Coral Reefs
https://doi.org/10.1007/s00338-025-02783-x

RESEARCH

Diet of herbivorous juveniles modulates growth, survival, and the timing of the ontogenetic diet shift to corallivory in crown-of-thorns sea stars

Daniela Llarena[1,2,3] · Maria C. Gomez Cabrera[2] · Peter C. Doll[1] · Sven Uthicke[2]

Received: 21 February 2025 / Accepted: 4 November 2025

Abstract Outbreaks of western Pacific crown-of-thorns sea stars (CoTS, *Acanthaster* cf. *solaris*) remain one of the foremost contributors to coral loss on Australia's Great Barrier Reef. For CoTS to reach maturity, juveniles feeding on crustose coralline algae (CCA) must complete an ontogenetic diet shift to reef-building corals. Here, we tested whether four different diets of CCA fed to herbivorous juveniles over 12 weeks influence the growth and survival of early-stage juveniles, and the timing of the ontogenetic diet shift to corallivory by introducing the juveniles to coral after 113 days of being offered CCA solely. Our results demonstrate considerable diet-mediated variation in growth rates (increase in number of arms, diameter, and surface area), with juveniles consuming the alga *Melyvonnea* sp. (mean diameter of 5.9 mm ± 1.16 SE after 12 weeks) growing significantly faster and larger, particularly compared to those consuming *Sporolithon* sp. (3.91 mm ± 0.96). Moreover, after 7 weeks of being offered coral, 100% of surviving juveniles fed *Melyvonnea* sp. transitioned to feeding on *Acropora kenti* contrasting with markedly lower transition rates for juveniles consuming *Lithophyllum* sp. (41%), *Lithothamnion* sp. (27%), and *Sporolithon* sp. (11%). Our results suggest that specific CCA (e.g., *Melyvonnea* sp.) promote elevated juvenile growth and earlier transition to corallivory, releasing CCA-feeding juveniles from stunted growth and high mortality, and facilitating earlier exponential growth and maturity as corallivores. The prevalence of these CCA on reefs may thus enhance individual fitness and recruitment success of CoTS, contributing to increased risk of population outbreaks and corresponding coral loss.

Keywords Coralline algae · Coral reef · Echinoderm · Recruitment · Marine ecology

Introduction

Crown-of-thorns sea stars (CoTS, *Acanthaster* spp.) are renowned for their rapid consumption of reef-building corals and considerable contributions to coral mortality across tropical coral reefs of the Indian and Pacific Oceans (De'Ath et al. 2012; Pratchett et al. 2017). While Anthropocene coral reefs also face the perils of climate change (Hughes et al. 2017), periodic population outbreaks of CoTS lead to extensive short- and long-term declines in coral cover and reef health (De'Ath et al. 2012), attracting substantial research attention since 1960s (reviewed by Pratchett et al. 2017). CoTS are native to Indo-Pacific coral reefs and have a negligible impact on these ecosystems at low densities (Uthicke et al. 2024). However, at elevated (or outbreak) densities, their collective feeding impact on coral assemblages can be detrimental, particularly for preferentially consumed taxa (e.g., genus *Acropora* in Pratchett et al. 2017), and threaten ecosystem functioning and resilience (Deaker & Byrne 2022b; Pratchett et al. 2021; Westcott et al. 2020).

Inherent biological and ecological traits of CoTS early life stages pre-dispose them to unstable population dynamics and major fluctuations in adult population sizes (Balu et al. 2021; Deaker & Byrne 2022a; Neil et al. 2022; Pratchett et al. 2021). Like many other echinoderms, CoTS have a bipartite life history, with planktotrophic pelagic larvae

Daniela Llarena
daniela.llarena@my.jcu.edu.au

1 College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia

2 Australian Institute of Marine Science, PMB No 3, Townsville, QLD 4810, Australia

3 AIMS@JCU, Australian Institute of Marine Science, James Cook University, Townsville, QLD 4811, Australia

Published online: 12 November 2025

settling onto the reef benthos and undergoing metamorphosis into benthic juveniles (Deaker & Byrne 2022a). Juvenile CoTS then usually remain herbivorous for 4 to 12 months post-settlement until an ontogenetic diet shift to corallivory (Deaker et al. 2020b; Deaker & Byrne 2022a; Neil et al. 2022; Yamaguchi 1974), although it is hypothesised that juveniles could stay hidden in rubble habitats for years and delay the diet shift until favourable conditions arise (Deaker et al. 2020a). Following their transition to feeding on reef-building coral, juvenile growth rates accelerate considerably until they reach sexual maturity within two years (Lucas 1984; Wilmes et al. 2020a).

Resource availability inherently contributes to the growth of CoTS, and minor diet-mediated changes in growth rate could significantly impact the time spent as small-bodied juveniles and thus individual fitness (Balu et al. 2021; Deaker & Byrne 2022a; Neil et al. 2022; Pratchett et al. 2021). Feeding ecology, although widely studied among adult CoTS, lacks extensive research in juveniles and the importance of herbivorous feeding preferences linked to the ontogenetic transition is largely overlooked. Crustose coralline algae (CCA) are demonstrated to be settlement cues, with distinct differences in settlement rates (Doll et al. 2023) among CCA species. Namely, *Melyvonnea* sp. (*Melyvonnea* cf. *madagascariensis* in Doll et al. 2023) has been shown to promote significantly higher settlement success than the previously regarded ‘gold standard’ of *Lithothamnion* cf. *proliferum* (Doll et al. 2023; Johnson et al. 1991; Johnson & Sutton 1994). In early life, CoTS diets are primarily composed of CCA, biofilms, and other forms of coralline algae in nature (Deaker et al. 2020b; Desbiens et al. 2023; Johansson et al. 2016; Wilmes et al. 2020b).Although juvenile CoTS can survive on a diet of biofilms, this has been shown to decrease their growth in comparison to their preferred diet of CCA (Deaker et al. 2020b). Conversely, juveniles have also been found to consume articulate coralline algae such as *Amphiroa* sp. with limited impacts on growth and survival to the coral-eating phase (Deaker et al. 2020b). The diet selectivity shown by CoTS, with clear feeding preferences on specific CCA such as *Melyvonnea* cf. *madagascariensis* and *Lithothamnion* cf. *proliferum* (Jensen et al. 2025), largely reflects settlement preferences (Doll et al. 2023). Following their ontogenetic diet shift to corals, CoTS have been documented to disproportionately consume *Acropora* spp. (Johansson et al. 2016; Keesing et al. 2019; Pratchett et al. 2009, 2014). Feeding selectivity of *Acanthaster* spp. is exhibited throughout life stages, with clear preferences on specific algal and coral species (Deaker et al. 2020b; Johansson et al. 2016; Neil et al. 2022). Any links between feeding preferences of herbivorous CoTS, growth rates, and the timing of the transition to coral consumption could be crucial to understanding individual survival as juveniles and population replenishment.

Like many echinoderms, CoTS experience high mortality in early life stages (Keesing et al. 2018; Keesing & Halford 1992b). As broadcast spawners, there is large variability in larval survival (Birkeland 1982; Wolfe et al. 2015). Subsequently, herbivorous juveniles are subject to competition for food availability and predation, affecting mortality rates (Jennings & Hunt 2011, 2014; Wolfe et al., 2025). The increased growth rate of juvenile CoTS is directly tied to their success, as they are less susceptible to predation with growth (Balu et al. 2021; Desbiens et al. 2023; Keesing et al. 2018; Wilmes et al. 2018; Wolfe et al. 2023). Lethal predation on juvenile CoTS beginning at 4 months (120 days) post-settlement decreased significantly, inferring that once large enough to transition to coral consumption, the threat of predation is considerably diminished (Balu et al. 2021). Individuals who continue to dwell in the rubble are more vulnerable to predation by epibenthic fauna, stressing the importance of finding food sources that facilitate growth during the herbivory stage and, in turn, an earlier transition to eating coral (Balu et al. 2021; Deaker et al. 2020b; Deaker & Byrne 2022a; Desbiens et al. 2023; Wilmes et al. 2017; Wolfe et al. 2023). The transition to corallivory itself is a significant bottleneck for CoTS, with potential damage or mortality caused by stinging nematocysts in coral (Birkeland & Lucas 1990; Deaker et al. 2021; Yamaguchi 1974). Sub-lethal or lethal injuries are more prevalent in smaller juveniles (Messmer et al. 2017). For the extraordinary fecundity of CoTS to translate to population outbreaks, large numbers of herbivorous juveniles must successfully transition to consuming coral, stressing the significance of understanding this complex and vulnerable stage of the CoTS life cycle (Pratchett et al. 2021).

Defining the age of CoTS at the onset of the dietary ontogenetic transition from herbivory to corallivory is critical to understanding their biology and the potential for diet-mediated variation in transition time to generate outbreaks from cohorts of juveniles. It is estimated in nature that the dietary shift occurs between 4 and 12 months post-settlement; yet, the accuracy of this is difficult to determine (Wilmes et al. 2020a; Zann et al. 1987). On the contrary, in aquaria conditions, the transition can be controlled and laboratory-based studies suggest transition age ranging from 4 to 6 months to over a year (Deaker & Byrne 2022b; Lucas 1984; Neil et al. 2022; Wilmes et al. 2020a; Yamaguchi 1974), and may be extended to six and a half years when no corals are offered (Deaker et al. 2020a). The discrepancy between ages in the field and laboratory settings is attributed to the optimal conditions provided in captivity with an abundance of food, lack of predation, and shelter from weather events in the case of early transition (Deaker et al. 2020a). In addition to Deaker et al. (2020a)’s hidden army theory, the lack of coral availability has been hypothesised to be a large factor in the delay in dietary transition to coral (Wilmes et al.

2020a). Likewise, the abundance of preferred coral induces early ontogenetic dietary shifts in juveniles (Wilmes et al. 2020a). Identifying factors which can promote an early transition to coral could thus prove crucial to understanding and mitigating CoTS outbreaks.

The aim of the present study was to explore whether the diet of herbivorous juvenile western Pacific CoTS (*Acanthaster* cf. *solaris*) influences their growth, survival, and the timing of the ontogenetic switch to corallivory. Specifically, we selected four different CCA taxa (*Lithothamnion* sp., *Sporolithon* sp., *Melyvonnea* sp., and *Lithophyllum* sp.), which are common on GBR midshelf reefs, where CoTS outbreaks occur (Dean et al. 2015; Doll et al. 2023), and have been shown to differ in their biology, ecology (Abdul Wahab et al. 2023; Doll et al. 2023) and their capacity to induce CoTS larval settlement (Doll et al. 2023). Here, we assessed the influence of four different CCA taxa on (i) the growth rate of juvenile CoTS, including both in herbivorous and corallivorous stages (number of arms, diameter, and surface area), (ii) their survival as herbivorous juveniles, including their ontogenetic diet shift, and (iii) the timing of the shift to corallivory. Because this shift in diet leads to accelerated juvenile growth and is essential for individuals to reach maturity (Lucas 1984; Wilmes et al. 2020a; Yamaguchi 1974), this study evaluates factors that underpin individual fitness and recruitment success, which may alter the incidence of CoTS population outbreaks.

Methods

A multi-part experiment assessing the influence of CCA diet on growth and survival of juvenile CoTS, and the timing of the ontogenetic diet shift to corallivory, was conducted at the Australian Institute of Marine Science (AIMS) National Sea Simulator (SeaSim) between 13 February 2024 and 13 May 2024.

Collection and maintenance of experimental specimens

To obtain juvenile CoTS for the experiment, larvae were reared in November 2023 as described in Uthicke et al. (2018), and settled on *Lithothamnion* sp. on December 3, 2023, as per Balu et al. (2021). Experimental treatments tested across all parts of the experiment included four crustose coralline algae (CCA) taxa (*Lithothamnion* sp., *Sporolithon* sp., *Melyvonnea* sp., and *Lithophyllum* sp.). CCA specimens were collected from Davies Reef (central GBR) and held in a 500 L flow-through seawater (FSW) holding tank at ambient conditions. They were identified using morpho-anatomical features as described by Harvey et al. (2005) and Doll et al. (2023) and cut into approximately 2 × 2 cm live chips in preparation for the experiment. *Acropora kenti* (sensu Bridge et al. 2024) specimens were collected from Davies and Chicken Reefs in the central GBR (GBRMPA permit G23/48998.1).

Experimental design

To test the effect of CCA diet on the growth and survival of juvenile CoTS, three replicate experimental assays were conducted for each of the four CCA treatments, for a duration of 5 weeks. For each experimental assay, a 5 L tank was placed within a FSW aquarium at SeaSim to maintain stable temperature (28 °C) throughout the duration of the experiments. Lighting was maintained as a 12-h light/dark cycle, and air was supplied through hoses fitted with filter tips, with each tank fitted with a 212-µm banjo filter to prevent the CoTS from escaping. The tanks were then randomly placed within the aquaria system. Four live CCA chips of similar size were placed into the respective treatment tanks of each species and left to acclimate for 24 h prior to the introduction of juveniles. After 24 h, ten juvenile CoTS (74-day post-settlement) were placed within each of the 12 experimental tanks. The tanks were cleaned weekly, removing all biofilm, and CCA was replenished once consumed to ensure that the quantity of food offered to the CoTS was not a limiting factor. Every 7 days, juveniles were placed in a Petrie dish with 2 ml of FSW and photographed using a Leica Stereo Microscope MZ16A DFC 500 Camera, with LAS software. Each image included a scale bar which was calibrated using the LAS software. Images were then analysed in ImageJ v0.5.8, to count the number of arms, measure body diameter by averaging the shortest cross section (from the tip of one arm across the central disc to the tip of the opposite arm) and the longest cross section, and to estimate (two-dimensional) body surface area.

To test the effect of CCA diet on the timing of the ontogenetic shift to corallivory and the survival of the juvenile CoTS during the transition, coral (*Acropora kenti*) was introduced to the experimental tanks on 25 March 2023 (113-day post-settlement), informed by (Neil et al. 2022), approximately 5 weeks after the start of the experiment. The tanks and CoTS specimens remained the same as the first part of the experiment, but for this second part, two live CCA chips and two fragments of *A. kenti* were placed within each experimental tank. Juveniles were monitored for evidence of transition from feeding on CCA to feeding on coral, recording the age of the CoTS (days post-settlement) at the time of transition. Weekly photographs and image analyses continued throughout the duration of the experiment to monitor growth and size of the individuals that transitioned to eating coral. Injuries sustained by the juvenile CoTS were assessed visually when photographed and documented (Appendix A, Fig. 6). The experiment concluded once half of the total number of living juveniles had transitioned to feeding on *A. kenti*.

Statistical analyses

All statistical analyses were conducted using RStudio (v. 2024.04.2 + 764). To account for variable sample sizes throughout the duration of the experiment, means were calculated for each juvenile CoTS growth metric (mean diameter, mean surface area, and mean number of arms) per week, based on replicates for each CCA treatment. To visualise differences in growth among CCA treatment groups, juvenile CoTS growth metrics were plotted over the duration of the experiment and fitted with a quadratic regression model (R-packages "ggplot2", "car", "dplyr", "mgcv"). Two-way analyses of variance with quadratic polynomial regression models (to account for time as non-linear) were conducted to test for variation in each growth metric among CCA treatment groups, and with time (Johnson & Field 1993). The fit of all models was assessed visually, and the normality of errors and homogeneity of variances were checked using Q-Q plots (Appendix A, Figs. 3–5). Post hoc tests to compare differences among CCA treatment groups and the average number of juvenile CoTS arms were conducted using a least square means test, where *p*-values were adjusted using the Tukey method (R-package "lsmeans"; Lenth 2016). Post hoc simultaneous tests for general linear hypotheses, with Tukey contrasts, where *p*-values are adjusted using a single-step method, were conducted to assess statistical differences at the end of the experiment, between CCA treatment groups and the average diameter of the juvenile CoTS, as well as differences between CCA treatment groups and the average surface area of the juvenile CoTS, due to significant interactions (treatment and time) for these two growth metrics (R-package "multcomp"; Hothorn et al. 2023).

To test for the variation in the probability of juvenile CoTS mortality among CCA treatments throughout the duration of the experiment, a Kaplan–Meier model was used (R-package "survival"; Landes et al. 2020). A Cox proportional hazards model was generated to determine the influence of the different CCA treatments on survival time. Differences in mortality between pairs of individual treatments were then tested using a pairwise_survdiff function for post hoc analysis, where *p*-values were adjusted using a Benjamini–Hochberg method to control for the false discovery rate (R-package ''survival"). To test for the probability of living individuals to transition to eating coral between CCA treatment groups throughout the duration of the experiment, a second Kaplan–Meier model was used (R-package "survival"). A Cox proportional hazards model was generated to determine the influence of the different CCA treatments on the transition time. Differences in transition time between individual treatments were then tested using a pairwise_survdiff function for post hoc analysis, where *p*-values were adjusted using a Benjamini–Hochberg method to control for the false discovery rate (R-package ''survival").

Results

Over the course of the 12-week feeding experiment, the arm number of juvenile CoTS varied among the CCA diet treatments (Table 1) but continuously increased in all treatments (Fig. 1a; Table 1). At 8 weeks, CoTS consuming *Melyvonnea* sp. had significantly more arms (mean of 13.33 arms ± 0.86 SE, $n = 21$) than the CoTS consuming the other three algal groups, especially compared to *Sporolithon* sp. (11.50 ± 1.96, $n = 10$; Fig. 1a; Table 2). *Lithothamnion* sp. (11.67 ± 1.88, $n = 18$) and *Lithophyllum* sp. (12.10 ± 1.86, $n = 20$) displayed similar arm numbers throughout the duration of the experiment (Fig. 1a). Post hoc tests revealed that the mean arm number for juvenile CoTS consuming *Melyvonnea* sp. (12.8 arms at twelve weeks) was significantly higher than that for the other three algal treatment groups ($p < 0.001$; Table 2): *Lithophyllum* sp. (11.7 arms, $p < 0.001$), *Lithothamnion* sp. (11.5 arms, $p = 0.007$), and *Sporolithon* sp. (10.8 arms), with no significant differences in arm number among the latter three groups.

Table 1 Two-way analyses of variance (ANOVA) testing the effects of CCA diet (treatment) on the mean number of arms, mean diameter, and mean surface area of CoTS juveniles over time. Treatment groups are the CCA species *Lithophyllum* sp., *Lithothamnion* sp., *Melyvonnea* sp., *Sporolithon* sp., and significant *p*-values are bolded

Response	Factor	Sum of squares	Degrees of freedom	*F*-value	*p*-value
Mean Number of Arms	Time (Week)	186.53	2	304.01	**< 0.001**
	Treatment	12.65	3	13.74	**< 0.001**
	Time (Week): Treatment	2.60	6	1.41	0.2371
Mean Diameter (mm)	Time (Week)	50.99	2	517.34	**< 0.001**
	Treatment	14.35	3	97.05	**< 0.001**
	Time (Week): Treatment	1.77	6	6.39	**< 0.001**
Mean Surface Area (mm^2)	Time (Week)	1616.65	2	429.62	**< 0.001**
	Treatment	520.23	3	92.17	**< 0.001**
	Time (Week): Treatment	125.13	6	11.08	**< 0.001**

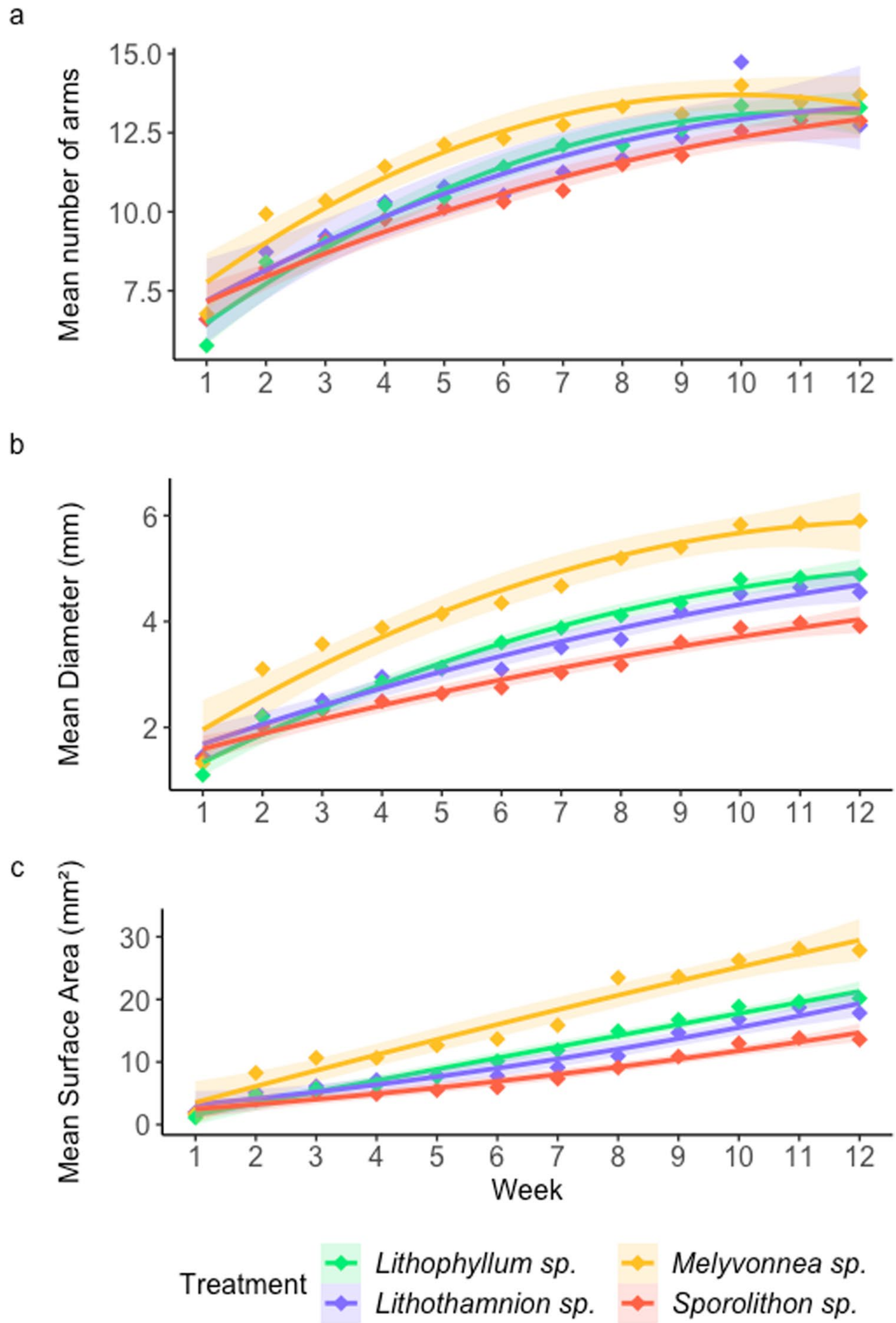

Fig. 1 The growth and size of herbivorous juvenile CoTS consuming four different crustose coralline algae species, expressed as **(a)** the mean number of arms over time (weeks), **(b)** mean diameter (mm) over time (weeks), and **(c)** mean surface area (mm^2) over time (weeks). Diamonds represent mean values and ribbons represent 95% confidence intervals for respective treatments. The data were fitted with a quadratic regression model, represented by the trend line

The mean diameter of juvenile CoTS varied significantly among CCA treatments and with time (Table 1; Fig. 1b); yet, the interaction term was also significant, (Table 1). Inspection of the size development over time suggested size differences between treatments existed throughout the experiment, but the magnitude of these differences varied, causing the interaction. CoTS consuming *Melyvonnea* sp. had a significantly (post hoc test, Table 3) larger diameter (5.9 mm ± 1.16 SE at twelve weeks, $n = 23$) than the CoTS consuming the other three CCA groups (*Sporolithon* sp. 3.91 ± 0.96, $n = 8$; Fig. 1b) at 12 weeks. At week 12, the diameter of CoTS consuming *Lithothamnion* sp. (4.55 ± 1.11 mm, $n = 15$) was similar to *Lithophyllum* sp. (4.88 ± 1.35 mm, $n = 17$) and their diameter was significantly smaller than CoTS consuming *Melyvonnea* sp. and larger than those consuming *Sporolithon* sp. (post hoc test, Table 3).

The mean surface area of juvenile CoTS varied significantly among CCA treatments and with time (Table 1; Fig. 1c); yet, the interaction term is significant ($p < 0.001$; Table 1). Similar to diameter, the significant interaction is likely caused by a difference in magnitude of these differences over time. CoTS consuming *Melyvonnea* sp. assumed the highest surface area (27.84 mm^2 ± 10.07 SE at twelve weeks, $n = 23$) compared to the other three CCA groups, especially *Sporolithon* sp. (13.58 ± 6.65, $n = 8$; Fig. 1c). CoTS consuming *Lithothamnion* sp. and *Lithophyllum* sp. displayed similar surface area to each other throughout the duration of the experiment (where after 12 weeks, *Lithothamnion* sp. 17.82 ± 8.43, $n = 15$, *Lithophyllum* sp. 20.16 ± 9.63, $n = 17$; Fig. 1c), but the surface area growth from these two species was clearly below CoTS consuming *Melyvonnea* sp., and above CoTS consuming *Sporolithon* sp. (Fig. 1c). These differences in mean surface area of CoTS were significant comparing between *Melyvonnea* sp. and all other algae, albeit only marginally so with *Lithophyllum* sp. (Table 4). Mean differences between the other algal pairs at week 12 were not significantly different (Table 4).

The survival probability during this experiment varied among juvenile CoTS consuming different CCA treatments, with no mortality recorded during the algal diet phase until 95 days post-settlement (Fig. 2b, Table 5). Pairwise comparisons using a log-rank test showed that juvenile CoTS feeding on *Melyvonnea* sp. had a significantly higher survival probability than individuals consuming

Table 2 Post hoc least square means tests comparing pairwise differences in mean number of juvenile CoTS arms between pairs of CCA treatment groups. Treatment groups are the CCA species *Lithophyllum* sp., *Lithothamnion* sp., *Melyvonnea* sp., *Sporolithon* sp., *p*-values were adjusted using the Tukey method, and significant *p*-values are bolded

Contrast	Estimate	Standard error	df	*t*-ratio	*p*-value
Lithophyllum sp—*Lithothamnion* sp.	0.26	0.341	36	0.75	0.877
Lithophyllum sp—*Melyvonnea* sp.	− 1.08	0.341	36	− 3.15	**0.017**
Lithophyllum sp—*Sporolithon* sp.	0.90	0.341	36	2.64	0.056
Lithothamnion sp—*Melyvonnea* sp.	− 1.33	0.341	36	− 3.90	**0.002**
Lithothamnion sp—*Sporolithon* sp.	0.65	0.341	36	1.89	0.249
Melyvonnea sp—*Sporolithon* sp.	1.98	0.341	36	5.79	**< 0.001**

Table 3 Post hoc simultaneous tests for general linear hypotheses, with Tukey contrasts, to test for pairwise differences in mean diameter of juvenile CoTS among CCA treatments at the end of the experiment (12 weeks). Treatment groups are the CCA species *Lithophyllum* sp., *Lithothamnion* sp., *Melyvonnea* sp., *Sporolithon* sp., *p*-values are adjusted using a single-step method, and significant *p*-values are bolded

Linear Hypotheses	Estimate	Standard error	*t*-ratio	*p*-value
Lithothamnion sp—*Lithophyllum* sp. = = 0	− 0.33	0.42	− 0.80	0.853
Melyvonnea sp—*Lithophyllum* sp. = = 0	1.02	0.38	2.69	**0.044**
Sporolithon sp—*Lithophyllum* sp. = = 0	− 0.98	0.51	− 1.92	0.226
Melyvonnea sp—*Lithothamnion* sp. = = 0	1.35	0.39	3.44	**0.006**
Sporolithon sp—*Lithothamnion* sp. = = 0	− 0.64	0.52	− 1.24	0.602
Sporolithon sp—*Melyvonnea* sp. = = 0	− 1.99	0.49	− 4.10	**< 0.001**

Table 4 Post hoc simultaneous tests for general linear hypotheses, with Tukey contrasts, to test for pairwise differences in mean surface area of juvenile among CCA treatments at the end of the experiment (12 weeks). Treatment groups are the CCA species *Lithophyllum* sp., *Lithothamnion* sp., *Melyvonnea* sp., *Sporolithon* sp., *p*-values are adjusted using a single-step method, and significant *p*-values are bolded

Linear Hypotheses	Estimate	Standard error	*t*-value	*p*-value
Lithothamnion sp—*Lithophyllum* sp. = = 0	− 2.34	3.27	− 0.72	0.889
Melyvonnea sp—*Lithophyllum* sp. = = 0	7.68	2.95	2.60	0.054
Sporolithon sp—*Lithophyllum* sp. = = 0	− 6.57	3.95	− 1.66	0.348
Melyvonnea sp—*Lithothamnion* sp. = = 0	10.01	3.06	3.27	**0.009**
Sporolithon sp—*Lithothamnion* sp. = = 0	− 4.24	4.04	− 1.05	0.718
Sporolithon sp—*Melyvonnea* sp. = = 0	− 14.25	3.79	− 3.77	**< 0.001**

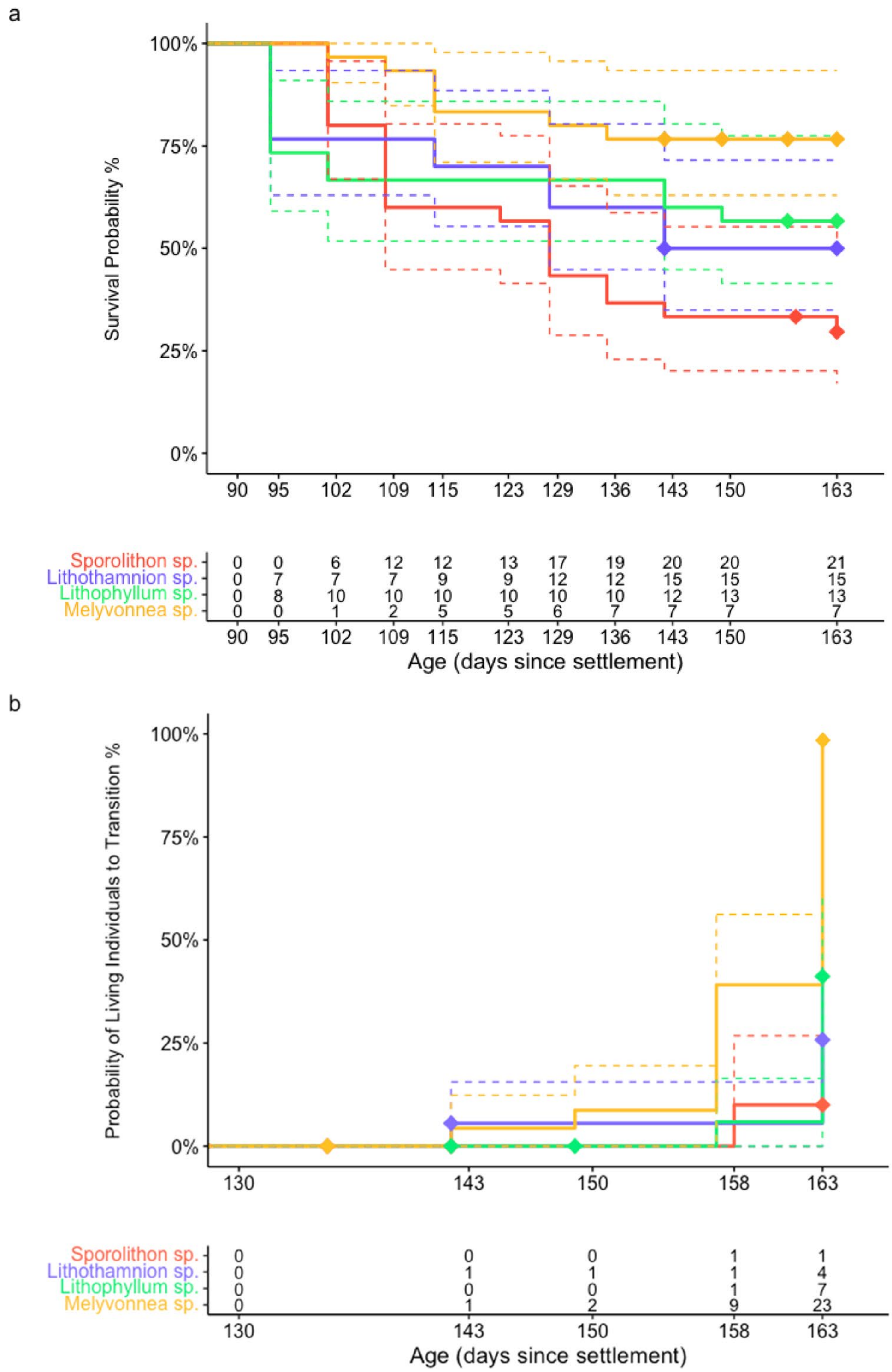

Fig. 2 Kaplan–Meier models illustrating the **(a)** survival probability of juvenile CoTS throughout the duration of the experiment and **(b)** probability of living individuals to transition to feeding on *Acropora kenti*, for each of the four CCA treatment groups: *Sporolithon* sp. (red), *Lithothamnion* sp. (blue), *Lithophyllum* sp. (green), and *Melyvonnea* sp. (yellow). The areas within the dotted lines represent the 95% confidence interval for each of the four treatment groups. Sample size at **(a)** 90 days and **(b)** 130 days is 120 (30 individuals per treatment group). The count ("events") of individual CoTS which have **(a)** died or **(b)** transitioned to eating *Acropora kenti* is displayed in the respective tables for each treatment group and experiment timepoint

Sporolithon sp. (Table 5), while all other comparisons were non-significant. At the end of the experiment, juvenile CoTS consuming *Lithophyllum* sp. had a 57% (17 CoTS, $n = 30$) survival rate, CoTS consuming *Lithothamnion* sp. had a 50% (15 CoTS, $n = 30$) survival rate, CoTS consuming *Melyvonnea* sp. had a 77% (23 CoTS, $n = 30$) survival rate, and CoTS consuming *Sporolithon* sp. had a 30% (9 CoTS, $n = 30$) survival rate (Fig. 2a).

The success and transition time to corallivory in juvenile CoTS varied considerably among CCA treatments, with higher shifts to coral consumption recorded for juvenile CoTS consuming *Melyvonnea* sp. compared to the other

Table 5 Pairwise comparisons using log-rank post hoc test for Kaplan–Meier Survival Analysis, comparing differences in survival probability between pairs of CCA treatments (*Lithophyllum* sp., *Lithothamnion* sp., *Melyvonnea* sp., *Sporolithon* sp.). *p*-values were adjusted using a Benjamini–Hochberg method, and significant *p*-values are bolded

Data		*Sporolithon* sp.	*Lithothamnion* sp.	*Lithophyllum* sp.
Mortality and treatment	*Lithothamnion* sp.	0.211	–	–
	Lithophyllum sp.	0.183	0.661	–
	Melyvonnea sp.	**0.002**	0.100	0.156

Table 6 Pairwise comparisons using log-rank post hoc test for transition Kaplan–Meier analysis, comparing differences in transition probability between pairs of CCA treatments (*Lithophyllum* sp., *Lithothamnion* sp., *Melyvonnea* sp., *Sporolithon* sp.). *p*-values were adjusted using a Benjamini–Hochberg method, and significant *p*-values are bolded

Data		*Sporolithon* sp.	*Lithothamnion* sp.	*Lithophyllum* sp.
Transition and treatment	*Lithothamnion* sp.	0.430	–	–
	Lithophyllum sp.	0.190	0.440	–
	Melyvonnea sp.	**< 0.001**	**< 0.001**	**< 0.001**

three treatments (Fig. 2a; Table 6). The first two CoTS to undergo the ontogenetic transition at 143-day post-settlement were on a diet of *Melyvonnea* sp. and *Lithothamnion* sp. (Fig. 2b). At the end of the experiment at 163 days, 23 CoTS consuming *Melyvonnea* sp. (100% of surviving CoTS, $n = 23$) had transitioned to feeding on coral, contrasting with only one CoTS that transitioned from a *Sporolithon* sp. diet (10%, $n = 9$; Fig. 2b). Meanwhile, seven CoTS feeding on *Lithophyllum* sp. (41%, $n = 17$) and four CoTS feeding on *Lithothamnion* sp. (26%, $n = 15$), transitioned to coral consumption by 163 days (Fig. 2b). Pairwise comparisons using a log-rank test showed significant differences between CoTS consuming *Melyvonnea* sp. and all three other CCA treatment groups in the timing of the transition ($p < 0.001$; Table 6). Transition time for all three remaining algal treatment groups is not significantly different from each other (Table 6). The pre-transition survival probability and transition probability are multiplicative for population outcomes (i.e., total recruitment success). At the conclusion of the experiment (Day 163), 76.7% of juveniles of the initial sample population ($n = 30$) had transitioned on a *Melyvonnea* sp. diet (i.e., 23 of 30), contrasting substantially lower proportions for juveniles feeding on *Lithophyllum* sp. (23.3%), *Lithothamnion* sp. (13.3%) and *Sporolithon* sp. (3.3%).

Discussion

Assessing the influence of crustose coralline algae diet on the growth and survival of herbivorous juvenile CoTS, and their diet transition to corals, this study adds novel insights into key parameters governing the survivorship of this keystone coral predator throughout its early life-history stages, and the proliferation of CoTS populations. Until recently, paradigms and research surrounding CoTS outbreaks were largely restricted to studies on adult populations or the larval stage (reviewed by Pratchett et al. 2017). The herbivorous juvenile stage of CoTS and their ontogenetic diet shift to corallivory are critical for recruitment success; yet, our understanding thereof remains highly fragmented (Pratchett et al. 2014, 2017, 2021). The present study provides novel evidence of an inherent link between the herbivorous diet of juvenile CoTS and key factors underpinning their survivorship, including the onset of the transition to coral consumption. The completion of this diet shift to corallivory represents an essential early life-history transition, accelerating growth rates and elevating recruitment success (Wilmes et al. 2020a). Thus, the considerable diet-mediated differences in growth rates and the transition to corallivory documented here may not only affect the fitness of individuals, but also contribute to the risk of population build-up.

Acanthaster spp. exhibits different growth rates depending on CCA diet among juveniles of the same species (Deaker et al. 2020b; Wilmes et al. 2020a). In the present study, the growth rate and fitness of juvenile CoTS were found to be influenced by algal diet, with *Melyvonnea* sp. promoting by far the highest growth and survival rates, with a 69% larger surface area and a 47% higher survival rate than the CCA with the lowest growth and survival rate *Sporolithon sp.* at the end of the experiment. Meanwhile, the alga *Lithophyllum* sp., closely followed by *Lithothamnion* sp., facilitated moderate growth of the juvenile CoTS. In captivity, when no coral is offered, juvenile CoTS have been observed to remain in the herbivorous stage for 4 to 12 months, sometimes years (Deaker et al. 2020a; Lucas 1984), post-settlement, growing roughly 2.6 mm per month

(Deaker & Byrne 2022a; Neil et al. 2022; Yamaguchi 1974; Zann et al. 1987). CoTS ranging between 120 and 150-day post-metamorphosis across the great barrier reef were observed to be between 4.41 and 9.28 mm in diameter (Wilmes et al. 2017), similarly to the juveniles measured in the present study, which averaged 4.81 mm in diameter. Notably, this diet-mediated growth in juvenile stage CoTS is reflective of the settlement preferences of CoTS larva observed by Doll et al. (2023), who reported a settlement rate of > 98% in the presence of *Melyvonnea* cf. *madagascariensis* within 48 h, compared to considerably lower rates (39–63%) for the other three CCA species used in the present study. This is ecologically important, as the post-settlement, early life-history stage presents major population bottlenecks for many echinoderms, yet the apparent links between settlement success, feeding preferences, and growth in juvenile CoTS could influence these dynamics, if juveniles remain on the substrate that they initially settled on (Doll et al. 2023).

The number of arms in juveniles can be used to initially infer growth of CoTS but plateaus toward the latter juvenile stages. The number of juvenile arms has previously been observed to cease increasing at 104 days post metamorphosis in CoTS averaging 10 mm in diameter without exposure to coral (Deaker et al. 2020a). The CoTS in the present study were offered *Acropora kenti* beginning at 113-day post-settlement, and some of the juveniles began to show a decrease in arm number which can be attributed to injuries associated with coral defences and mortality (Deaker et al. 2020a). However, the overall injury rate reported here was much lower than in the latter study, and due to the low number of CoTS transitioning on treatments other than *Melyvonnea* sp., injury rates could not be compared among treatments.

CoTS consuming *Melyvonnea* sp. exhibited greater growth and survival compared to CoTS consuming *Sporolithon* sp. The CoTS offered *Sporolithon* sp. were rarely seen consuming the alga, but rather found on the walls of the experimental aquaria either consuming biofilm or likely starving. Although documented as the primary diet of other juvenile echinoderms (Martinez et al. 2017), biofilm is an inadequate diet for juvenile CoTS and is associated with higher rates of mortality in later post-settlement juvenile stages (Deaker et al. 2020b). High mortality rates of juvenile CoTS have been attributed to body size in the wild, where CoTS 3 mm in diameter experienced a 2.6% d^{-1} mortality rate as compared to those 13 mm which experienced a 0.82% d^{-1} mortality rate (Keesing et al. 2018), where competition for food availability and predation can disproportionately affect smaller individuals (Jennings & Hunt 2011, 2014; Keesing & Halford 1992a; Wilmes et al. 2019.) In this aquarium-based study, the threat of predation is null, and the cause of mortality can instead be linked to starvation or under nourishment due to competition for available food sources between larger and stronger individuals outcompeting smaller, less nourished juveniles. This observation suggests that juvenile CoTS which can only access unfavourable CCA, such as *Sporolithon* sp., in the wild would be less likely to survive as a result of relatively low fitness. In turn, locations with high cover of preferred CCA, such as *Melyvonnea* sp., *Lithophyllum* sp., or *Lithothamnion* sp., could promote increased individual fitness and in situ survival. For population irruptions to occur, large numbers of juvenile CoTS must successfully grow and transition to corallivorous adults, which is only exacerbated when able to locate preferred CCA species on the reef, emphasising the ecological importance of diet-mediated effects on these key early life-history processes (Pratchett et al. 2021; Westcott et al. 2020).

The results of this present study indicate that the onset of early ontogenetic dietary shifts by juvenile CoTS can be attributed to the consumption of certain CCA. Importantly, the increased growth rate (and size) of herbivorous juveniles documented here inherently affects the size-mediated timing of the transition to corallivory (Wilmes et al. 2020a). The earliest CoTS to transition to eating coral were feeding on *Melyvonnea* sp. and *Lithothamnion* sp., and transitioned at 143-day post-settlement, similarly to observations by Neil et al. (2022), which recorded the earliest transition at 138-day post-settlement. In nature, the transition time is estimated to be around 6 to 15 months post-settlement (Wilmes et al. 2020a; Zann et al. 1987); however it is hypothesised that juveniles can remain hidden in the rubble zone and delay the transition until conditions are favourable and preferred coral is available (Deaker et al. 2020a; Wilmes et al. 2020a; Wolfe & Byrne 2024). Prolonging the time spent in the rubble does not provide protection from epibenthic fauna and may be disadvantageous to the success of juvenile CoTS (Balu et al. 2021; Deaker et al. 2020a; Deaker & Byrne 2022a; Desbiens et al. 2023; Wilmes et al. 2017; Wolfe et al. 2023). Instead, juveniles which have access to preferred CCA could reduce the length of earlier life stages and, in turn, transition to eating coral earlier. Importantly, the high pre-transition survival probability and high transition probability of juveniles feeding on *Melyvonnea* sp. are multiplicative for population outcomes, which is expected to result in sizeable total population replenishment facilitated relative to other species.

This study highlights an important role of CCA in moderating the early life-history dynamics of CoTS and corroborates the important contribution certain CCA make to recruitment success (Doll et al. 2023; Jensen et al. 2025). Specifically, the alga *Melyvonnea* sp. (*Melyvonnea* cf. *madagascariensis* in Doll et al. 2023), has already been shown to promote remarkably high larval settlement success in CoTS (Doll et al. 2023) and is preferentially consumed by early-stage juveniles (Jensen et al. 2025). This study confirms the relative importance of this alga across the early life-history stages of CoTS, highlighting both significant information gaps and important avenues for future research. The role of CCA, despite being essential across various CoTS life-history stages and transitions, is greatly underappreciated when considering factors underpinning the success of CoTS, and their propensity to undergo major population fluctuations (Pratchett et al. 2021). As an extension of the present study, a wider array of common CCA species and different coral species known to be consumed by juvenile CoTS in situ would provide improved understanding of this complex ontogenetic boundary. Moreover, metabolic and nutrient testing on the CCA used in experimental assays would increase understanding of feeding preferences and juvenile feeding ecology, critical to processes throughout the inherently vulnerable early life stages. Most importantly, we are lacking basic and critical information on the distribution and abundance of different CCA on coral reefs, and any environmental drivers thereof. Future research assessing CCA assemblages could not only provide information to contextualise the results of this present study, but also whether the spatial and temporal differences in CCA assemblages may explain some of the marked spatial and temporal heterogeneity in the adult abundance of CoTS.

In conclusion, we demonstrate that the consumption of certain CCA by early-stage juveniles results in (i) accelerated growth as herbivores, (ii) increased survival as herbivores, and (iii) increased likelihood of juveniles transitioning to corallivory early; an ontogenetic boundary which not only represents a change in diet and habitat, but also a shift from stunted growth while feeding on CCA to exponential growth as corallivores (Wilmes et al. 2020a). In turn, the growth (and size) of juvenile CoTS on both sides of this ontogenetic boundary, and the influence of diet thereon, decreases time to sexual maturity, whilst expected to increase survivorship and rates of recruitment. As a result, the distribution and abundance of any CCA that promotes faster growth, earlier maturity and elevated recruitment success of CoTS (e.g., *Melyvonnea* sp.) may play an underappreciated role in their population outbreaks and devastating effect on coral reef ecosystems.

Acknowledgements The authors thank all Australian Institute of Marine Science (AIMS) and National Sea Simulator staff involved with this experiment for their contributions, particularly Lee Bastin and Holland Elders. Thanks to Rhondda Jones for input to statistical analyses. Thanks to Ciemon Caballes and an anonymous reviewer for constructive comments. This research was supported by AIMS funding (SU) and AIMS@JCU. We acknowledge the Wulgurukaba and Bindal people as the Traditional Owners of the land on which this research was conducted. More broadly, we acknowledge the Traditional Owners of the Great Barrier Reef area and their continuing connection to their land and sea country.

Author contributions All authors contributed to the conception and design; D.L. and M.C.G. conducted the experiment; D.L. analysed the data with input from M.C.G., P.C.D., and S.U.; D.L. wrote the first draft with contributions by M.C.G., P.C.D., and S.U., and all authors reviewed the final manuscript.

Funding Australian Institute of Marine Science

Data availability The data generated as part of this study is available from Research Data JCU (DOI to be provided).

Declarations

Conflict of interest The authors declare no competing interests.

References

Abdul Wahab MA, Ferguson S, Snekkevik VK, McCutchan G, Jeong S, Severati A, Randall CJ, Negri AP, Diaz-Pulido G (2023) Hierarchical settlement behaviours of coral larvae to common coralline algae. Sci Rep. https://doi.org/10.1038/s41598-023-32676-4

Balu V, Messmer V, Logan M, Hayashida-Boyles AL, Uthicke S (2021) Is predation of juvenile crown-of-thorns seastars (*Acanthaster cf. solaris*) by peppermint shrimp (*Lysmata vittata*) dependent on age, size, or diet? Coral Reefs. https://doi.org/10.1007/s00338-020-02047-w

Birkeland C (1982) Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (*Echinodermata: Asteroidea*). Mar Biol. https://doi.org/10.1007/BF00396897

Birkeland C, Lucas JS (1990) *Acanthaster planci*: major management problem of coral reefs. In CRC Press

Bridge TCL, Cowman PF, Quattrini AM, Bonito VE, Sinniger F, Harii S, Head CEI, Hung JY, Halafihi T, Rongo T, Baird AH (2024) A tenuis relationship: traditional taxonomy obscures systematics and biogeography of the '*Acropora tenuis*' (*Scleractinia: Acroporidae*) species complex. Zool J Linn Soc. https://doi.org/10.1093/zoolinnean/zlad062

De'Ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci U S A. https://doi.org/10.1073/pnas.1208909109

Deaker DJ, Byrne M (2022a) Crown of thorns starfish life-history traits contribute to outbreaks, a continuing concern for coral reefs. Emerg Top Life Sci 6(1):67. https://doi.org/10.1042/ETLS20210239

Deaker DJ, Byrne M (2022b) The relationship between size and metabolic rate of juvenile crown of thorns starfish. Invertebr Biol. https://doi.org/10.1111/ivb.12382

Deaker DJ, Agüera A, Lin HA, Lawson C, Budden C, Dworjanyn SA, Mos B, Byrne M (2020a) The hidden army: corallivorous crown-of-thorns seastars can spend years as herbivorous juveniles. Biol Lett. https://doi.org/10.1098/rsbl.2019.0849

Deaker DJ, Mos B, Lin HA, Lawson C, Budden C, Dworjanyn SA, Byrne M (2020b) Diet flexibility and growth of the early herbivorous juvenile crown-of-thorns sea star, implications for its boom-bust population dynamics. PLoS ONE. https://doi.org/10.1371/journal.pone.0236142

Deaker DJ, Mos B, Lawson C, Dworjanyn SA, Budden C, Byrne M (2021) Coral defences: the perilous transition of juvenile crown-of-thorns starfish to corallivory. Mar Ecol Prog Ser. https://doi.org/10.3354/meps13660

Dean AJ, Steneck RS, Tager D, Pandolfi JM (2015) Distribution, abundance and diversity of crustose coralline algae on the Great Barrier Reef. Coral Reefs. https://doi.org/10.1007/s00338-015-1263-5

Desbiens AA, Mumby PJ, Dworjanyn S, Plagányi ÉE, Uthicke S, Wolfe K (2023) Novel rubble-dwelling predators of herbivorous juvenile crown-of-thorns starfish (*Acanthaster* sp.). Coral Reefs. https://doi.org/10.1007/s00338-023-02364-w

Doll PC, Uthicke S, Caballes CF, Diaz-Pulido G, Abdul Wahab MA, Lang BJ, Jeong SY, Pratchett MS (2023) Settlement cue selectivity by larvae of the destructive crown-of-thorns starfish. Biol Lett. https://doi.org/10.1098/rsbl.2022.0399

Harvey A, William W, Far T, Neill K, Nelson W (2005) Coralline algae of central New Zealand An identification guide to common ' crustose' species Coralline algae of central New Zealand. In NIWA Information Series (Issue 57)

Hothorn T, Bretz F, Westfall P, Heiberger RM, Schuetzenmeister A, Scheibe S (2023) Package 'multcomp'. Simultaneous Inference in General Parametric Models. In Cran

Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, Van De Leemput IA, Lough JM, Morrison TH, Palumbi SR, Van Nes EH, Scheffer M (2017) Coral reefs in the Anthropocene. Nature. https://doi.org/10.1038/nature22901

Jennings LB, Hunt HL (2011) Small macrobenthic invertebrates affect the mortality and growth of early post-settlement sea urchins and sea stars in subtidal cobble habitat. Mar Ecol Prog Ser. https://doi.org/10.3354/meps09131

Jennings LB, Hunt HL (2014) Spatial patterns in early post-settlement processes of the green sea urchin *Strongylocentrotus droebachiensis*. Mar Ecol Prog Ser. https://doi.org/10.3354/meps10667

Jensen K, Doll PC, Cabrera MCG, Diaz-Pulido G, Logan M, Uthicke S (2025) Feeding preferences and growth in herbivorous juvenile crown-of-thorns sea stars (*Acanthaster cf. solaris*). Mar Biol. https://doi.org/10.1007/S00227-025-04646-Z/FIGURES/6

Johansson CL, Francis DS, Uthicke S (2016) Food preferences of juvenile corallivorous crown-of-thorns (*Acanthaster planci*) sea stars. Mar Biol. https://doi.org/10.1007/s00227-016-2823-0

Johnson CR, Sutton DC (1994) Bacteria on the surface of crustose coralline algae induce metamorphosis of the crown-of-thorns starfish *Acanthaster planci*. Mar Biol. https://doi.org/10.1007/BF00349692

Johnson CR, Sutton DC, Olson RR, Giddins R (1991) Settlement of crown-of-thorns starfish: role of bacteria on surfaces of coralline algae and a hypothesis for deepwater recruitment. Mar Ecol Prog Ser 71:2. https://doi.org/10.3354/meps071143

Johnson CR, Field CA (1993) Using fixed-effects model multivariate analysis of variance in marine biology and ecology. In Oceanography and marine biology: an annual review Vol 31

Keesing JK, Halford AR (1992) Field measurement of survival rates of juvenile *Acanthaster planci*: techniques and preliminary results. Mar Ecol Prog Ser 85:1–2. https://doi.org/10.3354/meps085107

Keesing JK, Halford AR (1992) Importance of postsettlement processes for the population dynamics of *acanthaster planci* (l.). Mar Freshw Res. https://doi.org/10.1071/MF9920635

Keesing JK, Halford AR, Hall KC (2018) Mortality rates of small juvenile crown-of-thorns starfish *Acanthaster planci* on the Great Barrier Reef: implications for population size and larval settlement thresholds for outbreaks. Mar Ecol Prog Ser. https://doi.org/10.3354/meps12606

Keesing JK, Thomson DP, Haywood MDE, Babcock RC (2019) Two time losers: selective feeding by crown-of-thorns starfish on corals most affected by successive coral-bleaching episodes on western Australian coral reefs. Mar Biol. https://doi.org/10.1007/s00227-019-3515-3

Landes J, Engelhardt SC, Pelletier F (2020) An introduction to event history analyses for ecologists. Ecosphere. https://doi.org/10.1002/ecs2.3238

Lenth RV (2016) Least-squares means: The R package lsmeans. J Stat Softw 69:1–3. https://doi.org/10.18637/jss.v069.i01

Lucas JS (1984) Growth, maturation and effects of diet in *Acanthaster planci* (L.) (Asteroidea) and hybrids reared in the laboratory. J Exp Mar Biol Ecol. https://doi.org/10.1016/0022-0981(84)90214-4

Martinez AS, Byrne M, Coleman RA (2017) Filling in the grazing puzzle: A synthesis of herbivory in starfish. In Oceanography and Marine Biology: An Annual Review (Vol. 55). https://doi.org/10.1201/b21944

Messmer V, Pratchett M, Chong-Seng K (2017) Variation in incidence and severity of injuries among crown-of-thorns starfish (*Acanthaster* cf. *solaris*) on Australia's Great Barrier Reef. Diversity 9(1):12. https://doi.org/10.3390/d9010012

Neil RC, Gomez Cabrera M, Uthicke S (2022) Juvenile age and available coral species modulate transition probability from herbivory to corallivory in *Acanthaster* cf. *solaris* (crown-of-thorns seastar). Coral Reefs. https://doi.org/10.1007/s00338-022-02255-6

Pratchett MS, Schenk TJ, Baine M, Syms C, Baird AH (2009) Selective coral mortality associated with outbreaks of *Acanthaster planci* L. in Bootless Bay, Papua New Guinea. Mar Environ Res. https://doi.org/10.1016/j.marenvres.2009.03.001

Pratchett MS, Caballes CF, Wilmes JC, Matthews S, Mellin C, Sweatman HPA, Nadler LE, Brodie J, Thompson CA, Hoey J, Bos AR, Byrne M, Messmer V, Fortunato SAV, Chen CCM, Buck ACE, Babcock RC, Uthicke S (2017) Thirty years of research on crown-of-thorns starfish (1986–2016): scientific advances and emerging opportunities. Diversity 9(4):41. https://doi.org/10.3390/d9040041

Pratchett MS, Caballes CF, Cvitanovic C, Raymundo ML, Babcock RC, Bonin MC, Bozec YM, Burn D, Byrne M, Castro-Sanguino C, Chen CCM, Condie SA, Cowan ZL, Deaker DJ, Desbiens A, Devantier LM, Doherty PJ, Doll PC, Doyle JR, Dworjanyn SA, Fabricius KE, Haywood MDE, Hock K, Hoggett AK, Høj L, Keesing JK, Kenchington RA, Lang BJ, Ling SD, Matthews SA, McCallum HI, Mellin C, Mos B, Motti CA, Mumby PJ, Stump RJW, Uthicke S, Vail L, Wolfe K, Wilson SK (2021) Knowledge gaps in the biology, ecology, and management of the Pacific crown-of-thorns sea star *Acanthaster* sp. on Australia's Great Barrier Reef. Biol Bull 241(3):330. https://doi.org/10.1086/717026

Pratchett MS, Caballes CF, Rivera-Posada JA, Sweatman, HPA (2014) Limits to understanding and managing outbreaks of crown-of-thorns starfish (ACANTHASTER Spp.). In Oceanography and Marine Biology: An Annual Review (Vol. 52). https://doi.org/10.1201/b17143

Uthicke S, Liddy M, Patel F, Logan M, Johansson C, Lamare M (2018) Effects of larvae density and food concentration on crown-of-thorns seastar (*Acanthaster* cf. *solaris*) development in an automated flow-through system. Sci Rep. https://doi.org/10.1038/s41598-017-19132-w

Uthicke S, Pratchett MS, Bronstein O, Alvarado JJ, Wörheide G (2024) The crown-of-thorns seastar species complex: knowledge on the biology and ecology of five corallivorous *Acanthaster* species. Mar Biol. https://doi.org/10.1007/s00227-023-04355-5

Westcott DA, Fletcher CS, Kroon FJ, Babcock RC, Plagányi EE, Pratchett MS, Bonin MC (2020) Relative efficacy of three approaches to mitigate crown-of-thorns starfish outbreaks on Australia's Great Barrier Reef. Sci Rep. https://doi.org/10.1038/s41598-020-69466-1

Wilmes J, Matthews S, Schultz D, Messmer V, Hoey A, Pratchett M (2017) Modelling growth of Juvenile crown-of-thorns starfish on the northern Great Barrier Reef. Diversity 9:1. https://doi.org/10.3390/d9010001

Wilmes JC, Caballes CF, Cowan ZL, Hoey AS, Lang BJ, Messmer V, Pratchett MS (2018) Contributions of pre- versus post-settlement processes to fluctuating abundance of crown-of-thorns starfishes (*Acanthaster* spp.). Mar Pollut Bull. https://doi.org/10.1016/j.marpolbul.2018.07.006

Wilmes JC, Hoey AS, Messmer V, Pratchett MS (2019) Incidence and severity of injuries among juvenile crown-of-thorns starfish on Australia's Great Barrier Reef. Coral Reefs. https://doi.org/10.1007/s00338-019-01845-1

Wilmes JC, Hoey AS, Pratchett MS (2020a) Contrasting size and fate of juvenile crown-of-thorns starfish linked to ontogenetic diet shifts. Proc R Soc Lond B Biol Sci. https://doi.org/10.1098/rspb.2020.1052

Wilmes JC, Schultz DJ, Hoey AS, Messmer V, Pratchett MS (2020b) Habitat associations of settlement-stage crown-of-thorns starfish on Australia's Great Barrier Reef. Coral Reefs. https://doi.org/10.1007/s00338-020-01950-6

Wolfe K, Byrne M (2024) Dead foundation species create coral rubble habitat that benefits a resilient pest species. Mar Environ Res 202:106740. https://doi.org/10.1016/J.MARENVRES.2024.106740

Wolfe K, Graba-Landry A, Dworjanyn SA, Byrne M (2015) Larval starvation to satiation: influence of nutrient regime on the success of *Acanthaster planci*. PLoS ONE. https://doi.org/10.1371/journal.pone.0122010

Wolfe K, Desbiens AA, Pietsch E, Mumby PJ (2023) Habitat and distribution of the red decorator crab, *Schizophrys aspera*, a cryptic crown-of-thorns seastar predator. ICES J Mar Sci. https://doi.org/10.1093/icesjms/fsad136

Wolfe K, Desbiens AA, Patel F, Kwong S, Fisher E, Mumby PJ, Uthicke S, Knowlton N (2025) eDNA confirms lower trophic interactions help to modulate population outbreaks of the notorious crown-of-thorns sea star. Proceedings of the National Academy of Sciences of the United States of America. https://doi.org/10.1073/PNAS.2424560122/SUPPL_FILE/PNAS.2424560122.SAPP.PDF

Yamaguchi M (1974) Growth of Juvenile *Acanthaster planci (L.)* in the Laboratory. Pacific Scienc. 28(2)

Zann L, Brodie J, Berryman C, Naqasima M (1987) Recruitment, ecology, growth and behavior of juvenile *Acanthaster planci* (L.) (*Echinodermata: Asteroidea*). Bull Mar Sci. 41(2)