

Resource use and impact of three herbivorous damselfishes on coral reef communities

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ABSTRACT: Territorial damselfish are considered to be functionally important herbivores on coral reefs, promoting the abundance of preferred algae and depleting corals through a variety of 'farming' activities. However, the composition of algal and coral communities inside territories and patterns of feeding selectivity are known for only a few species. Here we compare substrata inside and next to territories of *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans*, 3 common damselfish in Papua New Guinea, and interpret patterns in relation to diets and patterns of feeding selectivity. The coral assemblages inside territories differed among fish species and also between defended and non-defended areas. Live corals dominated *P. dickii* territories, while those of *P. lacrymatus* and *S. nigricans* were primarily associated with algal substrata. Territories of *P. lacrymatus* were similar in coral composition to adjacent areas, while those of *P. dickii* and *S. nigricans* were associated with particular coral taxa. Territories of the 3 damselfish were similar in algal composition, with mixed turf algae (primarily blue-green algae *Polysiphonia* spp. and other filamentous red algae) more prominent inside territories and crustose coralline algae more prominent outside. Diets for the 3 species were also similar, as each species was primarily herbivorous and diets consisted of diatoms, blue-green algae, *Polysiphonia* spp. and other filamentous red algae. An experimental removal of *P. lacrymatus* showed that they promoted epiphyte loads without influencing macro-algal or coral cover. Our results suggest that while these 3 species of damselfish vary in their interactions with coral reef habitat, they selectively cultivate a similar range of epiphytic food algae on different substrata.

KEY WORDS: Algae · Coral reef · Diatoms · Diet · Feeding selectivity · Herbivory · Papua New Guinea · Pomacentridae · Territoriality

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INTRODUCTION

Herbivorous damselfish have been attributed a central role in determining the structure of coral and algal assemblages on coral reefs (Williams 1980, Wellington 1982, Hixon & Brostoff 1983, 1996, Carpenter 1986, Horn 1989). Damselfish can promote algal abundance and productivity, change algal species composition and disadvantage corals through a number of mechanisms. These include territorial behaviour directed at other herbivorous fish (Mahoney 1981, Hixon & Brostoff 1983, Hata & Kato 2003), cultivation of preferred algae or weeding of unwanted species

(Lassuy 1980, Hata & Kato 2002, Hata et al. 2002) and killing live coral tissue (Kaufman 1977, Potts 1977, Wellington 1982). These behaviours may favour algae in competitive interactions between algae and corals (Vine 1974, Lobel 1980, Sammarco et al. 1986). However, despite the potential importance of herbivorous damselfish, differences in the composition of benthic communities inside and outside territories are known for a relatively small number of the species that vigorously defend conspicuous algal 'farms' (Ceccarelli et al. 2001, Hata et al. 2002). Ceccarelli et al. (2001) argued that generalisations on the functional role of herbivorous damselfish would benefit from knowledge

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of the impacts of a wider range of species, many of which do not maintain conspicuous algal farms.

There are 3 steps necessary to gain an understanding of how damselfish influence benthic communities. First, the algal and coral composition of territories must be assessed and compared to adjacent, undefended areas (Montgomery 1980a,b, Sammarco 1983, Klumpp et al. 1987, Hixon & Brostoff 1996, Ferreira et al. 1998, Hata et al. 2003, Ceccarelli et al. 2005). Second, the preferred algal or coral resources being consumed must be identified (Ceccarelli et al. 2001). Finally, since damselfish may establish territories in places that differ from unoccupied areas, the overall impact of damselfish can only be demonstrated by experimentally removing them (Mahoney 1981, Kohda 1984, Hourigan 1986, Ceccarelli et al. 2005). These steps have only been completed for a few damselfish species, which may not represent the full range of responses in this behaviourally diverse guild of fishes.

If most damselfish influence benthic communities in a manner similar to larger, highly territorial species, we can predict a greater cover or biomass of algae inside territories (Ceccarelli et al. 2001). Also, since damselfish often kill particular coral species in order to promote algal growth, and since cultivated algae may overgrow corals, a reduction in coral cover might also be expected (Potts 1977, Wellington 1982). However, given that damselfish may also be defending territories from other corallivores (Wellington 1982, Glynn & Colgan 1988), the overall impact on corals may be positive. If damselfish are selectively cultivating preferred food algae, there should be a substantial difference in algal species composition inside and outside territories. Finally, after the removal of territory inhabitants, there should be a rapid depletion of algal biomass, which may ultimately promote coral cover. To date, most removal experiments have been conducted over short time periods at a scale of individual territories (Ceccarelli et al. 2001), and it is not clear to what degree this extends to a major impact on coral reef communities.

The aim of this study was to determine whether 3 territorial damselfish species exhibit any common patterns in terms of how the composition of corals and algae within their territories differs from neighbouring, undefended areas. The 3 different species chosen are abundant and occupy a range of coral reef habitats in Papua New Guinea. These include *Plectroglyphidodon lacrymatus*, the most common and aggressive territorial species dominating the reef crest (Ceccarelli et al. 2005), *P. dickii*, restricted in habitat to the narrow-growing edge of the reef crest and *Stegastes nigricans*, which is patchily distributed in protected back reef and lagoonal areas. All 3 species are highly aggressive, defending territories of 0.25 to 1.5 m² from

conspecifics, other herbivorous damselfish and grazers (including detritivores) from other fish families, such as parrotfish and surgeonfish.

If these territorial species promote the growth of certain algal taxa by excluding other herbivores and killing corals, it follows that their territories should differ from adjacent areas in cover and composition of algal and coral assemblages. This was tested by using a benthic sampling program, stratified according to fish species, and by sampling both inside and adjacent to territories. By integrating information on feeding substrata, diet and feeding selectivity, we also examined whether the 3 species promoted the abundance of preferred food. Finally, we undertook a long-term experimental removal of large aggregations of the most abundant species, *Plectroglyphidodon lacrymatus*, to determine whether it was a major determinant of benthic community structure in the reef crest habitat.

MATERIALS AND METHODS

Study sites and periods. The study was conducted at Kimbe Bay (5° 15' S, 150° 15' E) on the north shore of the island of New Britain, Papua New Guinea. This area is characterized by typical platform and fringing reef structures, and it supports a diverse suite of territorial damselfishes with broad Indo-Pacific distributions. Feeding substrata, diets and feeding selectivity were examined for large adult *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans*, sampled from various platform reefs in the vicinity of the Mahonia Na Dari Research Centre, where each species was abundant in different reef zones. Comparisons of benthic communities inside and next to territories, behavioural studies and collections for dietary analysis were made between April and July 2001.

Benthic communities inside territories and on adjacent undefended areas. The abundance and composition of coral and algal assemblages inside territories and in undefended areas immediately outside territories were quantified with the use of quadrats. We sampled a total of 72 adult damselfish of each species (24 fish from each of 3 different reefs) by placing a 25 × 25 cm quadrat on horizontal substrata inside and outside their territories. Sampling was not carried out until each damselfish was observed for a 15 min period to determine the spatial extent of the territory and to confirm that adjacent areas were not defended by conspecifics or other damselfish species. The percentage cover of coral genera and of macroscopic algal functional groups was estimated from the quadrats by ascertaining the proportion of the quadrat area covered by each category.

Multi-specific stands of filamentous algal turf were classified into either of 2 categories: 'Bushy' or 'Standard'. 'Bushy' turfs were multi-specific stands of filamentous turf, covered by a layer of epiphytes. 'Standard' turfs were also multi-specific stands of filamentous turf, but were not covered in epiphytes. In addition, other macro-algal groups were distinguished to genera, including crustose coralline algae, *Turbinaria*, *Amphiroa*, *Actinotrichia* and *Halimeda*.

To examine the fine structure of turf algal assemblages, samples were collected from a total of 15 territories for each species and from an area immediately adjacent to each of these territories. For each species, the territories of 5 individuals representing each species were sampled from 3 different reefs. The composition of these turf groups was later examined in the laboratory, and the algae comprising the turf were classified according to the following genera or recognizable forms: (a) 'gelid' red turfing algae, (b) blue-green algae, (c) *Laurencia*, (d) *Polysiphonia*, (e) 'peysonelids', (f) *Jania*, (g) *Coelothrix*, (h) crustose coralline algae, (i) *Hypnea*, and (j) *Dictyota*. 'Gelid' algae are a taxonomically diverse, but structurally similar turf-forming red algae (I. R. Price et al. unpubl. data). They have slender, cylindrical and corticated branches, but lack any other recognizable features in the field. 'Peysonelids' are an encrusting-form of red algae, impregnated with small amounts of calcium carbonate and have a spongy surface texture. The percentage composition of turfs was quantified in the laboratory by spreading the samples evenly in a dish marked with 100 random points. A stereo-dissector microscope was used to identify the algae under each point.

Bite substrata. The substrata from which the damselfish took bites were recorded for individuals of each species as observed, for 15 min intervals. As actual prey consumption was difficult to confirm during feeding observations, these bites may have included prey consumption, weeding or killing of coral polyps. A total of 72 individuals of each species were observed, with 24 being sampled from each of 3 different platform reefs. To reduce any effect of the diver's presence, the fish were monitored for 2 min before the observations were recorded. The number of bites on each identifiable component of substrata was recorded. Substrata were divided into: (a) Acroporid corals, (b) Favid corals, (c) Pocilloporid corals, (d) Porites corals, (e) Algal turfs, (f) Mixed *Amphiroa* + turfs, (g) Mixed *Turbinaria* + turfs and (h) coral-algal borders.

Diet and feeding selectivity. Twenty individuals of each damselfish species were collected from the same reefs where feeding substrata and algal composition were quantified. The contents of all the ingesta anterior to the pyloric caecae were extracted and analysed.

Percent cover of different food types was estimated by a point-intercept method using a microscope at $\times 100$ magnification. The food types were quantified by recording what was beneath each of the 81 points of a 9×9 ocular grid. Diet categories were the same as those used to quantify the composition of algal turfs. Additional categories were added to include diatoms, amorphous vegetative matter, sediment and invertebrate spicules.

To establish diet selectivity, a resource selection ratio (W_i) was used to compare algal use (stomach content) with algal availability (algae in territory) (Manly et al. 2002):

$$W_i = o_i/\pi_i$$

where o_i is the mean proportion that dietary category i makes up of the whole diet, and π_i is the mean proportion that algal category i makes up of the total available in the field. Bonferroni-corrected CI (adjusting for multiple tests) were calculated for each selection ratio according to the formula:

$$SE(W_i) = \sqrt{[o_i(1 - o_i)/(u_+ \pi_i^2)]}$$

where u_+ is the total number of resource categories used. When the CI encompassed a W_i value of 1, the fish were using algal types in proportion to their availability. Where the W_i was larger and did not overlap with 1, the resource was considered as selected. Conversely, when W_i was significantly less than 1, the resource was considered avoided, and a value of 0 was obtained for resources not consumed at all.

Estimates of diatom abundance. Due to the consistently high presence of diatoms found in the intestines of the 3 damselfish species, the abundance of diatoms inside and outside each of the territories was later estimated from an additional survey. To assess loads of epiphytic diatoms (a different algal species for each fish species), small (10 g) samples of the most abundant macro-alga were collected from inside the territories of 15 individuals for each fish species. These estimates were compared to equivalent samples of the same alga collected from outside territories. The abundance of diatoms present in the algal forms was recorded in the laboratory by quantifying the percent cover of diatoms associated with 10 g sample of the algae. Percent cover was estimated by observing the number of diatoms under each point of a 9×9 ocular grid using a microscope, as done for gut content analysis.

Experimental removal of *Plectroglyphidodon lacrymatus*. The most abundant territorial damselfish occupying the reef crest habitat, *P. lacrymatus*, was experimentally removed from large patches to examine its long-term effect on coral and algal cover. Removal and control plots, measuring 20 m along the reef crest and 12 m wide, were established on each of 3 reefs in March

2000. All individuals of *P. lacrymatus* were speared from the 3 removal plots, and sporadic immigrants continued to be removed by regular spearing until April 2001. Between 80 and 100 adults were removed from each experimental plot. It was hypothesised that if these damselfish were having an important influence on benthic assemblages within this reef zone by killing coral and farming algae, there would be a significant difference in the abundance and composition of algal and coral assemblages in the removal quadrats, compared with 3 control quadrats. The experimental plots were sampled to estimate algal and coral cover in April, 1 yr after the removal. Algal and coral cover was estimated using 5 random 10 m line-intercept transects laid within each experimental plot, with the substratum present beneath 100 random points along each transect recorded. The same coral and algal categories were used as in the comparisons of inside and outside territories, with coral colonies identified to genera, and algal types placed in standard categories.

Statistical analyses. Different data sets were used to make multiple comparisons between substrata inside and immediate adjacent to the same territories and also between experimental removals and control plots. Paired *t*-tests were used when variances were homogeneous, and non-parametric Kruskal-Wallis tests were used when this assumption was violated (Zar 1999). A Bonferroni-correction of alpha levels was made to adjust for the number of comparisons made using a particular data set (i.e. $0.05 k^{-1}$, where k = the number of comparisons). While all comparisons involved replicate fish sampled from 3 different reefs, data were pooled for presentation and final analysis where there were no differences among reefs.

RESULTS

Coral cover and composition in defended and undefended areas

Overall coral cover tended to be higher inside territories than in undefended areas for all 3 damselfish species (Fig. 1). However, the absolute cover inside territories and the magnitude of the difference between defended and undefended areas differed among species. *Plectroglyphidodon dickii* territories were dominated by live coral (~80% cover), twice that found in areas adjacent to territories (paired *t*-test, $t_{711} = 11.0$, $p < 0.016$). *P. dickii* territories contained over twice the amount of live coral found in territories of the other 2 species (Fig. 1). There was also significantly more live coral in the territories of *Stegastes nigricans* ($t_{711} = 4.03$, $p < 0.016$) and inside territories of *P. lacrymatus* ($t_{711} = 2.71$, $p < 0.016$) relative to adjacent areas.

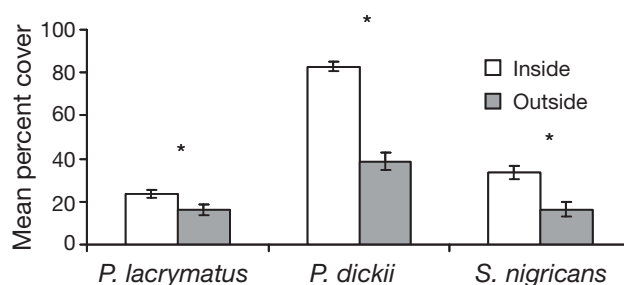


Fig. 1. *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans*. Mean percent cover of hard corals inside and adjacent to (outside) territories of 3 damselfish species ($n = 72$). *Significance at $p < 0.016$ for 3-paired *t*-tests. Error bars = 95% confidence limits (CL)

The magnitude of the difference between territories and adjacent undefended areas in the generic composition of coral assemblages depended on the species. The composition of assemblages inside *Plectroglyphidodon lacrymatus* territories was similar to areas outside (Fig. 2a). *P. dickii* territories contained significantly higher proportional cover of live *Acropora* and *Pocillopora* colonies, while undefended areas outside the territories were composed of a higher cover of *Favid* colonies (K-W test, $p < 0.007$) (Fig. 2b). Similarly, *Stegastes nigricans* territories were composed of a significantly higher proportion of live *Acropora* colonies (Fig. 2c). Areas outside territories were composed of a higher cover of live *Montipora* as well as a much higher proportion of sandy substrata.

Algal cover and composition in defended and undefended areas

Macroscopic algal composition within territories and in adjacent areas showed a consistent pattern among species. The most distinct difference between the algae inside and outside territories was the presence of 'bushy' turf algae, found at 20 to 30% cover in territories for all 3 species, but not found outside territories at all (Fig. 3). 'Standard' filamentous turfs dominated the substrata both inside and adjacent to territories for all species, but cover was consistently higher in the adjacent areas. The cover of crustose coralline algae outside territories was 3 to 4 times higher than in defended areas for all 3 species. There was a small but statistically significant increase in *Turbinaria* and *Amphiroa* inside territories of *Plectroglyphidodon lacrymatus* compared with adjacent areas (Fig. 3a). However, there was no detectable difference between defended and undefended areas in these lesser abundant macroalgae for *P. dickii* (Fig. 3b) or *Stegastes nigricans* (Fig. 3c).

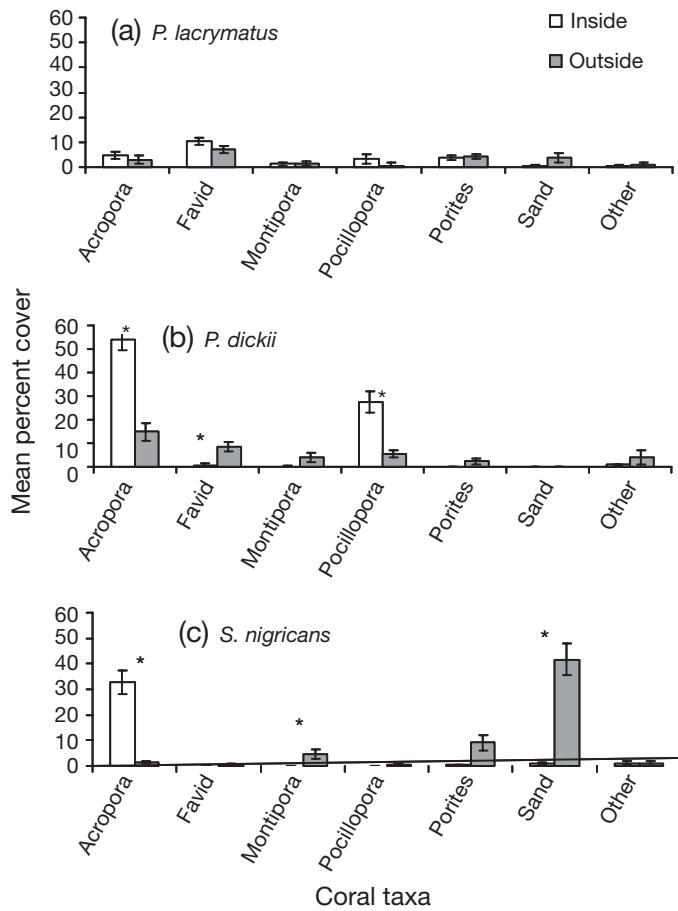


Fig. 2. *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans*. Mean percent cover of live coral assemblages inside and adjacent to (outside) territories of (a) *P. lacrymatus*, (b) *P. dickii* and (c) *S. nigricans* ($n = 72$). *Significance at $p < 0.007$ using multiple Kruskal-Wallis tests. Error bars = 95% CL

More detailed comparisons of the algal taxa that constitute filamentous turfs inside and outside territories revealed a number of differences not evident from the macro-algal survey (Fig. 4). Bushy and standard turfs were made up of a range of algal types, including 'gelids', blue-green algae, *Laurencia*, *Polysiphonia* and 'peysonelids'. The composition of filamentous turf algae outside territories was composed of a greater proportion of crustose coralline algae than inside territories for all 3 species (Fig. 4). The bushy turfs in territories of *Plectroglyphidodon dickii* were dominated by *Polysiphonia*, which was significantly higher than in turfs outside territories. Similarly, 'gelid' algae made up a greater proportion of bushy turfs in territories, compared with turfs outside territories. There were only minor differences among the 3 fish species in the composition of standard and bushy turfs (Fig. 4). Hence, territories appeared to be comprised of larger

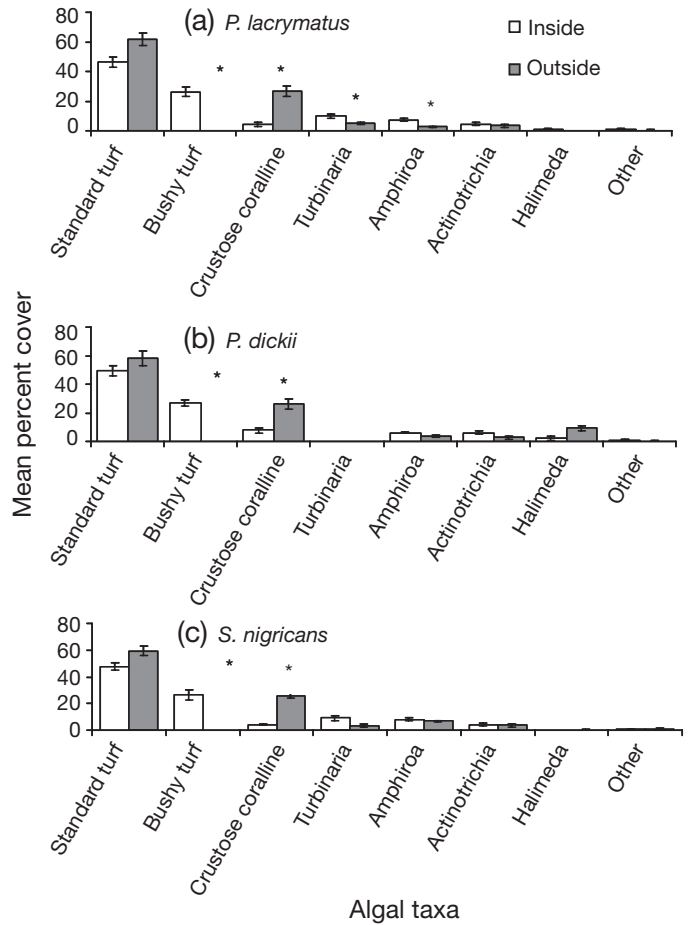


Fig. 3. *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans*. Mean percent cover of algal turf and macro-algal assemblages inside and adjacent to (outside) territories of (a) *P. lacrymatus*, (b) *P. dickii* and (c) *S. nigricans* ($n = 72$). *Significance at $p < 0.007$ using multiple Kruskal-Wallis tests. Error bars = 95% CL

individuals of the same algal taxa found outside, with the exception of crustose corallines.

Bite substrata

The 3 fish species differed according to the substrata from which most of their bites were made (Fig. 5). Over 70% of the bites observed for both *Plectroglyphidodon lacrymatus* and *Stegastes nigricans* were taken from filamentous turfs. *P. lacrymatus* occasionally took bites from a diverse range of other substrata (Fig. 5a), while bites by *S. nigricans* were restricted to algal turfs and acroporid corals (Fig. 5c). In contrast, over 80% of bites by *P. dickii* were from coral tissue, in particular *Acropora* and *Pocillopora*. They also occasionally took bites at other corals and algal turfs within their territories.

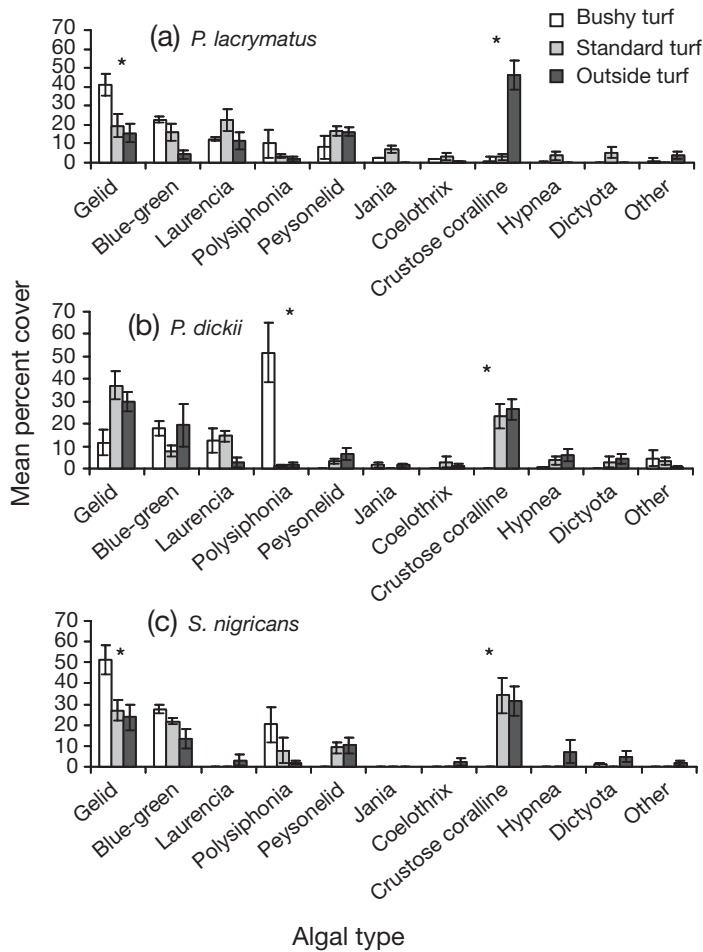


Fig. 4. *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans*. Percent mean cover of turf algal assemblages inside and adjacent to (outside) territories of (a) *P. lacrymatus*, (b) *P. dickii* and (c) *S. nigricans* ($n = 15$). *Significance at $p < 0.005$ using multiple Kruskal-Wallis tests. Error bars = 95% CL

Diet and feeding selectivity

Analysis of stomach contents indicated that the 3 species were primarily herbivores that selectively consumed a similar narrow range of algae found in their territories (Fig. 6). Diatoms were the most important algal food source for all 3 species, making up between 30 and 80% of the stomach content by volume. All species also consumed substantial amounts of 'gelid', blue-green algae and the red alga *Polysiphonia*, with the exact proportions varying among species. Feeding was clearly selective, given that the vast majority of algal types (over 80%) were not present in the stomach content (Fig. 6). Despite the fact that many of the bites made by *Plectroglyphidodon dickii* were from live coral, coral tissue was not found in their stomachs. A large proportion of the

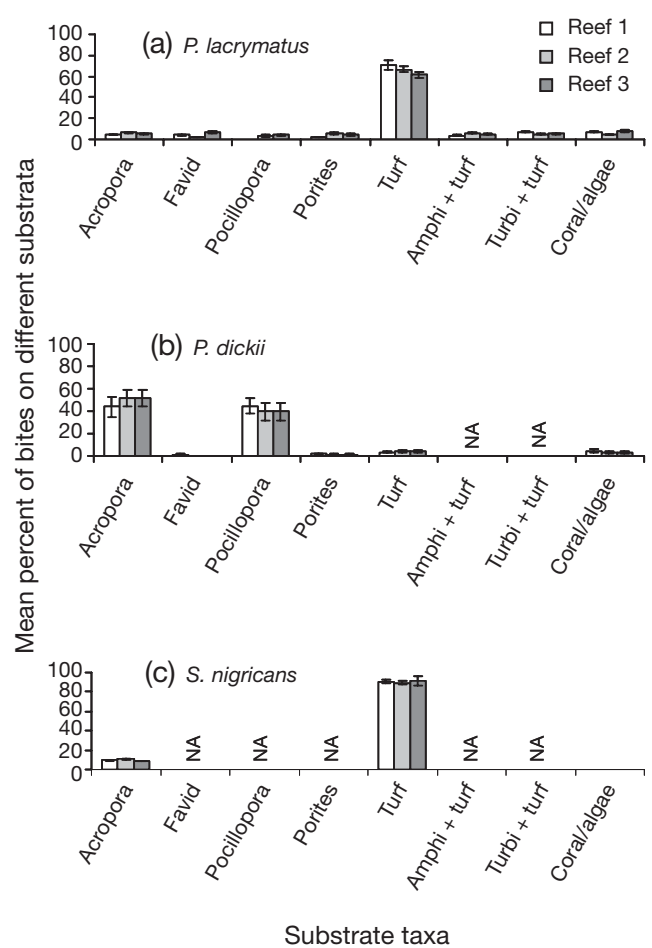


Fig. 5. *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans*. Mean percent of feeding bites on different substrata by (a) *P. lacrymatus*, (b) *P. dickii* and (c) *S. nigricans*. NA: substratum not present within territories of corresponding damselfish species ($n = 72$). Error bars = 95% CL

stomach content of *Stegastes nigricans* in the 'other' category was made up of amorphous material, which could not be identified, and sediment.

Because diatoms are microscopic, there was no measure from the field surveys of the percent cover of diatoms inside territories. However, it was clear that the 3 species showed a marked preference for these micro-algae. For other algal categories, comparisons of the percent-cover of algal types in the diet with percent-cover estimates from within territories revealed some consistent patterns of apparent selection (Table 1). The fish species consumed 'gelids', *Polysiphonia* or blue-green algae in greater amounts than expected on the basis of their availability. Most algal types were apparently avoided in the diet, but they may have been used as substrata from which diatoms were consumed.

Diatom abundance inside and outside territories

Damselfish appeared to facilitate rather than deplete the abundance of diatoms in their territories. The mean percent cover of diatoms attached to sub-samples of macro-algae inside territories was consistently more than twice that found attached to the same algae outside territories for all 3 species (Fig. 7). The differences between territories and adjacent areas were statistically significant for all species [paired *t*-tests: *Plectroglyphidodon lacrymatus*, $t_{14} = 6.01$, $p < 0.016$; *P. dickii*, $t_{14} = 5.25$, $p < 0.016$; *Stegastes nigricans*, $t_{14} = 6.99$, $p < 0.016$].

Experimental evaluation of the effects of *Plectroglyphidodon lacrymatus*

Data from the 1 yr experimental-removal of large patches of *Plectroglyphidodon lacrymatus* showed that this had no detectable influence on cover of major coral genera (Fig. 8a). The percent cover of all major coral genera was low, but this was the same both in removal plots and controls. There was also no difference in the percent cover of most of the major algal categories that were distinguished, with turfing algae dominating the substratum both in the presence and absence of *P. lacrymatus* (Fig. 8b). The exception was the higher proportion of bushy turfs in the controls compared with the removal plots. Bushy turfs were apparently reduced from approximately 20% cover to almost 0% in plots where *P. lacrymatus* had been removed.

DISCUSSION

A number of common and contrasting patterns of resource-use in the 3 territorial damselfish species were detected. The similarities confirm many of the generalizations about the role of damselfishes in coral reef ecosystems, while the differences add to the increasing diversity in the ways damselfishes acquire and maintain their food resources. While the overall structure of the habitat inside territories and feeding substrata differed markedly for the 3 species, the composition of turf algal assemblages, diets and patterns of feeding selectivity were remarkably similar, even though they occupy different reef zones. Although the differences in coral and algal composition between territories and adjacent territories grazed by other herbivorous fishes may not have been as great as reported for many other highly aggressive damselfish (Lobel 1980, Ceccarelli et al. 2001), preferred food algae were consistently higher within territories. Hence, knowledge of the diet and patterns of feeding selectivity

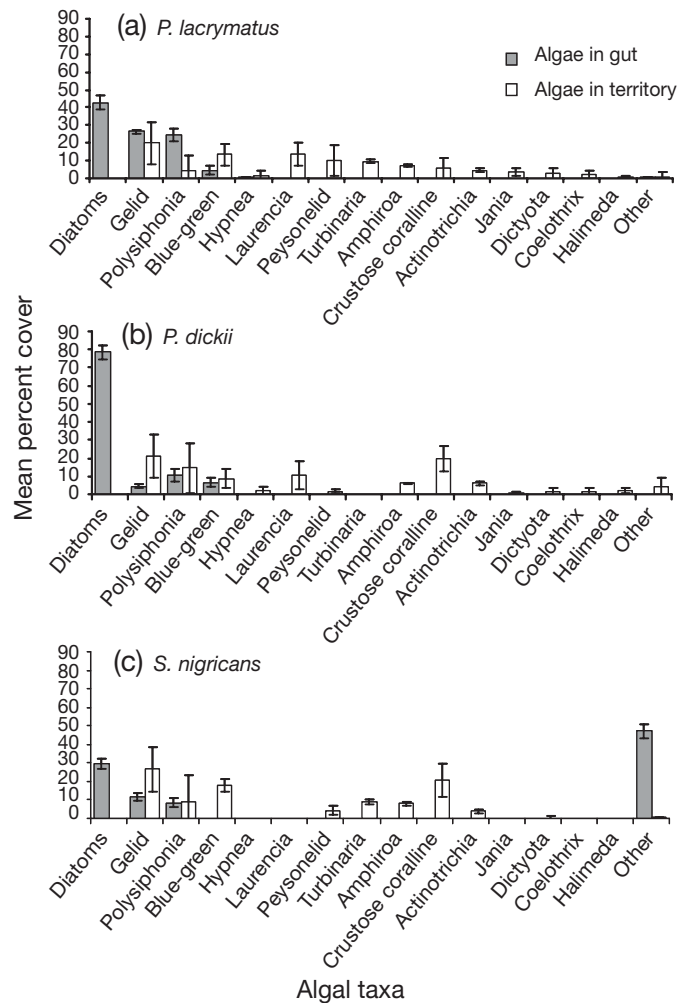


Fig. 6. *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans*. Mean percent cover of dietary items in the stomachs of (a) *P. lacrymatus*, (b) *P. dickii* and (c) *S. nigricans* with corresponding estimates of percent cover adjacent to territories. Percent cover of diatoms could not be estimated in field quadrats ($n = 20$). Error bars = 95% CL

were crucial to understanding how they interact with coral and macro-algal substrata and how much they impact the coral reef community as a whole.

This study has highlighted the importance of epiphytic algal communities, in particular diatoms, as a food resource for the 3 species of territorial damselfish examined (Lobel 1980). This confirms the widely held view that territorial damselfish are largely herbivorous (Lassuy 1980, Lobel 1980, Montgomery 1980b, Kamura & Choonhabandit 1986, Klumpp & Polunin 1989, Jones 1992). The 3 species examined are best described as 'micro-herbivores', actively feeding on diatoms, fine corticated rhodophytes (e.g. *Polysiphonia*) and cyanophytes (blue-green algae). Most of these algae appear to grow as epiphytes on mixed turf algal assem-

Table 1. *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans*. Resource selection ratios (W_i) and tests of significance for the different algal categories consumed by the 3 damselfish species. +: values significantly greater than 1 = algal selection; -: values significantly >1 = avoidance; 0: values ~ 1 = consumption/availability; N: present in territories, but not consumed

Algal taxa	<i>P. lacrymatus</i>		<i>P. dickii</i>		<i>S. nigricans</i>	
	W_i	Signif.	W_i	Signif.	W_i	Signif.
Gelid	2.32	+	0.99	0	2.15	+
<i>Polysiphonia</i>	10.19	+	3.37	+	4.63	+
Blue-green	0.60	0	3.43	+	0.05	-
<i>Hypnea</i>	0.94	0	N		N	
<i>Laurencia</i>	N		N		N	
Peysonelid	N		N		N	
<i>Amphiroa</i>	N		N		N	
Crustose coralline	N		N		N	
<i>Actinotrichia</i>	N		N		N	
<i>Jania</i>	N		N		N	
<i>Dictyota</i>	N		N		N	
<i>Coelothrix</i>	N		N		N	
<i>Halimeda</i>	N		N		N	

blages or on the larger macro-algae found in territories. The larger macro-algae do not appear to be consumed at all.

Most studies on territorial damselfish and their possible effects on coral and algal assemblages have stressed major differences in the abundance, biomass and diversity of algae between defended areas and adjacent, undefended substrata (Kaufman 1977, Lassuy 1980, Williams 1980, 1981, Hixon & Brostoff 1983, 1996, Horn 1989). In this study, the gross composition of the macro-algal assemblages inside territories was similar to non-defended areas for all 3 species, suggesting that the magnitude of the impact of these damselfish may not be as great as that of other species. However, territories of all 3 species consistently harboured a greater biomass of 'bushy' turfs with high levels of epiphyte loadings. The abundance of diatoms and the percent cover of preferred red algae were higher inside territories for all 3 species compared with adjacent, undefended areas. This pattern suggests that

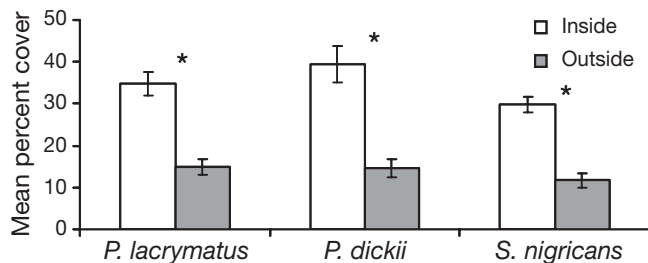


Fig. 7. *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans*. Mean percent cover of diatoms associated with 10 g samples of macro-algae from inside and adjacent to (outside) territories of 3 damselfish species ($n = 15$). *Significance at $p < 0.016$ for 3-paired t -tests. Error bars = 95% CL

they may be actively facilitating the abundance of preferred food algae. However, the contrasting composition of coral and algal substrata in territories of *Plectroglyphidodon lacrymatus*, *P. dickii* and *Stegastes nigricans* implies that each species is promoting the growth or abundance of epiphytic algal communities on different substrata.

Territorial damselfish probably fall along a continuum from highly aggressive species capable of killing large areas of coral and maintaining exclusive access to algal gardens to other species capable of less influence over their resources. In the 3 species studied here, the higher coral cover inside territories, compared with surrounding areas, likely

reflects habitat selection; although it is also possible that these species may actually promote coral growth by defending their coral shelters from corallivores (Wellington 1982, Glynn & Colgan 1988). However, the damselfishes themselves appear to be killing coral tissue to some degree. In the case of *Plectroglyphidodon lacrymatus*, experimental removal of adults over 1 yr showed little impact on coral cover, although the cover of algal turfs containing significant epiphyte loads underwent a significant decline. This result supports the experimental study of Ceccarelli et al. (2005), who reported that the dramatic effects of large, mobile grazers overshadowed the impact of this species on benthic communities. Even though this is a strongly territorial species, it is unlikely that individuals maintain exclusive access to the resources within territorial boundaries.

Plectroglyphidodon dickii characteristically defend live, branching coral colonies, mainly of the genera *Acropora* and *Pocillopora*. They maintain very distinct 'bushy' algal farms on small sections of the coral branches, which are also used as nest sites (G. P. Jones et al. unpubl.). Despite its herbivorous diet, a large proportion of the bites made by *P. dickii* were from live coral surfaces. Hence, it is likely that *P. dickii* is actively killing coral polyps without consuming them, thus increasing the area for algal growth inside their coral-dominated territories (Kaufman 1977, Robertson, et al. 1981, Wellington 1982). The extent of their impact on corals or algae needs to be confirmed by experimental removals.

Stegastes nigricans is also closely associated with living corals. It inhabits large patches of branching *Acropora* colonies in lagoonal areas. Compared with *Plectroglyphidodon dickii*, a larger proportion of the coral

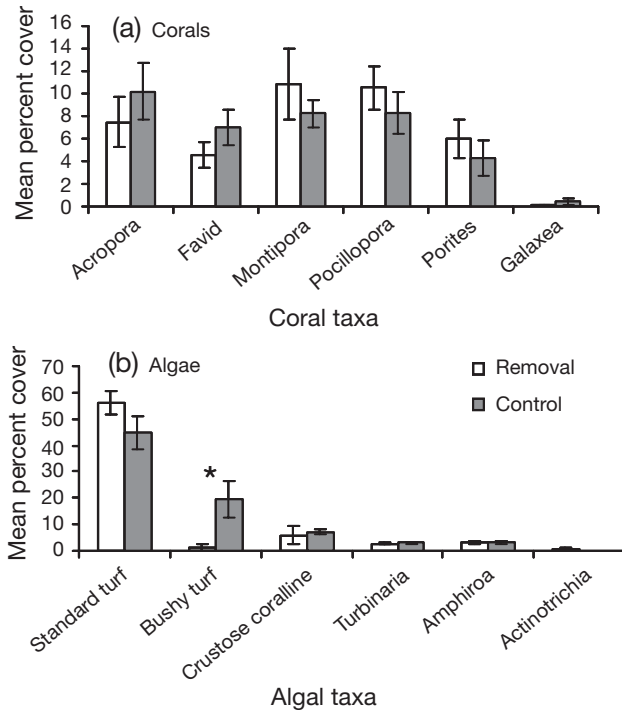


Fig. 8. *Plectroglyphidodon lacrymatus*. Mean percent cover of (a) algal turf and (b) macro-algal assemblages in experimental plots where *P. lacrymatus* had been removed for 1 yr in comparison to control plots. Data for 3 experimental and 3 control plots are pooled ($n = 15$). *Significance at $p < 0.01$ using multiple Kruskal-Wallis tests. Error bars = 95% CL

colonies associated with *S. nigricans* were dead, with only the growing tips of the branches still living. Most of the feeding by *S. nigricans* appears to be directed at epiphytic algae associated with turfing algae on the dead branches. Clearly, this damselfish species has a major impact on benthic communities at other locations (Klumpp et al. 1987), and further work is required to assess whether it is responsible for killing large areas of coral to promote algal growth in Papua New Guinea.

The results of this study support the theory that these 3 damselfish species are using algal turfs and macro-algae as a substratum for promoting the biomass of food. However, there does appear to be variation among species and locations in actual diets and what organisms are being promoted in territories. For example, Wilson & Bellwood (1997) showed that in *Hemiglyphidodon plagiometopon*, the algal turfs are used as a 'sieve' to trap organic detritus. In contrast, Zeller (1988) proposed that defended turfs were used to harbour invertebrates and other animal prey, and Hata & Nishihira (2002) showed that the habitat created by *Stegastes nigricans* promotes the abundance of foraminifera. In our study, all 3 species appeared to be promoting epiphytes such as diatoms and filamentous red algae.

The actual mechanisms by which diatoms and other epiphytes increase within territories require further investigation. All 3 species are aggressive toward other herbivores; therefore, as in other cases (Mahoney 1981, Hixon & Brostoff 1983, Hata & Kato 2003), the increase may be explained by a reduction in grazing intensity inside territories. However, damselfishes are not always effective at excluding schools of roving herbivores and other competitors (Russ 1987, Eagle & Jones 2004, Ceccarelli et al. 2005). Other mechanisms, such as weeding and habitat conditioning have been demonstrated in other systems (Jones 1992, Hata et al. 2002). It is likely that the proliferation of diatoms in territories can be attributed to more than one factor.

While large herbivorous fishes on coral reefs may be crucial in maintaining the structure of coral reef habitats (Steneck 1988, Hughes 1994, McCook 1999), the contribution of the many, small damselfish species may be subtle, but still important. Damselfish are clearly capable of promoting the abundance of micro-algae and small invertebrates in their territories. Furthermore, there are few areas of shallow reef habitat that are not occupied by territorial damselfish of some kind (Ceccarelli et al. 2001, 2005). Our study supports the view that herbivorous damselfish encompass a broad spectrum, from species capable of dramatically modifying the reef seascape by killing coral and thus promoting algal farms, to those effecting the abundance of a few algal taxa. Despite these diverse roles, many underlying similarities are also emerging. Their common effects on microscopic organisms such as diatoms may be an important link to higher trophic levels on coral reefs.

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