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REPORT

Outplanting of branching *Acropora* enhances recolonization of a fish species and protects massive corals from predation

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Abstract Damselfish of the genus *Stegastes* inhabit territories and cultivate algal gardens on branching corals of the genus *Acropora*, aggressively protecting their territories from other fish and preventing predation upon corals within the territory. This behaviour has important ecological impacts and could also be useful in reducing predation on outplanted corals during reef restoration efforts. However, the degree of protection from predators may depend on the ability of *Stegastes* spp. to recolonise outplanted or newly established coral colonies. Protection of bleaching-resilient massive corals within territories may be of particular importance due to the role of these corals in maintaining coral cover following bleaching events. This study examined whether the presence of *Stegastes* spp. reduces predation on the massive bleaching-resilient coral *Porites lutea* in the Mauritian lagoon, and whether *Stegastes* spp. readily colonise outplanted branching coral fragments and provide adjacent massive corals with indirect protection from predation. Predation levels on wild-occurring and outplanted *P. lutea* within and outside *Stegastes* spp. territories were measured. In addition, *Acropora muricata* branches were outplanted adjacent to wild *P. lutea* colonies outside *Stegastes* spp. territories, and recolonisation of these outplants by *Stegastes* spp. and the impacts of recolonisation on predation were monitored. Both wild and outplanted *P. lutea* colonies within *Stegastes* spp. territories sustained less predation damage compared to colonies outside territories. *Stegastes* spp. recolonized outplanted *A. muricata* colonies within six months of outplanting, and in doing so returned predation protection to adjacent *P. lutea* colonies. The ability of *Stegastes* spp. to colonise outplanted corals and provide indirect protection to adjacent massive bleaching-resilient corals may inform coral outplanting efforts in systems where *Stegastes* spp. are common. Encouraging *Stegastes* spp. recolonisation may help to reduce predation damage to corals within territories and potentially improve the success of rehabilitation efforts.

Keywords *Stegastes* · *Acropora* · *Porites* · Corallivory · Coral outplanting · Rehabilitation

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Introduction

Coral reef ecosystems are threatened by numerous anthropogenic impacts including ocean temperature increases, pollution, and overfishing. Various conservation and management approaches have been utilised to combat this, including the use of coral outplanting to restore degraded sites. In particular, the reintroduction of

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branching corals such as *Acropora* species has been utilised to increase habitat complexity and fish biodiversity through restoration of structural refugia (Lirman et al. 2010; Xin et al. 2016; Nithyanandan et al. 2018). Work has previously focussed on the effectiveness of coral restoration techniques and interspecific success rates in order to improve restoration success (Cabaitan et al. 2015). However, limited work has been done to analyse the contribution of other reef species to success in restoration efforts. Among the reef organisms that may affect the success of restoration are damselfish of the genus *Stegastes* (Gochfeld 2010; Johnson et al. 2011). *Stegastes* spp. form territories of $\sim$ 1–8 m^2 (Hata and Kato 2004; Osorio et al. 2006; Dromard et al. 2018; Blanchette et al. 2019) on and between *Acropora* colonies, upon which they cultivate gardens of filamentous algae, which form part of their omnivorous diet (Ceccarelli et al. 2011). *Stegastes* spp. territories and their associated algal gardens may cover up to 100% of the benthos on and around branching *Acropora* colonies (White and O'Donnell 2010; Johnson et al. 2011; Quadros et al. 2019), and they may significantly alter the algal species present in their territory, reducing growth of larger macroalgae by selectively removing indigestible species (Hata and Kato 2002, 2003, 2006; Ceccarelli et al. 2011). *Stegastes* spp. are highly territorial and will aggressively defend their territories against conspecifics and other fish species to prevent grazing of algae within territories (Johnson et al. 2011). Although territory size and degree of defence may vary among *Stegastes* species (Hata and Kato 2004), territorial defence is often limited to *Acropora* colonies and their underlying benthos (Jan et al. 2003). The territorial defence provided by *Stegastes* spp. may also indirectly protect organisms including corals within territories and increase coral biodiversity through the exclusion of coral predators (Rotjan and Lewis 2008; Gochfeld 2010; White and O'Donnell 2010). Predation by corallivorous fishes even at low levels is a significant stressor on coral colonies, resulting in tissue loss and potentially reduced coral growth, reproductive output, and survivorship of predated colonies at various developmental stages (Rotjan and Lewis 2008; Gochfeld 2010; Bonaldo and Bellwood 2011; Rice et al. 2019). While the presence of *Stegastes* spp. could have significant benefits to corals through predation reduction, *Stegastes* spp. may also negatively impact corals by encouraging algal growth in territories (Schopmeyer and Lirman 2015; Seraphim et al. 2020). Algae may compete with and overgrow corals, thus reducing coral growth and survivorship (Schopmeyer and Lirman, 2015), particularly with newly established and juvenile colonies (Casey et al. 2015). The effects of *Stegastes* spp. presence on hard coral cover are therefore complex (Emslie et al. 2012) but may be key to understanding the role of this widespread fish genus in coral conservation.

The preference of *Stegastes* spp. for *Acropora* means that loss of live *Acropora* and their associated branching structure due to bleaching or storm events may significantly reduce the habitat available to *Stegastes* and other fish species, though some *Stegastes* spp. have been observed to colonise other benthic habitats in times of stress (White and O'Donnell 2010), and may maintain their ecosystem functions such as predation protection in such habitats. The loss of corals due to environmental stressors may also impact corallivore populations through loss of their preferred food sources. This may result in increased grazing pressure on remaining corals, particularly by obligate corallivorous species that are unable to feed on other items, though such suboptimal diets may lead to reduced fitness for specialist corallivores adapted to feed on bleaching-susceptible corals (Pratchett et al. 2004; Rice et al. 2019). The loss of *Acropora*, and thus *Stegastes* spp., in coral reef habitats may therefore result in negative consequences for bleaching-resilient corals, though these may benefit from reduced algal overgrowth (Schopmeyer and Lirman 2015). Currently, little work has been done to examine the effects of *Stegastes* spp. loss on predation on bleaching-resilient massive corals.

Restoration techniques such as coral outplanting have been employed in various degraded reef systems to restore damaged coral and fish assemblages, with varying success (Cabaitan et al. 2015; Nava and Figueroa-Camacho 2017). The overall effectiveness of outplanting is not yet clear, partly due to the small area over which studies have been conducted compared to the very large areas of reef degradation (Montoya-Maya et al. 2016). However, outplanting of branching corals such as *Acropora* spp. may increase structural complexity within degraded reef areas, potentially attracting fish assemblages including *Stegastes* spp. that may have left the area due to lack of structural refugia. If *Stegastes* spp. form colonies on outplanted *Acropora* spp. corals, this may restore predation protection to outplanted and adjacent corals within territories, potentially facilitating growth and survival of said corals (Suefuji and van Woesik 2001). *Stegastes* spp. may, however, aggressively bite both wild and outplanted corals within newly established territories to encourage algal growth and remove coral species that may compete with algal cultivation (Chasqui-Velasco et al. 2007; Seraphim et al. 2020). However, algal overgrowth may be reduced by herbivorous fish species attracted to outplanted corals (Frias-Torres et al. 2015), large shoals of which may overwhelm the defensive functions of *Stegastes* spp. (Johnson et al. 2011). While *Stegastes* spp. recolonisation may have mixed effects upon coral colonies, these species quickly recolonise outplanted corals (Schopmeyer and Lirman 2015;

Seraphim et al. 2020) and it is thus likely that any restoration effort may be significantly affected by *Stegastes* spp. in areas where these fish are prevalent. It is therefore key to coral restoration and conservation in many reef habitats that the effects of *Stegastes* spp. presence on restoration projects are investigated, specifically with regard to their effects on bleaching-resilient massive corals in restoration areas, which remain understudied (Seraphim et al. 2020).

While the impacts of *Stegastes* spp. presence upon predation on the coral genera *Pocillopora*, *Acropora*, and *Montipora* have been previously studied (Gochfeld 2010; White and O'Donnell 2010), no such evidence yet exists for indirect protection of massive bleaching-resilient *Porites* spp. corals. Bleaching-resilient species such as massive *Porites* spp. often survive bleaching events that can kill their more susceptible coral counterparts (McClanahan et al. 2007; Pratchett et al. 2013) and are thus left behind in degraded areas, often with few or no *Stegastes* spp. (White and O'Donnell 2010), leading to a potential increase in predation upon these corals. In addition, while there is evidence that *Stegastes* spp. will recolonise and return predation protection to outplanted *Acropora* species (Schopmeyer & Lirman 2015), the ability of *Stegastes* spp. to return indirect predation protection to massive bleaching-resilient corals adjacent to outplanting areas is not understood.

We investigated these issues by surveying predation occurring on corals in the lagoon of Mauritius, an area known to contain abundant *Stegastes* spp. and subject to anthropogenic and climate-related stressors, causing loss of coral cover and biodiversity (Bhagooli and Kaullysing 2019; McClanahan and Muthiga 2020). Specifically, we quantified the extent of predation received by wild-occurring and outplanted *Porites lutea* in the absence of *Stegastes* spp. or in the presence of either of the two most common *Stegastes* spp. in this region—*Stegastes punctatus* and *Stegastes nigricans*. We also quantified predation on wild-occurring *P. lutea* adjacent to outplanted *Acropora muricata*, some of which was recolonised by *S. nigricans*. The study investigated the following predictions: (1) the presence of *Stegastes* spp. will reduce predation upon massive *P. lutea* within *Stegastes* spp. territories; and (2) *Stegastes* spp. will recolonise degraded areas following *A. muricata* outplanting into these areas, and recolonisation will reduce predation upon adjacent *P. lutea* within territories.

Materials and methods

Study Sites

Six sites were selected for study around Mauritius island; these were three sites under no legal protection, one fishing reserve site in which harvesting is prohibited, and two marine park sites in which harvesting is limited and closely regulated (Fig. 1).

Survey of fish and coral assemblage

Transects were surveyed at each site every two months from September 2018 to June 2019 to record coral, *Stegastes*, and corallivorous fish assemblages at each site. Corallivorous invertebrates were not included in the study, as little invertebrate predation was observed on *P. lutea* during pilot surveys, with the vast majority of existing scars on *P. lutea* colonies originating from fish predation. Four transects were assessed per site visit, with consistency between months ensured through the use of markers on the shore. Each transect was 30 m long and fish were recorded 5 m either side of the transect line, for a total area of 300 m^2 per transect (Bonaldo and Bellwood 2011; Friedlander et al. 2014). A measuring tape was used to measure the length of the transects, and human estimate for the width. Immediately after laying the tape, a free diver swam the length of the transect twice, once on each side of the transect line to ensure full coverage, filming ahead of them with an underwater camera. Footage was viewed in its entirety, with videos ranging from 1 to 4 min in length according to current and weather conditions. From the footage, the presence and numbers of corallivorous fish and *Stegastes* species and the benthic coral coverage at each site were determined. Corallivorous fish and *Stegastes* species observed off transects were also photographed to record all species present at each site. Corallivorous fish were defined as all fish species present in Mauritian waters known to predate corals (Supplementary Table 1) (Cole et al. 2008; FishBase 2020). To reduce the likelihood of individual corallivores being counted more than once, an underwater slate was used to make a note if it was suspected that the same individual had been captured more than once on the footage. The note was shown in the video recording to allow notes to be synced with recordings during later analysis. Coral cover included both live coral and recently deceased coral that retained its three-dimensional structure and therefore would still provide potential habitat for fish species. Coral cover was estimated to the nearest 5%, with 5% used as the minimum value where any individuals of a coral type were present.

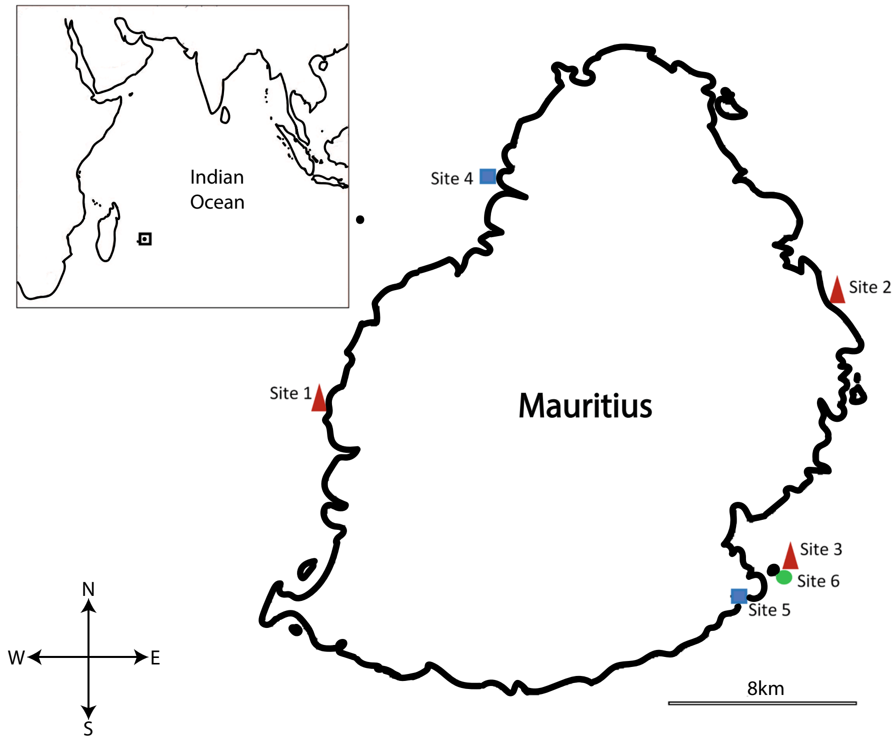

Fig. 1 Line map of Mauritius Island showing site locations and levels of legal protection. (1) Flic en Flac; (2) Belle Mare; (3) Blue Bay 1; (4) Balaclava; (5) Blue Bay 2; (6) Blue Bay 3. Red triangles indicate sites under no legal protection, blue squares indicate marine parks, and green circles indicate fishing reserves. Sites were selected for accessibility and presence of wild *Porites lutea* corals within and outside *Stegastes* spp. territories (figure adapted from Enchanted Learning, 2018 and d-maps, 2020)

Survey of predation on wild *P. lutea*

At each site, 11–15 *P. lutea* colonies within *Stegastes* spp. territories and 11–15 outside *Stegastes* spp. territories were surveyed every two months from September 2018 to June 2019 (Fig. 2). The surface area of surveyed colonies varied significantly (< 3 to > 9000 cm^2), due to low *P. lutea* abundance at some sites; colony surface area was thus included in statistical analysis. Colonies outside *Stegastes* spp. territories were defined as those occurring outside *A. muricata* aggregates and having no *Stegastes* spp. present within $\sim$ 0.5 m of the colony (Jan et al. 2003). Aggregates were defined as continuous expanses of *A. muricata*, potentially consisting of multiple colonies whose branches overlapped. *P. lutea* colonies within territories were defined as those within *A. muricata* aggregates with *Stegastes* spp. within $\sim$ 0.5 m of the colony (Jan et al. 2003). This was based on the observation that *Stegastes* spp. rarely ventured outside of *A. muricata* aggregates, with *Stegastes* observed to venture $\sim$ 0.3 m outside aggregates while chasing fish during pilot surveys. This value was increased to 0.5 m based on previous observations of the distance that *Stegastes* spp. will often venture outside their territories while chasing fish (Jan et al. 2003). In cases where fewer than 11 *P. lutea* colonies of either category were present, all available *P. lutea* were surveyed, and results were pooled across months. The minimum value of 11 was determined using a power analysis carried out on the pilot data from September, with up to four additional corals surveyed to increase power. *P. lutea* corals were not tagged, due to their shape making it difficult to reliably tag them. Instead, surveying areas were designated at each site, and corals were haphazardly selected within these areas each month. All observed corals fitting the criteria mentioned were surveyed up to a maximum of 15 colonies to reduce selection bias. Whether a coral colony was within the territory of *S. punctatus* or *S. nigricans* was recorded from photographs and transects. For each coral colony, all sides were photographed to show all bites, and to be able to measure coral colony surface area. Photography and analysis were carried out by the same person each time to ensure consistency. The app "SketchAndCalc (2019)" was used to measure coral area, with a tape measure included in each photograph for scale. Surface areas acquired were approximate due to the uneven nature of the *P. lutea* surface.

Microsoft photo editor was used to count bites, which were identified visually based on literature descriptions of their appearance. Bites were grouped into four categories: parrotfish, butterflyfish, damselfish, and other. Parrotfish bites appear as paired grooves, which can be single or up to five parallel grooves and may have a space in the middle where the jaws have closed, hence paired. All paired grooves were classed as parrotfish bites, as well as unpaired grooves if $\geq 2 \times$ as long as they were wide (Rotjan and Lewis 2008). Butterflyfish bites are not always visible, as some species remove only a single polyp. Where they are visible, they appear as small circular white marks with up

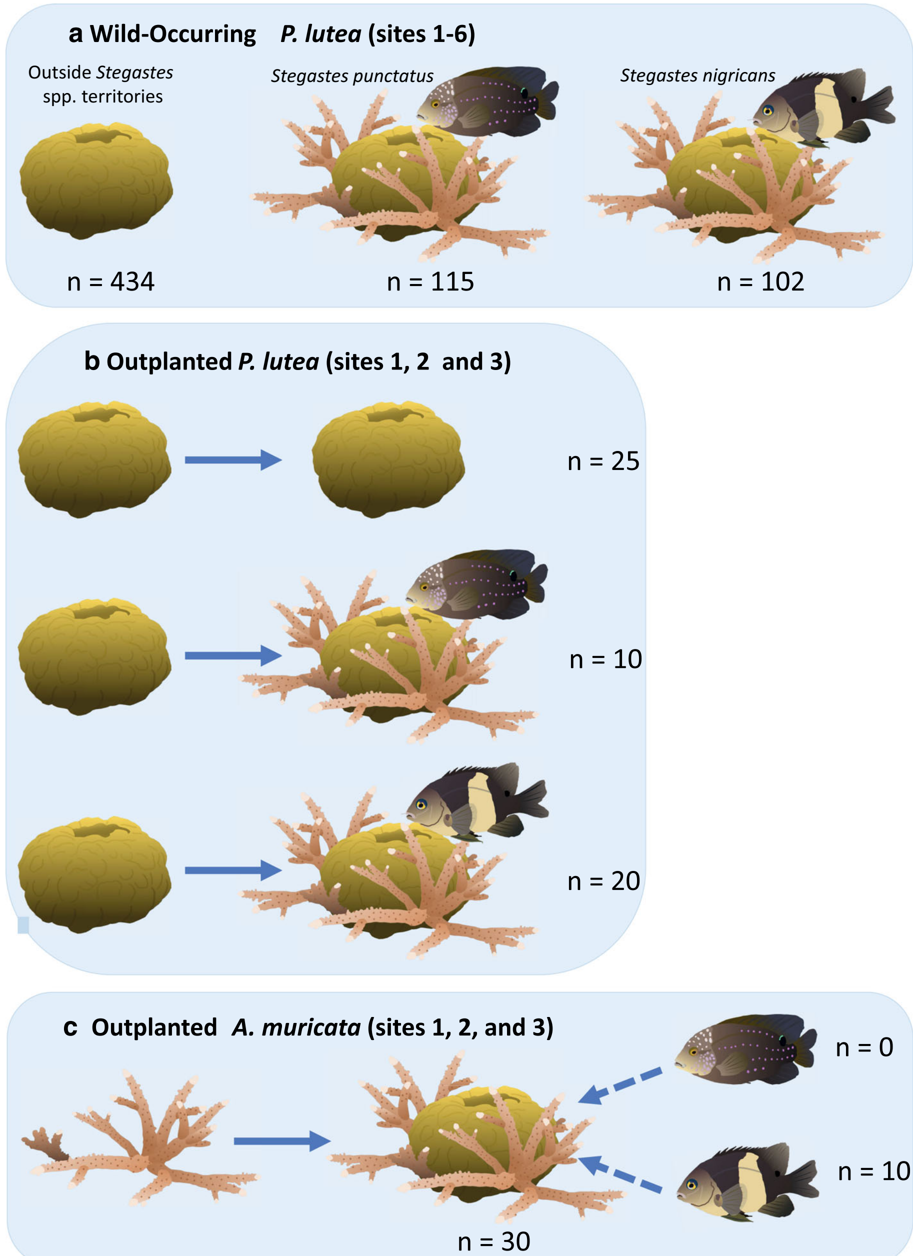

Fig. 2 Diagrams showing treatments carried out on *Porites lutea* corals. Treatment A represents wild-occurring *P. lutea*, treatment B represents outplanted *P. lutea*, and treatment C represents *Acropora muricata* outplanted to wild *P. lutea*. Solid arrows indicate outplanting; dashed arrows indicate potential recolonisation. n refers to the number of *P. lutea* within the treatment, or the total number recolonised. A total of 28 outplanted *P. lutea* and 12 *P. lutea* adjacent to outplanted *A. muricata* died or were lost during the study; data from these were included up to the point of coral death or loss. Vector drawings based on photos from I. Tiddy and Francois Libert

to 16 polyps removed, and an area of ≤ 1 cm^2. Damselfish bites form small circular marks with an undamaged centre (Rotjan and Lewis 2008). "Other" bites were defined as areas of damage that resembled bite marks in depth and extent of damage but did not fit the shape profile. This included single bites that were $< 2 \times$ as long as wide, and areas that may have been the result of parrotfish biting the same area several times (focussed biting) but where no individual grooves could be detected, meaning it could not definitively be said that parrotfish were responsible (Rotjan and Lewis 2008). These marks could have been made by trigger or pufferfish, but no literature on the shape of these bites on massive *Porites* spp. could be found. Average area of the different bite types was calculated from averages of $\sim$ 50 bite scars of each bite type on different *P. lutea* colonies, or from the maximum number of scars available if fewer than 50 were found throughout the survey. This was used to calculate percentage surface area damaged. This and bite density (bites cm^{-2}) were used as measures of corallivory upon *P. lutea*. It is likely that there was a tendency to underestimate the surface area of *P. lutea* due to its uneven nature. This meant that occasionally surface area damaged by bites would be calculated as covering a greater area than that of the coral itself. In these cases, the surface area damaged was recorded as 100%. Also included were other damaged areas that did not appear to result from fish corallivory, such as areas damaged by disease, borers, or other predators. These were included in the total area of the coral but marked out as additional damage not due to fish bites. Areas covered in sediment or algae were not included in the total area of the coral so as not to bias calculation of bitten areas, as these areas were not detectably bitten by corallivorous fishes.

Survey of predation on *P. lutea* outplanted within and outside *Stegastes* spp. territories

In addition to the surveys on haphazardly selected wild colonies, ten *P. lutea* colonies per site at each of the unprotected sites were outplanted from degraded areas with no *Stegastes* spp. into *Stegastes* spp. territories in December 2018 to January 2019 (Fig. 2). Colonies growing in sediment in isolated areas were outplanted directly to *A. muricata* aggregates and placed among the branches. Outplanted *P. lutea* were not fragmented but were picked up whole from the sediment to prevent damage to corals that could reduce the success of outplanting. Outplanted colonies were relatively small (surface area range 21–207 cm^2; average 80 cm^2) to allow colonies to be placed among *A. muricata* aggregates without damaging branching coral colonies. *P. lutea* colonies were not secured to minimise the amount of foreign material (e.g. plastic ties) introduced to the environment, but were placed between *A. muricata* branches to minimise displacement risk. Outplanting could not be carried out at protected sites due to licencing restraints. Outplanting was carried out into *A. muricata* aggregates found along transects, and *A. muricata* adjacent to outplants were tagged to identify the outplants in subsequent surveys. At sites two and three, corals were outplanted into *S. nigricans* territories, while at site one, corals were outplanted into *S. punctatus* territories. By way of a control, a further five to ten *P. lutea* from degraded areas were outplanted into degraded areas adjacent to other outplanted colonies (Fig. 2). These colonies were simply moved from degraded areas where they were found to those near to other outplanted colonies. Control colonies were also positioned along transect lines and tagged where allowed by their shape to allow re-identification. Corals were re-surveyed, and degree of predation measured in February–March, April, and June 2019. The photography and analysis methods used for outplanted *P. lutea* were the same as those described above for wild *P. lutea*. Data from wild and outplanted *P. lutea* were combined into a single dataset for analysis to increase statistical power and control for any effects of outplanting. Data from outplanted corals that died during the course of the study were collected up to the point of coral death. In addition, bites from a sub-sample of 28 corals randomly selected from the wild/outplant dataset were re-counted "blind", i.e. with the counter not aware of the position of the coral within or outside territories; these were then compared to the original dataset to ensure that the counter was not biased.

Outplanting of *A. muricata* to degraded areas and survey of predation on adjacent *P. lutea*

To gauge the ability of *Stegastes* spp. to recolonise degraded ecosystems following loss of *A. muricata* and any effect this may have on predation of adjacent *P. lutea*, forty *A. muricata* fragments (four per *P. lutea* colony), each consisting of a forked branch measuring approximately 30–40 cm in length, were outplanted to ten isolated *P. lutea* colonies at each of the unprotected sites in December 2018 (Fig. 2). *A. muricata* and *P. lutea* were fixed with cement and string to concrete blocks to reduce the chance of corals being swept away. *P. lutea* to which *A. muricata* branches were outplanted ranged in surface area from 4 to 313 cm^2 (mean 102 cm^2), as smaller corals were easier to affix to blocks. *A. muricata* branches were tagged and blocks positioned along transect lines to make it easier to return to outplants in subsequent months. Outplants were placed a minimum of 0.5 m from healthy *A. muricata* stands to reduce the likelihood that outplants would be within previously established *Stegastes* spp. territories (Jan et al. 2003). This was further ensured by observing the response of *Stegastes* spp. to outplants at the time of outplanting and moving outplants further away from territories if aggression (biting or chasing) was shown to the outplant or to the individual carrying out outplanting. Corals were re-surveyed in February–March, April, and June 2019. Predation was measured upon *P. lutea* adjacent to *A. muricata* corals, with wild *P. lutea* outside *Stegastes* spp. territories used as controls. The controls were not placed upon blocks to minimise the amount of foreign material introduced to the environment. The methods of *P. lutea* photography and analysis were the same as those described above. The presence or absence of *Stegastes* spp. inhabiting outplanted colonies was recorded at each re-surveying to assess whether recolonization occurred within the outplant survey period of six months, and any effect this may have upon predation of *P. lutea*. Data from each month of re-surveying were pooled for analysis due to limited sample size caused by death of *P. lutea* adjacent to outplanted *A. muricata*. Data from *P. lutea* that died during the study were collected up to the point of coral death. A sub-sample of 15 *P. lutea* adjacent to outplanted *A. muricata* was re-analysed "blind", i.e. with the counter not aware of the recolonisation status of the outplant; these were then compared to the original dataset to ensure that the counter was not biased.

Statistical analysis

Data were analysed using the data analysis software R (version 4.0.2). Linear mixed-effects models (LMEs) in the package lme4 were used to examine the data, and visual inspection of residuals from these models was used to verify normality and homogeneity of variance. Following inspection of model outputs, bite density and percentage surface area damaged were cube root transformed to increase normality and homogeneity of variance. LMEs were then constructed for survey and *P. lutea* outplant data, and for *A. muricata* outplant data. LMEs were constructed for each dataset using the response variables "bite density" and "percentage surface area damaged", respectively, while explanatory variables were altered according to the dataset. For the survey and *P. lutea* outplant data, the explanatory variables were "*Stegastes* species", "outplant status", and "*P. lutea* surface area", and the interaction term "*Stegastes* species*outplant status". Likelihood ratio tests were used to compare models without this interaction. The "Stegastes species" variable included "no Stegastes present" as a level, allowing predation level to be compared between corals within and outside territories. For *A. muricata* outplant data, the response variables were "*A. muricata* outplanting" (presence or absence of outplanted *A. muricata* adjacent to *P. lutea*), "*Stegastes* spp. recolonisation" (presence or absence of *Stegastes* spp.), and "*P. lutea* surface area".

Month, site, and individual coral identity were included as random effects in all LMEs. Coefficient values from final LMEs were utilised to determine significance and direction of effects. The coefficient of determination, or r^2, was calculated to examine the predictive capacity of models. The r^2 values included conditional and marginal r^2 values (r^2_c and r^2_m), which described the proportion of variance explained by fixed factors, and by both fixed and random factors, respectively (Nakagawa and Schielzeth 2013). Graphs were plotted using the ggplot2 package in R (4.0.2) (R Core Team 2020). All data for this study are available at Mendeley Data, https://doi.org/10.17632/572svz6nvb.2.

Results

Fish and coral assemblage at study sites

Mean hard coral cover ranged from ~ 41% (site one) to ~ 79% (site six). *A. muricata* was the most prevalent branching coral species at all sites, with the mean percentage of total benthic cover consisting of *A. muricata* ranging from ~ 23% (site five) and ~ 28% (site one) to ~ 58% (site six). Mean *P. lutea* cover ranged from < 1% (site six) to 5% (site one). *S. nigricans* and *S. punctatus* were present at all sites except site five, where only *S. punctatus* was present. A total of 1085 individual corallivorous fish of 20 species were observed on transect surveys, with a further five species observed off transects (Table 1).

P. lutea survey and outplanting

The most common bite type on both wild and outplanted *P. lutea* was parrotfish (82.5% of bites on wild and 78.3% of bites on outplanted), followed by butterflyfish (wild 8.79%, outplant 15.8%), other (wild 8.73%, outplant 5.92%), and damselfish (wild 0.02%, outplant 0.04%). Throughout the study, a total of 28 outplanted *P. lutea* were lost or died, mainly due to becoming dislodged from *Stegastes* spp. territories or covered with sediment, respectively. The *Stegastes* species*outplant status interaction was not retained in either model. Bite density and percentage surface area damaged were lower within the territories of both *S. nigricans* and *S. punctatus* compared to outside territories, but there were no significant differences in either metric between the territories of *S. nigricans* and *S. punctatus* (Table 2, Fig. 3, Fig. 4). Neither bite density nor surface area damaged varied between outplanted and wild corals, but both were greater on smaller corals (Table 2).

A. muricata outplanting

Out of 30 total outplants at three sites, ten were recolonised by *S. nigricans* within six months, with four colonies at site two being recolonised within two months of outplanting. No recolonisation was observed by *Stegastes* spp. other than *S. nigricans*. Recolonisation only occurred at outplants placed within 1 m of established *A. muricata* colonies containing *S. nigricans* territories. Within six months, recolonisation had occurred at 89% of outplants (eight out of nine) placed within one metre of healthy *A. muricata* stands at site two and at 20% of outplants (two out of ten) placed within one metre of healthy *A. muricata* at site one. A total of 12 *P. lutea* adjacent to outplanted *A. muricata* died during the course of the study. Three died following recolonisation by *S. nigricans*; of these two were buried by sediment and one was overgrown with filamentous algae. Of those that died prior to or without recolonisation, four were overgrown with larger macroalgae, two were overgrown with filamentous algae, and three died of unknown causes. An additional three *P. lutea* were partially overgrown with filamentous algae during the study; one following recolonisation by *S. nigricans*.

The most common bite type found on *P. lutea* adjacent to *A. muricata* outplants and on control colonies was parrotfish (78.6% of bites on colonies adjacent to outplants

Table 1 Numbers of corallivorous fish observed on transect surveys in the lagoon of Mauritius, and all species observed at sites (including off transects)

Family	No. of species observed	No. of individuals observed	Sites observed at	Species observed
Scarinae	2	920	All	*Chlorurus sordidus, S. ghobban*
Chaetodontidae	13	77	All	*Chaetodon auriga, C. citrinellus, C. guttatissimus, C. interruptus, C. kleinii, C. lunula, C. melannotus, C. trifascialis, C. trifasciatus, C. vagabundus, C. xanthocephalus, C. zanzibarensis, Forcipiger flavissimus*
Zanclidae	1	49	All	*Zanclus cornutus*
Labridae	2	25	All	*Gomphosus caeruleus, Thalassoma lunare*
Pomacentridae	1	4	3	*Plectroglyphidodon dickii*
Tetraodontidae	2	4	1, 2, 3, 4, 5	*Arothron nigropunctatus, Canthigaster valentini*
Monacanthidae	1	3	6	*Oxymonacanthus longirostris*
Balistidae	1	1	1	*Rhinecanthus aculeatus*
Blenniidae	1	1	2	*Exallias brevis*
Ostraciidae	1	1	1, 6	*Ostracion cubicus*

Table 2 Linear mixed-effects model results for factors contributing to bite number and percentage surface area damaged by bites on *P. lutea* coral outplanted and wild occurring within and outside *Stegastes* spp. territories. For the factor 'Treatment', 'wild occurring' is the reference level; for the factor 'Stegastes', 'outside territories' is the reference level. In each model, sampling month, site, and individual coral were included as random effects

Factor		Estimate	s.e	d.f	*t*	*p*	r^2_m	r^2_c
Bite Density (bites cm^{-2})							0.28	0.81
Intercept		0.866	0.047	9.465	18.39	< 0.0001		
Treatment								
	Outplant	0.037	0.032	372.0	1.151	0.251		
Stegastes spp.								
	S. nigricans	−0.264	0.021	660.5	−12.58	< 0.0001		
	S. punctatus	−0.266	0.022	671.7	−11.90	< 0.0001		
P. lutea surface area		− 0.0001	0.00002	653.1	−6.810	< 0.0001		
Surface Area Damaged (%)							0.30	0.81
Intercept		3.271	0.169	8.479	19.34	< 0.0001		
Treatment								
	Outplant	0.159	0.124	387.3	1.286	0.199		
Stegastes								
	S. nigricans	−1.051	0.080	662.1	− 13.15	< 0.0001		
	S. punctatus	−1.035	0.085	674.1	−12.20	< 0.0001		
P. lutea surface area		−0.0004	0.00006	609.9	−6.549	< 0.0001		

and 82.3% of bites on controls), followed by butterflyfish (outplant 12.1%; controls 12.2%) and other (outplant 9.4%; controls 5.5%). No damselfish bites were observed on *P. lutea* adjacent to outplants, or on control corals.

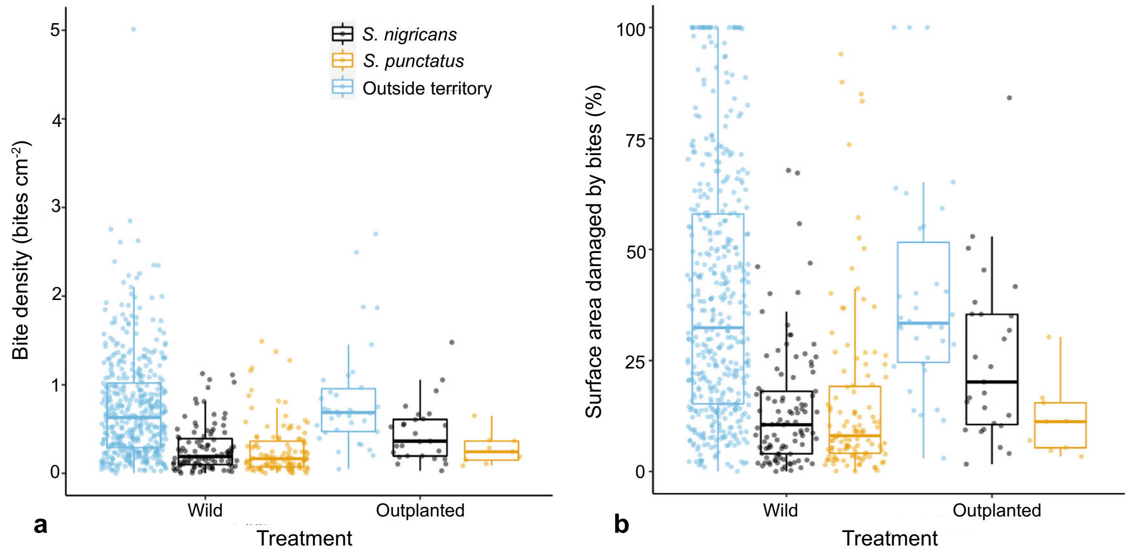

Fig. 3 **a** Bite density and **b** surface area damaged on naturally occurring and outplanted *Porites lutea* inside *Stegastes nigricans* (black) and *Stegastes punctatus* (yellow) territories, and outside *Stegastes* spp. territories (blue)

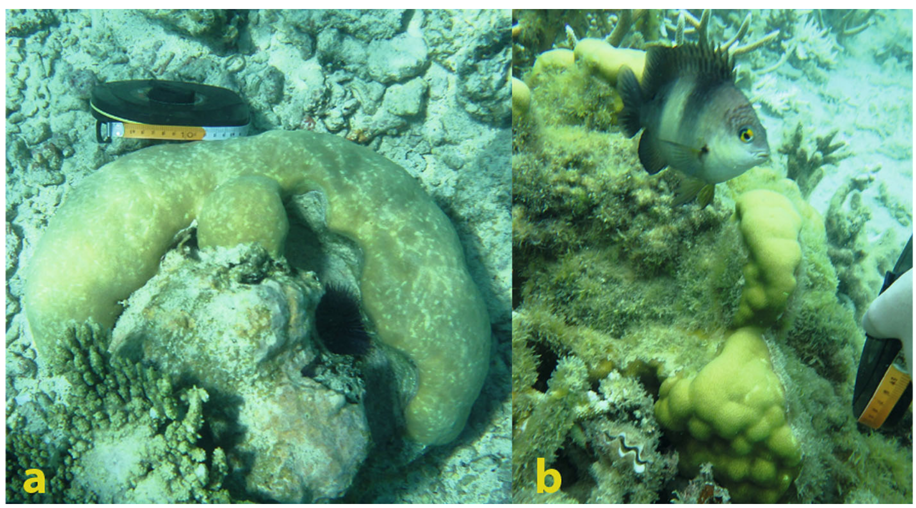

Fig. 4 **a** *Porites lutea* outside *Stegastes* spp. territories at site two, showing extensive bite damage (white marks) and **b** *P. lutea* within a *Stegastes nigricans* territory at site one showing minimal bite damage, and territorial behaviour by *S. nigricans* towards the surveyor (approaching tape measure to bite/chase)

Bite density and percentage coral surface area damaged were lower on corals recolonised by *S. nigricans* compared to corals where *S. nigricans* was absent (Table 3, Fig. 5). Neither bite density nor surface area damaged differed between *P. lutea* colonies with and without outplanted *A. muricata,* but both were higher on smaller colonies (Table 3).

Discussion

This study found that the presence of *Stegastes* spp. significantly reduces predation upon the massive bleaching-resilient coral *P. lutea*, in terms of both bite density and percentage surface area damaged. This was observed for both wild and outplanted *P. lutea* within *Stegastes* spp. territories. In addition, *S. nigricans* was capable of recolonising outplanted *A. muricata* and returning predation protection to adjacent *P. lutea*. This study therefore builds upon the results of Gochfeld (2010) and White and O'Donnell (2010) that *Stegastes* spp. presence can reduce predation upon corals within their territories. The results here also confirm previous reports that *Stegastes* spp. can recolonise degraded areas (Schopmeyer and Lirman 2015), though our findings suggest that the ability of *Stegastes* spp. to colonise outplanted corals may vary among sites and *Stegastes* species. The novel finding that *Stegastes* spp. can restore predation protection to massive corals within their territories through recolonisation of adjacent outplanted branching *A. muricata* may have significant conservation implications with regard to bleaching-resilient

Table 3 Linear mixed-effects model results for factors contributing to bite density and percentage surface area damaged by bites on *P. lutea* corals with or without adjacent *A. muricata* coral outplants, and with or without recolonisation by *S. nigricans*. For the factor 'treatment', 'control' (no outplanted *A. muricata*) is the reference level; for the factor '*Stegastes*', 'absent' is the reference level. In each model, sampling month, site, and individual coral were included as random effects

Factor		Estimate	s.e	d.f	t	p	r^2_m	r^2_c
Bite Density (bites cm^{-2})							0.15	0.71
Intercept		0.995	0.063	4.578	15.80	< 0.0001		
Treatment								
	With *A. muricata*	− 0.0397	0.0403	121.1	− 0.985	0.327		
Stegastes								
	Present	− 0.181	0.062	162.1	− 2.934	< 0.01		
P. lutea surface area		− 0.0005	0.00009	166.4	− 5.457	< 0.0001		
Surface Area Damaged (%)							0.14	0.78
Intercept		3.686	0.221	4.631	16.69	< 0.0001		
Treatment								
	With *A. muricata*	− 0.118	0.149	129.7	− 0.793	0.429		
Stegastes								
	Present	− 0.596	0.206	111.5	− 2.895	< 0.01		
P. lutea surface area		− 0.002	0.0003	160.4	− 5.348	< 0.0001		

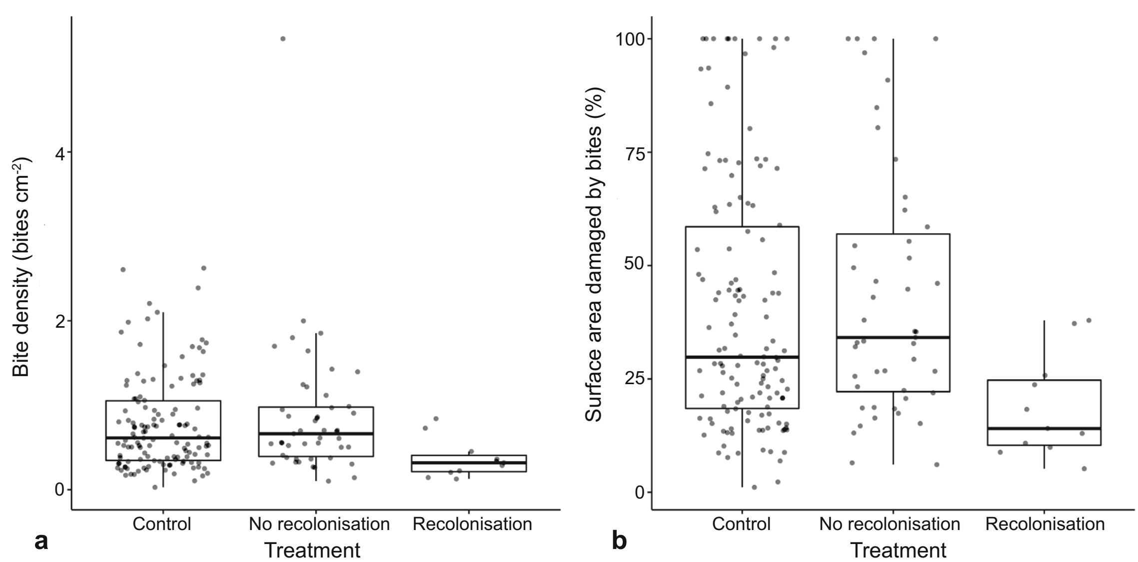

Fig. 5 **a** Bite density and **b** surface area damaged on *Porites lutea* adjacent to outplanted *Acropora muricata* two to six months after outplanting according to whether recolonisation by *Stegastes* spp. has occurred, and on controls

massive corals, and the reef restoration potential of *Stegastes* spp.

Branching *Acropora* spp. are often targeted for outplanting projects, due to their ecological importance, bleaching susceptibility, and the relative ease of propagating and outplanting branching compared to massive corals (Lirman et al. 2010; Young et al. 2012; Forsman et al. 2015; Xin et al. 2016; Nithyanandan et al. 2018). This restoration of branching coral cover has also been shown by this and previous studies to attract territorial *Stegastes* spp. (Schopmeyer and Lirman 2015). Several previous studies of the effects of *Stegastes* spp. on coral restoration efforts have highlighted the negative impacts of these fish on the survival and growth of corals within their territories, due to algal overgrowth and biting of corals to establish territories and facilitate algal lawn propagation (Chasqui-Velasco et al. 2007; Ceccarelli et al. 2011; Casey et al. 2015; Schopmeyer and Lirman 2015; Seraphim et al.

2020). While these studies provide strong evidence for the negative impacts of *Stegastes* spp. on coral restoration projects, the present study adds to the body of previous work (Suefuji and van Woesik 2001; Gochfeld et al. 2010; White and O'Donnell 2010; Johnson 2011) that has identified ways in which *Stegastes* spp. may facilitate restoration, namely through predation and erosion reduction. Specifically, the present study highlights the effects of *Stegastes* spp. recolonisation on massive bleaching-resilient corals such as *P. lutea*. These represent a group that may prove vital to reef conservation efforts using bleaching-resilient strains or species (Bhagooli and Taleb-Hossenkhan 2012; Pratchett et al. 2013; Morikawa and Palumbi 2019; Louis et al. 2020). *Stegastes* spp. have been previously shown to aid survival of juvenile corals following bleaching events by reducing incidental erosion from herbivores (Suefuji and van Woesik 2001), and the current study provides evidence that the benefits of *Stegastes* spp. to corals that survive bleaching events may also extend to predation reduction. Predation has the potential to be a significant stressor to massive bleaching-resilient corals following bleaching events, due to the loss of many branching coral species that would normally be preferentially fed upon (Pratchett et al. 2014; Rotjan and Lewis 2006, 2008). Therefore, encouraging *Stegastes* spp. to recolonise outplanted *Acropora* spp. following bleaching events may facilitate growth and survival of remaining corals, including both massive and bleaching-resilient branching strains within territories (Bhagooli and Taleb-Hossenkhan 2012; Louis et al. 2020). As bleaching events become more common, this may represent a way to utilise ecological processes to facilitate a shift to bleaching resilience among coral assemblages.

While *S. planifrons* (Schopmeyer and Lirman 2015), and now *S. nigricans*, have been shown to be capable of recolonising degraded coral habitats, the variation in recolonisation success among sites in the current study indicates that variation in local conditions may affect the ability of *S. nigricans* to recolonise outplanted corals. At site three, high levels of mortality of outplants and adjacent *P. lutea* may have reduced the number of potential habitats for colonisation. While outplant size has been previously shown to impact survival and recolonisation rates (Lirman et al. 2010; Schopmeyer and Lirman 2015), in this study, outplanted *A. muricata* fragments were all of similar size. Still, an effect of size cannot be ruled out and it would be beneficial for future studies to quantify this effect. Similarly, at site one high tourist activity resulting in mechanical damage to outplants may have reduced recolonisation success. Low existing branching coral cover at site one may also have reduced the density of *Stegastes* spp. present and thus the potential for recolonisation. The lack of recolonisation by *S. punctatus* was surprising but may have been due to congeneric competition resulting in exclusion of *S. punctatus* from established colonies close to transplant sites by *S. nigricans*.

In addition to inter-site variation, the lack of recolonisation of outplanted *A. muricata* placed more than one metre from established territories suggests that *S. nigricans* may be distance-limited in terms of their ability to recolonise. Alternatively, it is possible that it takes longer than six months for individuals to recolonise outplants placed further away. This may increase the difficulty associated with rehabilitating larger areas of degraded coral reefs, however could potentially be overcome through the direct reintroduction of *Stegastes* spp. individuals from established territories to outplanting sites. This may help juvenile outplanted corals to become established (Suefuji and van Woesik, 2001); however, introducing *Stegastes* spp. to new areas may also increase the incidence of coral biting by *Stegastes* spp. as individuals establish territories (Chasqui-Velasco et al. 2007). Given the impact of *Stegastes* spp. on reef ecosystems with regard to both algal farming and predation reduction potentially leading to increased diversity and survival of bleaching-resilient corals, such a project may be valuable to further examine the relative effects of *Stegastes* spp. on successful rehabilitation of degraded areas. An additional understudied factor is the influence of *Stegastes* spp. on invertebrate corallivores such as *Drupella* spp., which may also significantly affect coral health (Rotjan and Lewis 2008). This study did not analyse invertebrate corallivory due to low invertebrate predation upon *P. lutea* at the study sites, with only the sea snail species *Coralliophila violacea* and *C. radula* previously recorded as predating *P. lutea* in the Mauritian lagoon (Kaullysing et al. 2017, 2019). However, *Stegastes* spp. are known to dislodge herbivorous invertebrates from their territories (Hata and Kato 2004) and may do the same with invertebrate corallivores, representing another potential benefit of encouraging *Stegastes* spp. recolonisation as part of reef rehabilitation.

An important source of mortality to *P. lutea* colonies adjacent to outplanted *A. muricata* in this study was algal overgrowth, which is well documented for its negative effects on outplanting success and may be increased by *Stegastes* spp. presence (Dizon and Yap 2006; Young et al. 2012; Schopmeyer and Lirman 2015; van Woesik et al. 2018). In this study, although one *P. lutea* died and a further one was partially overgrown due to filamentous algae following recolonisation by *S. nigricans*, two *P. lutea* died and two were partially overgrown due to filamentous algae prior to or without recolonisation. In addition, several of those not recolonised were overgrown with larger macroalgae, which is more likely to occur where *Stegastes* spp. are absent (Hata and Kato 2002, 2003, 2006; Ceccarelli et al. 2011). Despite the evidence of algal cultivation by *Stegastes* spp. negatively impacting corals within territories (Schopmeyer and Lirman 2015), the low rate of algal overgrowth on *P. lutea* within recolonised territories in this study indicates that the benefits of *Stegastes* spp. presence with regard to reduced predation may outweigh the negative impacts of algal overgrowth for bleaching-resilient massive corals. For future studies, regular cleaning of outplanted corals and structures to which they are fixed could reduce the negative effects of algal overgrowth (Young et al. 2012). The loss of outplanted *P. lutea* colonies that occurred in the present study could also be reduced by fixing outplanted corals securely to outplanting sites, or through the use of larger coral colonies that may be less likely to be dislodged or buried. In addition, the size of outplanted colonies may also impact predation rates. While coral colony size is often unrelated to the amount of predation that they incur (Roff et al. 2011), for some coral species larger colonies receive greater amounts of predation per unit area (Burkepile 2012). The opposite effect was found in the current study, as smaller colonies received the most predation, with fewer bites being required to damage a large proportion of the total surface area of smaller corals. In addition, a smaller surface area means bites are more likely to overlap, resulting in a higher bite density but not necessarily contributing to a large increase in surface area damaged. In any case, the size of outplanted corals may be an important factor to consider in future studies in order to optimise coral survival as well as minimising the impacts on donor reefs.

The findings of this study indicate that *Stegastes* spp. play a significant role in predation protection of corals within their territories, including protection of bleaching-resilient corals which represent a significant asset in maintaining coral reef structure in the face of climate change. While few previous studies on species recolonisation and population restoration have focussed on coral reef fish, this study reaffirms that *Stegastes* spp. have the potential to recolonise outplanted *A. muricata* aggregates, although their success rate may vary between sites, and shows for the first time that in doing so they may return predation protection to bleaching-resilient corals. While the overall impact of *Stegastes* spp. on corals within their territories requires further investigation, this study adds to the growing body of work showing the positive impacts of these fish on coral assemblages and provides the first evidence that they may contribute to the preservation of bleaching-resilient corals, with potentially significant implications for reef conservation.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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