

Modification of benthic communities by territorial damselfish: a multi-species comparison

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Abstract The effects of territorial damselfish on coral reef benthos have been well-studied for a few relatively large-bodied species with visually distinct territories. Despite a growing body of research demonstrating their abundance, and their effects on algae, corals and other grazers, there has been little research on the effects of the territorial damselfish community as a whole. This study investigated the space occupation, territory composition, and diet of ten damselfish species at three locations: Magnetic and Orpheus Islands (Great Barrier Reef), and Kimbe Bay (Papua New Guinea). Territories were measured, and the composition of benthic communities inside and outside territories was assessed both in situ and from algal collections. The stomach contents of territorial damselfishes were also quantified. Although the larger, previously well-studied species had the most visible effect on the benthic community in their territories, all the smaller species also significantly affected the algal composition, normally with an increase of palatable algae. However, the composition of algal assemblages inside the territories of different species varied considerably. Damselfish territories were highly individual, not just among species, but also among locations. Diets were diverse and indicated a greater degree of omnivory and detritivory than previously thought. At all

locations, territories occupied a substantial proportion of the substratum: >25% on Magnetic Island, >50% at Orpheus Island, and ~50% in Kimbe Bay. Within individual zones, this figure was as high as 70%. The contribution of territorial damselfishes to a range of benthic patterns and processes is considerable, and future benthic studies may need to distinguish more closely between territory and non-territory areas.

Keywords Herbivores · Coral reef fishes · Algal diet · Benthic community · Patchiness · Territory

Introduction

Territorial damselfishes can be important determinants of benthic ecology and are a widespread and abundant component of coral reef fish communities (Doherty 1983; Meekan et al. 1995; Ceccarelli et al. 2001). They occur in most coral reef zones (Sale 1978; Robertson and Lassig 1980; Waldner and Robertson 1980), are often present in high densities (Scott and Russ 1987; Ceccarelli et al. 2005b; Arias-Gonzalez et al. 2006), and are considered the numerically dominant herbivores on some reefs/in some habitats (Scott and Russ 1987; Ceccarelli et al. 2001). Their territorial defence and farming activities alter the benthic communities within their territories (Hixon and Brostoff 1983). In some cases they have been attributed the status of keystone species, in terms of controlling algal diversity (Wellington 1982) and coral zonation (Ceccarelli et al. 2001).

Despite the high diversity in this guild, only a few species that maintain visually distinct mats of algal turf have thus far been tested for their effects on benthic communities (Robertson and Lassig 1980; Meekan et al. 1995; Lewis

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1997; Ceccarelli et al. 2005b). Many species in the genera *Pomacentrus* and *Chrysiptera* also defend territories, but how these territories differ from surrounding substrata is largely unknown. These species are usually more abundant and spatially more widespread than the larger, more conspicuous species (Robertson and Lassig 1980; Meekan et al. 1995). To gain a broader understanding of the wider effects of territorial damselfish on coral reef benthic communities, it is necessary to sample these smaller species as well.

The diverse nature of the studies conducted to date makes it difficult to define the overall effect of herbivorous damselfish on coral reef benthic communities. Studies exist on their distribution (Montgomery 1980; Santana 2001), diets (Robertson and Lassig 1980; Ebersole 1985; Bay et al. 2001), aggression rates (Hixon 1980), territory size (reviewed in Ceccarelli et al. 2001), and their ‘gardening’ or farming behaviour (Jones et al. 2006). So far, the group includes herbivores (Wilson and Bellwood 1997), detritivores (Zeller 1988), omnivores (Jones et al. 2006), and species that consume primarily microalgae (Robertson 1996; Bay et al. 2001). Aggression rates may be very different and directed at conspecifics, congeners, or other species (Brawley and Adey 1977). Territories may be discreet (Russ 1987), overlapping, or even shared (Ceccarelli et al. 2001). Territory composition can range from monocultures (e.g. Hata and Kato 2002) to high-diversity algal turfs (e.g. Hixon and Brostoff 1983), with a number of indirect effects to corals and other organisms (Wellington 1982; Zeller 1988; Jones et al. 2006). There are large differences in the biomass, productivity, diversity and taxonomic composition of algal turfs in damselfish territories (Ceccarelli et al. 2001). The importance of herbivorous damselfishes to benthic community composition on any one reef has not yet been investigated.

The objectives of the present study were to investigate the space occupation, territory composition and diet of ten damselfish species at three locations: Magnetic and Orpheus Islands [Great Barrier Reef (GBR)] and Kimbe Bay [Papua New Guinea (PNG)]. Specifically, the following questions were addressed: (1) How much space is occupied by the territorial damselfish community in each zone of the study reefs? (2) Do all the study species defend territories in which algal communities differ significantly from surrounding areas? (3) Are territorial damselfish primarily herbivores?

The effects of each species on their territories were linked to existing information about zonation patterns of territorial damselfish on each reef, to provide an estimate of the importance of the damselfish community in each location. Furthermore, the results of this study were combined with previous research to provide an up-to-date inventory of known effects of damselfish territorial behaviour.

Materials and methods

Study sites and species

The three sites chosen for this study were the shallow reef flats, reef crests and upper slopes (between 1 and 4 m in depth) of Magnetic Island (GBR) (19°S, 147°E), Orpheus Island (GBR) (18°36'S, 146°29'E), and Kimbe Bay (PNG) (05°26'S, 150°52'E). Each location had distinct territorial damselfish communities including both large (>10 cm) and small species (Table 1), different substratum characteristics, and unique benthic communities. All species investigated had discrete territories. Magnetic Island reefs consisted of an extensive inner sedimentary accumulation zone and a typical reef flat habitat (Mapstone et al. 1989). Reef habitats included reef flats dominated by dead corals and fleshy macroalgae, well-defined reef crests with high live coral cover and a shallow, gently descending reef slope with high live coral cover interspersed with large patches of *Sargassum* spp. and *Lobophora* spp. Orpheus Island reefs supported a lower cover of fleshy macroalgae (Baird and Marshall 2002), a more complex reef topography and a more diverse damselfish community than Magnetic Island (Table 1). The Kimbe Bay sites used for this study were platform reefs, and despite their proximity to the shore, water clarity was higher than at the other two sites, and the reefs resembled outer shelf reefs of the GBR. Topographic complexity and territorial damselfish diversity were highest on these reefs. Biophysical reef zones at each location were based on the specifications used in Ceccarelli et al. (2005b). Zonation and density data for each species used to obtain space occupation estimates at each location are from Ceccarelli et al. 2001 for Magnetic Island and Orpheus Island, and from G.P. Jones personal communication for Kimbe Bay (see Electronic Supplementary Material for Excel spreadsheet). The sampling methodology to obtain density estimates (visual belt transects) is described in Ceccarelli et al. (2005b).

Observations

All observation data were collected from 2001 to 2003 between the months of April and August each year. Individual fish were observed for 15 min, during which time the boundaries within which feeding and weeding activities took place were marked with lead weights. Generally the area defended by the damselfishes was highly irregular, but a ‘feeding patch’ existed within each territory where the majority of territory maintenance took place. This patch was often more compact and roughly circular in shape (see also Jan et al. 2003). Territory area was therefore calculated by measuring the circumference of each territory and using the formula for a circle of equivalent circumference. Territory size measurements multiplied by the densities of each

Table 1 Summary of locations and species used for the sampling of different characteristics

Location	Species	Size (cm)	Bite rate	Gut content	Territory large scale	Territory fine scale
Magnetic Island	<i>Pomacentrus tripunctatus</i>	10	25	25	25	25
	<i>Pomacentrus wardi</i>	10	25	25	25	25
	<i>Stegastes apicalis</i>	13	25	25	25	25
Total			75	75	75	75
Orpheus Island	<i>Pomacentrus tripunctatus</i>	10	25		25	25
	<i>Pomacentrus wardi</i>	10	25		25	25
	<i>Pomacentrus adelus</i>	8.5	25		25	25
	<i>Hemiglyphidodon plagiometapon</i>	18	25		25	25
	<i>Pomacentrus chrysurus</i>	9	25		25	25
Total			125	0	125	125
Kimbe Bay	<i>Pomacentrus tripunctatus</i>	10	25	25	25	25
	<i>Pomacentrus adelus</i>	8.5	25	25	25	25
	<i>Plectroglyphidodon lacrymatus</i>	10	25	25	25	25
	<i>Pomacentrus bankanensis</i>	10	25	25	25	25
	<i>Pomacentrus burroughi</i>	8	25	25	25	25
	<i>Stegastes lividus</i>	15		25		
	<i>Chrysiptera leucopoma</i>	8		25		
	<i>Chrysiptera unimaculata</i>	8		25		
	<i>Neoglyphidodon nigroris</i>	11	25		25	25
Total			150	200	150	150

‘Territory large scale’ refers to sampling conducted in situ on broad benthic categories, while ‘Territory fine scale’ refers to algal collection samples. ‘Size’ refers to maximum fish sizes recorded in Allen et al. (2003) and Randall (2005). Column totals are the total numbers of individuals for each characteristic

species allowed the estimation of how much space each species occupied in each zone.

After measuring the circumference, a 0.25 m² grid (split into 100 squares) was placed inside and then outside the territory. The outside sampling area was chosen on the basis of maximum proximity and maximum topographic similarity to the sampling area inside the territory. In areas of high damselfish abundance, outside sampling areas were marked during the focal individual observation period, and then observed for a further 15 min to ensure that no damselfish feeding occurred. In each sampling area, the benthos inside each square was recorded, providing an estimate of percent cover. Benthic categories were classified as coral-line algae (e.g. crustose coralline algae, Peyssonellidae), thin algal turf (<3 mm thick), thick algal turf (>3 mm thick), fleshy macroalgae (primarily *Sargassum* spp., *Padina* spp., *Dictyota* spp. and *Lobophora* spp.), corticated red algae (e.g. *Laurencia* spp. and *Hypnea* spp.), calcified algae (e.g. *Amphiroa* spp, *Jania* spp.) and live coral. Algal turf is defined as ‘...masses of tightly packed upright branches...’ (Hay 1981), and includes primarily filamentous taxa. In this study, algal turfs often included articulated coralline algae such as *Jania* spp. and *Amphiroa* spp., and microalgae (typically diatoms and cyanobacteria). Algal samples were then scraped from five 3 cm × 3 cm random collection points inside and five equivalent points outside the territory and fixed in 10% formalin as soon as possible after collection.

Directly after the observation period and algal collection, the focal individuals were anaesthetized with 30% clove oil, killed in ice water, and preserved in 10% formalin, with an incision in the abdomen to allow faster preservation of the gut contents. Due to logistic difficulties, all data were not obtained for all fish species (Table 1).

Laboratory analyses

Algal samples

Algal samples were spread evenly across a 10-cm Petri dish for the estimation of percent cover and taxonomic identification. A square grid (1 cm mesh size) was placed over the dish and the taxon under 50 intercept points was recorded. The frequency of occurrence of each taxon was converted into percent cover estimates. Taxa were identified to genus where possible, and to functional group where necessary (see Steneck and Dethier 1994; Ceccarelli et al. 2005b). Sediment and detritus directly associated with the algal samples were also quantified as percent cover.

Gut contents

While it is possible to determine the broad benthic category targeted by individual damselfish by counting numbers of bites on different substrata, gut contents analysis gives a much more accurate indication of what is removed from the

benthos. In the laboratory, the fish were weighed and measured (total length and standard length) and the ingested material above the pyloric caecae removed from the stomach and analysed in the same manner described above for territory samples.

Data analysis

Data were analysed with SPSS for Windows software. The area occupied by damselfish territories was estimated using the damselfish density, and the territory size measurements taken in each zone. Territorial damselfish space occupation was calculated reef-wide and for each designated reef zone, and the between-zone differences tested using analysis of variance (ANOVA). To provide a measure of the space taken up by all damselfish territories, the percentage of space occupied by all damselfish territories in each zone was calculated, and an overall average was calculated for each location. All percentage data was arcsine transformed. Tukey's post hoc tests were used to detect differences among categories of each factor. Multivariate ANOVA (MANOVA) was used to analyse differences at each location between benthic communities inside and outside the territories, and between gut contents. Tukey's post hoc tests were also produced to test the individual between-subjects effects of each analysis, with the appropriate correction factors. Canonical discriminant analysis (CDA) based on structure coefficients was then used to detect multivariate differences in benthic, algal and gut content composition between species of damselfish.

Despite the usefulness of CDA in showing the differences tested by MANOVA, it was found that, with the exception of differences in gut contents, principal components analysis (PCA) biplots were more useful in displaying the differences in the benthic and algal compositions between species. For these purposes, data were pooled for all locations. S-Plus for Windows software was used to produce the PCA biplots and the gut contents CDA plot. The PCA was based on the correlation matrix of the abundance of each category inside damselfish territories, and S-Plus produced 95% confidence ellipses around the group mean for each species. The CDA was also presented with 95% confidence limits around the group centroid of each fish species.

Results

Distribution and space occupation

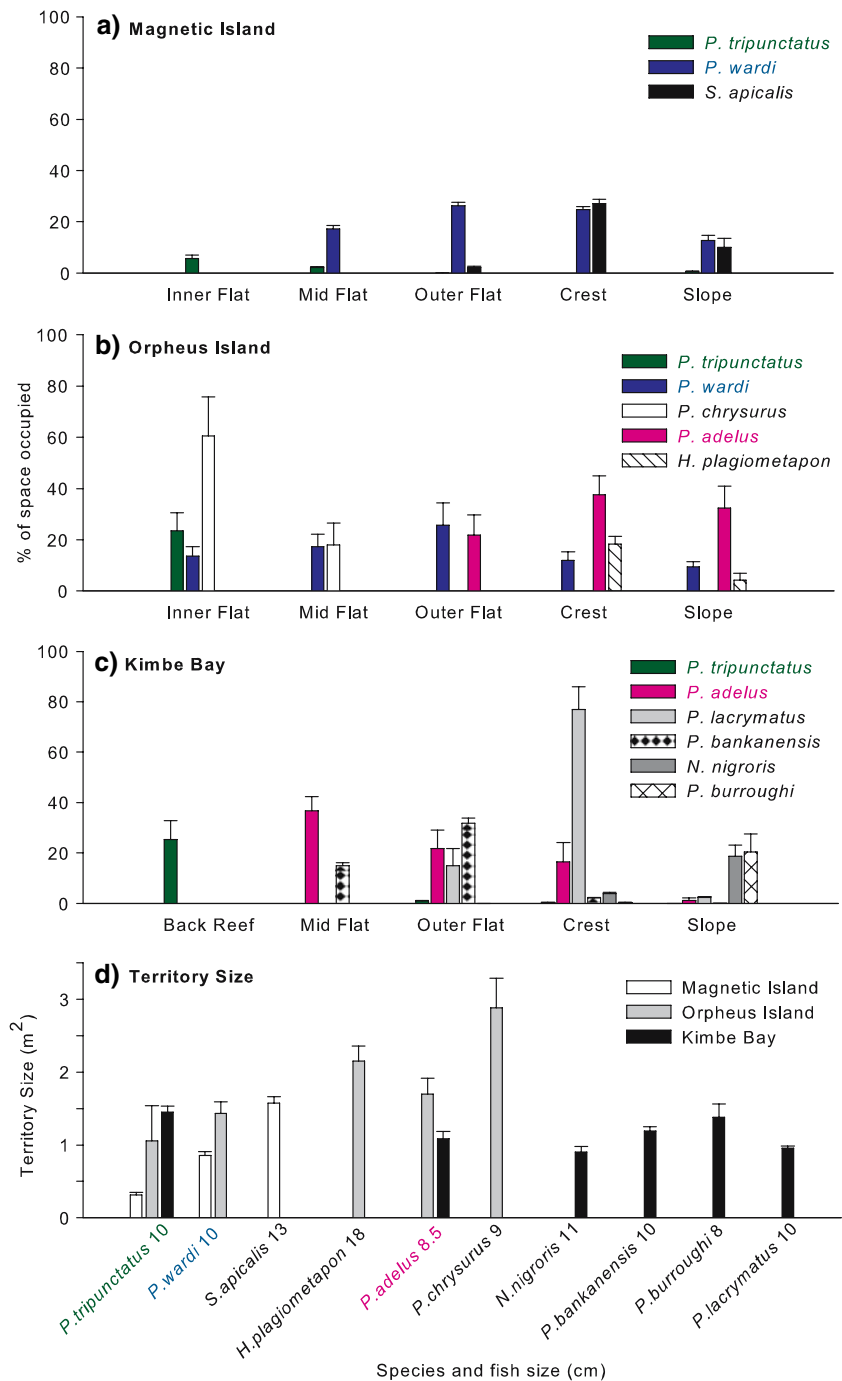
Across all zones on Magnetic Island, the individual territory sizes of all three species were significantly different (ANOVA: $F_{2,69} = 116.566$, $p < 0.001$), with *Stegastes*

apicalis defending the largest territories and *Pomacentrus tripunctatus* the smallest (Fig. 1d). The total space occupied by each species also differed significantly (ANOVA: $F_{2,69} = 30.708$, $p < 0.001$). Multiple comparisons showed that *P. wardi* occupied the most space, followed by *S. apicalis* and then *P. tripunctatus* (Tukey comparisons, all $p < 0.05$). Across all zones, an average of 25.8% (± 0.018 SE) of all available substrata was taken up by damselfish territories (Fig. 1a). On the Reef Crest; *P. wardi* and *S. apicalis* occupied almost 60% of the available space. On the Mid and Outer Reef Flat, 30% of the space was in territories belonging to *P. wardi*, whilst *P. tripunctatus* and *S. apicalis* occupied less than 4%. The sand and rubble Inner Reef Flat only supported *P. tripunctatus* territories, occupying 7% of the space.

Across the Orpheus Island fringing reefs, damselfish territory sizes also differed significantly (ANOVA $F_{4,45} = 5.031$, $p < 0.005$). *P. chrysurus* maintained the largest territories, followed by *Hemiglyphidodon plagiometapon* territories. These territory sizes differed from each other and from those of the other three species, *P. adelus*, *P. wardi* and *P. tripunctatus* (Tukey comparisons, both $p < 0.05$) (Fig. 1d). Species occupied varying proportions of total space across the reef flat (ANOVA, $F_{4,45} = 4.050$, $p < 0.05$), and multiple comparisons showed that *P. adelus*, *P. chrysurus* and *P. wardi* each occupied significantly more space, than *H. plagiometapon* and *P. tripunctatus* (Tukey comparison between the two groups of species, $p < 0.05$). An overall average of 58.8% (± 0.097 SE) of available substrata was taken up by damselfish territories (Fig. 1b). On the Inner Reef Flat, around 90% of the substratum was taken up by *P. tripunctatus*, *P. chrysurus* and *P. wardi* territories. The second most densely occupied zone was the Reef Crest, where almost 70% of substrata were taken up by *P. adelus*, *P. wardi* and *H. plagiometapon* territories. Only two or three species coexisted in each zone, and three of the five zones were dominated by one species.

The territory size of species found in Kimbe Bay also differed significantly (ANOVA, $F_{5,54} = 4.884$, $p < 0.005$). *P. tripunctatus*, *P. bankanensis* and *P. burroughi* defended territories that were significantly larger than those of *Plectroglyphidodon lacrymatus* and *Neoglyphidodon nigroris* (Tukey comparisons, $p > 0.05$ within groups, $p < 0.05$ between groups) (Fig. 1d). The territories of *P. adelus* were of intermediate size, and differed only from *P. tripunctatus* territories. Overall, *P. lacrymatus* occupied the most space on the reef (ANOVA, $F_{5,54} = 2.755$, $p < 0.05$), followed by *P. adelus* (Tukey comparison, $p > 0.05$). *P. burroughi*, *P. tripunctatus* and *N. nigroris* occupied the least space, although on the Back Reef, the most sparsely occupied zone, *P. tripunctatus* territories took up a quarter of the available space. An average of 46.6% (± 0.07 SE) of available substrata on the Kimbe Bay platform reefs was taken

Fig. 1 Percent of substratum occupied by damselfish territories on reefs at **a** Magnetic Island; **b** Orpheus Island; **c** Kimbe Bay; and **d** Territory sizes in m² for each species at each location (fish size from Table 1). Error bars = 1 SE. Species present at more than one location are shown in colour. *P.*: *Pomacentrus* (except for *Plectroglyphidodon lacrymatus*), *S.*: *Stegastes*, *H.*: *Hemiglyphidodon*, *N.*: *Neoglyphidodon*



up by damselfish territories belonging to six species (Fig. 1c). The most densely occupied zone was the Reef Crest, where almost 100% of the substratum was occupied by damselfish territories. The Reef Crest was also where the most species coexisted, even though most of this zone (77%) was occupied by *P. lacrymatus* (Fig. 1c).

Amongst locations, territory size varied significantly (ANOVA, $F_{2,137} = 37.142$, $p < 0.001$), but space occupation did not (ANOVA, $F_{2,137} = 1.501$, $p > 0.05$; Fig. 1). The smallest territories were those defended by *P. tripunctatus*

on Magnetic Island, while *P. chrysurus* maintained the largest territories on Orpheus Island. The variability in the territory sizes of different species was lowest in Kimbe Bay, and greater on Magnetic Island and Orpheus Island, where the smallest territories were approximately one-third to one-half the size of the largest territories, respectively. Territory sizes of species that were present at more than one location were not uniform in size; for instance, *P. tripunctatus* territories were approximately three times larger on Orpheus Island, and four times larger in Kimbe Bay, than

territories on Magnetic Island (ANOVA, $F_{2,27} = 23.832$, $p < 0.001$).

Benthic composition inside and outside territories

In all three sampling locations, the differences between territories and surrounding benthic communities varied among fish species (Table 2). Due to the differences in benthic composition among locations, the inside versus outside territory differences were represented separately for each sampling location (Fig. 2).

Benthic communities inside all fish territories on Magnetic Island were significantly different from those outside (MANOVA, $F_{7,48} = 22.98$, $p < 0.001$). The benthos outside damselfish territories was composed of large stands of fleshy macroalgae (40% cover), hard substrata covered in thin turf (22%), patches of high live coral cover (15%), and sandy patches (8%) (Fig. 2a). *P. tripunctatus* territories differed from undefended substrata primarily through the higher cover of thick turf and lower live coral cover. *P. wardi* and *S. apicalis* territories contained almost ten times more thick turf than surrounding areas and significantly lower cover of fleshy macroalgae. Additionally, *S. apicalis* territories contained, six times the cover of calcified algae and double the live coral cover of outside areas. *S. apicalis* territories differed significantly from the territories of *P. wardi* and *P. tripunctatus*, with highest cover of live coral and calcified algae, and the lowest cover of thin turf and macroalgae (MANOVA, CDA and Tukey comparisons on between-subject effects, all $p < 0.05$) (Fig. 2a).

Orpheus Island benthic communities differed between damselfish territories and undefended areas (MANOVA, $F_{7,84} = 11.675$, $p < 0.001$). The benthos outside territories was dominated by thin turf (62% cover), with few areas of live coral (13%), relatively low cover of macroalgae (10%) and few sandy patches (10%), while damselfish territories were composed of species-specific benthic assemblages. All damselfish territories had significantly more thick turf

than outside, especially *H. plagiometapon* territories, where thick turf reached ~80% cover and was approximately 40 times higher than outside territories and twice as much as the territories of all other damselfish species (Fig. 2b), where thick turf cover did not exceed 45%. The territories of *H. plagiometapon*, *P. adelus*, *P. chrysurus* and *P. wardi* also had significantly less thin turf than outside. *P. chrysurus* and *P. tripunctatus* territories had the highest cover of fleshy macroalgae (MANOVA, CDA and Tukey comparisons on between-subject effects, all $p < 0.05$) (Fig. 2b).

Benthic community structure in Kimbe Bay was also significantly affected by the presence of damselfish territories (MANOVA, $F_{7,102} = 9.254$, $p < 0.001$). Undefended areas had almost 30% live coral cover and large areas where thin turf dominated the benthos (almost 50% cover), whilst the cover of fleshy macroalgae was minimal (1%) (Fig. 2c). Thick turf cover was higher inside the territories of *P. adelus* (5 times more thick turf inside territories than outside), *P. bankanensis* (12 times more) and *P. lacrymatus* (almost 4 times more). *P. tripunctatus* territories had the highest cover of thin turf (80%), and *P. adelus* and *P. lacrymatus* defended territories containing high live coral cover (>40%) compared to outside (MANOVA, CDA and Tukey comparisons on between-subject effects, all $p < 0.05$) (Fig. 2c).

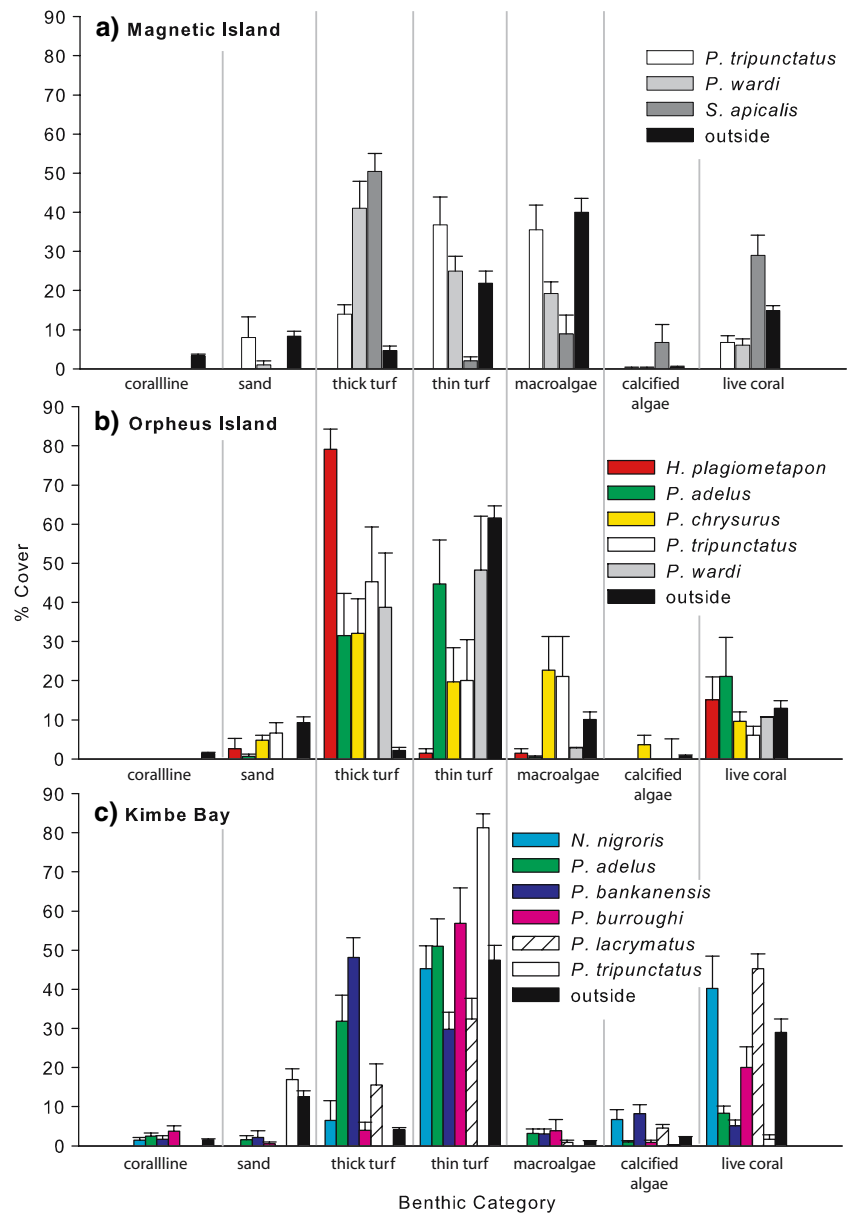
Most damselfish species could be distinguished by the relative cover of thick turf, thin turf and live coral in a PCA of all species that compared the benthic functional groups present in their territories (Fig. 3). *S. apicalis* and *H. plagiometapon* defended territories with particularly high cover of thick turf. A separate group, characterized by territories with high cover of thin turf and live coral, included *P. lacrymatus*, *N. nigroris* and *P. burroughi*. *P. lacrymatus* and *N. nigroris* were both usually found close to the reef crest, in areas of high coral cover, while *P. burroughi* defended territories on the reef slope, often near branching corals. The largest group was located near the origin of the four main vectors, suggesting the presence of more diverse

Table 2 Results of MANOVAs on differences between benthic communities from inside and outside damselfish territories, from direct sampling, algal collections and differences in gut contents

Test	Location	Test value	df	F	Significance
In situ benthic community	Magnetic Island	1.143	28,84	4.0	$p < 0.001$
	Orpheus Island	0.547	36,309	1.5	$p < 0.05$
	Kimbe Bay	0.947	45,520	2.699	$p < 0.001$
Algal collections	Magnetic Island	1.205	40,72	2.73	$p < 0.001$
	Orpheus Island	0.966	72,304	1.344	$p < 0.05$
	Kimbe Bay	1.246	90,475	1.752	$p < 0.001$
Gut contents	Magnetic Island	0.697	24,172	3.837	$p < 0.001$
	Kimbe Bay	2.57	119,434	2.116	$p < 0.001$

The test values refer to Pillai's Trace test statistics; and the df column includes the numerator and denominator degrees of freedom, separated by a comma

Fig. 2 Benthic composition inside and outside territories of damselfish communities for **a** Magnetic Island, **b** Orpheus Island, and **c** Kimbe Bay. The percent cover of different benthic categories was obtained with point intercept sampling on site. Each site represents a distinct damselfish community and slight variations in the major benthic categories. *P.*: *Pomacentrus* (except *Plectroglyphidodon lacrymatus*), *S.*: *Stegastes*, *H.*: *Hemiglyphidodon*, *N.*: *Neoglyphidodon*. Error bars = 1 SE



benthic communities in their territories (Fig. 3). Of this group, *P. bankanensis* territories appeared to contain the highest cover of thick turf, while *P. adelus* and *P. tripunctatus* territories were dominated by thin turf.

Algal composition inside and outside territories

At all three sampling locations, the differences in algal turf composition between territories and surrounding habitat varied among species (Table 2). The inside versus outside territory differences in algal turf composition were represented separately for each sampling location to distinguish the differences among locations (Fig. 4).

The algal community outside fish territories on Magnetic Island was significantly different from those inside damselfish territories (MANOVA, $F_{8,47} = 37.555, p < 0.001$), as it

was dominated by fleshy macroalgae (37% cover) with the only other major components being corticated red algae (14%) and detritus (11%). Inside damselfish territories, algal communities were much more varied (Fig. 4a). *P. tripunctatus* territories were made up primarily of detritus and corticated red algae (predominantly *Laurencia* spp.), which were present in approximately double the quantities found outside. *P. wardi* territories contained a higher cover of the delicate filamentous red *Polysiphonia* spp. than outside. *S. apicalis* defended the most distinct territories, with high cover of calcified and corticated red algae, particularly *Amphiroa* spp., *Gelidiopsis* spp. (both of which were absent outside) and the filamentous red algae, *Polysiphonia* spp., and a distinct lack of fleshy macroalgae (MANOVA, CDA and Tukey comparisons on between-subject effects, all $p < 0.05$).

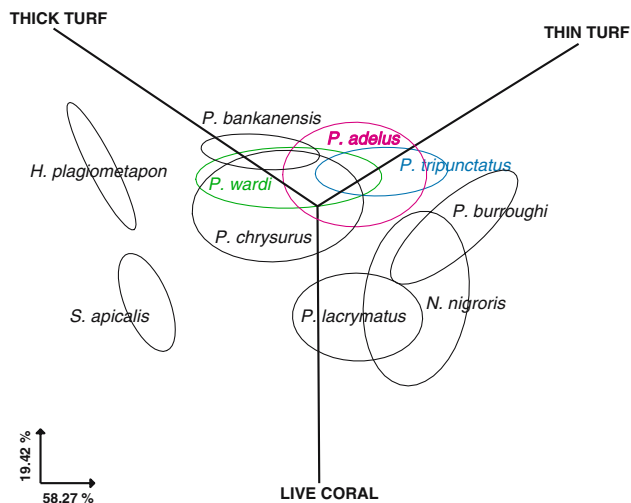


Fig. 3 Principal components analysis (PCA) biplot of benthic composition inside territories of all species, irrespective of location. PCA axes and loadings are shown in inset. Vectors represent trends in the original variables. Circles are 95% confidence intervals. *P.*: *Pomacentrus* (except *Plectroglyphidodon lacrymatus*), *S.*: *Stegastes*, *H.*: *Hemiglyphidodon*, *N.*: *Neoglyphidodon*

Areas outside territories on Orpheus Island were characterized by detritus (33%), followed by corticated algae (>20%), and differed significantly from damselfish territories (MANOVA, $F_{9,82} = 3.283$, $p < 0.005$) (Fig. 4b). *P. wardi* territories contained the highest cover of detritus (50%), while the cover of other territory components was similar to areas outside territories. *H. plagiometapon* territories included the highest cover of corticated red algae, mainly as *Gelidiopsis* spp. and *Hypnea* spp., but around a third less detritus than outside areas. *P. tripunctatus* territories contained the highest cover of the corticated red algae *Laurencia* spp. *P. adelus* territories, on the other hand, had almost four times more *Polysiphonia* than the territories of all other species (MANOVA, CDA and Tukey comparisons on between-subject effects, all $p < 0.05$).

Kimbe Bay algal communities outside territories were distinguished from those inside territories (MANOVA, $F_{9,100} = 9.521$, $p < 0.001$) by their high percentage of coralline algae (23%), combined relatively low cover of *Amphiroa* spp., corticated red algae, and filamentous red *Polysiphonia* spp. (Fig. 4c). However, the relatively high cover of thin turf (over 30% in all territories and outside, Fig. 2c) was reflected in the lower cover of most algal taxa compared with Magnetic and Orpheus Islands (Fig. 4). Most territories (except *P. tripunctatus*) contained approximately half the cover of coralline algae compared to outside territories, and most (except *N. nigroris* and *P. burroughi*) contained double the cover of corticated red algae. The territories of *P. adelus* and *P. bankanensis* were very similar, characterized by high cover of fleshy macroalgae and corticated red algae, especially *Laurencia* spp. *P. lacrymatus*

territories were dominated by corticated red algae, and distinguished by a higher cover of *Amphiroa* spp. compared to the territories of other species (MANOVA, CDA and Tukey comparisons on between-subject effects, all $p < 0.05$).

PCA indicated that the territory components causing most of the variability between species were detritus, corticated red algae and fleshy macroalgae. Of similar influence were algae of the genera *Amphiroa*, *Hypnea*, *Gelidiopsis* and *Polysiphonia* (Fig. 5). *H. plagiometapon* territories were distinguished by a high detrital content; *P. wardi* and *P. adelus* territories were characterized by high cover of *Polysiphonia*, while *P. chrysurus* territories were especially rich in corticated red algae. *S. apicalis* and *P. lacrymatus* territories were particularly high in the calcified algae *Amphiroa* spp. Most species and species groups tended to remain near the origin, suggesting that most species maintained algal communities with some degree of diversity.

Despite the propensity for similar algal taxa to recur from place to place, each species of damselfish maintained territories different from areas outside it and from the territories of other species. When a species was present at more than one location, the algal community composition inside its territories tended to vary between locations (*P. tripunctatus* and *P. wardi*, MANOVA for location by inside/outside algal community, $F_{18,174} = 2.64$, $p < 0.001$).

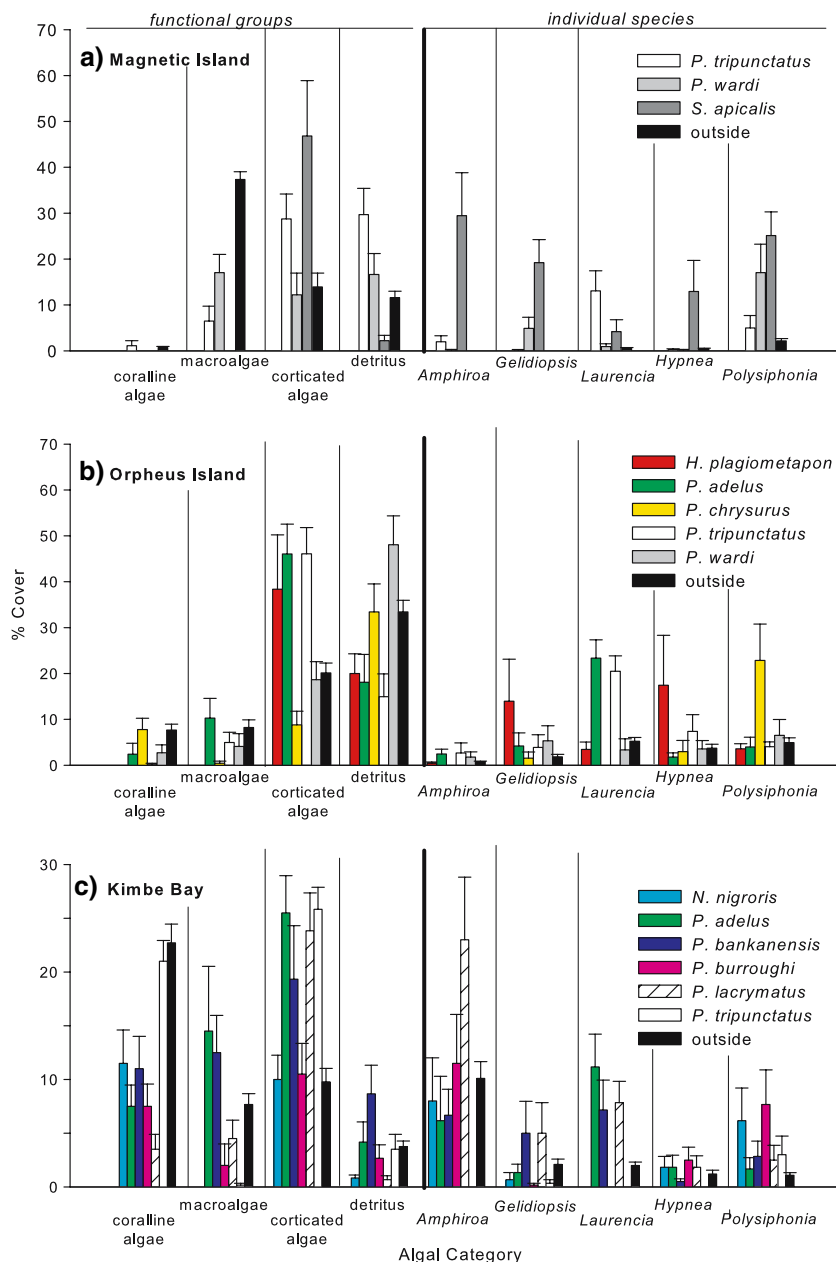
Gut contents

Gut contents analyses were carried out on three species on Magnetic Island (*P. tripunctatus*, *P. wardi* and *S. apicalis*) and eight species in Kimbe Bay (*P. tripunctatus*, *P. adelus*, *P. bankanensis*, *P. lacrymatus*, *P. burroughi*, *Chrysiptera leucopoma*, *C. unimaculata*, and *S. lividus*). At both locations, there were significant differences in the composition of the gut contents of different species (Table 2).

On Magnetic Island, *S. apicalis* had ingested primarily filamentous red algae, and overwhelmingly *Polysiphonia herpa*, while the stomach contents of *P. tripunctatus* and *P. wardi* contained a combination of algae and detritus (Fig. 6). The diet of *P. tripunctatus* consisted of significantly more detritus (50% of gut contents) and less filamentous algae (30%) than the other two species, while the detritus/algae ratio appeared almost exactly reversed for *P. wardi* and *S. apicalis* (Fig. 7; Tukey comparisons, all $p < 0.05$). Invertebrates made up a small portion of the diet of all three species.

In Kimbe Bay, detritus made up more than 50% of the diets of *C. leucopoma*, *C. unimaculata*, *P. lacrymatus*, *P. tripunctatus* and *S. lividus* (Fig. 6). The gut contents of the remaining three species, *P. adelus*, *P. bankanensis* and *P. burroughi*, consisted of between 60 and 80% corticated red algae and filamentous algae, and some (28–45%) detri-

Fig. 4 Composition of the algal communities inside and outside territories of damselfish communities for **a** Magnetic Island, **b** Orpheus Island, and **c** Kimbe Bay. The percent cover of different turf categories was obtained from laboratory analyses of algal collections. Both functional algal groups and individual genera are represented, separated by lines at the top of the figure, and by the thick line dissecting it. Each site represents a distinct damselfish community and slight variations in the major taxonomic categories present in the algal community. *P.*: *Pomacentrus* (except *Plectroglyphidodon lacrymatus*), *S.*: *Stegastes*, *H.*: *Hemiglyphidodon*, *N.*: *Neoglyphidodon*. Error bars = 1 SE



tus. Of the corticated red algae, *Hypnea* appeared to be the most important genus in the diets of many species, and *Polysiphonia* spp. was the dominant filamentous taxon contained in the stomachs (Fig. 6). Only one species, *P. lacrymatus*, had ingested substantial amounts of recognizable microalgae (10%; Fig. 7, Tukey comparisons all $p < 0.05$).

A discriminant analysis suggested that all species are omnivorous to some degree, with *S. apicalis* and *P. wardi* ingesting the highest proportion of algal matter (Fig. 7). All other species appeared to ingest a combination of detritus, delicate corticated and filamentous algae, and a small amount of animal matter. Despite the high degree of herbivory in the diet of *S. apicalis*, this species was also seen to actively target invertebrates.

Discussion

All the damselfish species included in this study guarded territories in which the cover and composition of algal turfs differed significantly from surrounding areas. Although the larger, previously well-studied species (e.g. *H. plagiometapon*, *Stegastes* spp.; see Table 1) appeared to have the most visible effects on benthic communities, this was not universally the case. For instance, territories of the relatively large *N. nigroris* contained benthic assemblages that were less distinct from those outside, compared to the territories of the smaller *P. tripunctatus* and *P. adelus*. Many of the smaller species (mostly members of the genus *Pomacentrus*) also had algal turf communities in their territories that

were significantly different from those outside territories. These results suggest that the influence of small damselfish on coral reef benthic communities may be more far-reaching than previously assumed.

The present study confirms the patterns found in previous research that suggest the primary effect all damselfish have in common is the increase of palatable algae, such as filamentous or corticated taxa, in their territories. While this

Fig. 5 PCA biplot of algal turf composition inside territories of all species, irrespective of location. PCA axes and loadings are shown in inset. Circles are 95% confidence intervals. Algal species and functional groups are shown in green. *P.*: *Pomacentrus* (except *Plectroglyphidodon lacrymatus*), *S.*: *Stegastes*, *H.*: *Hemiglyphidodon*, *N.*: *Neoglyphidodon*

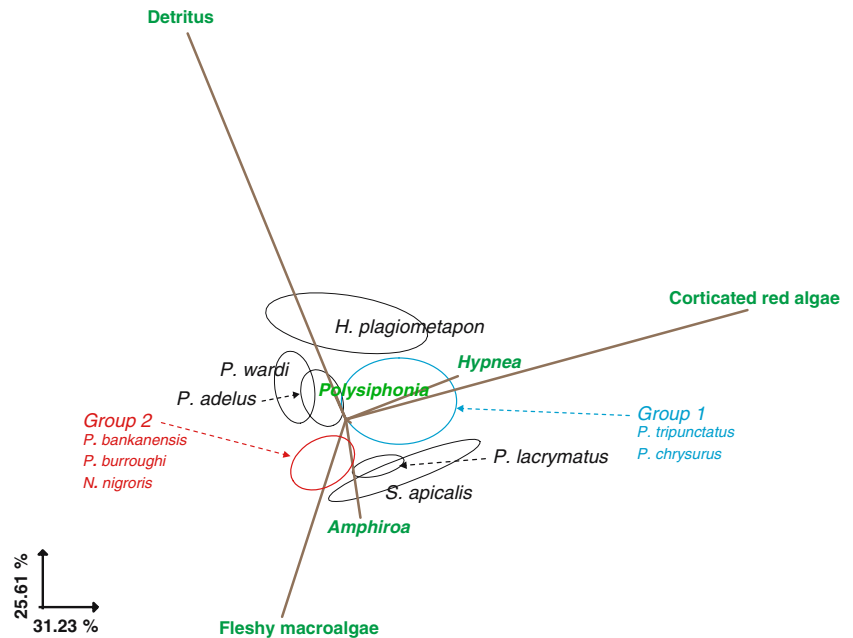
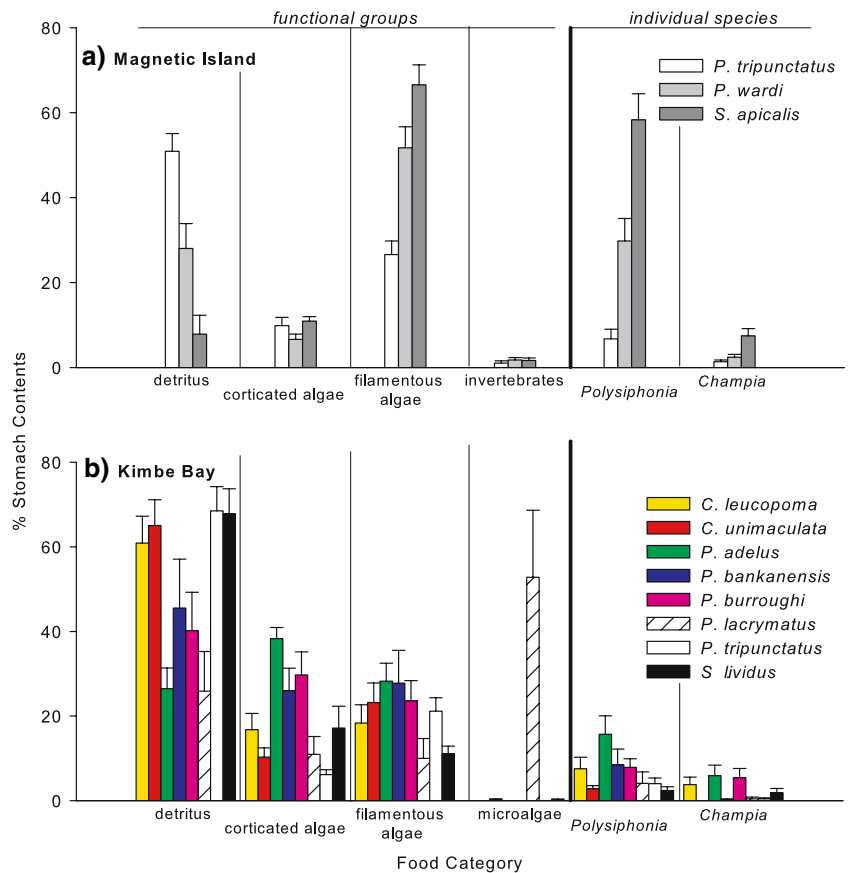


Fig. 6 Results of gut content analysis for fish caught at **a** Magnetic Island, and **b** Kimbe Bay. Both functional food groups and individual genera are represented, separated by lines at the top of the figure, and by the thick line dissecting it. Error bars = 1 SE. *P.*: *Pomacentrus* (except *Plectroglyphidodon lacrymatus*), *C.*: *Chrysiptera*



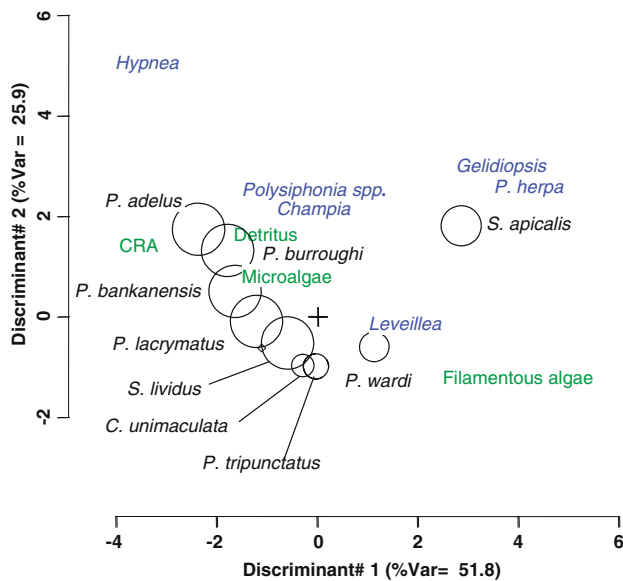


Fig. 7 Results of discriminant analysis on gut contents of nine species at two locations: Magnetic Island and Kimbe Bay. Circles are 95% confidence intervals around the fish species centroids. Food categories are represented in green (functional groups) and blue (individual species). *P.*: *Pomacentrus* (except *Plectroglyphidodon lacrymatus*), *C.*: *Chrysiptera*

study and some earlier studies have focused on differences in percent cover (Kamura and Choonhabandit 1986; Gobler et al. 2006; Jones et al. 2006), other studies have detected higher biomass (Sammarco 1983; Klumpp et al. 1987; Ferreira et al. 1998), diversity (de Ruyter van Steveninck 1984; Hinds and Ballantine 1987; Hixon and Brostoff 1996), and productivity (Klumpp et al. 1987; Russ 1987) inside damselfish territories compared to outside. The present study also confirms the general propensity for a predominance of delicate, filamentous taxa inside damselfish territories (Table 3). *Polysiphonia* spp., for instance, have been found to dominate the territories of over half the species investigated in all studies, across locations as diverse as the Great Barrier Reef, the Gulf of California, and the Caribbean, and on both coral and rocky reefs.

Despite these overall similarities, however, much higher diversity than previously assumed exists in the composition of algal turfs found inside territories of different species. Even for the same damselfish species, algal composition varied between locations, perhaps reflecting the composition of the available benthos. When comparing the findings of the present study to previous research, *H. plagiometapon* (for example) has been found to defend territories containing different species of corticated and blue-green taxa, depending on where studies were conducted. The differences in algal communities between species and locations found in the present study add to the wider diversity found in other studies from around the world. For instance, the

increase in erect calcified algae and distinctive lack of fleshy macroalgae in coastal *S. apicalis* territories and the high detrital content of *P. tripunctatus* territories can be added to findings of unique algal communities inside the territories of damselfish species (Table 3). These differences are likely to be a product of a number of interacting effects, including the direct farming activities of the damselfish (Hata and Kato 2004; Ceccarelli et al. 2005a), the existing benthic communities in each reef zone (Ceccarelli et al. 2005b), and possibly site selection (Bay et al. 2001). For example, *S. apicalis* and *P. lacrymatus* occurred primarily on exposed outcrops and reef crests (see also Klumpp et al. 1987; Zeller 1988; Ceccarelli et al. 2005b), therefore the turf in their territories was dominated by species resistant to relatively high wave action. In contrast, *P. tripunctatus* and *P. chrysurus* were found only in shallow inner reef (on fringing reefs) or back reef (on platform reefs) zones, and the detritus-rich composition of their territories tended to reflect a more sheltered environment. *S. nigricans*, *S. lividus* and *Plectroglyphidodon dickii* territories have been found almost exclusively in live colonies of branching acroporid corals (Jones et al. 2006), and the turf that grows there may be influenced by the quality of the substratum. The four species of the genus *Dischistodus* are spatially segregated, either by reef zone or topography, and maintain very different algal turfs (Bay et al. 2001). The idea that site selection affects algal turf composition in damselfish territories is supported by subtle differences in territory algal composition of individual species in different locations (Table 3). Territory size also varies considerably between species and locations, suggesting that complex factors interact to determine the extent of the area damselfish are able to cultivate and defend (e.g. Jan et al. 2003). Previous studies suggest that smaller territories can be defended more effectively and farmed more intensively, while larger areas require less active management to ensure an adequate food supply (Hata and Kato 2004).

Further factors influencing territory size may be the identity and abundance of potential competitors for space (e.g. other territorial damselfish) and food (e.g. invading roving herbivores). In the present study, *P. tripunctatus* maintained small territories that contained primarily detritus and corticated red algae on Magnetic Island, larger territories of similar composition on Orpheus Island, and territories dominated by coralline and corticated red algae in Kimbe Bay. Hata and Kato (2002, 2003, 2004) found that *S. nigricans* cultivated *Polysiphonia* monocultures at their study sites in Japan, but Jones et al. (2006) found territories of the same species dominated by corticated red algae in Papua New Guinea, and Gobler et al. (2006) recorded both *Polysiphonia* and *Ceramium* from territories in Fiji. In the Caribbean, *S. planifrons* territories were characterized by *Ceramium* spp. and *Polysiphonia* spp. in Jamaica (Brawley

Table 3 Summary of composition of dominant algal taxa inside damselfish territories from this and other studies

Species	Dominant taxa	Location	Reference	Sample size
<i>Hemiglyphidodon plagiometapon</i>	<i>Gelidiopsis</i> , <i>Polysiphonia</i> , <i>Microcoleus</i>	Yap	Lassuy (1980)	Not given
	<i>Lyngbya</i> , <i>Centroceras</i> , <i>Gracilariopsis</i>	GBR	Sammarco (1983)	3
	<i>Galaxaura</i> , <i>Hypnea</i> , <i>Gelidiopsis</i>	GBR	This study	25
<i>Microspathodon dorsalis</i>	<i>Polysiphonia</i> monoculture	Gulf of California	Montgomery (1980)	6
<i>Neoglyphidodon nigroris</i>	<i>Amphiroa</i> , <i>Polysiphonia</i> , corticated algae	PNG	This study	25
<i>Plectroglyphidodon dickii</i>	<i>Polysiphonia</i> monoculture	PNG	Jones et al. (2006)	72
<i>Plectroglyphidodon lacrymatus</i>	Blue-green and 'gelid' algae, <i>Polysiphonia</i>	PNG	Jones et al. (2006)	72
	<i>Amphiroa</i> , microalgae, <i>Gelidiopsis</i> , <i>Laurencia</i>	PNG	This study	25
<i>Pomacentrus adelus</i>	<i>Galaxaura</i> , <i>Polysiphonia</i>	GBR	This study	25
	<i>Turbinaria</i> , <i>Laurencia</i>	PNG	This study	25
<i>Pomacentrus bankanensis</i>	<i>Turbinaria</i> , corticated algae, microalgae	PNG	This study	25
<i>Pomacentrus burroughi</i>	Corticated algae, <i>Amphiroa</i>	PNG	This study	25
<i>Pomacentrus chrysurus</i>	<i>Laurencia</i> , macroalgae	GBR	This study	25
<i>Pomacentrus tripunctatus</i>	<i>Laurencia</i> , <i>Jania</i> , <i>Polysiphonia</i>	GBR	This study	25
	Corticated algae	GBR	This study	25
	Coralline and corticated algae	PNG	This study	25
<i>Pomacentrus wardi</i>	<i>Polysiphonia</i> , <i>Lobophora</i> , <i>Jania</i>	GBR	This study	25
	<i>Polysiphonia</i> , corticated algae	GBR	This study	25
<i>Stegastes apicalis</i>	Crustose coralline algae, <i>Udotea</i> , <i>Gelidiopsis</i> , <i>Lobophora</i> , <i>Polysiphonia</i>	Gulf of Thailand	Kamura and Choonhabandit (1986)	6
	<i>Amphiroa</i> , <i>Polysiphonia</i> , <i>Gelidiopsis</i>	GBR	This study	25
<i>Stegastes faciolutus</i>	<i>Centroceras</i> , <i>Calothrix</i> , <i>Taenioma</i> , <i>Ectocarpus</i>	Hawaii	Hixon and Brostoff (1983, 1996)	37
	Oscillatoriaceae, <i>Ceramium</i>	GBR	Russ (1987)	2
	<i>Polysiphonia</i> , <i>Ceramium</i> , filamentous and blue-green algae	Tonga	Gobler et al. (2006)	15
<i>Stegastes fuscus</i>	<i>Jania</i> , <i>Gelidium</i>	Brazil (rocky reef)	Ferreira et al. (1998)	30
<i>Stegastes lividus</i>	<i>Gelidiopsis</i> , <i>Polysiphonia</i> , <i>Centroceras</i> , <i>Sphacelaria</i>	Guam	Lassuy (1980)	not given
<i>Stegastes nigricans</i>	<i>Polysiphonia</i> , <i>Ceramium</i>	Fiji	Gobler et al. (2006)	20
	'gelid' algae, <i>Polysiphonia</i>	PNG	Jones et al. (2006)	72
	<i>Polysiphonia</i> monoculture	Japan	Hata and Kato (2004)	7
<i>Stegastes obreptus</i>	<i>Chondria</i> , <i>Calothrix</i>	Japan	Hata and Kato (2004)	7
<i>Stegastes planifrons</i>	52 species, none dominant	Puerto Rico	Hinds and Ballantine (1987)	6
	<i>Ceramium</i> , <i>Polysiphonia</i> , blue-green algae, <i>Lobophora</i> , <i>Halimeda</i>	Jamaica	Brawley and Adey (1977)	9
	<i>Coelothrix</i> , <i>Gelidiopsis</i> , blue-green algae, small articulated corallines	Florida	de Ruyter van Steveninck (1984)	9
<i>Stegastes partitus</i>	<i>Herposiphonia</i> , blue-green algae	Florida	de Ruyter van Steveninck (1984)	10
<i>Stegastes rectifraenum</i>	Filamentous green and blue-green algae, <i>Gracilaria</i> , <i>Jania</i>	Gulf of California (rocky reef)	Montgomery (1980)	11

Partially reproduced from Ceccarelli et al (2001), with results of later studies and this study added. Also added is the sample size (number of individual fish) used in each study. Results from this study do not include detritus, which was measured here but not by other studies

GBR Great Barrier Reef, PNG Papua New Guinea, 'gelid' algae corticated red algae

and Adey 1977), corticated red algae in Florida (de Ruyter van Steveninck 1984), and multi-species algal assemblages in Puerto Rico (Hinds and Ballantine 1987). Coral and rocky reefs in different geographic locations (e.g. Caribbean,

Atlantic Ocean, Indo-Pacific) support distinct damselfish communities; future studies comparing damselfish effects at these larger scales may find even greater differences in how damselfish affect benthic communities. Damselfish territo-

ries are therefore highly individual, not just between species, but also between locations, and are likely to be influenced by the local availability of palatable taxa.

The present study also found considerable variability in the diets of different species, although all included detritus in their diets (especially *P. tripunctatus*, *P. lacrymatus*, *P. bankanensis* and *P. adelus*). Detritus is a highly nutritious component of algal turfs, and recently some species previously thought to be herbivores have emerged as being detritivores (Wilson et al. 2003). Some elements of the detritus, such as diatoms, may be targeted in particular (Jones et al. 2006). The present study indicates that while none of the species examined can be classed as strict detritivores, most may be omnivorous. Most feed on specific algal taxa (especially filamentous algae), and this is one of the mechanisms considered to promote the distinct algal communities inside their territories (Klumpp et al. 1987; Jones 1992). This raises the question of the proportion of algal matter that must be consumed before a species can be classified as herbivorous. Opportunism in reef fishes is not uncommon, and recent work suggests that it can even take the form of ‘sleeping functional groups’ (Bellwood et al. 2006). The names ‘territorial herbivore’ and ‘herbivorous damselfish’ may only be accurate to describe a limited number of species, none of which were included in the present study.

At all three locations, damselfish territories occupied a substantial proportion of the reef substratum: over a quarter on Magnetic Island, more than half at Orpheus Island, and almost half in Kimbe Bay. Within individual reef zones, this figure was much higher. For example, almost 100% of the reef crest in Kimbe Bay was taken up by damselfish territories. Given the influence of damselfish on the feeding behaviour of other grazers (Robertson et al. 1976; Doherty 1983; Hata and Kato 2004) and on the benthos inside their own territories (reviewed by Ceccarelli et al. 2001), the overall importance of the damselfish community on coral reefs is considerable. Yet very few studies have attempted to quantify the overall contribution of the territorial damselfish community to grazer behaviour, coral zonation, algal community structure, productivity, or yield to other grazers on any given reef. For instance, the significant increase in filamentous algal cover found in all territories in the present study suggests that without damselfish territories, the overall yield of algal biomass to all grazers on the study reefs would be reduced. Russ (1987) found that the yield to large grazers were significantly higher inside the territories of *S. fasciolatus* than outside. Despite the aggressive behaviour of territorial damselfishes, their territories are often invaded by large schools of grazers (Robertson et al. 1976). Many reef crests were areas of high damselfish densities in the present study, a zone which also support the highest grazing intensity and algal yield to large grazers (Russ 2003). Measuring the relationship between damselfish

space occupation, grazing rates and algal yield may be a useful method to quantify the contribution of damselfish territories to processes linking primary producers and coral reef fishes.

The species- and location-specific nature of damselfish territories indicates that their contribution to patch diversity is not a simple case of comparing ‘territory’ patches to ‘non-territory’ areas. Instead, each damselfish species represents a different patch type, and the increased patchiness of reef zones with higher damselfish diversity may contain higher benthic biodiversity (Levin and Paine 1974; Levin and Hay 1996). This prediction is yet to be tested, but the present study demonstrates that to generalize the type of patch represented by a damselfish territory is not a viable approach. ‘Damselfish interference’ has disrupted the results of at least one study (Paddock et al. 2006). The implications of these results are that future studies wishing to avoid damselfish territories may need to avoid the territories of all damselfish species. Even small and inconspicuous species may affect the results of studies on algal production and distribution, studies on feeding behaviour of all grazers (including invertebrates), and possibly even coral settlement and survival. Accounting for the distributions of territorial damselfish distributions in future studies on coral reef benthic and grazing communities may avoid confounding results with the effects of damselfish activities.

Territorial damselfish clearly display higher levels of diversity in their diets and in the algal communities they promote than previously thought. Overall habitat complexity and algal diversity on any given reef may not only influence, but be a function of, the damselfish species composition on that reef. The results of this study confirm that, despite their drab appearance, territorial damselfish are important contributors to the overall biodiversity of coral reef benthic communities.

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