



Dead foundation species create coral rubble habitat that benefits a resilient pest species

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ABSTRACT

Critical loss of habitat is the greatest threat to biodiversity, yet some species are inherently plastic to and may even benefit from changes in ecosystem states. The crown-of-thorns sea star (CoTS; *Acanthaster* spp.) may be one such organism. CoTS are large corallivores native to the tropical Indo-Pacific and in unexplained high densities, can adversely affect entire coral reefs. Proximal causes of CoTS outbreaks remain elusive, so this phenomenon remains a daunting and costly challenge for reef conservation and management. Amplifying anthropogenic impacts and new empirical data point to the *degraded reef hypothesis* to explain the episodic nature of CoTS population outbreaks. We posit that loss of live coral paradoxically benefits CoTS juveniles, which accumulate in their rubble nursery habitat before conditions trigger their pulsed emergence as coral-eaters. We review trait plasticity across the CoTS life cycle and present the *degraded reef hypothesis* in an integrative understanding of their propensity to outbreak.

1. Resilience in degraded foundation habitat

Degradation and critical loss of habitat pose great threats to terrestrial and marine biodiversity (Brooks et al., 2002). In the marine environment, anthropogenic impacts on foundation species (e.g., oysters, corals, kelp) have cascading impacts on ecosystem structure and functioning (Wernberg et al., 2023). However, even dead foundation species provide crucial habitat (Barnhill et al., 2022; Engleman et al., 2023; Saldaña et al., 2023), and species able to adapt rapidly to altered ecosystem states can proliferate, as seen for synanthropic animals (e.g., cockroaches, crows, rats) in terrestrial environments (Shochat et al., 2006; Alberti et al., 2017). Species with stress resistance and plastic traits will have the upper hand in adjusting to altered habitat states to persist and thrive in the Anthropocene (Watson 2018; Thomas 2020).

For coral reefs, intensifying local and global stressors have profound impacts on community structure (Wolff et al., 2015; Morais et al., 2020). Many reefs have reached a tipping point where coral mortality outpaces recovery (Hughes et al., 2018), driving shifts toward alternate ecosystem states (Hughes 1994) and homogenisation of the reef framework through accumulation of coral rubble (Alvarez-Filip et al., 2009). As the remains of a foundation species (Barnhill et al., 2022; Saldaña et al., 2023), coral rubble helps to mediate ecosystem stability,

resilience, and transitions in structural and trophic dynamics (Wolfe et al. 2021, 2023b; Engleman et al., 2023). While coral degradation has major repercussions for live-coral dependant species (Jones et al., 2004; Stella et al., 2011; Rice et al., 2019), species that are inherently plastic and robust are likely to benefit and thrive. Many small organisms with rapid population cycles proliferate in dead coral and rubble where they avail of novel resources and microhabitat complexity (Fraser et al., 2021; Wolfe et al., 2023b). In addition, many organisms including corals, use rubble as a settlement and juvenile nursery habitat (Wolfe et al., 2021; Kenyon et al., 2023). As a result, and somewhat counter-intuitively, dead coral and rubble can host the greatest metazoan biodiversity on coral reefs (Enochs 2012; Stella et al., 2022). Species adapted to life in rubble may be winners in the future reef stakes, and help to buffer biodiversity loss and maintain nutrient and energy pathways as the living coral framework declines (Wolfe et al., 2023b).

2. The CoTS phenomenon

Crown-of-thorns sea stars (CoTS; *Acanthaster* spp.) are keystone coral predators that exhibit boom-bust population dynamics (Uthicke et al., 2009). They can exceed 10,000 individuals km² during unexplained outbreaks, which are a major cause of coral decline across the

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Indo-Pacific (Pratchett et al., 2014). Identification of the drivers of CoTS outbreaks is crucial to inform conservation and management to promote reef survival in the Anthropocene (Westcott et al., 2016; Pratchett and Cumming 2019). While the biology and ecology of *Acanthaster* have received intense interest (Pratchett et al. 2014, 2021a), the cause(s) of outbreaks remain elusive.

Proximal drivers of outbreaks have been debated for decades with hypotheses focused on anthropogenic impacts on the larval (*nutrient runoff hypothesis*) and adult (*predator removal hypothesis*) stages receiving most traction. The former hypothesis posits that elevated nutrients from eutrophic runoff generates phytoplankton blooms that enhance larval survival and settlement success (Birkeland 1982; Lucas 1982). The latter hypothesis posits that overfishing of predators alleviates top-down control of CoTS (Endean 1969; Dulvy et al., 2004). Evidence for these hypotheses remains largely equivocal and are derived from studies of the Pacific species, *A. cf. solaris*, in Australia and Japan (Pratchett et al., 2014). However, *Acanthaster* is taxonomically diverse (Vogler et al., 2008; Uthicke et al., 2023; Foo et al., 2024) and so applicability of these hypotheses with respect its broad Indo-Pacific distribution is unknown. A more holistic understanding of *Acanthaster* across all life stages, species, and their ranges is required.

For outbreaks of CoTS to occur, all life stages must be successful. As reviewed here, new empirical data on the early juvenile provide novel perspectives on CoTS population dynamics as reef degradation amplifies, pointing to the need to reconsider hypothetical models of outbreaks. How reef degradation contributes to and potentially amplifies CoTS success needs to be resolved (Wilmes et al., 2018; Pratchett and Cumming 2019). We posit the *degraded reef hypothesis* as an explanation of the pulsed nature of CoTS outbreaks. In this scenario, reef degradation

driven by local and global stressors (1) reduces live coral cover and increases dead coral, thereby increasing (2) the rubble recruitment habitat of CoTS larvae and (3) the rubble nursery habitat and algal food of the juveniles, and (4) in the absence of coral prey, multiple cohorts of herbivorous juveniles accumulate waiting for coral to recover (Deaker et al., 2020a; Deaker and Byrne 2022). Concurrently, a density-dependant feedback mechanism mediated by semiochemistry from adults may deter juveniles from switching to corallivory (Webb et al., 2024).

The *degraded reef hypothesis* posits that juveniles accumulate in the reef rubble until sufficient coral resources and/or adult competition is released. Thus, as adult outbreaks wane, cohorts of juveniles released from interference competition and given access to live coral serve as the proximate cause of episodic pulses of CoTS that emerge on the reef. Importantly, the *degraded reef hypothesis* integrates previous hypotheses, which we outline here to build a more holistic understanding of CoTS outbreaks.

3. Resilience of CoTS ontogeny across life stages in multiple habitats

Understanding nuances in the biology and ecology of CoTS is crucial to inform management of how to mitigate the drivers and impacts of outbreaks. Indisputably, CoTS are remarkable animals. The life cycle of CoTS is complex and involves a series of stages that occupy distinct habitats. Novel resilience and plastic traits associated with each life stage adds to the arsenal and tolerance of CoTS through stochastic environmental scenarios (Fig. 1), which empowers their success (Deaker and Byrne 2022).

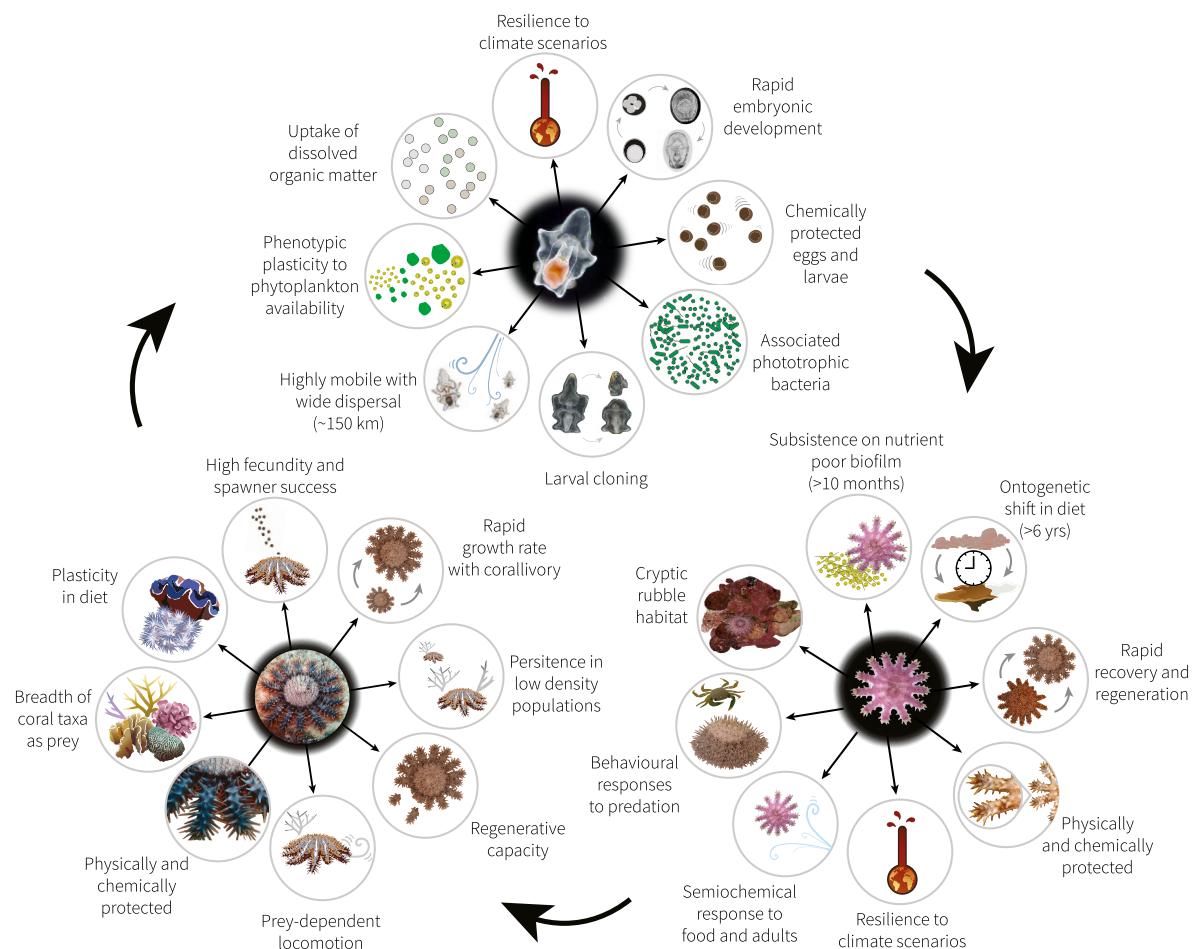


Fig. 1. Biological and ecological traits that contribute to the inherent resilience of CoTS across its ontogeny.

CoTS are highly fecund with large females producing >200 million eggs y^{-1} (Pratchett et al., 2021b). The planktotrophic larvae are robust to variations in phytoplankton levels ranging from starvation to satiation (Okaji et al., 1997; Wolfe et al., 2015b; Pratchett et al., 2017) with high food availability suggested to enhance their success (Fabricius et al., 2010); the *enhanced nutrients hypothesis*. However, CoTS larvae are resilient to oligotrophy (low nutrients) in their ability to (1) exhibit phenotypic plasticity by increasing the length of their feeding structures to avail of scarce resources (Wolfe et al., 2015a), (2) feed on alternate food sources, such as bacteria and dissolved organic matter (Olson 1987; Nakajima et al., 2016; Mos et al., 2024), and (3) host an autotrophic microbiome that may aid larval metabolic functioning (Carrier et al., 2018). CoTS larvae also clone, which may increase larval supply and dispersal, and may help maintain population levels to compensate for mortality (Allen et al., 2019). This artillery of traits contributes to the resilient nature of CoTS larvae (Fig. 1). Consequently, the rationale underpinning the *nutrient runoff hypothesis* is equivocal and links between runoff events and outbreaks remain tenuous (Wolfe et al., 2017; Clements et al., 2022; Kroon et al., 2023).

Post-settlement, CoTS begin their benthic life as tiny herbivorous sea stars typically hidden in coral rubble (Fig. 2), making them difficult to detect and study (Johnson et al., 1992; Wilmes et al., 2020b). Their preferred food is crustose coralline algae (CCA) (Doll et al., 2023a), which are abundant in rubble biomes (Wolfe et al., 2021). When coral prey is available, juveniles make the switch to a coral diet 4–12 mo post-settlement (Yamaguchi 1974; Zann et al., 1987; Deaker et al., 2020b), depending on coral species (Neil et al., 2022). As for the larvae, CoTS juveniles are extremely resilient to food scarcity and can persist for years on low energy food such as biofilm (Fig. 1). This diet plasticity allows for growth stasis and delays in the transition to corallivory (Box 1) likely modulated by food availability (Deaker et al., 2020a; Neil et al., 2022) and density dependant mechanisms (Box 2). Juveniles have physical defences and have protective responses to predators that enhance their survival (Deaker et al. 2021a, 2021b). Behavioural and phenotypic plasticity in the early benthic juvenile (Fig. 1) is the basis of the *juveniles in waiting hypothesis* (Deaker et al., 2020a), which posits that cohorts of juveniles build up in the reef infrastructure as a “hidden army” over multiple recruitment years to serve as a proximate source of cyclic CoTS outbreaks (Fig. 2).

Adult CoTS also have a suite of resilience traits (Fig. 1). Following their ontogenetic transition from herbivore to corallivore, CoTS exhibit rapid growth supported by their energy-rich coral diet (Fig. 2; Lucas 1984; Zann et al., 1987). Adults exhibit diet plasticity, preying on

diverse coral species, consuming alternate prey (e.g., soft corals, bivalves, algae) when coral declines (Yamaguchi 1975; Keesing 1990; Kuo et al., 2022), and exhibiting prey-dependent migration ($\sim 20 \text{ m day}^{-1}$) to aggregate around preferred species as coral declines (Ling et al., 2020). Adult CoTS upregulate immune responses which may counter pathogen transmission at high density (i.e., outbreaks; Mills 2012), and are physically and chemically defended, so predation risk is low and restricted to a few specialists (Cowan et al., 2017). However, many adults and juveniles show signs of predation (e.g., missing arms) (McCallum et al., 1989; Budden et al., 2019) and traces of CoTS eDNA in fish gut contents (Kroon et al., 2020) provide evidence of predation. Reefs protected from fishing are less prone to outbreaks (Dulvy et al., 2004; Kroon et al., 2021), adding support to the *predator removal hypothesis*. However, evidence of predation on live adult CoTS is sparse (Cowan et al., 2017). Predator-induced impacts on CoTS populations may be tightly linked to the juvenile stage in rubble (see Caveat 1) (Desbiens et al., 2023), as mortality at early life stages can have disproportionate effects on CoTS population size and outbreak potential (Keesing and Halford 1992b; Morello et al., 2014; Wilmes et al., 2018).

4. The degraded reef hypothesis: feedback between coral, CoTS and climate change

As live coral cover declines due to coral bleaching mortality and other stressors (e.g., cyclones, CoTS outbreaks), the parallel increase in structural erosion of these foundation species to rubble occurs (Sano et al., 1987; Alvarez-Filip et al., 2009). Rubble is a natural biome on coral reefs (Wolfe et al., 2021; Kenyon et al., 2023) and serves as the larval recruitment and juvenile nursery habitat of CoTS, providing early life stages with shelter and food (Wilmes et al., 2020b). In context of the *degraded reef hypothesis*, CoTS may benefit from increases in larval settlement cues and juvenile nursery habitat generated by amplified coral mortality (Fig. 3). This enhanced recruitment dynamic would be expedited by a reduction in coral polyps and planktivorous fishes (Sano et al., 1987), predators that modulate CoTS larval settlement and survival (Cowan et al. 2016a, 2016b, 2017).

Ocean heating is the dominant cause of reef degradation in the Anthropocene (Hughes et al., 2018). Consequent coral decline impacts all reef associated organisms, although species' responses vary. Thus, to assess the *degraded reef hypothesis*, the fate of both corals and CoTS in a changing climate must be considered. Mass bleaching mortality eliminates the main food of CoTS adults, imperilling CoTS populations. However, as above, adult CoTS exhibit diet plasticity and aggregate

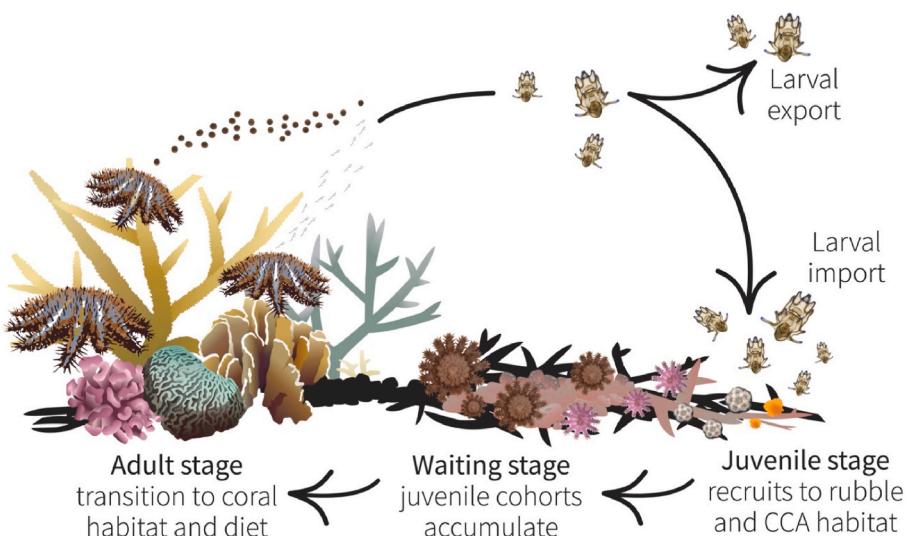


Fig. 2. The life cycle of CoTS involves a series of distinct stages with novel diets and habitat occupancy, including juvenile accumulation in coral rubble nursery habitat.

Box 1

Ontogenetic dietary transition in the early benthic juvenile

In predatory sea stars, juvenile plasticity with respect to environmental conditions contributes to their success (Nauen 1978; Ebert 1996; Byrne et al., 2023). This occurs in nature for *Marthasterias glacialis* and *Asterias rubens*, which delay their transition to the adult habitat and diet depending on prey availability (Nauen 1978), potentially balancing population density with respect to resource availability (Byrne et al., 2021). Juvenile sea stars can have a waiting stage (>6 years) in nature before switching to the adult diet, habitat and maturity (Byrne et al., 2021).

In CoTS, low availability of preferred prey can slow the transition of juveniles to the coral-feeding adult stage and maturity (Deaker et al., 2020b; Neil et al., 2022); the ‘Peter Pan’ phenomenon. In the absence of coral prey, juveniles can persist as herbivores (6.5 years in aquaria) in a prolonged growth stasis (Deaker et al., 2020a, 2020b; Wilmes et al., 2020a). In a scenario of low coral availability, including post-bleaching or outbreak disturbance, juvenile COTS have the potential to accumulate over recruitment events (i.e., years) before transitioning to corallivory. The broad size range of juveniles found in nature (Zann et al., 1987; Wilmes et al., 2020a) indicates such accumulation may occur, providing support to the *juvenile in waiting* (Deaker et al., 2020a) and *degraded reef* hypotheses. The age-size disconnect that comes with growth stasis must be resolved (see Caveat 2), to determine whether these ‘Peter Pans’ serve as a proximate driver of the pulsed nature of CoTS eruptions on the reef.

Box 2

Density-dependent transition and interference competition

In the marine environment, intra- and inter-specific chemical communication can modulate population and community structure (Hay 2009). Sea stars regularly respond to chemical cues that signal prey availability, predator presence, mature mates and settlement/nursery habitat (Motti et al., 2018) including CoTS (Beach et al., 1975; Ormond et al., 1976; Ling et al., 2020; Doll et al., 2023a). Adult interference competition, potentially conveyed by semiochemical cues, can be a selective force in the migration of juveniles from their nursery habitat (Moksnes 2004), as seen in the density-dependent ontogenetic transitions observed in predatory sea stars (Nauen 1978; Byrne et al., 2021).

CoTS juveniles exhibit avoidance in response to semiochemical cues from adults (Webb et al., 2024). Thus, the delay in juvenile transition to the adult stage may be coupled with a negative density-dependent feedback mediated by semiochemical communication (Byrne et al., 2023). Juveniles may delay their transition to corallivory to avoid competition for food, especially if adult density is high (i.e., outbreak populations). Conspecific chemical cues do not impair CoTS larval settlement to rubble (Doll et al., 2023b). Thus, reserve populations (“armies”) of juvenile CoTS may accumulate in rubble over successive recruitment periods until adult competition wanes and/or sufficient availability of live coral triggers their switch to corallivory (Deaker et al., 2020a), prompting rapid juvenile and population growth into outbreaks (Wilmes et al., 2016). This scenario may help to explain why some reefs require recurring voyages by culling teams to achieve sustained, reliable reductions of CoTS densities, especially involving small individuals (Westcott et al., 2020).

around surviving corals (Keesing et al., 2019), which would amplify coral decline and generation of rubble, supporting the *degraded reef hypothesis* feedback loop (Fig. 3). Such aggregations would increase CoTS reproductive success through enhanced Allee effects (Rogers et al., 2017) while abrupt increases in temperature during warming events can cause synchronous spawning (Caballes et al., 2021), with both mechanisms enhancing the reproductive capacity of CoTS to promote outbreaks.

As for their coral prey, adult CoTS are physiologically sensitive to increased temperature (Lang et al., 2022). In contrast, the larvae (Uthicke et al., 2015; Lang et al., 2023) and juveniles (Kamya et al., 2018; Byrne et al., 2023) are more resistant, which may be imprinted in the progeny of warm-adapted parents (Hue et al., 2022). In a warming world, juvenile CoTS may benefit from an increase in framework erosion to rubble following coral mortality (Alvarez-Filip et al., 2009), with the potential to survive heatwaves, subsist as herbivores within the rubble benthos, and accumulate in the ‘Peter Pan’ waiting phase until live coral recovers (Byrne et al., 2023). Recovery rates of coral from rubble states vary from years to decades based on the type, frequency and extent of disturbance (Kenyon et al., 2023). How juveniles persist in and respond to rubble of varying typologies requires attention, as high juvenile survival must be sustained to seed outbreaks while a prolonged waiting phase would be challenged by exogenous factors such as predation risk (see Caveat 1) and food availability (see Caveat 3).

While CoTS outbreaks may be less frequent on degraded reefs due to low cover of live coral prey (Pratchett et al., 2014), the *degraded reef hypothesis* posits that outbreaks will remain a threat to coral reefs due to

a negative feedback loop as reefs degrade (Fig. 3). In nature, ~90% of CoTS juveniles are found among dead reef structure (Wilmes et al., 2020b) where they are primed to generate waves of outbreak populations. Juveniles may accumulate in the benthos as herbivores until coral recovers to a density that triggers the switch to corallivory. It seems paramount to determine this trigger level, along with dietary profiles of juveniles and their predators in rubble.

5. Integration with long-standing hypotheses

The *degraded reef hypothesis* is not an exclusive explanation of CoTS outbreaks. The remarkable resilience and adaptability of CoTS to environmental stochasticity underpins their success (Deaker and Byrne 2022). We posit that a suite of amplifying and interacting anthropogenic stressors contribute to CoTS success (Fig. 3). For example, the catalyst of the *enhanced nutrients hypothesis* is a decline in water quality, conditions to which CoTS larvae show high resilience (Wolfe et al., 2017; Kroon et al., 2023). For the *predator removal hypothesis*, high fishing pressure can increase the susceptibility of reefs to CoTS outbreaks (Dulvy et al., 2004; Kroon et al., 2021). Thus, habitat degradation and alterations to community and trophic structure work in concert with the *degraded reef hypothesis*, complimenting long-standing hypotheses to explain CoTS outbreaks (Fig. 3).

It is unlikely that a single ‘one size fits all’ hypothesis (i.e., one that fits in all instances) applies to the *Acanthaster* outbreak phenomenon across species and their ranges. A multitude of interacting factors are likely to contribute to CoTS success with the relative contribution of

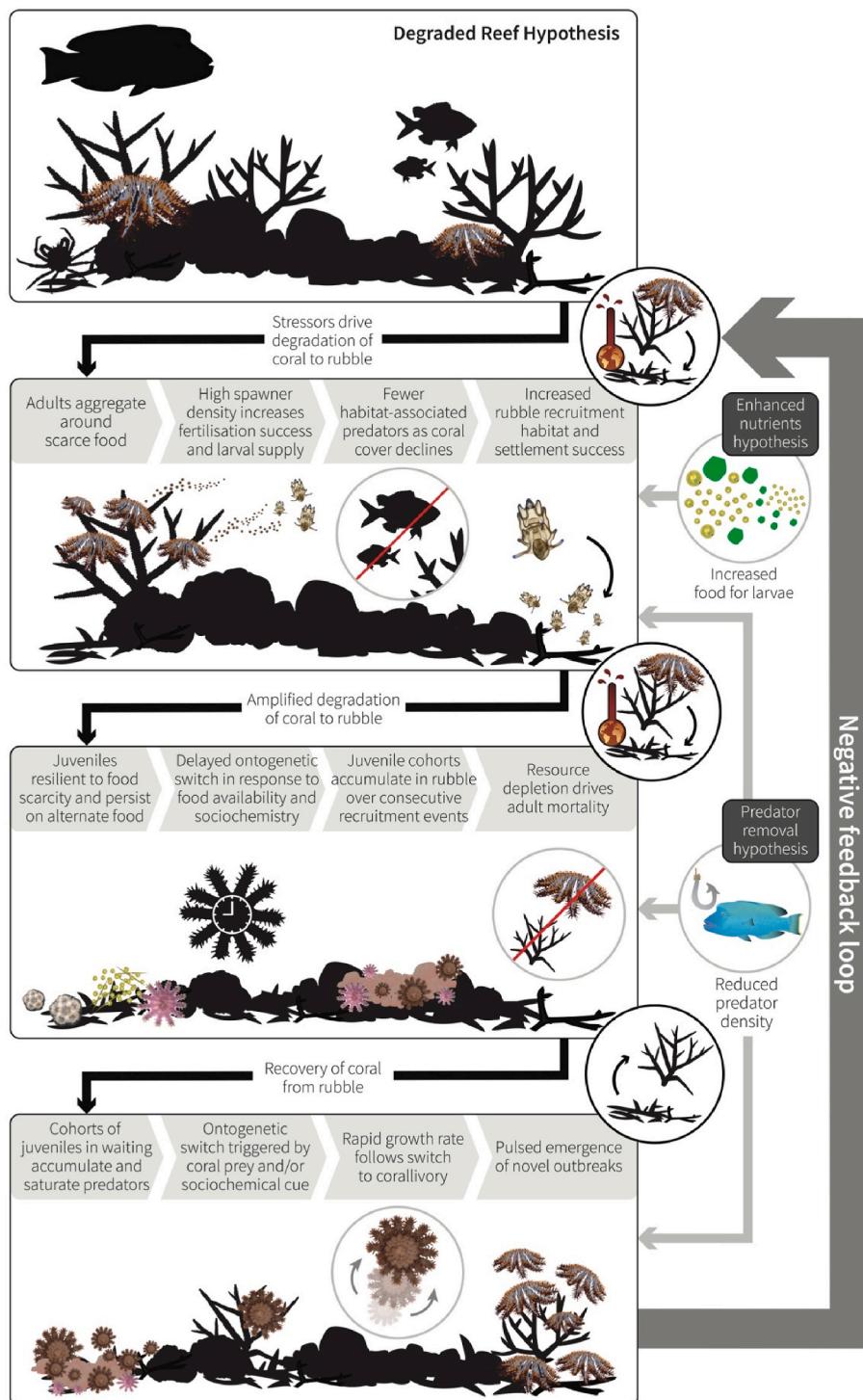


Fig. 3. Schematic representation of the *degraded reef hypothesis* to provide a systemic explanation of CoTS population outbreaks, including relevance to existing hypotheses and the negative feedback loop that exacerbates reef degradation.

each factor expected to vary at reef and regional scales and CoTS life-stage habitat. Holistic consideration of how CoTS respond to events and disturbances across their ontogeny provides a much deeper appreciation of their biology, plasticity, and the multifaceted nature of outbreak generation. Previous hypotheses have overlooked the resilience of CoTS across all life history stages and their tolerance to environmental stochasticity (Fig. 1), which the *degraded reef hypothesis* is the first to encapsulate and likely applies across *Acanthaster* species, though this is yet to be evaluated.

6. Evidence for the *degraded reef hypothesis*

- (1) *Adult behaviour amplifies structural erosion to degraded reefs:* Aggregation around remaining coral amplifies reef degradation.
- (2) *Increased settlement habitat and success in degraded reefs:* Amplified rubble generation and reduced larval predators benefit CoTS settlement and post-larval success in nursery habitat.
- (3) *Increased juvenile habitat and delayed transition:* Juvenile CoTS can live as herbivores for years and may paradoxically benefit from

- generation of rubble, accumulating over multiple cohorts; an underappreciated driver of CoTS outbreaks.
- (4) *Juvenile resilience to warming and climate feedback:* CoTS juveniles are resilient to heatwave conditions that bleach and kill corals with heat-adapted progeny adding to the resilience of future generations.
 - (5) *Rapid growth rates post-transition to corallivory:* Irruptions of CoTS in high densities from juvenile reserves is driven by rapid growth as coral predators.

7. Caveats

(1) Predation limitations and risk of an extended juvenile phase

Predation is a major bottleneck for post-larval CoTS (Keesing and Halford 1992b; Wilmes et al., 2018), so a prolonged juvenile phase may be risky. A diversity of predators consume juvenile CoTS in rubble (Desbiens et al., 2023) and benthic predator density may be inversely correlated to adult CoTS density (Wolfe et al., 2023a). However, most known predators of juvenile CoTS have low rates of predation and contribute more to injury than total consumption (Desbiens et al., 2023). Sublethal injury is likely to extend the waiting period, and thus exposure to secondary predation (Glynn 1984) while juveniles invest in recovery (Deaker et al. 2021a, 2021b). That 90% of juveniles found in rubble and dead coral show signs of sublethal predation demonstrates not only their susceptibility as prey, but their remarkable survival and regenerative capacity (Wilmes et al., 2019). While mortality rates of newly settled juveniles are estimated to reduce their population by $\sim 5\% \text{ d}^{-1}$ (Keesing and Halford 1992a), juvenile CoTS have an array of defensive behavioural responses to predators (Zann et al., 1987). Additionally, their toxicity may increase with age providing chemical defence during the waiting phase, though this remains to be determined, including whether scarce resources are selectively allocated to growth or chemical defence.

(2) Detecting accumulations of juveniles in nature

Juvenile CoTS in nature vary in size (Zann et al., 1987; Wilmes et al., 2020a) and given their capacity to exhibit growth stasis (Deaker et al., 2020a; Neil et al., 2022), are likely to be highly variable in age. To understand the potential of juveniles in waiting to contribute to CoTS outbreaks, cohorts of juveniles of a known age need to be tracked in nature, as done for other sea stars (Nauen 1978; Byrne et al., 2021). However, the ability to detect accumulations of CoTS juveniles over successive recruitment events in nature is challenging due to their cryptic rubble habitat. The marked age-size disconnect that comes with growth stasis hinders our capacity to predict their age in the wild based on size alone (Mead 1900; Barker and Nichols 1983). We urgently need methods to determine CoTS age, perhaps through morphological (e.g., tetracycline tagging; Stump and Lucas 1990), molecular (e.g., telomere length; Kwong et al., 2023) or epigenetic (e.g., DNA methylation) approaches, the latter of which has never been used in asteroids but has been highlighted as very useful tool for aging organisms (see: Yu et al., 2019; Parsons et al., 2023). The ability to accurately age juvenile cohorts will be a key tool in early detection of outbreak populations as juveniles accumulate in the rubble benthos.

(3) Susceptibility of CCA to stressors

While CoTS juveniles appear resilient to temperature in their waiting phase (Byrne et al., 2023), their CCA settlement cue and juvenile food source is susceptible to ocean change (Diaz-Pulido et al., 2012; Lang et al., 2023). How plastic the larvae and juveniles are to projected declines in CCA in a future ocean requires attention. That said, CoTS larvae settle to a range of coralline algal species (Doll et al., 2023a) and in the absence of CCA (Wolfe et al., 2015b), the juveniles avail of alternate food sources (Deaker et al., 2020b). In addition, some species of

coralline algae are tolerant of warming (Cornwall et al., 2019).

8. Management implications

Undeniably, CoTS outbreaks will continue to occur. If reef degradation promotes CoTS populations, management that holistically protects coral reef communities would be expected to increase resilience to outbreaks, as shown in protected (no-take) marine zones on the Great Barrier Reef (Westcott et al., 2020). Such natural pathways of resilience should be prioritised.

Manual culling of adults has been central to CoTS management across the Indo-Pacific at great cost (Pratchett et al., 2014), but with limited broad-scale success in suppressing CoTS densities or preventing coral loss (Endean 1969; Yamaguchi 1986; Pratchett and Cumming 2019; Pratchett et al., 2019). The *degraded reef hypothesis* suggests that physical mass-removal of adults may counterintuitively promote population productivity by releasing juveniles of adult competition, thereby facilitating the next generation to emerge; a catch-22 in marine management. The requirement of culling operators to conduct multiple expeditions to individual reefs to eradicate CoTS points to the presence of a reservoir of small CoTS undetected in the reef infrastructure (Westcott et al., 2020). Continual culling therefore becomes necessary as cohorts of juveniles emerge as coral-eaters. The apparent dependence on culling to minimise CoTS invasions may impede upon natural fluxes between coral recovery and CoTS predation, which were previously thought to promote coral diversity (Porter 1972) as an intermediate disturbance (Done et al., 1997). We posit here that this is exacerbated by reef decline in the Anthropocene, which has generated a path dependency in the perpetuity of manual control. Management innovations that target juveniles in rubble are likely to be effective in early suppression of outbreaks with knock-on benefits to reef resilience and recovery.

Failure to detect early stages of CoTS outbreaks prevents timely and efficient intervention (Pratchett and Cumming 2019). Surveillance of the early benthic life stage in the rubble is needed to gain a more comprehensive understanding of the “waiting stage” and age-size discrepancies (see Caveat 2). Given the difficulties sampling and surveying rubble biota (Wolfe et al., 2021), novel technologies will be needed to detect CoTS juveniles beyond manual searches. For example, eDNA has been used to detect larvae in the plankton (Uthicke et al., 2018). A similar approach could be used to detect juveniles and their predators in rubble to begin documenting relationships between habitat availability, predator distributions, and juvenile success.

9. Conclusions

Most research on CoTS outbreaks occurs in well-funded regions, largely guided by single causes hypotheses (larval nutrition, adult predation). Long-term solutions require a more holistic consideration of the multiple facets underlying CoTS outbreaks (Figs. 1 and 2), which the *degraded reef hypothesis* (Fig. 3) is the first to consider. In this complex world, there are likely to be many interacting factors that contribute to the success of CoTS. Most importantly, the inherently plastic biological traits of CoTS are likely to be the ‘secrets’ to their success and require attention (Box 3). In a changing climate, CoTS population resilience responds well to, and likely even benefits from, degrading reef condition and environmental stochasticity. From issues stemming from water quality, altered food webs, and reef degradation, the response of CoTS is rapid and adaptive. Management aiming to conserve coral reefs must consider CoTS not as a single issue, but as a symptom of ongoing environmental impacts that requires a broad response with knock-on benefits to reef ecosystems and their inhabitants (Pratchett and Cumming 2019).

Competing research statement

The authors declare no competing interests.

Box 3**Outstanding questions**

1. What triggers the transition (and delays) of juveniles to the coral-eating adult stage with respect to coral availability or density-dependent semiochemistry?
2. How do semiochemicals influence CoTS feeding, reproduction and ontogeny, including in context of potential management strategies involving push-pull methods?
3. Do juveniles exhibit nuanced feeding and transition responses with respect to coral availability and community structure, as observed for adults?
4. Does culling adults reinforce outbreaks by releasing juveniles from adult competition?
5. Have outbreaks historically occurred on reefs more prone or exposed to rubble generation, or reefs with higher rubble cover?

CRediT authorship contribution statement

Kennedy Wolfe: Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Maria Byrne:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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