Differences in composition of territories in relation to behaviour, stage, and depth of the three-spot damselfish, *Stegastes planifrons*, in Caribbean coral reefs

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Abstract

Coral reef diversity is correlated with the depth at which the reefs are found, the energy available for biological processes, and the species' roles and presence throughout the food chain. Can a specific species activity alter the whole ecosystem? Can a small-scale, short-term activity such as fish behaviour have a long-term effect on a larger scale, that of the reef? Can the life stage of a species mediate substrate competition? The three-spot damselfish (*Stegastes planifrons*) is hypothesized to regulate competition between substrate coverage by actively farming – protecting from herbivores and weeding – in order to regulate the algal species composition and percent coverage of the reef. This behaviour is observed in both juvenile and adult fish. Deeper patches are predicted to have less coral diversity and higher algal diversity; juvenile fish are predicted to have less diversity in their patches than adults. Coral and algal diversity are hypothesized to be negatively correlated. In this study, behaviour of the *S. planifrons* was classified into one of four categories (active patrolling, passing patrolling, farming, and hiding) and palatable algae surface area coverage was digitized from photographs; life stage was either juvenile or adult. Coral and algal genus diversity were measured along a depth gradient of 0-16 m where the diversity of the reef was thought to be the highest. A three-way ANCOVA was performed to test whether fish behaviour (a small-scale, short-term process), depth, or fish development stage (juvenile or adult) had a significant effect on coral or algal diversity (a large-scale, long-term process). Results showed a significant effect of fish behaviour category on algal genera diversity, and a significant effect of depth on both algal and coral genera diversity. Farming yielded significantly more algal coverage than hiding. This study shows that small-scale, short-term behaviours by *S. planifrons* can have an effect on algal genera diversity on coral reefs in Utila, Honduras.

Keywords: *Stegastes planifrons* (three-spotted damselfish); behaviours (short-term, small-scale); stage of development (juvenile, adult); depth; coral reef and algal diversity (long-term, large-scale); damselfish territories

Introduction

Coral reefs are important for diversity and productivity in marine ecosystems [1,2]. Patterns of coral reef diversity are predictable with depth – an increase in coral diversity with depth for the first 20m, followed by a decrease as light energy decreases with depth [3]. The shallower parts of the reef (above 12m) are the most vulnerable sections for disturbance because a higher abundance of fish, living coral, and algal coverage are found in these areas [3,4]. However, natural and human induced intermediate disturbances have in more recent years led to a higher diversity of algae, coral and fish at these depths [1-3,5].

Ecosystem biodiversity can be altered by certain species that act as mediators within natural processes. Damselfish

(*Pomacentridae*) are important species for marine benthic ecosystems [3,6-8]. Through herbivory on competitive dominants and controlled selective farming practices, they regulate the algal species composition and percent coverage, especially in shallow parts of the reef [3,7,9-12]. Herbivory consists of consuming algae while farming involves selective weeding of algae to increase the presence of another species [7,11]. Algae coverage is positively correlated with damselfish farming techniques since they crop the turf and palatable algae to maintain them at their optimum growth rate while removing unpalatable algal species [4,13,14]. Damselfish behaviour such as defence and farming can alter the percent algal coverage within their specific territory [7].

By selectively farming preferred palatable algae, damselfish affect interspecific competition between massive coral species (*Montastrea* spp.) and branching species (*Acropora* spp.), as well as coral and algal competition, for primary substrate since the main limiting resources that algae and coral compete for in coral reefs are light availability and space on the appropriate substrate [3,4,9,12,15-17]. Patches of algae on dead coral shade live coral heads, and prevent photosynthesis by the zooxanthellae that live inside hermatypic coral [18]. Algae also can colonize live coral tissue and induce abrasion by bacteria that settle next to the algae; this harms the coral and diverts energy resources into defence mechanisms rather than into growth [18].

Disturbances caused by damselfish have been described as small-scale (1m²), short duration (days or weeks) and frequent (lasting for months or years), thus contributing positively to a higher diversity in coral reefs through algal control (i.e. more productive algal patches, and more diverse sites) leading to more diverse fish populations and coral species presence [1,2,13]. Damselfish territories can be found covering up to 40-50% of substratum on shallow reefs [14]. Both coral and algal diversity are decreased with depth.

The algae farmed the most by damselfish – *Lobophora*, *Dictyota* and *Halimeda* – are the most common algae found in the Caribbean [14,15]. Farming by certain damselfish species creates monocultures of these algae [19-22]. These patches of monoculture algae are created by either active exclusion of other herbivore species by direct attack, or by selective weeding-cutting of the preferred algae which is left the most abundant in their specific territory [3,13,14,22,23].

Farming practices may also result in species-rich patches that differ between damselfish species [7,24]. In Japan, *Stegastes nigricans* farms red algae monocultures, affecting the algal species' ability to recover from disturbance [22,23,25].

In the Caribbean, other *Pomacentridae* species have been studied but no research has been conducted on the effects of their farming habits on algae composition, or on the effect that algae have on coral growth and recruitment [7,9,17,26]. Other studies have been performed in localized areas where high densities of aggressive and territorial *Pomacentridae* are found. *Stegastes planifrons* was observed in Utila due to their easily distinguishable features and their passive territoriality [personal observations].

The purpose of this study was to determine the effect that *S. planifrons* have on benthic composition inside their territories regardless of the depth at which they are found. Algal and coral diversity were chosen as variables due to their contribution to coral reef productivity. Damselfish control over algal diversity can indirectly lead to changes in coral diversity in that species of coral that colonize and grow faster will have better chances of survival within damselfish territories. Short observations of fish activities yielded an estimated regular activity that could be linked to the diversity of their territories. If *S. planifrons* controls algae and coral benthic coverage by its farming techniques and territorial

behaviours, then territory composition is not expected to differ significantly within the shallow range down to 15m. Also, if farming increases the benthic surface area coverage and genera of algae present in territories, then patches with higher algal diversity should have lower coral diversity due to inter-functional group competition for primary and secondary space on the substrate.

Materials and Methods

Data collection

The study sites were located on the south side of Utila, Bay Islands, Honduras (16°6'N, 86°55'W), on the Mesoamerican Barrier Reef. Daily data collection occurred over a two-week period in July 2011 throughout the coral reef: back reef, reef flat and outer slope [4]. Ranges of depths of the observed territories were from 0.4 m-15.6 m, and were sorted by depth classes (0.0-1.0m, 1.1-5.0m, 5.1-7.0m, 7.1-9.0m, 9.1-11.0m, 11.1-16.0m), fish behaviour, fish stage and substrate composition. Depth classes were based on the equipment used to collect the data; the first class was collected using snorkelling gear, while the deeper ones were done with SCUBA equipment. Depth, fish stage (juvenile or adult), territory composition and diversity (algae, coral, invertebrate, and other fish genera), and fish behaviour (active patrolling: chasing of other fish out of their territories; passive patrolling: swimming around their territories; hiding; farming: weeding, cutting and spitting algae outside their territories) were noted at each territory. Behaviours were noted at three stages of the observation period: initial, when first spotted; intermediate, when other observations were taking place; and final, after all observations were done, and the fish were no longer being physically disturbed by any external activity done by the collector. The behaviour that was used was the intermediate one as it appeared to be the most stable one of the three. Territories were chosen where an *S. planifrons* was spotted and observed for approximately five minutes or until all data were collected [14]. The territories' boundaries were recognized by the turf coverage and the defensive behaviour of the fish whenever their territory was invaded [14].

Digital photographs (Olympus Tough 8000 with Ikelite underwater housing, 1.6x1.2mp) were taken of each territory. Photographs of six territories from each depth class, and six replicates from each depth class ($n=36$ territories) were analyzed for palatable algal coverage using ImageJ software [27]. Photographs included either a central area of a territory, a larger area, or the full area of a territory depending on its location and the feasibility of obtaining the full territory. The algal coverage was determined as the area covered by turf and *Dictyota* spp. divided by the total area of the photographic frames. This proportion was later transformed to arcsine values for statistical analysis. Diversity was determined as the number of algal genera

present in each territory.

Data analysis

A total of 87 territories ($N=87$) were observed. Fish behaviour, fish stage and depth class were analyzed as independent variables in a three-way ANCOVA using the General Linear Model module of SYSTATW5 (SYSTAT Software Inc.). The analysis was done separately for the two territory composition dependent variables: number of algal genera and number of coral genera. Depth and behaviour were the two variables then tested for effect on genera diversity. The independent variables were depth (continuous: 0-16m), fish stage (categorical: adult or juvenile) and fish behaviour (categorical: farming, passive patrolling, active patrolling and hiding). As fish stage did not have a significant effect on algae genera diversity, it was removed from both models. Behaviour was significant for the algal diversity analysis and therefore a Tukey post hoc test was used to determine which of the four behaviour categories was significantly different from the others with respect to its effect of the number of algal genera present.

Results and Discussion

Depth and substrate composition

There was a significant difference in the diversity of algae ($M=2.4$ genera) and coral genera ($M=1.5$) present ($p<0.001$) along the depth gradient (Figure 1). The general trend of diversity is an increase with depth, for both algae ($r^2=0.135$, $SE=1.024$) and coral ($r^2=0.076$, $SE=0.983$) (Figure 1). Algae surface coverage increased in shallow waters (until 11 m), then decreased after this depth (Table 1). These results support evidence for higher productivity in shallower reefs and in damselfish territories [13].

Figure 1. Coral and algae genera present along the depth gradient where *S. planifrons* territories were observed. Data represent the mean number of genera (SE shown as error bar) present in each category. Algae was significant more diverse than coral ($p<0.001$) and more affected by depth.

Table 1. Depth categories and their correspondent arcsine ($^{\circ}$) value of algal benthic coverage of territories at different depths. Six territories per depth category were randomly chosen and analyzed for the algal coverage ($n=36$, $SE=2.58$).

Depth category (m)	0.0–1.0	1.1–5.0	5.1–7.0	7.1–9.0	9.1–11.0	11.1–16.0
Arcsine ($^{\circ}$) algae coverage	20.30	34.00	34.72	25.12	34.42	24.32

There was not a significant difference between the means of algal and coral genera; this provides indirect evidence that there is a low level of competition between these two functional groups for primary and secondary space. In the reefs surrounding Utila, there has been no evidence of either of the groups becoming the dominant competitor for space [personal observations]. However, diversity increased (Figure 1) with depth for both functional groups, and algae coverage decreased after the first 12 m within the depth gradient studied (Table 1) [3,4]. Algal diversity was more affected by depth ($r^2=0.135$, $p<0.001$) than coral diversity ($r^2=0.076$, $p=0.10$). The depth categories that had the lowest diversity were the first two (0.0-5.0m); this may be due to the physical location of the sites. The shallow reef flats might be more vulnerable to human-induced disturbances, since the sites studied are located closer to hotels and houses than the deeper sites located at the reef crest and along the wall. These results disagree with the Intermediate Disturbance Hypothesis where the most diverse sites should be the ones where the disturbances are promoting biodiversity instead of limiting it [5]. Human settlements can be an intermediate disturbance if controlled, or an excessive one that tends to limit biodiversity [28]. In Utila, human influence has a negative effect on the overall biodiversity and structure of marine and coastal ecosystems [28]. The diversity and depth relationship found in this study follow patterns previously described in coral reefs [3,4] where the coral and algae are found to be increasing within the depth studied (0-16m). Coral and algae diversity were significantly affected by depth rather than by fish behaviour.

Behaviour and stage

Fish were found either isolated inside their territories or sharing a territory with another damselfish. 80 sites of single individuals were observed. Adults were found to be the most active farmers (19 sites) compared to juveniles (9 sites), as well as hiding the most (9:1 for adults and juveniles, respectively). The two patrolling behaviours showed a smaller difference between fish stages. Adults and juveniles were found to be more frequently passively patrolling than actively (19 and 7 sites respectively for adults and 14 and 2 sites for juveniles) (Figure 2). Seven territories were found to have more than one individual; four behaviours were present. The ratio between adults and juveniles was the same

for passive patrolling and hiding (1 adult: 1 juvenile) but differed for farming (3 adults: 1 juvenile) and active patrolling (4 adults: 1 juvenile).

Figure 2. Frequency of fish behaviour categories observed throughout the territories where a single first was found ($N=80$). Adult ($n=54$) fish are more abundant in general than juveniles ($n=26$). Eight territories were found to have more than one fish and are not included in this graph. Fish stages were not significant for algal and coral diversity changes along the depth gradient studied.

Behaviour, algal, and coral coverage

The most abundant behaviour was passive patrolling (42.04%) followed by farming (32.95%), hiding (12.50%) and active patrolling (11.36%). Behaviour had no significant effect on coral genera diversity ($p=0.596$) (Figure 3, Table 2). Algae, however, was affected by fish behaviour ($p=0.024$, $df=3$). (Figure 4, Table 2). The most significant difference between behaviours was found to be between hiding and farming ($p=0.024$, $df=82$) (Figure 4, Table 3). Results show that farming yielded the most algal coverage followed by active patrolling, passive patrolling and hiding (Figure 4, Table 3).

Figure 3. Mean number of coral genera present in relation to the four behavioural categories of fish. Hiding had the most genera present ($M=2.27$, $SD=1.103$) followed by active patrolling ($M=2.20$, $SD=1.229$), farming ($M=1.79$, $SD=1.205$) and passive patrolling ($M=1.78$, $SD=1.104$).

Table 2. Two-way ANCOVA analyses with ocean depth (0-16m), and fish behaviour (farming, active patrolling, passive patrolling, and hiding) as the independent variables but with different dependent variables (A: number of genera of algae and B) number of genera of coral). Fish life stage did not have a significant effect on either algae or coral genera diversity; therefore it was removed from both models. * = significant at $\alpha=0.050$.

	SS	df	MS	F	p
A: Algae no. genera					
Depth	10.420	1.000	10.420	10.752	0.002
Behaviour*	9.669	3.000	3.223	3.426	0.024*
Error	79.469	82.000	0.969		
B: Coral no. genera					
Depth*	7.464	1.000	7.464	7.620	0.007*
Behaviour	1.860	3.000	0.620	0.633	0.596
Error	80.328	82.000	0.980

Figure 4. Mean number of algae genera present in relation to the four behavioural categories of fish. Farming had the most genera present ($M=3.10$, $SD=1.135$) followed by active patrolling ($M=2.80$, $SD=1.135$), passive patrolling ($M=2.351$, $SD=0.977$) and hiding ($M=2.272$, $SD=0.646$).

Table 3. Probability values for post hoc Turkey test. Multiple comparisons test the effect of fish behaviour (farming, active patrolling, passive patrolling, and hiding) on the number of genera of algae present (see Table 2 for ANCOVA).

	Active	Farming	Hiding	Passive
Active	1.000			
Farming	0.944	1.000		
Hiding	0.248	0.024*	1.000	
Passive	0.764	0.142	0.529	1.000

Overall, the results of this study are in agreement with literature pertaining to algal coverage increasing due to damselfish behaviour as farmers, excluders and grazer-controllers, and diversity trends [3,4,9,13,14,16,17,23]. The effect that algae cover has on coral appears to be insignificant, at least in the section of Mesoamerican reef that was studied, which supports the positive effect of damselfish on healthy coral reefs [17]. Algal coverage does not represent a threat to healthy living coral [23], as there is not significant

evidence from the results of studies of interspecific competition [16,17]. Algal diversity was not found to alter the coral diversity or adult coral mortality; instead, depth was the factor that had the most significant effect on coral diversity changes ($p=0.007$, $df=1$) (Table 2) [23]. The results found in this study are estimates of algal coverage within damselfish territories signalling greater productivity within these patches [13]. Further studies of algae chlorophyll- α concentrations will provide more evidence on the actual relevance of these territories, the effect that depth and fish behaviour have on them, and their overall role in marine ecosystems [29-31]. If chlorophyll- α concentrations were merged with the obtained results, then damselfish regulation of primary productivity and substrate coverage competition might be better understood [17]. Further work will yield better explanations on the function of the coral reef and the role of these fish.

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