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Superstars: Assessing nutrient thresholds for enhanced larval success of *Acanthaster planci*, a review of the evidence

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ABSTRACT

Crown-of-thorns starfish, *Acanthaster planci* (COTS), predation is a major cause of coral reef decline, but the factors behind their population outbreaks remain unclear. Increased phytoplankton food resulting from eutrophication is suggested to enhance larval survival. We addressed the hypothesis that larval success is associated with particular chl-*a* levels in tightly controlled larval:algal conditions. We used chl-*a* conditions found on coral reefs (0.1–5.0 µg chl-*a* L⁻¹), including nominal threshold levels for disproportionate larval success (≥1.0 µg chl-*a* L⁻¹). High success to the juvenile occurred across an order of magnitude of chl-*a* concentrations (0.5–5.0 µg chl-*a* L⁻¹), suggesting there may not be a narrow value for optimal success. Oligotrophic conditions (0.1 µg chl-*a* L⁻¹) appeared to be a critical limit. With a review of the evidence, we suggest that opportunistic COTS larvae may be more resilient to low food levels than previously appreciated. Initiation of outbreak populations need not require eutrophic conditions.

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1. Introduction

Predation by the corallivorous crown-of-thorns starfish (COTS), *Acanthaster planci*, is regarded as one of the most pervasive stressors on coral reefs (De'ath et al., 2012; Baird et al., 2013). COTS play an important functional role in the ecosystems where they reside, and in low densities can enhance coral diversity through preferential foraging (Keesing, 1990; Pratchett et al., 2014). However, periodic high-density population outbreaks of adult COTS have a major impact in causing coral mortality (Vine, 1973; Birkeland and Lucas, 1990; Kayal et al., 2012; Pratchett et al., 2014; Roche et al., 2015). Chronic high-density populations have also persisted for decades in some locations (Nakamura et al., 2014). High densities of COTS are reported to have deleterious impacts on tropical reef systems worldwide, as recorded for Brunei (Lane, 2012), the Chagos Archipelago (Roche et al., 2015), Fiji (Zann et al., 1990), French Polynesia (Kayal et al., 2012), the Great Barrier Reef (Lourey et al., 2000; De'ath et al., 2012), and Japan (Yamaguchi, 1986; Nakamura et al., 2014).

The driving forces behind COTS outbreaks have received considerable attention for decades, but the causes remain to be understood (Pratchett et al., 2014). Identifying the factors underpinning COTS outbreaks is fundamental to inform and establish management strategies for reefs impacted by this influential species (Westcott et al., 2016).

Here we focus on two major hypotheses proposed to explain the periodic outbreaks of COTS; the 'larval resilience' and 'enhanced nutrients' hypotheses (Birkeland, 1982; Lucas, 1982; Olson, 1987; Wolfe et al., 2015a, 2015b). It has been suggested that COTS outbreaks are primarily caused by enhanced larval survival due to eutrophication from riverine pollutant loads, which promote increased densities of their phytoplankton food (Birkeland, 1982; Lucas, 1982; Fabricius et al., 2010; Hock et al., 2014), with retention of larvae in reef groups that have enhanced phytoplankton concentrations (Wooldridge and Brodie, 2015). Nutrients from agricultural runoff generate increased phytoplankton/chlorophyll-*a* (chl-*a*) levels, particularly during high rainfall and flood events near catchment areas (Devlin et al., 2001; Brodie et al., 2005, 2007, 2016; Fabricius et al., 2010). Upwelling and runoff from seabird nesting sites also promote proliferation of phytoplankton and may provide COTS larvae with pulses of food that lead to outbreaks in regions not influenced by anthropogenic factors (Lane, 2012; Miller et al., 2015; Roche et al., 2015). As typical of planktotrophic developers, COTS larvae exhibit faster growth and more successful development at high food levels (Okaji, 1996; Fabricius et al., 2010), up to a limit (Wolfe et al., 2015a). Well-fed echinoderm larvae accumulate nutrient reserves with positive carryover effects for survival through to metamorphosis and early juvenile stages (Strathmann et al., 1992; Allison, 1994; George, 1999; Pechenik, 2006; Byrne et al., 2008; Prowse et al., 2008).

While the enhanced nutrients hypothesis has received considerable traction to explain COTS outbreaks, particularly on the Great Barrier Reef, high-density populations also occur in regions isolated from

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anthropogenically-driven eutrophy (Kayal et al., 2012; Lane, 2012; Pratchett et al., 2014; Miller et al., 2015; Roche et al., 2015). As a tropical species, COTS larvae are likely adapted to the oligotrophic conditions typical of coral reef ecosystems, and can also avail of alternative food sources such as dissolved inorganic matter and coral mucus derived nutrients (Olson, 1987; Olson and Olson, 1989; Nakajima et al., 2016). COTS larvae can survive and grow under low phytoplankton levels, albeit at a slower pace than well-fed larvae (Olson and Olson, 1989; Okaji, 1996; Fabricius et al., 2010; Wolfe et al., 2015a, 2015b). These larvae exhibit strong developmental plasticity matching their phenotype to environmental conditions, growing longer ciliated bands when nutrients are limited to increase their ability to capture scarce food particles (Wolfe et al., 2015b).

The flexible nature of COTS larvae may underline the boom-and-bust population characteristic of this species (Uthicke et al., 2009). Other sympatric asteroids with similar feeding larva do not exhibit marked population fluctuations. Thus, the opportunistic nature of COTS remains a challenge to understand. Adult COTS are highly fecund, with millions of eggs released by a single female during spawning, as well as large volumes of sperm (Conand, 1984; Kettle and Lucas, 1987; Babcock et al., 2016; Caballes et al., 2016). This suggests that success of a low proportion of the larval output of COTS may be sufficient to maintain high post-larval success and recruitment into adult populations. Given its extremely high fecundity, the progeny of a single female

could be sufficient to seed a population outbreak (Babcock et al., 2016). Clouds of COTS larvae have been detected on mid-shelf and offshore reefs across the northern Great Barrier Reef (Uthicke et al., 2015a). Although the larvae experience predation in the plankton (Pearson and Endean, 1969; Cowan et al., 2016), COTS eggs and larvae are also chemically protected with toxins that can deter predators (Lucas et al., 1979). It appears that COTS are built for larval resilience and post-larval success.

Several studies have reared COTS larvae on phytoplankton levels commensurate with chl-*a* levels suggested to enhance larval success in the field (Table 1). These studies endeavoured to identify nutrient thresholds that promote larval success, thus linking anthropogenic runoff-driven eutrophication with outbreaks. Trigger values for successful development of COTS larvae have been suggested in several studies where chl-*a* levels were empirically determined, with optimal development associated with nutrient enrichment $>2 \mu\text{g chl-}a \text{ L}^{-1}$ and poor development below this level (Okaji, 1996; Fabricius et al., 2010; Uthicke et al., 2015b) (Table 1). However, these studies used different methods and did not adjust for larval mortality and density. If algal densities are maintained while larval mortality ensues, more food becomes available for survivors, enhancing their growth and confounding results. As such, it is difficult to discern between absolute food levels per larvae, information needed to link with chl-*a* levels experienced in nature. Carefully controlled larval-nutrient conditions more closely reflect that

Table 1
Summary of feeding experiments on the success of *Acanthaster planci* larvae reared at varying chl-*a*/algal cell concentrations, with indication of settlement success; hyphen indicates no data.

Chl- <i>a</i> range ($\mu\text{g chl-}a \text{ L}^{-1}$)	Algal cell density (cells mL^{-1})	Larval survival (%)	Settlement success (%)	Larval density (per 100 mL)	Days	Temp	Algal species	Food renewal	Water changes	Reference
0–0.4 ^a	0–1000	0	–	25	26–44	28 °C	<i>Dunaliella primolecta</i>	Bi-daily	Bi-daily	Lucas, 1982
0.6 ^a	500	40	–				<i>Phaeodactylum tricornutum</i>			
1.2–6.0 ^a	1000–5000	100	–							
	10,000	50	–							
	50,000	100	–							
0.14	–	0	–	33	12	28–29 °C	<i>In situ</i> incubations			Olson, 1985
0.16	–	5	–							
0.2–0.3	1000–10,000	55	–	100	16	28–30 °C	<i>In situ</i> incubations			Olson, 1987
0.07–0.52	–	0	0	10	18–22	26.5–29 °C	<i>Dunaliella primolecta</i> Filtered natural seawater	Daily	Daily	Okaji, 1996 ^c
0.08–0.28	–	–	0 ^b	5	22	26.5–29 °C		Daily	Daily	
0.29	–	–	18.7 ^b							
0.01–0.4	–	–	0 ^b	7.5	22	–		Daily	Daily	
0.5	–	–	6.8 ^b							
0.75–0.8	–	–	32.2–38.6 ^b							
1–1.6	–	–	50.2–61.6 ^b							
0.19	–	–	0 ^b	5	22	27–29 °C		Daily	Daily	
0.28	–	–	88.3–97.2 ^b							
2.91	–	–	99–100 ^b							
5.25	–	–	100 ^b							
0.67	1100	10–90 ^d	0	100	24	28–30 °C	<i>Chaetoceros</i> sp. <i>Phaeodactylum tricornutum</i> <i>Dunaliella</i> sp.	Bi-daily	Bi-daily	Uthicke et al., 2015b
1.80	2800	30–75 ^d	0							
2.55	4200	10–70 ^d	Yes ^e							
4.85	7000	0–50 ^d	Yes ^e							
7.11	9800	0–60 ^d	Yes ^e							
0	0	63.2	0	100	16	27 °C	<i>Proteomonas sulcata</i>	Daily	Daily	Wolfe et al., 2015a
0.01	100	55.4	1.9							
0.1	1000	65.6	2.5							
1.0	10,000	66.2	37.5							
10	100,000	73	19.2							
0.1	1000	49	23	100	19	27.8 °C	<i>Proteomonas sulcata</i>	Daily	Daily	This study
0.5	5001	83	26							
0.8	8001	93	23							
1.0	10,002	93	31							
5.0	50,007	84	30							

^a Not empirical data.

^b Juvenile settlement success also included late brachiolaria larvae.

^c Data used for review by Fabricius et al. (2010).

^d Estimated from Supplementary Fig. 1 (Uthicke et al., 2015b).

^e No empirical data provided.

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