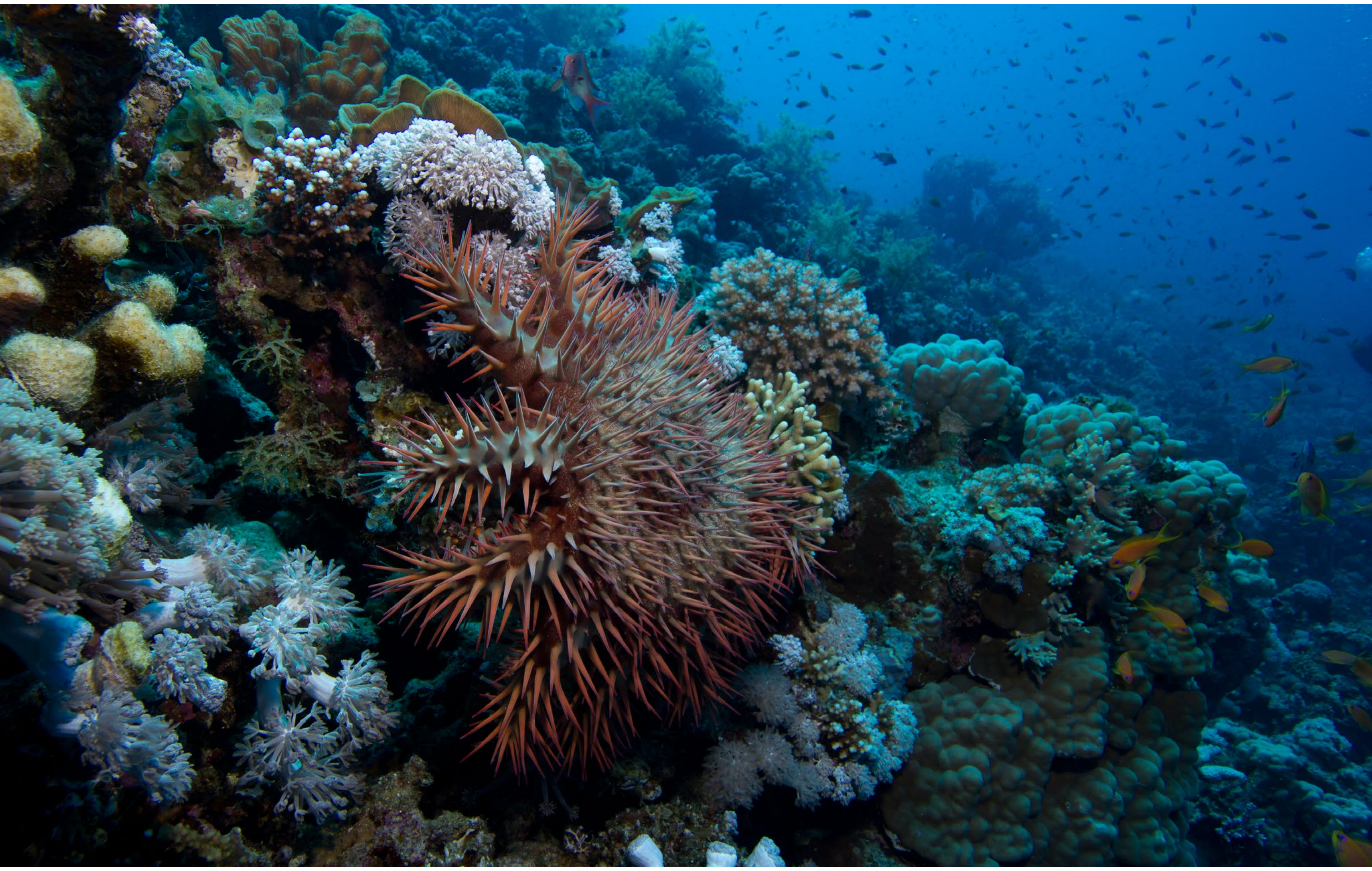
COTS Control Innovation Program

TECHNICAL REPORT

Predation on adult Pacific crown-of-thorns starfish (*Acanthaster cf. solaris*) relative to fisheries management zones on Australia's Great Barrier Reef

Peter C. Doll, Morgan S. Pratchett, Scott D. Ling, Sterling S. Tebbett,
Andrew S. Hoey, and Ciemon F. Caballes



Predation on adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) relative to fisheries management zones on Australia's Great Barrier Reef

Peter C. Doll[1], Morgan S. Pratchett[1], Scott D. Ling[2], Sterling S. Tebbett[1],
Andrew S. Hoey[1], and Ciemon F. Caballes[3]

1. College of Science and Engineering, James Cook University, Australia
2. Institute of Marine and Antarctic Studies, University of Tasmania, Australia
3. Marine Laboratory, University of Guam, USA

COTS Control Innovation Program | A research and development partnership to better predict, detect and respond to crown-of-thorns starfish outbreaks

Australian Government | REEF TRUST

Great Barrier Reef Foundation

AUSTRALIAN INSTITUTE OF MARINE SCIENCE

CSIRO

JAMES COOK UNIVERSITY AUSTRALIA

THE UNIVERSITY OF QUEENSLAND AUSTRALIA

Inquiries should be addressed to:

Peter C. Doll
College of Science and Engineering, James Cook University
peter.doll@jcu.edu.au

This report should be cited as

Doll PC, Pratchett MS, Ling SD, Tebbett SB, Hoey AS, Caballes CF (2025) *Predation on adult Pacific crown-of-thorns starfish (*Acanthaster *cf.* solaris*) relative to fisheries management zones on Australia's Great Barrier Reef*. A report to the Australian Government by the COTS Control Innovation Program (49 pp).

Funding Acknowledgement

The COTS Control Innovation Program aims to accelerate the development of innovative surveillance and control methods to manage outbreaks of coral-eating starfish on the Great Barrier Reef. The Program is a collaboration between the Great Barrier Reef Foundation, Australian Institute of Marine Science, Commonwealth Scientific and Industrial Research Organisation, James Cook University and The University of Queensland. The Program is funded by the partnership between the Australian Government's Reef Trust and the Great Barrier Reef Foundation.

Traditional Owner Acknowledgement

The COTS Control Innovation Program extends its deepest respect and recognition to all Traditional Owners of the Great Barrier Reef and its Catchments, as First Nations Peoples holding the hopes, dreams, traditions, and cultures of the Reef.

Disclaimer

Copyright

Contents

List of Figures

List of Tables

Acronyms and Abbreviations

COTS	Crown-of-thorns starfish
CCIP	Crown-of-thorns starfish Control Innovation Program
GBR	Great Barrier Reef
GBRMP	Great Barrier Reef Marine Park
AIMS LTMP	Australian Institute of Marine Science Long-Term Monitoring Program
PIT	Point-Intercept Transect
RNTBC	Registered Native Title Body Corporate
SALAD	Scooter-Assisted Large Area Diver-based (SALAD) surveys
TO	Traditional Owner

EXECUTIVE SUMMARY

Reef-wide population irruptions of coral-feeding crown-of-thorns starfish (COTS, *Acanthaster* spp.) are one of the foremost contributors to coral mortality and reef degradation throughout their tropical Indo-Pacific range. In contrast to other disturbances contributing to the plight of coral reefs (e.g. climate-induced coral bleaching), COTS are relatively amenable to direct management action. However, effective large-scale and long-term management of COTS populations, and intended protection of corals, requires an improved ecological underpinning of management strategies and understanding of the proximal cause(s) of their population irruptions. While high fecundity and other traits likely underpin much of the success of COTS and naturally predispose them to major population fluctuations, the initiation and spread of population irruptions has also been linked to the downstream effects of anthropogenic activities, particularly terrestrial runoff and overfishing.

The ‘predator removal hypothesis’ proposed that reduced abundance of predators (due to overfishing) releases COTS from the predation pressure that naturally regulates their populations. This has stimulated considerable interest in predation on COTS, both to unmask the root cause(s) of population irruptions and develop strategies to effectively moderate their impact. Targeted fisheries management could therefore play a valuable part in conserving the predator-mediated control of COTS abundance. However, this ‘zoning effect’ largely rests on patterns in the incidence of population irruptions and there is a need for experimental field studies to assess mechanistic links between zoning, predators, and predation pressure, which could have a major bearing on deciding appropriate management responses.

This study used standardised 24-hour predation assays to quantify and compare relative risk of predation on adult Pacific COTS (*Acanthaster* cf. *solaris*), particularly with respect to different fisheries management zones on Australia’s Great Barrier Reef (GBR). Within each of two regions, the northern GBR (Lizard Island region) and central GBR (Townsville region), reefs and sites (≥ 3 per reef) were selected within three GBR Marine Park (GBRMP) management zones: Marine National Park reefs, closed to fishing (‘green zones’ or no-take areas), Conservation Park zones in which fishing is restricted and mostly recreational (‘yellow zones’) and Habitat Protection zones which are open to fishing (‘blue zones’). ‘Green’, ‘yellow’ and ‘blue zones’ are thus expected to represent a gradient of increasing fishing pressure.

From 2022 to 2024, 72 predation assays were conducted across the two regions and differing GBRMP zones within each region. For each standardised predation assay, we assessed signs of full and partial predation on four adult COTS (mean diameter: 34.2 cm ± 0.4 SE), excluding caged controls. Time-lapse photography was used to capture predation events and identify key predators, while belt and point-intercept transects were surveyed at each site, primarily to assess local abundance of predatory fishes. Relative risk of predation was determined based on predation scores for each starfish deployed, ranging from 0 (no signs of predation) to 1 (entire starfish consumed), with partial predation scored from 0.05–0.95 based on the proportion of body area consumed.

The mean relative risk of in situ predation (i.e. estimated rate of predation) was 0.195 (± 0.021 SE) across 312 individual COTS assessed, excluding 31 caged controls. Of all individuals subject to any degree of predation (n = 89), 51.7% were fully consumed, while 21.3% and 27.0% were subject to either high (≥ 0.5 of body) or relatively low partial predation (< 0.5), respectively. Considerable predation and mortality was observed at many sampling sites, with up to 3 out of 4

COTS fully consumed at the assay level. This highlights that medium- to large-sized COTS are vulnerable to predation, despite their extensive physical and chemical anti-predator defences.

The majority of predation (97%) recorded using time-lapse was attributed to just three predatory reef-fish species. More than 55% of the predation recorded was solely ascribed to the spangled emperor (*Lethrinus nebulosus*), which was frequently recorded predating in schools. Most of the remaining predation was jointly ascribed to *L. nebulosus* in combination with one of two other species, observed predating on the same (set of) COTS: the starry puffer (*Arothron stellatus*; 35.5% jointly with *L. nebulosus*) and titan triggerfish (*Balistoides viridescens*; 6.1% jointly with *L. nebulosus*). Motile invertebrates (e.g. giant triton, *Charonia tritonis*) and many other reef fishes purported to feed on adult COTS (e.g. humphead wrasse, *Cheilinus undulatus*) are not likely to be effective and/or ecologically significant predators in the locations studied. This revised understanding of key predators (or the lack thereof) improves accuracy in capturing predation effects in demographic models.

Apparent differences in predation recorded relative to the three GBRMP management zones corroborate the ‘zoning effect’ in predatory regulation of COTS populations. The mean risk of in situ predation on adult COTS in ‘green zones’ (no-take; 0.278 ± 0.031 SE) was 3.6x higher compared to ‘blue zones’ (open; 0.077 ± 0.030 SE) and 2.8x higher than in ‘yellow zones’ (restricted; 0.099 ± 0.033 SE). Corresponding patterns were observed for both regions. Risk of predation in the northern GBR (Lizard Island region) was 3.5x and 3.0x higher in ‘green zone’ sites (0.265 ± 0.033 SE) compared to ‘blue’ (0.075 ± 0.037 SE) and ‘yellow zone’ sites (0.088 ± 0.040 SE), respectively. In the central GBR (Townsville region), risk of predation was 4.6x and 3.0x higher in ‘green zone’ sites (0.363 ± 0.090 SE) than in ‘blue’ (0.079 ± 0.052 SE) and ‘yellow zone’ sites (0.121 ± 0.060 SE), respectively. Moreover, the proportion of individuals that were fully (versus partially) consumed was higher in ‘green’ (54%) and ‘yellow’ (55%) zones compared to ‘blue zones’ (33%), while the proportion of partial consumption (< half of body), and thus potentially sublethal injury, was higher in ‘blue’ (56%) than in ‘green’ (22%) and ‘yellow zones’ (36%).

Novel insights into in situ predation on adult COTS relative to expected fishing pressure presented here add considerable evidence to the mechanistic basis of the ‘predator removal hypothesis’. In addition to species’ capacity to effectively kill starfish at high rates, the predator-mediated suppression of populations, and release thereof, inherently relies on the local abundance of key predators, and their vulnerability to overfishing and/or reef degradation. Our results suggest that the spangled emperor (*L. nebulosus*), a secondary target and by-product species of the Reef Line Fishery (in ‘blue zones’) and highly targeted recreational fishing species (in ‘blue’ and ‘yellow zones’), was more locally abundant at study sites closed to fishing. Notably, the biomass of *L. nebulosus* was 2.5 times higher in no-take zones (’green zones’) than fished reefs (‘yellow’ and ‘blue’ zones), corroborating previous reports based on GBR-wide surveys.

This study provides missing links underpinning the ‘predator removal hypothesis’, demonstrating that COTS are at markedly higher risk of predation in no-take zones, which is largely attributable to the fisheries species *L. nebulosus*. Whilst this presents an opportunity to refine ecosystem models for the targeted decision support of COTS control efforts, our results also highlight the applicability of targeted fisheries-based management. In conjunction with contemporary COTS control strategies, reduced fishing pressure on *L. nebulosus*, particularly in key areas in the initiation or spread of population irruptions, offers a promising biological control strategy to mitigate the threat COTS pose to coral reefs.

1. INTRODUCTION

1.1 Biology, ecology and management of crown-of-thorns starfish

The coral-feeding crown-of-thorns starfish (COTS; *Acanthaster* spp.) is one of the most well-known and extensively studied coral reef invertebrates (e.g. Moran 1986). Following planktonic larval and benthic herbivorous juvenile life-history stages, COTS undergo an ontogenetic dietary shift to feed on reef-building scleractinian corals (Wilmes et al. 2020). As corallivorous adults (**Figure 1**), COTS exhibit the traits this notorious coral predator is best known for, including a high feeding rate, fast growth, large body size and high fecundity (Birkeland 1989; Keesing and Lucas 1992). These traits are instrumental in the destructive effects of COTS (Deaker and Byrne 2022), which increasingly interact with the myriad of other stressors threatening the structure and function of reef ecosystems (Mellin et al. 2019; Bozec et al. 2021).

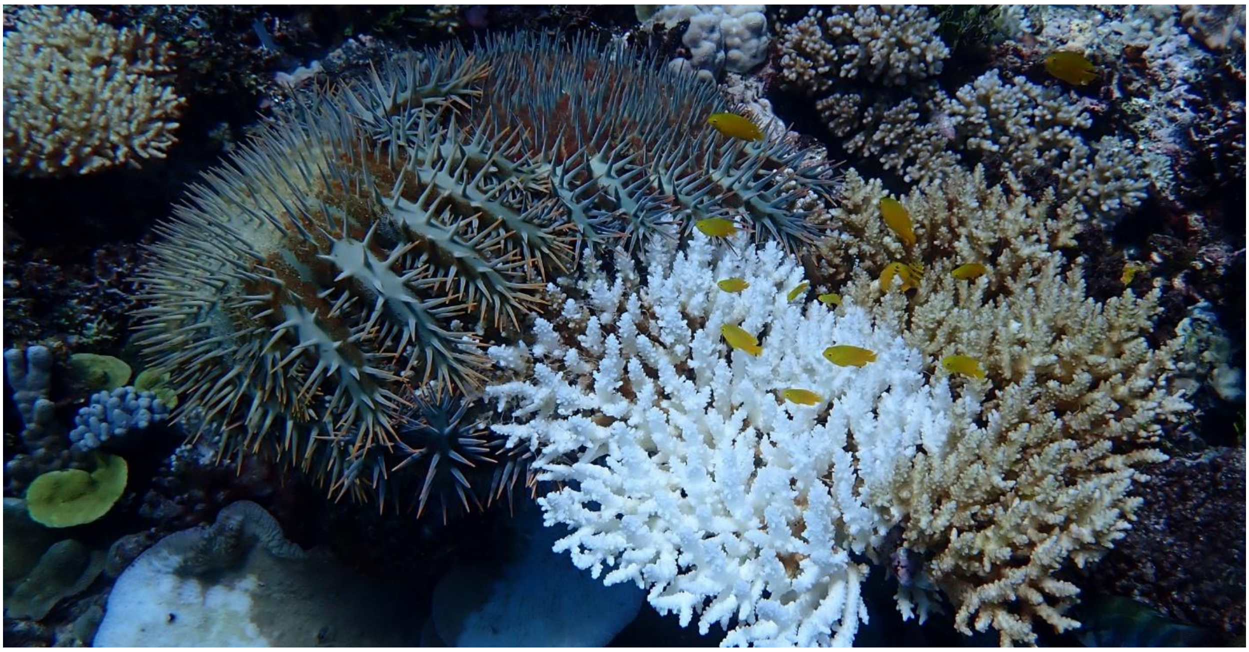


Figure 1. Three adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) feeding on coral colonies of the genus *Acropora* at Wilson Reef, southern Great Barrier Reef, in February 2021. A conspicuous feeding scar is visible in the foreground. Photograph: P. Doll

In comparison to other major stressors causing widespread coral mortality (e.g. mass coral bleaching events), COTS appear relatively amenable to localised action. Manual control programs, more recently involving lethal injections of COTS in situ, attempt to mitigate the effects of large COTS populations on priority reefs (Westcott et al. 2020; Matthews et al. 2024), although control efforts have historically lagged behind the establishment of population irruptions (Babcock et al. 2020). The prediction and mitigation of rapid population growth inherently depends on understanding the underlying biological and ecological factors (Pratchett et al. 2014). Resolving critical information gaps pertaining to the ecology of COTS and developing strategies to effectively manage its impact at scale continues to be a pivotal task for scientists, managers, and other stakeholders (Pratchett and Cumming 2019), especially given the escalating threats and widespread habitat degradation confronting Anthropocene reefs (Bellwood et al. 2019).

1.2 Consequences and causes of population irruptions

COTS are notorious for their propensity to undergo population irruptions (density > 15 ha^{-1}) which represent a perennial threat to tropical reef ecosystems throughout their tropical Indo-Pacific geographic range (Moran 1986). While considered a marine pest (Pratchett and Cumming 2019), COTS are native throughout their range and have a negligible impact on coral communities at low densities. At elevated densities however, adult COTS rapidly consume prey corals (**Figure 2**) and markedly reduce live coral cover at the scales of entire reefs and regions (e.g. Kayal et al. 2012). Due to their feeding preferences for some coral taxa, particularly Acroporidae, large populations of adult COTS can also reduce diversity of coral assemblages (Pratchett 2010). Because of the foundational role of corals on coral reefs, such changes to coral cover and diversity can have indirect, ecosystem-wide effects on many other reef organisms (e.g. Kayal et al. 2012).

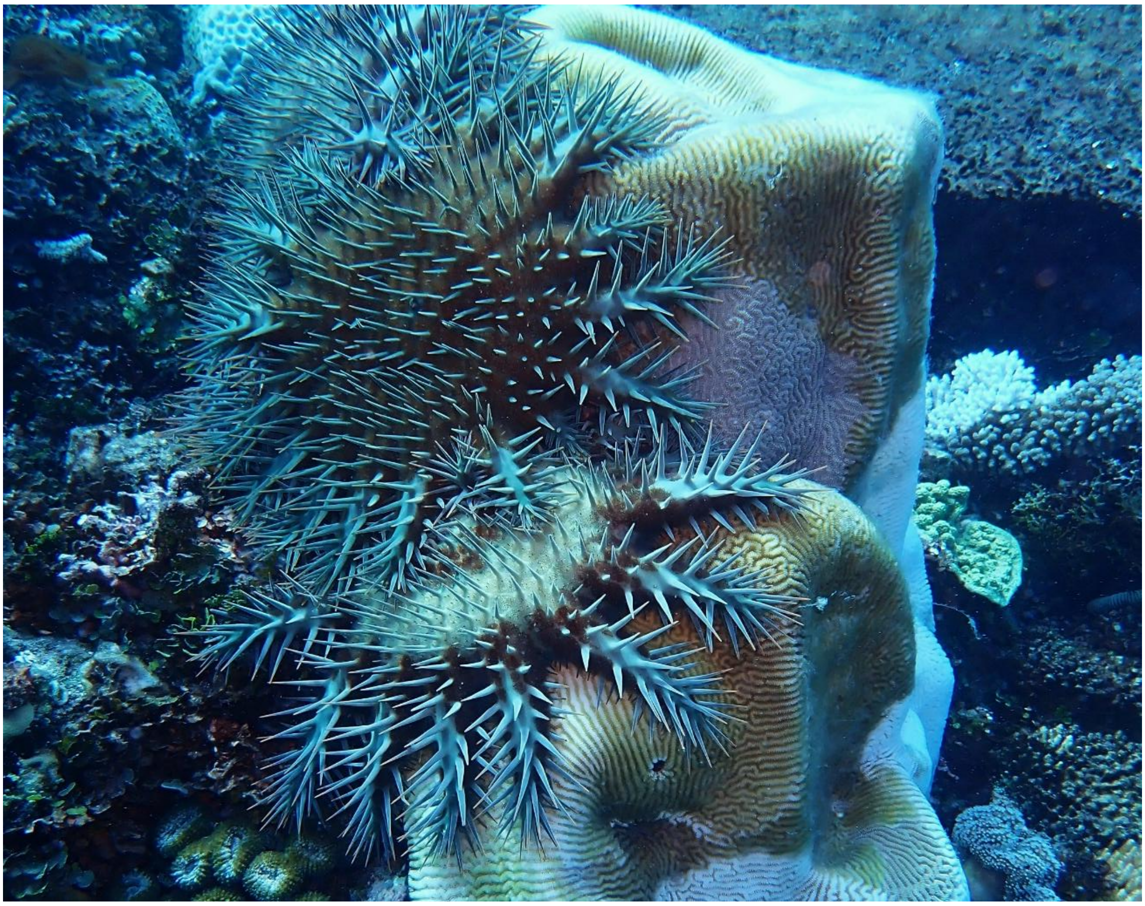


Figure 2. Four adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) feeding on a coral colony of the genus *Leptoria* during a population irruption in the Swains region, southern Great Barrier Reef (February 2021). Photograph: P. Doll

On Australia’s Great Barrier Reef (GBR), recurrent population irruptions of COTS represent one of the foremost contributors to ongoing coral loss (De’ath et al. 2012; Mellin et al. 2019). There have been four distinct waves of population irruptions of COTS recorded on the GBR since the 1960s (Pratchett et al. 2014), and the widely anticipated fifth population irruption has recently been shown to have commenced in northern and far northern sectors of the GBR (Chandler et al. 2023; Uthicke et al. 2024), which highlights the urgent necessity for innovation and action to mitigate new and renewed population irruptions. While there have been ongoing improvements in direct management actions (Westcott et al. 2020; Matthews et al. 2024), effective large-scale and long-term management of COTS is conditional upon an improved understanding of the proximal cause(s) of population irruptions (Babcock et al. 2016a).

The biology and traits of COTS naturally predispose them to population fluctuations (reviewed by Deaker and Byrne 2022), as seen in other echinoderms (Uthicke et al. 2009). Due to their extraordinary reproductive potential, minor changes in demographic rates can contribute to rapid population growth and the initiation of localised population irruptions (Uthicke et al. 2009; Doll et al. 2021; 2023). Thus, the ‘natural causes hypothesis’ views marked fluctuations in abundance as a natural consequence of the biological and ecological traits of COTS (Vine 1973), including their high fecundity and plasticity during early life-history stages and transitions. Other prominent hypotheses link the incidence of population irruptions to anthropogenic influences on COTS populations. The ‘terrestrial runoff hypothesis’ (or ‘larval starvation hypothesis’) links elevated survival rates of planktotrophic COTS larvae (and subsequent recruitment surges) to increased nutrient levels due to terrestrial runoff following major rainfall events (Birkeland 1982; Brodie et al. 2005; Fabricius et al. 2010; Wooldridge and Brodie 2015). The ‘predator removal hypothesis’ attributes population irruptions to the removal of predators that naturally regulate the abundance of COTS (Endean 1969; Sweatman 2008). On balance, a range of factors likely contribute to the incidence and spread of population irruptions, with anthropogenic influences on reef organisms and ecosystems disrupting processes that naturally regulate COTS populations in some locations (Pratchett et al. 2014).

1.3 Natural predators of crown-of-thorns starfish

More than 100 coral reef species, including many invertebrates and reef fishes, are reported to feed on COTS (reviewed by Cowan et al. 2017a; see also Desbiens et al. 2023), although it is largely unknown whether these putative predators can exert ecologically significant mortality, and thereby potentially regulate COTS populations. In fact, in situ feeding observations for a considerable proportion of these species were recorded only for moribund or dead COTS, while evidence of predation on healthy individuals remains scarce. Yet, despite their physical and chemical anti-predator defences, COTS are susceptible to predation throughout their life history, with different predatory groups acting at different stages (Cowan et al. 2017a). Planktonic COTS larvae are readily consumed by common planktivorous damselfishes (Cowan et al. 2016; 2017b), while rubble-dwelling crustaceans and other benthic invertebrates predate on COTS during their herbivorous early juvenile stage (Desbiens et al. 2023; CCIP-P-05 Wolfe et al. 2025). The pre-settlement and early post-settlement stages are likely significant demographic bottlenecks in the life-history of COTS (Deaker and Byrne 2022), however, predation on their larvae and early juveniles has been understudied. Thereafter, larger-bodied corallivorous juveniles and sub-adults remain susceptible to predation by motile benthic invertebrates (especially the giant triton, *Charonia tritonis*) and a suite of predatory fishes, including emperors, pufferfishes, and triggerfishes (reviewed by Cowan et al. 2017a).

The incidence of sublethal and lethal predation purportedly declines with age for COTS, due to increased body size and length of spines (McCallum 1987; 1989; Rivera-Posada et al. 2014a). Despite their physical (and chemical) defences, larger juvenile and adult COTS frequently exhibit injuries, commonly manifested as shortened or missing arms (Rivera-Posada et al. 2014a; Messmer et al. 2017; Caballes et al. 2022). In the absence of data on whole animal (or lethal) predation, this incidence of injuries (or sublethal predation) has previously served as a proxy for (differential) vulnerability of COTS to predation (McCallum et al. 1989; Messmer et al. 2017; Caballes et al. 2022). While not immediately fatal, rates of sublethal predation can still substantially affect population dynamics, increasing risk of disease and subsequent predation events (Glynn 1984; Caballes et al. 2022). Many groups of reef fishes have been observed to feed on injured adult COTS within reef habitats, including butterflyfishes, damselfishes, and wrasses (Glynn 1984), although such scavenging behaviour is generally not specific to COTS or thought to significantly alter COTS population dynamics. Thus, it is essential to differentiate between putative predators that opportunistically feed on injured or dead adult individuals (~ scavengers), and actual predators that feed on healthy individuals and have the capacity to kill COTS or significantly reduce their fitness (Cowan et al. 2017a).

The ecological importance of predation in regulating COTS populations depends largely on the capacity of predators to locate and effectively kill their prey (Cowan et al. 2017a). Giant triton (*C. tritonis*) immobilise COTS with a toxin before consuming the animal (Endean 1969) and the small-bodied harlequin shrimps (*Hymenocera picta*) are also known for their ability to kill much larger starfishes, including COTS (Wickler and Seibt 1970). Reef fishes predating on uninjured adults likely include the triggerfishes *Balistoides viridescens* and *Pseudobalistes flavimarginatus* (Ormond and Campbell 1973; Rivera-Posada et al. 2014b), the pufferfishes *Arothron hispidus* and *A. stellatus* (Ormond and Campbell 1973; Keesing and Halford 1992), and the humphead wrasse (*Cheilinus undulatus*; Chesher 1969; Ormond and Campbell 1973). However, these predators generally feed on other starfishes, echinoderms, and invertebrates, and do not appear to preferentially select for COTS to the exclusion of other suitable prey (Glynn 1984; Ormond and Campbell 1973), highlighting the relative abundance of alternative prey as an additional factor influencing the potential impact of predators on COTS abundance.

The capacity of predators to subject COTS populations to ecologically significant mortality rates is inherently constrained by the abundance of the predators and/or their individual capacity to consume considerable numbers of COTS. Understanding the actual impact of predators requires field-based predation and mortality estimates, however, quantitative data on COTS consumption is restricted to lab-based experimental studies to date (Cowan et al. 2017a). Field-based predation estimates are inherently difficult to obtain, but standardised predation assays have been widely employed to assess predation on other echinoderms (e.g. Young and Bellwood 2011) and provide comparable, relative estimates of in situ predation risk. *Charonia tritonis* were estimated to consume 0.7 adult COTS week^{-1} in caging experiments (Pearson and Endean 1969), although predation by this species can be limited to individual arms of the COTS and is not necessarily fatal (Chesher 1969). Large-bodied reef fishes appear to inflict significant damage, with some capable of killing and consuming entire adult starfish, such as *Arothron stellatus* (**Figure 3**). However, there doesn't appear to be one single species or group that plays an overwhelmingly large role (Cowan et al. 2017a). Despite an extensive list of potential predators based on in situ observations and/or eDNA gut analyses (e.g. Kroon et al. 2020), their relative functional roles and importance in the field remain largely unknown (Pratchett et al. 2021a). This limits our understanding of a key aspect of COTS population dynamics and highlights the importance of studying the risk of in situ predation.

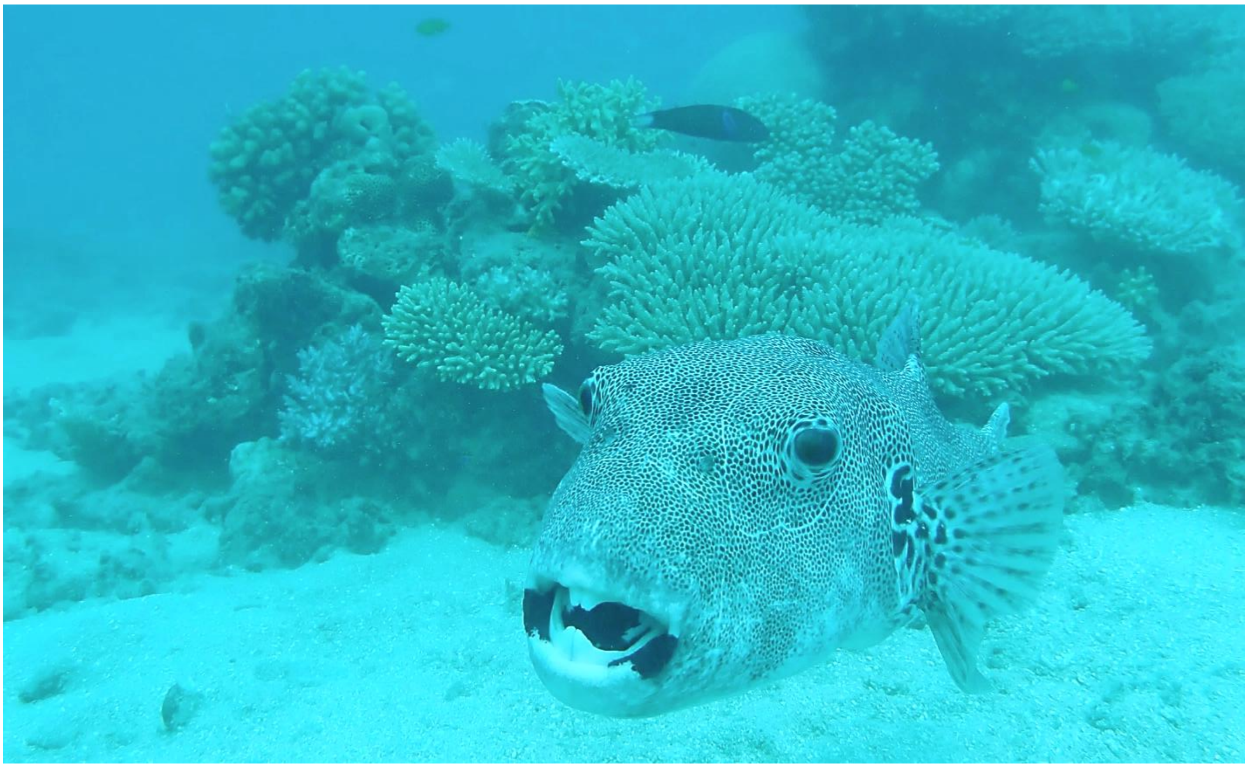


Figure 3. The Starry Puffer (*Arothron stellatus*), a large-bodied predatory fish that has been observed to consume adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) in less than 10 minutes (Keesing and Halford 1992). Photograph: P Doll.

1.4 The ‘predator removal hypothesis’

The ‘predator removal hypothesis’ (or ‘predatory release/overfishing hypothesis’) was one of the first hypotheses proposed to account for the (seemingly recent and/or increasing) occurrence of COTS population irruptions (Endean 1969). The original concept builds on the idea that COTS population irruptions are an unnatural phenomenon, caused by the effect of anthropogenic activities on COTS and coral reefs. Specifically, this hypothesis posits that the removal of COTS predators (through overfishing and/or habitat degradation) releases them from predation pressure that would normally regulate their population size (Sweatman 2008). This hypothesised release from top-down regulation has sparked considerable interest in links between fishing and predators of adult and juvenile COTS, both to uncover the cause(s) of population irruptions and effectively manage them.

The first recorded population irruptions of COTS on the GBR in the 1960s were linked to the substantial removal of giant triton (*Charonia tritonis*) in preceding decades (Endean 1969). Giant triton are capable of killing and consuming juvenile and adult COTS, albeit at relatively low rates and tend to preferentially feed on other starfish (Chesher 1969; Pearson and Endean 1969).

Nevertheless, Endean (1969) proposed that the overfishing of *C. tritonis*, particularly in the northern GBR, had relaxed the natural predator-mediated regulation on juvenile and sub-adult COTS, leading to elevated densities of large adults with greatly elevated reproductive potential (see Babcock et al. 2016b; Pratchett et al. 2021b). Endean (1969) suggested that it was the increased reproductive capacity of COTS that initiated population irruptions, rather than increased densities of adult starfish. The abundance of *C. tritonis* on the GBR is currently very low, such that these putative predators are unlikely to provide sufficient predation pressure to mitigate or prevent COTS population irruptions (Cowan et al. 2017a).

More recently, studies have proposed that overfishing of fish predators may have contributed to population irruptions of COTS, based on their increased incidence with increased fishing intensity, such as inside versus outside of no-take areas (Dulvy et al. 2004; Sweatman 2008; Kroon et al. 2021). The lines of evidence presented therein usually centre on large predatory fishes capable of consuming adult COTS. For top-down effects to be noticeable, predatory fishes do not only have to possess the capacity to consume considerable numbers of COTS at a high rate but must also be targeted by commercial or recreational fisheries. However, evidence that major fisheries target species (e.g. coral trout, *Plectropomus* spp.) are ecologically significant predators of COTS is lacking (Cowan et al. 2017a). Meanwhile, some known predators of adult COTS (e.g. *Arothron* spp.) are generally not vulnerable to overfishing, although some may be susceptible to the broader anthropogenic modification and degradation of coral reefs (Potts 1981). Notably, two Lethrinidae (*Lethrinus miniatus* and *L. nebulosus*) are secondary fisheries species on the GBR and have been reported to consume COTS (Kroon et al. 2020; 2021).

On the GBR, Sweatman (2008) demonstrated that the incidence of population irruptions on mid-shelf reefs was seven times lower within areas closed to fishing (‘green zones’ or no-take areas) compared to areas open to fishing (‘blue zones’). Subsequent analyses corroborated that population irruptions were less likely on reefs closed to fishing, where purported predatory fishes are 2.8x more abundant (Kroon et al. 2021). Moreover, the prevalence of injuries among COTS was significantly higher in no-take areas than other management zones (Caballes et al. 2022; see also Rivera-Posada et al. 2014a), presumably reflecting higher rates of predation (McCallum et al.1989). If predators mediate these apparent differences across gradients of fishing effort (Sweatman 2008; Kroon et al. 2021), we can expect to observe more predation on COTS in locations closed to fishing (i.e. no-take areas), corresponding with purported differences in the abundance of predators (e.g. Dulvy et al. 2004). However, this ‘zoning effect’ and proposed role for fisheries management in moderating population irruptions is thus far, largely based on patterns in the incidence of population irruptions. Experimental studies measuring and comparing predation on adult COTS are required to test the mechanistic basis of the ‘predator removal hypothesis’.

1.5 Objectives and impact pathway

The overarching objective of this project was to undertake field-based experiments and surveys to establish the relative risk of predation for adult COTS among reefs in different management zones that permit, restrict or prohibit fishing. Predator-mediated population regulation, and the release thereof, may be a major contributor to spatial heterogeneity in COTS abundance (Section 1.4). Yet, critical mechanistic links between fisheries management zoning, putative predators and predation on COTS remain unresolved. Understanding the underlying mechanisms of the apparent ‘zoning effect’ in the incidence of population irruptions has a major bearing on deciding appropriate management responses.

The specific objectives of this project were to:

- Develop a standardised experimental protocol to effectively quantify relative risk of in situ predation for adult COTS.
- Identify key predators responsible for lethal and sublethal predation on adult COTS.
- Compare the relative risk of predation for adult COTS at reefs within different fisheries management zones, including reefs closed to fishing (green zones or no-take areas), reefs at which fishing is restricted (yellow zones) and reefs where fishing is permitted (blue zones).
- Assess the relative abundance of key predators of adult COTS at the same reefs within different fisheries management zones.

This project (CCIP-P-06: Fish predation rates and zoning) forms part of the Prediction subprogram of the COTS Control Innovation Program (CCIP) (**Figure 4**) and has strong synergies with CCIP-P-05 (Benthic predation in rubble, Wolfe et al. 2025) and modelling projects within the CCIP Response subprogram (**Figure 4**), particularly CCIP-R-10 (Fish predator conservation for biocontrol, Ceccarelli et al. 2025). New insights gained on key predators and zoning effects are important to model population dynamics and refine ecosystem models for targeted decision support. The outputs associated with the CCIP-P-06 project objectives also provide an opportunity to assess the potential role of marine park zoning and/or predator-specific fisheries management in mitigating the impact of COTS population irruptions on coral assemblages.

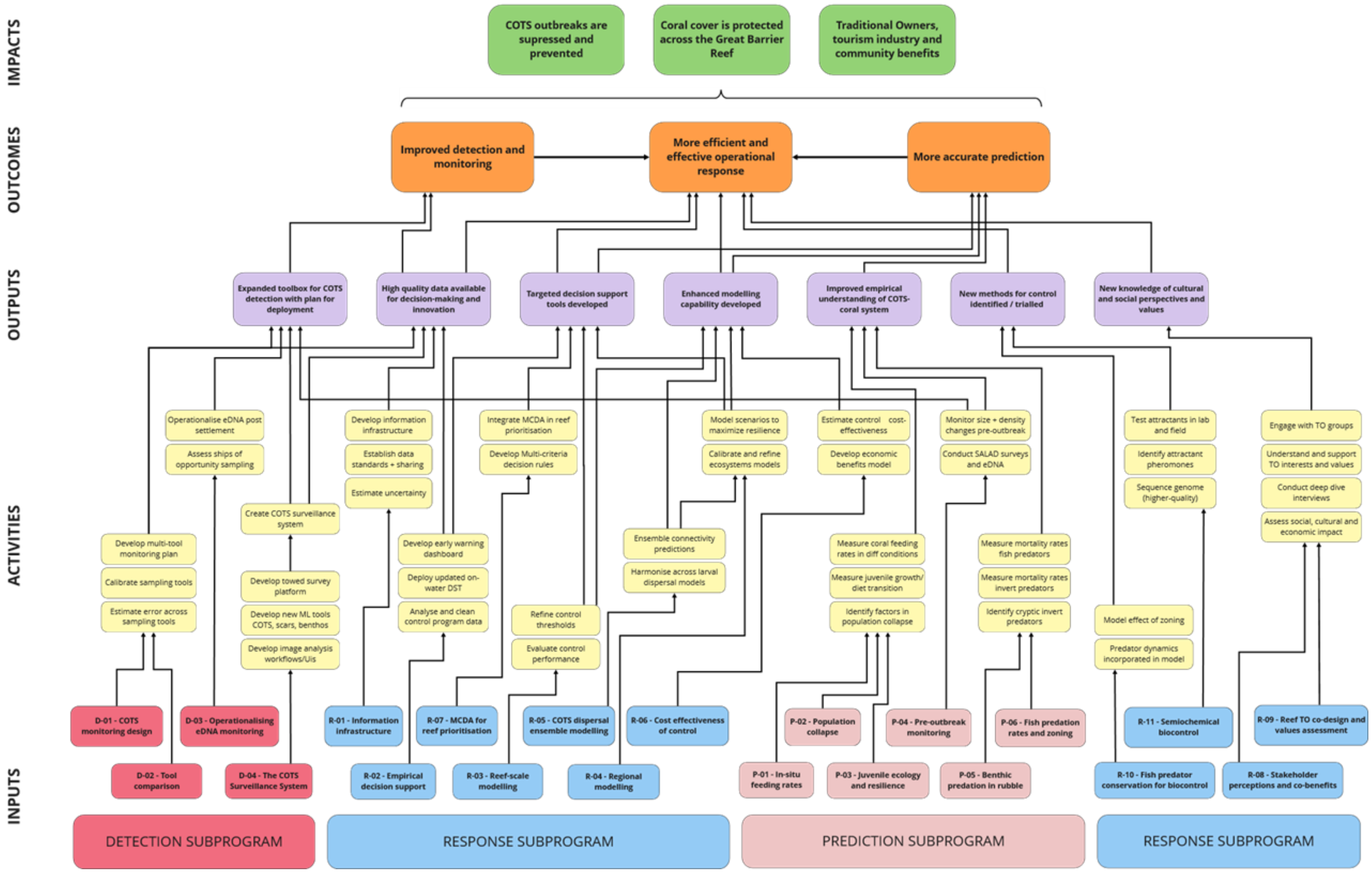


Figure 4. COTS Control Innovation Program (CCIP) program logic, showing how this project (CCIP-P-06: Fish predation rates and zoning) within the Prediction Subprogram (rose-coloured boxes) relates to other projects, as well as the overarching outputs, outcomes and impacts of the CCIP.

2. METHODS

This project was conducted over three years (2022–2024) but builds upon pilot studies conducted at Lizard Island (northern GBR; 2016, 2022) during which the specific methods and sampling design were tested and refined. The use of COTS mimics (made from freeze dried tissue of adult COTS embedded in agar) was originally considered as a potential test of relative predation rates but did not progress to field-based studies due to logistical and methodological problems. Therefore, only the short-term deployment of live COTS was trialled to test and refine the presentation and containment of the animals. A key component of this study was to assess the likelihood of predators to feed upon healthy adult COTS, such that we explicitly tested for differences in predation risk (and the species involved) between COTS that were tethered (where monofilament was inserted through a long needle that was used to drill through the ossified ring surrounding the mouth) versus staked (a single 12 mm diameter stake inserted through the oral disk). While much easier to deploy, it was expected that conspicuous injuries caused by staking the starfish would attract opportunistic predators or scavengers, more so than tethering. To test this, COTS of varying body size were deployed for up to four days using the two methods, with their condition monitored at regular intervals. The trials documented comparable rates of survival between the two deployment methods for both medium-sized (20–30 cm diameter) and large-sized COTS (> 35 cm) tested (**Figure 5**). The condition and survival of the deployed COTS decreased substantially within the first couple days of deployment (**Figure 5**), informing a standardised deployment duration of 24 hours for all subsequent predation assays. Given the increased time effort, safety risk and difficulty of the tethering method, the staking method was chosen for the subsequent components of the project, following a second trial with comparable results. The standardised protocol for in situ predation assays (see Section 2.2) and associated surveys (see Section 2.3) was finalised as part of this project in late 2022.

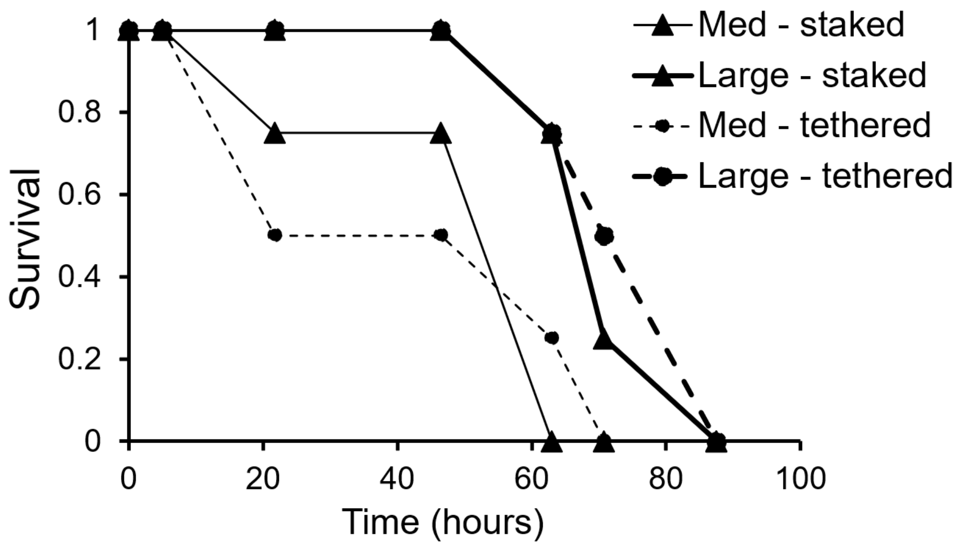


Figure 5. Comparison of survival rates of medium- (20–30 cm diameter) and large-sized (> 35 cm) Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*), using two deployment methods (staked versus tethered) over the 87.5-hour trial period at Lizard Island in 2016 (n = 4 per treatment, 16 COTS total). The condition of COTS was recorded at 7 time points (0-, 5-, 21.75-, 46.5-, 63-, 70.75-, and 87.5-hours following trial commencement).

2.1 Sampling design

Sampling for this project was focused on two distinct regions: reefs within the central sector (Townsville region) and reefs within the northern sector (Lizard Island region) of the GBR (**Figure 6**). These two study regions were selected based on the accessibility of reefs therein and their complementary GBRMP zoning. At the time the study was designed, the two regions also provided a natural gradient in COTS densities (Townsville region = moderate; Lizard Island region = low) to measure functional responses of putative predators, however, densities in the Lizard Island region rapidly increased from 2022–2024 (Chandler et al. 2023; Uthicke et al. 2024). Field work in these two regions furthermore maximised project effectiveness and synergies with other CCIP projects and stakeholders, including COTS density (see Section 2.3.3) and feeding data for CCIP-P-01 (Pratchett et al. 2025a), CCIP-P-04 (Pratchett et al. 2025b) and the COTS Control Program (reef prioritisation).

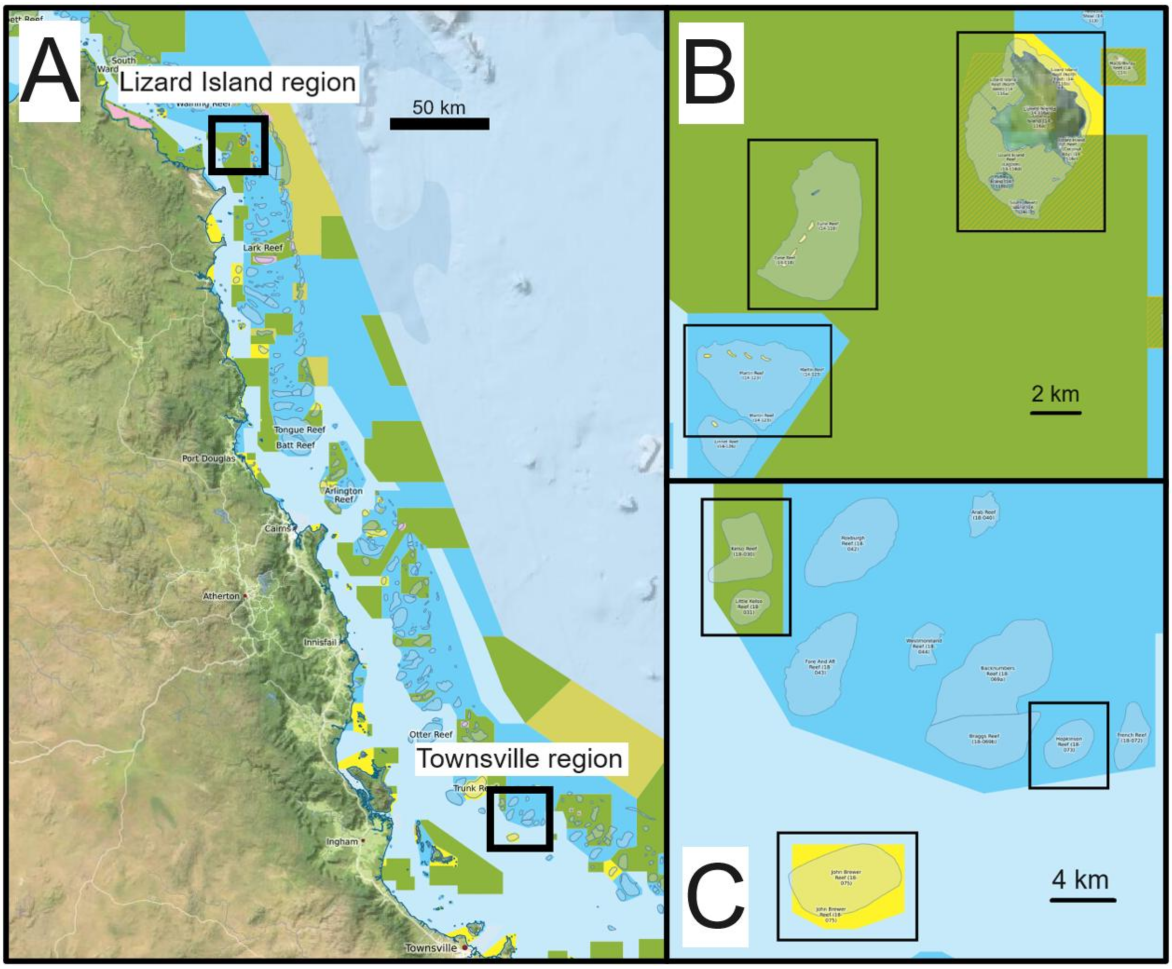


Figure 6. Maps of the **(A)** northern and central Great Barrier Reef (GBR), including the regions and reefs selected for predation assay sites and associated surveys (see also **Table 1**); **(B)** Lizard Island region in the northern GBR, and **(C)** Townsville region in the central GBR. Underlaying map colours indicate GBR marine park zones, including the 'green zones' (Marine National Park), 'yellow zones' (Conservation Park), and 'blue zones' (Habitat Protection) sampled in this study (zoning: eAtlas interactive mapping system).

To quantify risk of predation relative to local management arrangements, reefs and sites were selected within three GBRMP fisheries management zones for both regions (**Table 1**): *Marine National Park Zones* closed to fishing ('green zones' or no-take areas), *Conservation Park Zones* in which fishing is restricted ('yellow zones'), and *Habitat Protection Zones* where commercial and recreational fishing are permitted, albeit with some constraints on effort and fishing methods ('blue zones'). In 'yellow zones', no netting (other than bait netting) is permitted (contrasting blue zones) and fishing activities are predominantly recreational, while all commercial and recreational fishing is prohibited in 'green zones', except for traditional use of marine resources. 'Blue' (open), 'yellow' (restricted) and 'green zones' (closed) are thus generally viewed as a gradient of decreasing fishing pressure.

For each reef, three or more suitable sites were chosen for predation assays (see Section 2.2) and associated surveys (see Section 2.3), based on prior knowledge and/or observations during Scooter-Assisted Large Area Diver-based (SALAD) surveys/collection dives (see Section 2.3.3). A total of 60 standardised predation assays were completed in the northern sector over four field trips (12/2022, 05/2023–06/2023, 11/2023–12/2023, and 02/2024) and 18 assays were completed in the central sector over two field trips (07/2023 and 01/2024).

Table 1. Reefs selected for predation assay sites within Great Barrier Reef Marine Park (GBRMP) fisheries management zones of the northern GBR (Lizard Island region) and central GBR (Townsville region) sectors.

Zone (GBRMP)	Fishing	Northern GBR	Central GBR
Marine National Park	No-take	Eyrie Reef & Lizard Island (South/West)	Kelso Reef, Little Kelso Reef
Conservation Park	Restricted	Lizard Island (North/East)	John Brewer Reef
Habitat Protection	Permitted	Martin Reef	Hopkinson Reef

2.2 Standardised predation assays

Adult COTS for each predation assay were collected during SALAD surveys (see section 2.3.3) and/or additional collection dives on each of the relevant study reefs (Marine Parks permit G21/45711.1). Small-bodied (sub-adult) and extremely large-bodied individuals were excluded from predation assays. The body size of COTS used for predation assays ranged from 17 cm to 53 cm diameter. However, most individuals were 25–45 cm diameter, with an overall mean of 34.2 cm (± 0.4 SE). Individuals were carefully collected using tongs to minimise injury and stress, and they were moved to the surface in heavy duty catch bags. Between collection and subsequent assay deployment, COTS were held in nally bins (for short surface intervals; regular water changes) or larger tubs and tanks on marine vessels or at Lizard Island Research Station (for long surface intervals and overnight holding; flow-through systems).

For each standardised 24-hour predation assay, we set up an array of 4–5 individual COTS (**Figure 7**), immobilising each starfish with a single stake (40 cm length, 1.2 cm diameter) inserted through the oral disk. From 2023 onwards, we attached plastic-coated wire mesh plates (10 cm x 10 cm) to the stakes to sit on top of the starfish body and further reduce risk of escape (in the absence of predation). Predation assays were generally deployed on sand patches at the reef edge (mean depth of 5.3 m ± 0.3 SE; 2.1 m to 11.8 m range), with approximately 1 m between individual COTS. For approximately half of the predation assays completed, we deployed a fifth COTS as a caged control to control for the deterioration or loss of individuals independent of predation activity. These individuals were immobilised using single stakes through the oral disk and then protected from predators using a 40 cm x 40 cm x 15 cm (or 40 cm x 40 cm x 40 cm) cage made of plastic-coated wire mesh plates.

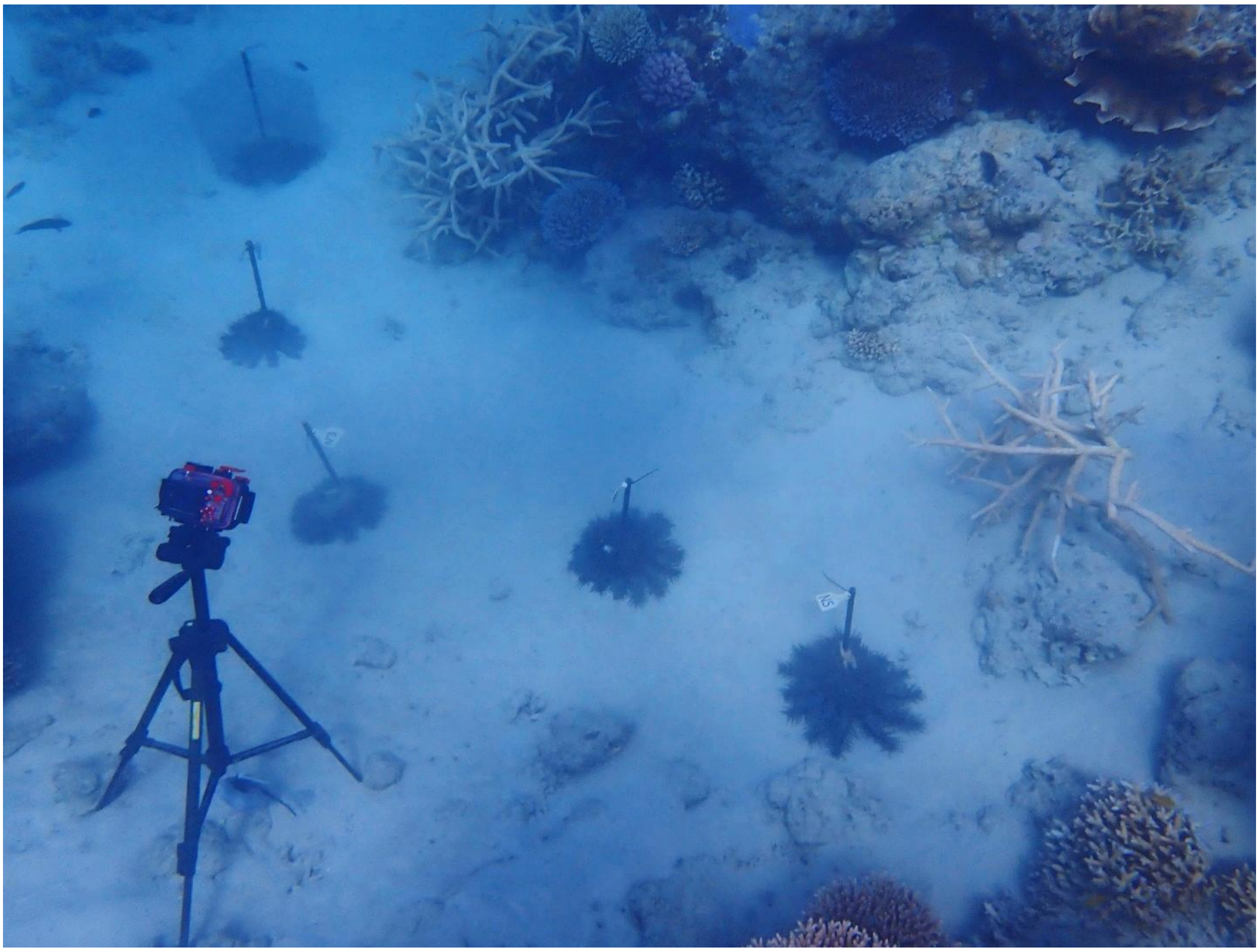


Figure 7. Standardised 24-hour predation assay used to quantify relative risk of in situ predation for adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*). Photograph: P Doll.

For each COTS deployed, we recorded the body size (diameter), reproductive status (empty vs gravid) and sex (if applicable) and any preexisting injuries. Individuals were sexed in situ by visually inspecting gonads obtained from a small arm incision. Time-lapse photography (images taken every 10 minutes using an Olympus TG-6 camera; see **Figure 7**) was used for 2–4 individuals per assay to capture relevant information (including predator identity and time of predation) for as many predation events as possible. Associated visual surveys of the local fish and benthic assemblages (see Section 2.3) were conducted in proximity of the assay sites.

Approximately 24 hours following deployment, we conducted the predation scoring for each individual starfish, which includes sublethal predation or injuries sustained over the duration of the assay. When an entire starfish was missing from the assay site, we conducted a search for COTS and feeding scars of the reef area in proximity of the assay site and checked the time-lapse footage (where applicable), to rule out that the missing individual had escaped (in the absence of predation). The site where each COTS was situated was carefully surveyed for signs of predation (e.g. arm(s) and/or spines), which in combination with the time-lapse footage, provided sufficient evidence to determine the predation of individuals. Moreover, the presence of putative predators in proximity of the assay site during the re-survey was noted and considered when analysing the time-lapse footage. Predation scores ranged from 0 (starfish alive and attached; no signs of predation or injuries) to 1 (entire starfish missing; evidence of predation) for each individual deployed. Partial predation was scored based on the proportion of body area missing, e.g. a score of 0.25 if approximately 25% of the body were missing due to predation.

2.3 Surveys of fish and benthic assemblages

2.3.1 Fish community surveys

The abundance, size and composition of predatory fishes was surveyed along four replicate 50 m x 5 m belt (250 m^2) transects near each predation assay site. Belt transects were generally positioned along the edge of the reef, along the base of the reef slope (i.e. where hard reef substratum often meets soft inter-reef habitat), in accord with the positioning of the predation assays and habitat requirements of large-bodied, roaming predatory fishes, including putative predators of adult COTS. The start of the belt transects was positioned at the site of the predation assay, with two transects, respectively, heading in opposite directions, following the reef contour. Along each belt transect, we identified all potential predatory fishes to species and recorded their abundance and size (nearest cm). The predominant reef-fish families for which the abundance and size of species was recorded included: Balistidae, Carangidae, Haemulidae, Holocentridae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Nemipteridae, Serranidae, Synodontidae, and Tetraodontidae. These include known and putative predators of adult COTS, such as the reef fish genera *Balistoides* (Balistidae), *Lethrinus* (Lethrinidae), *Plectropomus* (Serranidae) and *Arothron* (Tetraodontidae).

2.3.2 Point-Intercept Transect (PIT) benthic surveys

To assess whether benthic cover and habitat condition influences relative risk of predation, coral cover and benthic composition were documented with 50-m point-intercept transect (PIT) surveys at most assay sites. Four replicate 50-m PITs were surveyed within proximity of the predation assay site, following the transect path of the fish community surveys. Along each PIT, the organisms or substrate type underlying each of 100 uniformly spaced points (0.5 m apart) was recorded, following Pratchett et al. (2009). Hard corals were usually recorded to genus, using molecular-based classifications and the 2022 Coral Finder coral identification guide (Kelley 2022), with some genera sub-categorised by morphology (*Acropora*, *Porites*) and a few uncommon genera grouped to family. Soft corals and macroalgae were usually identified to genus, and the remaining underlying substratum was categorised as sponge, sand/rubble, or pavement. Hard coral cover was calculated as the proportion of points occupied by hard corals of the number of points occupied by reef substrate (excluding sand/rubble). Topographic complexity was estimated using the six-point scale (Wilson et al. 2007), where complexity scores range from 0 (homogenous habitat with no vertical relief) to 5 (very high topographic complexity at small and large scales).

2.3.3 Scooter-Assisted Large Area Diver-based (SALAD) surveys

To test whether the relative risk of predation or role of predators varies depending on the local density of adult COTS, this project conducted SALAD surveys in the proximity of most predation assay sites, following the protocol described in Chandler et al. (2023). This novel survey method integrates high-resolution search activities (to locate often cryptic adult COTS) within large area surveys along the reef crest and slope (Pratchett et al. 2022; 2024a; 2024b). Two divers, each towing a GPS unit, recorded the number of adult COTS and sets of feeding scars, providing estimates of recorded densities (number of COTS recorded) and inferred densities (number of COTS recorded plus the number of other distinct sets of feeding scars where the COTS was not located). For each COTS recorded, additional biological and ecological information was documented, including the size and exposure of the starfish.

2.4 Data analyses

The main objective of this research was to determine relative risk of in situ predation at reefs within different fisheries management zones, particularly between reefs closed (‘green zones’ or no-take areas) and open to fishing (‘blue zones’). Relative risk of predation was determined based on the predation observed for individual COTS during the standardised assays, ranging from nil predation (= 0) to full predation (= 1). Scores of partial predation (0.05–0.95) were determined based on the proportion of body area consumed. To calculate the relative proportions of full predation and partial predation (≥ 0.5 or < 0.5), all (full and partial) predation scores were summed to obtain a score of total predation events captured (using time-lapse photography). Boxplots and associated statistics for comparing relative risk of predation (and predator abundance) among management zones were generated in R (R Core Team 2023), including the ‘ggplot2’ package (Wickham 2016).

Time-lapse data (photograph 10 mins^{-1}, Olympus TG-6) were processed and analysed as soon as feasible upon re-survey of the assay and retrieval of the equipment. In the event of full or partial predation on any of the COTS deployed, all photographs for the respective assay were scanned for the appearance of putative predators. In the event of the footage showing a putative predator feeding on the COTS, the identity of the predator (species) and timing of predation was recorded. Similarly, the appearance of putative predators was noted even if a predation event was not captured by the time-lapse photographs. Opportunistic predation on injured COTS (~scavenging) following predation by another species was not included in analyses.

2.5 Stakeholder engagement

Significant stakeholder engagement underpinned the objectives and delivery of this project. Our CCIP-P-06 project team was joined by Dr Rick Abom from the Reef and Rainforest Research Centre (RRRC) on one of our mid-2023 field trips to the three reefs offshore from Townsville (Hopkinson Reef, John Brewer Reef, Kelso Reef). On this collaborative trip, Rick filmed a short-documentary-style information video, which was later edited, shared with CCIP, and published on the RRRC LinkedIn webpage. This video explains the background and methods of this COTS predation project (CCIP-P-06) and can be viewed by all stakeholders, including reef managers, COTS Control staff and Traditional Owners (TO). The original project team contacted Traditional Owner groups in the regions where field sampling was planned, including the Hope Vale

Congress Aboriginal Corporation RNTBC (Lizard Island). Regular contact was made with all TO groups to update them on project progress and alert them to annual research plans. Given the logistical and funding constraints it was not possible to have TO representatives accompany us on annual research voyages, but this will be key to future engagement and needs to be included in project planning and budgets from the outset. Project updates and data were shared and discussed with other stakeholders, particularly reef managers. The results of this COTS predation project (CCIP-P-06) were presented to stakeholders and end-users at CCIP symposia and the Reef Resilience Symposium 2024. Further stakeholder engagement eventuated through workshop-style or informal discussions with reef managers and modellers to share information and/or receive feedback on study design and data formatting to maximise the project and program pathway to impact. This significant two-way engagement, particularly with reef managers, throughout the duration of this project ensured that project objectives and outputs were well aligned with what is required to improve the ecological underpinning of COTS population modelling and management.

3. RESULTS

A total of 78 standardised predation assays were conducted across the two study regions, assessing in situ predation for 312 adult COTS (excluding 31 caged controls). The average risk of predation (~ relative predation) recorded across all 312 COTS was 0.195 (± 0.02 SE), reflecting the overall proportion of individuals that were fully (= 1), not (= 0), or partially (= 0.05–0.95) consumed. For COTS that appeared to have been subject to predation (n = 89), 51.7% were fully consumed, while 21.3% and 27.0% of individuals were subject to high (≥ 0.5 of body area; **Figure 8**) and relatively low partial predation (< 0.5), respectively. At the assay level (n = 4 COTS, excluding caged control), predation scores ranged from 0 (no full or partial predation of any COTS) to 0.875 (3 COTS fully consumed, 1 partially consumed).

Figure 8. Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) subject to high partial predation (≥ 50% of body area consumed) at Lizard Island, northern GBR. Such a high level of partial consumption likely indicates direct or indirect mortality following the predation event. Note signs of predation (spines, tip of arm) in proximity of the stake and starfish. Photograph: P. Doll.

3.1 Predators of adult crown-of-thorns starfish

The analysis of time-lapse photography data revealed a limited suite of predators responsible for recorded predation events (**Table 2**). Of a total of 89 predation events, the time-lapse recording allowed us to identify the predator(s) for 35 events (full or partial predation). More than half of the total predation (for which predators were identified) was attributed to the spangled emperor (*Lethrinus nebulosus*), which was often captured roaming and predating in schools (**Figure 9**). Most of the remaining predation events (41.6%) were also attributable to *L. nebulosus*, but in combination with either a starry puffer (*Arothron stellatus*) or a titan triggerfish (*Balistoides viridescens*). In these cases, the predation recorded could not be ascribed to an individual species, but rather the combination of both species predating on the same (set of) starfish (**Table**

2; **Figure 9**). The white-spotted puffer (*Arothron hispidus)* and giant triton (*Charonia tritonis*) were each captured feeding on COTS once and ascribed minor predation scores (**Table 2**).

Table 2. Proportion of total predation on adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) (for which predators were captured using time-lapse photography) ascribed to individual predators (or combinations of predators). In the rows of two species listed together, these predators were captured feeding on the same individual (or set of individuals) and the (partial) predation recorded could not be ascribed to a single species.

Predator(s)	Proportion of total predation captured
Lethrinus nebulosus	55.9 %
L. nebulosus + *Arothron stellatus*	32.8 %
L. nebulosus + *Balistoides viridescens*	10.1 %
Arothron hispidus	0.8 %
Charonia tritonis	0.4 %

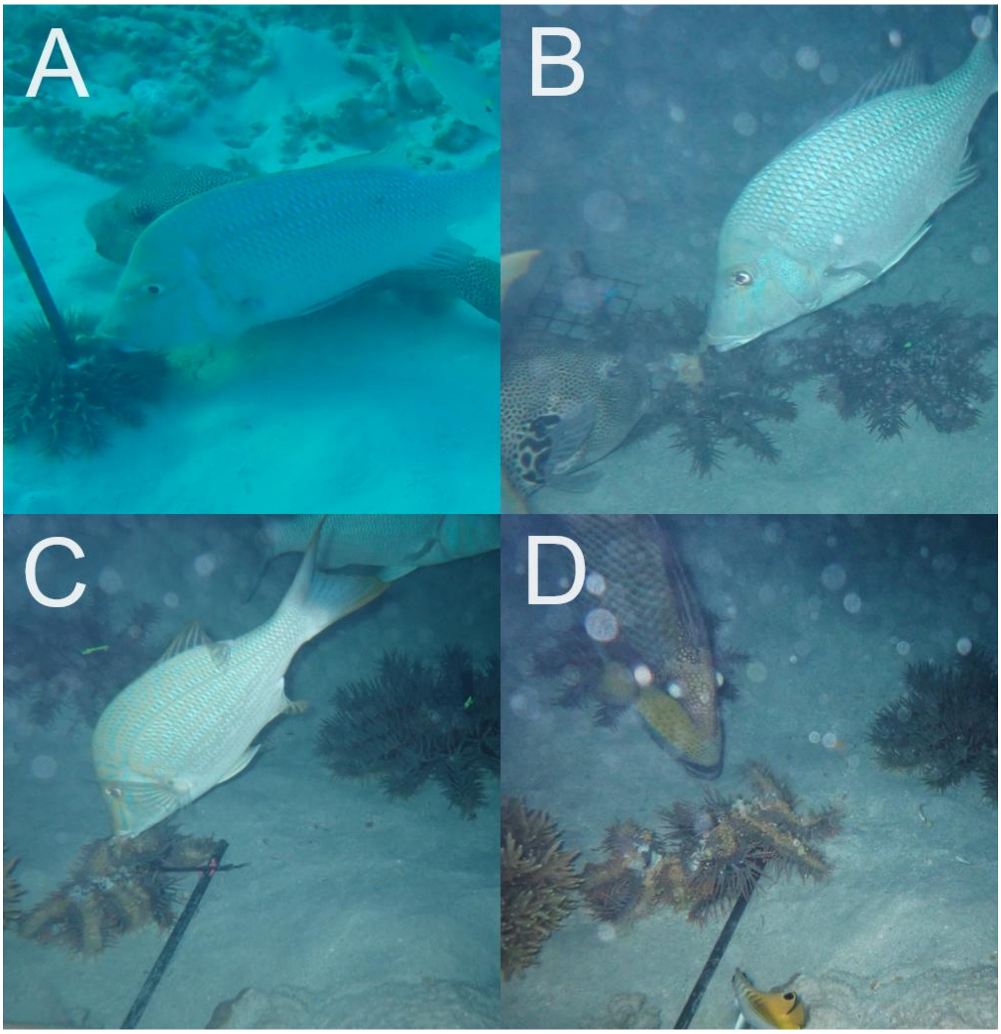


Figure 9. Predation events captured using time-lapse photography. Top row shows spangled emperors (*Lethrinus nebulosus*) and starry puffers (*Arothron stellatus*) in **(A)** proximity and **(B)** simultaneously feeding on the same adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*). Bottom row shows *L. nebulosus* and a titan triggerfish (*Balistoides viridescens*) feeding on the same individual 10 minutes apart **(C)** & **(D)**. Photographs: M. Pratchett and P. Doll.

3.2 Relative risk of predation across fisheries management zones

The mean risk of in situ predation recorded for staked COTS in ‘green zones’ (no-take; 0.278 ± 0.039 SE) was 3.6x higher compared to ‘blue zones’ (open; 0.077 ± 0.037 SE) and 2.8x higher than in the ‘yellow zones’ (restricted; 0.099 ± 0.040 SE) (**Figure 10**). Risk of predation recorded in ‘yellow’ and ‘blue’ zones was comparably low (**Figure 10**).

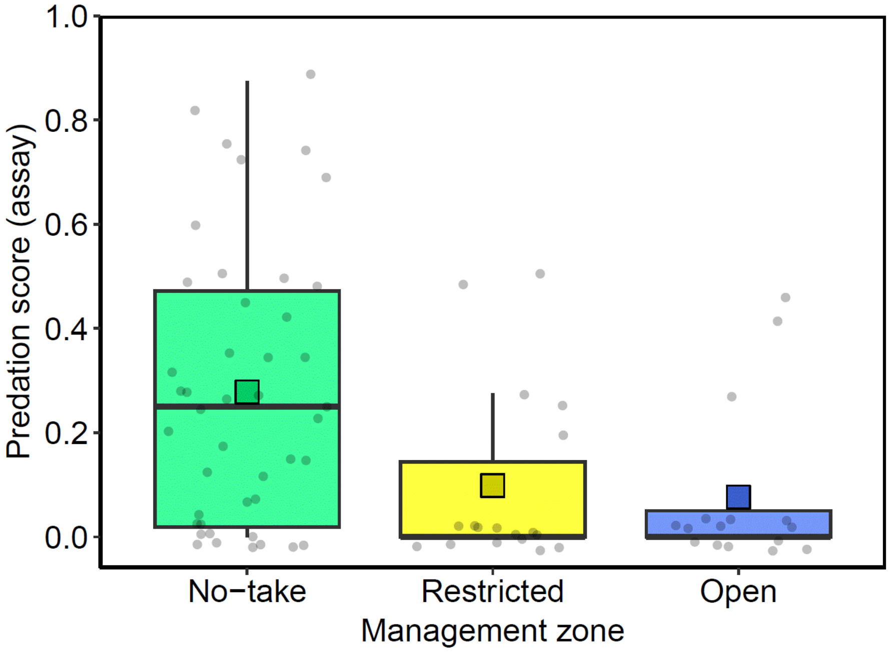


Figure 10. Boxplot showing the relative risk of in situ predation on adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at reefs (across regions) within different fisheries management zones: Marine National Park or ‘green zones’ (No-take), Conservation Park or ‘yellow zones’ (Restricted), and Habitat Protection or ‘blue zones’ (Open). Filled small squares (darker colour shades) represent means. Raw data are displayed as grey jitter points and represent mean assay-level predation scores (0-1) based on full (=1) and partial (=0.05–0.95) predation of individual COTS (n = 4 per assay).

While the overall pattern of predation across management zones was consistent between regions, the relative risk of predation recorded did vary (**Figure 11**). In the northern sector of the GBR (nGBR; Lizard Island Region), the mean risk of predation on COTS in ‘green zones’ (no-take; 0.265 ± 0.033 SE) was 3.5x higher compared to ‘blue zones’ (open; 0.075 ± 0.037 SE) and 3.0x higher than in the ‘yellow zones’ (restricted; 0.088 ± 0.040 SE) (**Figure 11**). In the central sector of the GBR (cGBR; Townsville Region), the mean risk of predation on staked COTS in ‘green zones’ (no-take; 0.363 ± 0.090 SE) was 4.6x higher compared to ‘blue zone’ sites (open; 0.079 ± 0.052 SE) and 3.0x higher than in the ‘yellow zone’ sites (restricted; 0.121 ± 0.060 se) (**Figure 11**).

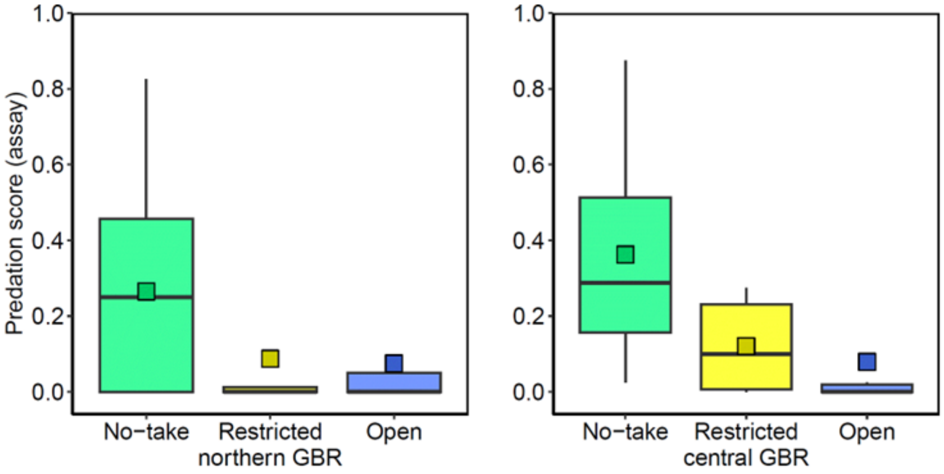


Figure 11. Boxplots showing the relative risk of in situ predation on adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at reefs within different fisheries management zones in the northern GBR (Lizard Island region) and central GBR (Townsville region): Marine National Park or 'green zones' (No-take), Conservation Park or 'yellow zones' (Restricted), and Habitat Protection or 'blue zones' (Open). Filled small squares (darker colour shades) represent means calculated using assay-level predation scores based on the full (=1) and partial (=0.05–0.95) predation of individual COTS (n = 4 per assay).

The relative proportions of adult COTS subject to full and partial predation varied among GBRMP fisheries management zones (**Table 3**). While 54% and 55% of individuals predated on in 'green zones' (no-take) and 'yellow zones' (restricted) were fully consumed (= 1), only 33% of individuals were fully consumed in 'blue zones' (open). However, the proportion of individuals predated on that were only partially consumed (< 0.5 of body) was higher in 'blue zones' (56%) compared to 'green' (22%) and 'yellow zones' (36%). The proportion of COTS that were fully or partially (≥ 0.5) consumed of the total number available in each zone was markedly higher in 'green zones' (21% and 10%) compared to 'yellow zones' (8% and 1%) and 'blue zones' (5% and 2%).

Table 3. Full or partial predation (based on body area consumption) on adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*), as a proportion of total predation recorded within each fisheries management zone: Marine National Park or 'green zones' (no-take), Conservation Park or 'yellow zones' (restricted), and Habitat Protection or 'blue zones' (open). The percentage value in brackets shows the total number of individuals recorded for each predation severity (per zone) divided by the total number of individuals available per zone (Green = 176, Yellow = 72, Blue = 64).

Zone (GBRMP)	Full predation (= 1)	Partial predation (≥ 0.5)	Partial predation (< 0.5)
Green (no-take)	54% (21%)	25% (10%)	22% (9%)
Yellow (restricted)	55% (8%)	9% (1%)	36% (6%)
Blue (open)	33% (5%)	11% (2%)	56% (8%)

3.3 Predator abundance and biomass across fisheries management zones

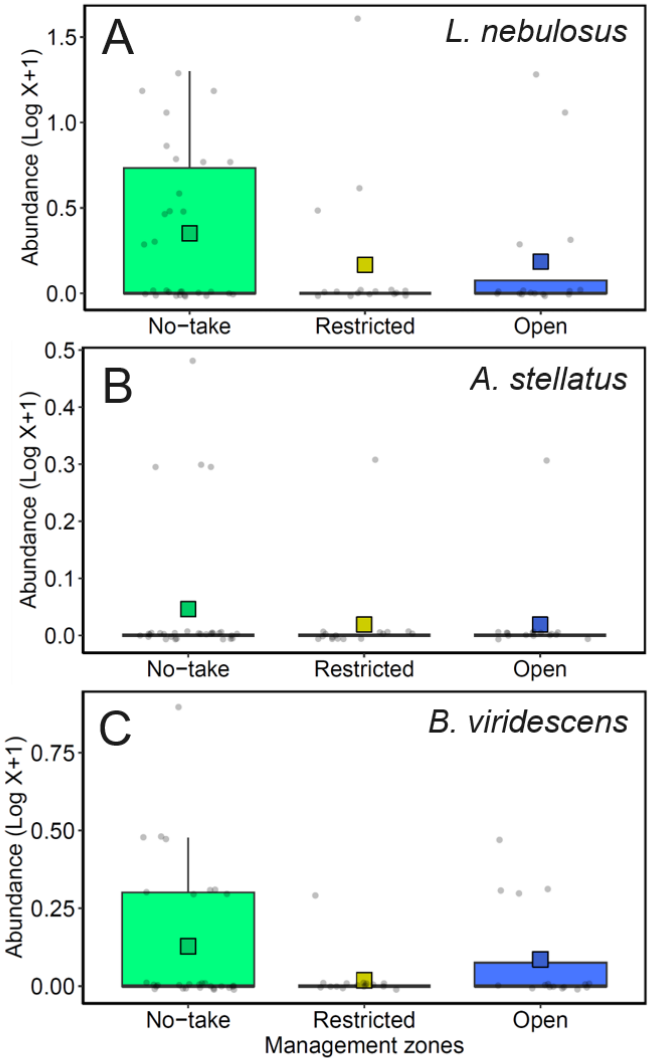


Figure 12. Boxplots showing the relative abundance of key predatory fishes in community belt-transect surveys, **(A)** spangled emperor (*Lethrinus nebulosus*), **(B)** starry puffer (*Arothron stellatus*), **(C)** titan triggerfish (*Balistoides viridescens*), at reefs within different fisheries management zones: Marine National Park or 'green zones' (No-take), Conservation Park or 'yellow zones' (Restricted), and Habitat Protection or 'blue zones' (Open). Filled small squares (darker colour shades) represent means. Raw data are displayed as grey jitter points and represent the summed abundance (log x+1) of each species recorded at the predation assay level (0.1 ha^{-1}). Note the different y axis values.

Variation in recorded densities of the predominant predators recorded to feed on COTS during standardised predation assays (see **Table 2**), was found to be generally higher in green zones (**Figure 12**), corresponding with the elevated risk of predation recorded at these sites. The mean density of *L. nebulosus* recorded per site (2.64 individuals 0.1 ha^{-1} ± 0.81 SE) was considerably higher compared to the densities of *A. stellatus* (0.11 ind. 0.1 ha^{-1} ± 0.05 SE) and *B. viridescens* (0.39 ind. 0.1 ha^{-1} ± 0.13 SE). The mean density of *L. nebulosus* was 55% higher at sites within 'green zones' (3.00 ind. 0.1 ha^{-1} ± 0.93 SE) than at sites within 'blue zones' (1.94 ind. 0.1 ha^{-1} ± 1.27 SE; **Figure 12**). Moreover, the mean density of *B. viridescens* was 92% higher in 'green zones’ (0.60 ind. 0.1 ha^{-1} ± 0.25 SE) than in ‘blue zones’ (0.31 ind. 0.1 ha^{-1} ± 0.15 SE). All three species were not recorded (or recorded in low numbers) at the majority of sampling sites, with *A. stellatus* being particularly rare (**Figure 12**).

The average biomass of *L. nebulosus* was 2.5 times higher in No-take zones (mean = 492.3 g 250 m^2 ± 130.9 SE; n = 117 transects; Marine National Park) than in fished zones (195.4 g 250 m^2 ± 80.9 SE; n = 127; Conservation Park and Habitat Protection zones).

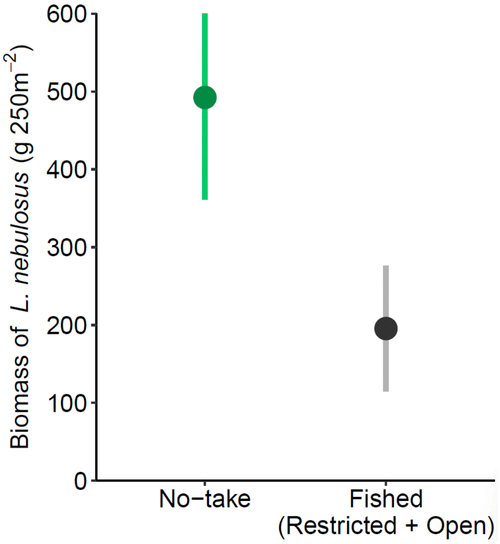


Figure 13. Mean biomass (± SE) of spangled emperor (*Lethrinus nebulosus*) in No-take zones (n = 117; ‘green zones’, Marine National Park) versus fished zones (n = 127; ‘yellow’ and ‘blue’ zones, Conservation Park and Habitat Protection) estimated from size and abundance data (5 x 50 m belt transect surveys) across both regions. A single outlier was replaced with highest non-outlier value. Replicate belt transects (n = 244 across 62 sites and 6 reefs) were surveyed at the same sites the predation assays were deployed in 2023–24.

4. DISCUSSION AND OUTPUTS

COTS are well-known for their propensity to undergo large-scale population irruptions that contribute to coral loss and reef degradation throughout the tropical Indo-Pacific, including the GBR (Moran 1986). The prediction and mitigation of population irruptions is fundamentally dependent on understanding the underlying biology and ecology of COTS, especially key processes that govern demographic rates (Pratchett et al. 2014). While their inherent life-history characteristics (especially exceptional fecundity; Babcock et al. 2016; Pratchett et al. 2021b) naturally predispose them to major and rapid changes in local abundance (Uthicke et al. 2009; Deaker and Byrne 2022), anthropogenic activities, such as terrestrial runoff (Birkeland 1982; Brodie et al. 2005; Fabricius et al. 2010; Wooldridge and Brodie 2015) and/or overfishing of predators (Endean 1969; Sweatman 2008), may also disrupt processes that naturally regulate COTS populations. The hypothesised release of COTS populations from top-down regulation has sparked significant interest in the links between fishing pressure and COTS predation (e.g. Dulvy et al. 2004), to understand driver(s) of population irruptions and effectively manage them. However, the ecological importance of predation as a process that may regulate COTS population dynamics depends largely on the ability of predators to kill their prey at ecologically significant rates (Cowan et al. 2017a).

Despite their extensive physical and chemical anti-predator defences (Deaker et al. 2021), our results suggest that large-bodied adult COTS are subject to considerable in situ predation by specialist fish predators. The incidence of lethal and sublethal predation on COTS is expected to decline with age and body size (McCallum 1987; McCallum et al. 1989; Rivera-Posada et al. 2014a). However, predators of the adult life stage can still cause significant injuries, with some predators capable of killing and rapidly consuming large adult COTS (Keesing and Halford 1992; this study). In fact, background predation pressure on adult COTS may be higher than expected in places where effective predators are relatively abundant, as we recorded significant mortality in some locations, with up to 3 (out of 4) starfish consumed during a 24-hour assay. Rates of partial (often sublethal) predation can also substantially affect population dynamics due to increased risk of disease and/or subsequent predation events (Glynn 1984; Caballes et al. 2022). For adult COTS, up to 60% of individuals have been reported to show evidence of recent injuries (McCallum et al. 1989). In the absence of data on lethal predation, the incidence of (sublethal) injuries, often manifested as short or missing arms (Rivera-Posada et al. 2014a; Messmer et al. 2017), had so far served as a proxy for relative predation pressure (McCallum et al. 1989; Messmer et al. 2017; Caballes et al. 2022). Here, we trialled and used an experimental approach to obtain estimates of predation risk (or relative predation) for adult COTS. This approach allowed us to assess the mechanistic basis of ‘zoning effects’ evident in the incidence of population irruptions, as well as the relative importance of putative predators.

4.1 Predators of adult crown-of-thorns starfish

Our results suggest that only few predatory reef-fish species are effectively exerting predation pressure on adult COTS, providing a revised and reduced list of predators compared to previous reports (reviewed by Cowan et al. 2017a). The importance of predation in regulating COTS populations depends largely on the capacity of predators to kill their prey at ecologically significant rates. Only three species demonstrated this capacity during our predation assays, whereby more than half of the total predation recorded could be solely ascribed to the spangled emperor (*Lethrinus nebulosus*), while most of the remaining predation was jointly ascribed to the combinations of *L. nebulosus* and the starry puffer (*Arothron stellatus*) or titan triggerfish (*Balistoides viridescens*). All three species had previously been reported to feed on healthy adult COTS, although for *L. nebulosus* this was solely based on gut content analyses, rather than direct observation of in situ predation (Ormond et al. 1973; Keesing and Halford 1992; Rivera-Posada et al. 2014b; Boström-Einarsson and Rivera-Posada 2016; Kroon et al. 2020). Whether these predators preferentially target COTS over other available prey remains unclear, considering all three species are known to feed on starfishes and other echinoderms, as well as molluscs, crustaceans, and some other benthic invertebrates (Carpenter and Allen 1989; Allen 1997; Matsuura 2001). Notably, *L. nebulosus* was frequently observed in schools, increasing their potential to cause substantial rates of injury and mortality among large adult COTS. In most cases of joint predation by *L. nebulosus* with another species on the same (set of) COTS, *L. nebulosus* were observed initiating the predation event, with a secondary predator (*A. stellatus* or *B. viridescens*) appearing soon after and generally targeting COTS that had already been attacked by *L. nebulosus*. These results suggest that *L. nebulosus* may be the foremost predator of adult COTS on the GBR, at least in the locations studied, and may thus play a fundamental role in the top-down control of COTS populations and incidence of population irruptions.

The limited number of effective predators presented here contrasts the extensive and ever-increasing suite of putative predators reported in past studies (reviewed by Cowan et al. 2017a, also see Kroon et al. 2020). Motile invertebrates known for their capacity to kill healthy COTS, at least at the sub-adult (or small adult) stage, include giant triton (*Charonia tritonis*) and harlequin shrimps (*Hymenocera picta*) (Endean 1969; Wickler and Seibt 1970). For example, *C. tritonis* were estimated to consume 0.7 adult COTS week^{-1} in caging experiments (Pearson and Endean 1969), however, predation by this species can be limited to individual arms and is not necessarily fatal for COTS (Chesher 1969, this study). Here, we only recorded *C. tritonis* during one predation assay, documenting the consumption of 1 COTS arm. Moreover, predatory reef fishes considered as putative predators of healthy adult COTS include the yellow-margin triggerfish *Pseudobalistes flavimarginatus* (Rivera-Posada et al. 2014a, Ormond and Campbell 1973), the white-spotted puffer *Arothron hispidus* (Ormond and Campbell 1973; Boström-Einarsson and Rivera-Posada 2016), and the humphead wrasse *Cheilinus undulatus* (Chesher 1969; Ormond and Campbell 1973). In this study, only limited (and sublethal) predation was recorded for *C. tritonis* and *A. hispidus*, suggesting their relative risk of in situ predation may be constrained by their relative abundance and/or capacity to consume large-bodied COTS at high rates.

An extensive list of reef fish taxa has been observed consuming injured, moribund and/or dead COTS (Cowan et al. 2017a; Kroon et al. 2020), highlighting the necessity to differentiate between these opportunistic predators (or scavengers) and predators that can kill and consume healthy individuals. Opportunistic predators include numerous species within the reef fish families Chaetodontidae, Labridae, Lutjanidae, Mullidae, Nemipteridae, Pomacanthidae, and Pomacentridae (Glynn 1984; Cowan et al. 2017a; Kroon et al. 2020; 2021), although the scavenging behaviour of these groups is generally not specific to COTS or likely to alter the population size of adult COTS. Other species (e.g. coral trout, *Plectropomus* spp.) have been reported to feed on COTS, mostly inferred from gut content analyses or DNA-based analyses of faecal or gut content samples (Kroon et al. 2020). *Plectropomus* spp. have since been considered in analyses linking fishing pressure on COTS predators and population irruptions (Kroon et al. 2021), however, adult coral trout are (obligate) piscivores and likely just scavenge on injured/dead COTS if the opportunity presents. Alternatively, the DNA detections of COTS in the stomach or faeces of putative predators may be a result of predation on earlier life-history stages of COTS and/or indirect food chain effects (Kroon et al. 2020). The absence of *Plectropomus* spp., and other putative predators inferred from gut contents and/or DNA, throughout the predation events captured in this study further corroborates that these reef fishes are generally not effective predators of adult COTS.

In general, large-bodied reef fishes with the morphological traits required to feed on motile invertebrates such as COTS can inflict significant damage, and we cannot rule out that additional fish species (other than the predators identified in this study) may be contributing to adult COTS predation and mortality in other locations. Importantly, the relative predation pressure different predatory fishes exert on adult COTS populations inherently depends on their local abundance and feeding preferences. Most of the aforementioned (putative) predators feed on other starfishes, echinoderms, and benthic invertebrates, without evidence of preferential selection for COTS over other suitable prey (Ormond and Campbell 1973; Glynn 1984). The relative abundance of alternative prey may thus be an underappreciated factor in the potential impact of predators on COTS.

Despite their anti-predatory defences, COTS are clearly susceptible to predation at all life stages, with different predatory groups acting at different stages, including many motile benthic invertebrates and small-bodied reef fishes (Cowan et al. 2017a; Desbiens et al. 2023). Many of the putative predators listed above (but not captured in our assays), including species inferred based on eDNA analyses (Kroon et al. 2020) may in fact be effective predators of COTS larvae, juveniles or sub-adults. While understudied compared to the adult stage, the pre-settlement and early post-settlement stages of COTS are thought to present considerable demographic bottlenecks (Wilmes et al. 2018; Deaker and Byrne 2022). The planktonic larval stages of COTS are readily consumed by damselfishes (Cowan et al. 2016; 2017b), while herbivorous (early-stage) juveniles are subject to predation by a suite of benthic invertebrates, including rubble-dwelling crustaceans (Desbiens et al. 2023; Wolfe et al. 2024). Thereafter, coral-feeding juveniles and sub-adults are susceptible to predation by motile benthic invertebrates (e.g. *C. tritonis*) and various groups of reef fishes (reviewed by Cowan et al. 2017a). Clearly, predation on COTS is multifaceted and highly complex, and the identity and relative roles of different suites of predators must be assessed for each life-history stage.

While major information gaps persist for the predators of pre-settlement and early-post settlement COTS (but see Desbiens et al. 2023; Wolfe et al. 2024), this study presents a revised understanding for the key predators of adult COTS. The trio of reef fishes captured in this study does not represent a comprehensive (or final) list of adult COTS predators, valid across the Indo-Pacific range of COTS, but rather species that can effectively consume adult COTS and thus appear capable to influence COTS population dynamics in the northern and central GBR. The identification of *L. nebulosus*, and to some extent *A. stellatus* and *B. viridescens*, as the foremost predator(s) of adult COTS improves accuracy in capturing predation effects in demographic models and provides an opportunity for targeted fisheries management in reducing the risk of COTS population irruptions.

4.2 The ‘zoning effect’: can no-take areas protect corals from COTS?

The ’predator removal hypothesis’ proposes that reduced abundance of predators (due to overfishing) releases COTS from the predation pressure that naturally regulates their populations, whereby the increased abundance of adult COTS (and concomitant reproductive potential) causes population irruptions (Endean 1969). This has stimulated considerable interest in predation on COTS, both to unmask the root cause(s) of population irruptions and develop strategies to effectively moderate their impact (Dulvy et al. 2004; Sweatman 2008; Kroon et al. 2021). Fisheries management, including no-take marine protected areas, could thus play a critical role in conserving (or re-establishing) this predator-mediated control of COTS abundance. However, this ‘zoning effect’ lacked ecological underpinning as evidence in support of it largely rested on broad-scale patterns in the incidence of population irruptions on reefs where fishing was or was not permitted (e.g. Sweatman 2008).

This study provides new insights into in situ predation on COTS relative to different management zones on the GBR, adding considerable evidence to the mechanistic basis of the ‘predator removal hypothesis’. If apparent differences in COTS abundance across gradients of fishing effort (Sweatman 2008; Kroon et al. 2021) are mediated by predators, we expect that the abundance of key predators and relative risk of predation would be much higher in areas closed to fishing. Our results corroborate this underlying assumption of the ‘zoning effect’ as they report a higher risk of predation for COTS on reefs closed to fishing (‘green zones’) compared to reefs where fishing is restricted or permitted (‘yellow’ and ‘blue zones’). The ‘zoning effect’ apparent in relative risk of predation was considerable and consistent for both regions studied, with ‘green zones’ reporting threefold higher predation scores than ‘yellow’ and ‘blue zones’ in both the northern (Lizard Island region) and central (Townsville region) sectors of the GBR. Moreover, adult COTS in ‘blue zones’ were less likely to be fully consumed by predators but instead reported high relative rates of partial consumption (less than half of body) or sublethal injuries, compared to COTS in ‘green’ and ‘yellow zones’, potentially due to the lower abundance of large-sized predators in fished zones. These findings correspond with reported differences in the incidence and severity of population irruptions (Sweatman 2008; Kroon et al. 2021) and prevalence of injuries for COTS on the GBR (Caballes et al. 2022), reinforcing the notion that increased predation risk in areas closed to fishing does have the capacity to moderate the local abundance of COTS, and could potentially prevent the establishment of population irruptions.

Our findings indicate that the relative risk of predation by spangled emperor (*L. nebulosus*) varies among the different fisheries management zones. The predator-mediated suppression of populations, and release thereof, inherently relies on a range of factors, including the local abundance of predators, and their vulnerability to overfishing and/or reef degradation. Our results suggest that the spangled emperor (*L. nebulosus*) was more locally abundant at study sites closed to fishing. Based on site-specific predator surveys, we estimate the biomass of *L. nebulosus* to be 2.5 higher in ‘green zones’ than on fished reefs (‘yellow’ and ‘blue’ zones) Analyses of larger-scale abundance (e.g. AIMS LTMP) and fisheries data for *L. nebulosus* and other predators are required to evaluate system-wide links between zoning and the dynamic role of predators in controlling COTS populations. For purported top-down effects to be noticeable at the scale of the GBR (e.g. Sweatman 2008), some key predators (see Section 4.1) must be targeted by fisheries. Kroon et al. (2021) demonstrated that fish biomass removal through commercial and recreational fisheries may be a major driver of COTS population irruptions. Many of the reef fish taxa included in their analyses are unlikely to directly drive this ‘zoning effect’ (Kroon et al. 2021), given limited evidence that major fisheries target species (e.g. coral trout, *Plectropomus* spp.) are effective predators of COTS (Cowan et al. 2017a). Nevertheless, it is possible that indirect effects of anthropogenic activity and/or the general degradation of reef ecosystems may contribute to the increased incidence and severity of population irruptions in fished areas (Cowan et al. 2017a).

The foremost predator of adult COTS identified in this study (spangled emperor, *L. nebulosus*) is a secondary target and by-product species of the Reef Line Fishery (> 40 t per annum, East Coast Queensland) and is a highly targeted recreational fishing species (Newman et al. 2021). In contrast, other identified predators of adult COTS, including the starry puffer (*A. stellatus*) and titan triggerfish (*B. viridescens*), are generally not targeted, although may be susceptible to the broader anthropogenic modification and degradation of coral reefs (Potts 1981). While *A. stellatus* and *B. viridescens* may have the capacity to consume COTS and disband aggregations if locally abundant, they are unlikely to effectively control populations of COTS as they are often rare (Endean 1977; Cowan et al. 2017a, this study). However, reduced populations of *L. nebulosus* outside of no-take zones (Kroon et al. 2021, this study), due to commercial (‘blue zones’) and recreational fishing pressure (‘yellow’ and ‘blue zones’), may be an important driver of heterogeneity in COTS abundance and the incidence or severity of population irruptions.

Past research on ‘zoning effects’ and their underlying processes has largely focused on sub-adult and adult COTS, with limited information on key predators of the larval and juvenile stages (but see Sweatman 1995; Cowan et al. 2016; 2017b, Desbiens et al. 2023), as well as their relative impact on COTS population dynamics and their vulnerability to anthropogenic stressors. For example, it is plausible that top-down effects of overfishing may result in reduced/elevated densities of key predators of juvenile COTS (e.g. *Schizophrys aspera*; Desbiens et al. 2023) in fished/unfished locations, although the trophic links underpinning this potential mechanism remain elusive. Apparent differences in adult abundances across these locations may thus be a result of differences in predation pressure on earlier life-history stages. Moreover, the collective consumption of COTS across life-history stages by different groups of predators may be compounded by indirect effects of anthropogenic activities on reef fishes that directly or indirectly influence COTS population dynamics, including widespread declines in reef biodiversity and productivity (Wilson et al. 2006).

Improved understanding of the underlying mechanisms of ‘zoning effects’ apparent in the incidence of population irruptions constitutes a critical step to explain and model the large heterogeneity in COTS abundance over space and time. This presents an opportunity to refine ecosystem models for the targeted decision support of COTS control efforts. Considering new information on in situ predation and key predators across management zones, our results also highlight a potential role for marine park zoning and targeted fisheries management of *L. nebulosus* in mitigating the considerable threat COTS pose to Anthropocene coral reefs.

4.3 Key outputs

The primary outputs of this project are:

- New knowledge on important predators of adult COTS. Contrary to past reports (and popular belief), only a small number of species were recorded predating on adult COTS during predation assays. The spangled emperor (*Lethrinus nebulosus*) emerged as the foremost predator of adult COTS. This result has implications for the potential role of targeted fisheries management in controlling COTS populations.

- New knowledge and empirical data on in situ risk of predation. Even large-bodied adult COTS are susceptible to in situ predation if effective predators are present, despite significant physical and chemical defences. These new insights have application for population modelling.

- New knowledge and empirical data on differences in risk of in situ predation on adult COTS on reefs within different GBRMP management zones, corroborating the hypothesis that predatory release may elevate COTS abundance in areas open to fishing. These results add evidence to the 'predator removal hypothesis' (Endean 1969; Sweatman 2008) and highlight a potential role for marine park zoning in managing COTS population irruptions.

- New datasets (relative risk of predation; abundance and size of predatory fishes; benthic cover and composition) to further assess the mechanistic basis of the 'predator removal hypothesis' and improve the ecological underpinning of COTS population monitoring, modelling, and management.

5. RESEARCH SYNERGIES AND NEXT STEPS

This study presents novel data on predators of, and predation on, adult COTS, which complements work undertaken to identify new predators of the early juvenile life stage (CCIP-P-05, Wolfe et al. 2025). The influence of predation on COTS populations is likely highly complex and multi-faceted, and the urgent need to understand key demographic processes (such as predation) across all life history stages is clear (Cowan et al. 2017a). The combined outputs of CCIP-P-05 (Wolfe et al. 2025) and CCIP-P-06 provide an opportunity to revise and supplement the ecological data that underpins COTS population modelling. Thus, strong links exist with modelling projects within the CCIP Response subprogram (**Figure 4**), particularly CCIP-R-10 (Fish predator conservation for biocontrol, Ceccarelli et al. 2025). New insights gained on key predators and zoning effects are important to model population dynamics and refine ecosystem models for targeted decision support (CCIP Response subprogram). The outputs associated with CCIP-P-06 (and potentially CCIP-P-05) also provide an important opportunity to assess the potential role of marine park zoning and/or predator-specific fisheries management in mitigating the impact of COTS population irruptions on coral assemblages.

Moreover, the research conducted in CCIP-P-06 compliments additional CCIP projects within the Prediction Subprogram (**Figure 4**). Notably, much of this research has been delivered in conjunction with other CCIP Prediction subprogram projects, especially CCIP-P-01 (Pratchett et al. 2025a) and CCIP-P-04 (Pratchett et al. 2025b), which collectively contribute to the improved understanding of COTS population irruptions and the ecological underpinning of management strategies. Overall, the outputs of this research, in conjunction with linked projects within and beyond the Prediction Subprogram, provide an extensive body of new insights and data that will facilitate considerable improvements to the monitoring, modelling and management of COTS populations.

5.1 Priorities for future research

Key priorities for future research into predatory release, and its role in COTS population irruptions, that have emerged through this project, include:

- Improved understanding of the distribution, abundance and fisheries take of key predators, particularly the spangled emperor (*Lethrinus nebulosus*). Analyses of larger-scale predator abundance data (e.g. AIMS LTMP, e.g. Kroon et al. 2021 including Lethrinidae), in conjunction with commercial and recreational catch estimates, could further resolve mechanistic links underpinning the purported 'zoning effect' and establish generality of our findings. Potential management scenarios surrounding *L. nebulosus* should be explored by complementary modelling. If spangled emperor are found to play a disproportionate role in the regulation of COTS populations, consideration should be given to providing increased protection from fishing, effectively increasing the potential benefits of fisheries management without necessarily modifying zoning.

- Ongoing large-scale sampling of COTS predation and surveys of putative predatory fishes at additional locations on the GBR, including reefs or regions of ecological interest. These should include putative initiation areas of population irruptions (other than the Lizard Island region), including the Cairns region and potentially the Cape Grenville regions

(Pratchett et al. 2024a; 2024b). Predation assays could make use of methodological advances (e.g. continual video recording of assay sites) for highly resolved predator and predation data. This includes the collection of both predator data and COTS density data along the same spatiotemporal scales.

- Longer-term tagging study (or alternative approaches) to provide field-based estimates of absolute predation and mortality rates for COTS. This study could bridge the gap between relative predation risk and mortality rates and may thus facilitate the use of predation data in population models. Importantly, this study should also explore the extent to which predation on COTS is density-dependent, identifying the rate of predation and the density of predators required to control COTS populations at a range of densities (i.e. prior to and during outbreaks).

6. MANAGEMENT IMPLICATIONS AND IMPACT

Coral reef scientists, managers, and other stakeholders are faced with the challenge of mitigating, if not preventing, the destructive effects of COTS population irruptions on Anthropocene reefs, which are increasingly compounded by the effects of climatic disturbances (Mellin et al. 2019; Bozec et al. 2021). In comparison to climatic disturbances, population irruptions of COTS are at least somewhat amenable to direct management action, largely through culling of adult COTS (Matthews et al. 2024). Improvements to management strategies and field-based culling activities are ongoing (e.g. single injection method; Rivera-Posada et al. 2014b). Nevertheless, the incidence of new and renewed population irruptions (Chandler et al. 2023; Pratchett et al. 2024a; 2024b; Uthicke et al. 2024), as well as the continuing devastation caused by COTS in some parts of the GBR (e.g. Swains), highlight the critical importance of further research and innovation to improve the ecological underpinning of direct or indirect population management approaches. Most notably, improved understanding of the proximal cause(s) of population irruptions, or factors contributing to their severity, would provide indirect pathways to effective conservation of coral reefs.

Our results indicate applicability of fisheries-based management, including marine park zoning, to prevent or mitigate COTS population irruptions, and their concomitant impact on coral reef ecosystems. Spatial zoning and no-take areas (or marine reserves) are used (on the GBR and globally) to effectively manage fisheries (Sala and Giakoumi 2018). On the GBR, no-take areas appear to have a major effect on COTS abundance and the incidence of population irruptions (Sweatman 2008; Kroon et al. 2021). Considering contemporary zoning and catch limits were not developed with consideration of COTS predators and primary fisheries target species (coral trout) are not consuming COTS (Kroon et al. 2021), the magnitude of the apparent 'zoning effect' reported (e.g. Sweatman 2008) is somewhat surprising. Nevertheless, the combined results of these and the present study suggest that protected reefs with 'healthy' predatory fish communities can directly or indirectly suppress COTS densities. For improved management of COTS populations, any future revisions to spatial zoning and/or additions of no-take areas should therefore consider the spatial distribution and abundance of COTS and their predators. Specifically, additional no-take areas within the initiation areas of population irruptions (Pratchett et al. 2024a; 2024b) and/or reefs of high ecological importance (e.g. recruitment, adult abundance, and larval dispersal/sink hotspots (e.g. Hock et al. 2014) could complement manual population control efforts.

Targeted species-specific management of key predators represents an alternative, and potentially much more tractable opportunity for effectively managing fisheries impacts that may cause or exacerbate population irruptions of COTS. Specifically, reduced fisheries take (or temporal closures) for key predatory fish(es) that have a disproportionate influence on COTS population dynamics presents a more direct and less-restrictive approach, compared to alterations of large-scale zoning plans (Kroon et al. 2021). Notably, the foremost predator identified in this study, *L. nebulosus*, is a secondary target and by-catch species of the Reef Line Fishery (> 40 t per annum, East Coast Queensland) and highly targeted recreational fishing species (Newman et al. 2021). Reduced commercial and/or recreational take of this species would improve the recovery potential of reduced biomass and functionality of this species and supplement the predator-mediated regulation of COTS populations. However, the recovery of biomass for *L. nebulosus* (or other reef fish predating on other COTS life-history stages) could take more than a decade (MacNeil et al. 2015), thus some of the contributions and benefits of targeted fisheries management to controlling COTS population irruptions may only be evident in the long term.

Contemporary management efforts to reduce COTS densities, largely centred around the manual control of adults (Matthews et al. 2024), may lack necessary capacity to effectively suppress COTS populations at scale, evident in established and enduring population irruptions in far northern and southern parts of the GBR (Pratchett et al. 2024a; 2024b). In contrast to widespread efforts to improve water quality, partly due to the ‘terrestrial runoff hypothesis’ (Birkeland 1982; Brodie et al. 2005; Fabricius et al. 2010; Wooldridge and Brodie 2015), the management of COTS predators has not been a major part of strategic management frameworks or the reef prioritisation process. The increasing evidence in support of the ‘predator removal hypothesis’ (Endean 1969; Sweatman 2008; this study) indicates that further emphasis on predator biocontrol as part of COTS management efforts may help regulate GBR populations. While there is not sufficient evidence that predatory release in and of itself can fully account for the initiation of COTS population irruptions, a reduction in anthropogenic stressors on COTS predators, by means of no-take areas or taxon-specific limits, represents a ‘no-regrets’ strategy to suppress COTS abundances, in conjunction with the contemporary control strategy. Our study highlights that these targeted fisheries-management approaches, considering the population dynamics of COTS and their foremost predators across life stages, may contribute to an effective reduction in the incidence and severity of population irruptions across the Indo-Pacific range of COTS, including the GBR.

7. ACKNOWLEDGEMENTS

This research was in part supported by funds from the Australian Research Council (ARC) grants CE140100020 (ARC Centre of Excellence for Coral Reef Studies) and FT200100949 (University of Tasmania). Thanks to Deborah Burn and Samuel Coenradi for field support, and to the Australian Museum's Lizard Island Research Station (particularly Anne Hoggett and Lyle Vail) and the skippers and crew of our research charter vessels (Wild Blue, Aroona, Delphi) for significant logistical support. We thank Mary Bonin and the anonymous reviewer for their constructive comments.

8. DATA ACCESSIBILITY

All data generated as part of this project are available from Research Data JCU using the DOI https://doi.org/10.25903/pjwy-4345 or the corresponding authors upon request.

9. REFERENCES

Allen GR (1997) Marine Fishes of Tropical Australia and South-east Asia. Western Australian Museum, Perth, Western Australia. 292 pp.

Babcock RC, Dambacher JM, Morello EB, Plagányi ÉE, Hayes KR, Sweatman HP, Pratchett MS (2016a) Assessing different causes of crown-of-thorns starfish outbreaks and appropriate responses for management on the Great Barrier Reef. PLoS One 11: e0169048. https://doi.org/10.1371/journal.pone.0169048

Babcock RC, Milton DA, Pratchett MS (2016b) Relationships between size and reproductive output in the crown-of-thorns starfish. Marine Biology 163:1-7. https://doi.org/10.1007/s00227-016-3009-5

Babcock RC, Plagányi ÉE, Condie SA, Westcott DA, Fletcher CS, Bonin MC, Cameron D (2020) Suppressing the next crown-of-thorns outbreak on the Great Barrier Reef. Coral Reefs 39(5): 1233-1244. https://doi.org/10.1007/s00338-020-01978-8

Bellwood DR, Pratchett MS, Morrison TH, Gurney GG, Hughes TP, Álvarez-Romero JG, Day JC, Grantham R, Grech A, Hoey AS, Jones GP (2019) Coral reef conservation in the Anthropocene: confronting spatial mismatches and prioritizing functions. Biological Conservation 236: 604-615. https://doi.org/10.1016/j.biocon.2019.05.056

Birkeland C (1989) The Faustian traits of the crown-of-thorns starfish. American Scientist 77(2): 154-163.

Birkeland C (1982) Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). Marine Biology 69:175-185. https://doi.org/10.1007/BF00396897

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: 223–228. https://doi.org/10.1007/s00338-015-1351-6

Bozec YM, Hock K, Mason RA, Baird ME, Castro-Sanguino C, Condie SA, Puotinen M, Thompson A, Mumby PJ (2021) Cumulative impacts across Australia's Great Barrier Reef: A mechanistic evaluation. Ecological Monographs 92(1): e01494. https://doi.org/10.1002/ecm.1494

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. https://doi.org/10.1016/j.marpolbul.2004.10.03

Caballes CF, Messmer V, Raymundo ML, Pratchett MS (2022) Prevalence and severity of sublethal injuries in crown-of-thorns starfish relative to marine reserves in the Great Barrier Reef. Aquatic Conservation: Marine and Freshwater Ecosystems 32(6): 993-1004. https://doi.org/10.1002/aqc.3762

Carpenter KE, Allen GR (1989) FAO Species Catalogue. Vol. 9. Emperor fishes and large-eye breams of the world (family Lethrinidae). An annotated and illustrated catalogue of lethrinid species known to date. FAO Fish. Synop. 125(9):118 p. Rome: FAO. (Ref. 2295)

Ceccarelli DM, Currey-Randall LM, Condie S, Barneche DR, Porobic Garate J, Emslie MJ, Kroon F (2025) Fish predator conservation to prevent crown-of-thorns starfish (COTS) outbreaks. A report to the Australian Government by the COTS Control Innovation Program.

Chandler JF, Burn D, Caballes CF, Doll PC, Kwong SL, Lang BJ, Pacey KI, Pratchett M (2023) Increasing densities of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at Lizard Island, northern Great Barrier Reef, resolved using a novel survey method. Scientific Reports 13: 19306. https://doi.org/10.1038/s41598-023-46749-x

Chesher RH (1969) Destruction of Pacific corals by the sea star *Acanthaster planci*. Science 165(3890): 280-283. https://doi/abs/10.1126/science.165.3890.280

Cowan ZL, Dworjanyn SA, Caballes CF, Pratchett MS (2016) Predation on crown-of-thorns starfish larvae by damselfishes. Coral Reefs 35: 1253-1262. https://doi.org/10.1007/s00338-016-1491-3

Cowan ZL, Pratchett M, Messmer V, Ling S (2017a) Known predators of crown-of-thorns starfish (*Acanthaster* spp.) and their role in mitigating, if not preventing, population outbreaks. Diversity 9(1): 7. https://doi.org/10.3390/d9010007

Cowan ZL, Ling SD, Dworjanyn SA, Caballes CF, Pratchett MS (2017b) Inter-specific variation in potential importance of planktivorous damselfishes as predators of *Acanthaster* sp. eggs. Coral Reefs 36: 653-661. https://doi.org/10.1007/s00338-017-1556-y

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. Marine Ecology Progress Series 665: 115-125. https://doi.org/10.3354/meps13660

Deaker DJ, Byrne M (2022) Crown of thorns starfish life-history traits contribute to outbreaks, a continuing concern for coral reefs. Emerging Topics in Life Sciences 6: 67-79. https://doi.org/10.1042/ETLS20210239

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. Proceedings of the National Academy of Sciences, USA 109(44):17995-17999. ttps://doi.org/10.1073/pnas.1208909109

Desbiens AA, Mumby PJ, Dworjanyn S, Plaganyi EE, Uthicke S, Wolfe K (2023) Novel rubble-dwelling predators of herbivorous juvenile crown-of-thorns starfish (*Acanthaster* sp.). Marine Biology 42: 579-591. https://doi.org/10.1007/s00338-023-02364-w

Doll PC, Messmer V, Uthicke S, Doyle JR, Caballes CF, Pratchett MS (2021) DNA-based detection and patterns of larval settlement of the corallivorous crown-of-thorns sea star (*Acanthaster* sp.). The Biological Bulletin 241: 271-285. https://doi.org/10.1086/717539

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. Biology Letters 19: 20220399. https://doi.org/10.1098/rsbl.2022.0399

Dulvy NK, Freckleton RP, Polunin NVC (2004) Coral reef cascades and the indirect effects of predator removal by exploitation. Ecology Letters 7: 410-416. https://doi.org/10.1111/j.1461-0248.2004.00593.x

Endean RG (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.

Endean R (1977) *Acanthaster planci* infestations of reefs of the Great Barrier Reef. In *Proceedings: the 3rd International Coral Reef Symposium*, Miami, Florida; Taylor DL, Ed.; University of Miami, Florida, USA 1: 185-191.

Fabricius KE, Okaji K, De'Ath G (2010) Three lines of evidence to link outbreaks of the crown-of-thorns seastar *Acanthaster planci* to the release of larval food limitation. Coral Reefs 29(3): 593-605. https://doi.org/10.1007/s00338-010-0628-z

Glynn PW (1984) An amphinoid worm predator of the crown-of-thorns sea star and general predation on asteroids in eastern and western pacific coral reefs. Bulletin of Marine Science 35: 54-71.

Hock K, Wolff NH, Condie SA, Anthony KR, Mumby PJ (2014) Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. Journal of Applied Ecology 51(5): 1188-1196. https://doi.org/10.1111/1365-2664.12320

Kayal M, Vercelloni J, Lison de Loma T, Bosserelle P, 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(10): e47363. https://doi.org/10.1371/journal.pone.0047363

Keesing JK, Halford A (1992) Importance of postsettlement processes for the population dynamics of *Acanthaster planci* (L.). Marine & Freshwater Research 41: 635-651. https://doi.org/10.1071/MF9920635

Keesing JK, Lucas JS (1992) Field measurement of feeding and movement rates of the crown-of-thorns starfish *Acanthaster planci* (L.). Journal of Experimental Marine Biology and Ecology 156(1) :89-104. https://doi.org/10.1016/0022-0981(92)90018-6

Kelley R (2022) Indo Pacific Coral Finder, 2022 edition, BYOGUIDES.

Kroon FJ, Lefevre CD, Doyle JR, Patel F, Milton G, Severati A, Kenway M, Johansson CL, Schnebert S, Thomas-Hall P, Bonin MC, Cameron DS, Westcott DA (2020) DNA-based identification of predators of the corallivorous Crown-of-Thorns Starfish (*Acanthaster* cf. *solaris*) from fish faeces and gut contents. Scientific Reports 10: 8184. https://doi.org/10.1038/s41598-020-65136-4

Kroon FJ, Barneche DR, Emslie MJ (2021) Fish predators control outbreaks of crown-of-thorns starfish. Nature Communications 12(1):6986. https://doi.org/10.1038/s41467-021-26786-8

MacNeil MA, Graham NAJ, Cinner JE, Wilson SK, Williams ID, Maina J, Newman S, Friedlander AM, Jupiter S, Polunin NVC, McClanahan TR (2015) Recovery potential of the world's coral reef fishes. Nature 520: 341-344. https://doi.org/10.1038/nature14358

Matsuura K (2001) Balistidae. Triggerfishes. p. 3911-3928. In K.E. Carpenter and V. Niem (eds.) FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Vol. 6. Bony fishes part 4 (Labridae to Latimeriidae), estuarine crocodiles. FAO, Rome. (Ref. 9770)

Matthews SA, Williamson DH, Beeden R, Emslie MJ, Abom RT, Beard D, Bonin M, Bray P, Campili AR, Ceccarelli DM, Fernandes L (2024) Protecting Great Barrier Reef resilience through effective management of crown-of-thorns starfish outbreaks. PLoS One 19(4): e0298073. https://doi.org/10.1371/journal.pone.0298073

McCallum HI (1987) Predator regulation of *Acanthaster planci*. Journal of Theoretical Biology. 127(2):207-220. https://doi.org/10.1016/S0022-5193(87)80131-5

McCallum HI, Endean R, Cameron AM (1989) Sublethal damage to *Acanthaster planci* as an index of predation pressure. Marine Ecology Progress Series 56: 29–36.

Mellin C, Matthews S, Anthony KR, Brown SC, Caley MJ, Johns KA, Osborne K, Puotinen M, Thompson A, Wolff NH, Fordham DA (2019) Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. Global Change Biology 25(7): 2431-2445. https://doi.org/10.1111/gcb.14625

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 2:12 https://doi.org/10.3390/d9010012

Moran PJ (1986) The *Acanthaster* phenomenon. Oceanography and Marine Biology: An Annual Review 24: 379-480.

Newman S, Trinnie F, Roelofs A, Hughes J, Saunders T (2021) Status of Australian fish stocks reports: Spangled Emperor (2020). Fisheries Research and Development Corporation. https://www.fish.gov.au/report/363-Spangled-Emperor-2020

Ormond RF, Campbell AC (1973) Formation and breakdown of *Acanthaster planci* aggregations in the Red Sea. In Proceedings of the 2nd International Coral Reef Symposium, Brisbane, Australia, 22 June–2 July 1973; Cameron, A.M., Campbell, B.M., Cribb, A.B., Endean, R., Jell, J.S., Jones, O.A., Mather, P., Talbot, F.H., Eds.; Volume 1, pp. 595–619.

Ormond RF, Campbell AC, Head SH, Moore RJ, Rainbow PR, Saunders AP (1973) Formation and breakdown of aggregations of the crown-of-thorns starfish, *Acanthaster planci* (L.). Nature 246(5429): 167-169. https://doi.org/10.1038/246167a0

Pearson RG, Endean R (1969) A preliminary study of the coral predator *Acanthaster planci* (L.) (Asteroidea) on the Great Barrier Reef. Fisheries Notes, Queensland Department of Harbours and Marine 3:27-55.

Potts DC (1981) Crown-of-thorns starfish - man-induced pest or natural phenomenon? Pages 55-86. In: Kitching RL, Jones RE (eds) The Ecology of Pests – Some Australian Case Histories, CSIRO Publishing, Melbourne.

Pratchett MS, Chandler JF, Figueira W, Dubuc A, Caballes CF, Doll PC (2025a) Spatiotemporal variation in feeding behaviour of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*), including highly resolved estimated of daily consumption rates. A report to the Australian Government by the COTS Control Innovation Program.

Pratchett MS, Doll PC, Chandler JF, Doyle JR, Uthicke S, Dubuc A, Caballes CF (2025b) Early detection of renewed population irruptions of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*, COTS) on Australia's Great Barrier Reef. A report to the Australian Government by the COTS Control Innovation Program.

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. Marine Environmental Research 67: 230-236. https://doi:10.1016/j.marenvres.2009.03.001

Pratchett MS (2010) Changes in coral assemblages during an outbreak of *Acanthaster planci* at Lizard Island, northern Great Barrier Reef (1995–1999). Coral Reefs 29: 717–725. https://doi.org/10.1007/s00338-010-0602-9

Pratchett MS, Cumming GS (2019) Managing cross-scale dynamics in marine conservation: pest irruptions and lessons from culling of crown-of-thorns starfish (*Acanthaster* spp.). Biological Conservation 238: 108211. https://doi.org/10.1016/j.biocon.2019.108211

Pratchett MS, Caballes CF, Rivera-Posada JA, Sweatman HPA (2014) Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). Oceanography and Marine Biology: An Annual Review 52: 133–200.

Pratchett MS, Caballes CF, Cvitanovic C, Raymundo ML, Babcock RC, Doherty PJ, Doll PC, Doyle JR, Dworjanyn SA, Fabricius KE, Haywood MDE, Hock K, Hoggett A, 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 (2021a) Knowledge gaps in the biology, ecology and management of pacific crown-of-thorns starfish, *Acanthaster* cf. *solaris*, on Australia's Great Barrier Reef. Biological Bulletin 241(3):330-346. ttps://doi.org/10.1086/717026

Pratchett MS, Nadler LE, Burn D, Lang BJ, Messmer V, Caballes CF (2021b) Reproductive investment and fecundity of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) on the Great Barrier Reef. Marine Biology 168(6): 87. https://doi.org/10.1007/s00227-021-03897-w

Pratchett MS, Caballes CF, Burn D, Doll PC, Chandler JF, Doyle JR, Uthicke S (2022) Scooter-assisted large area diver-based (SALAD) visual surveys to test for renewed outbreaks of crown-of-thorns starfish (*Acanthaster* cf. *solaris*) in the northern Great Barrier Reef. A report to the Australian Government by the COTS Control Innovation Program (32 pp). https://www.barrierreef.org/uploads/CCIP-EIP-02-Early-Investment-Project-COTS-Surveys-Final-Report.pdf

Pratchett MS, Chandler JF, Choukroun SM, Doll PC, Lang BJ, Kwong S, Chen CC, Emslie MJ, Caballes CF, Uthicke S, Matthews SA (2024a) Biophysical processes involved in the initiation and spread of population irruptions of crown-of-thorns starfish on the Great

Barrier Reef. Pages 290-305. In: Wolanski E, Kingsford MH (eds) Oceanographic Processes of Coral Reefs, CRC Press, Boca Raton.

Pratchett MS, Doll PC, Chandler JF, Doyle JR, Uthicke S, Dubuc A, Caballes CF (2024b) Early detection of renewed population irruptions of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) on Australia's Great Barrier Reef. A report to the Australian Government by the COTS Control Innovation Program.

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rivera-Posada J, Caballes CF, Pratchett MS (2014a) Size-related variation in arm damage frequency in the crown-of-thorns sea star, *Acanthaster planci*. Journal of Coastal Life Medicine 2: 187–195.

Rivera-Posada J, Pratchett MS, Aguilar C, Grand A, Caballes CF (2014b) Bile salts and the single-shot lethal injection method for killing crown-of-thorns sea stars (*Acanthaster planci*). Ocean & Coastal Management 102: 383-390. https://doi.org/10.1016/j.ocecoaman.2014.08.014.

Sala E, Giakoumi S (2018) No-take marine reserves are the most effective protected areas in the ocean. ICES Journal of Marine Science 75: 1166-1168. https://doi.org/10.1093/icesjms/fsx059

Sweatman HPA (1995) A field study of fish predation on juvenile crown-of-thorns starfish. Coral Reefs 14: 47–53. https://doi.org/10.1007/BF00304071

Sweatman HPA (2008) No-take reserves protect coral reefs from predatory starfish. Current Biology 18(14):R598-599. https://doi.org/10.1016/j.cub.2008.05.033

Uthicke S, Schaffelke B, Byrne M (2009) A boom–bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. Ecological Monographs 79(1):3-24. https://doi.org/10.1890/07-2136.1

Uthicke S, Doyle JR, Gomez Cabrera M, Patel F, McLatchie MJ, Doll PC, Chandler JF, Pratchett MS (2024) eDNA monitoring detects new outbreak wave of corallivorous seastar (*Acanthaster* cf. *solaris*) at Lizard Island, Great Barrier Reef. Coral Reefs https://doi.org/10.1007/s00338-024-02506-8

Vine PJ (1973) Crown of thorns (*Acanthaster planci*) plagues: the natural causes theory. Atoll Research Bulletin. 1973: 1-13.

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. Scientific Reports 10(1):12594. https://doi.org/10.1038/s41598-020-69466-1

Wickham H (2016) *ggplot2*: Elegant Graphics for Data Analysis. Springer-Verlag New York. https://ggplot2.tidyverse.org.

Wickler W, Seibt U (1970) Das Verhalten von *Hymenocera picta* Dana, einer Seesterne fressenden Garnele (Decapoda, Natantia, Gnathophyllidae). Zeitschrift fur Tierpsychologie 27: 352-368.

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.). Marine Pollution Bulletin 135: 332-345. https://doi.org/10.1016/j.marpolbul.2018.07.006

Wilmes JC, Hoey AS, Pratchett MS (2020) Contrasting size and fate of juvenile crown-of-thorns starfish linked to ontogenetic diet shifts. Proceedings of the Royal Society B 287: 20201052. https://doi.org/10.1098/rspb.2020.1052

Wilson SK, Graham NA, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Global Change Biology 12: 2220-2234. https://doi.org/10.1111/j.1365-2486.2006.01252.x

Wilson SK, Graham NA, Polunin NV (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Marine Biology 151(3): 1069-1076. https://doi.org/10.1007/s00227-006-0538-3

Wolfe K, Desbiens AA, Uthicke S, Patel F, Dworjanyn S, Riginos C, Byrne I, Fisher E, Mumby PJ (2025) Resolving the impact of benthic and cryptic predation on crown-of-thorns starfish (COTS). A report to the Australian Government by the COTS Control Innovation Program.
Wooldridge SA, Brodie JE (2015) Environmental triggers for primary outbreaks of crown-of-thorns starfish on the Great Barrier Reef, Australia. Marine Pollution Bulletin 101(2): 805-815. https://doi.org/10.1016/j.marpolbul.2015.08.049

Young MAL, Bellwood DR (2011) Diel patterns in sea urchin activity and predation on sea urchins on the Great Barrier Reef. Coral Reefs 30: 729-736. https://doi.org/10.1007/s00338-011-0754-2

Dr Peter Doll
College of Science and Engineering
James Cook University
peter.doll@jcu.edu.au

Prof Morgan Pratchett
College of Science and Engineering
James Cook University
morgan.pratchett@jcu.edu.au

COTS Control Innovation Program | A research and development partnership to better predict, detect and respond to crown-of-thorns starfish outbreaks

Australian Government
REEF TRUST
Great Barrier Reef Foundation
AUSTRALIAN INSTITUTE OF MARINE SCIENCE
CSIRO
JAMES COOK UNIVERSITY AUSTRALIA
THE UNIVERSITY OF QUEENSLAND AUSTRALIA