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Knowledge Gaps in the Biology, Ecology, and Management of the Pacific Crown-of-Thorns Sea Star *Acanthaster* sp. on Australia's Great Barrier Reef

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Abbreviations: COTS, crown-of-thorns sea stars (*Acanthaster* sp.); eDNA, environmental DNA; GBR, Great Barrier Reef.

Abstract. Crown-of-thorns sea stars (*Acanthaster* sp.) are among the most studied coral reef organisms, owing to their propensity to undergo major population irruptions, which contribute to significant coral loss and reef degradation throughout the Indo-Pacific. However, there are still important knowledge gaps pertaining to the biology, ecology, and management of *Acanthaster* sp. Renewed efforts to advance understanding and management of Pacific crown-of-thorns sea stars (*Acanthaster* sp.) on Australia's Great Barrier Reef require explicit consideration of relevant and tractable knowledge gaps. Drawing on established horizon scanning methodologies, this study identified contemporary knowledge gaps by asking active and/or established crown-of-thorns sea star researchers to pose critical research questions that they believe should be addressed to improve the understanding and management of crown-of-thorns sea stars on the Great Barrier Reef. A total of 38 participants proposed 246 independent research questions, organized into 7 themes: feeding ecology, demography, distribution and abundance, predation, settlement, management, and environmental change. Questions were further assigned to 48 specific topics nested within the 7 themes. During this process, redundant questions were removed, which reduced the total number of distinct research questions to 172. Research questions posed were mostly related to themes of demography (46 questions) and management (48 questions). The dominant topics, meanwhile, were the incidence of population irruptions (16 questions), feeding ecology of larval sea stars (15 questions), effects of elevated water temperature on crown-of-thorns sea stars (13 questions), and predation on juveniles (12 questions). While the breadth of questions suggests that there is considerable research needed to improve understanding and management of crown-of-thorns sea stars on the Great Barrier Reef, the predominance of certain themes and topics suggests a major focus for new research while also providing a roadmap to guide future research efforts.

Introduction

Crown-of-thorns sea stars (COTS; *Acanthaster* sp., excluding *Acanthaster brevispinus*) are among the most intensively studied coral reef organisms (Moran, 1986; Pratchett *et al.*, 2017). Scientific interest in COTS is due to marked spatiotemporal variation in their abundance (*e.g.*, Chesher, 1969; Moran *et al.*, 1992; Kayal *et al.*, 2012), particularly their capacity to occur at very high densities during population irruptions (also referred to as outbreaks; Birkeland, 1982). Crown-of-thorns sea stars are also one of the largest and most efficient coral predators, such that population irruptions often cause extensive coral loss (Moran, 1986; Pratchett *et al.*, 2014), contributing to sustained and ongoing degradation of reef ecosystems throughout the Indo-Pacific (Bruno and Selig, 2007; Trapon *et al.*, 2011; Mellin *et al.*, 2019). Despite their ecological importance and the corresponding research effort, some important unanswered questions remain about the biology, ecology, and management of COTS (*e.g.*, Pratchett *et al.*, 2017). Most importantly, there is persistent controversy regarding the causes of population irruptions of COTS and the efficacy of corresponding management actions that should be taken (Kenchington, 1987; Babcock *et al.*, 2016a; Hoey *et al.*, 2016; Pratchett and Cumming, 2019; Westcott *et al.*, 2020).

There are effectively two diametric views regarding the recent incidence of population irruptions of COTS on Australia's Great Barrier Reef (GBR): (i) major and recurrent population irruptions of COTS are a relatively recent and unnatural phenomenon, caused by anthropogenic changes in biological and/or habitat conditions that undermine or disrupt the factors that would otherwise regulate their densities (*e.g.*, Chesher, 1969; Randall, 1972; Endean, 1973), and (ii) population irruptions are a natural and recurring phenomenon that essentially went unnoticed prior to the 1960s (Vine, 1970; Weber and Woodhead, 1970) and are inherently linked to their particular life-history characteristics (Birkeland, 1989) and phenotypic plasticity, including their high fecundity in population irruptions (Stump, 1993; Uthicke *et al.*, 2009; Babcock *et al.*, 2016b; Pratchett *et al.*, 2021). A more nuanced view is that population irruptions do occur naturally but were previously rare and/or small-scale events that may have become more frequent, widespread, and severe as anthropogenic impacts have altered reef ecosystems (DeVantier and Done, 2007).

If population irruptions of COTS are caused or exacerbated by anthropogenic degradation of coastal environments and habitats (*e.g.*, due to over-fishing or eutrophication), it seems logical that redressing these issues would effectively prevent future population irruptions (Brodie *et al.*, 2005) or at least reduce their frequency of occurrence, intensity of impact, and spread through reef systems. There are, however, considerable challenges associated with effectively reversing historical and significant effects of anthropogenic activities in coastal environments (Fidelman *et al.*, 2013; Hughes *et al.*, 2017) and no certainty that these changes (if achieved) would necessarily prevent or reduce the frequency and intensity of future population irruptions (Pratchett *et al.*, 2014). Effective management of COTS is nonetheless warranted, even if population irruptions are a natural phenomenon, given that current levels of anthropogenically driven coral loss threaten the inherent resilience, structure, and function of reef ecosystems (Ortiz *et al.*, 2018; Bellwood *et al.*, 2019; Mellin *et al.*, 2019; Bozec *et al.*, 2020; Condie *et al.*, 2021).

In the northern and central GBR, there have been four documented waves of population irruptions of Pacific COTS (*Acanthaster* sp.), starting in about 1962, 1979, 1995, and 2010 (Pratchett *et al.*, 2014). Each of these population irruptions appears to have started on mid-shelf reefs in the northern section of the GBR, between Lizard Island (14° S) and Cairns (17° S). Once established within this region (the initiation box; Pratchett *et al.*, 2014), population irruptions spread latitudinally by about 1°–2° (100–200 km) every 3 years (Kenchington, 1977; Reichelt *et al.*, 1990), affecting (mostly mid-shelf) reefs along much of the length of the GBR (Vanhatalo *et al.*, 2016; Matthews *et al.*, 2020), except for the Swain Reefs in the southernmost section of the GBR, where primary outbreaks arise independently from those in the rest of the GBR (Miller *et al.*, 2015). Successive (or cyclical; Stump, 1996) population irruptions of COTS have contributed greatly to sustained declines in coral cover on the GBR (De'ath *et al.*, 2012; Mellin *et al.*, 2019), now being compounded by global environmental change (Hughes *et al.*, 2018b, 2019). The conservation of coral reefs globally is, therefore, critically reliant on immediate and significant reductions in greenhouse gas emissions (Van Hooidonk *et al.*, 2016). However, the increasing threat posed by accelerating environmental change also provides a renewed imperative to better manage other important and pervasive causes of coral loss, including population irruptions of COTS (Hoegh-Guldberg *et al.*, 2018; Westcott *et al.*, 2020; Condie *et al.*, 2021).

The purpose of this study was to establish critical and contemporary knowledge gaps pertaining to the biology, ecology, and management of COTS, to thereby inform renewed research imperatives and urgency toward better understanding and, ultimately, managing recurrent population irruptions of the Pacific COTS (*Acanthaster* sp.) on Australia's GBR (Babcock *et al.*, 2020; Westcott *et al.*, 2020). Our goal was not only to highlight well-known, existing knowledge gaps that still warrant critical research attention (though these are important), but also to explore new opportunities and emerging issues for COTS research (horizon scanning; Kark *et al.*, 2016). To do so, we draw on established horizon scanning methodologies (Sutherland and Woodroof, 2009; Rudd and Lawton, 2013) to elucidate the perspectives of established and contemporary Australian COTS research scientists to identify the most significant research gaps that are relevant to understanding and managing COTS populations on the GBR, without any prejudice given to the necessity of, impact of, or justification for the research being posed.

Materials and Methods

To establish critical and contemporary knowledge gaps pertaining to the biology, ecology, and management of COTS (*Acanthaster* Gervais, 1841, sp.), we used well-established horizon scanning research approaches. Horizon scanning is a participatory research approach that provides a structured and systematic methodology to elicit knowledge gaps and emerging issues by drawing upon the experience or knowledge of those involved in the process (Sutherland *et al.*, 2011). In relation to coastal and marine systems, horizon scanning approaches have already been utilized to develop research priorities relating to the impacts of climate change on coral reef fishes (Wilson *et al.*, 2010), the management of coral-dominated marine protected areas (Cvitanovic *et al.*, 2013), and recreational fisheries (Holder *et al.*, 2020), as well as coastal management (Rudd and Lawton, 2013). For this study, a core team (MSP, CFC, CC, and SKW) initiated and implemented the study following the methodology of Rudd *et al.* (2010). The core team was developed to ensure that there were individuals with expertise both on COTS (MSP and CFC) and on horizon scanning methods (SKW and CC).

To ascertain research needs, we approached scientists who are actively undertaking research or have previously published peer-reviewed international journal articles on Pacific COTS (*Acanthaster* sp.) within, or collected from, Australia's GBR. The identification of participants was based on expert working knowledge (by MSP and CFC), following the recent preparation of extensive literature reviews (Caballes and Pratchett, 2014; Pratchett *et al.*, 2014, 2017; Wilmes *et al.*, 2018). Each of 50 researchers was invited to submit research questions that they considered important to improve understanding and management of COTS and, thereby, to help reduce (or reverse) declining coral cover on the GBR. To constrain the scale and scope of research questions (*sensu* Sutherland *et al.*, 2009, 2013), researchers were asked to restrict their attention to important knowledge gaps that could conceivably be addressed within the timeframe of a typical research program (1–4 years). This was done in order to limit research questions to those that can be feasibly addressed within the typical duration of a research grant in Australia (*e.g.*, Australian Research Council grants). The authors also intend to repeat this horizon scanning exercise after five years to evaluate which knowledge gaps have been addressed within this timeframe. The geographic focus of this study was also restricted to Australia's GBR, reflecting the seemingly unique manifestation and proliferation of population irruptions in this region (Pratchett *et al.*, 2014), while also ensuring that proposed research activities (and suggestions arising) are directly aligned with a single and distinct management jurisdiction. Redressing emergent knowledge gaps and research questions will, however, have benefits for managing COTS throughout the Indo-Pacific.

Of the 50 invitees, 38 researchers representing at least 20 different institutions (either independently or as part of a consortium) contributed research questions. The specific responses varied greatly, ranging from very succinct research questions without any context or justification to extensive research proposals where it was difficult to identify distinct and salient research questions. Often, the research questions proposed contained several distinct components and/or questions. To obtain distinct, concise, and generally comparable research questions, it was necessary to disaggregate the salient components of all questions initially proposed. Participants were then presented with a list of all questions pertaining to their original submission for their approval. This greatly increased the number of distinct research questions being proposed by each researcher. In all, we had 251 distinct and concise research questions proposed, revised, and approved across all 38 participants. Five of these questions were, however, deemed by the core author group to be outside of the scope of this project (*e.g.*, not relevant to the GBR *per se*) and, therefore, were not included. Ultimately, we received 6 questions from most participants (range: 1–21 questions per participant), although 7 participants submitted >10 questions.

For the purpose of this study, the 246 research questions were organized into major themes by the core team of authors. Thematic allocation involved two steps. First, individual members of the core author team thematically characterized each question independently. The core team of authors then met to discuss individual approaches to thematic coding and discussed different options until consensus was reached as to the best approach. Nevertheless, it should be noted that the assignment of questions under the distinct themes and topics was subjective. During this process, redundant questions were also removed by the core author group; this reduced the total number of distinct research questions to 172. Unlike previous studies that have canvassed research experts to identify crucial knowledge gaps and research priorities on specific topics (*e.g.*, Wilson *et al.*, 2010), no attempt was made to explicitly score or rank research questions. While horizon scanning approaches (Sutherland *et al.*, 2011) allow researchers to elicit critical research gaps, they do not seek to assign an order of importance to the resulting research questions. Doing so would involve additional steps in the research design beyond the requirements of horizon scanning. Rather, the research questions presented herein and the redundancy of specific questions serve as the first step in identifying key knowledge gaps, emphasizing the distribution of questions posed across different themes and specific research topics.

Results and Discussion

Research questions ($n = 246$, including redundant questions) proposed by the 38 participants in this study were organized into 7 different themes (Fig. 1): feeding ecology, demography, distribution and abundance, predation, settlement, management, and environmental change. These are considered, in turn, below. Many of the questions posed could have easily been assigned to more than one theme but were assigned to only the most relevant theme. The distinction between some themes is also subjective. Most notably, predation and settlement are important demographic processes but were elevated to distinct themes, given their specific relevance in understanding and managing population irruptions of COTS, as well as the disproportionate number of questions posed on these topics. Nonetheless, there were a large number of questions (46) considered most relevant to demography, which, along with management (48 questions), were the largest themes, probably reflecting the increased breadth of these themes.

Research questions within each theme were further organized into distinct topics. Where relevant, these topics highlighted specific life-history stages of COTS, including larvae, juveniles (algal feeding), sub-adults (coral feeding), and adults, but also distinguished between specific factors or processes. The highest number of questions were found in these specific topics (nested within themes): (1) the incidence of population irruptions (16 questions); (2) the feeding (or nutritional) ecology of larval COTS (15 questions); and (3) the effects of ocean warming and marine heatwaves on COTS (13 questions). The distribution of independent questions across these topics provides preliminary insights into major priorities for future research. Note that some questions have already been studied to a greater or lesser degree but would benefit from additional research focus.

Feeding ecology

The feeding ecology (*e.g.*, preferences across different coral prey) of COTS has been extensively studied and is relatively well understood (*e.g.*, Ormond *et al.*, 1976; Keesing and Halford, 1992a; De'ath and Moran, 1998; Johansson *et al.*, 2016). This is because the feeding ecology of coral-feeding (adult and sub-adult) COTS is central to understanding their effects on coral assemblages and reef ecosystems (De'ath and Moran, 1998; Pratchett *et al.*, 2009; Baird *et al.*, 2013; Keesing, 2021). Moreover, there are important feedbacks between the availability of coral prey and foraging behavior of COTS (Ling *et al.*, 2020), with potential flow-on effects to the condition and demography of COTS (*e.g.*, Caballes *et al.*, 2016, 2017a); this, in turn, is likely important for understanding the cyclical nature of population irruptions on the GBR (Antonelli and Kazarinoff, 1984; Babcock *et al.*, 2020). Therefore, there is a recognized need for more resolved information on the feeding ecology of adult COTS to understand whether fluctuations in the availability of coral prey may explain boom-and-bust cycles of COTS populations, as well as reconcile the specific effects of elevated densities of large adult COTS on coral assemblages and on reef ecosystems more generally (Table 1).

The feeding ecology (or, more appropriately, the nutritional ecology) of larval COTS is also central to purported links between population irruptions and elevated nutrients during major flood and runoff events (Fabricius *et al.*, 2010). However, the current understanding of the nutritional ecology of COTS larvae comes mostly from experimental studies (*e.g.*, Lucas 1982; Fabricius *et al.*, 2010; Wolfe *et al.*, 2017); and there has been limited field sampling to validate these findings, mostly because of challenges associated with effectively sampling COTS larvae in the field (but see Uthicke *et al.*, 2015a). Many of the research questions that were posed under the theme of feeding ecology relate to field-based studies on the nutritional ecology of COTS larvae (Table 1), to explicitly test whether fluctuations in food availability and corresponding differences in larval condition and survival may explain population irruptions (*sensu* Olson, 1987). Accordingly, the question related to larval growth and mortality with varying levels of planktonic prey under natural conditions was posed by four separate participants (Table 1).

Demography

The uncertainty about what causes population irruptions of COTS (Kenchington, 1987; Babcock *et al.*, 2016a) reflects considerable gaps in the understanding of their population dynamics and demographic rates. Importantly, sporadic population irruptions of COTS are attributed to periodic disruptions in the factors (*e.g.*, predation, larval nutrition) that normally regulate their populations (Endean, 1969; Brodie *et al.*, 2005) and/or pronounced demographic shifts (Moore, 1990). This, therefore, requires more than simple baseline estimates of demographic rates and should include particular focus on variability in rates between

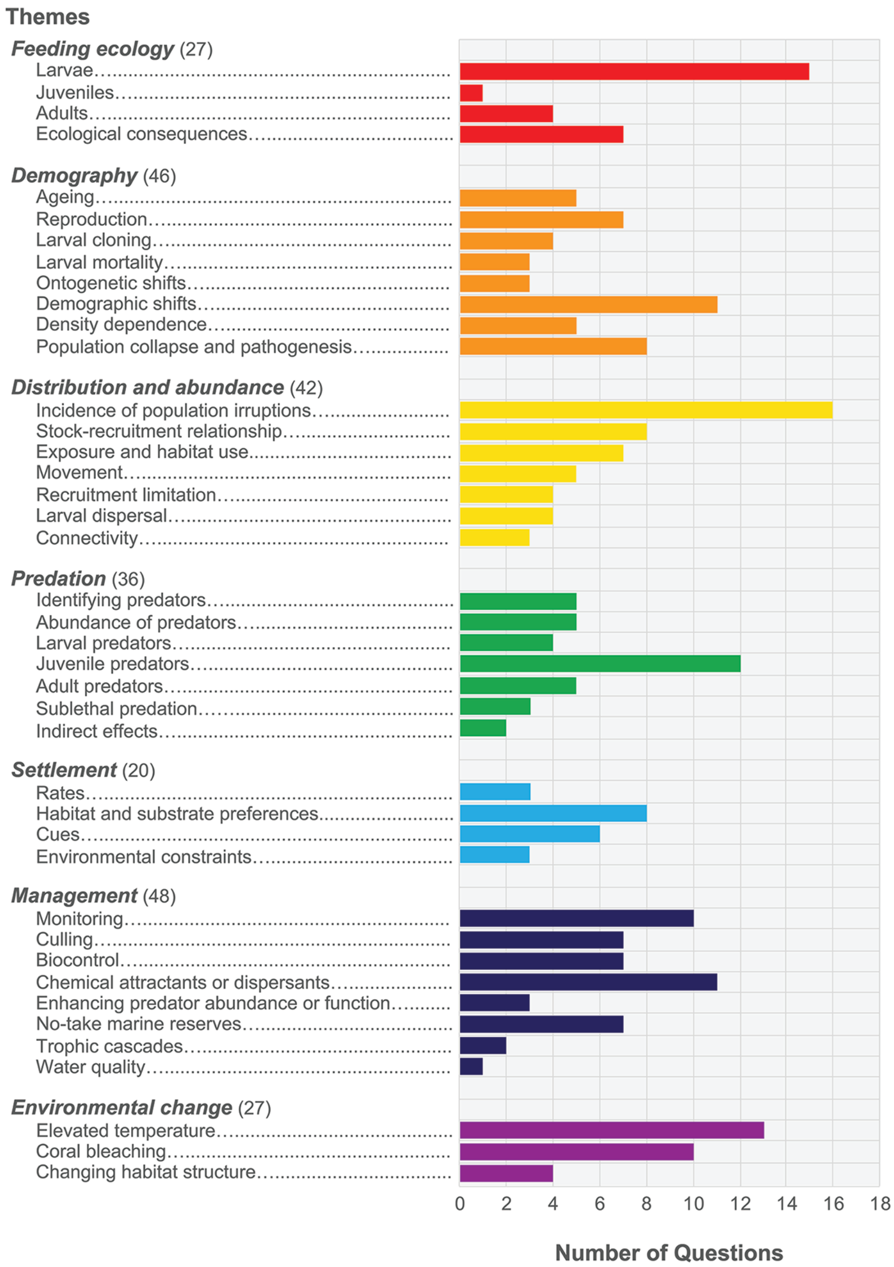

Figure 1. Distribution of original research questions related to the study of crown-of-thorns sea stars (*Acanthaster* sp.; $n = 246$, including redundant questions proposed by 5 different participants) across relevant themes and topics.

COTS populations (explicitly comparing between apparently stable low-density populations and irruptive populations) and the cause(s) of such variation (Moore, 1990; Stump, 1993). As such, estimates of demographic rates from COTS maintained in captivity may have limited utility in understanding natural population dynamics (Moran, 1986). Meanwhile, most field-based studies on COTS demography are initiated only after population irruptions are apparent and well established (*e.g.*, Wilmes *et al.*, 2018), partly because comparative research on low-density populations is very difficult (*e.g.*, Benzie and Stoddart, 1992) and also because there is limited appetite for COTS research outside of major population irruptions (Pratchett *et al.*, 2017). Hence, there remains a need for research comparing demography between stable, low-density populations *versus* irruptive (or outbreaking) populations, including larval abundance, settlement rates, and juvenile densities as well as adult growth, mortality, and behavior (Table 2).

Overall, knowledge gaps and research questions pertaining to the demography of COTS extend across a broad range of different life stages and demographic processes (Table 2).

Table 1

*Research questions (*n = *19) relevant to the feeding ecology (or nutritional ecology) of crown-of-thorns sea stars (COTS;* Acanthaster *sp.)*

Topic	Question	*N*
Larvae	• How long does the COTS facultative feeding period last?	1
	• How do larval growth and mortality vary with availability of planktonic prey under natural conditions?	4
	• How variable is the microbiome of larval COTS, and does this influence survival when food-limited?	3
	• Does the capacity of larval COTS to adopt microbes from the environment change with the baseline microbial community?	1
	• What water column conditions and human drivers favor or hinder COTS larvae and their food or predator environment?	1
	• Are COTS larvae more abundant in areas with elevated nutrients and/or higher abundance of phytoplankton?	2
	• How does stratification of food and water quality stressors influence COTS larvae?	1
	• Do high levels of suspended sediments and reduced salinity (as expected to occur during major flood events) offset effects of elevated nutrients on larval abundance and condition?	1
	• What is the natural diet of COTS larvae?	1
Juveniles	• What are the preferred prey of algal-feeding juveniles?	1
Adults	• What is the rate of coral loss caused by feeding activities of individual adult COTS, and how does this vary with body size and coral availability?	1
	• Can fluctuations in availability of coral prey explain boom-and-bust cycles of COTS populations?	1
	• What are the mechanisms behind COTS immunity to coral chemical defences?	1
	• What are the relative roles of olfactory *versus* visual systems in detecting prey at different scales?	1
Ecological consequences	• What impact did COTS have on coral assemblages and reef ecosystems prior to the 1960s?	1
	• How do local impacts of COTS vary with their population size and structure?	1
	• Do COTS prey on the entire colony, and can coral colonies recover after partial predation?	2
	• What are the broader ecosystem consequences of selective removal of preferred coral prey (mainly *Acropora*) on community structure?	2
	• Can COTS act as a vector or agent in spreading diseases to corals partially killed by predation?	1

Questions are organized by topics, mostly related to different life stages of COTS but also to the ecological consequences that arise due to localized depletion of prey corals. The number of individual researchers who asked each question is shown (*N*). The order of questions is in no way related to their priority.

This is attributable to persistent concerns about the validity of existing estimates of key demographic rates, because required research is greatly constrained by the limited capacity to tag and/or identify individual sea stars over necessary periods of several years (Pratchett *et al.*, 2017). Moreover, there are other potentially important demographic processes (such as larval cloning and persistence of algal-feeding juveniles) for which the incidence and potential importance have only recently become apparent (Allen *et al.*, 2019; Deaker *et al.*, 2020a, b; Hart *et al.*, 2021). Field-based studies on early life stages of COTS have also benefitted from recent advances in sampling methods (Uthicke *et al.*, 2015a; Wilmes *et al.*, 2020b), making it possible to tackle some of the important and perennial constraints to understanding population dynamics of COTS.

Distribution and abundance

Previous studies on the distribution and abundance of COTS on the GBR have mostly emphasized large-scale and long-term patterns in the initiation and spread of population irruptions (*e.g.*, Reichelt *et al.*, 1990; De'ath *et al.*, 2012), highlighting the important contribution of COTS to sustained declines in coral cover, which are apparent at regional scales. There are, however, important and significant differences in the abundance of COTS within and between reefs (*e.g.*, Vanhatalo *et al.*, 2016; Hock

Table 2

*Research questions (*n = *36) relevant to the demography of crown-of-thorns sea stars (COTS;* Acanthaster *sp.)*

Topic	Question	*N*
Ageing	• Are methods to estimate the age of COTS robust and reliable?	3
	• Is it possible to age juvenile starfish and thereby test for delayed ontogenetic shifts in the wild?	1
	• Can we use age-size relationships to assess cohort distributions?	1
Reproduction	• What is the exact timing of spawning by COTS on the Great Barrier Reef?	1
	• Do individual COTS spawn more than once per reproductive season?	1
	• What are key environmental factors that determine the timing and frequency of spawning?	1
	• Do COTS aggregate to spawn, and if so, where?	1
	• How does the reproductive potential of individual populations vary based on the distribution and abundance of adult COTS?	1
	• What is the natural incidence of self-fertilization, and how does this vary with local population densities, environment conditions, and prey availability?	2
Larval cloning	• What are the drivers of larval cloning?	3
	• Does larval cloning effectively increase planktonic larval duration?	1
Larval mortality	• What are natural rates of growth and mortality for COTS larvae in the field?	1
	• What are the constraints for the demography of COTS larvae in the planktonic phase?	1
	• What is the sensitivity of COTS larvae to environmental toxicants?	1
Ontogenetic shifts	• What are key determinants of ontogenetic diet shifts in juvenile COTS?	1
	• How long can algal-feeding juveniles persist and defer shifts to feeding on coral in the wild?	1
	• Do algal-feeding juveniles persist for over a year and accumulate over multiple settlement events?	1
Demographic shifts	• How do larval supply and predatory regulation interact to affect outbreak dynamics?	1
	• What environmental factors influence detectable changes in the abundance of larval COTS and subsequent initiation of primary outbreaks?	2
	• How do settlement rates and densities of algal-feeding juveniles vary both during outbreaks and in non-outbreak periods?	1
	• Are there differences in adult growth and mortality between outbreaking *versus* non-outbreaking populations?	1
	• Is there a difference in the behavior of COTS in low- *versus* high-density outbreaks?	1
	• How does population structure (size and age structure) vary between primary *versus* secondary outbreaks?	1
	• Can the density and size structure of low-density populations provide insights into the mechanisms leading to population outbreaks?	2
	• What regulates COTS populations, and has this changed with the advent of industrial agriculture and fisheries?	1
	• What are the most sensitive biological and ecological data uncertainties pertaining to the modeling of population dynamics of COTS and their impacts on the Great Barrier Reef?	1
Density dependence	• How are the size and growth of adult COTS affected by conspecific densities and prey availability?	1
	• How can food availability influence density-dependent nature of COTS behavior?	1
	• Is settlement success density dependent?	1
	• Is post-settlement growth density dependent?	1
	• Are post-settlement survival and development success density dependent?	1
Population collapse and pathogenesis	• What are the processes that drive the declines in the abundance of COTS in the aftermath of population outbreaks?	4
	• Do diseases play a critical role in population dynamics?	1
	• What role do starvation and susceptibility to disease play in the demise of population irruptions?	1
	• How do feeding history and reproductive investment interact to determine individual vulnerability to naturally occurring pathogens?	1
	• If disease is important in ending COTS outbreaks, what are the specific conditions that initiate elevated mortality?	1

Questions are organized by topics, mostly related to different demographic traits and potential shifts in demography. The number of individual researchers who asked each question is shown (*N*). The order of questions is in no way related to their priority.

et al., 2017; Matthews *et al.*, 2020). Most notably, there is a higher incidence of population irruptions on mid-shelf reefs, compared to inner-shelf (near-shore) or outer-shelf (offshore and oceanic) reefs (Matthews *et al.*, 2020). Exploring biological and environmental differences between reefs that do and do not sustain population irruptions might help to understand the cause(s) or driver(s) of population irruptions (Table 3). Research on biophysical conditions that explain which reefs are least or most affected by COTS also received considerable attention (a similar question asked by four participants).

Most questions regarding the distribution and abundance of COTS focus explicitly on spatiotemporal patterns in the incidence of population irruptions (Table 3). However, there is now capacity and interest in addressing more advanced ecological questions that consider relationships across different life stages (*e.g.*, comparing the larval supply to local densities of adult COTS;

Table 3

*Research questions (*n = 27*) relevant to the distribution and abundance, and in particular the incidence of population irruptions, of crown-of-thorns sea stars (COTS;* Acanthaster *sp.)*

Topic	Question	*N*
Incidence of population irruptions	• Are there reefs or regions that are consistently among the least or worst affected by COTS outbreaks (*i.e.*, bright and dark spots)?	1
	• What biophysical conditions best explain which reefs are least or worst affected by COTS, and how do these factors contribute to the initiation of outbreaks?	4
	• What drives cross-shelf variation in the incidence of COTS population irruptions?	2
	• Where exactly do primary outbreaks initiate in the northern Great Barrier Reef?	3
	• Do population irruptions occur in the absence of land runoff and elevated nutrients?	1
	• Do primary outbreaks arise from progressive accumulation of individuals across multiple years and cohorts?	1
	• Why is the onset of COTS population irruptions so regular?	1
	• Has there been any change in the frequency or severity of COTS outbreaks on the Great Barrier Reef over time?	2
	• Did recent population irruptions of COTS on Swain Reefs originate independently of the southward progression of outbreaks from the northern Great Barrier Reef?	1
Stock-recruitment relationship	• What is the key demographic bottleneck limiting adult COTS densities at individual reefs?	1
	• Is there evidence of recruitment limitation in COTS?	1
	• Is there a correlation between larval supply, settlement rates, and adult density at the scale of individual reefs?	6
Exposure and habitat use	• Where are juveniles between outbreaks?	1
	• How does the density of algal-feeding juveniles vary with environmental gradients?	1
	• How are coral-feeding juveniles distributed relative to adult conspecifics within and between reef habitats?	1
	• Do conspecific cues from adults impact the behavior of the juveniles?	1
	• Are juvenile COTS more active and exposed at night?	1
	• What is the prevalence of population irruptions of COTS on mesophotic reefs, and what impacts do they have on these slowly growing and rarely disturbed ecosystems?	2
Movement	• How much do COTS move over time, and are they capable of moving between reefs?	2
	• What are the relative roles of olfactory *versus* visual systems in navigation and movement?	1
	• Does large-scale migration contribute to the initiation of population irruptions of COTS on the Great Barrier Reef?	1
Larval dispersal	• How long is the planktonic larval duration of COTS under natural conditions?	1
	• What is the minimum larval duration, and how is it affected by environmental conditions?	1
	• What proportion of COTS larvae settle on their natal reef *versus* successfully disperse to other reefs?	2
Connectivity	• Does genetic structure of adult COTS confirm patterns of predicted larval connectivity based on hydrodynamic models?	1
	• Are there definitive “source” and “sink” reefs for COTS that are consistent through time?	1
	• Are predictions of connectivity models supported by empirical data on the differential occurrence of population irruptions of COTS among reefs and regions?	1

Questions are organized by topics, mostly related to different processes that may influence apparent and definitive differences in the distribution and abundance of COTS. The number of individual researchers who asked each question is shown (*N*). The order of questions is in no way related to their priority.

Hock *et al.*, 2017), which is important for assessing stock-recruitment relationships and the corollary, recruitment limitation (*sensu* Hughes *et al.*, 2000). Indeed, several researchers independently proposed the question to explore the correlation between larval supply, settlement rates, and adult density at the scale of individual reefs (Table 3). This research, along with improved understanding of larval dispersal (Dight *et al.*, 1990; Hock *et al.*, 2014) and post-settlement movement, will inform understanding about the ways in which COTS spread between reefs and will help resolve questions about which reefs are most vulnerable to population irruptions.

Predation

Long-term, multi-decadal reductions in the abundance of specific coral reef organisms (*e.g.*, giant triton, *Charonia tritonis*) that prey on COTS have long been considered a potential driver of population irruptions (reviewed in Cowan *et al.*, 2017). This has initiated extensive searches for potentially important predators of COTS (across all life stages), many of which have declined in abundance as a result of fishery exploitation or reef degradation. There is an ever-increasing range of reef organisms that have been observed or recorded to feed on COTS (Cowan *et al.*, 2017; Kroon *et al.*, 2020), though few of these putative predators are considered capable of killing adult COTS or effectively regulating local COTS densities. Understanding the importance of predation in the population dynamics of COTS is significantly constrained by a lack of empirical data on background mortality and natural predation rates. However, it appears that predation on early life stages (*e.g.*, larvae and newly settled COTS) may have the greatest potential to moderate or constrain COTS populations (Keesing and Halford, 1992b; Cowan *et al.*, 2016, 2020; Keesing *et al.*, 2018; Wilmes *et al.*, 2018); this is recognized as an important knowledge gap, given the lack of research on this topic (Table 4).

Most of the questions originally posed regarding predation on COTS were focussed on rates of predation and key predators of algal-feeding juveniles (12 questions; Fig. 1), showing that many different researchers consider this to be an important area of future research. The two most frequently posed questions relate to key predators and predation rates on juvenile COTS (each question posed by five participants; see Table 4). There is evidence that rates of predation on newly settled COTS may be substantial (Zann *et al.*, 1987; Keesing and Halford, 1992b; Keesing *et al.*, 2018). Moreover, early post-settlement mortality poses significant constraints on population replenishment and population dynamics of many reef organisms because of the high abundance and diversity of small cryptic predators (Goatley *et al.*, 2017; Sellers *et al.*, 2019). There is, however, a need for systematic sampling to comprehensively understand the identity of the most important cryptic predators and assess spatiotemporal variation in their abundance and potential links to anthropogenic changes (*e.g.*, fishing, habitat degradation), which could influence settlement success and explain inter-reef differences in the incidence of population irruptions.

Settlement

Settlement represents a critical change in morphology and ecology as individuals transition from planktivorous and planktonic larvae to sessile, benthic-feeding juveniles (Keesing and Halford, 1992b; Wilmes *et al.*, 2018), as for other coral reef organisms with a biphasic life history (Doherty *et al.*, 2004; Chong-Seng *et al.*, 2014). However, there have been considerable challenges to advancing research on settlement and early post-settlement processes for COTS, mainly because newly settled COTS are notoriously difficult to detect and effectively sample in the wild (Doherty and Davidson, 1988; Johnson *et al.*, 1991; but see Wilmes *et al.*, 2020a). Wilmes *et al.* (2020a, b) effectively sampled many thousands of newly settled COTS within shallow reef environments on the GBR and described habitat conditions (within spur and groove systems and rubble slips on obliquely exposed fore-reef habitats) that maximize detection of these very small COTS. Moreover, methods for measuring settlement rates of COTS have been developed (*e.g.*, Keesing *et al.*, 1993; Uthicke *et al.*, 2019) but are only just being implemented to explore spatiotemporal variation in settlement rates (Doll *et al.*, 2021). As such, there are many ($n = 20$) critical questions relating to the factors that promote or inhibit settlement success by COTS (Table 5). In particular, recent research (Wilmes *et al.*, 2020b) has challenged the prior assumption regarding settlement patterns of COTS on the GBR, which speculated that COTS predominantly settle in deep (>30-m) reef environments that cannot be effectively sampled by scuba divers (*e.g.*, Johnson *et al.*, 1991). The discovery of relatively high densities in shallow (and accessible) reef environments, as shown elsewhere in the world (*e.g.*, Fiji; Zann *et al.*, 1987, 1990), has ignited renewed interest in settlement preferences, substrates, and cues for COTS (Table 5). Most of the questions posed regarding settlement point toward the availability of preferred habitats and substrates, as well as the role of cues in the settlement process (Fig. 1).

Management

Since the first documented population irruptions of COTS in the 1950s and 1960s, it has been recognized that elevated densities of COTS pose a significant threat to coral reef ecosystems (Endean and Stablum, 1975), leading to concerted efforts to prevent or suppress population irruptions (Yamaguchi, 1986). Extensive removal and culling of COTS has occurred despite uncertainties about whether these population irruptions are caused or exacerbated by anthropogenic activities. This is because effective COTS management may provide the best opportunity to reverse ongoing coral loss throughout the Indo-Pacific (De'ath *et al.*, 2012; Westcott *et al.*, 2020; Condie *et al.*, 2021), which is important for sustaining the structure and function of reef systems

Table 4

Research questions (n = 21) relevant to predation on crown-of-thorns sea stars (COTS; Acanthaster sp.)

Topic	Question	N
Identifying predators	• Are there other reef organisms, not yet considered, that are potentially important COTS predators (*e.g.*, cryptic predators)?	2
	• Could stable isotope and DNA-based techniques be used to detect or confirm key predators of different COTS life stages?	2
	• Can we identify COTS DNA in gut samples of putative predators of juvenile and adult starfish?	1
Abundance of predators	• Are important COTS predators more abundant on reefs closed to fishing?	1
	• Are there differences in the abundance and composition of planktivores among reefs, which might functionally affect larval density and settlement rates?	1
	• What are key factors that determine contemporary abundance and distribution of the giant triton on the Great Barrier Reef?	3
Larval predators	• What are the natural predation rates on COTS gametes and larvae?	1
	• What are the key zooplanktivorous predators on COTS gametes and larvae?	2
	• Can planktivores effectively regulate COTS populations by feeding on gametes and larvae?	1
Juvenile predators	• What are natural predation rates on juvenile COTS, and how do these vary with density and local habitat structure?	5
	• What are the key predators of herbivorous and corallivorous juvenile COTS?	5
	• To what extent does the behavioral ecology of juvenile COTS moderate vulnerability to predation?	1
	• Does predation rate on juvenile COTS increase or decrease with ontogeny?	1
Adult predators	• To what extent do spines and toxins in adult COTS moderate vulnerability to predation?	1
	• What is the capacity of giant triton to prevent or suppress COTS outbreaks?	1
	• What is the natural diet of giant triton, and do they preferentially target COTS in the presence of alternative and consistently available prey?	2
	• What is the maximal range of detection of giant triton by COTS in the wild?	1
Sublethal predation	• How does sublethal predation affect growth and survival of COTS in the wild?	2
	• How do sublethal injuries affect fecundity and reproductive capacity of COTS?	1
Indirect effects of predators	• How do COTS respond to the presence or detection of giant triton and other predators in the wild?	1
	• Do predators moderate natural behavior and spawning success of adult COTS?	1

Questions are organized by topics, mostly related to identifying key predators across different life stages of COTS and understanding their specific effects on COTS populations. The number of individual researchers who asked each question is shown (*N*). The order of questions is in no way related to their priority.

Table 5

Research questions (n = 13) relevant to the settlement of crown-of-thorns sea stars (COTS; Acanthaster sp.)

Topic	Question	N
Rates	• How do rates of larval settlement of COTS vary spatially and temporally?	1
	• How do settlement rates vary between different reef substrates?	1
	• Do natural settlement rates vary with changes in the local abundance of specific crustose coralline algae species?	1
Habitat and substrate preferences	• Where do COTS settle across reefs within the outbreak initiation box?	1
	• Does limited availability of suitable settlement habitat constrain COTS settlement on inshore reefs?	2
	• How does early post-settlement survival vary between different reef habitats and substrates?	2
	• Do COTS settle predominantly in deep-water (>15-m) habitats?	2
	• Over what depth range do COTS settle and persist as algal-feeding juveniles?	1
Cues	• What are the specific habitat conditions and predominant cues that promote settlement in the wild?	3
	• Do conspecific cues from adult COTS influence larval settlement choices?	3
Environmental constraints	• Are there key environmental conditions that enhance or moderate settlement rates?	1
	• Are there factors that inhibit settlement of COTS even in the presence of suitable settlement habitats and cues?	1
	• How does water flow influence COTS settlement?	1

Questions are organized by topics, mostly related to different processes that influence settlement rates and patterns of COTS. The number of individual researchers who asked each question is shown (*N*). The order of questions is in no way related to their priority.

(Bellwood *et al.*, 2019). Thus far, manual control has been the most direct and effective way to suppress densities of COTS and minimize their impacts on coral cover and reef health (Westcott *et al.*, 2020). Improvements in surveillance and monitoring of COTS populations may further increase the effectiveness of these management actions for suppressing COTS populations by allowing for more timely intervention and strategic allocation of resources (Hock *et al.*, 2016, 2017; Babcock *et al.*, 2020; Bozec *et al.*, 2020). As such, there are several specific research questions that have been posed to assess current limitations and potential advances in the methods used to sample and monitor COTS, across all life stages (Table 6). Management actions to minimize fishing impacts (largely through the increasing establishment of no-take marine protected areas) and to improve water quality (by minimizing runoff of sediments, nutrients, and pollutants) also attract continued attention, because they represent no-regret strategies that contribute to the increased resilience of reef ecosystems (*e.g.*, Fabricius *et al.*, 2010; McCook *et al.*, 2010; Wooldridge and Brodie, 2015) and may ultimately moderate the incidence or severity of population irruptions of COTS (Sweatman, 2008; Wooldridge and Brodie, 2015; Westcott *et al.*, 2020). There is some evidence linking the reduction of fishing pressure *via* the establishment of no-take marine reserves to the effective suppression of population irruptions of COTS (Dulvy *et al.*, 2004; Sweatman, 2008; Vanhatalo *et al.*, 2016). On the GBR, Sweatman (2008) showed that the incidence of population irruptions of COTS was almost four times as high on mid-shelf reefs that were open to fishing, compared to no-take marine reserves, which was attributed to trophic cascades arising because of fisheries-induced depletion of large piscivorous fishes (Sweatman, 2008). Spatiotemporal modeling of population irruptions of COTS in the GBR also shows substantial declines in the relative intensity of population irruptions 10 years after the re-zoning of marine reserves in the GBR (Vanhatalo *et al.*, 2016). There are, however, yet to be any detailed studies quantifying rates of predation or mortality from COTS inside *versus* outside no-take marine reserves. Accordingly, most of the research questions posed on this topic are looking to advance understanding of how marine reserves work to moderate the incidence or severity of population irruptions of COTS *via* protection of potential predators (see also Table 4), which is a necessary step before redesigning or increasing fisheries restrictions.

Aside from continuing to improve the efficiency and effectiveness of established management approaches (*e.g.*, Westcott *et al.*, 2020), there is considerable interest in changing the way that COTS are managed on the GBR. Three researchers posed a similar question about the effectiveness, efficiency, and ways to improve the current surveillance techniques and culling procedures (Table 6). Given consistent and recurring patterns of population irruptions on the GBR (Pratchett *et al.*, 2014), there is, for example, potential to move beyond reactive management of established population irruptions toward proactively assessing and managing the risk of future population irruptions at strategically selected locations (Ling *et al.*, 2009; Hock *et al.*, 2016, 2017; Babcock *et al.*, 2020). This shift to proactive management calls for the development of new tools (*e.g.*, environmental DNA [eDNA] detection; Uthicke *et al.*, 2018) that will contribute to improved early warning of impending population irruptions (Table 6). There are also many important research questions that relate to, or will facilitate, innovative control activities (*e.g.*, biocontrol and/or use of attractant or repellent signaling molecules, semiochemicals) to improve the efficiency or reduce reliance on manual culling (Table 6). Additionally, however, there are concerns that some control measures could change the ecological trajectory of the COTS-coral interaction on the GBR from typically one of boom and bust to a more chronic trajectory (*e.g.*, Yamaguchi, 1986), where coral cover remains at low levels, preyed upon by persistent COTS populations and further impacted by other disturbances.

Environmental change

Sustained and ongoing environmental change will have important effects on coral reef ecosystems and species (Hoegh-Guldberg and Bruno, 2010; Hughes *et al.*, 2018a), such that future conservation and management need to explicitly account for widespread and accelerating changes in environmental and habitat conditions (Bellwood *et al.*, 2019). Previous research investigating the responses of COTS to projected changes in environmental conditions have investigated the effects of ocean warming and/or acidification on reproduction (Uthicke *et al.*, 2013; Caballes *et al.*, 2017b; Hue *et al.*, 2020) and larval development (Kamya *et al.*, 2014; Lamare *et al.*, 2014; Uthicke *et al.*, 2015b), as well as the feeding ecology and growth of both algal-feeding (Kamya *et al.*, 2016, 2017) and coral-eating (Kamya *et al.*, 2018) juvenile COTS. There has also been recent research exploring temperature sensitivity and thermal optima in adult COTS (Lang *et al.*, 2021). These studies consistently show that COTS are sensitive to projected changes in environmental conditions, though it is unclear whether environmental change will moderate (*e.g.*, Hue *et al.*, 2020) or exacerbate (Uthicke *et al.*, 2015b) population irruptions.

Aside from direct effects of elevated temperatures and other changing environmental conditions (*e.g.*, ocean acidification) on the physiology, replenishment, and persistence of COTS, ongoing environmental change is likely to significantly alter the structure of coral assemblages and reef ecosystems (*e.g.*, Hughes *et al.*, 2018b), as well as environmental and biological (*e.g.*, phytoplankton biomass and composition) conditions in surrounding waters (*e.g.*, Lough *et al.*, 2015). Most notably, severe mass bleaching and mass mortality of corals will alter the availability of coral prey for COTS, raising many questions about how this might affect the feeding behavior (Keesing *et al.*, 2019; Ling *et al.*, 2020), fitness, survival, distribution, and abundance of COTS (Table 7). There is also the potential for fitness, survival, and population dynamics of COTS to be altered by interactions between climate-driven environmental changes

Table 6

*Research questions (*n *= 38) relevant to the management of crown-of-thorns sea stars (COTS;* Acanthaster *sp.)*

Topic	Question	*N*
Monitoring	• Do current surveillance methods provide an accurate representation or suitable proxy for the overall abundance of COTS at individual reefs?	1
	• What proportion of COTS are detected or missed using different surveillance methods and in different habitats?	1
	• Can we use environmental DNA (eDNA) as an early-warning tool in conjunction with other monitoring?	2
	• How do eDNA detection and levels vary with local size and abundance of COTS *versus* other environmental factors (*e.g.*, current flow and sampling season)?	1
	• How can larval supply be measured?	1
	• Can COTS larval sampling be used to detect the early onset of new and renewed population irruptions?	1
	• How can settlement be measured?	1
	• Can changes in settlement rates or juvenile densities in the lead-up to initiation of population irruptions be detected?	1
	• Can eDNA (or RNA) be used to assess abundance of COTS when they are very small or rare?	1
Culling	• What changes in surveillance techniques and culling procedures will further enhance the efficiency and effectiveness of manual control?	3
	• What is the optimal allocation of current control capacity to maximize reef-wide ecological benefits?	1
	• What proportion of COTS are detected or missed during culling at a given reef location?	1
	• Are there potential negative effects (*e.g.*, creating chronic population irruptions) of ineffective culling?	1
	• Does the culling program release the juveniles from competition with adults, thereby triggering a transition to corallivory?	1
Biocontrol	• Can population irruptions of COTS be “controlled” biologically, and if so, what are the potential risks of such an approach?	2
	• Are there any COTS-specific microbial agents that could be used for biocontrol with minimal unintended consequences and that are socially acceptable?	1
	• Can immune systems be manipulated to compromise COTS physiology, health, and survival?	1
	• Is genetic control of COTS a viable option for COTS control, and are associated risks socially acceptable?	1
	• Can chemosensory systems and genome-encoded factors be used to disrupt COTS physiology, development, and behavior?	2
Chemical attractants or dispersants	• What are key limitations (*e.g.*, dispersal and dilution) to the use of semiochemicals in controlling COTS?	2
	• Are there potentially effective “attractants” that can be used to concentrate COTS in reef habitats and thereby enhance effectiveness of manual control?	1
	• Are there potentially effective “repellents” that can be used to disperse COTS in reef habitats to limit reproductive success and protect specific habitat areas?	2
	• Can feeding attractants isolated from select coral prey be used to control or disrupt COTS distribution and behavior?	1
	• What is the chemical nature of COTS-derived attractants, and is there a seasonal difference?	1
	• What are the specific chemical inducers of COTS spawning that may be exploited in modifying reproductive behavior and success?	1
	• Do COTS respond to conspecific alarm cues, and can these be exploited to influence the distribution and behavior of adult COTS in reef environments?	1
	• What are the specific chemical inducers of larval settlement that may be exploited in modifying larval distribution and settlement success?	1
	• What are the inherent vulnerabilities of the sensory systems of adult COTS that may be exploited in modifying behavior and fitness?	1
Enhancing predator abundance or function	• How can predatory risk to COTS across all life-history stages be maximized in terms of natural and human interventions?	1
	• What more can be done to increase numbers of important predators that might normally regulate COTS populations?	1

Table 6 (*Continued*)

Topic	Question	*N*
	• How can giant triton be cultured for the purpose of suppressing low-density populations of COTS?	1
No-take marine reserves	• Does spatial fisheries management (Great Barrier Reef Marine Park zoning) affect the incidence of population irruptions of COTS?	3
	• How does marine park zoning affect growth and mortality of COTS at all life-history stages as well as the interactions of their potential predators?	1
	• Will increasing the spatial extent of no-take areas serve to prevent or delay recurrence of population irruptions of COTS?	2
	• Are predation rates (lethal or sub-lethal) on adult COTS higher at reefs closed to fishing?	1
Trophic cascades	• Are there indirect effects of fishing on potentially important COTS predators?	1
	• How has fishing affected the abundance and function of not only target species but also lower trophic levels that are potentially important in regulating COTS populations?	1
Water quality	• What more can be done to reduce runoff of nutrients that may release COTS larvae from starvation?	1

Questions are organized according to topics that will either improve the effectiveness of existing management approaches or facilitate new management approaches for COTS. The number of individual researchers who asked each question is shown (*N*). The order of questions is in no way related to their priority.

Table 7

*Research questions (*n = *18) relevant to effects of environmental change on crown-of-thorns sea stars (COTS;* Acanthaster *sp.)*

Topic	Question	*N*
Elevated temperature	• Will population irruptions of COTS be more or less severe with ocean warming?	2
	• How will marine heatwaves affect the distribution and abundance of COTS?	4
	• What are the likely effects of ocean warming on reproductive biology?	1
	• How will projected ocean warming affect growth and survival of COTS larvae?	2
	• Can COTS larvae, juveniles, and adults withstand elevated temperatures associated with increasing incidence and severity of marine heatwaves?	1
	• How will ocean warming impact the growth and survival of algal-feeding juvenile COTS?	1
	• What is the preferred and optimal temperature for COTS, and does it vary depending on body size and prior thermal exposure?	1
	• How will feeding rates of adult COTS change with ocean warming?	1
Coral bleaching	• Will recurrent and ongoing coral bleaching lessen or worsen the effects of COTS outbreaks on coral assemblages?	1
	• Will declines in coral cover (especially *Acropora*) due to environmental change reduce the likelihood of population irruptions?	2
	• Do COTS prefer to feed on healthy or bleached coral?	1
	• Does coral loss caused by environmental disturbances (*e.g.*, mass bleaching) lead to aggregations of COTS in remnant patches of live coral?	1
	• How will recurrent mass bleaching influence the availability of preferred *versus* non-preferred coral prey for COTS, and will this affect COTS feeding behavior?	2
	• How will coral bleaching and corresponding changes in the availability of preferred coral influence the condition and fitness of coral-feeding COTS?	3
Changing habitat structure	• How will shifts in coral composition (away from *Acropora* dominance) affect the behavior and population dynamics of COTS?	1
	• How will changing environmental and habitat conditions influence local abundance of potential predators and corresponding predation rates on COTS?	1
	• Do cyclones increase the quantity and quality of rubble habitats, thereby promoting settlement and post-settlement survival of COTS?	1
	• Does lack of coral on degraded reefs (high seaweed cover, low crustose coralline algae cover) inhibit or delay ontogenetic shifts from herbivory to corallivory?	1

Questions are organized by topics, reflecting the different pathways by which impacts of environmental change affect COTS. The number of individual researchers who asked each question is shown (*N*). The order of questions is in no way related to their priority.

(*e.g.*, ocean warming) and other disturbances (*e.g.*, cyclones). In all, the effects of environmental change on the population dynamics and ecological impacts of COTS are likely to be very complex (*e.g.*, Haywood *et al.*, 2019) but need to be understood because they will have a major influence on future management needs and opportunities.

Conclusions

This study has highlighted many areas of potentially fruitful research for advancing the understanding and management of COTS in coming years. This is not to understate the very significant progress in COTS research over recent decades, which has effectively redressed many critical knowledge gaps (Moran, 1986; Pratchett *et al.*, 2017). Indeed, many of the research questions posed herein have arisen directly from new knowledge (*e.g.*, Allen *et al.*, 2019) or are possible only because of the recent sequencing of the COTS genome (Hall *et al.*, 2017) and development of novel sampling methods (Doyle *et al.*, 2017; Doyle and Uthicke, 2020). However, renewed impetus and opportunities for COTS research should carefully consider the myriad knowledge gaps and potential research questions. Herein, we present 172 distinct research questions considered to be important by at least 1 current or established researcher with relevant topical and geographical expertise. Thus, there is considerable need for a multi-disciplinary approach in addressing key knowledge gaps in COTS research. The predominant topics represented by the questions posed across all life-history stages of the sea star, which included the incidence of population irruptions, the feeding (nutritional) ecology of larval sea stars, effects of elevated temperature, and predation on juvenile COTS, should be a focus for new research. This will involve extensive field sampling, laboratory experiments, and modeling. The compilation of this list of potential research questions can now also be used to assess and prioritize the importance and urgency of redressing distinct knowledge gaps and to explore perceptional differences between different groups of stakeholders, following Cvitanovic *et al.* (2013).

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Author Contributions

The core research team (MSP, CFC, CC, and SKW) conceptualized, led, and coordinated the study, with data curation and analysis assistance from MLR. The remaining authors of this study were the participants, with authorship given in recognition of the significant intellectual input provided in the generation of research questions based on their high-level expertise. All authors listed reviewed and edited drafts of the manuscript.

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