Research Article

Origins and Implications of a Primary Crown-of-Thorns Starfish Outbreak in the Southern Great Barrier Reef

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The crown-of-thorns starfish (COTS) is a major predator of hard corals. Repeated COTS outbreaks in the Cairns and Central sections of the Great Barrier Reef (GBR) have been responsible for greater declines in coral cover than any other type of disturbance, including cyclones, disease, and coral bleaching. Knowledge of the precise timing and location of primary outbreaks could reveal the initial drivers of outbreaks and so could indicate possible management measures. In the central GBR, COTS outbreaks appear to follow major flooding events, but despite many years of observations, no primary outbreak has ever been unequivocally identified in the central and northern GBR. Here we locate a primary outbreak of COTS on the southern GBR which is not correlated with flooding. Instead it appears to have been the result of a combination of life history traits of COTS and prevailing oceanographic conditions. The hydrodynamic setting implies that the outbreak could disperse larvae to other reefs in the region.

1. Introduction

The crown-of-thorns starfish (COTS) (*Acanthaster planci*) is an obligate corallivore that causes dramatic losses of coral cover at high population densities and is a major challenge in coral reef management [1]. Populations of COTS alternate periods of low density, when individuals are sparsely distributed across large areas of reef, with briefer periods of much higher densities [2]. A single adult starfish can consume approximately 10 m^2 of coral per year and large "outbreak" populations have a major impact on local cover [3] that can persist for more than a decade [4]. Surveys on the Great Barrier Reef (GBR) span some 50 years, in which time there have been three series of outbreaks beginning in 1962, 1979, and 1993. Since the advent of systematic monitoring in 1986, two outbreaks have appeared in the Cairns Section of the GBR in 1993 and 2009 before subsequently spreading through the Central Section of the GBR. In 2012, coral cover on the GBR had fallen to half the value when surveys began, and COTS outbreaks have been responsible for a greater proportion of declines in coral cover on reefs in the Cairns and Central sections of the GBR than any other type of

disturbance including cyclones, diseases, and coral bleaching [5, 6]. This means that COTS are of critical concern on the GBR; particularly as a new series of outbreaks is currently developing on Cairns Section reefs and following the same pattern [7].

Outbreaks typically begin with an abrupt population increase from very low density. This change in abundance by orders of magnitude is termed a "primary outbreak" if it has not arisen through recruitment from other high-density populations nearby [8]. Explanations for primary outbreaks revolve round two types of drivers: natural (population fluctuations [9], aggregation behaviour of existing populations [10, 11], and/or food limitation [12]) and anthropogenic (enhanced larval survival due to nutrients in terrestrial runoff [13, 14] and increased postsettlement survival due to the removal of COTS predators [8]). In practice assigning cause(s) for COTS outbreaks is difficult; outbreaks may well result from a combination of factors that vary with time and location [15], or they may simply be an artefact of the dispersal of passive larva in the water column [16]. However primary outbreaks originate; secondary outbreaks are thought to result either from colonisation by immense

numbers of larvae spawned by existing high-density outbreaking populations that are carried to reefs downstream by prevailing currents or from adult migration between reefs [8].

The first widely documented outbreak population of COTS on the GBR was at Green Island in 1962 [17]. A variety of surveys were made at different times and locations between 1966 and 1974 to determine extent of COTS activity on the GBR [2]. From these it became apparent that outbreaks began in the Cairns section of the marine park and spread south through the central GBR with time [18, 19], as would be expected if planktonic larva dispersed passively in the water column. Systematic surveys over the next two decades confirmed this pattern for a second wave of outbreaks beginning in the late 1970s and also identified a northward spread of outbreaks [20]. This pattern had become well established by the third series of outbreaks beginning in 1993 [21].

Despite the 50-year history of COTS surveys on the GBR, the location of primary outbreaks has been difficult to pinpoint. To date, no primary outbreak on the GBR has been located with any precision, even though outbreaks in the Cairns Section first appear on reefs between 14.5° and 17°S [22]. While outbreaks were first reported at Green Island (16.75°S) near Cairns in 1962 [17], further research suggested that this was a secondary outbreak, and the original primary outbreak(s) had occurred north of Green Island in the 1950s [23]. In 1979 another large outbreak of starfish was observed on Green Island [24] and survey results and reliable unpublished data indicated that this outbreak was also secondarily derived from others located further north around 16°S [20]. Similarly, a third series of outbreaks beginning in 1993 was first detected near Lizard Island (14.5°S) [15, 21]. However the exact location of the primary outbreak in 1993 remained uncertain, as COTS increased on a number of nearby reefs about the same time [7]. More recent reports indicated increased COTS activity on reefs near Green Island from around 2010 [25]; however COTS numbers have been slowly building on reefs further north in the vicinity of the Lizard Island since 2005 [26]. Again the exact location of any primary outbreak was uncertain. Thus, despite an extensive history of surveys, primary outbreaks of COTS on the GBR remain a matter of conjecture.

Information on the location and timing of primary outbreaks of COTS could give valuable clues as to the causes. Primary outbreaks are potentially a pressure point for managing COTS on the GBR, as these initial aggregations lead to subsequent wide-spread outbreaks that cause such extensive destruction of coral communities over very large areas [27]. Although outbreaks have occurred on the GBR for eight millennia [28], the frequency of outbreaks in recent decades (in combination with other disturbances such as intense cyclones) is clearly unsustainable, leading to speculation that the frequency of outbreaks has increased [22] possibly due to enrichment of GBR waters with nutrients from agriculture in coastal watersheds [14]. The evidence that primary COTS outbreaks on the GBR are linked to enhanced nutrient input to the GBR lagoon is circumstantial [25]. The GBR is a mosaic of over 3000 individual coral reefs stretching nearly 2000 km from Torres Strait in the north (9°15′S) to Lady Elliot Island in the south (24°07′S) on the continental shelf of northeast
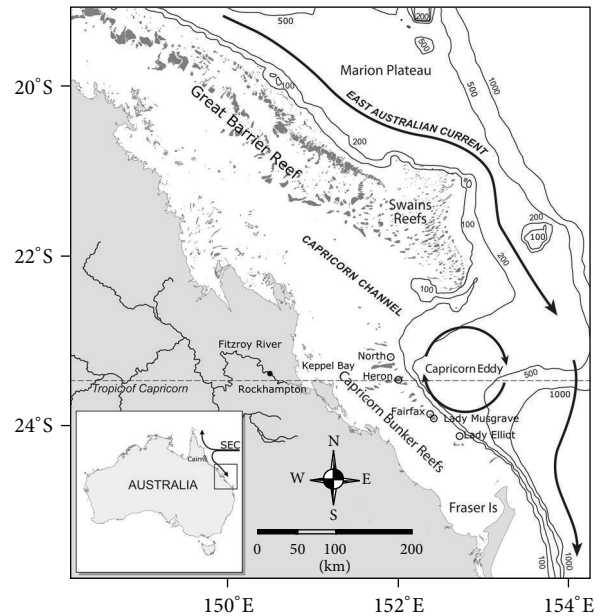

FIGURE 1: The Mackay/Capricorn Section of the GBR showing the location of the Swain Reefs and Capricorn-Bunker Reefs in relation to the coast. Isobaths represent depth in meters and show the edge of the continental shelf. Arrows show the general position of the South Equatorial Current and the East Australian Current and Capricorn Eddy. The mouth of the Fitzroy River is located southeast of Rockhampton and discharges into Keppel Bay.

Australia [29] and because of its large size, outbreaks may well occur independently and for different reasons in different parts of the GBR. Based on extensive surveys using manta tows to document the distribution of COTS outbreaks on the GBR since 1986 [7] we describe a primary outbreak discovered on some reefs in the Capricorn-Bunker Group in the southern GBR. We examine the possible causes, and we weigh the evidence for links to outbreaks in other parts of the GBR, based on the history of outbreaks on Capricorn-Bunker Reefs.

2. Methods

2.1. Physical Setting. Reefs in the Capricorn-Bunker Group are the southernmost extent of the GBR and are located 80 km offshore on the mid to outer continental shelf [30]. These reefs are distinctive, being mostly medium sized outer-shelf platform reefs, often with lagoons and sand cays [29]. To the north, the continental shelf widens at about 23°S from about 80 km to be more than 200 km wide, leaving a substantial gap of over 100 km, named the Capricorn Channel [31], between the northern extent of the Capricorn-Bunker Reefs and the Swain Reefs. The Swain Reefs are contiguous with the rest of the GBR and are a series of lagoonal and planar reefs located offshore on the margin of the continental shelf [29] (see Figure 1).

Reefs of the GBR are strongly influenced by the East Australian Current (EAC) which is derived from South Equatorial Current that crosses the Coral Sea to divide at

the Queensland Plateau around 18°S into two approximately equal branches [32]. The latitude of bifurcation can vary annually between 15° and 20°S [33, 34] with a mean of about 15.5°S [35]. The northward branch circulates clockwise around the northern Coral Sea and flows along the coastal line of the GBR (Cape York). The southern branch is the source of the EAC which flows southward along the outer GBR and ultimately into the Tasman Sea (Figure 1). In general the southward flow strengthens and moves onto the coast at about 17°S. This southward flow could be responsible for transport of COTS larvae between reefs, contributing to the cascade of outbreaks originating from reefs in the Cairns Section of the GBR [36]. With the sudden narrowing of the continental shelf as the EAC passes the Swain Reefs at the southern end of the GBR, a clockwise eddy (the Capricorn Eddy) is entrained, which drives a current northward along the continental slope adjacent to the Capricorn-Bunker Reefs [37]. The strength of the eddy varies seasonally with the southerly flow of the EAC. The northerly current resulting from the Capricorn Eddy is strongest during spring and early summer and circulates water around the Capricorn-Bunker Reefs [30]. Sea surface temperature in the Capricorn-Bunker Group averages 20°C in winter and 27-28°C in summer [30].

The major source of terrestrial input to the region is the Fitzroy River, which flows into Keppel Bay southeast of Rockhampton (Figure 1). The catchment extends over approximately 142, 500 km^2 and is topographically and geologically diverse. Land use is dominated by grazing and mining. The catchment was once extensively vegetated with Brigalow (*Acacia harpophylla*) that was largely cleared for grazing in the mid-20th century [38]. The Fitzroy is the second largest river that flows into the GBR lagoon [39] and has a mean annual discharge of approximately 5.9×10^6 megalitres [40]. Discharge is highly variable both seasonally and annually, with the magnitude and frequency of discharge dependent on the influence of the El Niño Southern Oscillation (ENSO) and summer cyclone activity [41]. In a typical year, the discharge of the Fitzroy River is relatively small, but large floods occur on average every 5–10 years [42].

2.2. Sampling Techniques. The Australian Institute of Marine Science (AIMS) has used the manta tow technique to survey reefs along the length of the GBR since 1986 as part of an ongoing Long Term Monitoring Program (LTMP). The manta tow technique involves towing a snorkel diver along the surface behind a small boat. The method provides a general description of large areas of reef and can be used to gauge broad changes in distribution and abundance of organisms. Manta tows are used to describe the broadscale pattern and extent of COTS activity on the GBR. Manta towing is used to survey entire perimeters of reefs, such that a reef constitutes the unit of survey. Two teams work in opposite directions around the reef to survey about half the perimeter each. A team consists of a boat driver and an observer who is towed along the surface slowly behind the boat holding on to a manta board at approximately 6 km/h (100 m per minute). The boat driver tows the observer parallel to the reef crest and close enough for the observer to see as much of the shallow (generally <10 m) reef slope as possible.

At two-minute intervals the boat stops, allowing the observer to record observations, including percent cover of living hard and soft coral, counts of COTS (including an estimate of their size), and associated feeding scars. The number of manta tows required to complete a survey of each reef perimeter will vary depending upon the size of the reef. On average a reef in the Swain region requires ~40 two-minute tows to complete, while a reef in the Capricorn-Bunker region requires ~60 tows. The method is documented in detail in a Standard Operational Procedure [43].

The AIMS LTMP has surveyed varying numbers of reefs in the Swain and Capricorn-Bunker regions each year since 1986 (see Table 1). While some reefs have been surveyed annually or biennially (key reefs), other reefs have been surveyed much less frequently. Sampling is designed to represent a broad overview of reefs in the two sectors (Figure 1), so the individual reefs that are surveyed within a sector have varied from year to year. More details of the surveys can be found in the Long Term Monitoring Report 2008 [4]. Surveys are made over the Austral summer, so the reporting period runs from 1 July to 30 June; for instance, the 2012 survey year includes reefs surveyed between July 2011 and June 2012.

The densities of COTS on a reef are expressed as the average number of COTS per tow. Two categories of outbreak are distinguished: Active Outbreak (AO) and Incipient Outbreak (IO). In principle, an Active Outbreak occurs when starfish densities reach levels where loss of coral tissue through starfish feeding is likely to be faster than the growth of the coral. Research into the feeding behaviour of COTS indicates that depletion of live coral cover on reefs will occur above a threshold of 1000 COTS km^{-2} (10 ha^{-1}) [3], while manta tow data, taking into account coral cover, indicated a threshold of ~1500 COTS km^{-2} [44]. This corresponds to approximately 0.22 COTS per two-minute tow. After consideration of the relative costs of Type I and Type II errors, the criterion for an Active Outbreak was revised upwards to approximately 1.0 COTS per two-minute manta tow [45]. This represents a starfish density that is highly likely to cause net decline in coral cover. Less dense populations (0.22–1.0 COTS per tow) are referred to as Incipient Outbreak representing COTS densities that may impact on coral cover.

3. Results

For the first two decades of manta tow surveys, small numbers of COTS were seen intermittently, mainly on reefs in the southern part of the Capricorn-Bunker region, and no outbreaks were recorded (Table 1). More recently, COTS numbers in this sector have increased steadily since 2008 (Figures 2 and 3), with the highest numbers recorded during surveys in 2014. The greatest numbers of COTS were seen at Fairfax Island Reef. COTS were first recorded below outbreak levels at 0.11 ± 0.01 (mean ± SE) COTS per tow on Fairfax Island Reef in 2010. When the reef was next surveyed in 2012, COTS numbers had increased to 0.97 ± 0.97 COTS per tow and the reef was declared an Active Outbreak. This was the first Active Outbreak to be recorded using manta tow on any reef in the Capricorn-Bunker Group since AIMS surveys began in 1986. The average size of COTS in all surveys exceeded 25 cm in

Table 1: Survey year and number of reefs surveyed including the number of reefs recorded with outbreaks in that year (figures given in brackets and include both Incipient and Active Outbreaks combined) in the Swain and Capricorn-Bunker Group. Mean COTS per two-minute tow and standard error (SE) are given for each survey year. A different suite of reefs is sampled in each survey year depending on sample design, weather, and logistical considerations. Survey years run from 1 July of the preceding calendar year to 30 June, so, for instance, the 2012 survey year represents reefs surveyed between July 2011 and June 2012.

| | Swain Reefs | | | Capricorn-Bunker Reefs | | |
Year	Number of reefs surveyed (number of outbreaking reefs)	Mean COTS	SE COTS	Number of reefs surveyed (number of outbreaking reefs)	Mean COTS	SE COTS
1986	32 (5)	0.134	0.062	8 (0)	0.012	0.012
1987	30 (7)	0.33	0.126	5 (0)	0	0
1988	28 (3)	0.227	0.124	6 (0)	0.002	0.002
1989			No survey			
1990	20 (4)	0.272	0.207	6 (0)	0	0
1991	21 (3)	0.222	0.158	5 (0)	0.005	0.005
1992	24 (4)	0.340	0.218	6 (0)	0	0
1993	9 (2)	0.781	0.671	4 (0)	0	0
1994	11 (2)	0.120	0.090	3 (0)	0	0
1995	15 (3)	0.142	0.079	3 (0)	0.006	0.006
1996	16 (3)	0.107	0.042	5 (0)	0.010	0.006
1997	8 (3)	0.872	0.445	5 (0)	0.012	0.012
1998	9 (4)	1.230	0.646	4 (0)	0	0
1999	7 (3)	0.431	0.225	4 (0)	0	0
2000	8 (3)	2.094	0.797	4 (0)	0	0
2001	8 (5)	18.775	7.371	4 (0)	0.005	0.005
2002	7 (4)	4.879	2.798	4 (0)	0	0
2003	7 (4)	4.077	2.227	4 (0)	0	0
2004	7 (3)	0.649	0.414	4 (0)	0.005	0.005
2005	13 (1)	0.050	0.033	4 (0)	0	0
2006	19 (1)	0.030	0.016	8 (0)	0	0
2007	6 (0)	0.005	0.004	4 (0)	0	0
2008	17 (0)	0	0	7 (0)	0	0
2009	7 (0)	0.011	0.011	4 (0)	0	0
2010	15 (0)	0.003	0.003	8 (0)	0.018	0.013
2011	7 (0)	0.002	0.002	3 (0)	0	0
2012	15 (0)	0.003	0.002	6 (1)	0.162	0.162
2013	7 (0)	0.023	0.018	4 (1)	0.066	0.066
2014	14 (0)	0.005	0.003	8 (2)	0.201	0.146

diameter, indicating that the individuals were three or more years old [43]. Subsequent surveys in 2014 showed Active Outbreak densities (1.16 ± 0.74 COTS per tow) persisted and that the population was highly concentrated in the back reef area. An Incipient Outbreak (0.40±0.16 COTS per tow, Figure 2) was also recorded on Lady Musgrave Island Reef in 2014. The outbreak was first observed on this reef in 2013 (0.26±0.1 COTS per tow). Prior to that, small numbers of COTS had been observed occasionally at Lady Musgrave Island Reef since the beginning of surveys in 1986 [7]. Once again starfish were all greater than 25 cm in diameter. As with the outbreak on Fairfax Island Reef COTS were concentrated on the sheltered back reef area where coral cover was the highest. Prior to

the discovery of these two outbreaks, reefs in the Capricorn-Bunker region of the GBR had only supported small COTS populations that were well below outbreak densities (Table 1). Other researchers recorded similarly low densities of COTS on reefs in the region for decades prior to the beginning of AIMS surveys [28] and the sector as a whole appears to have escaped the substantial effects of COTS outbreaks seen in other parts of the central and southern GBR [46].

By contrast, COTS were numerous in the Swain Reefs for the first two decades after 1986, with Active Outbreak levels of COTS recorded on one or more reefs in the region in nearly every year (Table 1). In particular from 1999 to 2003 COTS activity was high and greatly exceeded outbreak
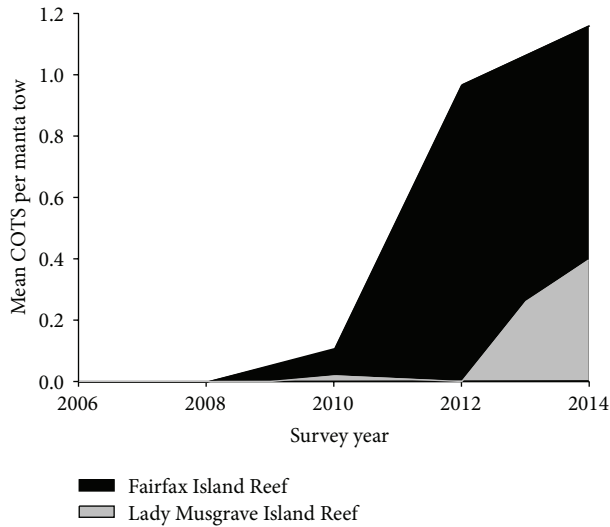
FIGURE 2: Recent change in abundance of COTS on Fairfax Island Reef (surveyed in 2006, 2008, 2010, 2012, and 2014) and Lady Musgrave Island Reef (surveyed in 2006, 2007, 2009, 2010, 2012, 2013, and 2014). Survey years run from 1 July of the preceding calendar year to 30 June, so, for instance, the 2012 survey year represents data from reefs that were surveyed between July 2011 and June 2012.
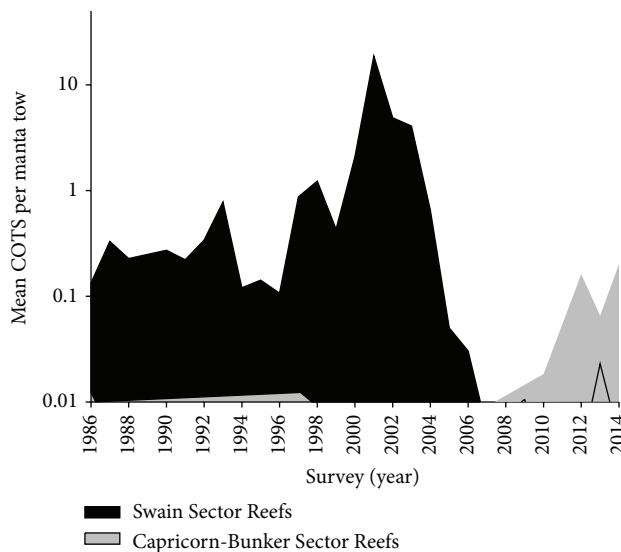

FIGURE 3: Historic change in COTS abundance on Swain Reefs compared to Capricorn-Bunker Reefs. Surveys conducted in both regions annually except for 1989. Survey years run from 1 July to 30 June, so, for instance, the 2012 survey year represents reefs surveyed between July 2011 and June 2012. Y-axis log scale, the small line peak in 2013, represents small numbers of COTS recorded from Swain Reef surveys in that year (see Table 1).

levels across the region (Figure 3). After 2004, COTS activity declined in the Swain Reefs and by 2007 no outbreaks were recorded. COTS activity has remained low on reefs in this region since, with the odd individual COTS observed but always well below outbreak densities (Table 1, Figure 3).
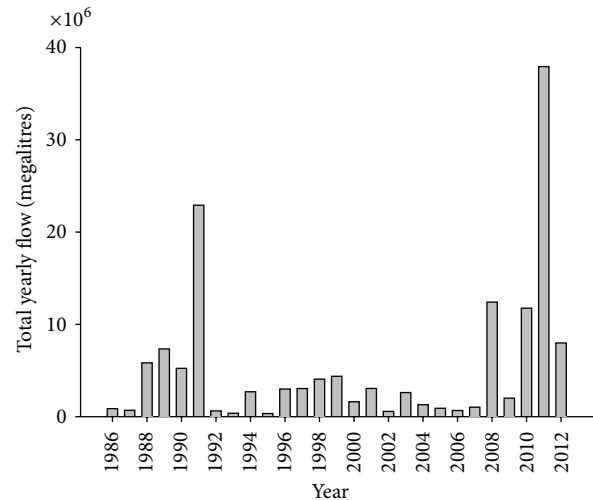

FIGURE 4: Total annual flow in megalitres for the Fitzroy River measured in "water years" at "The Gap" monitoring site. A water year runs from 1 October of the preceding calendar year to 30 September; for instance, the bar for 2012 water year in the figure represents total flow measured at "The Gap" between October 2011 and September 2012.

River flow data for the Fitzroy River for the period of AIMS broadscale surveys (1986 to 2012) shows that major flood events (where total annual river flow was more than double average total annual flow for the period 1986 to 2012) occurred in 1991 and 2011 with minor floods (where annual flow exceeded average annual flow for the period 1986 to 2012) in 1988, 1989, 1991, 2008, 2010, and 2012 (Figure 4). COTS are thought to breed in early wet season (November to January) and major flood events (where total early season river flow was more than double average early season flow for the period November to January) occurred at this time of year in 1991 and 2011 with minor flood events (where early season flow exceeded average early season flow for the period November to January) in 1996, 1999, 2001, and 2008 (Figure 5).

The outbreak at Fairfax Island Reef appears to be a primary outbreak because there were no known high-density COTS populations in the Swain Reefs that could have been sources of larvae. Unlike the repeated pattern in the Cairns Section of the GBR, this outbreak did not follow the occurrence of large flood plumes in the region.

4. Discussion

This is the first compelling example of a primary outbreak recorded from the GBR and, unlike outbreaks recorded in the Cairns Section of the GBR, the timing does not appear related to flooding in nearby catchments. While large population fluctuations are a characteristic of COTS [1, 47–49] the origins of outbreaks are often subtle and seldom due to a single cause [50]. COTS are among the most fecund of any marine species with annual gamete output per female of tens to hundreds of millions of gametes [51–53]. COTS also have the highest fertilisation efficiency recorded for any marine
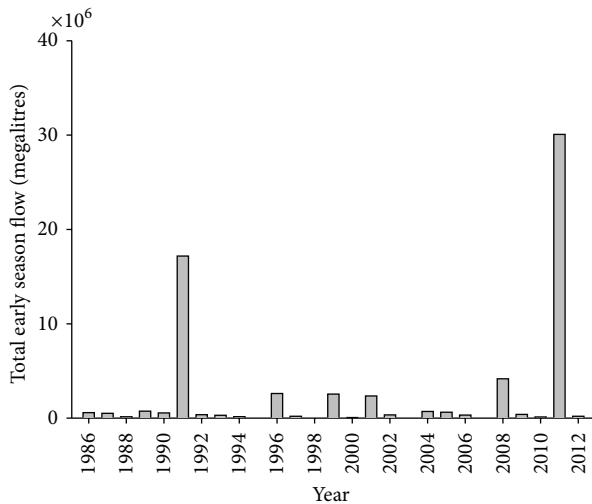
FIGURE 5: Total "early season flow" in megalitres for the Fitzroy River measured at "The Gap." Early season flow reflects measurement of total water flow from 1 November to 28 February, corresponding to the putative COTS spawning season. Thus the bar in the figure labelled 2012 represents total flow measured at "The Gap" between November 2011 and February 2012.

invertebrate [54], predisposing COTS to extreme population fluctuations [55]. Large aggregations may spawn billions of larvae; so a small increase in larval survival could cause population explosions [56]. Changes in oceanographic conditions, such as prevailing water currents and upwelling, have been correlated with increased survival and recruitment of COTS larvae [57–59] that have been linked to phytoplankton blooms [60–62]. Upwelling nutrients fuel the phytoplankton blooms, though eutrophication can also contribute [63–66]. The intensity and duration of phytoplankton blooms can potentially have profound impacts on survival of planktivorous larvae including COTS [67].

Since 1960, four series of outbreaks have begun in the region north of Cairns 2–5 years after the occurrence of floods where aggregate discharges from northern rivers (Burdekin to Daintree Rivers) in the early wet season (November–February) exceeded 10×10^6 megalitres [25]. A plausible explanation is that phytoplankton blooms resulting from increased nutrient loading in reef waters from floods have been the proximate cause of primary outbreaks in the region. The COTS outbreaks on reefs in the Capricorn-Bunker region do not show such a relationship with flooding. Assuming that COTS also spawn in December and January in the southern GBR [54] there have been a number of occasions over the past thirty years where floods, particularly early season floods, from the Fitzroy River may have engulfed Capricorn-Bunker Reefs. These include major early season floods in 1991 and 2011 and minor flood events in 1996, 1999, and 2008. Despite this history of floods, COTS outbreaks have not been recorded from this sector until recently. Capricorn-Bunker Reefs may be far enough off shore that they are rarely exposed to flood plumes [68]. For example, the major river flood of the Fitzroy River from Tropical Cyclone Joy

in 1991 generated a plume that reached the northern reefs of the Capricorn-Bunker region (75 km offshore) for a few days [69]. This was an exceptional event, only exceeded in recent years by flooding following Tropical Cyclone Tasha in 2011. While flood waters from the Fitzroy River may have impinged on Capricorn-Bunker Reefs in 2011, the COTS outbreak at Fairfax Island Reef was first observed in 2012 and comprised of starfish that were at least three years old (>25 cm in diameter), meaning that they must have been spawned at least two years prior to the flood. Thus these outbreaks did not begin 2–5 years after early season floods, unlike the pattern in the Cairns Section of the GBR. While there was a minor flood in 2008, the flow was moderate and only the largest plumes are known to have reached reefs in the southern Capricorn-Bunker region. Thus enhanced recruitment from eutrophication caused by early wet season floods is unlikely to have caused the current outbreaks on the Capricorn-Bunker Reefs.

Nutrient enrichment from upwelling can also lead to COTS outbreaks on coral reefs [59, 70]. In the Capricorn-Bunker region, the Capricorn Eddy draws cooler, nutrient-enriched oceanic water up into the shallows and transports it to the reefs, particularly during the summer [37, 71]. A twelve-year study of chlorophyll a concentrations on the GBR recorded the highest values for outer-shelf reefs anywhere on the GBR in the Capricorn-Bunker region (average $0.519\,\mu\mathrm{gL}^{-1}$, $P10 = 0.165$) [72], with significant variation among years. Chlorophyll a concentrations above $0.25\,\mu\mathrm{gL}^{-1}$ can lead to a much higher rate of development and survival of COTS larvae in laboratory studies [73]. Similarly, the optimal temperature for survival of COTS larvae in the laboratory is 25–32°C [74], which falls within the range of summer sea surface temperatures for the Capricorn-Bunker region. This suggests that conditions for enhanced recruitment of COTS larvae occur on a regular basis, though outbreaks have not been observed previously. This highlights the uncertain relationship between phytoplankton densities and survivorship of mass-spawned invertebrate planktotrophs generally. Until the relation between the two is better understood, the suggestion that the release from food limitation is the principal cause of enhanced COTS recruitment should be interpreted with caution [75].

The waves of outbreaks that have been observed to move through the central GBR are thought to be propagated by the immense numbers of larvae from outbreak densities of adults being carried to downstream reefs by the prevailing currents. It is surprising that more outbreaks have not been recorded on reefs in the Capricorn-Bunker Group because the region is potentially well-connected to the Swain Reefs where Active Outbreaks were consistently present for two decades (1986–2006). By the time the first outbreak in the Capricorn-Bunker region was observed at Fairfax Island Reef in 2012, some six years had elapsed since the last outbreak had been recorded from the Swain Reefs. This long interval makes it highly unlikely that the outbreak was the result of enhanced larval recruitment from large populations in the Swains.

Population release after removal of predators is another implied cause of COTS outbreaks [8]. Historically, both Fairfax Island Reef and Lady Musgrave Island Reef have

been subject to commercial and recreational fishing. However Fairfax Island Reef was rezoned to exclude fishing in 2006 and Lady Musgrave Island Reef has had a large area of reef perimeter protected from fishing since 1983. Prior to this time when the reefs were open for fishing no outbreaks were observed. Fishery targeted reef fishes have been shown to make a rapid recovery on the GBR once protection is introduced [76] and protection from fishing putatively reduces the ability of COTS to form outbreaks on other parts of the GBR [77]. However this link remains tenuous as more commonly fished large predatory fish do not usually prey upon COTS [78] and to date, no fish predator has been identified that can effectively regulate COTS populations, although predation on juveniles undoubtedly occurs [79]. This evidence, combined with the lack of outbreaking COTS populations prior to the fishing closures, strongly suggests predator removal is not an underlying cause for the outbreak.

Individual starfish can persist on a reef for nearly a decade [56]. Outbreaks in general and primary outbreaks in particular do not need to be the result of a single recruitment pulse; numbers may build up over a number of years to reach outbreak densities [80]. There are a number of examples described from the northern GBR that appear to follow this pattern [15, 21, 81]. This fits with what we know about the outbreak on Fairfax Island Reef.

Here we have described a primary outbreak of COTS on the GBR. This event is exceptional because the majority of outbreaks on the GBR are secondarily derived from larvae that spread among well-connected reefs after the initiation of one or more primary outbreaks [23]. These patterns of secondary outbreaks are also known from southern Japan [82, 83] but may occur amongst high island archipelagos in other parts of the Indo-Pacific [84]. An analyses of all reported Indo-Pacific outbreaks (246) since 1990 showed that while a majority of outbreaks (29% and 56%, resp.) were reported from high islands and continental shelves a significant proportion (14%) had also been reported from low islands or atolls [56]. That outbreaks had occurred on so many Indo-Pacific low islands and atolls is telling. This is because research into the genetic structure and connectivity among outbreak populations at 23 sites across the Pacific Ocean indicated that larval dispersal is highly constrained, and that high densities of larvae do not spread across open ocean expanses to initiate secondary outbreaks at distant reefs [49, 85]. Furthermore, where an outbreak has occurred on an isolated atoll or low island it can be often difficult to prescribe any anthropogenic forcing leading to the outbreak [56] other than overfishing [86]. Hence proposed mechanisms generally invoke other sources, usually nutrients that cause plankton blooms leading to enhanced larval survival including upwelling [59, 60], bioturbation, and resuspension of sediments by severe tropical storms and oceanographic features that create high productivity fronts [58]. Results presented here support the view that, given the lack of evidence for any clear anthropogenic drivers, the outbreak on Fairfax Island Reef is likely a result of one or a number of the myriad factors that affect larval survivorship and dispersal prior to settlement. Superficially this appears similar to cases recorded from low islands and atolls throughout

the Indo-Pacific where outbreaks cannot be readily linked to terrestrial runoff. More generally the link between the outbreak on Fairfax Island Reef and episodes of enhanced nutrients from oceanographic processes is less clear though ambient conditions would indicate they certainly exist. What is clear is that there is little evidence of a direct relationship with human activity which supports the idea that in some cases outbreaks can arise spontaneously with no immediate apparent explanation [75, 87]. Given the emergent complexity resulting from interactions between larval ecology, oceanographic, and postsettlement processes this is not surprising and the exact reason(s) for the Fairfax Island Reef outbreak remain enigmatic. Whatever the cause, the location of the primary outbreak at the southern end of the Capricorn-Bunker region has implications for the other nearby reefs. The Capricorn Eddy contributes to a north-westward flow within the region [88]. This flow is greater during the summer months when the EAC is stronger and the southeast trade winds are weak [37]. This effectively puts other reefs in the region "downstream" to those reefs currently supporting outbreaks. This northward flow is most prevalent during the summer months when COTS spawning is likely to occur. Drifter studies show that the orientation of the reef matrix in the Capricorn-Bunker region, approximately perpendicular to the main tidal flow, can result in trapping mechanisms, such as island wake eddies, that could keep particles within the reef array. This may represent a mechanism of both increasing dispersion of larvae along the reef matrix and, at the same time, containing them within this region [89]. As a result other reefs in this region may be subject to COTS outbreaks in the future.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

Acknowledgments

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