



Effects of territorial damselfish on corallivorous fish assemblage composition and coral predation in the Mauritian lagoon

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ABSTRACT

Predation is a significant stressor for many coral species. Understanding how predation interacts with factors such as climate change is key to coral conservation. Territorial damselfish of the genus *Stegastes* form territories on branching corals (genus *Acropora*) on which they cultivate algae, and while defending these territories, provide corals with indirect protection from predation. However, it is not known how the protection afforded by *Stegastes* spp. varies with corallivorous fish assemblage composition, nor whether corallivore assemblages themselves may be affected by the presence of *Stegastes* spp. and their associated *Acropora* spp. habitats. This study examined relationships among predation protection by *Stegastes* spp., branching *Acropora* coral cover, and the number and species richness of corallivorous fish present within a given area, namely the Mauritian lagoon in the western Indian Ocean. Predation on bleaching-resilient massive *Porites lutea* corals within and outside *Stegastes* territories was surveyed at sites around Mauritius island. Corallivorous fish assemblages, branching coral cover, and *Stegastes* spp. density were also surveyed at each site visit. Results show that high predation was correlated with the presence of high numbers of corallivores, but predation was lower within *Stegastes* spp. territories irrespective of all observed corallivore densities. Greater numbers of *Stegastes* spp. were correlated with increasing density of obligate corallivores. Non-Acroporid coral cover was positively correlated with species richness of obligate corallivores, while branching *Acropora* coral cover was negatively correlated with overall corallivore density. This study shows for the first time that predation on bleaching-resilient massive corals is lower within *Stegastes* spp. territories regardless of the number of corallivores present, adding to the growing body of knowledge on the complex relationships between *Stegastes* spp. and their environment. The findings also indicate possible effects of the presence of *Stegastes* spp. and their branching *Acropora* habitats on corallivorous fish density in areas with low coral diversity, which may warrant further study.

1. Introduction

The effects of stressors impacting coral reefs during the Anthropocene are becoming increasingly evident. Longstanding biotic stressors such as coral predation (Rice et al., 2019) have been identified as significant stressors to corals, leading to polyp and tissue loss (Bonaldo and Bellwood, 2011). This is often associated with reduced growth and

reproductive output and sometimes mortality of colonies subject to regular predation (Rotjan and Lewis, 2006, 2008; Rice et al., 2019). Predation may also make corals more vulnerable to competition with other benthic organisms such as algae, with high levels of predation leading to significantly reduced growth and survival for corals (Rotjan and Lewis, 2008; Rice et al., 2019) and potential phase shifts of reefs to more algae-dominated systems (Bhagooli et al., 2021). However,

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facultative corallivores including parrotfish may also feed on algae, reducing competition with corals (Jayewardene, 2009). The relationships between corals and their predators are therefore complex, and may be dependent on other organisms present within ecosystems if these influence the benthos and/or corallivore population dynamics. An understanding of the effects of biotic stressors on corals is key to identifying factors that may influence how coral reef ecosystems will respond to increasingly stressful environments brought about by anthropogenic changes.

Around the island of Mauritius, coral predation is mainly carried out by fish species and Crown-of-Thorns starfish *Acanthaster planci* Linnaeus 1758, though some invertebrates such as the sea snails *Drupella* Thiele 1925 and *Coralliophila* Adams 1853 spp. are known to predate corals, especially *Acropora* spp. Oken 1815 (Kaullysing et al., 2017, 2019, 2020). Around 50 corallivorous fish species have been observed in the waters of Mauritius (Cole et al., 2008; Rotjan and Lewis, 2008; FishBase, 2022; supplementary table 1). Their impact on corals varies from polyp-eating butterflyfish species that do not damage coral skeletons, to large “excavator” species such as the bumphead parrotfish *Bolbometopon muricatum* Valenciennes 1840 that remove large areas of coral skeleton (Rotjan and Lewis, 2008). Even facultative corallivores such as the bullethead parrotfish *Chlorurus sordidus* Forsskål 1775 may bite corals ≥ 2 times per minute (Bellwood and Choat, 1990; Rotjan and Lewis, 2008), which may translate to significant damage to corals where densities of these fish are high. The shallow lagoon surrounding the main island of Mauritius has historically been dominated by branching *Acropora* and foliose *Montipora* Blainville 1830 corals but with a high level of coral species diversity (McClanahan and Muthiga, 2020; Bhagooli et al., 2021). However, the Mauritian lagoon has experienced significant bleaching and loss of coral cover, particularly of rare and non-adaptive coral species, and a phase shift to algae-dominated benthos in recent years (Bhagooli et al., 2021). This loss has left behind monocultures of fast-growing *Acropora* spp. that provide structural complexity but are low in benthic species diversity (McClanahan and Muthiga, 2020; Tiddy et al., 2021). While *Acropora* spp. are relatively susceptible to bleaching (McClanahan et al., 2007), their occurrence in the Mauritian lagoon has decreased less dramatically in recent years compared with many other genera (McClanahan and Muthiga, 2020), possibly due to their adaptability (Louis et al., 2020) and fast rate of growth, meaning that in many degraded sites the majority of structural complexity and live coral is comprised of branching *Acropora* spp. (McClanahan and Muthiga, 2020; Tiddy et al., 2021).

Commonly found within *Acropora*-dominated systems in the Mauritian lagoon are bleaching-resilient massive corals of the genus *Porites* Link 1807 (McClanahan and Muthiga, 2020). These corals have been found to bleach less readily in response to heating events (McClanahan et al., 2007), including in the lagoon of Mauritius (McClanahan et al., 2005), and to be more likely to survive bleaching events compared with genera such as *Acropora*, *Montipora* and *Pocillopora* Lamarck 1816 (McClanahan et al., 2007; Grimsditch et al., 2010). While *Porites* species are less prone to bleaching and mortality as a result of high temperatures and therefore may be valuable conservation tools in reefs subject to bleaching damage (Marshall and Baird, 2000; Loya et al., 2001; Bhagooli and Taleb-Hossenkhan, 2012; Mattan-Moorgawa et al., 2012), significant loss of these corals at various sites around Mauritius has occurred in recent years (McClanahan and Muthiga, 2020). While this may be due to stressors other than high temperatures such as low chlorophyll (McClanahan and Muthiga, 2020) or corallivory, bleaching-resilient corals are often slow-growing and may be difficult to restore (Lough and Barnes, 2000; Lough, 2008; Goodkin et al., 2011; Lough and Cantin, 2014). Corallivory in diverse reef ecosystems often preferentially targets branching and tabular coral species such as *Acropora* species (Pratchett et al., 2004; Pratchett, 2005; Rotjan and Lewis, 2006; Cole et al., 2008), however facultative corallivores such as parrotfish species are known to predate massive coral species and may cause significant damage due to removal of areas of the coral skeleton (Rotjan

and Lewis, 2008; Bonaldo and Bellwood, 2011). In addition, if coral diversity is lost, predation pressure from obligate corallivores may switch to those coral species still present, further increasing predation pressure with the associated detriment to coral growth and survival and potential loss of bleaching-resilient species and genotypes (Pratchett et al., 2004; Rotjan and Lewis, 2006; Wilson et al., 2009; Rice et al., 2019; McClanahan and Muthiga, 2020).

Also found in large numbers in global reef environments are territorial damselfish of the genus *Stegastes*, of which six species are found in Mauritian waters including *S. nigricans* Lacépède 1802, *S. punctatus* Quoy & Gaimard 1825, and the endemic *S. pelicieri* Allen & Emery 1985. These small Pomacentrid fishes inhabit territories of $\sim 1\text{--}8\text{ m}^2$ on and around branching *Acropora* spp. stands within which they cultivate gardens of filamentous algae that form part of their omnivorous diet (Hata and Kato, 2002, 2004; Ceccarelli et al., 2011; Quadros et al., 2019). These gardens can cover up to 100% of the benthos within *Acropora* spp. stands including part of *Acropora* branches (White and O'Donnell, 2010; Johnson et al., 2011), and may represent a significant threat to corals within territories (Schopmeyer and Lirman, 2015) as *Stegastes* spp. encourage algal overgrowth and may bite or dislodge corals in order to improve algal coverage and prevent competition (Chasqui-Velasco et al., 2007; Schopmeyer and Lirman, 2015). However, *Stegastes* spp. also defend their territories aggressively against intruding fish and invertebrate species to prevent egg predation and competition for algae (Gochfeld, 2010; White and O'Donnell, 2010; Johnson et al., 2011; Tiddy et al., 2021). This territorial defence extends to associational protection of corals within *Stegastes* spp. territories, reducing coral vulnerability to fish predation (Gochfeld, 2010; White and O'Donnell, 2010; Tiddy et al., 2021). *Stegastes* spp. therefore have the potential to improve recruitment and survival of corals, including bleaching-resilient corals, in areas where predation is a significant threat. In systems such as the Mauritian lagoon where many sites are dominated by *Acropora*, a high proportion of live coral cover occurs within *Stegastes* spp. territories (Tiddy et al. pers. obs.). *Stegastes* spp. in partially degraded areas containing *Acropora* monocultures may therefore encounter greater numbers of corallivores targeting corals within territories than they are capable of defending against, leading to a reduction in associational protection of corals, including bleaching-resilient *Porites* spp. that may sometimes be found growing within territories (Tiddy et al., 2021). *Porites* corals outside territories are subject to significant predation pressure due to the large numbers of corallivorous parrotfish found within the Mauritian lagoon which target these corals (Bonaldo and Bellwood, 2011), but are protected when within territories (Tiddy et al., 2021). If territorial protection is reduced by increasing corallivore numbers, however, this may result in an increase in predation on *Porites* spp. even within territories, potentially furthering the decline of these bleaching-resilient corals within the Mauritian lagoon (McClanahan and Muthiga, 2020). *Porites* spp. are also highly susceptible to overgrowth by algal turf within *Stegastes* spp. territories (White and O'Donnell, 2010), meaning that if predation protection is reduced, survival within territories is likely to decline significantly. Facultative corallivores that also target algae may further contribute to damage on overgrown corals within territories, and may be attracted to the resources within *Stegastes* spp. territories (Johnson et al., 2011). Alternatively, if *Stegastes* spp. are capable of effective defence against high numbers of corallivores, this may negatively impact the ability of corallivores remaining in partially degraded areas to access resources, with fitness consequences for individual corallivores (Pratchett et al., 2004; Rice et al., 2019) and potentially fish assemblages.

It has been previously shown that *Stegastes* spp. presence reduces predation by corallivores on *Acropora* and *Montipora* coral species (Gochfeld, 2010; White and O'Donnell, 2010), and on massive bleaching-resilient *Porites lutea* Milne Edwards & Haime 1851 (Tiddy et al., 2021). However, it has not been shown how corallivore assemblages may affect predation on massive *P. lutea* within the Mauritian

lagoon, nor how they may affect the ability of *Stegastes* spp. to defend corals within their territories from predation. In addition, while overall and branching coral cover have been found to be associated with greater density and species richness of fish including corallivores (Johnson et al., 2011; Darling et al., 2017), it is not known how the presence of *Stegastes* spp. inhabiting the majority of branching *Acropora* stands may affect corallivore assemblage in an *Acropora*-dominated system. This study functions as a follow-up study to Tiddy et al. (2021) and had three aims: 1) to examine whether predation on massive bleaching-resilient *P. lutea* will be higher in areas containing greater density and/or species richness of corallivorous fish; 2) to determine whether the reduction in predation on *P. lutea* within *Stegastes* spp. territories persists when faced with greater numbers of corallivores; and 3) to investigate whether the presence of *Stegastes* spp. and their *Acropora* spp. habitats is correlated with changes in the density and species richness of corallivorous fish assemblages within the lagoon of Mauritius.

2. Materials and methods

2.1. Study sites

Some of the data utilised in this study, including *P. lutea* surveys, have been previously published in Tiddy et al. (2021); additional details of our methodology may be found in this publication or in the supplementary material to the present study. Surveying was carried out at six sites within the lagoon around Mauritius island (Fig. 1), every two months from October 2018 to June 2019.

2.2. Predation on *P. lutea*

At each site visit, 11–15 *P. lutea* corals within *Stegastes* spp. territories and 11–15 corals outside territories were surveyed. Where fewer than 11 corals within or outside territories were present, all those present were surveyed and results were pooled across months and sites. The minimum value of 11 was calculated based on a power analysis carried out on pilot data collected in September 2018. Corals were photographed on all sides in order to determine their surface area and to allow all bites originating

from corallivorous fish to be counted through picture analysis using the app “Sketch and Calc” (2019), with a ruler or tape measure included in each photograph for scale. Surface areas are approximate due to the non-planar nature of *P. lutea* surfaces, however the application used allows measuring of uneven areas to improve accuracy. Bites were marked in photos according to bite type in order to allow bite numbers and areas to be calculated. Corallivory on individual massive corals was calculated as bite density (bites cm^{-2}) and percentage of the coral surface area damaged by bites. In order to calculate the latter, the average surface area of each bite type was calculated based on an average of up to 50 bites from several individual corals. Bite type was determined according to size and form of damage to the coral, indicating which corallivore species likely made the bite. Butterflyfish bites tend to be small ($<1 \text{ cm}^2$) and remove polyps without damaging the coral skeleton, though size is variable and some species are “scrapers” that cause some damage to the coral skeleton (Cole and Pratchett, 2013). Parrotfish bites form paired grooves, often with a gap in the centre where the jaws have closed (hence “paired”), and often remove both polyps and coral skeleton. Damselfish bites form circles of removed polyps and skeleton with an undamaged centre (Rotjan and Lewis, 2008). An additional category was designated for ‘other bites’, meaning those that resembled fish bites in depth and extent of damage, but did not fit the shape profiles described. These could have been made by pufferfish or triggerfish, however no descriptions of the appearance of these bites on massive *Porites* spp. could be found in the literature, and we did not directly observe these species feeding on *Porites* spp. during surveys. We did not include bites originating from corallivorous invertebrates in our analysis, as none of these were observed on massive *P. lutea* during pilot surveys, and invertebrate predation upon massive *P. lutea* within the Mauritian lagoon is minimal (Kaullysing et al., 2017, 2019).

2.3. Transect surveying

Underwater transects were surveyed in order to quantify the density (fish 300 m^{-2} used in Poisson models due to requirement for integer data; fish m^{-2} used in Gaussian models) and species richness (number of species observed at each site visit) of corallivorous fish (Cole et al., 2008), the percentage of the benthos consisting of branching *Acropora* as well as the total cover of scleractinian corals, and the density of *Stegastes* spp. (fish m^{-2}) present at each site visit. Four video transects were surveyed per site visit, with each transect measuring 30 m in length and 5 m surveyed either side of the transect line, for a total of 300 m^2 surveyed per transect (Bonaldo and Bellwood, 2011; Friedlander et al., 2014). Video transects were used over visual surveys because of the difficulty associated with making accurate *in situ* counts of abundant, fast-moving species such as shoals of initial phase *Chl. sordidus*, whereas videos can be paused to allow fish to be identified and counted. In cases where corallivores were not shown clearly in footage, for example due to poor visibility, notes of their identities and approximate numbers were made on a slate at the time of surveying and shown in the footage to allow them to be synced with later analysis. Notes were also made if an individual appeared more than once in the footage to allow the subsequent sightings to be discounted. Depth was not recorded as the Mauritian lagoon does not vary much in depth (1–3 m). A snorkeler placed the transect line (tape measure), waited a few minutes to allow disturbed fish to return, then made two passes along the transect line (one on each side) filming ahead of them with an underwater camera. While placing transect lines may disturb fish assemblages (Emslie et al., 2018), in order to acquire standardised densities, it was necessary to lay some form of measuring device as transect lengths were too long to be estimated. As tidal action within the lagoon would have resulted in the loss of transect lines if these were placed prior to surveying, and time at sites was limited, it was necessary to carry out surveying immediately after laying the lines. Laying the line while filming (in order to prevent disturbance prior to recording) resulted in videos being shaky as handling a camera and paying out a transect line was very challenging

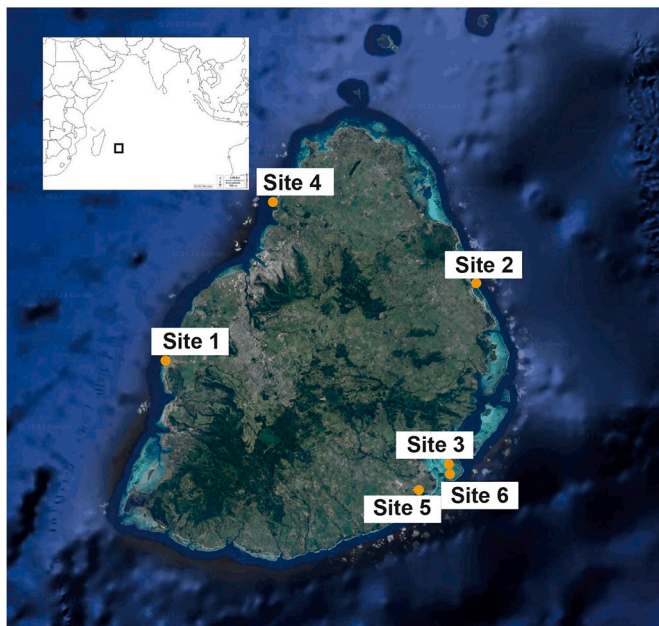


Fig. 1. Satellite map showing site locations within the Mauritian lagoon. Coordinates: Site 1: $-20.2788, 57.36582$; Site 2: $-20.1816, 57.78115$; Site 3: $-20.4086, 57.74452$; Site 4: $-20.0796, 57.50939$; Site 5: $-20.441, 57.70455$; Site 6: $-20.4211, 57.74607$.

for a single swimmer. While this likely resulted in an underestimate of fish numbers, our methodology was consistent across sites and thus sites can still be compared. The transect line was used to measure the length of the transect, with human estimate used for width, as the width either side of the transect (5 m) was small enough to be estimated with reasonable accuracy and it was not possible to carry additional tape measures in order to measure width along the transect. Footage was later analysed for coral cover, and presence and number of corallivore species and *Stegastes* spp. It is likely that there was a tendency to underestimate *Stegastes* spp. numbers due to the propensity of these fish to hide among *Acropora* branches within their territories, although the camera was held at a 45° angle to maximise capture of fish in the benthos as well as those swimming ahead of the surveyor. However, given that *Stegastes* spp. almost exclusively inhabit *Acropora* colonies in the Mauritian lagoon (Tiddy et al., 2021), this underestimation was likely fairly uniform across sites. Additional corallivore species not recorded on transects were photographed or noted on an underwater slate, and the species seen on and off transects were then combined to give total species diversity from each site visit.

Coral cover was estimated from transect footage by pausing the video every three metres of tape, for ten points either side of the transect (method adapted from Kenyon et al., 2006; reviewed in Jokiel et al., 2015), and visually estimating (Wilson et al., 2007) the most prevalent form of benthic cover present in the frame. The results of this were used to calculate the prevalence of each form of benthic cover (branching *Acropora*, massive *Porites* spp., other coral species, non-filamentous algae, sand, or coral rubble) to the nearest 5%. Dead coral that still retained its structure was counted as coral. Where filamentous algae covered part or all of *Acropora* branches i.e., within *Stegastes* spp. territories, this was recorded as branching *Acropora* cover as long as the branching structure was clearly present.

2.4. Data analysis

All statistical analyses were carried out in R (version 4.0.3) (RStudio Team, 2022). Graphs were plotted in the ggplot package (Wickham, 2016). Prior to data analysis, data was checked for outliers by calculating z-scores, with values having a z-score greater than ± 3 being excluded. This resulted in two of 609 (final $n = 607$) data points being excluded from the predation dataset, and seven of 218 data points (final $n = 211$) being excluded from the corallivore assemblage dataset. Two models were constructed to examine correlation of corallivore assemblage and *Stegastes* spp. presence with degree of predation on *P. lutea*. Linear mixed models (LMMs) with Gaussian (normal) distributions were constructed in the lme4 package (Bates et al., 2015). Model assumptions of linearity and normality and homoscedasticity of residuals were verified by visual inspection of residual-fit plots and histograms of model residuals. Bite density and surface area damaged data were cube root transformed, as the untransformed data did not meet distribution assumptions, however this was corrected by transformation. In these models, the explanatory variables were "parrotfish density", "butterflyfish density", "other corallivore density", "corallivore species richness", "*Stegastes* species", "*P. lutea* surface area (cm^2)", and the interaction terms "parrotfish density**Stegastes* species", "butterflyfish density**Stegastes* species", "other corallivore density**Stegastes* species", and "corallivore species richness**Stegastes* species". The term "*Stegastes* species" included a level for "*Stegastes* not present" i.e., corals outside *Stegastes* spp. territories. The response variables were "bite density" and "surface area damaged by bites" respectively. Damselfish density was not included due to very low numbers of damselfish bites recorded throughout the survey, though these bites were still included in models. "Month" and "Site" were included as random effect variables. It was assumed in these models that groups of corallivores would react similarly to *Stegastes* spp. presence, though only one species of parrotfish was observed on our transects, removing the issue of inter-species variation. In the case of butterflyfish and other corallivores, a PCA analysis carried

out on species-specific abundance data found no correlation with *Stegastes* spp. density or any other factor (see supplementary material). This indicates no detectable statistically significant differences between species in our study, though this may be due to low numbers of most individual corallivore species.

A further two models were constructed in order to identify factors correlated with corallivorous fish assemblage. These were generalized linear mixed models (GLMMs) plotted in the glmmTMB package (Brooks et al., 2017) using a Poisson distribution, as this produced a better residual distribution for our count data and also allows comparison of zero-inflated models with non-zero-inflated models. In the case of corallivore density, a zero-inflated Poisson distribution was used due to the large number of zero counts in the data. In these models, the explanatory variables were initially "non-*Acropora* coral cover (%)" (referring to coral cover other than *Acropora* spp., including massive *Porites* spp.; this was used in place of total coral cover due to high collinearity between this and *Acropora* coral cover), "*Acropora* coral cover", "*Stegastes nigricans* density", "*S. punctatus* density", "corallivore diet" (facultative or obligate), and the interaction terms "*Acropora* coral cover**S. punctatus* density", "*Acropora* coral cover**S. nigricans* density", "corallivore diet**S. punctatus* density", "corallivore diet**S. nigricans* density", "corallivore diet**Acropora* coral cover", and "corallivore diet*non-*Acropora* coral cover". The response variables were "overall corallivore density" and "overall corallivore species richness". The random effect variables "Month" and "Site" were also included in all models.

Akaike's information criterion (AIC) was used to compare models with and without interaction variables to find the best fit model in each case, using the AICcmodavg package (Mazerolle, 2023). For Poisson distributions (GLMMs), zero-inflated models were also tested for fit against equivalent non-zero-inflated models using AIC. To determine how well the final models would predict outcomes, we calculated the coefficient of determination (r^2) for all final LMMs. This included both the level of variance explained by fixed and random variables together (r_m^2) and by fixed variables alone (r_f^2) (Nakagawa and Schielzeth, 2013). The level of variance explained by each explanatory variable, reported as partial r^2 (r_p^2), was calculated using the partR2 package (Stoffel et al., 2021). Final LMMs were also checked for normality of residual variance by examining Q-Q plots of residuals. Calculating R^2 for zero-inflated Poisson distributions (GLMMs) is not possible (Nakagawa and Schielzeth, 2013), however final models were tested for residual distribution, including overdispersion, using the DHARMA package (Hartig, 2022), and ΔAIC produced by including each interaction variable (comparative to the best fit model) is reported to give an indication of the variance explained by each interaction.

3. Results

3.1. Fish and coral surveys

Of the six *Stegastes* spp. present in Mauritian waters (FishBase, 2022), three were observed on transect surveys: *S. nigricans*, *S. punctatus*, and *S. limbatus* Cuvier 1830 (McClanahan et al., 2021). *S. nigricans* and *S. punctatus* were by far the most common, with a total of only 37 individuals of *S. limbatus* observed at sites 1, 3, and 6 on transects. By comparison, 2991 individuals of *S. nigricans* and 1473 individuals of *S. punctatus* were observed in total across all sites, except at site 5 (Fig. 1) where only *S. punctatus* was observed. A total of 1085 individual corallivores belonging to 20 species were observed on transects, with an additional five species observed off transects during site visits (Table 1). The most common species observed on transects was the facultatively corallivorous bullethead parrotfish *Chlorurus sordidus*, followed by the Moorish idol *Zanclus cornutus* Linnaeus 1758, also a facultative corallivore, and the melon butterflyfish *Chaetodon trifasciatus* Park 1791, an obligate corallivore.

The most prevalent branching coral at all survey sites was *Acropora muricata* Linnaeus 1758, which covered 11–74% (site visit average) of

Table 1

Numbers and site locations of corallivorous fish species (Cole et al., 2008; Rotjan and Lewis, 2008) observed on transects, in decreasing order of abundance. Families are shown in parentheses. An additional five species not recorded on transects were observed at sites; these were *Forcipiger flavissimus* (Chaetodontidae; butterflyfish; occasional) at site 1, *Chaetodon guttatissimus* (Chaetodontidae; butterflyfish; obligate) and *Scarus ghobban* (Scaridae; parrotfish; facultative) at site 2, *C. kleinii* (Chaetodontidae; butterflyfish; facultative) at site 3, and *C. interruptus* (Chaetodontidae; butterflyfish; facultative) at site 4.

Species	Corallivore type	Diet	Site(s) recorded	Total abundance on transects (individuals)
<i>Chlorurus sordidus</i> (Scaridae)	Parrotfish	Facultative	All	920
<i>Zanclus cornutus</i> (Zanclidae)	Other	Facultative	All	49
<i>Chaetodon trifasciatus</i> (Chaetodontidae)	Butterflyfish	Obligate	2, 3, 5, 6	30
<i>Gomphosus caeruleus</i> (Labridae)	Other	Facultative	1, 2, 4, 5, 6	20
<i>Chaetodon trifascialis</i> (Chaetodontidae)	Butterflyfish	Obligate	2, 4, 5	12
<i>Chaetodon auriga</i> (Chaetodontidae)	Butterflyfish	Facultative	1, 4, 5	10
<i>Chaetodon melannotus</i> (Chaetodontidae)	Butterflyfish	Obligate	1, 3, 6	8
<i>Chaetodon lunula</i> (Chaetodontidae)	Butterflyfish	Facultative	1, 2, 3, 5, 6	6
<i>Chaetodon vagabundus</i> (Chaetodontidae)	Butterflyfish	Facultative	1, 2, 4, 5	6
<i>Thalassoma lunare</i> (Labridae)	Other	Facultative	2, 3	5
<i>Plectroglyphidodon dickii</i> (Pomacentridae)	Other	Facultative	3	4
<i>Chaetodon zanzibarensis</i> (Chaetodontidae)	Butterflyfish	Obligate	1, 4	3
<i>Oxymonacanthus longirostris</i> (Monacanthidae)	Other	Obligate	6	3
<i>Arothron nigropunctatus</i> (Tetraodontidae)	Other	Facultative	2, 5	2
<i>Canthigaster valentini</i> (Tetraodontidae)	Other	Facultative	3, 5	2
<i>Chaetodon citrinellus</i> (Chaetodontidae)	Butterflyfish	Facultative	6	1
<i>Chaetodon xanthecephalus</i> (Chaetodontidae)	Butterflyfish	Facultative	5	1
<i>Exallias brevis</i> (Blenniidae)	Other	Facultative	2	1
<i>Ostracubicus</i> (Ostraciidae)	Other	Facultative	2	1
<i>Rhinecanthus aculeatus</i> (Balistidae)	Other	Facultative	1	1

the benthos on transects and made up the majority (by percentage cover) of total coral cover on 79 of 109 transects surveyed. Massive bleaching-resilient corals, the most prevalent being *Porites* spp., made up a relatively small percentage of coral cover (site visit average 0–10%) at survey sites.

3.2. Correlations between corallivore assemblage and predation rates

All interactions were retained in all models examining correlations between corallivore assemblage and predation rates, with the exceptions of the interaction terms of *Stegastes* spp. presence with corallivore

species richness and with butterflyfish density. These were removed from both models due to high collinearity with the species richness term and the *S. punctatus* presence term respectively, leading to equation estimates that were at odds with plotted data (“suppressor effect”, Falk and Miller, 1992).

Predation on *P. lutea* was significantly positively correlated with corallivorous parrotfish density (bite density $p < 0.001$, $t = 3.535$, $r_p^2 < 0.0001$; surface damaged $p < 0.001$, $t = 3.587$, $r_p^2 < 0.0001$) and with butterflyfish density in the case of surface damaged ($p = 0.028$, $t = 2.209$, $r_p^2 = 0.005$), but was not associated with other corallivorous fish density (supplementary table 2; Fig. 2). Corallivore species richness was not correlated with either measure of predation (supplementary table 2).

3.3. Correlations between *Stegastes* spp. presence and predation rates

The presence of *S. nigricans* was associated with a 62% reduction in bite density ($\bar{x} = 0.296$ bites cm^{-2} , 95% CI = 0.243–0.349 bites cm^{-2} , $p < 0.001$, $t = -4.024$, $r_p^2 = 0.005$) (Fig. 2) and a 64% reduction in surface area damaged ($\bar{x} = 14.8\%$, 95% CI = 12.0–17.6%, $p < 0.001$, $r_p^2 = 0.008$, $t = -4.39$, Hedge’s $g = 1.23$) (Fig. 2) on *P. lutea* within compared to outside territories (bite density $\bar{x} = 0.784$ bites cm^{-2} , 95% CI = 0.725–0.842 bites cm^{-2} ; surface damaged $\bar{x} = 41.5\%$, 95% CI = 38.7–44.2%) (supplementary table 2), as described in Tiddy et al. (2021). Both bite density ($\bar{x} = 0.214$ bites cm^{-2} , 95% CI = 0.171–0.258 bites cm^{-1}) and surface area damaged ($\bar{x} = 11.3\%$, 95% CI = 8.77–13.8%) were 73% lower within *S. punctatus* territories. Though this was not statistically significant in the model (supplementary table 2), the interaction terms between *S. punctatus* presence and density of parrotfish and other corallivores were negatively correlated with both bite density (parrotfish $p < 0.001$, $t = -3.455$, $r_p^2 = 0.042$; other $p < 0.001$, $t = -4.676$, $r_p^2 = 0.013$) and surface area damaged (parrotfish $p < 0.001$, $t = -4.259$, $r_p^2 = 0.051$, other $p < 0.001$, $t = -4.801$, $r_p^2 = 0.015$), indicating reduced predation within territories and greater reductions at higher densities of corallivores (Fig. 2). The interactions between *S. nigricans* presence and corallivore density were not significantly correlated with either measure of predation (supplementary table 2; Fig. 2).

P. lutea colony surface area was significantly negatively correlated with all predation metrics (bite density $p < 0.001$, $t = -17.15$, $r_p^2 = 0.2161$; area damaged $p < 0.001$, $t = -16.03$, $r_p^2 = 0.1873$), indicating higher predation damage on smaller *P. lutea* colonies (supplementary table 2).

3.4. Correlations between *Stegastes* spp., *Acropora* cover, and corallivore assemblage

The interactions of corallivore diet with *S. punctatus* and *S. nigricans* presence were retained in both models ($\Delta\text{AIC} = 0$) (supplementary table 3). The interaction of diet with total non-Acroporid coral cover was retained in the species richness model ($\Delta\text{AIC} = 0$) (supplementary table 3), however both the interaction and the fixed effect of non-Acroporid coral cover had to be removed from the density model due to high collinearity with the random effect variable “Site”, leading to variable suppression (Falk and Miller, 1992). The interaction of corallivore diet with *Acropora* coral cover was only retained in the species richness model (species richness $\Delta\text{AIC} = 0$, density $\Delta\text{AIC} = 11.78$). The interactions between *Stegastes* spp. and total *Acropora* cover were both removed from the species richness model (*S. nigricans* $\Delta\text{AIC} = 2.23$, *S. punctatus* $\Delta\text{AIC} = 2.26$). Both of these interactions were in the best fit density model according to AIC ($\Delta\text{AIC} = 0$), but were removed due to high collinearity with the *Acropora* cover term, leading to variable suppression (Falk and Miller, 1992).

Significantly fewer obligate corallivores were observed in our study ($p < 0.001$, $z = -9.434$), with an overall lower species richness of obligate corallivores ($p < 0.001$, $z = -7.116$) (supplementary table 3). Total *Acropora* cover was not significantly correlated with corallivore

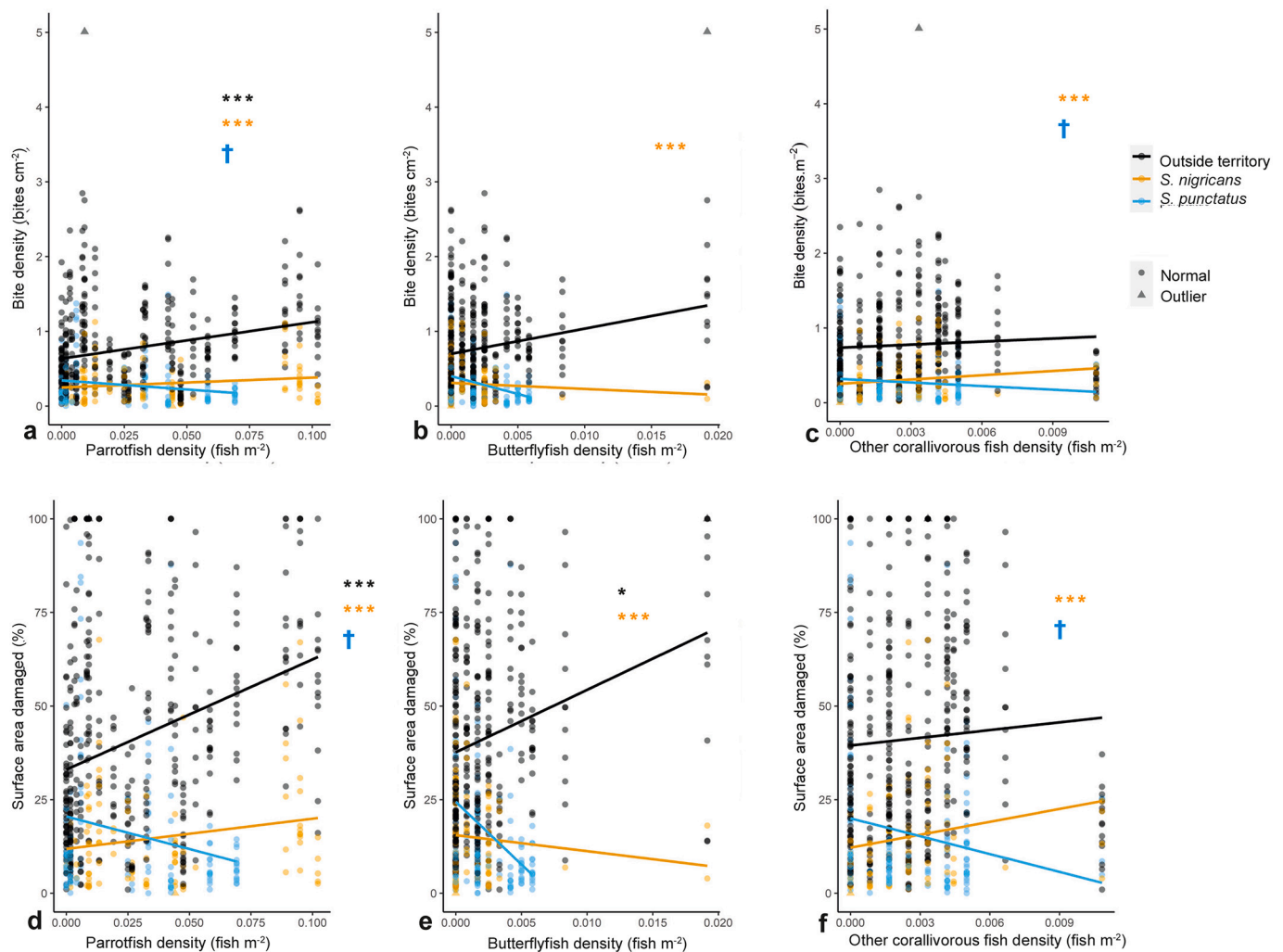


Fig. 2. Bite density on *Porites lutea* according to a) corallivorous parrotfish density, b) corallivorous butterflyfish density, c) other corallivorous fish density, and presence of *Stegastes* spp. Surface area damaged on *P. lutea* according to d) corallivorous parrotfish density, e) corallivorous butterflyfish density, f) other corallivorous fish density, and presence of *Stegastes* spp. * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Black stars indicate an effect of corallivore density, while blue or orange stars indicate a significant effect of *Stegastes* spp. and † indicates a significant interaction effect of corallivore density with *S. nigricans* (orange) or *S. punctatus* (blue). Outlier datapoints that were excluded from statistical analysis are shown as triangles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species richness, but was negatively correlated with corallivore density ($p = 0.005$, $z = -2.355$) (supplementary table 3; Fig. 3). While no overall effect of total non-Acroporid coral was found, the interaction between non-Acroporid coral cover and corallivore diet was positively correlated with corallivore species richness ($p = 0.009$, $z = 2.618$, Fig. 3), indicating greater species richness of obligate corallivores where more non-Acroporid coral was present. Neither *Stegastes* spp. was correlated with corallivore species richness, or with overall corallivore density (supplementary table 3). In contrast, both interaction terms between *Stegastes* spp. density and corallivore diet were significantly positively correlated with corallivore density (*S. punctatus* $p < 0.001$, $z = 5.758$, Fig. 4; *S. nigricans* $p < 0.001$, $z = 4.065$, Fig. 4), indicating that greater densities of obligate corallivores were found where *Stegastes* densities were higher (supplementary table 3). A conceptual diagram illustrating our results may be found in Fig. 5.

4. Discussion

Our results show that the presence of territorial *Stegastes* spp. was correlated with reduced predation on bleaching-resilient *P. lutea* corals, even in areas subject to increased predation damage associated with

high numbers of corallivorous fish. In addition, while *Acropora* cover was associated with a reduction in the density of corallivorous fishes, abundance of both *Stegastes* spp. was correlated with an increase in the density of obligate corallivorous fishes. The overall effects of *Stegastes* spp. on reef ecosystems, particularly vulnerable systems, has been the cause of some debate with regards to their various ecological functions. Several studies have found significant negative effects of *Stegastes* spp. on scleractinian corals due to their algal farming behaviour, which can increase algal overgrowth on corals and therefore coral mortality rates, including of outplanted corals (Chasqui-Velasco et al., 2007; Ceccarelli et al., 2011; Casey et al., 2015; Schopmeyer and Lirman, 2015; Seraphim et al., 2020). In contrast, the positive effects of *Stegastes* spp. on coral survival and wellbeing, including of juvenile and outplanted corals, through reduction of predation and incidental erosion have also been highlighted in a number of studies (Suefuji and van Woesik, 2001; Gochfeld, 2010; White and O'Donnell, 2010; Tiddy et al., 2021). While other studies have recorded corallivore density and/or species richness in relation to *Stegastes* spp. (Gochfeld, 2010; White and O'Donnell, 2010), the present study provides the first statistical evidence of lower predation rates within *Stegastes* spp. territories regardless of corallivore densities. Our results also indicate that *Stegastes* spp. presence is

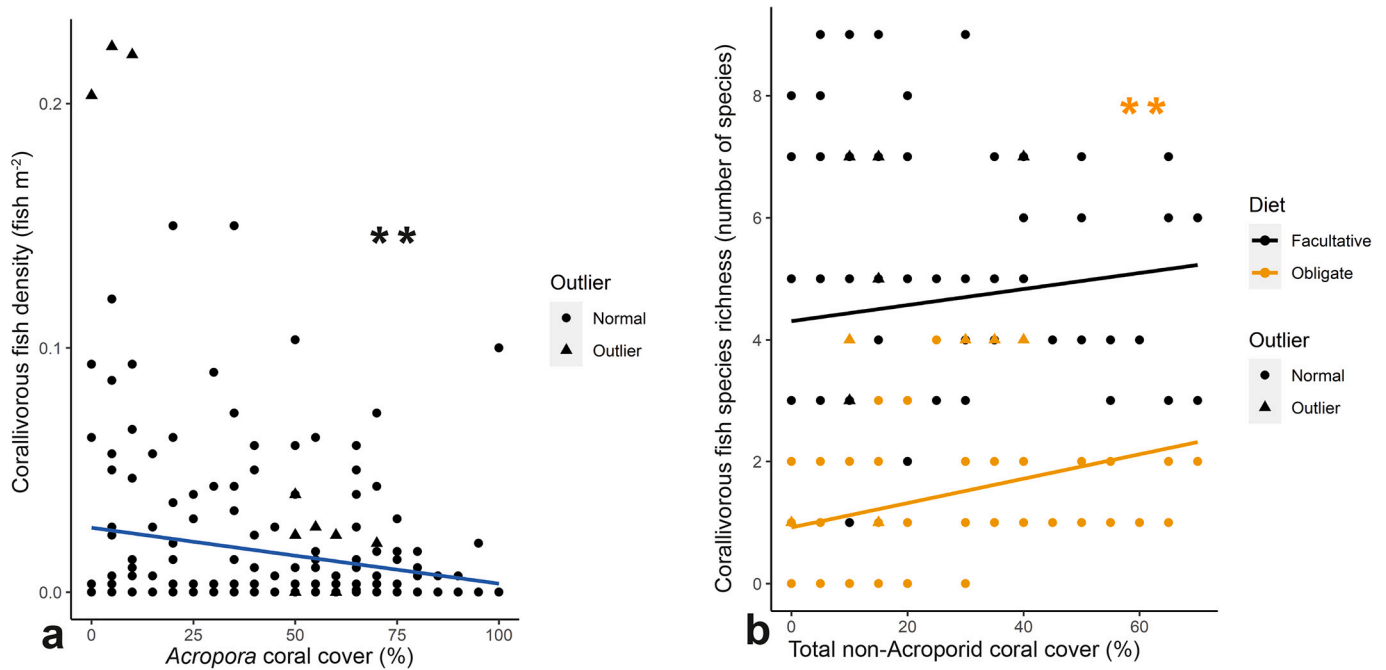


Fig. 3. a. Negative correlation between branching *Acropora* coral cover and corallivorous fish density, and b. Positive correlation between total non-*Acroporid* coral cover and obligate corallivorous fish species richness. Black stars indicate a significant correlation between the explanatory and response variables. Orange stars indicate a significant effect of diet (obligate versus facultative). * indicates a significant effect at $p < 0.05$, while ** indicates $p < 0.01$, and *** indicates $p < 0.001$. Outlier datapoints that were excluded from the dataset are shown as triangles.

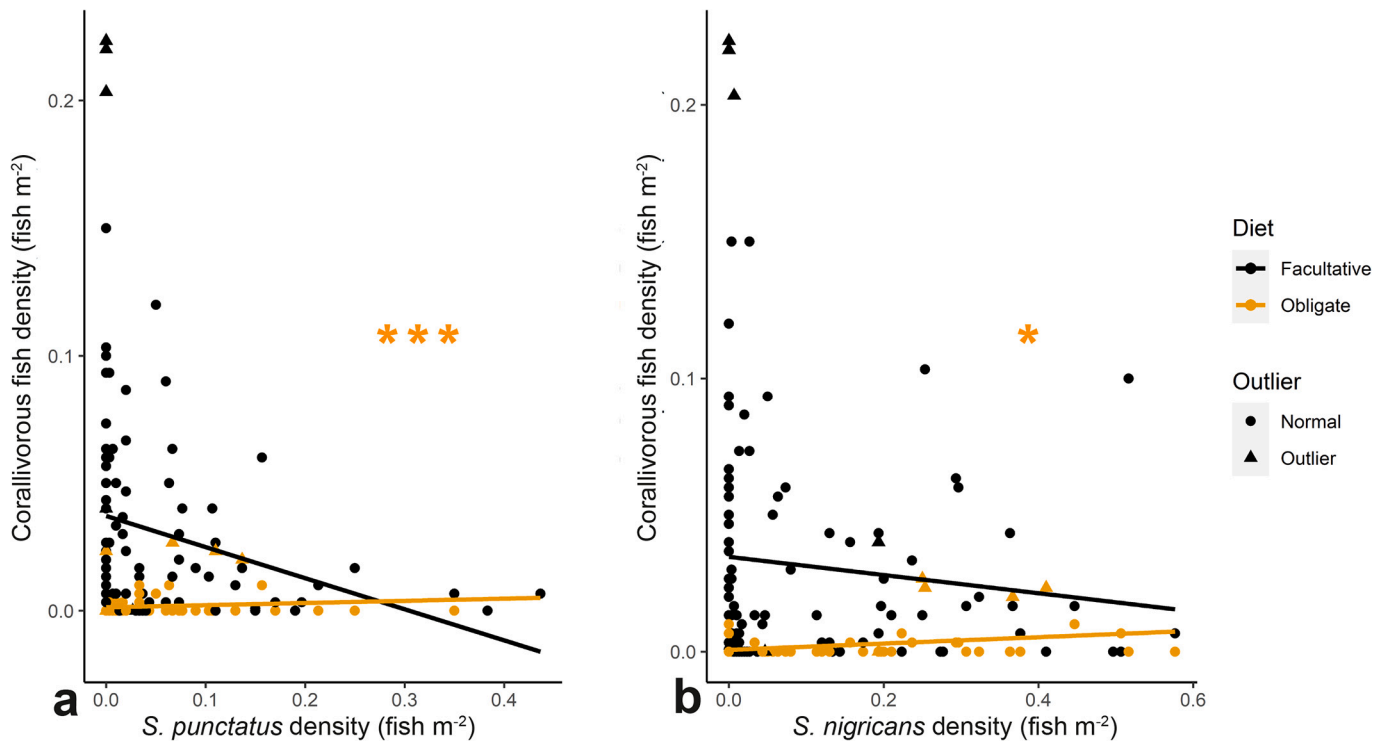


Fig. 4. a, Positive correlation between *Stegastes punctatus* density and obligate corallivorous fish density, and b. Positive correlation between *S. nigricans* density and obligate corallivorous fish density. Orange stars indicate a significant effect of diet (obligate versus facultative). * indicates a significant effect at $p < 0.05$, while ** indicates $p < 0.01$, and *** indicates $p < 0.001$. Outlier datapoints that were excluded from the dataset are shown as triangles.

correlated with increased density of obligate corallivorous fish species. While this may lead to an increase in biomass of these species in areas tending towards a loss of fish biomass and species richness (Appadoo et al., 2022), such an increase may also be associated with increased

coral predation rates outside territories.

Increasing corallivore density, as well as incidence of large ‘excavator’ corallivores such as triggerfish and some parrotfish species, has been previously associated with increases in predation damage upon

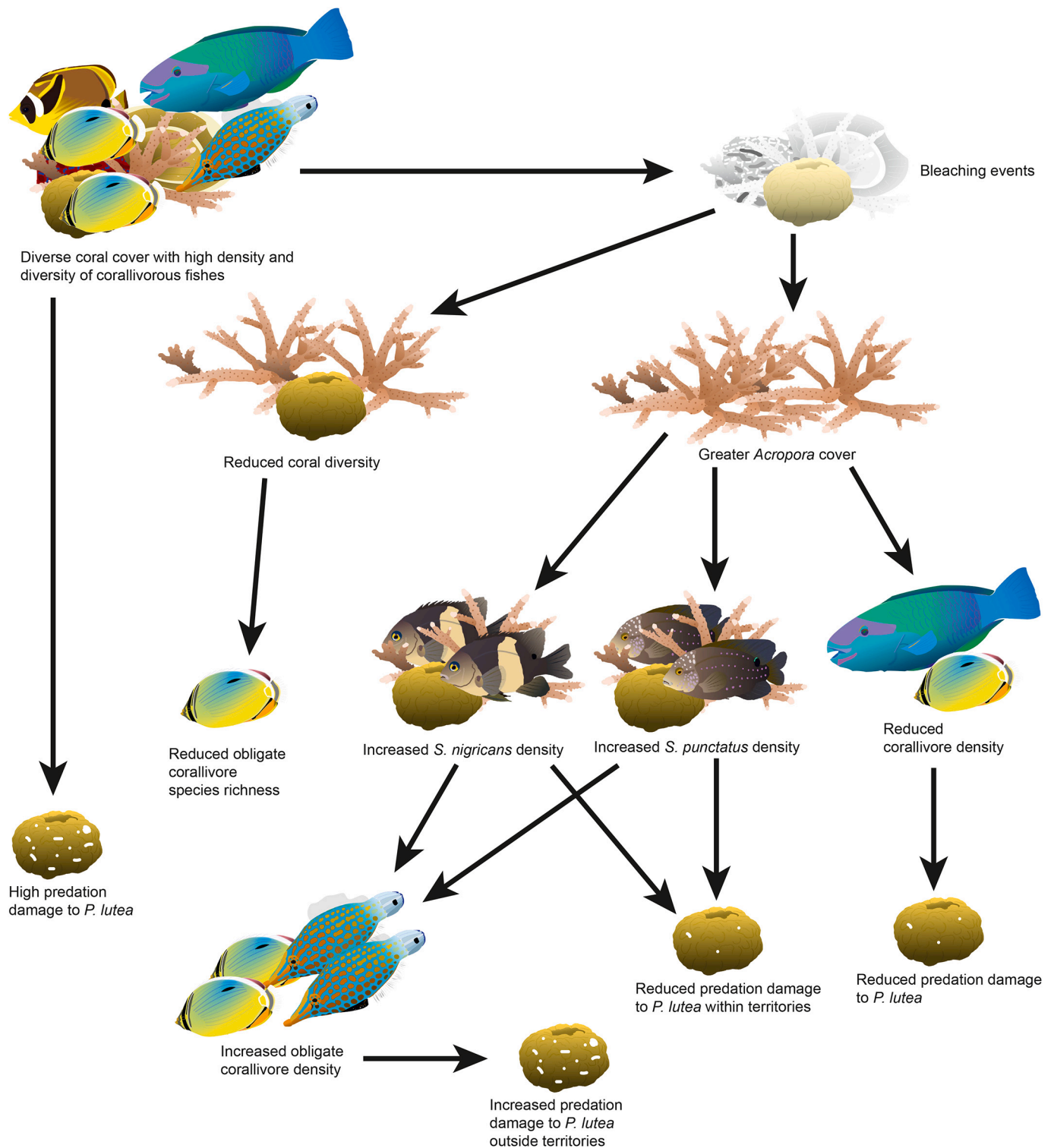


Fig. 5. Conceptual diagram showing relationships among *Acropora* monocultures, *Stegastes* spp. densities, corallivorous fish density and species richness, and predation on massive *Porites lutea* indicated by our results. Vector drawings based on photos by I. Tiddy, Francois Libert, Save our Seas Foundation, Project Noah, Phillip Colla, and Fishes of Australia.

corals (Cole et al., 2008; Rotjan and Lewis, 2008; Rice et al., 2019). Our results provide further evidence of this, particularly in the case of parrotfish and butterflyfish, which we found to be associated with an increase in predation on *P. lutea*. Parrotfish including *Chlorurus* species such as *Chl. sordidus*, the most common corallivore observed in our surveys, may preferentially predate massive corals (Bonaldo and Bellwood, 2011), meaning that this increase likely does not indicate a shift

in diet from other coral species following bleaching events but rather selective corallivory of *P. lutea* by increasing numbers of corallivores. However, butterflyfish species including some observed in our surveys, such as *C. trifascialis*, have been found to actively avoid predated *Porites* spp. (Berumen and Pratchett, 2008), indicating that predation on these may be the result of lack of access to preferred food sources. While corals within territories appear to experience reduced predation, both

preferential and opportunistic predation have the potential to be highly detrimental to *P. lutea* outside *Stegastes* spp. territories, particularly as excavator species such as *Chl. sordidus* can cause significant damage to coral skeletons (Bonaldo and Bellwood, 2011; Rotjan and Lewis, 2008). Our results showed no effect of the density of “other” corallivores on predation, though large numbers of “other” bites were identified. This may be because our methods of transect surveying likely led to an overall underestimation of fish numbers, particularly of fast-moving species such as wrasse, due to disturbance caused by laying the transect line (Emslie et al., 2018). We also found no correlation of predation with corallivore species richness. This may be because the presence or absence of a small number of a few rare species such as the speckled butterflyfish *Chaetodon citrinellus* had a large influence on our species richness metrics, however low numbers of these species may not have had a significant impact on predation rates.

The presence of *Stegastes* spp. has been found to reduce predation pressure on corals of various genera (Gochfeld, 2010; White and O'Donnell, 2010), including massive *Porites* corals, within territories (Tiddy et al., 2021). It has not previously been shown, however, that predation upon bleaching-resilient *P. lutea* within *Stegastes* spp. territories continues to be reduced in areas where predation pressure outside territories is relatively high. The lower rates of overall predation within territories observed in the present study indicate that the ability of *Stegastes* spp. to defend their territories against predation persists where high numbers of corallivores are present. Interestingly, while the presence of *S. punctatus* was correlated with reduced predation relative to the density of both parrotfish and other corallivores, this was not the case for *S. nigricans*, though overall bite density within territories was still lower. This may indicate reduced defensiveness by *S. nigricans* against smaller or facultative corallivores such as juvenile parrotfish and some pufferfish species, which may be perceived as less of a threat when they invade territories (Johnson et al., 2011). In the case of *S. punctatus*, the reduction in predation at high corallivore densities may indicate an increase in aggression by *S. punctatus* towards corallivores at higher densities of the latter. It has been found that species such as corallivores and egg stealers, towards which *Stegastes* spp. show high aggression, tend to be more common near *Stegastes* spp. territories (Johnson et al., 2011), possibly due to attraction of these fish to territories. This attraction may lead to greater aggression towards these species, if they are perceived by *Stegastes* spp. as common threats (Cleveland, 1999). It is also possible that body size of *Stegastes* spp. plays a role, as *S. punctatus* tend to be larger than *S. nigricans* within the Mauritian lagoon (Tiddy et al. pers. obs.). Body size of *Stegastes* spp. may both affect the ability of *Stegastes* spp. to successfully defend their territories, and the degree to which the foraging behaviour of corallivores is altered due to the degree of perceived threat from a fish larger or smaller than themselves. Larger fish may also be more aggressive in defending territories, possibly due to greater aggression being required to secure high-quality territories which tend to be held by larger fish (Cleveland, 1999). Our study did not quantify body size of individual fish, but this may be beneficial for future studies to examine. Predation was also found to be negatively correlated with *P. lutea* size as found in Tiddy et al. (2021). This may be due to our predation metrics, as fewer bites are required to damage a larger proportion of the coral on smaller corals (Tiddy et al., 2021).

While *Stegastes* spp. may prevent corallivore access to territories, territories also contain resources, and presence of *Stegastes* spp. and their *Acropora* habitats may themselves impact corallivore assemblage composition. Branching corals such as *Acropora* spp. provide structural refugia as well as the preferred food source of many corallivores (Pratchett et al., 2004; Pratchett, 2005; Johnson et al., 2011; Darling et al., 2017), however the lack of coral diversity in *Acropora*-dense areas within the Mauritian lagoon may lead to fewer corallivores in these areas. We found greater species richness of obligate corallivores in areas with greater non-*Acroporidae* coral cover, as well as lower overall corallivore density in areas with high *Acropora* cover. This indicates that the *Acropora* monocultures found in much of the Mauritian lagoon may not

provide sufficiently diverse coral cover to meet the dietary requirements of some corallivores. In an environment subject to regular bleaching and storm events (Bhagooli and Kaullysing, 2019), fast-growing and adaptable *Acropora* species (Louis et al., 2020) may outcompete other susceptible corals following disturbances, leading to a lack of benthic and possibly fish diversity (McClanahan and Muthiga, 2020). This may also explain why we found fewer obligate compared with facultative corallivorous fishes, as obligate corallivores may be more affected by limited coral diversity while facultative corallivores can take advantage of other food sources. A review by Pratchett et al. (2008) found that obligate corallivore populations decline quickly after coral loss, however herbivore and generalist populations may persist for longer.

Our results regarding corallivore density around *Stegastes* spp. territories are in line with previous work which found that *Stegastes* spp. may increase density of other fish species, including corallivores, possibly due to increased resource availability within territories (Johnson et al., 2011). We found significant positive correlations between *Stegastes* spp. density and obligate corallivore density. *Stegastes* spp. territories may be host to various coral species (Gochfeld, 2010), which in areas of low coral diversity may represent rare resources that attract obligate corallivorous fish. As we found greater predation rates on corals outside territories in areas with more corallivores, such an increase in corallivore density may equate to a significant increase in predation risk to corals outside territories, if corals within territories are difficult to access. Therefore, while the presence of *Stegastes* spp. may play a role in increasing corallivorous fish density in areas otherwise experiencing a loss of fish abundance (Appadoo et al., 2022), this may increase the disparity between predation rates within and outside territories, and reduce survivorship of corals subject to greater predation as a result (Rotjan and Lewis, 2006, 2008). These connections are speculative, however, and empirical study, such as removing *Stegastes* spp. from *Acropora* patches (White and O'Donnell, 2010) and evaluating corallivore food preference within the Mauritian lagoon at sites with high coral diversity would be needed to clarify the relationship between *Acropora* cover, *Stegastes* spp., corallivore assemblages, and coral predation. We found no increase in species richness associated with *Stegastes* spp. presence, indicating that the increase in corallivore density was driven by greater numbers of more common species.

Our study is limited by the level of noise in our dataset (e.g., Fig. 2), which leaves potential for outliers to play a role in driving trends. While datasets were examined for outliers, and these were removed if their inclusion affected our results, we cannot rule out the possibility of some trends being driven by our large sample size as opposed to strong biological effects. It is also likely that other environmental factors affect fish assemblage and interactions with benthic diversity in this complex system, contributing to the large amount of variation observed in our data. Nevertheless, our results show that *Stegastes* spp. may have an effect on corallivore density within our study system. It would be beneficial, however, for further studies in other systems to examine the effects of *Stegastes* spp. presence and density on corallivore assemblage.

To summarise, our findings add a novel element to the ongoing discussion on the effects of *Stegastes* spp. on degraded and recovering reef ecosystems. While multiple studies have investigated the positive and negative effects of *Stegastes* spp. on corals within territories (Gochfeld, 2010; Schopmeyer and Lirman, 2015; Seraphim et al., 2020; Suefuji and van Woesik, 2001; Tiddy et al., 2021; White and O'Donnell, 2010), the present study is unique in investigating the ability of *Stegastes* spp. to defend against increasing numbers of corallivores. In line with previous findings (Cole et al., 2008; Rotjan and Lewis, 2008; Rice et al., 2019), we found that increasing corallivore density is associated with increased incidence of predation on bleaching-resilient massive *P. lutea*, likely as a result of selective corallivory by parrotfish (Bonaldo and Bellwood, 2011) and opportunistic corallivory by butterflyfish (Berumen and Pratchett, 2008). Within territories, however, we found that predation remained low, indicating that *Stegastes* spp. may be able to defend against relatively high numbers of corallivores. We also found

Stegastes spp. density to be correlated with increased density of obligate corallivore species, belying the trend shown for their *Acropora* coral habitats. While possibly due to attraction to resources within territories, this association may also result in increased predation on corals outside territories, and we recommend empirical study to investigate this. The results of the present study contribute to our understanding of the complex relationships between territorial *Stegastes* spp. and their environments, which may be key to understanding the dynamics of stressors affecting corals in systems such as the Mauritian lagoon where *Stegastes* spp. are common. As anthropogenic stressors become near-ubiquitous in coral reef systems, understanding these interactions may form the basis for future research into effective conservation and restoration.

CRedit authorship contribution statement

I.C. Tiddy: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Visualization, Writing – original draft, Writing – review & editing. **D. Kaullysing:** Methodology, Investigation, Resources, Writing – review & editing. **D.M. Bailey:** Methodology, Formal analysis, Writing – review & editing, Supervision. **S.S. Killen:** Formal analysis, Visualization, Writing – review & editing. **A. Le Vin:** Methodology, Writing – review & editing, Supervision. **R. Bhagooli:** Conceptualization, Methodology, Investigation, Resources, Funding acquisition, Supervision, Project administration, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2023.151960>.

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