

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

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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.

CHAPTER 1: GENERAL INTRODUCTION

Herbivory is one of the key processes determining the diversity, structure and dynamics of plant communities (McNaughton 1979; Lubchenco and Gaines 1981; Hay 1997; Adler et al. 2001). Herbivores also control the biomass and productivity of plant assemblages (McNaughton 1979) and can determine the habitat structure and resources available to all other animals in the community (Foster 1987; Zeller 1988; Palacin et al. 1998; Adler et al. 2001; Fournier et al. 2003; Garcia-Charton et al. 2004). The diversity of herbivores and the functional roles of individual species vary among systems. There is substantial variation among herbivores in diet, feeding mechanisms and interactions among species (Foster 1987; Bellwood and Choat 1990; Coley and Barone 1996; Kotanen and Rosenthal 2000). This provides a challenge to identifying general patterns, as not all species play a functional role in the system, and of those that do, roles can vary among different types of herbivore (Ogden and Lobel 1978; Horn 1989; Bellwood and Choat 1990; Purcell and Bellwood 1993; Steneck 2001). Impacts on plant communities arise through a wide range of mechanisms, including the different effects of feeding rates and selectivity (McNaughton et al. 1988; Horn 1989), weeding (Lassuy 1980; Hata and Kato 2002), trampling (McNaughton et al. 1988), removal of substratum (Choat 1991) and by nutrient enrichment from defecation (Sterner 1986; Plaganyi and Branch 2000). The ultimate goal of determining which herbivore species or identifiable groups of species are most important, and the means by which they influence plant communities, has not been achieved for most ecological communities.

On coral reefs, herbivorous fish are known to play one of the most important roles in structuring algal and coral communities (Choat 1982; Horn 1989; Hay 1991; Hixon 1996; McCook 1999). However, there is a great diversity of herbivorous fish on coral reefs, and the magnitude and nature of their impacts are likely to vary among different behavioural groups. The largest impacts on coral reef benthic communities have been attributed to the families Scaridae (parrotfish), Acanthuridae (surgeonfish) and Siganidae (rabbitfish, Choat 1991), which I will collectively refer to as ‘Foragers’ in this thesis (Figure 1). Members of these three families often graze in large, wide-ranging schools, with individuals feeding in a relatively non-selective manner (Horn 1989). Grazing by these fish can control algal standing crops (Hatcher 1983) and change the algal community composition from erect algae to grazer-resistant crustose algae (Lewis 1986; Scott and Russ 1987). Foragers can significantly reduce the biomass of fleshy macroalgae, and influence the competitive balance between algae and corals in favour of reef-building corals (Miller 1998; Russ and McCook 1999; Jompa and McCook 2002). The specific feeding activities and diets of foragers vary among species, from strict herbivory to diets largely composed of detritus (Choat 1991; Purcell and Bellwood 1993), so not all species play the same ecological role.

Highly site-attached, territorial species, primarily damselfish (Pomacentridae) comprise the second well-documented group of fish herbivores on coral reefs (Ceccarelli et al. 2001). They are often considered ‘farmers’ because they appear to cultivate distinct ‘gardens’ of algae, which they defend from conspecifics and all other herbivores (both farmers and foragers; Figure 1). It is widely accepted that territorial herbivores also have distinct effects, and in some cases, may be “keystone” species on coral reefs (Williams 1980a; Wellington 1982; Hixon and Brostoff 1983; Hixon 1996). Various mechanisms have been proposed to explain their effects (Figure 1), including

selective feeding (Jones 1992), ‘weeding’ (Lassuy 1980; Hata and Kato 2002), killing surrounding coral tissue (Potts 1977; Robertson et al. 1981; Santana 2001), fertilizing their territories (Klumpp and Polunin 1989) and reducing grazing rates by excluding other grazers (Hixon and Brostoff 1983). Their impacts on the reef benthos include modifying algal biomass (Sammarco 1983; Wilkinson et al. 1985; Hixon and Brostoff 1996), altering algal productivity and taxonomic composition (Ruyter van Steveninck 1984; Klumpp et al. 1987; Russ 1987), affecting the recruitment, growth and survival of corals (Sammarco et al. 1986; Gleason 1996) and increasing invertebrate densities (Zeller 1988). Although these activities are restricted to the area encompassed by individual territories, it has been estimated that on some reefs these territories can take up between 11% and 70% of the available substratum (Ceccarelli et al. 2001). However, abundances, territory sizes, feeding mechanisms and levels of aggression vary among species, and it has been suggested that the hypothesized role of farmers may apply to only a small subset of species (Ceccarelli et al. 2001). It is therefore likely that the effects of these fish dominate in some areas on coral reefs, while the activities of larger schooling grazers may be concentrated in areas of reduced damselfish abundance (Doherty 1983).

While there is a general consensus that foragers have a major effect on benthic communities, the ecological significance of farmers is less clear (Figure 1). Generalizations about the effects of farmers on benthic communities have ignored the potential for spatial variability in the farmer community, both within and between reefs, and most have not considered temporal variations in both farmer populations and the benthic reef community. Furthermore, the relationship between foragers and farmers has not been fully explored (Ceccarelli et al. 2001). While several studies address the aggressive behaviour of farmers towards foragers, the effects of foragers on farmer

populations and their territories remain unexplored. The mechanisms by which farmers “manage” their territories have been subjected to some preliminary testing (Mahoney 1981; Hixon and Brostoff 1983; Carpenter 1986; Hourigan 1986), but all previous experiments have tended to assume that the primary mechanism was the reduction of grazing by other herbivores through defence (Hixon and Brostoff 1996). More sophisticated experimental designs are needed to separate the different mechanisms by which farmers affect the structure and succession of benthic communities in their territories. This thesis will address these fundamental limitations to our understanding of farmers’ behaviour, their interactions with foragers, and their consequent role in coral reef ecosystems.

In Chapter 2, the spatial and temporal variability in the effects of farmers on benthic communities will be explored. Many studies have found that there is clear within-reef habitat partitioning in the farmer community, both on the Great Barrier Reef (Sale 1976; Robertson and Lassig 1980; Meekan et al. 1995; Bay et al. 2001) and in the Caribbean (Itzkowitz 1977; Waldner and Robertson 1980; Gutierrez 1998). Most species are restricted to certain reef zones and depths, and there can be major changes in species composition along depth gradients (Robertson and Lassig 1980) or on reefs with different substratum characteristics (Ohman et al. 1998; Bay et al. 2001; Santana 2001). Despite these clear zonation patterns in farmer distributions, there are no studies that address the question of whether farmer effects on their territories also vary within a reef. A few studies have addressed temporal change in farmer effects (Montgomery 1980b; a; Klumpp et al. 1987; Ferreira et al. 1998), and they all noted seasonal differences in algal standing crop both inside and outside territories. These spatial and temporal patterns suggest that the nature and magnitude of the impacts of farmers may depend on the reef zone and the season in which sampling takes place. Chapter 2 will test the hypothesis

that the effects of farmers on the algal turf cover and taxonomic composition in their territories varies among reef zones or between seasons.

The impact of farmers may also vary considerably among species. It is already known that behavioural traits, such as levels of aggression, are not necessarily the same for all farmer species (Ebersole 1985; Robertson 1996; Bay et al. 2001), just as diet has not been established for most species (Wilson and Bellwood 1997). Dietary analyses suggest that many species may be opportunistic omnivores rather than strict herbivores (Allen 1975; Meekan et al. 1995). Not all species identified as farmers maintain visually differentiated algal turfs. The genera most commonly studied tend to be those at the larger and more aggressive end of the scale, such as *Dischistodus* and *Stegastes* (Ebersole 1977; Potts 1977; Cleveland 1999), which also tend to have well-defined, visually distinct algal turfs in their territories. Smaller species of *Pomacentrus* and *Chrysiptera* are also territorial (Low 1971), and they tend to be more abundant and widely distributed than the larger genera (Meekan et al. 1995; Ceccarelli et al. 2001), although their territories appear undifferentiated from the surrounding substratum. Chapter 3 will include a number of these smaller species in a comparative study on farmer territoriality. This chapter will test the hypothesis that the magnitude and nature of the effects of different species varies according to patterns of diet, feeding selectivity and aggression. Geographic locations that differ in the diversity of farmers will be compared to assess the degree of variation within and among species.

While the effects of farmers on foragers through aggression have been widely documented (Robertson et al. 1976; Hixon 1996), the effects of forager activities on farmers have never been explored. Foragers represent a potential cost to farmers, in terms of the energy expended on territorial defence (Cleveland 1999). Schools of foragers also frequently invade territories (Robertson et al. 1976) and may deplete algal

abundance on a regular basis (Figure 1). Foragers may also modify the structure of reef habitats, potentially influencing the availability of critical resources used by farmers. Measuring the effects of foragers on farmers is a crucial step towards understanding both the dynamics between these two groups, and some of the mechanisms involved in creating and maintaining the unique benthic communities found inside farmer territories. Herbivore exclusion cages are the most commonly used method for measuring the effects of herbivores on benthic communities. However, they have never been employed to test the effects of foragers on farmers. Chapter 4 will describe an experiment where the herbivore exclusion cages are large enough to include a community of farmers. Different indicators will be used to assess the effects of foragers on farmers, including population densities of local farmer species, their territory sizes and the algal turf composition in their territories.

The different mechanisms by which farmers create and maintain their territories have undergone only preliminary experimental testing. There is a range of mechanisms by which farmers may establish and maintain territories that are different from the surrounding substrata (Figure 1). These may be broadly categorized into those that may reduce the abundance of preferred food algae and modify algal composition through selective feeding (Jones 1992), and ‘farming’ activities (Irvine 1980; Lassuy 1980), which are defined as activities that directly promote the establishment and growth of algal ‘crops’. The second category of mechanisms includes ‘weeding’ out unpalatable algal species (Lassuy 1980; Lobel 1980; Branch et al. 1992; Hata and Kato 2002), substrate preparation, which may involve killing coral and other activities (Potts 1977; Lobel 1980; Robertson et al. 1981; Wellington 1982; Santana 2001), and nutrient enrichment from waste products excreted by resident farmers (Polunin and Koike 1987; Klumpp and Polunin 1989; Ferreira et al. 1998). Furthermore, farmers may maintain

“gardens” of algae by reducing herbivory by other organisms through active defence (Hixon and Brostoff 1983). Experimental removals of farmers are known to cause a substantial increase in feeding by foragers within territories, with a concomitant reduction in algal biomass (Mahoney 1981; Kohda 1984; Hourigan 1986; Foster 1987). However, the simple removal of farmers from their territories does not distinguish between the effects on the benthos of the increased feeding by foragers in undefended territories and the effects of the cessation of farmer activities (Ceccarelli et al. 2001). A more complex experimental design is necessary to successfully separate forager effects from farmer effects, and to distinguish between the effects of different farmer activities. Chapter 5 will test the hypotheses that foragers and farmers have different effects on the structure of benthic coral reef communities, and that farmers increase algal abundance by reducing the impact of foragers through defence. A fully orthogonal farmer removal/forager exclusion experiment will be conducted, allowing the separation of the direct effects of the two groups, in addition to the detection of effects arising from their interaction (the aggressive exclusion of foragers by farmers).

Foragers and farmers may have contrasting effects on algal communities because they differ in the way they modify the development of algal communities through succession (Hixon and Brostoff 1996; Hata and Kato 2003). Algal succession can be modified by the activities of farmers, leading either to a highly diverse algal turf community (Hixon and Brostoff 1996) or a monoculture of preferred food algae (Hata and Kato 2002). However, the ways in which foragers influence succession outside territories, and the interactive effects of the two groups, have received little attention. As farmers may only establish territories in specific micro-habitats (Bay et al. 2001), the potential exists that patterns of succession will naturally differ between areas occupied by farmers and adjacent areas. Chapter 6 will test the separate and interactive effects of

farmers and foragers on the development of algal communities, and will distinguish them from natural spatial variation in patterns of algal succession. An experiment will be conducted to test the hypotheses that foragers and farmers have different effects on algal succession, and that farmers alter the course of succession differently through direct farming activities and through the location of their territories.

The conclusions from each chapter in this thesis will be used to evaluate the generalizations commonly made about farmers and foragers. The relative importance of the two behavioural groups of herbivores, and the potential bi-directional interactions between them, can only be assessed by careful observations and experiments. This thesis will provide the first comprehensive set of studies that aims to clarify how coral reef benthic communities are affected by each group and the relationship between them.

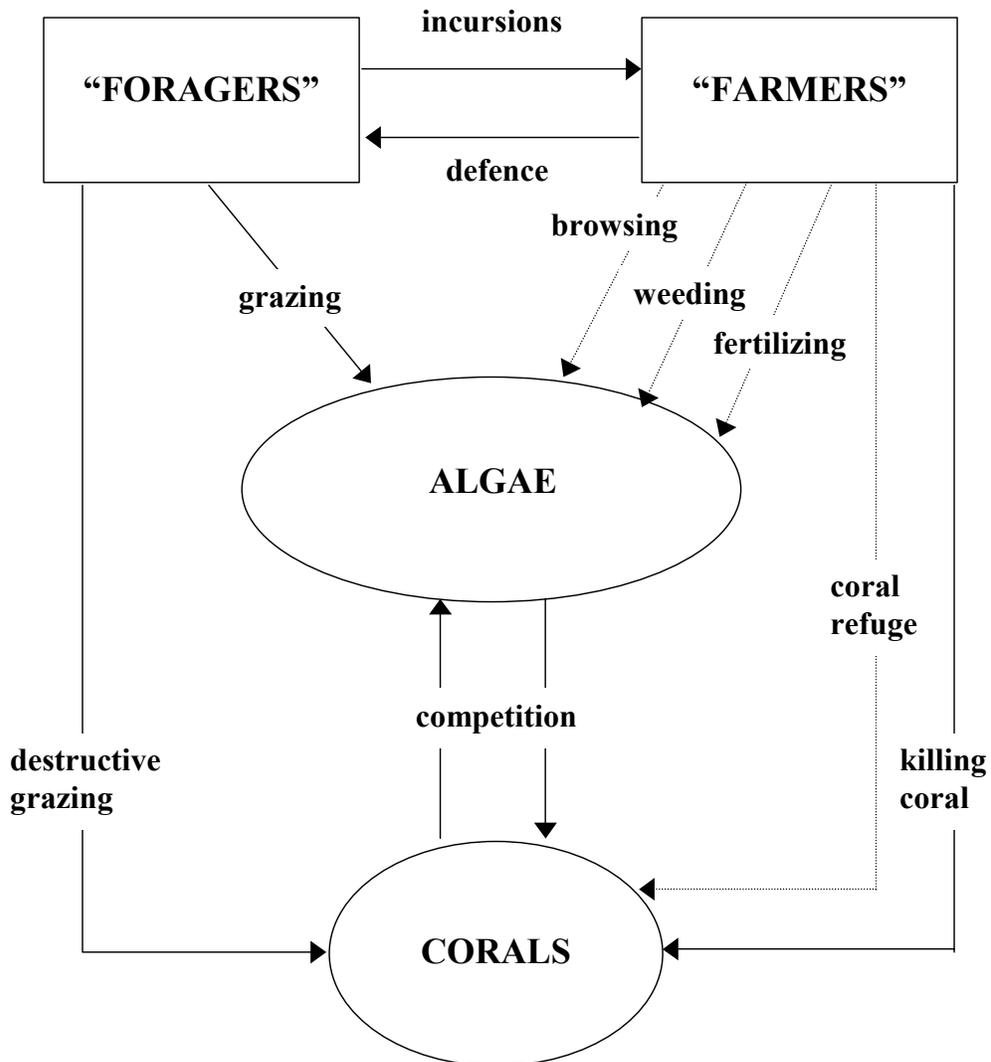


Figure 1. Flow diagram of relationships between foragers, farmers, algae and corals. “Algae” encompasses both turf algae and fleshy macroalgae. “Corals” encompass both recruits and adult colonies. Solid lines represent well-established and widely accepted mechanisms, and dotted lines represent mechanisms about which there are inconclusive or insufficient data.

CHAPTER 2: SPATIAL AND TEMPORAL PATTERNS IN THE EFFECTS OF FARMERS ON BENTHIC COMMUNITIES ON A COASTAL CORAL REEF

Introduction

Territorial damselfish, or “farmers”, are known to affect a wide range of organisms, including algae (Hixon 1996), corals (Sammarco and Carleton 1981; Wellington 1982), fish (Green 1996) and mobile invertebrates (Zeller 1988). Their effects have been so dramatic that they have been attributed a “keystone” role in reef ecology (Wellington 1982; Hixon and Brostoff 1983). However, the evidence that these generalizations apply to all species and habitats has been questioned (Ceccarelli et al. 2001). Most studies on farmers have been restricted to a few species in a single habitat at one point in time, restricting our ability to evaluate their overall significance. To assess the role farmers play in structuring coral reef benthic communities, there is a need for fundamental information on how much space they occupy in different habitats, and how the composition of their territories varies in space and time.

Farmers are often considered a guild, with attributes that have been defined from studies on a few focal species (Ceccarelli et al. 2001). Generalizations have almost invariably been based on species with strong aggressive behaviour and whose territories contain algal assemblages distinct from those found in undefended areas (Klumpp et al. 1987). Furthermore, general statements about the importance of farmers have come from studies based on a single species (Russ 1987), or a select group of species (Klumpp et al. 1987). Recently, some of the smaller, less conspicuous farmer species have been shown to affect the benthos in their territories (Ceccarelli et al. 2001). To

estimate the role of farmers on any coral reef, it is necessary to encompass the whole guild.

While farmers and benthic biota display clear zonation patterns across reefs (Waldner and Robertson 1980; Lewis 1999; Bay et al. 2001), how this spatial variation alters their influence on the benthos has not been described. Farmers may not represent 'keystone species' in all reef zones, with their effects varying depending upon spatial variation, species composition and abundance. Temporal variation in the effects of farmers on algae is also poorly understood (but see Klumpp et al. 1987; Ferreira et al. 1998). Temporal changes on the composition of farmer assemblages and the algal composition of their territories may alter perceptions as to their ecological role.

Spatial and temporal variations in the role of farmers may differ among reef systems. Studies of farmer effects in the Caribbean include a range of reef types, but all studies on the Great Barrier Reef to date have focussed on mid- or outer-shelf reefs (Ceccarelli et al. 2001). On these oligotrophic reefs, high densities of large herbivorous fish control algal biomass, promoting the establishment and growth of corals (Pennings 1996). On some inshore reefs, farmers are the only herbivores present in high densities (Russ 1984b). The biomass of fleshy macroalgae such as *Sargassum* spp. is naturally higher on inshore reefs (McCook and Price 1997; Wachenfeld et al. 1998). There are dramatic spatial and temporal changes in the structure of macroalgal communities on coastal reefs. The zonation of algal communities is well-developed on inshore reefs (Morrissey 1980; Mapstone et al. 1989) and the seasonal winter die-off and summer blooms of *Sargassum* spp. create a dynamic seascape (Vuki and Price 1994).

The goal of this study was to describe spatial and temporal patterns in the structure of farmer communities and associated algal assemblages on a single, coastal fringing reef habitat (Magnetic Island) on the Great Barrier Reef. Patterns in fish

abundance and territory size were combined to assess the space occupied by farmers and quantify their overall influence on benthic communities. I then used these patterns to evaluate whether conclusions about the importance of farmers and their interactions with benthic organisms are dependent upon the place and time of sampling. The specific questions I addressed were as follows:

1. What is the spatial partitioning of the farmer community on inshore reefs, and how does this partitioning coincide with the zonation of benthic biota?
2. What are the temporal patterns of change in farmer populations and how does this relate to changes in algal assemblages?
3. How much space does each farmer species occupy in each zone, and does space occupation change over time?
4. What are the apparent effects of all the farmer species occurring on the study reef on the cover and species composition of benthic communities in their territories?
5. Do these effects vary across zones and between seasons?

Materials and Methods

Study site and species

The study was conducted between June 2000 and November 2002 in Nelly Bay on Magnetic Island (19°17S, 146°86E), a high continental island situated 8 km off the coast of North Queensland, Australia (Figure 1). The distribution of macroalgae and corals on reef flats and reef slopes in Nelly Bay, Geoffrey Bay, Picnic Bay, Arthur Bay and Florence Bay has previously been documented in a baseline study conducted in

response to a proposed development in Nelly Bay (Mapstone et al. 1989). Detailed physical and biological information exists for Geoffrey Bay, Magnetic Island (Morrissey 1980). Nelly Bay is subject to similar physical conditions as it has a similar orientation and terrestrial geological features.

Nelly Bay has an extensive fringing reef, consisting of an inner sedimentary accumulation zone and a typical reef flat habitat. The distance between the reef crest and the beginning of the inner sedimentary accumulation zone ranges from approximately 200 m to 400 m. The seagrasses *Halodule uninervis* and *Halophila ovalis* dominate the benthic biota in the sedimentary accumulation zone, with macroalgae restricted to banks of rubble and dead microatolls interspersed within the zone. On the reef flat proper, the community structure is dominated by fleshy macroalgae, such as *Sargassum* spp. (Morrissey 1980; Mapstone et al. 1989; Vuki and Price 1994). Coral cover is higher on the reef slope than on the reef flat, with *Montipora* spp. being the most abundant and widespread coral genus (Mapstone et al. 1989).

Preliminary observations indicated that the community of farmers in Nelly Bay was made up of *Pomacentrus tripunctatus*, *P. wardi* and *Stegastes apicalis*. These three species defend territories from other grazers, conspecifics and congeners. They vary slightly in size, with *P. tripunctatus* being the smallest, *P. wardi* growing to slightly larger sizes and *S. apicalis* being significantly larger than the other two (Allen 1975).

Spatial patterns in fish and benthic communities

Five distinct reef zones were recognized in this study, according to a previous classification (Lewis 1999, Table 1). In each zone, three 20 m transects were employed for benthic point intercept sampling. Benthos was recorded three times at each meter: once at the point under the transect, once a meter to the right of the point, and once a meter to its left. Benthic categories included in this survey were thin algal turf (<3 mm

thick), thick algal turf (>3 mm thick), fleshy macroalgae, corticated red algae (of intermediate robustness, between delicate filamentous algae and tough fleshy macroalgae), sponges, bivalves and corals (recorded by growth form). Fleshy macroalgae and corticated red algae were identified to genus or species level where possible. Fish counts were conducted along the same 20 m transects employed for the substratum and benthic surveys in a belt 4 m wide. All farmers were counted using SCUBA, at mid- or high tide. Where possible, fish were counted in the morning hours so as not to confound density estimates with diurnal differences in fish behaviour. Benthic point intercept sampling and fish counts were conducted between June 2000 and April 2002, at intervals of three months.

Data were analysed using SPSS for Windows[®] software. Farmer densities and percent cover of key benthic taxa were calculated for each zone, and the between-zone differences tested using Multivariate Analysis of Variance (MANOVA). Temporal changes in farmer densities and benthic taxa were tested using multivariate Repeated Measures ANOVA.

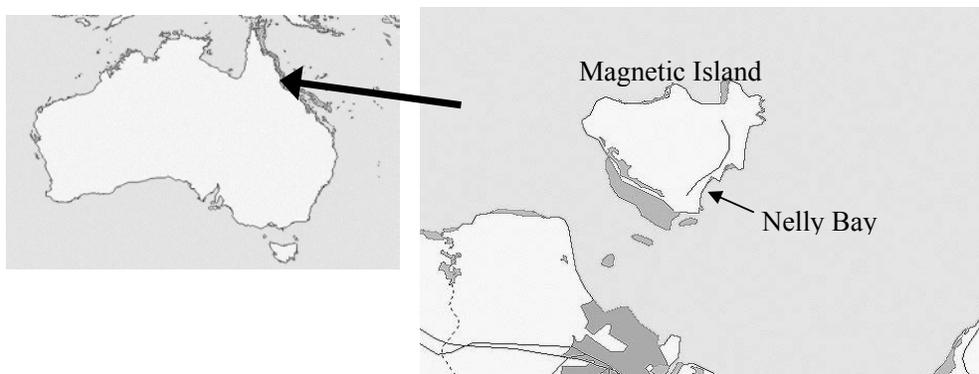


Figure 1. Map showing Magnetic Island and the position of Nelly Bay, where the study was conducted.

Table 1. Categorization of substratum zones (from Lewis 1999).



Space occupation and territory composition

The starting point of each transect was used as a site for the measurement of territory size and the collection of algal turf in the territories of the three species. From each point, the three closest territories of each species present were located and marked. Individual fish were observed for 15 minutes, during which time the territory boundaries were marked with lead weights. Territory area was calculated by measuring the circumference of each territory and using the formula for an ellipse of equivalent circumference. Territory size measurements multiplied by densities of each species allowed the estimation of how much space each species occupied in each zone.

The algal assemblages inside and immediately outside territories were quantified by collecting algal scrapings. At the end of the observation period, five point collections were made from substrata where fish had been seen to feed: for example, if the fish was observed taking bites from a *Sargassum* leaf, this leaf was then collected for analysis. The equivalent five substrata were then collected from an undefended area outside the territory. These samples were preserved in 10% formalin immediately after collection for analysis in the laboratory. These observations and collections took place at the same times as the overall benthic surveys and fish counts.

Each algal turf sample was emptied into a Petri dish and spread evenly across its surface for the estimation of percent cover and taxonomic identification. A square grid (1 cm mesh size) was placed over the dish and the taxon and/or substratum category under each intercept point was recorded. Large pieces of fleshy algae, such as *Sargassum* spp., *Padina* spp., *Lobophora* spp., *Dictyota* spp. and *Colpomenia* spp., were classified as substrate types, along with dead coral, rock and rubble. Taxa were identified to genus where possible, and to functional group (Steneck and Dethier 1994) where necessary. The overall percent cover of algal turf was estimated for each sample.

As above, data were analysed using SPSS for Windows[®] software to test for differences in space occupation and inside/outside territory differences in the percent cover of different taxa between reef zones using MANOVA. Temporal changes in these parameters were tested using multivariate Repeated Measures ANOVA.

Results

Spatial patterns in fish and benthic communities

There was a clear and significant zonation pattern in the overall distribution of the three farmer species in Nelly Bay ($F_{(d.f.=240)} = 26.132, p < 0.05$). *Pomacentrus*

tripunctatus was found on the inner reef flat and the mid reef flat, with only small numbers extending to the outer flat, *Stegastes apicalis* established territories primarily on the reef crest and was occasionally seen on the reef slope, and *P. wardi* appeared to be a spatial generalist, occurring in all zones except the inner flat (Figure 2a). With the exception of the inner reef flat, *P. wardi* was also consistently the most abundant species on this reef.

Benthic community structure also exhibited a clear zonation pattern (Figure 2b; MANOVA $F_{(d.f.=88)}=10.003$, $p<0.001$). Most surfaces on the inner reef flat were covered by thin turf and macroalgae. The cover of thin turf declined across the reef as other organisms became more abundant. Fleishy macroalgae increased in cover across the reef flat, occupying ~30% of the available space on the inner reef flat and reaching ~70% cover on the outer reef flat. The decline in macroalgal cover on the crest and slope was concurrent with the higher live coral cover in these zones. Live coral was present in very low abundance on the reef flat, but covered ~40% of the reef crest and 30% of the reef slope. Thick turf was found primarily inside farmer territories and the zonation pattern of thick turf related well to the patterns of farmer zonation and abundance (Figure 2a).

Of the five most common algal genera, *Sargassum* clearly dominated every reef zone. It increased significantly with increasing distance from the shore, before eventually declining on the crest and slope (Figure 2c; $F_{(d.f.=6)}=45.96$, $p < 0.001$). *Lobophora* and *Colpomenia* were less abundant but also followed this trajectory. *Padina* and *Dictyota* were most abundant on the inner reef flat and declined to very low cover on the reef crest and slope (Figure 2c). *Colpomenia*, *Padina* and *Dictyota* never covered more than 10% of sampled substrata.

Temporal variation in fish abundance and benthic community structure

The densities of all three species of farmers remained more or less consistent across reef zones over time (Figure 3). The density of *Pomacentrus tripunctatus* was almost constant on the inner reef flat and the mid reef flat, although in the summer of 2002 recruitment was very high and overall *P. tripunctatus* densities increased accordingly (Figure 3a). *P. wardi* densities were highest, and temporally most consistent, on the reef crest (Figure 3b). In the other zones *P. wardi* densities fluctuated over time. *Stegastes apicalis* densities were substantial only on the reef crest, where seasonal changes were not significant, but in the colder months small *S. apicalis* colonies were found on the outer reef flat and on the reef slope (Figure 3c).

The benthic community composition, including both algae and corals, varied significantly between seasons and distinctly within each zone (MANOVA interaction for Zone and Season: $F_{d,f=528} = 2.119$, $p < 0.001$). The strongest seasonal pulse was found in *Sargassum* spp., which bloomed in summer. These blooms were significantly more pronounced on the mid and outer reef flat than in other zones (Figure 4a). During *Sargassum* blooms, several components of the benthos declined, either because their percent cover decreased or because they were hidden by *Sargassum* plants. The benthic categories and taxa most affected by *Sargassum* blooms were thick filamentous turf on the outer flat (Figure 4b), *Lobophora* spp. on the outer flat and reef crest (Figure 4c), and live coral cover (Figure 4d).

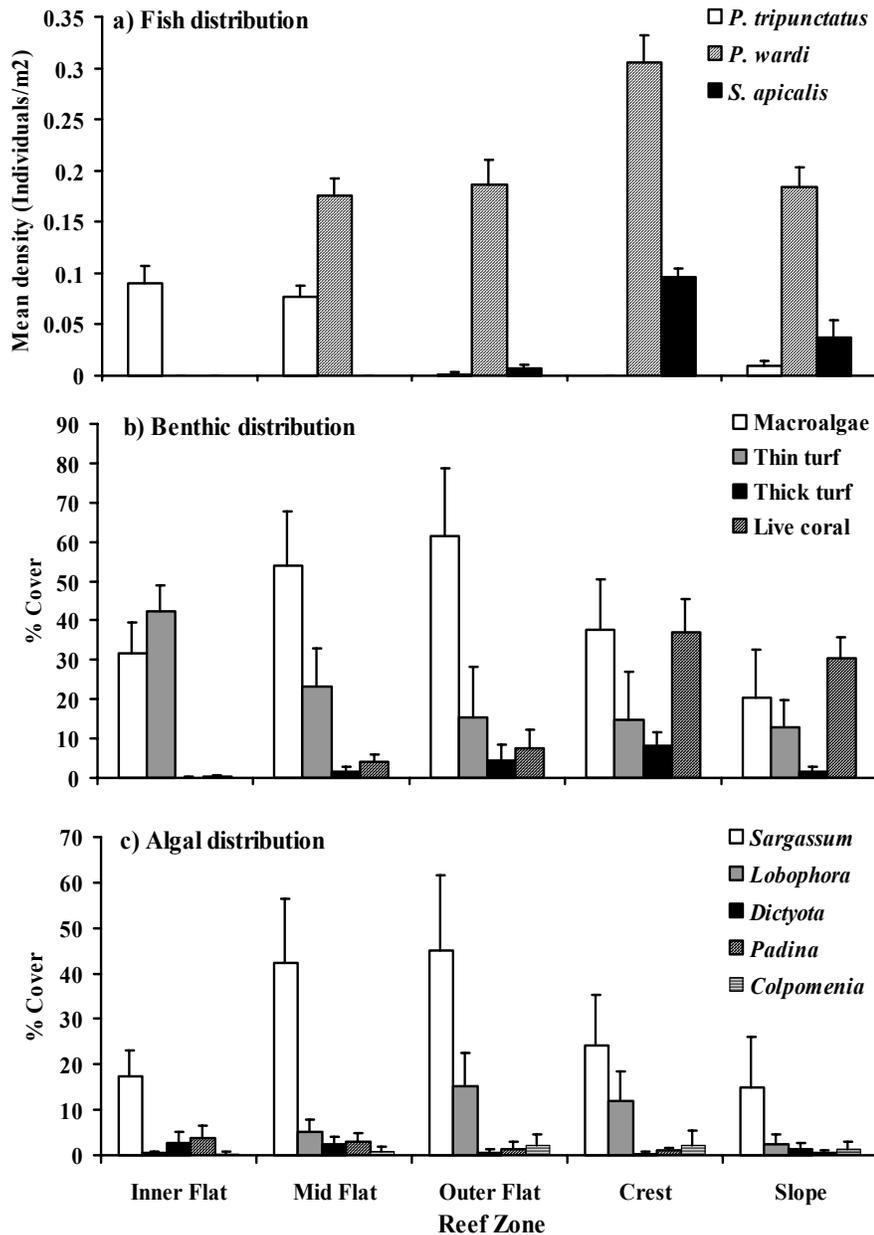


Figure 2. a) Spatial zonation patterns in *Pomacentrus* (*P.*) *tripunctatus*, *P. wardi* and *Stegastes* (*S.*) *apicalis* across five reef zones in Nelly Bay. b) Zonation patterns in the four dominant benthic categories as defined by percent cover during point intercept sampling. c) Zonation patterns in the five dominant macroalgal genera found on the Nelly Bay reef. Includes fleshy (*Sargassum*) and more delicate foliose macroalgae. Note differences in the y-axes for figures b) and c). Error bars for all 3 figures = 1 S. E.

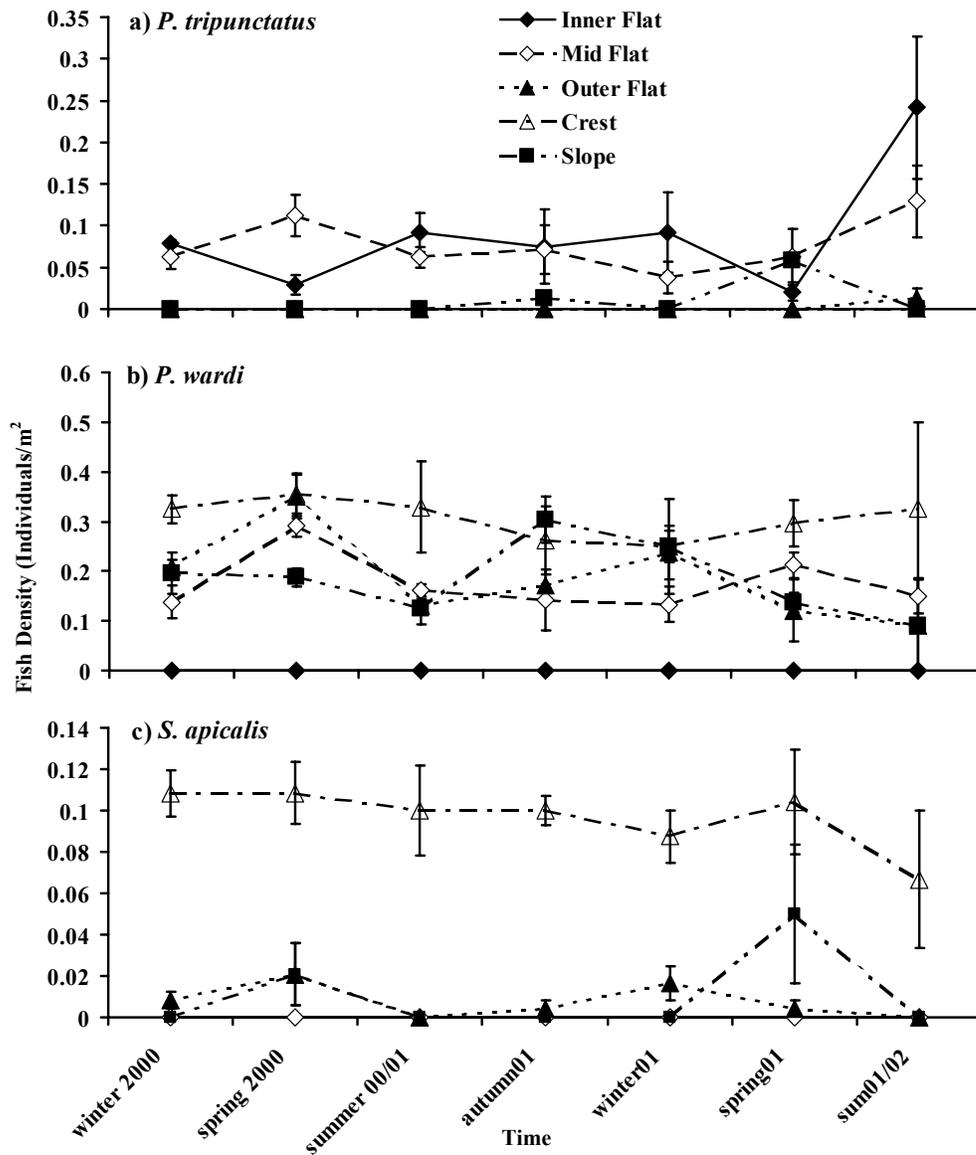


Figure 3. Temporal variability in densities of a) *Pomacentrus (P.) tripunctatus* (Time x Zone: $F_{(d.f.=6)} = 3.301$, $p < 0.05$), b) *P. wardi* (Time x Zone: $F_{(d.f.=18)} = 4.18$, $p < 0.05$) and c) *Stegastes (S.) apicalis* (Time x Zone: $F_{(d.f.=6)} = 2.933$, not significant) in the five reef zones in Nelly Bay. Note the differences in y-axes for the three species. Error bars = 1 S.E.

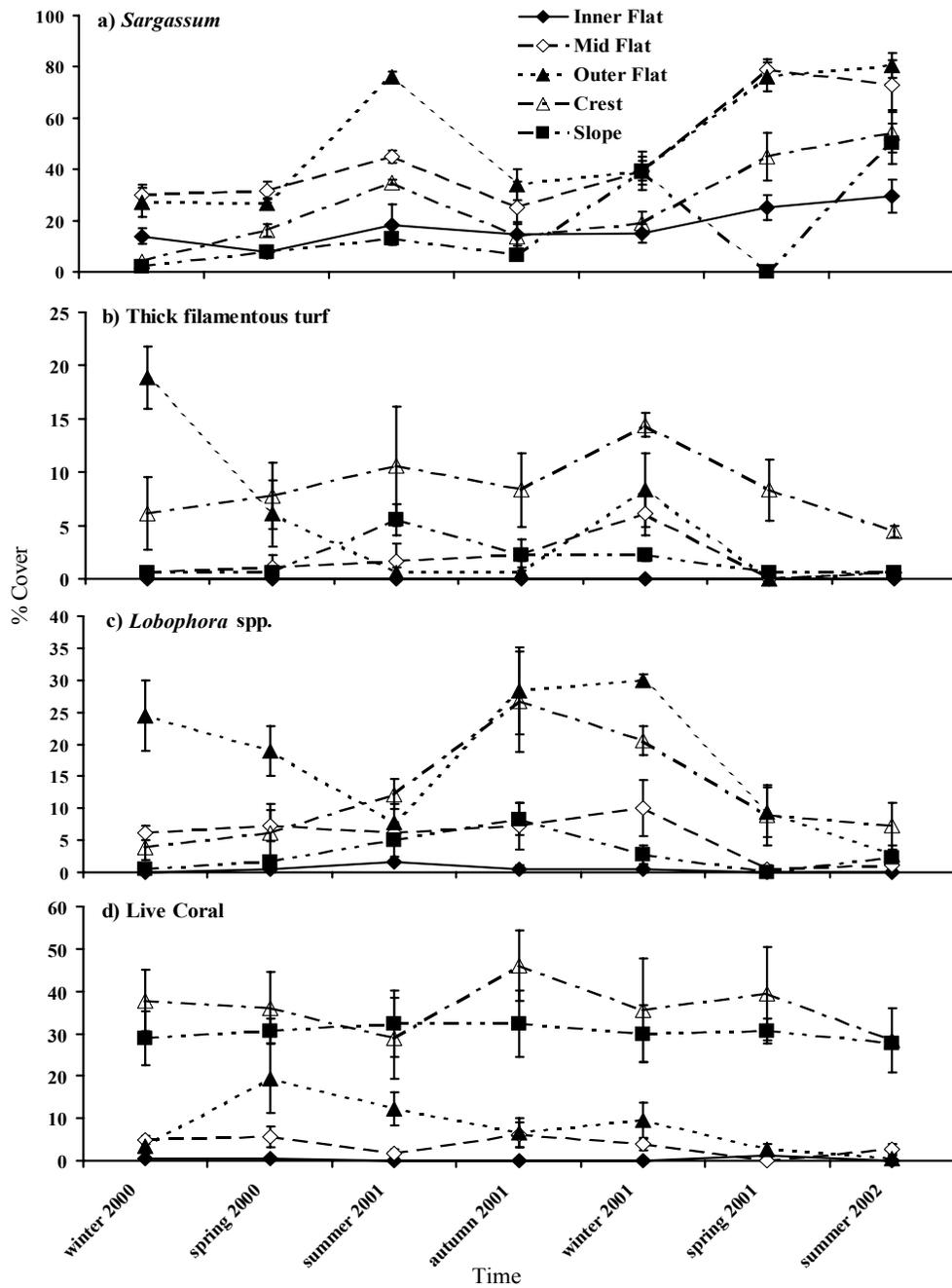


Figure 4. Temporal variations in the percent cover of four dominant benthic components across the five reef zones on the Nelly Bay reef. Note differences in the y-axes. Error bars = 1 S.E.

Space occupation of farmer territories

Stegastes apicalis clearly defended the largest territories ($1.56 \text{ m}^2 \pm 0.09$ S.E.) and *Pomacentrus tripunctatus* the smallest ($0.23 \text{ m}^2 \pm 0.01$ S.E.), with the territory sizes of all three species being significantly different from the others (*P. wardi* territories: $0.62 \text{ m}^2 \pm 0.03$ S.E.; $F_{(d.f.=2)} = 116.566$, $p < 0.001$). Furthermore, the territories of *P. tripunctatus* and *P. wardi* varied significantly between zones (Figure 5a). The territories of *P. tripunctatus* were significantly larger on the inner reef flat than on the mid reef flat, where it coexisted with *P. wardi* ($F_{d.f.=1} = 11.843$, $p < 0.05$). The territories of *P. wardi* were significantly larger on the outer reef flat than in any other zone (Figure 5a, $F_{d.f.=3} = 14.248$, $p < 0.05$). In zones where two species co-occurred, the territories of the smaller species were significantly smaller than those in zones that were not shared with a larger species (Figure 5a).

Calculations of the proportion of substratum taken up by farmer territories revealed that on the reef crest, almost 60% of the available space was taken up by *P. wardi* and *S. apicalis* territories (Figure 5b). On the mid and outer reef flat, 30% of the space was contained within *P. wardi* and *P. tripunctatus* territories. *P. tripunctatus* territories occupied between 5% and 7% of the inner reef flat (Figure 5b), which consisted primarily of sand and rubble.

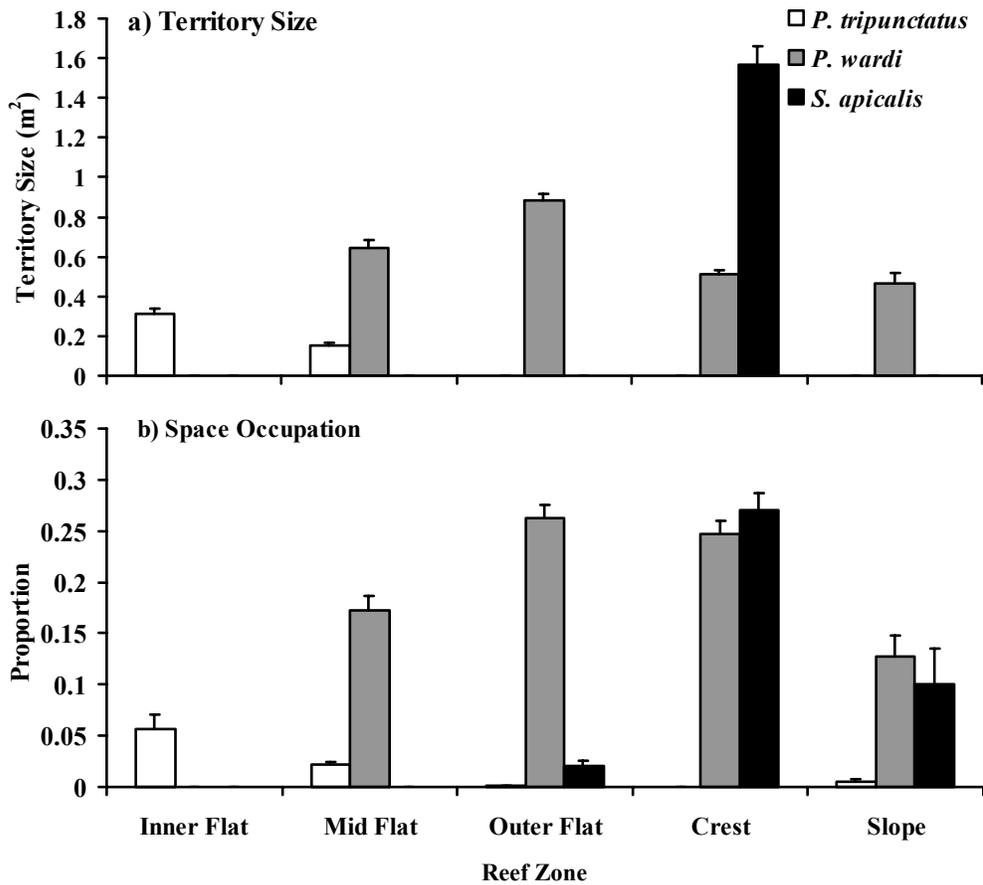


Figure 5. a) Mean territory size (measured in m²) of individuals of the three species of farmers in the five reef zones of Nelly Bay. b) Space occupation, measured as the proportion of available space in each zone taken up by farmer territories, in the five reef zones in Nelly Bay. Space occupation was calculated using farmer density estimates and territory area measurements. *P.*: *Pomacentrus*, *S.*: *Stegastes*. Error bars = 1 S.E.

Benthic communities inside and outside territories: spatial patterns

Substrata inside territories were consistently covered with a higher percentage of algal turf and epiphytes than similar substrata adjacent to territories (Table 2). Inside/outside territory differences in percent cover of turf and epiphytes varied significantly between species, but were consistent among zones. Both fleshy macroalgae and hard substrata, such as rubble, rock and dead coral were fed on by farmers, and were represented separately (Figure 6). Only *Pomacentrus tripunctatus* territories contributed to variation between zones; inside territories, the cover of turf was similar on fleshy macroalgae and hard substrata on the inner flat, but on the mid flat, percent cover was higher on fleshy macroalgae than on hard substrata. In *P. wardi* territories, fleshy macroalgae consistently appeared to be the preferred substratum for the cultivation of epiphytic algae, as percent cover was higher on fleshy macroalgae than on hard substrata across zones. In contrast, algal turf in *Stegastes apicalis* territories grew primarily on hard substrata. Outside territories, percent cover was equally distributed between fleshy macroalgae and hard substrata, with the exception of the inner flat, where more algal turf grew on hard substrata, and the outer flat, where fleshy macroalgae were more overgrown (Figure 6).

The composition of the algal turf community inside the territories of all three species was significantly different from the turf found in undefended areas. This difference varied between the two zones occupied by *P. tripunctatus* territories ($F_{(d.f.=14)} = 3.345, p < 0.05$). Terrigenous sediment covers substantial portions of the substratum of both zones occupied by *P. tripunctatus*, and was therefore measured inside and outside territories. Sediment particles were present on all forms of substratum categories. In *P. tripunctatus* territories, sediment loads were significantly reduced in comparison to adjacent undefended areas in both zones (Figure 7a). On the other hand,

detritus was more abundant inside territories in both zones (Figure 7b), and of all components of the algal turf communities in and around *P. tripunctatus* territories, detritus had the highest cover. The cover of the delicate erect calcified algae *Jania* spp. was higher inside territories than outside (Figure 7c), as was the cover of delicate filamentous red algae that were a possible food source for *P. tripunctatus* (Figure 7d). Surprisingly, the taxon most often found in high abundance inside the territories of other farmers, *Polysiphonia* spp., was found in higher abundance outside the territories of *P. tripunctatus* on the inner reef flat, while its cover on the mid reef flat was higher inside territories. Despite the statistical significance of these differences, *Polysiphonia* spp. was generally found in very low cover both inside and outside territories (Figure 7e). *Leveillella* spp. also occurred in higher abundance inside territories in both zones (Figure 7f). The cover of corticated red algae in general was higher inside territories in both zones (Figure 7g), especially of *Laurencia* spp. (Figure 7h).

Table 2. Analysis of Variance testing differences in overgrown substrata inside and outside territories, between species and in different zones. Factors representing significant effects are marked in bold.

Source	SS	df	MS	F	p
Zone	5 652.844	4	413.211	3.486	0.008
Species	11 471.330	3	3 823.777	9.431	0.000
In/Out	435 272.309	1	435 272.309	1 073.595	0.000
Zone x In/Out	3 619.401	4	904.850	2.232	0.064
Species x In/Out	13 357.564	3	4 452.521	10.982	0.000
Error	423 273.368	1044	405.434		

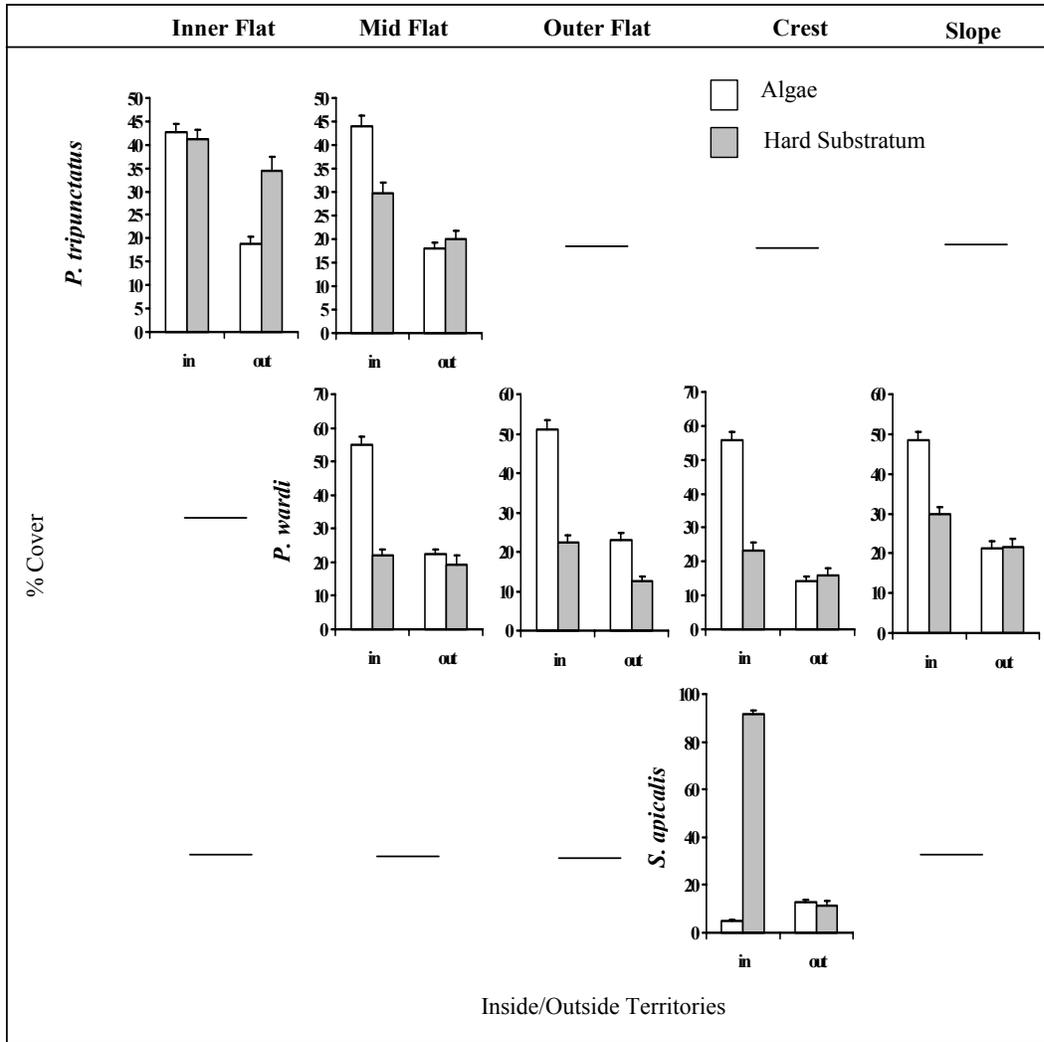


Figure 6. Percent cover of algal turf (on hard substrata) or epiphytes (on fleshy macroalgae). “Fleshy macroalgae” include all fleshy macroalgal taxa shown in Figure 2c. Percent cover is shown for each species in the zones of its occurrence, both inside (‘in’) and outside territories (‘out’). ‘-’ is used for reef zones where species did not occur, and percent cover was not calculated. Note the differences in y-axes. *P.*: *Pomacentrus*, *S.*: *Stegastes*. Error bars = 1 S.E.

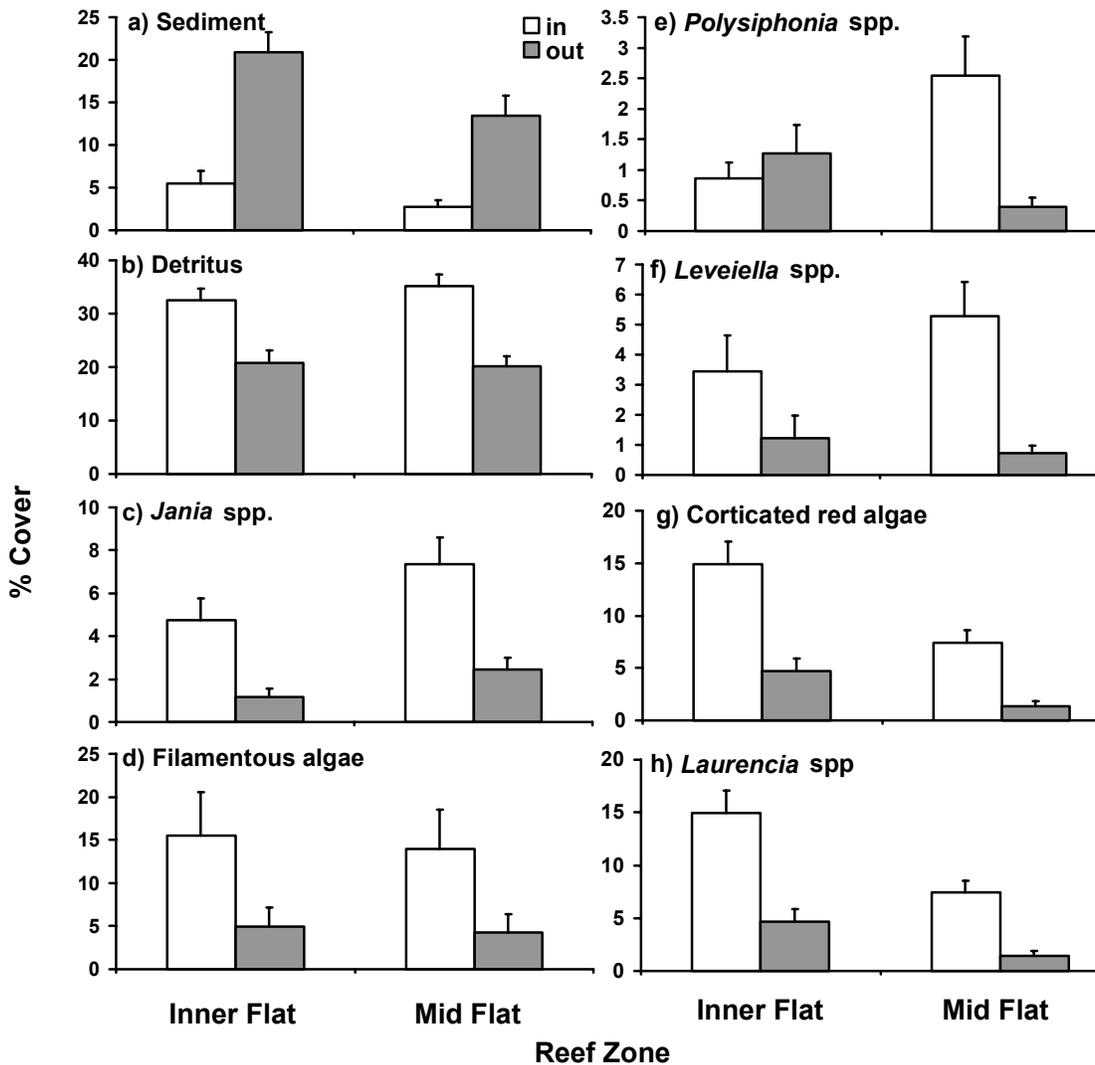


Figure 7. Percent cover of a) sediment, b) detritus and (c-h) algal taxa inside and outside *Pomacentrus tripunctatus* territories. All figures show benthic categories that were significantly different between inside and outside territories at the $p < 0.05$ level. Note the differences in the y-axes. Error bars = 1 S.E.

The differences in algal turf communities inside and outside *P. wardi* territories were not consistent between zones (Multivariate $F_{(d.f.=42)} = 3.541$, $p < 0.001$). Sediment loads were higher outside territories than inside, and this difference was significantly larger on the reef slope than on the reef flat and crest (Figure 8a). The cover of detritus was higher inside territories across all zones where *P. wardi* was present (Figure 8b). The cover of *Jania* spp. was approximately three times higher inside territories than outside on the mid and outer reef flat, but on the crest and slope it was only slightly higher inside territories than outside. Furthermore, the overall cover of *Jania* was highest on the mid reef flat (Figure 8c). As expected, the cover of filamentous algae was always significantly higher inside territories than outside. This difference was greatest on the reef crest, with filamentous turf covering over 40% of substrata inside territories and only around 7% in undefended areas (Figure 8d). *Polysiphonia* was the genus that conformed most closely to this pattern, as it was always significantly more abundant inside territories than outside (Figure 8e). The largest differences in *Polysiphonia* cover inside and outside territories were found on the mid reef flat, where *Polysiphonia* was almost absent outside territories, and on the crest, where its cover inside territories was an order of magnitude higher than outside (Figure 8e).

Corticated red algae were consistently found to be more abundant inside *P. wardi* territories, where their cover was approximately five-fold that found outside territories throughout all zones (Figure 8f). Corticated red algae of the genus *Laurencia* were found to be higher inside territories than outside primarily on the mid reef flat (Figure 8g), while the tougher corticated red algae *Gelidiopsis* spp. were consistently found almost only inside territories (Figure 8h).

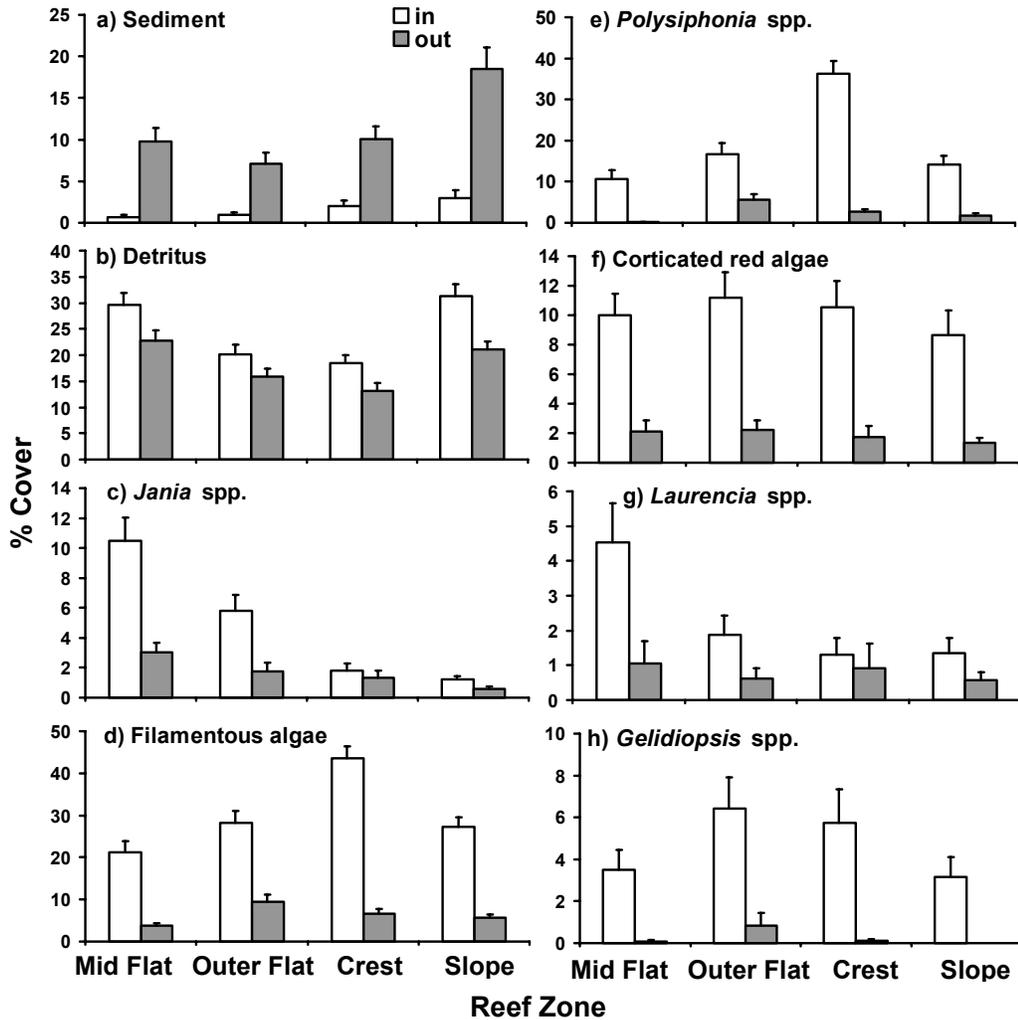


Figure 8. Percent cover of a) sediment, b) detritus and (c-h) algal taxa inside and outside *Pomacentrus wardi* territories in the four reef zones of its distribution. All figures show benthic categories that were significantly different inside and outside territories at the $p < 0.05$ level. Note the differences in the y-axes. Error bars = 1 S.E.

S. apicalis was the only species of this farmer assemblage that defended territories in which algal turfs were visibly different from surrounding areas. The distinct community structure of algal assemblages was also evident from the algal turf collections ($F_{(d.f.=11)} = 183.99$, $p < 0.001$). Sediment and detritus were more abundant outside territories, with sediment almost absent inside territories (Figure 9a). Filamentous red algae covered almost 60% of substrata inside territories, compared with 10% in surrounding areas. Of the filamentous red algae inside *S. apicalis* territories, more than half were of the genus *Polysiphonia* (Figure 9b). Corticated red algae, which were otherwise almost absent in reef crest turf communities, covered 30% of *S. apicalis* territories, and consisted almost exclusively of the species *Gelidiopsis scoparia* (Figure 9c). The most visually striking component of *S. apicalis* territories is the large stands of *Amphiroa* spp., and to a smaller extent *Jania* spp., both of which were not otherwise found on the reef crest (Figure 9d).

Benthic communities inside and outside territories: temporal patterns

There were small but significant variations in overall percent cover of algal turfs over time, with variability between inside and outside territories and among zones (Time x Zone x Inside/Outside: $F_{(d.f.=7)} = 2.728$, $p < 0.05$). Inside *Pomacentrus tripunctatus* territories, there was an initial shift in the dominant substratum overgrown with algal turf from hard substrata to fleshy macroalgae (Figure 10a). Both substratum types had higher turf cover inside territories consistently over time, with the exception of a significant increase in the cover of turf on hard substrata in the last six months of the study, possibly in response to the coral bleaching even in 2002 (Figure 10a). The difference between inside and outside territories of *P. wardi* was more striking, with the percent cover of epiphytes on fleshy macroalgae varying between 20% and 80%, but essentially remaining higher than outside territories over time. Percent cover of algal

turf on hard substrata inside *P. wardi* territories was not significantly different from percent cover outside territories (Figure 10b). The highest overall percent cover of algal turf was found on hard substrata inside *Stegastes apicalis* territories, where it ranged between 84% and 100%. Hard substrata outside territories were initially overgrown to approximately 44%, but percent cover then declined over the following six months and remained at around 5% for the remaining time of the study (Figure 10c).

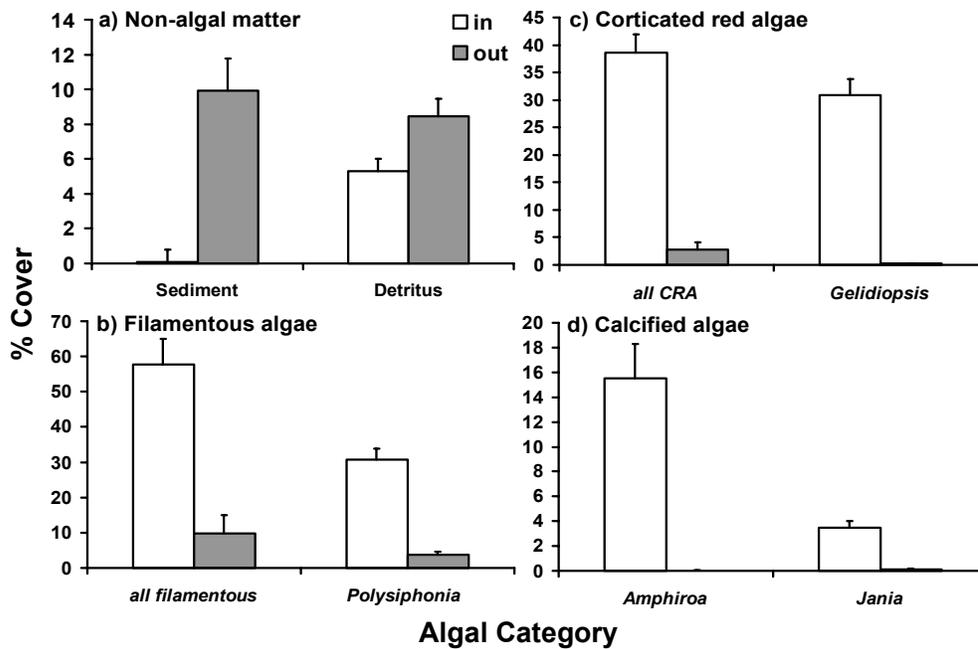


Figure 9. Percent cover of a) sediment and detritus, b) filamentous algae and *Polysiphonia*, c) corticated red algae (CRA) and *Gelidiopsis*, d) erect calcified algae inside and outside *Stegastes apicalis* territories on the reef crest. All figures show benthic categories that were significantly different between inside and outside territories at the $p < 0.05$ level. Note the differences in the y-axes. Error bars = 1 S.E.

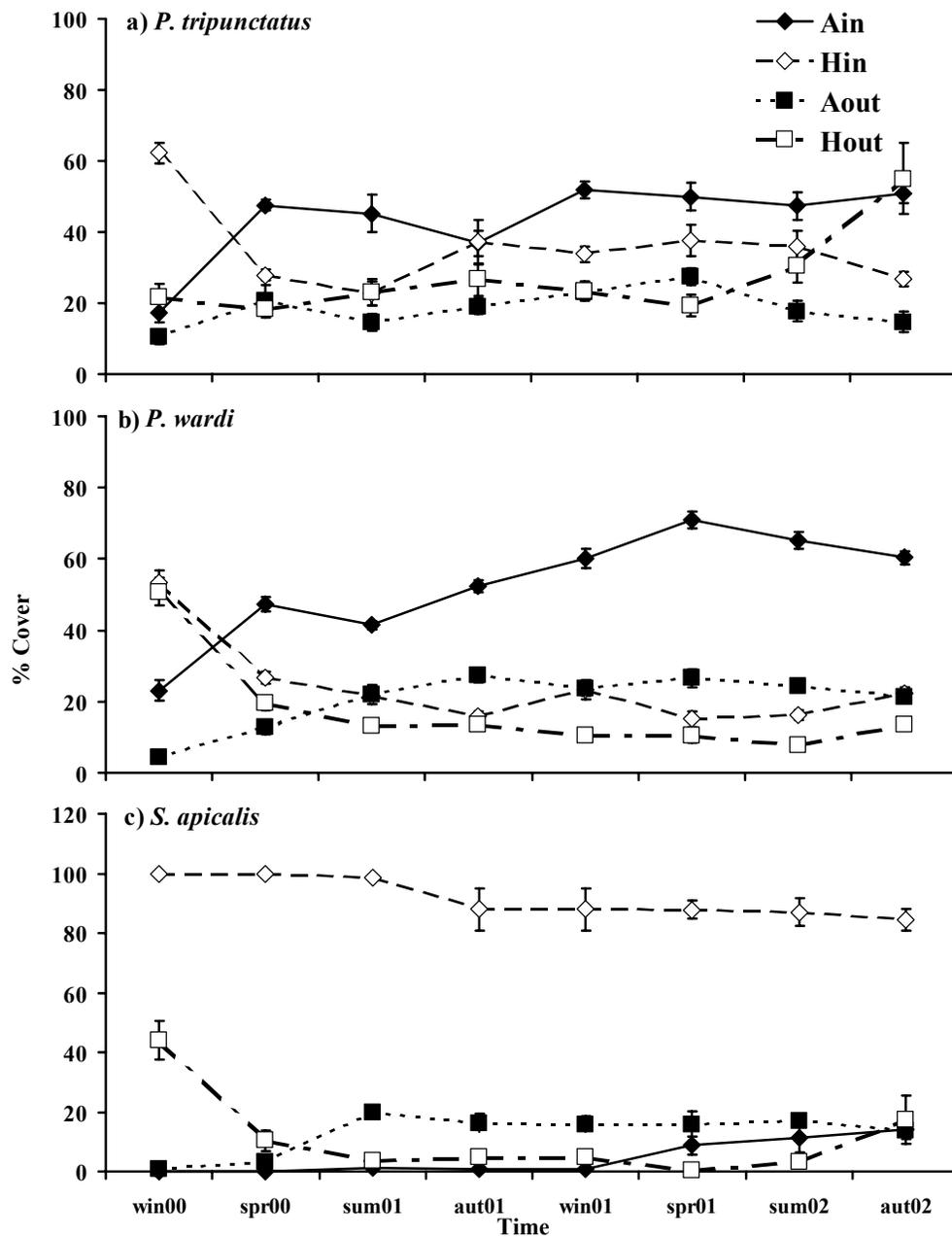


Figure 10. Temporal changes in the overall percent cover of algal turf and epiphytes inside and outside the territories of a) *Pomacentrus tripunctatus*, b) *Pomacentrus wardi*, c) *Stegastes apicalis*. Different lines and symbols represent different substrata. Ain: Fleshy macroalgae inside territories, Hin: hard substrata inside territories, Aout: Fleshy macroalgae outside territories, Hout: hard substrata outside territories. Win: winter; spr: spring; sum: summer; aut: autumn. Error bars = 1 S.E.

There were significant seasonal changes in the difference between inside and outside *P. tripunctatus* territories, and these seasonal pulses varied among reef zones (MANOVA: $F_{(d.f.=45)} = 1.409$, $p < 0.05$). Sediment was consistently higher outside *P. tripunctatus* territories, but the lowest cover of sediment was found inside territories on the mid flat (Figure 11). There was a strong and significant increase in sediment cover outside territories in both zones towards the end of 2002, and this increase occurred three months earlier on the mid flat than on the inner flat.

The cover of *Polysiphonia* spp. was not significantly different between inside and outside territories on the inner flat, except for a brief bloom outside territories in the winter of 2000 (Figure 12). On the mid flat, *Polysiphonia* cover was significantly higher inside territories, with brief blooms in both winters.

Seasonal changes were also significant inside and outside *P. wardi* territories, and seasonal patterns varied among reef zones (MANOVA $F_{(d.f.=135)} = 1.231$, $p < 0.05$). Sediment cover was uniformly low, except for the high sediment load found outside territories in the winter of 2000. On the mid and outer flat, sediment was almost absent inside territories, and outside territories sediment cover ranged between 17% (outer flat) and 30% (mid flat) (Figure 13). On the crest and slope, sediment cover was not only higher outside territories (33% and 55%, respectively), it was slightly raised inside territories as well (11% and 13%, respectively). Sediment returned to low cover (below 10%) more quickly inside territories than outside (Figure 13). The cover of *Amphiroa* spp., despite being uniformly low, nevertheless displayed significant seasonal patterns. There were small *Amphiroa* “blooms” inside territories in both springs of the study period on the mid flat, in the second summer on the outer flat, in both summers on the crest, and none at all on the reef slope (Figure 14). The cover of filamentous algae was very low outside territories in all zones. Inside territories, filamentous algal cover was

higher than outside throughout the sampling period, with no significant differences between zones (Figure 15).

There were no significant seasonal changes in the difference between inside and outside *S. apicalis* territories (MANOVA Pillai's Trace $F_{(d.f.=45)} = 1.265$, NS). Of the three species in Nelly Bay, it appeared that *S. apicalis* territories were the most distinct when compared to areas outside territories, but also the most stable in terms of seasonal changes.

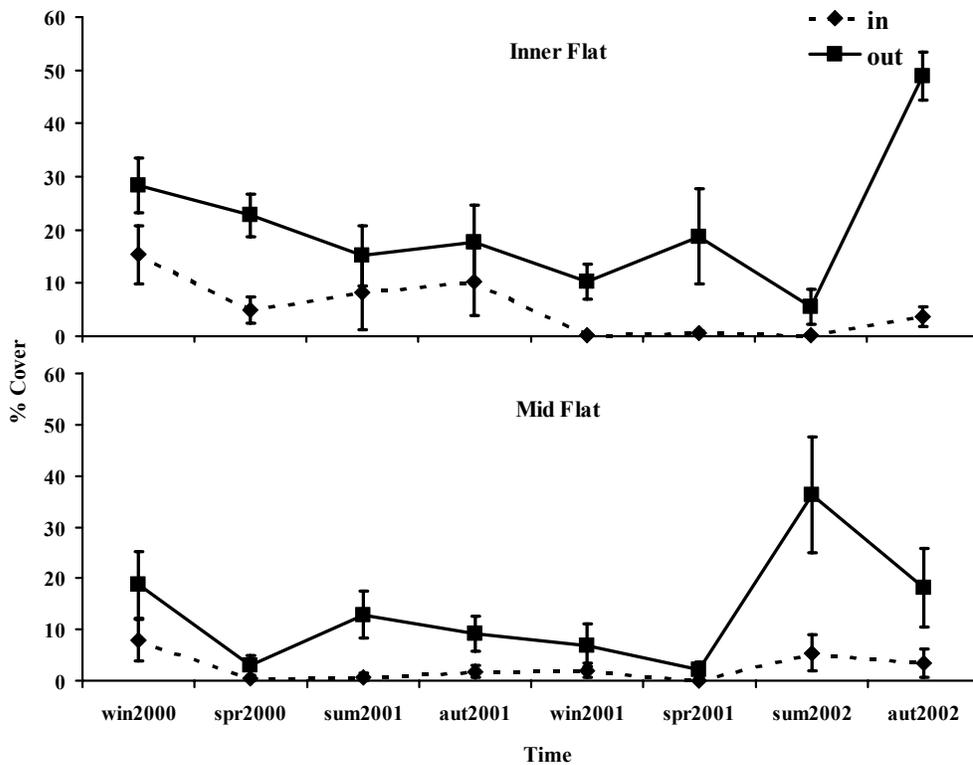


Figure 11. Temporal variation in % cover of sediment inside and outside *Pomacentrus tripunctatus* territories a) on the inner reef flat and b) on the mid reef flat. There was a significant interaction between time, zone and inside/outside territories ($F_{(d.f.=3)} = 4.161$, $p < 0.01$). Win: winter; spr: spring; sum: summer; aut: autumn. Error bars = 1 S.E.

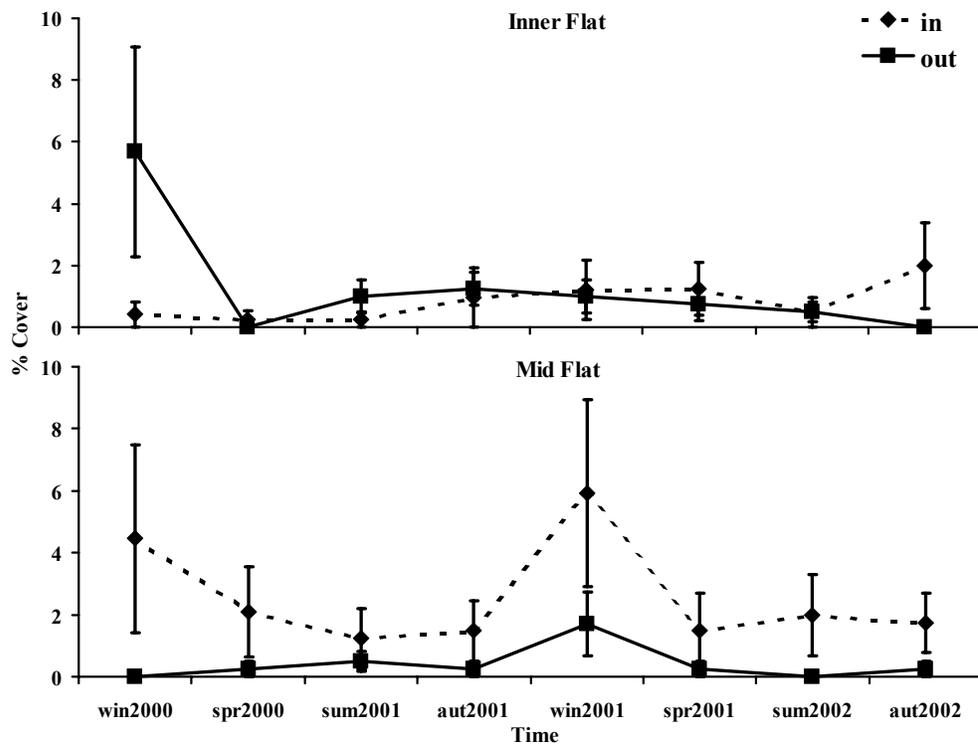


Figure 12. Temporal variation in % cover of *Polysiphonia* spp. inside and outside *Pomacentrus tripunctatus* territories a) on the inner reef flat and b) on the mid reef flat. There was a significant interaction between time, zone and inside/outside territories ($F_{(d.f.=3)} = 3.01, p < 0.05$). Win: winter; spr: spring; sum: summer; aut: autumn. Error bars = 1 S.E.

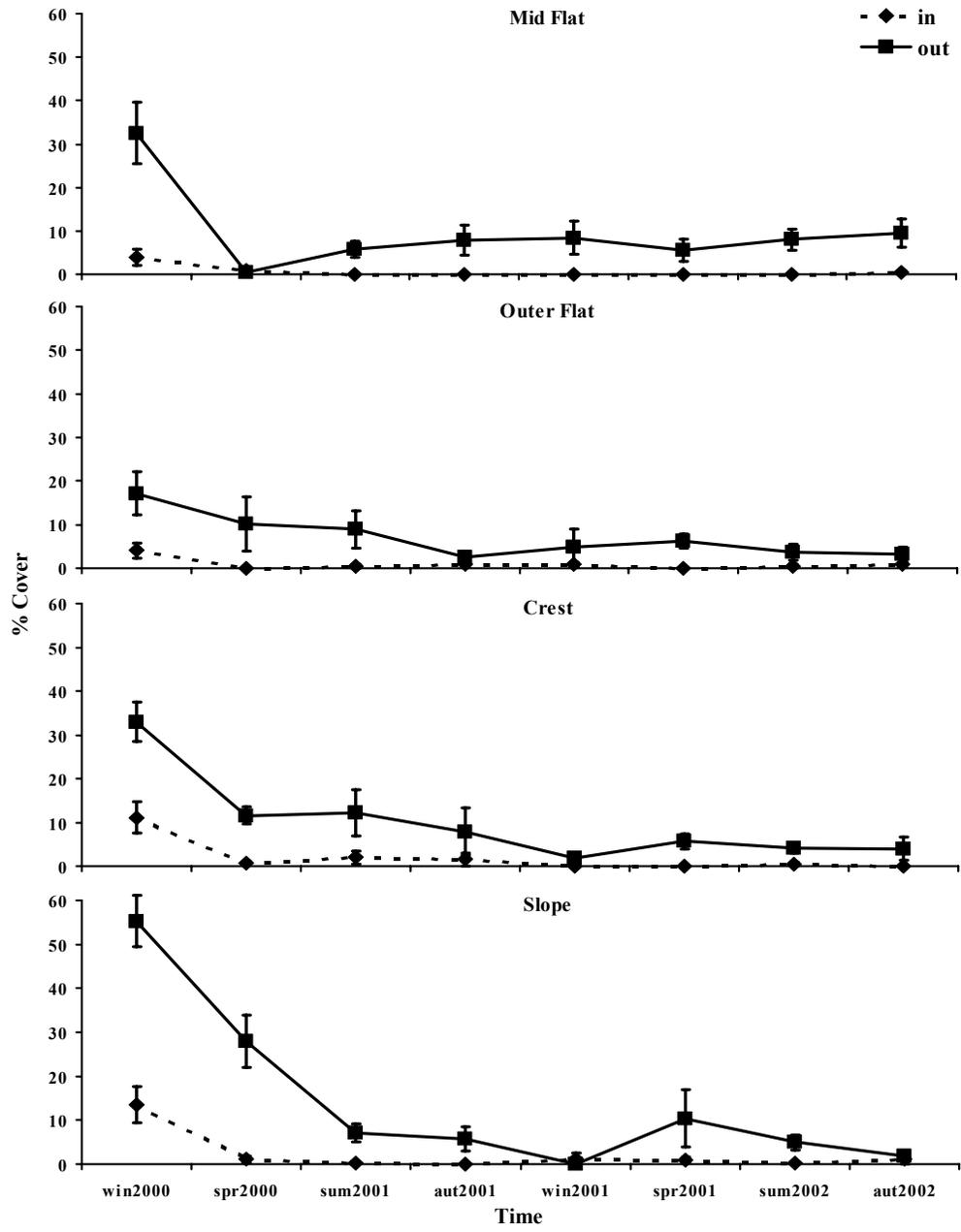


Figure 13. Temporal variation in % cover of sediment inside and outside *Pomacentrus wardi* territories a) on the mid reef flat, b) on the outer reef flat, c) on the reef crest and d) on the reef slope. There was a significant interaction between time, zone and

inside/outside territories ($F_{(d.f.=9)} = 2.132, p < 0.05$). Win: winter; spr: spring; sum: summer; aut: autumn. Error bars = 1 S.E.

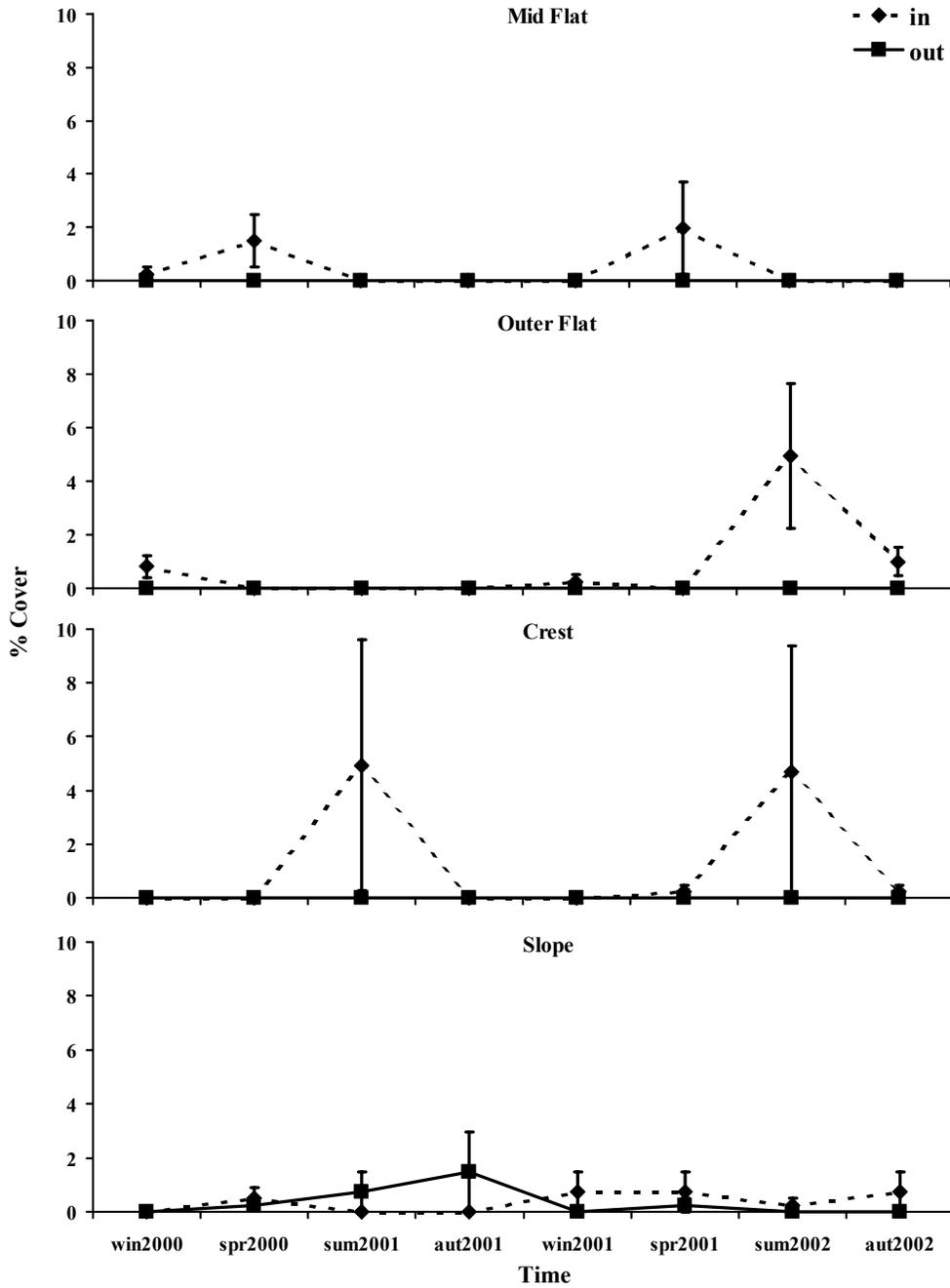


Figure 14. Temporal variation in % cover of *Amphiroa* spp. inside and outside *Pomacentrus wardi* territories a) on the mid reef flat, b) on the outer reef flat, c) on the

reef crest and d) on the reef slope. There was a significant interaction between time, zone and inside/outside territories ($F_{(d.f.=9)} = 2.25, p < 0.05$). Win: winter; spr: spring; sum: summer; aut: autumn. Error bars = 1 S.E.

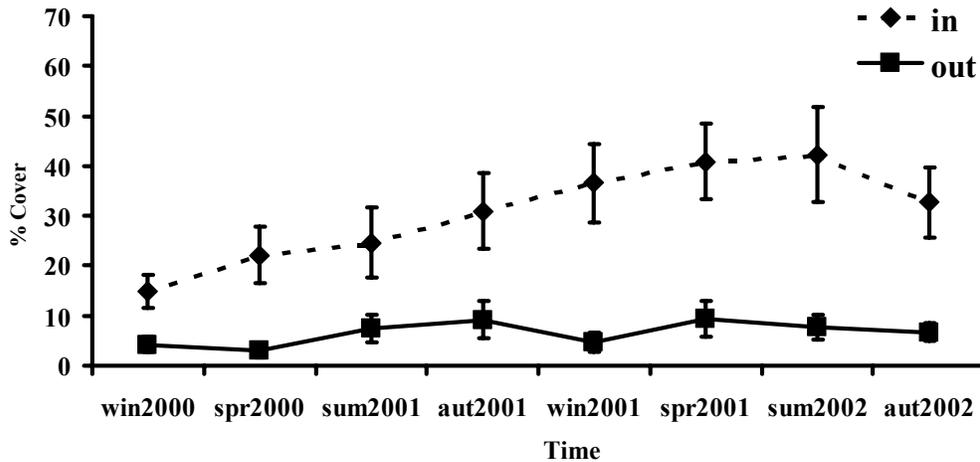


Figure 15. Temporal variation in % cover of filamentous algae inside and outside *Pomacentrus wardi* territories, with average % cover pooled over all zones where *P. wardi* occurs: Mid flat, Outer flat, crest and slope. Win: winter; spr: spring; sum: summer; aut: autumn. Error bars = 1 S.E.

Discussion

Generalizations about the effects of farmers are problematic because they overlook differences between species, spatial variability and temporal patterns (Ceccarelli et al. 2001). The results of this study confirm that farmers can have different effects in different reef zones because of the distinct patterns of zonation that can occur in both farmer and algal communities. Furthermore, there was significant temporal variability in the composition of the benthic community and in the effects of farmers on their territories, although overall zonation patterns tended to remain consistent over time.

There are several studies on the effects of farmers on benthic communities that include information on the taxonomic differences between turf communities inside and outside territories (reviewed by Ceccarelli et al. 2001). None of these studies takes into account the natural local distribution of the study species (both farmers and benthos). It is possible that these studies have chosen species with restricted within-reef distributions, but at least two typically occupy several reef zones (Waldner and Robertson 1980): *Stegastes planifrons* (Brawley and Adey 1977; Ruyter van Steveninck 1984; Hinds and Ballantine 1987) and *S. partitus* (Ruyter van Steveninck 1984). This confirms the need for most studies on farmer effects to consider the within-reef spatial distribution of farmers.

Differences among farmer species

This study provides a clear indication of the differences that can exist between species in terms of how they affect benthic communities. The effects of two of the species studied here were previously unknown, and possibly considered negligible, as both *Pomacentrus tripunctatus* and *P. wardi* maintain territories that are visually undifferentiated from surrounding substrata (pers. obs.). Despite the findings that *Stegastes apicalis* clearly had the strongest effects on benthic communities, both in terms of overall percent cover and in terms of the taxonomic structure of the algal turf, *P. tripunctatus* and *P. wardi* also had significant effects on the benthos in their territories. In all zones, the territories of *P. tripunctatus* and *P. wardi* contained at least twice as much, and sometimes up to an order of magnitude more, detritus, filamentous algae and delicate corticated red algae when compared to undefended areas. Algal turf collections revealed significantly higher cover of several taxa of palatable algae (Paul and Hay 1986) inside the territories of both species. *S. apicalis*, on the other hand, defended territories covered in a thick mat of *Gelidiopsis*, *Amphiroa* and *Jania*, which

provide a framework for dense stands of *Polysiphonia*. These territories were very different in appearance from surrounding areas.

Generalizations about the effects of farmers on benthic communities have come from studies on species that maintain territories similar to those of *S. apicalis* in terms of their difference from surrounding substrata (Ceccarelli et al. 2001). The subtle but significant effects of *P. tripunctatus* and *P. wardi* suggest two things. Firstly, generalizations about the magnitude of the effects of individual farmer species on benthic communities are likely to be overestimates because they are based on farmers that have the strongest effects on benthic communities. Secondly, generalizations about the spatial extent of farmer influence are likely to be underestimates because small species with seemingly undifferentiated territories have largely been ignored.

Differences between reef zones

Assumptions about the influence of farmers on benthic communities may be strongly affected by the reef zone chosen for sampling. Most striking are the six-fold increase in *Polysiphonia* cover in *Pomacentrus tripunctatus* territories on the mid flat, but not on the inner reef flat, and the increase in *Jania* and *Laurencia* cover in *P. wardi* territories on the mid and outer flat, but not the crest and slope. Comparing studies on the same species in different geographic locations has revealed that many species maintain territories with slightly different algal turf taxa depending on where sampling occurs. For instance, *Stegastes apicalis* territories were dominated by both robust algae (*Gelidiopsis*, *Lobophora*) and delicate filaments (*Polysiphonia*) in the Gulf of Thailand (Kamura and Choonhabandit 1986), almost only filamentous species (*Herposiphonia*, *Centroceras*) on Davies Reef, Great Barrier Reef (Klumpp and Polunin 1989), and an assemblage of erect calcified algae (*Amphiroa*), tough corticated algae (*Gelidiopsis*) and

filaments (*Polysiphonia*) in Nelly Bay (this study). However, no study has considered within-reef variability in territory composition until now.

Linking farmer distribution and territory composition with overall benthic zonation is important when considering that reef zones may be different in their substratum and benthic characteristics. The availability of food and suitable substrata in their immediate habitat may have a strong influence on the ability of farmers to promote their preferred food algae (Ceccarelli et al. 2001). Territories of all three species were associated with substrata that experienced significantly higher levels of percent cover, both in the form of algal turf on hard substrata and epiphytes on fleshy macroalgae. However, the percent cover of turf on hard substrata was the same inside and outside *P. tripunctatus* and *P. wardi* territories. The results of this study suggest that these two species may do less to change the overall percent cover of turfs on hard substrata, but significantly increase the growth of epiphytes on fleshy macroalgae. This may have subtle effects on these fleshy macroalgae in terms of their distribution and their susceptibility to other grazers.

Many studies suggest that epiphytes have negative effects on their host plants, by inhibiting light (Cebrian et al. 1999) and carbon dioxide absorption (Sand-Jensen 1977), increasing drag and reducing reproductive output (D'Antonio 1985), and attracting mesograzers to the host plant (Karez et al. 2000). Farmer territories may be areas of increased epiphytic load on macroalgae, therefore representing patches of increased vulnerability of fleshy macroalgae due to their increased palatability to mesograzers, which may in turn affect mesograzers densities (Zeller 1988). Long-term effects on macroalgae are likely to be difficult to determine due to the strong seasonal cycle of *Sargassum* populations (McCourt 1984).

The distribution of farmer territories across reef zones may also be important in relation to the reef-wide distribution of both food algae and other grazers. Russ (1987) found that the yield of algal tissue to all grazers (including the resident farmers) were possibly higher inside the territories of *Stegastes fasciolatus* than outside. His study posed the question “If ... the actions of territorial fishes affect such important trophodynamic processes as rates of production of algae and consumption by grazers, how important and widespread might such effects be on coral reefs?”. The present study did not measure algal production and algal removal by grazers, but it broadens the within-reef spatial and temporal context in which studies on farmer effects have been conducted. Furthermore, this study demonstrates that studies on whole-reef algal production and consumption by grazers must take into account farmer species that do not visibly alter the composition of their territories. This study and other studies have found that space occupation of farmer territories is highest on the reef crest (Robertson and Lassig 1980; Russ 1984a; Meekan et al. 1995). A recent study suggested that large grazers aggregate in areas of highest algal production (Russ 2003), which in many cases is the reef crest (Barnes and Devereux 1984; Klumpp and McKinnon 1989; Klumpp and Polunin 1990). Future studies could investigate whether these high algal production and grazing rates are found on reef crests because sampling often occurs inside farmer territories.

The results of this study show that the space occupation of farmer territories, when taking into account the entire farmer community, encompasses much larger areas than previously thought. For instance, if this study had followed the example of other studies and included only *S. apicalis*, the reef-wide space occupation would be restricted to the reef crest and consist of ~30%. Inclusion of *P. tripunctatus* and *P. wardi* increased the space occupation estimate to include all reef zones, with a whole-

reef average of 43% (+/- 3.3SE), and a total space occupation on the reef crest of 52%. The contribution of these territories to the benthic structure of Nelly Bay becomes much greater when considering all three farmer species. A simple calculation using the space occupation of *P. wardi* and *S. apicalis*, and the proportional increase in filamentous algae contributed by the territories of both species, estimates that farmer territories increase filamentous algal cover on the reef crest by approximately 325%. Furthermore, the presence of *S. apicalis* territories reduces the cover of fleshy macroalgae on the reef crest by ~30%.

Temporal patterns

A further element often overlooked in studies of farmers and their effects on benthic communities is the possible temporal dynamics in territory composition. Despite small differences inside *Pomacentrus tripunctatus* and *P. wardi* territories, the overall spatial patterns found in this study were essentially stable over time. Sediment cover declined more rapidly inside the territories of *P. wardi* than outside, and failed to increase inside *P. tripunctatus* territories during high sedimentation rates in the summer and autumn of 2002. These findings suggest that farmers either actively clear sediment from their territories or modify their territory composition in a way that clears sediment or inhibits sedimentation. Sediment loads have been found to be detrimental for *Sargassum* spp. on Magnetic Island (Umar et al. 1998). Further work is needed to study the effects of farmer territories on *Sargassum*, in particular, because there may be a complicated interaction between the increased epiphytic load that may be detrimental for *Sargassum*, offset by the decreased sediment load which may be beneficial. The seasonal nature of *Sargassum* spp. (Vuki and Price 1994) would necessitate a temporal approach, as effects could be long-term and associated with regeneration, growth and

reproductive potential rather than an immediately measurable effect on biomass or size (Umar et al. 1998).

Temporal variations may not be of the same importance in every environment, however, many studies take place in locations that experience seasonal changes in the physical environment. Here, the seasonality in the physical environment was reflected in the life cycle of the dominant benthic component of the habitat, the fleshy macroalgae *Sargassum* spp. The less visible components of the benthos, both inside and outside farmer territories, responded to these changes. Differences in temporal dynamics of some algal taxa in *P. tripunctatus* and *P. wardi* territories suggest that the time of sampling may have a significant effect on findings of inside/outside territory differences. Previous studies that have measured seasonal changes in farmer territories have found significant changes in biomass (Klumpp et al. 1987), productivity (Ferreira et al. 1998) and even species composition of algal turfs (Ferreira et al. 1998).

Comparison with offshore reefs

This study was conducted on an inshore reef of the Great Barrier Reef (GBR), an environment characterized by strong fluctuations in the physical and chemical environment (Morrissey 1980; Wachenfeld et al. 1998). How do the patterns found on this reef relate to most other farmer studies on the GBR, all of which have been conducted on offshore reefs? Most offshore reefs have higher species richness of farmers (Williams 1982; Russ 1984b), and the results of this study suggest that each species may have different effects on benthic communities. Each reef zone is therefore likely to be affected by a more complex combination of different farmer effects, and more space may be occupied by farmer territories in each zone. Temporal patterns are also likely to be different, due in part to the lack of a highly seasonal benthic community, such as the *Sargassum*-dominated community in Nelly Bay. Being closely

associated with the benthos, farmers on offshore reefs are therefore likely to be subject to a more constant environment than those on inshore reefs. To determine the extent of these patterns, inshore–offshore comparisons of farmers and their effects on benthic communities are necessary.

Conclusions

This study has indicated the importance of incorporating more farmer species, the space occupied by their territories, and the spatial and temporal patterns in their effects on benthic communities when searching for the importance of their role on coral reefs. Not all farmers have the same dramatic effects on benthic communities as those studied more often, and the general assumption that all farmers have strong and visible effects is an overestimate. However, they occupy more space than previously thought, more species than expected significantly alter benthic communities in their territories, and these effects vary in space and time. The general role of farmers on coral reefs, and the importance of spatial and temporal patterns, may therefore have been underestimated.

CHAPTER 3: A MULTI-SPECIES COMPARISON OF FARMERS AND THEIR EFFECTS ON CORAL REEF ALGAL COMMUNITIES

Introduction

Territorial herbivorous damselfishes, or ‘farmers’, are a widespread and abundant component of coral reef fish communities (Doherty 1983; Meekan et al. 1995; Ceccarelli et al. 2001). They occur in most coral reef zones (Sale 1978; Robertson and Lassig 1980; Waldner and Robertson 1980) and are often present in high densities (Sammarco and Williams 1982; Klumpp et al. 1987). They are the numerically dominant herbivores in some areas (Williams 1982; Russ 1984b; Scott and Russ 1987). Their territorial defence and farming activities often alter the benthic communities within their territories (Ceccarelli et al. 2001), and in some cases they have been attributed the status of keystone species, controlling algal diversity (Hixon and Brostoff 1983) and coral zonation (Wellington 1982). However, it is not clear to what extent farmers represent a single functional group of herbivores with a common role in coral reef ecosystems.

Despite the high diversity in this guild, research on their effects on benthic communities has been restricted to a few species that maintain visually distinct mats of algal turf, such as *Stegastes planifrons* and *Hemiglyphidodon plagiometapon* (Ceccarelli et al. 2001). Many species in the genera *Pomacentrus* and *Chrysiptera* also defend territories, but how these territories differ from surrounding substrata is largely unknown. Recently, it has been shown that some of these smaller species have significant effects on the algae in their territories (Chapter 2). These species are usually more abundant and spatially more widespread than the larger, more conspicuous species

(Robertson and Lassig 1980; Meekan et al. 1995; Lewis 1997). To gain a broader understanding of the effects of farmers on coral reef benthic communities, it is necessary to focus on the full range of territorial species.

A more comprehensive understanding of the functional role of farmers must include a description of their diets and patterns of feeding selectivity (Bay 1999; Santana 2001). The group appears to be represented by a diversity of feeding modes, including herbivory (Santana 2001), detritivory (Wilson and Bellwood 1997) and omnivory (Zeller 1988). Among herbivores, there appear to be microalgal feeders primarily consuming diatoms (Bay 1999; Santana 2001) and species that consume filamentous and corticated algae (Montgomery 1980a; Bay 1999). This range of diets challenges the assumption that all farmers affect the algal composition and biomass through selective feeding alone (Lobel 1980; Jones 1986). However, diets and feeding selectivity are unknown for most species. An investigation of the stomach contents of different species provides a useful place to begin evaluating diets (Wilson and Bellwood 1997). Comparing proportions of food items in gut contents to the available proportions of those items inside territories is a valuable method for establishing the potential for selective feeding (Manly et al. 1993; Santana 2001).

Evaluations of the effects of farmers on benthic communities often ignore the amount of space they actually occupy on coral reefs (Ceccarelli et al. 2001). Territories of different farmer species may be discreet (Brawley and Adey 1977), overlapping (Russ 1987) or even shared (Robertson and Polunin 1981), affecting the area and nature of their influence on coral reefs. A farmer species maintaining isolated territories surrounded by undefended benthos is likely to have quantitatively different effects from species that form large colonies with contiguous territories. Focussing on just one farmer species cannot provide information about the overall significance of the farmer

community on any given reef (Klumpp et al. 1987; Hata and Kato 2002). Here I sample a wide range of farmer species and relate their effects on benthic communities to the extent of space occupation by the guild as a whole.

Despite the broad geographic distribution of many species of farmers (Allen 1975), generalizations about farmer effects have tended to arise from studies at a single location. Comparisons of territory composition in some species of farmers reveal that the composition of algal turf in their territories can vary according to their location. For instance, the territory composition of *Stegastes apicalis* was different according to whether sampling occurred in the Gulf of Thailand (Kamura and Choonhabandit 1986), on Davies Reef, Great Barrier Reef (Klumpp and Polunin 1989), or in Nelly Bay, Magnetic Island (Chapter 2). The abundance and diversity of farmers clearly vary on local and geographic scales, which may have implications for the importance of this guild in coral reef ecosystems.

The objectives of this study were to investigate the diet, feeding selectivity, territory composition and space occupation of 10 farmer species at three locations: Magnetic Island, Great Barrier Reef (GBR), Orpheus Island (GBR) and Kimbe Bay, New Britain, Papua New Guinea (PNG). The following questions were addressed:

1. What are the diets of different farmer species, and which potential food items are selected or avoided?
2. What are the differences in benthic structure and algal turf composition between inside and outside the territories of different species at each location?
3. What are the differences in territory size between farmer species, and how much space do they occupy at each location?

Materials and Methods

Study sites

The three sites chosen for this study were Magnetic Island, GBR (19°17S, 146°86E), Orpheus Island, GBR (18°36S, 146°29E) and Kimbe Bay, PNG (5°26S, 150°52E; Figure 1). Each location had a distinct farmer community (Table 1), different substratum characteristics and different benthic communities. Magnetic Island reefs were composed of extensive reef flats dominated by dead corals and fleshy macroalgae, well-defined reef crests with high live coral cover and shallow, gently descending reef slopes with high live coral cover interspersed with patches of *Sargassum* spp. and *Lobophora* spp. Orpheus Island was more characteristic of mid - shelf reefs of the GBR, with high live coral cover (recovering from the 1998 bleaching event) and low cover of fleshy macroalgae. The reef topography was more complex than on Magnetic Island and the farmer community more diverse (Table 1). The Kimbe Bay sites used for this study were platform reefs, and despite their proximity to the shore, water clarity was higher than at the other two sites, and the reefs resembled outer shelf reefs of the GBR. Topographic complexity and farmer diversity were highest on these reefs. All field data were collected between the months of April and August, in the years from 2001 to 2003.

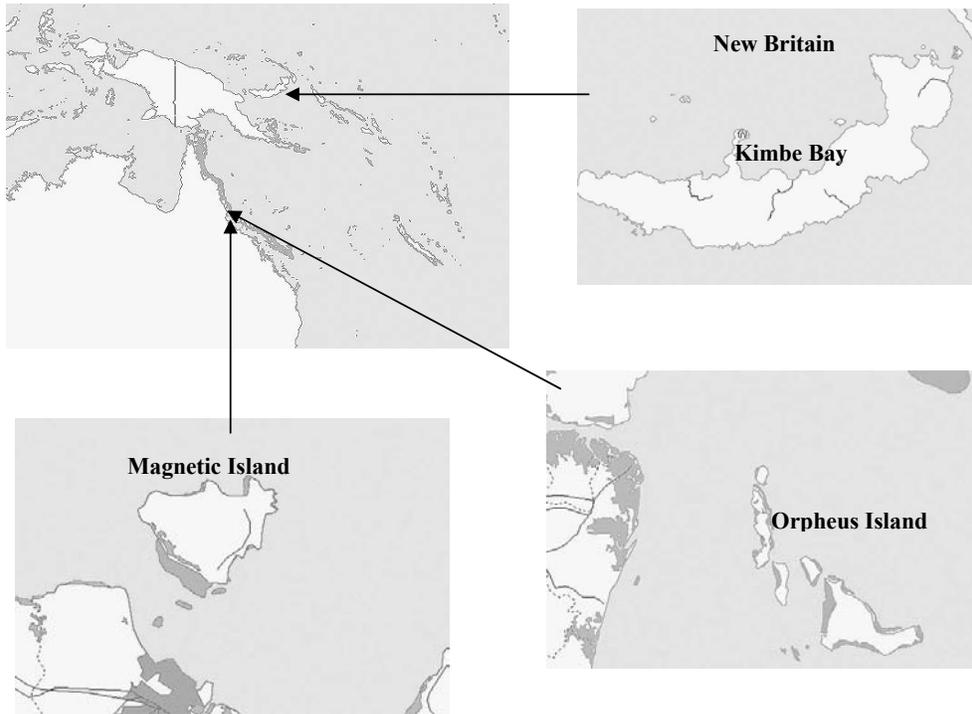


Figure 1. Maps of the three locations used for the study. Magnetic Island and Orpheus Island are located on the Central Great Barrier Reef, while Kimbe Bay is on the northern shore of New Britain, Papua New Guinea.

Table 1. Summary of locations and species used for the sampling. M.I.: Magnetic Island; O.I.: Orpheus Island; K.B.: Kimbe Bay. The four ecological characteristics across the top row were not sampled for every species in each locations; ‘X’ marks where sampling of different characteristics occurred.

Location	Species	Gut Content	Selectivity	Inside/outside differences: benthos	Inside/outside differences: algal turf
M. I.	<i>Pomacentrus tripunctatus</i>	X	X	X	X
	<i>Po. wardi</i>	X	X	X	X
	<i>Stegastes apicalis</i>	X	X	X	X
O. I.	<i>Hemiglyphidodon plagiometapon</i>			X	X
	<i>Po. adelus</i>			X	X
	<i>Po. wardi</i>			X	X
	<i>Po. tripunctatus</i>			X	X
	<i>Po. chrysurus</i>			X	X
K. B.	<i>Po. adelus</i>	X	X	X	X
	<i>Po. bankanensis</i>	X	X	X	X
	<i>Plectroglyphidodon lacrymatus</i>	X	X	X	X
	<i>Po. tripunctatus</i>	X	X	X	X
	<i>Po. burroughi</i>	X	X	X	X
	<i>S. lividus</i>	X			
	<i>Chrysiptera leucopoma</i>	X			
	<i>C. unimaculata</i>	X			
	<i>N. nigroris</i>			X	X

Distribution of study species

The former community at each location was distributed according to clear zonation patterns. On Magnetic Island, *Pomacentrus tripunctatus* occupied shallow reef flat zones, *S. apicalis* was found almost only on the reef crest, and *Po. wardi* occupied all zones except the shallowest inner reef flat zone (Figure 2a). Orpheus Island and Kimbe Bay reefs were also inhabited by some species with restricted distributions and others that occurred more widely (Figure 2b, c). On Orpheus Island, *Po. tripunctatus* and *Po. chrysurus* occupied the shallow reef flat although the distribution of *Po. chrysurus* extended more widely across the reef flat. *Hemiglyphidodon plagiometapon* occupied primarily the reef crest. *Po. adelus* was distributed across the outer reef flat, crest and slope, and *Po. wardi* occurred across all zones (Figure 2b). In Kimbe Bay there was a shallow back reef specialist (*Po. tripunctatus*), reef crest specialists (*Plectroglyphidodon lacrymatus*, *Neoglyphidodon nigroris*), a reef slope specialist (*Po. burroughi*) and species with broader distributions (*Po. adelus*, *Po. bankanensis*). Overall, the most abundant species was *Pl. lacrymatus* on the reef crest in Kimbe Bay (Figure 2c).

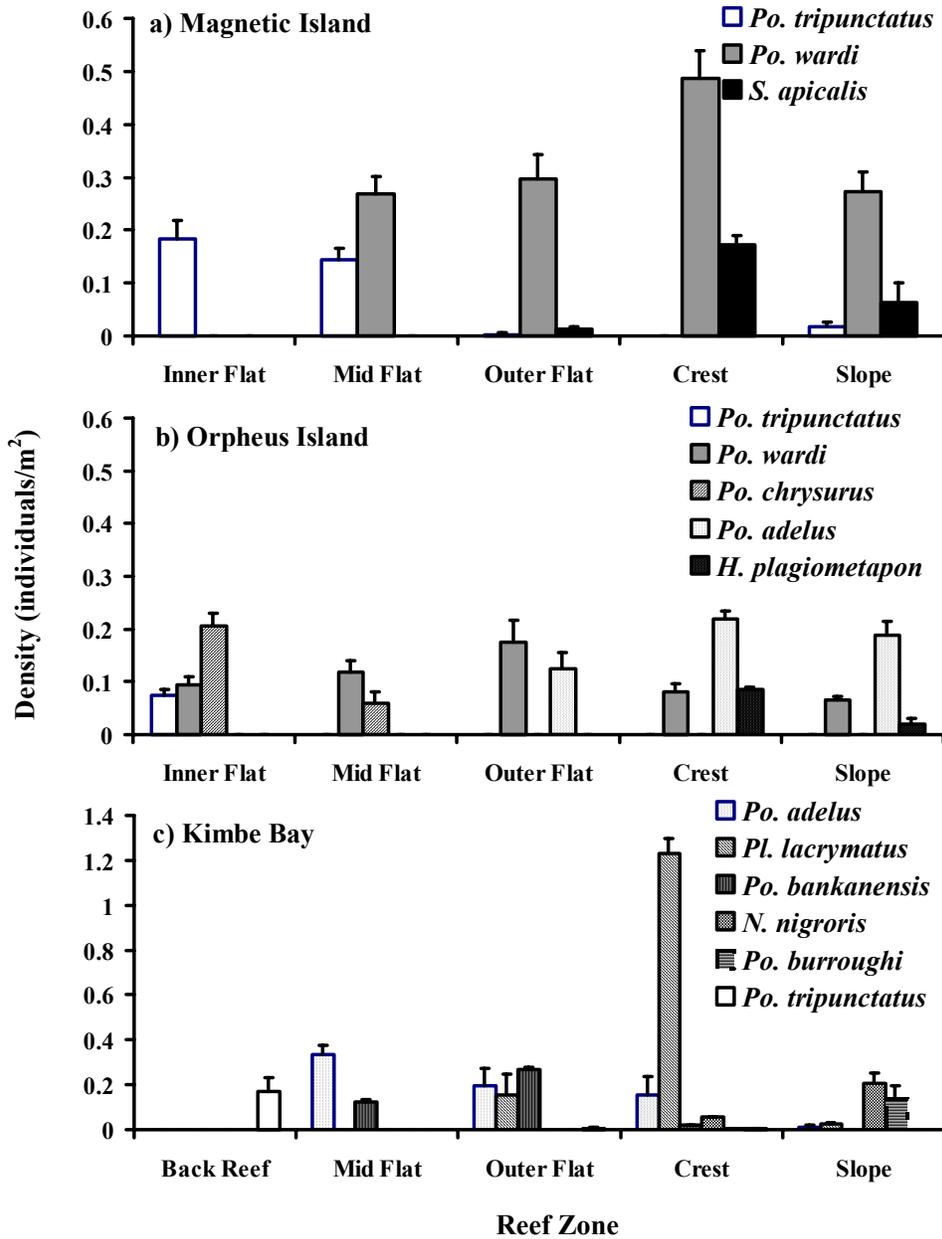


Figure 2. Zonation patterns of farmer communities a) on Magnetic Island, b) on Orpheus Island and c) in Kimbe Bay. Density estimates (individuals/m²) are given for each species in each reef zone. Note the difference in the y-axis of Figure c). *Po.*: *Pomacentrus*, *S.*: *Stegastes*, *H.*: *Hemiglyphidodon*, *Pl.*: *Plectroglyphidodon*, *N.*: *Neoglyphidodon*. Error bars = 1 S.E.

Diet and selectivity

Twenty individuals were collected from each location for gut content analysis. Prior to collection, territories were mapped and algal samples were taken to quantify availability and calculate selectivity (see below). The focal individuals were anaesthetized with 30% clove oil diluted in ethanol, administered from a spray bottle, and then caught with a hand net. They were killed in ice water and preserved in 10% formalin, with an incision in the abdomen to allow faster preservation of the gut contents. Due to logistic difficulties, all data characteristics were not sampled for each species (Table 1).

Once in the laboratory, the fish were weighed and measured (both total length and standard length were recorded) and their stomachs were extracted for gut contents analysis. As the objective of the study was to determine the effects of farmers on algae, I was more interested in what the fish had ingested than in what was assimilated. The ingested material within the stomach, above the pyloric caecae, was extracted and spread evenly over a Petri dish that had a 1 cm² grid drawn underneath. The matter under each of 50 random points was recorded to the highest possible taxonomic resolution. The genus name '*Polysiphonia*' will be used to include the filamentous genera *Polysiphonia*, *Herposiphonia* and *Lophosiphonia* found in stomach contents, as they are not easily distinguished as fragments. This will be applicable only to polysiphonous filamentous algae found in stomach contents.

The preference index Manly's α (Krebs 1999) was used to calculate food preference on pooled territories for each species as a measure of selectivity in the farmer's feeding behaviour :

$$\alpha_i = \frac{r_i}{n_i} \left(\frac{1}{\sum r_j/n_j} \right)$$

Where:

α_i = Manly's α (preference index) for prey type i

r_i, r_j = Proportion of prey type i or j in the diet (i and $j = 1, 2, 3 \dots m$)

n_i, n_j = Proportion of prey type i or j in the environment

m = number of prey types possible

The α values are normalized so that:

$$\sum_{i=1}^m \alpha_i = 1.0$$

When selective feeding does not occur, $\alpha_i = 1/m$ (m = total number of prey types). If α_i is greater than $(1/m)$, then prey species i is preferred in the diet. If α_i is less than $(1/m)$, prey species i is avoided in the diet. Differences in diets between species were analysed using Multivariate Analysis of Variance (MANOVA) and Principal Components Analysis (PCA), and all data were analysed with the software packages SPSS for Windows[®] and S-Plus[®].

Comparisons of inside and outside territories

After establishing the territory boundaries of 20 randomly selected individuals for each species, a 0.25 m² grid split into 100 squares was placed inside each territory, and then outside each territory. The outside territory sampling area was chosen on the basis of maximum proximity and maximum topographic similarity to the sampling area inside the territory. In each sampling area, the benthos inside each square was recorded, providing an estimate of % cover of the following categories: sand, encrusting coralline algae ('coralline algae'), thin turf (<3mm), thick turf (>3mm), fleshy macroalgae, erect

calcified algae ('calcareous algae'), and live coral. Algal turfs were then collected randomly from 5 points inside and 5 points outside the territory and fixed in 10% formalin as soon as possible after collection.

Each algal sample was emptied into a Petri dish and spread evenly across its surface. A square grid (1 cm mesh size) was placed over the dish and the taxon and/or substratum category under each intercept point was recorded. Taxa were identified to genus where possible, and to functional group where necessary (Steneck and Dethier 1994). Percent cover of each turf algae taxonomic or functional category was estimated for each sample. Community-level inside–outside territory differences were tested using MANOVA and Principal Components Analysis (PCA), both for samples obtained in the field and collections of algal turf.

Territory size and space occupation

Zonation data for each species at each location were collected previously (for Magnetic Island and Orpheus Island, see Ceccarelli et al. 2001). Twenty randomly selected focal individuals for each species were observed for 15 minutes, the territory boundaries were marked with lead weights, and at the end of the observation period the territory circumference was measured. Territory area was estimated by using the formula for calculating the area of an ellipse with the same circumference as the territory. To estimate space occupation in the different zones of each reef, the zone-specific density of each species was multiplied with the average territory area of this species. Differences in space occupation between species and zones were then tested using ANOVA.

Diet and selectivity

Gut contents

Stomach contents analyses were carried out on three species on Magnetic Island (Pomacentrus tripunctatus, Po. wardi and Stegastes apicalis) and 8 species in Kimbe Bay (Po. trlpunctatus, Po. adelus, Po. bankanensis, Po. burroughi, Plectroglyphidodon lacymatus, Chyslptera leucopoma, C. unimaculata, and S. lividus). At both locations, there were significant differences in the composition of the stomach contents of different species (MANOVA for Magnetic Island: $F_{(d.f.=24)} = 3.837$, $p < 0.001$; for Kimbe Bay: $F_{(d.f.=119)} = 2.116$, $p < 0.001$).

On Magnetic Island, S. apicalis ingested mainly filamentous red algae (primarily Polysiphonia), while the stomach contents of Po. tripunctatus were dominated by detritus (Figure 3a). The diet of Po. wardi appeared to be more varied, consisting of algae and detritus. Around 50% of Po. wardi stomach contents consisted of filamentous algae, but this was supplemented to nearly 30% by detritus and smaller amounts of the delicate corticated red algae and Champia. Only S. apicalis had animal matter (primarily small cmstaceans) in its stomach, however, proportions were low.

In Kimbe Bay, detritus made up more than 50% of the diets of C. leucopoma, C. unimaculata, Pl. lacymatus, Po. tripunctatus and S. lividus (Figure 3b). The remaining three species, Po. adelus, Po. bankanensis and Po. burroughi, also had large amounts of detritus in their stomachs, but between 60% and 80% of their gut contents were made up of corticated red algae and filamentous algae. Polysiphonia spp. were the dominant filamentous taxa to appear in the stomachs (Figure 3b). Only one species, Pl. lacymatus, had ingested substantial amounts of microalgae (10%), as recognizable under a stereomicroscope.

The highest proportion of gut contents of only two species, *S. apicalis* and *Po. wardi*, was made up of algal matter. All other species appeared to ingest a combination of detritus, delicate corticated and filamentous algae, and a small amount of animal matter.

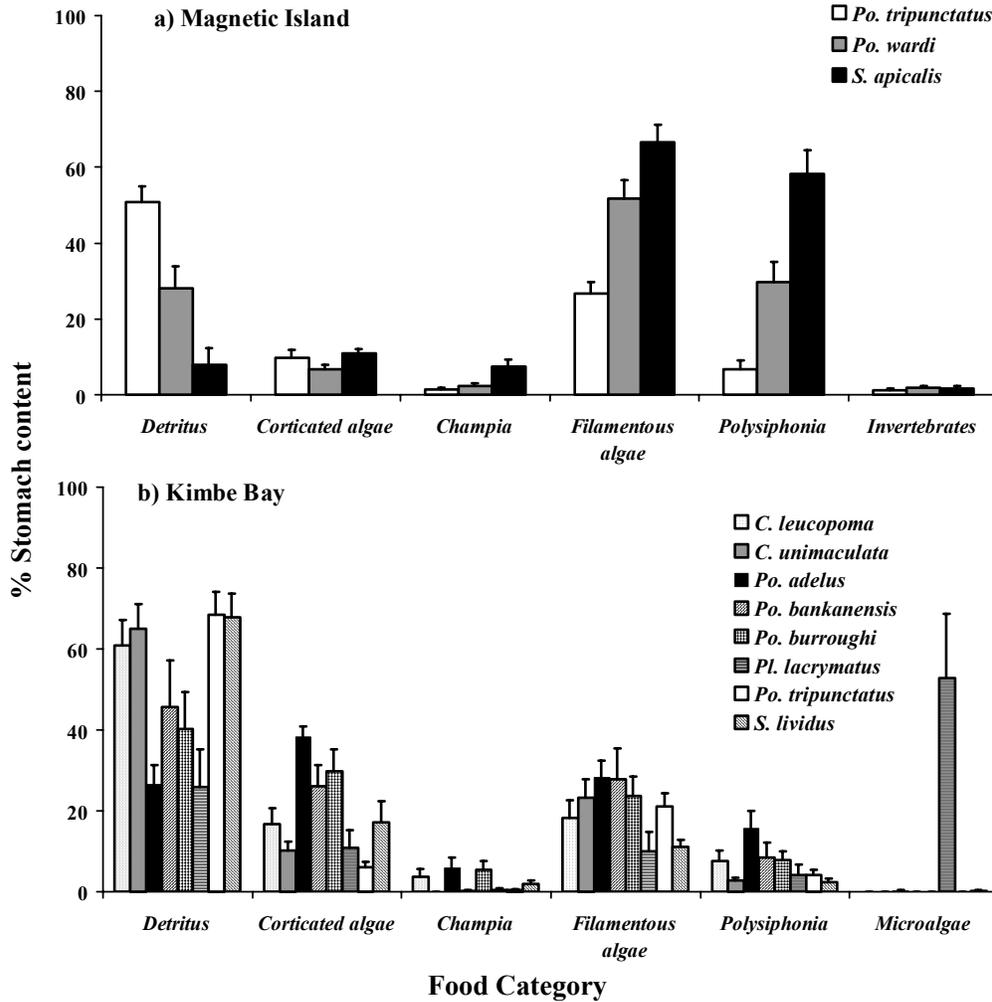


Figure 3. Results of gut content analysis for fish caught on Magnetic Island and in Kimbe Bay. *Po.*: *Pomacentrus*, *S.*: *Stegastes*, *C.*: *Chrysiptera*, *Pl.*: *Plectroglyphidodon*. Error bars = 1 S.E.

Selectivity

Selectivity indices confirmed that some species actively select detritus. That is, detritus appears in the gut contents in a higher proportion than would be expected, given its availability in their territories (Figure 4a). The highest proportion of detritus was consumed by *Plectroglyphidodon lacrymatus*, followed by *Pomacentrus bankanensis* and *Po. tripunctatus*. Surprisingly, *Po. tripunctatus* selectively consumed detritus both on Magnetic Island and in Kimbe Bay, despite substantial differences in the territory composition of this species in the two locations (see below). *Po. adelus* also consumed more detritus than expected, while *Stegastes apicalis* appeared to avoid ingesting detritus. *Po. wardi* and *Po. burroughi* ingested proportions of detritus similar to those available in their territories. Fleshy macroalgae were avoided by all species that maintained territories containing fleshy macroalgae (Figure 4b), while corticated red algae were preferred by some species, but not others. Stomachs of *Po. wardi* contained corticated red algae in proportion to their occurrence in their territories, while *Po. adelus* and *Po. bankanensis* appeared to avoid these algae (Figure 4c). *Po. tripunctatus* selected corticated algae on Magnetic Island but not in Kimbe Bay, even though their territories in Kimbe Bay contained double the proportion of corticated red algae than those on Magnetic Island (see below). The species *S. apicalis*, *Pl. lacrymatus* and *Po. burroughi* actively selected corticated algae as part of their diets (Figure 4c). All species appeared to strongly favour filamentous algae (Figure 4d), especially *Polysiphonia* spp., which consistently made up more than 85% of the filamentous taxa found inside territories. Invertebrates, however, were avoided by all species (Figure 4e).

For a more detailed analysis of algal selectivity, the algal genera *Leveiella*, *Champia*, *Laurencia* and *Hypnea* were analysed separately (Figure 5). *Leveiella* only grew as an epiphyte on fleshy macroalgae on Magnetic Island, and was selected by *Po.*

wardi and *S. apicalis*, but avoided by *Po. tripunctatus* (Figure 5a). *Champia* was relatively rare in most territories, but was nevertheless selected by *Po. wardi*, *S. apicalis*, and *Po. burroughi* (Figure 5b). *Po. tripunctatus* and *Po. adelus* avoided *Champia*, and it did not grow inside the territories of the other species. Of the two most abundant corticated red algal taxa, *Laurencia* was mostly avoided and *Hypnea* was mostly selected. *Laurencia* was only consumed in amounts proportional to its availability by *S. apicalis*, and avoided by all other species (Figure 5c). *Hypnea*, on the other hand, was highly selected by all species except *Po. wardi*, which avoided it, and *S. apicalis*, which maintained territories without measurable amounts of *Hypnea* (Figure 5d).

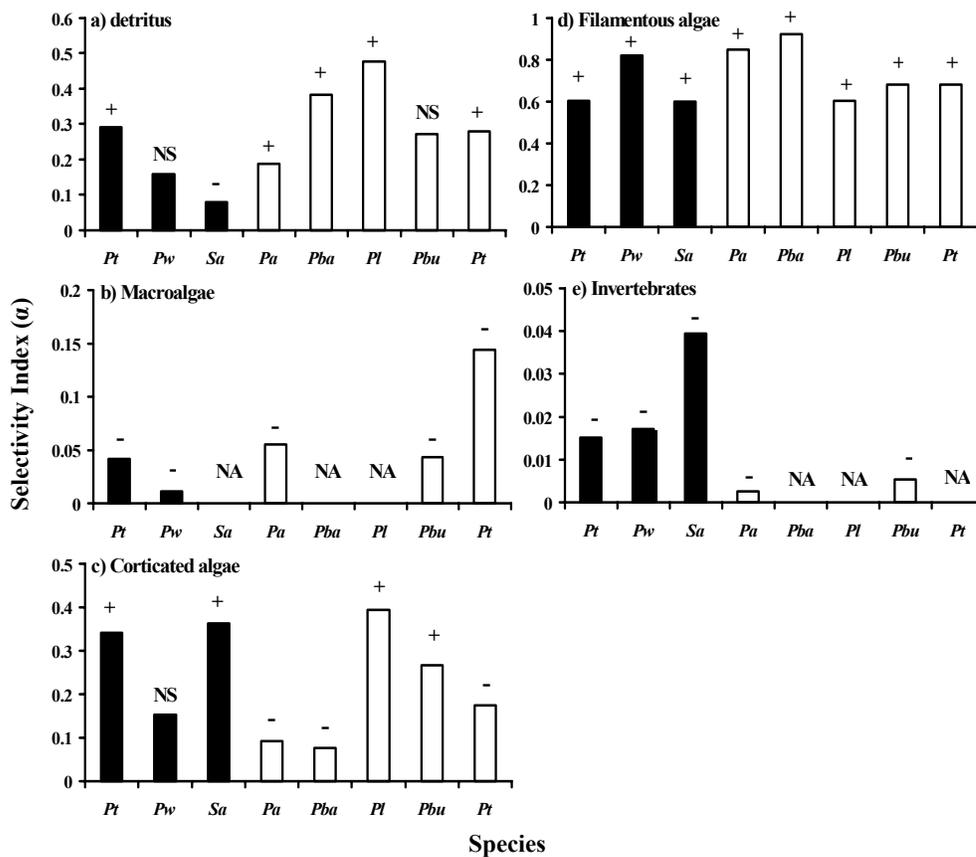


Figure 4. Selectivity indices for seven species in two separate locations on the functional groups of available food items. Black bars: Magnetic Island; white bars: Kimbe Bay; +: food item selected; -: food item avoided; NS: food item consumed in proportion to availability; NA: food item not available. *Pt*: *Po. tripunctatus*, *Pw*: *Po. wardi*, *Sa*: *S. apicalis*, *Pa*: *Po. adelus*, *Pba*: *Po. bankanensis*, *Pl*: *Pl. lacrymatus*, *Pbu*: *Po. burroughi*.

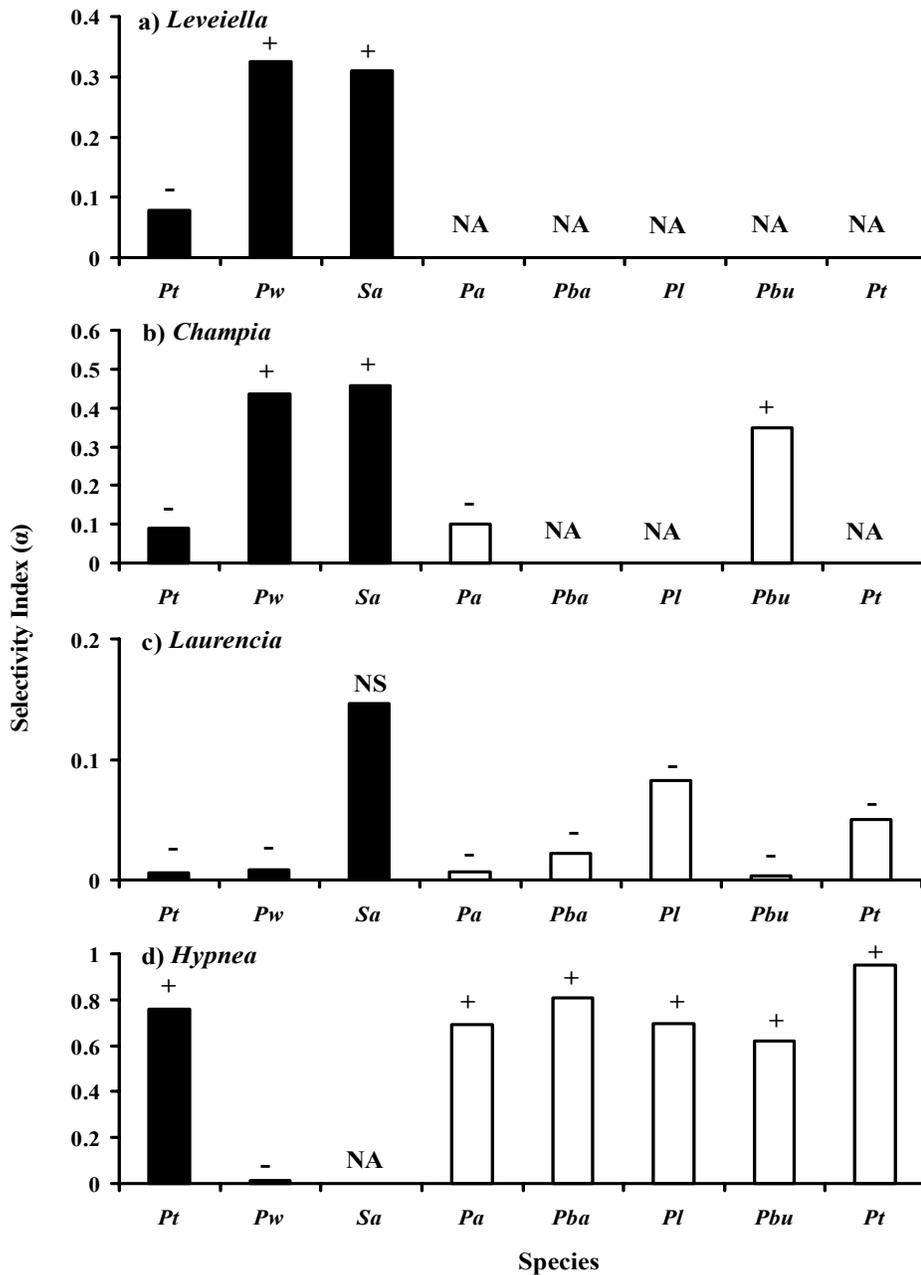


Figure 5. Selectivity indices for seven species in two separate locations on four dominant algal taxa. Black bars: Magnetic Island; white bars: Kimbe Bay; +: food item selected; -: food item avoided; NS: food item consumed in proportion to availability; NA: food item not available. *Pt*: *Po. tripunctatus*, *Pw*: *Po. wardi*, *Sa*: *S. apicalis*, *Pa*: *Po. adelus*, *Pba*: *Po. bankanensis*, *Pl*: *Pl. lacrymatus*, *Pbu*: *Po. burroughi*.

Principal Components Analysis (PCA) for Magnetic Island showed a clear dietary separation between *Po. tripunctatus* and the other two species, and a slight overlap between the gut contents of *Po. wardi* and *S. apicalis* (Figure 6). The differences between all three species were primarily caused by varying amounts of detritus and filamentous algae in general, and *Polysiphonia* in particular, found in the stomach contents. *Po. tripunctatus* consumed the most detritus and the least filamentous algae, while the diet of *S. apicalis* was dominated by filamentous algae. The diet of *Po. wardi* tended to be more similar to that of *S. apicalis* than *Po. tripunctatus*, but contained a more diverse array of food items, including detritus, corticated algae, *Champia* and filamentous algae. In this community, *S. apicalis* was the species that could be classified with the highest confidence as a herbivore, *Po. tripunctatus* as a detritivore and *Po. wardi* as an omnivore (Figure 6).

PCA for the damselfish community in Kimbe Bay showed a more complex distribution of diets (Figure 7). Four groups could be distinguished in this analysis. Group 1, made up of *Po. tripunctatus*, *C. leucopoma*, *C. unimaculata* and *S. lividus*, was separated from the other groups along the first Principal Component (PC1) on the horizontal axis, which was highly correlated with increasing amounts of detritus. Group 2, including *Po. bankanensis* and *Po. burroughi*, was separated from Group 1 along PC1 by having a more herbivorous diet that comprised a number of corticated and filamentous algal taxa. There was considerable overlap between Group 1 and Group 2, suggesting that both groups supplemented their diet with either algae (in the case of Group 1) or detritus (Group 2). *Po. adelus* was included in Group 2, but did not overlap with Group 1, indicating that *Po. adelus* may be the most herbivorous species in this community. PC2 (the vertical axis) was highly correlated with high cover of microalgae, and separated the diet of *Pl. lacrymatus* from the diets of all other species

(Figure 7). It is notable that in both locations, reef crest and slope species (*S. apicalis*, *Pl. lacrymatus*, *N. nigroris*, *Po. burroughi*, *Po. bankanensis*) tended to ingest more algae, while the diets of the inner reef flat and back reef species (*Po. tripunctatus*) included more detritus.

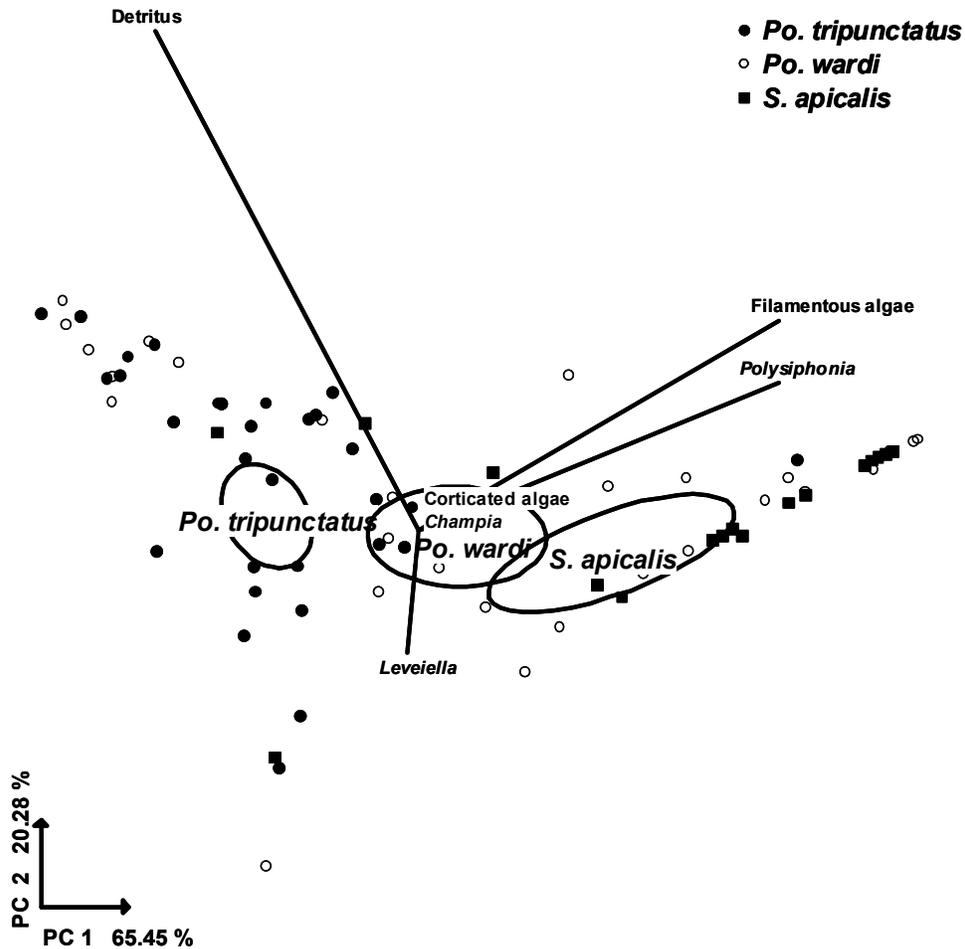


Figure 6. Principal Components Analysis (PCA) describing diets of *Po. tripunctatus*, *Po. wardi* and *S. apicalis* on Magnetic Island, based on gut contents. The ellipses represent the 95% confidence intervals for each species. Principal Component (PC) 1 is highly correlated with filamentous algae/*Polysiphonia*, accounting for 65.45% of the variability in the data. PC 2 is highly correlated with detritus and *Leveiella*, and accounts for 20.28% of variation. PC1 and PC 2 together encompass 85.73% of the variability in the data. *Po.*: *Pomacentrus*, *S.*: *Stegastes*.

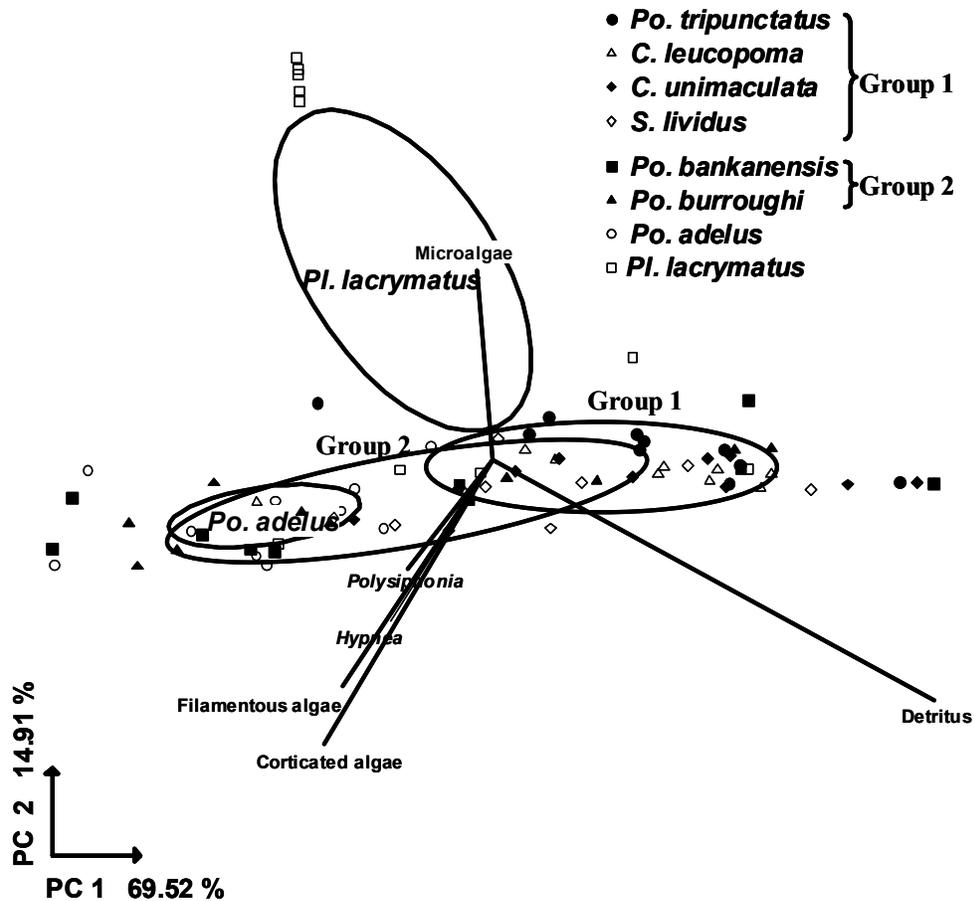


Figure 7. Biplot describing diets of *Po. tripunctatus*, *C. leucopoma*, *C. unimaculata*, *S. lividus*, *Po. bankanensis*, *Po. burroughi*, *Po. adelus* and *Pl. lacrymatus* in Kimbe Bay, based on gut contents. The ellipses represent the 95% confidence intervals for each species. Principal Component (PC) 1 is correlated with detritus, accounting for 69.52% of the variability in the data. PC 2 is correlated with microalgae, filamentous algae and corticated algae, and accounts for 14.91% of variation. PC1 and PC 2 together encompass 84.43% of the variability in the data. *Po.*: *Pomacentrus*, *C.*: *Chrysiptera*, *S.*: *Stegastes*, *Pl.*: *Plectroglyphidodon*.

Comparison of benthic assemblages inside and outside territories

Percent cover of benthos

In all three locations, there were significant differences between territories and surrounding benthic communities, which also varied among species (MANOVA for Magnetic Island: $F_{(d.f.=28)} = 4.0$, $p < 0.001$; for Orpheus Island: $F_{(d.f.=36)} = 1.5$, $p < 0.05$; for Kimbe Bay: $F_{(d.f.=45)} = 2.699$, $p < 0.001$). Due to the differences in benthic composition between locations, the inside–outside territory differences are presented separately for each sampling location (Figure 8).

The benthos on Magnetic Island was composed of large stands of fleshy macroalgae (40% cover), primarily *Sargassum* spp. and *Lobophora* spp., sandy patches (8%), hard substrata covered in thin turf (22%) and patches of high live coral cover (15%) (Figure 8a). *Pomacentrus tripunctatus* territories differed from the benthic community surrounding them in containing a higher cover of thick turf inside territories. *Po. wardi* territories contained almost 10 times more thick turf than surrounding areas, around three times more dead coral, and approximately half the cover of fleshy macroalgae (Figure 8a). *Stegastes apicalis* territories contained over 10 times more thick turf than surrounding areas, six times the cover of *Amphiroa* spp., double the live coral cover and five times the dead coral cover. In contrast, thin turf covered 10 times less area inside *Stegastes apicalis* territories than outside, and fleshy macroalgae were four times less abundant.

Orpheus Island reefs were dominated by non-living surfaces covered in thin turf (62% cover), with few areas of live coral (13%), relatively low cover of fleshy macroalgae (10%) and few sandy patches (10%). By contrast, *Hemiglyphidodon plagiometapon* territories were covered in uniform stands of thick turf (80% cover).

This was 40 times higher than outside territories and approximately double the cover of thick turf found in the territories of all other species (Figure 8b). The cover of thick turfs found in the territories of the other sampled species did not exceed 45% cover. *Po. adelus* territories contained higher live coral cover than all other sampled areas, while *Po. chrysurus* and *Po. tripunctatus* territories contained the highest cover of fleshy macroalgae (primarily *Galaxaura* spp. and *Padina* spp.). *Po. wardi* territories contained higher cover of thick turf (38%) and significantly less fleshy macroalgae than undefended areas (Figure 8b).

Kimbe Bay sites had the highest overall live coral cover of the three locations (almost 30%; Figure 8c). There were also large areas left bare by recent crown-of-thorns starfish outbreaks, which were covered in thin turfs (almost 50%). The cover of fleshy macroalgae was minimal (1%). *Neoglyphidodon nigroris* territories were similar in benthic community structure to surrounding areas, consisting of high thin turf cover (45%) and live coral cover (40%), with small patches of thick turf (6.5%) and erect calcified algae (6.7%) such as *Amphiroa* and *Actinotrichia*. Only three of the sampled species appeared to promote thick turf in significantly higher cover than undefended areas. These were *Plectroglyphidodon lacrymatus* (almost four times more), *Po. adelus* (five times more) and *Po. bankanensis* (12 times more). It is noteworthy that these are all reef crest species (Figure 2) with substantial amounts of algae in their diets (Figure 7). *Po. tripunctatus* territories, which occurred primarily on the shallow back reef, contained the highest cover of thin turf (80%), precluding the growth of almost anything else in their territories. The reef slope species, *Po. burroughi*, had territories that were distinguished by thick clumps of microalgae (around 10%). None of the species on the Kimbe Bay reefs had territories with the high cover of thick algal turf that is usually characteristic of farmer territories, with the exception of *Po. bankanensis*. Furthermore,

three of the sampled species defended territories containing reasonably high live coral cover: the widespread farmer *Po. adelus* (40%), the reef slope species *Po. burroughi* (20%) and the reef crest species *Pl. lacrymatus* (45%; Figure 8c).

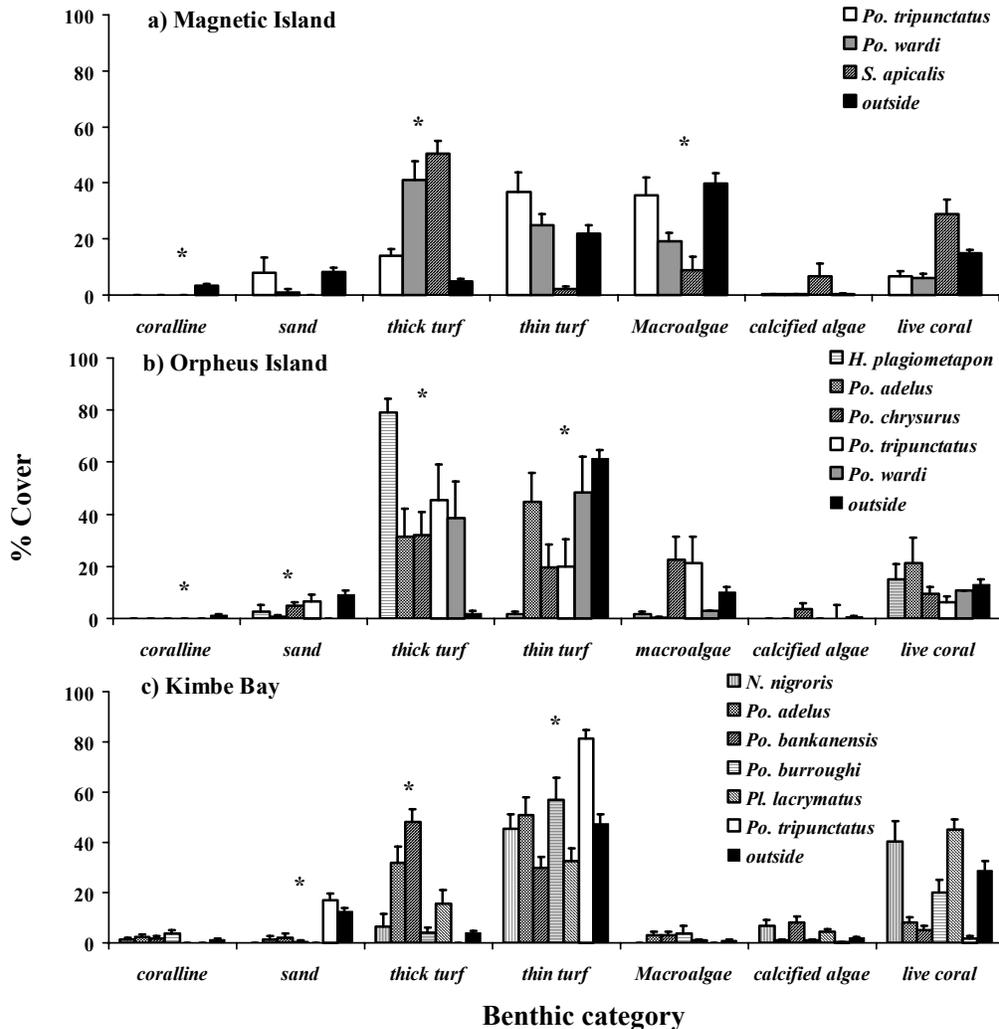


Figure 8. Benthic composition inside and outside territories of farmer communities for a) Magnetic Island, b) Orpheus Island and c) Kimbe Bay. The percent cover of different benthic categories was obtained with point intercept sampling on site. Each site represents a distinct farmer community. * shows a significant difference between species at $p < 0.05$. *Po.*: *Pomacentrus*, *S.*: *Stegastes*, *H.*: *Hemiglyphidodon*, *N.*: *Neoglyphidodon*, *Pl.*: *Plectroglyphidodon*. Error bars = 1 S.E.

Community-level differences were further explored using Principal Components Analysis (PCA). In all three locations, the differences between benthic communities inside and outside the territories of most species were as great as the differences among species (Figure 9). Benthic communities sampled outside the territories of each species did not generally overlap, due to the spatial zonation of both farmer species and benthic biota. Benthic samples obtained outside territories were therefore not pooled, but grouped according to the overlap of confidence ellipses around the group means (indicating a strong similarity in community structure).

Of the three species on Magnetic Island, *Po. tripunctatus* defended territories with most similarities to surrounding areas (Figure 9a). Sand, thin algal turf and to a lesser extent fleshy macroalgae dominated both inside and outside *Po. tripunctatus* territories. The benthic community making up areas surrounding the territories of *Po. wardi* were characterized by high fleshy macroalgal cover (especially *Lobophora* and *Sargassum*). The separation between group means obtained outside and inside *Po. wardi* territories occurred evenly along PC1 (correlated with an increase in thick algal turf) and PC2 (correlated with an increase in thin algal turf). Essentially, in an environment dominated by fleshy macroalgae, *Po. wardi* maintained territories covered in algal turf. The largest differences occurred between inside and outside *S. apicalis* territories. *S. apicalis* territories were covered in thick turf and dead coral in a reef zone otherwise occupied by fleshy macroalgae and thin turf on dead coral surfaces (Figure 9a).

Unlike Magnetic Island, Orpheus Island exhibited an almost complete separation between benthic communities inside and outside territories (Figure 9b). This separation appeared to be defined by differences in the cover of algal turf, with areas outside territories associated with thin turf and those inside territories with thick turf.

Within these two broad groups, there was further variability. The shallow inner reef flat species *Po. tripunctatus* and *Po. chrysurus* maintained territories surrounded by a high cover of fleshy macroalgae, and containing a combination of fleshy macroalgae and thick turf. The areas outside *Po. wardi* territories overlapped with Group 1 (areas outside the territories of *Po. adelus* and *H. plagiometapon*), and were characterized by high cover of thin turf. Although the composition of areas outside their territories overlapped strongly, assemblages inside *Po. wardi* and *Po. adelus* territories were very different from those inside *H. plagiometapon* territories. *Po. wardi* and *Po. adelus* territories contained both thin and thick turf, whereas *H. plagiometapon* territories were dominated by the highest cover of thick turf of all five species sampled on Orpheus Island.

There was much less separation among inside and outside farmer territories in Kimbe Bay (Figure 9c). Areas outside territories were much more affected by the background benthic zonation patterns found on the Kimbe Bay reefs. The zone where *Po. tripunctatus* was found was dominated by sand, and this environment was clearly altered inside *Po. tripunctatus* territories to contain more algal turf. All other species maintained territories in areas of higher benthic diversity; the fact that group means were concentrated around the centre of the PCA biplot suggests that no benthic component dominated. Species that defended territories with benthic communities similar to surrounding areas were the reef slope species *Po. burroughi* and the reef crest species *N. nigroris*. *Po. bankanensis* and *Po. adelus* territories, which were more widely distributed across reef zones, were characterized by high proportions of thick algal turf, while on the reef crest, the territories of *N. nigroris* and *Pl. lacrymatus* contained high cover of live coral (Figure 9c).

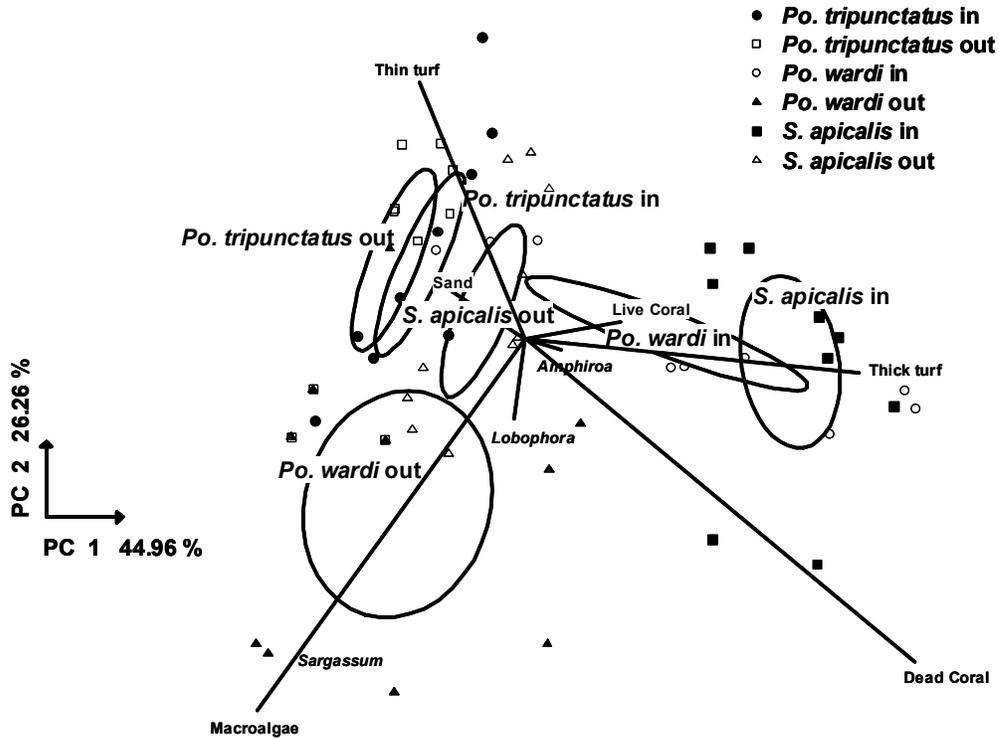


Figure 9a. PCA (Principal Components Analysis) Biplot of overall benthic composition inside and outside territories of all species on Magnetic Island. The ellipses represent the 95% confidence intervals for each species. Group means are separated along Principal Component (PC)1 by increasing thick turf, and PC 2 accounts for almost all other vectors. PC 1 and PC 2 explain 44.96% and 22.26% of the variability in the data respectively, and 67.22% together. *Po.*: *Pomacentrus*, *S.*: *Stegastes*.

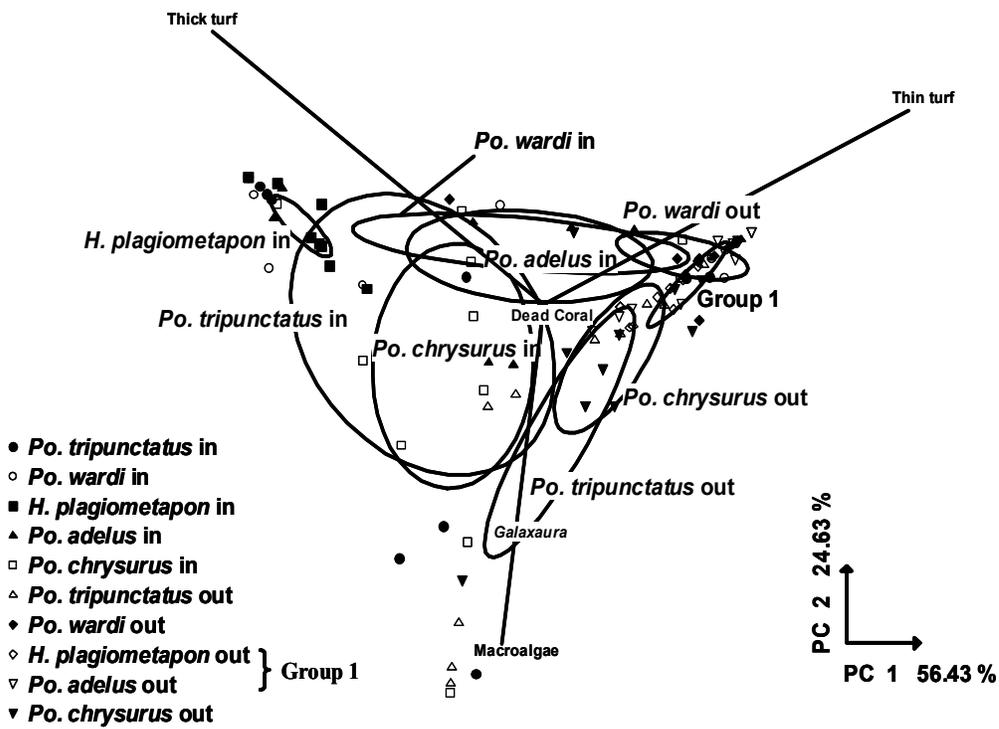


Figure 9b. Biplot of overall benthic composition inside and outside territories of all species on Orpheus Island. The ellipses represent the 95% confidence intervals for each species. Group means are separated along Principal Component (PC) 1 by increasing thick turf in one direction and thin turf in the other, and PC 2 is correlated with % cover of macroalgae. PC 1 and PC 2 explain 56.43% and 24.63% of the variability in the data respectively, and 81.06% together. *Po.*: *Pomacentrus*, *H.*: *Hemiglyphidodon*.

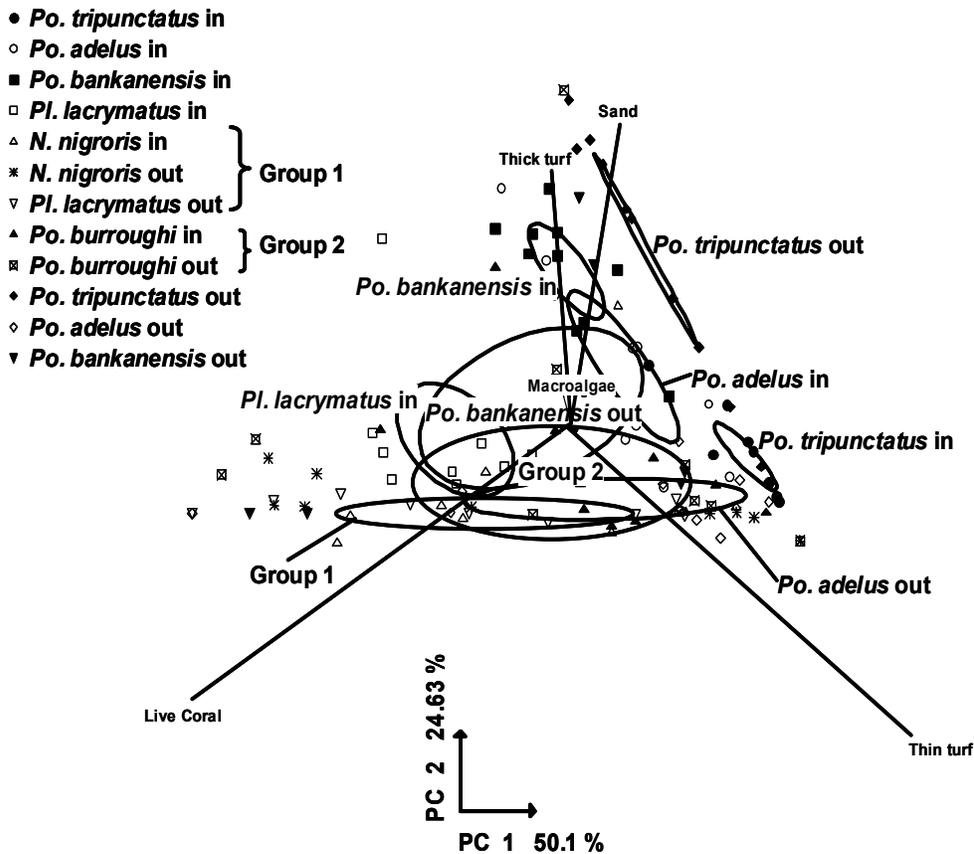


Figure 9c. Biplot of overall benthic composition inside and outside territories of all species in Kimbe Bay. The ellipses represent the 95% confidence intervals for each species. Principal Component (PC) 1 is correlated with live coral and thin turf, and PC 2 is correlated with % cover of sand and thick turf. PC 1 and PC 2 explain 50.1% and 24.63% of the variability in the data respectively, and 74.73% together. *Po.*: *Pomacentrus*, *N.*: *Neoglyphidodon*, *Pl.*: *Plectroglyphidodon*.

Composition of algal turfs

In all three sampling locations, there were significant differences between territories and surrounding algal turf composition, which varied among species

(MANOVA for Magnetic Island: $F_{(d.f.=40)} = 2.73$, $p < 0.001$; for Orpheus Island: $F_{(d.f.=72)} = 1.344$, $p < 0.05$; for Kimbe Bay: $F_{(d.f.=90)} = 1.752$, $p < 0.001$). As with the percent cover of benthos, the inside–outside territory differences are presented separately for each sampling location (Figure 10).

The algal community on Magnetic Island was dominated by fleshy macroalgae (37%, particularly *Sargassum*), with the only other major components being corticated red algae (14%) and detritus (11%). Inside farmer territories, algal turfs were much more varied (Figure 10a). In general, farmers with a high proportion of detritus in their stomachs (c.f. Figure 3) also defended territories high in detrital cover. Turfs in *Pomacentrus tripunctatus* territories were made up primarily of detritus and corticated red algae (mostly *Laurencia*), which occurred in double the quantities inside territories than outside. Fleshy macroalgae and *Polysiphonia* were also present, but never more than 13% (Figure 10a). *Po. wardi* territories contained the most diverse algal assemblages, reflecting the diversity of their stomach contents, with almost even quantities of detritus, *Jania*, the fleshy macroalgae *Sargassum* and *Lobophora*, corticated red algae (mainly *Gelidiopsis*) and the delicate filamentous red alga *Polysiphonia* (Figure 10a). *Stegastes apicalis*, the most herbivorous of the three species on Magnetic Island, defended territories dominated by *Amphiroa*, *Gelidiopsis* and *Polysiphonia*. This made *S. apicalis* the most distinct when compared to undefended areas; both *Amphiroa* and *Gelidiopsis* were absent on the reef crest outside territories.

Algal assemblages on Orpheus Island were dominated by detritus (33%), followed by *Galaxaura* (16%) (Figure 10b). There were also small but consistent amounts (generally not above 10% cover) of crustose coralline algae, *Laurencia*, *Hypnea*, and *Polysiphonia*. The algal community in *Po. wardi* territories was very similar, with the exception of *Galaxaura* (three times less than outside) and detritus

(higher than outside at almost 50% cover). *Hemiglyphidodon plagiometapon* territories contained the highest cover of *Gelidiopsis* and *Hypnea*, but around a third less detritus than areas outside territories, and relatively low cover of *Polysiphonia* (Figure 10b). *Po. chrysurus* and *Po. tripunctatus* territories contained the highest cover of corticated red algae, the highest proportion of which was made up of *Laurencia*. On the other hand, *Po. adelus* territories contained almost four times more *Polysiphonia* than the territories of all other species (Figure 10b).

Algal communities in Kimbe Bay were composed of 5–10% cover of *Turbinaria*, *Amphiroa* and corticated red algae, and a very high percent cover of crustose coralline algae (23%; Figure 10c). Algal composition inside the territories differed substantially between species, and appeared to reflect the composition of stomach contents for most species. The cover of crustose coralline algae was halved in the territories of most species compared to outside territories (except in the case of *Po. tripunctatus*), and the territories of many species (except *Neoglyphidodon nigroris* and *Po. burroughi*) were covered in double the abundance of corticated red algae when compared to undefended areas. The algal turfs in *N. nigroris* territories were usually very thin and contained small amounts of corticated red algae, *Amphiroa* and *Polysiphonia* (Figure 10c). Algal assemblages in *Po. adelus* and *Po. bankanensis* territories were very similar, characterized by high cover of *Turbinaria* and *Laurencia*, and other corticated red algae. The primary difference was that *Po. bankanensis* territories contained around double the cover of both *Actinotrichia* and detritus when compared with *Po. adelus* territories. A further difference was that *Po. bankanensis* territories contained a relatively high cover of microalgae, similar to *Plectroglyphidodon lacrymatus* territories. Interestingly, little microalgae were found at this scale in *Po. burroughi* territories (see Figure 10c), possibly due to the patchy

distribution of microalgae in their territories. *Pl. lacrymatus* territories were dominated by corticated red algae, and distinguished by a higher cover of *Amphiroa* than the territories of other species.

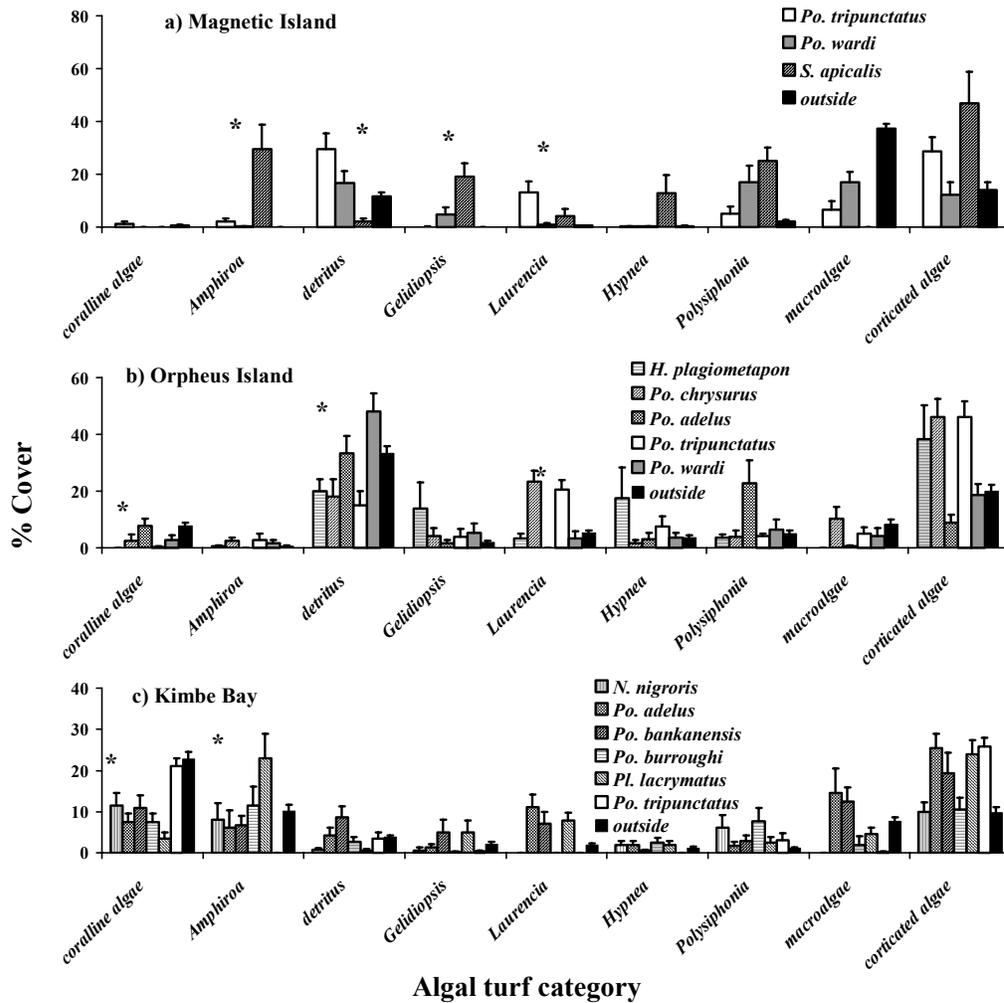


Figure 10. Composition of algal assemblages inside and outside territories of farmer communities for a) Magnetic Island, b) Orpheus Island, and c) Kimbe Bay. The percent cover of different turf categories was obtained from laboratory analyses of algal turf collections. Each site represents a distinct farmer community. * shows a significant difference between species at $p < 0.005$. Note the differences in the y-axes. *Po.*: *Pomacentrus*, *S.*: *Stegastes*, *H.*: *Hemiglyphidodon*, *N.*: *Neoglyphidodon*, *Pl.*: *Plectroglyphidodon*. Error bars = 1 S.E.

PCA conducted on algal composition inside and outside territories on each location showed that while there was a clear separation between outside territories and inside territories on Magnetic Island and in Kimbe Bay, the territories of most species on Orpheus Island tended to represent enhanced cover of a subset of the algal species present in surrounding areas (Figure 11). In all three locations, areas outside territories were sampled independently for each species, but a strong overlap in the algal composition outside territories allowed the confidence ellipses around the group means to be pooled.

On Magnetic Island, a clear community-level separation existed between algal assemblages outside territories and those inside the territories of *Po. tripunctatus*, *Po. wardi* and *S. apicalis* along the vector of high macroalgal cover (outside territories) and the vector of filamentous and corticated algae (inside territories; Figure 11a). There was some overlap in the composition of algal communities occurring in the territories of *Po. wardi* and *Po. tripunctatus*. *S. apicalis* territories were completely separated from those of the other two species along the vectors describing higher proportions of filamentous algae, *Amphiroa* and corticated red algae (Figure 11a).

On Orpheus Island, algal assemblages outside territories were composed of relatively balanced proportions of the available taxa, including macroalgal genera such as *Padina* and *Galaxaura* (Figure 11b). Algal composition inside territories fell into two major groups; one was made up of the territories of *H. plagiometapon*, *Po. tripunctatus* and *Po. chrysurus*, and the other contained *Po. adelus* and *Po. wardi*. The first group was defined by a tendency for territories to be dominated by corticated red algae, and the second was characterized by higher proportions of filamentous algae and detritus (Figure 11b).

Algal communities outside territories in Kimbe Bay were characterized by high cover of coralline algae and fleshy macroalgae, and there was very little overlap between the algal composition outside territories and those inside territories (Figure 11c). The territories of *Po. tripunctatus*, with high cover of corticated and coralline algae, and those of *Pl. lacrymatus*, with high microalgal cover, were the most distinct when territory composition was compared between species. Group 1, which included *Po. adelus* and *Po. bankanensis* territories, overlapped with Group 2 (*Po. burroughi* and *N. nigroris* territories) and *Pl. lacrymatus* territories. Its orientation along PC 2 suggests that high proportions of detritus, fleshy macroalgae and corticated algae characterized the territories of these species. In contrast, the orientation of Group 2 (*Po. burroughi* and *N. nigroris*), and its tendency to overlap with both Group 1 (*Po. adelus* and *Po. bankanensis* territories) and areas outside territories indicates a high proportion of corticated red algae and crustose coralline algae.

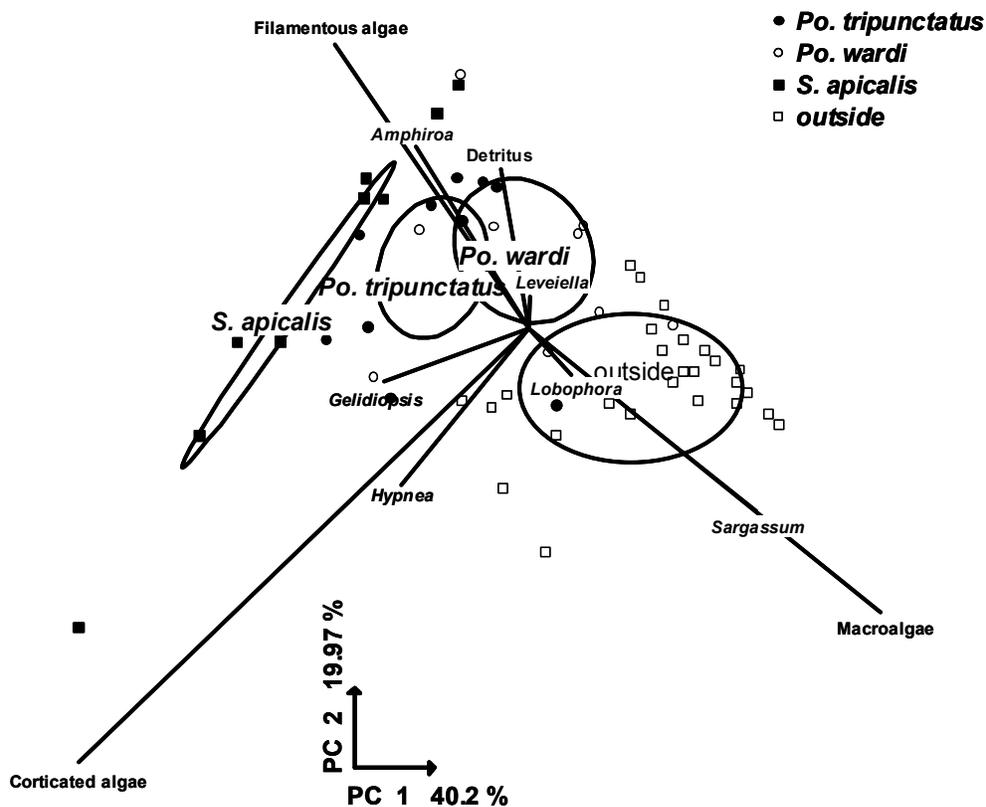


Figure 11a. Principal Components Analysis (PCA) Biplot of algal composition inside and outside territories of all species on Magnetic Island. The ellipses represent the 95% confidence intervals for each species and outside territories. ‘Outside’ turf composition was sampled independently for each species and a new confidence ellipse drawn around the three group means due to strong overlap. The distribution of species along Principal Component (PC) 1 is influenced by its correlation with the % cover of fleshy macroalgae and corticated red algae, and PC 1 explains 40.2% of variability in the data. PC2 is correlated with the % cover of detritus and filamentous algae, and accounts for 19.97% of the variation. PC 1 and PC 2 together account for 60.17% of the variability in the data. *Po.*: *Pomacentrus*, *S.*: *Stegastes*.

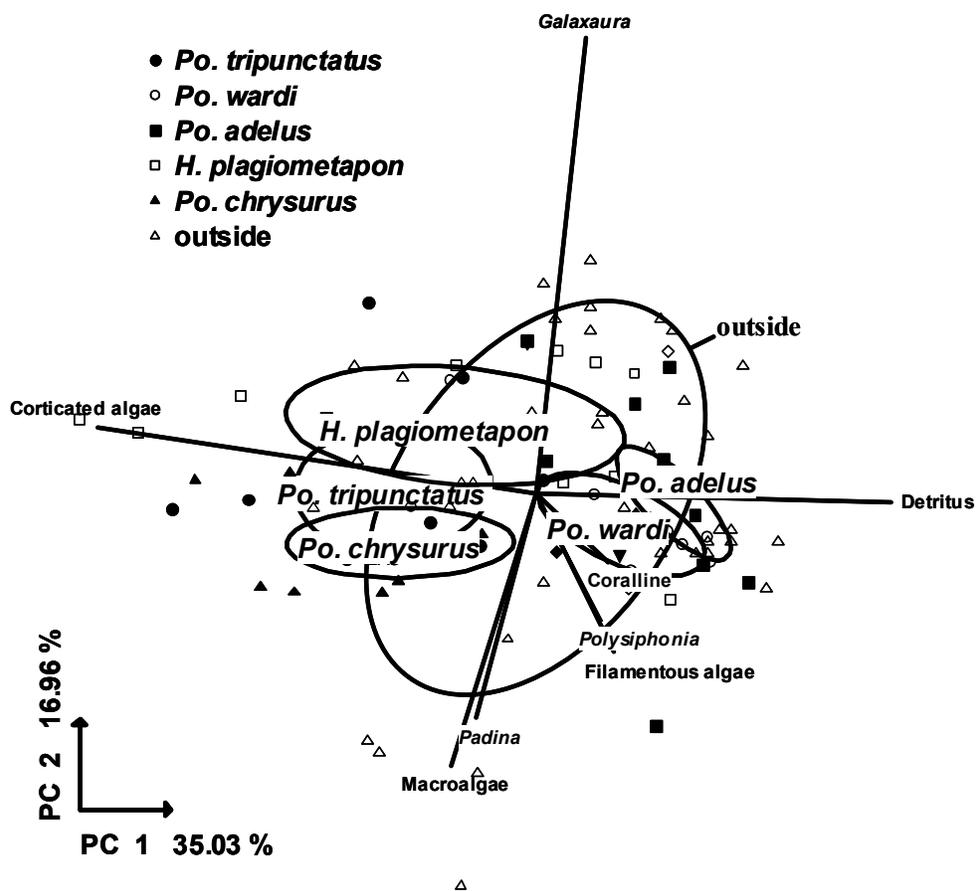


Figure 11b. Biplot of algal composition inside and outside territories of all species on Orpheus Island. The ellipses represent the 95% confidence intervals for each species and outside territories. ‘Outside’ turf composition was sampled independently for each species and a new confidence ellipse drawn around the three group means due to strong overlap. Principal Component (PC) 1 is correlated with the % cover of detritus and corticated red algae, and PC 1 explains 35.03% of variability in the data. PC2 is correlated with the % cover of fleshy macroalgae, although the vectors for *Padina* and *Galaxaura* separate out in opposite directions, and accounts for 16.96% of the variation. PC 1 and PC 2 together account for 51.99% of the variability in the data. *Po.*: *Pomacentrus*, *H.*: *Hemiglyphidodon*.

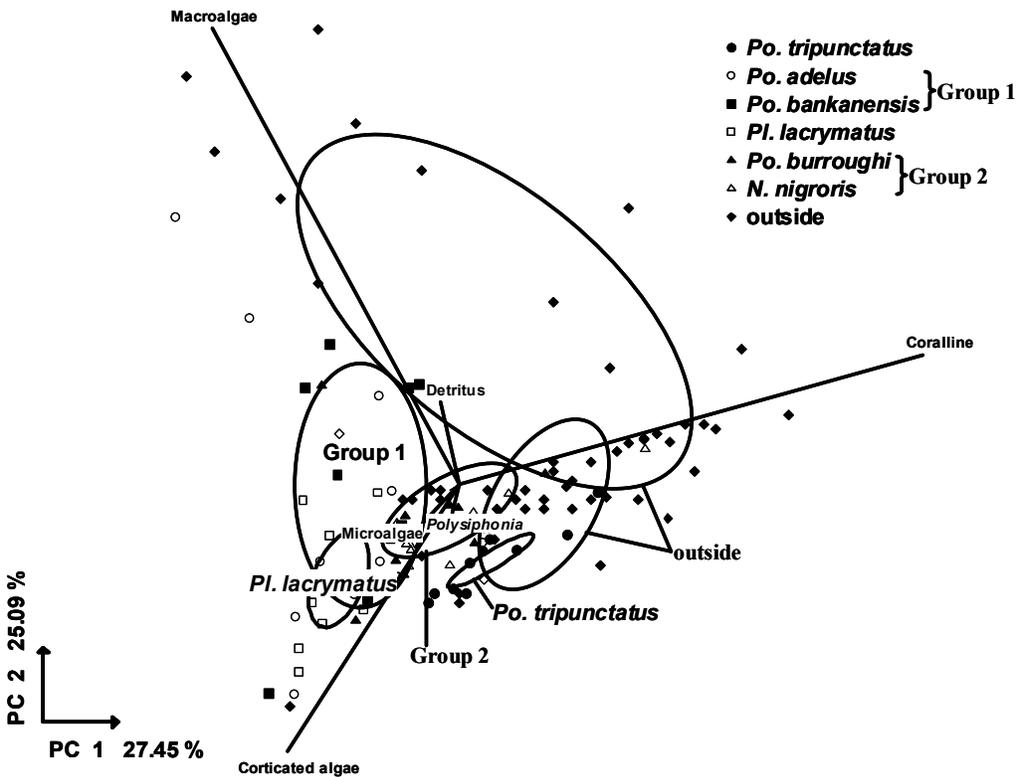


Figure 11c. Biplot of algal composition inside and outside territories of all species in Kimbe Bay. The ellipses represent the 95% confidence intervals for each species and outside territories. ‘Outside’ turf composition was sampled independently for each species and a new confidence ellipse drawn around the three group means due to strong overlap. The distribution of species along Principal Component (PC) 1 is influenced by its correlation with the % cover of coralline algae, PC2 is correlated with the % cover of fleshy macroalgae and corticated red algae. PC 1 and PC 2 explain similar proportions of the variability in the data (27.45% and 25.09%, respectively, and 52.54% together). *Po.*: *Pomacentrus*, *N.*: *Neoglyphidodon*, *Pl.*: *Plectroglyphidodon*.

Distribution and space occupation

The largest differences in territory size between different species occurred on Magnetic Island, the location with fewest species (Figure 12). The territories of each species were significantly different from all the others, with *Pomacentrus tripunctatus* defending the smallest territories and *Stegastes apicalis* the largest (Figure 12a). On Magnetic Island, *Po. tripunctatus* territories were also significantly smaller than they were on Orpheus Island (Figure 12b) or in Kimbe Bay (Figure 12c). On Orpheus Island, *Po. wardi* defended the smallest territories and *Po. tripunctatus* the largest, with only moderate differences between the five species (Figure 12b). Territories in Kimbe Bay showed the least variation between species, with no significant differences between species in territory size (Figure 12c). Overall, the average farmer territory size was significantly greater on Orpheus Island ($2.24 \text{ m}^2 \pm 0.16 \text{ S.E.}$) than the other two locations (Magnetic Island: $0.91 \text{ m}^2 \pm 0.1 \text{ S.E.}$; Kimbe Bay: $1.1 \text{ m}^2 \pm 0.04 \text{ S.E.}$; ANOVA $F_{(d.f.=2)} = 43.317$, $p < 0.001$).

Across the Magnetic Island fringing reefs, an average of $25.8 \pm 0.018\%$ of available substrata was taken up by non-overlapping farmer territories. Calculations of the proportion of substratum taken up by farmer territories revealed that on the reef crest, almost 60% of the available space was taken up by *Po. wardi* and *S. apicalis* territories (Figure 13a). On the mid and outer reef flat, 30% of the space was contained within primarily *Po. wardi* territories. *Po. tripunctatus* territories took up between 5% and 7% of the inner reef flat (See also Chapter 2; Figure 13a), which consisted primarily of sand and rubble.

Farmer territories occupied an average of $58.8 \pm 0.097\%$ of available substrata on Orpheus Island fringing reefs (Figure 13b). On the inner reef flat, around

90% of the substratum was taken up by *Po. tripunctatus*, *Po. chrysurus* and *Po. wardi* territories. The second most densely occupied zone was the reef crest, where almost 70% of substrata were taken up by *Po. adelus*, *Po. wardi* and *Hemiglyphidodon plagiometapon* territories (Figure 13b).

On a reef-wide scale, an average of 53.7 +/- 7.2 % of available substrata on the Kimbe Bay platform reefs was contained within farmer territories, and farmer territories occupied over 90% of reef crest substrata (Figure 13c). The most densely occupied zone was the outer reef flat, just behind the reef crest, where almost 70% of substrata were occupied by the territories of *Po. bankanensis*, *Po. adelus* and *Plectroglyphidodon lacrymatus*. Even on the back reef, the most sparsely occupied zone, *Po. tripunctatus* territories took up a quarter of the available space. The reef crest was the zone where most species coexisted, however, the space was clearly dominated by *Po. adelus* and *Pl. lacrymatus*, which together took up around 40% of the available substratum (Figure 13c).

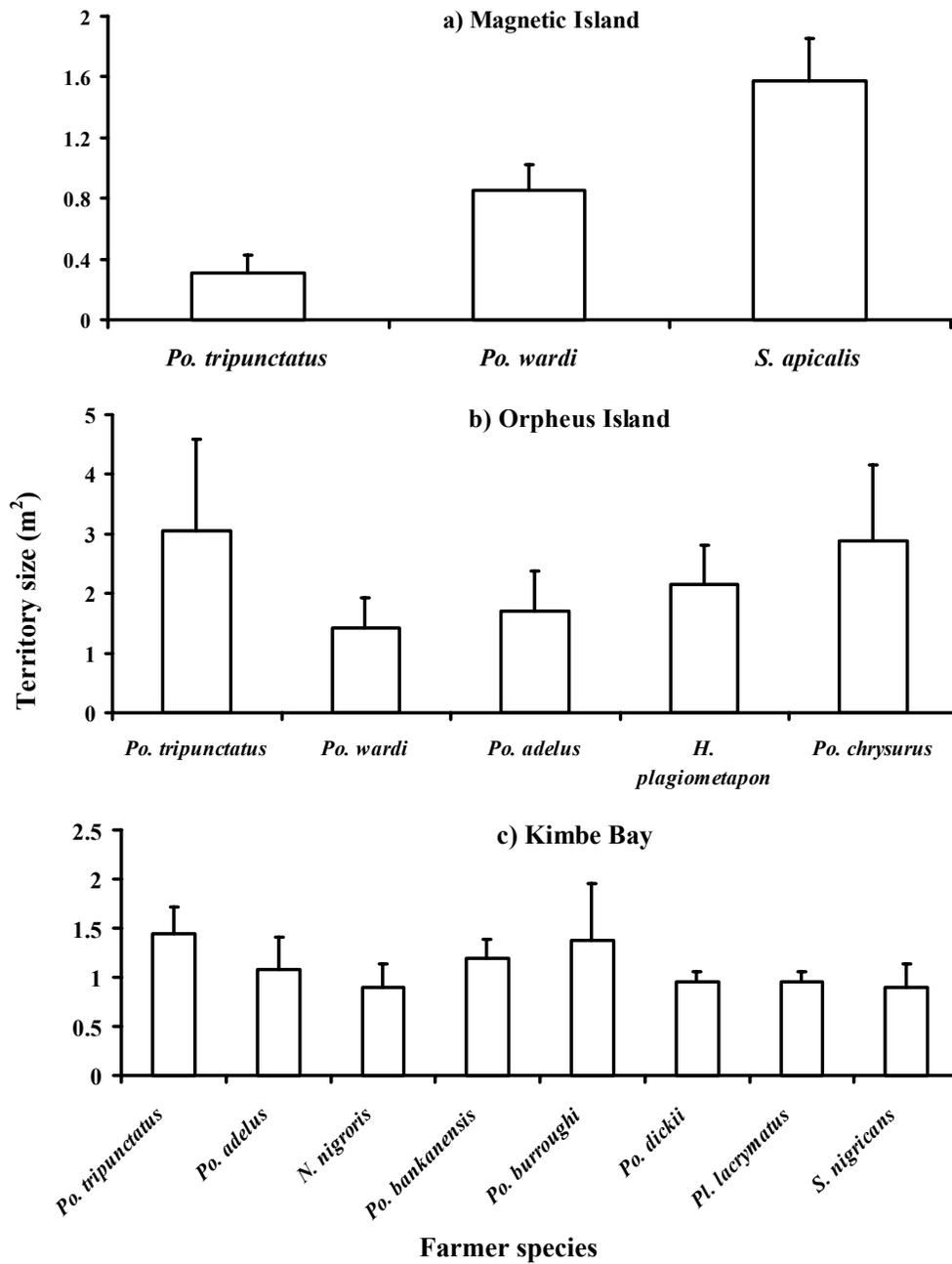


Figure 12. Differences in territory size (measured in m²) between species on a) Magnetic Island, b) Orpheus Island and c) Kimbe Bay. Note the differences in the y-axes. *Po.*: *Pomacentrus*, *S.*: *Stegastes*, *H.*: *Hemiglyphidodon*, *N.*: *Neoglyphidodon*, *Pl.*: *Plectroglyphidodon*. Error bars = 1 S.E.

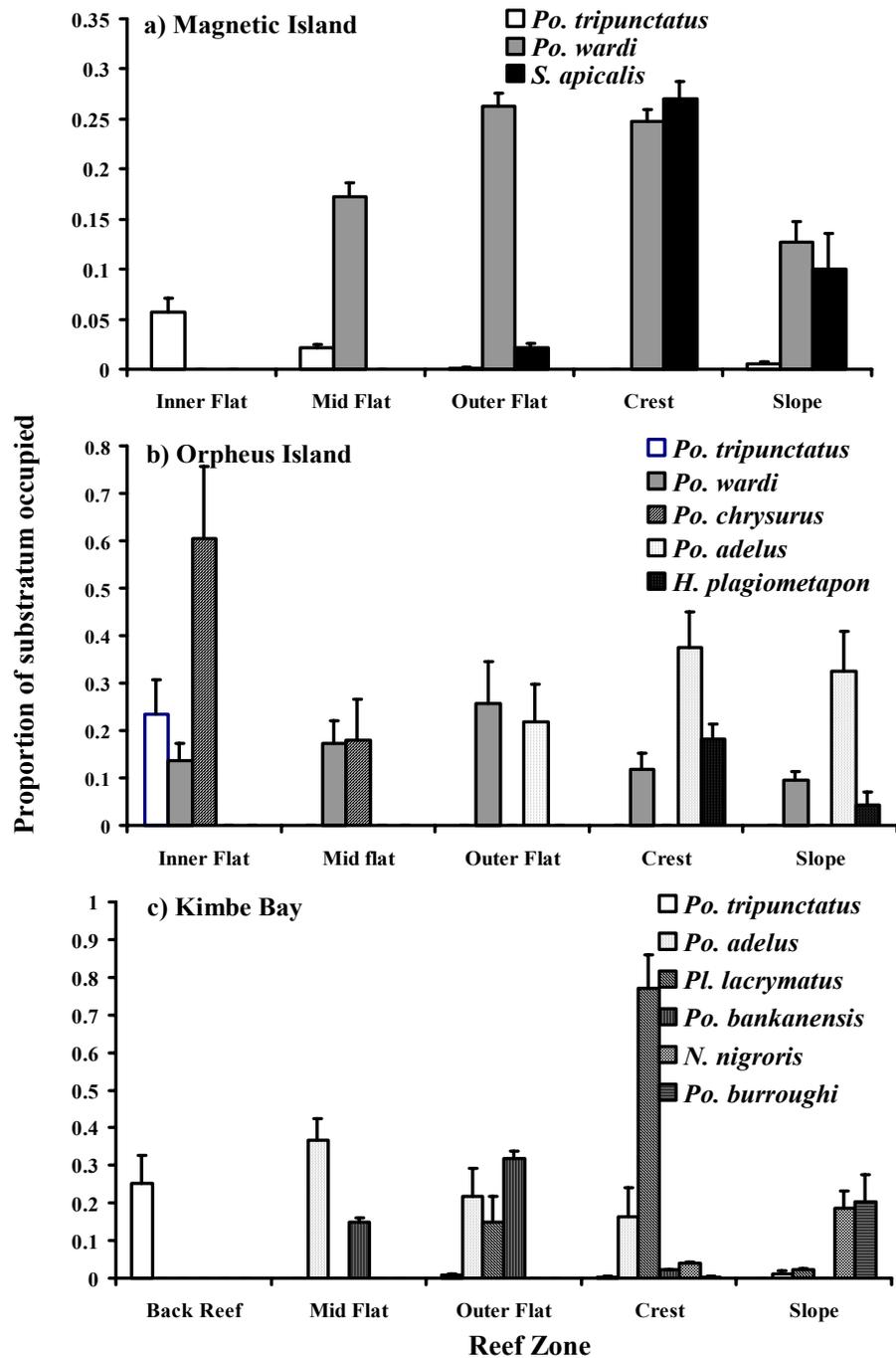


Figure 13. Proportion of substratum occupied on a) Magnetic Island, b) Orpheus Island and c) Kimbe Bay reefs by the territories of territorial damselfish. Note the differences in the y-axes. *Po.*: *Pomacentrus*, *S.*: *Stegastes*, *H.*: *Hemiglyphidodon*, *N.*: *Neoglyphidodon*, *Pl.*: *Plectroglyphidodon*. Error bars = 1 S.E.

Discussion

The results of this study confirm that farmers have diverse diets, and that they select or avoid different food items. They appear to be modifying the substratum inside their territories in different ways, often reflecting their dietary preferences. Although the larger, previously well-studied species tended to have the largest effects on the benthic communities in their territories, all the smaller species (mostly members of the genus *Pomacentrus*) also had significant effects on the algal turf in their territories. In addition, a substantial proportion of most reef zones was occupied by farmer territories, indicating that the effects on the scale of individual territories amount to a significant impact across the reef as a whole.

What do farmers eat?

The diets of most farmers appeared to be related to their zonation patterns and the proportions of different taxa in their territories. The shallow inner reef flat and back reef species that defended territories with a high proportion of detritus also ingested primarily detritus. By contrast, the territories of species restricted to the reef crest and slope contained more algae, and these species appeared to be more herbivorous.

Considerable variations were found in the diets and levels of feeding selectivity of the studied farmer species. Only *Stegastes apicalis* could be classified as a strict herbivore, selectively consuming *Polysiphonia*, *Leveilla* and *Champia*. The degree of dependence on algae versus detritus varied among species. A number of species actively selected detritus (*Pomacentrus tripunctatus*, *Po. bankanensis*, *Po. adelus* and *Plectroglyphidodon lacrymatus*), while a further two did not avoid it (*Po. wardi*, *Po. burroughi*). Detritus is a highly nutritious component of algal turfs, and recently some fish that were thought to be herbivores have emerged as being detritivores (Wilson et al. 2003). In this study, it was found that most species ingested both detritus and algae and,

with the exception of *S. apicalis*, could not be classified as either strict herbivores or detritivores.

The degree to which farmer species appeared to select more algae or detritus was directly linked to their cross-reef zonation patterns and the availability of food items in their territories. *Po. tripunctatus* is a shallow water specialist (Birdsey 1989; Boonayanate 1992), maintaining territories with a high proportion of detritus, and this species also had the highest percentage of detritus in its diet. All the species present in high densities on the reef crest or the reef slope (*S. apicalis*, *Po. wardi*, *Pl. lacrymatus*, *Po. burroughi*, *Po. adelus* and *Po. bankanensis*) ingested lower proportions of detritus, and also defended territories with lower detrital loads. This pattern was consistent among the two locations where diets were examined.

Selective feeding is said to be one of the mechanisms by which farmers cultivate the distinct algal turf in their territories (Jones 1992), either by promoting particularly palatable or productive species or by keeping select species in their most productive phase of growth (Klumpp et al. 1987; Jones 1992). The results of this study indicate that all the examined species selectively consume some algae, and that the amount of algae in the diet may be related to the magnitude of each species' effect on the algae in their territories. This was clearly the case in the territories of *S. apicalis*; as well as being the most distinctly herbivorous species, its territories also contained the most developed algal turf 'lawns'. There was also a strong relationship between the dietary selectivity and the magnitude of inside–outside territory differences in *Po. wardi*, *Pl. lacrymatus*, *Po. adelus* and *Po. bankanensis*. To be able to more accurately predict the relationship between diet and effects on benthic communities, information about diet and selectivity must be more closely linked to between-zone differences in territory composition.

The use of selectivity indices to measure feeding preferences may not be appropriate to farming fishes that alter the composition of their territories in favour of preferred food algae. Comparing food items in the gut to those in the territories (Bay 1999; Santana 2001) may lead to a result of avoidance or neutrality because food items in the territory already exist in higher proportions than would be expected if algae were not being cultivated. Ultimately, food preferences must be tested under controlled conditions, such as conducting food choice experiments in a laboratory environment.

How do farmers influence algal communities?

The present study and previous literature all suggest that the primary effect of most farmers appears to be the increase of filamentous algae in their territories, either in terms of biomass (Sammarco 1983; Klumpp et al. 1987), productivity (Klumpp et al. 1987; Russ 1987) or percent cover (Santana 2001). However, there also appear to be species-specific effects that are not universal to all farmers. The high cover of microalgae in the territories of *Plectroglyphidodon lacymatus* (Santana 2001) and *Pomacentrus burroughi*, the increase in erect calcified algae and decreased fleshy macroalgae in *Stegastes apicalis* territories, and the high detrital content of *Po. tripunctatus* territories are patterns that have previously remained largely unexplored. The territories of most species also contain enhanced cover of corticated red algae (except *Po. wardi*, *Po. adelus*, *Po. burroughi* and *Neoglyphidodon nigroris*). Many species not included in this study have previously been shown to have significant effects on algal communities in their territories *S. fasciolatus* (Hixon and Brostoff 1996), *S. lividus* (Lassuy 1980), *S. nigricans* (Klumpp et al. 1987), *Pl. dickii* (Santana 2001), *Dischistodus melanotus*, *D. perspicillatus*, *D. pseudochysopocilus* and *D. prosopotaenia* (Bay 1999).

The patterns found in this study, whereby inner reef and back reef species consume large amounts of detritus and defend territories high in detritus, and reef crest species tend to have less detritus and more algae both in their territories and in their diets, has implications for the cross-reef distribution of detritus. Several studies have reported lower proportions of detritus in the algal turfs of reef crests, when compared to reef flats and back reef slopes (Crossman et al. 2001; Purcell and Bellwood 2001). Future studies could investigate whether these patterns are related to the distribution of farmer territories. For example, the cross-reef distribution of detritus within algal turfs could be different on reefs such as those on Orpheus Island, where the reef crest is dominated by a recognized detritivore such as *H. plagiometapon* (Wilson and Bellwood 1997).

The significant contribution to filamentous turf cover found in all species in this study suggests that farmer territories may be sites of increased algal yield to other grazers. Russ (1987) found that rates of yield to large grazers were significantly higher inside the territories of *S. fasciolatus* than outside. Despite the aggressive behaviour of farmers, their territories are often invaded by large schools of grazers (Robertson et al. 1976). There appears to be a relationship between the finding that reef crests are often areas of concentrated farmer territories (present study), high grazing intensity by large grazers (Steneck 1997), and high yield to large grazers (Russ 2003). However, other studies indicate that algal productivity, rather than biomass, drives herbivory, and that the mass-specific productivity in farmer territories is likely to be lower than in a closely cropped turf (Carpenter 1986). To test this pattern adequately, future research could measure the correlation between the densities of farmer territories, the rate of grazing and the algal yield to grazers on different reef zones.

By creating patches of benthos significantly different from surrounding areas, all the species in this study contributed to the overall patchiness of the benthic community on the study reefs. The species-specific nature of the farmer-mediated patches indicates that the diversity of patches is greatly increased (Levin and Paine 1974). Regional comparisons of patches created by farmer territories indicated that where farmer diversity was higher, the mosaic formed by the territories of each species and the background between-zone patch diversity became more complex. Some species created territories with unique benthic communities, while the territories of other species shared attributes with surrounding areas, the territories of other species, or both. Clearly, the term ‘farmer’ is more applicable to some species than others, despite the ability of all species in this study to defend territories against intruders. Regional comparisons of farmer communities also allowed the evaluation of how applicable generalizations about each species are, with surprising results. For example, on Magnetic Island, benthic communities inside *Po. tripunctatus* territories were very similar to those in surrounding areas, while there was only a small similarity on Orpheus Island and none at all in Kimbe Bay. Algal turf composition showed the opposite trend: *Po. tripunctatus* promoted algal turf taxa that were very different from the background species pool on Magnetic Island, but on Orpheus Island and in Kimbe Bay *Po. tripunctatus* territories included a subset of the available taxa. *Po. adelus* and *Po. wardi* occurred in two of the three locations, and the territories of these species also varied in their differences from surrounding substrata according to their location. This indicated that generalizations must be made with great caution even when referring to a single species.

How important are they?

At the three locations included in this study, the reef crest and the zone directly landward of it were consistently the zones of highest space occupation by farmers. Their overall importance to benthic communities on corals reefs is highlighted by the fact that in many reef zones, a high proportion of available space is under the jurisdiction of one or more farmer species. Previous studies have found between 11% (Wellington 1982) and 70% (Ferreira et al. 1998) of available space occupied by farmer territories, and at least six further studies report values somewhere in between (reviewed by Ceccarelli et al. 2001). However, most previous studies have reported the space occupation estimates for a single species. The complex distribution and space occupation patterns found in this study highlight the fact that generalizing the importance of farmers based on one or a few species can be problematic, and that a community-level approach may be more valuable.

It is possible that previous studies estimated the space occupation of only a few species because the smaller and more widespread farmer species were deemed unimportant (Ceccarelli et al. 2001). In demonstrating that even smaller farmer species affect the benthic structure in their territories, the results of this study suggest that farmer communities may be of greater importance than previously thought because the inclusion of smaller species greatly increases the overall space occupation of farmer territories. This implies that the contributions of farmer territories to the amount of food available to other grazers is also greater than previously thought. On reefs with greater farmer diversity, space occupation is likely to be greater, and the spatial mosaic created by their territories is likely to be more diverse.

Conclusions

The idea that farmers promote their preferred food in their territories is not a new one, but how the diets and spatial distribution of different farmer species relate to the distribution patterns of benthic communities has never been explored. Species appear to vary in their position along a continuum between strict herbivory and detritivory. It appears that farmers with a greater proportion of detritus in their diets have greater amounts of detritus in their territories, and are distributed in reef zones where algal turfs are more likely to contain more detritus. Conversely, more herbivorous farmers may establish territories in reef zones where algal turfs contain less detritus and more algae. It is possible that species with more specialized diets (i.e. at the more extreme ends of the continuum between detritivory and herbivory) engage in more active ‘management’ of the algal turfs in their territories. Selectivity indices may not be an appropriate method for measuring food preferences in farmers, therefore selective feeding will be difficult to demonstrate as a ‘farming’ mechanism. However, other methods by which farmers alter benthic communities in their territories may be more amenable to experimental testing. The results of this study suggest that while not all farmers are likely to be keystone species, many more species than has been assumed do appear to influence the benthic communities in their territories. Greater areas than expected are therefore likely to be under the influence of farmers. This implies that farmers affect algal biomass, productivity and community structure, invertebrate communities, coral recruitment and survival, and forager grazing rates on a larger scale than previously thought.

CHAPTER 4: THE EFFECTS OF FORAGERS ON FARMERS AND THEIR TERRITORIES

Introduction

Two of the most important herbivorous fish groups on coral reefs are foragers (scarids, acanthurids and siganids) and farmers (primarily territorial pomacentrids). Foragers feed in a wide-ranging, relatively non-selective manner and can have destructive effects on both benthos and substratum (Bellwood and Choat 1990; Choat 1991). They are often the dominant group of herbivores on coral reefs in terms of density and biomass (McClanahan 1997). In contrast, farmers defend territories in which they feed and nest (Ceccarelli et al. 2001), and are active in determining the composition of algae within their territories (Lassuy 1980; Lobel 1980; Hata and Kato 2002). Some farmers are assumed to play a central role in determining the structure of algal and coral communities by moderating the effects of other grazers (Williams 1980a; Wellington 1982; Hixon and Brostoff 1983; Hixon and Brostoff 1996). However, foragers are rarely completely excluded by farmer aggression (Robertson et al. 1976) and may affect both farmer populations and the benthic assemblages in their territories. How the relationship between foragers and farmers affects benthic communities has yet to be explored.

Interactions between farmers and foragers usually take the form of the farmers' aggressive exclusion of foragers (Ceccarelli et al. 2001), causing foragers to concentrate their grazing activities in areas of low farmer densities (Doherty 1983), but the effects of foragers on farmers are not completely understood. The tendency for

foragers to form schools facilitates their invasion of farmer territories (Robertson et al. 1976), implying that despite the aggressive behaviour of farmers, there is at least some grazing by foragers inside farmer territories. More direct effects of foragers on farmers could include the energetic cost to farmers involved in excluding foragers from territories. One approach in measuring this energetic cost has been to assess farmers' oxygen consumption during attacks on foragers, which showed that aggressive behaviour in two species of *Stegastes* required minimal energy expenditure (Cleveland 1999). This contradicts predictions that territorial defence is energetically costly to the individuals defending a resource (Charnov 1976; Maynard Smith 1978; Martindale 1982). However, alternative indicators of foragers' effects on farmers, such as population density, territory size and algal turf composition, have not been tested.

In territorial organisms, population density is usually closely related to territory size, with larger territory sizes leading to lower population densities. If the energy expenditure needed by farmers to defend their territories from foragers restricts the size of the territory they are able to defend, then the presence of foragers could cause increased population densities (Hixon 1980). If different farmer species are affected differently by foragers, then the activities of foragers could affect the relative abundance of farmer species. This may, in turn, determine which farmer species are able to occupy more space, and therefore affect larger proportions of the benthic community. In this way, foragers could potentially influence the extent of the effects of different farmer species.

If defending territories affects the ability of farmers to cultivate or promote optimal quantity or quality of food algae, then foragers will also influence the effect of farmers on benthic communities. This effect can arise not only through the exclusion of foragers (and associated costs to farmers), but also by the occasional invasion of farmer

territories. Both of these disturbances to farmer activities could alter the algal turf community in farmer territories from a strictly farmer-mediated turf assemblage.

In November 2000, a large herbivore exclusion experiment was established in Pioneer Bay, Orpheus Island, Great Barrier Reef. Cages that excluded large foragers, but included farmers, were constructed and maintained over approximately 30 months. As a result of forager exclusion, the benthic community structure inside the cages experienced a dramatic phase shift from coral/turf dominance to an assemblage dominated by large fleshy macroalgae up to 3 m high (primarily *Sargassum* spp.; Figure 1). The biomass of fleshy macroalgae in the cages was 9–20 times higher than in open and partially caged plots by the end of the experiment. This led to a number of other changes in the benthic community, including detrimental effects on hard corals (slower recovery from bleaching, lower recruitment, thinner tissue), shifts in the community structure of understory taxa, and changes in food-web structure (T. Hughes et al., in prep.). This experiment indicated that the overfishing of large grazing fish would cause a phase-shift from coral-dominated to algal-dominated reefs, and would significantly impair the resilience of hard coral communities in the face of major disturbances such as bleaching events. In addition, this experiment provided the ideal conditions for testing the effects of foragers on farmers. The size of the cages allowed me to test the effects of foragers on an existing community of farmers and the composition of their territories. More specifically, I aimed to test the hypotheses that the absence of large roving herbivores will affect:

- i) population densities of farmers,
- ii) territory size of farmers, and
- iii) biomass and taxonomic composition of algal turfs in and around farmer territories.

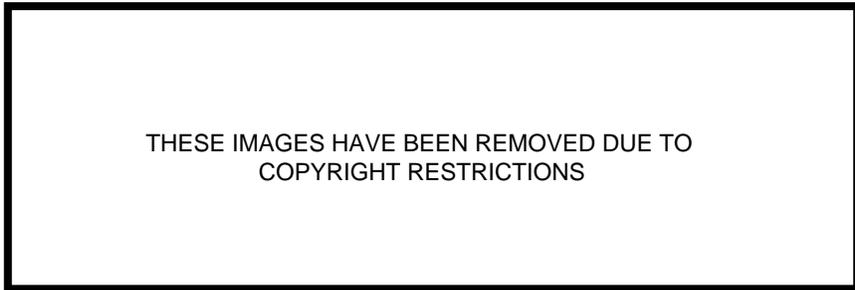


Figure 1. Photographs of benthic communities on the reef crest of Pioneer Bay before and after the cages were established. Photographs supplied by L.J. McCook.

Materials and Methods

Study site and species

The experiment was located in the reef crest zone of Pioneer Bay, Orpheus Island, Great Barrier Reef (18°36S, 146°29E). During the experiment (between October 2000 and August 2003), the coral community on the Pioneer Bay reef was recovering from the 1998 coral bleaching event (Baird and Marshall 2002; Wilkinson 2003) and was dominated by dead coral surfaces covered in closely cropped algal turfs and coralline algae. Three farmer species were abundant enough in this reef zone to be included in the experiment: *Hemiglyphidodon plagiometapon*, *Pomacentrus wardi* and *P. adelus*. The first species, *H. plagiometapon*, defended territories dominated by fine filamentous algal turfs directly on the reef crest and in a band extending approximately 5 m landward and 3 m seaward of the crest. *P. wardi* and *P. adelus* are smaller and slightly less aggressive species with a much broader distribution across the reef flat (see Chapter 3). Of the latter two species, *P. wardi* is usually larger and more aggressive than *P. adelus* (Ceccarelli, unpubl. data).

Experimental design

The experimental design consisted of three treatments: 1) open plots that allowed free access to all foragers, 2) caged plots that excluded large foragers; and 3) partial cages to control for cage artefacts. Four replicates were included for each treatment. Open plots were not manipulated and were used to provide a measure of natural variation in the reef crest community of Pioneer Bay. Fully caged plots excluded all foragers longer than 1 cm, and were used to simulate the overexploitation of foragers, and partially caged plots allowed access to foragers. Each plot measured 5 by 5 metres, and the corners of the open plots were marked with steel 'star pickets'. For the

full and partial cages, emergent fences were constructed of plastic mesh (1 cm² for the bottom 2 metres, and 2 cm² for the top 1.5 metres) on a frame of galvanized steel pipes. Cages were unroofed, but 3.5 m high, in order to break the water surface at the highest high tide. Open, partially caged and fully caged plots were alternated along the reef zone parallel to the reef crest. The cages were constructed in October 2000 and the mesh removed in May 2003, and they were cleaned approximately every 10 days.

Sampling regime

Sampling was conducted between November 2000 and August 2003, at intervals of between 4 and 10 weeks. At each sampling occasion, farmers were counted in all the plots, with recruits and adults recorded separately. To estimate territory size, three territories per species were randomly selected in each treatment, and the resident farmers observed for 15-minute periods to determine the territory boundaries. Territory circumference was measured after placing lead weights around the territory boundaries during the observation period. Territory area was estimated by measuring the circumference of each territory and using the formula for an ellipse of equivalent circumference. Territory size measurements were not conducted for *Hemiglyphidodon plagiometapon*, as they were not present in densities high enough throughout the plots. Changes in farmer densities and territory sizes were compared across treatments using Repeated Measures Analysis of Variance.

Four individuals per species were randomly selected for sampling of algal turf inside and outside territories in each treatment. Sample size was limited to avoid intruding on other experiments taking place within the plots at the same time. Algal turfs were sampled by collecting scrapings from 3 by 3 cm plots. Scrapings were taken within each territory, and from undefended adjacent areas similar in terms of substratum

composition and topographic complexity. The turf was scraped off the substratum and collected into a stocking using suction, then preserved in 10% formalin.

Samples were examined under a dissecting microscope using a grid with 1 cm squares over a Petri dish. The identity of the algae under 45 random intercepts was recorded, providing an estimate of the percent cover of different algal groups. Algae were identified to genus or species level where possible. In many cases it was more appropriate to estimate percent cover of functional groups (Steneck and Dethier 1994). The three functional groups referred to in this study were fleshy macroalgae (such as *Sargassum* spp. and *Padina* spp.), filamentous algae, and corticated red algae (such as *Hypnea* spp. and *Laurencia* spp.). Corticated algae are described as having ‘cortication’, or the ‘formation of 1 or more secondary peripheral cell layers in an algal thallus’, and are therefore not as delicate as filamentous algae, but less robust than fleshy or leathery macroalgae such as *Sargassum* (Price and Scott 1992).

The biomass of the algal turf samples in the different treatments was also assessed. The samples were decalcified in 10% hydrochloric acid and dried for 24 hours at 60°C before weighing. Biomass was calculated as unit weight (grams) per unit area (cm²). Changes over time in taxonomic composition and biomass were compared across treatments, and between inside and outside territories (nested within treatments for analysis of variance). All data were analysed with Repeated Measures Analysis of Variance (ANOVA), using SPSS for Windows[®], and a nested Repeated Measures ANOVA design was used to analyse biomass and territory composition data.

Results

Farmer density and territory size

There was a significant change in the relative densities of *Pomacentrus adelus* and *P. wardi* in response to the exclusion of foragers (Table 1). The density of *P. wardi* increased 2.2–3.4 fold from its original density (Figure 2a), while *P. adelus* densities dropped by more than 100% (Figure 2b). These density shifts over time did not occur in open and partially caged plots. Once the cages were removed, both species returned to the densities found outside the cages within a few weeks. Recruitment patterns of *P. adelus* and *P. wardi* were also significantly affected by forager exclusion (Table 1). Both species recruited in the summer months and in open and partially caged plots and there were more *P. adelus* recruits than *P. wardi* in these treatments. In the cages, *P. wardi* recruit densities were significantly higher than outside (Figure 2c), while *P. adelus* recruitment was significantly lower in the cages compared to open and partially caged plots (Figure 2d).

The territories of *P. wardi* were significantly larger than those of *P. adelus* ($1.27 \text{ m}^2 \pm 0.09$ and $0.97 \text{ m}^2 \pm 0.06$ respectively), but the exclusion of foragers did not lead to a consistent change in the territory size of either species (Figure 3). There was a small but statistically significant increase in the territory sizes of both species in the cages, and the increase in *P. wardi* territories occurred earlier than in *P. adelus* territories (Table 1). However, the territories of both species returned to their previous sizes after approximately 5 months (Figure 3).

Table 1. Results of Repeated Measures ANOVA on densities of adult and recruit *Pomacentrus wardi* and *P. adelus*, and their territory sizes. The ‘values’ column shows the multivariate statistic used in each analysis. ¹ Roy’s Largest Root, ² Pillai’s Trace.

Effect	Source of Variation	Value	df	F	p
Adult farmer density	Time x Treatment x Species	60.777 ¹	16	15.194	0.009
Recruit farmer density	Time x Treatment x Species	1.970 ²	32	16.187	0.000
Territory size	Time x Treatment	0.725 ²	26	2.405	0.001
	Time x Species	0.353 ²	13	2.262	0.018
	Time x Treatment x Species	0.366 ²	26	0.947	0.544

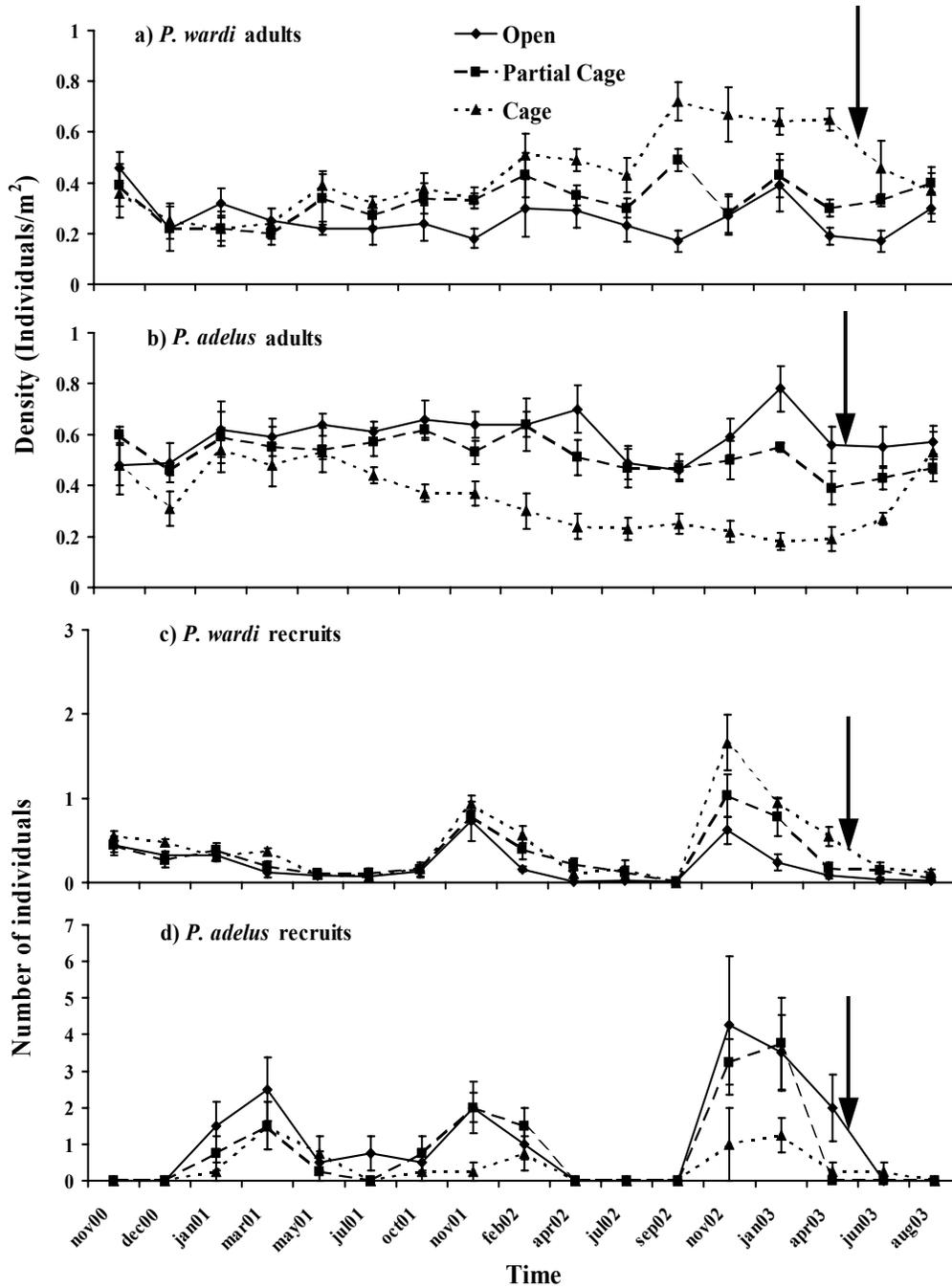


Figure 2. Changes in densities of adults (a and b) and in recruit numbers (c and d) over time in the three treatments. Densities of adults were measured as numbers of individuals per m², while recruit abundance was measured as individuals per 5m². Arrows show when the cages were removed. *P.*: *Pomacentrus*. Note the differences in the y-axes of figures c) and d). Error bars = 1 S.E.

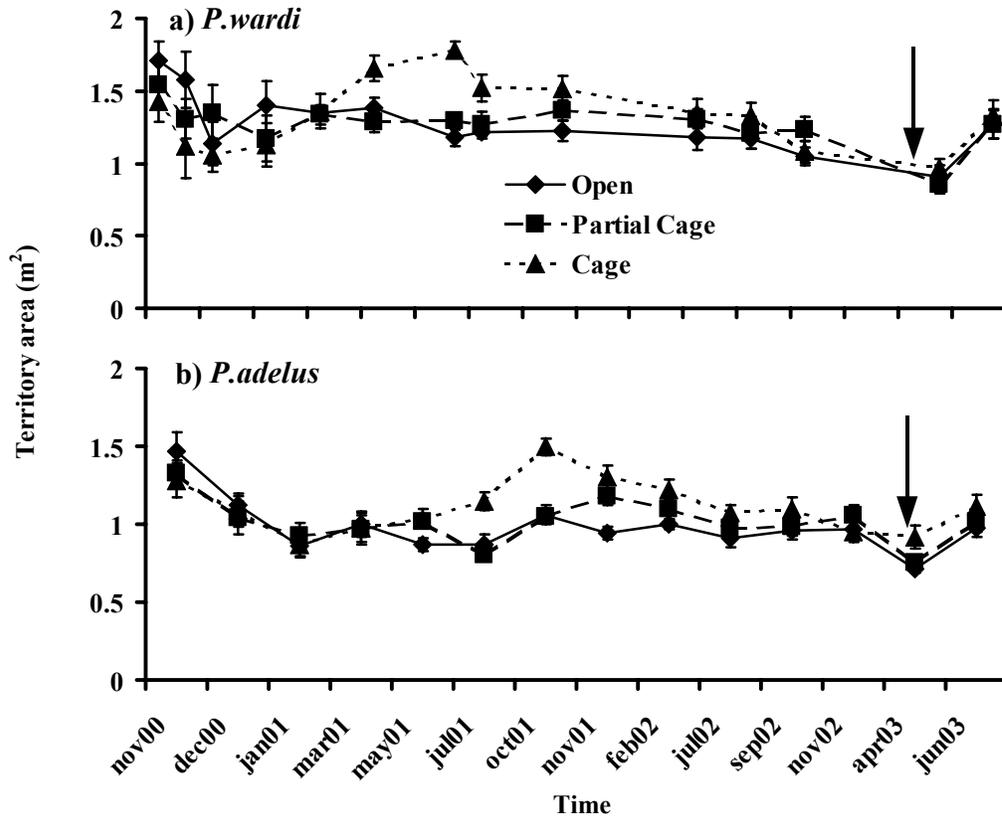


Figure 3. Changes over time in the territory area of the two numerically dominant farmer species. Arrows show when the cages were removed. *P.*: *Pomacentrus*. Error bars = 1 S.E.

Algal turf biomass and percent cover

The biomass of algal turf increased significantly in the cages through the early months of the experiment, and 7 months later (May 2001) it remained consistently higher than in partially caged and open plots until the cages were removed in June 2003 (Figure 4).

No significant changes in algal biomass were evident in farmer territories occupying the open and partially caged plots (Figure 4a, 4b). The significant biomass increase in the cages, however, took place primarily inside farmer territories, despite strong fluctuations over time (Figure 4c). The low biomass outside territories remained stable throughout the experimental months. Biomass was significantly higher outside territories than inside only after the cages had been removed (Table 2, Figure 4c).

The percent cover of algal turf in unmanipulated plots was significantly higher in farmer territories than in undefended areas (Table 2). Algal turf never covered more than 40% of the substrata outside territories. It was significantly higher in *Pomacentrus adelus* territories, higher still in *P. wardi* territories and almost always above 60% inside *Hemiglyphidodon plagiometapon* territories (Figure 5a). The pattern inside partial cages was similar (Figure 5b). In contrast, the percent cover of algal turf inside the full cages was consistently above 40% throughout the experiment both inside and outside all territories, until the cages were removed and the original pattern was restored (Figure 5c).

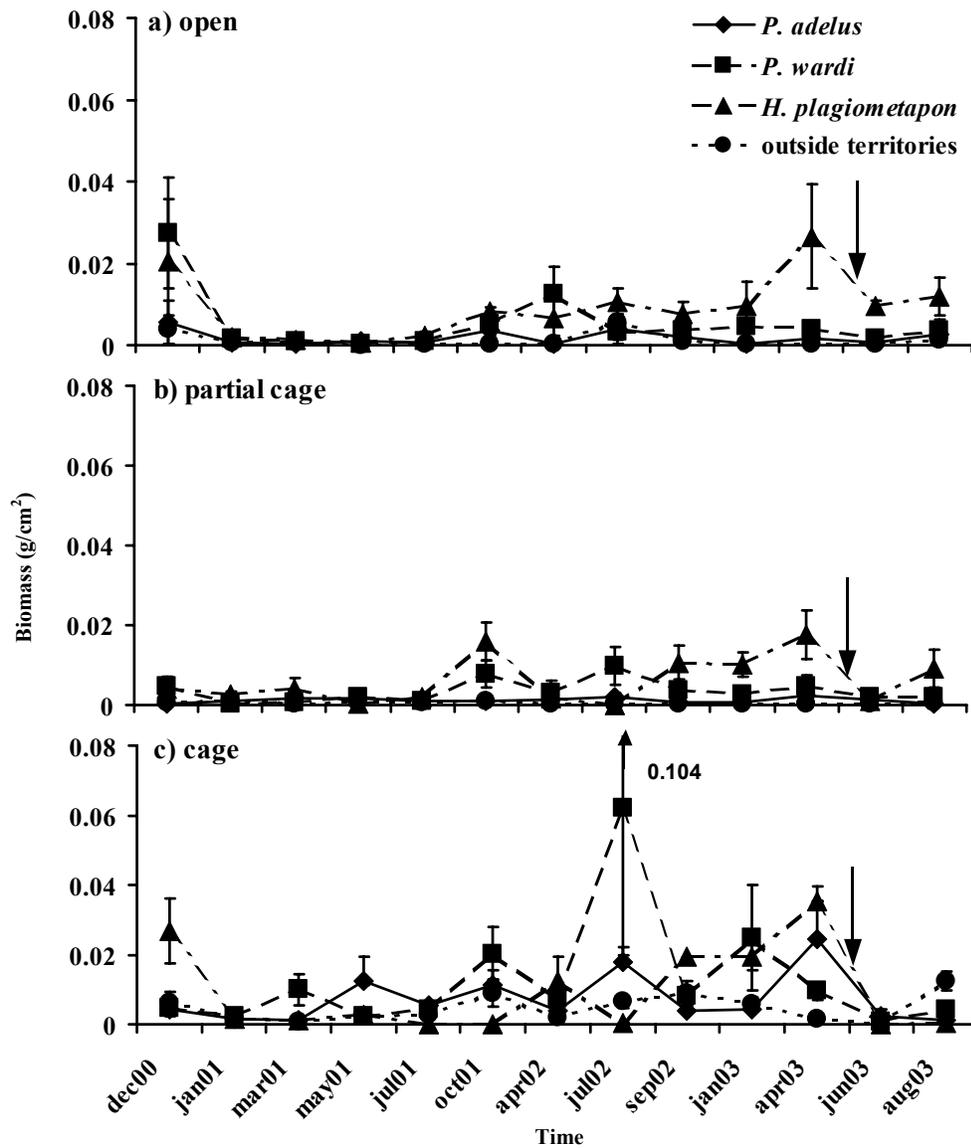


Figure 4. Changes in turf biomass over time a) in open plots, b) in partially caged plots and c) in fully caged plots. Biomass was estimated as unit weight (g) per unit area (cm²). Arrows show when the cages were removed. *P.*: *Pomacentrus*, *H.* *Hemiglyphidodon*. Error bars = 1 S.E.

Table 2. Results of Repeated Measures ANOVA on characteristics of algal turf collected inside the territories of *P. wardi*, *P. adelus* and *H. plagiometapon*, and outside territories. “Position” defines inside/outside samples for each farmer species. Characteristics include biomass and cover, and overall taxonomic composition. Results are given for the components of the algal turf community that changed significantly as a result of the experiment. Interactions between time, treatment and position were not available due to the nested ANOVA design, where position was nested within treatment (represented as ‘Position (Treatment)’). The ‘values’ column denotes the result of the multivariate statistic used in each analysis. ¹ Pillai’s Trace, ² Roy’s Largest Root.

Effect	Source of Variation	Value	d.f.	F	p
Biomass	Time x Treatment	0.8991	24	2.996	0.000
	Time x Position (Treatment)	3.2921	180	1.361	0.004
% Cover	Time x Treatment	1.1001	28	3.664	0.000
	Time x Position (Treatment)	1.1032	14	3.624	0.000
Community composition	Time x Treatment	0.2061	28	2.999	0.000
	Time x Position (Treatment)	1.9261	504	1.675	0.000
Fleshy macroalgae	Time x Treatment	1.0681	28	3.439	0.000
	Time x Position (Treatment)	2.2811	84	2.015	0.000
Corticated red algae	Time x Treatment	1.0941	28	3.625	0.000
	Time x Position (Treatment)	2.4901	84	2.331	0.000
Filamentous algae	Time x Treatment	0.9681	28	2.812	0.000
	Time x Position (Treatment)	2.0931	84	1.760	0.000
<i>Polysiphonia</i>	Time x Treatment	0.7381	28	1.753	0.026
	Time x Position (Treatment)	1.3742	14	4.513	0.000
<i>Hypnea</i>	Time x Treatment	0.8711	28	2.316	0.002
	Time x Position (Treatment)	1.9661	84	1.601	0.003

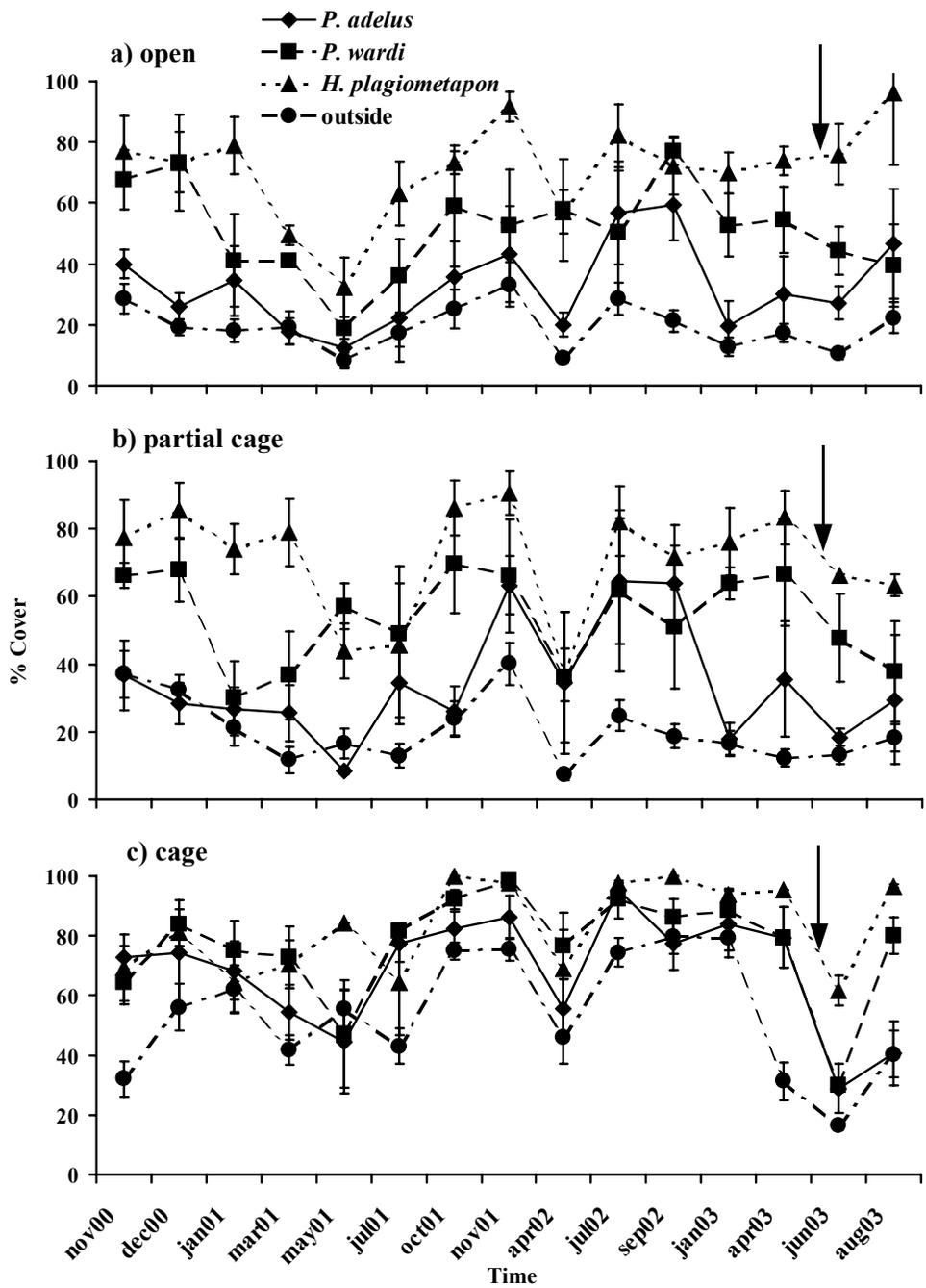


Figure 5. Changes in the percent cover of algal turfs over time a) in open plots, b) in partial caged and c) in full cages. Arrows show when the cages were removed. *P.*: *Pomacentrus*, *H.*: *Hemiglyphidodon*. Error bars = 1 S. E.

Composition of algal turf

The algal turf assemblage on the Pioneer Bay reef crest was significantly affected by the exclusion of large foragers, but the effect varied inside and outside farmer territories (Table 2). The functional groups most strongly influenced by the absence of foragers were corticated red algae (primarily *Hypnea* spp., *Chondria* spp. and *Laurencia* spp.) and fleshy macroalgae (primarily *Padina* spp. and *Sargassum* spp.). In open plots and partially caged plots, corticated red algae were generally found in low cover everywhere (Figure 6a) except in the territories of *Hemiglyphidodon plagiometapon* and *Pomacentrus wardi* (Figure 6b). When foragers were excluded, the cover of corticated red algae also increased in *P. adelus* territories and outside territories (Figure 6c).

In examining how foragers affect the role of farmers in structuring benthic communities, it may be important to establish whether most of the potential for fleshy macroalgal growth, in the form of juvenile plants and holdfasts within the algal turf, occurs inside or outside the territories of farmers. If it occurs inside, it would also be interesting to see whether some species are more responsible for this increase than others. The presence of fleshy macroalgae in the algal turf was estimated as percent cover. Overall, the cover of fleshy macroalgae was significantly higher in the cages than open and partially caged plots for most of the duration of the experiment ($F_{(d.f.=84)} = 3.439, p < 0.001$) (Figure 7a). The cover of fleshy macroalgae was generally low in the open and partially caged plots, with small and occasional peaks in cover primarily inside the territories of *H. plagiometapon* and *P. wardi* (Figure 7b). In the cages, the cover of fleshy macroalgae was very variable, but almost never as low as in the open and partially caged plots. Outside territories, there were peaks in the cover of fleshy macroalgae in the summer months of 2001 and 2002. Inside the territories of *H.*

plagiometapon, the peaks in macroalgal cover occurred during the winter months, reaching values of up to 40% cover (Figure 7c). It appears that the overall increase in fleshy macroalgae in the caged plots is being driven by the higher cover of these algae inside *H. plagiometapon* territories.

The temporal dynamics of selected taxa were analysed to estimate the effects of forager exclusion on taxa commonly used by farmers as food. The genera *Polysiphonia*, a filamentous red alga, and *Hypnea*, a corticated red alga, are commonly found in farmer territories and in the gut contents of many herbivores (see Chapter 3), and their abundance was used as an indication of the amount of available food inside and outside territories. *Polysiphonia* spp. increased significantly in the cages shortly after they were established, and remained higher than in the other treatments until the cages were removed (Figure 8a). The cover of *Polysiphonia* in the cages declined in April of each year, suggesting a seasonal die-off, and in the summer months of one year *Polysiphonia* bloomed in the partial cages. Repeated Measures ANOVA showed that inside the cages, the cover of *Polysiphonia* was significantly higher inside territories than outside, with open or partially caged plots having the lowest cover of *Polysiphonia* irrespective of the presence or absence of territories (Table 2). Percent cover of *Polysiphonia* was very variable, indicating different temporal dynamics inside the territories of each species (Figure 8b), but there was a general increase in the cover of *Polysiphonia* in caged plots (Figure 8c).

The cover of *Hypnea* spp. was slightly higher in the cages in the latter half of the experiment, and then bloomed in April 2003, just before the cages were removed (Figure 9a). This sudden and short-lived increase, which did not occur in open plots (Figure 9b), occurred almost exclusively inside caged farmer territories (Figure 9c). In the spring of 2001 and the autumn of 2003, *Hypnea* blooms were found only inside *H.*

plagiometapon territories, while the cover of *Hypnea* was significantly higher in *P. adelus* territories than anywhere else in the winter of 2002 (Table 2). Forager exclusion therefore significantly affected the territories of *P. adelus* and *P. wardi*, leading to an increase in food quantity (biomass) and quality (*Polysiphonia* and *Hypnea*), but also to an increase in the amount of unpalatable fleshy macroalgae inside the territories of all three species.

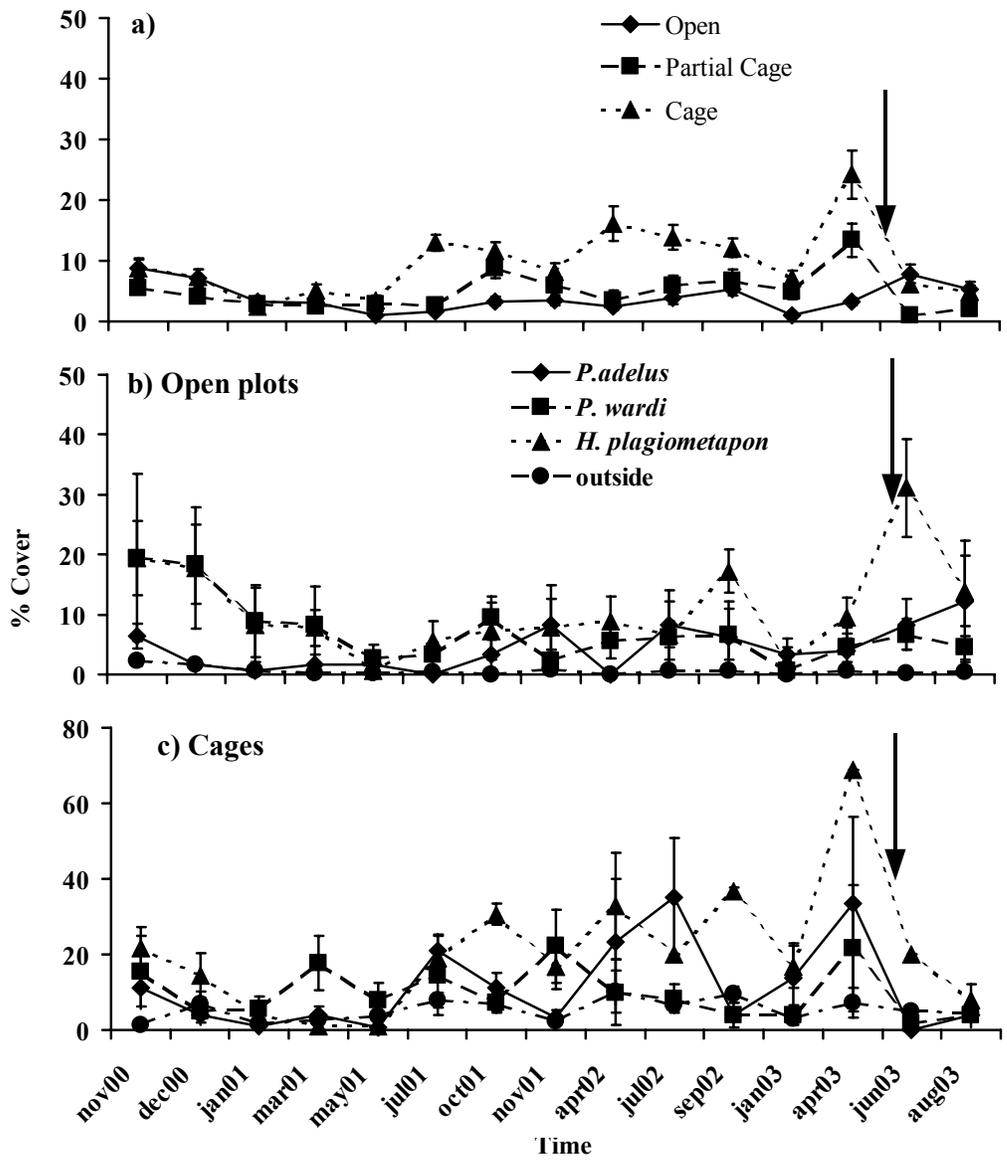


Figure 6. Changes in the percent cover of corticated red algae a) pooled for each treatment, b) in open plots, separated by farmer territories (with outside territories pooled to avoid congestion), and c) in caged plots, where percent cover was significantly higher in farmer territories than outside. Values in partial cages were not significantly different from open plots and are not shown here. Arrows show when the cages were removed. Note the differences in the y-axis of figure c). *P.*: *Pomacentrus*, *H.*: *Hemiglyphidodon*. Error bars = 1 S.E.

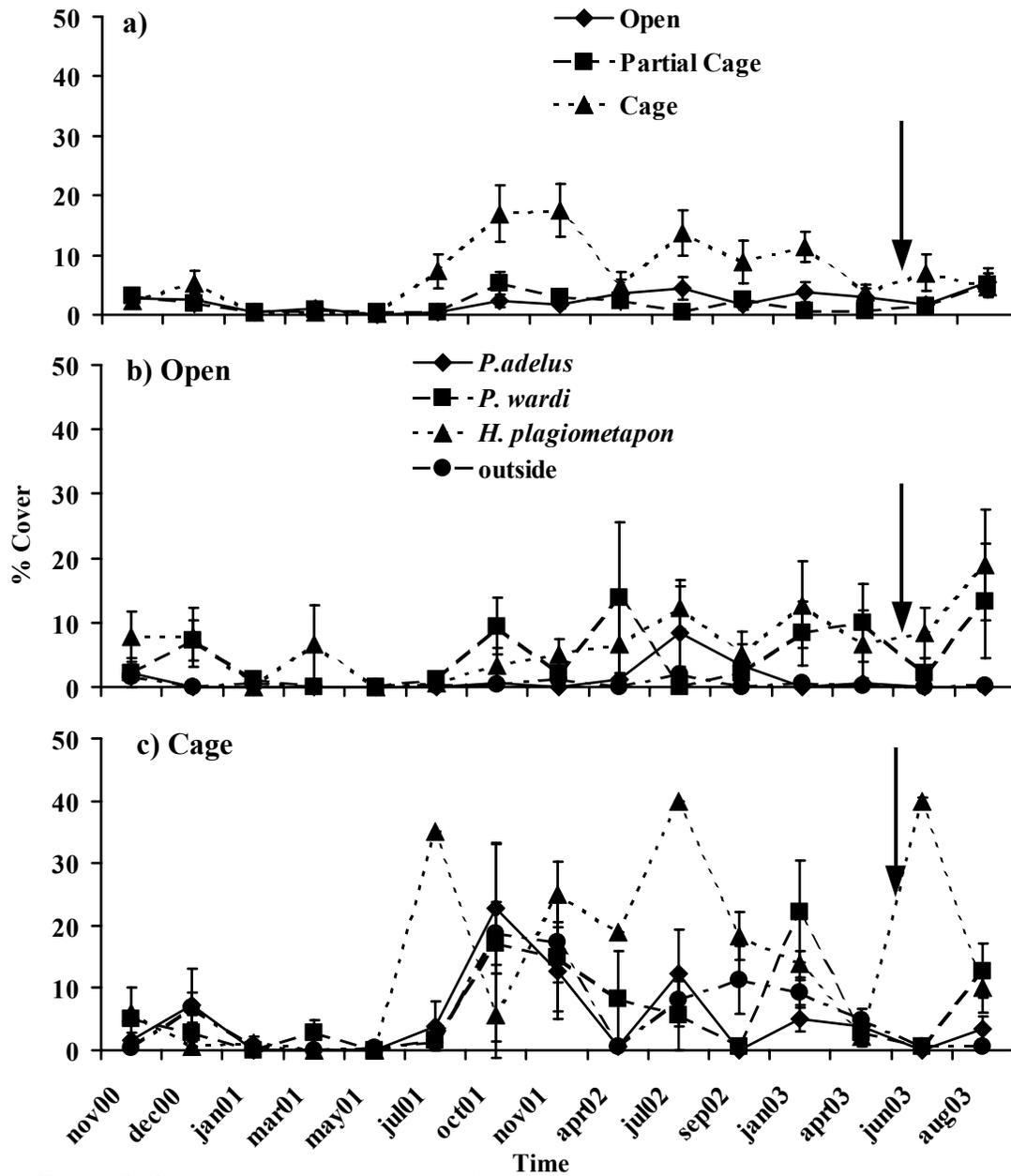


Figure 7. Changes in the percent cover of fleshy macroalgae a) in the three treatments, b) in open plots, separated by farmer territories (with outside territories pooled) and c) in caged plots, where percent cover was highest in *H. plagiometapon* territories than outside. Values in partial cages were not significantly different from open plots and are not shown here. Arrows show when the cages were removed. *P.*: *Pomacentrus*, *H.*: *Hemiglyphidodon*. Error bars = 1 S.E.

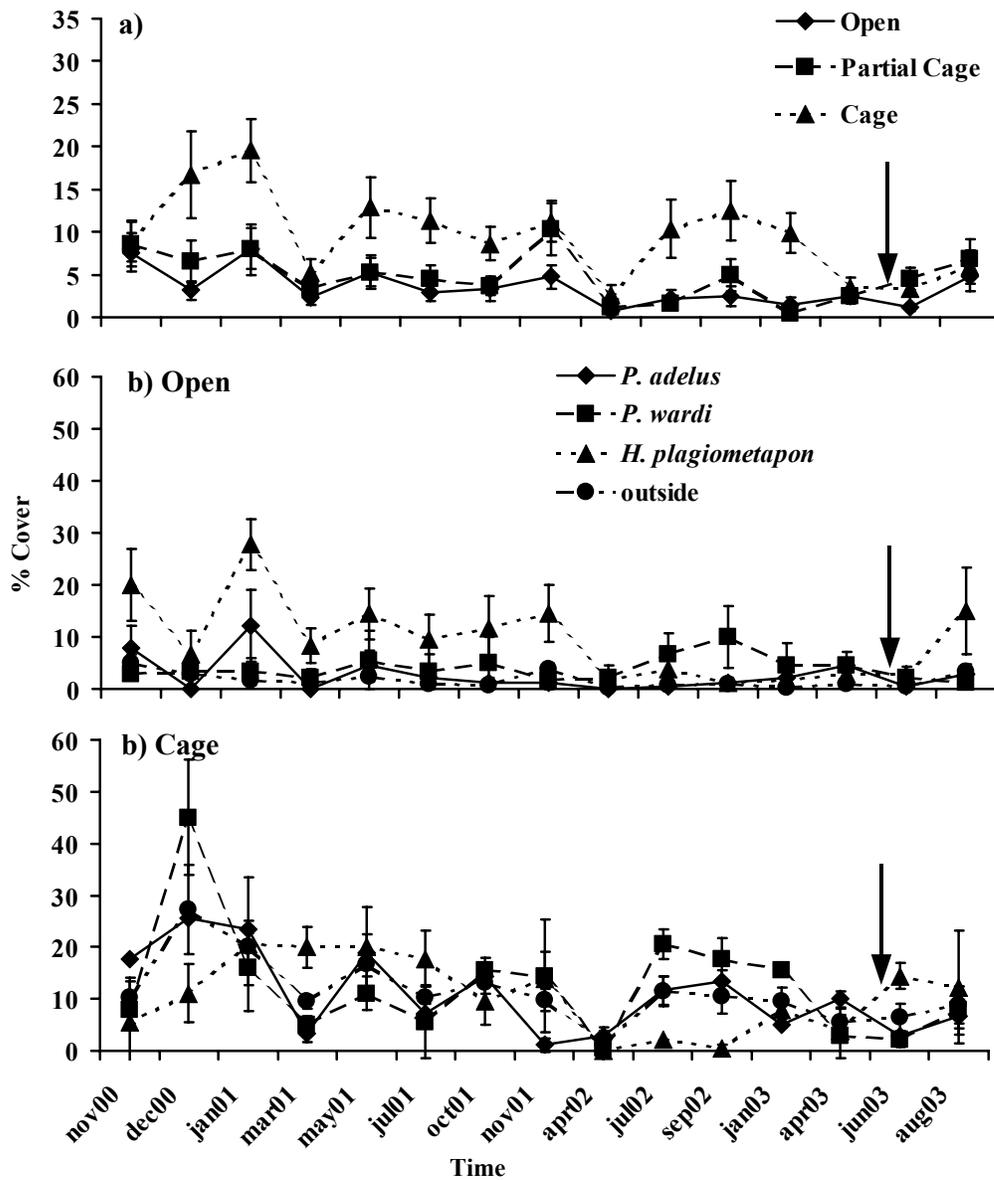


Figure 8. Changes in the percent cover of *Polysiphonia* spp. a) in the three treatments, b) in open plots and c) in caged plots separated by farmer territories (with outside territories pooled). Values in partial cages were not significantly different from open plots and are not shown here. Arrows show when the cages were removed. *P.*: *Pomacentrus*, *H.*: *Hemiglyphidodon*. Error bars = 1 S.E. Note differences in the y-axes.

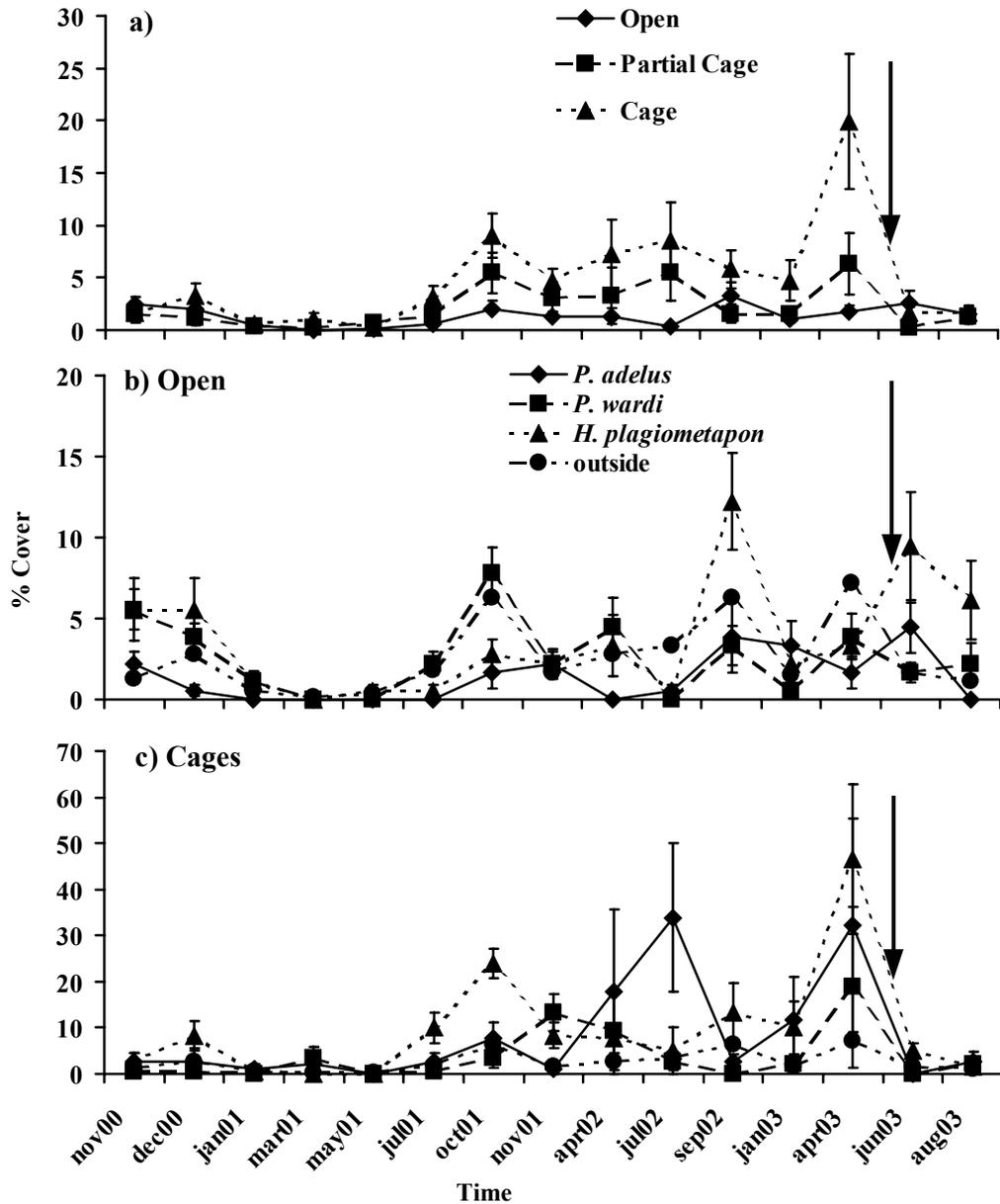


Figure 9. Changes in the percent cover of *Hypnea* spp. a) in the three treatments, b) in open plots and b) in caged plots separated by farmer territories (with outside territories pooled). Values in partial cages were not significantly different from open plots and are not shown here. Arrows show when the cages were removed. *P.*: *Pomacentrus*, *H.*: *Hemiglyphidodon*. Error bars = 1 S.E. Note differences in the y-axes.

Discussion

The changes in farmer populations and their territories inside forager exclusion cages could have been caused by three possible mechanisms. Firstly, the cages may have excluded predators, leading to a decrease in predation levels on farmers, which in turn may have brought about shifts in relative densities of the two more abundant farmers. Similarly, the decreased need to hide from predators may have allowed more time and energy for territory cultivation, which then caused shifts in the benthic community structure of territories. This is unlikely, however, as many predatory serranid fishes found crevices in the substratum and were often seen inside the cages (pers. obs.).

Secondly, and most obviously, cages reduced competition from large foragers, potentially increasing competition between the two congeners *Pomacentrus wardi* and *P. adelus* in favour of the larger species (*P. wardi*). The exclusion of foragers also meant that algal turf in farmer territories was no longer being periodically consumed by competitors, and could therefore increase in quantity and quality.

Thirdly, removing access to foragers caused a significant shift in habitat structure (from two-dimensional coral/turf dominance to three-dimensional *Sargassum* forests), perhaps creating an environment more suitable to *P. wardi* and to certain algal turf taxa. It is most likely that the observed patterns were caused by a combination of reduced competition from foragers and a shift in habitat structure.

The two more common species of farmers in Pioneer Bay, *P. wardi* and *P. adelus*, responded to the exclusion of foragers with a shift in relative numeric dominance in both adults and recruits. Both explanations for the patterns observed in the cages imply that they were caused by forager exclusion, either directly (reduced competition between foragers and farmers) or indirectly (habitat shift through decreased

herbivory), and this study cannot distinguish between them. The habitat of *P. adelus* and *P. wardi* overlaps across a wide reef zone extending from the outer reef flat to just below the reef crest (Chapter 3), and given that their territories do not overlap intra- or interspecifically, it is reasonable to assume that they may compete for space in which to establish their territories (Doherty 1983; Robertson 1984). Of the two species, *P. wardi* is the larger and more aggressive (unpubl. data) and would therefore be expected to occur in greater densities (Itzkowitz 1977; Williams 1978) and defend larger territories (Hixon 1980). In the shared reef zone of Pioneer Bay, *P. adelus* is generally more abundant than *P. wardi*. When foragers were excluded, this situation was reversed.

The increase in *P. wardi* densities occurred concurrently with a massive growth of *Sargassum* spp. inside the cages, a fleshy macroalga that is usually absent from the Pioneer Bay reef crest. As described in Chapter 2, *P. wardi* inhabits *Sargassum* beds at other locations on the inner GBR, so it is possible that the changes in farmer population density were habitat-driven. If this is the explanation, then the effect of foragers on farmer populations lies in their ability to modify the habitat to the preference of some farmer species and the detriment of others, and it can still be considered an indirect effect of forager activities on farmer populations.

Recruitment patterns of *P. adelus* and *P. wardi* were significantly affected by the exclusion of foragers, but adult densities changed 6 months before any recruitment was recorded. Therefore, changes in recruitment alone cannot entirely account for the significant shift in adult densities. The most likely explanation for the change in recruitment patterns is that the growth of large stands of fleshy macroalgae in the cages created a favourable habitat for *P. wardi* recruits, which doubled in density in the cages, and a less favourable habitat for *P. adelus* recruits, which were less than half as abundant in the cages than in open and partially caged plots. Habitat choice is a

common occurrence during the settlement and recruitment of fishes on coral reefs (Booth and Wellington 1998; Ohman et al. 1998), and large stands of fleshy macroalgae provide a very different habitat to a coral/turf-dominated reef (Carr 1994).

Adult *P. wardi* densities were higher than *P. adelus* densities only in the absence of foragers, but *P. wardi* was able to maintain larger territories than *P. adelus* irrespective of the need to defend them against larger competitors. Any effect of forager exclusion on farmer territory size was small and short-lived. Competition theory predicts that competition will determine the size of the territory that can be defended (Davies 1978; Schoener 1983). In these models, there is a trade-off between the defence of large territories that compensate for low food quality (Schoener 1983), and the defence of smaller territories restricted by increased intrusion pressure, which in turn is driven by high food quality (Grant 1997). In this study, the absence of a persisting or large change in territory size when competition from foragers was removed could be a product of three potential processes.

Firstly, the increase in three-dimensional space availability presented by tall, erect *Sargassum* plants may have reduced the need for a two-dimensional expansion in territory area (see Chapter 2). Secondly, the uncaged farmers in this study may have been able to maintain optimal territory sizes despite the need to defend them from foragers. Thirdly, competition for space affecting territory size may have occurred primarily between the two congeneric farmers (Bay et al. 2001), rather than between farmers and foragers, with foragers adding only minor competitive pressure on territory size. It is likely that a combination of the first and third processes was responsible for the observed patterns, as there was an increase in the three-dimensional space available, and at least one farmer species (*P. wardi*) has been observed to promote the growth of peiphytes on *Sargassum* leaves and stalks (Chapter 2). There was also frequent

aggression between *P. wardi* and *P. adelus* (pers. obs.). To adequately test the three proposed reasons for the lack of change in territory size, each would need to be more rigorously tested. The results of this study also raise the question of the adequate length of time for experimental tests of mechanisms affecting territory size, as results may be affected by the length of the experimental time period.

Forager exclusion caused an increase in the quantity and quality of food resources in farmer territories. Algal turf biomass and cover were higher inside all farmer territories than outside, in accordance with the results of most studies on farmer territories (Brawley and Adey 1977; Sammarco 1983; Klumpp et al. 1987; Hixon and Brostoff 1996). If defending territories meant that farmers invested less energy in the “cultivation” of optimal food quantity, we would expect algal biomass and cover to increase in the absence of foragers. An increase in food quantity in the cages would also provide an indirect measure of defence effectiveness. That is, if farmers adequately defend their food resources from foragers, there should be little change once those resources are further defended by a cage.

In uncaged and partially caged plots, there was a clear difference in algal biomass between the three species: *Hemiglyphidodon plagiometapon* territories held the highest biomass, followed by *P. wardi*, while in *P. adelus* territories biomass was only slightly higher than outside territories. In the absence of foragers these differences became negligible, suggesting that in this farmer community defence effectiveness was closely linked to the size of farmer species. The largest species, *H. plagiometapon*, experienced the least change in food quantity in the absence of large competitors, while territories of the smallest species, *P. adelus*, changed the most.

The algal groups that changed most in the absence of foragers were the highly palatable red filamentous algae *Polysiphonia* spp., corticated red algae (especially the

palatable *Hypnea* spp.), and combined fleshy macroalgae (including primarily *Sargassum* spp., *Padina* spp. and *Galaxaura* spp). Interestingly, *Polysiphonia* spp. increased uniformly inside the cages, both outside territories and in the territories of all three species. It is commonly found that the activities of farmers promote the growth of *Polysiphonia* spp. and other red filamentous algae (Brawley and Adey 1977; Lassuy 1980; Sammarco 1983; Kamura and Choonhabandit 1986); therefore this taxon can be considered a widely preferred food alga. Even in the territories of *H. plagiometapon*, reportedly a detritivore, filamentous algae can serve the purpose of trapping detritus and can therefore be classed as desirable (Wilson and Bellwood 1997).

Corticated red algae are also often found growing in farmer territories (Lassuy 1980; Ruyter van Steveninck 1984; Ferreira et al. 1998). *Hypnea* spp., in particular, is often present in the gut contents of farmers (Chapter 3), and like *Polysiphonia*, its percent cover may be used as an indicator of food quality in farmer territories. The response of *Hypnea* to forager exclusion was significant in *H. plagiometapon* and *P. adelus* territories, where it grew to cover 47% and 34% of territories respectively, compared with 10% and 4% (respectively) in open plots. This suggests that foragers affect the ability of these species to promote or cultivate corticated red algae in general and *Hypnea* spp. in particular.

In the territories of *H. plagiometapon*, both corticated red algae and fleshy macroalgae increased in the absence of foragers. If *H. plagiometapon* maintains a mat of filamentous turf in its territories to trap detritus, larger algae may inhibit this process. Incursions by foragers into *H. plagiometapon* territories could be helpful in removing large corticated algae and macroalgal holdfasts, instead of only reducing the biomass of more palatable algae. The relationship between foragers and farmers needs to be

explored in greater depth to understand the complex nature of these interactions more clearly.

This study provides evidence that farmer populations and the composition of their territories are affected by the activities of foragers, both through competition and through the forager-mediated coral/turf dominated environment. Furthermore, the influence of farmers on coral reef benthic communities may be the result of a complex interaction between foragers and farmers, where, despite the need to defend their food resources, some farmer species rely on forager intrusions to remove tough, unpalatable algae.

By affecting the relative densities of *P. wardi* and *P. adelus*, forager activities can influence the extent of the impact each species is able to have on the benthic community of the reef crest zone. Where previously benthic communities were affected primarily by the activities of *P. adelus*, in the absence of foragers *P. wardi* became the spatially dominant species and therefore influenced a larger proportion of the benthic community.

This experiment was conducted on a reef zone where the more abundant farmers were species with relatively subtle effects on benthic communities (Chapter 3); reef zones dominated by farmers with stronger effects may yield larger shifts in the benthic community structure as a response to the absence of foragers. The absence of large foragers is often associated with reef degradation (Hughes 1994; Hughes et al. 1999; McCook 1999), through the loss of top-down control on fleshy macroalgae. Potential forager-mediated shifts in the relative abundance of farmers towards larger farmers with higher algal turf biomass in their territories could exacerbate reef decline through the detrimental effects of thick algal turfs, including the trapping of sediment (Steneck 1997), the smothering of reef-building corals and coralline algae, and the

inhibition of coral recruitment (Sammarco and Carleton 1981; Birrell et al. in press).

This study has also shown that algal turfs in farmer territories can be the potential source for the growth of fleshy macroalgae. The effects of foragers on farmers can therefore influence not only farmer populations, but modify the overall role of farmer communities in structuring benthic assemblages.

CHAPTER 5: CONTRASTING EFFECTS OF FORAGERS AND FARMERS ON CORAL REEFS

Introduction

On coral reefs, the greatest effects of feeding by herbivorous fish are usually attributed to foragers (scarids, acanthurids and signanids), due to their ability to reduce algal biomass and the destructive effects of some species (Carpenter 1986; Steneck 1988; Horn 1989; Bellwood and Choat 1990). However, some farmers (pomacentrids) have been attributed a central role in determining the structure of algal and coral communities because of their ability to directly promote algal abundance, kill coral and moderate the effects of foragers (Williams 1980b; Wellington 1982; Hixon and Brostoff 1983). The relative effects of foragers and farmers, and the interactive effects of these herbivores have not been fully examined. Algal communities on coral reefs are subject to different influences, depending on the dominant group of herbivores present: 1) biomass reduction by foragers in areas where foragers are abundant; and 2) modification by farmers in areas of high farmer densities. Many studies have focussed on the effects on benthic communities by either foragers (Choat and Bellwood 1985; Lewis 1986; Miller and Hay 1996) or farmers (Lassuy 1980; Wellington 1982; Ferreira et al. 1998; Hata and Kato 2002). However, both foragers and farmers are usually present and their interaction may have a major influence on the structure of coral reef assemblages.

Of the different possible farming activities, the aggressive exclusion of other grazing fishes has received the most attention. Experimental farmer removals usually

result in an influx of other grazing fishes, such as parrotfish and surgeonfish (Mahoney 1981; Hourigan 1986), causing a rapid decline of algal standing stocks within territories. This implies territorial defence as an important mechanism, but the experimental design does not allow the effects of defence to be isolated from the other potential effects of farmers. Where farmers are removed there is a concomitant increase in forager feeding and a reduction in all other potential farming activities (direct feeding effects, weeding, substrate preparation and fertilizing). A more sophisticated experimental design is necessary to distinguish the effects of farmers and other grazers on reef algae and corals.

In this study, I test the hypotheses that foragers and farmers have different effects on the structure of benthic coral reef communities, and that farmers increase algal abundance by reducing the impact of foragers through defence, using a reef zone with a high density of both farmer territories and foragers. To do this, I distinguish between the effects of farmers (largely *Plectroglyphidodon lacrymatus* and *Pomacentrus adelus*) and a suite of foragers (primarily acanthurids and scarids) on algal assemblages on a coral reef in Papua New Guinea. I carried out an experiment in which the effects of the two behavioural groups of herbivores were distinguished; the farmer - effect was measured by damselfish removal and the forager -effect was measured by exclusion using fences. An orthogonal design enabled me to separate the direct effects of the two groups, in addition to detecting effects arising from their interaction (the aggressive exclusion of foragers by farmers).

Materials and methods

Study site and species

I conducted this study on two inshore reefs in Kimbe Bay, West New Britain Province, Papua New Guinea (5°26'S, 150°52'E), between April and June 2001. The farmer community on and directly landward of the reef crest was dominated by *Plectroglyphidodon lacrymatus* and *Pomacentrus adelus*, but included a host of other partially herbivorous damselfish. The dominant farmer on this reef zone was *Pl. lacrymatus*, maintaining territories dominated by thick turfing algae and covered in a layer of blue-green algae, and behaving aggressively towards larger herbivorous and detritivorous fishes, such as parrotfish (*Scarus dimidiatus*, *S. quoyi* and *S. bleekeri*) and surgeonfish (*Ctenochaetus striatus*, *C. strigosus* and *Acanthurus lineatus*).

Abundance of foragers and farmers

I conducted fish counts along belt transects on the reef crest and on the reef slope just seaward of the crest (<2 m in depth) to determine forager densities, using four 200 m² transects in each zone on two reefs. Farmers were counted in the 2 x 2 metre quadrats that were later used as experimental plots, to obtain densities specific to the study area. Farmer density estimates were obtained from 15 plots on the reef crests of two reefs.

Benthic communities inside and outside farmer territories

Twenty individuals of each species (*Plectroglyphidodon lacrymatus* and *Pomacentrus adelus*) were observed in order to map territories, identify undefended areas, and to compare with adjacent undefended areas so as to examine the potential of

their influence on benthic communities. Each individual was observed for 30 minutes, the perimeter of their territory was marked with lead weights, and a chain was laid around the territory circumference. Territory area was estimated by using the formula for calculating the area of an ellipse with the same circumference as the territory. Territory size measurements multiplied by the densities of each species allowed the estimation of how much space farmers occupied on the reef crest.

Algal scrapings from small plots (25 cm²) were taken randomly from within the territory and from adjacent undefended areas. The samples were fixed and preserved in 10% formalin and examined under a dissecting microscope using a grid with 1 cm squares over a Petri dish. The identity of the algae under 45 random intercepts was recorded, providing an estimate of the percent cover of different algal types. Algae were routinely identified to genus level, and, where possible, to species level (Table 1). Percent cover values inside territories were compared to those outside for each farmer species using analysis of variance (ANOVA). The taxonomic composition inside and outside territories was analysed using multivariate analysis of variance (MANOVA) and displayed by Principal Components Analysis (PCA).

Forager exclusion and farmer removal experiment

An orthogonal combination of experimental removals of farmers and emergent forager exclusion fences was used to separate the effects of the two groups and quantify their interaction (Figure 1). The treatments also included a fence control to account for any direct effect of fences on algal communities. All treatments were applied to six replicate 4 m² experimental plots on the reef crest.

Emergent fences were constructed for the fence control (Treatment 1) and large holes were cut in all four sides to allow access to all herbivores. The unmanipulated

control (Treatment 2) consisted of unfenced plots marked at the corners. A comparison of treatments 1 and 2 measures the potential effect of the fence artefact alone (Figure 1).

Treatment 3 consisted of farmer removal without a fence. The effect of the experimental removal of farmers was measured by a comparison of treatments 3 and 2 (Figure 1). In the literature, such removals are used to measure the effect of farmer territoriality on algal communities (Mahoney 1981; Hourigan 1986). Comparing treatments 2 and 3 measures all potential effects of farmers, including their own feeding or farming activities, plus additional effects due to the influence of the farmers on foragers. These effects can only be distinguished by additional treatments in which foragers are excluded.

Emergent fences to exclude all foragers were constructed for treatments 4 and 5 (Figure 1). Resident farmers were left at natural densities in treatment 5, but were removed in treatment 4. As farmers are absent in both treatments 3 and 4, this comparison measures the effects of foragers, without the potentially confounding effects of farmers. As treatments 4 and 5 only differ with respect to the presence of farmers, a comparison of these treatments measures the direct effects of farmers without confounding effects of foragers.

The potential effect of farmers that could be explained only by defending areas from foragers was measured by the statistical interaction between the forager exclusion and the farmer removal treatments. That is, if farmer removal has an effect on algal communities when foragers have access (treatments 2 vs. 3), but not where they are excluded (treatments 4 vs. 5), this can be attributed to defence. All treatments were compared using MANOVA, with a priori planned comparisons for all between-treatment comparisons.

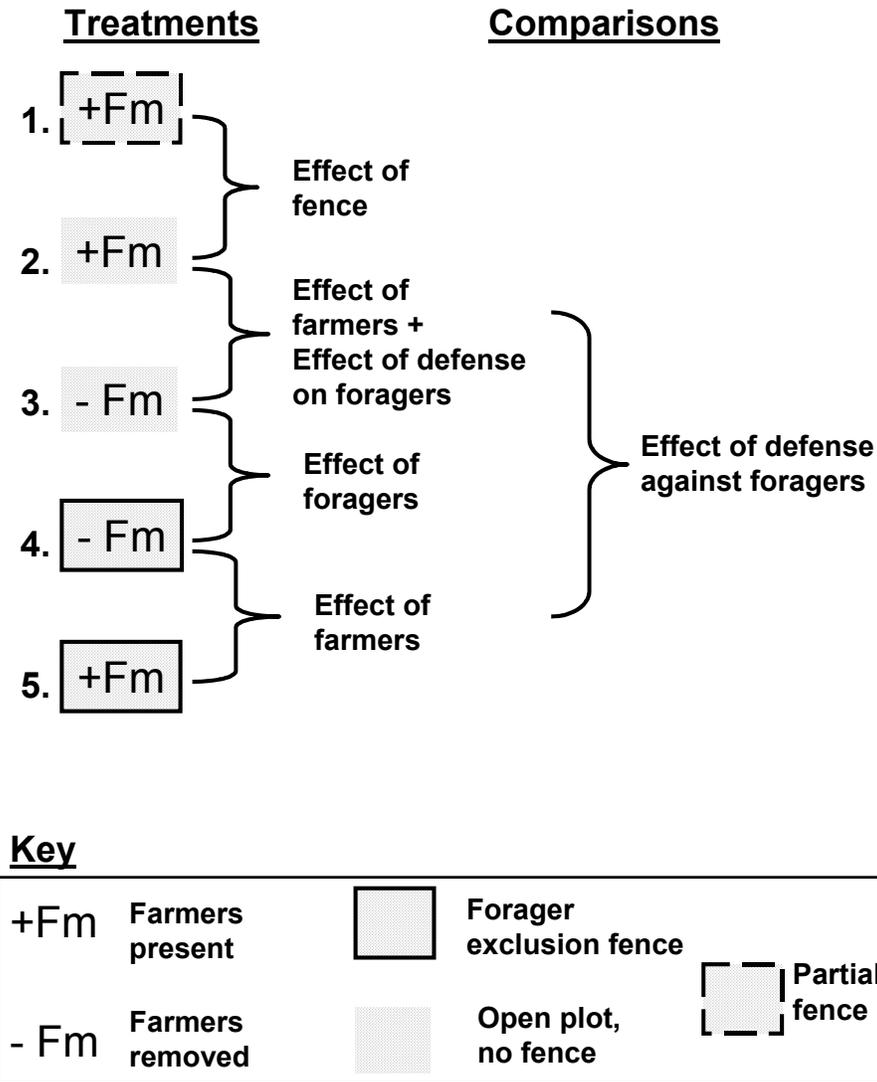


Figure 1. Experimental design and planned comparisons to distinguish the effects of farmers and foragers and their interactions on algal and coral communities. ‘Fm’: Farmers, ‘Fg’: Foragers.

Experimental protocol

In April 2001, I established a series of 4 m² plots at least 5 m apart along the reef crest, where the substratum was submerged at all phases of the tide and the maximum tidal height was 1 m above the substratum. This allowed me to use open-top fences rather than cages, to minimize the potential effects of shading. To reduce the potential for spatial confounding, the six replicates of each of the five different treatments were alternated in sequence along the reef crest.

Exclusion and partial fences were supported by 1.3 m lengths of steel reinforcement bar that were hammered in and cemented at the corners and halfway along each side of the square. Wire fencing mesh (8 m lengths; mesh size 1 cm²) were attached to the reinforcement rods with cable ties and thin wires. The full fences were sealed at the bottom with chicken wire and fencing staples. For the partial fences, panels of mesh approximately 1.5 m long and 0.6 m high were cut out on each side. The fences were cleaned weekly.

All herbivorous fish in the plots were counted before the construction of the fences and again at the end of the experiment 2 months later. Fish counts were used to determine the effectiveness of the fences in excluding foragers, and to assess the use of partial fences and open plots by foragers. All *Plectroglyphidodon lacrymatus* and *Pomacentrus adelus* were removed from treatments 3 and 4 immediately after the fences were established, and immigrating farmers were removed as soon as they were noticed during the duration of the experiment.

To estimate the percent composition of the benthic communities a grid with a 1 cm mesh size was strung onto a 1 m² quadrat. The quadrat was sequentially placed in each of the 4 m² of the plot. The benthic organism present under each of 25 random

points was recorded, giving 100 random points for the whole plot to provide an estimate of percent cover. The benthic categories included thin turf (<3 mm thick), thick turf (>3 mm thick), microalgae (blue-green algae and diatoms), encrusting coralline algae, macroalgae classified to genus, sponges, sand and live, bleached or dead coral classified by growth form. The benthos was sampled before the fences were established, 2 weeks after their construction and at the end of the experiment 2 months later.

Algal turf was collected from each plot to quantify the effects of the treatments on the algal community composition and their biomass. Before the construction of the fences, five randomly selected 5 cm² quadrats were scraped in each plot with a paint scraper and the algae were collected into a stocking using a suction airlift. The samples were fixed in 10% formalin and examined under a dissecting microscope using a grid with 1 cm squares over a Petri dish. The identity of the algae under 45 random intercepts was recorded, providing an estimate of the percent cover of different algal types. All algae were identified to genus or species level where possible (Table 1).

Results

Farmer territories: space occupation and benthic communities

The reef zone chosen for the experiment supported a diverse community of foragers and farmers (Figure 2). It was a zone clearly dominated by farmers, as their densities were approximately seven times higher than those of foragers (2-tailed t-test: $t_{(16)} = 2.682$, $p < 0.05$). *Plectroglyphidodon lacrymatus* was the farmer found in highest densities, followed by the smaller and less aggressive *Pomacentrus adelus* (Figure 2). Using the territory measurements and density estimates, I calculated that 87.4 +/- 4.3%

of the substratum in a 10 m band behind the reef crest was occupied by *Pl. lacrymatus* and *Po. adelus* territories.

There were significant differences in algal community structure inside and outside the territories of *Pl. lacrymatus* and *Po. adelus* (MANOVA results for Pillai's Trace $F_{(d.f.=20)} = 4.734$, $p < 0.05$). Coralline algae dominated outside territories, but all other taxa were more abundant inside territories, especially *Laurencia* spp., *Polysiphonia* spp., microalgae, pooled filamentous algae and corticated red algae. Principal components analysis showed that there was some overlap between communities outside territories and those inside *P. adelus* territories, but communities inside *P. lacrymatus* territories formed a distinct group, defined by high abundances of *Amphiroa* spp., microalgae and corticated red algae (Figure 3). The proportion of substratum covered in turfing algae inside territories of *P. lacrymatus* (77.83% \pm 2.8 S.E.) was significantly higher than adjacent undefended areas (61.5% \pm 5.1; $t_{(d.f.=18)} = 2.77$; $P < 0.05$). In contrast, the percent cover of turf inside territories of *P. adelus* (68% \pm 6.1 S.E.) was not significantly different ($t_{(d.f.=18)} = 0.397$; $p > 0.05$) from the mean cover in adjacent areas.

Validation of the experiment

A comparison of benthic community structure in partially fenced plots with unfenced plots indicated that there were no effects directly attributable to the presence of the fence, either from field estimates of percent cover or laboratory analysis of algal turf composition (Table 2).

Repeated censuses of experimental plots showed that farmers were successfully prevented from migrating into removal plots and foragers were excluded from fully fenced areas. In plots where farmers had been removed, their numbers were

reduced from an average of 9.833 (± 0.6 S.E.) to 0, and the only farmers that were subsequently counted and removed in these plots were recruits and juveniles (2.16 ± 0.3 S.E.). The differences in the average number of foragers between partially fenced plots before the establishment of the fences (2.33 ± 0.61 S.E.) and after (2.66 ± 0.56 S.E.), when compared to open control plots (before: 4.0 ± 0.93 S.E., after: 3.16 ± 1.22 S.E.), were not significant, indicating that of partial fences did not cause a change in the use of these plots by foragers (2-way ANOVA, interaction of Time x Treatment, $F_{(d.f.=2)} = 0.48, p > 0.05$).

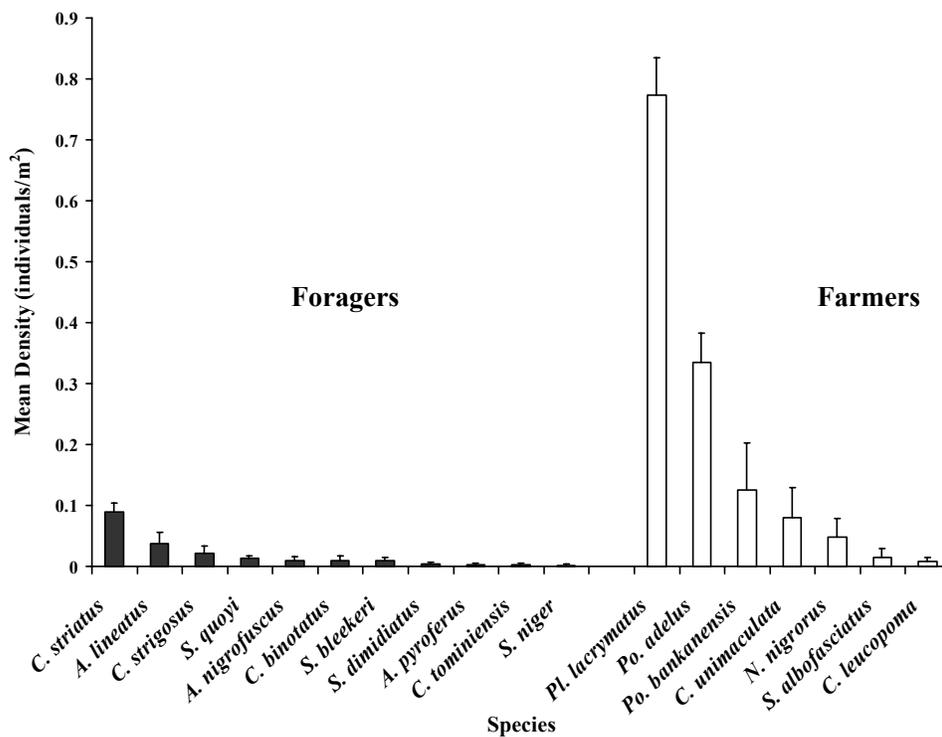


Figure 2. Densities of foragers and farmers on the study reefs, taken from around the crest area from 0 to 2 metres in depth. Solid black bars represent mean densities of foragers, and white bars represent mean densities for farmers. Genus names for foragers are: *C.*: *Ctenochaetus*, *A.*: *Acanthurus*, *S.*: *Scarus*. Genus names for farmers are: *Po.*: *Pomacentrus*, *Pl.*: *Plectroglyphidodon*, *C.*: *Chrysiptera*, *N.*: *Neoglyphidodon*, *S.*: *Stegastes*. Error bars = 1 S.E.

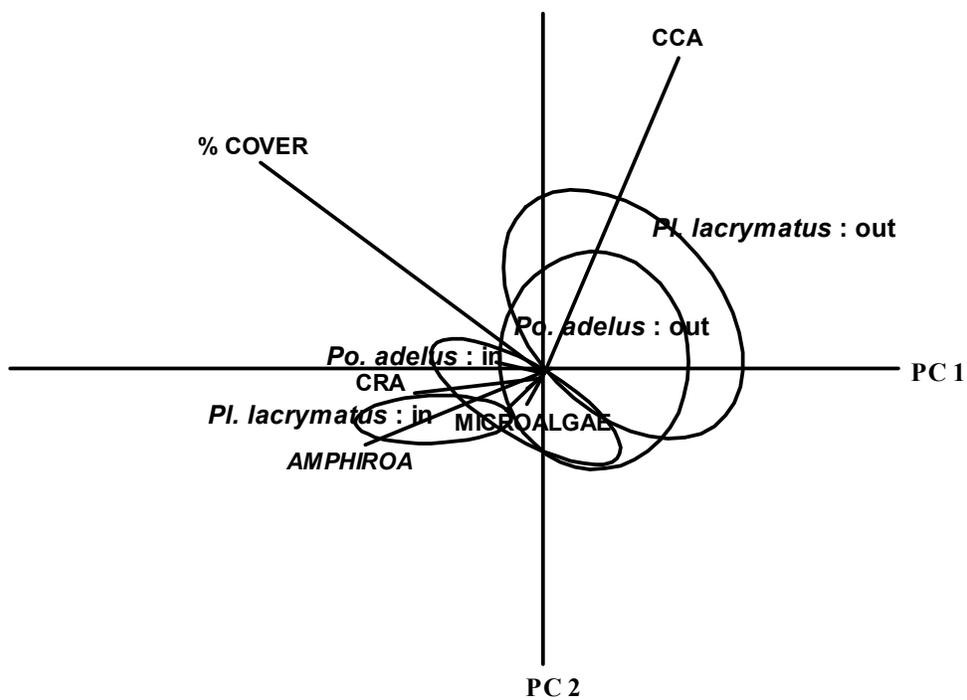


Figure 3. Principal Components Analysis (PCA) of the structure of benthic communities inside and outside territories of *Pomacentrus (Po.) adelus* and *Plectroglyphidodon (Pl.) lacrymatus*. Principal Component (PC)1 explains 12.65% of the variance, PC2 describes 7.56%. The cumulative % explained by PC1 and PC2 = 20.21%. CRA: Corticated red algae. CCA: Crustose coralline algae. Benthos inside *Pl. lacrymatus* territories forms a group separated from the rest along the vectors of increased microalgae, corticated red algae and *Amphiroa* spp.

Table 1. Summary of taxa present in each functional group.

Functional group	Genus	Species	
Microalgae	<i>Hormothamnion</i>		
Filamentous algae	<i>Champia</i>	<i>parvula</i> <i>vieillardii</i>	
	<i>Callithamnion</i>		
	<i>Ceramium</i>	<i>macilentum</i> <i>sympodiale</i>	
	<i>Spermothamnion</i>		
	<i>Heterosiphonia</i>	<i>crispella</i>	
	<i>Herposiphonia</i>	<i>secunda</i> f. <i>secunda</i> <i>secunda</i> f. <i>tenella</i>	
	<i>Polysiphonia</i>	<i>infestans</i> <i>scopulorum</i> <i>upolensis</i>	
	Corticated red algae	<i>Pterocladia</i>	<i>caerulescens</i>
		<i>Gelidiella</i>	<i>acerosa</i> <i>pannosa</i>
		<i>Wurdemannia</i>	<i>miniata</i>
		<i>Hypnea</i>	<i>cervicornis</i> <i>pannosa</i> <i>spinella</i>
		<i>Gelidiopsis</i>	<i>intricata</i>
		<i>Coelothrix</i>	<i>irregularis</i>
<i>Lomentaria</i>		<i>corallicola</i>	
<i>Chondria</i>		<i>dangeardii</i> <i>simpliciuscula</i>	
<i>Laurencia</i>		<i>carolinensis</i> <i>crustiformans</i> <i>implicata</i> <i>perforata</i> <i>succisa</i>	
<i>Acanthophora</i>		<i>spicifera</i>	
Fleshy macroalgae		<i>Gracilaria</i>	<i>arcuata</i>
		<i>Turbinaria</i>	<i>ornate</i>
		<i>Padina</i>	<i>tenuis</i>
	<i>Dictyota</i>		
	<i>Hypoglossum</i>	<i>caloglossoides</i>	
	<i>Haloplegma</i>	<i>duperreyi</i>	
	<i>Haraldiophyllum</i>	<i>sinuosum</i>	
Erect calcified algae	<i>Amphiroa</i>		

Table 2. Summary of the effects of each comparison. Effects on benthic categories were obtained with the *in situ* benthic surveys, while effects on specific taxa result from the laboratory analyses of collected algal turf. The last two benthic categories relate to corals of different morphology. 0 is no effect, ↑ is a significant increase in % cover, and ↓ represents a significant decline in % cover. The arrows are doubled in cases where the effect is large. In cases where there was a significant difference in the rate of change in % cover, this is symbolized by an arrow for the direction of the change, and r.o.i. for ‘rate of increase’ and r.o.d. for ‘rate of decline’.

	Fence	Farmer removal	Forager exclusion	Farmer (forager exclusion)	Defence
Benthic categories					
Microalgae	0	↑ then ↓	↑↑ then ↓	0	0
Thin turf (<3mm)	0	0	↓	0	0
Thick turf (>3mm)	0	0	↑	0	0
Fleshy macroalgae	0	0	↑	0	0
<i>Acropora</i> (bushy)	0	0	↓	0	0
Encrusting (bleached)	0	↑	↓	0	0
Specific taxa/groups					
<i>Ceramium</i>	0	↑	↓ (r.o.i)	0	0
<i>Polysiphonia</i>	0	0	0	↑	0
Filamentous algae	0	↓ (r.o.i.)	0	0	0
<i>Hypnea pannosa</i>	0	0	↑	↑↑	0
Corticated red algae	0	0	0	↑	0
<i>Padina</i>	0	↑	↑↑	0	0
<i>Amphiroa</i>	0	0	0	↓	0

Effect of farmer removal

The removal of farmers from open plots (comparison of treatments 2 and 3) resulted in a number of changes in algal community structure (Figure 4). A microalgal bloom that took place in the unmanipulated open plots was not reflected in plots where farmers had been removed (Figure 4a). Farmer removal also influenced the cover of bleached corals with an encrusting growth form. The small increase in the cover of

bleached encrusting corals was statistically significant, and was deemed biologically significant in view of the short time frame of the experiment (Figure 4b). Within the algal turf samples, delicate filamentous red algae of the genus *Ceramium* increased when farmers were removed (Figure 4c). This taxon was pooled with other filamentous red algae, and the removal of farmers resulted in slowing down the rate of increase in filamentous algal cover (Figure 4d). The foliose macroalgae *Padina* spp. (Figure 4e) began to increase in cover as soon as farmers were removed.

Effects of foragers (in absence of farmers)

The exclusion of foragers had the most widespread effects on algal community structure (Treatment 3 vs. Treatment 4) (Figure 5). The microalgal bloom already observed in open plots (Figure 4a) was significantly greater when foragers were removed and, at its peak, microalgae covered around 20% of substrata inside the fences (Figure 5a). Thin filamentous turf appeared to decline in cover (Figure 5b), but the rapid growth of algal turfs protected from foragers resulted in their inclusion in the thick filamentous turf category, which increased significantly (Figure 5c). The cover of fleshy macroalgae increased significantly when foragers were excluded, and concurrently there were small but statistically significant declines in the cover of some corals, namely *Acropora* colonies with bushy morphologies (Figure 5e), and bleached encrusting corals (Figure 5f).

Interestingly, the cover of the delicate rhodophyte *Ceramium* spp. was able to grow significantly higher in the presence of foragers than in their absence (Figure 5g). It is possible that this taxon represents an early successional species that is only able to persist when free space is available. In the forager exclusion fences, the growth of mid-successional corticated rhodophytes, such as *Hypnea pannosa* (Figure 5h), and foliose

macroalgae, such as *Padina* spp. (Figure 5i), may have inhibited the growth of *Ceramium* spp.

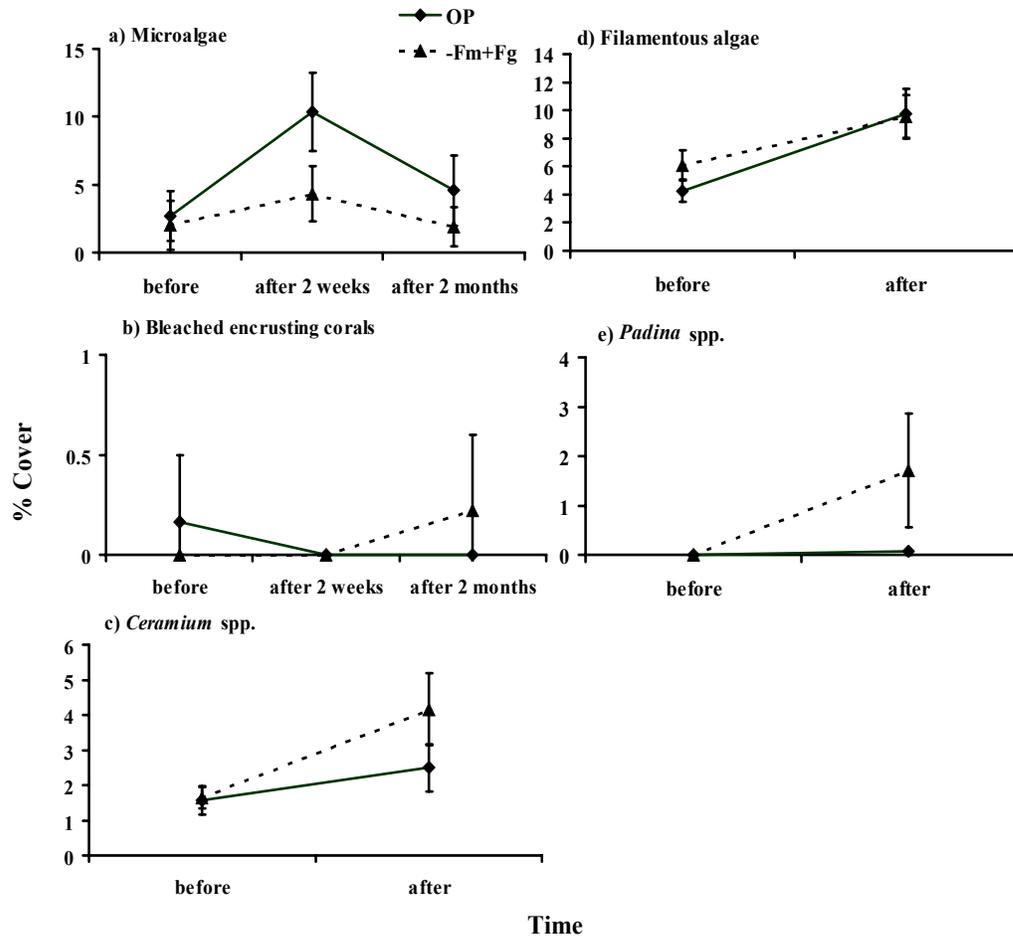


Figure 4. The effects of farmer removal on the benthic and algal turf communities. Treatment 3 (farmer removal) is compared with treatment 2 (control). Only categories exhibiting statistically significant differences are plotted. Benthos sampled *in situ* by point intercept were sampled three times (before – after 2 weeks – after 2 months), while algae scrapings were examined twice (before – after). Note differences in the y-axes. ‘OP’: Open Plots, ‘Fm’: Farmers, ‘Fg’: Foragers. Error bars = 1 S.E.

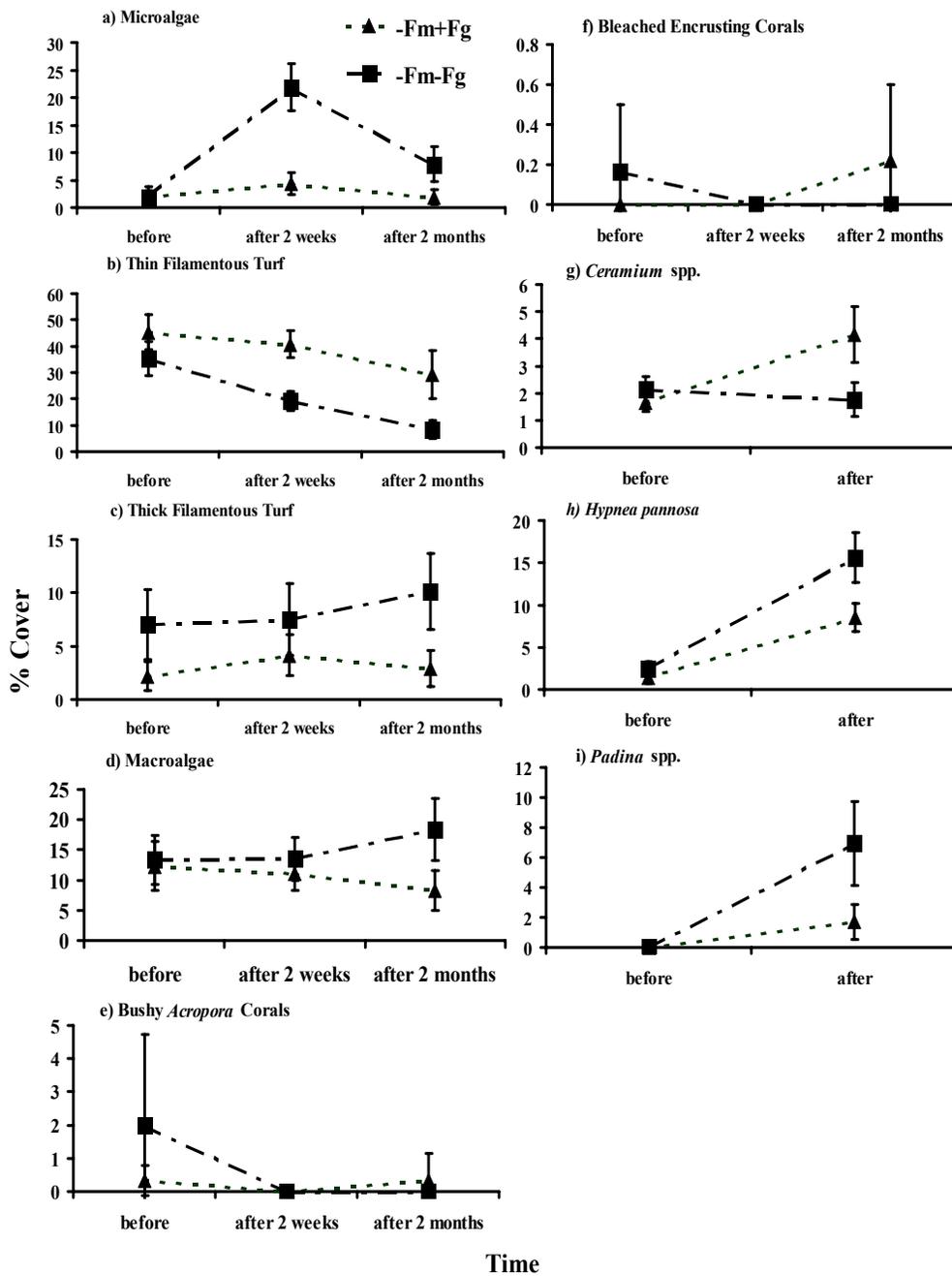


Figure 5. Effects of foragers on % cover of benthic organisms where farmers have been removed. Treatment 4 (forager exclusion) is compared with treatment 3 (foragers not excluded). ‘Macroalgae’: Fleshy macroalgae. Benthos sampled *in situ* by point intercept were sampled three times (before – after 2 weeks – after 2 months), while algae scrapings were examined twice (before – after). ‘Fm’: Farmers, ‘Fg’: Foragers. Note differences in the y-axes. Error bars = 1 S.E.

Effects of farmers (in absence of foragers)

The direct effects of farmers, in the absence of foragers, were only detectable on the scale of algal turf scrapings. Comparing fenced plots without (treatment 4) and with (treatment 5) farmers provided a clear indication that farmers directly affect the algal turf composition. The cover of *Polysiphonia* spp. increased significantly inside forager exclusion fences, but only when farmers were present (Figure 6a). On a larger scale, the corticated rhodophyte *Hypnea pannosa* grew to cover around 35% of fenced substrata where farmers were present, compared to only 15% of plots in which farmers were removed (Figure 6b). When *H. pannosa* was pooled with all other corticated red algae present (Table 1), the resulting difference between fenced plots with and fenced plots without farmers was almost 50% and 30%, respectively (Figure 6c). In contrast, the presence of farmers appeared to be detrimental to the cover of *Amphiroa* spp., which increased significantly in the fenced removal plots and remained stable in the fenced plots where farmers were present (Figure 6d).

Effects due to farmer defence against foragers

If farmers have an effect on benthic communities as a result of excluding foragers, treatments 2 and 3 (the effects of farmer removal) should differ markedly in comparison to the difference between treatments 4 and 5 (the effects of forager exclusion). There was no statistical interaction between the two comparisons, suggesting that the changes to benthic communities caused by the activities of farmers were not significantly affected by the absence of foragers. In other words, the effects on benthic communities due to farmer defence against foragers were minimal.

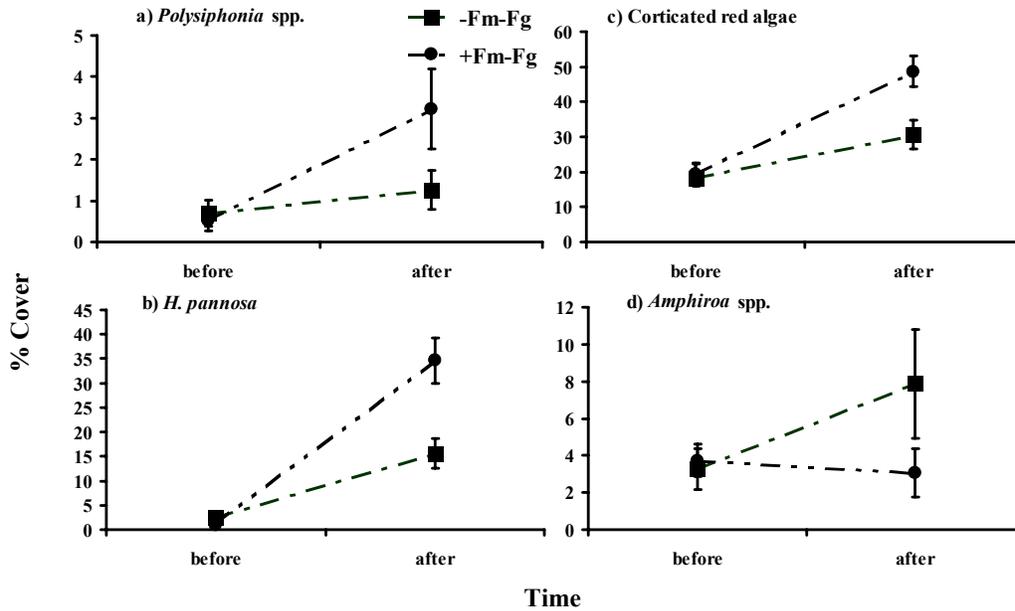


Figure 6. Effects of farmers on algal turf communities, where foragers have been excluded. Treatment 5 (farmers present) is compared with treatment 4 (farmers removed). ‘Fm’: Farmers, ‘Fg’: Foragers. Note differences in the y-axes. Error bars = 1 S.E.

Discussion

Experimental exclusion of foragers (Carpenter 1986; Lewis 1986) and removals of farmers (Mahoney 1981; Hourigan 1986) have independently shown that both groups can have dramatic effects on benthic community structure. However, the relative importance of the two groups and the interaction between them have not previously been determined. In this experiment, the orthogonal combination of the experimental removal of territorial farming species and the fence exclusion of foragers provides a

resolution to this problem. The experiment showed that the two behavioural groups of herbivorous fishes exhibit quantitative and qualitative differences in their impacts on coral reef habitats in Kimbe Bay, Papua New Guinea.

Despite the high density of farmers on the reef crest and the high proportion of space they occupy (~88%), foragers had a greater overall impact on benthic algal assemblages than farmers. A small and qualitatively different effect of farmers was also detected (by comparing the farmer removal treatment with the control in the two treatments that had foragers excluded). These effects can be attributed directly to the farmers and cannot be explained by forager exclusion.

Unexpectedly, there was no measurable effect of farmers' aggressive defence on the benthic communities within their territories, with the difference between farmer removals and controls being the same, regardless of whether foragers had access or not. Removing farmers in the situation where foragers had access did not lead to a rapid reduction in turf cover, as previously noted in farmer removal experiments (Mahoney 1981; Hourigan 1986). In fact, some algal taxa increased in cover, suggesting that foliose macroalgae and even some filamentous algae are suppressed by farmers. Although this is surprising, it provides an explanation for the strong effect of foragers in a farmer-dominated reef zone. These farmers appear to be relatively ineffectual in excluding foragers from grazing in their territories, although they do appear to be able to alter algal communities by other means.

Exclusion of foragers resulted in rapid and substantial effects, regardless of whether farmers were present or not, supporting the view that these grazers are functionally important on coral reefs (Steneck 1988; Horn 1989; Bellwood and Choat 1990; Russ and McCook 1999). Foragers clearly reduce the biomass of dominant macroalgae and turfing algae, prevent microalgae from settling, and increase the space

available for acroporid corals and coralline algae. The effects on corals were small but noteworthy due to the short timeframe of the experiment. These findings are not new, as large foraging fish have long been implicated in suppressing macroalgal biomass and in facilitating the competitive advantage of hard corals (Hughes 1994; McCook 1999). However, the effects of exclusion of foragers in this case was the same, regardless of whether farmers were present or not, indicating that farmers do not appear to play a major role in modifying the effects of foragers or displacing their activities. In contrast to foragers, the effects of farmers on algae were species-specific and only detected by examining differences in the composition of algal turfs. These results support the hypothesis that farmers directly cultivate or benefit certain food algae (Irvine 1980; Lobel 1980; Montgomery 1980b; Hata and Kato 2002). Filamentous and corticated algae known to be an important component of the diet of farmers, e.g. *Polysiphonia* (Montgomery 1980b; Jones 1986), declined when farmers were removed and foragers were excluded. Conversely, a calcified unpalatable taxon (*Amphiroa*) increased.

Surprisingly, the effects of farmers that could be attributed to the aggressive exclusion of foragers from their territories were minimal in this system. This contrasts with previous studies where differences inside and outside territories have been attributed to the ability of farmers to reduce grazing pressure by foragers (Sammarco and Williams 1982; Hixon and Brostoff 1983; Gleason 1996; Hixon and Brostoff 1996). Here, the effect of farmer removal was not significantly altered by the presence of forager exclusion fences and could only be attributed to other farmer activities.

One possible explanation for the difference between these results and those in the literature is that the farmer species dominating the reef crest habitat in Papua New Guinea (*Pl. lacrymatus* and *Po. adelus*) are less effective in excluding schools of foragers than others that have been studied. Although farmers may increase algal

productivity within their territories (Klumpp et al. 1987; Russ 1987; Ferreira et al. 1998), this may be offset by increased incursions by foragers. The direct efforts of farmers in promoting palatable algal species with high growth rates within the boundaries of their territories (Klumpp et al. 1987) may enhance the overall yield of algae to foragers (Russ 1987). The results of this study suggest that farmers may play an important role in enhancing reef productivity and influencing the feeding patterns of foragers, but by facilitation rather than exclusion. Farmer aggression is probably circumvented by schooling of foragers (Robertson et al. 1976). The terms forager and farmer are umbrellas for a wide range of species with different diets, feeding modes and abilities to impact on coral reef habitats. Clearly, there is considerable variation among species in both groups, with herbivorous and detritivorous feeding prevalent in both groups (Wilson and Bellwood 1997; Wilson et al. 2003). With further refinement of experimental techniques, the functional importance of individual species may be determined. More sophisticated experimental designs will also be required to isolate the exact mechanisms by which farmers cultivate specific algae.

These results support prevailing views that foragers have a major impact on coral reefs, and that farmers cultivate selected algae, but challenge the hypothesis that farmers have a strong influence on habitat structure by reducing disturbance by foragers. Instead, this study provided a testable hypothesis that farmers can directly enhance the abundance and productivity of particular algae, and that these increased resources are exploited by both resident farmers and foragers, because farmers do not appear to be able to maintain exclusive access to their resources.

CHAPTER 6: THE INTERACTION BETWEEN FARMERS AND FORAGERS AND THEIR INFLUENCE ON ALGAL SUCCESSION ON CORAL REEFS

Introduction

Differences between farmer territories and adjacent areas have been attributed to the different grazing rates of foragers and farmers (Hixon and Brostoff 1996), or active ‘management’ of algal turf inside territories by farmers (Chapter 5, Lassuy 1980; Hata and Kato 2002; 2003). Farmers can modify succession through a number of different mechanisms. The activities of farmers can inhibit succession, halting it at a stage of high diversity (Hixon and Brostoff 1996), or divert it, leading to a monoculture of preferred food algae (Hata and Kato 2003). Not only can they modify the grazing intensity of foragers inside territories (Hixon and Brostoff 1996), but they can also ‘weed’ undesirable algae from their territories (Lassuy 1980; Hata and Kato 2002), selectively consume preferred species (Klumpp et al. 1987; Jones 1992), and fertilize algae by defecating on algal farms (Polunin and Koike 1987; Klumpp and Polunin 1989; Ferreira et al. 1998). Most of these mechanisms remain untested, and there is little conclusive evidence to suggest that one mechanism is more important than the others.

Only a few studies have researched the natural trajectories of succession in benthic communities surrounding farmer territories. In contrast to the inhibition of succession by farmers, foragers have been shown to divert succession through heavy grazing, leading to low-diversity communities of grazer-resistant species. Experimental evidence for the mechanisms by which foragers affect succession has been limited to environments subject to high grazing pressure by foragers (Hixon and Brostoff 1996). The algal community only reached relative successional maturity inside herbivore

exclusion cages outside territories, where grazing was virtually absent (Hixon and Brostoff 1996). In order to fully distinguish the effects of both foragers and farmers, and the extent of their interactions, cages need to be employed both inside and outside territories.

It is possible that farmers select specific locations for territories, where the development of benthic communities naturally differs from surrounding areas. Site selection has been demonstrated for some species of farmers (Bay et al. 2001), but the effect this has on benthic communities and their development inside territories has not been investigated. Only one study measured succession in caged territories to identify whether it was the location of the territory or the activities of the farmers (in this case, *Stegastes nigricans*) that caused the observed patterns of succession (Hata and Kato 2003). This recent study found that it was not the position of the territories on the reef, but the access of the resident farmer to the substratum that brought about the typical monoculture found inside *S. nigricans* territories.

Of the different possible mechanisms affecting algal communities in farmer territories, the aggressive exclusion of other grazing fishes has received the most attention. It is commonly accepted that the exclusion of foragers decreases grazing rates inside territories, leading to higher algal turf biomass and a change in the algal community structure (Sammarco and Carleton 1981; Hixon and Brostoff 1983; Sammarco 1983). This assumption implies that farmers are highly successful at excluding foragers, and that farmer grazing rates in their territories are low. Two findings challenge this assumption. Firstly, it was recently established that direct farming activities (selective feeding and weeding) were the primary mechanism by which some farmer species modified algal assemblages inside territories (Chapter 5, Hata and Kato 2002). Secondly, grazing rates inside farmer territories can be as high, or

higher, than those occurring in surrounding areas (Russ 1987; Booth 1998). Exclusion cages have been shown to successfully inhibit grazing by foragers; it is unclear whether farmers also represent effective forager exclusion treatments.

Caging experiments offer a successful way to distinguish between the mechanisms that can modify benthic communities on coral reefs (Carpenter 1986). However, to date no study has been designed to isolate the effects of farmers and foragers, and to evaluate the effect of their interactions on patterns of algal succession on coral reefs. In this study, cages were combined with settlement tiles both inside and adjacent to farmer territories to separate the different mechanisms affecting succession. The following questions are addressed:

1. What are the patterns of succession inside and outside farmer territories?
2. How do foragers influence succession outside farmer territories?
3. How do the direct activities of farmers affect succession inside territories?
4. Is succession in farmer territories affected by their location? That is, are patterns of succession inside farmer territories independent of the activities of farmers and foragers?
5. Are the effects of forager exclusion by farmers different from the effects of forager exclusion by a cage?

Materials and Methods

Study site and species

The experimental evaluation of succession was conducted at Nelly Bay, Magnetic Island (19°17S, 146°86E), from December 2002 to December 2003.

Experimental plots were established along the reef crest, where there is an extensive population of *Stegastes apicalis*. In this habitat, *S. apicalis* is the dominant farmer, aggressively defending territories of approximately 1 m², in which the algal turf is visually distinct from surrounding areas. Large stands of *Sargassum* spp. or patches of high live coral cover characterize the benthos adjacent to the territories. Foragers occur in low densities on the reef crest (< 0.02 individuals/m², Ceccarelli, unpubl. data) and include primarily the scarids *Scarus rivulatus* and *Sc. ghobban*, the siganids *Siganus doliatus* and *Si. argenteus*, and the acanthurids *Naso unicornis* and *Acanthurus blochii*.

Territoriality in *Stegastes apicalis*

To establish the rate of incursion by other fish into *Stegastes apicalis* territories, 25 focal territories were chosen randomly and the resident farmers were observed for 15-minute periods. During the observation period, the number and identity of all fish swimming into the *S. apicalis* territory were recorded. I also recorded rates of aggression, in the form of attacking behaviour, and the identity of the attacked fish. Fish were then grouped into the following categories: conspecifics, other pomacentrid fish (including both other farmers and opportunistic omnivores such as *Abudefduf* spp.), foragers and Labridae (wrasses; potentially egg predators).

Experimental design

I used a fully orthogonal experimental design to separate the effects of foragers and farmers, and to distinguish between direct management of farmers and territory location, on the successional composition of the benthic community. The experimental

design included caged and uncaged treatments both inside and outside *S. apicalis* territories. It also included control treatments for the effects of the cage artefacts on benthic communities both inside and outside farmer territories (Figure 1). Five replicates of each treatment were allocated randomly to and around farmer territories on the reef crest.

Pair-wise comparisons of the treatments enabled seven relevant hypotheses to be tested.

1. Comparing uncaged tiles outside territories (treatment 1) with uncaged tiles inside territories (treatment 2) determined the successional patterns inside and outside territories, without isolating any specific mechanisms. Differences could be due to grazing activities of both groups and possible farming activities of farmers, the interactions of foragers and farmers, and the effects of territory location. This comparison was designed to test the hypothesis that succession differs inside and outside farmer territories.
2. Comparing uncaged tiles outside territories (treatment 1) with caged tiles outside territories (treatment 3) measured the effects of foragers alone on algal succession. Here I test the hypothesis that grazing by foragers alters the development of algal communities outside farmer territories.
3. Comparing uncaged tiles inside territories (treatment 2) with caged tiles inside territories (treatment 4) estimated the effects of farmer activities on the communities in their territories. This includes all potential farmer effects except fertilization, as this could potentially still occur on caged tiles inside territories. Therefore, this comparison tests the hypothesis that the feeding and weeding activities of farmers modify succession in their territories.

4. Comparing caged tiles outside territories (treatment 3) with caged tiles inside territories (treatment 4) allowed me to identify the a priori effects of territory location on the natural succession of benthic communities undisturbed by foragers or farmers. Here, I test the hypothesis that farmer territories are located in areas where succession naturally follows a different trajectory from surrounding areas.
5. Comparing uncaged tiles inside territories (treatment 2) with caged tiles outside territories (treatment 3) provided an estimate of how differently benthic succession progresses on tiles where foragers were excluded by farmers, compared with tiles where they were excluded by a cage. This comparison tests the hypothesis that farmers represent a different mechanism than simply forager exclusion.
6. Comparing uncaged tiles outside territories (treatment 1) with partially caged tiles outside territories (treatment 5) tested the effects of the cage artefact on the composition and succession of the benthic community outside territories.
7. Comparing uncaged tiles inside territories (treatment 2) with partially caged tiles inside territories (treatment 6) tested the effects of the cage artefact, other than the effect of excluding foragers, inside territories.

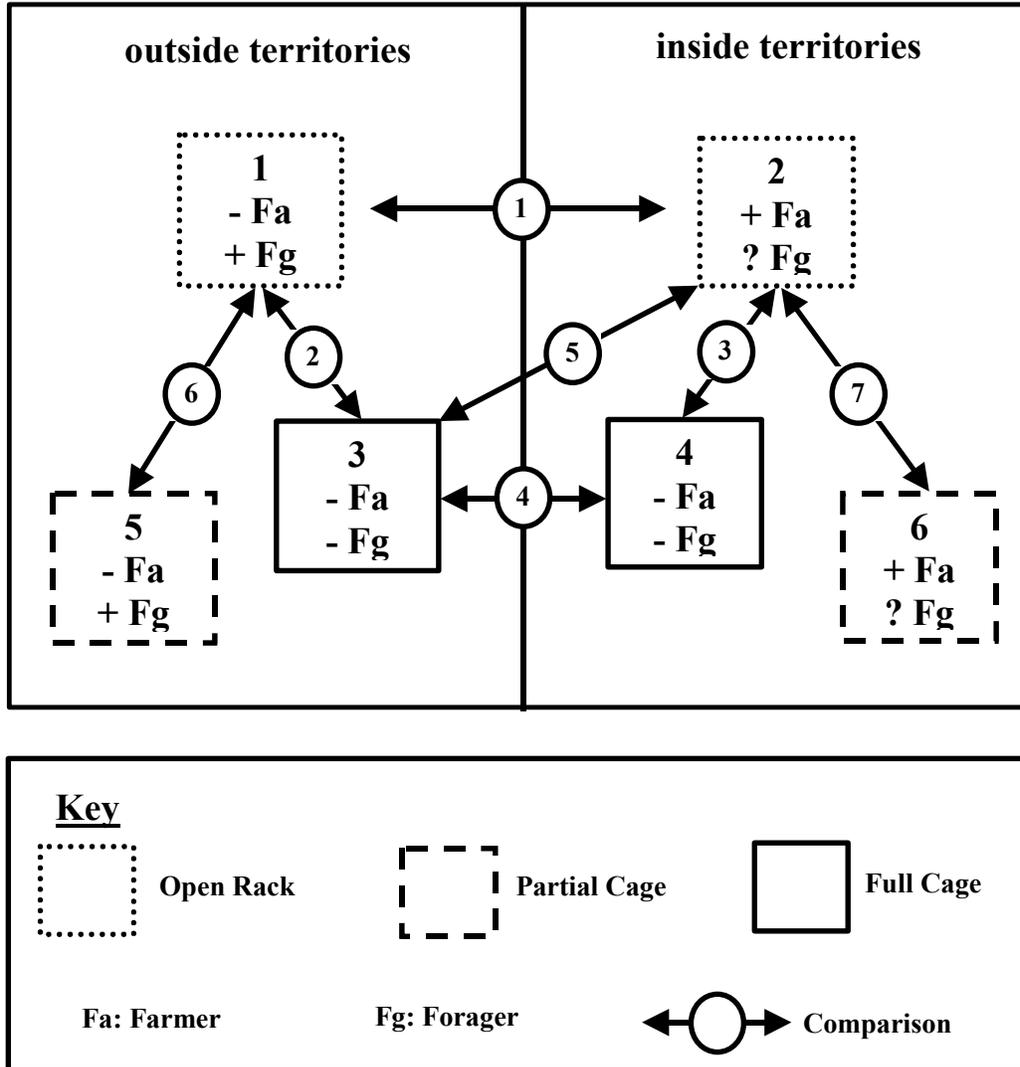


Figure 1. Sampling design for the tile experiment, showing the effects measured with each comparison between treatments.

Experimental protocol

Ten rugose ceramic tiles, 5 by 10 cm in area, were fixed to metal racks using stainless steel bolts and wing nuts, with rubber washers placed between the tile and both the base of the rack and the bottom of the wing nut (Figure 2). I then secured 30 metal racks to the reef substratum. Fifteen of these racks were placed inside randomly chosen *S. apicalis* territories, and 15 in nearby areas that were as similar as possible to *S. apicalis* territories in terms of elevation and exposure. Oyster mesh (16 mm mesh size) was tied around five randomly selected racks inside territories and five outside territories, completely enclosing the tiles. A further 10 racks (also 5 inside and 5 outside territories) were partially enclosed by the oyster mesh. The last 10 racks were left uncaged.

The tiles were sampled every 3 months over the year, resulting in four sampling occasions. At each sampling occasion, two tiles were removed from each rack, resulting in a sample size of 10 tiles per treatment per sampling occasion. The tiles were enclosed in clip seal plastic bags for transportation and frozen immediately. The tops of the tiles were sampled by scraping all benthos from the tile into a Petri dish, and using a 1 cm grid placed over the dish to randomly sample the benthos under each of 54 points. Taxa were identified to genus, and to species where possible. For the purposes of exploring succession on the tiles, algae were also summarized into functional groups (Table 1, Steneck and Dethier 1994).

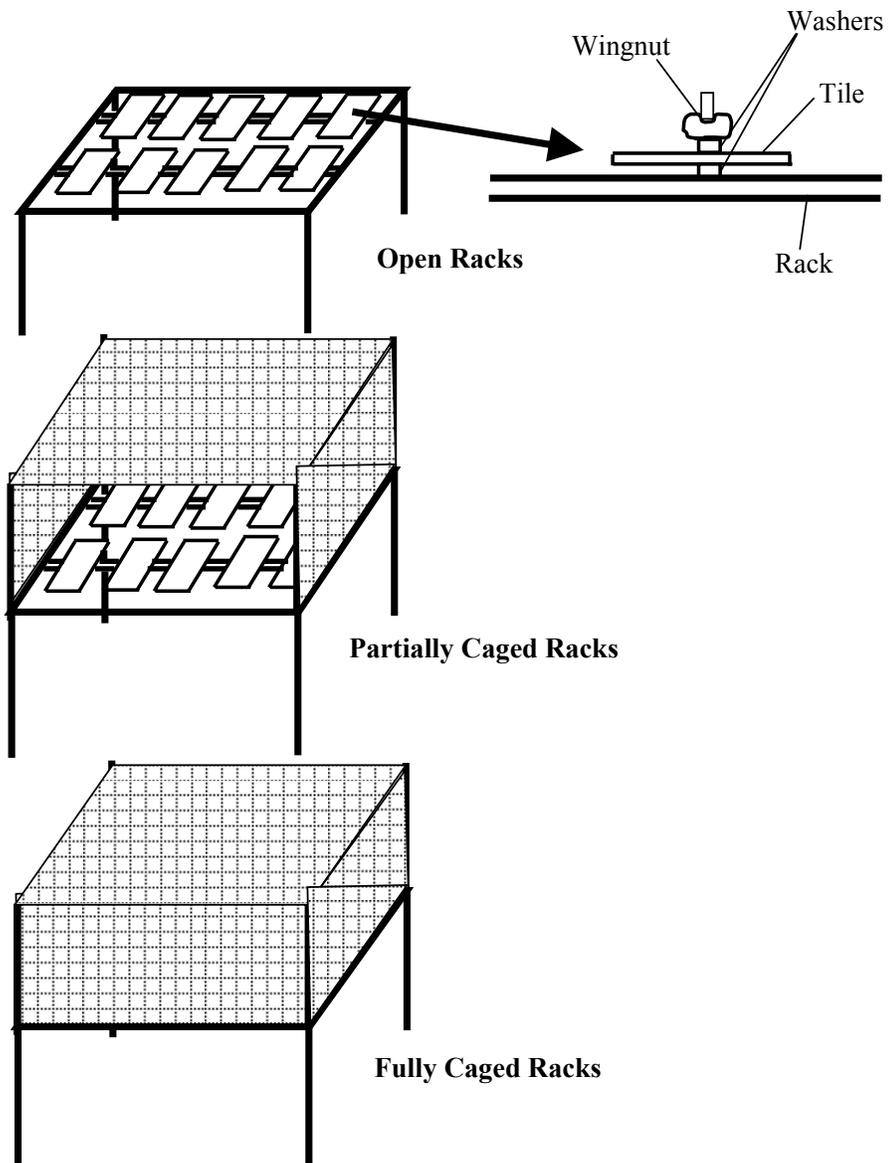


Figure 2. Diagram of the experimental racks, including the detail of how each tile was attached to the metal racks.

Table 1. Functional groups as used to classify algae in this study, adapted from Steneck and Dethier (1994). * Identified as ‘corticated macrophytes’ by Steneck and Dethier (1994). # Includes corticated foliose algae and leathery macrophytes (Steneck and Dethier 1994).

Algal functional group	Commonly found in Nelly Bay	
Microalgae	Diatoms and blue-green algae	
Filamentous algae	<i>Polysiphonia</i>	<i>herpa</i> <i>ferulacea</i> <i>infestans</i>
	<i>Herposiphonia</i>	<i>secunda</i>
	<i>Ceramium</i>	<i>macilentum</i> <i>sympodiale</i>
	<i>Callithamnion</i>	
	<i>Spermothamnion</i>	
	<i>Champia</i>	<i>parvula</i> <i>veillardii</i>
	<i>Tolypocladia</i>	
	<i>Leveiella</i>	
Corticated red algae*	<i>Laurencia</i>	<i>implicata</i> <i>succisa</i> <i>crustiformans</i>
	<i>Hypnea</i>	<i>pannosa</i> <i>spinella</i>
	<i>Gelidiopsis</i>	<i>scoparia</i> <i>intricata</i>
Fleshy macroalgae#	<i>Padina</i> <i>Dictyota</i> <i>Sargassum</i>	
Erect calcified algae	<i>Amphiroa</i> <i>Jania</i>	
Peyssonellidae	<i>Peyssonellia</i>	
Encrusting coralline algae	<i>Porolithon</i> <i>Neogoniolithon</i>	

Data analysis

Species richness, diversity (H') and evenness (J' , Zar 1984) were estimated for benthic communities on the tile tops. Multivariate ANOVA was used for community-level analyses, with a priori planned comparisons for each set of treatments as described in Figure 1. I chose a fully orthogonal design rather than repeated measures ANOVA due to the limited scope for the latter analysis to provide tests of between-subjects effects. In addition to graphical representation of significantly affected taxa, algae were summarized into functional groups for a graphical representation of successional change in the overall algal turf community.

Results

***Stegastes apicalis* aggression rates**

Foragers were effectively excluded from *S. apicalis* territories. No successful incursions occurred during any of the observation periods, and no aggression towards foragers was observed (Figure 3). Conspecifics and wrasses (Labridae) were attacked 100% of the time they entered *S. apicalis* territories, and other pomacentrid fish were often ignored, as demonstrated by the relatively low proportion of attacks towards them (Figure 3).

Comparison 1: Succession inside and outside farmer territories

The hypothesis that patterns of algal succession differ as a result of either farmer effects, forager effects or their interaction was supported. Different algal assemblages developed on uncaged tiles inside territories, where they were exposed to

farmer activities, from those that were found on uncaged tiles outside territories, which were exposed to the grazing and other activities of foragers (Figure 4). The temporal change in the benthic community varied between open tiles inside and outside territories (Pillai's Trace value 0.363, $F_{(d.f.=14)} = 8.358$, $p < 0.01$). In general, the community inside territories was ultimately dominated by early-succession filamentous red algae, which covered double the area inside territories than outside territories. Outside farmer territories, the assemblage developed more evenly, including over 20% fleshy macroalgal cover by the end of the experiment (Figure 4).

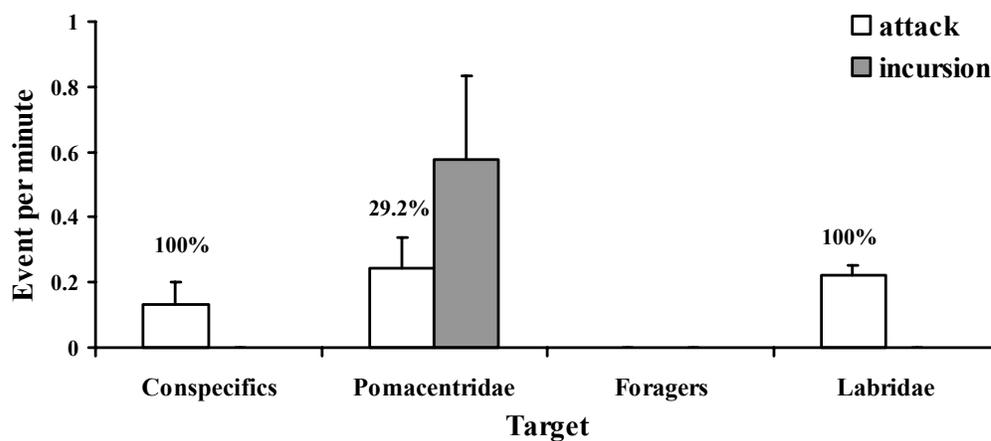


Figure 3. Incursion rates into *Stegastes apicalis* territories by four groups of possible competitors, and rates of attacks by *S. apicalis* against the four groups. Error Bars = 1 S.E.

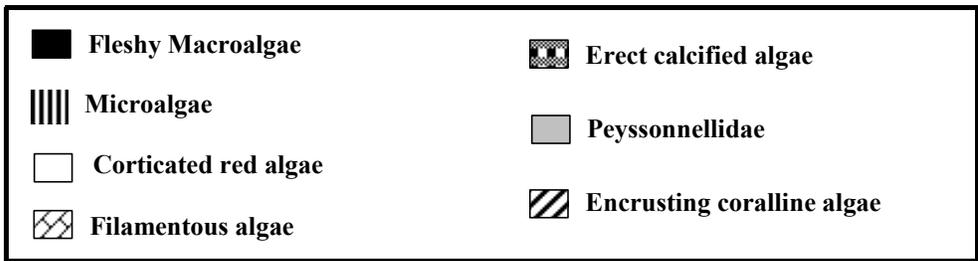
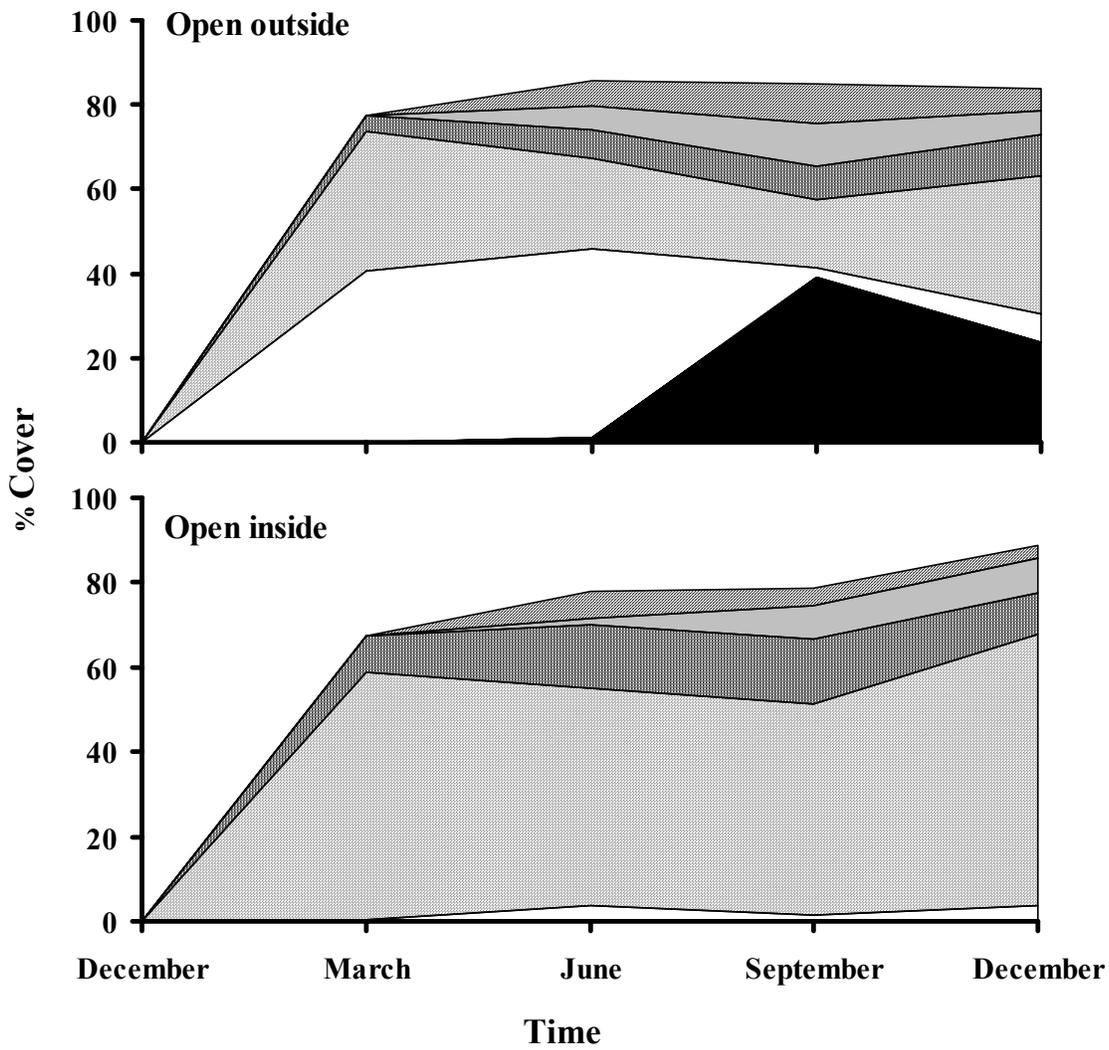


Figure 4. Comparison of algal succession inside and outside farmer territories: succession of seven algal functional groups on uncaged tiles outside and inside *Stegastes apicalis* territories, as measured by changing % cover of each functional group over time.

The cover of fleshy macroalgae increased to almost 40% between June and September on the tiles outside territories, but remained very low on tiles inside territories (Figure 5a). Detrital cover, on the other hand, increased much faster on the tiles inside territories. By the end of the year, however, the cover of detritus in both treatments had declined to approximately 15% (Figure 5b).

Corticated red algae grew outside territories in the first 6 months, then declined back to a similar low cover as on tiles inside territories, where there was no significant increase in cover (Table 2). Outside territories, this group was replaced by fleshy macroalgae. *Laurencia implicata*, the dominant member of the genus *Laurencia* to grow on the experimental tiles, grew to cover ~50% of tiles outside territories, but declined dramatically after 6 months (Figure 5c). The cover of *Polysiphonia herpa* increased steadily to around 70% inside territories, but remained at around 30% outside territories for the duration of the experiment (Table 2, Figure 5d). The cover of *Callithamnion* spp. bloomed in the first 3 months on all the tiles, and subsequently declined, but the bloom inside territories reached approximately double the percent cover compared with tiles outside territories (Figure 5e).

Species richness, diversity and evenness of the algal community developed similarly inside and outside territories (Figure 6). However, while species diversity and evenness followed almost identical trajectories inside and outside territories (Figure 6b, c), species richness outside territories was higher than inside territories 6 months after the beginning of the experiment (Figure 6a). The time of sampling may therefore have significant impacts on studies of how herbivory affects species richness.

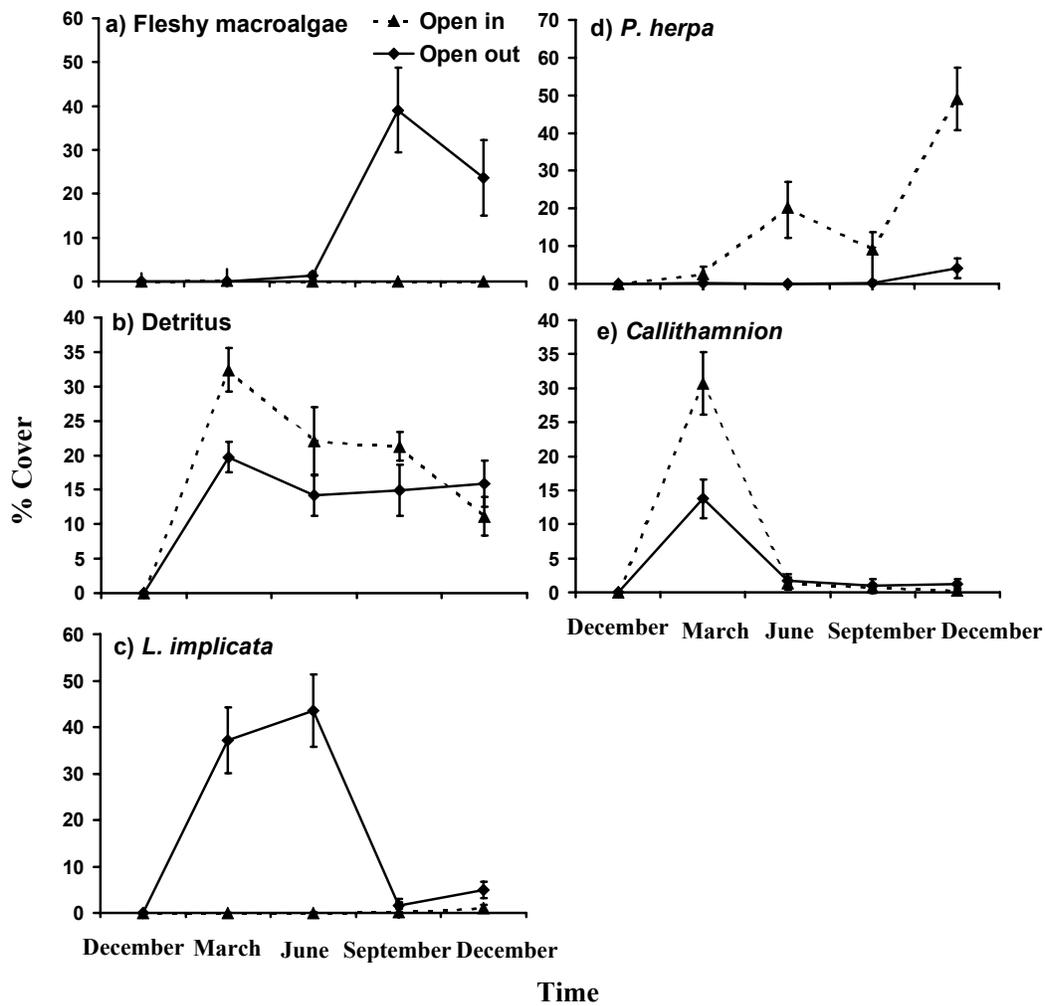


Figure 5. Comparison of algal succession inside and outside farmer territories: changes in the percent cover of individual taxa significantly affected by the differences between mechanisms acting on uncaged tiles inside and outside *Stegastes apicalis* territories. *P.*: *Polysiphonia*, *L.*: *Laurencia*. Note the different y-axes. Error bars = 1 S.E.

Table 2. MANOVA results for analysis of algal community structure on the tiles. F-values are given for variables showing a significant response to the tested mechanisms. – symbolizes variables that did not show a significant response to the treatments. F-values for Peyssonnellidae affected by cage effects are given for inside and outside territories (inside/outside). *P.*: *Polysiphonia*, *L.*: *Laurencia*. Taxa that did not respond significantly to any treatment include: *Polysiphonia ferulacea*, *P. infestans*, *Herposiphonia* spp., *Ceramium* spp., *Spermothamnion*, *Champia* spp., *Tolypocladia*, *Leveillea*, *Gelidiopsis* spp., and *Jania*.

	Inside/ outside	Forager effects	Farming effects	Location effects	Exclusion effects	Cage effects
Detritus	7.77	6.105	19.519	–	24.272	–
Microalgae	–	5.667	–	5.235	4.026	–
Fleshy macroalgae	9.243	4.652	–	15.851	23.585	–
Corticated red algae	35.531	6.474	31.681	5.619	9.069	–
<i>Hypnea</i> spp.	–	8.103	4.834	–	7.915	–
<i>L. implicata</i>	43.608	16.449	23.284	6.084	4.611	–
<i>Chondria</i> spp.	–	–	–	4.116	–	–
Filamentous algae	–	7.997	–	–	–	–
<i>Polysiphonia</i> spp.	–	11.824	7.363	–	–	–
<i>P. herpa</i>	60.142	–	58.695	–	54.231	–
<i>Callithamnion</i> spp.	6.104	–	8.45	–	9.777	–
<i>Amphiroa</i> sp.	–	–	15.655	13.234	–	–
Peyssonnellidae	–	45.19	76.578	–	46.234	10.04/7.32
Encrusting corallines	–	7.398	4.567	12.736	–	–
Diversity (H')	–	4.895	–	4.392	–	–

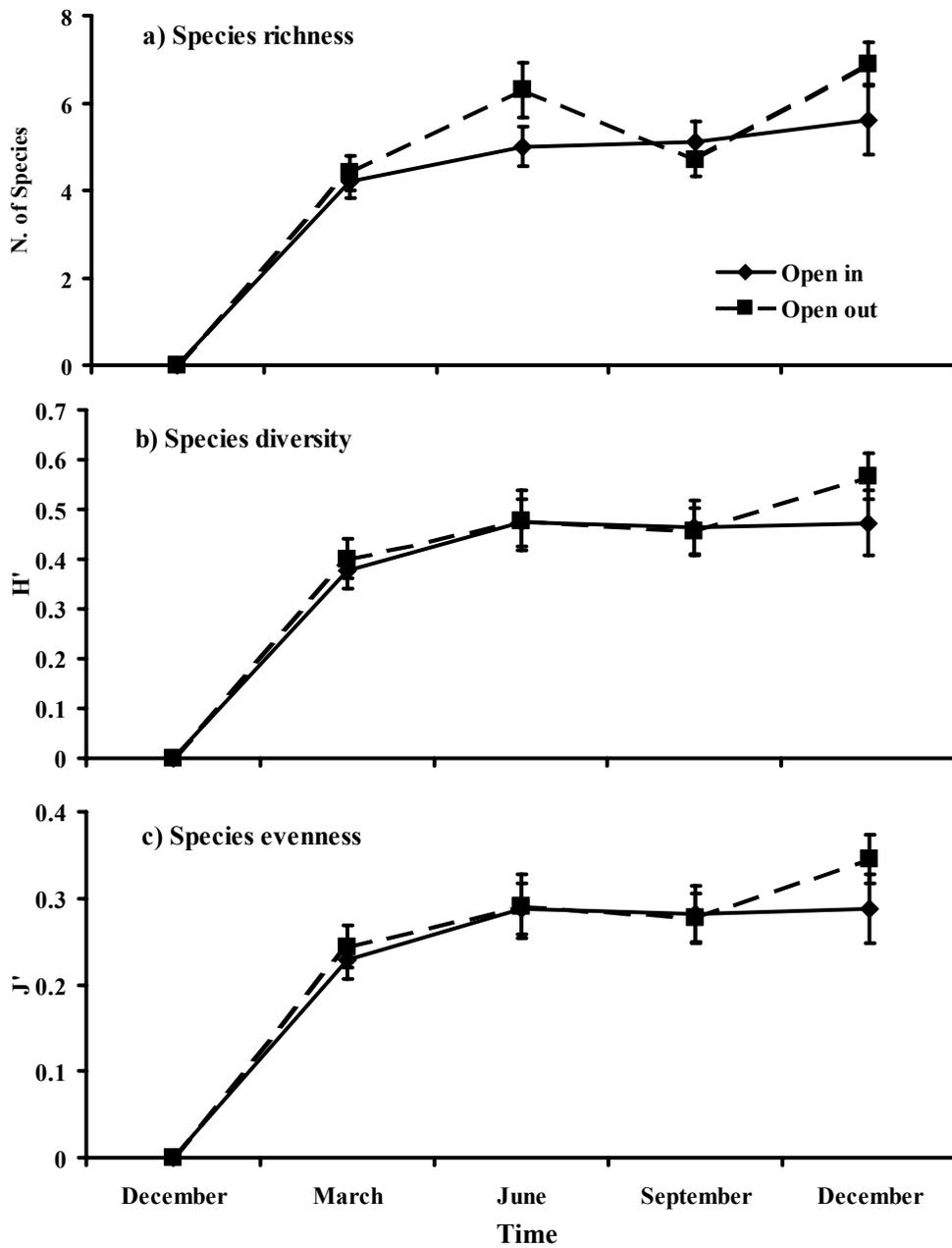


Figure 6. Changes in diversity inside and outside farmer territories, as measured by average a) species richness, b) diversity (H') and c) evenness (J'). Error bars = 1 S.E.

Comparison 2: Forager effects

Foragers had a major impact on the development of algal communities outside farmer territories, confirming the hypothesis that grazing by foragers can modify succession. The temporal change in the algal community varied between open and caged tiles (Pillai's Trace value 0.372, $F_{(d.f.=14)} = 8.688$, $p < 0.01$).

Where foragers had access, succession proceeded from early-successional filamentous algae to a community rich with corticated red algae and fleshy macroalgae (Figure 7). Where foragers were excluded, the cover of filamentous algae increased rapidly, but was quickly replaced almost completely by crustose algae such as Peyssonellidae (Figure 7). Fleshy macroalgae became established earlier in the absence of foragers, but reached higher cover in their presence (Table 2). Furthermore, species richness, evenness (J) and species diversity were significantly higher on open tiles (exposed to foragers) than on caged tiles, although this difference did not occur until the last 3 months of the experiment (Figure 8).

Corticated red algae grew twice as quickly on the open tiles, but were replaced by other taxa in the middle of the year. The cover of this group on the caged tiles reached only 10–20%. This pattern was closely followed by the cover of *Laurencia implicata* (Table 2, Figure 9a). Microalgae bloomed in June on the caged tiles (this increase was small, but significant) and then disappeared, while on the open tiles this bloom did not occur (Figure 9b).

After the initial growth of filamentous turf, there was a significant decline in its cover only on the caged tiles (Table 2). The cover of filamentous red algae *Polysiphonia* spp. bloomed, then declined, on the caged tiles, as opposed to a gradual but significant increase on the open tiles (Figure 9c). Foliose calcified algae of the family Peyssonellidae grew to dominate the benthic community on caged tiles (Figure 9d).

Encrusting coralline algae, on the other hand, became established only on tiles exposed to grazing by foragers (Figure 9e).

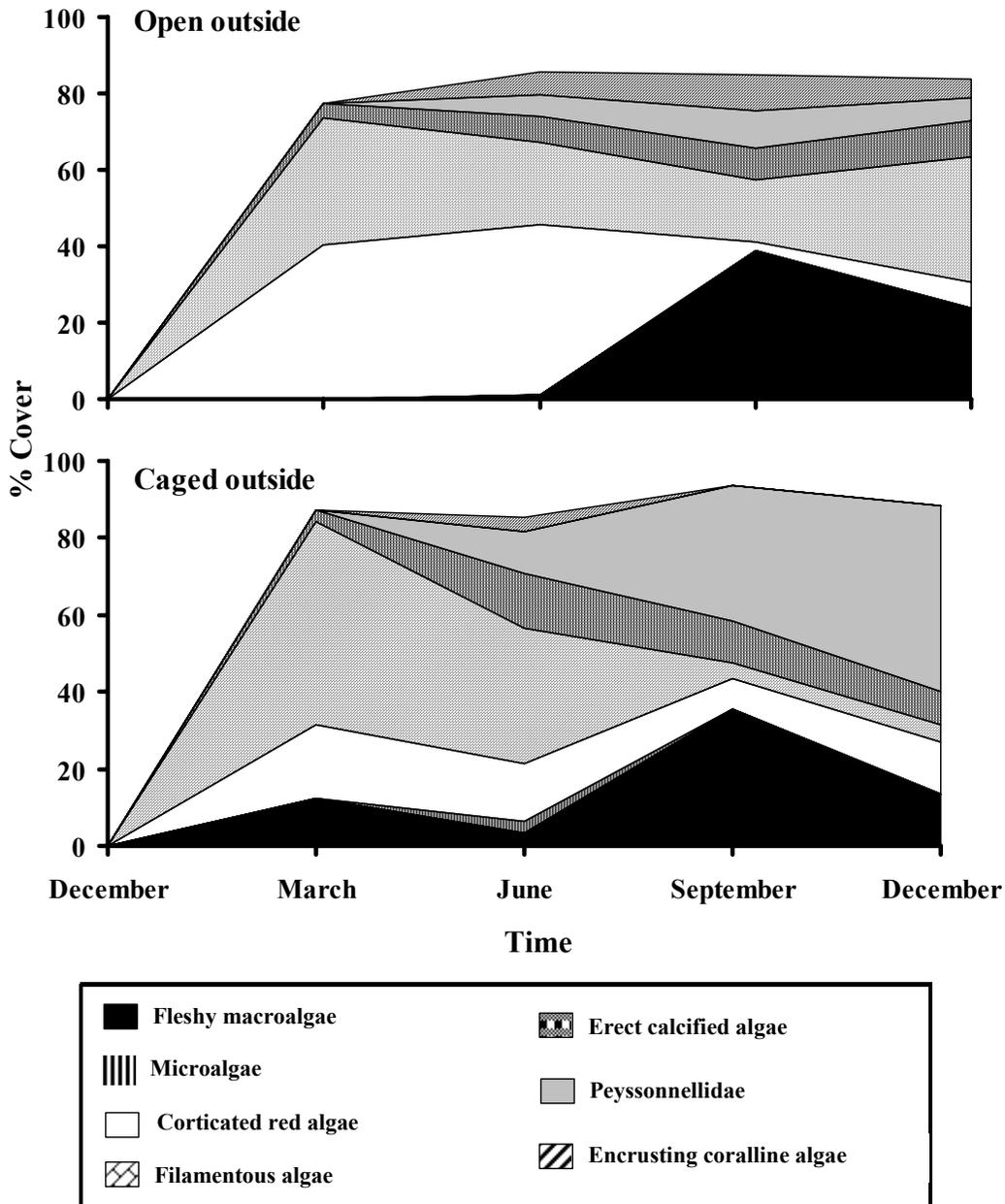


Figure 7. Effects of foragers: succession of seven algal functional groups on uncaged and caged tiles outside *Stegastes apicalis* territories, as measured by changing % cover of each functional group over time.

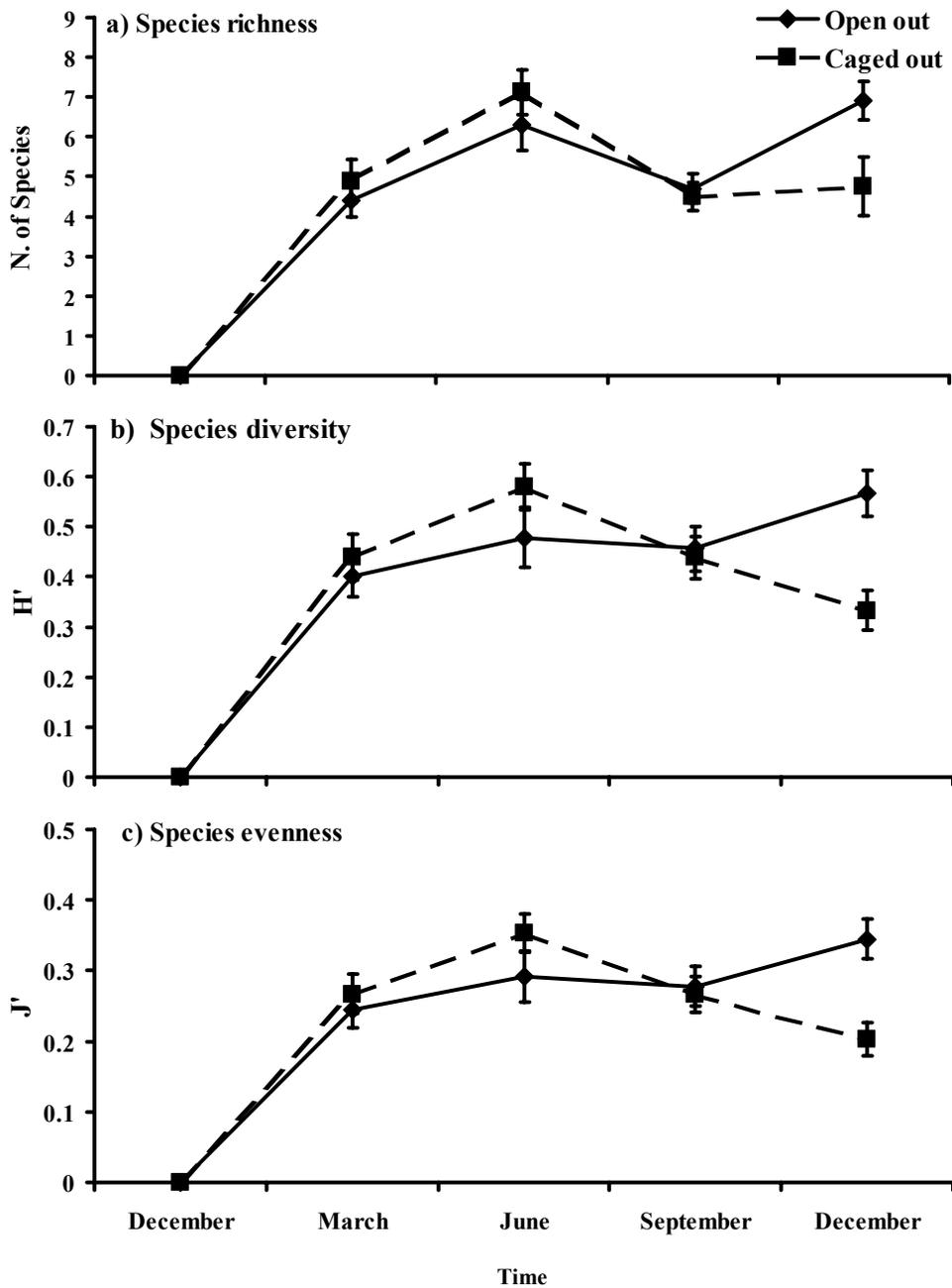


Figure 8. Effects of foragers: changes in algal diversity on uncaged and caged tiles outside *S. apicalis* territories, as measured by average a) species richness, b) diversity (H') and c) evenness (J'). Error bars = 1 S.E.

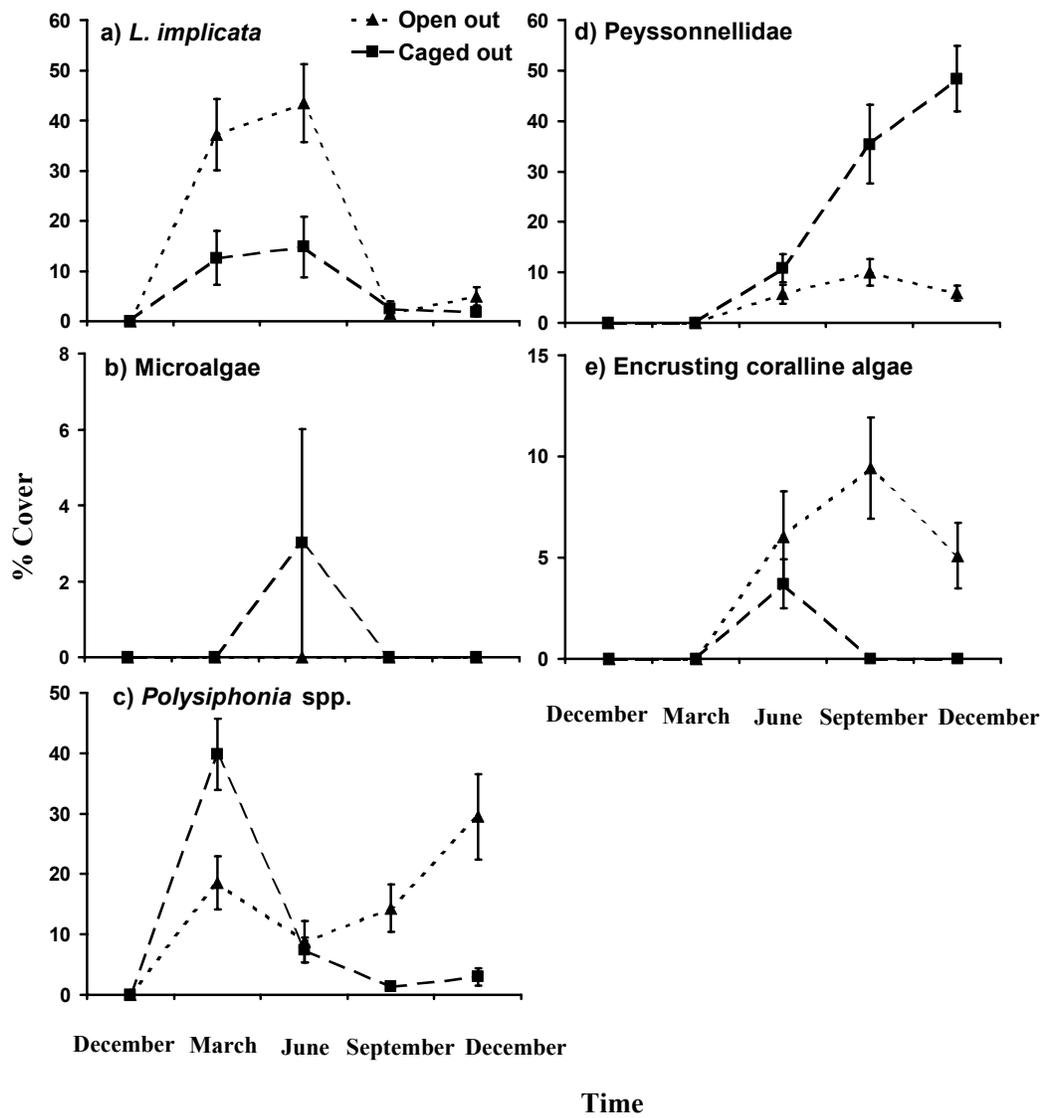


Figure 9. Effects of foragers: changes in the percent cover of individual taxa significantly affected by the differences between mechanisms acting on uncaged and caged tiles outside *Stegastes apicalis* territories. *L.*: *Laurencia*. Note the differences in y-axes. Error bars = 1 S.E.

Comparison 3: Direct farming effects

The benthic community on the tiles was significantly altered by farmer activities within territories, supporting the hypothesis that feeding and weeding by

farmers affect algal succession (Pillai's Trace value 0.514, $F_{(d.f.=14)} = 15.473$, $p < 0.01$).

The comparison of open and caged tiles inside farmer territories suggests that succession was halted at an earlier stage when farmers had access to the benthos (Figure 10), and where farmers had no access it proceeded to include corticated red algae and erect calcified algae (Figure 10). Calcified algae of the family Peyssonnellidae dominated these tiles at the end of the experiment.

The cover of detritus increased rapidly in both caged and uncaged treatments inside territories, reaching 30% cover on open tiles and 18% cover on caged tiles (Figure 11a). Both the rate of increase and the rate of decline were higher on the tiles to which farmers had access, and by the end of the experiment the tiles in both treatments were covered to only ~10% in detritus (Figure 11a). There was a general pattern of decline in cover of benthic algae on the caged tiles after the first 3 months of the experiment, driven primarily by corticated red algae, which bloomed in the cages in the first 3 months and were then replaced by other taxa over the course of the year. The cover of algae of the genus *Hypnea* experienced a brief but substantial bloom in the second half of the year (Figure 11b). *Laurencia implicata*, however, followed the increase-and-decline pattern of pooled corticated red algae more closely (Table 2; Figure 11c).

The cover of *Callithamnion* spp. underwent a bloom-and-decline pattern only on open tiles (Figure 11d). Members of the genus *Polysiphonia*, such as *P. herpa* (Figure 11e), were dominating the turf on the tiles by the end of the year, covering around 60% of the available substratum. Calcified algae, such as *Amphiroa* (Figure 11f) and Peyssonnellidae (Figure 10), on the other hand, grew primarily on the caged tiles.

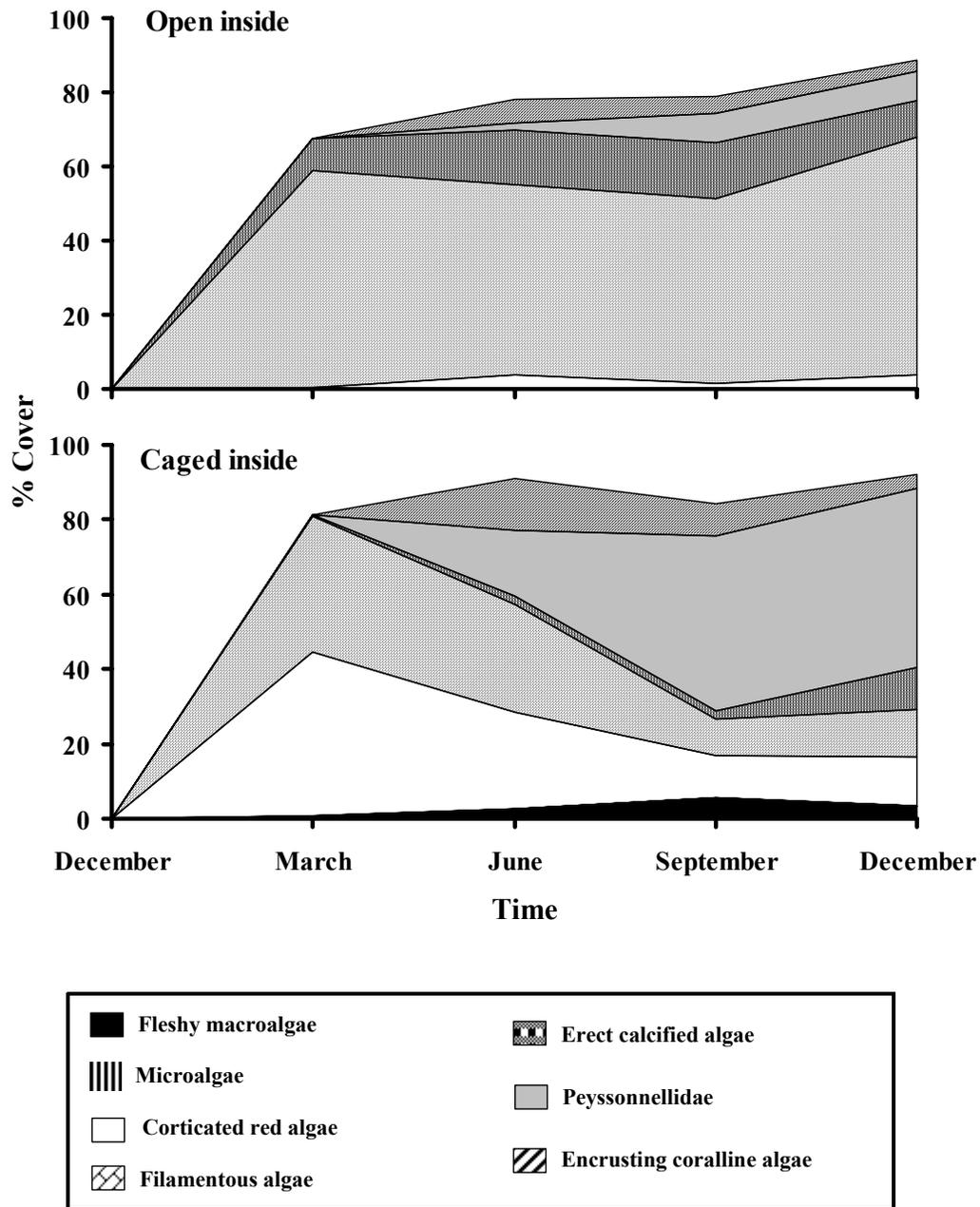


Figure 10. Effects of farming: succession of seven algal functional groups on uncaged and caged tiles inside *Stegastes apicalis* territories, as measured by changing % cover of each functional group over time.

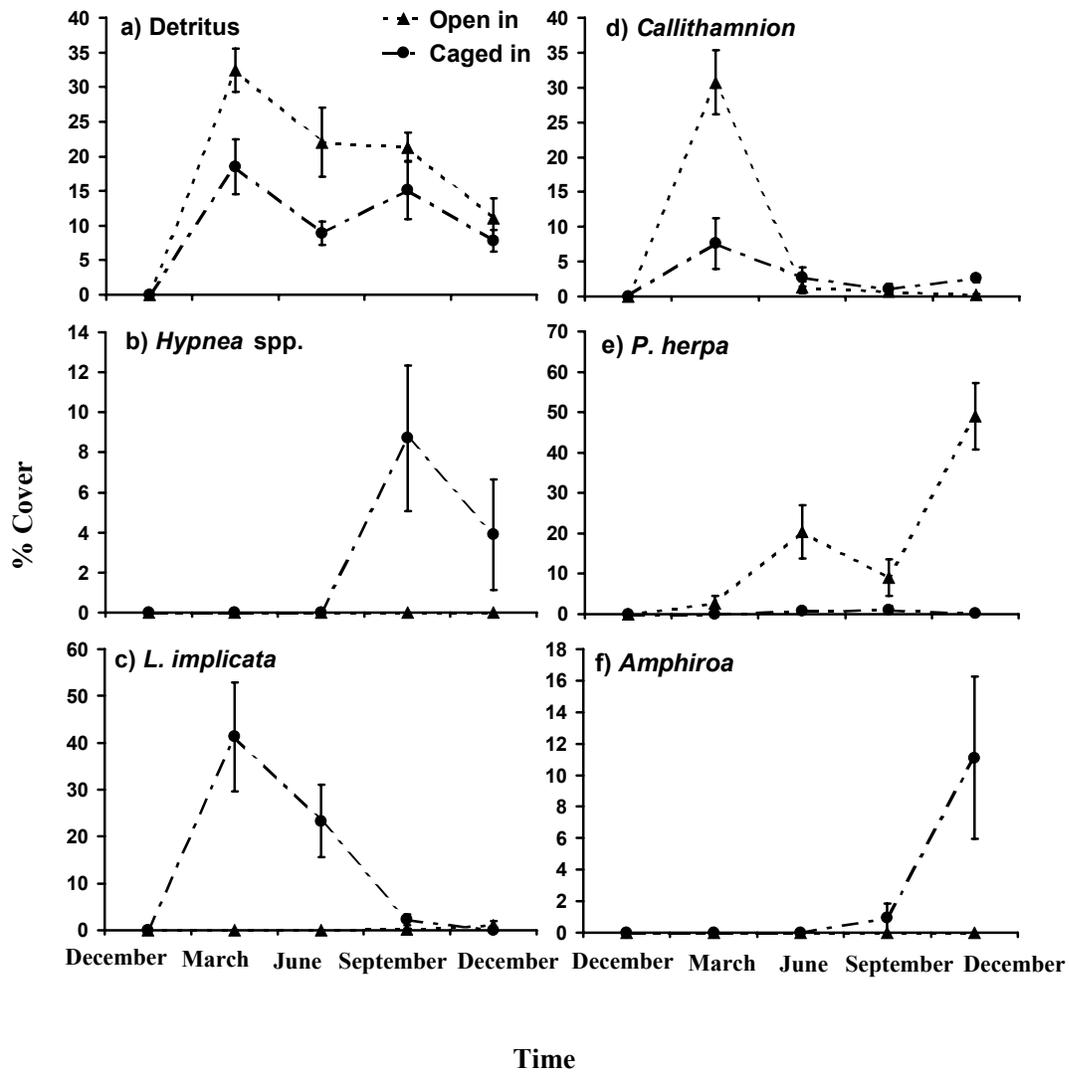


Figure 11. Effects of farming: changes in the percent cover of individual taxa significantly affected by the differences between mechanisms acting on uncaged and caged tiles inside *S. apicalis* territories. *P.*: *Polysiphonia*, *L.*: *Laurencia*. Note the differences in y-axes. Error bars = 1 S.E.

Comparison 4: Territory location effects

The results of this comparison supported the hypothesis that algal communities develop differently inside and outside territories, in the absence of grazing by foragers or farmers. Comparing caged tiles inside and outside territories revealed that the location of farmer territories, without any direct manipulation by farmers, can have a significant effect on the benthic community (Pillai's Trace value 0.290, $F_{(d.f.=14)} = 5.990$, $p < 0.01$). Inside territories, calcified algae replaced filamentous and corticated algae within 6 months of the beginning of the experiments, and almost 70% of the tile area was covered by the foliose calcified algae Peyssonnellidae, encrusting coralline algae and, to a smaller extent, erect calcified algae (*Amphiroa* spp. and *Jania* spp.) by the end of the year (Figure 12). Outside the territories, dominant filamentous algae were replaced by high macroalgal cover, and fleshy macroalgae were in turn replaced by tougher calcified algae (Figure 12).

The location of territories had a significant effect on species diversity. Species richness, diversity and evenness were significantly higher inside territories than outside territories at the end of the experiment, suggesting that territories are located in areas more suitable to the development of greater algal diversity (Table 2, Figure 13). However, this pattern was reversed earlier in the year; diversity on caged tiles outside territories increased at a higher rate, so that it was initially higher than diversity inside territories. Six months after the beginning of the experiment, it declined to become significantly lower than diversity inside territories (Figure 13).

Corticated red algae were significantly affected by territory location. There was a small but significant effect on algae of the genus *Chondria*, which bloomed on the caged tiles outside territories early in the year and then declined again (Figure 14a). Furthermore, there was a four-fold increase in cover of algae of the genus *Laurencia*,

(especially *L. implicata*) inside territories in the first 3 months, but the percent cover of these taxa had declined significantly by the end of the year (Figure 14b). Calcified erect algae of the genus *Amphiroa* increased in cover in the last 3 months of the experiment, but only on the caged tiles inside territories (Figure 14c). There was a small but significant increase in the cover of microalgae, but only on caged tiles outside territories (Table 2, Figure 14d). Fleshy macroalgae also grew to cover a much higher proportion of caged tiles outside territories; despite a decline in winter (6 months after the start of the experiment), it grew to cover up to 35% of caged tiles outside territories (Figure 14e). In contrast, encrusting coralline algae grew primarily on caged tiles inside territories, reaching a peak of ~15% cover and subsequently declining in cover at the end of the experiment (Figure 14f).

While some of these effects were useful in explaining the differences in algal succession inside and outside territories, there were several patterns that could not be explained by the location of farmer territories. The effects of location accounted for the lack of macroalgal growth inside territories (Figure 14e), but not for the dramatic increase in palatable algae inside territories (Figure 5d). Furthermore, the effects of location did not account for the suppression of *Laurencia implicata* inside territories (Figure 5c), as this species was able to grow on caged tiles inside territories (Figure 14b). These patterns could be explained as being affected primarily by direct farming activities inside territories (see Comparison 3).

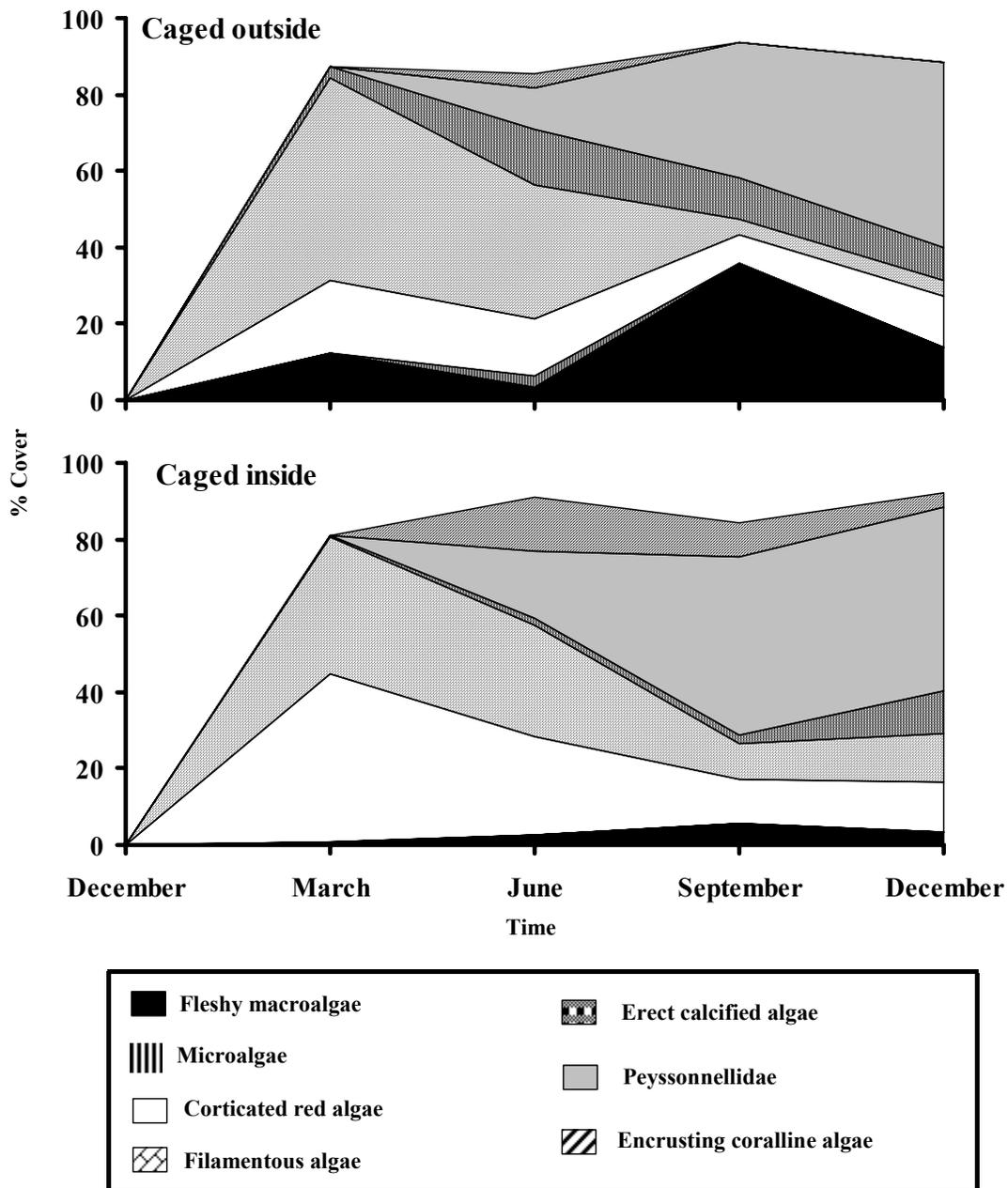


Figure 12. Effects of territory location: succession of seven algal functional groups on caged tiles outside and inside *Stegastes apicalis* territories, as measured by changing % cover of each functional group over time.

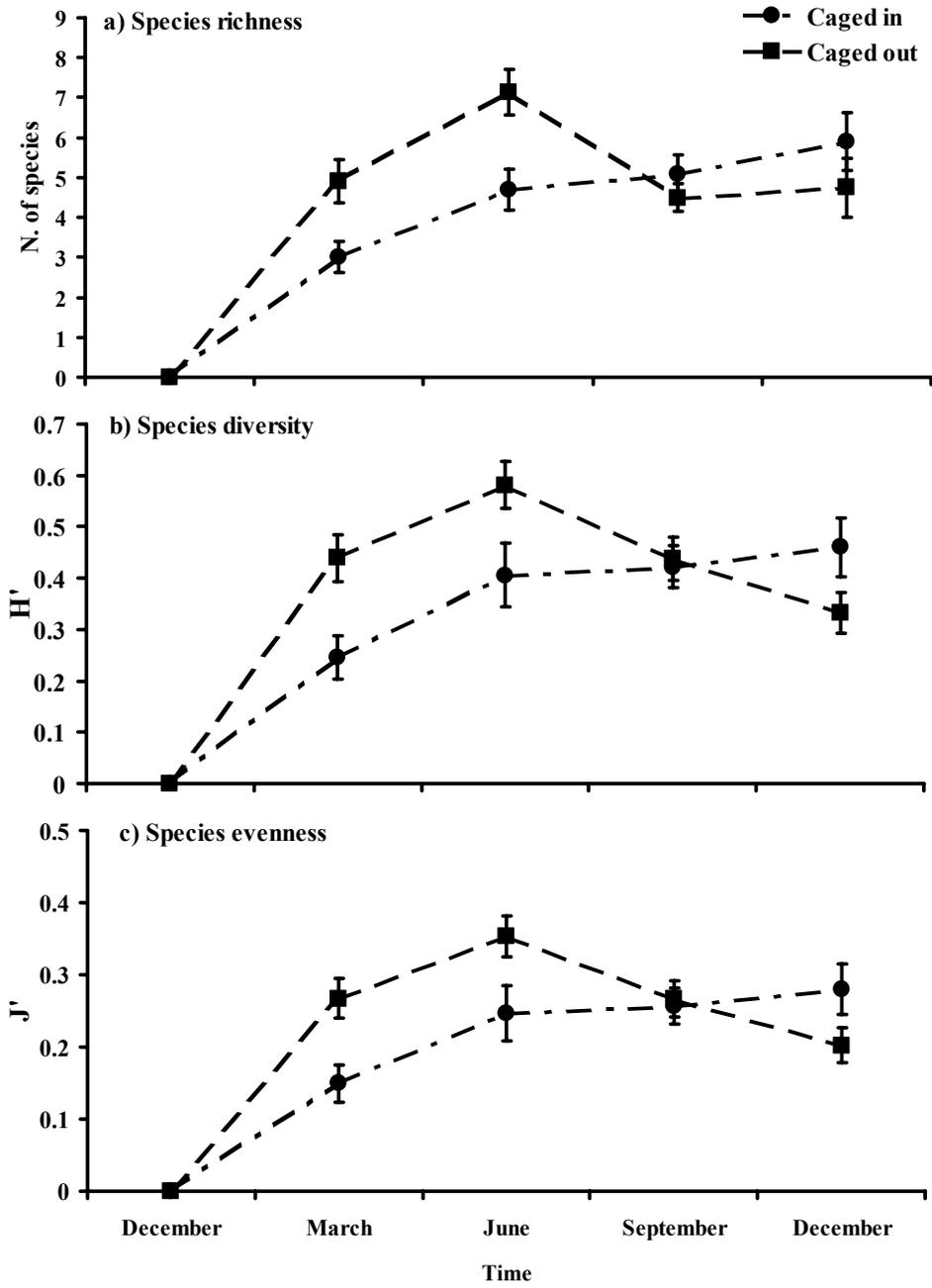


Figure 13. Effects of territory location: changes in algal diversity on caged tiles outside and inside *Stegastes apicalis* territories, as measured by average a) species richness, b) diversity (H') and c) evenness (J'). Error bars = 1 S.E.

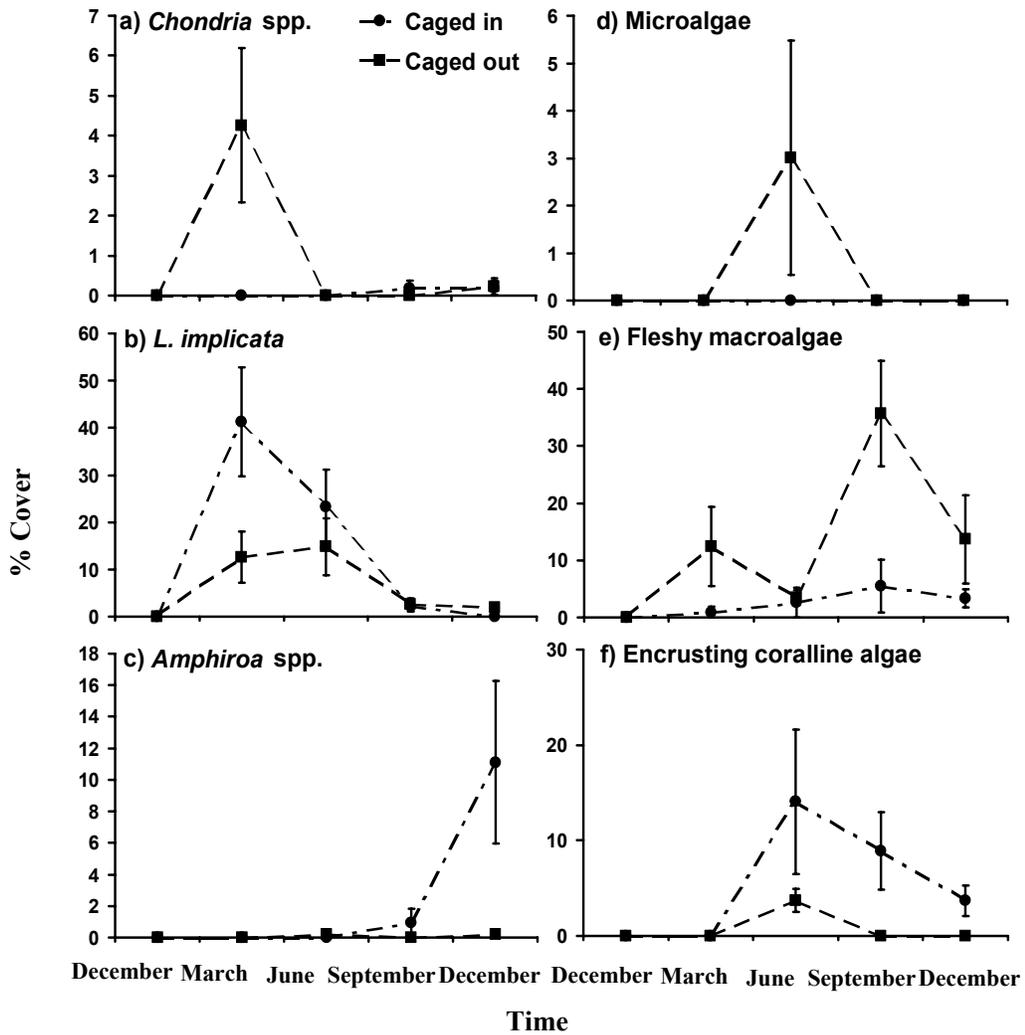


Figure 14. Effects of territory location: changes in the percent cover of individual taxa significantly affected by the differences between mechanisms acting on caged tiles outside and inside *S. apicalis* territories. *L.*: *Laurencia*. Note the differences in y-axes. Error bars = 1 S.E.

Comparison 5: Exclusion effect

The results of this comparison supported the hypothesis that the effects of farmers on succession cannot be explained by their exclusion of foragers. The succession of algal communities on the tiles progressed very differently in farmer territories than in cages outside territories (Pillai's Trace value 0.473, $F_{(d.f.=14)} = 14.143$, $p < 0.01$). The dense stands of filamentous algae that developed on uncaged tiles inside territories did not develop on caged tiles outside territories (Figure 15). Filamentous algae dominated caged tiles for a short time before being replaced by fleshy macroalgae, which were in turn replaced by Peyssonellidae (Figure 15).

The benthic groups with the strongest response to the two treatments were detritus, fleshy macroalgae, some corticated red algae, filamentous algae and Peyssonellidae (Table 2). Detritus accumulated much more rapidly on open tiles inside territories than on caged tiles outside territories, but then declined until tiles in both treatments contained about 10% detritus within the algal turf (Figure 16a). Fleshy macroalgae grew only on caged treatments outside territories. The increase in fleshy macroalgae occurred in two 'steps', separated by a decline in the cover of macroalgae in winter (June) (Figure 16b). Corticated red algae of the genus *Laurencia* also grew only on caged tiles outside territories. The cover of *Laurencia* grew to approximately 15% in the first 6 months of the experiment, and then almost disappeared (Figure 16c), as the available space was occupied first by fleshy macroalgae, and then by Peyssonellidae (Figure 15). The delicate red filamentous alga *Polysiphonia herpa* grew only on the open tiles inside territories (Figure 16d), growing to gradually dominate the algal community after an initial bloom of *Callithamnion* spp. (Figure 16e). On the caged tiles outside territories, calcified algae of the family Peyssonellidae grew to occupy half the

available space, while on the open tiles inside territories its cover never exceeded 10% (Figure 16f).

Comparisons 6 and 7: Cage effects

The cage artefacts were found to have minimal effects on the development of benthic communities on the tiles. The only taxa to be affected significantly by the cage artefact were calcified algae of the family Peyssonellidae. This effect occurred both inside and outside territories (inside $F_{(d.f.=14)} = 10.037, p < 0.05$; outside $F_{(d.f.=14)} = 7.327, p < 0.05$, Figure 17). However, the percent cover of Peyssonellidae in partial cages was intermediate between open tiles and fully caged tiles, but much more similar to open tiles (partial cages: 16.54% \pm 4.5 S.E.; open tiles: 12.19% \pm 1.9 S.E.; full cages: 31.55% \pm 5.7 S.E.). This pattern between treatments suggests that cages affected levels of herbivory, rather than shading and water movement (Figure 17).

There were no other significant changes in the algal biomass and community composition that could be directly attributed to the presence of the cage artefacts. Benthic communities on partially caged tiles inside territories developed similarly to those on open tiles inside territories ($F_{(d.f.=14)} = 1.148$, NS), and partially caged tiles outside territories followed a similar trajectory of succession as open tiles outside territories ($F_{(d.f.=14)} = 1.553$, NS).

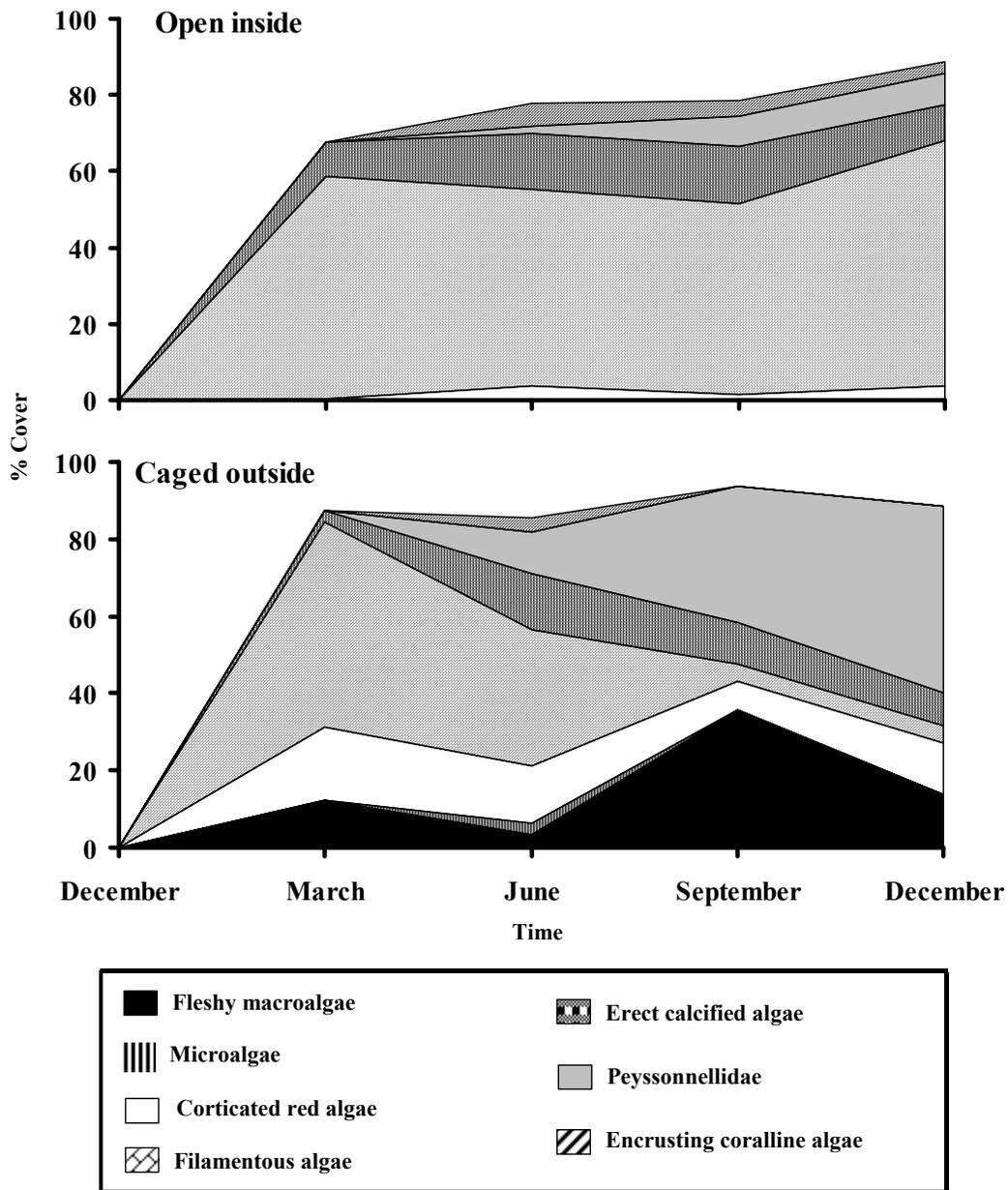


Figure 15. Effects of exclusion: succession of seven algal functional groups on caged tiles outside and uncaged tiles inside *Stegastes apicalis* territories, as measured by changing % cover of each functional group over time.

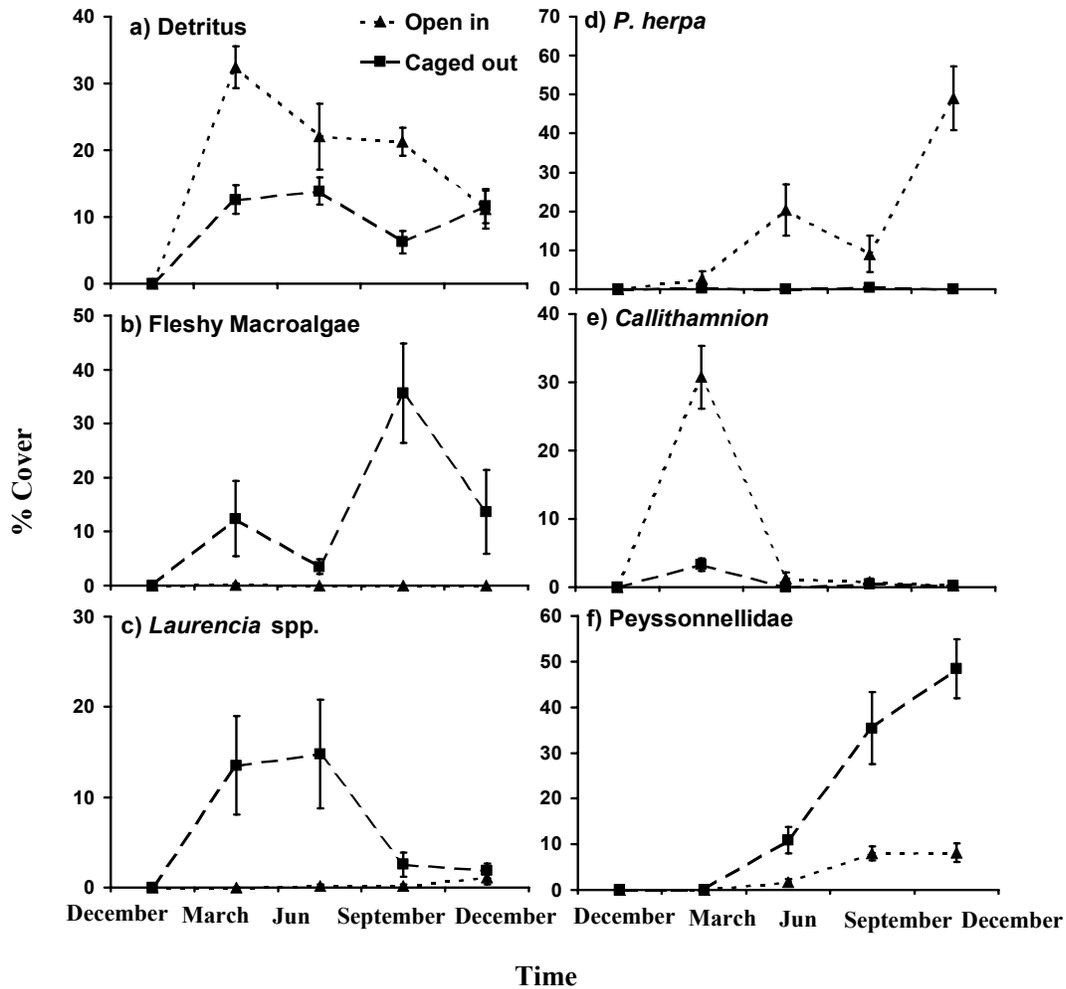


Figure 16. Effects of exclusion: changes in the percent cover of individual taxa significantly affected by the differences between mechanisms acting on caged tiles outside and uncaged tiles inside *Stegastes apicalis* territories. *P.*: *Polysiphonia*. Note the differences in y-axes. Error bars = 1 S.E.

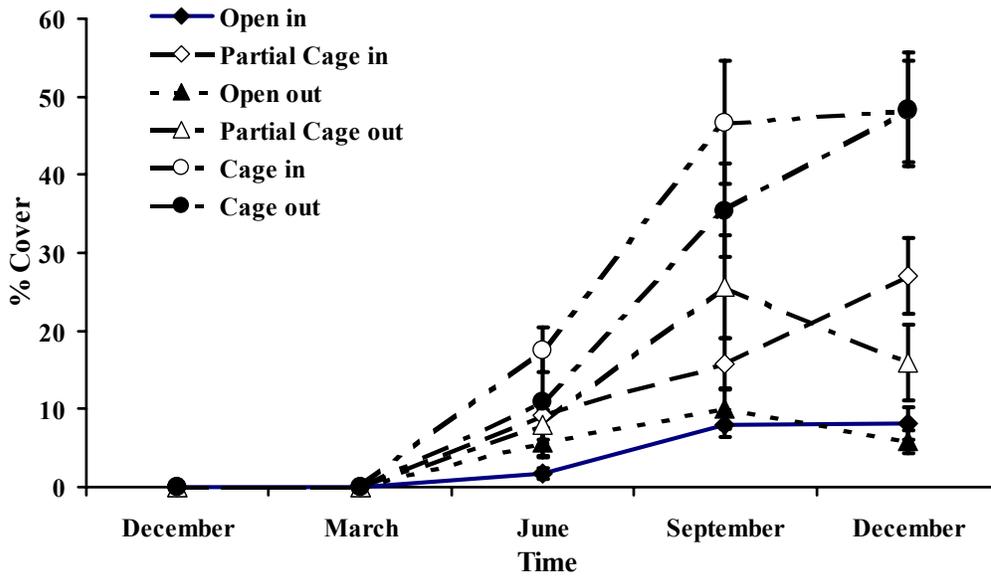


Figure 17. Effects of partial cages inside and outside territories on the % cover of Peyssonnellidae, compared with open tiles (inside and outside territories) and fully caged tiles (inside and outside territories). Error bars = 1 S.E.

Discussion

Herbivorous fish have often been found to modify the natural development of algal communities, both in temperate marine habitats (Sousa 1979; Farrell 1991) and on coral reefs (Glynn 1990; Hay 1991). However, the effects of different kinds of herbivores on this process are often poorly understood. On coral reefs, algal communities undisturbed by grazing fish are said to proceed from an initial stage dominated by diatoms, blue-green algae and filamentous algae to a more diverse assemblage composed of filamentous, corticated and fleshy algae, reaching a 'mature'

community dominated by calcified algae and fleshy macroalgae (Littler et al. 1983; Hay 1991; Hixon and Brostoff 1996; Hata and Kato 2003). In previous studies, foragers were found to divert trajectories of succession to a community dominated by grazer-resistant algal taxa (Godwin 1929; Hixon and Brostoff 1996). Farmers, on the other hand, have been shown to inhibit succession in order to promote monocultures of preferred filamentous algae (Hata and Kato 2003), or to cultivate highly diverse assemblages of palatable taxa (Hixon and Brostoff 1996). In this study, four different trajectories of succession were detected, depending on whether algal assemblages were under the influence of foragers, farmers, the absence of both, or a particular location on the reef crest.

Succession inside and outside farmer territories

The comparison of settlement tiles inside and outside territories encompassed all the effects of farmers (including the location of their territories) and all the effects of foragers. Succession followed different trajectories inside and outside territories. It appears that succession inside territories was inhibited, remaining at a stage where it was dominated by filamentous taxa, while succession outside territories progresses in a manner more similar to the way suggested by the traditionally accepted model of succession described above. However, simply comparing succession inside and outside territories does not identify the mechanisms acting on these different trajectories. In farmer territories, succession could be affected by the direct activities of farmers, the exclusion of foragers, the location of territories, or a combination of all these mechanisms. Outside territories, it is unclear whether the observed patterns occur because of the activities of foragers, or despite them. To detect the mechanisms

influencing succession inside and outside farmer territories it is necessary to include a number of caging treatments, both inside and outside territories.

The effects of foragers on succession

In Nelly Bay, foragers affected succession by inhibiting the growth of calcified algae of the peyssonellid family, but they did not hinder the establishment of fleshy macroalgae such as *Padina* and *Sargassum*. Feeding by large foragers is usually held as the reason for reducing algal biomass (Carpenter 1986; Steneck 1988; Bellwood and Choat 1990; Pennings 1996; but see Williams et al. 2001). When their role in affecting the succession of benthic communities is mentioned, it is usually implied that facilitation occurs, allowing succession to proceed towards a relatively ‘mature’ community (Sousa and Connell 1992). Alternatively, high grazing pressure can divert succession to an alternative community dominated by crustose coralline algae not otherwise found in ungrazed systems (Hixon and Brostoff 1996). In this study, foragers did not suppress macroalgal growth, leading to a benthic community dominated by *Sargassum* spp. and other fleshy macroalgae (Morrissey 1980; Lewis 1999). The activities of foragers on the Nelly Bay reef crest facilitated a diverse ‘mid-successional’ assemblage that included corticated red algae and fleshy macroalgae, but inhibited the growth of ‘late-successional’ Peyssonellidae and crustose coralline algae.

The effects of farmers on succession

The effects of farmers on algal succession were more dramatic than the effects of foragers. Where the activities of foragers affected succession in a way that allowed several functional groups of algae to coexist after 12 months, farmers stopped

succession at a stage where filamentous algae dominated the benthic assemblage. The activities of farmers have been previously recognized for their ability to alter the naturally occurring trajectory of succession (Lassuy 1980; Hixon and Brostoff 1996; Hata and Kato 2003). Recent studies by Hata and Kato (2002, 2003) showed that the weeding activities of *Stegastes nigricans* were directly responsible for the halted succession inside their territories. The degree to which succession is modified inside other farmer territories is variable (Lassuy 1980; Hinds and Ballantine 1987; Hixon and Brostoff 1996), suggesting that each farmer species may use a different mechanism for maximising the abundance of palatable algae in its territories (Ceccarelli et al. 2001). *S. apicalis* appears to directly promote an algal assemblage dominated by *Polysiphonia herpa* inside its territories, which is also found in large proportions in the stomach contents of this species (Chapter 3). This study provides a further alternative to the two patterns already found in the literature: *S. apicalis* neither arrested succession to the point of promoting a monoculture (Montgomery 1980b; Hata and Kato 2003), nor modified it to form a highly diverse algal assemblage (Hixon and Brostoff 1983). Despite suppressing corticated and fleshy macrophytes, *S. apicalis* did not eradicate calcified algae, possibly because the latter group can act as a substrate on which to promote the growth of palatable filamentous epiphytes.

In the first 3 months of the experiment, diversity inside farmer territories was significantly higher on open tiles than on caged tiles. Although the location of farmer territories also had a positive effect on diversity (diversity on caged and uncaged tiles inside territories did not differ at the end of 12 months), the increase in diversity due to location was slower than the increase caused directly through farming activities of *S. apicalis*. This suggests that the activities of farmers, enhance algal diversity during early succession. Previous studies have found either a strong increase in diversity and/or

species richness inside territories (Lassuy 1980; Hixon and Brostoff 1983; Ruyter van Steveninck 1984; Hinds and Ballantine 1987), or very low diversity (Montgomery 1980a; Hata and Kato 2002). The result of this study suggest that findings on farmer effects on algal species richness or diversity may be related to the time allowed for algal development in farmer territories.

Does location matter?

The results of this study suggest that farmers select sites for their territories where the trajectory of succession differs from surrounding areas. The location chosen by farmers to establish their territories had a positive effect on diversity, but a negative effect on the growth of fleshy macroalgae. Succession on caged tiles inside territories did not include a stage of high macroalgal cover, and the algal community that developed at the end of the year was more diverse than the assemblage on caged tiles outside territories. The effect of the location of farmer territories on algal succession has remained virtually untested (but see Hata and Kato 2003), despite the demonstration that site selection occurs in some farmer species (Wellington 1992; Bay et al. 2001). It appears that *Stegastes apicalis* established territories in locations less suitable for the growth of unpalatable fleshy macroalgae. However, the direct activities of *S. apicalis* were more important than the location of territories in the promotion of preferred food algae.

Both the activities of foragers and the location of farmer territories led to increased levels of algal diversity after 12 months. However, both the effects of foragers and the effects of location on diversity varied according to the amount of time that had elapsed from the beginning of the experiment, highlighting the fact that different

herbivore effects on algal diversity cannot be generalized without first examining the temporal or successional context in which they occur.

Are farmers simply forager exclusion treatments?

Farmers and cages had different effects on algal succession, supporting the hypothesis that the effects of farmers on their territories are not equivalent to a forager exclusion treatment. Succession on caged tiles outside territories included a stage dominated by filamentous algae, but they were replaced by corticated and fleshy macroalgae, and these were then replaced by calcified algae, while succession on uncaged tiles inside territories remained dominated by filamentous algae.

Studies using farmer territories as ‘low grazing’ treatments (Gleason 1996) assume that grazing by farmers represents a lesser impact on benthic communities than grazing by foragers (Ogden and Lobel 1978; Horn 1989). Furthermore, it is commonly assumed that the exclusion of foragers by farmers further reduces grazing rates inside territories (Hixon 1996). The results of this study indicate that the exclusion of foragers by farmers, even when it appears to be highly successful, does not have the same effect on algal communities as the exclusion of foragers by a cage. Clearly, the other mechanisms acting on farmer territories (the location of territories combined with farming activities of the resident fish) are more important in creating the distinct algal turfs associated with farming fish (Hata and Kato 2003). Therefore, the extent to which farmer territories are modified by the other activities of farmers (territory location and ‘farming’) make them largely inappropriate as sites of ‘low grazing pressure’. The modification of grazing rates through farmer aggression can no longer be considered the primary mechanism by which farmers create the benthic assemblages inside their territories.

Relative importance of farmers and foragers

In this study, foragers had a moderate impact on algal succession, but their grazing regime on open tiles did not lead to an algal assemblage that differed dramatically from ungrazed tiles. The visually dominant fleshy macroalgae that occur in high densities on the Nelly Bay reef (Chapter 2, Mapstone et al. 1989) were not suppressed by foragers. Farmers, however, defended territories in which they promoted algal communities that were visually distinct from surrounding areas. Despite the widely accepted view that foragers are the dominant herbivores on coral reefs (Lewis 1986; Bruggemann et al. 1994), this may not be true where they occur in low densities (Williams et al. 2001). Other studies have found that on reefs with low forager densities, sea urchins can become the dominant herbivores (Ogden and Lobel 1978; Carpenter 1997). In this study, the reef crest in Nelly Bay may be a zone where farmers are the dominant herbivores, both in terms of their densities (see Chapter 2) and their effects on the algal development in their territories.

The role of fertilization

A mechanism that remains to be experimentally tested is whether farmers fertilize their territories in order to produce a higher growth rate in the taxa they prefer (Klumpp et al. 1987; Polunin and Koike 1987; Plaganyi and Branch 2000). Comparing caged tiles outside territories with caged tiles inside territories to measure the effects of fertilization is problematic because it is potentially confounded with the effects of territory location and assumes that fertilization by foragers does not affect algal

communities outside territories. Future studies need to measure fertilization more directly, and should include a range of farmer species in different locations.

Conclusions

Foragers influence algal succession on coral reefs, however the magnitude of their impact is strongly dependent on their abundance, and they are not always able to significantly reduce the biomass of fleshy macroalgae. Farmers do not simply act as herbivore exclusion treatments, but appear to actively cultivate algal assemblages in their territories. Their activities affect not only established algal communities, but modify algal succession to promote a high abundance of palatable algae. Differences in succession inside and outside territories could also be partially explained by habitat selection, whereby farmers establish territories in locations less suitable to the growth of unpalatable algae. Inshore reefs with low forager densities may represent environments where farmers replace foragers as the herbivore group with the greatest effects on coral reef algae.

CHAPTER 7: GENERAL DISCUSSION

This thesis has reaffirmed the differing roles of farmers and foragers in coral reef ecosystems, and expanded our knowledge of the complex interactions between these two behavioural groups of herbivore. Farmers and foragers have quantitatively and qualitatively different effects on algal assemblages. The effects of farmers can vary among geographic locations, reef zones and species. However, general patterns suggest that even species without obvious algal mats in their territories significantly modify algal assemblages in their territories. The activities of foragers are integral to the maintenance of existing benthic communities, and their absence can cause phase-shifts from coral-dominated to algal-dominated reefs. The impacts of foragers on farmers have been demonstrated for the first time. Conversely, farmers may be less effective in modifying the activities of foragers than previously assumed. In the first experimental separation of the potential mechanisms by which farmers affect their territories, it was found that the direct feeding and weeding activities of farmers were more important than the exclusion of foragers. In this discussion I will draw together recurrent themes that have emerged in this thesis concerning the role of farmers, the role of foragers, their reciprocal influences on one another and the consequence of both groups for the structure of coral reef communities.

Role of farmers

On a worldwide basis, by 2001 the effects of approximately half of the damselfish species that defend territories had been addressed (Ceccarelli et al. 2001). Almost all studies documented the effects of members of the genera *Dischistodus*, *Stegastes*, *Plectroglyphidodon*, *Hemiglyphidodon* and *Microspathodon*, which tend to

be relatively rare and spatially restricted (Klumpp et al. 1987; Meekan et al. 1995). Only one previous study addressed the effects of a member of the widespread and abundant genus *Pomacentrus*. This thesis has contributed information about the effects of six further species (*Pomacentrus wardi*, *P. adelus*, *P. tripunctatus*, *P. chrysurus*, *P. burroughi*, and *Neoglyphidodon nigroris*), all of which were previously thought to have little impact on benthic communities.

This thesis confirms that farmers are a diverse group, and that their role varies according to their distribution, their space occupation, their diet and the relative abundance of each species in the community. Each species appears to add further detail to our understanding of the role of farmers in modifying benthic assemblages. These roles can range from the creation of very distinct algal assemblages that also affect corals and invertebrates in those that may be considered keystone species (Williams 1980a; Wellington 1982; Hixon and Brostoff 1983) to those that defend territories with inconspicuous boundaries, but nevertheless cause significant changes in the abundance and taxonomic composition of algae in their territories (Chapters 2 and 3). Despite their variability, all the species studied in this thesis increased the abundance of palatable algae in their territories, and therefore maintained algal turf communities significantly different from surrounding areas.

In some habitats, almost all the available space was occupied by farmer territories. The farmers that were found to significantly affect their territories included species that tend to be more abundant and widespread than farmers with more specialized habitat requirements (Chapter 3, Robertson and Lassig 1980). Combining information about the widespread distribution of these smaller species with the findings that they have significant effects on their territories (Chapters 2 and 3) increases the perception of the spatial extent of the influence of farmers as a group.

The diversity of their effects on benthic communities and the extent of their space occupation on reef substrata (Chapter 3) has implications for the effects of farmers on overall patchiness on coral reefs. Sammarco and Carleton (1981) suggested that the distinct patches created by farmer territories may serve to increase overall coral reef heterogeneity. Given the different effects of farmers on their territories, the number of distinct patches may increase with increasing numbers of farmer species (Chapter 3). The results of this thesis suggest that the contribution of farmers to the overall patch diversity of coral reefs may be greater than previously thought.

The results of Chapter 3 suggest that dietary preferences may reflect the proportions of benthic components that are likely to be promoted inside farmer territories. The diets of most farmers appear to exist along a continuum between strict herbivory and detritivory, with many species consuming both algae and detritus. The proportions of algae and detritus in their guts were reflected in the composition of their territories and in the naturally occurring distribution of detritus and algae across reef zones. This suggests that farmers may select habitats where their preferred food is likely to be abundant, and then “cultivate” algal assemblages in their territories to further increase the proportions of palatable items.

This thesis contains the first of only two studies to experimentally demonstrate that farmers actively promote the algal turf in their territories (see also Hata and Kato 2003). Previous studies have attributed the distinct algal turfs in farmer territories to the effects of the reduction in grazing pressure from foragers (Hixon and Brostoff 1983; Hourigan 1986; Ferreira et al. 1998). Only one previous study has included an experimental design able to unambiguously separate the effects of “farming” from other mechanisms acting on farmer territories (Hata and Kato 2003). The results of this thesis suggest that the structure and development of algal communities inside territories can be

modified directly by the activities of farmers (selective feeding and weeding; Chapters 5 and 6), and not necessarily by the reduction in the grazing rates of foragers.

Chapter 6 has provided strong evidence that farmers can select locations for their territories that may be ideal for the growth of food algae or less suitable for unpalatable algae. It seems surprising that despite the knowledge that habitat selection is common in farmers (Wellington 1992; Ohman et al. 1998; Bay et al. 2001), only one previous study has tested whether this would affect the benthic composition in their territories (Hata and Kato 2003). That study found no *a priori* effect of location on the territory composition of *Stegastes nigricans*. Using a different species, *S. apicalis*, Chapter 6 found that the location of territories significantly affected the successional trajectory of algal assemblages. Rather than contradicting the previous study, these findings highlight the diversity of the effects of different farmer species and the possible variability between geographic locations.

Some studies on coral reefs could be affected by whether sampling takes place inside or outside farmer territories. This can include research on algal community structure and succession, nitrogen fixation, grazer behaviour and distribution, invertebrate distribution, fish recruitment, and also the recruitment, zonation survival and growth of corals (see review by Ceccarelli et al. 2001). Sampling locations in future studies may benefit from taking into account the local distribution of farmer species. The results of this thesis suggest that considering the full range of farmer species may be more useful than focussing only on species with visually distinct territories.

Role of foragers

It is widely accepted that foragers reduce the biomass of fleshy macroalgae, facilitating the competitive dominance of corals on coral reefs (Hatcher 1983; Steneck

1988; McCook 1996; Carpenter 1997; McCook 1997). Their decline has often been associated with phase-shifts from coral-dominated reefs to reefs dominated by algae (Hughes 1994; Lapointe 1997; McClanahan and Muthiga 1998; Hughes et al. 1999; McCook 1999). On Orpheus Island and in Kimbe Bay, the experimental exclusion of foragers resulted in a large increase in macroalgal cover and biomass (Chapters 4 and 5), at the expense of the health of the coral community (in terms of sub-lethal stress and recovery from disturbance), corroborating previous findings. Therefore, this thesis confirms that where foragers are abundant, they have a major influence on macroalgal abundance, and consequently, on the health of coral communities.

The effects of foragers are fundamentally different from those of farmers (see also Carpenter 1986; Steneck 1988; 2001). The effects of farmers are restricted to their territories, therefore their reef-wide effects as a group are dependent on the extent of their space occupation. In contrast, the wide-ranging and often schooling nature of forager behaviour means that their activities often affect the overall structure of coral reef benthic communities. On reefs with high forager densities, their grazing behaviour generally reduces the abundance of palatable algae, while cultivation by farmers tends to increase it (Chapters 4, 5 and 6). The differences in impact magnitude between these two groups of herbivores were highlighted in the three experimental chapters of this thesis. In Chapter 4, the exclusion of foragers on an Orpheus Island reef caused a phase-shift from a turf/coral assemblage to a benthic community dominated by fleshy macroalgae. In Chapter 5, the absence of foragers on a Kimbe Bay reef caused increases in palatable algae and shifts in live coral cover within a short time. The results of Chapter 6 showed that foragers can affect succession, inhibiting calcified algae from replacing fleshy macroalgae. On Orpheus Island and Kimbe Bay reefs, the dramatic shifts in overall benthic community structure occurred despite the presence of farmers.

In all three cases, the role of foragers was to maintain the overall composition of benthic communities on the reef, even when this did not lead to the suppression of fleshy macroalgae (e.g. Magnetic Island).

The relative importance of foragers and farmers in reducing macroalgal biomass has never been questioned, as the control of macroalgal abundance has always been considered a key role of foragers. Generalizations about this role are usually based on studies conducted on offshore reefs with high densities of foragers (Pennings 1996), or environments from which foragers have largely disappeared (Hughes 1994). A recent study suggested that foragers may not always be able to control the biomass of macroalgae, especially on reefs with low coral cover (Williams et al. 2001). In this thesis, the inshore reefs of Magnetic Island provided sites with low forager densities and relatively low coral cover, and foragers did not hinder the growth of macroalgae on settlement tiles (Chapter 6). In this situation, farmers (*Stegastes apicalis*) were responsible for reducing the abundance of fleshy macroalgae; without the territories of this species, there would be a 30% increase in the cover of macroalgae on the reef crest (Chapter 2). This suggests that there are situations in which farmers are more important than foragers in reducing the biomass of fleshy macroalgae.

Effects of foragers on farmers

It is generally assumed that during competitive interactions between foragers and farmers, farmers are the superior competitors that successfully defend territories from foragers. Thus it is the effect of farmers on foragers that has received the most attention. However, Chapter 4 suggests that the impact of foragers on farmers requires further investigation. When the ability of farmers to exclude foragers was supplemented by exclusion cages, both food quantity and food quality increased inside territories (Chapter 4). For some species of farmers, the territory composition that is ultimately

maintained is probably not brought about by the activities of farmers alone, but through an interaction with foragers (defence and intrusion, Chapter 4). Some species may rely on occasional grazing by foragers to aid in the removal of undesirable algae, while similar incursions into the territories of other farmer species may prove detrimental to the quantity and quality of palatable algae (Chapter 4).

Farmers may be affected by forager-mediated habitat changes as well as by changes in the abundance of foragers as competitors (Chapter 4). Farmer species are often distributed according to habitat characteristics (Ebersole 1985; Tolimieri 1995; Bay et al. 2001). The forager exclusion experiment in Chapter 4 provided the opportunity to observe the consequences to farmers of a change in habitat structure from coral/turf dominance to algal dominance. In this experiment, the farmer species that increased in abundance during the bloom of fleshy macroalgae was one which was found to inhabit large stands of *Sargassum* in another location (Chapters 2 and 3). The effects of foragers on habitat structure can influence which farmers occupy the most space and therefore have the largest impacts on benthic communities. In Chapter 4, the absence of foragers favoured a relatively large farmer species with relatively greater biomass of algal turfs in their territories. In this situation, the absence of foragers may have contributed to reef decline not only directly (through the lack of top-down control on macroalgae), but also indirectly through the spread of thicker farmer-controlled algal turfs and their detrimental effects to coralline algae (Steneck 1997) and corals (Risk and Sammarco 1982; Sammarco et al. 1986).

Effects of farmers on foragers

The results of Chapter 5 suggest that farmers may not necessarily be maintaining exclusive access to the resources in their territories. Similarly, the results of Chapters 4 and 5 suggest that farmers may not all be equally as successful at excluding

foragers as previously thought. The aggressive exclusion of foragers from farmer territories has been considered a highly effective and influential mechanism, both in modifying algal assemblages inside territories (Hixon and Brostoff 1983) and in affecting forager feeding behaviour (Robertson et al. 1976). However, it has also been shown that, aggression rates can vary between farmer species both in their intensity and in their targets (Bay et al. 2001). Many species behave aggressively towards conspecifics and congeners, and not exclusively towards invading foragers (Ebersole 1985; Robertson 1996; Bay et al. 2001).

The well-known strategy of schooling by foragers (Robertson et al. 1976) serves to periodically introduce very high grazing rates into farmer territories (pers. obs.). Farmers can increase algal productivity within their territories (Montgomery 1980b; Klumpp et al. 1987; Russ 1987; Ferreira et al. 1998), which may attract increased incursions by foragers. That is, feeding effort by foragers may be concentrated where farmer territories are abundant, instead of where they are rare as previously suggested (Doherty 1983). Recent studies have found that the highest algal productivity, forager biomass (Steneck 1997), algal yield to grazers and forager feeding effort was concentrated on reef crests (Russ 2003). Farmer territories can also occupy the most space in this reef zone (Chapter 3), but correlations between the extent of farmer territory occupation and the algal yield to foragers have yet to be explored. Farmer territories may therefore represent patches of high algal yield to foragers, possibly affecting forager feeding behaviour through facilitation rather than exclusion.

Unresolved issues

This thesis has added to the knowledge of how farmers modify benthic composition and food availability in their territories, but a number of farmer effects have not been fully explored. Only a few studies have examined how farmers affect

coral reef nutrient dynamics (Wilkinson and Sammarco 1983; Wilkinson et al. 1985; Russ 1987), and even these studies estimated only nitrogen content or nitrogen fixation. Work also remains to be done on how different species of farmers can affect corals. Potential sub-lethal effects on corals (e.g. growth rates, tissue thickness, fecundity) remain to be examined (but see Santana 2001).

Spatial and temporal variability must be considered, or at least acknowledged, in future studies on herbivore effects. Large-scale studies of farmer and forager impacts on different types of coral reefs, and at different latitudes, have yet to be conducted. Such studies could clarify the relative importance of farmers and foragers on different reef types. They would also add to our understanding of patch dynamics and diversity on coral reefs, especially on reefs with diverse farmer communities.

There are “farming mechanisms” which to date have been widely accepted but never rigorously tested. Selective feeding (Jones 1992) is not the same as weeding (Lassuy 1980; Hata and Kato 2002), and these two mechanisms cannot be expected to affect the benthos in the same way. However, these two activities have never been separated. Due to the propensity for territories to be dominated by preferred food algae, selectivity indices as a method to detect selective feeding may only be useful in situations where food availability can be controlled (Chapter 3). There is also ambiguity about the occurrence and effectiveness of fertilization inside territories, with some species defecating in patches of territory separate from feeding patches (Polunin and Koike 1987), and others defecating outside the territory boundaries (pers. obs.). It is possible that fertilization is another mechanism that is employed more by some species than others.

Foragers may not be equally effective in suppressing macroalgae on all reefs (Williams and Polunin 2001; Williams et al. 2001). This thesis has confirmed that the

effects of foragers on benthic communities vary on different reefs (see also McCook 1996). The role of foragers on the inshore reefs of the GBR would benefit from further study, especially in the light of current concerns over water quality and the degradation of reefs closer to human influence (McClanahan 2002).

The results of this thesis suggest that the effects of foragers on farmers need to be explored further, to help with the understanding of the extent to which foragers affect the species composition and distribution patterns of farmers. The results of Chapter 4 also imply that some farmer species might benefit from forager incursions, because grazing by foragers aids in the removal of unpalatable algae in their territories. The extent to which this is the case, and whether it applies to some farmer species more than others, remains to be rigorously tested.

A study on the effects of forager incursions into farmer territories would also benefit from information about the effectiveness of different farmer species in excluding foragers. In this thesis, at least one farmer species was found not to affect its territory composition by excluding foragers, however levels of aggression may differ between farmer species. It is also unclear whether some species of farmers maintain territories with algal turfs that are more attractive to foragers than others, and how the distribution of these territories might affect forager behaviour. Examining the relationship between forager feeding patterns, algal productivity and farmer territory distribution may provide valuable information about the utilization of primary productivity by both groups of herbivores.

Conclusions

In summary, this thesis confirms that farmers and foragers both play important roles on coral reefs, and that these roles are fundamentally different. The effects of farmers on their territories vary spatially and among species, but all the species included

in this thesis significantly affected benthic communities. Farmers actively cultivate algal assemblages in their territories that are higher in palatable taxa than adjacent areas. The spatial extent to which farmers influence coral reef communities is greater than was expected, indicating that their territories may contribute resources to a wide range of grazers. The role of foragers is unambiguously more wide-reaching than that of farmers in terms of affecting algae and corals on a large scale. Forager activities are important in structuring the habitat of coral reef organisms, including farmers. The interactions between foragers and farmers can affect not only farmer population densities, but also the quantity and quality of algal turfs in farmer territories. The different activities of these two groups of herbivorous fish combined are important in maintaining the structure of benthic communities on coral reefs.

In the face of declining coral reef health on a global scale, significant reductions in the abundance of either group could have consequences not only for benthic communities, but also for other herbivores. Both the overexploitation of large foragers and habitat degradation may alter the relationships between different types of herbivore. Overfishing of large foragers can cause phase-shifts in the overall benthic ecology of the reef, and the resulting change in habitat can affect farmer communities. Habitat degradation caused by destructive fishing practices and declining water quality can detrimentally affect potential farmer habitat, and a loss of farmer territories may significantly reduce food resources available to foragers. Furthermore, phase shifts to algal-dominated reefs may fundamentally alter the interactions between these two important groups of herbivorous fish. This thesis has found that both groups contribute significantly to the maintenance of the existing benthos on coral reefs, and the survival of both groups must be ensured to safeguard coral reef ecosystems.

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APPENDIX 1

Ceccarelli, D. M., Jones, G. P. and McCook, L. J. (2001) Territorial damselfish as determinants of the structure of benthic communities on coral reefs. *Oceanography and Marine Biology: an annual review* 39, 355-389

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