



# Global patterns of herbivorous reef fish productivity: the role of *Prionurus laticlavus* in the Galápagos

Sterling B. Tebbett<sup>1</sup> · Helen F. Yan<sup>1</sup> · Lucas L. Lutzenkirchen<sup>1</sup> · Alexandre C. Siqueira<sup>1</sup> · David R. Bellwood<sup>1</sup>

Received: 15 July 2023 / Accepted: 26 January 2024 / Published online: 28 February 2024  
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**Abstract** Herbivorous fishes play important roles on coral reefs, acting as key trophic conduits of primary productivity. Whilst these roles are widely appreciated on tropical reefs, the relative contribution of fishes which inhabit marginal reefs, such as *Prionurus* surgeonfishes, is not well understood. Here, we examine the extent to which herbivorous fish productivity varies amongst global ecoregions, specifically considering the relative contribution of *Prionurus*. We also compare the productivity of *Prionurus* to that of other herbivorous fishes in relation to water temperatures. Our analysis revealed that the Eastern Galápagos Islands support the highest levels of herbivorous fish productivity recorded to date, with *Prionurus laticlavus* accounting for over 94% of that productivity. Moreover, *Prionurus* productivity peaked at relatively cool water temperatures (~22–25 °C), although patterns were driven by *P. laticlavus*. These results highlight the exceptional herbivorous fish productivity in the Eastern Galápagos Islands and the disproportionate contribution of *P. laticlavus* in this locality.

**Keywords** Algal turf · Coral reefs · Cropping surgeonfishes · Galápagos Islands · Herbivory · Marginal reef systems

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00338-024-02473-0>.

✉ Sterling B. Tebbett  
sterling.tebbett@my.jcu.edu.au

<sup>1</sup> Research Hub for Coral Reef Ecosystem Functions and College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

## Introduction

In the marine environment, the diversity of herbivores reaches its zenith in warm, tropical, clear-water locations (Floeter et al. 2005; Steneck et al. 2017). Such locations are typified by productive coral reef habitats, where the interactions between algal/plant primary productivity and piscine herbivory can be particularly pronounced (Choat 1991; Longo et al. 2019). Indeed, fish-based herbivory is widely accepted as a critical ecosystem function on coral reefs, with fishes controlling the growth of algae (Burkepile and Hay 2008; Tebbett et al. 2023) as well as acting as conduits that pass primary productivity up food chains (Bejarano et al. 2013; Robinson et al. 2019). However, the productivity of herbivorous reef fish assemblages is currently unclear at global scales, especially for marginal coral reef locations (sensu Schoepf et al. 2023) where the relative role of key fishes may be overlooked.

One group of herbivorous fishes that has received little attention in the literature are species in the surgeonfish genus *Prionurus*. This may be in part due to the intriguing global distribution patterns of this genus, with *Prionurus* species only occurring in cooler anti-tropical locations and equatorial areas with cold water upwellings e.g. the Galápagos Islands, and subtropical east Australia (Ludt et al. 2015). This differs from other surgeonfish genera, as well as most species from other key herbivorous fish groups (e.g. parrotfishes and rabbitfishes), which are typical components of tropical coral reef fish faunas (Choat 1991; Cheal et al. 2012; Heenan et al. 2016; Tebbett et al. 2022). Despite their unusual distribution patterns, previous observations have suggested that *Prionurus* can be remarkably abundant in the locations where they occur (Montgomery et al. 1980; Choat 1991; Pessarrodona et al. 2022; Riofrío-Lazo et al. 2022). Nevertheless, given the

marginal nature of these locations compared to tropical coral reefs, it may be expected that the productivity of *Prionurus*-dominated herbivorous fish communities is only a fraction of that found on diverse, warm, tropical coral reefs. Whether this expectation holds at global scales is currently unclear.

The aim of the current study, therefore, is to assess the extent to which herbivorous reef fish productivity varies amongst global ecoregions and consider the relative contribution of *Prionurus* spp. therein. To provide further insights into these global-scale patterns, we also examine how *Prionurus* spp. productivity aligns with other groups of herbivorous fishes, including their closest ecological counterparts (other surgeonfishes), and how the productivity of these groups relates to a key environmental gradient: water temperature. In doing so, we shed light on the productivity of a globally distributed group of herbivorous reef fishes and highlight the implications of these results for our understanding of herbivory on coral reefs and marginal reef systems.

## Materials and methods

### Fish survey data

To examine large-scale patterns in herbivorous reef fish productivity, we used reef fish community survey data from the publicly available Reef Life Survey dataset (<https://reeflifesurvey.com>). This global dataset of fish surveys is based on a standardised method and the systematic collection of data in a broad range of geographic locations (Edgar and Stuart-Smith 2014; Edgar et al. 2020). Each reef fish survey is based on an underwater visual census of the reef fish community in two 250 m<sup>2</sup> survey blocks (Edgar and Stuart-Smith 2014). Our goal with this dataset was to assess the productivity of major groups of roving nominally herbivorous fishes on coral reefs (i.e. Acanthuridae [surgeonfishes], Kyphosidae [chubs], scarine labrids [parrotfishes], and Siganidae [rabbitfishes]; Choat 1991; Tebbett et al. 2023) in shallow water (1–10 m) reef habitats. Only nominally herbivorous fishes from these groups (i.e. species that feed primarily on primary producers or particulate/detrital material) were considered in the analyses (Table S1). All species that feed predominantly on other trophic resources, such as planktivorous surgeonfish species, were excluded from analyses to ensure they did not bias results. However, it should be noted that many ‘herbivorous’ fishes still exhibit a marked degree of dietary flexibility and, under certain circumstances (e.g. when zooplankton are particularly dense), have been observed feeding on other nutritional resources (Randall 2001; Tebbett et al. 2023).

### Calculation of reef fish productivity

We followed the methods set forth by Morais and Bellwood (2018, 2020) to calculate the productivity of herbivorous fishes. Here, productivity was quantified as the biomass accumulated via ontogenetic growth of all surviving individuals of a community over the course of one day. In short, we used a suite of ecological traits and methodological attributes (i.e. maximum size, diet, position in the water column, survey water temperature, and aging method) to explain and predict standardised growth rates for all fishes. Then, based on the body size of surveyed individuals, we predicted the biomass of somatic growth expected over the course of one day. Finally, because we applied rates of mortality based on body size (Gislason et al. 2010), we bootstrapped this entire process and generated mean estimates of productivity of individual herbivorous fish (see Morais and Bellwood 2018, 2020 for more details).

### Statistical analyses

Initially, we explored variation in total herbivorous fish productivity across different ecoregions. Due to small sample sizes in some ecoregions, we limited our analysis to ecoregions with 20 or more individual blocks, with conjoining blocks averaged for each survey to limit the influence of spatial dependence. Moreover, due to the focus on tropical/subtropical species, we limited our global analysis to reef areas between  $\pm 32^\circ$  from the equator. This ensured that all coral reef and key marginal reef ecoregions were included in the analysis (such as Lord Howe Island), whilst limiting the inclusion of surveys from well outside the natural distribution of coral reefs. We note that this may have resulted in the exclusion of some temperate reef areas that may host herbivorous fishes including some *Prionurus* (Ludt et al. 2015). However, the abundance of other tropical herbivorous families is limited in these temperate areas (Choat 1991), which limits the scope for comparison in our study and results in substantial zero-inflation. Therefore, after applying these filters, the final global-scale dataset was based on surveys across 1548 sites in 38 ecoregions.

We tested for variation in the total productivity of herbivorous fishes amongst different ecoregions using a generalised linear mixed-effects model (GLMM) based on a tweedie error distribution and log-link function. Ecoregion was treated as a categorical fixed effect, whilst sampling year nested within site identity were treated as random effects to account for any lack of spatial and temporal independence derived from resampling of the same sites in some ecoregions. Model fit and assumptions were examined based on simulated model residuals (Hartig 2020), being satisfactory in all cases. To ensure our insights were not biased by outliers or ecoregion classification, we repeated the analysis

above after excluding the highest 1% of total productivity values and by using geographic location (58 locations had 20 or more blocks) rather than ecoregion as the fixed effect. All model fitting and checking procedures followed those described above. On all subsequent plots, the relative contribution of *Prionurus* spp. to total roving herbivorous fish productivity, based on the raw data, was overlaid to visualise the contribution of this group of fishes at a global scale (note that of the six species of *Prionurus*, only *P. laticlavus*, *P. maculatus*, and *P. microlepidotus* were observed in the dataset).

Following the global-scale analysis, we examined the relationships between sea surface temperature (SST) and the productivity of *Prionurus* spp. (both together and separately for each species) as well as all other surgeonfishes and all other nominal herbivores (i.e. acanthurids [excluding *Prionurus* spp.], scarine labrids, kyphosids, and siganids). To do this, we used the mean site-level (i.e. same geographic coordinates) productivity of each respective species/group. Due to the zero-inflated nature of the data, and the fact that we were only interested in the relationship between the productivity of the species/groups and sea surface temperature, we only examined data where the productivity of a species/group was greater than zero based on the entire Reef Life Survey dataset (i.e. not just limited to between  $\pm 32^\circ$ ). Moreover, to ensure relationships were not biased by outlying datapoints, we excluded the highest 1% of productivity values in all cases. Based on the geographic coordinates of each site, we extracted data on mean long-term SST from Bio-Oracle (Assis et al. 2018). Subsequently, the relationship between the productivity of each species/group and SST was explored using separate GLMMs with Gamma error distributions and log-link functions. In all cases, the productivity of each species/group was fitted as the response variable, whilst SST was treated as a continuous fixed effect. During the modelling process, a degree of nonlinearity was detected, which was accounted for by fitting SST with a second-order polynomial term. Ecoregion was also included as a random effect in all cases to account for the lack of spatial independence at this scale. Model fits and assumptions were assessed as above. All statistical analyses were performed in the software R (version 4.2.2; R Core Team 2022) using the *glmmTMB* (Brooks et al. 2017) and *DHARMA* (Hartig 2020) packages.

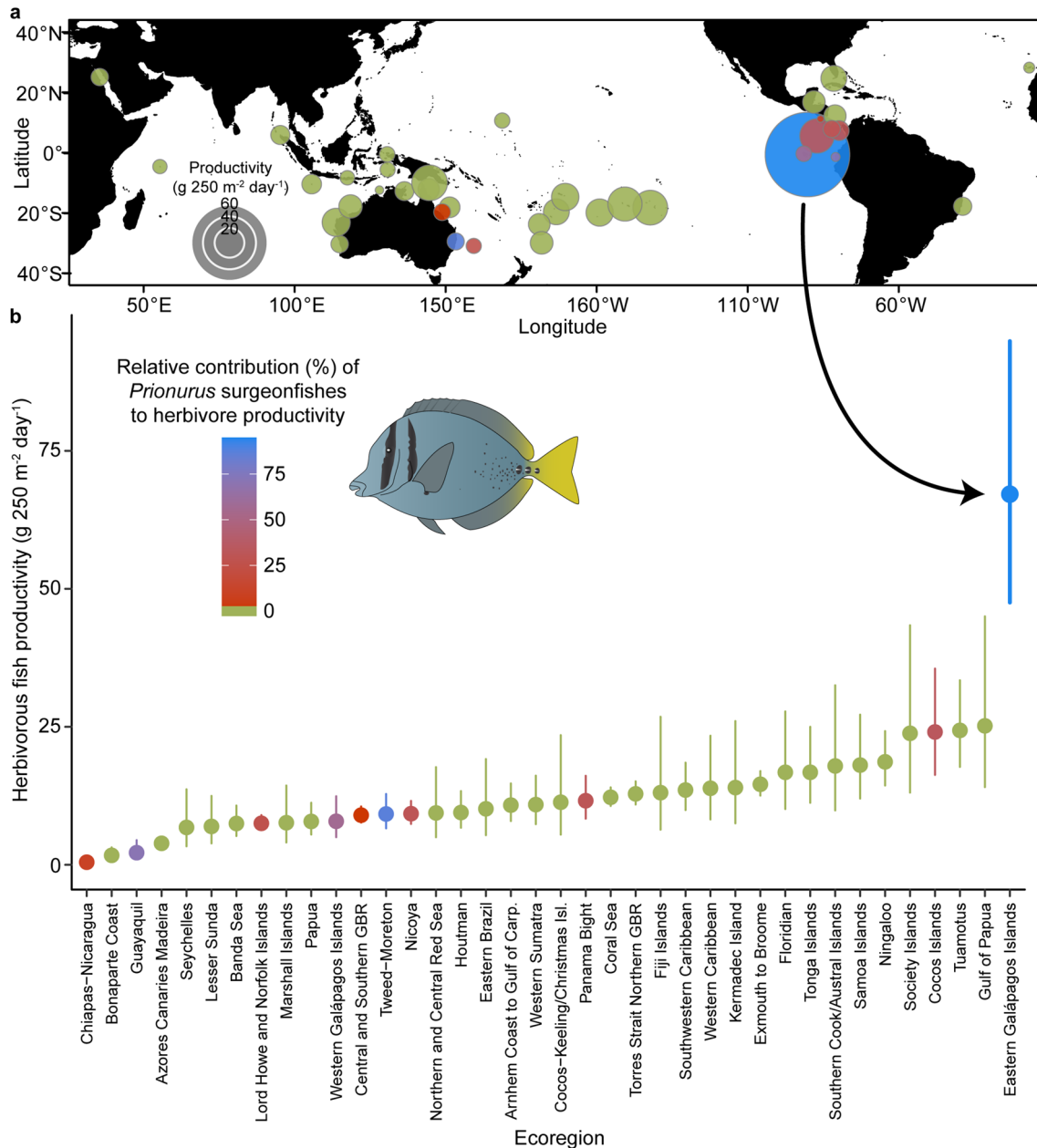
## Results and discussion

By exploring patterns in global nominally herbivorous reef fish productivity, we found that the Eastern Galápagos Islands had by far the most productive assemblages out of all 38 ecoregions examined (Fig. 1). Indeed, a GLMM revealed that herbivorous fish productivity in the Eastern

Galápagos Islands averaged ( $67.15 \pm 11.84$  g  $250\text{ m}^{-2}$  day $^{-1}$  [mean  $\pm$  SE]), which was significantly higher than all other ecoregions and over 2.6-fold higher than the second highest ecoregion (Gulf of Papua;  $25.17 \pm 7.46$  g  $250\text{ m}^{-2}$  day $^{-1}$ ) ( $p < 0.05$  in all cases; Table S2; Fig. 1). Importantly, even after excluding the highest 1% of productivity values or considering geographic location classifications rather than ecoregions, the (Eastern) Galápagos Islands still exhibited the highest productivity (Figs S1, S2; Table S2). This exceptional productivity was underpinned by a single species *P. laticlavus* (see Ludt et al. 2019), which accounted for over 94% of all herbivorous fish productivity in the Eastern Galápagos Islands (Fig. 1).

The Galápagos Islands are renowned for their exceptional biogeography, with a major biogeographic division falling along the East–West axis (Glynn and Wellington 1983; Edgar et al. 2004; McKinley et al. 2023). The Western Galápagos Islands experience nutrient-rich upwellings and cooler waters, whilst the Eastern Galápagos Islands are typified by warmer waters and less upwellings (Wellington et al. 2001; Kingsford et al. 2023). Consequently, the Western Galápagos Islands exhibit significantly lower herbivorous fish productivity, averaging 8.5-fold less than that of the Eastern Galápagos Islands (Fig. 1). The exceptional herbivorous reef fish productivity found in the low-upwelling Eastern Galápagos Islands is underpinned by *P. laticlavus* and aligns with the findings of Kingsford et al. (2023). Specifically, Kingsford et al. (2023) showed that the average *P. laticlavus* abundance ( $> 300$  ind.  $500\text{ m}^{-2}$ ) and biomass ( $> 240$  kg  $500\text{ m}^{-2}$ ) was highest in shallow low-upwelling regions of the Galápagos, with this trophic pathway supported by the high cover of short filamentous turf-like algae across the barren reef-scape.

Algal turfs can represent a particularly productive nutritional resource, being widely recognised for their capacity to underpin herbivorous trophic pathways on reefs (Hatcher 1988). The dentition (multidenticulate spatulate-like teeth [Tyler 1970]) as well as feeding behaviour (predominantly turf grazing) and/or gut contents (predominantly turf-forming algae) (Montgomery et al. 1980; Moreno-Sánchez et al. 2014; Basford et al. 2016; Brandt et al. 2022) all suggest that *Prionurus* spp. are cropping surgeonfishes that feed on turf algae. Given the equatorial position of the Eastern Galápagos Islands (i.e. high light availability) and oceanic position (i.e. low sediment loads), turfs may be particularly productive in this region (Klumpp and McKinnon 1989; Tebbett et al. 2018). Moreover, the cover of turfs appears to be particularly high in this region with low cover of other benthic space holders such as corals (Kingsford et al. 2023). Such productivity and high turf cover could support *P. laticlavus* productivity in the Eastern Galápagos (also see Kingsford et al. 2023). However, herbivory rates on algae are invariably controlled by temperature, with higher herbivory rates in



**Fig. 1** The global distribution of roving nominally herbivorous fish (acanthurid, scarine labrid, siganid, and kyphosids) productivity in 38 ecoregions around the world. **a** World map showing the ecoregion surveyed and the spatial arrangement of herbivorous fish productivity. **b** The mean predicted productivity and 95% confidence intervals for

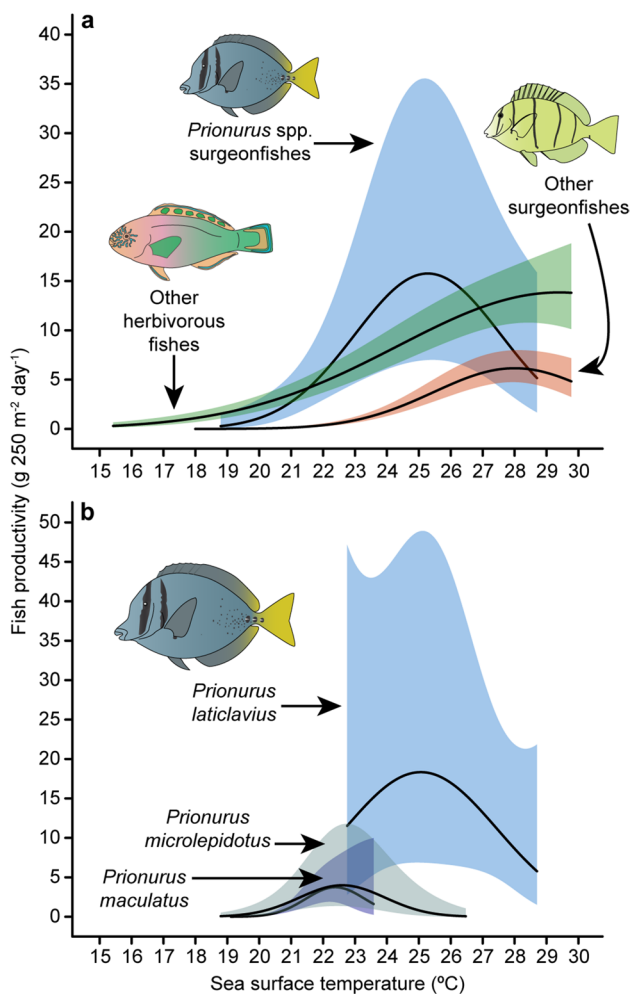
each ecoregion from a generalised linear mixed-effects model. Note colour gradient shows the relative contribution (%) of *Prionurus* spp. to total herbivorous fish productivity, ranging from zero (green), low (red), and high (blue). GBR = great barrier reef, Isl. = islands, Carp. = Carpentaria

warmer temperatures (Carr et al. 2018; Brandt et al. 2022). Therefore, it may be expected that surgeonfish productivity would peak in waters warmer than those inhabited by *Prionurus* spp.

By comparing the productivity of *Prionurus* spp. with that of all other tropical nominally herbivorous fishes examined as well as all other surgeonfishes, across SST, we revealed marked differences in the relationships (Fig. 2;

Table S3). Specifically, we found that the productivity of *Prionurus* spp. peaked at ~25 °C, whilst the other groups of herbivorous fishes peaked at warmer temperatures (Fig. 2a). However, by specifically exploring the relationship between SST and the productivity of each of the three *Prionurus* species observed in the dataset, it became clear that *P. laticlavius* disproportionately shaped the relationship (Fig. 2). Indeed, the productivity of both *P. maculatus*





**Fig. 2** **a** The relationship between sea surface temperature and *Prionurus* surgeonfish productivity (blue) as well as the productivity from all other surgeonfishes (orange) and all other nominally herbivorous fishes (acanthurids, scarine labrids, siganids, and kyphosids) considered in this study (green). **b** The relationship between mean long-term sea surface temperature and the productivity of the three species of *Prionurus* surgeonfish observed in the dataset; note the overwhelming contribution of *P. laticlavius* to *Prionurus* productivity in **a**. The black lines denote mean predicted productivity, whilst the coloured ribbons show the 95% confidence intervals from generalised linear mixed-effects models. Note the y-axis scales differ

and *P. microlepidotus* peaked at ~22–23 °C, whilst the productivity of *P. laticlavius* peaked at ~25 °C and at a productivity level roughly four-fold higher than the other two *Prionurus* species (although the relationship between SST and *P. laticlavius* productivity was not significant (Table S3)). These results suggest that *P. laticlavius* may be more productive in warmer waters than the other two *Prionurus* species examined.

It is critical to note that whilst the Reef Life Survey dataset is based on a single method and represents one of, if not the, most spatially comprehensive reef fish survey datasets

publicly available (Edgar et al. 2020), only three of the six *Prionurus* species were observed in the dataset examined. This means it is currently unclear how productive the other three species (i.e. *P. biafraensis*, *P. chrysurus*, and *P. scalprum*) are, and if they rival *P. laticlavius* in the Eastern Galápagos. Notably, both *P. biafraensis* and *P. scalprum* have previously been reported as relatively abundant and major herbivores throughout their natural ranges (Canterle et al. 2020; Azevedo Silva et al. 2022; Vergés et al. 2022). Nevertheless, given the exceptional productivity of *P. laticlavius* in the Eastern Galápagos (Fig. 1; Kingsford et al. 2023), and the tendency for this species to form large feeding aggregations (which may readily be detected in fish surveys) and reach a relatively large size (60 cm) (Randall 2001) it seems unlikely that the other *Prionurus* species are as ecologically successful (from a productivity point of view) as *P. laticlavius*.

Given the understudied nature of *Prionurus* spp. when compared with their tropical relatives, the exact mechanisms underlying the high productivity of *P. laticlavius* in the Eastern Galápagos is currently unclear. Detailed studies, particularly in respect to the morphology and physiological capacity of *P. laticlavius*, as well as other *Prionurus* species, will be necessary to uncover how they succeed in areas where other surgeonfishes do not. In addition, given the reliance of *Prionurus* species on turf-based nutritional resources, the nature of turfs in the Eastern Galápagos, relative to other locations, warrants specific examination in the future. Indeed, as it is now recognised that the nature of turfs can vary dramatically under different scenarios (e.g. Connell et al. 2014; Pessarrodona et al. 2022) it could be that the Eastern Galápagos represents a global ‘sweet spot’ of turf productivity typified by turfs of a tropical/subtropical nature with low sediment loads and fuelled by the high solar irradiance on the equator. Ultimately, our analysis highlights the Eastern Galápagos as a global outlier in terms of nominally herbivorous reef fish productivity, with *P. laticlavius* responsible for underpinning these exceptional levels of biomass production.

**Acknowledgements** We thank the Reef Life Survey Team and their volunteers for the publicly available data. These data are managed through and were sourced from, Australia’s Integrated Marine Observing System (IMOS)— IMOS is enabled by the National Collaborative Research Infrastructure Strategy (NCRIS). We also thank CR Hemington for vector images of fishes and the reviewers for insightful comments.

**Funding** Open Access funding enabled and organized by CAUL and its Member Institutions. This work was funded by the Australian Research Council (DRB; grant number FL190100062).

**Data availability** All raw data are publicly available from Reef Life Survey (<https://reeflifesurvey.com>).

## Declarations

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

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