

The Behavioral mechanism of Damselfish Algal Farming and its Ecological Effects on Coral Reef Ecosystems

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Abstract:

Coral reefs are one of the most diverse and productive ecosystems, and their biodiversity and ecological stability are very important. Within coral reef ecosystems, the algal-farming damselfishes are some damselfish species that have a unique territorial behavior of cultivating algal farms. Current studies on the behavioral mechanism of damselfish algal farming and its ecological impacts on coral reef ecosystems are summarized in this review. It focuses on the interactions, farming practices, and territorial strategies of algal-farming damselfishes. Algal-farming damselfish have been shown to manage their algal farms through selective weeding, which alters the reef's benthic composition, defending against invaders like urchins, and promoting their preferred algae. Recent research notes that environmental stressors like coral bleaching and ocean acidification may increase the disruption of damselfish algal farms on the coral-algae balance in favor of algae dominance. Government organizations can develop more effective coral reef conservation plans by using the species as an indicator of ecosystem health, and understanding how damselfish algal farming operates is crucial for predicting reef development trends in the context of climate change.

Keywords: Damselfish; Algal farming; Interspecific interaction; Farming mutualism; Coral reef conservation.

1. Introduction

Composed of calcium carbonate skeletons and biological communities, coral reefs are one of the most diverse and productive ecosystems that support about a third of marine fish species [1]. Moreover, coral reefs contribute significantly to local economies through fisheries and tourism, and they protect shore-

lines from storms and wave erosion [2]. However, coral reef resilience is currently increasingly challenged by climate change and human disturbances; climate change leads to coral bleaching and ocean acidification [3]. Coral bleaching is the expulsion of symbiotic algae under stress, leaving corals pale and vulnerable, and ocean acidification is the decline in seawater pH due to the uptake of anthropogenic CO₂,

which brings serious consequences for calcifiers like corals [4, 5]. Under these circumstances, damselfish (Pomacentridae) has shown high potential value as an indicator species to monitor benthic habitat on coral reefs [6]. They are territorial, “having a major influence on the structure of algal, coral, other invertebrate, and fish assemblages on coral reefs” [7]. Their widespread and abundant territories that occupy a large proportion of shallow reef habitats significantly modify coral reef benthic habitats [7]. Among their behavioral traits, algal farming is particularly influential. Algal-farming damselfishes control their farm algal composition by defending against herbivores and even “remove scleractinian corals... biting the living tissue” to create bases to grow denser algae [6]. The cultivation mutualism between algal-farming damselfish and the alga is a worthy phenomenon to research and monitor coral health. Although damselfishes’ farming behavior has been studied for decades, existing research is often fragmented, and many studies focus on specific regions, such as Moorea Island in French Polynesia [6]. The purpose of this review is to synthesize current knowledge on the behavioral mechanisms of damselfish algal farming and evaluate its ecological effects on coral reef ecosystems under climate change. We address both natural and anthropogenic stressors and highlight new conservation strategies and directions for future research.

2. The Behavioral Mechanism of Damselfish Algal Farming

2.1 Overview of Damselfishes

Damselfishes (Teleostei: Pomacentridae) are a marine fish family with a wide variety of 428 species [8, 9]. The diverse species of damselfishes are widespread worldwide in mainly Indo-Pacific tropical seas; they are common in the coral reef range and make a large proportion of reef inhabitants [8, 9]. Many species are highly territorial herbivores that consume benthic algae, while others are omnivores that feed on algae, plankton, and benthic invertebrates; some species are noted for their extreme aggressiveness [8, 9]. Many planktonic damselfish form large schools of fish above coral heads, while the territorial algal-farming damselfish usually live alone and strongly repel intruders [10]. Among their diverse behaviors, algal farming stands out as one of the most remarkable and research-worthy characteristics.

2.2 Territoriality and Defense of Farming Grounds

Certain marine herbivores exhibit “farming” behavior, a specialized resource management system. Within a fixed

territory, individual herbivores modify benthic plants by favoring a specific kind of algae to increase the availability and quality of their food [11]. The territorial behavior and farming strategy vary among algal-farming damselfish species. Previous research found that “algal farms maintained by different species of territorial herbivorous damselfishes vary in size, algal biomass, and species composition” [11]. The relatively small territory size of *Stegastes nigricans* ranged from 55 to 280 cm in radius, about 0.5–2 m², as measured by maximum distance of attack (MDA); their territory size was inversely related to algal abundance, indicating that food availability is a key determinant of defended area [12]. When the algal-farming damselfish were confronted with both a neighbor and a non-neighbor intruder simultaneously, territory owners attacked the neighbor first, suggesting neighbors pose greater threats [12]. Their bite frequency was significantly negatively correlated with algae abundance—the fish became more aggressive when food was insufficient; moreover, aggressiveness increases as the distance shortens [12]. The algal-farming damselfishes’ aggressive behaviors include charging, chasing, biting, and head-butting intruders [7, 11, 12]. Beyond aggressively defending their territories, algal-farming damselfishes actively manage algae farming through selective weeding and careful cultivation.

2.3 Algal Cultivation and Selective Weeding

Based on farming strategies, algal-farming damselfishes are categorized into three kinds: intensive farmers (small, dense farms), extensive farmers (large, mixed-culture farms), and intermediate farmers (unweeded, mixed-culture farms) [13]. For example, the *Stegastes nigricans* owns small, monoculture farms while the *S. obrepus* owns large-scale, mixed-culture farms [11].

Cultivation mutualism is the “relationships in which the consumer promotes the growth and net survival of the species it consumes” [14]. Algal-farming damselfish such as *Stegastes nigricans* maintain monocultures of the red alga *Polysiphonia* sp. 1, which is “rich in biomass, highly productive, and the most digestible alga species for this fish” [13]. They selectively weed out inedible or calcareous algae. An obligate mutualism occurs between *Stegastes nigricans* and its cultivated algae: it is highly vulnerable to grazing and weak in competition, and therefore persists only within the protection of damselfish territories [13]. Many other algal-farming damselfish species maintain mixed-culture algal farms where diverse algae species are not exclusively dependent on the fishes’ cultivation [11, 13]. In most cases, selective weeding alters benthic algal composition on coral reefs. What’s more, damselfishes also have a direct impact on the reef structure itself through substratum modification via coral removal.

2.4 Substratum Modification through Coral Removal

In some reef zones, algal-farming damselfishes' territories occupied about 70% of the reef substrate, showing their important role in modifying the reef's environment [7]. People observed white scars of about 1 cm in diameter appearing on corals near damselfish territories. They were analyzed to be "bite lesions caused by the removal of coral tissue and upper layers of skeleton," which was proposed for clearing space to grow algae [14].

By biting away live tissue of scleractinian corals, algal-farming damselfishes actively removed corals and exposed the skeletons, which then serve as substratum for the development of dense algal lawns [6]. This disruption of coral-algae competition benefits algal growth at the expense of corals, yet the interspecific interactions driven by algal-farming damselfishes are even more sophisticated.

2.5 Interspecific Interactions

In Hawaii, *Stegastes marginatus*, a damselfish species, defends its farm of invasive algae but also acts as an opportunistic browser to consume the invasive algae, showing its two-way effect on promoting the persistence of invading species or restricting their outbreak [15].

Besides producers, algal-farming damselfish actively interact with other herbivores, one of which is the sea urchin. Sea urchins are important herbivores that feed on marine plants and benthic algae, strongly influencing reef community structure, switching algal turfs into barrens [16, 17]. The damselfish prevent the creation of barrens through attacks and expulsions of urchins from their farms and adjacent turfs. The intruders are removed through handling efficiency. Although the green urchins are the biggest threat, pencil urchins (with large, smooth, and few spines) are attacked more quickly and fiercely, while the green urchins (with short, sharp, and numerous spines) are picked and pushed away carefully and cautiously [16]. Damselfishes' direct negative effect on urchins by preventing them from grazing has an indirect positive effect on algae growth.

Moreover, researchers found that damselfish territories sometimes serve as refuges for invertebrates; demersal plankton such as amphipods and isopods, benthic invertebrates like juvenile crabs, snails, polychaetes, and brittlestars inhabit inside the algal mat [18]. Since the algal-farming damselfish actively drive away intruding fish from their algal farms, the invertebrates gain protection from predators [18]. Thus, algal-farming damselfishes play a crucial role in regulating the abundance and distribution of benthic organisms on coral reef systems [18].

3. The Ecological Effects on Coral Reef Ecosystems

3.1 Coral-Algae Competition

At coral-algal boundaries, turf algae directly compete with corals for space and light, making coral recovery more difficult. Global warming and repeated mass bleaching events have shifted many reefs from coral-dominated to algae-dominated states [14]. Herbivorous fishes usually facilitate reef resilience by consuming algae, reducing competition. On the contrary, algal-farming damselfishes promote and protect algae growth within their territories [14]. Damselfish farming behavior —bite off coral tissues to provide substratum space to cultivate algae —brings even more disruption to coral-algae competition, benefits algal growth at the expense of corals [19, 20]. Moreover, some researchers find that "the farms of several *Stegastes* species (e.g., *S. apicalis* and *S. nigricans*) can act as reservoirs of pathogens that cause coral diseases" [6]. In short, increased abundance of damselfish has been linked to higher prevalence of coral disease and reduced coral cover, indicating that algal-farming damselfishes can weaken reef resilience and ecosystem functioning when predator control is lost [20].

3.2 Effects on Benthic Communities and Biodiversity

In most cases, damselfish territories serve as refuges for invertebrates, providing a predator-free habitat under the algal mat; the fish also alter the composition and abundance of certain benthic organisms like sea urchins in their territories [16]. Algal-farming damselfish significantly change the composition of benthic communities, but although they enhance the biomass of selected algal species, their weeding behavior in some of their monoculture farms decreases biodiversity [11]. The selective weeding and the exclusion of other herbivores prevent diverse species from inhabiting or foraging in the area, limiting community diversity [11]. With less biodiversity, the resilience of coral reefs also declines. In short, algal-farming damselfishes act as ecosystem engineers whose influence has both benefits and drawbacks for coral reef ecosystems.

3.3 Responses to Environmental and Human Stressors

3.3.1 Climate Change: Bleaching & Acidification

Coral reef resilience is currently increasingly challenged by climate change and human disturbances; climate change leads to coral bleaching and ocean acidification [3]. Coral bleaching is the expulsion of symbiotic algae under

stress, leaving corals pale and vulnerable, and ocean acidification is the decline in seawater pH due to the uptake of anthropogenic CO₂, which brings serious consequences for calcifiers like corals [4, 5].

Bleaching events increase coral mortality rate and reduce the structural complexity of reef habitats, then diminish biodiversity and coral's ecological functions [3]. Acidification weakens the ability of corals and crustose coralline algae to calcify, accelerating reef framework erosion and reducing the stability of benthic communities [4, 5].

These stressors also magnify the ecological role of algal-farming damselfishes. As corals die or weaken due to bleaching or acidification, more substrata becomes available for algal colonization: the damselfishes exploit these disturbed habitats by expanding their algal farms, accelerating the shift from coral to algal dominance [7, 14, 19].

3.3.2 Overfishing & Local Human Impacts

Overfishing is the act of “catching or removing too many fish in an aquatic system such that the breeding population becomes too depleted to recover” [21]. Overfishing first causes the decline of larger fish species, and when exploitation intensifies, it can also reduce mesopredators such as small groupers and snappers [19]. The reduction of mesopredators allows the damselfish population to increase, and they will clear more coral tissues to cultivate algae, which damages the hard coral [19]. Due to the excessive number of damselfish, their behavior of repelling urchins is magnified, and it largely reduces the ability of originally controllable algae to be cleared by sea urchins [22]. In some cases, the natural recovery of the urchin population is hindered by the damselfish [22].

Besides overfishing, local human impacts also include artificial noise from motorboats, which negatively impacts fish physiology and behaviors [23]. The noise on the parental-care behaviors of the Ambon damselfish *Pomacentrus amboinensis*, a damselfish species that has male-only egg care. Researchers find that when disturbed by the noise of motorboats during the breeding season, males spend more time on vigilance, but less time on egg fanning, which may reduce the survival rate of embryos due to the decrease of oxygen supply to the eggs and bad eggs removal [23]. Although it is not a typical kind of algal-farming damselfish, its strong territoriality and sensitivity provide valuable analogies for understanding how algal-farming damselfishes might also be affected under similar stressors [23].

3.4 Potential as Ecological Indicator Species

Damselfishes can be regarded as ecological indicator species due to their unique traits. They are highly sensitive to ecological stressors and interact strongly with other

species, with responses to environmental changes that are drastic enough to be observed clearly [6, 23]. In addition, their strong territoriality ties them closely to specific habitats, making them relatively easy to monitor or experiment on [7, 9]. Furthermore, their cultivation of algal farms reflects coral–algae competition, offering valuable indicators of reef health [13, 18].

4. Conclusion

All in all, the discussed behavioral mechanisms of damselfish include territoriality, algal farming with selective weeding, substratum modification, and interspecific interactions. Algal-farming damselfish occupy territories and drive away intruders in aggressive ways. Within their farms, they practice selective weeding to remove inedible algae and promote the growth of their preferred algae. This algal cultivation forms a cultivation mutualism: algae survive better under the care of damselfish, while damselfish depend on algae for food. Damselfish also bite off coral tissues to create substrate to provide space for algal growth. With sea urchins, damselfish repel them from consuming the algae. On the other hand, damselfish algal farms sometimes offer a predator-free refuge for small invertebrates.

Algal-farming damselfishes bring both positive and negative impacts on coral reef ecosystems. In coral–algae competition, damselfish reinforce algal dominance by biting coral tissue to grow algae. In some monoculture algal farms, damselfish increase the biomass of their favorite algae but reduce diversity through selective weeding. Bleaching and acidification create more substrata that allow damselfish to expand their farms and reinforce algal dominance again. Overfishing resulted in the removal of mesopredators like groupers, which led to uncontrolled increases in the damselfish population, which brings excess algae protection. Human disturbance also affects damselfish. Motorboat noise disrupts parental care in some sensitive damselfish species, reducing egg survival rate.

The paper summarizes the behavioral mechanism of damselfish algal farming and its ecological impact on coral reef ecosystems, and it helps to understand the coral-algal balance, evaluate the potential of damselfish as an indicator species, and offers insights to address climate change challenges and human disturbances on damselfish and coral reefs. Future research should monitor cross-regional algal-farming damselfish behavior, further evaluate their role as ecological indicator species, and develop improved strategies for both damselfish and coral reef conservation under climate change.

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