Juvenile age and available coral species modulate transition probability from herbivory to corallivory in *Acanthaster cf. solaris* (Crown-of-Thorns Seastar)

Rachel C. Neil¹,²,³ • Maria Gomez Cabrera² • Sven Uthicke²

Received: 22 November 2021 / Accepted: 31 March 2022 / Published online: 20 April 2022 © The Author(s) 2022

**Abstract** Prior to transitioning to a coral diet, juvenile *Acanthaster cf. solaris*, the Crown-of-Thorns Seastar (COTS), feed on crustose coralline algae. Although a detailed understanding of juvenile ecology is crucial to predict and prevent outbreaks, the exact timing of the transition is unresolved. Two experiments were conducted to measure time and size of COTS at the transition, and investigate potential modulating effects of different coral species. COTS began early transitions at similar sizes (7.5–8.5 mm), and these first transitions were observed around 136–145 d. Between 175 and 191 d, a 50% transition in the presence of *Acropora tenuis* was measured. After 175 d, the percentage of COTS cohorts that had transitioned was significantly lower in *A. millepora* (38%) and *Stylophora pistillata* (7%) compared to *A. tenuis* (51%). These data fill important knowledge gaps in juvenile ecology, and the influence of coral species on transition suggests an undescribed feedback mechanism between prey and predator.

**Keywords** Crown-of-Thorns Seastar • Coral • Herbivory • Crustose coralline algae • Juvenile

**Introduction**

Corallivorous Crown-of-Thorns Seastars (COTS), *Acanthaster* sp., are significant contributors to coral reef decline in the Indo-Pacific region (De’ath et al. 2012; Kayal et al. 2012). Predicting and managing COTS outbreaks requires a thorough understanding of their life cycle, particularly as the causes of outbreaks remain unresolved (Pratchett et al. 2014; Westcott et al. 2020). After a planktonic larval period, juvenile COTS settle and metamorphose among crustose coralline algae (CCA) covered substrate, where they remain feeding on biofilms and CCA until transitioning to corallivory at 4–12 months post-settlement (Yamaguchi 1974; Zann et al. 1987; Deaker et al. 2020a; Wilmes et al. 2020b).

The transition to coral is an important bottleneck in the life cycle of the COTS. This is the point at which COTS become a threat to corals, as well as driving an increase in COTS growth-rate and a transition from juvenile to adult morphology (Yamaguchi 1974; Wilmes et al. 2020a). During this time COTS may be damaged or killed by corals as the seastars start to actively seek them (Deaker et al. 2021), as well as changing the COTS’ habitat and exposure to other forms of predation (Wilmes et al. 2019). Aquarium studies found that this transition occurs as early as 4 months, once COTS reached ~8 mm in diameter (Yamaguchi 1974), while studies of in situ juveniles estimated the first point of transition occurred 13–15 months post-settlement (Zann et al. 1987).

While past studies have identified the approximate age and size that COTS begin their transition, field studies are...
hampered by the difficulty of ageing juveniles (Wilmes et al. 2017; Deaker et al. 2020b), and aquarium-based studies typically begin their investigations into the behaviour of transitioning COTS well after they have surpassed the reported minimum size and age (Yamaguchi 1974; Johansson et al. 2016; Deaker et al. 2021). Clarifying this early transition point and behaviour of cohorts during this period is important for predicting outbreaks of COTS, as most aspects of juvenile ecology critical for understanding and modelling outbreaks are still ‘largely unresolved’ (Pratchett et al. 2017, 2021), and population models require knowledge of the transitions between life history stages and the factors influencing these.

This study aimed to address this knowledge gap by investigating the age and size juvenile COTS transition from CCA feeding to corallivory in two independent experiments. We aimed to identify the earliest and smallest size that transition would occur, and how long it takes for 50% and 100% of a cohort to transition. In addition, based on known feeding preferences (Johansson et al. 2016) and the potential of injury through coral defences (Deaker et al. 2021), we tested if offering Acropora tenuis, a species preferred by juveniles, Acropora millepora, a neutral species, or Stylophora pistillata, a species avoided by juveniles, would alter transitions.

**Methods**

We obtained COTS (Acanthaster cf. solaris) juveniles for both experiments by rearing larvae derived from spawning 5 males and 5 females as described in Uthicke et al. (2018). Larvae were settled and juveniles raised as per Balu et al. (2021) and Kwong et al. (2021).

**Age and size of COTS transitioning to preferred food A. tenuis**

In this experiment conducted in 2020, 24 5L flow-through aquaria were continuously supplied with 27.5 °C filtered seawater at 0.25L min⁻¹. Each aquarium was fitted with a 100 μm outlet filter to prevent COTS from escaping the tanks, and light was supplied by eight Aqua Illumination® Hydra® LEDs at an intensity of 100 μmol m⁻² s⁻¹, in a 9:15 light:dark cycle.

Two fragments of Acropora tenuis ~ 5 cm and two chips of CCA ~ 2 cm in diameter were added to each aquarium. A. tenuis was chosen as juvenile COTS show a preference for feeding on this species, thus it seems logical that juveniles would preferentially transition to this food source (Johansson et al. 2016). Corals were collected from Backnumbers Reef (18° 31.043’S, 147° 8.475’E) on the Great Barrier Reef under permit G12/35236.1, and introduced to the experimental systems with the CCA 10 days prior to the start of the experiment. This allowed time for corals and CCA to acclimate to the systems, and during this time corals that showed signs of stress were removed and replaced. Twenty-four juvenile COTS (116 d post settlement) were measured, and their arms counted via high-resolution photography using a Leica MS5 dissecting microscope with a calibrated ToupCam digital camera, then one COTS was added to each experimental tank. At this age, juvenile COTS averaged 3.24 mm ± 0.22 mm (mean ± s.e., n = 24), less than half the size reported in the literature that they transition to corals (~ 8 mm), but large enough that they could be observed with the naked eye (Yamaguchi 1974; Lucas 1984; Wilmes et al. 2020a).

Juveniles were then monitored weekly for evidence of transition from feeding on CCA to feeding on coral (Fig. 1B). After active feeding on coral fragments was observed, the age of the COTS was recorded, then the COTS photographed and measured (Fig. 1A). This experiment was run until all COTS had transitioned to determine the time period required for all individuals to transition.

**Effect of available coral species on transitioning COTS cohorts**

The second experiment was conducted in 2021, offering three different coral species: Acropora tenuis, Acropora millepora and Stylophora pistillata. This allowed us to test the effect of preferred species A. tenuis compared to less preferred A. millepora and typically avoided S. pistillata (Johansson et al. 2016) on the behaviour of the COTS as they began to feed on corals. Twelve 5 L flow-through aquaria were set in a similar manner as per experiment 1 in relation to light, light cycle and water flow. Ten juvenile COTS at 119 days post-settlement, averaging 3.41 mm ±
0.10 mm (mean ± s.e., n = 120) in diameter, were added to each tank with 2–3 CCA fragments ~ 3 cm in diameter. Each tank was assigned a random coral species, then two coral fragments ~ 5 cm in length were offered to the COTS per experimental tank (N = 4 tanks per coral treatment). Coral fragments were checked daily for COTS or any damage; if a coral was found damaged or if a COTS was found eating it, this would be replaced with a fresh coral fragment. COTS found eating coral were removed from the experimental tank, measured and age recorded, then placed in a separate tank. This experiment was terminated after 8 weeks, 175 d post settlement.

Statistical analyses

All statistical analyses were conducted in RStudio v1.3.1073 (R Core Team 2020). A Kaplan–Meier model was used to analyse the probability of COTS in experiment 1 transitioning at each time point (R-package “survival” (Therneau 2020)). The probability of juvenile COTS transitioning to coral at the end of the second experiment, and the survival of COTS under the different treatments, was tested with a generalised linear mixed effects model for binomial data (R-package “lme4” (Bates et al. 2015)). The model included a random effect representing the repeated (N = 4) tanks for each treatment. Differences between individual treatments were then tested using Tukey test for post hoc analysis (R-package “multcomp”, (Hothorn et al. 2008)). A Welch two-sample t-test was also conducted to test for differences in COTS sizes at the start of each experiment.

Results and Discussion

In the first experiment, the earliest transition to coral feeding was recorded at 145 d for a juvenile 7.91 mm in diameter, while the smallest COTS to transition was 7.13 mm at 222 d (Fig. 2A). By 191 d, 50% (95% CI = 33.5%-74.6%) of the cohort had transitioned (pT50 = 191 d) to feeding on A. tenuis, and after 239 d all 24 specimens had transitioned (pT100 = 239 d) with no mortality occurring during the experiment (Fig. 2A). The mean size COTS transitioned to feeding on A. tenuis was 8.73 mm ± 0.23 mm (mean ± s.e., n = 24, ranging 7.13 mm to 11.16 mm) with 14.5 ± 0.217 arms (Fig. 2B).

During the second experiment, the timing of the first transition to coral (136 d) and size of juveniles (7.85 mm) was similar to the previous experiment (Fig. 3) (details in Supplementary Table 1). This experiment was concluded at 175 d (~ 6 months) post-settlement when > 50% of the A. tenuis cohort had transitioned to coral feeding. With one exception (a < 4 mm specimen), individuals at the time of transition were 5.77—10.22 mm in diameter, with a mean diameter of 7.65 ± 0.20 mm, 14.4 ± 0.174 arms and first transition age of 162 ± 1.66 d (mean ± se).

Comparing the likelihood of COTS transitioning to feeding on different coral species, binomial generalised linear mixed effects models suggested significant differences between the coral treatments (χ² = 10.58, DF = 2, p = 0.0050). By 175 d the probability of transition was 0.38 when offered A. millepora, 0.51 with A. tenuis and only 0.07 (2 specimens) in the presence of S. pistillata. The probability of transition was not statistically different between the two Acropora species (Tukey’s post hoc test, z = 1.141, p = 0.4803), whereas availability of both A. millepora (z = -2.506, p = 0.0313) and A. tenuis (z = -3.245, p = 0.003) resulted in significantly higher probabilities of transitioning to coral when compared to S. pistillata (Fig. 4). Thus, species available in the environment will have an important influence on the transition probability.

The time for ~ 50% to transition in the presence of A. tenuis (191 vs 175d) is comparable between the two experiments, albeit slightly earlier in the second experiment. There were no significant differences in the size of COTS at the start of each experiment (Welch two-sample t-test, t34.339 = -0.70686, p = 0.4844), suggesting this difference was not because of variation in the sizes of COTS going into the experiments. The size of COTS that transitioned to A. tenuis was also similar across experiments, and similar to previously reported transitions around four months post-settlement at 8 mm in diameter (Yamaguchi 1974). The consistent results across different cohorts separated by several decades indicate that these values could be used to predict the behaviour of transitioning COTS, making this an important finding for COTS management and population modelling, as we have identified the age and size COTS enter the exponential growth period of their life and the point they become a threat to corals via predation.

Overall, mortality in the second experiment was 20.8% (25 total), with no significant differences between the different treatments (Pr > |z|) > 0.05, details in Supplementary Table 2). In the first experiment, no mortality was observed among COTS. It is likely that the difference in mortality was due to the different experimental set-ups – less COTS in total (24 compared to 120) and only one COTS per tank compared to the 10 per tank in the second experiment, or potentially slight differences in batch quality. No escaped COTS were observed around the outsides of tanks or near the outlets, so it is likely that they died. Deaker et al. (2021) reported that within the first two-months of being offered coral, 37.8% of their 10-mo juveniles had been injured or killed by the Acropora sp.,
while Wilmes et al. (2019) found that in the wild, smaller COTS (3 mm) had higher incidence of predatory damage compared to larger (12 mm) juveniles from the same habitat. Mortality rates in wild juveniles have been reported as high as 2.6% d⁻¹, with most of it (73%) attributed to the effect of predators (Keesing et al. 2018). Since there were no predators in our experimental tanks, it is likely that the source of mortality in this study was injuries sustained from coral defences while transitioning to a coral diet (Deaker et al. 2021).

COTS that transitioned to feeding on *A. tenuis* (n = 18) and *A. millepora* (n = 12) were similar in size, 7.68 mm ± 0.31 mm and 7.48 mm ± 0.32 mm, respectively, while the two that transitioned to *S. pistillata* had a larger mean size at 8.43 ± 0.10 mm (Fig. 3). These results emphasize that the availability of coral species plays a role in COTS diet transition. This follows past research suggesting some coral species (e.g., *Echinopora* sp.) can be lethal to COTS juveniles during transition (Johansson et al. 2016; Deaker et al. 2021), though even preferred *Acropora* corals can cause damage or mortality in COTS (Deaker et al. 2021). *Stylophora* coral, demonstrated here to delay a transition to coral diet, has previously been shown to be non-preferred food for juvenile COTS (Johansson et al. 2016). Some papers have suggested it is an important food source of adult COTS (Pratchett 2007; Pratchett et al. 2014), while other research suggests it is not preferred but also not actively avoided (Pratchett et al. 2014). The

**Fig. 2** A The probability of Crown-of-Thorns Seastar (COTS) transitioning to feeding on *A. tenuis* in the first experiment based on a modified Kaplan–Meier model. Green shading represents the 95% confidence interval. B Age and size of juvenile COTS when they first transitioned from feeding on crustose coralline algae to coral. Dashed line indicates the age COTS were introduced to the experiments, prior to which they had been feeding solely on CCA.
The number of nematocysts reported for *Acropora* and *Stylophora* is similar (~20⁴ cm⁻¹), though the haemolytic activity of *Stylophora* is 600-fold higher than that of *Acropora* (Ben-Ari et al. 2018), and it has been suggested that this haemolytic activity is associated with defence against predators (Ben-Ari et al. 2018). This offers a hypothesis as to why COTS prefer certain coral species over others, which should be investigated in future experiments.

Here we have demonstrated that COTS must reach a size of 7.5 – 8.5 mm in diameter before transitioning to coral diets, and that this observation was consistent across two distinct larval cohorts and previous aquarium studies (Yamaguchi 1974). Under laboratory conditions, the probability of transition equals zero for animals < 136d, independent of food supply, while with preferred food available juveniles have a 0.5 probability of transitioning after 175–192 d, and 1 after 236 d. We observed that transition was delayed when less attractive food was available, providing data needed for population dynamic modelling. Future research could test transition probabilities along gradients of coral density and different species composition, and relate this to field data. This could be used to test for a potential undescribed prey/predator feedback mechanism and elucidate the likelihood of a ‘hidden army’ of long-term CCA feeding COTS standing by to seed the next outbreaks (Deaker et al. 2020b).

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00338-022-02255-6.

**Acknowledgements** The authors acknowledge the Traditional Owners of the land and sea country where this research was conducted, the Wulgurukaba and Bindal peoples. We pay our respect to their Elders, past, present and emerging, and acknowledge their continuing spiritual connection to their land and sea country.

We are grateful for the support of the AIMS SeaSim team during these experiments, and would like to thank Rachel’s supervisors Craig Humphrey, David Bourne and Andrew Heyward for their help with conceptualisation and initial set-up for experiment one. We are also grateful to Frances Patel and Lee Bastin for assistance.

**Funding** Open Access funding enabled and organized by CAUL and its Member Institutions.

**Declarations**

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

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

**References**

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 wittata*) dependent on age, size, or diet? Coral Reefs 40:641–649

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:1–48
Ben-Ari H, Paz M, Sher D (2018) The chemical armament of reef-building corals: inter- and intra-specific variation and the identification of an unusual actinoporin in *Stylophora pistilata*. Sci Rep 8:251

Deaker DJ, Mos B, Lin HA, Lawson C, Budden C, Dvorjanyn SA, Byrne M (2020) Diet flexibility and growth of the early herbivorous juvenile crown-of-thorns sea star, implications for its boom-bust population dynamics. PLoS One 15:e0236142

Deaker DJ, Aguer A, Lin HA, Lawson C, Budden C, Dvorjanyn SA, Mos B, Byrne M (2020b) The hidden army: coronilivorous crown-of-thorns seastars can spend years as herbivorous juveniles. Biol Lett 16:20190849

Deaker DJ, Mos B, Lawson C, Dvorjanyn SA, Budden C, Byrne M (2021) Coral defences: the perilous transition of juvenile crown-of-thorns starfish to corallivory. Mar Ecol Prog Ser 665:115–125

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 109:17995–17999

Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models. Biom J 50:346–363

Johansson CL, Francis DS, Uthicke S (2016) Food preferences of juvenile coronilivorous crown-of-thorns (*Acanthaster planci*) sea stars. Mar Bio 163:1

Kayal M, Vercelloni J, Lison de Loma T, Chancerelle Y, Geoffroy S, Stievenart C, Michonneau F, Penin L, Planes S, Adjeroud M (2012) Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. PLoS One 7:e47363

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 597:179–190

Kwong SLT, Villacorta-Rath C, Doyle J, Uthicke S (2021) Quantifying shedding and degradation rates of environmental DNA (eDNA) from Pacific crown-of-thorns seastar (*Acanthaster cf. solaris*). Mar Bio. https://doi.org/10.1007/s00227-021-03896-x

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 79:129–147

Pratchett M (2007) Feeding preferences of *Acanthaster planci* (*Echinodermata: Asteroidea*) under controlled conditions of food availability. Pacific Science 61:113

Pratchett M, Caballes CF, Rivera-Posada JA, Sweatman HPA (2014) Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster spp.*). In: Hughes RN, Hughes DJ, Smith IP (eds) Oceanography and marine biology: an annual review. CRC Press, pp 133–200. https://doi.org/10.1201/b17143-4

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, Dvorjanyn SA, Fabricius KE, Haywood MDE, Hock K, Hoggett AK, Hoj L, Keesing JK, Kenchington RA, Lang BJ, Ling SD, Matthews SA, McCallum HL, Mellin C, Mos B, Motti CA, Mummy 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 241:330–346

Pratchett M, Caballes C, Wilmes J, Matthews S, Mellin C, Sweatman H, Nadler L, Brodie J, Thompson C, Hoey J, Bos A, Byrne M, Messmer V, Fortunato S, Chen C, Buck A, Babcock R, Uthicke S (2017) Thirty Years of Research on Crown-of-Thorns Starfish (1986–2016): Scientific Advances and Emerging Opportunities. Diversity 9

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Therneau TM (2020) _A Package for Survival Analysis in R_. R package version 3.1–12

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 8:642

Westcott DA, Fletcher CS, Kroon FJ, Babcock RC, Plaganyi 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 10:12594

Wilmes J, Matthews S, Schultz D, Messmer V, Hoey AS, Pratchett MS (2017) Modelling growth of juvenile crown-of-thorns starfish on the northern great barrier reef. Diversity 9:1

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 38:1187–1195

Wilmes JC, Hoey AS, Pratchett MS (2020a) Contrasting size and fate of juvenile crown-of-thorns starfish linked to ontogenetic diet shifts. Proc Biol Sci 287:20201052

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 39:1163–1174

Yamaguchi M (1974) Growth of Juvenile *Acanthaster planci* (L.) in the laboratory. Pac Sci 28:123–113

Zann L, Brodie J, Berryman C, Nagasima M (1987) Recruitment, ecology, growth and behavior of juvenile *Acanthaster planci* (L.) (*Echinodermata: Asteroidea*). Bull Mar Sci 41:561–575

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.