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Drivers and Stability of Clownfish-Anemone Symbiotic Mutualism

Zihan Yang

Beijing National Day School, Beijing, China
yangzihan20090519@gmail.com

Abstract. The marine heatwaves driven by global warming has been affecting the mutualistic interactions within coral reef ecosystems for years. One typical example of this relationship: the symbiotic relationship between clownfish and host sea anemones, is also facing this gradually increasing problem. The 2023 Red Sea heatwave results in a significant increase in temperature, causing massive coral bleaching around the region and severe decrease in clownfish population. Because of this event, the public started paying attention to this fragile and precious mutualistic relationship. This review synthesizes recent researches and sorts biological, non-biological and human-related factors shaping clownfish-anemone mutualism. Within these factors, active food-provisioning behavior by clownfish is a key positive biological factor, as it can improve the growth of host sea anemones as well as increasing the available survival area of clownfish family. Coral bleaching led by ocean warming will break the symbiotic relationship between clownfish and sea anemones by reducing the amount of hosts with normal functions even though clownfish have the ability of 'olfactory capacity' to help them detect other healthy hosts. Thermal-tolerant symbiont strains, a new method invented to help recover the mutualistic relationship between anemones and clownfish, shows theoretical restoration potential yet cannot be directly transferred from coral research to sea anemone systems. Human-caused threats including aquarium trade collection and coastal pollution remain comparatively under-quantified despite their obvious destructive effects. This paper clarifies interacting drivers of this iconic marine mutualism and supplies reference information for future reef conservation practice.

Keywords: Anemone, mutualistic, clownfish

1. Introduction

Coral reefs support exceptionally high marine biodiversity, and interspecies mutualism maintains the stability of reef community structure [1, 2]. The obligate association between clownfish and sea anemones serves as a classic textbook example of marine mutualism, yet recent mass-bleaching events demonstrate how rapidly this partnership can collapse under environmental pressure [3]. Host sea anemones offer clownfish anti-predator shelter and safe spawning substrate, and clownfish in return deliver nutrients, water agitation and partial anti-predator defence for their cnidarian hosts [3, 4] Under accelerating global climate change, however, such tightly coevolved symbiotic systems

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have become highly vulnerable to anthropogenic environmental disturbance, with frequent mass bleaching events threatening long-term population persistence of both partners.

Global research on clownfish-anemone symbiosis has developed rapidly over the past decade with expanding interdisciplinary coverage [1, 5]. Early studies predominantly focused on basic adaptive mechanisms, including juvenile mucus acclimation processes, host specificity patterns and general nutritional exchange pathways. Recent behavioural experiments have overturned traditional assumptions of passive nutrient exchange, confirming that clownfish exhibit highly selective, condition-dependent food provisioning behaviour that actively promotes host anemone growth and fitness [4]. Parallel ecological investigations have revealed that thermal stress and anemone bleaching not only reduce host survival rates but also alter clownfish physiology, social structure and reproductive output, severely undermining population recruitment [5, 6]. Despite these advances, existing literature generally separates biological behavioural mechanisms from climate stress research, while human-induced multiple stressors remain poorly integrated into systematic analytical frameworks. Most reviews focus narrowly on either symbiotic adaptation or climate impacts, lacking comprehensive summarization of positive and negative regulatory pathways across biological, environmental and anthropogenic dimensions.

Given the above research gaps, this review systematically integrates up-to-date empirical findings to clarify major driving factors shaping the stability of clownfish-anemone mutualism. The research framework sequentially discusses beneficial biological mechanisms dominated by food provisioning, destructive non-biological stressors represented by ocean warming and anemone bleaching, and underestimated human disturbance impacts. This study aims to clarify synergistic and antagonistic interactions among multiple influencing factors, highlight current research limitations, and provide scientific references for future reef ecological protection and symbiosis restoration strategies.

2. Biological and environmental drivers shaping clownfish-anemone mutualism

2.1. Food-provisioning as a reinforcing biological mechanism for symbiosis

Active food provisioning represents one of the most meaningful newly verified behavioural interactions within clownfish-anemone systems. Traditional understanding assumed nutrient input mostly originated from clownfish metabolic waste excretion. Recent controlled laboratory observations on Amphiprion clarkii and its host Entacmaea quadricolor prove that clownfish actively capture food items and deliberately transfer suitable prey fragments toward host anemone oral discs. Food particles transported by the clownfish will be absorbed directly by the anemone tissue, providing particular amount of nutrients for the host, and this supplement of nutrition doesn't rely on the inner-mutualistic photosynthetic substances. This active food provisioning process results in a positive feedback loop, which further strengthens the mutualistic relationship between clownfish and host sea anemones [4].

Through the food provisioning process, there are two specific standards of clownfish from choosing food: the size of food particle, and the type of food. When obtaining food pieces with a diameter of less than 7 millimeters, clownfish usually ingest these food to fulfill the demand of itself.

Larger pieces reaching ten millimetres or above are commonly carried across tentacles and attached onto host tissue for anemone ingestion. Animal-origin food including krill, clam meat and squid tissues follow this size-dependent allocation pattern. Green algal fragments also undergo size sorting during behavioural transfer. Hard brown macroalgae and sponge fragments are consistently

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rejected by clownfish and neither consumed nor delivered to hosts, indicating clownfish can discriminate food quality and filter out material unsuitable for carnivorous cnidarian physiology. Selective resource delivery avoids supplying low-value organic material and improves net nutritional efficiency for the host anemone [4].

Extra nutrient input from clownfish provisioning directly accelerates host somatic growth. Enlarged anemone tentacle surface area creates expanded shelter capacity and supports larger clownfish social groups [4, 7]. Inside each social unit, dominant individuals obtain priority access to shelter and nutrition. The increase in group size of clownfish further affects the growth and reproduction of themselves. Larger host sea anemones can provide a more stable surface for nesting, and increase the success rate of clownfish reproduction. In the social class of clownfish population, its social status is equal to its size. The largest clownfish in a population will evolve into a fertile female, while the others will remain in male state or stay immature [7, 8]. This sexual change highly rely on a stable living habitat and continuous resource supply rather than the process similar to vertebrates. Nutrition brought by this mutualistic relationship can promote the increase in body length for both male and female clownfish, while in a beneficial symbiotic relationship, females can usually reach a larger average body length.

Positive feedback plays an important role in this whole biological process. Larger numbers of clownfish can result in a larger amount of food supply, which speeds up the growth of host sea anemones. Hosts with a greater size can carry more group members while supplying stronger protection from defending predators [4, 7]. This low risk of being eaten provides clownfish a better opportunity to feed after leaving the tentacles of host anemones, and further helps it gain additional food resources, which will be taken back to the anemone. However, this continually strengthening cycle completely rely on stable environmental conditions. If outer pressure disrupts the physiological state of host, this advantageous behavior can no longer stabilize the mutualistic relationship between clownfish and sea anemones.

Despite providing nutrients directly, continuous food supply can also improve the hosts' physiological stability and immunity. Sea anemones with sufficient nutrition can maintain a denser tentacle structure, a higher symbiont survival rate, and stronger ability of adjusting immunity, which further improves the living standards of host clownfish. A stable health condition can decrease the strength of competition within social groups, and improve survival rate of the whole family. This multi-level biological regulation makes food provisioning a foundational stabilizing factor for long-term symbiotic persistence under normal environmental conditions. Nevertheless, this cooperative behavior shows an obvious host specificity in natural reef environments. Not all anemone species are able to obtain sufficient food from clownfish, instead, clownfish only put their effort in those sea anemones that are easier to form a symbiotic relationship with them. Host anemones with weaker symbiont activity or poor adaptive compatibility rarely obtain continuous food supplementation, which further widens the fitness gap between high-quality and low-quality host individuals. This selective cooperative relationship acts as a natural selection mechanism, making stabler mutualistic pairs benefit more in a coral reef communities, and optimizes the overall structural matching degree of clownfish-anemone populations in local ecosystems.

2.2. Climate-driven bleaching of anemones and disruption towards symbiosis

Ocean conditions have transformed rapidly under anthropogenic carbon emission pressure. The global ocean absorbs approximately one-third of atmospheric carbon dioxide, triggering interconnected shifts including ocean acidification, sea-level rise and widespread seawater warming [1, 2]. The rate of present-day marine environmental change exceeds most geological records from

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the past three hundred million years. Like reef-building corals, host sea anemones depend on intracellular Symbiodiniaceae symbionts to obtain photosynthetic nutrition. Thermal stress forces anemone hosts to expel photosymbiont communities and produces bleaching phenotypes. Bleached anemones lose major energy sources and face high mortality risk without fast environmental recovery [6].

After host bleaching events, clownfish rely on inherent olfactory sensing ability to detect chemical signals released by intact healthy anemone individuals and may conduct host switching behaviour. This behavioural coping strategy can theoretically rescue symbiotic associations when alternative hosts remain accessible. Yet mass regional bleaching drastically reduces the abundance of unbleached anemone individuals. Suitable host options become extremely limited across impacted reef areas. Even if clownfish maintain normal sensory capacity, insufficient habitat resources prevent successful relocation. In the Red Sea 2023 heatwave survey, near-total local anemone bleaching led to roughly a 95 percent decline of symbiotic clownfish abundance because few intact hosts remained available for population persistence [6]. Despite of causing a drop in population of clownfish, some clownfish living in partially-bleached host anemones will even present higher concentration of stress hormone, lower frequency of spawning, and much lower survival rate of eggs. This will further suppress its potential of population recovery for subsequent generations.

Symbiont community composition largely determines cnidarian thermal tolerance. Coral restoration research has explored experimental evolution approaches to cultivate heat-resistant Symbiodiniaceae strains through multi-generational laboratory thermal selection. After eighty to one hundred twenty generations of gradual temperature elevation, evolved symbiont strains confer improved bleaching resistance for coral holobionts without obvious growth trade-offs under normal ambient temperature. Although such biotechnological ideas sound promising for anemone conservation, researchers cannot simply copy coral-derived results onto sea anemone systems. Host-symbiont compatibility rules differ substantially between corals and anemones. Sea anemone-specific symbiont strains may respond differently under thermal selection pressure. Real application for clownfish host anemone restoration still needs independent targeted laboratory verification.

Thermal bleaching also triggers subtle but persistent behavioural degradation in clownfish populations. Resident individuals on bleached hosts exhibit reduced foraging activity, increased hiding behaviour and weakened territorial defence, further lowering individual fitness [5, 6]. Over prolonged heat stress periods, the breakdown of symbiotic interaction disrupts natural behavioural rhythms and may even cause local population segregation, gradually eroding the complete reef community structure. Such sublethal negative impacts are often overlooked in short-term field surveys but profoundly determine long-term ecosystem recovery capacity. In addition, persistent thermal stress disrupts the synchronized life cycle rhythm between clownfish and host anemones. Bleached anemones delay tissue regeneration and tentacle regrowth, failing to provide stable spawning grounds for clownfish during breeding seasons. The mismatch between host recovery cycle and clownfish reproductive cycle reduces offspring survival rates and inhibits population renewal. Unlike instantaneous population decline caused by extreme heatwaves, this long-term ecological desynchronization slowly degenerates symbiotic community functions, making it difficult for damaged reef systems to achieve natural restoration even after seawater temperature returns to normal levels.

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2.3. Human-associated disturbance and interactive stress effects

In published articles, there are less researches specific to the effect of human-caused pressure on clownfish-anemone symbiosis, although multiple anthropogenic behaviors have caused measurable damage to coastal coral reef ecosystem. The increase in Carbon dioxide concentration in the atmosphere will directly lead to ocean warming and acidification. Petrol pollution near the sea will release toxic chemicals, which can break up the inner tissue of anemones and disrupt the sensory functions of clownfish. Wild collection for the global ornamental aquarium trade removes large quantities of both clownfish and their host anemones from natural reefs. Many captured anemones cannot survive during transportation and captive raising, which may further decrease their local wildlife population. At the same time, eutrophication from in-land streams will affect water quality, and change the competitive relationship between benthic reef organisms.

Various anthropogenic pressures rarely effect the relationship independently. Pollution, over-fishing, and global warming usually happen at the same time in a same coral reef, bringing a sophisticated impact. Nutrient enrichment may sometimes accelerate anemone growth under benign temperature conditions, yet eutrophic environments amplify bleaching severity once heat stress arrives. Overfishing will remove reef predator and herbivore species, reshaping the whole-reef trophic web, and indirectly altering survival probability for clownfish-anemone assemblages. Since it's hard to separate different anthropogenic pressures in real-world experiments, recent understandings to these mechanisms remain fragmented. Most researched nowadays stay at observational levels, while lacking a quantitative analysis of how do each factor changes the stability of symbiotic relationship.

The rapid development of coastal urbanization and marine tourism also results in a continuous disruption to the mutualistic relationship between clownfish and host sea anemones [9, 10]. Frequent human activities and vessel movements produce suspended sediment plumes that reduce underwater light intensity, inhibiting photosynthetic efficiency of anemone symbionts and subtly weakening host nutritional supply. Long-term but low-intensity human disturbance will gradually decrease anemone vitality, making symbiotic communities easier to be affected by extreme heat waves. Comparing to sudden natural disasters, these continuous anthropogenic disturbance is less visually obvious, but still breaks down the mutualistic relationship in a long term perspective.

Despite these factors, human-caused ecological cascade effects amplifies the degradation of symbiotic relationships. Coastal eutrophication will cause benthic algae to over-reproduce, and these algae will compete with sea anemones for sunlight and space. Gradually, these algae may stick on the ocean floor, limiting the survival area for host anemones. The shrinkage of living space makes clownfish communities gather in fragmented coral reef habitats, which further leads to an increase in intraspecific competition, and lowers group stability. These indirect human-driven ecological changes form a vicious cycle with climate stress, jointly restricting the survival and development of clownfish-anemone symbiotic systems in tropical coastal reefs [2, 9].

Conservation strategies built on current knowledge include global greenhouse-gas emission reduction to mitigate marine heatwave frequency, local water-quality regulation and trade restriction on wild-collected clownfish and host anemones. Advanced biotech solutions such as experimentally evolved symbionts remain hypothetical for anemone restoration. Field validation is essential before such techniques can serve practical reef protection purposes.

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3. Conclusion

This paper assembles available research findings about multiple interacting drivers that govern the clownfish and host sea anemone mutualistic relationship. Positive biological feedback comes from the selective 'food provisioning' of clownfish. This behavior can activate the growth of host sea anemone, which increases area for protection, and can help clownfish form larger social communities as well as improving their reproductive performances. Coral bleaching led by climate change results in severe destructive pressure. Although clownfish still has the ability of finding new hosts with their olfactory capacity, extreme bleaching events could still lead to breakdown of local symbiotic relationships. Biotechnological progress achieved on coral symbiont modification cannot be directly applied for sea anemone conservation due to host-symbiont compatibility differences. Human threats such as aquarium trade harvesting and coastal pollution are ecologically meaningful, but still lack quantitative analysis. In real coral reef ecosystems, the interplay of complex factors may enlarge the damage regarding to this mutualistic relationship between clownfish and host sea anemones. Summarizing these mechanisms supports integrated conservation thinking for coral-reef-associated mutualistic partnerships. There are still many limitations regarding this research, including a lack of data towards human disturbance factors, the experiments testing the effect caused by multi-factors, and a limited amount of experiments focusing on the evolution of anemone-specific symbiont. Most research conclusions rely heavily on short-term observations, but lack a long-term continuous experiment for clownfish-anemone relationship in the natural world. Future studies should primarily focus on multi-factor experiments and long-term coral reef detection. Researchers need to test heat-evolved symbiont strains specifically for host sea anemone species rather than only drawing inference from coral studies. More field research is also needed, quantifying population influence from aquarium collection and coastal runoff pollution. Conservation management should integrate global climate mitigation with local coastal regulation measures to preserve this iconic marine mutualism.

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