

**HERBIVOROUS FISHES AS DETERMINANTS OF THE STRUCTURE OF  
CORAL REEF COMMUNITIES: FARMERS, FORAGERS AND THEIR  
INTERACTIONS**

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## STATEMENT OF ACCESS

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## ABSTRACT

Herbivorous fish are considered integral to the maintenance of healthy coral reef ecosystems. However, the impacts of different kinds of herbivorous fishes on algal and coral assemblages, and the consequences of interactions among them, have not been fully assessed. Two groups of fish with very different feeding behaviours and potential impacts on benthic communities are the territorial herbivores, (primarily damselfish; termed ‘farmers’ throughout this thesis), and the more mobile, often schooling herbivores, (primarily parrotfish and surgeonfish; termed ‘foragers’). Although farmers have been attributed the status of keystone species on coral reefs, the importance of this group has not been sufficiently evaluated. Farmers can affect benthic communities through selective feeding, ‘weeding’, exclusion of foragers through aggression, and habitat selection. However, the specific mechanisms by which farmers maintain the typical algal turfs in their territories have not been isolated. The overall goal of this thesis was to assess the relative importance of farmers and foragers, and the interactions between them, in determining the structure and dynamics of benthic communities on coral reefs.

The specific objectives of this thesis were to explore the role of farmers on coral reefs, to distinguish their role from that of foragers, and to experimentally distinguish among the potential mechanisms by which farmers maintain the benthic assemblages within their territories. I collected extensive observational data to assess the spatial and temporal variability in farmer effects, both within and between reefs. A comparative study allowed me to determine the effects of several farmer species with previously unknown impacts. I then used a series of experiments to determine the effects of foragers on farmers, the effects of farmers on foragers, and to separate the mechanisms by which both groups and their interactions affect benthic communities. The first chapter of this thesis introduces common generalizations about the role of farmers, and questions their validity in relation to previously existing information.

In Chapter 2, I describe the spatial variability and seasonality in the effects of three farmer species on their territories on a coastal coral reef. There were distinct patterns of zonation in both farmers and benthic communities, and the effects of farmers on algal assemblages in their territories varied across reef zones. Each species in this study maintained territories with different algal assemblages, indicating that there is no general effect of farmers on algal composition. The overall benthic community was

strongly seasonal, but the composition of algal assemblages in farmer territories varied in response to episodic events (cyclones, coral bleaching, etc.). These results suggest that studies on farmer effects may need to take account of the reef zone and the season in which sampling takes place.

Chapter 3 establishes the effects of different farmer species on benthic communities and assesses levels of feeding selectivity as a possible mechanism for modifying algal assemblages inside territories. I compared the diets, territory composition and space occupation of ten farmer species across three geographic locations representing different reef types. Overall, farmer territories occupied between 11% and 60% of reef substrata, and between 52% and 100% of reef crest habitats, suggesting that they are likely to be important contributors to coral reef community structure. All the farmers included in these studies significantly modified the algal assemblages in their territories by promoting the abundance of preferred food items. Diets varied along a continuum from detritivory to herbivory, and both the distribution of farmers on the reef and the benthic composition of their territories reflected the proportions of algae and detritus in their diets. This suggests that diet can give a strong indication to the likely nature and magnitude of farmer effects on their territories. The differences among species make it overly simplistic to consider them a single ecological grouping, but their space occupation as a community, and consequently the spatial extent of their influence, has previously been underestimated.

In Chapter 4, I explored the effects of foragers on farmers, their territory sizes and the benthic communities in their territories. A forager exclusion experiment showed that foragers had a major impact on the dynamics of two abundant farmers (*Pomacentrus adelus* and *P. wardi*), and altered their relative abundance in favour of the larger species, *P. wardi*. Territory size was enlarged only briefly when foragers were absent, but the results suggest that foragers can hinder the ability of some farmers to maintain optimal quantity and quality of food algae in their territories. Foragers were previously only thought to affect farmers through the energetic cost of territory defence, but this study suggests that foragers may also determine relative densities of farmers and the composition of their territories.

Chapter 5 focusses on an experiment designed to distinguish between the effects of farmers and foragers on algae and corals, and to assess the effects of forager exclusion and direct farming as mechanisms by which farmers affect benthic communities. The experiment was conducted on an oligotrophic reef in Papua New

Guinea and is based on an orthogonal combination of a farmer removal treatment and a forager exclusion treatment. It showed that foragers had quantitatively greater and qualitatively different effects on benthic community structure than farmers. Where foragers were excluded, there were substantial increases in the cover and biomass of macro-algae and a decline in some corals, regardless of the presence of farmers. Where farmers were removed there was a moderate decline in the cover of some palatable algal species, regardless of whether foragers had access. No effect of the exclusion of foragers by farmers could be detected, providing the first experimental evidence that direct farming activities can be more important than forager exclusion in the promotion of distinct algal turfs in farmer territories.

In Chapter 6, the separate effects of foragers and farmers on algal succession, and their interactions, were tested on an inshore reef with high macroalgal cover. Grazing by foragers, farmer activities, and the *a priori* differences in the location of territories had different effects on algal succession on settlement tiles. Benthic communities developed differently where foragers were excluded by farmers, compared with where they were excluded by cages. Foragers did not suppress fleshy macroalgae, but inhibited succession to exclude calcified and crustose algae. Farmers had more dramatic effects on succession than foragers on this reef, suppressing macroalgae and promoting dense stands of palatable filamentous algae. The results suggest that territories were established in locations less suitable to the growth of fleshy macroalgae, and were subsequently “cultivated” by farmers. This study provides further evidence of the importance of farming as a mechanism for modifying benthic communities, and challenges the notion that foragers have stronger effects than farmers on all reef types.

In summary, not all farmers have the same dramatic effects on benthic communities as those emphasized in the literature. However, more species than previously thought have significant effects on their territories, suggesting that the spatial extent to which farmers influence coral reef communities may be greater than expected. The interactions between foragers and farmers are complex, and can have consequences not only for farmer population densities, but also for the quantity and food quality of algal turfs in farmer territories. It is becoming increasingly evident that the effects of farmers are not always limited to the aggressive exclusion of foragers, and that the relative importance of foragers and farmers may vary on different reef types. Both foragers and farmers play important roles in the maintenance of the existing benthic

structure of coral reefs, and it seems likely that the loss of either group could lead to significant shifts in coral reef community composition.

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## **STATEMENT ON SOURCES**

### **DECLARATION**

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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