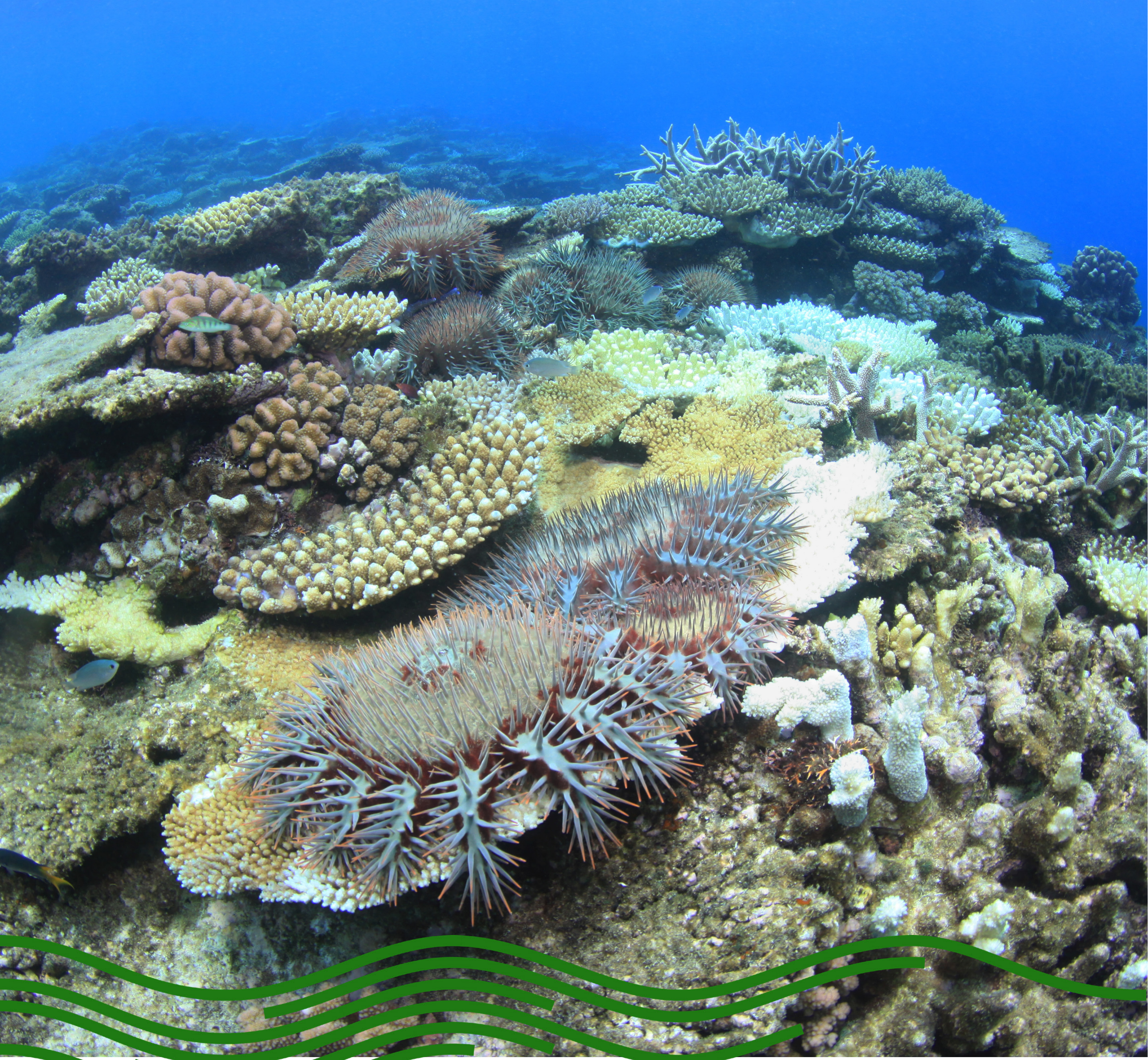

2022 Scientific Consensus Statement

Question 4.3 What are the key drivers of the population outbreaks of crown-of-thorns starfish (COTS) on the Great Barrier Reef, and what is the evidence for the contribution of nutrients from land runoff to these outbreaks?

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Cover image credit: Ciemon Caballes.

Explanatory Notes for readers of the 2022 SCS Syntheses of Evidence

These explanatory notes were produced by the SCS Coordination Team and apply to all evidence syntheses in the 2022 SCS.

What is the Scientific Consensus Statement?

The Scientific Consensus Statement (SCS) on land use impacts on Great Barrier Reef (GBR) water quality and ecosystem condition brings together scientific evidence to understand how land-based activities can influence water quality in the GBR, and how these influences can be managed. The SCS is used as a key evidence-based document by policymakers when they are making decisions about managing GBR water quality. In particular, the SCS provides supporting information for the design, delivery and implementation of the Reef 2050 Water Quality Improvement Plan (Reef 2050 WQIP) which is a joint commitment of the Australian and Queensland governments. The Reef 2050 WQIP describes actions for improving the quality of the water that enters the GBR from the adjacent catchments. The SCS is updated periodically with the latest peer reviewed science.

C_2O Consulting was contracted by the Australian and Queensland governments to coordinate and deliver the 2022 SCS. The team at C_2O Consulting has many years of experience working on the water quality of the GBR and its catchment area and has been involved in the coordination and production of multiple iterations of the SCS since 2008.

The 2022 SCS addresses 30 priority questions that examine the influence of land-based runoff on the water quality of the GBR. The questions were developed in consultation with scientific experts, policy and management teams and other key stakeholders (e.g., representatives from agricultural, tourism, conservation, research and Traditional Owner groups). Authors were then appointed to each question via a formal Expression of Interest and a rigorous selection process. The 30 questions are organised into eight themes: values and threats, sediments and particulate nutrients, dissolved nutrients, pesticides, other pollutants, human dimensions, and future directions, that cover topics ranging from ecological processes, delivery and source, through to management options. Some questions are closely related, and as such readers are directed to Section 1.3 (Links to other questions) in this synthesis of evidence which identifies other 2022 SCS questions that might be of interest.

The geographic scope of interest is the GBR and its adjacent catchment area which contains 35 major river basins and six Natural Resource Management regions. The GBR ecosystems included in the scope of the reviews include coral reefs, seagrass meadows, pelagic, benthic and plankton communities, estuaries, mangroves, saltmarshes, freshwater wetlands and floodplain wetlands. In terms of marine extent, while the greatest areas of influence of land-based runoff are largely in the inshore and to a lesser extent, the midshelf areas of the GBR, the reviews have not been spatially constrained and scientific evidence from anywhere in the GBR is included where relevant for answering the question.

Method used to address the 2022 SCS Questions

Formal evidence review and synthesis methodologies are increasingly being used where science is needed to inform decision making, and have become a recognised international standard for accessing, appraising and synthesising scientific information. More specifically, ’evidence synthesis’ is the process of identifying, compiling and combining relevant knowledge from multiple sources so it is readily available for decision makers[1]. The world’s highest standard of evidence synthesis is a Systematic Review, which uses a highly prescriptive methodology to define the question and evidence needs, search for and appraise the quality of the evidence, and draw conclusions from the synthesis of this evidence.

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[1] Pullin A, Frampton G, Jongman R, Kohl C, Livoreil B, Lux A, ... & Wittmer, H. (2016). Selecting appropriate methods of knowledge synthesis to inform biodiversity policy. *Biodiversity and Conservation*, 25: 1285-1300. https://doi.org/10.1007/s10531-016-1131-9

In recent years there has been an emergence of evidence synthesis methods that involve some modifications of Systematic Reviews so that they can be conducted in a more timely and cost-effective manner. This suite of evidence synthesis products are referred to as **'Rapid Reviews'**[2]. These methods typically involve a reduced number of steps such as constraining the search effort, adjusting the extent of the quality assessment, and/or modifying the detail for data extraction, while still applying methods to minimise author bias in the searches, evidence appraisal and synthesis methods.

To accommodate the needs of GBR water quality policy and management, tailormade methods based on Rapid Review approaches were developed for the 2022 SCS by an independent expert in evidence-based syntheses for decision-making. The methods were initially reviewed by a small expert group with experience in GBR water quality science, then externally peer reviewed by three independent evidence synthesis experts.

Two methods were developed for the 2022 SCS:

- The **SCS Evidence Review** was used for questions that policy and management indicated were high priority and needed the highest confidence in the conclusions drawn from the evidence. The method includes an assessment of the reliability of all individual evidence items as an additional quality assurance step.
- The **SCS Evidence Summary** was used for all other questions, and while still providing a high level of confidence in the conclusions drawn, the method involves a less comprehensive quality assessment of individual evidence items.

Authors were asked to follow the methods, complete a standard template (this 'Synthesis of Evidence'), and extract data from literature in a standardised way to maximise transparency and ensure that a consistent approach was applied to all questions. Authors were provided with a Methods document, *'2022 Scientific Consensus Statement: Methods for the synthesis of evidence'*[3], containing detailed guidance and requirements for every step of the synthesis process. This was complemented by support from the SCS Coordination Team (led by C_2O Consulting) and the evidence synthesis expert to provide guidance throughout the drafting process including provision of step-by-step online training sessions for Authors, regular meetings to coordinate Authors within the Themes, and fortnightly or monthly question and answer sessions to clarify methods, discuss and address common issues.

The major steps of the Method are described below to assist readers in understanding the process used, structure and outputs of the synthesis of evidence:

1. **Describe the final interpretation of the question.** A description of the interpretation of the scope and intent of the question, including consultation with policy and management representatives where necessary, to ensure alignment with policy intentions. The description is supported by a conceptual diagram representing the major relationships relevant to the question, and definitions.
2. **Develop a search strategy**. The Method recommended that Authors used a S/PICO framework (Subject/Population, Exposure/Intervention, Comparator, Outcome), which could be used to break down the different elements of the question and helps to define and refine the search process. The S/PICO structure is the most commonly used structure in formal evidence synthesis methods[4].
3. **Define the criteria for the eligibility of evidence for the synthesis and conduct searches.** Authors were asked to establish **inclusion and exclusion criteria to define the eligibility of**

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[2] Collins A, Coughlin D, Miller J, & Kirk S (2015) The production of quick scoping reviews and rapid evidence assessments: A how to guide. UK Government. https://www.gov.uk/government/publications/the-production-of-quick-scoping-reviews-and-rapid-evidence-assessments

[3] Richards R, Pineda MC, Sambrook K, Waterhouse J (2023) 2022 Scientific Consensus Statement: Methods for the synthesis of evidence. C_2O Consulting, Townsville, pp. 59.

[4] https://libguides.jcu.edu.au/systematic-review/define

evidence prior to starting the literature search. The Method recommended conducting a **systematic literature search** in at least **two online academic databases**. Searches were typically restricted to 1990 onwards (unless specified otherwise) following a review of the evidence for the previous (2017) SCS which indicated that this would encompass the majority of the evidence base, and due to available resources. In addition, the geographic **scope of the search for evidence** depended on the nature of the question. For some questions, it was more appropriate only to focus on studies derived from the GBR region (e.g., the GBR context was essential to answer the question); for other questions, it was important to search for studies outside of the GBR (e.g., the question related to a research theme where there was little information available from the GBR). Authors were asked to provide a rationale for that decision in the synthesis. Results from the literature searches were screened against **inclusion and exclusion** criteria at the title and abstract review stage (**initial screening**). Literature that passed this initial screening was then read in full to determine the eligibility for use in the synthesis of evidence (**second screening**). Importantly, all literature had to be **peer reviewed and publicly available.** As well as journal articles, this meant that grey literature (e.g., technical reports) that had been externally peer reviewed (e.g., outside of organisation) and was publicly available, could be assessed as part of the synthesis of evidence.

4. **Extract data and information from the literature**. To compile the data and information that were used to address the question, **Authors were asked to complete a standard data extraction and appraisal spreadsheet**. Authors were assisted in tailoring this spreadsheet to meet the needs of their specific question.
5. **Undertake systematic appraisal of the evidence base**. Appraisal of the evidence is an important aspect of the synthesis of evidence as it provides the reader and/or decision-makers with valuable insights about the underlying evidence base. Each evidence item was assessed for its spatial, temporal and overall relevance to the question being addressed, and allocated a relative score. The body of evidence was then evaluated for overall relevance, the size of the evidence base (i.e., is it a well-researched topic or not), the diversity of studies (e.g., does it contain a mix of experimental, observational, reviews and modelling studies), and consistency of the findings (e.g., is there agreement or debate within the scientific literature). Collectively, these assessments were used to obtain an overall measure of the level of confidence of the evidence base, specifically using the overall relevance and consistency ratings. For example, a high confidence rating was allocated where there was high overall relevance and high consistency in the findings across a range of study types (e.g., modelling, observational and experimental). Questions using the **SCS Evidence Review Method** had an **additional quality assurance step**, through the assessment of reliability of all individual studies. This allowed Authors to identify where potential biases in the study design or the process used to draw conclusions might exist and offer insight into how reliable the scientific findings are for answering the priority SCS questions. This assessment considered the reliability of the study itself and enabled authors to place more or less emphasis on selected studies.
6. **Undertake a synthesis of the evidence and complete the evidence synthesis template** to address the question. Based on the previous steps, a narrative synthesis approach was used by authors to derive and summarise findings from the evidence.

Guidance for using the synthesis of evidence

Each synthesis of evidence contains three different levels of detail to present the process used and the findings of the evidence:

1. **Executive Summary**: This section brings together the evidence and findings reported in the main body of the document to provide a high-level overview of the question.
2. **Synthesis of Evidence:** This section contains the detailed identification, extraction and examination of evidence used to address the question.
    - ***Background***: Provides the context about why this question is important and explains how the Lead Author interpreted the question.

  - ***Method:*** Outlines the search terms used by Authors to find relevant literature (evidence items), which databases were used, and the inclusion and exclusion criteria.
  - ***Search Results:*** Contains details about the number of evidence items identified, sources, screening and the final number of evidence items used in the synthesis of evidence.
  - ***Key Findings:*** The **main body of the synthesis**. It includes a summary of the study characteristics (e.g., how many, when, where, how), a deep dive into the body of evidence covering key findings, trends or patterns, consistency of findings among studies, uncertainties and limitations of the evidence, significance of the findings to policy, practice and research, knowledge gaps, Indigenous engagement, conclusions and the evidence appraisal.
3. **Evidence Statement:** Provides a succinct, high-level overview of the main findings for the question with supporting points. The Evidence Statement for each Question was provided as input to the 2022 Scientific Consensus Statement Summary and Conclusions.

While the Executive Summary and Evidence Statement provide a high-level overview of the question, it is **critical that any policy or management decisions are based on consideration of the full synthesis of evidence.** The GBR and its catchment area is large, with many different land uses, climates and habitats which result in considerable heterogeneity across its extent. Regional differences can be significant, and from a management perspective will therefore often need to be treated as separate entities to make the most effective decisions to support and protect GBR ecosystems. Evidence from this spatial variability is captured in the reviews as much as possible to enable this level of management decision to occur. Areas where there is high agreement or disagreement of findings in the body of evidence are also highlighted by authors in describing the consistency of the evidence. In many cases authors also offer an explanation for this consistency.

Peer Review and Quality Assurance

Each synthesis of evidence was peer reviewed, following a similar process to indexed scientific journals. An Editorial Board, endorsed by the Australian Chief Scientist, managed the process. The Australian Chief Scientist also provided oversight and assurance about the design of the peer review process. The Editorial Board consisted of an Editor-in-Chief and six Editors with editorial expertise in indexed scientific journals. Each question had a Lead and Second Editor. Reviewers were approached based on skills and knowledge relevant to each question and appointed following a strict conflict of interest process. Each question had a minimum of two reviewers, one with GBR-relevant expertise, and a second ‘external’ reviewer (i.e., international or from elsewhere in Australia). Reviewers completed a peer review template which included a series of standard questions about the quality, rigour and content of the synthesis, and provided a recommendation (i.e., accept, minor revisions, major revisions). Authors were required to respond to all comments made by reviewers and Editors, revise the synthesis and provide evidence of changes. The Lead and Second Editors had the authority to endorse the synthesis following peer review or request further review/iterations.

Contents

Acknowledgements

We are grateful to Jane Waterhouse (C_2O Consulting), Mari-Carmen Pineda (C_2O Consulting) and Rob Richards (Evidentiary) for guidance in preparing this document and early comments on the search strategy. We also thank Stephen Lewis for providing river discharge data used for Figure 4 and Maria Byrne for comments and expert advice on previous drafts. Thanks to Barbara Robson, Guillermo Diaz-Pulido and Ian Prosser for discussions about the narrative synthesis. We also acknowledge the following people for contributing literature submissions for this question: Marie Vitelli (AgForce), Matthew Leighton (Bundaberg CANEGROWERS), Elisa Westmore (CANEGROWERS) and Frederieke Kroon (Australian Institute of Marine Science). Finally, we especially acknowledge the Traditional Custodians of the places on which all the work from the body of evidence we have compiled was conducted, and recognise their continuing connection to land, water, and community.

Executive Summary

Question

Question 4.3 What are the key drivers of the population outbreaks of crown-of-thorns Starfish (COTS) on the Great Barrier Reef, and what is the evidence for the contribution of nutrients from land runoff to these outbreaks?

Background

Population outbreaks of the corallivorous crown-of-thorns starfish (COTS) represent one of the most significant biological disturbances on coral reefs and remain one of the principal causes of coral loss on the Great Barrier Reef (GBR) and throughout the Indo-Pacific region. Managing COTS populations, specifically, preventing or suppressing outbreaks and mitigating their effects on coral reefs, is conditional upon identifying the proximal causes of pronounced fluctuations in population size. The question of what causes or initiates population outbreaks of COTS on the GBR is largely unresolved, partly due to uncertainties regarding when outbreaks first occurred: one viewpoint is that outbreaks are natural phenomena that have occurred repeatedly in the past while the other is grounded on the premise that outbreaks are recent and novel events resulting from anthropogenic changes to the environment.

This question is interpreted as referring to the main drivers of COTS outbreaks in the GBR, with emphasis on the role of nutrients from land-based runoff in the initiation of primary outbreaks. This Evidence Review focuses on the three most prominent hypotheses put forward to explain the initiation of population outbreaks of COTS on the GBR: i) *natural causes hypothesis*, ii) *predator removal hypothesis*, and iii) *nutrient hypothesis*. At the outset, this question reviews and compares the weight of available evidence for each of the hypotheses proposed to explain the initiation of primary outbreaks in the northern GBR. More emphasis is placed on appraising the evidence for the role of nutrients from land runoff in the initiation of COTS outbreaks. This process includes looking at the evidence supporting or refuting each assumption in the evidential chain necessary to establish the relationship between nutrients from land runoff and the initiation of COTS outbreaks. Evidence relevant to some of these causal links are reviewed or summarised in other questions addressed in the 2022 Scientific Consensus Statement (SCS).

Methods

- A formal Rapid Review approach was used for the 2022 Scientific Consensus Statement (SCS) synthesis of evidence. Rapid reviews are a systematic review with a simplification or omission of some steps to accommodate the time and resources available[5]. For the SCS, this applies to the search effort, quality appraisal of evidence and the amount of data extracted. The process has well-defined steps enabling fit-for-purpose evidence to be searched, retrieved, assessed and synthesised into final products to inform policy. For this question, an Evidence Review method was used.
- Two academic databases were used for the search: Web of Science and Scopus.
- All studies on the possible drivers of COTS outbreaks in the GBR were considered. Studies on drivers of outbreaks of COTS outside the GBR were considered where relevant, for comparison. The search strategy looked for items *“crown-of-thorns starfish” OR “crown-of-thorns sea star” OR “Acanthaster” OR “crown-of-thorns”*. For the Web of Science search, all fields were searched to be as inclusive as possible. For the Scopus search, searches were restricted to the Abstract, Title and Keyword fields to avoid including studies where these keywords were mentioned only in the references.

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[5] Cook CN, Nichols SJ, Webb JA, Fuller RA, Richards RM (2017) Simplifying the selection of evidence synthesis methods to inform environmental decisions: A guide for decision makers and scientists. *Biological Conservation* 213: 135-145. https://doi.org/10.1016/j.biocon.2017.07.004

- The broad search approach initially identified 366 studies that were relevant to COTS. Extensive second screening identified 183 studies which directly or indirectly addressed drivers of COTS outbreaks.
- In addition to the Evidence Appraisal, a further assessment of the reliability (assessment of the internal validity) of studies was included in this review (e.g., items that were considered relevant in scope but whose methods or approaches were less reliable were noted).

Method limitations and caveats to using this Evidence Review

For this Evidence Review, the following caveats or limitations should be noted when applying the findings for policy or management purposes:

- Only studies written in English were included.
- With a few exceptions, only GBR derived studies were included.
- Only two academic databases were searched: Web of Science and Scopus.

Key Findings

Summary of evidence to 2022

The fact that no one hypothesis can fully account for the spatiotemporal patterns in the occurrence of COTS outbreaks suggests that multiple processes may be involved. While distinct population outbreaks of COTS across the Indo-Pacific exhibit certain similarities, there is no reason to presume that these are all triggered by the same drivers. Taken together, the body of available evidence suggests that outbreaks in the GBR are most likely driven by a combination of some aspect of the most prominent hypotheses discussed above. For instance, it is plausible that under natural conditions, adult COTS may gather in specific locations, and if their spawning coincides with high river runoff events, which lead to nutrient enrichment and phytoplankton blooms, it can enhance the survival and growth of COTS larvae. This, in turn, leads to increased rates of larval settlement and dense aggregations of juvenile COTS, despite extensive predation by epibenthic fauna on newly settled COTS in at least some contexts. The absence of an overarching cause to definitively explain the occurrence and spatiotemporal distribution of COTS outbreaks reflects the inherent unpredictability of some key variables and the logistical challenges involved in measuring key parameters in the field.

The key findings are:

- Primary outbreaks of COTS are triggered by the spatiotemporal convergence of a combination of factors, which are distinct aspects within the three most prominent hypotheses: i) *natural causes hypothesis*, ii) *predator removal hypothesis*, and iii) *nutrient hypothesis*.
- COTS outbreaks mostly occur on midshelf reefs in the GBR.
- COTS possess inherent life history traits that predispose populations to significant spatial and temporal fluctuations. This is supported by evidence of high fecundity, high fertilisation rates, and fast growth that predisposes them to naturally occurring extreme fluctuations in reproductive success and population size. These traits, coupled with the time required for recovery and regrowth of their coral prey, may explain the periodicity (~14 to 17 years) of recurrent outbreaks events on the GBR.
- The evidence shows that in areas where fishing is prohibited, the incidence of COTS outbreaks is generally lower, while the prevalence of sublethal injuries on COTS is higher, compared to areas open to fishing. In addition, laboratory, field experiments and modelling studies also indicate that predation rates on post-settlement juveniles can be significant and may regulate crown-of-thorns starfish populations.
- Nutrient loads delivered to inshore waters and some midshelf sections of the GBR (particularly between Cooktown and Cairns where midshelf reefs are closer to the coast) have increased as a result of historical agricultural development in the GBR catchment area.
- The concentration and availability of nutrients increases following large river discharges, although COTS outbreaks do not consistently occur in the aftermath of large river discharge events.

- Phytoplankton blooms and shifts in phytoplankton community structure resulting from nutrient enrichment during flood events have been documented, although there is some uncertainty whether phytoplankton concentration (chlorophyll-a levels) or specific phytoplankton species that become dominant during blooms, or a combination of both, is necessary to drive enhanced survivorship and development rates in crown-of-thorns starfish larvae.
- Survival, growth, and development rates are generally higher for well-fed larvae, but there is a lower and upper threshold for optimal food levels.
- The fundamental assumption that larval supply is generally limiting, such that outbreaks arise as a result of pronounced and temporary increases in larval survivorship due to enhanced food supply, has yet to be explicitly tested.
- Outbreaks of COTS on the GBR start on midshelf reefs in the Northern sector of the GBR (between Cairns and Lizard Island, and possibly further north), an area commonly referred to as the COTS 'initiation area'. The 'initiation area' overlaps with the area where nutrient-enriched river discharge enter the midshelf waters of the GBR on a regular basis. Larvae produced by primary outbreak populations are subsequently retained on source reefs or dispersed to reefs south of the 'initiation area' according to prevailing hydrodynamic regimes, thereby resulting in secondary outbreaks.

Recent findings 2016-2022

Out of the 183 studies included in this Evidence Review, 81 (over 44%) have been published since the 2017 SCS. This can be attributed to both the emergence of new and recurring population outbreaks in the past decade, as well as the recent influx of significant support and funding specifically allocated for COTS research. The main findings from these recent studies are:

- Climate change (ocean warming and changes in seawater chemistry) may have direct effects on reproduction and on the early life history stages of COTS, as well as on juvenile and adult COTS.
- Recent developments in environmental DNA (eDNA) technology have highlighted its applicability as a tool for monitoring and studying COTS at different life history stages in the field, especially when used alongside fine-scale survey methods.
- There is a growing list of inherent life history and demographic traits relevant to COTS that predispose them to outbreaks.
- There is a growing list of previously unknown COTS predators at different life history stages, particularly predators of gametes, larvae, and juveniles.
- Juvenile COTS have habitat preferences that are distinct from adult COTS and are able to delay diet transition from herbivory to corallivory according to the availability of preferred coral prey.
- Assessment of the role of fisheries management and zoning on COTS populations in the GBR suggests that managing fishing pressure on putative predators can be successful in mitigating COTS populations within relatively short timeframes.
- Re-evaluation of larval starvation show that survival, growth, and development rates are generally higher for well-fed larvae, but there is a lower and upper threshold for optimal food levels.

In addition, since 2017 there have been several reviews that detail key knowledge gaps relevant to COTS research on the biology and ecology of COTS, as well as on the comparative efficacy of management approaches in the GBR.

Significance for policy, practice, and research

Given that there are likely multiple drivers of COTS outbreaks, a multifaceted approach is necessary to improve our understanding of these drivers and mechanisms, and to implement effective management strategies. Active control measures are being advocated for COTS on the GBR, including spatially limited efforts within the outbreak 'initiation area'. Regardless of improvements in the effectiveness of direct control measures, it is important to recognise that these solutions can only offer temporary or short-term relief in mitigating the impacts of COTS on coral reef ecosystems. Achieving long-term or permanent solutions requires a deeper understanding of the underlying drivers of COTS outbreaks, especially if outbreaks are indeed triggered or exacerbated by human activities, such as elevated nutrient levels from terrestrial runoff or overfishing. Improving water quality through minimising sediment, nutrient, and pollutant runoff, and implementing stricter regulations on fishing activities, particularly through the establishment of no-take marine protected areas, will not only help prevent or suppress COTS outbreaks but also contribute to the overall health and stability of coral reef ecosystems in the GBR.

Key uncertainties and/or limitations

It is important to acknowledge that each of the three major hypotheses presented have some factual basis or provide seemingly plausible explanations for the occurrence of COTS outbreaks. However, it should be noted that inconsistencies exist within each hypothesis, and none of them can fully account for the occurrence of these outbreaks. The hypotheses are primarily based on correlations, and the establishment of causation has not been definitively demonstrated. Additionally, it is worth highlighting that in several cases, the studies were not specifically designed to address the particular hypothesis in question but rather contained tangentially relevant findings that indirectly supported a specific hypothesis. Furthermore, some of these hypotheses rely on evidence that is inconclusive and open to multiple interpretations. The persistent uncertainties are in part related to inherent challenges in explicitly testing key predictions, but new research methods and developments (e.g., sampling COTS larvae, establishing key settlement habitat) now provide much greater opportunity to address these knowledge gaps.

Evidence appraisal

The overall relevance of the body of evidence to the question was rated as Moderate (5), while the relevance rating for studies included under each hypothesis was also Moderate, with scores of 5, 6, and 6 (out of 9) for *natural causes*, *predator removal,* and *nutrient hypothesis,* respectively. A total of 183 studies were included in the body of evidence to address the question on what drives the initiation of COTS outbreaks in the GBR. This is considered to be a High proportion of the total available evidence base, representing a High diversity of approaches with Moderate consistency of findings relevant to the question.

Overall, there is a Moderate level of confidence in the body of evidence based on Moderate consistency and Moderate overall relevance of the studies. The majority of the studies included in this Evidence Review had a Moderate to High rating (74%) in terms of relevance to the hypothesised drivers of COTS outbreaks in the GBR. Consistency was rated as Moderate, as there were some notable studies under each hypothesis that had marginally inconsistent results. The High reliability score for the studies included was also factored in when assessing the level of confidence in the body of evidence compiled to address this question. Taken together, the diverse approaches to address various aspects of this question will improve our understanding of the key drivers of COTS outbreaks in the GBR.

1. Background

Population outbreaks of the corallivorous crown-of-thorns starfish (COTS) represent one of the most significant biological disturbances on coral reefs (De'ath et al., 2012; Moran, 1986; Pratchett et al., 2014) and remain one of the principal causes of widespread declines in live coral cover on the Great Barrier Reef (GBR) (Mellin et al., 2019), despite emerging effects of climate change and coral bleaching (Hughes et al., 2017). COTS occur throughout the Indo-Pacific (Moran, 1986), though recent molecular sampling has revealed that there are at least four strongly differentiated clades with restricted and largely distinct geographic distributions (Pacific, northern Indian Ocean, southern Indian Ocean, Red Sea), which are proposed to represent distinct species (Haszprunar & Spies, 2014; Vogler et al., 2008). Notably, *Acanthaster planci,* which is restricted to the northern Indian Ocean, is readily distinguishable from the Pacific species (nominally referred to as *Acanthaster solaris*; Haszprunar et al., 2017) based on colour and morphology (Pratchett et al., 2017a). Distinguishing between these species is important because species-specific differences in behaviour and biology may account for geographic variation in the apparent incidence and/ or severity of population outbreaks (Pratchett et al., 2017a). Densities of COTS vary greatly both spatially and temporally, and population outbreaks are generally defined based on their ecological impacts (Plagányi et al., 2020), whereby the capacity to deplete local coral assemblages increases with both the size and density of adult COTS (Pratchett, 2010). Population outbreaks may also be inferred based on the population dynamics of COTS, where outbreaks are often reported to arise very suddenly, within a few years (Chesher, 1969; Kayal et al., 2012). Factors that contribute to mass settlement of planktonic larvae, thereby resulting in sudden and pronounced increases in the local abundance of COTS (e.g., Birkeland, 1982; Lucas, 1973), are likely to be different from those that facilitate slow and sustained increases in starfish densities (Johnson, 1992a). The sustained and gradual accumulation of COTS from multiple successive recruitment events may represent a mechanism by which outbreaks are initiated ("primary outbreaks"; Endean, 1974; Johnson, 1992b; Stump, 1996), which then give rise to further secondary outbreaks on nearby or downstream reefs (Moran et al., 1992). On the GBR, it is currently believed that primary outbreaks occur in the area between Cairns and Lizard Island, which give rise to waves of secondary outbreaks that propagate both north and south (Kenchington, 1977; Reichelt et al., 1990a; Vanhatalo et al., 2017).

Understanding the key drivers of COTS outbreaks on the GBR (and throughout the Indo-Pacific) is fundamental for establishing relevant management responses (Babcock et al., 2016a). In particular, effective long-term management will require a holistic understanding of the anthropogenic pressures and/or changes in environmental and habitat conditions that cause or contribute to the initiation of primary outbreaks. Several different hypotheses have been put forward to explain the initiation of population outbreaks of COTS (Caballes & Pratchett, 2014; Moran, 1986; Pratchett et al., 2014), the extent to which outbreaks are caused or exacerbated by anthropogenic activities is still unclear.

The *natural causes hypothesis* argues that spatial and temporal variation in COTS densities are natural phenomena attributable to their inherent life history characteristics (Dana, 1970; Moore, 1978; Newman, 1970; Vine, 1970). Most importantly, highly fecund mature females can produce more than a million fertilised eggs annually per individual under favourable conditions (Babcock et al., 2016b; Pratchett et al., 2021a), which may be sufficient to initiate a population outbreak. This view was initially supported by historical records, mostly from anecdotal information, suggesting that COTS were abundant and had a wide distribution in the past (Dana, 1970; Newman, 1970; Vine, 1973). However, Branham (1973) speculated that these anecdotal accounts could have been in reference to normal spawning aggregations (although there is no conclusive evidence to prove that COTS aggregate to spawn) of COTS rather than outbreaks. Birkeland (1981) and Flanigan & Lamberts (1981) also proposed that the incorporation of COTS in Micronesian and Samoan cultures, respectively, could be indicative of its abundance in the past, but Moran (1986) argues that the occurrence of outbreaks in the past cannot be inferred from the cultural importance of COTS since this could be attributable to their sinister appearance and toxicity regardless of major population fluctuations. Another line of evidence that outbreaks have occurred in the past comes from the examination of COTS skeletal elements found in abundance periodically in sediment cores over many thousands of years (Frankel, 1978; Henderson, 1992; Walbran et al., 1989a). These attempts to establish a relationship between past outbreak events and the contribution of COTS skeletal elements to surface sediment have been criticised because of assumptions about post-outbreak mortality patterns, dispersion of skeletal ossicles, and dating methodology (Fabricius & Fabricius, 1992; Keesing et al., 1992; Moran et al., 1986; Pandolfi, 1992). To further support the concept that outbreaks are a consequence of natural processes, Dana et al. (1972) postulated that aggregation and migrations may be a behavioural response to the food limitation imposed by typhoon damage to coral reefs. Although this notion explains why individuals in outbreaks are all adult-sized, the amount of coral damage required to result in food limitation is much greater than that observed for most storms (Pearson, 1975).

In contrast to the *natural causes hypothesis*, there are several hypotheses that attribute outbreaks of COTS to anthropogenic changes to tropical coastal environments. Critically, it has been argued that the contemporary diversity and structure of coral reef communities could not have been attained if COTS outbreaks occurred at the current frequency and intensity throughout key periods in their evolution and development (Birkeland & Lucas, 1990; Chesher, 1969; De'ath et al., 2012; Randall, 1972). If COTS outbreaks were a regular feature of coral reef dynamics, it is argued that coral assemblages would be dominated by non-preferred coral species (Randall, 1972). When considering the global occurrence of COTS outbreaks, it has been pointed out that almost all of the major outbreaks have occurred near centres of human populations (Chesher, 1969; Dulvy et al., 2004; Nishihira & Yamazato, 1974; Randall, 1972), reinforcing the belief that the increased frequency and intensity of recent outbreaks are caused by anthropogenic alterations of environmental and habitat conditions. Hypotheses supporting this view include the *reef destruction hypothesis* (Chesher, 1969), *pollution hypothesis* (Randall, 1972), and the more prominent *predator removal hypothesis* (Endean, 1973) and larval starvation or terrestrial runoff hypothesis, collectively referred to as the *nutrient hypothesis* hereafter (Birkeland, 1982; Brodie, 1992; Brodie et al., 2005; Fabricius et al., 2010; Lucas, 1982).

The *reef destruction hypothesis* proposed by Chesher (1969) assumes that corals are the primary predators of COTS larvae; therefore, decreasing coral abundance as a result of destructive human activities (i.e., dredging, blasting, and poor land use practices) subsequently leads to outbreaks. However, this does not explain the presence of outbreaks in areas that are not subject to these destructive activities (Endean, 1977). The *pollution hypothesis* suggests that increased input of chemical pollutants, particularly chlorinated hydrocarbon pesticides (e.g., DDT, Dieldrin), into nearshore waters is responsible for reducing the abundance of predators of larval and juvenile COTS (Randall, 1972). Nonetheless, attempts to establish a connection between chemical pollutants and their distribution concerning COTS and coral reefs have not provided substantial evidence in support of this hypothesis.

The *predator removal hypothesis* infers that COTS populations are normally regulated by high rates of predation on post-settlement life stages and that outbreaks arise as a consequence of the release from predation pressure due to direct overharvesting of COTS predators (Endean, 1973). Several species (mostly coral reef fishes) have been recorded to prey upon juvenile and/or adult COTS, as well as COTS gametes and larvae (Cowan et al., 2017a). Indirectly, fishing pressure on large piscivores may trigger trophic cascades by reducing the densities of benthic carnivorous fishes and relieving predation pressure on invertebrates that feed on small COTS (Sweatman, 2008). There is not, as yet empirical evidence to support the existence of such trophic cascades, but there is significant and increasing evidence that COTS are vulnerable to a range of different predators. Benthic epifauna have been found to be important predators of small COTS that are very cryptic and are often inaccessible to fish predators (Keesing & Halford, 1992a). Significantly higher frequencies of sublethal arm damage on COTS within zones where fishing is prohibited or restricted, have been suggested to indicate the importance of predation in regulating COTS populations (Caballes et al., 2022).

Lastly, the *nutrient hypothesis* first proposed by Birkeland (1982) in reference to the occurrence of outbreaks on high islands in Micronesia and Polynesia, states that enhanced nutrient supply from river runoff (usually after periods of extremely heavy rainfall around high islands and continental land masses), elevates levels of primary production resulting in a phytoplankton bloom. This, in turn, is expected to enhance the larval survival of COTS by reducing mortality from starvation (Lucas, 1982) or through more rapid larval development, decreasing exposure to other sources of mortality such as predation (Birkeland & Lucas, 1990). Aside from river runoff, upwellings and sediment resuspension during storms (Furnas & Mitchell, 1986), and broad oceanographic features like the transition zone chlorophyll front (Houk et al., 2007) could also be responsible for enhanced phytoplankton levels. The proposed link between increased nutrient runoff and primary outbreaks of COTS has contributed, in part, to the prioritisation of investment into water quality management on GBR catchments. However, more recent research and reviews have highlighted some inconsistencies or unresolved issues relevant to this hypothesis (Lane, 2012; Pratchett et al., 2014).

For the purported link between elevated nutrient runoff and primary outbreaks of COTS to hold, the evidential chain and associated questions below must be clearly established:

1. Evidence for the increase in nutrient load of runoff into GBR coastal waters from North Queensland rivers following agricultural development on catchments (addressed in Questions 2.3, Lewis et al., and 4.4, Prosser & Wilkinson, this Scientific Consensus Statement (SCS)).
2. Evidence for the increase in the concentration and availability of nutrients following heavy river discharge and land runoff (addressed in Question 4.1. Robson et al., this SCS).
    - What is the nutrient composition?
    - Which specific nutrients increase following heavy discharge from rivers?
    - Which constituents of these nutrients are present or dominant during this period?
3. Evidence for phytoplankton blooms and shifts in phytoplankton community composition as a result of elevated nutrients and the persistence of these conditions immediately following the spawning period of COTS in the GBR (addressed, in part, by Questions 4.1, Robson et al., and 4.2, Diaz-Pulido et al., this SCS).
    - Does the absence of nutrients from river runoff significantly limit phytoplankton production to the point that COTS larval populations are negatively impacted?
    - Which specific nutrients or nutrient constituents drive these blooms?
    - Which phytoplankton species or size classes are dominant during these blooms?
    - What is the spatiotemporal distribution of phytoplankton blooms in the GBR?
    - When is the spawning period of COTS in the GBR?
4. Evidence for enhanced growth and survival of COTS larvae in high food (phytoplankton) conditions.
    - What are the cell-specific chlorophyll levels of dominant phytoplankton species (or size classes) during blooms?
    - Which species (or size class) of phytoplankton are preferred by COTS? What are the growth and development rates for COTS given a specific diet of phytoplankton?
    - What is the evidence for nutritional limitation of COTS larvae?
    - What are the threshold values (i.e., chlorophyll *a*, phytoplankton concentration) for enhanced larval performance?
5. Evidence that high settlement rates from high densities of larvae completing development lead to primary outbreaks.
    - Does the stock-recruitment relationship hold for COTS?
    - Are settlement and recruitment limited by larval density or microsite availability?
    - What factors regulate post-settlement survival and growth?
    - Do conditions exist where COTS delay transition to corallivory?
6. Evidence that increased larval output from the ‘initiation area’ triggers secondary outbreaks on other reefs.
    - Is there an outbreak ‘initiation area’ in the GBR and if so, where are the boundaries delineating this zone?
    - Which factors limit the formation of secondary outbreaks?
    - Do favourable conditions (i.e., high phytoplankton availability) also need to exist on sink reefs?

- What is the estimated pelagic larval duration (PLD) for COTS?

1.1 Question

Primary question	**Q4.3** What are the key drivers of the population outbreaks of crown-of-thorns starfish (COTS) on the Great Barrier Reef, and what is the evidence for the contribution of nutrients from land runoff to these outbreaks?

The question is interpreted as referring to the main drivers of COTS outbreaks in the GBR, with emphasis on the role of nutrients from land-based runoff in the initiation of primary outbreaks. This Evidence Review focused on the three most prominent hypothesis that have been put forward to explain the initiation of outbreaks of COTS on the GBR: i) *natural causes hypothesis*, ii) *predator removal hypothesis*, and iii) *nutrient hypothesis*. At the outset, this question reviews and compares the weight of available evidence for each of the hypotheses proposed to explain the initiation of primary outbreaks in the northern GBR. More emphasis is placed on appraising the evidence for the role of nutrients from land runoff in the initiation of COTS outbreaks. This process includes looking at the evidence supporting or refuting each assumption in the evidential chain necessary to establish the relationship between nutrients from land runoff and the initiation of COTS outbreaks. Evidence relevant to some of these causal links are reviewed or summarised in other questions addressed in the SCS.

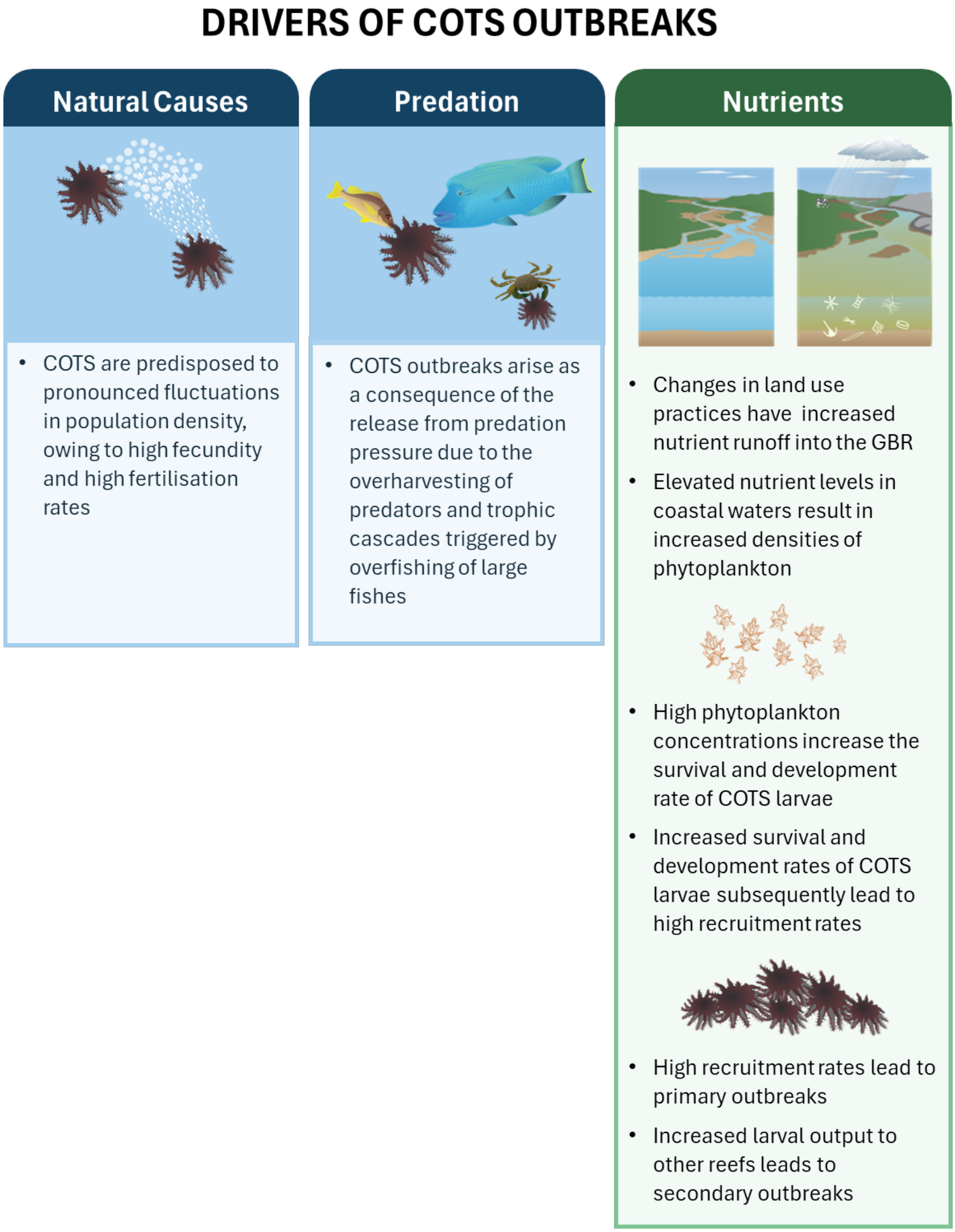
1.2 Conceptual diagram

The conceptual diagram in Figure 1 illustrates and defines the proposed drivers of COTS outbreaks in the GBR, with emphasis on the role of nutrients from land runoff on the initiation of outbreaks. The weight of evidence supporting each hypothesis is compared and evidence for each causal link under the nutrient hypothesis evidential chain is thoroughly appraised.

1.3 Links to other questions

This synthesis of evidence addresses one of 30 questions that are being addressed as part of the 2022 SCS. The questions are organised into eight themes: values and threats, sediments and particulate nutrients, dissolved nutrients, pesticides, other pollutants, human dimensions, and future directions, that cover topics ranging from ecological processes, delivery and source, through to management options. As a result, many questions are closely linked, and the evidence presented may be directly relevant to parts of other questions. The relevant linkages for this question are identified in the text where applicable. The primary question linkages for this question are listed below.

Links to other related questions	**Q2.3** What evidence is there for increases in land-based runoff from pre-development estimates in the Great Barrier Reef? **Q4.1** What is the spatial and temporal distribution of nutrients and associated indicators within the Great Barrier Reef? **Q4.2** What are the measured impacts of nutrients on Great Barrier Reef ecosystems, what are the mechanism(s) for those impacts and where is there evidence of this occurring in the Great Barrier Reef? **Q4.4** How much anthropogenic nutrient (nitrogen and phosphorus species) is delivered to the Great Barrier Reef ecosystems (including the spatial and temporal variation in delivery), what are the most important characteristics of anthropogenic nutrients, and what are the primary sources?



DRIVERS OF COTS OUTBREAKS

Natural Causes

- COTS are predisposed to pronounced fluctuations in population density, owing to high fecundity and high fertilisation rates

Predation

- COTS outbreaks arise as a consequence of the release from predation pressure due to the overharvesting of predators and trophic cascades triggered by overfishing of large fishes

Nutrients

- Changes in land use practices have increased nutrient runoff into the GBR
- Elevated nutrient levels in coastal waters result in increased densities of phytoplankton
- High phytoplankton concentrations increase the survival and development rate of COTS larvae
- Increased survival and development rates of COTS larvae subsequently lead to high recruitment rates
- High recruitment rates lead to primary outbreaks
- Increased larval output to other reefs leads to secondary outbreaks

Figure 1. Conceptual diagram representing the scope and interpretation of Question 4.3. Alternative drivers of population outbreaks of crown-of-thorns starfish (COTS) are not necessarily mutually exclusive. In this synthesis, emphasis is given to the role of nutrients (shown in green), and the chain of evidence required to clearly establish the role of nutrients.

2. Method

A formal Rapid Review approach was used for the 2022 SCS synthesis of evidence. Rapid reviews are a systematic review with a simplification or omission of some steps to accommodate the time and resources available[6]. For the SCS, this applies to the search effort, quality appraisal of evidence and the amount of data extracted. The process has well-defined steps enabling fit-for-purpose evidence to be searched, retrieved, assessed and synthesised into final products to inform policy. For this question, an Evidence Review method was used.

2.1 Primary question elements and description

The primary question is: ***What are the key drivers of the population outbreaks of crown-of-thorns starfish (COTS) on the Great Barrier Reef, and what is the evidence for the contribution of nutrients from land runoff to these outbreaks?***

S/PICO frameworks (Subject/Population, Exposure/Intervention, Comparator, Outcome) can be used to break down the different elements of a question and help to define and refine the search process. The S/PICO structure is the most commonly used structure in formal evidence synthesis methods[7] but other variations are also available.

- **Subject/Population:** Who or what is being studied or what is the problem?
- **Intervention/exposure:** Proposed management regime, policy, action or the environmental variable to which the subject populations are exposed.
- **Comparator**: What is the intervention/exposure compared to (e.g., other interventions, no intervention, etc.)? This could also include a time comparator as in ‘before or after’ treatment or exposure. If no comparison was applicable, this component did not need to be addressed.
- **Outcome:** What are the outcomes relevant to the question resulting from the intervention or exposure?

Table 1. Description of primary question elements for Question 4.3.

Question S/PICO elements	Question term	Description
Subject/ Population	Crown-of-thorns starfish in the GBR	Crown-of-thorns starfish (COTS) have generally been regarded to be *Acanthaster planci* throughout the Indo-Pacific; however, molecular sampling has revealed that there are at least four geographically separated species located in: i) the Red Sea (*Acanthaster benziei*), ii) the Northern Indian Ocean (*Acanthaster planci*), iii) the Southern Indian Ocean (*Acanthaster mauritiensis*), and iv) the Pacific Ocean (*Acanthaster* cf. *solaris*). Although specific differences in their biology and behaviour are yet to be explored, all four putative species inhabit coral reef environments and feed almost exclusively on scleractinian corals. This review will mostly assess evidence for COTS from the GBR; however, since the taxonomic identity and nomenclature of COTS from the western Pacific remains

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[6] Cook CN, Nichols SJ, Webb JA, Fuller RA, Richards RM (2017) Simplifying the selection of evidence synthesis methods to inform environmental decisions: A guide for decision makers and scientists. *Biological Conservation* 213: 135-145

[7] https://libguides.jcu.edu.au/systematic-review/define and https://guides.library.cornell.edu/evidence-synthesis/research-question

Question S/PICO elements	Question term	Description
		uncertain, *Acanthaster* cf. *solaris* or *Acanthaster* sp. are used in more recent literature.
Exposure & qualifiers	Land runoff; Nutrients	The sources of nutrients in the GBR are covered in more detail under Question 4.4 (Prosser & Wilkinson, this SCS). The focus will be on bioavailable nutrients (e.g., nitrate, ammonia, phosphate) from land runoff brought by river discharge; although other drivers of nutrient enrichment in the GBR will also be discussed (e.g., upwelling, sediment resuspension).
Comparator (if relevant)	Other key drivers of COTS population outbreaks (i.e., natural causes, predator removal)	Although the main focus of this Evidence Review is on the role of nutrients from land runoff in the initiation of outbreaks, other hypotheses put forward to explain the initiation of COTS outbreaks (i.e., natural causes, predation) will also be discussed.
Outcome & outcome qualifiers	Phytoplankton blooms; COTS outbreaks	Phytoplankton blooms will be covered more extensively in Question 4.2 (Diaz-Pulido et al., this SCS) but will be included in this Evidence Review as it relates to COTS larval diet, development, and survival. Measurements of chlorophyll concentration are often used as a proxy for levels of phytoplankton biomass in the water column. The spatiotemporal distribution of COTS outbreaks will be discussed to relate to specific drivers and potential links to nutrients.

Table 2. Definitions for any terms used in Question 4.3.

Definitions	
Crown-of-thorns starfish (COTS)	Coral-eating species of starfish native to the Great Barrier Reef and reefs throughout the Indo-Pacific region.
Population outbreak	Pronounced increases in abundance of crown-of-thorns starfish that result in coral mortality beyond what can be sustained by local resources.
Key drivers	Hypotheses (e.g., nutrient hypothesis), and/ or key processes inherent in these hypotheses, put forward to explain the initiation of COTS outbreaks
Nutrients	Mainly nitrogen (N) and phosphorus (P) in different bioavailable constituents (i.e., inorganic, organic, particulate).
Land runoff	Runoff from a terrestrial source brought by river discharge.
GBR	The Great Barrier Reef World Heritage Area.

2.2 Search and eligibility

a) Search locations

Searches were performed on:

- Web of Science (searching in ALL fields)
- Scopus (searching Abstract, Title and Keyword fields)

b) Search terms

Table 3 shows a list of the search terms used to conduct the online searches.

Table 3. Search terms for S/PICO elements of Question 4.3.

Question element	Search terms
Subject/Population	Crown-of-thorns starfish
Exposure or Intervention	Nutrients
Comparator (if relevant)	Other key drivers (natural causes, predator removal)
Outcome	Population outbreaks

c) Search strings

Table 4 shows the search strings used to conduct the online searches.

Table 4. Search strings used for electronic searches for Question 4.3.

Search strings
Web of Science: ALL(“crown-of-thorns starfish” OR “crown-of-thorns sea star” OR *Acanthaster* OR crown-of-thorns)
Scopus: TITLE-ABS-KEY("crown-of-thorns starfish" OR "crown-of-thorns sea star" OR *Acanthaster* OR "crown-of-thorns starfish")

d) Inclusion and exclusion criteria

Table 5 shows a list of the inclusion and exclusion criteria used for accepting or rejecting evidence items.

Table 5. Inclusion and exclusion criteria for Question 4.3 applied to the search returns.

Question element	Inclusion	Exclusion
Subject/Population	All studies on the possible drivers of COTS outbreaks in the GBR. Studies on drivers of outbreaks outside the GBR (for comparison).	Studies that only mention COTS but are not the subject of the paper. Studies outside the GBR that are not specific to COTS.
Exposure or Intervention	Nutrients from river discharge into GBR catchments. Other nutrient sources, e.g., upwelling, sediment resuspension (for comparison).	Nutrient dynamics outside the GBR. Studies not relevant to COTS outbreak drivers.
Comparator (if relevant)	Studies on other drivers.	Studies not relevant to COTS outbreak drivers.
Outcome	COTS outbreaks.	Studies not relevant to COTS outbreaks (e.g., physiology, taxonomy).
Publication	Peer reviewed and published articles and reports.	Pre 1990 and not relevant to the question. Abstract only, no full text available. Non peer reviewed studies. Magazine article/Special Issue Preface.
Language	English language	Not English language
Study type	Field, laboratory, modelling studies	Correction / Erratum / Response

3. Search Results

A total of 1,651 studies were identified through online searches for peer reviewed and published literature. Six studies were identified manually from personal collections, as well as 18 pre-1990 studies that proposed key hypotheses and were therefore considered vital in addressing the question. Manual additions represented 1.4% of the total evidence. After initial and secondary screening, 183 studies were eligible for inclusion in the synthesis of evidence (Table 6; Figure 2). Only one study was unobtainable.

Table 6. Search results table, separated by A) Academic databases, B) Search engines (i.e., Google Scholar) and C) Manual searches. The search results are provided in the format X(Z)/ Y, where: X (number of relevant evidence items retained for second screening); Y (total number of search returns or hits); and Z (number of relevant returns that had already been found in previous searches).

Date	Search strings	Sources	
A) Academic databases		Web of Science	Scopus
21/02/23	(“crown-of-thorns starfish” OR “crown-of-thorns sea star” OR “Acanthaster” OR “crown-of-thorns”)	312/951	329(299)/700
B) Search engines (e.g. Google Scholar)			
	(Not used)		
Total items online searches		***1,651 (98.6%)***	
C) Manual search			
Date	Source	Number of items added	
	Lead Author personal collection	6	
	References pre-1990	18	
Total items manual searches		***24 (1.4%)***	

For the Web of Science search, all fields were searched to be as inclusive as possible. For the Scopus search, searches were restricted to the Abstract, Title and Keyword fields to avoid including studies where these keywords were mentioned only in the references. Out of the 951 hits from the Web of Science search, 312 studies were retained for second screening. From the Scopus search, 329 studies out of 700 search returns were retained for second screening, of which, 299 had already been found in the previous Web of Science search.

There were 366 papers (342 from online searches, 6 from the Lead Author’s personal collection, and 18 pre-1990 studies manually added by the Lead Author) retained following initial screening. After screening of the full text, 183 literature items were retained for inclusion in the synthesis. Of the nine papers submitted by external audiences, all were also identified through the online searches and were included in the full-text (secondary) screening.

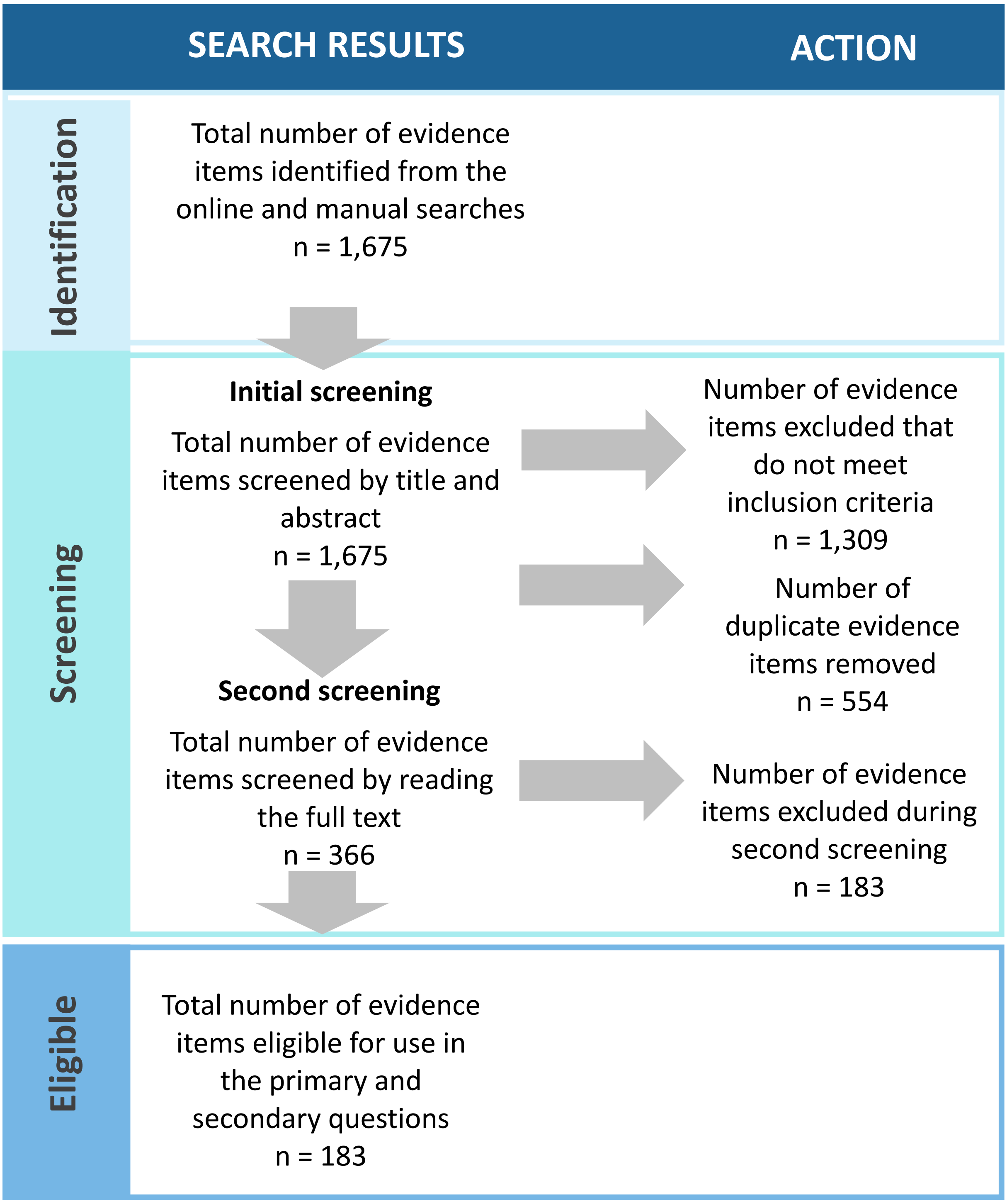


Figure 2. Flow chart of results of screening and assessing all search results for Question 4.3.

4. Key Findings

4.1 Narrative synthesis

4.1.0 Summary of study characteristics

Searches of peer reviewed literature were conducted using two online academic databases: Web of Science and Scopus. The broad online search approach initially identified 342 studies from title and abstract screening that were relevant to COTS and a further 24 studies were manually added. Extensive second, full-text screening identified 183 studies which directly or indirectly addressed drivers of COTS outbreaks (Table 7). Most of these studies were from 1990 to 2022, although 18 studies published before 1990 were included as these were studies that were important in the formulation of hypotheses on the causes of COTS outbreaks. Relevant studies conducted outside the GBR were also included to compare drivers of outbreaks in other locations (GBR = 128; Australia Non-GBR = 2; Covers most of the geographic distribution of COTS = 23; Outside Australia = 30).

Table 7. Summary of the body of evidence considered in this review detailing the type of study across different hypothesised drivers for COTS outbreaks.

COTS Outbreak Drivers	Study Type				Driver Totals
	Experimental (Field-based, Lab-based)	Observational / Analytical	Conceptual/ Review/ Modelling	Mixed (Combination of 2-3 Types)	
Natural	13	21	6	2	**42 *(23%)***
Predation	9	13	10	0	**32 *(17%)***
Nutrients	14	13	13	0	**40 (22%)**
Multiple	7	17	18	3	**45 (25%)**
Hydrodynamics	0	5	6	0	**11 (6%)**
Other	12	1	0	0	**13 (7%)**
Study Type Totals	**55 *(30%)***	**70 *(38%)***	**53 *(29%)***	**5 *(3%)***	**183**

The distribution of studies addressing each of the three major hypotheses was roughly even (Table 7): natural (42 studies, 23%), predation (32 studies, 17%), nutrients (40, 22%). However, it is important to note that in several cases, the studies were not designed to explicitly test the specific hypothesis, but rather contained indirect or anecdotal information that lend support for a specific hypothesis. The distinctions between these studies will be discussed in more detail in the sections below. It is acknowledged that these hypotheses are not mutually exclusive, which partly explains the relatively high number of studies that addressed (explicitly or implicitly) multiple hypotheses at the same time (45 studies, 25%). Studies that examined the role of hydrodynamics (11 studies, 6%) in the dispersal or retention of COTS larvae, as a mechanism for driving secondary outbreaks were also included in the body of evidence, together with studies that addressed other (13 studies, 7%) potential drivers of COTS outbreaks, such as climate change and deep-water recruitment.

The distribution of studies considered in the Evidence Review was also fairly even in terms of the primary study type (Table 7, Figure 3). Most of the studies included used an observational approach via direct measurements or further analyses of observational data (70 studies, 38%). This type of study is important in assessing the distribution and behaviour of COTS in the wild, but often makes it difficult to disentangle the specific drivers of observed phenomena. Out of the 183 studies included, 55 (31%) used manipulative experiments in a laboratory or field setting. These studies have the advantage of isolating specific effects of variables tested but may not have broad applicability when conditions do not resemble the complexities in the wild. Modelling and conceptual studies or reviews (53 studies, 29%)

also make up a significant proportion of the body of evidence included in this review and are often spatially and temporally generalisable. Conceptual studies and reviews rely heavily on published literature, while models often rely on assumptions that still need to be verified through experiments or observations.

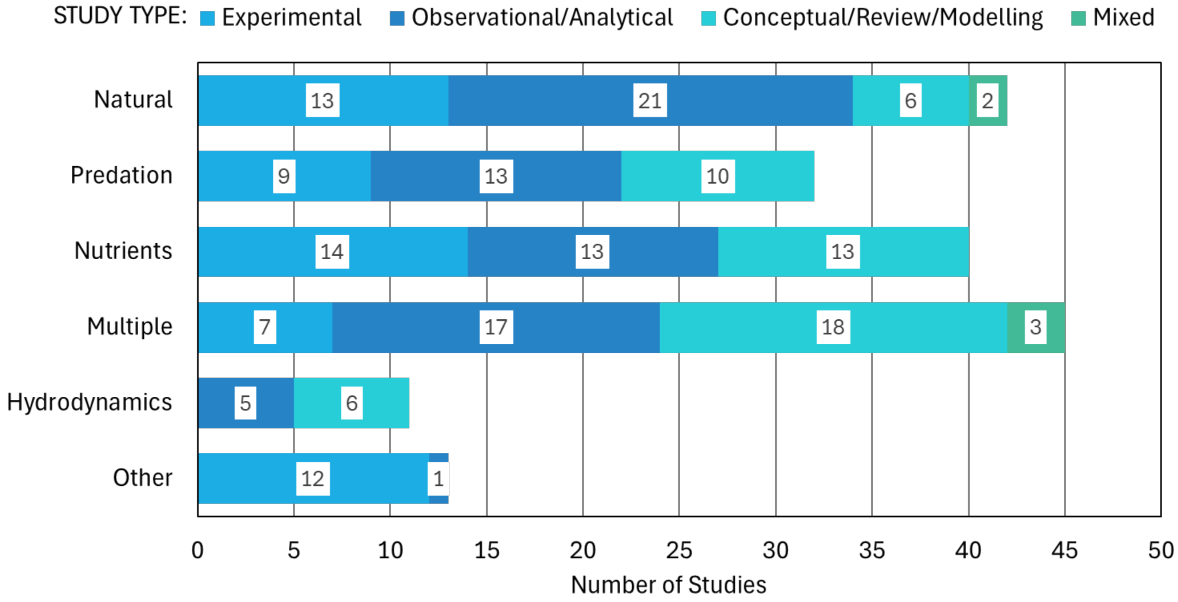


Figure 3. Summary of the body of evidence considered in this review by the primary type of study across hypothesised drivers of COTS outbreaks.

4.1.1 Summary of evidence to 2022

Given the extensive geographic span across which COTS outbreaks occur (see Figure 8 and Figure 9 in Pratchett et al., 2014), this review also considered studies that have examined the drivers of outbreaks outside the GBR. Answers to this question may involve a much more intensive study of each process and the relationships between them in order to determine the critical pathways in the system. Despite the high quantity of studies on this species, it is possible that some of the key variables in the system may be inherently unpredictable; and given the logistical challenges of measuring key parameters in the field, parts of the question on what drives COTS outbreaks may never be precisely predictable or even quantifiable, but understanding should increase as knowledge of the specific processes improves.

4.1.1.1 Natural causes

The type of studies included in this review, which were relevant to the *natural causes hypothesis* (42 studies; see Table 7), were predominantly observational/analytical (21: 50%), with 13 experimental (31%), 6 conceptual/review/modelling (14%), and 2 mixed (5%). Most of these studies have emphasised key traits (e.g., exceptional fecundity) of COTS that would predispose them to natural fluctuations in abundance, while there has (as yet) been limited attempt to bring together the latest data and understanding of their biology and ecology to present a really compelling demonstration of how outbreaks may arise naturally.

The *natural causes hypothesis* argues that COTS outbreaks are not necessarily caused or triggered by significant and recent anthropogenic changes in marine environments and habitats (Dana, 1970; Newman, 1970; Vine, 1970), but are part of the normal population fluctuations typical of marine organisms with planktotrophic larvae (Uthicke et al., 2009). In general, studies that did not show evidence of external or anthropogenic drivers of COTS outbreaks were categorised under ‘Natural Causes’ and out of the 42 studies included, only eight studies explicitly proposed or supported the *natural causes hypothesis* (7 out of the 8 were studies published pre-1990). Moore (1978) argued that although COTS conform broadly to r-strategies, they also exploit longer-lived habitats; therefore, periodic outbreaks are inherent to COTS. As a mechanism for the formation of outbreaks, Dana et al. (1972) suggested that these aggregations are redistributions of existing populations which at some point in their recent history have been brought together under conditions of food limitation, such as cyclones. This is supported in part by surveys conducted around the island of Oahu in Hawai'i, where the localised outbreaks represented an active aggregation towards reef areas with high cover of preferred coral prey (Kenyon & Aeby, 2009). Indeed, COTS are attracted to chemical signals from preferred coral species (Ormond et al., 1973), can travel relatively large distances (Mueller et al., 2011; Pratchett et al., 2017b), and have the ability to delay diet shift to corallivory in the absence of coral prey (Deaker et al., 2020a).

One of the key pieces of evidence to support the *natural causes hypothesis* is proof that outbreaks have occurred in the past and are not recent phenomena. Several attempts have been made to establish a relationship between past outbreak events and the contribution of COTS skeletal elements to surface sediment (Frankel, 1978; Henderson, 1992; Walbran et al., 1989a). However, these attempts have been widely criticised because of assumptions regarding post-outbreak mortality patterns, dispersion of skeletal ossicles, and dating methodology (Fabricius & Fabricius, 1992; Keesing et al., 1992; Moran et al., 1986; Pandolfi, 1992). Exceptional biological features possessed by COTS, such as enormous fecundity (Babcock et al., 2016b; Pratchett et al., 2021a), high fertilisation rates (Babcock & Mundy, 1992; Benzie & Dixon, 1994), and relatively fast growth to reproductive maturity (Kettle & Lucas, 1987; Lucas, 1984) reinforce the notion that this species is predisposed to significant, but periodic, oscillations in population size (Uthicke et al., 2009). More recent studies have identified and validated these key life history and demographic traits that predispose COTS to population outbreaks, such as extreme reproductive potential (e.g., Babcock et al., 2016b; Pratchett et al., 2021a), larval plasticity in response to varying food conditions (e.g., Caballes et al., 2017b; Carrier et al., 2018; Wolfe et al., 2015a), larval cloning (e.g., Allen et al., 2019; Hart et al., 2021; Uthicke et al., 2021), dietary and reproductive flexibility (Caballes et al., 2021; Deaker et al., 2020a; Haywood et al., 2019; Uthicke et al., 2019), resilience to variable food environments (Caballes et al., 2017b; Nakajima et al., 2016; Wolfe et al., 2017), and phenotypically plastic growth dynamics (Deaker et al., 2020a; Wilmes et al., 2020a). The timing of primary outbreaks has also been found to follow a predictable pattern, with an average time period of approximately 15-17 years observed between the onset of successive outbreaks (Condie et al., 2018; Reichelt et al., 1990a; Vanhatalo et al., 2017). Explaining the specific timing or periodicity for the initiation of recurrent outbreaks is very difficult based on chronic or sustained changes in environmental or habitat conditions but must relate to stochastic or cyclical processes (Seymour & Bradburys, 1994; Wooldridge et al., 2015). One likely explanation for this pattern is the coupled oscillation between predator and prey, where COTS populations experience rapid growth and subsequent decline as they consume coral on reefs, coupled with the time needed for coral recovery on affected reefs. The lengthening of this period may be influenced by factors such as prolonged coral recovery time due to phenomena like coral bleaching and more severe cyclones (Mellin et al., 2019; Seymour & Bradbury, 1994).

Taken together, these findings show that **COTS possess inherent biological and demographic traits that predispose them to extreme fluctuations in reproductive success and population size** and that **coupled oscillations in the abundance of COTS and their coral prey explain the periodicity (~14 to 17 years) of recurrent outbreak events on the GBR**. Despite this, the role of extrinsic variables associated with anthropogenic impacts in triggering outbreaks or modulating population fluctuations cannot be discounted; more specifically, it is likely that anthropogenic impacts on water quality and reef habitats and assemblages have exacerbated the incidence or severity of COTS outbreaks, and/or undermined the capacity of reef ecosystems to withstand these perennial disturbances (Pratchett et al., 2014).

4.1.1.2 Predation

The type of studies included in this review which were relevant to the *predator removal hypothesis* (32 studies; see Table 7) were predominantly observational/ analytical (41%), with nine experimental (28%), and 10 conceptual/review/modelling (31%). Most of these studies have identified putative predators that may be important in regulating population outbreaks under specific conditions, though there is limited empirical evidence that COTS densities are consistently low in areas where predators are abundant. This highlights the challenges involved in collecting this evidence as specific reefs have to be identified and studies have to be conducted prior to the formation of primary outbreaks.

The *predator removal hypothesis* assumes that COTS populations are normally regulated by predation or predation risk. The cryptic behaviour of smaller COTS are proposed to have evolved as a predator avoidance strategy with larger starfish achieving a refuge in size (Keesing, 1995). Modelling exercises have also shown this hypothesis to be plausible under certain functional response and density-dependent conditions (Keesing & Halford, 1992a; McCallum, 1987; 1990; Ormond et al., 1990). However, it is difficult to identify at what stage in the life cycle predation is likely to exert sufficient influence to either moderate population replenishment, or directly suppress their local abundance. Sweatman (1995) attempted to document fish predation on juvenile COTS in the field, but did not observe significant levels of predation by large fish, even when juvenile COTS were presented to fish that were previously reported to feed on COTS (i.e., lethrinids). Alternatively, McCallum (1987) suggested that predation on low-density adult populations is the most likely phase in the outbreak cycle and stage in COTS life history, which outbreaks can be effectively suppressed. Although a large proportion of studies that addressed the *predator removal hypothesis* are observational (41%, 13 out of 32), it is noteworthy that none of these studies have actually documented or quantified active lethal predation by fish on COTS.

The key evidence for the role of predators in regulating COTS populations come from comparing the incidence of outbreaks between reefs that are open and closed to fishing (Kroon et al., 2021; McCook et al., 2010; Sweatman, 2008). Spatiotemporal modelling of COTS outbreaks in the GBR showed that the relative intensity of COTS outbreaks within no-take reefs substantially declined 10 years after the implementation of the Great Barrier Reef Marine Park (GBRMP) re-zoning plan in 2004 (Vanhatalo et al., 2017). Using the density of human populations on several islands in Fiji as a proxy for fishing intensity, Dulvy et al. (2004) found that COTS densities were higher on reefs where fishing intensity was high and the density of fish predators was low. In the GBR, Sweatman (2008) showed that the incidence of COTS outbreaks was 3.75 times higher on GBR midshelf reefs that were open to fishing compared to no-take marine reserves. Re-examination of the link between no-take zones and the likelihood of COTS outbreaks using more current data yielded similar results, albeit with less statistical difference between reefs that are open and closed to fishing (Sweatman & Cappo, 2018). Kroon et al. (2021) modelled the response of COTS density to fish biomass removal and found that densities are 2.8-fold higher on reefs that are open to fishing, suggesting that COTS densities increase systematically with increasing fish biomass removal, including for known COTS predators. Nevertheless, there is limited evidence that any exploited fishes are significant predators of COTS (reviewed in Cowan et al., 2017a). The application of DNA technology to detect COTS in fish faecal and gut content samples has emerged as a useful tool in identifying predators, although food web transfer of COTS DNA cannot be ruled out for some fish species (Kroon et al., 2020). Alternatively, a plausible positive link between commercially exploited fishes and predation on COTS could involve a trophic cascade where higher numbers of large piscivores in no-take areas reduce densities of benthic carnivorous fishes such as wrasses, consequently causing ecological release of invertebrates that prey on juvenile COTS in the rubble (Sweatman, 2008). This is supported by field experiments demonstrating that epibenthic fauna caused significant levels of mortality in juvenile COTS (Keesing & Halford, 1992b; Keesing et al., 1996; 2018). However, there is currently no published data from the GBR on the distribution and abundance of benthic invertebrates inside and outside of no-take zones.

Although not immediately fatal, sublethal injuries on COTS can be used as an index of relative predation intensity (McCallum et al., 1989). Caballes et al. (2022) found that the prevalence of sublethal injuries was significantly higher for COTS collected from reefs within no-take areas, where fishing is effectively prohibited, compared to reefs where fishing is permitted, which could be a possible mechanism to explain the lower incidence of COTS outbreaks on reefs that are closed to fishing (Kroon et al., 2021; McCook et al., 2010; Sweatman, 2008). Taken together, this body of evidence suggests that higher densities of putative predators, particularly larger benthic feeding fishes (Kroon et al., 2020), within no-take marine reserves (Kroon et al., 2021), may serve to moderate populations and perhaps even suppress localised COTS outbreaks.

Overall, **the incidence of COTS outbreaks is generally lower, while the prevalence of sublethal injuries on COTS is higher, in areas where fishing is prohibited, and a higher abundance of putative predators is expected**. Moreover, laboratory and field experiments, as well as modelling studies, indicate that **predation rates on post-settlement juveniles are often significant and have the potential to regulate**

COTS populations. Despite all the circumstantial evidence outlined above, there is limited empirical data on comparative rates of predation mortality – whether this is due to large fish consuming adult COTS or small fish and benthic invertebrates consuming juvenile COTS, or both. Furthermore, conceptual models and empirical evidence for trophic cascades on the GBR are poorly developed. Despite these caveats, manipulating predator density is currently the only area in which management appears to have positive effects in mitigating the impacts of COTS, excluding direct culling.

4.1.1.3 Nutrients

Overall, the type of studies included in this review which were relevant to the *nutrient hypothesis* (40 studies; see Table 7) is evenly distributed: 14 experimental (35%), 13 observational/ analytical (32.5%), 13 conceptual/review/modelling (32.5%). However, only 17 (42.5%) out of the 40 studies explicitly provide evidence in support of the contribution of nutrients from terrestrial runoff to COTS outbreaks in the GBR. Most of the studies directly addressing the *nutrient hypothesis* are conceptual, review, or modelling (12 out of 17, 70.6%), which highlight the complexities of this hypothesis. For the *nutrient hypothesis* to explain COTS outbreaks in the GBR, evidence for key individual links in the complete chain of evidence (see below) need to be established. The evidence for individual elements in the evidential chain and the key knowledge gaps are highlighted below. Taken together, the findings show that**:** 1) the increase in nutrient load of runoff into GBR coastal waters from North Queensland rivers following agricultural development on catchments is well documented; 2) the concentration and availability of nutrients increases following heavy river discharge and land runoff, although COTS outbreaks do not consistently occur in the aftermath of heavy river discharge events; 3) phytoplankton blooms and shifts in phytoplankton community structure resulting from nutrient enrichment during flood events have been documented in the past, although the question remains whether phytoplankton concentration (chlorophyll *a* levels) alone, or specific phytoplankton species that become dominant during blooms, or both conditions are necessary, to drive enhanced survivorship and development rates in COTS larvae; 4) survival, growth, and development rates are generally higher for well-fed COTS larvae, but there is a lower and upper threshold for optimal food levels based on laboratory-based experiments; 5) the fundamental assumption that larval supply is generally limiting, such that outbreaks arise due to pronounced and temporary increases in larval survivorship, has yet to be explicitly tested; and 6) outbreaks of COTS on the GBR appear to start on midshelf reefs in the northern sector (perhaps even the far northern sector) of the GBR and larvae produced by these primary outbreaks are subsequently retained on natal reefs or dispersed to reefs south of the putative 'initiation area' according to prevailing hydrodynamic regimes, thereby resulting in secondary outbreaks.

Evidence for the increase in nutrient load of runoff into GBR coastal waters from North Queensland rivers following agricultural development on catchments (addressed in Question 2.3, Lewis et al., and Question 4.4, Prosser & Wilkinson, this SCS)

Based on water quality monitoring studies, proxy records, and modelling exercises, Lewis et al., (Question 2.3, this SCS) state that there is strong evidence to support the conclusion that loads of nutrients have increased from most basins of the GBR since the arrival of Europeans. Models suggest that nearly half of the total dissolved inorganic nitrogen (DIN) load exported from the GBR catchments is from the Wet Tropics Natural Resource Management (NRM) region, and half of the total DIN load exported to the GBR lagoon is derived from the sugarcane cropping areas. Prosser and Wilkinson (Question 4.4, this SCS) add that there is high confidence from both observations and model results that export of DIN to the marine environment is approximately double compared to pre-development exports, as a result of fertiliser added nitrogen being lost to rivers and sugarcane is by far the largest fertiliser-adding land use. Based on the evidence, or lack thereof, it is now widely accepted that COTS outbreaks, at the recent frequency and intensity observed, did not occur in the distant past (see discussion under "Natural Causes" above). These findings demonstrate that **the increase in nutrient load of runoff into GBR coastal waters from North Queensland rivers following agricultural development on catchments is well documented.**

Evidence for the increase in the concentration and availability of nutrients following heavy river discharge and land runoff (addressed in Question 4.1. Robson et al., this SCS)

In their evidence synthesis, Robson et al., (Question 4.1, this SCS) state that there is strong evidence to support the conclusion that elevated nutrient concentrations are associated with freshwater discharge from rivers, particularly in flood plumes during the wet season (November to April). Nutrient concentrations vary from year to year and are elevated in years of high river discharge and storm activity. These nutrient-rich flood plumes extend throughout the inshore region of the GBR and sometimes reach midshelf waters after major flood events. Direct observations (e.g., Devlin & Brodie, 2005), satellite imagery (e.g., Furnas et al., 2013; Schroeder et al., 2012), and modelling (e.g., King et al., 2002) clearly show that major flooding events can affect the inshore and midshelf sections of the Wet Tropics region, and nutrient-rich plumes from the large floods in the Burdekin and Herbert Rivers can flow northward into and beyond the proposed 'initiation area' of COTS primary outbreaks, north of Cairns (Brodie et al., 2017). This purported 'initiation area' (Fabricius et al., 2010) overlaps with the area where nutrient-rich river discharge enters the midshelf waters of the GBR on a regular basis (Brodie et al., 2005). When the chronology of the initiation of primary outbreaks over the last 70 years (1962, 1979, 1994, 2010; see Pratchett et al., 2014) was overlaid on top of estimates of annual river discharge, particularly the river discharge during the period when COTS larvae are in their pelagic feeding stage (early wet season), a pattern emerges wherein outbreaks appear to start 2-5 years after a wet season with discharge that exceeded 10 km^3 before the end of February (Figure 4). This shows that the initiation of outbreaks between Cairns and Lizard Island seemed to follow (2- to 5-year lag for COTS to reach adult stage) large runoff events that occurred in the early wet seasons beginning in 1957, 1973, 1991, and 2008 (Fabricius et al., 2010). If the previously recorded periodicity of population outbreaks continues, it is likely that another wave of outbreaks will commence between 2023 and 2026 (Babcock et al., 2020), although it remains to be seen whether this will be preceded by heavy river discharge, as suggested by Furnas et al. (2013). Pratchett et al. (2014) argued that not all major flood events in the GBR have initiated outbreaks, although Fabricius et al. (2010) did stress that large floods must occur between November and January to benefit COTS larvae.

Without considering its direct link to COTS, there is strong evidence that **the concentration and availability of nutrients increases following heavy river discharge and land runoff**, although a recent analysis by Kroon et al. (2023) suggests that oceanographic processes such as upwelling and intrusive events may be more important in the interannual variability of nutrient concentrations in midshelf waters in the Wet Tropics than previously understood. Studies outside the GBR, where the role of terrestrial runoff from river discharge is absent or negligible, have emphasised the importance of upwelling events in causing localised increases in nutrient concentration (Houk & Raubani, 2010; Mendonça et al., 2010; Roche et al., 2015). In the southern GBR, Miller et al. (2015) suggest that a primary outbreak in the Capricorn-Bunker Group appears to have been associated with elevated chlorophyll *a* concentrations brought by upwelling events. Although Miller et al. (2015) considered the role of one southern river (Fitzroy River), Brodie et al. (2017) argue that while the Fitzroy River discharge only influences the northern section of the Capricorn-Bunker Group reefs during rare large flood events that are coupled with favourable wind conditions, the five rivers to the south of the Fitzroy are also known to influence phytoplankton dynamics in the southern Capricorn-Bunker Group, which may influence the survivorship of COTS larvae in this region. Nevertheless, as Pratchett et al. (2014) pointed out, **COTS outbreaks do not consistently occur in the aftermath of heavy river discharge events**, especially when relevant lags in development are taken into account, which suggests that other variables may play an important role in triggering outbreaks. It is also possible that low salinity associated with major flood plumes will reduce survival of COTS larvae and thereby mediate any beneficial effects of elevated nutrients during heavy river discharge events (Clements et al., 2022).

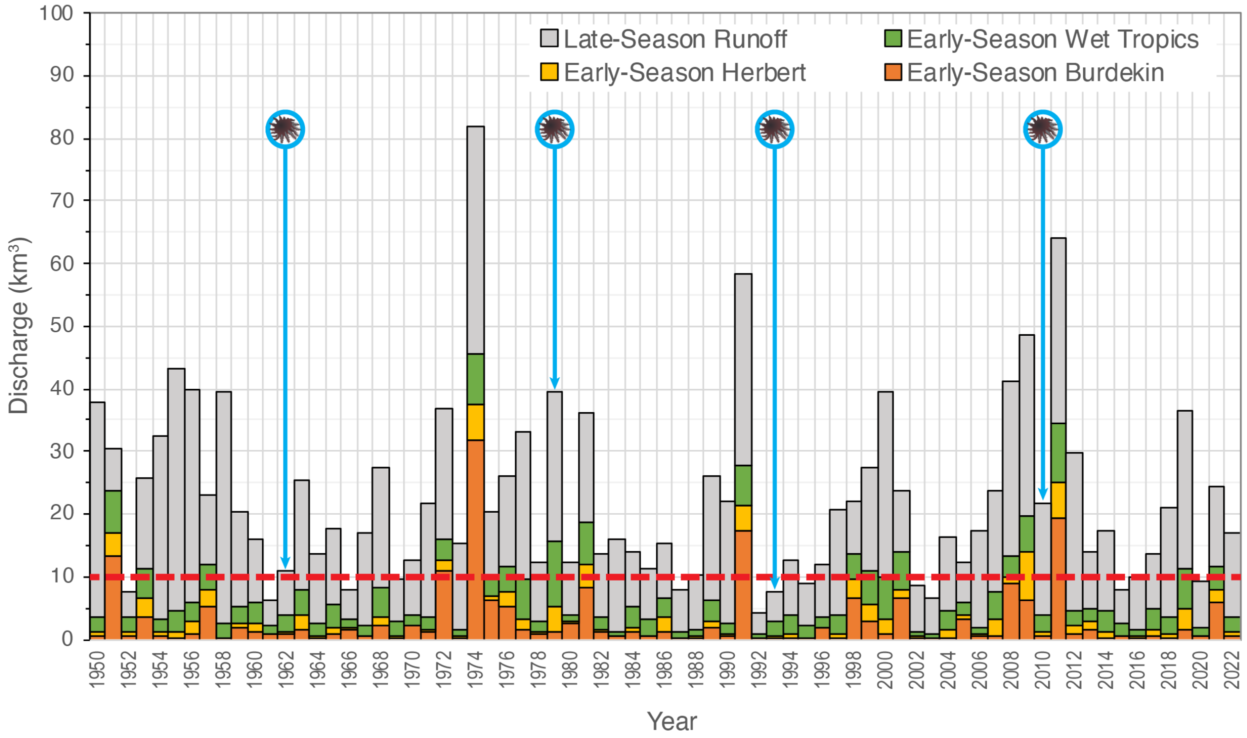


Figure 4. Estimated annual river runoff (total bars) during wet seasons from 1950 to 2022. Coloured segments (i.e., yellow, green, orange) show estimated early wet season (Nov-Feb) freshwater runoff into the north and central Great Barrier Reef. Runoff data was integrated from the Daintree, Barron, Mulgrave-Russell, Johnstone, Tully, Herbert and Burdekin Rivers. The Burdekin and Herbert flow data were lagged 28 and 14 days, respectively, to allow for transport into the Cairns – Lizard Island outbreak region. The blue vertical arrows indicate nominal years of COTS outbreak initiation, and the red horizontal dashed line shows a runoff volume of 10 km^3. Modified from Furnas et al. (2013); post-2012 data provided by Stephen Lewis (JCU TropWATER).

Evidence for phytoplankton blooms and shifts in phytoplankton community composition as a result of elevated nutrients and the persistence of these conditions immediately following the spawning period of COTS in the GBR (addressed, in part, by Question 4.2, Diaz-Pulido et al., this SCS)

In their review, Diaz-Pulido et al. (Question 4.2, this SCS) show that there is strong evidence that phytoplankton blooms follow heavy discharge of nutrient-rich flood plumes from rivers and that this has been well documented in many regions of the GBR, including the central and northern GBR, within the proposed 'initiation area' (see discussion on 'COTS initiation area' below). Brodie et al. (2007) have demonstrated that chlorophyll *a* measurements are a reliable indicator of exponential increases in phytoplankton biomass and this has been used to assess water quality in the GBR (see Question 4.2, Diaz-Pulido et al., this SCS). In their microscopic analysis of phytoplankton community structure from samples collected during flood plume periods, Devlin et al. (2013) found that the highest phytoplankton cell counts were also associated with the highest concentrations of chlorophyll *a*. Aside from increased phytoplankton biomass, elevated nutrient concentrations during heavy river discharge can also result in rapid changes in the composition of phytoplankton communities in the GBR lagoon, from a picoplankton-dominated system to one dominated by diatoms and dinoflagellates (Furnas et al., 2005). Increased concentrations of DIN and intermediate salinity have been identified as the main drivers of shifts in community structure towards larger size classes of phytoplankton during high flow events (Devlin et al., 2013). High chlorophyll *a* concentrations were mainly driven by very high counts of the nanoplankton species, particularly, *Skeletonema* sp., a small diatom that responds quickly to elevated nutrients and is typically abundant in eutrophic systems. Aside from its potential role as a spawning cue for COTS (Caballes & Pratchett, 2017), to date, there have been no studies on whether feeding on *Skeletonema* sp. can enhance survival of COTS larvae. The peak spawning period of COTS in the GBR is between November and December (Babcock & Mundy, 1992; Uthicke et al., 2019), but can be protracted up to February depending on interannual variation in summer temperatures (Caballes et al., 2021). While most of the changes in phytoplankton biomass and community structure associated with elevated nutrients are short-lived, some have been documented (associated with flood plumes), albeit rarely, to coincide with the pelagic feeding larval phase of COTS (Devlin et al., 2001). Although **phytoplankton blooms and shifts in phytoplankton community structure resulting from nutrient enrichment during flood events have been documented in the past, the question remains whether phytoplankton concentration (chlorophyll *a* levels) or specific phytoplankton species that become dominant during blooms, or a combination of both, is necessary, to drive enhanced survivorship and development rates in COTS larvae** (see discussion on larval diet in next section). A better understanding of the evolution and composition of phytoplankton blooms and the nutrient constituents that drive them is critical.

Evidence for enhanced growth and survival of COTS larvae in high food (phytoplankton) conditions

One of the foundational assumptions of the nutrient hypothesis is that larvae are normally food limited (Fabricius et al., 2010; Lucas, 1982). *In situ* culturing experiments by Olson (1987) disputed this assumption and demonstrated that COTS larvae were able to develop at near-maximal rates in the absence of phytoplankton blooms, suggesting that larvae could make up food limitation by ingesting bacteria and other food sources such as dissolved organic matter. However, subsequent studies have shown that larvae are unable to ingest bacteria (Ayukai, 1994) and that based on ingestion rates, it is unlikely that cyanobacteria form a sufficient component of the diet of COTS larvae (Okaji et al., 1997). Although COTS larvae are also able to take up dissolved free amino acids (Hoegh-Guldberg, 1994), their concentrations in natural seawater are probably too low to make a significant contribution to larval nutrition (Ayukai, 1994). Nevertheless, the 12 experimental studies (see Table 8) that investigated the feeding ecology of COTS larvae are generally in agreement that well-nourished larvae have relatively better survivorship and faster developmental rates (Caballes et al., 2017b; Clements et al., 2022; Lucas, 1982; Mellin et al., 2017; Okaji, 1996; Olson, 1985; 1987; Pratchett et al., 2017c; Uthicke et al., 2015a; 2018b; Wolfe et al., 2015b; 2017), which is typical for asteroids and other marine invertebrates with planktotrophic larvae. To date, the direct effect of specific nutrient components on COTS larvae has not been investigated. Instead, studies on the feeding ecology of COTS larvae have used a range of cell densities for cultures of phytoplankton species and corresponding chlorophyll *a* concentrations as a proxy for nutrient enrichment. Only 3 out of the 12 studies (Olson, 1985; 1987; Okaji, 1996) were conducted in the field, all using modifications of *in situ* culture chamber apparatus designed by Olson (1985). Despite switching chambers every two days, following Olson (1985), Okaji (1996) found that the chambers created an artificially enriched food environment for the larvae (chlorophyll concentration within chambers above ambient levels), presumably due to retention of algal contaminants, and decided to abandon this approach in favour of using freshly collected filtered seawater at varying levels of enrichment to simulate changes in natural phytoplankton abundance and community structure. This series of experiments were later described in Fabricius et al. (2010) to show that the odds of COTS larvae completing development increases ~8-fold with every doubling of chlorophyll concentrations up to 3 μg L^{-1}, above which, completion of development was predicted to be certain. More recent experiments (Clements et al., 2022; Pratchett et al., 2017c; Wolfe et al., 2015b; 2017), using a single species diet of the tropical microalgae, *Proteomonas sulcata*, however, have recorded moderate levels of larval survivorship and settlement at chlorophyll concentrations well below (0.1 μg L^{-1}) the thresholds reported by Fabricius et al. (2010). These differences may be explained by variation in the chlorophyll concentrations of different microalgae, whereby cell densities used by Pratchett et al. (2017c) and Wolfe et al. (2015b) are very high (1–100 × 10^3 cells·mL^{-1}) relative to the cell densities used by Fabricius et al. (2010), suggesting that *P. sulcata* has a very low cell-specific chlorophyll concentration (Brodie et al., 2017). Experiments by Wolfe et al. (2015b) and Pratchett et al. (2017b), show that high cell densities of *P. sulcata* were more deleterious for larval survival and settlement. Studies using a mixed diet of 2-3 species of phytoplankton (Caballes et al., 2017b; Uthicke et al., 2018b) did not observe the negative effect documented at extreme algae cell densities outside the natural range, including flood event conditions. This suggests that conducting experiments with COTS larvae raised on a single phytoplankton species has the potential to significantly bias results depending on how preferred the single species is as a dietary component. In contrast, a mixed diet comprised of a variety of phytoplankton species may be more reflective of natural conditions. Low salinity waters, which coincide with nutrient enrichment, during high river runoff events, have also been recently shown to be detrimental to COTS bipinnaria larvae (Clements et al., 2022). However, the levels of salinity (22–25‰) that were shown to be deleterious to COTS larvae most likely only affect the top layer and it is not yet known whether COTS larvae can swim to more favourable halocline layers along the water column. Recent studies have also revealed that climate change introduces complexities in the association between food concentration and larval condition (Hue et al., 2022; Kamya et al., 2014; Uthicke et al., 2015a). Overall, these findings show that **survival, growth, and development rates are generally higher for well-fed COTS larvae, but there is a lower and upper threshold for optimal food levels**. Given the inconsistencies highlighted above, further studies are warranted, particularly comparing specific cell densities and quantifying cell-specific chlorophyll values (sensu Mellin et al., 2017) when using chlorophyll concentrations as a proxy for food availability, as well as testing the influence of food availability on nutritional condition of COTS larvae in the field.

Table 8. Summary of experiments on the feeding ecology of larvae from GBR COTS showing survival or development rates under different levels of algal food cell density or chlorophyll concentration. DIET: 0.45-FSW = 0.45-µm filtered seawater, 2-FSW = 2-µm filtered seawater, 25-FSW =25-µm filtered seawater, AES = alga enriched seawater; CHL = chlorophyll concentration ($\mu g\ L^{-1}$); ALG = algal food density (cells mL^{-1}); SURV = survival (%); DEVT = development (% of larvae at most advanced stage when experiment was terminated: NBP = normal bipinnaria, MBR = mid-brachiolaria, LBR = late brachiolaria, SET = settled or metamorphosed juvenile); DENS = larval density (number of larvae per 100 mL); DAYS = duration of experiment. Values for survival and development were estimated using PlotDigitizer 3.1.5 (https://plotdigitizer.com) for studies that only show this information in graphs.

Study	DIET	CHL	ALG	SURV	DEVT	DENS	DAYS	Key findings
Lucas, 1982	*Dunaliella primolecta*	0	0	0	0 LBR	24	27	Larval development through the brachiolaria stages, with production of a starfish primordium, depended on the environmental food regime. All phytoplankton species tested supported at least some survival through complete larval development, but there were marked differences in rates of development and survival on the different diets. Food availability in the field was generally low or marginal for the nutritional requirements of COTS larvae, suggesting that food is a major environmental influence on survival and development of COTS larvae in the GBR.
		0.65[a]	500	54	23 LBR	24	43	
		1.3 [a]	1,000	63	52 LBR	24	44	
		6.5 [a]	5,000	83	78 LBR	24	27	
			10,000	45	37 LBR	24	27	
			50,000	47	38 LBR	24	27	
	Phaeodactylum tricornutum	0	0	1	0 LBR	24	27	
		0.4 [a]	1,000	22	0 LBR	24	27	
		2 [a]	5,000	78	70 LBR	24	27	
		3.9 [a]	10,000	67	67 LBR	24	27	
			50,000	1	1 LBR	24	27	
			100,000	1	1 LBR	24	27	
	Dunaliella tertiolecta		5,000	80	59 LBR	24	22	
			5,560	77	61 LBR	24	22	
	Amphidinium carterae		912	46	3 LBR	24	33	
			5,000	28	23 LBR	24	33	
	Pavlova lutheri		5,000	55	0 LBR	24	41	
			14,090	84	12 LBR	24	41	
	Prymnesium parvum		5,000	20	9 LBR	24	22	
			6,650	28	6 LBR	24	20	
	Porphyridium purpureum		1,090	55	9 LBR	24	33	
			5,000	55	15 LBR	24	34	
Olson, 1985	Ambient seawater	0.15-0.16		40-58	68-84 MBR	27	12	Larvae that survived appeared healthy, active, showed little or no signs of dedifferentiation, and

Study	DIET	CHL	ALG	SURV	DEVT	DENS	DAYS	Key findings
								developed normally over 12 days.
Olson, 1987	Ambient seawater	0.2-0.3	0	54	13 SET	30	16	Enrichment of diet resulted in no significant difference in survivorship (compared to larvae feeding only on natural seawater) and only a slight difference in development rates.
	D. primolecta		1,000-10,000	56	36 SET	30	16	
Okaji, 1996	0.45-FSW	0.07		6	0 SET	10	26	Using the combined results from these experiments, Fabricius et al. (2010) proposed these chlorophyll thresholds: At <0.25 μg L^{-1}, a negligible proportion of larvae complete development, suggesting starvation. At 0.25–0.8 μg L^{-1}, this proportion is moderate, but development is slow and body sizes of larvae and juveniles remain small, suggesting severe food limitation. Finally, at >2 μg L^{-1}, larval developmental success is high, developmental speed is fast, and both larvae and juveniles grow to their maximum observed size, suggesting release from trophic limitation.
	2-FSW	0.17	4[b]	35	0 SET	10	26	
	25-FSW	0.40	214[b]	81	0 SET	10	26	
	AES	8.06	3,000-4,000	50	18 SET	10	26	
	0.45-FSW	0.08		94	0 SET	10	16	
	2-FSW	0.25	4[b]	55	0 SET	10	16	
	25-FSW	0.52	234[b]	87	0 SET	10	16	
	AES	8.54	3,000-4,000	82	64 SET	10	16	
	2-FSW	0.08	163[b]	58	0 LBR+SET	5	26	
	25-FSW	0.29	437[b]	71	19 LBR+SET	5	30	
	AES	7.48	3,000-4,000	60	63 LBR+SET	5	22	
	25-FSW	0.28	385[b]	77	0 LBR+SET	5	22	
	AES	5.70	3,000-4,000	66	89 LBR+SET		22	
	2-FSW	0.19	4[b]	76	0 LBR+SET	5	22	
	25-FSW	0.28	207[b]	42	88 LBR+SET	5	24	
	50% NES	2.91	2,435[b]	85	100 LBR+SET	5	22	
	100% NES	5.25	4,441[b]	70	100 LBR+SET	5	22	
	2-FSW	0.19	4[b]	51	0 LBR+SET	5	22	
	25-FSW	0.28	207[b]	57	97 LBR+SET	5	22	
	50% NES	2.91	2,435[b]	74	99 LBR+SET	5	22	
	NES	5.25	4,441[b]	61	100 LBR+SET	5	22	
	NES	0.10			0 LBR+SET	7.5	22	
	NES	0.20			0 LBR+SET	7.5	22	
	NES	0.40			0 LBR+SET	7.5	22	
	NES	0.80			32 LBR+SET	7.5	22	
	NES	1.60			50 LBR+SET	7.5	22	
	NES	0.01			0 LBR+SET	7.5	22	
	NES	0.25			0 LBR+SET	7.5	22	
	NES	0.50			7 LBR+SET	7.5	22	
	NES	0.75			39 LBR+SET	7.5	22	
	NES	1.00			62 LBR+SET	7.5	22	
Uthicke et al., 2015a	Mixed Diet: *Chaetoceros sp. (31%)*	0.67	1,100		11 MBR+LBR	100	24	This study also examined the effects of temperature. When
		1.8	2,800		17 MBR+LBR	100	24	

Study	DIET	CHL	ALG	SURV	DEVT	DENS	DAYS	Key findings
	P. tricornutum (61%) *Dunaliella sp. (8%)*	2.55	4,200		22 MBR+LBR	100	24	results for food concentration were considered in isolation, there was a 5-fold increase in the proportion of late brachiolaria at 24 days across the range of food concentrations tested.
		4.85	7,000		38 MBR+LBR	100	24	
		7.11	9,800		56 MBR+LBR	100	24	
Wolfe et al., 2015b	*Proteomonas sulcata*	0	0	63	0 SET	100	16	Chlorophyll levels of 1 µg L^{-1}, were optimal for larval success. Development was less successful above and below this food treatment.
		0.01	100	55	2 SET	100	16	
		0.1	1,000	66	2 SET	100	16	
		1	10,000	66	37 SET	100	16	
		10	100,000	73	19 SET	100	16	
Caballes et al., 2017b	Mixed Diet: *Dunaliella tertiolecta (30%)* *Chaetoceros muelleri (70%)*		0	28	0 MBR+LBR	67	16	This study also examined the interactive effects of maternal nutrition. None of the starved larvae reached the mid-to-late brachiolaria stage at 16 days. There was no significant difference in the survival, development, and competency of larvae between high and low food treatments.
			1,000	54	13 MBR+LBR	67	16	
			10,000	56	15 MBR+LBR	67	16	
Pratchett et al., 2017c	*P. sulcata*	0.1	1,000	26	10 SET	120	17[c]	Larval survival was greatest at intermediate algal concentrations (10,000 cells mL^{-1}). Rates of settlement were also highest at intermediate food levels and peaked at 22 days post-fertilisation.
		1	10,000	40	28 SET	120	17[c]	
		10	100,000	22	21 SET	120	17[c]	
Mellin et al., 2017	*P. tricornutum*	0.31[d]	1,000, 3,000			100	7	This study did not measure larval condition, but quantified ingestion rates, as it relates to the quality of algal food. Greatest energy gain in the single species experiment was from the ingestion of high concentration of *Dunaliella sp.* In the mixed-species experiment, the greatest energy gain was obtained from the ingestion of *Dunaliella sp.* and *Chaetoceros sp.* followed by that of *Dunaliella sp.* mixed with *T. lutea.*
	P. lutheri	0.58[d]	1,000, 3,000			100	7	
	Tisochrysis lutea	0.35[d]	1,000, 3,000			100	7	
	Dunaliella sp.	1.05[d]	1,000, 3,000			100	7	
	Chaetoceros sp.	0.75[d]	1,000, 3,000			100	7	
	Mixed Diet: Dunaliella sp. (50%) *T. lutea* (50%)		1,000, 3,000			100	7	
	Mixed Diet: Dunaliella sp. (50%) *Chaetoceros* sp. (50%)		1,000, 3,000			100	7	
	Mixed Diet: Dunaliella sp. (50%) *P. lutheri* (50%)		1,000, 3,000			100	7	

Study	DIET	CHL	ALG	SURV	DEVT	DENS	DAYS	Key findings
	Mixed Diet: *Dunaliella* sp. (50%) *P. tricornutum* (50%)		1,000, 3,000			100	7	
Wolfe et al., 2017	*P. sulcata*	0.1	1,000	49	23 SET	100	19	Survival was highest for larvae reared at 0.8–1.0 µg chlorophyll L^{-1}. Around 30% of larvae had settled in the two highest chlorophyll treatments (1.0–5.0 µg L^{-1}), while settlement in the lower food treatments was 23–26%.
		0.5	5,001	83	26 SET	100	19	
		0.8	8,001	93	23 SET	100	19	
		1	10,002	93	31 SET	100	19	
		5	50,007	84	30 SET	100	19	
Uthicke et al., 2018b	Mixed Diet: *Dunaliella* sp. (60%) *Tisochrysis lutea* (40%)	0.33	761	7[e]		44	15	This study also examined the effect of larval density. Increasing food concentrations increased the probability of reaching late-brachiolaria stage. Larvae under low densities at a given algae concentration being further developed than those under higher densities.
		0.22	506	1[e]		77	15	
		0.21	481	5[e]		158	15	
		0.33	558	3[e]		50	15	
		0.32	540	5[e]		86	15	
		0.25	428	4[e]		178	15	
		0.72	1,031	4[e]		52	15	
		0.72	1,020	3[e]		76	15	
		0.63	892	1[e]		184	15	
		1.01	1,075	2[e]		61	15	
		0.87	932	2[e]		111	15	
		0.71	760	1[e]		228	15	
		0.45	481	4[e]		62	15	
		0.38	402	3[e]		112	15	
		0.28	302	1[e]		222	15	
Clements et al., 2022	*P. sulcata*	0.1	0	88	88 NBP	100	7	This study also examined the effect of salinity. Food concentration, at the levels tested, did not have a significant effect on larval survival and development. Salinity levels <22-25‰ were deleterious to larvae.
		1	10,000	70	70 NBP		7	
		5	20,000	83	73 NBP		7	

[a] chlorophyll values derived from published measurements for these species

[b] density of eukaryotic cells (cells mL^{-1})

[c] duration of experiment was 50 days, but data for survival and settlement estimated from non-linear splines at 17 days

[d] cell-specific chlorophyll concentration (pg cell^{-1})

[e] values represent daily mortality rates, instead of % survival

Evidence that high settlement rates from high densities of larvae completing development lead to primary outbreaks

High densities of COTS larvae and high recruitment are a fundamental precursor of elevated densities of adult COTS and population outbreaks. Establishing stock-recruitment relationships is essential in validating links between enhanced larval survival and recruitment, particularly as it relates to the *nutrient hypothesis*, which hinges entirely on the notion that survival of high densities of larvae from a single mass spawning event consequently translates to high recruitment. Despite this, observations of newly settled COTS in the field are rare (Yokochi & Ogura, 1987; Zann et al., 1990). Although there was limited success in finding newly settled COTS in the GBR, more recent work by Wilmes et al. (2016;

2020a; 2020b) demonstrated that 0+ year juveniles can be effectively sampled in the field. Alternatively, outbreaks may also develop through an accumulation of distinct cohorts from multiple recruitment events (Pratchett, 2005). Deaker et al. (2020a) also suggest that under extremely poor coral conditions, juveniles can delay transition to corallivory for several years until conditions become more favourable, which could lead to the build-up of juveniles that seed outbreaks. Population outbreaks around Lizard Island almost certainly developed through several consecutive years of high recruitment from 1994 to 1998 (Pratchett, 2005), making links to individual stochastic events (e.g., individual flooding events) somewhat tenuous (Pratchett et al., 2014). However, Fabricius et al. (2010) argue that these consecutive years of successful recruitment can be accounted for by an unusual frequency of flooding events reaching this part of the shelf in 1991, 1994, 1995 and 1996. To date, **the fundamental assumption that larval supply is generally limiting, such that outbreaks arise due to pronounced and temporary increases larval survivorship, has yet to be explicitly tested** due to the inability to quantify larval supply, settlement, and recruitment in the field. New methods aimed at measuring these processes are being developed and tested (Doll et al., 2021; Uthicke et al., 2015b; Wilmes et al., 2020b) and will provide new opportunities to test questions pertaining to recruitment limitation. In particular, recent developments in environmental DNA (eDNA) technology has highlighted its applicability as a tool for monitoring and studying COTS at different life history stages in the field, especially when used alongside fine-scale survey methods (e.g., Doll et al., 2021; Doyle & Uthicke, 2020; Doyle et al., 2017; Kwong et al., 2021; Uthicke et al., 2018a; 2022).There are still unresolved questions as to whether high local densities of larvae (larval supply) are required to achieve high rates of effective settlement. Critical to understanding the *nutrient hypothesis*, it is especially important to establish whether increased food availability and nutritional condition of late-stage larvae lead to higher larval survival and settlement success, thereby enhancing population replenishment. Further studies to explore recruitment limitation or stock-recruitment relationships are also warranted. There are also important questions about how far and how fast COTS can move within and among reef habitats after they have settled, which will determine relevant scales of recruitment limitation (Mueller et al., 2011; Pratchett et al., 2017b).

Evidence that increased larval output from the 'initiation area' triggers secondary outbreaks on other reefs

Although this link in the evidential chain may not directly pertain to the role of nutrients in the initiation of primary outbreaks, studies on the patterns and mechanisms involved in the spread of outbreaks are important as the location and timing of outbreak initiation is critical in assessing the role of factors (e.g., nutrients) proposed to drive COTS outbreaks. This was the rationale for including studies (11 out of 183) that examined the role of hydrodynamics in the propagation of outbreaks (larval dispersal and larval retention).

Not all reefs on the GBR experience COTS outbreaks (Reichelt et al., 1990a) and the initiation and spread of these outbreaks usually follow a predictable pattern (Moran et al., 1992; Vanhatalo et al., 2017). Each documented wave of outbreaks (1962, 1979, 1994, 2010; see Pratchett et al., 2014), originated from midshelf reefs located between Lizard Island (14.6°S) and Cairns (17°S), an area commonly referred to as the COTS 'initiation area' (Fabricius et al., 2010; Kroon et al., 2023; Pratchett et al., 2014). It is possible however, that population outbreaks of COTS may originate on reefs located at even lower latitudes, north of the designated 'initiation area' (e.g., Vanhatalo et al., 2017), and that the proliferation of COTS observed around the Lizard Island region could be attributed to the secondary accumulation of larvae produced by established COTS populations at reefs situated further north (see section *4.5 Knowledge gaps*). In contrast, van der Laan and Hogeweg (1992) argue that models using random and directional currents do not necessarily imply that there is a seed area in the northern GBR. Based on the re-analyses of size-frequency distributions of COTS populations from several distinct reefs during the first documented outbreak wave, Kenchington (1977) proposed that population outbreaks began in the northern GBR and spread southwards through localised larval dispersal. Sequential progression of population outbreaks occurred as each distinct population matured, spawned, and contributed to the production of larvae, which subsequently colonised reefs further south. This was later confirmed by detailed data on the spatiotemporal occurrence of population outbreaks at individual reefs along the GBR (Moran et al., 1992; Reichelt et al., 1990a; Vanhatalo et al., 2017) and by genetic analyses showing that outbreak populations on the GBR are derived from a single source most likely within the 'initiation area' (Benzie, 1992; Benzie & Stoddart, 1992; Benzie & Wakeford, 1997).

It is widely recognised that the substantial quantity of larvae generated by densely populated and well-nourished starfish during primary outbreaks inevitably result in subsequent secondary outbreaks on reefs located downstream (Pratchett et al., 2017a). The moderate connectivity among reefs facilitates a wave of secondary outbreaks carried by prevailing currents away from the 'initiation area' (Hock et al., 2014; Moran et al., 1992; Vanhatalo et al., 2017). Apart from hydrodynamics, dispersal distance is primarily limited by the time that larvae spend in the plankton (planktonic larval duration, PLD). While COTS may settle in as little as 9 days post-fertilisation (reviewed in Caballes & Pratchett, 2014), Pratchett et al. (2017c) demonstrated that COTS larvae can remain competent to settle up to 43 days post-fertilisation, which has significant implications for long-distance larval dispersal. Settlement peaks around 22 days post-fertilisation (Pratchett et al., 2017c), and COTS larvae typically disperse over distances ranging from tens to hundreds of kilometres between reefs (Dight et al., 1990a; 1990b; Hock et al., 2014), if not entrained within the confines of their natal reef (Black, 1993; Black & Moran, 1991).

Although larval delivery via hydrodynamic connectivity predominantly influences when and where secondary outbreaks arise, the delivery of high densities of COTS larvae to individual reefs would not necessarily result in the establishment of population outbreaks if there were local constraints on larval survival and development or high rates of post-settlement mortality (Wilmes et al., 2018). Previous discussions on the influence of river discharge and nutrient pulses on the GBR have mainly focused on the initiation of primary outbreaks (Brodie et al., 2005; Fabricius et al., 2010). It is, however, possible that primary outbreaks can propagate over extended periods without major flood events, while the subsequent spread of outbreaks might benefit from such events due to increased food availability and higher larval survival across larger reef areas. Brodie et al. (2017) suggest that suitable phytoplankton conditions provided by increased nutrient discharges from relevant rivers may also facilitate secondary outbreaks. This is highlighted by modelling work that indicates that larval connectivity and flood plume exposure were the best predictors for COTS outbreaks across the GBR (Matthews et al., 2020a).

Generally, these findings indicate that **outbreaks of COTS on the GBR appear to start on midshelf reefs in the northern sector (perhaps even the far northern sector) of the GBR and larvae produced by these primary outbreaks are subsequently retained on natal reefs or dispersed to reefs south of the putative 'initiation area' according to prevailing hydrodynamic regimes, thereby resulting in secondary outbreaks**. However, even if a reef receives a substantial number of well-fed and competent larvae, settlement and post-settlement survival can still be constrained by factors such as habitat structure, availability of coralline algae or coral prey, and the local abundance of potential predators (Keesing & Halford, 1992a; Wilmes et al., 2018). Moreover, advection of larvae towards reefs with favourable settlement substrate (Doll et al., 2023; Johnson et al., 1991) and suitable habitat for post-settlement juveniles (Wilmes et al., 2018; 2020b) is viewed as an important prerequisite for successful recruitment (Black & Moran, 1991; Johnson, 1992a; 1992b; Wilmes et al., 2018).

4.1.2 Recent findings 2016-2022 (since the 2017 SCS)

Approximately 81 of the 183 studies included in this Evidence Review (over 44%) have been published since the 2017 SCS. The main themes from these recent studies are:

- The potential impacts of climate change (warming and ocean acidification) on the early life history stages and predictions on the persistence of COTS populations under climate change scenarios (e.g., Allen et al., 2017; Caballes et al., 2017a; Haywood et al., 2019; Hue et al., 2020; 2022; Kamya et al., 2016; 2017; Keesing et al., 2019; Lang et al., 2021; 2022; Sparks et al., 2017).
- Applicability of eDNA technology as a tool for monitoring and studying COTS at different life history stages in the field (e.g., Doll et al., 2021; Doyle et al., 2017; Doyle & Uthicke, 2020; Kwong et al., 2021; Uthicke et al., 2018a; 2022).
- Identification and validation of key life history and demographic traits that predispose COTS to population outbreaks (reviewed in Deaker & Byrne, 2022a), such as extreme reproductive potential (e.g., Babcock et al., 2016b; Pratchett et al., 2021a), larval plasticity in response to varying food conditions (e.g., Caballes et al., 2017b; Carrier et al., 2018), larval cloning (e.g.,

Allen et al., 2019; Hart et al., 2021; Uthicke et al., 2021), dietary and reproductive flexibility (Caballes et al., 2021; Deaker et al., 2020b; Haywood et al., 2019; Uthicke et al., 2019), resilience to variable food environments (Caballes et al., 2017b; Nakajima et al., 2016; Wolfe et al., 2017), and phenotypically plastic growth dynamics (Deaker et al., 2020a; Wilmes et al., 2020a).

- Identification of new COTS predators at different life history stages, particularly predators of gametes, larvae, and juveniles (e.g., Balu et al., 2021; Cowan et al., 2016a; 2016b; 2017a; 2017b; 2020; Desbiens et al., 2023; Johansson et al., 2016; Kroon et al., 2020).
- New insights into the feeding ecology, habitat associations, and growth of juvenile COTS (Deaker & Byrne, 2022b; Deaker et al., 2020a; 2020b; 2021; Johansson et al., 2016; Neil et al., 2022; Wilmes et al., 2016; 2019; 2020a; 2020b).
- Assessment of the role of fisheries management and zoning on COTS populations in the GBR (Caballes et al., 2022; Kroon et al., 2021; Matthews et al., 2020a; Messmer et al., 2017; Sweatman & Cappo, 2018; Westcott et al., 2020; Wilmes et al., 2019).
- Re-evaluation of the link between water quality and COTS outbreaks in the GBR (Brodie et al., 2017; Caballes & Pratchett, 2017; Caballes et al., 2017b; Clements et al., 2022; Kroon et al., 2023; Mellin et al., 2017; Pratchett et al., 2017c; Uthicke et al., 2018b; Wolfe et al., 2017).

In addition, since 2017 there have been several reviews on the key knowledge gaps relevant to COTS research (Pratchett et al., 2017a; 2021b; Wilmes et al., 2018), as well as on the comparative efficacy of management approaches in the GBR (Babcock et al., 2016a; 2020; Matthews et al., 2020a; Pratchett & Cumming, 2019; Westcott et al., 2020).

4.1.3 Key conclusions

While distinct population outbreaks of COTS across the Indo-Pacific exhibit certain similarities, there is no reason to presume that these are all triggered by the same drivers. Indeed, the fact that no one hypothesis can fully account for the spatiotemporal patterns in the occurrence of COTS outbreaks suggests that multiple processes may be involved. Taken together, the body of available evidence suggests that outbreaks in the GBR are most likely driven by a combination of some aspect of the most prominent hypotheses discussed above. For instance, it is plausible that outbreaks may occur under natural conditions where COTS numbers and densities are sufficiently high, and when spawning coincides with high river runoff events that lead to nutrient enrichment and phytoplankton blooms, the survival and growth of COTS larvae are consequently enhanced. This, in turn, reduces the vulnerability of COTS larvae to planktivorous predators, allowing them to settle in high densities and form dense aggregations of juveniles, particularly if predation by epibenthic fauna is limited by the presence of large piscivores. The absence of a single overarching cause to definitively explain the occurrence and spatiotemporal distribution of COTS outbreaks reflects the inherent unpredictability of some key variables and the logistical challenges involved in measuring key parameters in the field.

Primary outbreaks of COTS are likely triggered by the spatiotemporal convergence of a combination of factors, which are distinct aspects within the three most prominent hypotheses: i) *natural causes hypothesis*, ii) *predator removal hypothesis*, and iii) *nutrient hypothesis*.

The key points of supporting evidence are:

- COTS outbreaks mostly occur on midshelf reefs in the GBR.
- COTS possess inherent life history traits that predispose populations to significant spatial and temporal fluctuations. This is supported by evidence of high fecundity, high fertilisation rates, and fast growth that predisposes them to naturally occurring extreme fluctuations in reproductive success and population size. These traits, coupled with the time required for recovery and regrowth of their coral prey, may explain the periodicity (~14 to 17 years) of recurrent outbreaks events on the GBR.
- The evidence shows that in areas where fishing is prohibited, the incidence of COTS outbreaks is generally lower, while the prevalence of sublethal injuries on COTS is higher, compared to areas open to fishing. In addition, laboratory, field experiments and modelling studies also indicate that predation rates on post-settlement juveniles can be significant and may regulate COTS populations.

- Nutrient loads delivered to inshore waters and some midshelf sections of the GBR (particularly between Cooktown and Cairns where midshelf reefs are closer to the coast) have increased as a result of historical agricultural development in the GBR catchment area.
- The concentration and availability of nutrients increases following large river discharges, although COTS outbreaks do not consistently occur in the aftermath of large river discharge events.
- Phytoplankton blooms and shifts in phytoplankton community structure resulting from nutrient enrichment during flood events have been documented, although there is some uncertainty whether phytoplankton concentration (chlorophyll-*a* levels) or specific phytoplankton species that become dominant during blooms, or a combination of both, is necessary to drive enhanced survivorship and development rates in COTS larvae.
- Survival, growth, and development rates are generally higher for well-fed larvae, but there is a lower and upper threshold for optimal food levels.
- The fundamental assumption that larval supply is generally limiting, such that outbreaks arise as a result of pronounced and temporary increases in larval survivorship due to enhanced food supply, has yet to be explicitly tested.
- Outbreaks of COTS on the GBR start on midshelf reefs in the Northern sector of the GBR (between Cairns and Lizard Island, and possibly further north), an area commonly referred to as the COTS 'initiation area'. The 'initiation area' overlaps with the area where nutrient-enriched river discharge enter the midshelf waters of the GBR on a regular basis. Larvae produced by primary outbreak populations are subsequently retained on source reefs or dispersed to reefs south of the 'initiation area' according to prevailing hydrodynamic regimes, thereby resulting in secondary outbreaks.

4.1.4 Significance of findings for policy, management and practice

Given that there are likely multiple drivers of COTS outbreaks, a multifaceted approach is necessary to improve our understanding of these drivers and mechanisms, and to implement effective management strategies. Active control measures are being advocated for COTS on the GBR, including spatially limited efforts within the 'initiation area' (Babcock et al., 2020; Rogers & Plagányi, 2022; Westcott et al., 2020). Regardless of improvements in the effectiveness of direct control measures, it is important to recognise that these solutions can only offer temporary or short-term relief in mitigating the impacts of COTS on coral reef ecosystems. Achieving long-term or permanent solutions requires a deeper understanding of the underlying drivers of COTS outbreaks, especially since all the evidence suggests that outbreaks are likely to be triggered or exacerbated by human activities (e.g., elevated nutrient levels from terrestrial runoff and/or overfishing). It becomes crucial to explicitly address these factors to reduce the likelihood of recurrent outbreaks or, at the very least, diminish the frequency of future occurrences.

Measures are already being taken in certain locations to address water quality and fisheries management as proactive and no-regret management strategies. The establishment of a network of no-take marine reserves and implementation of the amalgamated zoning plan for the GBRMP in 2004 (Day et al., 2019) has reduced fishing pressure and helped stem declines in fish abundance and biomass (Emslie et al., 2015; 2020). Studies comparing the incidence of COTS outbreaks or the prevalence of sublethal injuries (relative index of predation) between management zones in the GBRMP, suggest that managing fishing pressure can be successful in mitigating COTS populations within relatively short timeframes. To improve water quality in the GBR, catchment and land management programs were implemented starting in 2003 to reduce sediment and nutrient loads from river runoff (Brodie et al., 2012). To date, however, there is still insufficient evidence that these interventions have resulted in detectable long-term changes in nutrient levels in GBR inshore waters (Waterhouse et al., 2021) or within the vicinity of the COTS 'initiation area' (Kroon et al., 2023) and considerable uncertainty remains around the timeframes for achieving such changes (Kroon, 2012). Given this, it is unlikely that water quality management programs alone would have a quantifiable effect on ongoing COTS outbreaks in the GBR (Babcock et al., 2016a; Kroon et al., 2023; Westcott et al., 2020). Nevertheless, improving water quality through minimising sediment, nutrient, and pollutant runoff, and implementing stricter regulations on fishing activities, particularly through the establishment of no-take marine protected areas, will certainly enhance the resilience of reef ecosystems, especially against the backdrop of unprecedented climate change (Anthony, 2016; MacNeil et al., 2019; Mellin et al., 2016). These actions may not only help prevent or suppress COTS outbreaks but also contribute to the overall health and stability of coral reef ecosystems in the GBR.

4.1.5 Uncertainties and/or limitations of the evidence

Each of the three major hypotheses put forward to explain the initiation of outbreaks of COTS on the GBR (see *Conceptual Diagram*) are supported to a greater or lesser extent by experimental studies, or appear to explain the specific spatiotemporal occurrence of outbreaks on the GBR. However, the support for each of these hypotheses is primarily based on correlations, and the establishment of causation has not been definitively demonstrated. There are therefore, persistent uncertainties as to the relative contribution or importance of different factors in causing or exacerbating outbreaks of COTS on the GBR. Additionally, it is worth highlighting that in several cases, the studies were not specifically designed to address the particular hypothesis in question but rather contained tangential information that has since been used to support a specific hypothesis. Furthermore, some of these hypotheses rely on evidence that is inconclusive and open to multiple interpretations. The persistent uncertainties are in part related to inherent challenges in explicitly testing key predictions, but new research methods and developments (e.g., sampling COTS larvae, establishing key settlement habitat) now provide much greater opportunity to address these knowledge gaps. Moreover, there are likely to be multiple and varied factors involved in the initiation and propagation of outbreaks of COTS on the GBR, such that, multifactorial studies will be required to further understand the underlying factors involved.

4.2 Contextual variables influencing outcomes

The documented occurrence of distinct episodes of population outbreaks on the GBR, that appeared to be initiated in the northern GBR in approximately 1962, 1979, 1994 and 2010 and subsequently spread southwards (Pratchett et al., 2014; Vanhatalo et al., 2017), is the foremost data used to assess the validity of contrasting theories regarding the drivers of outbreaks. However, these data may have limited utility in testing for congruence with fine-scale changes in environmental or habitat conditions. For example, limited temporal and spatial resolution of existing monitoring of GBR reefs, especially in the far northern GBR (Vanhatalo et al., 2017), as well as limited capacity to effectively survey COTS at low densities (Pratchett et al., 2017a), make it difficult to say exactly when and where outbreaks originate on the GBR. There has also not been consistent monitoring of relevant environmental and ecological variables throughout this period, which precludes rigorous tests of association, and also makes it hard to account for systematic changes in environmental conditions throughout this period (e.g., ocean warming).

Table 9. Summary of contextual variables for Question 4.3.

Contextual variables	Influence on question outcome or relationships
Climate change	COTS, as well as their coral prey, are increasingly subject to environmental change caused by anthropogenic forcing in global climate systems (Byrne, 2011; Hughes et al., 2017; Przeslawski et al., 2008). Projected changes in ocean temperatures and seawater chemistry are expected to have direct effects on reproduction and on the early life history stages of COTS (Allen et al., 2017; Caballes et al., 2017a; Hue et al., 2020; 2022; Kamya et al., 2014; Lamare et al., 2014; Sparks et al., 2017; Uthicke et al., 2013; 2015a), as well as on juvenile (Kamya et al., 2016; 2017; Lang et al., 2023; Uthicke et al., 2013) and adult COTS (Lang et al., 2021; 2022). Notably, Uthicke et al. (2015a) found that elevated temperatures predicted under climate change scenarios combined with sufficient food, may shorten larval development time and increase survival, thereby increasing outbreak potential of COTS. Further examination is required to fully understand the cumulative impacts of environmental change on the individual fitness and population viability of COTS. However, these effects may be of limited significance when compared

Contextual variables	Influence on question outcome or relationships
	to the substantial threat posed by climate change to the availability of coral prey (Hughes et al., 2017), which disproportionately impacts *Acropora* spp. and other corals (Hughes et al., 2018a) that are favoured by COTS. Importantly, the loss of these preferred coral species will lead to declines in the quality and quantity of progeny (Caballes et al., 2016; 2017b), leading to significant consequences for population replenishment, independent of any direct effects of environmental change. Widespread and significant bleaching and subsequent coral mortality throughout the 'initiation area' may ultimately constrain the initiation of future COTS outbreaks or delay their onset. However, the possibility that new 'initiation areas' will emerge under future environmental conditions cannot be discounted.
Climate variability	The level of larval retention and self-recruitment on the GBR can vary among years due to fluctuations in ocean current velocities influenced by the El Niño-Southern Oscillation (ENSO). Weak or variable currents, which occur during neutral phases of the Southern Oscillation Index (SOI) may promote strong larval retention or very limited dispersal by causing the regional larval connectivity network to fragment into smaller local reef clusters (Wooldridge & Brodie, 2015). This may result in increased survivorship of COTS larvae in cases where these reef clusters share enhanced phytoplankton levels (Brodie et al., 2017) or consequently lead to the progressive accumulation of COTS within a given location (Pratchett, 2005). Some mass coral bleaching events (loss of COTS coral prey) in the tropical Pacific and the GBR have been attributed to El Niño conditions (Hughes et al., 2018b). Predictions suggest that more frequent La Niña periods will likewise result in increased rainfall extremes, larger river discharge events, and elevated pollutant loads (Cai et al., 2015). Models also suggest that lowest summer chlorophyll *a* concentrations are associated with El Niño events, while La Niña events were associated with the highest chlorophyll *a* values (Wooldridge & Brodie, 2015).
Availability and spatiotemporal extent of fine-scale data	The reliance on spatiotemporal patterns (Matthews et al., 2020b; Vanhatalo et al., 2017) in the occurrence (and especially, the initiation) of population outbreaks to identify key drivers (Matthews et al., 2020a) is problematic given the lack of highly resolved information on changes in the abundance and demography of COTS at relatively low densities (Pratchett, 2005). Addressing this issue (which is now possible with new and innovative monitoring tools) will greatly increase understanding of when, where, and potentially how, outbreaks arise.
Ongoing COTS control operations	There is extensive culling of COTS underway across the GBR, with demonstrated benefits for suppressing COTS densities and reducing coral loss at specific reefs (Westcott et al., 2020). While these efforts are essential for the immediate mitigation of coral loss and for minimising the spread of outbreaks (Rogers et al., 2017; Plagányi et al., 2020), they do pose a challenge to research on key demographic traits of COTS and the long-term dynamics of COTS populations on the GBR as these activities often result in 'artificial' and abrupt declines in COTS populations.

4.3 Evidence appraisal

Relevance

The relevance of the overall body of evidence to the questions was rated as Moderate (5) and relevance scores for each individual indicator are summarised in Table 10. The overall relevance rating for studies included under each hypothesis was Moderate, with scores of 5, 6, and 6 (out of 9) for *natural causes*, *predator removal,* and *nutrient hypothesis,* respectively (Table 10).

The overall relevance of the study approach and reporting of results to the question was given a Moderate (2.0) score due to the inclusion of studies that were not designed to explicitly test the specific hypothesis, but rather contained indirect or anecdotal information that lend support for or tangentially address a specific hypothesis. Of the 183 articles included in this Evidence Review, 64 (35%) were rated High, 71 (39%) were rated Moderate, and 47 (26%) were rated Low for overall relevance to the question. Average ratings for relevance to the question for studies included under each hypothesised driver are shown in Table 10. Out of the 42 studies included under the *natural causes hypothesis*, 15 (36%) were rated High, 15 (36%) were rated Moderate, and 12 (29%) were rated Low for overall relevance to the question. For the *predator removal hypothesis*, 14 (44%) were rated High, 14 (44%) were rated Moderate, and 3 (9%) were rated Low, out of the 32 studies included, for overall relevance to the question. Out of the 40 studies included under the *nutrient hypothesis*, 18 (45%) were rated High, 17 (43%) were rated Moderate, and 5 (13%) were rated Low for overall relevance to the question.

In terms of spatial generalisability, overall relevance was rated as Moderate (1.7 out of 3.0). This is mainly due to the inclusion of 32 studies from outside the GBR (17%). Experimental and observational studies in the field conducted on a few reefs within one sector of the GBR or experimental studies that used COTS specimens from a single population also influenced the moderate score for spatial relevance. Of the 183 articles included in this Evidence Review, 27 (15%) were rated High, 59 (32%) were rated Moderate, and 82 (45%) were rated Low for spatial relevance. Table 10 displays the average ratings indicating the spatial relevance of studies to the respective hypothesised drivers of COTS outbreaks. Among the 42 studies considered for the *natural causes hypothesis*, 5 (12%) received a High rating, 16 (38%) were rated Moderate, and 21 (50%) were rated Low in terms of spatial relevance. Regarding the *predator removal hypothesis*, out of the 32 studies considered, 4 (13%) were rated High, 9 (28%) were rated Moderate, and 15 (47%) were rated Low in terms of spatial generalisability. Within the *nutrient hypothesis*, the 40 included studies received ratings of 9 (23%) as High, 17 (43%) as Moderate, and 13 (33%) as Low for their spatial relevance to the question.

The temporal generalisability of the studies included in this Evidence Review was assessed and rated as Moderate (1.7 out of 3.0) overall. This rating was influenced by the inclusion of short-term experimental and observational studies, which often scored low in terms of temporal relevance to the question. Furthermore, the Moderate score for temporal relevance was also impacted by the inclusion of studies that relied on temporally limited datasets, although this provides a framework for future studies to revisit with updated biological, ecological, and environmental data. This is especially critical for the validation of models that are based on outdated assumptions and parameters. Among the 183 articles reviewed, 16 (9%) received a High rating, 76 (42%) were rated as Moderate, and 74 (40%) were rated as Low in terms of their temporal relevance to the question. Table 10 presents the average ratings, illustrating the temporal relevance of the studies to the hypothesised drivers of COTS outbreaks. For the *natural causes hypothesis*, out of the 42 studies considered, 4 (10%) received a High rating, 22 (52%) were rated as Moderate, and 14 (33%) were rated as Low in terms of their temporal relevance. Regarding the *predator removal hypothesis*, out of the 32 studies examined, 3 (9%) were rated as High, 14 (44%) as Moderate, and 34 (47%) as Low in terms of their temporal relevance. In relation to the nutrient hypothesis, the 40 included studies received ratings of 6 (15%) as High, 16 (40%) as Moderate, and 17 (43%) as Low in terms of temporal generalisability.

Table 10. Summary of relevance rating of each individual indicator for included studies across different hypothesised drivers for COTS outbreaks.

HYPOTHESISED DRIVER	RELEVANCE OF APPROACH/ RESULTS Low: 1 Mod: 2 High: 3	SPATIAL GENERALISABILITY Low: 1 Mod: 2 High: 3	TEMPORAL GENERALISABILITY Low: 1 Mod: 2 High: 3	RELEVANCE RATING Low: 1-3 Mod: 4-6 High: 7-9
Natural	2.1	1.6	1.8	**5**
Predation	2.4	1.6	1.7	**6**
Nutrients	2.3	1.9	1.7	**6**
Multiple	2.1	1.5	1.6	**5**
Hydrodynamics	2.0	2.2	1.5	**6**
Other	1.0	1.2	1.3	**4**
OVERALL	**2.0**	**1.7**	**1.7**	**5**

Consistency, Quantity and Diversity

A total of 183 studies were included in the body of evidence to address the question on what drives the initiation of COTS outbreaks in the GBR. This is considered to be a High Quantity of studies (high proportion of the total available number of studies), representing a High diversity of approaches (see Table 7; Figure 3) with Moderate Consistency of results relevant to the question.

Overall, the types of approaches used to address the question were almost evenly distributed: 30% experimental, 38% observational/analytical, 29% conceptual/review/modelling, and 3% a combination of 2-3 different study types. Out of the 42 studies considered under the *natural causes hypothesis*, 50% (21) were observational or analytical, while 31% (13) were experimental, 14% (6) were conceptual/review/modelling, and 5% (2) were a combination of two or more study types. Among the 32 studies examined in relation to the *predator removal hypothesis,* 41% (13) employed observational or analytical methods, while 31% (10) adopted conceptual, review, or modelling approaches, and 28% (9) of the studies used experimental methodologies. For the *nutrient hypothesis*, there was a relatively even distribution of study types, whereby 35% (14) used experimental approaches, 33% (13) were observational or analytical methodologies, and 33% (13) were conceptual or review or modelling studies.

The Moderate rating for consistency was mainly due to marginally inconsistent findings among key studies addressing a specific hypothesis. The main point of contention for the *natural causes hypothesis* is whether COTS outbreaks have occurred in the distant past. One side suggests that the aggregation of skeletal elements within sediment samples is proof that outbreaks have occurred in the geologic past, while the other side has argued that this conclusion is not warranted given the multiple shortcomings of this approach. While there is a growing body of correlative evidence to support the *predator removal hypothesis*, other studies did not observe similar patterns. The primary area of debate regarding the *nutrient hypothesis* is whether there is marked spatiotemporal patterns in the condition and survival of COTS larvae that is attributable to changes in the availability of relevant phytoplanktonic prey, and whether this in turn, is sufficient to account for increasing settlement and abundance of COTS.

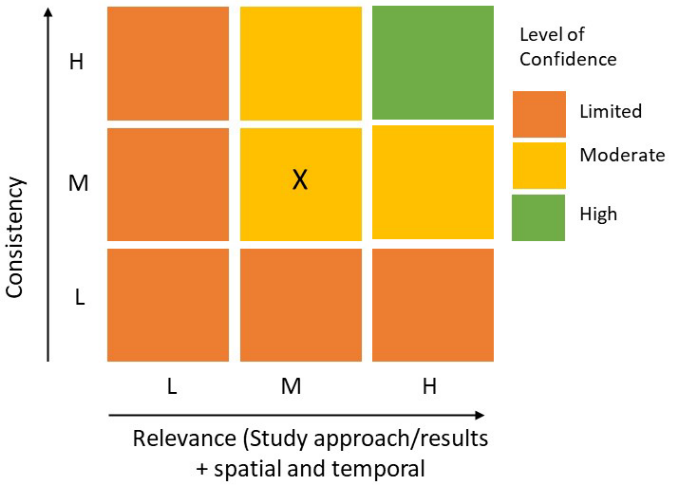
Additional Quality Assurance (Reliability)

The reliability (internal validity) assessment revealed that the majority of studies (146 out of 183; 80%) were rated as High, indicating strong reliability. Only 20% of studies (36 out of 183) received a Low rating. This assessment underscores that the experimental, observational, and analytical studies included in this Evidence Review were well-designed and appropriately replicated. Similarly, review, modelling, and conceptual studies were based on sound assumptions and supported by existing literature. The main concerns regarding reliability were primarily associated with assumptions made in modelling studies, the reliability of data used to support conclusions, and issues pertaining to methodologies and sample sizes. It is important to note that many of these limitations were acknowledged by the authors themselves, and appropriate caveats are provided in the narrative synthesis.

Confidence

Overall, there is a Moderate level of confidence in the body of evidence based on: Moderate Consistency and Moderate Overall Relevance of the studies considered (see Confidence Matrix in Table 11). The majority of the studies included in this Evidence Review had a Moderate to High rating (74%) in terms of relevance to the hypothesised drivers of COTS outbreaks in the GBR. Consistency was rated as Moderate, as there were some notable studies under each hypothesis that had marginally inconsistent results (see examples above). The High reliability score for the studies included was also factored in when assessing the level of confidence in the body of evidence compiled to address this question. Taken together, the diverse approaches to address various aspects of this question will improve our understanding of the key drivers of COTS outbreaks in the GBR.

Table 11. Summary of results for the evidence appraisal of the whole body of evidence in addressing Question 4.3. The overall measure of Confidence (i.e., Limited, Moderate and High) is represented by a matrix encompassing overall relevance and consistency. The final row summarises the additional quality assurance step needed for questions using the SCS Evidence Review method.

Indicator	Rating	Overall Measure of Confidence
Relevance (overall)	Moderate (5)	
-To the Question	Moderate	
-Spatial	Moderate	
-Temporal	Moderate	
Consistency	Moderate	
Quantity	High (183 studies)	
Diversity	High (38% observational / analytical, 30% experimental, 29% conceptual / review/ modelling approaches and 3% mixed)	
Reliability	High	- Most studies (80%) rated High in the reliability assessment, with only 20% rating Low. - The common causes of ‘low’ reliability were due to assumptions used in modelling studies, reliability of data used to contextualise conclusions and issues related to methodologies used and sample size. - Studies rating ‘low’ reliability were identified during the evidence appraisal stage and concerns associated with the findings of these studies were highlighted during the synthesis stage.

4.4 Indigenous engagement/participation within the body of evidence

Indigenous engagement and/or direct participation within the body of evidence was non-existent.

4.5 Knowledge gaps

Recent reviews have highlighted key knowledge gaps in the biology and ecology of COTS.

Table 12. Summary of knowledge gaps for Question 4.3.

Gap in knowledge (based on what is presented in Section 4.1)	Possible research or Monitoring & Evaluation (M&E) question to be addressed	Potential outcome or Impact for management if addressed
Demography and dynamics of low-density (pre-outbreak) populations.	How does the demography of COTS populations change with increasing density, and what are the key indicators for potential outbreaks?	Early warning for outbreaks before they cause widespread coral damage and inform control efforts.
Delineation of the COTS ‘initiation area’.	Where are the geographic boundaries of the COTS ‘initiation area’ and can new methods to intensively survey COTS populations detect the early onset of outbreaks?	Would enable pre-emptive culling to contain or prevent the initiation of new or renewed population outbreaks.
Predation rates in the field, as well as the identity of the main predators and their ecological linkages with respect to potential trophic cascade interactions.	What are the relative (or absolute) rates of predation on juvenile and adult COTS in different habitats, regions and management zones? What are the main predators and what is their role in food web interactions?	Establish potential benefits of improved fisheries management, including the extent and distribution of fully protected marine protected areas, to moderate the incidence or severity of COTS outbreaks.
Ecology of juveniles in the field.	What are the growth and survival rates of early post-settlement stages of COTS in the wild, relative to local habitat and environmental conditions?	Confirm or refute the capacity of COTS to delay ontogenetic shifts in resource use (Deaker et al., 2020a, b), which might otherwise buffer changes in larval supply and population replenishment.
Reliable method to accurately age COTS.	What is the age structure of COTS populations in the GBR?	Clarify the extent to which COTS outbreaks develop from multiple cohorts through successive recruitment, due to sustained settlement or persistence of algal feeding juveniles.
Cumulative reproductive potential of COTS populations based on size, abundance and distribution of mature individuals.	Do fecundity and fertilisation rates vary as a function of size, density, and behaviour of adult COTS?	Further refine reproductive thresholds to establish the capacity to constrain population replenishment through manual culling.

Gap in knowledge (based on what is presented in Section 4.1)	Possible research or Monitoring & Evaluation (M&E) question to be addressed	Potential outcome or Impact for management if addressed
Standardised methods to quantify larval feeding rates and survival using diets of phytoplankton algal species that are particularly dominant during flood events in the GBR.	Do COTS larvae feed on phytoplankton species that are dominant during flood events (e.g., *Skeletonema* sp.) and what are the consequences of this diet in terms of larval performance?	Establish critical link between enhanced COTS larval survival to phytoplankton blooms, as well as define thresholds for larval survival and development.
Comparative analyses of larval condition in the wild, relating this to local environmental and habitat conditions (e.g., food availability).	Does the condition and survival of COTS larvae vary according to local environmental (i.e., phytoplankton concentration) and habitat conditions within the outbreak initiation area?	Confirm whether COTS larvae are typically food-limited, and understand potential impact of stochastic events on larval condition and survival.
Recruitment limitation, and also the converse, stock-recruitment relationships.	What limits recruitment in COTS? Is recruitment density dependent (larval density) or microsite-limited (condition or availability of settlement habitat)?	Understand nature and scale of stock-recruitment relationships for COTS to understand the local and regional benefits of different management approaches.

5. Evidence Statement

The synthesis of the evidence for **Question 4.3** was based on 183 studies, primarily undertaken within the Great Barrier Reef (but including others for comparison) and published between 1990 and 2023. The synthesis includes a *High* diversity of study types (38% observational/analytical, 30% experimental, 29% conceptual/review/modelling approaches and 3% mixed) and has a *Moderate* confidence rating (based on *Moderate* consistency and *Moderate* overall relevance of studies).

Summary of findings relevant to policy or management action

Population outbreaks of the coral-eating crown-of-thorns starfish represent one of the most significant biological disturbances on coral reefs and remain one of the principal causes of widespread declines in live coral cover on the Great Barrier Reef. Understanding the key drivers of outbreaks on the Great Barrier Reef is fundamental for establishing relevant management responses. There are several hypotheses to explain why outbreaks occur, but they have been typically considered as discrete entities. The most prominent hypotheses include natural causes due to inherent life history characteristics, and others that take into account anthropogenic influences such as the effects of predator removal on different life stages, and water quality changes causing enhanced larval success. This synthesis finds supporting evidence for each of these hypotheses and proposes that the hypotheses are more likely to be complementary rather than mutually exclusive, with a combination of elements resulting in a 'perfect storm' that can trigger an outbreak. Combining evidence from the different hypotheses will contribute to a more complete understanding about when, where and how population outbreaks will occur.

Supporting points

- Crown-of-thorns starfish outbreaks mostly occur on midshelf reefs in the Great Barrier Reef.
- The body of evidence suggests that primary outbreaks of crown-of-thorns starfish on the Great Barrier Reef are most likely driven by a combination of the most prominent hypotheses: natural causes, predator removal, and enhanced nutrients.
- *Natural causes hypothesis:* This hypothesis argues that crown-of-thorns starfish naturally possess inherent life history traits that predispose populations to significant spatial and temporal fluctuations. This hypothesis is supported by evidence of high fecundity, high fertilisation rates, and fast growth that predisposes them to naturally occurring extreme fluctuations in reproductive success and population size. These traits, coupled with the time required for recovery and regrowth of their coral prey, may explain the periodicity (~14 to 17 years) of recurrent outbreaks events on the Great Barrier Reef.
- *Predator removal hypothesis*: This hypothesis argues that crown-of-thorns starfish populations are normally regulated by high rates of predation on post-settlement life stages and that outbreaks arise when predator populations are reduced (e.g., through fishing). The evidence shows that in areas where fishing is prohibited, the incidence of crown-of-thorns starfish outbreaks is generally lower, while the prevalence of sublethal injuries on crown-of-thorns starfish is higher, compared to areas open to fishing. In addition, laboratory, field experiments and modelling studies also indicate that predation rates on post-settlement juveniles can be significant and may regulate crown-of-thorns starfish populations.
- *Nutrient hypothesis:* This hypothesis argues that enhanced nutrient supply from river runoff (especially after extreme rainfall events) increases primary production, particularly in coastal and inshore marine waters, resulting in a phytoplankton bloom. Phytoplankton blooms could be beneficial for crown-of-thorns starfish larvae by increasing food supply, thereby promoting faster growth and lower mortality. The following evidential chain was established for this review:
    1) Nutrient loads delivered to inshore waters and some midshelf sections of the Great Barrier Reef (particularly between Cooktown and Cairns where midshelf reefs are closer to the coast) have increased as a result of historical agricultural development in the Great Barrier Reef catchment area;

2) The concentration and availability of nutrients increases following large river discharges, although crown-of-thorns starfish outbreaks do not consistently occur in the aftermath of large river discharge events;
3) Phytoplankton blooms and shifts in phytoplankton community structure resulting from nutrient enrichment during flood events have been documented, although there is some uncertainty whether phytoplankton concentration (chlorophyll-*a* levels) or specific phytoplankton species that become dominant during blooms, or a combination of both, is necessary to drive enhanced survivorship and development rates in crown-of-thorns starfish larvae;
4) Survival, growth, and development rates are generally higher for well-fed larvae, but there is a lower and upper threshold for optimal food levels;
5) The fundamental assumption that larval supply is generally limiting, such that outbreaks arise due to pronounced and temporary increases in larval survivorship due to enhanced food supply, has yet to be explicitly tested; and
6) Outbreaks of crown-of-thorns starfish on the Great Barrier Reef start on midshelf reefs in the Northern sector of the Great Barrier Reef (between Cairns and Lizard Island, and possibly further north), an area commonly referred to as the COTS ‘initiation area’. The ‘initiation area’ overlaps with the area where nutrient-enriched river discharge enter the midshelf waters of the Great Barrier Reef on a regular basis. Larvae produced by primary outbreak populations are subsequently retained on source reefs or dispersed to reefs south of the ‘initiation area’ according to prevailing hydrodynamic regimes, thereby resulting in secondary outbreaks.

- The evidence to date suggests that water quality management programs in isolation will have a limited effect on controlling crown-of-thorns starfish outbreaks on the Great Barrier Reef. However, improving water quality through minimising sediment, nutrient, and pollutant runoff, and implementing stricter regulations on fishing, particularly through no-take marine protected areas, offers the best resistance to a natural pest while simultaneously enhancing the resilience of reef ecosystems to withstand or recover from outbreaks.
- In summary, while crown-of-thorns starfish may be naturally predisposed to outbreaks because of key life history traits, it is likely that anthropogenic impacts on water quality and predator fish stocks have exacerbated the incidence or severity of outbreaks, and/or undermined the capacity of reef ecosystems to withstand these cyclic pest irruptions.

6. References

The ‘Body of Evidence’ reference list contains all the references that met the eligibility criteria and were counted in the total number of evidence items included in the review, although in some cases, not all of them were explicitly cited in the synthesis. In some instances, additional references were included by the authors, either as background or to provide context, and those are included in the ‘Supporting References’ list.

Body of Evidence

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Appendix 1: 2022 Scientific Consensus Statement author contributions to Question 4.3

Theme 4: Dissolved nutrients – catchment to reef

Question 4.3: What are the key drivers of the population outbreaks of Crown-of-thorns Starfish (COTS) on the Great Barrier Reef, and what is the evidence for the contribution of nutrients from land runoff to these outbreaks?

Author team

Name	Organisation	Expertise	Role in addressing the Question	Sections/Topics involved
1. Ciemon Caballes	Marine Laboratory, University of Guam College of Science and Engineering, James Cook University	COTS biology and ecology	Lead Author	All Sections
2. Katie Sambrook	C_2O Consulting	Evidence review, ecology	Contributor	Searches and data extraction, evidence appraisal and final revision of overall report
3. Morgan Pratchett	College of Science and Engineering, James Cook University	COTS ecology	Contributor; Expert Advice	Executive Summary, narrative synthesis and final revision of overall report