resulting in DNA damage. The persistent impact of climate change on these organisms compromises their

DNA repair mechanisms, resulting in increased mutations and heightened sensitivity in subsequent generations. Rising temperatures have also been shown to impair coral reproductive capacity.[17] In addition, environmental stressors such as pH fluctuations and increased water toxicity may result in the activation of mobile nucleotide sequences, known as transposable elements. Deleterious mutations are known to result from the transposable elements inserting themselves into a gene.[18] In the face of extreme environmental stressors, only the most resilient corals continue to adapt and successfully reproduce, causing the gene pool to become narrower and reducing the overall biodiversity in aquatic ecosystems.

A diverse array of traits within a genetically diverse population increases the probability of characteristics favorable for survival under changing conditions being present in that population. Equipped with survival-supporting genetic traits, coral populations can potentially adapt to stressors such as temperature fluctuations.[19] Furthermore, genetic diversity enhances disease resistance within coral populations, resulting in a wider range of immune responses and defense mechanisms such as the production of antimicrobial compounds, improved tissue repair, and stronger symbiotic relationships with beneficial microorganisms. Genetic diversity, thus, equips corals with increased adaptive potential, disease resistance, and overall resilience.[20]

The Coral Microbiome: Tiny Partners, Big Impact

Corals establish diverse mutualistic relationships that enhance their survival capabilities and adaptation to novel environments. While associations with sea sponges or reef sharks involving nutrient exchange and mutual support are macroscopic, some microscopic relationships within coral microbiomes are also crucial for the functioning of reef ecosystems. In addition to zooxanthellae, coral microbiomes also comprise bacteria and archaea, which exhibit distinct spatial distribution patterns across various reef compartments, including sediments, water columns, coral tissues, and skeletal structures. The coral holobiont demonstrates significant spatial heterogeneity in its microbial composition, reflecting the diverse functional roles these microorganisms play in reef survival. While some microorganisms facilitate primary production through photosynthesis, others are pivotal to essential processes such as cell signaling, motility, and nitrogen cycling. Multiple environmental parameters, including silicate or carbonate presence, depth gradients, and geographical location, influence the distribution of bacterial communities within reef sediments and water columns and significantly affect the metabolism of the microbial communities.

The composition of the coral microbiome differs from the microorganisms in surrounding waters and sediments. While oligotrophic bacteria that thrive in nutrient-deficient environments, recycle nutrients, and fixing nitrogen and carbon cycles predominate the outer reef crest and are crucial facilitators of coral nutrition, copiotrophic bacteria that thrive in nutrient-rich environments and contribute to the degradation of pollutants and algal blooms provide protective functions for coral polyps.[21] The contrast between the roles and resilience of micro- and macroorganisms associated with corals is also noteworthy. Coral-associated microbes protect the production of antimicrobial compounds and competitive exclusion of pathogenic microorganisms, in addition to providing nutrition through phosphorus cycling and various catabolic processes. These microbial populations can rapidly adapt in response to environmental stressors and enhance holobiont survival.[22] On the other hand, macroorganisms serve more limited functions, primarily removing parasites and dead tissue from coral surfaces. They exhibit lower resilience and greater vulnerability to increasing ecological disturbances.

The coral genome specifies the metabolic and physical requirements and plays a fundamental role in determining the microbiome composition. Certain genetic factors also influence the recruitment and retention of microbial colonies, as seen in the *Poscillopora damicornis* and *Acropora coral* species that selectively facilitate the growth of the beneficial bacteria, *Endozoicomonas*, which enhance nutrient cycling and stress response mechanisms in the coral species.[23] Corals express genes that enhance antioxidant defense systems, synthesize surface proteins that selectively mediate the inclusion or exclusion of microorganisms, and optimize metabolic interactions with symbiotic zooxanthellae in response to extreme thermal stress and other environmental stressors.

The overall organization of the microbial community is influenced by the differences in the abilities of the various bacteria to colonize and proliferate within the holobiont, resulting in species-specific responses among coral species.[22,24] This intricate relationship between coral genetics and microbial community assembly underscores the complexity of host-microbe interactions in coral reef ecosystems.

Evolving Together: Dynamic Coral-Microbe Relationships

The maintenance of homeostatic conditions within the holobiont is crucial for enabling microbiome adaptation concurrent with coral responses to ecological pressures. Notably, coral immune systems demonstrate refined selectivity over time to retain beneficial bacteria such as *Endozoicomonas* that secrete steroid hormones, which catalyze the breakdown of toxic reactive oxygen species to less harmful compounds during thermal stress. Reciprocal adaptation enables corals to selectively filter out less useful microorganisms, optimizing the microbiome composition of the holobiont to maximize mutual benefits.

Significant codivergence has been observed between *Endozoicomonas* bacteria and their coral hosts, resulting in stable, long-term symbiotic relationships. Furthermore, critical metabolic functions in coral reefs, including calcification and nitrogen fixation, are mediated by metabolic collaborators.[25,26] These collaborations facilitate nutrient production tailored to the requirements of the coral host, thereby compensating for metabolic capabilities absent in the coral. The genetic traits of corals play a pivotal role in regulating microbial populations, thereby preventing detrimental microbial overgrowth and maintaining a community composition aligned with its physiological requirements.[26] as the impact of climatic stressors, including oceanic acidification and elevated temperatures

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on the holobiont causes the coral to exhibit significant changes in genomic expression and immune responses.

Photosymbionts such as *Symbiodinium* demonstrate rapid evolutionary adaptability and modulate the composition of the microbiome in a manner conducive to enhanced thermal tolerance for the host coral. The microbial component of the holobiont has shorter generation times and high mutation rates due to its simplicity in size and function. While this facilitates rapid reproduction compared to the coral host, the high mutation rates result in frequent errors during DNA replication that are less likely to be corrected and have the potential to provide significant evolutionary advantages to the holobiont, increasing resilience to environmental challenges.[27,28] These symbiotic organisms also reduce the carbon requirements of the host corals in oligotrophic environments, thereby optimizing nutrient cycling. This enables corals to colonize and thrive in otherwise inhospitable environments, providing more opportunities for growth and regeneration.[28]

Implications for Reef Conservation

The interplay of factors affecting reef restoration is crucial to the optimization of microfragmentation procedures. Coral populations with varying genomic compositions respond differently to restoration processes, demonstrating varying abilities to acclimatize to changing conditions and nutrient availability.[27] The beneficial microbial population within the coral microbiome provides protection against pathogenic bacteria, enhances their ability to recycle nutrients, and initiates nitrogen fixation in oligotrophic waters.[28]

However, environmental challenges such as rising sea temperatures and oceanic acidification weaken the coral microbiome and have deleterious effects on immune responses to microfragmentation processes. These stressors also have the potential to slow coral growth during the restoration process, further emphasizing the importance of the interplay of ecological factors and stressors. Furthermore, genetic homogeneity among corals can have detrimental effects on their ability to respond to environmental changes. The microbial communities associated with the corals also influence the recovery rate of corals in stressful conditions. Thus, a comprehensive understanding of all the interconnected factors is pivotal for achieving better outcomes post-fragmentation and improving the success of reef restoration efforts. Larval enhancement, a reef restoration approach that complements microfragmentation, focuses on improving coral survival during the early developmental stages by enhancing larval growth and fertility rates. This approach improves genetic diversity among corals and supports the long-term effectiveness of microfragmentation. However, changes in the genetic diversity of corals induced by larval enhancement can alter the coral-associated microbiome composition, potentially compromising coral resilience to environmental changes. Furthermore, the insufficiency of appropriate substrate for the coral larvae to latch onto and grow can also directly impact the survival rate of these coral larvae.[29] Despite these potential hurdles, continuing research and development for reef restoration techniques ensure a collective increase in the likelihood of sustaining and recovering reef colonies globally.

■ Strengths and Limitations

This review demonstrates several strengths in its analysis of microfragmentation-based coral restoration. It highlights the connections between coral genetics, microbiome composition, and the effectiveness of microbiome-based restoration, thereby providing valuable insights for future conservation efforts. The review integrates existing knowledge on microfragmentation with the emerging results of research on coral-microbe interactions, thereby providing a holistic perspective on reef restoration. The investigation of multiple restoration approaches combined with a comprehensive assessment of the biological and environmental factors affecting reef recovery further strengthens the practical applications of the review. Furthermore, the integration and analysis of findings from several studies derived from this review provide actionable insights for restoration practitioners.

Despite the significant contributions of the study, it is important to acknowledge several limitations. Existing research lacks sufficient long-term data on outcomes of microfragmentation across different coral species and environments, limiting the ability of this review to predict long-term success rates.

The understanding of the specific mechanisms governing coral-microbe interactions during restoration remains obscure, warranting further investigation. The absence of standardized protocols for assessing restoration success across different geographical regions hinders comparative analysis and optimization of techniques. Additionally, current research provides limited insight into the cost-effectiveness and scalability of combined restoration approaches. Finally, there is a pressing need for more comprehensive research on the impact of climate change on restoration outcomes, particularly as marine environments continue to face increasing stressors.

■ Conclusion

This review elucidates the complex interplay between the coral holobiont, environmental stressors, and genetic expression, factors that are crucial to the success of restoration of coral reefs through microfragmentation. The findings underscore the ability of corals to maintain beneficial microbes and genetic traits during reproduction, enhancing their chances of survival under changing environmental conditions. The study also emphasizes the crucial role of evolutionary dynamics and microbial interactions in contemporary reef recovery efforts.

The exponentially increasing challenges associated with the conservation and preservation of reefs have warranted the need for unique and determined preservation efforts. In addition to being indisputable biodiversity hotspots, coral reefs also contribute significantly to oceanic health by facilitating the cycling of nutrients and maintaining the marine ecosystem. The preservation of coral diversity and the sustenance of their mutualistic relationships are indispensable to prevent the ecosystem from collapsing and to enhance the long-term results of microfragmentation as an effective restoration strategy.

The insights that have emerged from this review contribute significantly to the existing knowledge of coral resilience in the face of deteriorating conditions of the marine environment. This review navigates the complex labyrinth of interconnections between the factors crucial for the success of micro fragmentation as an effective reef rehabilitation and restoration strategy that would stand the test of time and increasing environmental challenges. The interpretations derived from the findings of the study enunciate both the limitations and advantages of reef rehabilitation methods.

Further research into species-specific responses, standardization of restoration protocols, and investigation of the long-term effects on the restored coral reefs, enzyme activity within the reefs, and the health of the marine ecosystem could improve the success rate of coral restoration methods. Studies focused on the development of cost-effective and scalable rehabilitation solutions have the potential to make the conservation and restoration of coral reefs more reliable and accessible, ultimately supporting the re-establishment of balance in pelagic ecosystems.

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