Coral Reefs
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RESEARCH

Daily feeding rates of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) vary with body size and coral cover across the Great Barrier Reef

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Abstract The ecological effects of high densities of crown-of-thorns starfish (CoTS, *Acanthaster* spp.) are driven by their cumulative feeding pressure on coral assemblages, making accurate predictions of feeding impacts essential for management. Despite this, a limited understanding of the spatiotemporal dynamics of feeding behaviour, and the environmental and biological drivers underlying them constrains our capacity to predict feeding impacts. We quantified daily feeding rates for 565 individual Western Pacific CoTS (*Acanthaster* cf. *solaris*) across a broad gradient of environmental conditions and population densities on Australia's Great Barrier Reef (GBR). CoTS body size and local coral cover emerged as the strongest predictors of daily feeding rates, whilst population density, season, and water temperature had no significant effect. Notably, large CoTS (>40 cm) at high coral cover sites consumed over ten times more coral tissue compared to smaller individuals (15–25 cm) at low coral cover sites, with mean daily consumption rates of 221.99 and 18.86 cm^2 (planar area), respectively. These estimates of daily feeding are aggregated across all different coral genera consumed. We present estimates of daily feeding rates for different size classes and coral cover that are directly compatible with existing monitoring methodologies used on the GBR, providing ecologically relevant parameters to improve outbreak impact modelling and enable more accurate forecasting of coral loss for targeted CoTS control on the GBR.

Keywords Crown-of-thorns starfish · Feeding ecology · Ecosystem management · Great Barrier Reef

Introduction

Crown-of-thorns starfish (CoTS, *Acanthaster* spp.) are highly effective and efficient coral feeders (Birkeland 1989), capable of consuming and thereby killing large quantities of reef-building hard corals (order Scleractinia). At low densities of CoTS, the net ecological effect of their feeding is negligible, especially in areas with higher cover of fast-growing corals (Glynn 1974; Pratchett et al. 2009; Plagányi et al. 2020). However, at very high densities, during population outbreaks (Chesher 1969; Kayal et al. 2012), the cumulative effects of their feeding can be substantial and cause severe and widespread coral depletion (Birkeland and Lucas 1990; Pratchett 2010; Tkachenko and Hoang 2022). The occurrence and ecological impacts of population outbreaks tend to vary regionally, possibly reflecting interspecific differences in the biology and behaviour of CoTS (Kettle and Lucas 1987; Pratchett et al. 2017; Foo et al. 2024), of which there are at least five species with generally distinct geographic ranges (Uthicke et al. 2024).

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Population outbreaks of the Western Pacific CoTS (*Acanthaster* cf. *solaris*) are one of the foremost contributors to coral reef degradation in the Western Pacific (Bruno and Selig 2007; Mellin et al. 2019; Pratchett et al. 2021), compounding upon other increasing disturbances, such as mass coral bleaching causing coral loss and shifts in coral composition. *Acropora* spp., in particular, are sustaining major losses, as both the preferred prey of CoTS (De'ath and Moran 1998b; Pratchett 2007), and one of the most susceptible taxa to climate-induced mass coral bleaching (e.g. Loya et al. 2001) and severe tropical storms (Madin and Connolly 2006; Keesing et al. 2019). Whilst these fast-growing corals have traits that allow for rapid recovery following disturbance events (Emslie et al. 2026), the confluence of major population outbreaks of CoTS and mass coral bleaching has led to extensive and rapid depletion of *Acropora* corals in some areas (Foo et al. 2024, Garing et al. 2026), leading to regional shifts in the structure of coral assemblages (Pratchett 2010, 2020). Effective CoTS management is therefore crucial for minimising coral reef degradation and enhancing reef resilience in the face of escalating environmental change (Condie et al. 2021; Castro-Sanguino et al. 2023).

CoTS have evolved extremely efficient feeding mechanisms for feeding on hard corals, everting their stomachs to simultaneously digest large areas of coral tissue (Brauer et al. 1970; Birkeland and Lucas 1990). When everted, the stomach covers a planar area roughly equivalent to the size of the oral disc (Birkeland and Lucas 1990), though it can effectively cover highly complex surfaces, such that the overall tissue surface area consumed increases with the three-dimensional complexity of corals (Chandler et al. 2025). Corresponding increases in the tissue surface area of coral that is consumed may explain CoTS feeding preferences for complex corals, and especially tabular and corymbose *Acropora* spp. (Keesing 2021). Despite the important ecological effects that result from CoTS feeding, few studies have directly quantified individual daily feeding rates. Initial estimates of feeding rates (378 $cm^2.day^{-1}$, Chesher 1969; 150 $cm^2.day^{-1}$, Glynn 1974) were derived from broad-scale assessments of cumulative coral loss, which were then standardized by local densities of adult CoTS. While valuable as first approximations, these estimates were inherently coarse, relying on population-level losses rather than direct observations of individual feeding behaviour. This limitation was addressed by Keesing and Lucas (1992), who followed individually tagged CoTS and quantified feeding activity by measuring the linear dimensions of recent feeding scars, which are conspicuous for the first few days following a feeding event (Chandler et al. 2025). This approach provided more detailed data on both the number and size of corals consumed by individual starfish, expressed as the two-dimensional planar area of coral killed, and enabled rates of coral loss from CoTS feeding to be assessed relative to available coral cover (Plagányi et al. 2020). Although more precise than earlier methods, this study did not account for variation among individuals, populations or regions, or capture three-dimensional extent of coral tissue consumed, somewhat limiting our ability to interpret impacts of feeding. Critically, feeding rates are likely to scale with body size, reflecting increased metabolic rates (Kettle and Lucas 1987).

Research on the feeding behaviour of CoTS has progressed since the 1990s (Foo et al. 2024; Millican et al. 2024), although many knowledge gaps still remain (Pratchett et al. 2021, 2026). Recently, Chandler et al. (2025) provided new insights into daily variation in the feeding behaviour of CoTS over successive days using highly resolved methodologies afforded by underwater close-range photogrammetry. The study reported mean daily feeding rates of 198.4 $cm^2.day^{-1}$ ($\pm$23.86 SE), based on the planar area of different corals consumed, but highlighted significant individual variation. Most importantly, it was apparent that individual CoTS do not necessarily feed every day. Whilst this was an important contribution to our knowledge of CoTS feeding potential and strategies, this intensive tracking study was limited to a small number of CoTS (n = 8) and conducted at one location (Lizard Island, northern GBR). Feeding rates of CoTS are, however, likely to be influenced by intrinsic (e.g. metabolic demands of starfish; Kettle and Lucas 1987) and extrinsic (e.g. quantity and quality of food available) factors (Wright et al. 2005), and expected to vary over a continuum of biological and environmental conditions (Keesing and Lucas 1992). Previous large-scale comparisons of CoTS activity patterns (De'ath and Moran 1998a) and feeding preferences (De'ath and Moran 1998a) revealed limited differences among reefs in the southern GBR. Rather, activity patterns were influenced mainly by CoTS size and time of day (De'ath and Moran 1998a), whereas feeding preferences were largely dependent on CoTS densities and relative availability of different prey corals (De'ath and Moran 1998b). These studies did not explicitly consider individual feeding rates, but suggested that feeding behaviour of *A.* cf. *solaris* is likely to be very consistent over wide geographical scales and latitudinal gradients ((De'ath and Moran 1998a).

This study aimed to assess large-scale (regional) variation in daily feeding rates of *A. cf. solaris* to explore spatial, seasonal, and other individual- and environmental-level drivers, as well as potential density-dependent effects. This study builds upon information presented in previous studies (Chandler et al. 2024, 2025) to derive estimates of feeding rates from instantaneous estimates of the size of feeding scars, which is necessary to facilitate large-scale estimates and comparisons. More specifically, linear measurements of feeding scares are converted to 2D planar area and 3D tissue surface area using conversions derived for 15 different morphotaxa (Chandler et al. 2024). Estimates of the size of feeding scars are then aggregated

across different corals to calculate daily feeding rates of individual CoTS. In addition to investigating drivers of daily feeding rates, these data will provide insights into how CoTS balance feeding trade-offs under varying coral cover and population density regimes, and the implications for energetic intake and, ultimately, population dynamics. Keesing and Lucas (1992) showed that feeding rates of CoTS varied among individuals depending on body size and season. However, feeding rates will also be dependent upon the distribution, abundance and composition of coral prey (Burn et al. 2020). Understanding how feeding rates vary under different conditions is central to understanding the cumulative ecological impacts of CoTS, especially during severe population outbreaks. This is critical for establishing and projecting the relative contribution of CoTS to ongoing coral loss and reef degradation (Condie et al. 2021; Castro-Sanguino et al. 2023), and guiding the prioritization of management interventions.

Methods

Field surveys

To test for large-scale differences in the feeding behaviour of *A.* cf. *solaris*, Scooter-Assisted Large Area Diver-based (SALAD) surveys were conducted (Chandler et al. 2023) across five distinct regions of the central, northern and far northern GBR (Townsville, Cairns, Lizard, Princess Charlotte Bay and Cape Grenville; Fig. 1) between March 2023 and March 2024. These regions differed not only in CoTS densities and average body size, but also had marked

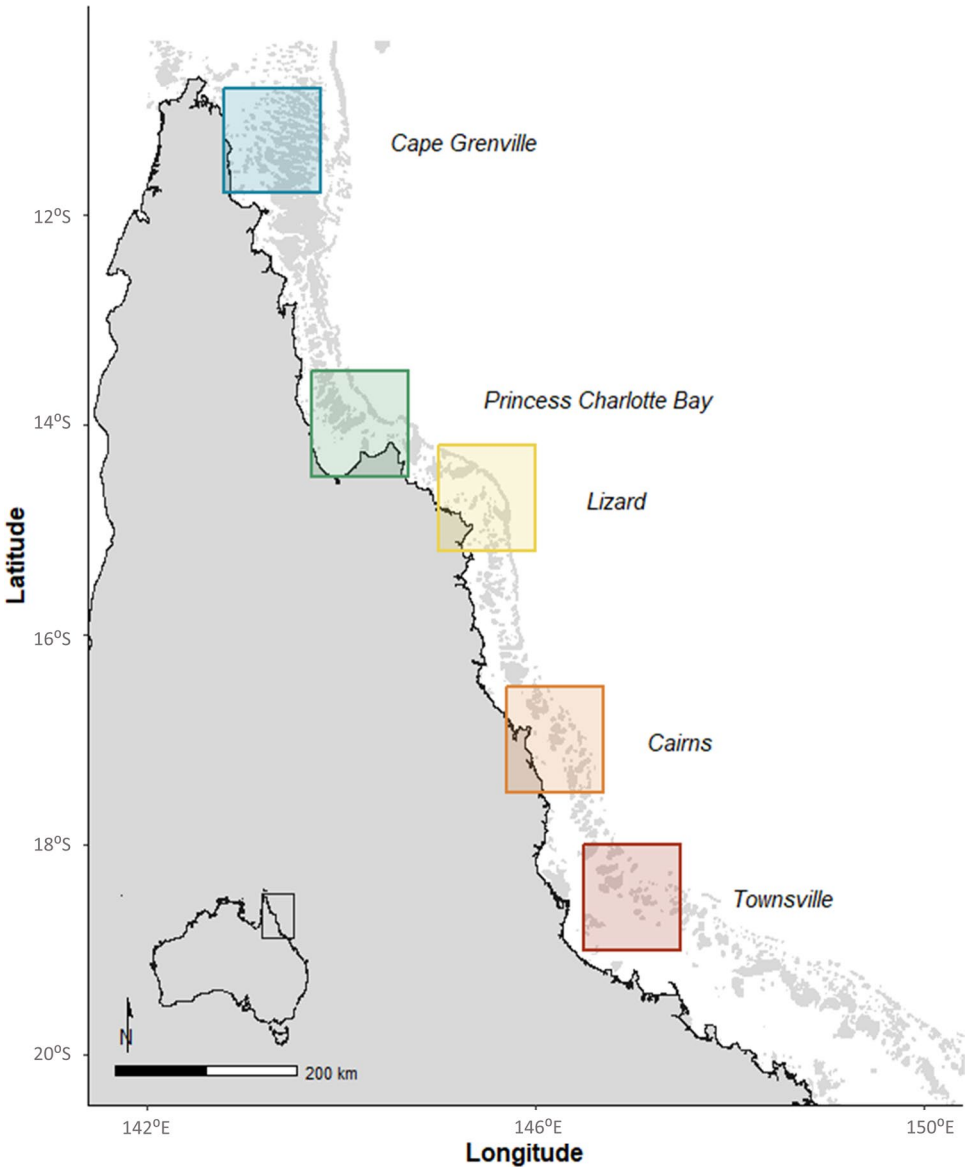

Fig. 1 Map of the central and northern Great Barrier Reef, showing five distinct regions (Cape Grenville, Princess Charlotte Bay, Lizard, Cairns and Townsville) where sampling was undertaken in 2023–2024 (for specific reefs surveyed in each region see Supplementary Material; Table S1). SALAD surveys were used to collect feeding data across this wide latitudinal gradient

differences in coral cover and composition (Table 1). Data collected in May–October, when water temperatures were 24–26^{0}C were classed as 'Winter', whilst data collected from November–April, where water temperatures were 27–31^{0}C were classed as 'Summer'.

SALAD surveys were conducted at 3–5 reefs within each region (Supplementary Material; Table S1), with the choice of reefs and sites largely determined by logistics and accessibility. During each SALAD survey, the detection of conspicuous clusters of feeding scars triggered a thorough search of the local environment to locate the responsible starfish and to rule out feeding by multiple individuals or alternative sources of coral mortality (e.g. coral disease or predation by *Drupella* spp.). Feeding data were only recorded when scars could be confidently attributed to a single starfish feeding in isolation, which made it challenging to collect such data in areas with very high CoTS densities.

For each CoTS detected, maximum diameter was measured, and associated fresh feeding scars were recorded. Fresh scars were defined as coral colonies showing clear evidence of recent consumption (tissue sloughing, mucous coverage, or bare white skeleton not yet overgrown by turf algae; Chandler et al. 2025). Each fresh scar was identified to coral genus, and its maximum diameter measured with a flexible tape. From these linear dimensions, two-dimensional planar area and three-dimensional surface area estimates were calculated using genus-specific calibration curves (see below).

Daily feeding rates were then estimated for each starfish based on the number and cumulative areal extent of attributable scars. The number of days over which scars were assumed to have been produced was standardized according to scar persistence; 5 days during summer surveys (November–April) and 7 days during winter surveys (May–October) (Chandler et al. 2025).

SALAD surveys provided estimates of CoTS densities (Chandler et al. 2023), which were used to test for density-dependent variation in feeding behaviour (especially daily feeding rates). Coral cover and composition were also recorded at the start and end of each SALAD survey using 50 m Point Intercept Transects (PIT) with data averaged over the two transects. The benthic substrate directly beneath the transect line was recorded at 50 cm intervals, with scleractinian corals identified to genus. Body size of CoTS and also average coral cover were treated as a categorical variables to enable direct assessment of interactions between size class and coral cover. The PIT data for total coral cover for each survey site were placed into one of four coral cover categories ($\leq 15\%, > 15\%$ to $\leq 30\%, > 30\%$ to $\leq 50\%, > 50\%$) and *Acropora* categories ($\leq 10\%, > 10\%$ to $\leq 30\%, > 30\%$). Similarly, CoTS were placed into one of four body size categories (≤ 15 cm, > 15 cm to ≤ 25 cm, > 25 cm to ≤ 40 cm, > 40 cm). These size categories are the same as those used by the GBR CoTS culling teams when collecting size-structure data, ensuring our predicted feeding rates can be readily applied to management datasets.

Converting field measurements to 2D/3D surface area

Daily feeding rates were explored using three different metrics; i) number of coral colonies, ii) combined planar (2D) area (cm^2) of all feeding scars, and iii) total (3D) tissue surface area (cm^2) of all feeding scars, following Chandler et al. (2025). To estimate the 2D and 3D surface area of feeding scars, we used empirically derived calibrations for each of 15 distinct morphotaxa (Chandler et al. 2024) to convert measurements of the maximum diameter of the scar (cm), into projected (2D) planar area (cm^2), and total (3D) tissue surface area. Estimates derived from calibration curves inherently contain uncertainty, as the empirical relationships between coral scar diameter and measured 2D and 3D surface area exhibited residual variation not explained by the model (Chandler et al. 2024). However, it would not have been possible to directly and accurately measure the 2D and 3D surface area of all feeding scars recorded herein ($n > 2{,}600$ feeding scars), whilst the use of existing calibration curves provides an opportunity to explore regional differences in these different metrics of feeding rate.

Data analyses

Generalized linear mixed effects models (GLMM) were fitted to investigate environmental and biological drivers of individual differences in daily feeding rates among all CoTS ($n = 565$). Separate GLMMs were fitted for each of

Table 1 Summary of sampling effort and selected ecological variables at each region, including the range of values recorded. Population density data was collected via SALAD surveys, coral cover data were collected using 50 m PIT ($n = 2$) per SALAD survey

Region	Total coral cover (%)		*Acropora* cover (%)		CoTS Density (ha^{-1})		CoTS Diameter (cm)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Cape Grenville	27.40	10.73–45.00	9.79	0.00–33.00	17.94	1.92–37.5	393.06	180–550
Princess Charlotte Bay	36.53	18.01–52.14	17.65	2.72–44.41	17.25	1.70–33.74	291.29	120–450
Lizard	46.04	12.71–90.34	28.75	6.17–75.75	27.88	2.89–61.11	430.99	110–660
Cairns	21.88	13.18–38.92	4.18	2.16–5.78	6.38	5.96–8.96	384.34	270–500
Townsville	27.07	5.65–48.88	19.90	0.00–44.00	30.80	1.96–73.68	335.57	10–620

the three metrics (number of colonies, projected surface area and total tissue surface area). All feeding rate data were log-transformed to meet normality assumptions and back transformed for presentation of results. Data were modelled against a gaussian distribution with an identity link function.

Given the range of possible predictors, Boosted Regression Tree (BRT) machine learning algorithms were performed for GLMM variable selection. The full set of predictor variables considered were CoTS body size, population density, total coral cover (%), *Acropora* cover (%), season, month, water temperature, latitude, region and reef. GLMM variable selection processes were conducted separately for each of the three measures of daily feeding rate (number of colonies, planar area and 3D surface area); however, the same set of predictors were retained in each case. BRT analysis indicated that season, month and latitude had minimal influence on daily feeding rates and were therefore excluded from the final models. CoTS body size, population density and coral cover had the strongest relative influence for all three feeding rate metrics. For continuous predictors (CoTS body size, population density, total coral cover, *Acropora* cover), data were categorized into discrete bins to facilitate the generation of model-derived feeding estimates, which would be a key output of this study for ecological modelling, and also to allow for assessment of interactions between variables. The variable selection process for each of the three models is detailed in the Supplementary Material (Table S2, S7, S12).

Relevant combinations of fixed and random effects were tested and retained only if they improved the fit of the GLMM model, based on the Akaike Information Criterion (AICc) (Supplementary Material; Table S3, S8, S13). The model that was selected (lowest AIC score) included: CoTS body size category, total coral cover category and population density category (with no interactions), with site as a random effect with random intercepts. Neither season nor *Acropora* cover improved model fit (AIC score) and were therefore excluded; however, it is noteworthy that *Acropora* cover resulted in a model with only a marginally lower AIC score (within 2 units). Total coral cover and *Acropora* cover data in this study were strongly positively correlated ($R^2 = 0.77$, $F = 1914$, $df = 1, 548$, $p < 0.001$) so were not included within the same model.

Tukey's pairwise comparisons were calculated using estimated marginal means to test for significant differences in feeding rates between groups (coral cover categories and size categories). A 95% confidence interval (CI) was generated for pairwise comparisons. Values where no overlap in CI occurred were considered to be statistically significant. Predicted daily feeding rates were calculated and plotted for combinations of size and coral cover categories whilst holding density constant. Predictions were generated using the emmeans package in R (Lenth, 2023), and visualized with ggplot2 (Wickham 2016).

Models were fitted in R (v4.3.1; R Core Team 2021) using the glmmTMB package (Brooks et al. 2017). Model diagnostics were assessed with the DHARMa package (Hartig 2018), which indicated no major violations of distributional assumptions or overdispersion and confirmed adequate model fit. Figures were produced using the ggplot2 package (Wickham 2016).

Results

Sampling effort

Daily feeding rates were quantified for a total of 565 individual CoTS from 208 SALAD surveys conducted at 24 reefs across the five regions on the GBR. Feeding rates were calculated by measuring more than 2,600 feeding scars associated with the 565 CoTS. Environmental conditions varied markedly among and within regions (Table 1). Coral cover ranged from 5.66% at Lynchs Reef (Townsville region) to 90.34% at Eagle Reef (Lizard region), with *Acropora* cover spanning 0–75.11%. CoTS densities varied by more than two orders of magnitude, from just 1.69 CoTS·ha^{-1} at Corbett Reef (Princess Charlotte Bay region) to 73.68 CoTS·ha^{-1} at Banfield Reef (Townsville region). Temperature varied with season and latitude, from 24 °C at John Brewer Reef (Townsville region) in winter to 31 °C at Lizard Reef (Lizard region) in summer. Notably, contrasting site conditions were observed, including reefs with high coral cover and low CoTS densities (e.g. Hopkinson Reef in the Townsville region) and reefs with both high coral cover and high CoTS densities (e.g. Eagle Reef in the Lizard region). This variation provided strong contrasts for evaluating the relative influence of coral cover and population density on feeding rates. Although the study employed a regional sampling design, feeding rates were analysed in relation to the continuous environmental variables that exist across the range of reefs sampled.

Daily Feeding rates

For all three feeding metrics (number of colonies, 2D planar area and 3D tissue surface area), CoTS body size was the strongest and most consistent predictor ($p < 0.001$), with feeding rates increasing markedly from the smallest to the largest body size classes (Fig. 2). Population density had no significant effect on feeding rates for any metric ($p > 0.05$). Coral cover showed a positive relationship with feeding rates when expressed as 2D planar area and 3D tissue surface area, but not when measured as the number of colonies predated on (Supplementary Material; Figure S4).

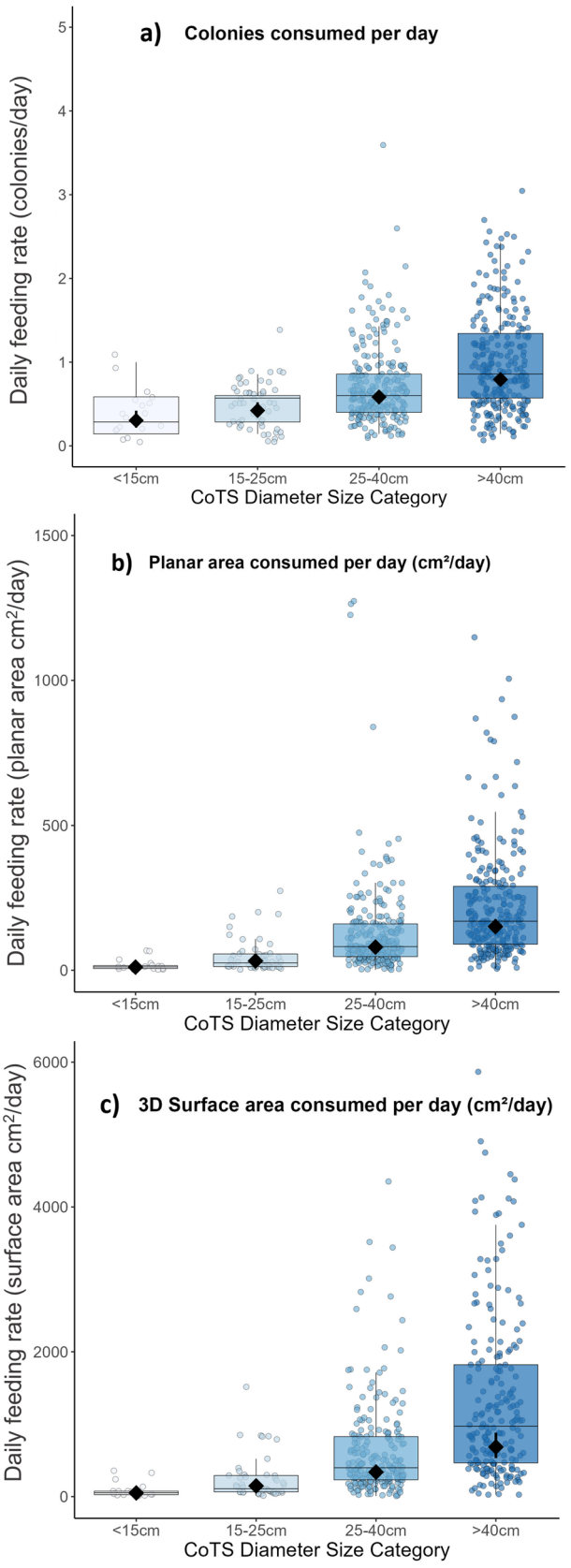

Fig. 2 Box plot of daily feeding rates for CoTS in different size classes for **(a) number of colonies**, **(b) 2D planar area** (cm^2 day^{-1}) and **(c) 3D tissue surface area** (cm^2 day^{-1}). Data are based on the overall number and extent of feeding scars attributed to each individual CoTS, considering all different (15) morphotypes of coral prey. Predicted means are shown as black diamonds. Observed daily feeding rate data recorded for each starfish are also presented as individual points. Boxes and whiskers display 25-75th and 5-95th percentile ranges of true data, respectively, thick lines indicate median values

Number of coral colonies

The predicted number of colonies preyed upon among all starfish was 0.81 colonies.day^{-1} ± 0.02 SE (range: 0.14–3.6), with the model explaining 16.1% of the variation (13.3% from fixed effects). Pairwise contrasts found significant size-based differences between most size classes (Supplementary Material; Tables S6, S11, S16), but coral cover and population density had no detectable effect on the number of colonies predated on ($p > 0.05$).

Planar (2D) area

The predicted daily planar area consumed among all starfish was 164.04 cm^2.day^{-1} ± 8.30 SE (range: 1.58–2,135.29 cm^2 day^{-1}), with 43.8% of the model variation explained (35.8% from fixed effects). Estimated marginal means of predicted planar daily feeding rate increased for each body size class (Fig. 2; Supplementary Material; Tables S5, S10, S16). Coral cover category had a significant positive effect on predicted planar daily feeding rate ($p < 0.05$); however, post hoc analysis revealed that significant differences were only observed between the highest coral cover category (> 50%) and all other categories (> 50%/0–15%, $p = 0.03$; > 50%/15–30%, $p = 0.04$; > 50%/30–50%, $p = 0.01$).

Tissue (3D) surface area

The predicted daily 3D tissue surface area consumed among all starfish was 900.46 cm^2.day^{-1} ± 42.93 SE (range: 8.00–7,420.72 cm^2 day^{-1}), with 43.5% of variation explained (34.0% from fixed effects). Estimated marginal means of predicted 3D daily feeding rate increased for each body size class (Fig. 2; Supplementary Material; Tables S5, S10, S16). Coral cover had a significant positive effect ($p < 0.05$) on 3D daily feeding rate; however, significant differences were only observed between the highest coral cover category (> 50%) and categories 0–15% ($p = 0.03$) and 30–50% ($p = 0.03$). There was no significant difference between the highest coral cover category and category 15–30% ($p = 0.11$).

To facilitate application of these findings in outbreak forecasting and management, we generated predictive daily feeding rates from GLMM modelled data for each combination of CoTS size class and coral cover category, which are presented in Fig. 3 and Table 2. These values allow direct estimation of cumulative feeding pressure for populations where size structure and local coral cover are known, providing a more accurate basis for modelling ecological impacts

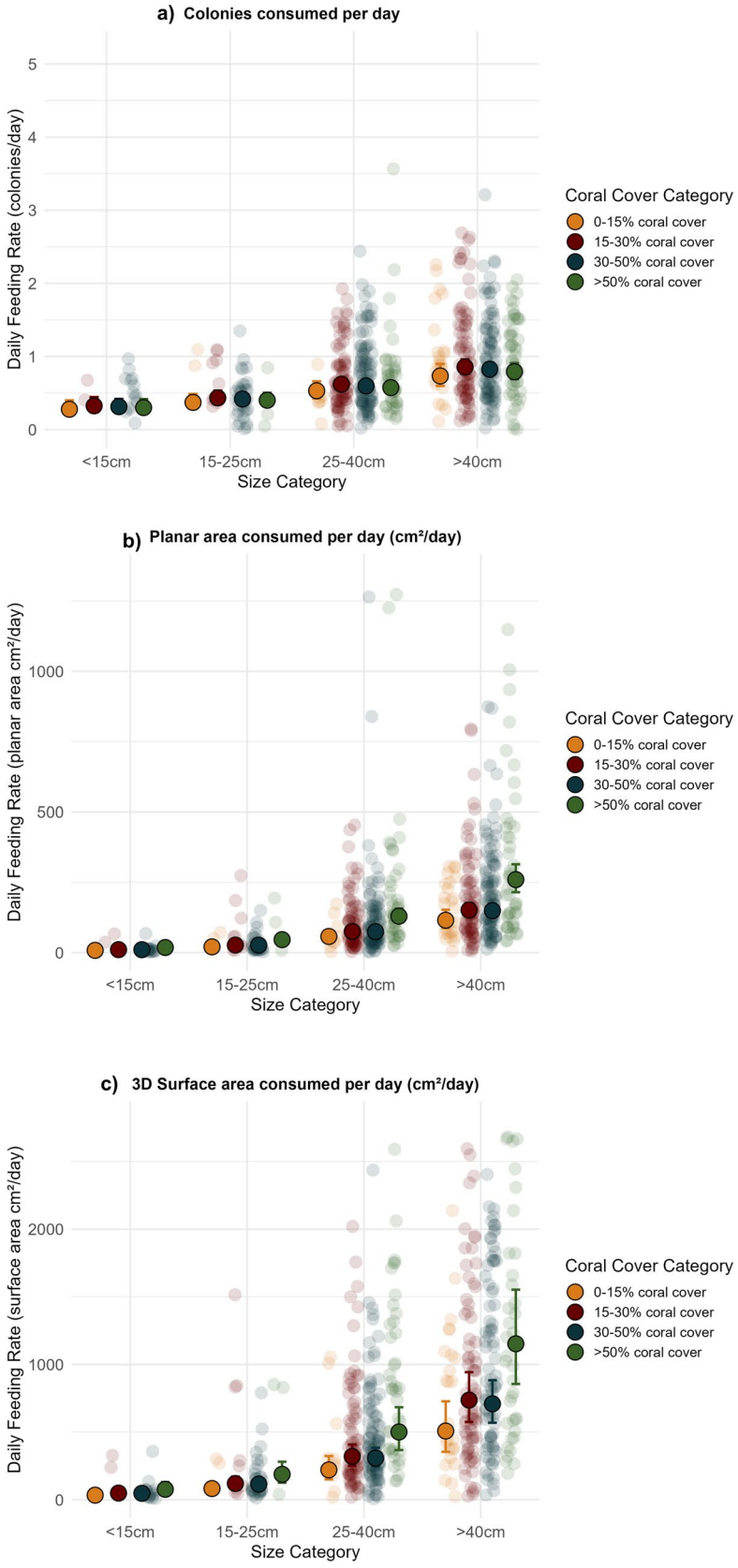

Fig. 3 Daily feeding rates for CoTS, showing variation due to prey availability (coral cover) within different size classes for **(a) number of colonies**, **(b) 2D planar area** (cm^2 day^{-1}) and **(c) 3D tissue surface area** (cm^2 day^{-1}). Dark coloured points with error bars represent the predicted value and 95% confidence intervals, faded points represent raw daily feeding rate data for individual starfish (see also Table 2)

Table 2 Predicted values of daily feeding rate from GLMM modelled data. Modelled feeding rates are provided for different size categories of CoTS (rows) and coral cover categories (columns). Daily feeding rate is presented as **a) Number of colonies** consumed per day, **b) Planar (2D) area** of coral consumed per day (cm^2) and **c) total (3D) surface area** consumed per day (cm^2)

	0–15% Coral cover			15–30% Coral cover			30–50% Coral cover			> 50% Coral cover		
Diameter (cm)	Prediction	Lower CI	Upper CI	Prediction	Lower CI	Upper CI	Prediction	Lower CI	Upper CI	Prediction	Lower CI	Upper CI
A) Number of colonies												
15-25	0.38	0.28	0.52	0.41	0.32	0.53	0.40	0.33	0.50	0.38	0.29	0.50
25-40	0.53	0.41	0.68	0.57	0.49	0.68	0.56	0.48	0.65	0.53	0.43	0.64
> 40	0.75	0.59	0.94	0.81	0.68	0.97	0.79	0.68	0.92	0.75	0.62	0.90
B) Planar (2D) area												
15-25	18.86	12.45	28.59	23.25	16.49	32.76	22.61	16.67	30.66	36.73	25.14	53.67
25-40	52.17	37.06	73.44	64.29	50.80	81.38	62.53	50.91	76.80	101.59	76.97	134.09
> 40	114.00	82.58	157.38	140.49	110.37	178.83	136.64	111.26	167.81	221.99	169.95	289.97
C) Total (3D) tissue surface area												
15-25	84.60	54.61	131.04	121.16	84.43	173.87	114.89	83.37	158.34	191.40	128.42	285.27
25-40	231.56	161.59	331.85	331.65	258.81	424.98	314.50	253.32	390.46	523.92	391.23	701.61
> 40	536.98	382.45	753.95	769.07	596.60	991.39	729.30	587.47	905.36	1214.92	917.20	1609.28

than uniform per-capita rates. The categories used match those routinely recorded by GBR culling teams and long-term monitoring programmes such as Great Barrier Reef Marine Park Authority (GBRMPA) and Australian Institute of Marine Science (AIMS) Long-Term Monitoring Programme, ensuring outputs are directly compatible with management datasets. Where data on both variables are not available, predicted values for size classes alone and for coral cover categories alone are provided (Supplementary Material; Table S10) to allow application across a broader range of survey datasets.

Modelled means increased considerably at high coral cover sites (> 50%) for both planar and 3D surface area estimates of feeding, a trend consistent across all size classes but most pronounced for CoTS > 40 cm (Fig. 3b,c). Feeding rates were lowest at sites with 0–15% coral cover, whilst intermediate categories (15–30%, 30–50%) showed relatively consistent feeding levels. Whilst predicted values of surface area are considerably greater at higher coral cover categories, and considerably lower at low coral cover categories, in contrast, the number of colonies predated on per day remained similar across coral cover classes and increased only with body size.

Discussion

This study revealed considerable variation in daily feeding rates among individual CoTS, which was partly explained by size-based differences in feeding behaviour. Notably, the predicted planar area of corals consumed by large CoTS (> 40 cm) at high coral cover sites (221.99 $cm^2.day^{-1}$) was 10-times higher than for smaller individuals (15–25 cm) at low coral cover sites (18.86 $cm^2.day^{-1}$). These results show that it is not appropriate to assume that cumulative feeding capacity of CoTS during population outbreaks is solely affected by population size.

The mean planar area of corals consumed by CoTS in this study (164.04 $cm^2.day^{-1} \pm 8.30$ SE) is within the range of prior estimates (198.4 $cm^2.day^{-1} \pm 23.86$ SE, Chandler et al. 2025; 194–445 $cm^2.day^{-1}$, Souter 2007; 155–234 $cm^2.day^{-1}$, Keesing and Lucas 1992; 116–187 $cm^2.day^{-1}$, Pearson and Endean 1969). However, this is at the low end of estimated daily feeding rates (Foo et al. 2024), which may reflect the inclusion of non-feeding days in the dataset (Chandler et al. 2025). Crucially, this study has demonstrated the limitations of using a population-wide feeding rate, as both environmental factors (e.g. coral cover) and individual traits (e.g. body size) were found to strongly influence feeding rates. The large variation among individual CoTS recorded within our study (where the planar area of coral consumed ranged from 1.58 to 2,135 $cm^2.day^{-1}$) demonstrates the range of factors at play, some of which cannot be accounted for (e.g. nutritional history, metabolic demands) and further, several factors are likely acting synergistically to affect the feeding behaviour of individuals.

Body size was the strongest predictor of daily feeding rates for CoTS, both in terms of total (3D) surface area, planar (2D) area and number of colonies consumed. This finding is supported by other studies recording large individuals to consume more coral in comparison with small individuals (Keesing and Lucas 1992), which is attributable to both the increased feeding potential afforded by larger body sizes as well as mass-specific increases in metabolic demands of larger individuals (Yamaguchi 1974; Kettle and Lucas 1987; Lang et al. 2021; Deaker and Byrne 2022). Large individuals have bigger stomachs and can consume a greater area of coral in a single feeding bout, but they also face reduced predation risk and are therefore less constrained when they feed (Keesing 1995; Cowan et al. 2017; Ling et al. 2020).

Total coral cover had a significant positive effect on feeding rates, with particular influence at high coral cover sites (> 50%). However, this trend was only apparent for planar area and overall 3D tissue surface area consumption, not the number of colonies predated upon. So, whilst CoTS consume more coral tissue area in high cover sites, they do not increase the number of distinct colonies that are predated upon, suggesting that it is the increased size of corals that affords greater feeding rates. Most high coral cover sites on the GBR are dominated by complex branching corals such as *Acropora*, and indeed in this study 78% of variation in total coral cover was explained by *Acropora* cover. Complex branching corals, including *Acropora* and *Pocillopora* have higher tissue surface area, compared to other corals of similar size or maximum dimensions (Chandler et al. 2024), which greatly increases the overall tissue surface area of coral consumed with each feeding bout. This increased feeding efficiency likely explains apparent preference for *Acropora* spp. (Keesing 2021), which can also have important influence on the biology (Caballes et al. 2016) and behaviour of CoTS (Ling et al. 2020). Ling et al. (2020) showed that when local abundance of *Acropora* spp. is high (> 30%), CoTS exhibit high site fidelity and conspicuous homing behaviour, but when *Acropora* cover is low, CoTS tend to roam and move large distances in search of prey. This aligns with our findings and raises questions about the energetic constraints faced by CoTS in these food-limited environments, which we know are expending more energy (searching effort) and receiving lower energetic intake (low surface area of corals) compared to CoTS in high cover environments. Living in these constrained environments is likely to have consequences for individual condition and fitness (e.g. Caballes et al. 2016) and starvation has been proposed as a key factor in the collapse of high-density populations; however, this hypothesis has never been verified in situ (Pratchett et al. 2021). Assessing the physiological condition

of CoTS in prey-depleted environments will be crucial for understanding outbreak longevity and predicting population dynamics under future scenarios where coral cover declines and structurally complex corals become rare (Pratchett 2010; Dietzel et al. 2020). If *Acropora*-dominated environments are essential for sustaining high CoTS densities, it is possible that widespread coral loss could impose natural constraints on future outbreaks.

Previous studies have suggested that feeding rates fluctuate seasonally (Keesing and Lucas 1992; Foo et al. 2024) potentially due to temperature-mediated metabolic demand (Lang et al. 2021) and seasonal gametogenesis (Lucas 1973; Keesing and Lucas 1992; Caballes et al. 2021). However, we did not find a significant effect of season or water temperature on feeding rates (see also Souter 2007). The design of our study, which spanned 8° of latitude, allowed us to investigate the effect of temperature in isolation from the gametogenetic stage by surveying across a gradient of water temperatures during the same 2-week periods. There was no evidence that feeding rate was linked to water temperature, though the temperature range was relatively narrow (2–3 °C) and there was also likely to be a multitude of other environmental factors contributing to variability over this latitudinal gradient. When data from a single site (Lizard Island) were compared between winter (25–26 °C) and summer (27–28 °C), feeding rates were moderately higher in summer, particularly during the spawning period. Resolving the effects of temperature on feeding rates is essential for understanding CoTS' feeding capacity under future climate scenarios. Laboratory studies have shown that CoTS metabolism increases with temperature (Lang et al. 2021), suggesting that energy demand and corresponding feeding rates may increase with ocean warming. If CoTS do increase their feeding rate with sustained increases in baseline ocean temperatures then this could present a double threat for corals as they face elevated thermal stress alongside increased CoTS predation rates (Haywood et al. 2019; Keesing et al. 2019). Conversely COTS may struggle to meet increased energetic demands on coral reefs with limited cover of suitable coral prey. More work in this area is necessary to predict values of daily feeding under dynamic warming scenarios.

Density-dependent feeding rates have been observed in various echinoderm species, particularly sea urchins (Benedetti-Cecchi et al. 1998; Wright et al. 2005), which can lead to significant ecological shifts. In this study, we found no significant effect of population density on daily feeding rates regardless of the method used to measure feeding. This finding aligns with Foo et al. (2024), who similarly reported no relationship between population density, outbreak status, and planar feeding rates for CoTS. One possible explanation is that the population densities observed in this study (0–73.7 CoTS.ha^{-1}, Table 1) are very moderate compared to severe outbreaks (e.g. > 1,000 CoTS.ha^{-1}; Kayal et al. 2012), and behavioural shifts may only become apparent at very high densities. Alternatively, effects of increasing population density may scale directly with size and abundance of CoTS (i.e. *per-capita* feeding rates are insensitive to density), and individual feeding rates are more sensitive to corresponding changes in the distribution, abundance and composition of prey corals. Our method of establishing feeding rates from instantaneous observations also becomes increasingly difficult at high densities, as it is not clear which individual may be responsible for different feeding scars. It may, however, be possible to simply measure the total extent of feeding scars within different sites and habitats and then divide by presumed densities, so long as detectability is also carefully considered (see Pratchett et al. 2026). This approach lacks individual resolution, but may be necessary to test for changes in feeding rates across large differences in CoTS densities.

Insights from this study highlight the critical importance of integrating environmental (coral cover and composition) and biological (body size) factors when assessing the ecological consequences of CoTS outbreaks. A key outcome of this study is the development of predictive daily feeding rates for CoTS, stratified by size class and coral cover, presented in Table 2. Derived from extensive empirical data, these predictive values of feeding represent a novel, management-ready tool for quantifying potential coral loss during outbreaks, enabling higher accuracy in CoTS impact forecasting than models that scale directly with CoTS densities. By using the same size-class categories as GBR culling teams and coral cover categories aligned with GBMPA and AIMS Long-Term Monitoring Program protocols, these predictions can be applied immediately to existing survey data to estimate cumulative feeding impacts. Where datasets are only available for one variable (either size structure or coral cover) predicted feeding rates for each variable in isolation are also provided in the Supplementary Material. Managers can therefore use these outputs flexibly, combining local population data with the relevant feeding rate values to forecast coral loss either as benthic area (2D) or tissue surface area (3D), depending on whether the goal is to project cover decline or assess energetic intake and outbreak persistence potential. With informed management decisions providing the best chance for safeguarding the resilience of the reef, this approach directly links monitoring data to actionable thresholds for intervention, providing a powerful basis for prioritizing control efforts and safeguarding reef resilience (Babcock et al. 2014).

Conclusion

Effectively predicting and modelling ecological impacts of CoTS outbreaks is contingent upon accurate assessments

of daily feeding rates *per capita*. Estimates of daily feeding which inform management decisions must account for the considerable variation in daily feeding that is associated with environmental and biological conditions. The finding that CoTS body size is the strongest predictor of feeding rate, whilst population density had no significant effect, challenges conventional outbreak models that assume a uniform *per-capita* feeding pressure. The integration of coral cover as a modulating factor for feeding rate (especially when measured in 2D planar and 3D surface area) underscores the nonlinear nature of CoTS impact, where higher coral availability not only supports greater consumption but also amplifies the feeding rates of larger individuals. This has direct implications for modelling coral mortality, particularly in high cover areas where even moderate densities of large CoTS can exert disproportionately high predation pressure. The provision of predictive values of daily feeding across combinations of these variables enables more precise forecasting of coral loss. These predictions can be readily integrated into existing monitoring and management frameworks, allowing real-time estimates of cumulative feeding impacts from population size-structure and habitat data, which may be used to reassess intervention thresholds and streamline the prioritization of control efforts. Further, this study identified the influential role that local coral coverage is having on feeding behaviour (and likely physiological condition) of CoTS, which may account for cyclical changes in their population dynamics on the GBR and thus be of critical importance in the distribution and initiation/collapse of population outbreaks (Babcock et al. 2020). This highlights the need to quantify coral cover, including *Acropora* cover, across all ongoing monitoring and modelling efforts used to inform CoTS management. Overall, the study enhances predictive capacity for CoTS-driven coral decline by offering size-structured, context-dependent feeding estimates, thereby moving beyond simplistic models and allowing for more accurate, spatially nuanced assessments of ecological risk.

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Data availability All data analysed as part of this study is available from Research JCU, which will be released from embargo on publication. Contact data manager Josie Chandler josie.chandler@my.jcu.edu.au to request earlier access to this data.

Declarations

Conflict of interest The authors declare no competing interests.

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