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Review

Known Predators of Crown-of-Thorns Starfish (*Acanthaster* spp.) and Their Role in Mitigating, If Not Preventing, Population Outbreaks

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Abstract: Predatory release has long been considered a potential contributor to population outbreaks of crown-of-thorns starfish (CoTS; *Acanthaster* spp.). This has initiated extensive searches for potentially important predators that can consume large numbers of CoTS at high rates, which are also vulnerable to over-fishing or reef degradation. Herein, we review reported predators of CoTS and assess the potential for these organisms to exert significant mortality, and thereby prevent and/or moderate CoTS outbreaks. In all, 80 species of coral reef organisms (including fishes, and motile and sessile invertebrates) are reported to predate on CoTS gametes (three species), larvae (17 species), juveniles (15 species), adults (18 species) and/or opportunistically feed on injured (10 species) or moribund (42 species) individuals within reef habitats. It is clear however, that predation on early life-history stages has been understudied, and there are likely to be many more species of reef fishes and/or sessile invertebrates that readily consume CoTS gametes and/or larvae. Given the number and diversity of coral reef species that consume *Acanthaster* spp., most of which (e.g., *Arothron* pufferfishes) are not explicitly targeted by reef-based fisheries, links between overfishing and CoTS outbreaks remain equivocal. There is also no single species that appears to have a disproportionate role in regulating CoTS populations. Rather, the collective consumption of CoTS by multiple different species and at different life-history stages is likely to suppress the local abundance of CoTS, and thereby mediate the severity of outbreaks. It is possible therefore, that general degradation of reef ecosystems and corresponding declines in biodiversity and productivity, may contribute to increasing incidence or severity of outbreaks of *Acanthaster* spp. However, it seems unlikely that predatory release in and of itself could account for initial onset of CoTS outbreaks. In conclusion, reducing anthropogenic stressors that reduce the abundance and/or diversity of potential predatory species represents a "no regrets" management strategy, but will need to be used in conjunction with other management strategies to prevent, or reduce the occurrence, of CoTS outbreaks.

Keywords: *Acanthaster* (Acanthasteridae); fisheries closures; marine parks; predation; predator removal hypothesis; chemical defences; saponins; population regulation; top-down control; trophic cascades

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1. Introduction

Adult crown-of-thorns starfish (CoTS; *Acanthaster* sp.) have numerous long, very sharp and toxic spines (Figure 1). In addition, the dermal tissues of CoTS (and all of their organs) contain high concentrations of chemicals, including saponins [1,2] and plancitoxins [3], which are both unpalatable [4] and highly toxic [5–7]. Intuitively therefore, one might expect that these starfish are effectively protected and largely immune from predation (e.g., [8]). In reality, there are few organisms that are completely immune to predation at any or all stages of their life cycle. Rather, well-developed anti-predatory defences reduce the range of predators to which prey species are vulnerable [9], but may or may not affect overall rates of predation and the extent to which prey populations are controlled by predators. Accordingly, there is an increasing number of coral reef organisms (fishes and invertebrates) reported to predate on CoTS [10,11], including some predators (e.g., *Arothron* pufferfishes) that feed almost exclusively on adult CoTS when they are in abundant supply (e.g., during outbreaks). Such predators may be important in supressing the abundance of prey species [12] as well as influencing the behaviour, habitat-associations, and population dynamics of even well-armoured and/or chemically defended prey species (e.g., [13]).

Despite their physical and chemical defences, post-settlement stages (juvenile and adults) of CoTS often exhibit injuries, largely manifested as missing arms [11,14,15]. These injuries are believed to occur when predators are only able to remove one or a few arms before the starfish escapes or avoids further damage by hiding within the reef matrix [15]. If however, there are high rates of partial predation at specific reef locations [11] then it is expected at least some CoTS will also be killed outright and/or consumed in entirety. The cryptic nature and nocturnal behaviour of CoTS, especially when small (<12 cm diameter) or at low densities [11,16] further suggests that they must be highly vulnerable to predators. In controlled experiments, survivorship of laboratory reared *Acanthaster* spp. settled to natural substrates is effectively zero, owing to very high rates of predation by naturally occurring predators [17–19]. Recent research also demonstrates that CoTS larvae are highly vulnerable to predation [20], despite having the highest concentrations of anti-predator chemicals (discussed later). Cowan et al. [20] showed that CoTS larvae are readily consumed by many common planktivorous damselfishes, and often in preference to other asteroid larvae.

While there is now general acceptance that CoTS are vulnerable to predation (e.g., [11,21]), on-going controversies relate to whether known predators would ever be capable of regulating CoTS populations, and mitigating, if not preventing outbreaks. More specifically, attention is focussed on whether anthropogenic impacts (via fishing or habitat degradation) have supressed the abundance of key predators, thereby accounting for the seemingly recent and/or increasing occurrence of CoTS outbreaks [10].

Figure 1. Adult crown-of-thorns starfish are defended against predators by numerous long, very sharp and toxic spines. Photographic credit: Scott Ling, Dick’s Reef, Swains Region, southern Great Barrier Reef (22°18′ S, 152°39′ E).

1.1. The Predator Removal Hypothesis

The *predator removal hypothesis* was one of the first hypotheses proposed to account for CoTS outbreaks [22]. Following trophic-cascade concepts as a result of ecological extinction of functional echinoderm predators such as sea otters (e.g., [23–25]), lobsters [26] and large benthic predatory fishes [27], this hypothesis (like many other hypotheses put forward in the 1960s and 1970s, such as the *nutrient enrichment hypothesis*, e.g., [28–30]) is predicated on the idea that CoTS outbreaks are an unnatural phenomenon, caused by anthropogenic modification and degradation of coral reef environments [31]. The initial formulation of the *predator removal hypothesis* related to apparent overfishing of the giant triton (*Charonia tritonis*) on the GBR in the decades immediately preceding the first documented outbreak of CoTS in 1962 [22]. Notably, ~10,000 giant tritons were removed from the GBR each year from 1947 to 1960 by trochus fishermen and commercial shell collectors [22]. Densities of triton must have been significant to sustain this level of removal, or at the very least, much higher than they are now. While there is no empirical data on their abundance, *C. tritonis* are exceedingly rare on the GBR, and have been since the 1960s, perhaps reflecting the legacy of excessive removals in the 1950s [32].

Endean [22] argued that the effective loss of giant triton from reefs in the northern GBR relaxed normally strong regulatory pressure on abundance of juvenile and sub-adult CoTS, leading to increased abundance of large adult starfish that were capable of initiating outbreaks by virtue of their massive combined reproductive output. Adding weight to this hypothesis, outbreaks of CoTS were reported from other locations (e.g., Fiji and Western Samoa) where *C. tritonis* had also been extensively harvested, whilst outbreaks had not been reported in areas (e.g., Malaysia, Philippines and Taiwan) where *C. tritonis* were abundant [22]. The ability of *C. tritonis* to provide the sufficient top-down control necessary to regulate CoTS populations has since been questioned (e.g., [33]) largely based on their generally low rates of feeding and the apparent reluctance to eat CoTS when provided with alternative prey.

Though the role of giant triton in regulating abundances of CoTS (past, present, or future) is still not resolved, the *predator removal hypothesis* has evolved through time to place increasing emphasis on fish predators. Attention has focused on large predatory fishes capable of consuming adult starfish (e.g., [33–35]), which are targeted by fisheries and/or have declined in abundance due to localized fishing activities. Explicit and direct evidence that any of the major fisheries target species (e.g., coral trout, *Plectropomus* sp.) are significant predators of crown-of-thorns starfish is meagre [34]. However, some studies [33,36,37] have reported increased incidence and/or severity of outbreaks of CoTS along gradients of increasing fishing effort. On the GBR, Sweatman [37] showed that reefs open to fishing were seven times more likely to experience an outbreak of crown-of-thorns starfish (57% of reefs affected) compared to reefs effectively closed to fishing within no-take marine reserves (8% of reefs affected). While the mechanistic basis of these patterns has not been critically tested, increasing evidence of links between fishing and starfish outbreaks [36,37] has fuelled significant interest in predation, both to understand the cause(s) and ultimately manage CoTS outbreaks.

1.2. Objectives of This Review

The purpose of this review is to synthesise existing knowledge of potentially important CoTS predators, considering their individual and collective capacity to influence population dynamics of CoTS. There is an ever-increasing list of putative predators (e.g., [11,38,39], Table 1), largely based on anecdotal observations of different coral reef organisms (mainly fishes) feeding on dead or dying CoTS within reef environments. Our intention in this review is to differentiate between organisms that opportunistically feed on dead or injured CoTS (scavengers), versus those predators that feed on live and healthy starfish and either kill them outright or reduce their individual fitness and/or reduce population level fitness by altering patterns in abundance and distribution. It is possible, for example, that the mere presence of benthic predators could disperse adult CoTS that might otherwise aggregate to spawn, and thereby reduce fertilization success. Moreover, this review will explicitly consider potential predators at different stages in the life cycle of CoTS, especially pre-settlement (e.g., gametes, larvae) and early post-settlement life stages, which is quite possibly the most significant bottleneck in their life-history [40–42]. Where possible, we report or derive estimates of the rates of mortality due to predation across different life-history stages of CoTS.

Having established the range of putative CoTS predators, this review will consider empirical and theoretical evidence that supports (or refutes) the potential role of predators in moderating (if not preventing) CoTS outbreaks. If predation underlies observed differences in the incidence or severity of outbreaks across gradients of fishing pressure [36,37], we would expect to find that the specific predators would be significantly more abundant in areas with little or no fishing, with corresponding increases in effective rates of predation on juvenile and/or adult CoTS within these areas. Persistent controversy around the role of predation in regulating abundance of CoTS (e.g., [11,36,37]) highlights many deficiencies in previous research approaches and points to the definitive need for experimental studies that explicitly test the mechanistic underpinnings of the *predator removal hypothesis*.

2. Known Predators of Crown-of-Thorns Starfish

A total of 80 species of coral reef organisms are reported to feed on CoTS, including 24 motile and sessile invertebrates versus 56 species of coral reef fishes (Table 1). However, most species have been observed feeding on moribund and dead individuals in the field, while observations of predation on healthy, uninjured starfish are comparatively rare. Similarly, field observations of species feeding on the gametes of CoTS are also extremely limited, and field observations of predation upon larvae are simply not feasible. Gut content analysis has also been largely unsuccessful in identifying putative predatory species (e.g., [43]). However, there have been significant advances in the field of environmental DNA (eDNA) analysis in recent years [44] and it is likely that this technique could be utilised to both identify previously unknown predators, and establish the frequency with which known predators actually consume CoTS. One suggested method to do this would be to collect faeces of presumed CoTS predators and test this for presence of CoTS DNA. However, there are limitations to this technique. Most notably, it is not possible to distinguish between particular life stages of prey species, nor whether specific prey species were alive or dead when consumed [44], which is important in understanding the role of predators in structuring populations of CoTS. Such experiments should be supplemented with benthic surveys to confirm presence of juvenile or adult starfish, and plankton tows to confirm presence/absence of CoTS larvae (see [45]). This could provide an indication of the CoTS life stage from which DNA found in predator faeces has originated, and would be particularly beneficial for predators such as damselfish which may prey upon both pre- and post-settlement life stages (e.g., [20,28]).

Table 1. Species that feed on different life stages and states of health of *Acanthaster* spp. "F" denotes that the particular predator has been directly observed feeding on a particular life stage in the field, which also includes where starfish were made unnaturally available; "L" denotes where feeding is inferred based on studies in a laboratory/aquarium; "G" denotes that *Acanthaster* remains have been recovered from the stomach of the predator; I = not directly witnessed.

Predator	Sperm	Eggs	Larvae	Juvenile	Adult–Healthy	Adult–Injured	Adult–Moribund/Dead	Reference
Fishes								
Angelfish								
Holacanthus passer						L		[39]
Pomacanthus semicirculatus							F	[38]
Pomacanthus sexstriatus							F	[38]
Bream								
Scolopsis bilineatus							F	[46]
Butterflyfish								
Chaetodon aureofasciatus							F	[46]
Chaetodon auriga						L	FL	[11,38,46]
Chaetodon auripes	F							[47]
Chaetodon citrinellus						L		[39]
Chaetodon plebeius							F	[46]
Chaetodon rafflesi							F	[46]
Chaetodon rainfordi							F	[46]
Chaetodon vagabundus							FL	[46,48]
Damselfish								
Abudefduf sexfasciatus		F	L					[20,22]
Acanthochromis polyacanthus			L				L	[20,48]
Amblyglyphidodon curacao		F	L					[20,28]
Chromis atripectoralis			L					[20]
Chromis caerulea						L	F	[11,38]
Chromis dimidiata			L					[49]
Chromis viridis			L					[20]
Chrysiptera rollandi			L					[20]
Dascyllus aruanus			L					[20]
Dascyllus reticulatus			L					[20]
Neoglyphidodon melas							F	[46]
Neoglyphidodon oxyodon							F	[46]

Table 1. *Cont.*

Predator	Sperm	Eggs	Larvae	Juvenile	Adult–Healthy	Adult–Injured	Adult–Moribund/Dead	Reference
Neopomacentrus azysron			L					[20]
Pomacentrus amboinensis			L					[20]
Pomacentrus chrysurus							F	[46]
Pomacentrus moluccensis			L			L	FL	[11,20,38,46]
Pomacentrus wardi							F	[46]
Stegastes acapulcoensis						F		[39]
Stegastes nigricans							F	[46]
Emperors								
Lethrinus atkinsoni				F			FL	[46,50]
Lethrinus miniatus				F				[50,51]
Lethrinus nebulosus					G		F	[46,51]
Goatfish								
Parupeneus multifasciatus							F	[46]
Gobies								
Cryptocentrus sp.							F	[38]
Groupers								
Epinephelus lanceolatus				FG				[52]
Pufferfish								
Arothron hispidus				F	FL	L	FL	[11,39,43,46,48,53]
Arothron manilensis							L	[46]
Arothron meleagris							F	[39]
Arothron nigropunctatus							F	[38]
Arothron stellatus					F			[47]
Triggerfish								
Balistapus undulatus							F	[46]
Balistoides viridescens				L	FL		L	[11,43,46,48,53]
Pseudobalistes flavimarginatus				L	FGL			[11,43,54]
Rhinecanthus aculeatus							L	[48]
Sufflamen verres							F	[39]

Table 1. *Cont.*

Predator	Sperm	Eggs	Larvae	Juvenile	Adult–Healthy	Adult–Injured	Adult–Moribund/Dead	Reference
Wrasses								
Cheilinus diagrammus							F	[38]
Cheilinus fasciatus							F	[38]
Cheilinus undulatus					FG			[43,51,55,56]
Coris caudomacula							F	[46]
Halichoeres melanurus							L	[48]
Thalassoma hardwicke							F	[38]
Thalassoma lucasanum						FL		[11,39]
Thalassoma lunare							FL	[46,48]
Thalassoma nigrofasciatum							F	[46]
Motile invertebrates								
Acanthaster planci							F	[38]
Alpheus sp.							F	[38]
Bursa rubeta				I	I			[57] in [21]
Cassis cornuta					L			[55]
Charonia tritonis				F	FL		F	[22,28,32,38]
Cymatorium lotorium					I			[43]
Dardanus sp.					I			[43]
Diadema mexicanum							F	[39]
Dromidiopsis dormia					I			[57] in [21]
Hymenocera elegans/picta				L	F	F		[39,58,59]
Murex sp.					L			[55]
Neaxius glyptocercus				I	I			[60] in [21]
Panulirus penicillatus				L				[18]
Pherecardia striata				F		F	F	[39,59]
Trapezia flavopunctata			L					[19]
Trapezia bidentata			L					[19]
Trapezia cymodoce			L					[19]
Trizopagurus magnificus							F	[39]
Xanthidae				L				[49]
Sessile invertebrates								
Paracorynactis hoplites				F	F			[61]
Platygyra sp.			L					Cowan Pers. obs.
Pocillopora damicornis			L					[8]
Pseudocorynactis sp.					F			[62]
Stoichactis sp.					L			[55]

2.1. Pre-Settlement Predation

Most of the putative CoTS predators feed or scavenge on post-settlement life stages (juveniles and adults) compared to pre-settlement stages (Figures 2 and 3). However, this probably reflects limited research directed at identifying potential predators on CoTS eggs and larvae and/or difficulties in documenting predation on these early life-history stages. Coral reefs typically support very high abundance and diversity of planktivorous species, including many different reef fishes (e.g., [20,28,47,63]) as well as sessile invertebrates, such as corals [8], which may consume CoTS propagules during spawning, as well as feeding on CoTS larvae when they settle. CoTS are one of the most fecund invertebrates [64], with very high fertilisation rates [65,66], but intuitively, most eggs and larvae must fail to survive. As for other marine species with planktonic larvae, significant rates of pre-settlement mortality are also likely to arise due to predation [67,68]. Yet, given their exceptional reproductive potential [64], even small changes in the proportion of larvae that survive and settle will lead to vast differences in the absolute number of juvenile and adult starfish.

Early studies suggested that CoTS eggs and larvae were largely immune from predation due to unpalatable chemical defences (saponins) contained within [4]. However, more recent examination of predation upon both eggs [69] and larvae [20] reveals that these are indeed readily consumed by a range of highly abundant, planktivorous damselfishes. Given that this group of predators can be extremely abundant on coral reefs, it is likely that they play an important role in reducing the proportion of CoTS that survive through to settlement, and high densities of damselfishes should be considered important for the buffering capacity of coral reefs. Given that all the planktivorous damselfishes tested in the recent studies [20,69] consumed CoTS material, albeit to varying extents, it is highly likely that there are more predators of the pre-settlement stages that are yet to be identified. Furthermore, the actual suite of predators that prey upon the early life stages of CoTS is likely to span a far greater taxonomic range, from benthic species such as those already identified (e.g., [8,19], Table 1) to large pelagic fishes, such as manta rays and whale sharks.

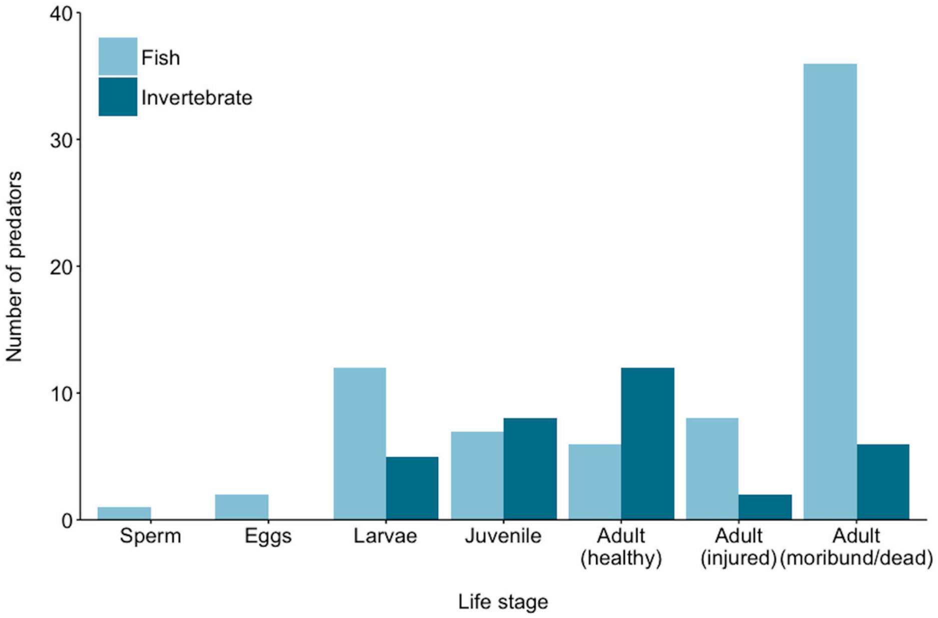

Figure 2. Putative predators of crown-of-thorns starfish across each major life stage. Predators at each life stage are not mutually exclusive. This figure is based on references from Table 1.

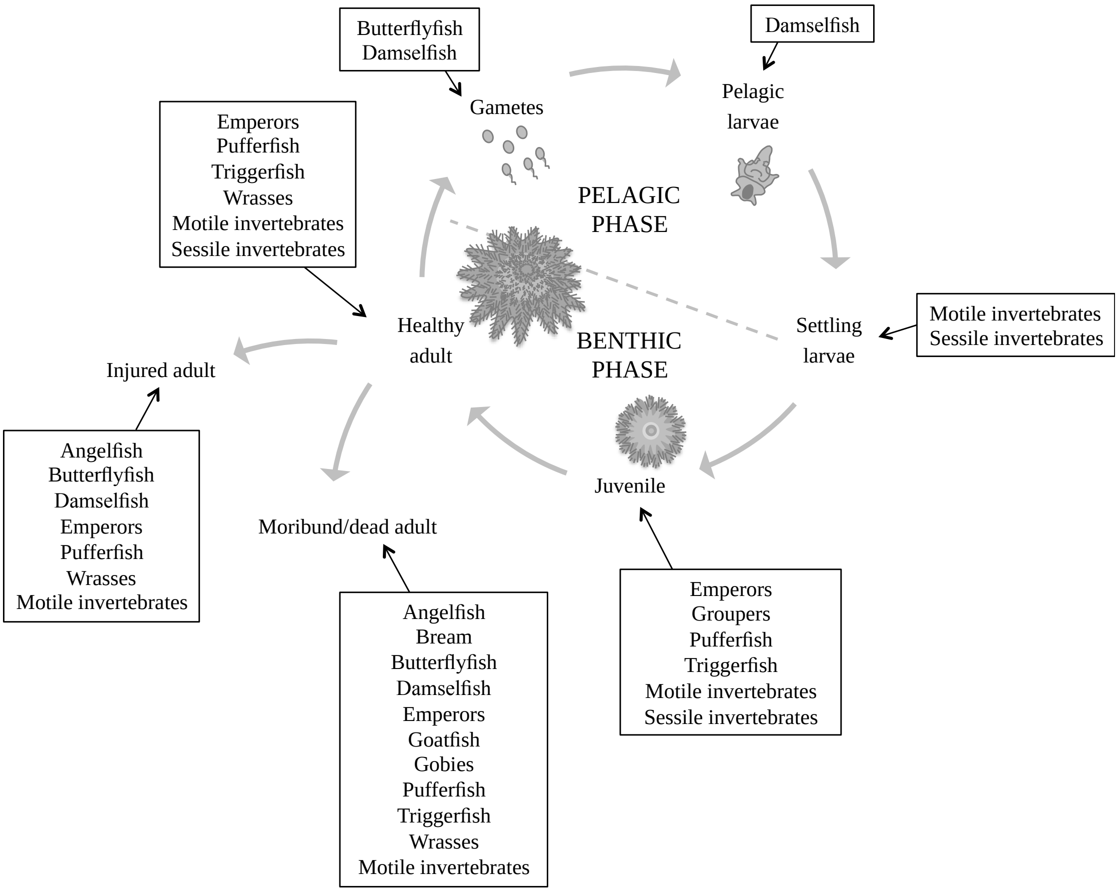

Figure 3. Main predatory groups acting at different life stages of crown-of-thorns starfish. This figure is based on references from Table 1.

2.2. Post-Settlement Predation

A key component of the vulnerability of larvae is their susceptibility to predation during settlement. Larvae preferentially settle in habitats with fine-scale topographic complexity [49], which is likely to be an adaptation to minimise early post-settlement mortality. However, a wide range of potential predators are abundant within the reef matrix (e.g., [11,17,39,70]). Benthic predators and filter feeders, including corals such as *Pocillopora damicornis*, may exact a heavy toll on the settling larvae of coral reef asteroids, including *Acanthaster* spp. [8]. Keesing and Halford [47] estimate mortality at settlement and during metamorphosis to be in excess of 85%. Furthermore, Cowan et al. [19] observed that 55% of brachiolaria larvae that settled to rubble with naturally attached crustose coralline had undergone metamorphosis after 48-h when substrates had been cleaned of potential predators, compared to 0% when polychaete predators were present. If predation represents a significant threat to settling larvae, this should have provided sufficient selective pressure for the evolution of behavioural mechanisms to evade predators, as seen in juveniles and adults in low-density populations. Cowan et al. [19] used static choice chambers to determine whether such mechanisms are present to assist larvae in avoiding settlement on or near predators, revealing that larvae are able to both detect, and respond to, the presence of predators within settlement substrates; larvae were attracted to rubble with naturally attached crustose coralline algae that had been cleaned of predators, but were deterred from these substrates when polychaete predators were present. Whether similar mechanisms are present to enable juveniles to detect and actively avoid predators in the reef matrix remains to be tested.

Following settlement, many marine organisms experience very high early post-settlement mortality (e.g., asteroids [8]; bivalves [71]; fish [72]; corals [73]), to the extent that this is a recognised demographic bottleneck for some taxa [73]. Although Sweatman's [50] measurements of predation by fishes on laboratory-reared juvenile CoTS (25–79 mm diameter) revealed very low predation rates (0.13% per day), predation on juvenile CoTS is due mainly to epifaunal invertebrate predators, which are highly abundant on coral reefs (e.g., [17,70]). For example, survivorship of laboratory reared CoTS that are settled to freshly collected rubble is effectively zero, owing to very high rates of predation on newly settled larvae by naturally occurring predators (e.g., polychaetes) within the rubble [17].

In the eastern Pacific, Glynn [39] demonstrated that the harlequin shrimp *Hymenocera picta* and a polychaete worm *Pherecardia striata* were significant predators of CoTS [39,59,74]. Moreover, there have not been any outbreaks, or persistently high numbers of CoTS on reefs in Panama, where these two predators are found in high abundance, and where populations of alternative prey (ophidiasterids) are scarce. Although both field [74] and laboratory studies [43,74,75] demonstrate that the shrimp has difficulties attacking larger and more active CoTS, it is expected that they are highly effective predators of smaller, more cryptic CoTS within the reef matrix [39]. The observed preference of *H. picta* for other asteroid prey species, particularly smaller ophidiasterids [43], and the strong preference of *P. striata* for crustacean tissue over tissue from CoTS [39] emphasises how the relative scarcity of alternative prey may be an important factor influencing the capacity of a potential predator to manipulate the population dynamics of CoTS [74]. If they are important in regulating populations of CoTS, this may occur within a relatively restricted geographical area.

The polyp *Pseudocorynactis* sp. may also play an important role in the population control of CoTS [62] in areas where it occurs in high abundances, such as Sogod Bay, Philippines. *Pseudocorynactis* sp. prey on a range of echinoderms and has been observed ingesting adult CoTS up to 250 mm in diameter [62]. Furthermore, *Pseudocorynactis* sp. preferentially settles under coral ledges and in reef crevices, where it likely predates on cryptic juvenile and sub-adult CoTS [62].

3. Rates of Predation on Crown-of-Thorns Starfish

Understanding of the importance of predation in the population dynamics of CoTS is significantly constrained by a lack of empirical data on background mortality rates and natural predation rates. Quantifying mortality rates of CoTS in the field is tractable, but requires significant investment to follow the fate of a large number of uniquely tagged or recognizable individuals (*sensu* [76]) across a broad size range of individuals and in different habitats. The biggest limitation to such experiments is the limited capacity to tag CoTS (e.g., [77]). Previous methods used to distinguish individual starfish (staining, branding, tagging and dyeing) were only effective for days to weeks, limiting any capacity to get meaningful long-term data on rates of mortality [77]. Identifying more permanent tagging solutions is essential, but even short-term tagging and tethering experiments could yield important information about the vulnerability of CoTS to predation.

Short-term tagging and tethering experiments have been used to effectively estimate or compare predation vulnerability for a range of echinoderms, especially echinoids or urchins (e.g., [76,78,79]). These studies typically use very short observations ($\leq$3 days) to estimate predation rates, though some recent studies have been conducted over several months; Ling and Johnson [76] successfully tagged and tethered the urchin *Centrostephanous rodgersii*, and measured subsequent survivorship >100 days. At present, there are few direct, quantitative estimates of predation or mortality rates for CoTS in the field, which are critical for establishing the importance of predation in limiting the densities of starfish at individual reefs [21].

Previous research on CoTS predators has focused on estimating maximum rates of starfish consumption by individual predators and extrapolating this to account for natural densities of these predators (e.g., [28,80,81]). This is based on the belief that effective control of outbreak populations is fundamentally reliant on high rates of predation to compensate for rapid population growth of CoTS when outbreaks begin. However, it is not the rate of feeding per se that is important in determining whether a predator can effectively regulate prey densities [12], but changes in the rates of predation in response to spatial and temporal gradients in prey abundance. Predators that are capable of consuming large numbers of CoTS, by virtue of their high abundance and/or individual capacity to consume large numbers of CoTS [20], may be important in suppressing local CoTS densities. Cowan et al. [20] showed that a wide range of planktivorous damselfishes will feed on CoTS larvae, some of which (*D. aruanus* and *P. amboinensis*) have very high satiation limits. The capacity of these fishes to consume large numbers of CoTS larvae, combined with high densities of these fishes (as well as many other planktivorous fishes that may also readily feed on CoTS larvae) could be critical in limiting settlement rates [42,82] and thereby moderating the local severity of outbreaks. It is unlikely however, that these fishes could actually prevent an outbreak from ever occurring, unless either (i) they selectively target CoTS larvae (over other potentially more abundant prey) even at very low prey densities, and thereby prevent initiation of outbreaks; or (ii) their combined feeding capacity exceeds the very large number of CoTS larvae that can cause the rapid and pronounced onset of some outbreaks.

Early research on putative CoTS predators largely dismissed the importance of generalist reef predators, suggesting instead that important predators would have to be highly specialized (preferentially feeding on CoTS to the exclusion of almost all other potential prey) and feed on adult CoTS [80]. Importantly, if there are specialist predators that are highly effective in finding and killing CoTS even when they occur at very low densities, then it may be these predators that are key in preventing outbreaks from ever occurring [82]. However, effective CoTS predators must be sufficiently generalist to consume alternative prey [82] and thereby sustain themselves during non-outbreak periods when CoTS are scarce. If predation (or lack thereof) is a potential cause of CoTS outbreaks, it seems that we should also be focusing on predators that target pre-settlement, settlement, and post-settlement pre-reproductive stages [41,42]. Most notably, predation by benthic invertebrates on newly settled starfish appears, at present, to be the most significant bottleneck in their life-history [42], but this may be largely attributable to underestimates of predation rates on CoTS during other life-stages.

Quantitative data on predation rates is rare and in most cases comes from experimental studies that aim to determine maximum predation rates by specific organisms (e.g., [17,20,28,47,61]), or modelling efforts that predict the rate of predation needed to prevent outbreaks (e.g., [33,41,82,83]). Based on caging experiments, the triton shell *C. tritonis* is estimated to consume 0.7 adult starfish per week [28], however attacks are not always fatal [55] and this predator prefers to feed on other starfish when given a choice [28]. Furthermore, pre-fishing numbers of *C. tritonis* remain largely unknown and it is unlikely that this invertebrate was ever present in sufficiently high numbers to prevent outbreaks [84,85]. Starfish numbers are persistently low in areas where the corallimorph *P. hoplites* [61] or harlequin shrimp *H. picta* together with the lined fireworm *P. striata* [59] are abundant. Consumption rates of adult starfish (up to 340 mm diameter) by *P. hoplites* are estimated to be 29.5 g day^{-1} [61]. In the eastern Pacific, Glynn [59] reported that 5%–6% of the CoTS were being attacked by *H. picta* at any time, and 0.6% of the starfish population were preyed upon by both *H. picta* and *P. striata*. Approximately 50% of CoTS being attacked by *H. picta* ultimately died, compared to close to 100% for CoTS being attacked by both *H. picta* and *P. striata*, and these two predators are particularly effective in regulating numbers of juvenile starfish [59]. Keesing and Halford [17] measured significant mortality rates on post-metamorphic starfish (5.05% day^{-1} on 1-month old starfish and 0.85% day^{-1} on 4-month old starfish), due to predation by epibenthic fauna contained within dead coral rubble. This is much higher than the attack rate on juvenile starfish (1%–1.5%) that McCallum [40] suggested would be sufficient to limit the occurrence of CoTS outbreaks, based on demographic modelling. Cowan et al. [20] conducted a series of laboratory experiments, measuring maximal predation rates by a wide range of planktivorous damselfishes upon CoTS larvae, reporting consumption rates ranging from 14 larvae h^{-1} by *C. viridis*, up to 158 larvae h^{-1} by *D. aruanus*.

Ormond and Campbell [43] suggest that the predatory behaviour of large fishes (the pufferfish *A. hispidus*, and triggerfishes *P. flavimarginatus* and *B. viridescens*) may have the capacity to control densities of adult CoTS in the Red Sea, and may be capable of disbanding aggregations in their early stages. It is however, unlikely that these species would be effective in controlling CoTS populations across the entire Indo-Pacific region as they are not universally common [86]. However, triggerfishes (particularly, *Balistapus undulatus*) may nonetheless be important maintaining the structure of coral reef ecosystems, by predating on rock-boring urchins [87]. There may be other large predatory fishes capable of regulating densities of adult CoTS; Keesing and Halford [47] observed the pufferfish *A. stellatus* to be capable of consuming adult starfish (20 cm diameter) in less than 10 min. Further, Ormond et al. [33] reported greater mean densities of lethrinids and large fish predators from the Red Sea, where no major outbreaks of CoTS were known to have occurred, compared to the GBR, where two cycles of large scale outbreaks had occurred [33]. Further, within the GBR, mean predatory fish densities were found to be reduced on reefs that were experiencing major outbreaks [33]. Fish species examined were commercially targeted or frequently caught as bycatch, and variations in population densities of predatory fish between sites was compatible with fisheries data on fishing intensity, therefore the pattern of difference in CoTS populations could be explained by differing fishing intensities between locations [33].

3.1. Sub-Lethal Injuries

Discussions to this point have focused on instances of whole animal or lethal predation, but sublethal (or partial) predation is often very apparent and well documented among echinoderms [88,89]. For CoTS, very high proportions of adults (up to 60%) have evidence of recent injuries (most apparent as missing arms), which is attributed to partial predation [15]. Even if the predation is not immediately fatal, sublethal attacks may still have an important influence on population dynamics. In the short term, open injuries and exposed internal organs may increase the likelihood of pathogenic infections and disease transmission among individuals [90–92] and can also increase susceptibility to further attacks [39]. Even if starfish effectively repair injuries caused by partial predation, effective declines in the size of individuals caused by sub-lethal predation will reduce food intake [88,93,94]. Crown-of-thorns starfish also regrow damaged or missing arms [28,95], which will require re-allocation of nutrients to regeneration, which could otherwise have been used for immune defence [11], reproduction or somatic growth [88,93]. The removal of arm tips, and consequent removal of the eyespot, may additionally result in reduced foraging efficiency due to the loss of vision, which is important for navigating between reef structures and locating prey [96].

There are strongly opposing views about the inferences of high incidence of partial predation in populations of crown-of-thorns starfish. In general, high incidence of sub-lethal predation has been considered to be generally reflective of high intensity of predation (e.g., [11,15]), such that high rates of partial mortality serve as a proxy for high levels of overall mortality. In the Philippines, Rivera-Posada et al. [11] showed that the incidence of injuries on CoTS was highest within a no-take marine reserve, and supporting information on the high diversity and abundance of reef fishes corroborate the idea that overall intensity of predation would likely be much higher inside versus outside of this reserve. Conversely, high incidence of partial mortality may reflect low intensity of predation pressure [16] because when predation is intense it would be expected that most predation events would result in complete mortality. As such, high incidences of starfish with partial injuries point to the strong regenerative capacity of starfish [14] and may suggest that predation is predominantly sub-lethal for crown-of-thorns starfish. Schoener [97] suggested that there is no reason to expect any relationship between rates of injuries versus rates of predation-driven mortality, because the efficiency of predation (the proportion of attacks that cause death) is independent of the attack rate or incidence of predation. For the asteroid *Asterias amurensis*, high density populations have been observed to be completely annihilated by an incursion of thousands of spider crabs (*Leptomithrax gaimardii*) that moved to shallow reefs in large numbers [89]. Additionally, where crab incursions involved fewer individuals, high rates of sub-lethal injury (~70% of starfish population injured) occurred independently of mass predator-driven mortality [89]. In this example, the high mobility of spider crabs can lead to overwhelming local impacts on starfish populations but this impact is highly variable across space and time [89]. Ultimately, a dedicated research project is needed to test the relationship between rates of partial versus complete predation mortality. However, in the absence of any empirical data on overall rates of predation mortality, the incidence of injuries serves as the best proxy to test for variation in vulnerability to predation among locations and with size of starfish [15].

A common trend among echinoderm species is for the incidence of sub-lethal injuries to decline with increasing body size [14,78,88,89,93,98] reflecting general declines in the vulnerability to predation. Accordingly, Messmer et al. [14] observed a clear linear decline in both rate and severity of predation with increasing starfish size. Rivera-Posada et al. [11] reported highest incidence of arm damage in the intermediate (11–20 cm diameter) size class however. This pattern may be explained by changes in behavioural and physical characteristics with increasing size, whereby intermediate sized individuals may have greatest exposure to predators, while smaller starfish (<10 cm) tend to remain hidden but are also more likely to be completely consumed [16]. Reduced incidence of sublethal predation in largest individuals (≥21 cm) may be explained by increased length of spines [11] and satiation of predators following removal of a smaller proportion of the total body mass. Disparity between the trends observed in these studies may be a result of differing sample size or differing suites of predators between the locations on the GBR [14] versus in the Philippines [11].

Sub-lethal and/or 'trait-mediated' effects of predators [89] can include alteration of behaviour and spatial patterns in echinoderms, in addition to changes in adult abundances and local spatial distributions, which are important for the reproductive ecology of free-spawning marine invertebrates as they influence rates of fertilization success [99]. For CoTS, fertilization success may be close to 100% when spawning individuals are adjacent to each other [100], thus any predator that is capable of dissipating an aggregation, or sufficiently reducing adult density, is likely to have a significant impact on zygote production. Humans have been shown to indirectly alter spatial distributions of asteroids, leading to much higher rates of fertilization in human-driven hotspots of zygote production [97]. In this way, sub-lethal predatory effects, leading to reduced individual reproductive performance, in combination with alteration to spatial configurations at the time of spawning may impact on zygote production for asteroids [99], potentially influencing the occurrence of secondary outbreaks for CoTS [101].

3.2. Population Modelling

Population simulation models provide a means of exploring the possible role of predation (or other natural causes of mortality) in regulating populations of CoTS (e.g., [82]), especially given little or no empirical data on satiation levels and feeding efficiency of potential predators or predation rates on larval and juvenile CoTS. Simulation models indicate that changes to predation rates during the pre-reproductive, post-settlement stage may be particularly relevant in understanding the dynamics of CoTS populations [40,41,82]. Notably, given their exceptional reproductive capacity, small changes in proportional survivorship or settlement success of CoTS larvae will result in large changes in adult abundance. Accordingly, McCallum [41] argues that relatively subtle changes in the abundance of predators (e.g., caused by exploitation) and/or predation rates, will reduce the level of local recruitment required to overcome (or satiate) predators.

The potential ecological importance of predation as a regulatory factor upon CoTS populations depends largely upon the ability of predators to find and consume prey [102]. Quantification of the functional response, described by the intake rate of prey as a function of prey density [103], is a common method that provides insight into the dynamics of predator–prey systems [104–106]. Functional responses may be classified into three types. A type I response assumes a linear increase in the intake rate with increasing food density, generally up to a maximum value, beyond which the intake rate is constant [107]. Type II is characterized by a decelerating intake rate [107] and assumes that the predator is limited by its ability to process food [108,109]. Type III is associated with an accelerating intake rate, associated with prey switching behaviour (preferential consumption of the most common type of prey [110]), up to a saturation point [107]. Predators that exhibit prey-switching behaviour, feeding more frequently on CoTS in response to a marked increase in their local abundance, may be capable of dissipating an aggregation in its early stages [53]. In order to persist when population densities of CoTS are low, predators should be able to take a range of prey, exhibiting an increased feeding response in reaction to a rapid increase in the CoTS population [53]. Predators exhibiting these type II and type III functional responses [103] are typical of vertebrate predators, reinforcing the focus on fish, and are supported in McCallum's [15,82] population models. In laboratory feeding experiments on *Acanthaster* spp. larvae, planktivorous damselfishes exhibit primarily a type II functional response, indicating their capacity to consume sufficient larvae to suppress settlement rates when larvae are already scarce, thereby contributing to very low natural densities of CoTS recorded outside of outbreak periods [20]. However, very high densities of larvae, which are a necessary condition for the rapid and pronounced onset of outbreaks, are likely to swamp even the combined consumption capacity of all planktivorous reef fishes [40].

4. Conclusions

Crown-of-thorns starfish are vulnerable to predation from a wide range of coral reef organisms, and at all stages of their life cycle. Despite identification of potentially key predators, and groups of predators, natural predation rates in both outbreaking and non-outbreaking populations remain largely unknown. This considerably limits our understanding of the role of predation in structuring the population dynamics of CoTS and of approaches to managing their often-devastating impacts on coral reef ecosystems. Whilst predation is likely to be important in suppressing settlement rates and contributing to naturally low densities of CoTS, the initiation and spread of outbreaks cannot, at present, be definitively attributed to changes (presumably declines) in the abundance of predators and/or changes in predation rates (e.g., [111]). Babcock et al. [111] showed that there are likely to be multiple factors that contribute to outbreaks of CoTS, such that a diverse range of management strategies will be required to prevent, or reduce the occurrence, of outbreaks. Maximising the number and diversity of putative CoTS predators is nonetheless, a "no regrets" strategy to minimise the risk of CoTS outbreaks and increase the resilience of coral reef ecosystems, generally. In the meantime, further research into potential predators, as well as estimates of predation and mortality across all life-stages of CoTS, is still warranted. More specifically, rates of pre- and post-settlement predation should be explicitly compared along known gradients in abundance of putative CoTS predators (e.g., inside and outside of marine reserves with marked differences in the abundance and diversity of fishes that feed on CoTS). New technologies provide improved opportunities to explore spatial and temporal variation in the demographics of CoTS populations, for example, DNA screening of diets for large numbers of potential CoTS predators [44,112], plus increased potential to tag and track benthic species within reef environments [113]. Such novel approaches along with remote sensing techniques will provide new insights into changes in the population dynamics and/or environmental conditions during the onset of population outbreaks.

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