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Farming damselfishes shape algal turf sediment dynamics on coral reefs

Authors:

Sterling B. Tebbett *, Tory J. Chase, David R. Bellwood

Addresses:

[1]ARC Centre of Excellence for Coral Reef Studies; and College of Science and Engineering, James Cook University, Townsville, Queensland 4811, Australia

***Corresponding Author:**

Email: sterling.tebbett@my.jcu.edu.au

Phone: (07) 47815729

Abstract

Farming damselfishes are well known for shaping benthic communities on reefs, in terms of both cultivating algae and increasing productivity. However, their capacity to shape relationships between algal turfs, detritus and sediments remains largely unknown, despite the importance of such relationships on reefs. We therefore examined the relationships between sediment loads and both algal turf length and detritus levels, inside and outside farming damselfish territories, at two reefs on the Great Barrier Reef. We found that, while sediment loads are tightly coupled with algal turfs outside territories, the nature of this coupling was fundamentally different inside damselfish territories, with significantly longer algal turfs and higher detritus levels prevailing, irrespective of sediment loads. These modified algal turf-sediment relationships may be a key factor in explaining, a) the significantly higher productivity levels reported from within farming damselfish territories and b) the ability of farming damselfishes to persist in high-sediment locations.

Keywords

Algal turf; Coral reef; Damselfish; Herbivory; Productivity; Sediment

1. Introduction

Coral reefs are changing rapidly as the impacts of anthropogenic stressors intensify (Hughes et al., 2017; Stuart-Smith et al., 2018). After climate change, land-based sediments are one of the greatest threats to reef ecosystems, with the interactions between sediments and algal turfs, and the fishes that modify them, becoming a major focus of future reef management approaches (Tebbett and Bellwood, 2019). This is because the coverage of algal turfs is increasing on many coral reefs following coral loss (Bellwood et al., 2019a; Holbrook et al., 2016). Furthermore, these algal turfs can rapidly accumulate inorganic sediments (Latrille et al., 2019), which can modify key ecosystem functions including herbivory/detritivory (Duran et al., 2019; Goatley et al., 2016) and coral settlement (Ricardo et al., 2017; Speare et al., 2019). However, the nature of these algal turf-sediment relationships is complex, as longer algal turfs can accumulate more sediment (Latrille et al., 2019), while sediment accumulation facilitates the development of longer algal turfs (Goatley et al., 2016), but slows the growth rate of these algae (Tebbett and Bellwood, 2020). Furthermore, these processes can be modified by fishes which can both remove sediments (Goatley and Bellwood, 2010) and crop algal turfs (Clausing et al., 2014). Understanding, and disentangling, this complexity is becoming increasingly important on anthropogenically disturbed coral reefs (Bellwood et al., 2019b).

Farming damselfishes are a charismatic and conspicuous component of coral reef fish assemblages. Their ability to modify benthic algal composition (Cabaitan et al., 2018; Ceccarelli, 2007; Hata and Kato, 2004; Russ, 1987), and therefore shape productivity through the maintenance of algal lawns (Ferreira et al., 2018; Klumpp et al., 1987), is widely documented. However, the nature of the relationship between sediments and the length of these algal turfs, as well as the relationship between sediments and nutritional resources (i.e. organic detritus) within these algal turfs, has received limited attention. Indeed, it is currently unclear if, and to what extent, these relationships differ inside damselfish territories relative to algal turfs outside damselfish territories. This is despite repeated suggestions that farming damselfishes may modify benthic sediment dynamics (Ceccarelli et al., 2005; Eurich et al., 2018; Hata and Nishihira, 2002), and that sediments may shape the nature of algal turfs inside their territories (Casey et al., 2014; Ceccarelli et al., 2001). Importantly, examining how key relationships differ inside compared to outside damselfish territories may help explain why algae inside territories are more productive, as studies have revealed that sediment is one of the key moderators of algal turf productivity. Indeed, increasing sediments lead to marked decreases in algal turf productivity on both tropical coral reefs (Tebbett et al., 2018a; Tebbett and Bellwood, 2020) and temperate reef systems (Irving and Connell, 2002a; 2002b). The aim of this study, therefore, was to examine the nature of the relationship between sediments and algal turf length, and sediments vs. detritus, inside versus outside damselfish territories.

2. Methods

2.1 Study sites

This study was conducted between March and April 2019 in Mermaid Cove, Lizard Island, in the Northern Great Barrier Reef (GBR), and from April to May 2019 in Pioneer Bay, Orpheus Island, in the Central GBR (Fig. S1). Both study locations were relatively sheltered and leeward facing. Lizard Island is a mid-shelf reef located approximately 30 km from the mainland, while Orpheus Island is an inner-shelf reef located approximately 15 km from the mainland. As these islands are on different shelf positions they are exposed to different sediment dynamics, particularly terrestrial sediment input (Fabricius et al., 2014), with higher algal turf sediment levels recorded on reef crests at Orpheus Island (796.99 ± 224.17 g m^{-2} [mean ± SE]) compared to Lizard Island (184.57 ± 45.67 g m^{-2}) (Tebbett and Bellwood, 2019). In both locations the species of farming damselfishes examined occurred in approximately equal densities and were the most abundant species at each location. Overall, farming damselfishes were relatively abundant at each location, but were patchily distributed.

2.2 Field sampling

Algal turf particulate samples (particulates = inorganic sediments + organic material < 2 mm) were collected from suitable surfaces within the territories of two damselfish species (11-13 samples per species, at each location). Study species were *Plectroglyphidodon lacrymatus* and *Stegastes nigricans* at Lizard Island and *P. lacrymatus* and *Stegastes apicalis* at Orpheus Island (Fig. 1a, b ,c). Suitable surfaces were flat, smooth, free of particulate-retaining pits, macroalgae and encrusting organisms, and in shallow-water (1-5 m) reef habitats between the crest and mid-flat (following Purcell and Bellwood, 2001). Only one sample was taken per territory and all territories contained an adult damselfish of the respective species. Territories generally measured 1-2 m^2 and were located on contiguous reef. For each sample, algal turf length was initially quantified by measuring 10 haphazardly selected algal turf filaments using the depth probe of vernier callipers following the procedure outlined in Tebbett and Bellwood (2019). Particulates trapped within the algal turfs were then sampled from within a 58 cm^2 PVC ring using a submersible electronic vacuum sampler (modified after Purcell, 1996) that readily removes inorganic sediments and organic detritus but not algae (Crossman et al., 2001; Purcell 1996; Purcell and Bellwood 2001). Damselfish species were selected based on: a) their abundance at the study locations, and b) their propensity to produce thick algal ‘lawns’ within their territories (Ceccarelli, 2007; Hata and Ceccarelli, 2016). Note the *S. nigricans* species category may have included an occasional *S. punctatus*. These two species were fused herein (following Johnson et al., 2011) due to: a) identification difficulties, and b) the propensity for both species to form adjacent interconnected territories.

Baseline relationships between algal turfs, detritus and sediments were provided via algal turf particulate samples (n = 60 Orpheus Island, n = 63 Lizard Island) collected from suitable algal turf-covered surfaces (following the same criteria as above) outside damselfish territories using the same vacuum sampling method. All outside-territory sampling was conducted on the same field trips (i.e. within days of each other) and from the same locations (i.e. the same reef and habitat at each location). The data from outside damselfish territories were sourced from Tebbett and Bellwood (2020). Samples were processed following Gordon et al., (2016), i.e. dried, weighed, bleached with hydrogen peroxide (H_2O_2), re-dried and re-weighed to yield total benthic particulate mass (inorganic and organic particulates), inorganic sediment mass and mass of organic particulates (detritus). Herein, detritus was considered non-living organic particulate material that is likely to contain live organisms in the form of microalgae and microbes (following Crossman et al., 2001; Wilson et al., 2003). Full details of sample processing can be found in the supporting information Text S1.

2.4 Statistical analysis

The nature of the relationships between inorganic sediment mass (independent variable) and algal turf length (dependent variable), the proportion of organic particulates in total particulates by mass (dependent variable) and total organic detritus mass (dependent variable), were compared inside vs. outside damselfish territories using generalised linear models (GLMs). In all cases, data were examined separately for each location due to differences in the damselfish species examined. In all cases substratum type (damselfish species territory or outside territory), and inorganic sediment mass (logged and mean centred) were initially fitted as interacting fixed effects. The most parsimonious model was then selected based on the corrected Akaike Information Criterion (AICc) (Table S1). Models examining the relationship between algal turfs or organic detritus load and sediment mass were based on a Gamma distribution with a log link, while models examining the relationship between proportion of organic detritus and sediment mass were based on a beta distribution with logit link. Model assumptions were assessed using residual plots, all of which were satisfactory. Post-hoc pairwise means comparisons with a Tukey’s adjustment were undertaken to examine within-factor differences for additive models. All statistical analyses were performed in the software R (R Core Team, 2018) using the *tidyverse* (Wickham, 2017), *glmmTMB* (Brooks et al., 2017) and *emmeans* (Lenth, 2019) packages.

3. Results and discussion

Algal turf length always increased with increasing sediment loads, however, the nature of this relationship differed fundamentally inside versus outside damselfish territories (Fig. 1d, e). Regardless of the damselfish species or location in question, algal turfs were always significantly longer inside damselfish territories compared to outside territories across the same range of sediment loads (Fig. 1d, e; Table S2, S3). The extent of this difference was dependent on the damselfish species. At Lizard Island the GLM revealed that *P. lacrymatus* and *S. apicalis* territories contained algal turfs that were 2.1 and 2.5-fold longer than algal turfs outside territories, at the mean sediment load, respectively (Table S2). While at Orpheus Island the GLM revealed that *P. lacrymatus* and *S. nigricans* territories contained algal turfs that were 1.8 and 3.3-fold longer than algal turfs outside territories, at the mean sediment load, respectively (Table S2). Indeed, this resulted in a significant difference between damselfish species (*S. nigricans* and *P. lacrymatus*) at Lizard Island (*p* <0.001; Table S3). Regardless of the location, or species, it is clear that algal turf length-sediment relationships are fundamentally different inside when compared to outside damselfish territories.

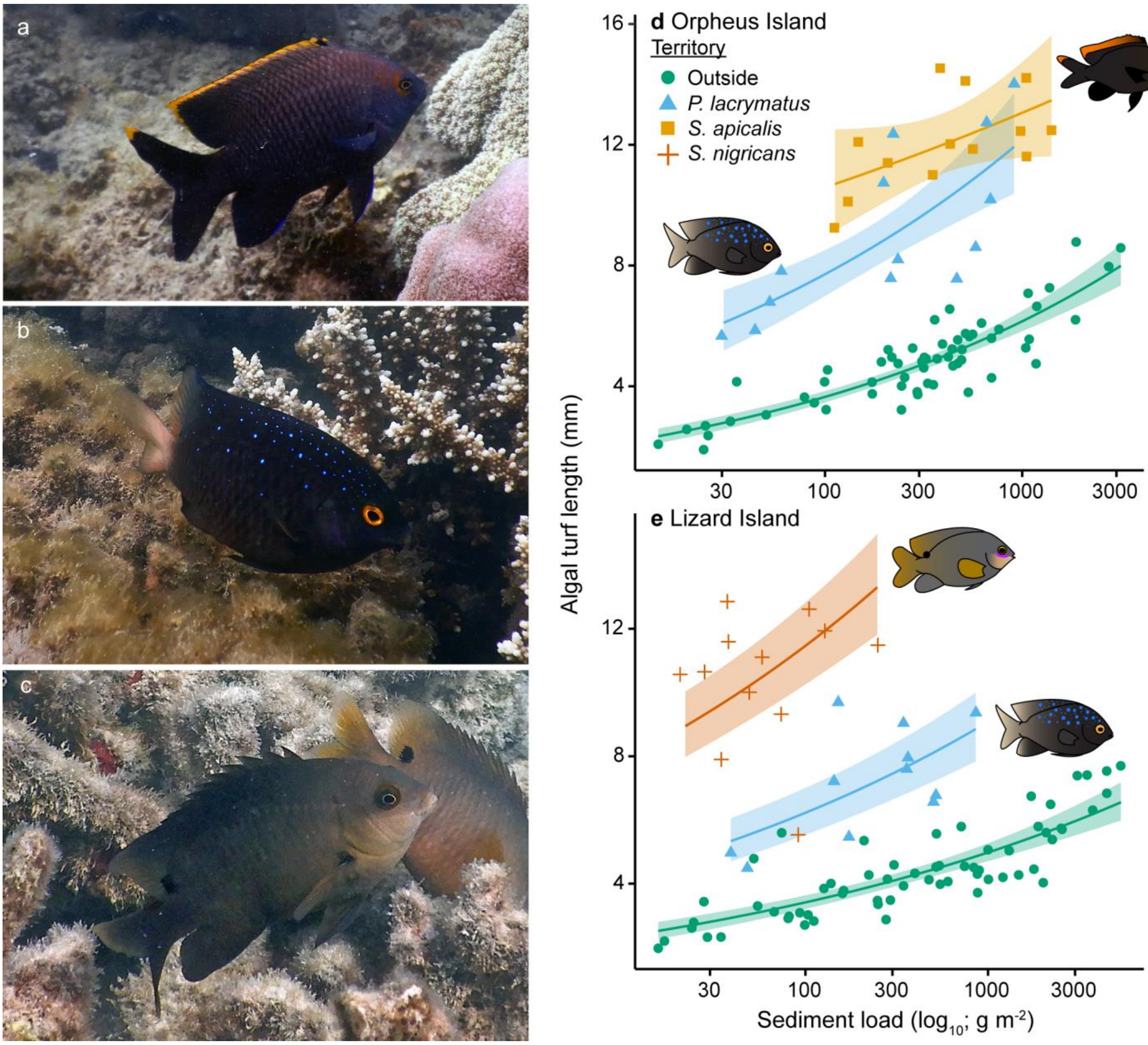

Figure 1 Farming damselfishes and thick algal ‘lawns’ within their territories: a) *Stegastes apicalis*, b) *Plectroglyphidodon lacrymatus* and c) *Stegastes nigricans* (Photographs: a, b T.J. Chase, c S.B. Tebbett). The relationship between sediment load and algal turf length inside and outside damselfish territories on coral reefs at d) Orpheus Island and e) Lizard Island. Coloured lines are the mean predicted fits of generalised linear models, shaded areas are the upper and lower 95% confidence intervals, and coloured dots are the raw data points. Fish genus abbreviations: *P.* = *Plectroglyphidodon*, *S.* = *Stegastes*.

When trapped within algal turfs, sediments can constrain the growth of algae (Tebbett and Bellwood, 2020), through mechanisms such as the development of anoxic conditions in the underlying sediment layers (Clausing et al., 2014). However, this relationship does not operate in just one direction, because as algal turfs become longer, they also have a greater propensity to trap and retain more sediment (Latrille et al., 2019). Indeed, outside damselfish territories, algal turfs generally trap progressively more sediment as they get longer (Fig. 1d, e), until a saturation point where algal turf growth slows (Steneck, 1997; Tebbett and Bellwood, 2020). Interestingly, this relationship does not appear to operate in the same way inside damselfish territories as algal turfs grow ~1.8-3.3-fold longer without accumulating the same levels of sediment as would be expected in algal turfs outside of territories (Fig. 1d, e; Table S3). There may be two primary reasons for this lack of sediment accumulation: a) damselfishes selectively cultivate algae that has a limited capacity to trap sediments, or b) damselfishes directly reduce sediment loads. The evidence suggests that the later mechanism is the most parsimonious explanation and is the predominant driver.

The available evidence suggests that the later mechanism is operating. There are three lines of evidence. 1) it has been repeatedly shown that longer algal turfs, regardless of location and associated differences in taxonomic composition, accumulate far more sediment than shorter turfs (reviewed in Tebbett and Bellwood, 2019). This even applies to plastic turf analogues (which clearly have a fundamentally different composition to natural turfs) (Latrille et al., 2019). 2) It could be argued that farming damselfishes only cultivate algae that has a limited ability to trap sediment and therefore the composition of algae in their territories overrides the standard relationship between length and sediment mass. However, Hata and Nishihira (2002) have suggested that the algae found inside some *S. nigricans* territories has a greater propensity to trap sediment than algae outside territories. Finally, 3) the magnitude of the results we documented need to be placed in perspective. Algae of ~10 mm length inside

S. nigricans territories contains less sediment than one would expect to accumulate on sedpods (i.e. smooth concrete mounds that mimics a corals surface) (Field et al., 2013; Latrille et al., 2019). This low accumulation is quite remarkable. It appears highly unlikely that long filamentous algae would have the same propensity to trap sediment as smooth concrete.

In addition to the above evidence, it is widely accepted that other fishes such as surgeonfishes and parrotfishes actively reduce algal turf sediment loads (reviewed in Tebbett and Bellwood, 2019), and damselfishes have previously been shown to directly reduce sediments on corals (Chase et al., 2020). In terms of farming damselfishes their capacity for directly removing benthic items from their territories has been widely documented (reviewed in Ceccarelli et al., 2001; Hata and Ceccarelli, 2016). Indeed, both Ceccarelli et al. (2005) and Eurich et al. (2018) posited that farming damselfishes directly reduce sediment loads inside their territories (but see Hata and Nishihira, 2002). Based on the above evidence, it would appear that damselfishes may be actively modifying sediments, raising the question: why would damselfishes modify sediments?

Part of the explanation is likely to relate to the relationship between inorganic sediments and the nutritional value of organic particulates (detritus) trapped in algal turfs. Many species of farming damselfishes, including the species examined herein, incorporate at least some detritus in their diets (Ceccarelli, 2007; Eurich et al., 2019; Wilson and Bellwood, 1997), but as inorganic sediment loads increase, the relative level of nutritionally rich organic detritus in the particulates often decreases precipitously (Gordon et al., 2016; Tebbett and Bellwood, 2020). Indeed, our data revealed that regardless of the location or damselfish species in question, the relative level of detritus in benthic particulates always decreased with increasing sediment loads (Fig. 2a, b). However, the relative detritus levels, as well as the absolute mass of detritus, remained significantly higher in all damselfish species territories, compared to outside territories, across the same range of sediment loads (Fig. 2; Table S2, S3). It may be that damselfishes are actively modifying the relative proportion of sediments in their territories, limiting the extent to which sediments 'water-down' detrital yields.

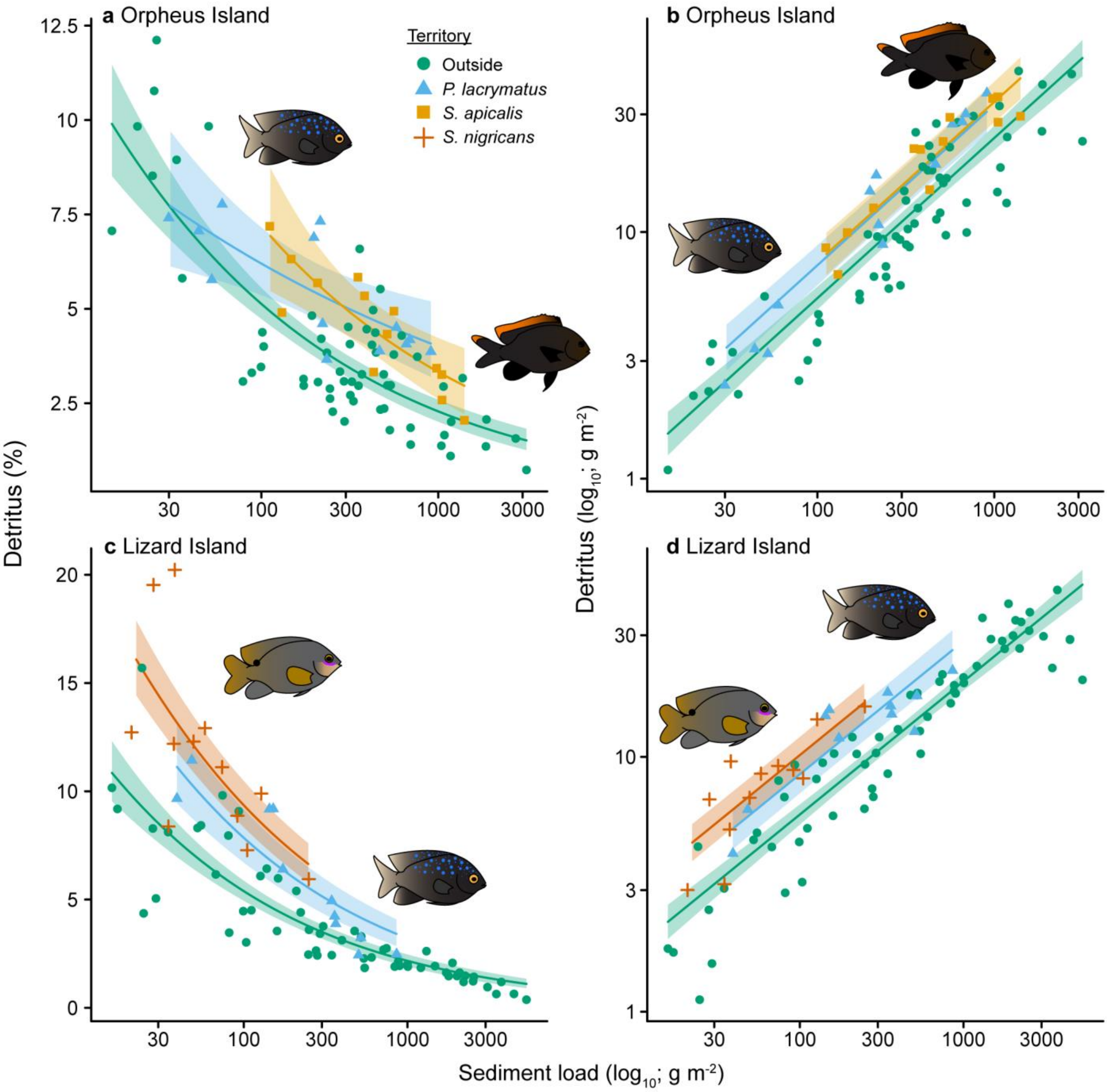

Figure 2 The relationship between sediment load and a, c) the relative detrital levels (in benthic particulates by mass) and b, d) total organic detritus mass, inside and outside damselfish territories on coral reefs at a, c) Orpheus Island and b, d) Lizard Island. Coloured

lines are the mean predicted fits of generalised linear models, shaded areas are the upper and lower 95% confidence intervals, and coloured dots are the raw data points. Herein, detritus was considered to be non-living organic particulate material that is likely to contain life in the form of microalgae and microbes (following Crossman et al., 2001; Wilson et al., 2003). Fish genus abbreviations: *P. = Plectroglyphidodon, S. = Stegastes.*

Damselfishes may also modify sediment loads to enhance the productivity of algal turfs inside their territories; turf productivity in territories is substantially higher than in turfs outside territories (Klumpp et al., 1987; Montgomery, 1980). While factors such as additional nutrients (Blanchette et al., 2019; Klumpp et al., 1987) and selective cultivation of productive algal species (Ceccarelli et al., 2001; Klumpp et al., 1987) may enhance productivity, the alteration of sediment loads is likely to play a considerable, albeit previously overlooked, role. Indeed, recent evidence has revealed that even minor sediment increases can lead to marked declines in algal turf productivity (Tebbett et al., 2018a; Tebbett and Bellwood, 2020). Therefore, to maintain high algal turf growth inside territories it may be essential for damselfishes to keep sediment levels at relatively low levels.

It is interesting to note that the nature of the relationships between sediment, algae and detritus inside damselfish territories may incentivise the ‘raiding’ of these territories by other herbivorous/detritivorous fishes. Indeed, it has been widely documented that roving herbivorous/detritivorous fishes form schools to overwhelm damselfish and gain access to the resources in their territories (Foster, 1985; Robertson et al., 1976). In doing so, these fishes would gain access to algae and detritus that is relatively free of sediment, therefore yielding higher nutritional returns per bite compared to feeding on algal turfs outside of territories (also see Russ, 1987). It is possible that other school forming herbivorous/detritivorous fishes actually benefit from the presence of farming damselfishes in high-sediment locations as territories may offer ‘oases’ of nutritional resources (including, for example, juvenile parrotfishes that may live within damselfish territories for part of their early ontogeny [Bellwood and Choat, 1989]).

It is currently unclear how, and indeed if, damselfishes modify sediments within their territories; this will require further experimental investigation. However, damselfishes have been observed directly removing material from their territories (Ceccarelli et al., 2001; Irving, 2019), and some have specific ‘toilet’ sites at the boundaries of their territories where they deposit ingested sediments (DRB pers. obs.); as in the surgeonfish *Ctenochaetus striatus* (Goatley and Bellwood, 2010). Regardless of the mechanisms involved, the fundamentally different nature of relationships between sediments, algae and detritus inside compared to outside damselfish territories was marked. Indeed, it is remarkable to think that just as human farmers manage their soil, farming damselfishes could be managing sediments in their territories to facilitate the production of nutritional resources.

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