

Algal assemblages associated with *Stegastes* sp. territories on Indo-Pacific coral reefs: Characterization of diversity and controls on growth

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Abstract

Herbivorous fish occupy an important niche in coral reef ecosystems. Specifically, damselfish of the genus *Stegastes* have been shown to have a significant impact on coral community structure and algal assemblages. This study investigated the algal communities associated with *Stegastes* territories of the Indo-Pacific (Fiji, Solomon Islands, and Tonga), while concurrently examining the effects of nutrient enrichment and herbivore exclusion (alone and in unison) on these communities. Results evidenced differences in species composition, percent cover, and algal growth rate between *Stegastes* territories and non-*Stegastes* sites and between control sites and treatment sites. *Stegastes* territories consistently displayed a greater abundance of turf algae than non-*Stegastes* sites; the two main genera of turf algae observed at all sites were *Polysiphonia* and *Ceramium*. Although non-*Stegastes* sites in Fiji, the Solomon Islands, and Tonga showed a greater percent coverage of macroalgae, they contained fewer algal species compared to *Stegastes* territories. In Fiji, red macroalgae decreased in the herbivore exclusion treatments, while brown macroalgae increased significantly in the herbivore exclusion and nutrient treatments. The combined effect of the herbivore exclusion and nutrient treatment at this location yielded a significantly increased turf algae growth rate compared to control sites. Growth rates of turf algae in the Solomon Islands and Tonga increased significantly in caged treatments, suggesting that damselfish of the genus *Stegastes* can play an important role in maintaining cropped algal beds. In summation, the results demonstrated that *Stegastes* sustains distinct algal assemblages which may be disrupted by reduced grazing and/or eutrophication.

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1. Introduction

Herbivorous fish maintain an important position in the coral reef system, as they influence algal growth and

diversity and alter coral community structure (Steneck, 1988; Ceccarelli et al., 2001; Smith et al., 2000; Thacker et al., 2000). Herbivorous grazing has been shown to affect algal diversity in many ways. Herbivores can enhance algal diversity by exposing new substrates upon which algae can grow, by consuming the more competitive algae — relieving competition for the non-dominating algae, and by fertilizing their grazing areas with fecal material (Smith et al., 2000; Thacker et al., 2000).

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Conversely, they can also decrease algal diversity by selective removal of specific species (Thacker et al., 2000).

Bottom-up factors, such as nutrient loading, have also been shown to affect coral reef communities, particularly in regions where the top-down control of herbivorous grazing has been reduced (Steneck, 1988; Lapointe, 1997; Smith et al., 2000; Thacker et al., 2000). In reef environments where key herbivores have been removed by overfishing, a phase shift can occur, as coral-dominated communities are succeeded by an overgrowth of macroalgae (Hughes, 1994). For example, reefs in the western Atlantic became overgrown with macroalgae when *Diadema antillarum* populations were drastically reduced by disease and herbivorous fish populations were diminished by overfishing (Hughes, 1994; Jackson et al., 2001). Studies conducted on the reefs around the globe also suggest that excess nutrients promote enhanced productivity and biomass of macroalgae (Lapointe, 1997; Miller et al., 1999; Smith et al., 2000; Thacker et al., 2000). Moreover, Littler and Littler (1984) suggest that macroalgae dominate when nutrients are high and grazing is low.

One group of herbivorous grazers that is known to have a significant impact on coral reef structure and algal abundance is the damselfish family (Pomacentridae), in particular, the genus, *Stegastes* (Ceccarelli et al., 2001). *Stegastes* is found throughout coral reef ecosystems and is known to be herbivorous and territorial (Allen, 1975; Montgomery, 1980a,b; Ferreira et al., 1998; Hata and Kato, 2002). Damselfish territories can have a greater

biomass, rate of productivity, and species diversity of algae than areas on the reef not defended by these fish (Brawley and Adey, 1977; Montgomery, 1980a,b; Hixon and Brostoff, 1981, 1996; Klumpp et al., 1987; Zeller, 1988). The daily activities of damselfish, which include farming for preferred species, killing corals, and guarding their territory from other herbivorous fish, play an important role in structuring the algal community on the reef (Potts, 1977; Irvine, 1980; Lassuy, 1980; Lobel, 1980; Montgomery, 1980a; Polunin and Koike, 1987; Klumpp and Polunin, 1989; Branch et al., 1992; Ferreira et al., 1998; Hata and Kato, 2002). This is demonstrated by *Stegastes fasciolatus*, which typically defends a lush feeding territory that consists of primarily filamentous algae-covered reef rock (Myers, 1999; Hata and Kato, 2002). *S. fasciolatus* has been observed to aggressively drive away other fish, particularly competitive herbivores (Amesbury and Myers, 1982; Losey, 1982). The selective feeding habits of the damselfish may reduce the abundance of specific algal species and create space for the preferred species (Lobel, 1980; Montgomery, 1980b; Zeller, 1988). In addition, the highly territorial behavior of many damselfish reduces grazing by other fish in the area (Doherty, 1983). Previous studies of *Stegastes* have shown that damselfish territories maintain a higher biomass of algae than undefended areas (Hixon and Brostoff, 1981, 1996; Klumpp et al., 1987).

The goal of this study was to assess the effect of grazing by *Stegastes* spp. on algal assemblages within coral reefs of the Indo-Pacific, while concurrently examining the relative impact of nutrient loading on the

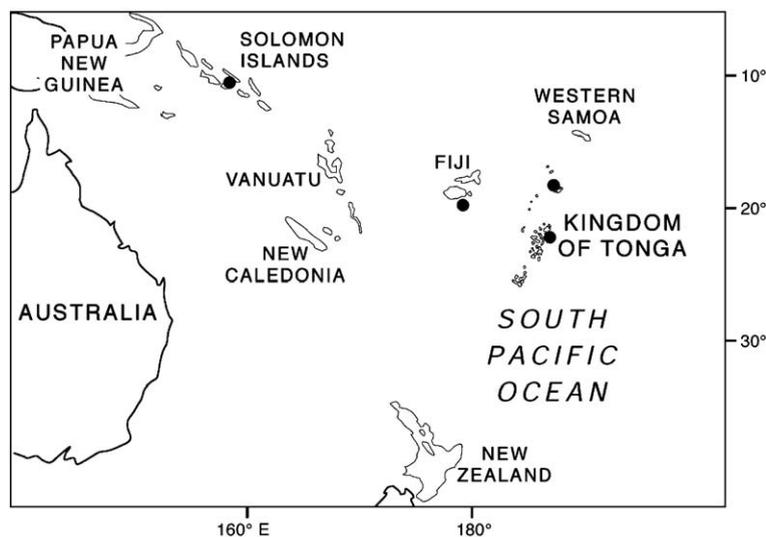


Fig. 1. A map depicting the four study locations: Dravuni, Fiji; Uepi Island, Solomon Islands; Vava'u, Tonga (northern point); Ha'apai, Tonga (southern point).

Table 1
Methodological approach for each study site

Country	Island	<i>Stegastes</i> sp. studied	Experiment conducted	Analysis conducted during each experiment
Fiji	Dravuni	<i>S. nigricans</i>	Caged grazer exclusion, nutrient addition	Growth rate of turf algae, change in percent cover
Solomon Islands	Uepi	<i>S. nigricans</i> , <i>S. lividus</i>	Caged grazer exclusion, nutrient addition	Growth rate of turf algae, change in percent cover
Tonga	Vava'u	<i>S. fasciolatus</i>	Caged grazer exclusion only	Growth rate of turf algae, change in percent cover
Tonga	Ha'apai	<i>S. fasciolatus</i>	Caged grazer exclusion only	Growth rate of turf algae, change in percent cover

growth of algae in their territories. Herbivory has long been recognized as having a profound mitigating effect on the algae of coral reefs (Hatcher and Larkum, 1983; Hay, 1985; Carpenter, 1986), while nutrient enrichment may dramatically increase algal biomass on reefs (Lapointe, 1997). The objective of this study was to examine the interaction between these opposing factors on algal growth within *Stegastes* territories. In this study, observations were made and short term experiments were conducted on the shallow tropical reefs of Fiji, the Solomon Islands, and Tonga, where most aspects of coral reefs have been poorly studied despite the impact human population expansion has had on some of these ecosystems (Hoffman, 2002; Graham et al., 2005). Our results bring insight into the critical role *Stegastes* spp. plays in these coral reefs and provide an understanding of how the loss of these fish and/or eutrophication may impact the growth of algae in these systems.

2. Materials and methods

Research was conducted on three island nations in the Indo-Pacific: Fiji, the Solomon Islands, and Tonga (Fig. 1; Table 1). Experiments were conducted on the windward fringing reefs of Dravuni Island, Fiji (18° 48' S, 178° 36' E; Fig. 1), a 200-acre island which hosts the University of the South Pacific field station and is surrounded by the Osborne Atoll (also known as the Great Astrolabe Reef). *Stegastes* territories, occupied by the Dusky Gregory, *Stegastes nigricans*, were abundant throughout the shallow fringing reefs of Dravuni Island, covering dead coral rock and large, dead round corals. In the Solomon Islands, our study sites were the shallow reefs of Uepi Island (8° 24' S, 157° 55' E; Fig. 1), a 400 km² island which is a barrier reef to New Georgia and Vangunu in the Solomon Islands. The *Stegastes* territories around Uepi Island were found on and within dead, branching staghorn coral on the reef platform of a trench connecting the lagoon with the open sea. The territories studied in the Solomons were occupied by the Dusky Gregory, *S. nigricans* and the Bluntnout Gregory, *Stegastes lividus*. Research was also performed on two island groups within the Kingdom of Tonga: Ha'apai (19° 48' S, 174° 22' W; Fig. 1) and Vava'u (18° 40' S, 173° 56'

W; Fig. 1). In the Ha'apai group, the study was conducted in Pangai on the leeward side of the island of Lifuka. Within the Vava'u island group, research was conducted on the main island near Utulei, at a site located adjacent to the Port of Refuge. Tongan sites were generally patch reefs surrounded by a sandy substrate located within 50 m of shore. These territories were inhabited by *S. fasciolatus*, and algal beds were maintained within 5 to 10 m of water. Each site was selected for the relatively pristine nature of the coral reef systems and the proximity of services which could facilitate SCUBA diving.

In each location, the algal communities within *Stegastes* territories and non-*Stegastes* sites were assessed, with each site typically comprised of ~ 1 m² area. The damselfish within the territories were identified to species level. Percent cover of algae was estimated within *Stegastes* territories and non-*Stegastes* sites (Fiji, $n=20$; Solomons, $n=30$; Tonga, $n=15$) using 100 cm² quadrats placed within each site (Fiji and Solomons, $n=15$; Tonga, $n=6$). Percent cover was estimated by noting the genus of algae present within each quadrat and the approximate area occupied by each alga. Replicated observations of quadrats by independent observers yielded nearly identical estimates of percent cover using these techniques during this study. Non-*Stegastes* sites were generally located within <5 m of *Stegastes* territories and represented regions of similar depth and reef morphology. The relative abundance of algae within quadrats was sometimes more than 100% due to epiphytic growth and algal layering. In all locations, samples of algae were taken from each site by means of a razor blade ($n=5$ per site) and identified visually and/or by light microscopy to the genus level (Littler and Littler, 2003). The algae were grouped by division (Rhodophyta — red, Chlorophyta — green, Phaeophyta — brown) and as 'turf-forming' or 'macroalgae'.

Experiments were conducted to evaluate the impact of grazer exclusion and nutrient loading on algal growth in *Stegastes* territories (Table 1). In Fiji and the Solomon Islands, 12 *Stegastes* territories were utilized: three were caged, three had nutrients added, three had both, and three were used as controls ($n=3$ for all). In Tonga, three caged sites and three control sites were examined. Cages

had all visible fish removed at the commencement of experiments and remained fish-free throughout the experiments. At nutrient treatment sites, Osmocote slow-release fertilizer was placed into weighted nylon sacks, positioned on the bottom. At the end of experiments, recovering, drying and weighing nutrient sacks indicated that 1.2 ± 0.6 (avg \pm stdev) g *N* and 0.36 ± 0.18 g *P* were released into the water column per day during experiments. The depth of all cages was approximately 3 m. In Fiji and the Solomon Islands, the 0.5 m³ cages were made of PVC piping and covered with monofilament netting with a 1 cm mesh size, which attenuated incoming irradiation by $13.3 \pm 7.1\%$ (as measured by a submersible Li-1400 LiCorr light meter). Skirts, constructed from window screening, were used to completely enclose the territory along the uneven

bottom. The cages were arranged in three replicated areas, each containing three treatments and a control. Experiments were carried out for 7 days in Fiji and 5 days in the Solomon Islands. In Tonga, the 0.30 m³ cages were constructed of monofilament netting with 2 cm openings. These enclosures were left over three different territories for 5 days in Ha'apai and for 8 days in Vava'u. Estimated water flow rates based on particle movement (m s^{-1}) were not measurably different between locations inside and outside of either cage type. Height of turf algae (Fiji, $n=9$; Solomons, $n=15$; Tonga, $n=15$) was measured with rulers at the start and the end of each experiment in order to calculate growth rate. Individual height measurements were pooled within each treatment or control replicate to obtain replicate means. Upon the conclusion of each experiment, the

Table 2
Algal species composition within and outside of *Stegastes* territories on Indo-Pacific coral reefs

Algae	Type	Fiji		Solomons		Ha'apai, Tonga		Vava'u, Tonga	
		Territory	Outside	Territory	Outside	Territory	Outside	Territory	Outside
<i>Acetabularia</i> sp.	Green	X	X						
<i>Amphiroa</i> sp.	Red, macro						X	X	X
Blue green, filamentous	Turf			T		T			
<i>Boodlea</i> sp.	Green					X		X	
<i>Botryocladia</i> sp.	Red, macro	X							
<i>Bryopsis</i> sp.	Green					T	X		
<i>Caulerpa</i> spp.	Green	X	X					X	X
<i>Ceramium</i> sp.	Red, turf	T		T		T		T	
<i>Champia</i>	Red, turf			T					
<i>Chladophora</i> sp.	Green					T			
<i>Codium</i> sp.	Green	X							
<i>Dictyosphaeria</i> sp.	Green	X							
<i>Dictyota</i> sp.	Brown	X						X	X
<i>Digenea</i> sp.	Red, macro		X					X	
<i>Galaxaura</i> sp.	Red, macro	X	X				X		
<i>Gelidiella</i> sp.	Red, macro	X				X	X		
<i>Halimeda</i> sp.	Green	X	X			X	X	X	X
<i>Hypnea</i> spp.	Red, macro				X			X	
<i>Laurencia</i> sp.	Red, macro						X		
<i>Liagora</i> sp.	Red, macro		X						
<i>Lobophora</i> sp.	Brown					X		X	
<i>Laurencia</i> sp.	Red, turf			T					
<i>Monosporus</i> sp.	Red, macro							X	
<i>Padina</i> sp.	Brown					X	X	X	X
Parenchymatous, red	Red, turf	T	X	T					
<i>Peyssonnelia</i> sp.	Red, macro	X	X						
<i>Polysiphonia</i> sp.	Red, turf	T		T		T		T	
<i>Pterocladia</i> sp.	Red, macro	X							
<i>Struvea</i> sp.	Green					X			
<i>Turbinaria</i> sp.	Brown					X	X		X
<i>Valonia</i> sp.	Green	X							
<i>Ventricaria</i> sp.	Green	X							
<i>Wrangelia</i> sp.	Red, turf			T				T	

'X' indicates the presence of the non-turf algae within the region, whereas 'T' signifies that the algae is a primary turf component. Red algae are divided into macroalgae and fine filamentous algae which are part of the algal turf within territories.

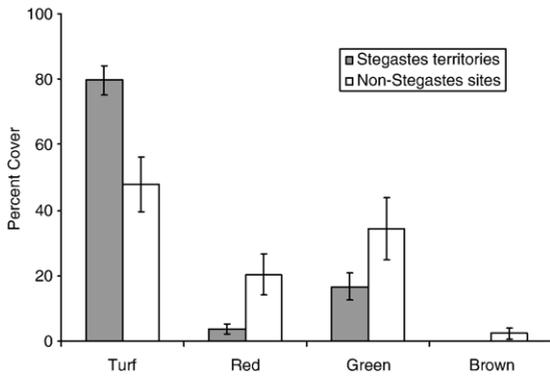


Fig. 2. Mean percent coverage of turf algae and macroalgae (red, green, and brown) within *Stegastes* territories (gray bars) and non-*Stegastes* sites (white bars) in Fiji. Error bars represent ± 1 standard error of replicate measurements.

relative abundance of algae within each marked treatment site was resurveyed utilizing 100 cm² quadrats placed within each site ($n=15$).

In total, this study consisted of four experiments: a grazer removal experiment in Ha'apai, Tonga; a grazer removal experiment in Vava'u, Tonga, a nutrient addition-grazer removal experiment in the Solomon Islands; and a nutrient addition-grazer removal experiment in Fiji (Table 1). Algal growth rates from each experiment involving only caged and uncaged *Stegastes* territories were analyzed using the Student's *t*-test. The effect of both nutrient addition and grazer removal on algal growth rate was determined using a two-way ANOVA. When a significant effect was found for the response variable, multiple comparison tests (Tukey's Studentized range) were used to test for significant differences between levels within the treatment. Statistical comparisons of algal composition within *Stegastes* sp. territories and adjacent non-*Stegastes* regions were made via Student's *t*-tests. Statistical outliers of replicated data points were identified using the Dixon test prior to statistical analysis. Data were transformed when necessary to meet assumptions on normality. Results in all comparisons were considered to be significant when $p < 0.05$. All statistical analyses were conducted using Sigma Stat Version 2.03 statistical software package.

3. Results

3.1. Fiji

Stegastes territories, occupied by the Dusky Gregory, *S. nigricans*, were abundant throughout the shallow fringing reefs of Dravuni Island, Fiji, covering dead coral rock and large, dead round corals. Algal species

composition differed between *Stegastes* territories and non-*Stegastes* sites (Table 2, Fig. 2). The dominant algae inside *Stegastes* territories were turf algae (Fig. 2). The three main genera of turf algae collected from the sites were identified as *Polysiphonia* sp., *Ceramium* sp., and a parenchymatous, *Polysiphonia*-like algae (Table 2).

Stegastes territories showed significantly greater coverage of turf algae ($80 \pm 4.4\%$ = mean \pm standard error) than non-*Stegastes* sites in Fiji ($48 \pm 8.3\%$; Fig. 2; $p < 0.01$; *t*-test). In addition, non-*Stegastes* territories showed greater coverage of macroalgae relative to *Stegastes* territories (Fig. 2). For example, red macroalgae cover within non-*Stegastes* sites ($20 \pm 6.2\%$) was significantly greater than the red macroalgae cover within *Stegastes* territories ($3.7 \pm 1.6\%$; Fig. 2; $p < 0.05$; *t*-test). Relative to *Stegastes* territories, non-*Stegastes* sites were found to have greater green algae cover ($34 \pm 9.5\%$ v. $17 \pm 4\%$) and brown algae cover ($2.3 \pm 1.6\%$ v. $0 \pm 0\%$), although differences were not statistically significant (Fig. 2). Both *Stegastes* territories and non-*Stegastes* sites contained the green algae *Caulerpa* sp. and *Halimeda* sp., and the red algae *Galaxaura* sp., and *Peyssonnelia* sp. (Table 2). However, the algae found within the *Stegastes* territories also included *Pterocladia* sp., *Botryocladia* sp., *Valonia* sp., *Gelidiella* sp., *Ventricaria* sp., *Codium* sp., *Dictyota* sp., and *Dictyosphaeria* sp. (Table 2), suggesting a greater diversity of macroalgae, despite a lower abundance, within *Stegastes* territories.

During experiments conducted in Fiji, the growth rate of the cage and nutrients treatment (0.72 ± 0.04 mm day⁻¹) was substantially larger than all other treatments (Fig. 3). Two-way ANOVA indicated a significant treatment effect of both cages ($p = 0.003$) and nutrients ($p = 0.013$), as well as indicating significant interaction between the two treatments ($p = 0.017$; Table 3). The percent cover of turf algae did not change significantly

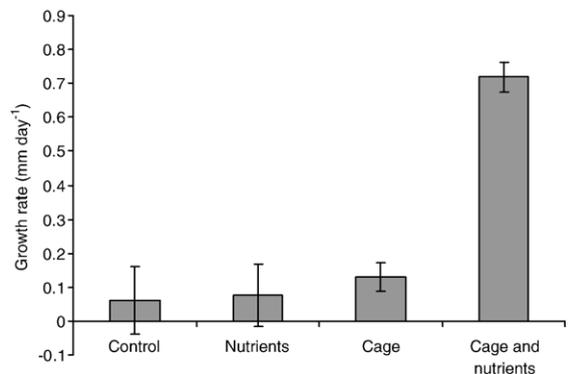


Fig. 3. Mean turf algae growth rates within control and experimental sites around Dravuni Island, Fiji. Error bars represent ± 1 standard error of triplicate sites.

Table 3

Two-way ANOVA tables for algal growth rates and changes in percent cover of the red algae within the experimental manipulations of *Stegastes* territories in Fiji

Source	df	SS	MS	F	P
<i>Turf algae growth rates</i>					
Nutrient	1	0.268	0.268	12.214	0.013
Cage	1	0.492	0.492	22.454	0.003
Nutrient × cage	1	0.234	0.234	10.684	0.017
Error	6	0.132	0.022		
Total	9	1.309	0.145		
<i>Percent cover of red macroalgae</i>					
Nutrient	1	156.74	156.74	2.72	0.143
Cage	1	266.67	266.67	4.63	0.068
Nutrient × cage	1	156.74	156.74	2.72	0.143
Error	7	403.33	57.62		
Total	10	1028.73	102.87		

Other groups of algae did yield a significant change in percent coverage during experiments (see Results).

within or among treatment groups during the experiment (Fig. 4). However, caging had a marginally significant effect on the percent coverage of red macroalgae (two-way ANOVA; $p=0.068$; Table 3), as the control group had substantially more coverage ($5.5\pm 1.9\%$) than the caged treatments, both of which contained no red macroalgae by the end of the experiment (Fig. 4). All treatments showed an increase in brown algae coverage (nutrient treatment= $11\pm 11\%$; cage= $4.4\pm 4.4\%$; cage and nutrient= $40\pm 40\%$) relative to the control group ($0\pm 0\%$; Fig. 4), although treatment effects were not significant. There were no significant differences between the green macroalgae abundance of the control and other groups (Fig. 4).

3.2. Solomon Islands

The *Stegastes* territories around Uepi Island were found on and within dead, branching staghorn coral. The territories studied were occupied by the Dusky Gregory, *S. nigricans* and the Bluntnout Gregory, *Stegastes lividus*. Almost all *Stegastes* territories were covered in 100% turf algae, dominated by a long turf alga, short turf algae, or both morphologies. The longer, bushier turf alga was composed of *Wrangelia* sp. The algae that appeared red, short, and fibrous were composed primarily of *Ceramium* sp., *Laurencia* sp., *Champia* sp., and *Polysiphonia* sp. (Table 2). The only macroalgae found within the non-*Stegastes* sites was identified as *Hypnea* sp. (Table 2). There was a remarkable difference in the relative abundance of algae between *Stegastes* territories and non-*Stegastes* sites. On average, non-*Stegastes* sites had significantly more macroalgae ($16\pm 4.5\%$) and

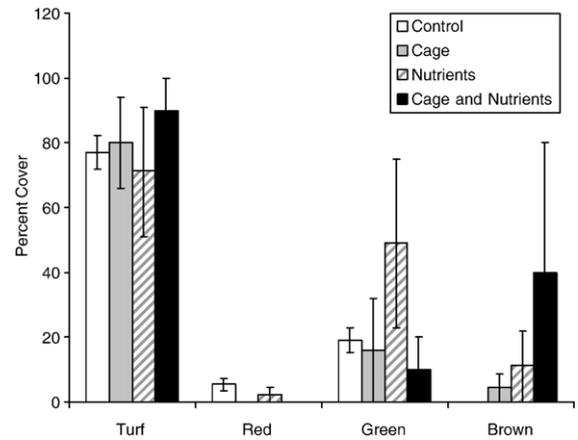


Fig. 4. Mean percent coverage of turf algae and macroalgae (red, green, and brown) within experiment sites around Dravuni Island, Fiji: Control (white bars), caged (gray bars), nutrient enriched (lined bars), and caged with nutrient enrichment (black bars). Error bars represent ± 1 standard error of triplicate sites.

significantly less turf algae ($7.0\pm 4.0\%$) relative to *Stegastes* territories ($0\pm 0\%$ and $97\pm 1.4\%$; Fig. 5; $p<0.001$; t -test).

All experimental treatments showed increased growth of turf algae in the Solomon Islands (Fig. 6). However, the largest growth rates of turf algae occurred within the cage treatment (0.77 ± 0.18 mm day⁻¹) and the cage and nutrient treatment (0.88 ± 0.23 mm day⁻¹; Fig. 6). A two-way ANOVA indicated that cages were the only treatment effect which yielded significantly enhanced growth rates ($p<0.05$) as the impact of nutrients and the interaction of nutrients with cages was not significant (Table 4). No changes in algal composition were noted during this experiment (data not shown).

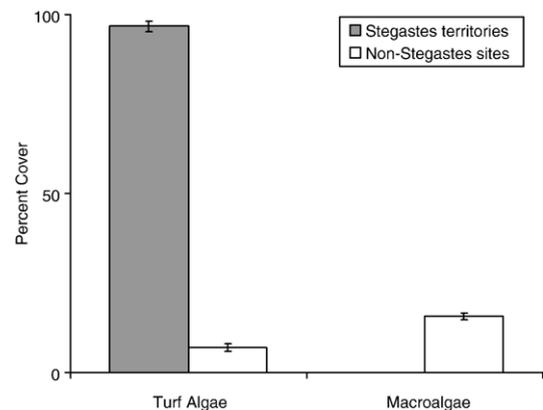


Fig. 5. Mean percent coverage of turf algae and macroalgae in *Stegastes* territories (gray bars) and non-*Stegastes* sites (white bars) in the Solomon Islands. Error bars represent ± 1 standard error of replicate measurements.

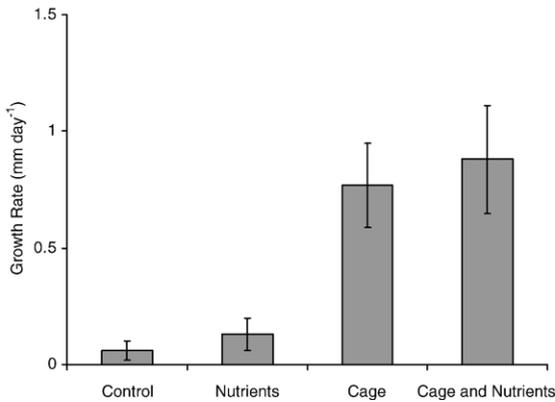


Fig. 6. Mean turf algae growth rates within experiment and control sites around Uepi Island, Solomon Islands. Error bars represent ± 1 standard error of triplicate sites.

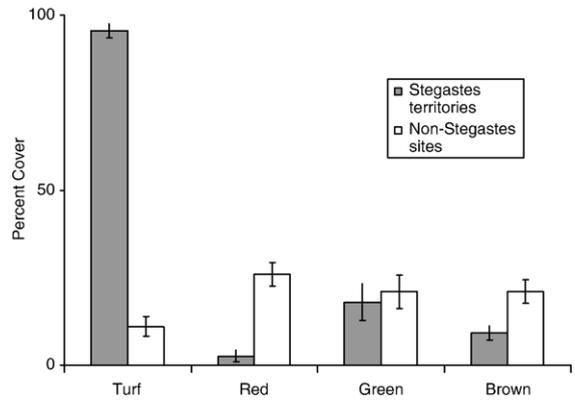


Fig. 7. Mean percent coverage of turf algae and macroalgae (red, green, and brown) in *Stegastes* territories (gray bars) and non-*Stegastes* sites (white bars) in Ha'apai, Tonga. Error bars represent ± 1 standard error of replicate measurements.

3.3. Tonga

The experimental and observational sites of Tonga were generally patch reefs surrounded by a sandy substrate located within 50 m of shore. The territories were inhabited by *S. fasciatus*, and algal beds were maintained within 5 to 10 m of water. The turf algae within *Stegastes* territories in Vava'u, Tonga were composed of *Amphiroa* sp., *Ceramium* sp., *Monosporus* sp., *Wrangelia* sp., and *Polysiphonia* sp. (Table 2). Macroalgae such as *Boodlea* sp., *Caulerpa* spp., *Dictyota* sp., *Digenea* sp., *Halimeda* sp., *Hypnea* sp., *Lobophora* sp., and *Padina* sp. were also present inside the territories (Table 2). On Ha'apai, Tonga, the turf algae within *Stegastes* territories were composed of *Bryopsis* sp., *Polysiphonia* sp., *Cladophora* sp., *Ceramium* sp., and a fine, filamentous, blue green alga (Table 2). The macroalgae present within *Stegastes* territories included *Turbinaria* sp., *Padina* sp., *Struvea* sp., *Lobophora* sp., *Halimeda* sp., and *Gelidiella* sp. (Table 2). *Bryopsis* sp. was the only turf alga found in non-*Stegastes* sites on Ha'apai. The macroalgae found within non-*Stegastes* sites included *Galaxaura* sp., *Laurencia* sp., *Amphiroa* sp., *Turbinaria* sp., *Halimeda* sp., and

Gelidiella sp. In Ha'apai, the coverage of turf algae within *Stegastes* territories (96 ± 6.0%) was significantly greater than within non-*Stegastes* sites (13 ± 8.2%; Fig. 7; $p < 0.05$; *t*-test). Macroalgae cover was greater within non-*Stegastes* territories (red = 26 ± 3.3%; green = 21 ± 4.8%; brown = 21 ± 3.3%) than within *Stegastes* territories (red = 2.5 ± 1.7%; green = 18 ± 5.3%; brown = 9.2 ± 2.0%), although only red and brown macroalgae showed a significantly greater coverage (Fig. 7; $p < 0.05$; *t*-test).

Caging *Stegastes* territories in Tonga did not alter species composition or the relative abundance of macroalgae (data not shown). While caging yielded slightly increased turf algae growth (0.05 ± 0.03 mm day⁻¹) in Ha'apai, rates were not significantly different from the control (-0.02 ± 0.02 mm day⁻¹; Fig. 8). However, in Vava'u the growth rate of the cage treatment was

Table 4
Two-way ANOVA table for turf algae growth rates within the experimental manipulations of *Stegastes* territories in the Solomons

Source	df	SS	MS	F	p
<i>Turf algae growth rates</i>					
Nutrient	1	0.023	0.023	0.434	0.529
Cage	1	1.621	1.621	30.026	<0.001
Nutrient × cage	1	0.001	0.001	0.0261	0.876
Error	8	0.432	0.054		
Total	11	2.077	0.189		

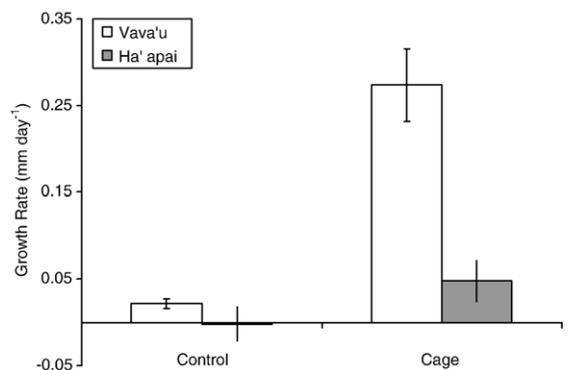


Fig. 8. Mean turf algae growth rates within experiment and control sites around Vava'u (white bars) and Ha'apai (gray bars), Tonga. Error bars represent ± 1 standard error of triplicate sites.

significantly greater than the control group ($0.27 \pm 0.07 \text{ mm day}^{-1}$ vs. $0.02 \pm 0.01 \text{ mm day}^{-1}$; Fig. 8; $p < 0.05$; t -test).

4. Discussion

During this study, we documented the unique algal assemblages that *S. nigricans*, *S. lividus*, and *S. fasciatus* maintain on the shallow reefs of Fiji, the Solomon Islands, and Tonga. Our short term experiments established the key role *Stegastes* spp. plays in maintaining algal turf height and species composition and concurrently revealed the impact of nutrient loading on the turf algal community. Although the species of *Stegastes* we examined differed among locations, the ecological role of these grazers and consequences of their removal were remarkably similar across this region. Together, these results highlight the distinct impact of *Stegastes* spp. on the ecology of Indo-Pacific reefs.

Stegastes territories differed noticeably among Fiji, the Solomon Islands and Tonga. In Fiji, the *Stegastes* territories were found on dead coral rock and were abundant throughout the fringing reefs. In contrast, *Stegastes* territories in the Solomon Islands were found only on and within dead, branching, staghorn coral, while *Stegastes* sites in Tonga were found on nearshore patch reefs. Furthermore, macroalgae present in regions with *Stegastes* territories differed among sites. In the Solomon Islands, most non-*Stegastes* sites contained all live coral, although some exhibited live coral with a dead base partially covered by only *Hypnea* sp. (Fig. 5). Both within and outside of *Stegastes* territories, the abundance of macroalgae (green, red and brown) was greater in Fiji and Tonga than in the Solomons Islands. Non-*Stegastes* sites were not dominated by a single algal species in either location (Figs. 2 and 7) which is consistent with Hata et al. (2002), who also found non-damsel fish sites lacking a dominant algae type. Furthermore, the presence of *Halimeda* and *Liagora* in Fiji (Table 2) and of *Halimeda* in Ha'apai, Tonga, (Table 2) in non-*Stegastes* sites is consistent with reports of these genera in non-damsel fish sites of Jamaica (Brawley and Adey, 1977). Observed differences among Indo-Pacific sites suggest that *Stegastes* can employ ecologically flexible strategies to adapt to and create territories in various environments. Despite the differences attributable to location, these sites did share several characteristics and were affected by experimental treatments in a similar manner.

During our study, the percent cover of turf algae within *Stegastes* territories was significantly greater than in non-*Stegastes* sites (Fiji, $80 \pm 4.4\%$ v. $48 \pm 8.3\%$, Fig. 2; Solomon Islands, $97.0 \pm 1.4\%$ v. $7.0 \pm 4.0\%$, Fig. 5; Tonga

$96 \pm 2.0\%$ v. $13 \pm 2.8\%$, Fig. 7), a finding consistent with prior studies (Brawley and Adey, 1977; Lassuy, 1980; Hinds and Ballantine, 1987; Russ, 1987; Ferreira et al., 1998). *Polysiphonia* and *Ceramium* were part of the turf algae consortium in *Stegastes* territories found at all four island groups (Table 2) and have been reported as main components of damsselfish territories in the Great Barrier Reef, Guam, Jamaica, and Okinawa, Japan (Brawley and Adey, 1977; Lassuy, 1980; Russ, 1987; Hata et al., 2002). Their consistent presence over an extensive geographical range in *Stegastes* spp. territories and their absence from most non-*Stegastes* sites in the same region suggest that the damsselfish manipulate their territories to specifically select for these genera of algae. Damsselfish may augment turf algal abundance within their territories through multiple mechanisms. Several studies have presented evidence that damsselfish remove unpalatable algae; thus, their weeding behavior promotes the growth of preferred algae (Irvine, 1980; Lassuy, 1980; Lobel, 1980; Montgomery, 1980b; Branch et al., 1992). Damsselfish have also been observed to destroy coral, creating an increased surface area for new algal growth (Potts, 1977; Lobel, 1980; Roberston et al., 1981; Wellington, 1982). Although there is little direct evidence, it has been suggested that damsselfish promote the growth of preferred algae via defecation over these groups (Polunin and Koike, 1987; Klumpp and Polunin, 1989; Ferreira et al., 1998). Territorial behavior, which decreases grazing by other herbivores within territories, is a final method by which damsselfish may increase preferred algal abundance within their domain (Doherty, 1983). During our study, we observed damsselfish engaged in all of these activities except for coral destruction.

Relative to *Stegastes* territories, non-*Stegastes* sites generally contain a greater coverage of macroalgae. For example, in Fiji and Ha'apai, Tonga there was a greater coverage of red, green, and brown macroalgae in non-*Stegastes* sites relative to *Stegastes* territories (Figs. 2 and 7). Since significant differences were observed only among red and brown macroalgae (Figs. 2 and 7), *Stegastes* spp. may be more focused on algae in these groups than in the green macroalgae group. These observations are consistent with our experiments, which demonstrate that *Stegastes* spp. may selectively remove and cultivate specific classes of macroalgae. For example, unaltered *Stegastes* territories in Fiji exhibited a significantly greater abundance of red macroalgae ($5.5 \pm 1.9\%$) than the cage and cage plus nutrient treatments, both of which contained no visible red macroalgae (Fig. 4). In addition, treatments showed an increase in coverage of brown macroalgae from the control (Fig. 4). These findings suggest that some red macroalgae within territories may be maintained and farmed by *Stegastes* spp., while brown macroalgae appear

to be selectively removed. Such a conclusion is consistent with the work of Miller and Hay (1996) on temperate reefs who found that fish herbivores preferred to consume red macroalgae over less palatable brown algae. The higher percent coverage of red macroalgae in non-experimental, non-*Stegastes* territories ($20 \pm 6.2\%$; Fig 2) relative to caged treatments suggests animals besides *Stegastes* that were excluded by cages may support elevated densities of red algae in these regions.

Our results demonstrate that relative to adjacent regions, there is greater algal diversity in *Stegastes* territories of the Indo-Pacific reefs (Table 2), a finding consistent with prior research conducted in Guam and Hawaii that found a greater diversity of algae in the territories of *S. lividus* and *S. fasciatus* respectively (Lassuy, 1980; Hixon and Brostoff, 1981, 1996). According to Connell's (1978) intermediate disturbance hypotheses, which predicts that moderate disturbance results in the highest diversity, *Stegastes* spp. territories should perhaps be expected to contain a highly diverse algal community as grazing reduces the dominant algal competitor. The grazing and territorial behavior of *Stegastes* spp. within their territories, serves to maintain a delicate balance between the extreme grazing of numerous herbivorous fish and a complete lack of grazing (Hixon and Brostoff, 1983, 1996; Ferreira et al., 1998).

Removal of *Stegastes* spp. from their territories yielded enhanced growth of turf algae in some but not all experiments. In Fiji, only the cage and nutrient treatment showed a significant increase in turf algae growth ($0.72 \pm 0.04 \text{ mm day}^{-1}$ vs. $0.06 \pm 0.06 \text{ mm day}^{-1}$; Fig. 3), suggesting that in this area increases in nutrients or reductions of grazing alone would not be sufficient to cause a significant increase in turf algae growth. A study conducted by Thacker et al. (2000) using Osmocote nutrients similar to the type used in our experiments reported that experimental nutrient enrichment had a negligible effect on algal biomass. However, in the present study, nutrient enrichment affected the algal community synergistically with reduced grazing in Fiji (Fig. 4, Table 3). Lapointe (1997) showed that in areas, such as Jamaica and southeastern Florida, where studies identified reduced herbivory as the principal factor inducing macroalgae-dominated phase shifts, nutrients may have also contributed significantly to the shift. In a study conducted at Puako Reef on the leeward side of the island of Hawaii, Smith et al. (2000) found that algal biomass was greatest in areas both exposed to nutrients and excluded from grazing. Similarly, on Fijian reefs, it appears that together these stresses can cause a significant increase in the short-term growth rate of the turf algae.

In contrast to experiments in Fiji, in the Solomon Islands and Tonga, a significant increase in turf growth rate resulted from herbivore exclusion and not nutrient enrichment (Figs. 6 and 8). The enclosure experiments in Vava'u, Tonga, and Uepi, Solomon Islands, demonstrated that, in the absence of grazing by *Stegastes* spp., the algal turf bed grew significantly greater than rates in the presence of this species. Such a result is consistent with an array of literature which has demonstrated that reduced herbivory on coral reef environments can lead to an overgrowth of algae (Hughes, 1994; Miller et al., 1999; Jackson et al., 2001; Bellwood et al., 2004).

While there was a notable growth of algal beds within enclosures during many of our experiments, caging *Stegastes* spp. territories in Ha'apai did not yield a significant increase in turf algae growth rates, possibly due to the shorter time allowed for growth. The duration of the experiments (days) presented here provides insight into the short term changes which may arise from decreased grazing and/or eutrophication. It is possible that over a longer time frame the algal community would reach a new state of equilibrium which may or may not be reflected by our short term observations.

Our results emphasize the important role that herbivory plays on reef algal communities and point to reduced grazing as a primary factor creating change in the algal community composition. It is evident that *Stegastes* spp. manipulates the algal community within its territories, creating a balance among various species and between the algal and coral communities. At the conclusion of our experiments in Fiji, the characteristics of territories subjected to herbivore exclusion and nutrient enrichment appeared similar to non-*Stegastes* sites, with regard to percent coverage of some macroalgae. The nutrient treatment displayed an increase in green macroalgae, while every treatment showed increased brown macroalgae coverage (Fig. 4). This is consistent with the observations that percent coverage of macroalgae was greater in non-*Stegastes* sites at all locations (Figs. 2, 5, 7), and suggests that fewer damselfish and eutrophication could lead to a phase shift in which macroalgae dominate the reefs, as has already occurred on some coral reefs (Hughes, 1994; Jackson et al., 2001; Bellwood et al., 2004). Consequently, the pristine ecosystems of Fiji, the Solomon Islands, and Tonga may be similarly susceptible to phase shifts and reef degradation.

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