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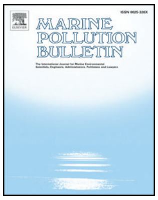

Environmental triggers for primary outbreaks of crown-of-thorns starfish on the Great Barrier Reef, Australia

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ABSTRACT

In this paper, we postulate a unique environmental triggering sequence for primary outbreaks of crown-of-thorns starfish (COTS, *Acanthaster planci*) on the central Great Barrier Reef (GBR, Australia). Notably, we extend the previous *terrestrial runoff hypothesis*, viz. nutrient-enriched terrestrial runoff → elevated phytoplankton 'bloom' concentrations → enhanced COTS larval survival, to include the additional importance of strong larvae retention around reefs or within reef groups (clusters) that share enhanced phytoplankton concentrations. For the central GBR, this scenario is shown to occur when El Niño-Southern Oscillation (ENSO) linked hydrodynamic conditions cause the 'regional' larval connectivity network to fragment into smaller 'local' reef clusters due to low ocean current velocities. As inter-annual variations in hydrodynamic circulation patterns are not amenable to direct management intervention, the ability to reduce the future frequency of COTS outbreaks on the central GBR is shown to be contingent on reducing terrestrial bioavailable nutrient loads ~20–40%.

1. Introduction

Outbreaks of crown-of-thorns starfish (COTS, *Acanthaster planci*) remain a major cause of coral mortality on the Great Barrier Reef (GBR, Australia) and elsewhere in the Indo-Pacific, contributing to widespread and accelerating degradation of coral reef environments (reviewed by Pratchett et al., 2014). Field observations from the 28-year period (1985–2012) identify damage from COTS as the second largest contributor to recent declines in GBR coral cover, accounting for a loss of 1.24% year^{-1} (De'ath et al., 2012).

Identifying the origin of primary COTS outbreaks is thus a priority for successful management of the GBR, especially if outbreaks are linked to anthropogenic impacts that are amenable to change. Two hypotheses that specifically consider a contributing role for anthropogenic impacts have been widely debated. They are: (i) the *predator removal hypothesis*, which postulates that more juveniles survive to maturity due to the removal of fish predators through human exploitation (reviewed in Birkeland and Lucas, 1990), and (ii) the *terrestrial runoff hypothesis*, which postulates that the survival of COTS larvae is most often constrained by the nutrient-limited abundance of phytoplankton food sources, such that if (by chance) populations of adult COTS spawn at around the same time that a major rainfall–runoff event washes large amounts of terrestrial nutrients into coastal waters, then more larvae would survive than might normally be the case — thereby increasing the risk of a population outbreak (Birkeland, 1982; Brodie et al., 2005; Fabricius et al., 2010; Wolfe et al., 2015).

Whilst only circumstantial evidence currently exists in support of the *predator removal hypothesis* (reviewed by Pratchett et al., 2014), a growing body of empirical evidence appears to support the central tenets of the *terrestrial runoff hypothesis* (Lucas, 1982; Okaji, 1996; Okaji et al., 1997; Fabricius et al., 2010; Wolfe et al., 2015; Uthicke et al., 2015). This also includes the broader consideration that elevated nutrient supply and hence phytoplankton biomass, as indicated by elevated seawater chlorophyll-*a* concentrations, can arise from river discharge (Birkeland, 1982; Wooldridge et al., 2006) as well as oceanographic features such as fronts (Houk et al., 2007) and upwelling zones (Houk and Raubani, 2010). Central to the emerging evidence, are larval nutrition experiments which confirm that the planktotrophic larvae of *A. planci* feed on the nano- and microplankton (>3 μm cells) (Okaji et al., 1997; Fabricius et al., 2010; Wolfe et al., 2015) that multiply at high seawater nutrient levels. Indeed, by using cultured microalgae it has been shown that larval development is optimal at 1.0–6.5 μg L^{-1} chlorophyll-*a* (chl-*a*), or at phytoplankton cell concentrations of >1000 cells mL^{-1} — with continuously increasing survivorship up to 10,000 cells mL^{-1} (Uthicke et al., 2015). Few larvae complete their development at <0.8 μg L^{-1} (Lucas, 1982; Okaji, 1996; Okaji et al., 1997; Fabricius et al., 2010; Wolfe et al., 2015). Uncertainty remains as to the exact period of delay (~2–3 years) between predicted enhanced larval survivorship and the COTS development period into visible, adult starfish (reviewed by Fabricius et al., 2010; Pratchett et al., 2014). This may be a real phenomenon, perhaps related to resource availability of coral and/or coralline algae cover for juvenile COTS feeding. Else, it may

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simply record the uncertainty associated with correctly identifying which floods (and/or upwelling) events actually promote the exceedence of phytoplankton biomass thresholds (chl-$a > 0.8\ \mu g\ L^{-1}$) that favour enhanced larval survivorship. Inaccurate detection of the precise timing of outbreaks is also a real possibility due to the limits of large-scale reef monitoring.

The *terrestrial runoff hypothesis* is generally put forward to explain so called primary outbreaks (cf. Endean, 1974) whereas secondary outbreaks are considered the result of massive larval production from a primary outbreak impacting on 'down current' reefs (Kenchington, 1977). Such secondary outbreaks have been successfully reconstructed and explained by hydrodynamic modelling of larval transport (Dight et al., 1990a,b; Hock et al., 2014). There is some evidence, however, that hydrodynamic circulation patterns on the GBR may also influence the occurrence of primary outbreaks. For example, hydrodynamic models for the central GBR indicate that weak along-shelf current flow during COTS spawning periods often precedes the buildup of primary COTS outbreaks (Black et al., 1995; Burrage et al., 1997). Long-term fluctuations in the strength and direction of these along-shelf currents are dominated by the El Niño-Southern Oscillation (ENSO), whose 7–15 year response dynamic also approximates the time-scale between historical primary outbreaks on the central GBR (Birkeland and Lucas, 1990).

In this paper, we investigate the possibility that both enhanced larval survival (cf. *terrestrial runoff hypothesis*) and hydrodynamic circulation patterns that promote strong 'local' reef interconnectedness are required to trigger primary COTS outbreaks on the central GBR. In particular, we reconstruct data for historical COTS outbreak events to investigate the co-occurrence, environmental drivers and inter-annual variability of potential triggering thresholds for the summer 'bloom' intensity of phytoplankton biomass and local reef connectivity.

2. Study area

The reefs and other ecosystems of the GBR are embedded on a shallow continental shelf (Fig. 1), wherein water depths increase to a maximum of 100 m before the shelf break and average about 35 m. The matrix of reef structures on the outer margins of the shelf creates an incomplete barrier to the deep oceanic waters of the Coral Sea (Brinkman et al., 2001). The shallowness and width (>50 km–100 km) of the GBR lagoon plays an important role in the retention of imported material (Brodie et al., 2012), distinguishing the GBR system from many other Indo-Pacific coral reefs surrounded by deeper water. The nutrients and sediments that are held and/or recycled in the inner- to mid-shelf region of the GBR lagoon have a large terrestrially derived component (Furnas, 2003; Furnas et al., 2011). The numerous river systems that drain the 423,000 km^2 catchment adjoining the GBR lagoon provide the primary delivery mechanism for this terrestrial material (Furnas, 2003; Brodie et al., 2012).

The initiation and spread of COTS outbreaks on the GBR have been very consistent in all four recorded outbreaks, including the current outbreak that started in 2010/11 (reviewed by Pratchett et al., 2014). Each of the outbreaks has been initiated on mid-shelf reefs in the north-central (Wet Tropics) region of the GBR (the 'initiation box'; Fig. 1 inset) between Lizard Island (14.6°S) and Cairns (16.6°S). The reefs in the vicinity of Green Island off Cairns (16°45′ S, 145°56′ E) appear to be a particularly important focal point. The first outbreak was observed at Green Island in 1962 (Barnes, 1966), the second also at Green Island in 1979 (Endean, 1982), and the third first detected by tourist operators at Michaelmas Cay (a reef neighbouring Green Island) in 1993, and also at Lizard Island considerably further north (Wachenfeld et al., 1998). A chronic COTS population persists on outer shelf reefs in the nutrient upwelling Pompeys and Swains reef regions (Sweatman et al., 2000), but is considered unrelated as an initiation source for historical primary outbreaks on the central GBR.

The load of terrestrial sediment and pollutants discharging into the GBR lagoon has increased greatly with the development of the river catchments for agriculture over the past 150 years (e.g., Kroon et al., 2012). Loads have increased by up to five times for suspended sediment from some rivers, and up to six times for dissolved inorganic nitrogen (DIN) (Mitchell et al., 2009; Kroon et al., 2012). Whilst various organic and inorganic forms of terrestrial nitrogen become bioavailable in the marine environment, it is the DIN component that is considered the principal source capable of causing nutrient enrichment on the mid-shelf reefs (Wooldridge et al., 2015). The essentially conservative mixing properties of DIN during the early stages of flood plume transport means that the risk of DIN-enriched flood waters reaching inshore, mid-, and even outer-shelf reef areas increases considerably as end-of-river DIN concentrations rise (Devlin and Brodie, 2005). A predictive modelling framework exists for the central GBR which links end-of-river DIN concentrations and the ensuing flood plume intensity ('bloom') of phytoplankton biomass — as indicated by the concentration of photosynthetic pigment, chl-*a* (Wooldridge et al., 2006, 2015). For the mid-shelf reef complex surrounding Green Island, the model predicts an exceedence of the enhanced COTS larvae survival threshold (chl-$a > 0.8\ \mu g\ L^{-1}$; Fabricius et al., 2010) with a statistical expectation of ~1 in every 7–10 years (i.e. annual exceedence probability ~15%, Wooldridge et al., 2015; Fig. 2). This is in contrast with reef waters further north surrounding Lizard Island, where the model predicts an extremely low (essentially 0% likelihood) of chl-$a > 0.8\ \mu g\ L^{-1}$; being consistent with long-term (1993–1999) field observations wherein the $0.8\ \mu g\ L^{-1}$ threshold was never exceeded during the summer wet season period (Brodie et al., 2007). Such an outcome can be explained in terms of the limited agricultural development, lower rainfall–runoff volumes and subsequent lower end-of-river DIN loads that mix into the reef waters surrounding Lizard Island (Wooldridge et al., 2006, 2015).

The net circulation over the GBR shelf is forced by the tides, wind and oceanic inflows from the adjoining Coral Sea (Brinkman et al., 2001; Choukroun, 2010). The general structure of the oceanic currents adjacent to the continental shelf is discussed in Church (1987) and Burrage et al. (1995), and is depicted schematically in Fig. 3A. A broad oceanic inflow system, the South Equatorial Current (SEC) which is part of the South Pacific gyre, meets the continental shelf and bifurcates at a latitude similar to Green Island (16°S), although the latitude of this bifurcation is subject to temporal variation. The SEC splits to form two boundary currents whose influence is felt on the shelf as low frequency long-shelf currents. These are the southward flowing East Australia Current (EAC), and the northward flowing North Queensland and Hiri Currents. The strength of oceanic inflows from the SEC, and the resultant impact upon shelf currents show inter-decal fluctuations that are consistent with the 7–15 year response dynamic of the ENSO (Burrage et al., 1997). Both hydrodynamic simulation models and drogue drifter data indicate that when combined with prevailing south-easterly trade winds, the oceanic inflows from the SEC can result in a 'decoupling' of inner-shelf currents from the mid- to outer-shelf currents at a latitude similar to Green Island (16°S) (King and Wolanski, 1992; Cahill and Middleton, 1993; Dight et al., 1990a; Brinkman et al., 2001; Choukroun, 2010). This can result in significant northward flows on the inner shelf, whilst flows are strongly southward on the mid- to outer-shelf (see Fig. S1). This shear provides an efficient dispersal mechanism (i.e. shear dispersion) such that small across-shelf excursions in the location of larval release points can result in very large differences in the direction and distance that larvae are advected along and across the shelf (see e.g., Fig. 3B). Model simulations indicate that larvae released from reefs around Green Island travel in a northward direction ~20% of the time, related in part, to the occurrence of the La Niña phase of ENSO (Dight et al., 1990b).

3. Methods

Given the often cited significance of Green Island and its neighbouring reefs as a focal location for the initiation of primary COTS outbreaks on the central GBR (e.g., Birkeland and Lucas, 1990;

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