



Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef

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ABSTRACT

Herbivory is an important mechanism affecting algal succession, particularly on coral reefs where the relationship between algae and corals is largely controlled by herbivores. However, different functional groups of herbivores may have contrasting effects on succession, which may explain different trajectories of coral reef recovery after disturbance. Here, the effects of different herbivore groups (roving herbivores = *foragers* and territorial damselfish = *farmers*) were isolated by a multi-factorial experiment carried out on a coastal coral reef with high macroalgal cover, high farmer densities and relatively low forager abundance. The effects of foragers and farmers were distinguished by monitoring algal succession on settlement tiles placed inside and outside exclusion cages, with orthogonal treatments established inside and outside damselfish territories (with appropriate cage controls). Within 12 months, algal assemblages on ungrazed tiles inside exclusion cages proceeded rapidly from fine filamentous turfs, to corticated algae, to tough erect (e.g. *Amphiroa* spp.) and foliose (e.g. Peyssonnellidae) calcified algae. Farmers had a dramatic impact on succession, essentially arresting the development of the algal community at a point where it was dominated by palatable filamentous algae of the genus *Polysiphonia*. Fleshy macroalgae such as *Sargassum* spp. were excluded from farmer territories. In contrast, foragers did not suppress fleshy macroalgae, but rather, appeared to decelerate succession and promote a relatively diverse assemblage. In contrast to forager-dominated reefs, farmer territories did not appear to function solely as forager exclusion areas or promote algal diversity as a result of intermediate grazing pressure. The relatively strong effects of farmers observed here may represent a future scenario for coral reefs that are increasingly subject to overfishing of large grazing fishes.

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1. Introduction

Understanding the succession of coral reef benthic communities is becoming increasingly important as reefs face multiple natural and anthropogenic disturbances (Hughes et al., 2003; Webster et al., 2005; Halpern et al., 2008). One of the key factors governing the recovery of coral communities is the maintenance of settlement space and the reduction of algal overgrowth through the actions of herbivores (Mumby, 2006; Hughes et al., 2007; Birrell et al., 2008; Burkepile and Hay, 2010). The dominant coral reef fish herbivores include foragers (roving grazers that feed over large tracts of substratum, such as parrotfishes, surgeonfishes and rabbitfishes) and farmers (primarily damselfishes that defend feeding territories from foragers) (Choat

and Bellwood, 1985; Bellwood, 2003; Ceccarelli et al., 2005a). The effects of these different behavioral groups are likely to vary in space and time, depending on their relative abundance and the strength of their interactions.

Foragers have been attributed a central role in facilitating the dominance of corals over algae (Hughes, 1994; McCook, 1996; 1999; Szmant, 2001; Burkepile and Hay, 2008). They divert algal succession through intensive grazing, leading to low-diversity communities of grazer-resistant species, such as crusts and fast-growing algal turfs that are competitively inferior to adult corals (Hixon and Brostoff, 1996; Thacker et al., 2001; Hughes et al., 2007; Burkepile and Hay, 2008; Sotka and Hay, 2009; Burkepile and Hay, 2010). Farmers can halt succession at an early stage, facilitating turfs of high diversity (Hixon and Brostoff, 1996) or creating monospecific turfs of preferred food algae (Hata and Kato, 2003). Trajectories of algal succession on coral reefs are generally expected to progress from bare space to a microalgal film, and then to filamentous turf algae and crustose coralline algae, followed in turn by corticated algae, fleshy macroalgae, and erect and foliose calcified algae (McClanahan, 2000; McClanahan et al., 2001; Diaz-Pulido and McCook, 2002; Diaz-Pulido et al., 2007). The relative

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effects of foragers and farmers and the mechanisms by which they influence succession require further investigation.

The differences between farmer territories and adjacent areas have often been attributed either to the grazing regimes of foragers outside territories or active “management” of algal turf and exclusion of other grazers inside territories (Lassuy, 1980; Hixon and Brostoff, 1996; Hata and Kato, 2003, 2004; Ceccarelli et al., 2005a; Gobler et al., 2006). The potential mechanisms by which farmers control the benthic communities inside their territories include the reduction in forager grazing inside territories (Hixon and Brostoff, 1996; Ceccarelli et al., 2005a), the ‘weeding’ of undesirable algae from their territories (Lassuy, 1980; Hata and Kato, 2002), the selective consumption of preferred species (Klumpp et al., 1987; Jones, 1992) and the fertilization of algae by defecating on algal farms (Polunin and Koike, 1987; Klumpp and Polunin, 1989; Thacker et al., 2001). There is little conclusive information on when or where one mechanism is more important than the others (Ceccarelli et al., 2001) and simply monitoring differences in succession inside and outside territories cannot distinguish among these effects. Given that farmers and foragers exhibit different activities and feeding modes, and farmers exclude foragers from their territories, isolating their different effects and interactions can be difficult.

Our understanding of how herbivory affects succession on coral reefs comes predominantly from oligotrophic systems with large forager populations that effectively control algal biomass outside farmer territories (McCook, 1996; McCook and Price, 1997; Ceccarelli et al., 2006). However, there is increasing evidence of reefs with high macroalgal cover and biomass (Littler and Littler, 1984; McCook, 1996; Williams et al., 2001; Paddock et al., 2006). Such situations may become more prevalent under increasing eutrophication and temperatures, especially in coastal areas with lower forager abundance, or in situations where foragers have been overfished (Littler et al., 2006). It is important to understand the interacting effects of foragers and farmers on the benthic succession of these reefs, as farmers may become more important for mediating their recovery from disturbance. Given that farmers can collectively dominate large tracts of coral reefs, occupying up to 90% of some reef zones (Ceccarelli et al., 2001; Ceccarelli, 2007), it is critical to understand how they influence patterns of succession.

The purpose of this study was to carry out a fully orthogonal herbivore exclusion experiment on a coastal coral reef to examine patterns of succession in both farmer territories (where cages excluded farmers) and areas outside territories accessed by foragers (where cages excluded foragers). The experiment included exclusion treatments (full cages), cage controls and uncaged controls were to separate the effects of the farmer species (in this case, *Stegastes apicalis*) and forager grazing (mainly *Scarus rivulatus*, *Scarus ghobban*, *Siganus doliatus*, *Siganus argenteus*, *Naso unicornis* and *Acanthurus blochii*). The following specific hypotheses were tested:

- I. The trajectory of algal succession is different inside and outside *S. apicalis* territories.
- II. Outside *S. apicalis* territories, algal succession differs depending on the access or exclusion of foragers.
- III. Inside *S. apicalis* territories, algal succession differs depending upon the access or exclusion of the farmer. That is, direct farming activities (i.e., activities in addition to excluding foragers) alter the trajectory of succession that would otherwise occur inside their territories.

2. Material and methods

2.1. Study site and system

This experiment was conducted in Nelly Bay, on Magnetic Island, Great Barrier Reef (19°17' S, 146°86'E), for 12 months from December

2002. Experimental plots were established along the reef crest, where the abundant *S. apicalis* is the dominant farmer species (Ceccarelli, 2007). Individual *S. apicalis* aggressively exclude other grazers and potential egg predators from territories of approximately 1 m², in which the algal turf is visually distinct from surrounding areas (D. Ceccarelli, unpublished data). Large stands of *Sargassum* spp. and patches of high live coral cover characterize the benthos directly outside the territories. Forager densities on the reef crest are typical of inshore reefs (<0.02 individuals/m²) and include primarily the scarids *Scarus rivulatus* and *Scarus ghobban*, the siganids *Siganus doliatus* and *Siganus argenteus*, and the acanthurids *Naso unicornis* and *Acanthurus blochii*.

2.2. Experimental design and planned comparisons

A fully orthogonal experimental design (Fig. 1) was used to separate the effects of foragers and farmers on the successional composition of the benthic community, and to distinguish between the influence of direct management by farmers (other than excluding foragers) and territory location.

The following comparisons of the treatments enabled the testing of hypotheses I to III (Fig. 1):

- A. To test Hypothesis I, we compared uncaged tiles outside territories (Treatment 1) with uncaged tiles inside territories (Treatment 2). While this establishes whether the trajectory of algal succession is different inside, versus outside, of territories, additional comparisons are necessary to determine whether differences are due to grazing activities of either herbivore group, possible farming activities, or the interactions of foragers and farmers.
- B. To test Hypothesis II, we compared caged tiles outside territories (Treatment 5) with cage controls outside territories (Treatment 3). This measures the effects of foragers with any cage artifacts

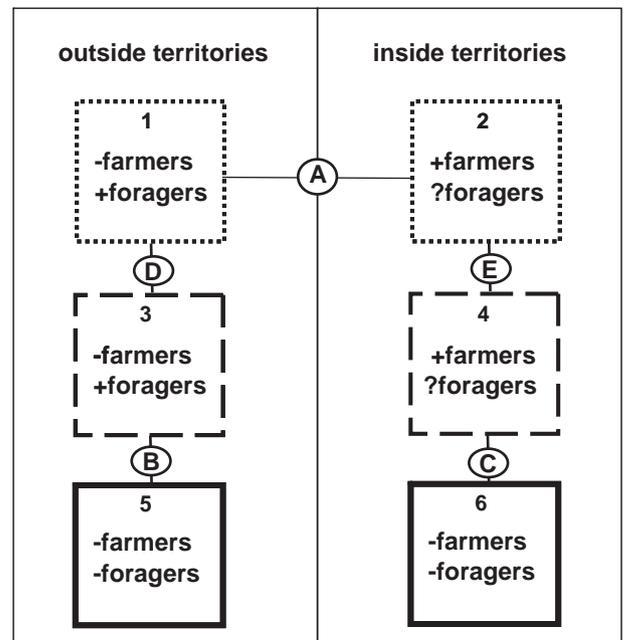


Fig. 1. Sampling design for the experiment, showing orthogonal design and the effects measured with each comparison. Comparison labels correspond with hypotheses tested for each pair of treatments (Comparisons A–C test Hypotheses I to III). Dotted lines: open plots; dashed lines: partial cages; unbroken lines: full cages. Farmers: Territorial damselfish; Foragers: Roving herbivores. In treatments 2 and 4, where foragers are excluded by farmer aggression, it is assumed that foragers may have some influence. The numbers correspond to treatments, which were replicated 5 times. Each square represents a rack of 10 tiles, and collections were made 4 times over a 12 month period.

removed. It tests whether algal succession differs depending on the access or exclusion of foragers outside *S. apicalis* territories, taking into account any cage artifact effects.

- C. To test Hypothesis III, we compared caged tiles inside territories (Treatment 6) with cage controls inside territories (Treatment 4). This allowed us to estimate the effects of direct farmer activities, other than the exclusion of foragers, on the communities in their territories, taking into account any cage artifact effects. This includes all potential effects resulting from direct farming activities (i.e. activities in addition to excluding foragers) on the trajectory of succession that inside their territories. In addition to testing the main hypotheses, we also examined whether the cages themselves were influencing patterns of succession.
- D. Comparing uncaged tiles outside territories (Treatment 1) with partially caged tiles outside territories (Treatment 3) tested the effects of the cage artifact on the composition and succession of the benthic community outside territories.
- E. Comparing uncaged tiles inside territories (Treatment 2) with partially caged tiles inside territories (Treatment 4) tested the effects of the cage artifact, other than the effect of excluding foragers, inside territories.

2.3. Experimental protocol

Succession was examined by examining colonization of ceramic tiles. Ten rugose ceramic tiles, 5 by 10 cm in area, were fixed to metal racks (0.5 m by 0.5 m) 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 (Appendix A). 30 metal racks were then secured to the reef substratum with a mallet, bringing the tiles were as close to the benthos as possible. Five replicates of each treatment were allocated randomly to positions inside and outside territories on the reef crest. Fifteen racks were placed inside randomly chosen *S. apicalis* territories, and fifteen in nearby areas that were as similar as possible to *S. apicalis* territories in terms of topography 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 ten racks (also 5 inside and 5 outside territories) were partially enclosed by the oyster mesh, and used as cage controls. Observations during the course of the experiment indicated that both foragers and farmers grazed inside the open-sided cages. The last set of 10 racks was left uncaged. Sets of racks were haphazardly distributed within each habitat type, with at least 3 m between individual racks.

The tiles were collected four times over the year, approximately every three months. At each sampling occasion, two tiles were removed from each rack and treated as subsamples (10 tiles per treatment per sampling occasion = 240 tiles over 12 months). The tiles were enclosed in clip seal plastic bags and frozen immediately upon leaving the study site. The tops of the tiles were sampled with a stereomicroscope with a 1 cm grid, identifying the benthos under each of 54 randomly chosen points. Taxa were identified to genus, or to species where possible, and detritus was also quantified as a potential food source for the resident farmers. For the purposes of exploring succession on the tiles, algal taxa were also summarized into functional groups (Appendix B, Steneck and Dethier, 1994).

2.4. Statistical analyses

Diversity was assessed by calculating the Shannon–Weaver Diversity Index H' , as outlined in Krebs (1989). Multivariate ANOVA was used for community-level analyses, with a priori planned comparisons for each combination of treatments (and testing the Time \times Treatment interaction term) as described above. The results of

the MANOVA (carried out in SPSS for Windows[®]) included individual effects for each variable in the analysis, while automatically controlling for errors associated with using each treatment in multiple comparisons. We used non-metric, multi-dimensional scaling analysis (MDS, Clarke and Gorley, 2006) on the Bray–Curtis resemblance matrix of transformed arcsine percentage cover of each species to delineate the community-level successional trajectories of the six treatments, using Primer[®].

3. Results

3.1. Comparison A: Succession inside and outside farmer territories

The hypothesis that succession differs significantly in areas accessed by either farmers or foragers as a result of independent effects or their interaction was supported. Different algal assemblages developed on uncaged tiles inside territories and exposed to farmer activities, from those that were found on uncaged tiles outside territories, which were exposed to the activities of foragers (Table 1, Fig. 2a). Uncaged tiles inside territories were covered in filamentous algae such as *Polysiphonia* spp. within the first three months and changed very little for the rest of the year, while the algal community on uncaged tiles outside territories developed further within the same timeframe, towards higher cover of fleshy macroalgae and calcified Peyssonnellids (Fig. 2a).

More detailed taxonomic assessments showed that on uncaged tiles inside territories, *Callithamnion* spp. bloomed within the first three months and then declined to below 5% cover by the middle of the year, but algae of the genus *Polysiphonia* continued to flourish and became dominated by *Polysiphonia herpa* (Fig. 3). Uncaged tiles outside territories rapidly progressed from fine filamentous turf to more complex corticated algae and subsequently fleshy macroalgae. These tiles initially developed less filamentous algae (e.g., only half the cover of *Callithamnion* as on tiles inside territories, Fig. 3) and then progressed to a 50% cover of more complex, corticated algae such as *Laurencia implicata*. By the end of the year, a 20% cover of fleshy macroalgae had grown on these tiles (Fig. 3). Detrital cover increased more rapidly on the tiles inside territories than on tiles outside territories. By the end of the year, however, the cover of detritus in both treatments had declined to approximately 15% (Fig. 3).

3.2. Comparison B: Forager effects

Foragers had a major impact on the development of algal communities outside farmer territories, affecting all major benthic and algal groups (Table 2), confirming the hypothesis that grazing by foragers can significantly modify succession, even when present in low densities (Table 1, Fig. 2b). Caged tiles outside territories represent the closest treatment to ungrazed succession, and the algal community developed rapidly towards an assemblage dominated by fleshy macroalgae and tough, calcified taxa. Where foragers had

Table 1

Results of MANOVA with a priori planned comparisons for the succession of the algal assemblage on the tiles. The results presented are those from the Time \times Treatment interaction test. Cage effect results are given for inside and outside territories.

Comparison	Pillai's Trace Value	F _(14,205)	p
A. Combined effect	0.363	8.358	0.0001
B. Forager effect	0.234	2.17	0.0001
C. Farming effect	1.182	3.102	0.0001
D. Cage effect inside ^a	0.141	2.398	0.04
E. Cage effect outside ^a	0.125	2.096	0.013

^a Between-subjects tests show that only Peyssonnellidae were affected by the cage artifact, both inside and outside territories (Table 2).

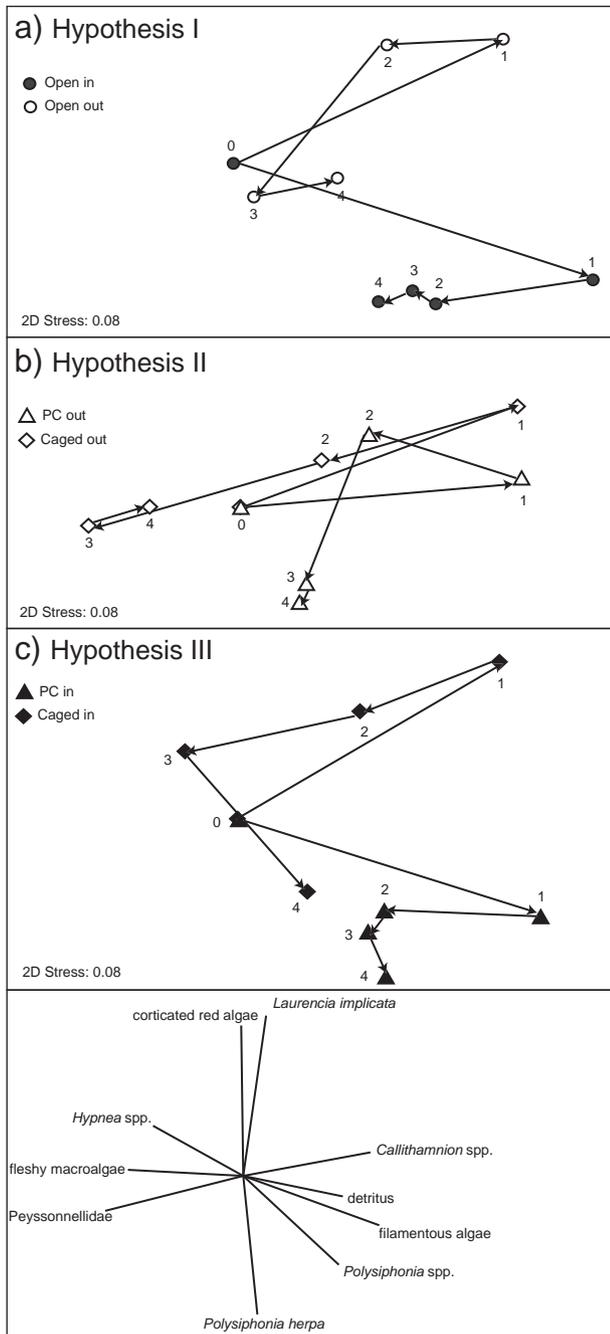


Fig. 2. MDS of the successional trajectories of the algal assemblages in the 6 treatments relative to the major benthic groups (Bray–Curtis similarity matrix of arcsine-transformed percent cover estimates). Arrows show the temporal trajectory of each treatment, starting from deployment of the tiles (Time 0). The MDS is presented in four panels for ease of interpretation, with the bottom panel depicting the eigenvectors for each tested benthic category or algal taxon. Successional trajectory panels correspond to a) Hypothesis I/Comparison A; b) Hypothesis II/Comparison B; c) Hypothesis III/Comparison C. PC: partial cages.

access, succession proceeded from early-successional filamentous algae to a community rich with corticated red algae and fleshy macroalgae (Fig. 2b).

Within the first three months, partially caged tiles outside territories were covered primarily in *Callithamnion* sp. and a smaller percentage of *L. implicata* and *Polysiphonia* spp., and then progressed to a fleshy macroalgal cover of approximately 20% (Fig. 4). Where foragers were excluded, the cover of filamentous algae increased rapidly, but was quickly replaced by crustose algae such as *Peyssonnellidae* (Fig. 2b). The

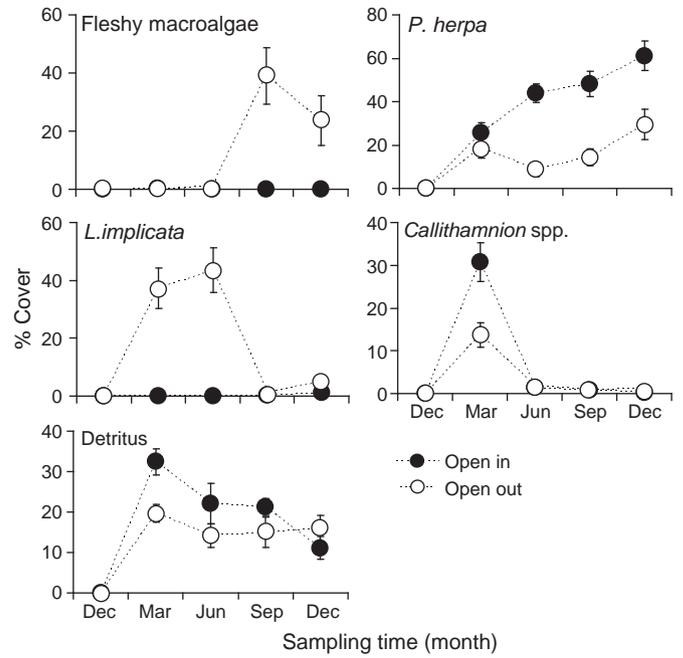


Fig. 3. Effects of foragers and farmers (Comparison A) on individual taxa, as measured by changing % cover over time. Note differences in the y-axes. Error bars = 1 S.E.

caged tiles initially developed higher cover of *Polysiphonia* spp., but only half the cover of corticated red algae (Fig. 4). Algal diversity (H') increased significantly as a result of forager access to tiles outside territories, reaching an average of 0.46 (± 0.06 S.E.) on partially caged tiles and 0.33 (± 0.04 S.E.) on closed tiles outside territories.

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. The results presented are those from the Time \times Treatment interaction test. 'NS' symbolizes variables that did not show a significant response to the treatments. Arrows show the direction of the effect. Two arrows pointing in opposite directions indicate either a brief suppression or a short-lived 'bloom' caused by the relevant effect. For example, in Row 4, Column 5, arrows indicate that farmer manipulation resulted in the initial suppression of corticated red algae, followed by an increase. Arrows for the Combined Effects column indicate the trajectory inside territories. F-values for *Peyssonnellidae* affected by cage effects are given for inside and outside territories (inside/outside). Taxa that did not respond significantly to any treatment include: *Polysiphonia ferulacea*, *Polysiphonia infestans*, *Herposiphonia* spp., *Ceramium* spp., *Spermothamnion* spp., *Champia* spp., *Tolyptocladia* spp., *Gelidiopsis* spp., and *Jania* spp.

	A. Combined effects	B. Forager effects	C. Farmer effects	D. and E. Cage effects
Fleshy macroalgae	9.243↓	4.478↑	NS	NS
Corticated red algae	35.531↓	NS	4.326↑	NS
<i>Hypnea</i> spp.	NS	NS	3.253↑	NS
<i>L. implicata</i>	43.608↓	NS	7.64↑	NS
<i>Chondria</i> spp.	NS	4.365↑	NS	NS
Filamentous algae	NS	3.372↑	NS	NS
<i>Polysiphonia</i> spp.	NS	7.381↑	4.962↑	NS
<i>P. herpa</i>	60.142↑	NS	7.027↑	NS
<i>Callithamnion</i> spp.	6.104↓	2.967↑	13.167↓	NS
<i>Amphiroa</i> sp.	NS	NS	4.348↓	NS
<i>Peyssonnellidae</i>	NS	4.571↓	4.293↓	10.04/7.32↑
Encrusting corallines	NS	2.799↓	2.137↓	NS
Detritus	7.77↑↓	6.371↑↑	4.417	NS
Diversity (H')	NS	4.586↑	3.968↓	NS

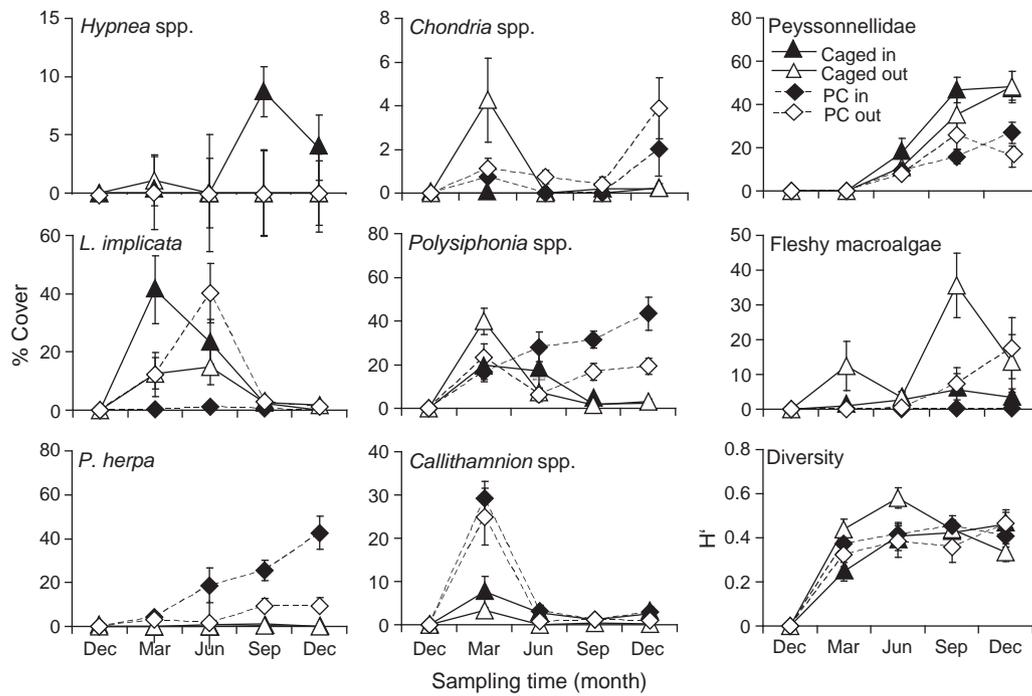


Fig. 4. Effects of foragers and farmers (Comparisons B and C, respectively) on individual taxa, as measured by changing % cover over time (note that the y-axis for the last panel 'Diversity' represents the Shannon–Weaver Index H'). The effects of foragers are shown by comparing 'caged out' with 'partial cage (PC) out' treatments (Comparison B). The effects of farmers are shown by comparing 'caged in' with 'PC in' treatments (Comparison C). Note differences in the y-axes. Error bars = 1 S.E.

3.3. Comparison C: Farmer effects

The benthic community on the tiles was significantly altered by farmer activities within territories, supporting the hypothesis that direct management (weeding and selective feeding) by farmers affects algal succession (Table 1). Farmers significantly affected the trajectories of most benthic groups (Table 2). In fact, the community-level response to the treatments was essentially split between tiles to which the farmers had access, and tiles where farmers had no access (Fig. 2c). Partially caged tiles inside farmer territories showed a trajectory that indicated a decelerated or halted succession, with the algal assemblage remaining at an early stage dominated by delicate filamentous algae. These tiles were quickly dominated by polysiphonaceous algae to the exclusion of most other taxa. Caged tiles inside territories initially developed similarly to caged tiles outside territories, but over the following nine months, corticated red algae gave way to an assemblage of encrusting coralline algae, Peyssonellidae and the erect calcified algae of the genus *Amphiroa* (Fig. 4).

3.4. Comparisons D and E: Cage effects

The cage artifacts 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 artifact, both inside and outside territories, were calcified algae of the family Peyssonellidae (Table 2, Fig. 5). The difference in percent cover of Peyssonellidae was greater between partial cages and full cages than between partial cages and open treatments (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.).

4. Discussion

Understanding algal succession and the influence of herbivory is central to the development of knowledge about how coral reef ecosystems may respond to and recover from increasing anthropogenic pressures (e.g., Diaz-Pulido and McCook, 2002). However,

different herbivore groups can exhibit quantitative and qualitative differences in their influence on successional trajectories (Hixon and Brostoff, 1996). The results of this study highlight the pronounced and different effects farmers and foragers can have on coral reef benthic succession. *S. apicalis* on a fringing inshore reef of the Great Barrier Reef actively manipulated the algal community in their territories to grow a dense turf of palatable algae. Overall, the numerically dominant farmers had more dramatic effects than foragers on algal succession in this system. However, foragers also directly impacted succession, effectively decelerating the rate of succession to a diverse community that included macroalgae.

Succession followed different trajectories inside and outside territories, indicating differential effects of the two herbivore groups through a variety of potential mechanisms. It appears that succession was dramatically decelerated under the influence of farmers, remaining at an 'early' stage where it was dominated by filamentous

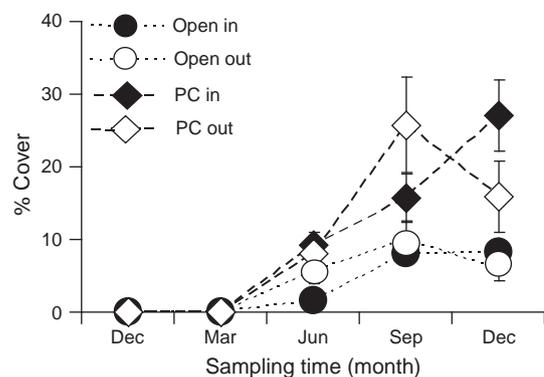


Fig. 5. Effects of cage artifacts (Comparisons D and E) on Peyssonellidae, as measured by changing % cover over time. The caging effects outside territories are shown by comparing 'Open out' with 'PC out' treatments (Comparison D). The caging effects inside territories are shown by comparing 'Open in' with 'PC in' treatments (Comparison E). Note differences in the y-axes. Error bars = 1 S.E.

algae of the genus *Polysiphonia*. Hixon and Brostoff (1996) also found that succession inside damselfish territories was decelerated, but at a later stage, resulting in a highly diverse mid-successional algal assemblage. In our study it was the foragers that appeared to play the role of ‘intermediate impact’ grazers, facilitating a diverse assemblage of corticated and fleshy macroalgae over the 12-month period. This difference in outcome may reflect variation in the relative abundance of the two herbivore groups in the different study systems.

4.1. Effects of foragers

Feeding by large herbivores is usually responsible for reducing algal biomass (Steneck, 1988; Bellwood and Choat, 1990; McCook, 1996; Pennings, 1996; McCook and Price, 1997; Williams et al., 2001; Paddack et al., 2006) and, in some cases, enhancing coral cover (Burkepile and Hay, 2008). The role of grazing pressure by herbivores usually results in the ‘facilitation’ or acceleration of succession to proceed towards a relatively ‘mature’ community – one dominated by fleshy macroalgae, calcified and encrusting algae (Sousa and Connell, 1992; Zanini et al., 2006) or in the diversion of succession to an alternative community not otherwise found in ungrazed systems (Hixon and Brostoff, 1996; Littler et al., 2006). In our study, the activities of foragers on the reef crest decelerated succession to result in a diverse ‘mid-successional’ assemblage that included corticated red algae and fleshy macroalgae, but not a ‘late-successional’ assemblage of fleshy macroalgae and erect calcified algae. Foragers did not prevent the establishment of fleshy macroalgae such as *Sargassum* spp. and *Padina* spp.

4.2. Effects of farmers

The effects of farmers on algal succession were completely different and much more dramatic than the effects of foragers, stopping 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). 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 varies (Lassuy, 1980; Hinds and Ballantine, 1987; Hixon and Brostoff, 1996), suggesting that each farmer species may use a different mechanism for maximizing the abundance of palatable algae in its territories (Ceccarelli et al., 2001; Hata and Kato, 2004). Inside its territories, *S. apicalis* appears to directly and actively promote an algal assemblage dominated by *P. herpa*. Gut contents analysis conducted on *S. apicalis* on Magnetic Island found a dominance of polysiphonaceous algae, but included corticated red algae and detritus, which were also present inside territories (Ceccarelli, 2007). This study provides an alternative to the two patterns already found in the literature: *S. apicalis* neither cultivated a monoculture (Montgomery, 1980; Hata and Kato, 2003), nor enhanced overall algal diversity (Hixon and Brostoff, 1983), but actively promoted a unique algal assemblage most suitable to its resource requirements. These results add to the evidence that different species of damselfishes manipulate the development of algal communities in their territories based on a combination of their preferences and the availability of food algae in their immediate environment (Hata et al., 2010).

In our study, farmers were not equivalent to cages, suggesting that the effects this species of farmer were not solely due to forager exclusion. Succession on caged tiles outside territories included an early stage dominated by filamentous algae, a later stage with corticated and fleshy macroalgae, which were then replaced by calcified algae, while succession on uncaged tiles inside territories remained dominated by filamentous algae. Grazing by farmers has generally

been demonstrated to have a lesser impact on benthic communities than grazing by foragers (Ogden and Lobel, 1978; Horn, 1989; Ceccarelli et al., 2005a). Furthermore, it is commonly assumed that the exclusion of foragers by farmers further reduces grazing rates inside territories (Hixon and Brostoff, 1996), although grazing has been found to be highest inside territories by some studies (Russ, 1987; Booth, 1998). In fact, some damselfish territories may parallel frequently grazed areas referred to as ‘grazing lawns’ in terrestrial systems (van der Graaf et al., 2005). Although it may be relevant to some farmer species, the modification of grazing rates through farmer aggression can no longer be considered the primary mechanism by which all farmers create the benthic assemblages inside their territories.

4.3. 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 (Ceccarelli et al., 2005b) were not suppressed by foragers at the densities found there. A threshold exists below which grazer densities cannot control macroalgal dominance on coral reefs (Mumby et al., 2007). While this threshold has been modeled in the context of overfishing of foragers, it may also apply across natural gradients of forager abundance.

In contrast, *S. apicalis* defended territories in which they promoted algal communities that were visually and taxonomically distinct from surrounding areas. Other studies have also concluded that the impact of herbivory on any given reef will reflect the type of herbivore; for instance, reefs with low fish herbivore densities can instead show the denuding effects of herbivorous sea urchins (Ogden and Lobel, 1978; Carpenter, 1997). Similarly, the relative importance of foragers and farmers may change along environmental and geographic gradients, with farmers becoming more effective at controlling or changing algal communities as forager influence decreases. On some reef systems, farmer territories of a single species have been found to occupy up to 87% of the substratum (Ceccarelli et al., 2005a). On the Nelly Bay reef crest, approximately 30% of the substratum is occupied by *S. apicalis* territories (Ceccarelli et al., 2005b); the pronounced effects of these farmers are therefore structuring benthic communities on one-third of the reef crest. Typically, each reef zone is shared by a number of cohabiting farmer species, each with subtly different effects on benthic communities (Ceccarelli, 2007).

The significance of farmer and forager effects for mediating coral–algal interactions depends strongly on the resulting algal community. Thick turfs and fleshy macroalgae have been found to be the most damaging to coral survival and regeneration, but crustose coralline algae can enhance recruitment (Birrell et al., 2008; Arnold et al., 2010). However, the direct interaction between corals and thick turfs, which tend to dominate farmer territories, can be further complicated by activities of the farmers themselves, which can actively kill corals (Jones et al., 2006), but can also exclude coral predators (e.g., Glynn and Colgan, 1988; Gochfeld, 2010) and external bioeroders (e.g., Sammarco and Williams, 1982). Therefore, while most research suggests that foragers are crucial to coral resilience (Mumby and Steneck, 2008; Hughes et al., 2010), there is still not enough information to determine whether farmer effects are beneficial or detrimental to coral communities.

4.4. Conclusions

Farmers do not simply act as herbivore exclusion treatments, but actively select suitable locations for their territories and subsequently actively cultivate them, dramatically altering the successional pathways and benthic communities within them. In this system, farmers

appear to replace foragers as the herbivore group with the greatest effects on coral reef algae. It remains to be tested whether this is also the case on reefs where large herbivores have been overfished, but in areas of high occupancy by damselfish territories, farmers may exert a strong control on succession. This study suggests that including farmers may be necessary in research that aims to adequately quantify the effects of fish herbivory on coral reefs. Coastal coral reefs under increasing anthropogenic pressure may be areas in which the generally accepted paradigms of herbivore control on macroalgae no longer apply.

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