



Contributions of pre- versus post-settlement processes to fluctuating abundance of crown-of-thorns starfishes (*Acanthaster* spp.)

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ABSTRACT

Numerous hypotheses have been put forward to account for population outbreaks of crown-of-thorns starfishes (CoTS, *Acanthaster* spp.), which place specific importance on either pre- or post-settlement mechanisms. The purpose of this review is to specifically assess the contributions of pre- versus post-settlement processes in the population dynamics of CoTS. Given the immense reproductive potential of CoTS (> 100 million eggs per female), persistent high densities would appear inevitable unless there were significant constraints on larval development, settlement success, and/or early post-settlement growth and survival. In terms of population constraints, pre- and post-settlement processes are both important and have additive effects to suppress densities of juvenile and adult CoTS within reef ecosystems. It is difficult, however, to assess the relative contributions of pre- versus post-settlement processes to population outbreaks, especially given limited data on settlement rates, as well as early post-settlement growth and mortality. Prioritising this research is important to resolve potential effects of anthropogenic activities (e.g., fishing) and habitat degradation on changing population dynamics of CoTS, and will also improve management effectiveness.

1. Introduction

Crown-of-thorns starfishes (CoTS, *Acanthaster* spp.) are native inhabitants of coral reefs throughout the Indo-Pacific (Birkeland and Lucas, 1990). Although formerly regarded as a single pandemic species, *Acanthaster planci* [Linnaeus, 1758], throughout its geographical range, genetic analyses (using microsatellite markers) have revealed there are at least four different species of CoTS with distinct, but overlapping, geographic ranges (Vogler et al., 2008; Haszprunar and Spies, 2014; Haszprunar et al., 2017). In the Indian Ocean there are two nominal species; *A. planci* [Linnaeus, 1758] which occurs throughout the northern Indian Ocean from the Sea of Oman to North Sumatra, and *A. mauritiensis* [de Loriol, 1885], found mainly in the western Indian Ocean, but also Chagos and Christmas Island (Vogler et al., 2012). There is also a third distinct, and currently undescribed species from the Red Sea, which is purported to have fewer arms and may also have comparatively limited toxicity (Haszprunar et al., 2017). In the Pacific, there appears to be a single species (Vogler et al., 2008), for which the most likely valid name is *Acanthaster solaris* [Schreber, 1795]

(Haszprunar et al., 2017).

Despite genotypic and phenotypic differences, there are no obvious dissimilarities in the biology of coral reef CoTS, and all four nominal species have been reported to undergo population outbreaks (Haszprunar et al., 2017). Adult CoTS feed on scleractinian corals (e.g., Ormond et al., 1976; Glynn, 1988; De'ath and Moran, 1998; Pratchett, 2007) and at low densities (< 10 starfish per hectare) have negligible impact on the abundance of prey corals and associated reef processes (e.g., Glynn, 1973; Zann et al., 1990). However, CoTS outbreaks (defined herein as pronounced increases in the abundance of CoTS to levels that cannot be sustained by pre-existing levels of coral prey) are a major contributor to ongoing coral loss and associated degradation of coral reef ecosystems (e.g., De'ath et al., 2012; Kayal et al., 2012; Baird et al., 2013; Pisapia et al., 2016). In extreme cases, outbreak densities of CoTS can exceed 100,000 starfish ha⁻¹ and cause significant and widespread depletion of reef-building corals (e.g., Cheshier, 1969; Kayal et al., 2012), with concomitant effects on the biodiversity, productivity, structure and functioning of coral reef ecosystems (Pratchett et al., 2014, 2017a).

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When outbreaks of CoTS were studied in the 1960s, it was assumed that they represented new and unprecedented phenomena linked to sustained and ongoing exploitation of marine species (Endean, 1977) or inputs of excess nutrients or pollutants to coastal waterways (Chesher, 1969). It is possible however, that outbreaks of CoTS occur naturally (Vine, 1973; Caballes and Pratchett, 2017), due to variation in key demographic rates linked to environmental fluctuations or inherent stochasticity. Fundamentally, disruption to (or natural variability in) any of the mechanisms that typically regulate population size has the potential to lead to pronounced changes in local abundance (e.g., Andrewartha and Birch, 1954). However, species with high intrinsic rates of population growth are predisposed to very large fluctuations in abundance (e.g., Uthicke et al., 2009) and CoTS have extremely high reproductive potential (Endean, 1982; Conand, 1984; Babcock et al., 2016a), combined with early maturation and relatively rapid somatic growth (Moran, 1986).

Numerous hypotheses have been put forward regarding the explicit causes or triggers of CoTS outbreaks (reviewed by Moran, 1986; Birkeland and Lucas, 1990; Pratchett et al., 2014). These hypotheses place specific importance on either i) factors affecting pre-settlement life stages and processes (e.g., *larval recruitment hypothesis*, Lucas, 1973; *terrestrial run-off hypothesis*, Birkeland, 1982) or ii) changes in the behaviour and survivorship of post-settlement individuals (e.g., *predator removal hypothesis*, Endean, 1969; *adult aggregation hypothesis*, Dana et al., 1972; *prey-threshold hypothesis*, Antonelli and Kazarinoff, 1984). While ultimate causes of outbreaks may be many and varied (e.g., Babcock et al., 2016b), the relative importance of pre-settlement processes in initiating primary outbreaks continues to be debated (Johnson, 1992; Pratchett et al., 2014, 2017a; Rogers et al., 2017). Larval supply to individual reefs will undoubtedly be constrained by production, growth, survival, and dispersal of larvae, but post-settlement processes may alter the patterns established at settlement and ultimately limit the number of CoTS that actually grow and ultimately feed on reef-building corals. Consequently, biological and physical processes that occur during and after settlement may be just as important, if not more important, in regulating population size and conversely, initiating outbreaks (Keesing and Halford, 1992b).

Despite the potential importance of early post-settlement processes in structuring the dynamics of CoTS populations, this phase of the life history has received remarkably limited scientific attention. This is due, at least in part, to difficulties in detecting newly settled CoTS in natural environments, especially on the Great Barrier Reef (Doherty and Davidson, 1988; Johnson et al., 1992). However, emerging technologies (Uthicke et al., 2015a, b; Doyle et al., 2017) and existing protocols (Keesing et al., 1993; Wilmes et al., 2016) provide opportunities to effectively sample and study CoTS at various stages throughout their early life history, from planktonic larvae, through settlement, and during the formative period (first 12-months) immediately following settlement (Wilmes et al., 2016). The purpose of this review, therefore, is to critically evaluate the relative contributions of pre- versus post-settlement processes in regulating the abundance and initiating population outbreaks of CoTS. Where possible, data on demographic rates during distinct life-history phases will be presented and summarised. The specific focus on pre- versus post-settlement processes (and particularly, early post-settlement processes) differentiates this review from other major reviews on CoTS (e.g., Moran, 1986; Birkeland and Lucas, 1990; Caballes and Pratchett, 2014; Pratchett et al., 2014, 2017a), which tend to provide a broad overview of the specific biology of CoTS and/or consider predominant hypotheses put forward to account for population outbreaks and corresponding management actions.

2. Pre-settlement processes

Many of the hypotheses put forward to explain the initiation of CoTS outbreaks (e.g., *larval starvation* and *terrestrial runoff* hypotheses; Birkeland, 1982; Lucas, 1982; Brodie, 1992; Brodie et al., 2005)

emphasise factors affecting larval production, development and survival. Importantly, it is often assumed that there are major natural constraints on larval development and survival, meaning that settlement rates are normally very low despite potentially very high fecundity and reproductive potential (Cheney, 1974). Anthropogenic factors (e.g., eutrophication of coastal ecosystems) that relax normal constraints on larval development and survival may therefore, represent important causes or triggers of population outbreaks (Birkeland and Lucas, 1990). Alternatively, outbreaks of CoTS may represent a natural and inherent manifestation of population instabilities associated with their extreme fecundity and reproductive potential (Vine, 1973; Uthicke et al., 2009). However, CoTS outbreaks do not necessarily arise due to sudden and dramatic increases in larval supply and mass settlement of planktonic larvae, though this has been documented in some locations (Yokochi and Ogura, 1987; Zann et al., 1987). Elsewhere, CoTS outbreaks may arise from progressive accumulation of individuals over multiple successive recruitment events (Pratchett, 2005).

When considering factors that may cause or contribute to population outbreaks, it is important to distinguish between primary versus secondary outbreaks. Primary outbreaks arise independently (Endean, 1973), caused by inherent changes in demography at one or more stages in the life-cycle, which may lead to either subtle and sustained increases in local population size (Pratchett, 2005) or sudden and dramatic spikes in local population densities (Zann et al., 1987). Understanding the factors that contribute to initiation of primary outbreaks is fundamental to effective long-term management (Pratchett et al., 2014). Secondary outbreaks, by contrast, are an almost inevitable outcome resulting from marked increases in larval supply following increases in abundance of adult/reproductive CoTS on nearby or upstream reefs, and simply reflect the inevitable spread of primary outbreaks (Harrison et al., 2017).

2.1. Fecundity

Crown-of-thorns starfishes are purported to have exceptional fecundity (Conand, 1984; Babcock et al., 2016a), which provides for very high reproductive potential. However, the phenomenal reproductive capacity of CoTS is largely inferred based on the mass of ripe gonads, while relying on very preliminary estimates of oocyte concentrations (90,000 oocytes gm^{-1}) estimated by Conand (1984) from limited sampling ($n = 10$) of a single population of *A. cf. solaris*. By combining the estimates of oocyte concentrations with measures of total mass of ovarian tissues, Conand (1984) estimated that each female CoTS was capable of producing up to 60 million eggs. By extrapolating to larger bodied CoTS based on known relationships between diameter and gonad weight, Babcock et al. (2016a) extended the upper estimates of fecundity for *A. cf. solaris* to > 100 million oocytes, which may be as high as 200 million for the largest reported CoTS (62 cm diameter) in Pratchett (2005). Fecundity of female CoTS increases exponentially with body size, due partly to allometric increases in weight relative to diameter, though larger females also invest disproportionately in gametogenesis (Kettle and Lucas, 1987; Caballes and Pratchett, 2014; Babcock et al., 2016a).

Aside from the size of adult CoTS, the fecundity and reproductive potential of *A. cf. solaris* is also dependent upon their recent feeding history and physiological condition (Caballes et al., 2016, 2017a). Caballes et al. (2016) showed that CoTS with unfettered access to *Acropora* corals during the final stages of gametogenesis had > 25% larger gonads (standardised for body size) compared to starved individuals. CoTS fed on *Acropora* also had 10% larger gonads compared to individuals restricted to feeding on *Porites* corals, potentially highlighting the importance of coral composition rather than overall coral cover. These differences in reproductive investment also translated into significant increases in the development rate, survival and size of the progeny (Caballes et al., 2016, 2017a). Overall, well-fed female CoTS

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