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Regional-scale variation in the distribution and abundance of farming damselfishes on Australia's Great Barrier Reef

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Abstract Territorial damselfishes that manipulate ("farm") the algae in their territories can have a marked effect on benthic community structure and may influence coral recovery following disturbances. Despite the numerical dominance of farming species on many reefs, the importance of their grazing activities is often overlooked, with most studies only examining their roles over restricted spatial and temporal scales. We used the results of field surveys covering 9.5° of latitude of the Great Barrier Reef to describe the distribution, abundance and temporal dynamics of farmer communities. Redundancy analysis revealed unique subregional assemblages of farming species that were shaped by the combined effects of shelf position and, to a lesser extent, by latitude. These spatial patterns were largely stable through time, except when major disturbances altered the benthic community. Such disturbances affected the functional guilds of farmers in different ways. Since different guilds of farmers modify benthic community structure and affect survival of juvenile corals in different ways, these results have important implications for coral recovery following disturbances.

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Introduction

The feeding actions of grazing reef fishes can often enhance coral recovery following disturbances, by regulating algal biomass and providing suitable substrate for coral settlement. Grazers fall into two broad functional groups: large, roving grazers and small, territorial grazers (Ceccarelli et al. 2001). The distribution, abundance and biology of large, roving grazers, primarily rabbitfishes (Siganidae), parrotfishes (Labridae) and surgeonfishes (Acanthuridae), have received considerable attention, as have the roles of these fishes in maintaining ecosystem function and reef resilience (Choat and Bellwood 1985; Horn 1989; Bellwood and Choat 1990; Hoey and Bellwood 2008; Cheal et al. 2010, 2012). Whilst the reproduction, recruitment and behaviour of territorial grazers, predominantly damselfishes (Pomacentridae), have also been studied extensively (e.g. Feary et al. 2007; Medeiros et al. 2010; White and O'Donnell 2010; Johnson and Hixon 2011), basic information on their broad distribution and abundance and understanding of their wider role in structuring benthic communities are very limited.

Because of their small body size and limited foraging ranges, territorial, grazing damselfishes (hereafter: farmers) are assumed to have much less influence on benthic community structure than do large, roving grazers (Ceccarelli et al. 2005b). However, several small-scale studies hint at a more pervasive role. Farmers have been shown to shape

algal community structure (Hata and Kato 2003, 2004; Ceccarelli et al. 2005a; Jones et al. 2006), to influence the patterns of coral recruitment, survival, diversity and zonation (Wellington 1982; Gleason 1996; Gochfeld 2010) and to modify the grazing activities of roving herbivores through their aggressive territorial defence (Jones 1992; Hixon and Brostoff 1996). Collectively, farmer territories can cover over 90 % of the reef substratum in some reef zones, and they can be important in structuring benthic reef communities, especially where they are abundant (Kaufman 1977; Williams 1980; Williams and Sale 1981; Hixon and Brostoff 1996; Hata and Kato 2004; Ceccarelli et al. 2011).

An important first step to understanding the more general effects of farmers on benthic community function is to quantify their distribution, abundance, temporal dynamics and response to disturbances over large spatial scales. Numerous studies have investigated the distribution and abundance of farmers at individual reefs or within reef zones (Williams and Hatcher 1983; Russ 1984a, b; Sale et al. 1984; Doherty 1987; Ceccarelli et al. 2005a; Ceccarelli 2007; Hoey and Bellwood 2010). On the Great Barrier Reef (GBR), the abundance of many reef fish groups varies along and across the continental shelf (Williams and Hatcher 1983; Russ 1984a; Hoey and Bellwood 2008; Emslie et al. 2010), but no such patterns of distribution and abundance have been described for farmers. Here we use a long-term and spatially extensive data set to describe broad-scale spatial patterns in the distribution and abundance of farmers on the GBR. We then ask whether these patterns are stable through time across a mosaic of

subregional disturbance histories and consider the ecological implications of such patterns.

Methods

Seventeen species of farmers (Table 1) were censused as part of the Long-Term Monitoring Programme (LTMP) at the Australian Institute of Marine Science (AIMS). The LTMP monitors reef communities across 9.5° of latitude of the Great Barrier Reef (GBR, Fig. 1). Reefs in six latitudinal sectors were surveyed annually from 1993 to 2005, and biennially since 2005. Replicate reefs were surveyed within each of three positions across the continental shelf (i.e. inner-shelf, mid-shelf and outer-shelf) where these were available. However, due to the geography of the GBR, there are no suitable inner- or mid-shelf reefs in the Capricorn-Bunker sector, and no suitable inner-shelf reefs in the Swain sector, resulting in 15 combinations of sector and shelf position (hereafter "subregion").

Farmers were sampled in a standard habitat on each survey reef: the reef slope on the north-east flank, with surveys generally conducted mid-slope (6–9 m). The north-east flanks of GBR reefs are situated at an oblique aspect to the prevailing south-easterly wind and swell, ensuring accessibility even during rough weather and consistency in exposure-related reef assemblage structure.

Between two and five reefs were surveyed within each subregion. Farmers were surveyed along five permanent belt transects (50 × 1 m) in each of three sites in the standard habitat on each reef (n = 15 transects per reef per

Table 1 Species of farmers included in this study, with guild assignations. References are given in support of each species' assignation

| Guild	Species	Reference
Extensive	*Dischistodus prosopotaenia*	Hoey and Bellwood (2010)
	Hemiglyphidodon plagiometopon	Ceccarelli (2007), Hoey and Bellwood (2010)
	Plectroglyphidodon lacrymatus	Hoey and Bellwood (2010)
	Pomacentrus wardi	Ceccarelli (2007)
	Stegastes fasciolatus	Hixon and Brostoff (1996)
Intensive	*Dischistodus melanotus*	Ceccarelli (personal observation)
	D. pseudochrysopoecilus	Hoey and Bellwood (2010)
	Plectroglypgidodon dickii	Jones et al. (2006)
	Stegastes apicalis	Ceccarelli (2007)
	Stegastes nigricans	Hata and Kato (2004)
Indeterminate	*Neoglyphidodon nigroris*	Ceccarelli (2007)
	Plectroglyphidodon johnstonianus	Ceccarelli (personal observation)
	Pomacentrus adelus	Ceccarelli (2007)
	Pomacentrus bankanensis	Ceccarelli (2007)
	Pomacentrus chrysurus	Ceccarelli (2007)
	Pomacentrus grammorhynchus	Ceccarelli (personal observation)
	Pomacentrus vaiuli	Ceccarelli (personal observation)
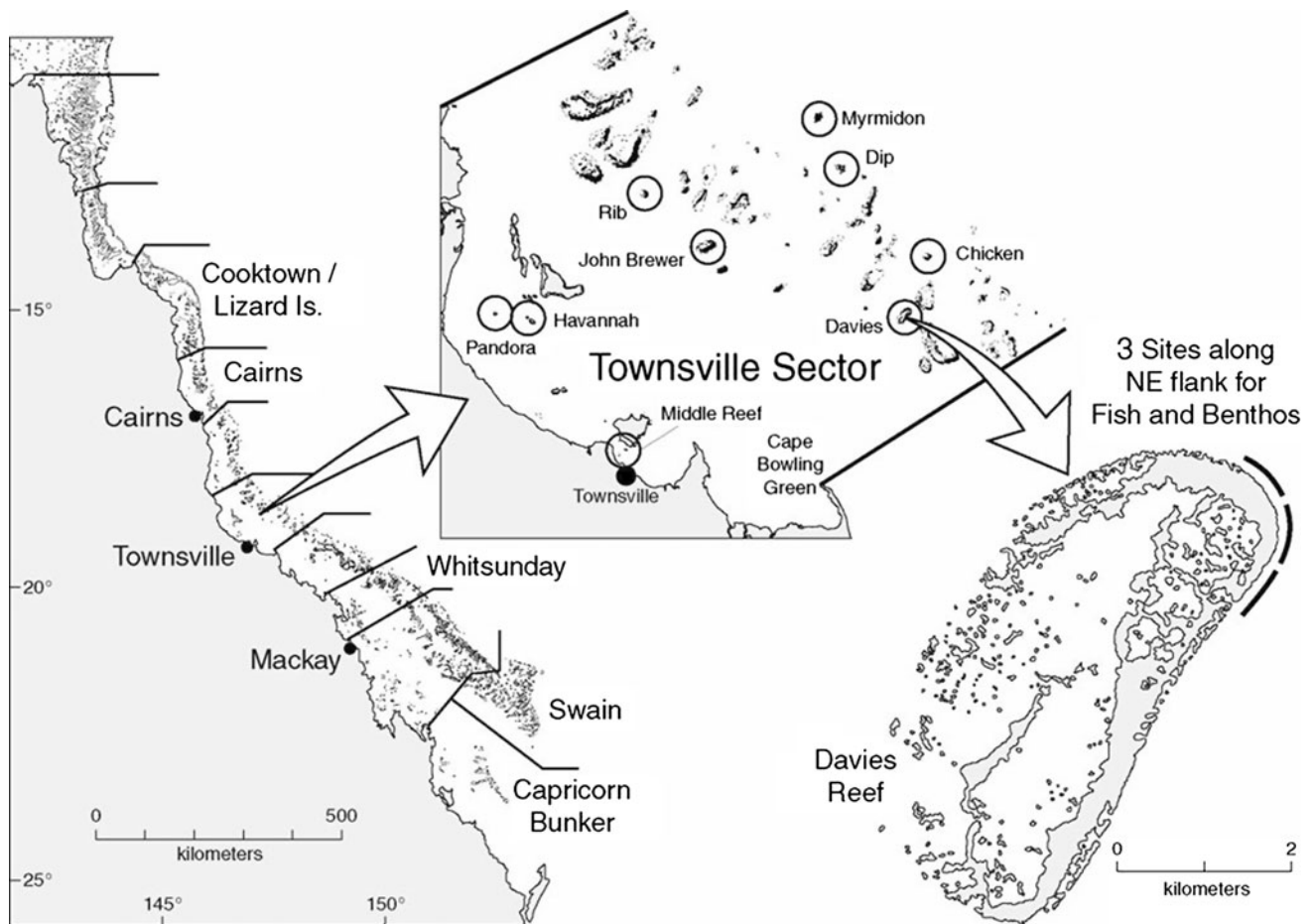
Fig. 1 LTMP survey design. The *left panel* shows the latitudinal sectors. The *inset figures* show the cross-shelf component with replicate reefs within each of the three shelf positions (inner-, mid- and outer-shelf), and the three survey sites in a standard habitat on the north-east reef slope at each reef

year). The start and finish of permanent transects were marked with metal stakes, with smaller metal rods spaced at 10-m intervals along each transect. The observer swum along the transect recording all farmer species in a 1-m wide belt. A second diver then followed the observer deploying a transect tape along the markers.

As there is considerable interspecific variation in how farmers affect the benthic communities within their territories (Hata and Kato 2004; Ceccarelli 2007; Hoey and Bellwood 2010), we analysed farmer distributional patterns in terms of total farmer abundance and the abundance of three separate guilds, which were distinguished by their weeding and defensive behaviours and the types of algal assemblages they maintain. Hata and Kato (2004) identified two guilds: (1) "intensive" farmers that weed intensively and defend relatively small territories containing low diversity algal turfs very aggressively. These territories are readily distinguishable from the surrounding benthos and (2) "extensive" farmers that weed and defend their territories less intensively and maintain relatively large

territories with diverse algal assemblages that are distinct from the algae outside their territories. Subsequent studies have identified a third guild of farming species: (3) "indeterminate" farmers—referring to species that have subtle effects on the composition of algal assemblages within their territories, though these remain visually similar to the surrounding areas. These fishes weeded less intensively and defended their territories less aggressively than the other categories of farmers (Ceccarelli unpublished data). Each farmer species was assigned to one of these three farming guilds (Table 1).

Broad patterns in farmer communities were explored graphically using redundancy analysis (RDA, Legendre and Legendre 1998). The abundances of the 17 species in each site at each reef were fourth-root transformed prior to analysis. RDA is a form of direct gradient analysis in which the community patterns are constrained by variation explained by environmental predictors (e.g. sector and shelf). We also explored the specific temporal and spatial profiles of abundance of guilds of farming fish throughout

the GBR using general additive mixed models (GAMMs, Wood 2010). Farmer abundances were modelled (Poisson distribution) for each farmer guild through time (thin-plate spline with three knots) nested within reefs (random factor). Whilst these models provide highly informative visual explorations of the specific nature of trends, they do not provide inferential information concerning predictor levels or their effect sizes. For this reason, the spatial and temporal variation in the abundance of farmers was modelled using a generalised linear mixed effects model (GLMM, Bolker et al. 2008) with Poisson errors (log-link), followed by Wald's F tests incorporating between-within degrees of freedom estimates. Data from all sites on each reef were pooled, and separate models were fitted for the total numbers of each guild of farmers separately and for the sum of all farmers. Each model included the fixed effects of sector (Cooktown-Lizard Island, Cairns, Townsville, Whitsunday, Swain and Capricorn-Bunker), position on the continental shelf (inner, mid and outer) and year (modelled as polynomial splines with three knots) plus their interactions. Effects involving sector, shelf position and interactions were estimated as specific sets of contrasts on a composite factor to compensate for missing cells (Logan 2010). Reefs (nested within sector by shelf) were included as random factors to account for spatial variation, pseudoreplication and temporal autocorrelation arising from multiple and repeated observations from the same reefs. Observation-level random effects were also fitted in order to account for over-dispersion in the models by constraining the theoretical variance to one.

We then investigated the potential role of benthic variables in structuring farmer communities by examining the relationship between farmer abundance, and the cover of both hard corals and turf algae. Data were aggregated to total abundance of farmers per reef per year and average per cent cover of hard coral and turf algae per reef per year. Separate linear models were fitted in each subregion regressing the abundance farmers, for all farmers collectively and the three guilds and each species independently, against per cent cover of hard coral and turf algae, using the "lm" function in R (R Development Core Team 2011).

As a preliminary investigation of the variability of the changes in farmer abundance following different types of disturbances, we analysed an example of each of four specific disturbance events: (1) an outbreak of the crown-of-thorns starfish, *Acanthaster planci*, on mid-shelf reefs in the Townsville sector (1997–2003), (2) a bleaching event in the Townsville inner-shelf subregion (1997–1999), (3) a storm in the Capricorn-Bunker sector (2007–2009), and (4) an outbreak of white syndrome coral disease in the Cooktown-Lizard Island outer-shelf subregion (1999–2005) These four disturbance events caused average declines in hard coral cover of 24.0 ± 16.2 (mean ± SE)

%, 18.2 ± 2.0 %, 40.2 ± 9.9 %, and 8.6 ± 1.4 %, respectively (Sweatman et al. 2000, 2005, 2008). These disturbances were chosen because they occurred on more than one reef within a subregion; they were not confounded by other disturbance events; and the magnitude of change in hard coral cover was among the highest recorded, thus representing a replicated, worst-case scenario.

The effects of these specific disturbances were estimated by fitting generalized linear mixed effects models (GLMMs) to abundances of farmers (by guild and all farmers combined) averaged within time windows representing Pre, During and Post disturbance (fixed factor) nested within reefs (random factor). Farmer abundances were compared among three time periods of the disturbance event: (1) During versus Pre, (2) Post versus During and (3) Post versus Pre. All GLMMs were run in R (R Development Core Team 2011), using the glmer (lmer package; Bates et al. 2011) and wald.test functions (aod package; Lesnoff and Lancelot 2010).

Results

There were distinct inner-, mid- and outer-shelf communities of farmers on the GBR. In the RDA bi-plot, Axis 1 separated farmer assemblages according to their location across the continental shelf and explained most of the variation (58.8 %), whilst Axis 2 partitioned reefs by latitude in each shelf position (Fig. 2). Inner-shelf assemblages were characterised by two indeterminate farmer species: *Pomacentrus adelus* and *Neoglyphidodon nigroris* (Fig. 2, ESM Table 1). However, the dominant farming guild varied with latitude: indeterminate farmers were numerically dominant in the two northern inner-shelf subregions whilst extensive farmers were predominant on reefs in southern inner-shelf subregions (Fig. 3). In contrast, outer-shelf assemblages were characterised by a mix of all three farmer guilds: the intensive farmer *Plectroglyphidodon dickii*, the extensive farmer *Plectroglyphidodon lacrymatus*, and the indeterminate farmers *Plectroglyphidodon johnstonianus* and *Pomacentrus bankanensis*. Mid-shelf assemblages included both species with inner-shelf and species with outer-shelf distributions that extended their range onto the mid-shelf (Fig. 2, ESM Table 1). Interestingly, farmer communities on mid-shelf reefs of the two northern sectors (Cooktown-Lizard Island and Cairns) did not match their a priori shelf assignments (Fig. 2). Assemblages on three reefs of the Cairns mid-shelf were more similar to those on outer-shelf reefs, largely due to high abundances of *P. lacrymatus* and *P. dickii* (Fig. 2, ESM Table S1). In contrast, farmer communities on mid-shelf reefs of the Cooktown-Lizard Island sector and on one reef in the Cairns sector were more similar to inner-
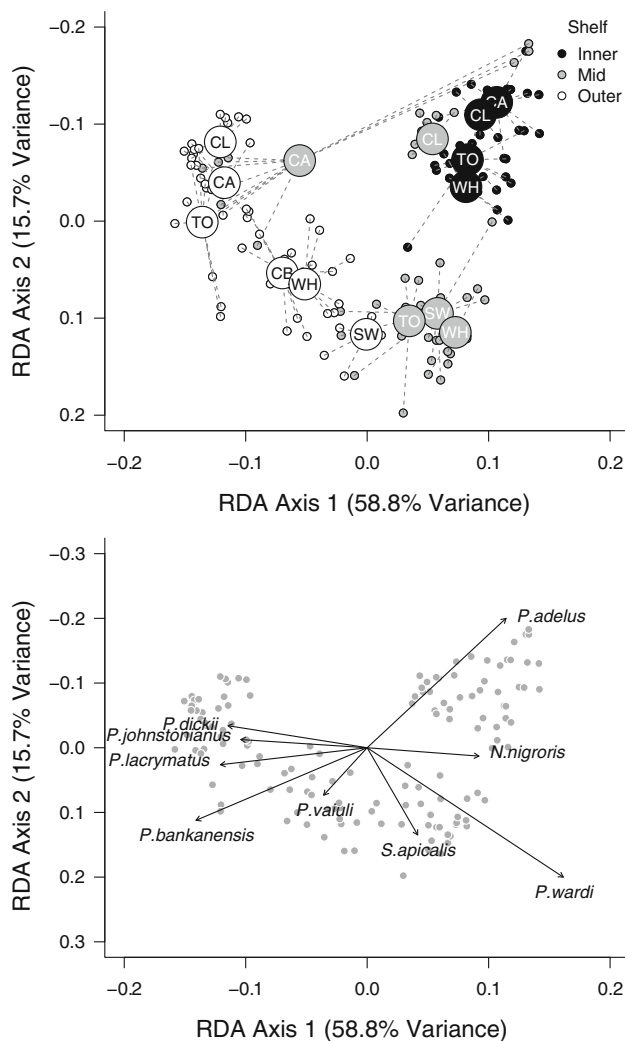
Fig. 2 The structure of GBR farmer communities in different positions on the continental shelf. The *top panel* shows the ordination of the first two axes of a redundancy analysis on abundances of 17 farmer species. *Axis 1* represents cross-shelf differences in farmer community structure, whilst *Axis 2* displays variation with latitude. *Small dots* represent abundances of farmers per site (250 m²) on each survey reef (averaged over time). *Large dots* represent the community centroids for each sector, *shaded* by shelf position (*black* = inner-shelf, *grey* = mid-shelf, *white* = outer-shelf). Abbreviations within the centroids identify the sectors (*CL* Cooktown-Lizard Island, *CA* Cairns, *TO* Townsville, *WH* Whitsunday, *SW* Swain, *CB* Capricorn-Bunker). *Dotted lines* join individual sites to their centroids and so represent the variation around the centroid. The *bottom panel* displays vectors for species, indicating the proportion of variation that is explained by variation in abundance of each species. Genus abbreviations are P = *Pomacentrus* and *Plectroglyphidodon*, N = *Neoglyphidodon*, S = *Stegastes*

shelf communities, with large numbers of *P. adelus* (Fig. 2, ESM Table S1). Whilst spatial factors accounted for the majority of variation (range 70.5 % for all farmers to 92.3 % for intensive farmers; Table 2), the significant interaction between shelf and latitudinal sector indicated that there was no simple cross-shelf or latitudinal patterns

in the dominant guild (Table 2; Fig. 3). Overall, farmers were most abundant in the Cairns and Townsville sectors, peaking in mid-shelf subregions (Fig. 3, ESM Table S1). Abundances were lowest in the Whitsunday inner-shelf and the Cooktown-Lizard Island mid-shelf subregions (Fig. 3, ESM Table S1).

Extensive farmers were the most abundant guild on the GBR; their numbers peaked on mid-shelf reefs of every sector except Cooktown-Lizard Island, where abundance was highest on inner-shelf reefs (ESM Table S1). This pattern was due mainly to the contrasting distributions of *Pomacentrus wardi* (largely absent from outer-shelf communities) and *P. lacrymatus* (which was mostly absent from inner-shelf communities). Together these two species constituted 51 % of all farmers in this study (ESM Table S1). The abundance of indeterminate and intensive farmers varied but with no clear cross-shelf or latitudinal (sector) patterns (Fig. 3, ESM Table S1). Indeterminate farmers were the second most abundant guild, represented by seven species, five of which accounted for 98 % of the guild's abundance (ESM Table S1). The abundance of indeterminate farmers was highest on reefs in the Cairns mid- and inner-shelf, the Townsville mid- and outer-shelf, and the Cooktown-Lizard Island inner-shelf subregions. Lowest abundances occurred on inner- and mid-shelf reefs in the Whitsunday sector. The patterns were driven by the distributions of individual species. For example, the two most abundant species of indeterminate farmers, *Pomacentrus bankanensis* and *P. adelus*, had contrasting distributions. *P. bankanensis* was virtually absent from inner-shelf reefs in all sectors whilst *P. adelus* was largely restricted to inner-shelf reefs (ESM Table S1). Intensive farmers were the least abundant guild and had the lowest species richness, with two of the five species, *Stegastes apicalis* and *P. dickii,* accounting for 89 % of the guild's abundance (ESM Table S1). The abundance of intensive farmers was highest on mid- and outer-shelf reefs, particularly in the three northern sectors (ESM Table S1), whilst they were virtually absent from inner-shelf communities.

The relationships between total farmer abundance, abundance of each farmer guild and abundances of individual farmer species and hard coral cover showed no consistent spatial patterns among the subregions (ESM Table S2). The same was true for the relationships between total farmer abundance, abundance of the three farmer guilds and abundances of individual farmer species and cover of turf algae (ESM Table S3). For example, the abundance of the intensive farmer guild was significantly related to hard coral cover in eight of fifteen subregions; however, two of these relationships were negative and six were positive (ESM Table S2). Similarly, the abundances of extensive and indeterminate famers were each both positively and negatively related to hard coral cover in
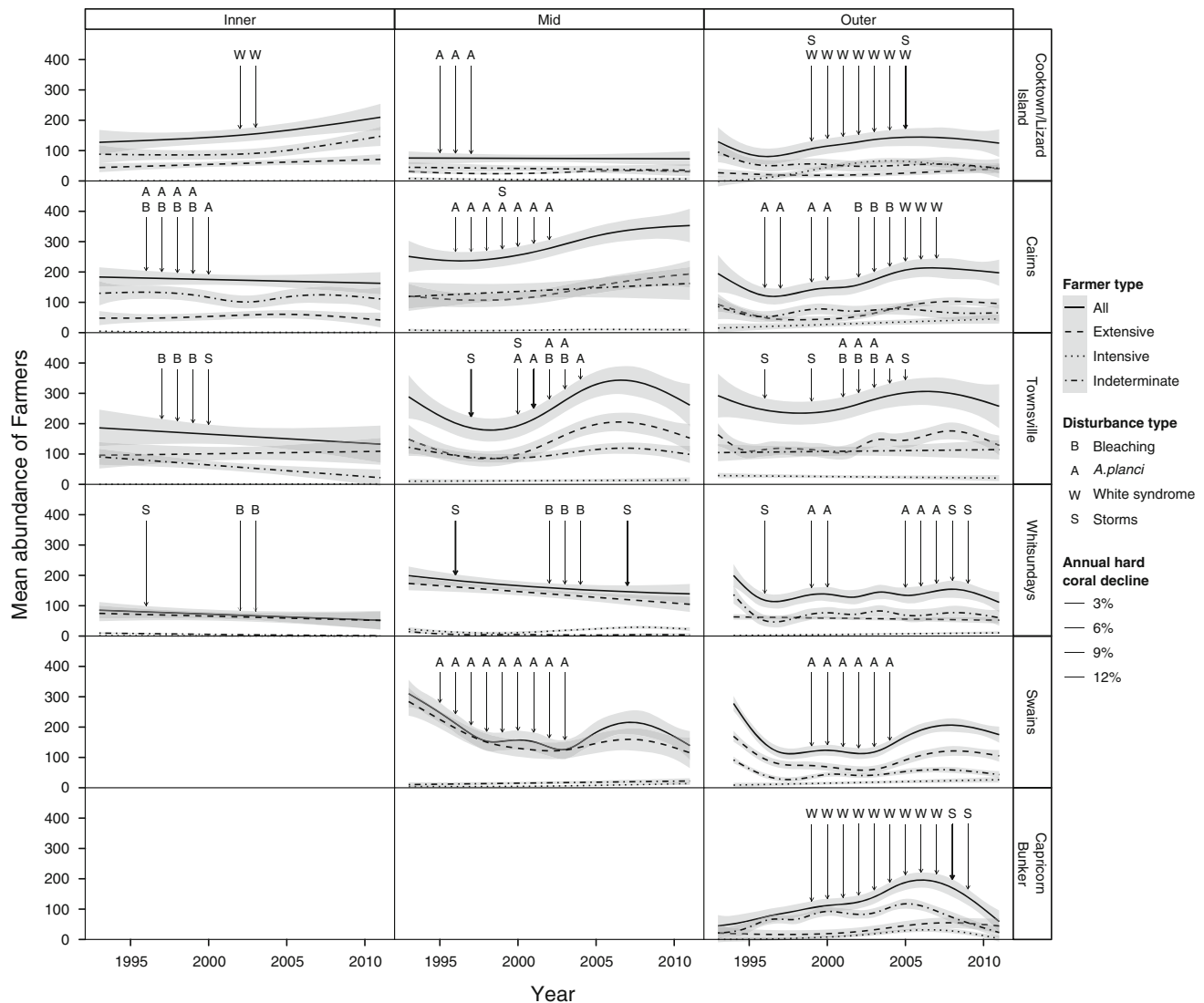
Fig. 3 Temporal and spatial trends in abundance of farming fishes on the GBR. *Curves* represent temporal profiles of total abundance of farmers and of the three guilds (All = total abundance, Extensive = extensive farmer abundance, Intensive = intensive farmer abundance, Indeterminate = indeterminate farmer abundance) as modelled from general additive mixed models (GAMMs) per reef (750 m²). *Arrows* show the timing of different disturbances on any reef within a given subregion (shelf position within each sector). B = Bleaching, A = *Acanthaster planci*, W = White syndrome, S = Storms. The *thickness of the arrows* represents the magnitude of disturbance in terms of per cent hard coral decline. *Grey shaded bands* about the modelled trend lines are 95 % CI

different subregions (ESM Table S2). Results were similar for individual farmer species. Surprisingly, two species that are known to be closely associated with hard corals, *Plectroglyphidodon dickii* and *P. johnstonianus,* only showed significant relationships between abundance and hard coral cover in three of the fifteen subregions (ESM Table S2). The nature of the relationships between turf algal cover and the abundance of all farmers, the three farmer individual species with turf algae, was also highly variable among subregions (ESM Table S3).

The extent of temporal changes in farmer assemblages varied among subregions and appeared related to each subregion's disturbance history (Table 2—sector by shelf

by time interaction, Fig. 3). Temporal change explained a much smaller proportion of the total variance in farmer abundance than spatial factors did, ranging from 7.7 % in intensive farmers to 29.5 % for the total community (Table 2). Thus, whilst there was some variation over time, spatial patterns were generally maintained (Fig. 3). Temporal variation in the abundance of farmers appeared to be related to the disturbance history of each subregion; however, the response varied among farmer guilds and disturbance types (Figs. 3, 4). Overall, farmer abundances increased following an outbreak of *A. planci* on Townsville mid-shelf reefs, decreased following a storm on Capricorn-Bunker outer-shelf reefs, and changed little following

Table 2 Marginal hypothesis tests exploring patterns of total farmer and guild abundance across inner-, mid- and outer-shelf reefs in five sectors over time

Parameter	Num DF	Den DF	All			Extensive			Intensive			Indeterminate		
			% var explain	F value	P value	% var explain	F value	P value	% var explain	F value	P value	% var explain	F value	P value
Sector	4	32		8.6	0.000		16.22	0.000		2.18	ns		19.90	0.000
Shelf	2	32		4.65	0.017		24.77	0.000		4.53	0.019		5.53	0.009
Sector*Shelf	8	32		5.82	0.000		3.38	0.006		13.26	0.000		7.82	0.000
Spatial			70.5			76.97			92.31			84.32		
Year	3	594		45.15	0.000		61.68	0.000		26.32	0.000		12.54	0.000
Sector*Year	12	594		12.13	0.000		12.68	0.000		5.38	0.000		9.42	0.000
Shelf*Year	6	594		37.89	0.000		15.13	0.000		20.10	0.000		37.48	0.000
Sector*Shelf*Year	28	594		7.29	0.000		5.66	0.000		12.34	0.000		5.26	0.000
Temporal			29.5			23.03			7.69			15.68		

Estimates were from a variety of generalised linear mixed effects models (GLMMs). All = total farmer abundance, Extensive = extensive farmer abundance, Intensive = intensive farmer abundance, Indeterminate = indeterminate farmer abundance. *ns* non significant result

bleaching and white syndrome coral disease on Townsville inner-shelf and Cooktown-Lizard Island outer-shelf reefs respectively (Table 3; Fig. 4). The increase following the *A. planci* outbreak was caused by an increase in the abundance of extensive and, to a lesser extent, indeterminate farmers (Table 3; Fig. 4a). In contrast, reductions in both intensive and indeterminate farmers caused the reduction in overall farmer abundance following the storm (Table 3; Fig. 4c).

Discussion

We identified strong spatial structure in assemblages of farming damselfishes on the GBR, shaped primarily by position on the continental shelf and to a lesser extent by latitude, resulting in unique subregional assemblages. The spatial patterns we found concur with the broad-scale distributions of other groups of fishes on the GBR, including large roving herbivores (Williams 1982; Russ 1984a, b; Hoey and Bellwood 2008; Cheal et al. 2012; Wismer et al. 2009) and butterflyfishes (Emslie et al. 2010). The cross-shelf variation we found suggests broad-scale underlying processes that are linked to broad environmental gradients between the coastal and oceanic waters. These environmental gradients have also been shown to drive cross-shelf distributions in other organisms (reviewed in Wilkinson and Cheshire 1988). To our knowledge, there have been no other distributional studies of farming damselfishes on this scale, either on the GBR or in other tropical regions. Consequently, this work represents a baseline of knowledge about the distribution and abundance of these fishes on the GBR.

We found that abundance of farming fishes varied across the shelf, but the pattern differed with latitude. This was mainly because the assemblages on mid-shelf reefs in the Cairns sector resembled those on outer-shelf reefs whilst assemblages on mid-shelf reefs in Cooktown-Lizard Island sector resembled those on inner-shelf reefs. This may reflect the narrow continental shelf in these sectors: the continental shelf is only 40–50 kms wide in the northern sectors, compared with 100–200 kms further south. The narrow continental shelf may compress inshore–offshore biophysical gradients and lead to greater variation among mid-shelf reefs. For example, turbid inshore environments may extend proportionally further across the shelf in the northern sectors, expanding the suitable habitat for inner-shelf species offshore. Alternatively, the small distances across the shelf in northern sectors may increase connectivity among reefs from different shelf positions, leading to reduced variation in community structure. Whilst large-scale patterns in farmer community structure have yet to be examined in other tropical regions, studies to date have

Fig. 4 Changes in abundance per reef (750 m²) of farming fishes before, during and after disturbances in the **a** Townsville mid-shelf subregion, **b** Townsville inner-shelf subregion and **c** Capricorn-Bunker subregion and **d** Cooktown-Lizard Island outer-shelf subregion. Means and confidence intervals were derived from generalised linear mixed effects models (GLMMs), and thus statistical significance can be inferred from non-overlapping confidence intervals between time periods for each guild
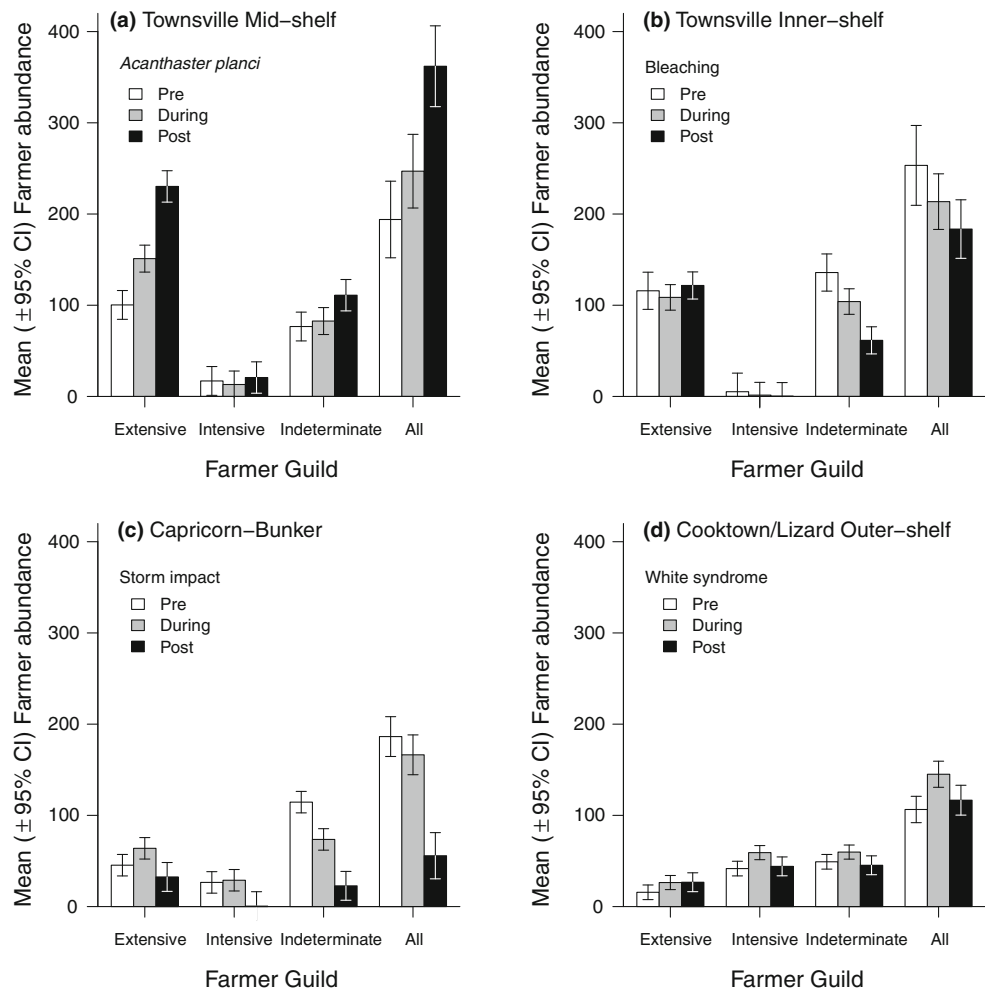
found similar variability. There have been macro-ecological comparisons of farmer territoriality, feeding rates and body size in the Caribbean (Panama), the Atlantic coast of Brazil, Baja California, Papua New Guinea, the GBR and the Indian Ocean off Madagascar (Barneche et al. 2009). However, almost all existing research in the western Atlantic (Ferreira et al. 1998), the Gulf of California (Montgomery 1980), the central Pacific (White and O'Donnell 2010) and the north-west Pacific (Kamura and Choonhabandit 1986; Hata and Kato 2004) has concerned selected species on individual reefs, so has not provided comparable distributional data.

We did not find any generalisations regarding relationships between farmer abundance and benthic community structure. The variability in this relationship among subregions could be interpreted as evidence that (1) living coral cover and algal turf influence farmer communities, but the nature of the relationship varies geographically; or (2) that farmers are not associated with total coral cover, but may be influenced by the distribution of particular coral taxa or growth forms. The lack of relationship, even for species that

are known to closely associate with hard coral such as *Plectroglyphidodon dickii* and *P. johnstonianus,* suggests that the taxonomic resolution of the present study was not sufficient to detect such relationships. The use of growth form categories such as branching, submassive or table corals might have revealed consistent relationships. This uncertainty concerning the role of benthic variables in structuring farmer communities on the GBR highlights the need to incorporate greater taxonomic and spatial resolution into future investigations of these potential relationships.

Different farmer species use algal resources differently and can have markedly different effects on the benthic communities within their territories (Hata and Kato 2004; Ceccarelli et al. 2005a, b; Ceccarelli 2007; Hoey and Bellwood 2010). The fine-scale benthic characteristics of each subregion are likely to be influenced by the dominant farmer assemblage, especially in areas where farming species are abundant. For example, extensive farmers cultivate a mixed turf of diverse filamentous and macro-algae (Ceccarelli 2007). They are less successful in excluding other grazers from their territories than intensive farmers

Table 3 Mean effects size (±95 % CI) and Tukey's *P* values (contrasting each time pairing) for various farmer guilds in response to selected disturbances

Source	Farmer guilds											
	Extensive		Intensive		Indeterminate		All	
	Effect size	*P* value	Effect size	*P* value	Effect size	*P* value	Effect size	*P* value
Acanthaster planci								
During versus Prior	**50.77 (25.8, 75.8)**	0.024	−3.90 (−28.8, 21.1)	0.622	5.99 (−19.0, 31.0)	0.751	**52.97 (1.3, 104.7)**	0.100
Post versus During	**79.15 (50.6, 107.6)**	0.002	7.65 (−20.8, 36.1)	0.228	28.34 (−0.1, 56.8)	0.002	**115.03 (56.1, 174.0)**	0.000
Post versus Prior	**129.92 (99.3, 160.5)**	0.000	3.75 (−26.8, 34.3)	0.721	**34.33 (3.7, 64.9)**	0.000	**168.00 (104.7, 231.3)**	0.000
Bleaching								
During versus Prior	−7.25 (−52.8, 38.3)	0.857	−3.73 (−49.3, 41.8)	0.872	−31.82 (−77.4, 13.7)	0.232	−39.74 (−133.4, 53.9)	0.670
Post versus During	13.07 (−23.2, 49.4)	0.905	−1.12 (−37.4, 35.2)	0.481	**−42.53 (−78.8, −6.2)**	0.006	−30.07 (−103.6, 43.5)	0.689
Post versus Prior	5.82 (−41.0, 52.7)	0.980	−4.85 (−51.7, 42.0)	0.926	**−74.35 (−121.2, −27.5)**	0.000	−69.81 (−166.5, 26.90)	0.315
Storm impact								
During versus Prior	18.50 (−11.4, 48.4)	0.152	2.37 (−27.5, 32.20)	0.952	**−40.88 (−70.7, −11.0)**	0.000	−20.00 (−56.3, 16.30)	0.512
Post versus During	−31.38 (−67.9, 5.2)	0.028	−28.38 (−64.9, 8.2)	0.011	**−50.88 (−87.4, −14.3)**	0.000	**−110.62 (−155.1, −66.1)**	0.000
Post versus Prior	−12.88 (49.4, 23.7)	0.542	−26.00 (−62.6, 10.6)	0.021	**−91.75 (−128.3, −55.2)**	0.000	**−130.63 (−175.1, −86.1)**	0.000
White syndrome								
During versus Prior	10.68 (−9.4, 30.8)	0.158	17.48 (−2.6, 37.6)	0.001	10.64 (−9.4, 30.7)	0.596	**38.64 (15.1, 62.2)**	0.003
Post versus During	0.34 (−23.6, 24.2)	0.886	−15.06 (−39.0, 8.8)	0.091	−14.46 (−38.4, 9.4)	0.231	**−28.45 (−56.3, −0.6)**	0.101
Post versus Prior	11.02 (−13.3, 35.4)	0.117	2.42 (−21.9, 26.8)	0.590	−3.82 (−28.2, 20.5)	0.704	10.19 (−18.2, 38.6)	0.752

Effect sizes for extensive, intensive and indeterminate farmer guilds were derived from a generalised linear mixed effects models (GLMMs) incorporating both disturbance timing (Pre, During and Post) and farmer guilds. Effects sizes for total farmers combined (All) were derived from a separate GLMM incorporating only disturbance timing. Confidence intervals not overlapping zero are presented in bold to highlight significant effects. Tukey's contrasts represent simultaneous comparisons following simple main effects of disturbance timing for each guild separately

(Hata and Kato 2004), which increases the probability that coral spat will be killed by feeding activities of large mobile grazers (Gleason 1996). On the other hand, the intensive farmers may actively exclude macroalgae from their territories and cultivate a unique monospecific turf. They can be associated with patches of high coral cover on some reefs (Ceccarelli et al. 2011) and have been observed to maintain a turf-free zone around newly settled corals (Ceccarelli, personal observation).

The abundance and functional composition of farmer assemblages remained relatively stable through time, except when intense disturbances caused large declines in hard coral and/or structural complexity. Whilst only preliminary, our results identified shifts in the functional composition of the overall farmer assemblages following disturbances and disturbances of different types affected the abundance of the three farmer guilds in different ways. This is true for other groups of fishes, such as roving herbivores (Cheal et al. 2008; Emslie et al. 2008; Graham et al. 2007) and butterflyfishes (Emslie et al. 2011). Disturbances that reduced structural complexity and hard coral cover (i.e. storms) led to declines in both indeterminate and intensive farmers, whilst extensive farmers remained largely unaffected. These declines are likely to reflect reductions in the availability of shelter as structurally complex coral skeletons are converted to rubble (Graham et al. 2006; Wilson et al. 2009). In contrast, disturbances that killed coral but had a limited effect on structural complexity caused variable responses; there was little change with coral bleaching or coral white syndrome disease, but the abundance of extensive farmers increased markedly following an outbreak of A. planci. This may be because the dead coral skeletons provide greater area for algal colonisation and consequently for farming. It is not readily apparent why farmers did not show similar responses following bleaching- or disease-induced coral mortality, but it may be related to the magnitude of the coral loss and/or the composition of coral and farmer assemblages in the respective subregions. Whatever the mechanisms, such spatial and temporal variation in the functional composition of farmer assemblages could have implications for coral recovery as different farmer guilds can affect coral spat settlement and survivorship through their territorial and weeding behaviours. However, it must be noted that these analyses were exploratory and were only intended to add context to the temporal patterns of farmer abundance. A robust analysis incorporating appropriate controls (which are difficult to define given the inherent spatial variability in farmer community structure among subregions) is beyond the scope of the present work and is a priority for future studies.

The effect of farmers on coral recruitment and early survival is still largely unexplored, but early results are conflicting. On the one hand, farmers can kill adult coral tissue and coral recruits through their farming activities and by cultivating thick filamentous turfs within their territories (Wellington 1982). Alternatively, *Stegastes nigricans*, *S. lividus*, *P. dickii* and *Hemiglyphidodon plagiometopon* defend their territories against large, mobile grazers and corallivores, which can enhance survivorship of corals that might otherwise be damaged by scraping and excavating grazers (Sammarco and Carleton 1981; Sammarco et al. 1986; Glynn and Colgan 1988; Gleason 1996; Letourneur et al. 1997). This results in an increase in overall coral diversity (Gochfeld 2010). Whilst indeterminate farmers probably have limited effects on corals, extensive farmers may promote the type of algal community that is most hostile to recruiting corals: thick, multi-specific algal turfs that include fleshy macroalgae (Birrell et al. 2008). Intensive farmers, with their intensive defensive behaviour, may successfully exclude fishes that may cause damage or mortality to corals. Deeper understanding of how farming damselfishes affect the recruitment and subsequent survival of coral spat is important, particularly given the predicted increases in frequency of disturbances (Sheppard 2003; Donner et al. 2005) and the high abundance and ubiquity of these fishes in coral reef systems.

Spatial variation in coral cover has been negatively related to farmer abundance in some systems (e.g. Sandin et al. 2008). However, it is difficult to identify the link between coral cover and farmer abundance without knowing the sequence of changes. This study shows that declines in hard coral cover affected the abundance of farming species in ways that varied both spatially (among reefs and subregions) and with the type of disturbance. The disturbances we examined in this study may be categorised by their effects on live coral cover and structural complexity: those that reduced the cover of living coral whilst retaining structural complexity (A. planci outbreaks, coral bleaching and coral white syndrome) and those that reduced both coral cover and complexity (storms). Where coral mortality occurred without reduction in structural complexity, farmers either increased in abundance or changed little following disturbance. Thus, these responses may reflect the availability of new substrate for algae and the persistence of shelter afforded by coral skeletons. In contrast, farmer abundance decreased markedly following storms. This is likely to be a direct response to the decline in habitat complexity. Abundance of both indeterminate and intensive farmers declined markedly, whilst extensive farmers remained relatively unchanged. Such changes could impede coral recovery as the territories of extensive farmers appear the least hospitable to coral recruits. There was also evidence for lagged response to coral decline, which may represent the effects of increased competition for reduced shelter on these disturbed reefs. Our results add

to the growing body of evidence of the importance of habitat complexity in shaping reef fish community structure (Graham et al. 2006, 2008; Wilson et al. 2009; Emslie et al. 2008). Where mortality occurred without reduction in structural complexity, farmers generally increased in abundance, probably in response to the availability of new substrate for algal colonisation and the retention of shelter afforded by coral skeletons. This variability means farmer responses need to be considered carefully in the light of each individual disturbance, and not just assumed to increase in abundance where coral cover has declined appreciably.

Overall, this study has shown that there is clear, large-scale spatial structure in the communities of farming damselfishes on GBR reefs. The subregional differences in community structure of farming damselfishes identified in this study, and butterflyfishes and large roving herbivores in other similar studies (Emslie et al. 2010; Cheal et al. 2012), question the generality of conclusions from small-scale manipulative experiments: results obtained on patch reefs at one location on the GBR may not necessarily apply in locations in other subregions. Furthermore, the lack of consistent relationship between farmer abundance and measured benthic variables across all subregions highlights the potential difficulties in extrapolating the findings of small-scale studies to broader spatial scales. A preliminary investigation of the effects of disturbances demonstrated that different types of disturbance have contrasting effects on the three guilds of farming damselfishes. This study provides the basis for a more detailed investigation into the effects of different disturbance types, for studies of how farming fishes use territorial space and for an experimental investigation of the rates of coral recruitment and survival inside and outside of territories that would extend our knowledge of how this ubiquitous but often overlooked group of fishes contribute to coral reef ecosystem function.

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