

# CROWN OF THORNS STARFISH (*Acanthaster* spp.) & THE GREAT BARRIER REEF

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*Photo Credit: Joe Littell*

## INTRODUCTION

Coral reefs are one of the most productive and diverse ecosystems on the planet. The wealth of ecosystem services provided by coral reefs are highly valued by millions of people. Scleractinian corals, or hard corals, form the structure of coral communities within a reef (Wescott et al. 2016). The structural complexity of coral reefs supports diverse assemblages of fishes and other marine species (Graham and Nash 2013). Barrier reefs protect shorelines from storms and surge, as well as stabilize mangroves and seagrass beds. Corals purify water and recycle carbon dioxide to the atmosphere. In addition, coral reefs support thriving recreational and commercial fisheries as well as the tourist industry.

Coral reefs are considered one of the world's most threatened ecosystems, with coral decline understood as a general global phenomenon (Bruno and Selig 2007). Climate change, along with acute large-scale disturbances combined with anthropogenic pressures stemming from mismanagement of natural resources, suggest an uncertain future for reefs across the globe

(Pratchett et al. 2014). Coral abundance, health, and diversity of species are vital to the ecological functioning of reef ecosystems.

Australia's iconic Great Barrier Reef (GBR) is the world's largest coral reef ecosystem, spanning more than 2300 kilometers along the Queensland coastline (Figure 1.). Inscribed in 1981 for its natural "outstanding universal value", the GBR World Heritage Area encompasses 348,000 square kilometers and includes 1050 islands. The more than 400 species of hard corals found on the GBR comprise a habitat covering 26,000 square kilometers (GBRMPA 2014). The network of more than 2900 separate reefs forms 30 distinct bioregions and make up 10% of the world's coral reefs (Spalding et al. 2001). The ecological and biological processes of the GBR represent major stages of earth's evolutionary history, with globally significant marine fauna and vegetation groups of immense diversity. The natural beauty of the GBR below and above the water reflects one of the richest and most complex natural ecosystems on earth and is therefore one of the most significant habitats for biodiversity conservation.



Figure 1. Map showing the extent of the Great Barrier Reef. Britannica, 2022.

The national and international community also values the GBR for its importance to the cultural, social, and economic well-being of the more than one million people living in its catchment (GBRMPA 2014). Tourism, fishing, recreation, traditional use, research, defense, shipping, and ports are among the wide range of activities supported by the GBR. A marine protected area conserves the reef environment and benefits Australia's economy, generating billions of dollars each year and supporting over 70,000 jobs (Deloitte Access Economics 2013).

The GBR has experienced a decline in hard-coral cover over the past several decades. Corals are sensitive to the rising temperatures and ocean acidification caused by the world's changing climate, water pollution from terrestrial runoff and dredging, destructive fishing, overfishing, and coastal development. An increase in the frequency and intensity of tropical cyclones, warming ocean waters, and population outbreaks of Crown of Thorns Starfish (CoTS, *Acanthaster* spp.) have caused mass mortality of corals as well as reduction in coral growth rates (De'ath et al. 2012). Renewed outbreaks of CoTS on the GBR occurring simultaneously with mass bleaching events due to climate change continues to cause significant degradation of the reef (Wescott et al. 2020). As such, close and continuous monitoring of CoTS populations and evaluation of management effectiveness is crucial. Although knowledge gaps remain with regard to the exact cause(s) of CoTS outbreaks, and effective CoTS management remains costly, CoTS outbreaks are a principal cause of coral loss that is amenable to direct and immediate action (Pratchett et al. 2017).

With advances in technology, research continues to evolve and expand our knowledge of CoTS outbreaks, impacts, and management. Opportunities for research and conservation have also expanded to include a variety of participants. Tourists and volunteers from the general public can assist in monitoring and control of CoTS populations by reporting sightings and participating in control programs. Increasing awareness of the threat posed by outbreaking populations of CoTS can foster collaboration between scientists and the public, resulting in immediate protection of the GBR and other reef ecosystems where CoTS are a threat.

This publication focuses on the Pacific Crown-of-Thorns Starfish (CoTS) and its impacts from predation on corals of the GBR. It contains information on CoTS identification, ecology, and impacts to humans and the environment. The intended audience is tourists of Australia and Australian residents.

## CoTS IMPACTS TO CORAL REEFS

Although rare, the Crown-of Thorns Starfish (CoTS) is a natural inhabitant of coral reef ecosystems in the Indo-Pacific Region, and occasionally occurs in large populations termed

*outbreaks* (Moran and De'ath 1992). Outbreaking populations of CoTS have been identified as a major driver of coral decline across the Indo-Pacific (De'ath et al. 2012, Pratchett et al. 2014). Hard coral on the GBR has seen extensive damage from predation by CoTS over the past several decades. From 1985 to 2012, hard coral cover declined by ~50% on the GBR, with 42% of the loss attributable to impacts of predation by CoTS (De'ath et al. 2012).

The runoff of soils, fertilizers, and pesticides from agricultural and coastal development, which has also significantly affected inshore coral reefs, has likely increased CoTS outbreak frequencies (Brodie et al. 2005). Recurrent outbreaks of CoTS have the potential to alter biotic communities and compound ongoing, multiple threats to the existence of the GBR (Wescott et al. 2016). If corals do not have enough time to recover between outbreaks, the reef ecosystem undergoes a "phase shift", entering a new state dominated by algae, soft corals, and sponges covering the dead coral rubble. This results in a reduction from a dimensionally complex reef with high coral cover to a habitat low in coral cover and reduced ecosystem diversity (Graham and Nash 2013).

In 2010, the GBR experienced the initial stages of the most recent CoTS outbreak, the fourth since the 1960's (Pratchett et al. 2014). Following a common pattern, primary outbreaks begin approximately every 15 to 17 years in the region known as the "initiation zone" between Lizard Island and Cairns on reefs offshore from the Wet Tropics river catchment (Wooldridge and Brodie 2015). Waves of secondary outbreaks spread southward in warmer months (December and January) when adults spawn, as larvae are transported from the initiation zone by ocean currents. Spreading at a rate of 60 Kilometers per year, these outbreaks can persist for a period of 10 years or more. Outbreaks have had devastating and widespread effects, sometimes reducing live hard coral cover by 90% in the immediate area of the outbreak (Pratchett et al. 2014).

Removal of the primary cause of outbreaks would be the most efficient way of controlling CoTS population eruptions (GBRMPA 2019). However, no definitive answer has been given as to the initial drivers of CoTS outbreaks (Pratchett, et al. 2014). Continued improvements in CoTS management is necessary due to the consequences of the interactions of CoTS impacts and other drivers of coral decline (De'ath, et al. 2012). Research suggests factors that contribute to CoTS outbreaks may include biological traits of the starfish itself, nutrient run-off, fishing pressure, coral prey availability, and current flow patterns (GBRMPA 2020).

Along with tropical cyclones, coral bleaching events, fishing pressure, coral disease, and flooding events, CoTS impacts compound the cumulative pressure exerted on coral health and the GBR. Anthropogenic influences combined with climatic events are thought to increase the severity of impacts from CoTS outbreaks. Of all the threats to the GBR, minimizing CoTS impacts is the most feasible action that will reduce the pressure exerted on reef (De'ath, et al. 2012).

## MANAGING CoTS POPULATIONS

Manual control programs to manage CoTS population outbreaks have been implemented since the 1960's (Kenchington 1978). Early programs involved physically extracting starfish and burying them on land (Pratchett et al. 2019). Efforts to cut-up, remove, and bury starfish are slow, resource intensive, and pose risk to divers from their venomous spines (Bostrom-Einarsson 2016). Documentation suggests these activities were poorly

designed, focusing on putting divers in the water at locations with high CoTS densities and killing as many individuals as possible until resources were depleted (Zann and Weaver 1988). Although success at initial outbreaks was achieved, attempts at broad-scale control was considered a failure, leading to a focus on protecting high-value tourism sites in subsequent outbreaks on the GBR (Wescott et al. 2016). Limited success in reducing CoTS densities or coral loss (Pratchett et al. 2019) has been attributed to the lack of a strategic approach in implementing programs (Zann and Weaver 1988). In recent years, the development of single-shot injection methods (Figure 2.) for culling CoTS along with strategic deployment of manual control have significantly improved the efficacy of programs to control high CoTS densities and reduce impacts to coral reefs (Rivera-Posada et al. 2014; Wescott et al. 2016; Wescott et al. 2020).



Figure 2. Diver injecting CoTS with vinegar. © 2022 Great Barrier Reef Foundation.

## IDENTIFYING CoTS

Crown-of-Thorns Starfish have been documented in the Indo-Pacific from the Red Sea, but have never been found in Atlantic or Caribbean waters (Pratchett 2014). They have been found in a wide range of latitudes, from 34°N (Yamaguchi 1986), to 32°S (DeVantier & Deacon 1990). First described and classified in the 1700's (Rumpf 1705, von Linne 1758), *Acanthaster planci* was previously thought to represent all CoTS as a single species. DNA barcoding showed that there are at least four geographically separated species throughout the Indo-Pacific (Vogler et al. 2008,). The Pacific Crown-of-Thorns Starfish (*Acanthaster cf. solaris*) is distributed throughout the Pacific Ocean and is the only species known to occur within the GBR.



Figure 3. Close-up view of *Acanthaster cf. solaris* arms and spines. Ocean Gardener 2020.

Like other starfish, CoTS are in the phylum Echinodermata, which are relatives of sand dollars and sea urchins. CoTS are the world's second largest starfish, measuring up to one meter in diameter (Birkland 1989), and are the only starfish considered a threat to coral reefs (Glynn and Krupp 1986). They have 10-20 flexible arms extending from the center of their body. Although adult CoTS are large and are easily spotted in the water, juveniles are much smaller, cryptic in nature, and are rarely seen. CoTS exhibit drastic variation in color among individuals (Haszprunar 2017), although *A. cf. solaris* is usually observed as having a multi-colored pattern with distinct shades of green, blue, grey, purple, red and/or pink on the top (aboral side) of their body.

Adult CoTS are covered with numerous long and sharp spines, measuring 40-50 millimeters in length, which serve to protect them from predators (Moran 1986). When disturbed, the starfish curl up into a spiny ball. These spines are harmful to both humans and marine life, as they are coated with a toxin. Skin penetration wounds are known to be excruciatingly painful, and pain can last for hours or days. Associated symptoms include persistent nausea, fever, or even permanent abscesses, apoptosis, hemolysis, and bone destroying processes (Haszprunar 2017).

## BIOLOGY AND ECOLOGY

Biological traits of CoTS exhibited throughout their lifecycle are strongly suggestive of their prevailing nature. Both male and female adults are very fecund. Research has shown that large female *A. cf. solaris* individuals are capable of producing 106 million relatively large and nutrient dense eggs per year, and adult males can produce nearly 53 billion sperm (Pratchett et al. 2021).

On the GBR, adult CoTS spawn in the summer (December-January) in dense populations and are thought to spawn once a year (Caballes et al. 2021). During this process eggs are fertilized, and hatch approximately one day later (Pratchett et al. 2014) into a planktonic phase as larvae floating in the water column. Dispersing widely with ocean currents, CoTS larvae have a flexible diet which includes phytoplankton, dissolved organic matter and bacteria in the absence of phytoplankton (Pratchett et al. 2014). If food levels are low, they can adjust the size of their feeding structures to increase their ability to capture food (Wolfe et al. 2015). CoTS larvae are known to reproduce asexually by cloning, increasing population size and thereby increasing survival (Allen et al. 2019). Typically, larvae spend 2-3 weeks in this phase before settling on a preferred substrate of coralline algae in the reef matrix (Deaker and Byrne 2022).

Two days after settling, CoTS undergo metamorphosis and grow five arms to become juvenile starfish (Figure 4., stage G) measuring 0.3-0.7 mm in diameter (Henderson and Lucas 1971, Yamaguchi 1973). Three weeks later, the starfish's body turns pink, camouflaging them against the algae on which they feed. The herbivorous juveniles continue adding arms and spines as they grow (Pratchett 2014). As early as 4-6 months of age (8-18 mm diameter), they emerge from rubble and begin feeding on coral (Yamaguchi 1974). Rapid growth increases CoTS's chances of survival after metamorphosis and continues to accelerate until they reach reproductive maturity (>2 years, 200 mm diameter) (Lucas 1984).

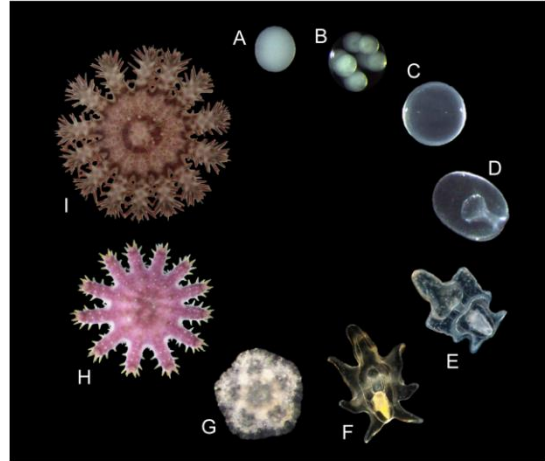


Figure 4. The life cycle of a crown of thorns starfish. (A) an unfertilised egg, (B) the eight-cell stage, (C) a blastula, (D) a gastrula with the archenteron, (E) a feeding bipinnaria with fully developed digestive tract (photo Dr Jonathan Allen) (F), a brachiolaria with anterior arms used for benthic settlement (photo Dr. Paulina Selvakumaraswamy) (G) a newly settled juvenile, (H) the older herbivorous stage juvenile and, finally, (I) the corallivorous stage (Deaker and Byrne 2022).

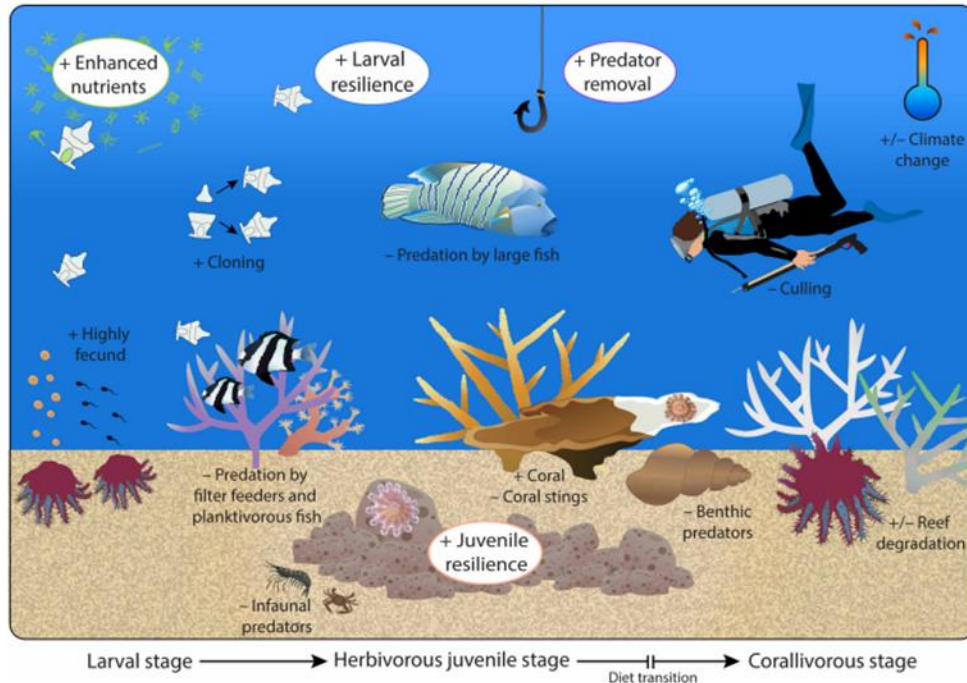


Figure 5. Processes and traits that may have positive (+) or negative (-) effects on CoTS species success. Symbols sourced from Integration and Application Network, University of Maryland Center for Environmental Science (<https://ian.umces.edu/media-library/>).

CoTS have an exceptionally large stomach in relation to an individual's total biomass, probably accounting for its ability to grow rapidly (Birkland 1989). Using hundreds of small, sucking tube feet in each arm, the starfish slowly moves onto the surface of the corals. It pushes its stomach out through its mouth on the underside, spreading the stomach across the surface of the coral beneath it to about its own diameter. They are nocturnal and can travel at speeds up to 20 meters per hour. Preying on nearly all species of coral, CoTS can consume 10 square meters of coral per year.

CoTS are one of the largest and most efficient predators on scleractinian corals (Moran 1986). In naturally low numbers on healthy reefs, they play an important role in benefiting the ecosystem by consuming faster growing corals, allowing slower growing corals to catch up. This promotes coral diversity within the reef. However, when CoTS appear in outbreak numbers, they have the potential to devastate large tracts of reef.

Massive outbreaks occur periodically when the number of individual starfish suddenly rises above their naturally low density of 1 starfish per hectare to 15 starfish per hectare. Feeding exclusively on coral, CoTS continue to threaten the health and resilience of the GBR when their consumption of coral tissue exceeds coral growth during outbreaks (GBRMPA 2019). An outbreaking CoTS population is estimated to be capable of consuming 0.18% of hard coral biomass per day on an average reef, with significant coral loss occurring when densities climb beyond 1000 individuals/km (Wescott et al. 2016).



Predator release is one of the first concepts hypothesized to account for CoTS outbreaks (Cowan et al. 2017). The predator release hypothesis suggests CoTS populations are regulated by natural predators, feeding mainly on juvenile starfish, and that exploitation of predators by humans leads to CoTS outbreaks (Endean 1969). Heavily overfished from 1947-1960, the removal of the giant triton marine snail (*Charonia tritonis*) from the GBR has been thought responsible for the first documented outbreak in 1962 (Endean 1969). Since then, a diverse range of reef fish and invertebrates including harlequin shrimp, humphead Maori wrasse (Figure 5.), spangled emperor, red throat emperor, starry pufferfish, Queensland grouper, and titan triggerfish have been reported to consume pelagic larvae and benthic juvenile, sub-adult and adult CoTS (Cowan et al. 2017). Evidence has suggested a link between CoTS outbreaks and fishing pressures whereby reefs in fished Habitat Protection Zones had almost four times the number of outbreaks as reefs in no-take Marine National Park Zones, resulting in reduced coral cover (Sweatman 2008).

The nutrient enhancement hypothesis states that “high nutrient availability increases phytoplankton biomass which enhances larval growth and survival leading to mass recruitment events and outbreaks” (Kroon et al. 2021). Nutrient levels are nine times higher in rivers flowing to the central and southern areas of the GBR, compared with pre-European settlement (De’ath et al. 2012). Evidence suggests that current water quality conditions on the GBR are enhancing CoTS survival, reproduction, establishment, and spread (Allen et al. 2019).

## WHAT’S BEING DONE

Although removal of fish species that directly prey on, or indirectly influence predation on CoTS may affect CoTS density, predation management has never been implemented as a strategy to control CoTS outbreaks (Kroon et al. 2021). Research has shown that coral reefs protected from fishing have lower CoTS abundances and are less likely to experience outbreaks, indicating the applicability of fisheries-based management (Sweatman 2008; Kroon 2021). In addition, no-take marine reserves have been shown to recover 2-3 times faster from damage caused by CoTS outbreaks than those open to fishing (Mellin et al. 2016). Continued research showing the effects of removing CoTS predators through recreational and commercial fisheries may reveal the applicability of fisheries-based management to prevent and control outbreaks (Kroon 2021).

Improving water quality is a long-term preventative action to indirectly reduce frequency of CoTS outbreaks while enhancing the resilience of corals on the GBR (Commonwealth 2018). Various water quality improvement programs for the GBR have been implemented since 2003, focusing on changes in agricultural practices to reduce land-based pollution to waters flowing from catchments adjacent to the GBR (Kroon et al. 2016). The Australian and Queensland

Government's Reef Quality Improvement Plan 2050 has set targets that, if met, may result in positive outcomes for the GBR (GBRMPA 2020). The CoTS Strategic Management Framework admits that current mitigation measures are unlikely to meet these targets, as progress has slowed. However, the Australian Government maintains that improvements to water quality are a high priority and are critical for CoTS management (GBRMPA 2020).

Of all the threats to the GBR, minimizing CoTS impact is the most feasible action that will reduce the pressure exerted on reef (De'ath, et al. 2012). Currently, the most effective way to manage outbreaks is through manual control by killing individual starfish (Wescott et al. 2020). The CoTS Control Program developed by the Great Barrier Reef Marine Park Authority in 2012 now operates on modern principles of Integrated Pest Management and utilizes a decision support tool to guide on-water operations (Fletcher et al. 2020; Wescott et al. 2016; Wescott et al. 2020). The strategic approach for managing CoTS populations in the GBR Marine Park outlined in the Strategic Management Framework combines tactical responses during an outbreak with preventative actions aimed at improving water quality and protecting natural predators of CoTS.

## WHAT YOU CAN DO

Protecting the GBR from harmful effects of CoTS as well as other negative impacts is not limited to the efforts of scientists and reef professionals. The GBRMPA and the Queensland Government encourage community members to participate in the Strategic Management of CoTS. Anyone can report sightings of CoTS to the Marine Park Authority through the [Eye on the Reef Sightings app](#). The Marine Park's rangers and CoTS Control Program vessel crews use this information to guide more in-depth assessments of CoTS populations and risk of outbreaks.

Community members may also actively engage in culling CoTS in the Marine Park. Interested individuals may apply for CoTS control permits free of charge and submit them through the [Permit Application Portal](#). Information on safety and best practices for effectiveness of CoTS culling activities can be found in the GBRMPA's [CoTS Control Guidelines](#). A lethal injection of appropriate concentrations of bile salts or household vinegar is the current method recommended for culling CoTS. A single injection into the body can kill a CoTS within 24-48 hours without harming any other reef organisms (Rivera-Posada et al. 2014; Boström-Einarsson and Rivera-Posada 2016).

In general, users and visitors of the GBR can contribute to CoTS management by practicing good reef stewardship. This means following [responsible reef practices](#) such as compliance with GBRMPA zoning regulations, proper waste disposal, and exercising caution to prevent damage to corals when boating, fishing, and snorkeling/diving. These practices contribute to overall reef

health and ensure that efforts to increase reef resilience, such as CoTS control, are not undermined (GBRMPA 2020).

## REFERENCES

1. Allen, J.D., Richardson, E.L., Deaker, D., Agüera, A. & Byrne, M. 2019. Larval cloning in the crown-of-thorns sea star, a keystone coral predator. *Mar. Ecol. Prog. Ser.* 609, 271–276.2.
2. Birkeland, C. 1989. The Faustian traits of the crown-of-thorns starfish. *Am. Sci.*, 77, 154–163.
3. Boström-Einarsson, L. & Rivera-Posada, J. 2016. Controlling outbreaks of the coral-eating crown-of-thorns starfish using a single injection of common household vinegar, *Coral Reefs* 35(1): 223.
4. Britannica, The Editors of Encyclopaedia. "Great Barrier Reef". Encyclopedia Britannica, 29 Aug. 2022, <https://www.britannica.com/place/Great-Barrier-Reef>.
5. Brodie, J., Fabricius, K., De'ath, G. & Okaji, K. 2005. Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. *Marine Pollution Bulletin* 51(1-4): 266-278.
6. Bruno, J. F. & Selig, E. R. 2007. Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. *Plos One* 2, e711.
7. Caballes, C.F., Byrne, M., Messmer V. & Pratchett, M.S. 2021. Temporal variability in gametogenesis and spawning patterns of crown-of-thorns starfish within the outbreak initiation zone in the northern Great Barrier Reef. *Mar. Biol.* 168:13.
8. Commonwealth of Australia and State of Queensland 2018, Reef 2050 Water Quality Improvement Plan 2017-2022, Reef Water Quality Protection Plan Secretariat.
9. Cowan, Z.L., Pratchett, M., Messmer, V. and Ling, S. 2017. Known predators of crown-of-thorns starfish (*Acanthaster* spp.) and their role in mitigating, if not preventing, population outbreaks, *Diversity* 9(1): 7.
10. De'ath, G., Fabricius, K., Sweatman, H. & Puotinen, M. 2012. The 27–year decline of coral cover on the Great Barrier Reef and its causes. *Proc. Natl Acad. Sci. USA* 109, 17995–17999.
11. Deloitte Access Economics. 2013. Economic contribution of the Great Barrier Reef 2011-2012, *Great Barrier Reef Marine Park Authority, Townsville*.
12. DeVantier, L.M. & Deacon, G. 1990. Distribution of *Acanthaster planci* at Lord Howe Island, the southernmost Indo-Pacific reef. *Coral Reefs* 9, 145–148.
13. Edean, R. 1969. *Report on investigations made into aspects of the current Acanthaster planci (crown of thorns) infestations of certain reefs of the Great Barrier Reef*. Queensland Department of Primary Industries (Fisheries Branch), Brisbane, Australia.

14. Fletcher, C.S., Bonin, M.C. and Westcott, D.A. 2020. *An ecologically-based operational strategy for COTS control: integrated decision making from the site to the regional scale*. Report to the National Environmental Science Programme, Reef and Rainforest Research Centre Limited, Cairns.
15. Glynn, P.W. & Krupp, D.A. 1986. Feeding biology of a Hawaiian sea star corallivore, *Culcita novaeguineae* Muller & Troschel. *Exp. Mar. Biol. Ecol.* 96, 75–96.
16. Graham, N.A., Wilson, S.K., Jennings, S., Polunin, N.V., Bijoux, J.P. & Robinson, J. 2006. Dynamic fragility of oceanic coral reef ecosystems. *Proc. Natl Acad. Sci. USA* 103(22): 8425- 8429. 17.
17. Graham, N. & Nash, K.L. 2013. The importance of structural complexity in coral reef ecosystems, *Coral Reefs* 32(2): 315-326.
18. Great Barrier Reef Marine Park Authority 2014, *Great Barrier Reef Region Strategic Assessment: Strategic assessment report*, GBRMPA, Townsville.
19. Great Barrier Reef Marine Park Authority. 2019. *Great Barrier Reef outlook report 2019*, Great Barrier Reef Marine Park Authority, Townsville.
20. Great Barrier Reef Marine Park Authority, 2020. *Crown-of-thorns starfish strategic management framework*. Great Barrier Reef Marine Park Authority, Townsville.
21. Haszprunar, G., Vogler, C. & Wörheide, G. 2017. Persistent gaps of knowledge for naming and distinguishing multiple species of crown-of-thorns seastar in the *Acanthaster planci* species complex. *Diversity* 9, 22.
22. Henderson, J.A. & Lucas, J.S. 1971. Larval development and metamorphosis of *Acanthaster planci* (Asteroidea). *Nature* 232, 655–657.
23. Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., et al. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301: 929–933.
24. Kenchington, R.A. 1978. The Crown-of-thorns Crisis in Australia: A Retrospective Analysis. *Environmental Conservation* 5(01), 11-20.
25. Kroon, F. J., Torburn, P., Schafelke, B. & Whitten, S. Towards. 2016. protecting the Great Barrier Reef from land-based pollution. *Glob. Change Biol.* 22, 1985–2002.
26. Kroon, F.J., Barneche, D.R. & Emslie, M.J. 2021. Fish predators control outbreaks of Crown-of-Thorns Starfish. *Nat. Commun.* 12, 6986.
27. Lucas, J.S. 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.
28. Lucas, P. H. C., Webb, T., Valentine, P. S. & Marsh, H. 1997. *The outstanding universal value of the Great Barrier Reef world heritage area*.
29. Mellin, C., MacNeil, A. M., Cheal, A. J., Emslie, M. J. & Caley, J. M. 2016. Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.* 19, 629–637.
30. Moran, P.J. 1986. The *Acanthaster* phenomenon. *Oceanogr. Mar. Biol. Annu. Rev.* 24, 379–480.

31. Moran, P.J. and De'ath, G. 1992. Estimates of the abundance of the crown-of-thorns starfish *Acanthaster planci* in outbreaking and non-outbreaking populations on reefs within the Great Barrier Reef, *Marine Biology* 113: 509-515.
32. Pratchett, M.S., Caballes, C.F., Cvitanovic, C., Raymundo, M.L., Babcock, R.C., Bonin, M.C., Bozec, Y.M., Burn, D., Byrne, M., Castro-Sanguino, C., Chen, C.M., Condie, S.A., Cowan, Z.L., Deaker, D.J., Desbiens, A., Devantier, L.M., Doherty, P.J., Doll, P.C., Doyle, J.R., Dworjanyn, S.A., Fabricius, K.E., Haywood, M.D., Hock, K., Hoggett, A.K., Hoi, L., Keesing, J.K., Kenchington, R.A., Lang, B.J., Ling, S.D., Matthews, S.A., McCallum, H.I., Mellin, C., Mos, B., Motti, C.A., Mumby, P.J., Stump, R.J.W., Uthicke, S., Vail, L., Wolfe, K. & Wilson, S.K. 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. *The Biological Bulletin* 241:3, 330-346
33. Pratchett, M.S., Caballes, C. F., Rivera-Posada, J. A. & Sweatman, H. P. A. 2014. Limits to our understanding and managing outbreaks of Crown-of-Thorn Starfish (*Acanthaster* spp.). *Oceanogr. Mar. Biol. Annu. Rev.* **52**, 133–200.
34. Pratchett, M.S., Nadler, L.E., Burn, D. *et al.* 2021. Reproductive investment and fecundity of Pacific crown-of-thorns starfish (*Acanthaster cf. solaris*) on the Great Barrier Reef. *Mar Biol* **168**, 87.
35. Rivera-Posada, J., Pratchett, M. S., Aguilar, C., Grand, A. & Caballes, C. F. 2014. Bile salts and the single-shot lethal injection method for killing crown-of-thorns sea stars (*Acanthaster planci*). *Ocean Coast. Manag.* 102, 383–390.
36. Spalding, M.D., Ravilious, C. & Green, E.P. 2001. *World atlas of coral reefs*, University of California, Berkeley.
37. Sweatman, H. 2008. No-take reserves protect coral reefs from predatory starfish. *Current Biology* 18(14): R598- R599.
38. Vogler, C., Benzie, J., Lessios, H., Barber, P. & Wörheide, G. 2008. A threat to coral reefs multiplied? Four species of crown-of-thorns starfish. *Biol. Lett.* 4, 696–699.
39. Westcott, D.A., Fletcher, C. S, Babcock, R. & Plaganyi-Lloyd, E. 2016. A strategy to link research and management of crown-of-thorns starfish on the Great Barrier Reef: An Integrated Pest Management approach. Report to the National Environmental Science Programme. *Reef and Rainforest Research Centre Limited, Cairns* (80pp.)
40. Westcott, D.A., Fletcher, C.S., Kroon, F.J. *et al.* 2020. Relative efficacy of three approaches to mitigate Crown-of-Thorns Starfish outbreaks on Australia's Great Barrier Reef. *Sci. Rep.* 10, 12594.
41. Wolfe, K., Graba-Landry, A., Dworjanyn, S.A. & Byrne, M. 2015. Larval phenotypic plasticity in the boom-and-bust crown-of-thorns seastar, *Acanthaster planci*. *Mar. Ecol. Prog. Ser.* 539, 179–189.
42. Wooldridge, S.A. & Brodie, J.E. 2015. Environmental triggers for primary outbreaks of crown-of-thorns starfish on the Great Barrier Reef, Australia. *Marine Pollution Bulletin* 101(2): 805-814.

43. Yamaguchi, M. 1973. Early life histories of coral reef asteroids, with special reference to *Acanthaster planci* (L.). In *Biology and Geology of Coral Reefs Biology* (Jones, O.A. and Endean, R., eds), pp. 369–387, Academic Press, New York & London.
44. Yamaguchi, M. 1974. Growth of juvenile *Acanthaster planci* (L.) in the laboratory. *Pacific Science* 28: 123–138.
45. Yamaguchi, M. 1986. *Acanthaster planci* infestations of reefs and coral assemblages in Japan: a retrospective analysis of control efforts. *Coral Reefs* 5, 23–30.
46. Zann, L., Weaver, K. 1988. An evaluation of crown-of-thorns starfish control programs undertaken on the Great Barrier Reef. In '*Proceedings of the 6th International Coral Reef Symposium Vol. Vol. 2: Contributed Papers.*' (Eds JH Choat, D Barnes, M Borowitzka et al). (International Coral Reef Society: Townsville, Australia)