

Review Article

Crown of thorns starfish life-history traits contribute to outbreaks, a continuing concern for coral reefs

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Crown of thorns starfish (COTS, *Acanthaster* sp.) are notorious for their destructive consumption of coral that decimates tropical reefs, an attribute unique among tropical marine invertebrates. Their populations can rapidly increase from 0–1 COTS ha⁻¹ to more than 10–1000 COTS ha⁻¹ in short order causing a drastic change to benthic communities and reducing the functional and species diversity of coral reef ecosystems. Population outbreaks were first identified to be a significant threat to coral reefs in the 1960s. Since then, they have become one of the leading causes of coral loss along with coral bleaching. Decades of research and significant investment in Australia and elsewhere, particularly Japan, have been directed towards identifying, understanding, and managing the potential causes of outbreaks and designing population control methods. Despite this, the drivers of outbreaks remain elusive. What is becoming increasingly clear is that the success of COTS is tied to their inherent biological traits, especially in early life. Survival of larval and juvenile COTS is likely to be enhanced by their dietary flexibility and resilience to variable food conditions as well as their phenotypically plastic growth dynamics, all magnified by the extreme reproductive potential of COTS. These traits enable COTS to capitalise on anthropogenic disturbances to reef systems as well as endure less favourable conditions.

Introduction: the crown of thorns problem

Crown of thorns starfish (COTS, *Acanthaster* sp.) are endemic to tropical coral reefs. After a planktonic larval phase, they begin their benthic life as herbivores and are best known for their subsequent corallivorous stage which begins when the juveniles reach a size of >8 mm diameter (Figure 1). The adults can span up to a metre in diameter, have a flexible, multiarmed body (10–20 arms) and an eversible stomach that wraps around the coral to consume them [1]. In one year, an individual COTS is estimated to consume as much as 12 m² of coral tissue compared with 1.0 m² yr⁻¹ for the other corallivorous sea star *Culcita novaeguineae* [2, 3]. The fast growth and large body size of COTS, rapid consumption of coral and their dietary flexibility as well as their ability to cover a large spatial extent of reefs make these sea stars the most destructive coral predator.

Corals are the backbone of tropical reefs. With global warming causing back-to-back bleaching events and more intense and severe tropical cyclones [4, 5], coral reefs are in peril. This negative trajectory is exacerbated by the mortality caused by COTS outbreaks which increases the time needed for reefs to recover [6, 7], especially as COTS can consume new coral recruits [8] and selectively feed on *Acropora* species that are susceptible to bleaching [9]. If reefs are not able to recover, they can be lost in a process called a ‘phase shift’ where the ecosystem shifts to a new state, a seascape dominated by algae, soft corals and sponges covering reef rubble [10]. Reduced coral cover after an outbreak has ecosystem-wide consequences. The loss of branching corals and the complex three-dimensional habitat that they create is particularly devastating for associated species that do not have the capacity

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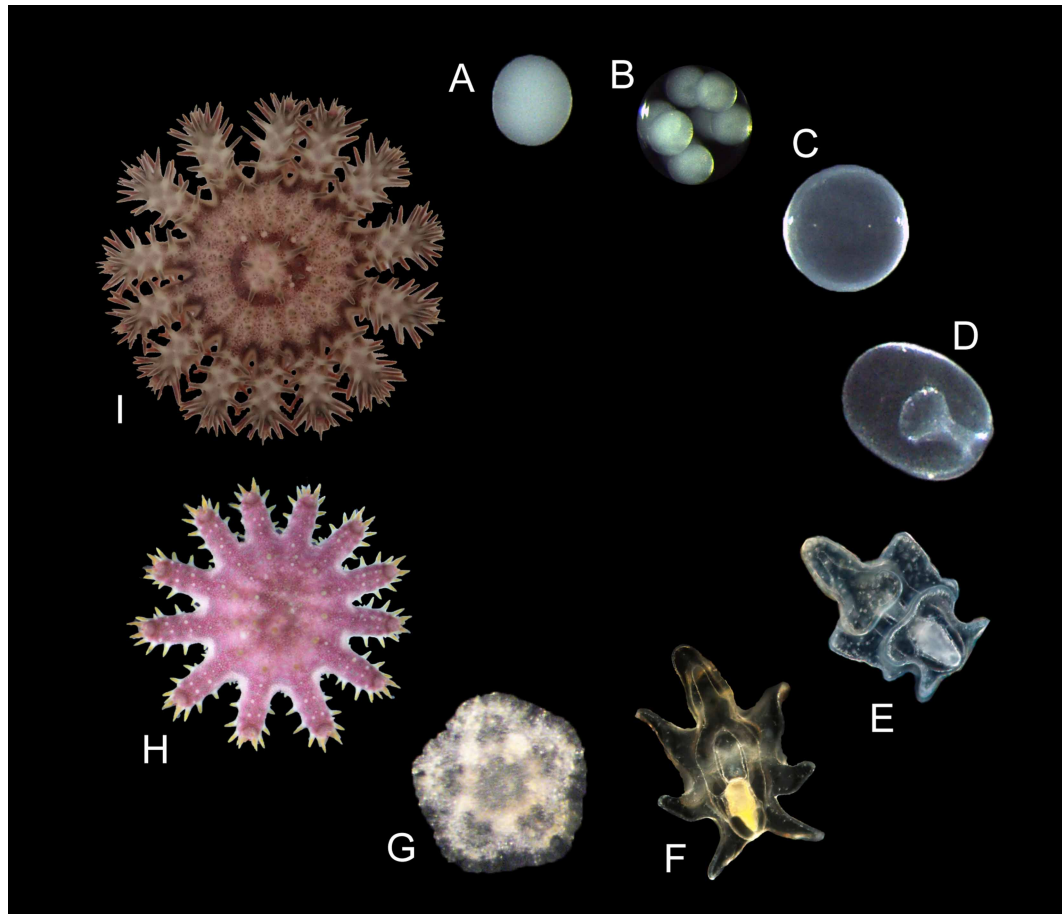


Figure 1. The life cycle of a crown of thorns starfish.

(A) an unfertilised egg, (B) the eight-cell stage, (C) a blastula, (D) a gastrula with the archenteron, (E) a feeding bipinnaria with fully developed digestive tract (photo Dr Jonathan Allen) (F), a brachiolaria with anterior arms used for benthic settlement (photo Dr. Paulina Selvakumaraswamy) (G) a newly settled juvenile, (H) the older herbivorous stage juvenile and, finally, (I) the corallivorous stage.

to find alternative habitat, as well as for a diversity of obligate coral feeding species. COTS outbreaks have been directly linked to declines in damselfish [11], and collapse of butterflyfish populations [12] in parallel with increased abundance of herbivorous fishes [13, 14]. Additionally, selective feeding on preferred coral species by COTS can significantly alter coral assemblages on reefs [15, 16].

COTS are best known for their boom-bust population dynamics with extreme fluctuations in adult abundance followed by population collapse as coral food levels decrease leaving behind an expanse of dead coral [17]. As a natural boom-and-bust species, outbreaks are likely to be an inherent feature of COTS under natural conditions and have been occurring for thousands of years [18]. Since the 1960's, the frequency of outbreaks on the Great Barrier Reef (GBR) has increased from once in every 50–80 years to occurring at ~15 year intervals [19, 20]. Why outbreaks have become more frequent is not known but may be linked to anthropogenic perturbation(s) [21, 22]. Regardless of the causes, the success of this species is underpinned by its highly resilient and opportunistic nature, particularly of the early life history stages.

Potential drivers of outbreaks

Several hypotheses have been proposed to explain the drivers of population outbreaks. The terrestrial run-off hypothesis has received the most traction [22]. Initially proposed by Charles Birkland in the 1980s [23], this hypothesis posits that temporal pulses of enhanced larval survival and settlement are driven by an increase in

their phytoplankton food in blooms generated by eutrophic terrestrial runoff following high rainfall [19, 23, 24]. Outbreaks in isolated atolls and reefs far from a coastline not exposed to anthropogenic runoff are suggested to be caused by nutrient input from bird guano or upwelling that result in increased phytoplankton to support COTS larvae [24, 25]. It would be of interest compare these different bloom scenarios and their influence on COTS populations.

Decreased abundance of COTS predators is also likely to contribute to population outbreaks. The predator removal hypothesis was originally suggested by Endean in the 1960s [26] and has been gaining support over the past 15 years. Extensive harvesting of the giant triton snail (*Charonia tritonis*) in the 1960s [27] and later fishes [28, 29] that prey on COTS has been followed by outbreaks occurring at shorter time intervals [19]. Protected (no-take) GBR marine park areas have lower numbers of COTS and less frequent outbreaks compared with fished areas [29, 30]. In models of coral reef dynamics, no-take areas are less susceptible to outbreaks [31]. COTS with sublethal injuries are also more frequent in areas closed to fishing [32, 33]. The predator removal hypothesis is also supported by the morphological and behavioural adaptations of COTS that are likely to have evolved to counter predation including their cryptic colouration, their cover of venomous spines [34], toxic eggs [35], the avoidance responses of larvae and adults to predator cues [36, 37] and their ability to curl into a spiny ball when disturbed to protect their soft ventral tissue [38, 39]. Reefs with a more intact fish guild, more large predatory fishes and resilient trophic dynamics have higher ecosystem health and would be expected to have a greater resistance to COTS outbreaks [40].

While links between outbreaks and these proposed mechanisms are often tenuous and have been a subject of debate [22, 41, 42], they are used to inform COTS management strategies [43]. It is likely that both enhanced larval survival and predator removal contribute to COTS success. Additionally, post-settlement processes [44–46] and prevailing oceanic currents [42] can lead to rapid population growth in a single spawning year or the accumulation of sea stars over multiple spawning years [22, 47, 48]. The early life history stages of broadcast spawning marine invertebrates are vulnerable population mortality bottlenecks [49, 50]. The disproportionate success of early life history stages is a feature of echinoderms that have boom-and-bust population dynamics [17]. Thus, the biology of the larval and juvenile stage of COTS is critical to our understanding of the outbreak phenomenon.

Why are COTS so successful?

Reproduction in COTS involves synchronous spawning in summer (December–January in the GBR) [51, 52]. COTS are highly fecund, releasing up to 100 million eggs per individual female suggesting that outbreaks can be seeded even at low population densities [53]. Although they are dioecious, there is evidence of hermaphroditism indicating potential for self-fertilisation [54]. Aggregation by adults during spawning [55] would increase the chances of syngamy and promote genetic diversity [56, 57]. The eggs of COTS at ~220 μm diameter are unusually large for a sea star with planktotrophic development [58]. Larger eggs benefit fertilisation by providing a larger target size for sperm [59]. These eggs also have a comparatively higher nutritional content for offspring that may increase the facultative feeding period of the larvae during which an exogenous food source (i.e. phytoplankton) is not needed [60]. This reduces the dependency of the very early vulnerable larval stage compared with species that have smaller eggs [61, 62].

The extreme fecundity of COTS together with dense adult populations can generate plumes of larvae in the plankton [63]. Larvae are proposed to be retained near natal reefs by prevailing oceanic conditions [42]. In the Northern GBR this is suggested to occur between Cairns and Townsville in an area known as the ‘initiation box’ of COTS outbreaks [22]. Over their 2–3 week planktonic larval duration, COTS larvae are also likely to disperse widely in currents between reefs and seed COTS populations far from the source reef. This is indicated by the detection of COTS environmental-DNA across a 350 km expanse of the GBR after spawning, regardless of proximity to adult populations [63]. Notably, population genetics show that outbreaks in isolated islands (Hawaii and Moorea) and archipelagos across the central Pacific are independent of each other with low larval exchange across open ocean [64].

With respect to their feeding biology, COTS larvae are highly plastic, reflecting the phenotypic plasticity trait well known for echinoderm larvae [65, 66]. The larvae can adjust their morphology with respect to food levels. In low food conditions, COTS larvae increase the size of their feeding structures (ciliated bands) to increase food capture [67]. This observation, together with the results of *in situ* experiments showing that COTS larvae can develop well in naturally low nutrient reef conditions [68, 69], prompted the larval-resilience hypothesis [67]. High survival of COTS larvae has been reported in low to moderate chlorophyll-*a* concentrations (0.5–5 $\mu\text{g L}^{-1}$) as a proxy of phytoplankton food levels in the environment [19, 70, 71]. Values within this

range (0.6–1.0 $\mu\text{g L}^{-1}$) are common in coastal waters of the GBR and in areas susceptible to outbreaks during the wet season when COTS larvae are in the plankton [24, 72]. The larvae also have a flexible diet including dissolved organic matter [73, 74] as well as potentially having phototrophic bacterial symbionts [75]. Larval plasticity is likely to increase survivorship in variable food conditions and allow them to quickly avail of enhanced food levels and flourish in favourable conditions.

As for many echinoderms [76, 77], COTS are able to reproduce asexually by larval cloning [78]. Cloning, along with the possibility for self-fertilization, has been detected in genetic analyses of COTS populations in Japan and the GBR and in models of these data [79–81]. The bipinnaria larval stage of COTS (Figure 1E) clone through bisection of the body into anterior and posterior portions which then regenerate to make a complete, fully functional larva within days of separation (Figure 2). Cloning has been suggested to increase in optimal nutrient conditions (1.7 $\mu\text{g chl-a L}^{-1}$) compared with low nutrient conditions (0.17 $\mu\text{g chl-a L}^{-1}$) [78]. Cloning also occurs in brachiolaria larvae (Figure 1D) by budding a new larva from the posterior end as seen in field caught larvae (see budding larvae in Figure 3 [82]). It is not yet known if a single larvae can clone multiple times. For other sea star species, it has been suggested that some larvae may be perpetual cloners and remain in the plankton as ‘eternal’ larvae for extended periods of time and disperse widely without settling [83]. This ability may amplify their population numbers, increase their planktonic larval duration and dispersal as well as reduce their visibility to predators such as planktivorous fish [28].

Settling larvae select a suitable substrate in the reef matrix with a preference for crustose coralline algae (CCA). Larvae have also been found to be attracted to conspecific cues and the distribution of larvae around reefs in models and patterns of larval settlement across the GBR suggest that COTS larvae may be attracted to areas with adult populations thereby increasing population replenishment [2, 36, 84]. Additionally, well-fed larvae can settle spontaneously on biofilms in the absence of a coralline algal cue [72]. The potential for plasticity in settlement behaviour at the competent larval stage is typical of echinoderms [85, 86] and may increase the distribution of newly settled COTS in the reef infrastructure.

Two days after settlement, COTS larvae metamorphose into five-armed algae-eating juveniles, 0.3–0.7 mm in diameter [87, 88] (Figure 1G). As the juveniles grow, they add arms and spines (Figure 1H). Herbivorous

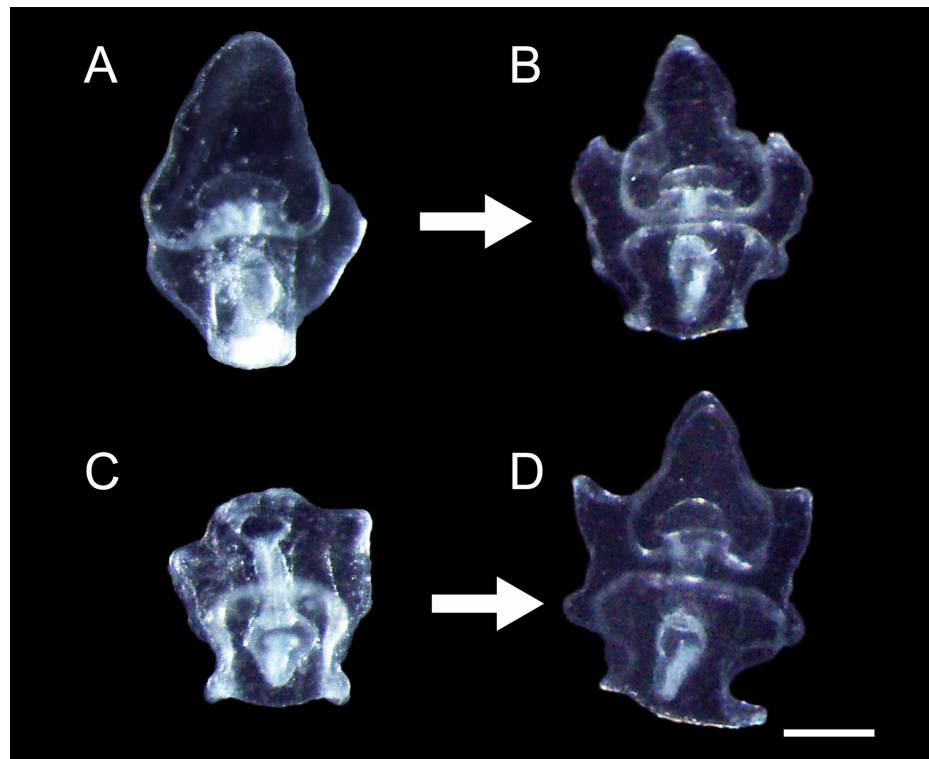


Figure 2. Cloning crown of thorns starfish larvae.

Partially regenerated head (A) and body (C) clone and the regenerated larvae (B and D) after four days. Scale bar = 200 μm .

juveniles are able to float in water tension, a possible and unprecedented avenue for dispersal during the benthic stage [89]. In nature, juveniles are most commonly found on CCA, their known settlement substrate and food source [90–92], as well as articulated and other growth forms of coralline algae [93]. Juvenile growth is diet-dependent with faster growth on CCA compared with articulated coralline algae (eg. *Amphiroa* sp.) [89], likely due to differences in digestibility and nutritional quality [94]. Although their growth was minimal over 10 months (1–3 mm diameter), juveniles can also survive on biofilm, a potentially ubiquitous food source in marine environments [89]. Once offered CCA, these juveniles resume their growth, attesting to their ability to withstand low food levels [89]. The dietary flexibility of juvenile COTS reduces their vulnerability to food scarcity when traversing the reef rubble matrix in search of coral (50 m on Suva reef, Fiji) [90].

Juveniles emerge from the rubble to start preying on coral as early as 4–6 months of age (8–18 mm diameter) [44, 95]. Corallivorous juveniles and adults consume a range of coral species as well as filamentous and foliose algae when coral is scarce, further demonstrating the dietary resilience of COTS [16, 96]. As they grow, their visual spatial resolution used to recognise suitable coral reef habitat and food increases [97]. During the first 40 days of the diet switch to coral, juveniles may be damaged or killed by coral tentacles [95, 98]. Injured juveniles are able to regenerate lost tissue, as typical of echinoderms [99, 100], with a predicted recovery time for damaged arms of ~3.5 months [98]. Despite coral stings, the juveniles persevere in their quest for coral prey although some revert to CCA during the regeneration-recovery period. Despite the potential fitness cost of sublethal injuries [101], 90% of juveniles in field surveys had arm damage showing their ability to survive [102].

The ability of juvenile COTS to exhibit rapid growth compared with other sympatric sea stars is likely to increase recruitment into adult populations and lead to the sudden appearance of outbreaks [1]. In a series of laboratory studies, algae-eating juvenile COTS reached a diameter of 4.5 mm in ~90 days, ~2.8- and 1.5-fold faster than those of *Linckia laevigata* (surface grazer) and *Culcita novaeguineae* (corallivore), respectively [88, 103, 104]. Once they transition to coral, the growth of COTS accelerates until they reach reproductive maturity (>2 years, 200 mm diameter) [95, 105]. The comparatively fast growth rate of COTS may be due to somatic growth that does not involve production of an energetically costly heavily calcified body wall as seen in most tropical sea stars [106]. Additionally, the disproportionately large size of their eversible stomach relative to their body diameter enhances food intake (COTS: 50%, *L. laevigata*: 8%, *C. novaeguineae*: 40%) [107, 108]. As juveniles become less susceptible to lethal predation with growth [46, 109, 110], the rapid growth of COTS is likely to increase post-settlement survival. This size-related refuge from predators is reflected in the change to foraging more openly during the day from cryptic, nocturnal foraging as juveniles [111, 112].

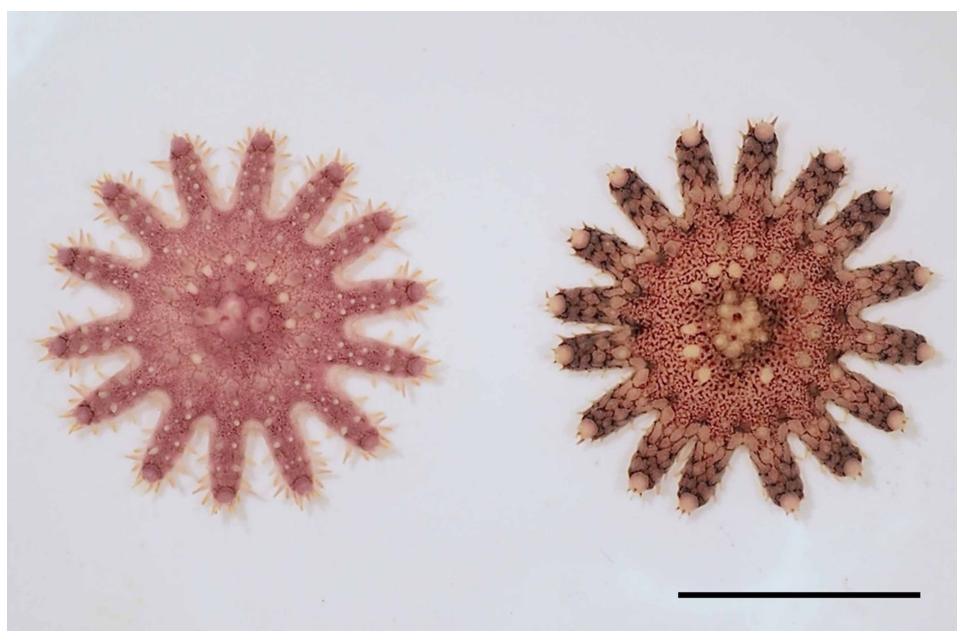


Figure 3. Herbivorous crown of thorns starfish aged ~1 year (left) and 6.5 years (right).

Scale bar = 10 mm.

If coral is not readily available, juveniles can pause their growth at ~18 mm diameter and have the potential to survive on a diet of algae for years (Figure 3). This extended herbivorous phase has been observed in the laboratory setting [44, 105, 113] and modelled to occur in the field [114]. In the laboratory, a prolonged herbivorous phase of six year had no impact on their continued growth on a coral diet [44]. While smaller COTS are likely to have increased risk of predation [109], juveniles <10–20 mm diameter have also been found at least one year after settlement in the GBR [115]. The capacity of COTS to have an indeterminate herbivorous juvenile stage prompted the juveniles-in-waiting hypothesis, positing that juveniles can accumulate in the reef rubble over spawning years before seeding an outbreak of adults [44]. An extended juvenile stage is not uncommon among predatory sea star populations in nature and has been found for *Asterias rubens* with juveniles pausing growth as they wait for increased food abundance and reduced competition from adults [116, 117] and *Marthasterias glacialis* with juveniles that remained in their nursery habitat over six years [118]. As well as diet-dependent growth and sublethal injuries from coral stings, a number of factors may influence the timing of the herbivory-corallivory ontogenetic switch in COTS including the proximity of coral to the nursery habitat [90], low coral abundance due to a cyclone or bleaching, or competition from adults, and predation pressure.

Crown of thorns starfish will remain a concern and burden

COTS are one of the most extensively studied sea stars and remain an ongoing research priority in many tropical regions [22, 25, 81, 119–121]. Identifying the key traits and highly adaptive biology of COTS across life stages such as their recently recognised phenotypic plasticity is crucial to understand the outbreak phenomenon. COTS appear to be an extreme expression of the plasticity characteristic of echinoderms within a single species. Thus, it is unlikely that outbreaks can be prevented, but perhaps can be curbed if the factors that influence their survival are better understood and addressed (Figure 4).

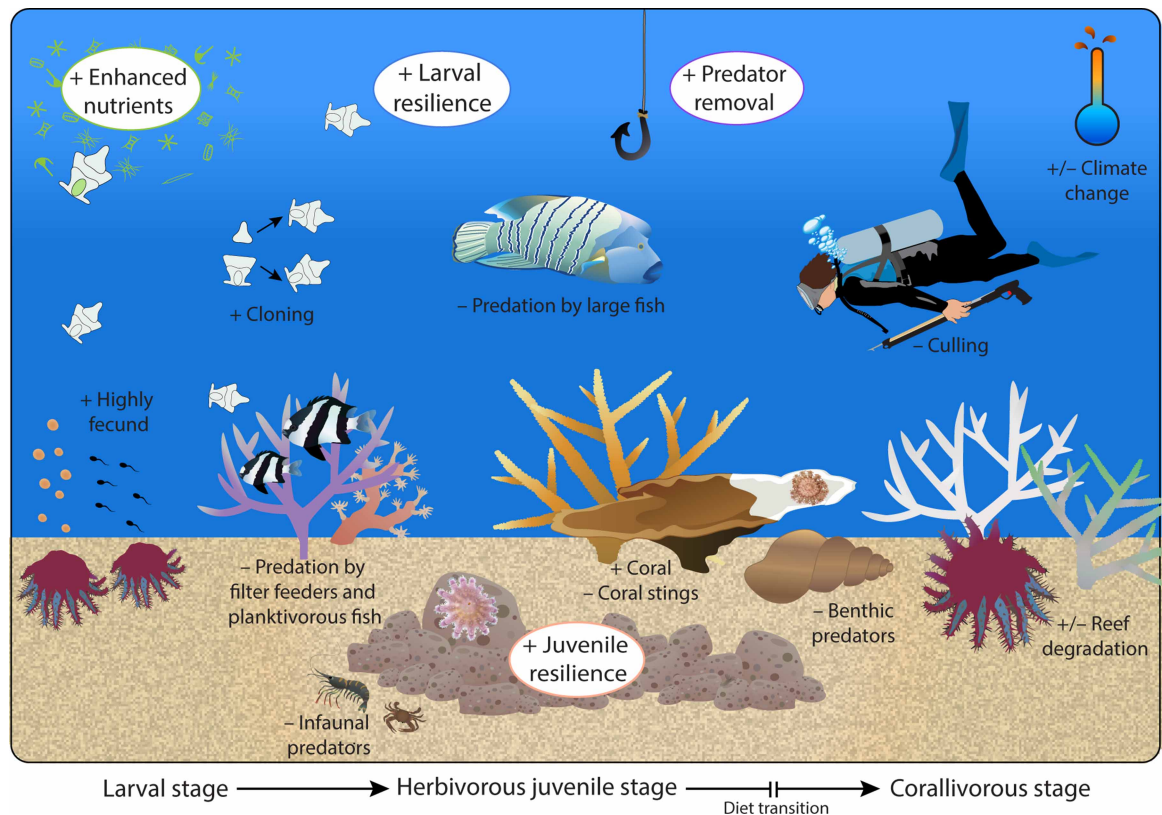


Figure 4. Processes and traits that are likely to have a positive (+) or negative (-) effect on the success of crown of thorns starfish.

Symbols sourced from Integration and Application Network, University of Maryland Center for Environmental Science (<https://ian.umces.edu/media-library/>).

Over the past 10 years, substantial financial investment has been made into COTS control by the Australian Government with AUD\$44.9 million in 2012 and AUD\$57.8 million in 2018 directed towards research, water quality management and killing COTS [122]. Of this, AUD\$21.7 million in 2012 and AUD\$23.2 million in 2018 have been invested into manual culling programs [123]. Since the 1950s, widely implemented programs across the Indo-Pacific have removed over 18 million COTS [43, 122]. In Australia, the lethal injection method is now used to increase the efficiency of COTS removal (Figure 5). Without a means to eradicate the causes of outbreaks, culling is the only tool available to directly lower COTS densities and reduce coral loss during an active outbreak, particularly for priority reefs used by the tourism industry [20, 30, 57]. These programs can benefit from early detection of COTS and warning systems of outbreaks through predictive modelling of at-risk reefs [20], targeted collections of juveniles [115] and enhanced surveillance which, in Australia, involves SCUBA and manta tows surveys undertaken by COTS control teams [124, 125]. Recent development of environmental DNA can also be used to detect the presence of adult starfish in the water surrounding outbreaking reefs [126, 127].

Identifying proactive measures to prevent or minimise outbreaks would be the most effective way of protecting coral reefs and increasing the success of coral restoration programs. Larval success may be curtailed by a reduction in agricultural runoff and thereby a reduction in phytoplankton food levels [128], although the link between runoff and outbreaks remains equivocal. Stronger evidence is emerging on the importance of COTS predators in reducing outbreaks [29, 31, 40, 122]. Additionally, reef degradation from anthropogenic activities may increase the susceptibility of reefs to outbreaks. The degree of degradation has been positively correlated with COTS abundance in chronic outbreak populations in Japan [129]. Destructive and unmanaged fishing practises, pollution, sedimentation and erosion from marine and terrestrial development and unregulated tourism reduce the functional and species diversity of coral reefs [129, 130]. Coral loss reduces habitat for fishes that prey on the benthic stage of COTS as well as planktivorous fishes that, alongside coral polyps themselves, create a ‘wall



Figure 5. Crown of thorns starfish culling by lethal injection, Great Barrier Reef, Australia.

Photo: Matthew Curnock.

of mouths' that prey on COTS larvae [28, 88, 131] and can substantially reduce the quantity of zooplankton entering a reef [132]. Furthermore, increased rubble habitat in damaged areas may promote the settlement and survival of early juvenile COTS [2].

The threat of COTS may be further exacerbated by climate change, which is by far the biggest threat to coral reefs. In contrast with the sensitivity of corals to ocean warming, COTS larvae and the herbivorous and corallivorous juvenile stages have enhanced growth in warmer temperatures [133–137]. The juveniles are also robust to ocean acidification [133, 134]. However, larval development is negatively impacted by higher temperatures (above +2°C) and in combination with reduced pH [135, 136]. Adults acclimated to climate change conditions (+2°C, −0.35 pH), produce smaller eggs although with little impact on fertilisation success [121]. The impact of parental acclimation on offspring development of COTS is not known and has been shown to be species-specific with both positive and negative effects across echinoderms [138]. Furthermore, coral consumption by COTS may increase as the ocean warms and during heatwaves as their metabolism increases with temperature up to 31°C (+2°C) [133, 139]. COTS outbreaks and the increased intensity of heatwaves, cyclones and coral bleaching cause widespread coral damage [4]. However, coral loss also reduces the availability of coral prey for COTS. Without coral, COTS outbreaks will not occur.

Summary

- Outbreaks of COTS are an ongoing threat to an already imperilled Great Barrier Reef and other tropical reefs throughout the Indo-Pacific.
- The extreme success of this species is likely to be a combination of its highly resilient and opportunistic traits and anthropogenic activities that advantage COTS.
- While killing COTS is the only option available to management in the effort to reduce coral loss, this approach is unlikely to prevent future outbreaks due to the inherent biology and high fecundity of COTS.
- Taking a precautionary and proactive approach to COTS management by understanding and addressing the factors that are likely to increase COTS survival will benefit coral reef ecosystem health.
- Regardless of addressing the causes of COTS outbreaks, immediate action against climate change is crucial to curb the global decline in coral reefs.

Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

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Abbreviations

CCA, crustose coralline algae; COTS, Crown of thorns starfish; GBR, Great Barrier Reef.

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