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Corallivore assemblage, feeding behavior, and cover of *Acropora* corals drive fish corallivory on tropical reefs

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Abstract

Understanding spatial patterns and drivers of corallivory is essential for assessing reef resilience and identifying recovery pathways. Fish corallivory patterns arise from the complex direct and indirect effects of key factors, including food availability (cover of preferred corals), the nature of the corallivore assemblage (richness and biomass), how the corallivores choose to feed (intensity and bout duration), and the local risk profile (predator biomass and habitat structural complexity). While some linkages within this network are well studied, such as the generally positive relationship between coral cover and the abundance of corallivores, the manner and extent to which they can explain overall corallivory rates is less clear. In this study, we used structural equation modeling to provide an integrated assessment of the relative importance of these key elements in both directly and indirectly explaining patterns of total corallivory by fishes (bites in 30 min). We used remote underwater video sampling at four reefs spanning approximately 1800 km across the Torres Strait (TS) and Great Barrier Reef (GBR) in northeast Australia to quantify corallivory. Total corallivory and corallivore biomass were significantly higher in back- than fore-reef habitats, while neither corallivore feeding behavior (intensity or duration) nor richness varied across spatial scales. Due to distinct benthic and corallivore assemblages, separate analyses were conducted for GBR and TS sites. Structural equation modeling showed that among GBR sites, corallivore richness, feeding intensity, and event duration were direct positive drivers of corallivory, while the cover of *Acropora* corals was both a direct and indirect (via its effect on corallivore richness, feeding intensity, and event duration) positive driver of corallivory. In contrast, TS sites, dominated by large massive corals and near-monospecific corallivore assemblages, showed no relationship between corallivory and any assemblage or behavioral metrics. Our findings showed little evidence in either area that

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predation risk (biomass of piscivores) affected corallivory either directly or through changes in feeding behavior.

KEYWORDS
behavioral ecology, Chaetodontidae, ecological function, feeding activities, indirect effects, resilience

INTRODUCTION

Coral reefs are highly biodiverse ecosystems that support complex food webs. However, the effects of climate change and local anthropogenic pressures are increasingly impacting reefs, leading to reductions in the cover of scleractinian corals (Hughes et al., 2017, 2018), shifts in benthic communities (Reverter et al., 2022), flattening of the reef structure (Alvarez-Filip et al., 2009), and changes in composition and diversity of fish assemblages (Pratchett et al., 2018; Richardson et al., 2018). Corallivorous fish, particularly obligate corallivores (Cole et al., 2008), are generally the first and most adversely impacted by coral mortality due to their dependency on live coral for food (Pratchett et al., 2006; Wilson et al., 2006). However, the influence is not unidirectional; corallivores, through their feeding, may exacerbate stress on the remaining corals by feeding more intensely on recently bleached or diseased corals (Cole et al., 2009), concentrating their feeding on surviving preferred coral species (Gomez et al., 2025; Rice et al., 2019), or modifying coral heterotrophic feeding patterns potentially affecting internal resource allocation and/or growth (Hsu, Hoey, Warren, et al., 2026). Understanding the drivers of corallivory is therefore crucial for assessing reef resilience and informing management strategies.

Many studies have shown the importance of benthic communities, especially the cover and composition of corals, in shaping assemblages of corallivorous fishes through the provision of food and/or shelter. For example, *Acropora*-dominated habitats support the highest abundance and richness of butterflyfishes on the Great Barrier Reef (GBR) (Emslie et al., 2010). Similarly, the abundance of hard coral with a "competitive" life history (sensu Darling et al., 2012), mainly *Acropora* and *Pocillopora*, has been positively related to the biomass of corallivorous fishes across 157 coral reef sites in the Indo-Pacific (Darling et al., 2017). While habitat-driven changes in the abundance and composition of corallivores may directly influence rates of corallivory, these relationships may be mediated by behavioral responses (i.e., feeding intensity and duration). Notably, these elements of feeding behavior (how long and how intensively they feed during a feeding bout) of corallivores can be shaped by the availability of preferred corals (Chandler et al., 2016; Gunn et al., 2022), as well as the perceived risk of predation (e.g., abundance of predators and availability of suitable refugia; Gaynor et al., 2019; Mitchell & Harborne, 2020).

While it is possible to identify the potential drivers of overall corallivory and even elements of corallivorous fish behavior on a reef, potential interactions among these elements (i.e., composition of corallivore assemblage, predation risk, and availability of preferred corals) are likely to be quite complex. Feeding intensity and duration are expected to be positively related to the availability of preferred coral prey, as obligate corallivores take more bites when their preferred coral prey (typically branching and tabular corals) are available (Pratchett, 2005, 2007). However, these corals are important contributors to reef structural complexity (Darling et al., 2017), with tabular corals, in particular, providing shelter for large piscivorous reef fish (Kerry & Bellwood, 2012, 2015). This raises the question of whether corallivory is directly suppressed through direct consumptive effects of predators on corallivore populations, or indirectly through non-consumptive effects (i.e., changes in feeding behavior under elevated predation risk). Moreover, feeding behavior of corallivorous fishes and access to preferred coral prey may be affected by both resource availability and interspecific competition. When coral prey are abundant (i.e., not limiting), corallivory is hypothesized to be positively related to feeding behavior (feeding intensity and duration), species richness and abundance of corallivores, as interspecific competition can be mitigated through resource partitioning, enabling the coexistence of different species (Munday et al., 2001). In contrast, when preferred coral prey is limited (e.g., following a cyclone or coral bleaching event), some corallivorous fishes may switch to prey on other, less preferred, coral taxa (Semmler et al., 2022) and/or spend more time searching for preferred corals (Berumen & Pratchett, 2006; Cole & Pratchett, 2014), potentially leading to a reduction in total corallivory per unit area. In addition to the biotic factors discussed above, the feeding behavior of corallivorous fishes can be influenced by abiotic ones such as wave exposure (Karkarey et al., 2020; Krajewski et al., 2010; Noble et al., 2014). For example, two species of corallivorous butterflyfishes spent less time searching

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and feeding but more time traveling at wave-exposed compared to sheltered sites, despite similar coral cover and reef topography (Noble et al., 2014).

On the northeast coast of Australia, coral reefs occur across approximately 15 degrees of latitude, from the Torres Strait (TS) in the north to the southern GBR, and feature large regional and within-reef variations in both fish and benthic communities (Emslie et al., 2010; Hoey & Bellwood, 2007; Mellin et al., 2019). This region represents an ideal system to evaluate drivers of corallivory across a broad range of different reef contexts. In this study, we combined information on feeding behavior (from remote underwater video [RUV]), benthic habitat composition and structural complexity (from large area imaging), and fish assemblage structure (from underwater visual census [UVC]) to understand drivers of corallivory at 16 sites spanning the TS and GBR. Specifically, we (1) compared spatial variation in total corallivory (i.e., total bite rates), feeding behavior (the intensity [in bites per minute] and duration of feeding during individual feeding events), and corallivore fish assemblage (richness and biomass) within and among reefs; (2) explored spatial variation in assemblage-level corallivory (multivariate characterization of corallivory based on species-specific bite rates rather than species numerical abundance) and benthic communities across the study regions; and (3) used structural equation modeling to evaluate the relative importance of the direct and indirect linkages in driving overall corallivory.

MATERIALS AND METHODS

Study sites

This study was conducted on four offshore reefs on the northeast coast of Australia from January to May 2023 (Figure 1): Lizard Island, Davies Reef, and Heron Island in the northern, central, and southern regions of the GBR, respectively, and Masig Island in the TS. Within each reef, two sheltered back-reef sites and two exposed fore-reef sites were selected based on wave exposure. Each site was at a depth of approximately 5 m and consisted of four plots (each 12 m × 6 m). Plots were spaced approximately 10 m apart, with minor adjustments made to picket installation based on local substrate suitability. There was a total of 64 plots at 16 sites across the four reefs. Total corallivory, feeding behaviors, and richness of corallivores, benthic composition, and structural complexity were quantified at the plot level, while fish assemblages at each site were quantified along two belt transects that encompassed plots 1 and 2, and plots 3 and 4, respectively. All data were collected as part of the EcoRRAP project (Australian Institute of Marine Science [AIMS], 2023).

Remote underwater video

Fish foraging activities within each of the 64 plots were recorded using unbaited RUV. A GoPro camera (HERO 11 Black, GoPro, USA) was mounted approximately 1 m above the benthos on a preexisting star picket with the field of view capturing approximately 15 m^2 of the plot. The GoPros were deployed between 10:00 and 13:00, recorded for >70 min (1080p, 60 fps, wide view), with a total of 64 videos recorded (~75 h) across all plots.

Corallivory

Foraging of obligate corallivorous fish from the video footage was quantified using EventMeasure (SeaGIS, Australia) following the methods of (Hsu et al., 2025). Obligate corallivores were defined as species whose diets consist of more than 80% live coral tissue (following Cole et al., 2008). Facultative corallivorous fish were excluded as they were rarely observed on the video footage and took very few bites from live coral. To minimize any potential effects of divers deploying and/or retrieving cameras on fish behavior, the middle 30 min of each video was analyzed, a duration which has been shown to yield precise and accurate estimates of bite rates of corallivorous fishes (Hsu et al., 2025). For each video, the time an obligate corallivorous fish entered and subsequently left the field of view was recorded, and all bites taken during that time were counted. A feeding event was defined as any obligate corallivorous fish that entered the field of view and was observed to take bites from live hard or soft coral. Bites on non-coral substrata were excluded. While we assumed biting on live coral targeted coral tissue or mucus, obligate corallivores may occasionally ingest non-coral taxa associated with the colony; however, this accounts for a small percentage (<3%) of the ingested material (Nagelkerken et al., 2009).

From this data, we defined two components of feeding behavior for every event: (1) event duration (time in the field of view) and (2) feeding intensity (bites taken during an event divided by the duration of that event). They were averaged for all events across the entire assemblage in a video to generate an overall estimate of average event duration and feeding intensity for each plot. Total corallivory was quantified as the total number of bites of all corallivorous fish per 30-min video. We

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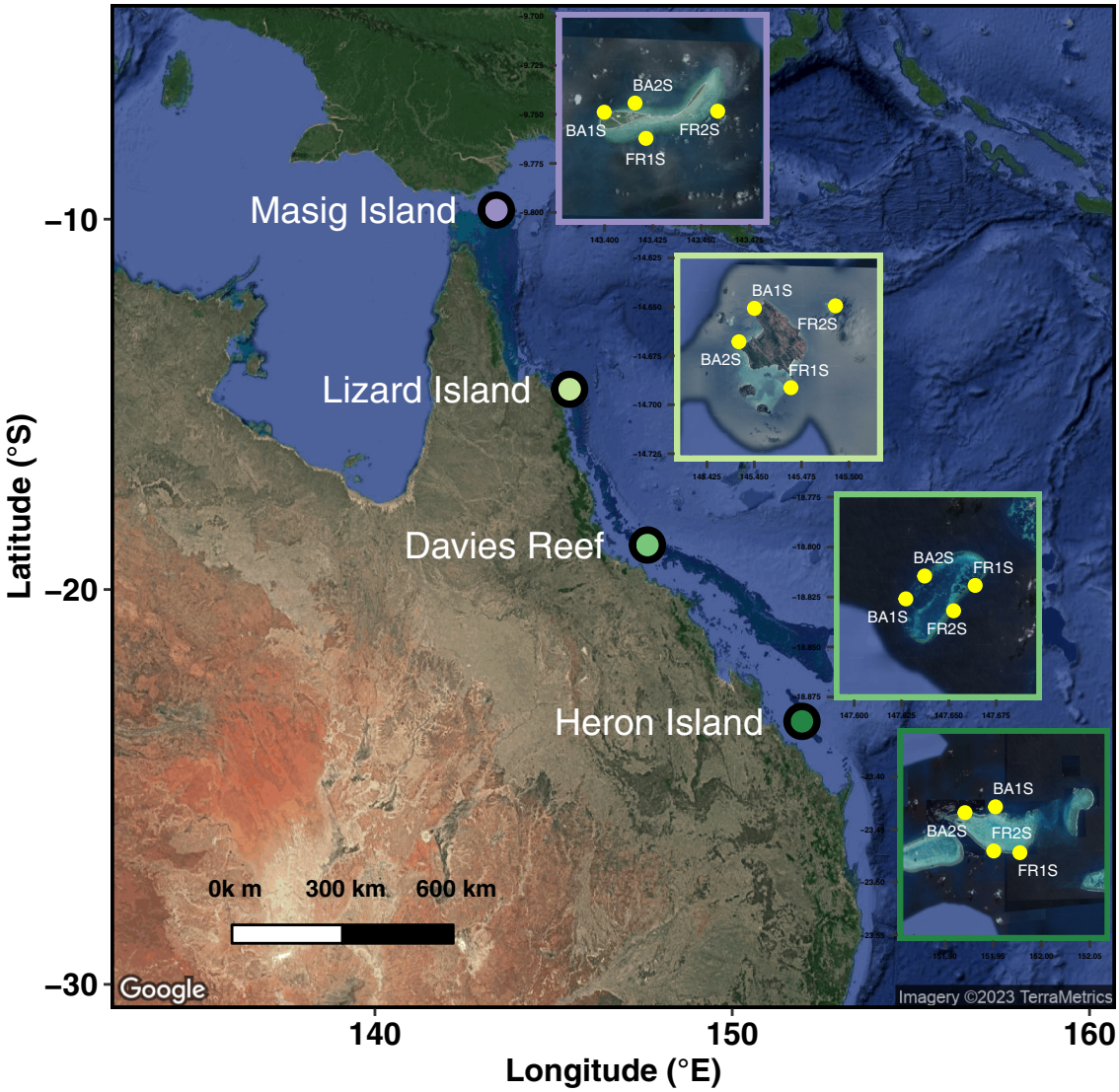


FIGURE 1 Study sites on the northeast coast of Australia.

acknowledged that quantifying the total number of bites is a proxy for corallivory and does not take into account the volume of coral tissue consumed per bite. Directly quantifying the coral tissue removed per bite would need to be conducted under controlled (aquaria) conditions (e.g., butterflyfishes; Cole et al., 2011), and is not amenable to field-based studies. The species richness of obligate corallivorous fish observed during each video was also recorded, irrespective of whether they were observed feeding. To simultaneously understand the number of bites taken and the species composition of corallivorous fish across study sites, we defined "assemblage-level corallivory" as the multivariate characterization of corallivory within a plot, derived using the species-specific bite rates (total number of bites taken per 30 min) for all species seen in the video.

Fish assemblage metrics: Biomass of corallivores and piscivores

Fish assemblages were quantified at each site by a SCUBA diver using UVC along two belt transects laid parallel to the depth contour and running through the center of the plots. All fishes within a 5-m wide belt (i.e., 2.5 m either side of the diver's path) were recorded while the transect tape was simultaneously deployed (following Hoey et al., 2020). The first transect spanned the distance from the leading edge of the first plot to the trailing edge of the second, while the second transect extended from the start of the third plot to the end of the fourth. Each transect was approximately 30 m in length, with the exact length of each transect calculated from the top-down view of the 3D reef model for each site

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(see details below). All fish within the transect area were identified to species and their total length estimated to the nearest cm. Abundance was transformed to biomass using species-specific length-mass relationships: $M = a\mathrm{TL}^b$, where M is the mass in grams, TL is the total length in centimeters, and a and b are species-specific constants referenced from FishBase (Froese & Pauly, 2025). Biomass (in grams per square meter) was then standardized by the transect area and further aggregated for obligate corallivores and piscivores as defined by Cole et al. (2008) and Mihalitsis and Bellwood (2019), respectively (Appendix S1: Table S1).

Structural complexity: Surface rugosity

Photogrammetry was used to reconstruct 3D reef models following Gordon et al. (2023) and Gordon et al. (2025). Briefly, ground control points were placed within each plot, and plots were mapped using two DSLR cameras (Nikon D850 + NIKKOR 20 mm f/1.8 lens, two photographs per second), resulting in 1700–2700 photographs per plot. The 3D models were built using the software Metashape Pro v1.7.6 (Agisoft LLC, Russia), following Gordon et al. (2025), and subsequently used to generate 2D orthomosaics, a top-down image of the entire plot (72 m^2). Surface rugosity was then extracted from the 3D models following Gordon et al. (2025), which is the ratio of 3D surface area over the 2D surface area projected onto the plane of best fit, as a proxy for reef structural complexity (hereafter referred to as rugosity).

Benthic communities and coral composition

Benthic composition within each plot was quantified using images extracted from the 2D orthomosaic by ReefCloud (González-Rivero et al., 2020), a supervised machine learning digital annotation tool. Before analyzing images, ReefCloud was trained using approximately 26,000 manually annotated points on images across two depths (5 and 12 m) and 17 reefs on the GBR and the TS (see Gordon et al., 2023 for detailed site information), including a subset of the images used in this study. The developed model had an accuracy (f1 score) of approximately 80% and was applied to automate the identification of benthic composition in the 64 plots in the present study. This process involved the extraction of 12 randomly selected non-overlapping images (80 × 50 cm) from the 2D orthomosaic within each plot, capturing approximately 6.6% of the area in each plot. This coverage is three times higher compared to that of the photo-quadrat surveys (~2.16%) used in the Long-Term Monitoring Program of the GBR (LTMP, AIMS, Australia), with 40 photographs (45 × 30 cm) annotated from a 5 × 50 m transect. Fifty random points were scattered in each image (10 with human expert annotations, 40 automatically annotated using the ReefCloud model). The benthos underneath each point were first classified into 72 taxa and then aggregated into 25 morpho-taxonomic groups (14 hard coral, five soft coral, five algae, and sponge) that represent likely prey for corallivorous fishes (see the full list of taxa in Appendix S1: Table S2).

Data analyses

Given the complexity of the data and potential influence of divergent fish assemblages across the large latitudinal range in this study, the analyses were structured into three steps. We first evaluated how geographical factors influenced patterns of corallivory (overall and behavioral components) and corallivorous fish assemblages (richness and biomass), and then evaluated how "assemblage-level corallivory" (multivariate assemblage based on species-specific bite rates) and associated benthic communities varied across these same spatial gradients. The results of these first two steps were then used within a structural equation modeling approach to evaluate the relative importance of the direct and indirect linkages within the network of potential drivers of overall corallivory at a location: food availability (i.e., cover of the six major coral prey), the nature of the corallivore assemblage (richness and biomass), corallivore feeding behavior (intensity and bout duration), and the local risk profile (predator biomass and habitat structural complexity). The details of each step are described in greater detail below. Data wrangling and plotting were performed using base R functions and the packages, *tidyverse* (Wickham et al., 2019), *cowplot* (Wilke, 2020), and *ggrepel* (Slowikowski, 2024), while statistical analyses were conducted with the packages listed below in R v4.4.2 (R Core Team, 2025).

Spatial variations in total corallivory, feeding behavior, richness, and biomass of corallivores

To assess spatial variation in total corallivory, feeding intensity and duration, and richness and biomass of corallivores, we modeled each response variable as a function of spatial factors with a linear mixed model (LMM) using the function "lmer" in the package, *lmerTest* (Kuznetsova et al., 2017), with plot as the unit of

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replication. Reef, habitat, and their interaction were included as fixed effects, while the interaction between reef and site was treated as a random effect. The significance of fixed effects in each LMM was tested using a type III ANOVA based on Satterthwaite's method (Kuznetsova et al., 2017), followed by estimated marginal means with Tukey's honestly significant difference (HSD) test for pairwise comparison using the function "emmeans" (Lenth, 2024) if significant differences were detected among groups. Total corallivory was square-root transformed to meet the assumption of normality of residuals, and the random effect in the model on corallivore biomass was excluded due to zero variance explained (i.e., singular fit).

Spatial variations in assemblage-level corallivory and benthic communities

Differences in assemblage-level corallivory and benthic communities between habitats and among reefs were visualized using non-metric multidimensional scaling (nMDS) with a Bray–Curtis dissimilarity matrix and separately analyzed using a two-way permutational ANOVA (PERMANOVA) with reef, habitat, and their interaction as fixed effects with 999 permutations. The analyses were based on the total number of bites by each species of corallivore and the percent cover of each benthic morpho-taxonomic group within each plot, respectively. Rare morpho-taxonomic groups (maximum cover <5% across all plots) were excluded from the analyses, resulting in 15 morpho-taxonomic groups characterizing benthic communities. Both assemblage-level corallivory and benthic communities showed significant reef × habitat interaction (see *Results*); therefore, pairwise PERMANOVA on the Bray–Curtis dissimilarity matrix, with Bonferroni correction, was used to test for differences between back- and fore-reef habitats at each reef. Where differences were identified, similarity percentages (SIMPER) analysis was used to identify corallivore species and benthic morpho-taxonomic groups that distinguished assemblage-level corallivory and benthic communities, respectively. nMDS, PERMANOVA, and SIMPER were conducted using the functions, "metaMDS," "adonis2," and "simper" in the package *vegan* (Oksanen et al., 2024), while pairwise PERMANOVA was performed using "pairwise.adonis2" in the package *pairwiseAdonis* (Martinez Arbizu, 2017). Moreover, the cover of each benthic morpho-taxonomic group was compared between TS sites (Masig) and GBR sites (Lizard, Davies, and Heron) using the Wilcoxon rank-sum test, owing to the unique assemblage-level corallivory at Masig (see *Results*).

Drivers of corallivory

Structural equation modeling (SEM) was used to understand the relative importance (both directly and indirectly) of the potential drivers (i.e., feeding intensity, event duration, richness and biomass of corallivores, biomass of piscivores, rugosity, and cover of coral prey) on corallivory. This technique integrates the outputs of a set of linear models (LMs) that describe the relationships between all possible predictors and response variables in a single network and gives standardized regression coefficients and *p*-values to each hypothesized pathway (Lefcheck & Freckleton, 2016).

Seven defined sets of LMs were constructed to relate potential predictor variables to each response variable (see Table 1 for summary), the outcomes of which were integrated using SEM to clarify the strength and paths (direct and indirect) of all relationships. Specifically, the cover of the following six coral prey was used as the benthic explanatory variables: tabular *Acropora*, corymbose *Acropora*, massive *Porites*, arborescent *Acropora*, *Montipora*, and *Pocillopora*. Collectively, these six coral morpho-taxa were the major feeding substrata among all corallivores recorded in this study, accounting for approximately 87% of bites recorded. Moreover, these coral morpho-taxa are major contributors to the physical structure of reefs (Darling et al., 2017) and have been shown to influence the abundance and biomass of piscivorous fishes through the provision of shelter (Kerry & Bellwood, 2012, 2015; Urbina-Barreto et al., 2022).

Based on the previous analysis, it was clear that the assemblage-level corallivory and benthic communities were very different in the TS when compared to the GBR (see *Results*: *Assemblage-level corallivory and benthic communities*), and thus these regions were modeled separately. All factors were first standardized to *z*-scores, analyzed by LMs (as listed in Table 1), followed by SEM, and visualized in a hierarchical network plot using the package, *qgraph* (Epskamp et al., 2012), where variables in the upper and lower levels were the response and predictors, respectively. Marginal effects of each LM were computed by the function "ggpredct" in the package *ggeffects* (Lüdecke, 2018) for visualization.

To identify significant predictors and avoid overfitting, each component model was optimized prior to the SEM following a similar approach as in Bowd and Lindenmayer (2024). Collinearity among variables was assessed by examining the variance inflation factor (VIF) values using the function "vif" in the package, *car* (Fox & Weisberg, 2019). VIF value exceeding 10 indicates serious multi-collinearity (O'brien, 2007); therefore, variables with the highest VIFs were sequentially removed from

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TABLE 1 Component model specification for linear models.

		Predictors						
		Corallivore behavior		Corallivore assemblage		Predation risk	Structural complexity	
Response variables		Feeding intensity	Event duration	Species richness	Biomass	Piscivore biomass	Rugosity	Coral prey
Overall corallivory	Total corallivory	✓	✓	✓	✓	✓	✓	✓
Corallivore behavior	Feeding intensity			✓	✓	✓	✓	✓
	Event duration			✓	✓	✓	✓	✓
Corallivore assemblage	Species richness					✓	✓	✓
	Biomass					✓	✓	✓
Predation risk	Piscivore biomass						✓	✓
Structural complexity	Rugosity							✓

the model, and collinearity was reassessed after each step until all VIF values were below 10. The optimal models were then selected by examining the small-sample corrected Akaike information criterion (AIC_c) in stepwise backward elimination using the function "glmulti" in the package, *glmulti* (Calcagno, 2020). The distribution of residuals for each optimized model was checked using a Q–Q plot and tested for normality using the Shapiro–Wilk test. If model residuals were not normally distributed, the respective response variable was transformed and refitted to a new model. Total corallivory (GBR and TS) was cube-root transformed, and piscivore biomass (GBR) and event duration (TS) were fourth-root transformed.

Once optimized, the seven LMs were analyzed by a piecewise structural equation model (SEM) using the function "psem" in the package, *piecewiseSEM* (Lefcheck & Freckleton, 2016), which further tests conditional independence to see if there are missing relationships present among the unconnected variables, using Shipley's test of directed separation (Shipley, 2000). Fisher's *C* further tests if the model predictions fit the observed data (goodness-of-fit), and AIC values are computed.

RESULTS

Summary of corallivory

A total of 4329 bites were recorded from 839 feeding events across the 64 plots. The mean (±SE) feeding intensity and event duration across all plots were 12.31 ± 0.55 bites min^{-1} and 0.40 ± 0.03 min, respectively. Twelve obligate corallivores were recorded, including nine butterflyfishes (*Chaetodon aureofasciatus*, *C. baronessa*, *C. lunulatus*, *C. melannotus*, *C. unimaculatus*, *C. ornatissimus*, *C. plebeius*, *C. rainfordi*, and *C. trifascialis*), two mucus-feeding wrasses (*Labrichthys unilineatus* and *Labropsis australis*), and one damselfish (*Plectroglyphidodon johnstonianus*).

Spatial variations in total corallivory, feeding behavior, richness, and biomass of corallivores

Total corallivory, defined as the total number of bites by the entire corallivore assemblage, varied significantly between habitats (ANOVA, $F_{1,8} = 11.815$, $p < 0.01$; Figure 2b), and was twice as high in back-reef habitats (91 ± 10.6 bites per 30 min) compared to fore-reef habitats (45 ± 6.7 bites per 30 min). The biomass of corallivores varied significantly among reefs ($F_{3,24} = 3.498$, $p < 0.05$; Figure 2i) and between habitats ($F_{1,24} = 6.643$, $p < 0.05$; Figure 2j). Biomass was 4.6 times higher at Heron (2.65 ± 0.62 g m^{-2}) than at Masig (0.58 ± 0.33 g m^{-2}; Tukey's HSD test, $p < 0.01$), and twice as high in back-reef habitats (2.21 ± 0.47 g m^{-2}) compared to fore-reef habitats (1.03 ± 0.29 g m^{-2}, $p < 0.01$). No other spatial predictors (i.e., reef, habitat, or the reef × habitat interaction) significantly explained the variation in total corallivory, feeding intensity, event duration, and the richness and biomass of corallivores (Figure 2).

Assemblage-level corallivory and benthic communities

Corallivorous fish assemblages were less diverse at Masig Island, TS (1.4 ± 0.2 species per plot) than at the three GBRs (3.0 ± 0.3 species per plot), with *C. aureofasciatus*

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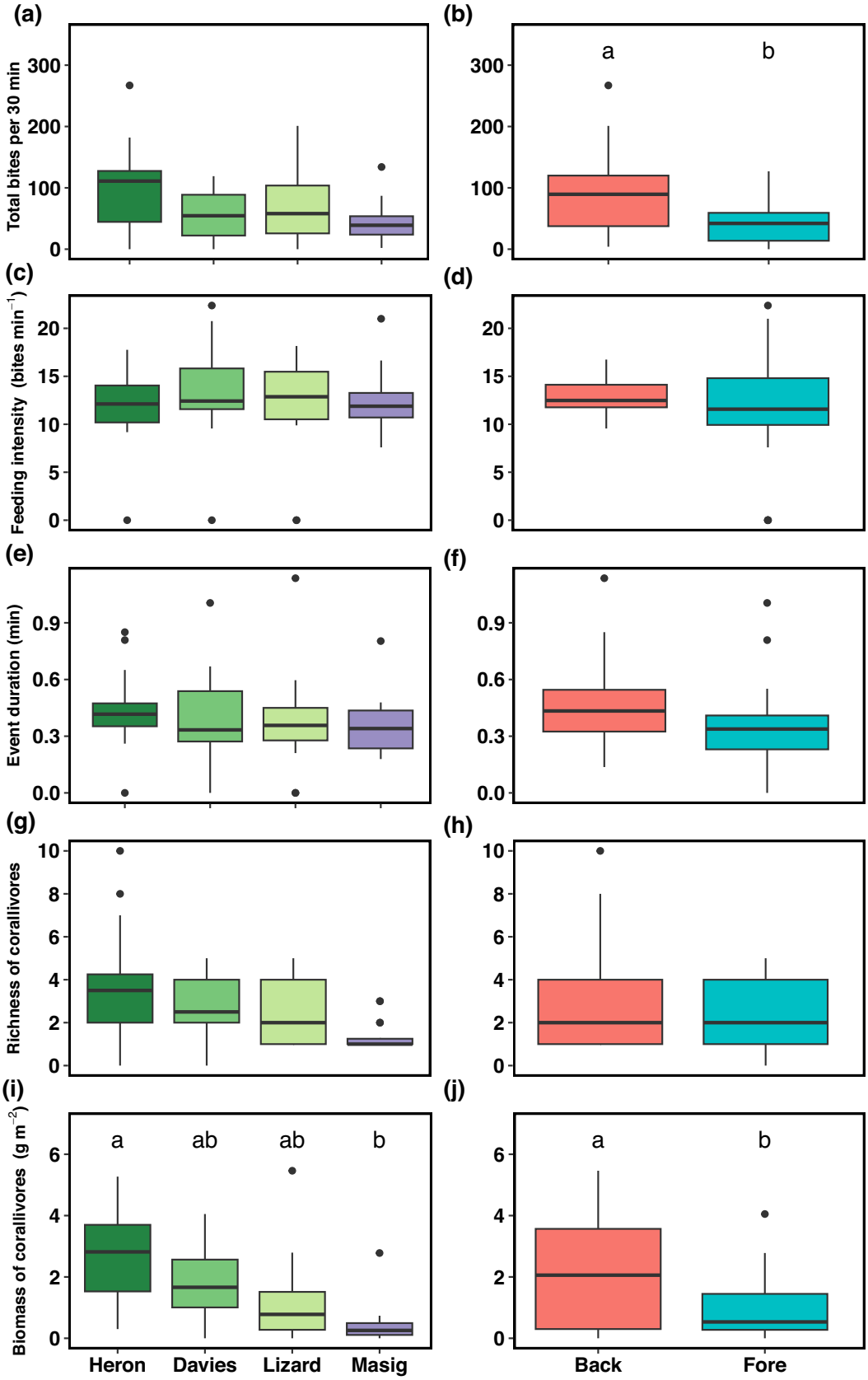


FIGURE 2 Legend on next page.

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being the only species observed foraging in 13 of the 16 plots at Masig. There was a significant reef by habitat interaction (PERMANOVA: $F_{3,52} = 1.885$, $p < 0.05$), with differences in assemblage-level corallivory (i.e., species-specific bite rates) between back- and fore-reef sites only at Heron (pairwise PERMANOVA: $F_{1,13} = 3.567$, $p < 0.01$; Figure 3). The difference was driven by more number of bites of *C. trifascialis* and *C. rainfordi* at the back-reef than fore-reef at Heron (SIMPER, $p < 0.01$ and $p < 0.05$, respectively).

There was a significant reef by habitat interaction (PERMANOVA: $F_{3,56} = 9.372$, $p < 0.001$) with significant differences in benthic communities (i.e., morpho-taxonomic groups in per cent cover; Figure 4 and Appendix S1: Table S3) between back- and fore-reef sites on each of the four reefs (pairwise PERMANOVA, all $p < 0.05$). Morpho-taxonomic groups driving the differences between habitats varied among reefs. Sites at Heron were characterized by higher cover of arborescent *Acropora* (SIMPER, $p < 0.01$) and tabular *Acropora* ($p < 0.001$) at the back-reef sites, while higher cover of turfs ($p < 0.05$) and other massive hard coral ($p < 0.01$) at the fore-reef sites. Sites at Lizard were characterized by higher cover of arborescent *Acropora* ($p < 0.01$) and corymbose *Acropora* ($p < 0.01$) at the back-reef sites, while higher cover of *Pocillopora* ($p < 0.05$) at the fore-reef sites. Sites at Davies were characterized by higher cover of corymbose *Acropora* at the fore-reef sites ($p < 0.001$). Sites at Masig were characterized by higher cover of massive *Porites* ($p < 0.001$), other branching hard coral ($p < 0.001$), and branching soft coral ($p < 0.05$) at the back-reef sites, while higher cover of turfs ($p < 0.05$), massive soft coral ($p < 0.001$), and *Pocillopora* ($p < 0.01$) at the fore-reef sites. Moreover, GBR sites were characterized by higher cover of corymbose *Acropora* (Wilcoxon rank-sum test, $p < 0.001$; Appendix S1: Table S4), tabular *Acropora* ($p < 0.001$), *Montipora* ($p < 0.01$), turfs ($p < 0.001$), crustose coralline algae (CCA, $p < 0.001$), and articulate calcareous algae ($p < 0.001$), while TS sites were characterized by higher cover of massive *Porites* ($p < 0.001$), "other" branching hard coral ($p < 0.01$), branching soft coral ($p < 0.001$), and massive soft coral ($p < 0.001$) (Figure 4).

Drivers of corallivory within regions

The optimized LMs are summarized in Table 2, which were included in the SEM to evaluate the direct and indirect relationships among drivers of corallivory among GBR and TS sites (Figure 5). Partial effects of each model for GBR and TS sites were visualized in Appendix S1: Figures S1 and S2, respectively.

The test of directed separation of SEM showed that no significant relationships were missed, and Fisher's C statistics indicated good model fits among GBR ($C = 53.93$, df $= 80$, $p = 0.989$, AIC $= 796.53$) and TS sites ($C = 60.43$, df $= 66$, $p = 0.670$, AIC $= 227.98$). Overall, the complexity and nature of the network of drivers and responses were quite different between the GBR and TS sites (see Table 2 for the full summary of coefficients).

Among the GBR sites (Figure 5a), total corallivory was positively correlated with corallivore feeding behavior (i.e., feeding intensity and duration), richness of corallivores, and tabular *Acropora*. Behavior, richness, and biomass of corallivores were mainly influenced by the cover of coral prey. Event duration was positively associated with arborescent *Acropora* while negatively associated with *Pocillopora* and *Montipora*. Feeding intensity was positively associated with corymbose *Acropora* and rugosity. Corallivore assemblage metrics were positively correlated with the cover of acroporid corals only (arborescent and tabular forms for biomass while arborescent and corymbose forms for richness). Aside from the direct pathways described above, arborescent and corymbose *Acropora* had indirect positive effects on total corallivory through the pathways of richness of corallivores and corallivore behavior. There was no negative effect from the biomass of piscivores or structural complexity on total corallivory, corallivore behavior, or corallivore assemblage metrics. The biomass of piscivores was positively correlated with *Montipora*, *Pocillopora*, and arborescent *Acropora* but was not associated with rugosity. Rugosity was positively correlated with tabular *Acropora*, massive *Porites*, and *Montipora*.

Unlike GBR sites, total corallivory among the TS sites (Figure 5b) was poorly explained and only negatively

FIGURE 2 Total corallivory (a) among reefs and (b) between habitats, feeding intensity (c) among reefs and (d) between habitats, event duration (e) among reefs and (f) between habitats, richness of corallivores (g) among reefs and (h) between habitats, and biomass of corallivores (i) among reefs and (j) between habitats. Letters in panels (b), (i), and (j) indicate the significant difference among reefs and between habitats, respectively (ANOVA with Tukey's honestly significant difference [HSD] test). Nonsignificant comparisons are not shown. The lower edge, middle line, and upper edge of each box represent the first (Q1), second (median), and third (Q3) quartiles, respectively. Whiskers extend to the smallest and largest values within 1.5 times the interquartile range from the lower and upper quartiles, while values beyond this range are outliers shown as solid circles.

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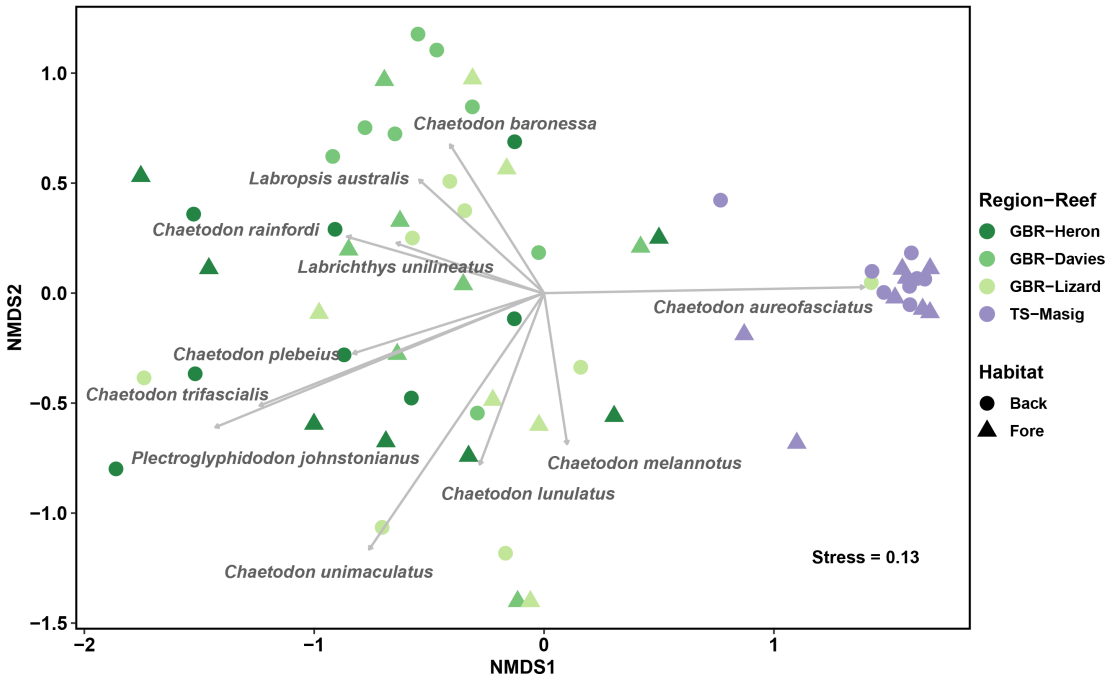


FIGURE 3 Non-metric multidimensional scaling (nMDS) showing variation in assemblage-level corallivory between habitats and among reefs on the Great Barrier Reef (GBR) and Torres Strait (TS). The nMDS is based on a Bray–Curtis dissimilarity matrix of corallivorous bites by species across 60 plots (the other four plots with zero bites are not shown).

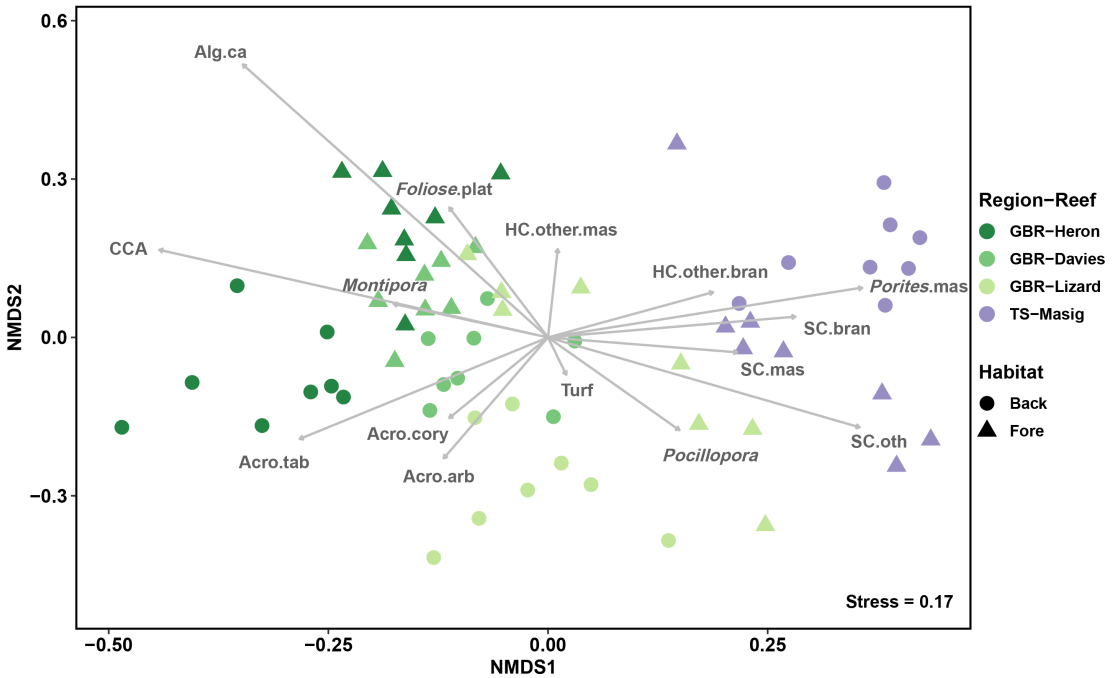


FIGURE 4 Non-metric multidimensional scaling (nMDS) showing variation in benthic communities between habitats and among reefs on the Great Barrier Reef (GBR) and Torres Strait (TS). The nMDS is based on a Bray–Curtis dissimilarity matrix of benthic cover across 64 plots. The 15 benthic morpho-taxonomic groups are labeled using abbreviations (see Appendix S1: Table S2 for the full description).

associated with the cover of *Montipora*. Moreover, feeding intensity was not significantly predicted by any of the variables measured. In contrast, event duration was negatively associated with the rarest hard coral, tabular *Acropora* (0.47% ± 0.1%; Appendix S1: Table S4), while positively associated with the biomass of piscivores. The

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TABLE 2 Component model specification for structure equational modeling (SEM) among Great Barrier Reef (GBR) and Torres Strait (TS) sites.

Region	Response	R^2	Predictor	Coefficient	SE	df	*p*
GBR	Total corallivory	0.82	Feeding intensity	0.32	0.07	43	***
			Event duration	0.39	0.07	43	***
			Richness of corallivores	0.46	0.07	43	***
			Tabular *Acropora*	0.16	0.07	43	*
	Feeding intensity	0.26	Corymbose *Acropora*	0.38	0.13	45	**
			Rugosity	0.27	0.13	45	*
	Event duration	0.36	Tabular *Acropora*	0.23	0.13	42	0.0939
			Corymbose *Acropora*	0.23	0.13	42	0.0984
			Arborescent *Acropora*	0.30	0.13	42	*
			Montipora	−0.29	0.14	42	*
			Pocillopora	−0.30	0.14	42	*
	Richness of corallivores	0.34	Corymbose *Acropora*	0.29	0.12	44	*
			Arborescent *Acropora*	0.41	0.12	44	**
			Montipora	0.26	0.12	44	*
	Biomass of corallivores	0.38	Tabular *Acropora*	0.49	0.12	45	***
			Arborescent *Acropora*	0.35	0.12	45	**
	Biomass of piscivores	0.56	Tabular *Acropora*	0.18	0.11	43	**
			Arborescent *Acropora*	0.36	0.11	43	**
			Montipora	0.64	0.11	43	***
			Pocillopora	0.53	0.12	43	***
	Rugosity	0.41	Tabular *Acropora*	0.46	0.12	44	***
			Montipora	0.30	0.12	44	*
			Massive *Porites*	0.36	0.12	44	**
TS	Total corallivory	0.28	*Montipora*	−0.53	0.23	14	*
	Event duration	0.55	Biomass of piscivores	1.10	0.31	13	**
			Tabular *Acropora*	−1.12	0.31	13	**
	Richness of corallivores	0.69	Tabular *Acropora*	−0.59	0.19	12	**
			Pocillopora	1.47	0.30	12	***
			Massive *Porites*	1.49	0.31	12	***
	Biomass of corallivores	0.72	Arborescent *Acropora*	0.37	0.17	12	*
			Montipora	−0.34	0.16	12	0.0601
			Pocillopora	0.98	0.18	12	***
	Biomass of piscivores	0.79	Tabular *Acropora*	0.89	0.13	13	***
			Montipora	−0.42	0.13	13	**
	Rugosity	0.25	Massive *Porites*	0.50	0.23	14	0.0506

Note: Feeding intensity among TS sites was not explained by any of the variables and was excluded in the SEM.
*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

richness of corallivores was positively associated with the most abundant hard coral, massive *Porites*, followed by *Pocillopora*, while negatively associated with tabular *Acropora*. The biomass of corallivores was positively associated with *Pocillopora* and arborescent *Acropora*. The biomass of piscivores was positively correlated with tabular *Acropora* while negatively correlated with *Montipora* but was not associated with rugosity. Massive *Porites* had a nonsignificant but marginal positive effect on rugosity ($p = 0.0506$, Table 2).

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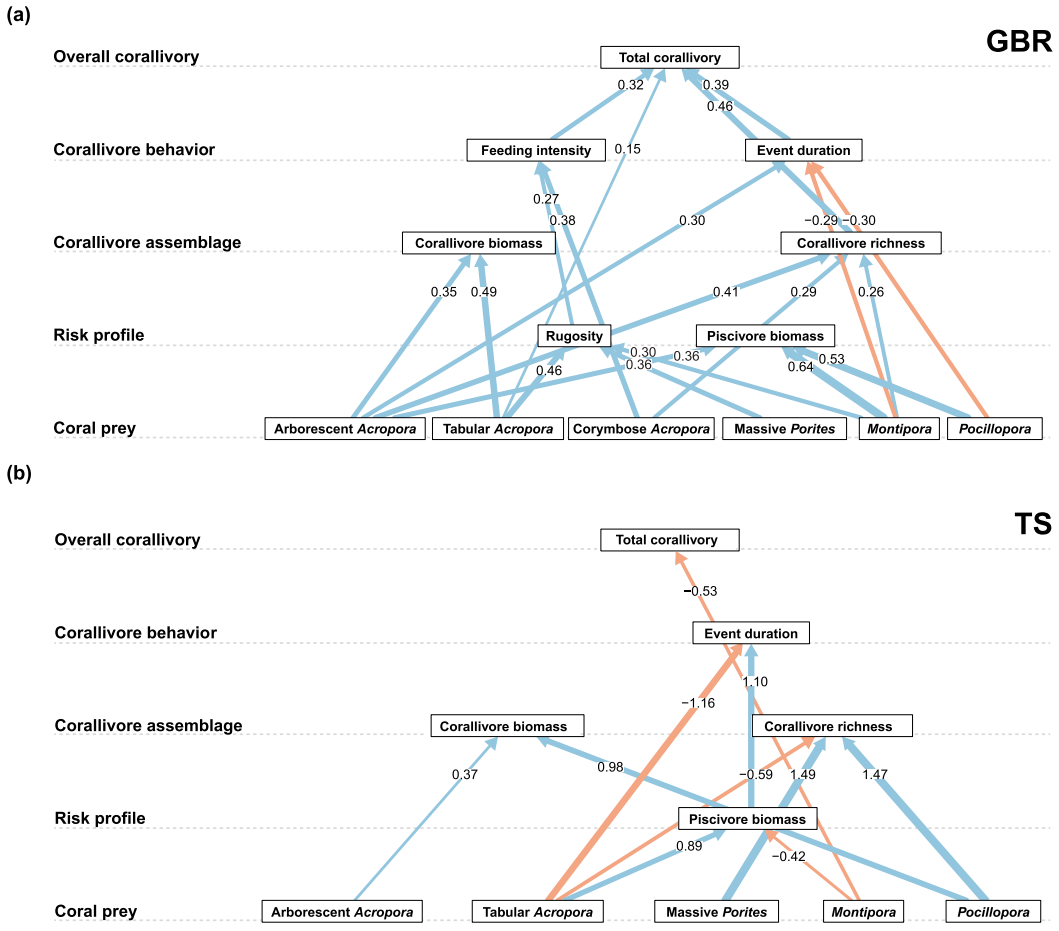


FIGURE 5 Structural equation models (SEMs) on drivers of corallivory among (a) Great Barrier Reef (GBR) and (b) Torres Strait (TS) sites, respectively. Variables at the upper and lower levels are the response and predictors, respectively. Blue and orange arrows represent positive and negative relationships, respectively, and only significant relationships are shown. The thickness of arrows represents the relative strength of relationships.

DISCUSSION

The positive relationships between total coral cover and the abundance of corallivorous fishes are well established (Emslie et al., 2010; Pratchett et al., 2006; Wilson et al., 2006). A similar positive relationship between total coral cover and the biomass of corallivores is also observed in this study (see further details in Appendix S1: Figure S3). However, variation in corallivore assemblages is seldom linked to their behavior, and in turn to rates of total corallivory. This study reveals that total corallivory (in bites per 30 minutes) and two measures of feeding behavior of obligate corallivores (bite intensity and bout duration) are relatively consistent among reefs. In contrast, assemblage-level corallivory (multivariate species-specific bite rates) was spatially variable (among reefs and habitats) and related to variation in benthic composition across the same spatial scales. This study highlights that it is not only the numerical properties of the corallivore assemblage (especially species composition) that directly drive overall rates, but also the behavioral elements of how they feed (intensity and duration). Predation risk, while acknowledged to be an important process regulating the abundance and behavior of reef fish (Boaden & Kingsford, 2015; Rasher et al., 2017), did not have a strong effect on corallivory rates either directly or indirectly via feeding behavior in this study.

Spatial variation in total corallivory explained by assemblage-level corallivory and benthic communities

Total corallivory varied little among the studied reefs despite their broad geographic distribution across approximately 1800 km in northeast Australia, suggesting that

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the obligate corallivores exert a similar amount of corallivory (as measured by bites) among reefs despite significant differences in the composition and biomass of corallivorous fishes and coral cover. The consistency in feeding pressure of obligate corallivores contrasts with that of herbivores, another important functional group on coral reefs, where rates of herbivory have been shown to vary among habitats and reefs on the GBR (Hoey & Bellwood, 2007), among regions (Kindinger et al., 2024) and among different modes of feeding (i.e., browsers, scrapers, and excavators, Hoey, 2018). However, we acknowledge that total bite rates are used as a proxy for corallivory, and actual corallivory (i.e., the amount of coral tissue removal) will depend on the volume of coral tissue removed per bite. In contrast to the pattern among reefs, total corallivory varied significantly between habitats, with bite rates twice as high at sheltered back-reef compared to exposed fore-reef sites. This difference likely reflects the two-fold higher corallivore biomass observed in back-reef compared to fore-reef sites. A similar result was found in the assemblage-level corallivory, where more bites of two corallivorous species occurred at back-reef than fore-reef sites at Heron. These findings align strongly with the coral community present at sites, where the cover of preferred coral was higher at back-reef than fore-reef sites. These results are consistent with studies which have shown that wave exposure drives variation in benthic communities (Williams et al., 2013; Wismer et al., 2009), influencing corallivore assemblages (Emslie et al., 2010) and ultimately rates of corallivory.

Limited spatial variation in the feeding behavior of corallivores

In contrast to total corallivory, there was no significant variation in either feeding intensity or event duration between habitats or among reefs. This differs from a previous study that reported the feeding behavior of two of the four species corallivore examined was influenced by exposure (Noble et al., 2014). However, unlike the present study where coral cover differed between habitats, and hence exposure, coral cover was similar across exposure gradients in Noble et al. (2014). Such species-specific responses are probably not surprising as feeding rates of obligate corallivores are known to vary among species (Gregson et al., 2008; Pratchett et al., 2014) due to different diet compositions, selectivity, and specialization (Pratchett, 2007). The consistency in the feeding behavior traits evaluated here despite variation in the underlying coral cover and assemblage-level corallivory is noteworthy. This suggest that obligate corallivores as a feeding guild need to maintain a relatively high feeding intensity, compared to facultative corallivores and non-coral feeders (Gregson et al., 2008), and invest a similar amount of time foraging to meet their energetic demands across the spatial scales. This may in turn explain the limited variation in total corallivory among reefs. It is also possible that habitats and reefs are poor explanatory variables, at least for the two components of feeding behavior evaluated in this study (i.e., intensity and duration). Indeed, the results of the SEM in the present study identify several factors that are more mechanistically linked to the overall corallivory of reef sites.

Contrasting reef assemblages between GBR and TS sites

The initial aim was to compare assemblage-level corallivory and benthic communities among the four reefs studied. However, the unique assemblage-level corallivory among the TS sites, constituted mainly of a single species, *C. aureofasciatus* (Goldstripe Butterflyfish), has led to further investigation of reef assemblages at Masig Island separately from the other three reefs on the GBR. Despite being an obligate corallivore, this species has a more general diet, enabling persistence in the face of severe loss of live coral cover (Pratchett et al., 2006). Moreover, it can thrive in habitats with limited access to acroporid corals and preferentially selects *Porites* (Emslie et al., 2010; Pratchett, 2007), which aligns with the characteristics of benthic communities at Masig sites with high covers of massive *Porites* and soft coral, typical of a turbid environment similar to inshore reefs on the central GBR (Osborne et al., 2013), where few obligate corallivores can survive. In contrast, corallivory at Lizard, Davies, and Heron sites on the GBR is performed by a higher diversity of corallivore assemblages than Masig sites in the TS, with the former supported by higher cover of acroporid corals, which are the major diet preferentially selected by corallivorous butterflyfishes (Pratchett, 2005; Pratchett, 2007). The finding of less speciose corallivore assemblages in the TS than GBR sites seems contradictory to the general prediction of increasing species richness with latitudes (Diamond & Roy, 2023), suggesting the influence of other major factors, which, in this study, are likely the high turbidity from local sources in the central TS (Harris & Baker, 1991).

Direct influences of feeding behavior and richness of corallivores on total corallivory

Total corallivory at GBR sites was directly and positively influenced by feeding intensity, event duration, and the

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richness of corallivores, with richness emerging as the strongest predictor. Corallivorous butterflyfishes often live in sympatry with high dietary overlap among species and limited niche partitioning (Pratchett, 2005), suggesting stronger interspecific competition as richness increases. However, competition can be mitigated through differences in selectivity (Pratchett, 2007) or when the shared resource is not limited (Munday et al., 2001). Although highly specialized butterflyfishes (e.g., *C. trifascialis* and *C. baronessa*) may defend territories and display aggression toward subordinate species (Berumen & Pratchett, 2006), the heterogeneous distribution of corals permits subordinate species to access resources, known as the incomplete competitive exclusion (Pratchett, 2005). Thus, the diverse and abundant acroporid corals at GBR sites likely meet the energetic demands of multiple species, mitigating competition and underpinning the positive relationship between corallivory rates and species richness.

Aside from the numerical characteristic of corallivore assemblages (i.e., richness), this study has also identified the two components of feeding behavior as important positive drivers of total corallivory, with higher rates associated with more intense and prolonged feeding bouts among the GBR sites. This demonstrates that individual behaviors can directly scale up to influence total corallivory across all corallivorous fishes when coral prey is diverse and abundant. Comparable links between feeding behavior and ecosystem function have also been reported for herbivory, but through a different mechanism, where macroalgal removal increases with the proportion of group-feeding bites (Hyndes et al., 2013). In contrast to patterns evident at the GBR sites, total corallivory at the TS sites is not driven by either feeding behavior or assemblage metrics of corallivores, likely reflecting the near-monospecific corallivory pattern, where the community response is largely driven by numerical properties of a single species.

Direct and indirect influences of coral availability on total corallivory, feeding behavior, and assemblage of corallivores

Common coral prey had direct effects on all the corallivore-related variables, including the total corallivory rates, feeding behavior, and assemblages, among the GBR and TS sites. However, the response and magnitude of changes varied between the two regions. Different morphologies of acroporid corals had positive effects on total corallivory, feeding intensity, and event duration among the GBR sites. As expected, when acroporid corals are more abundant, feeding intensity and duration increase as they comprise the major diet of corallivores and are preferentially selected (Pratchett, 2005; Pratchett, 2007). This aligns with the positive relationship between species-specific bite rates and resource availability in a previous study (Blowes et al., 2017). Moreover, butterflyfish spend more time defending territories and foraging than exploring (Gunn et al., 2022), especially the highly specialized species, whose territories are inversely associated with food density (Berumen & Pratchett, 2006; Irons, 1989). Therefore, they become more spatially aggregated with higher covers of preferred coral prey, resulting in a higher total number of corallivorous bites per unit area.

Apart from the direct positive effect of tabular *Acropora* on total corallivory, arborescent and corymbose *Acropora* have indirect positive effects on total corallivory mediated by the richness and feeding behavior of corallivores. The positive effect of acroporid corals on the richness of corallivores aligns with the findings from a long-term monitoring study on butterflyfish across the GBR (Emslie et al., 2010) and a broad-scale study across the Indo-Pacific (Darling et al., 2017). In contrast, massive *Porites* and *Pocillopora*, instead of acroporid corals, are found to be the main positive predictors of corallivore richness and biomass among our TS sites. Massive *Porites* and soft coral dominated the coral composition in this region, and the cover of acroporid corals was low, failing to support diverse corallivore assemblages. As such, the same positive effect of acroporid corals on total corallivory observed among GBR sites was not present among TS sites. Instead, total corallivory among the TS sites was only negatively associated with the cover of *Montipora*. This coral prey comprises much smaller portions of the diet of the dominant corallivore, *C. aureofasciatus*, and is less preferred than *Porites* and *Acropora* (Pratchett, 2005; Pratchett, 2007). Furthermore, coral availability has limited effects on corallivore feeding behavior among the TS sites. The only exception is the negative effect of tabular *Acropora* on event duration despite its low cover (<0.5% on average) in benthic communities, which is likely driven by the shelter provided for large piscivores (Kerry & Bellwood, 2015), but it is contradictory to the positive relationship between event duration and the biomass of piscivores discussed in the following section.

Limited influences of predation risk on total corallivory and corallivore feeding behavior

Our prediction that the local risk profile (predation pressure and structural environment) would influence

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corallivory via non-consumptive effects generally did not hold. While the structural complexity of sites in the GBR was positively related to the cover of three of the six most abundant coral prey, and this complexity was positively related to feeding intensity. These growth coral forms (in particular tabular corals) have been shown to serve as resting and ambush habitats for large reef fish (Kerry & Bellwood, 2012). The elevated feeding intensity may, therefore, be driven by a potential increase in the risk of predation in these high complexity areas. We did find a positive effect of tabular *Acropora* on the biomass of piscivores among the TS sites, however, this was not observed among the GBR sites. Combined with the absence of negative effects of the biomass of piscivores on any of the corallivore-related variables examined in either region suggests that the observed variability in feeding intensity was not strongly related to predation risk. Indeed, the majority of mortality of butterflyfish has been shown to occur early in the life stages, with limited mortality of adult individuals (Leahy et al., 2016). Moreover, most piscivore (~68%) recorded in this study are diurnal benthic piscivores (e.g., grouper and coral trout, Mihalitsis & Bellwood, 2019), which rarely consumed butterflyfish (Kingsford, 1992; St John, 1999).

The biomass of piscivores had an unexpected positive effect on event duration among the TS sites. This positive relationship appears spurious as it is driven by the two outliers with the highest piscivore biomass measured on the same transect (Appendix S1: Figure S2), turning negative and nonsignificant once the outliers are excluded. While no negative effect of predation risk on corallivores was found in this study, the biomass of piscivores has been shown to be negatively related to the feeding rate of an herbivorous fish but not its space use (Davis et al., 2017). However, another study using a fiberglass model of a grouper to simulate acute predation risk to herbivorous fish found increased feeding rate but decreased overall herbivory and changes in size structure (Catano et al., 2016). Therefore, combining both acute and chronic predation risks (Madin et al., 2010) with information on size structure may help better understand the effects of the landscape of fear (Gaynor et al., 2019) on corallivores. Alternatively, the lack of a detectable predator effect may stem from the limited scale of our UVC transects (~300 m^2 per site). Some piscivorous species are highly mobile with large home ranges. For example, the common coral trout (*Plectropomus leopardus*) has home ranges of up to 2000 m^2 and can travel up to 7.5 km (Samoilys, 1997). Consequently, our sampling effort of two transects per site may not have effectively sampled the local piscivore assemblage at each site.

CONCLUSIONS

This study shows that the corallivory function provided by obligate corallivores is quite consistent across coral reefs but varies by benthic habitats, likely reflecting differences in exposure. Furthermore, with an integrative and rigorous modeling approach, this study has highlighted the strong influence of not only the richness but also the feeding behavior of corallivores in driving the overall corallivory on a reef, and reaffirmed the bottom-up effects of coral availability on corallivory, feeding behavior, and assemblage of corallivores. This study has also shown little evidence that predation risk and reef structure are driving risk-mitigation behaviors, which then influence overall corallivory. In the context of coral loss following climate change, the current finding suggests that there will be consequences not only on the assemblage characteristics but also on the function and behavior of corallivores. Overall, this work contributes to better understanding of the spatial and ecological drivers of corallivory. Harnessing these ecological processes can play a crucial role in developing effective reef management strategies and restoration projects (Ladd et al., 2018).

AUTHOR CONTRIBUTIONS

Tsai-Hsuan Tony Hsu: Writing—original draft; conceptualization; data curation; investigation; methodology; validation; visualization; formal analysis. **Andrew S. Hoey:** Writing—original draft; conceptualization; investigation; methodology; validation; resources; funding acquisition; supervision. **Renata Ferrari:** Writing—review and editing; investigation; resources; funding acquisition. **Maren Toor:** Writing—review and editing; investigation. **Sophie Gordon:** Writing—review and editing; investigation. **Tiny Remmers:** Writing—review and editing; investigation. **James Smallhorn-West:** Writing—review and editing; investigation. **Agustina Piccaluga:** Writing—review and editing; investigation. **Will F. Figueira:** Writing—original draft; conceptualization; investigation; methodology; validation; resources; funding acquisition; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Hsu, Hoey, Ferrari, et al., 2026) are available from Sydney eScholarship: https://doi.org/10.25910/hevd-0g28. R script (Hsu, 2026) is available from Zenodo: https://doi.org/10.5281/zenodo.22102838.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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