Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 7 December 2016 doi:10.20944/preprints201612.0041.v1

Peer-reviewed version available at *Diversity* **2017**, *9*, 17; doi:10.3390/d9010017

Review

Potential Enhanced Survivorship of Crown of Thorns Starfish Larvae due to Near-Annual Nutrient Enrichment during Secondary Outbreaks on the Central Mid-Shelf of the Great Barrier Reef, Australia

Jon Brodie [1,2,*], Michelle Devlin [3] and Stephen Lewis [4]

1 ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville QLD 4811, Australia
2 Coasts, Climate, Oceans Consulting (C2O), Townsville QLD 4810, Australia
3 The Centre for Environment, Fisheries and Aquaculture Science (Cefas), Lowestoft NR33 0HT, UK; michelle.devlin@cefas.co.uk
4 TropWATER, James Cook University, Townsville QLD 4811, Australia; stephen.lewis@jcu.edu.au
* Correspondence: jon.brodie@jcu.edu.au; Tel.: +61 (0) 407127030

Abstract: The Great Barrier Reef (GBR) is currently experiencing widespread crown of thorns starfish (CoTS) outbreaks as part of the fourth wave of outbreaks since 1962. It is believed that outbreaks have become more frequent on the GBR and elsewhere in the Indo-Pacific associated with anthropogenic causes. The two widely accepted potential causes are (1) anthropogenic nutrient enrichment leading to increased biomass of phytoplankton, the food of the planktonic stage of larval CoTS; and (2) overfishing of predators on the juvenile to adult stages of CoTS, for example, commercial fished species such as coral trout. In this study, we show the evidence for the nutrient enrichment causation hypothesis is strong based on a large number of recent studies in the GBR. We also hypothesise that secondary outbreaks in the region between Cairns and Townsville can also be enhanced by nutrient enriched conditions associated with the annual nutrient discharge from Wet Tropics rivers.

Keywords: crown of thorns starfish; Great Barrier Reef; nutrient enrichment; larval survivorship

1. Introduction

The crown of thorns starfish (*Acanthaster planci* – CoTS) is a specialized coral-feeder and is found across the Indo-Pacific. Populations of *A. planci* display cyclic oscillations between extended periods of low-density with individuals sparsely distributed among large reef areas, and episodes of unsustainable high densities commonly termed ‘outbreaks’. The outbreaks result in mass mortalities of corals with typically second-order and long-term consequences on various reef communities. CoTS outbreaks usually spread widely across reef ecosystems in the Indo-Pacific driven over large distances by larval transport, and commonly lead to increases in benthic algae, a loss of coral-feeding assemblages, an overall collapse of reef structural complexity, and a decline in coral biodiversity and productivity [1,2].

CoTS is a naturally occurring animal on Indo-Pacific coral reefs and seem to “normally” occur in low densities on most reefs. However our knowledge of the density of CoTS on reefs before 1960 is very limited. CoTS have caused widespread damage to many coral reefs in the Indo-Pacific over the past six decades as population ‘explosions’ have occurred at regular intervals [1,3,4,5]. There have been several opposing views as to the origin of the outbreaks including both a “natural occurrence” hypothesis through to various anthropogenic causes’ hypotheses [6]. However given the huge numbers of animals which were found on reefs across the Indo-Pacific by the 1970s [1] it has been suggested that these “outbreaks” could not have occurred in the past, or alternatively not at the frequency at which they were occurring by the 1990s. Hence a range of anthropogenic possible "causes" were postulated (reviewed in [1,5,6,7]).

Human causes suggested for the CoTS population outbreaks include removal of predators (especially fish such as the commercially fished coral trout) [8,9] and/or increased larval survivorship due to increased phytoplankton food stocks associated with nutrient enrichment [6,10,11,12]. However the cause (or causes) of the outbreaks remains a controversial issue and there are several opposing views in the literature [5]. One view postulates that population outbreaks are a natural phenomenon due to the inherently unstable population sizes of highly fecund organisms such as *Acanthaster planci* [13]. Outbreaks have also been attributed to anthropogenic changes to the environment of the starfish with a range of possible causes including: removal of adult predators, particularly fish [8] and the gastropod *Charonia tritonis* [1]; changes to population structures of predators on larval and juvenile stages, caused by chemical (possibly pesticide) pollution [14,15]; destruction of larval predators, particularly corals, by construction activities on reefs; and larval food supply (phytoplankton) enhancement from nutrient enriched terrestrial runoff [6].

This contribution examines the latest research on the nutrient enrichment hypothesis for CoTS outbreaks with a specific focus on the GBR, north-eastern Australia. We highlight the importance of understanding the life history stages of CoTS development and the influence of nutrients on the larval stage. The completing hypotheses for CoTS outbreaks are considered and for the first time we examine the potential role of river-discharged nutrients on triggering and sustaining secondary CoTS outbreaks on the central GBR. We also reinterpret recent works on the potential causes of CoTS outbreaks in the southern GBR.

2. Mortality of COTS at different life history stages

The nutrient enrichment hypothesis for CoTS outbreaks centres on the increased survivorship at the larval stage of development, although there is little robust knowledge on the rates of mortality of their different life stages. Keesing and Halford [16,17] studied mortality rates at the small settled juvenile stage (0.5 – 5.5 mm) and found high rates (6.49 % d^{-1}) for 1 month old starfish (mean size = 1.1 mm). The mortality rates decreased considerably with increasing age at 1.24 % d^{-1} for 4 month old starfish (2.7 mm) and 0.45 % d^{-1} for 7 month old starfish (5.5 mm) [16,17]. The results highlighted that mortality rates in these early life stages may be strongly influenced by both predators (epibenthic fauna) and food availability [18].These experiments, involving exclusion of predators, indicated that the major source of mortality was predation by epibenthic fauna for juvenile CoTs. Results also show that in the presence of adequate food supply juvenile *A. planci* move very little which suggests that juvenile survival will be enhanced by settling in areas where predation will be minimal.

It has been suggested that the larval stage, especially at the brachiolaria stage where the larval requires an external food source, is likely to have high mortality [6,10] but there are no field data to support this hypothesis [7]. However laboratory experiments show that in food limited conditions few larvae are able to reach competency [10,12,19,20,21]. In addition it is known that fish such as damsel fish are able to eat CoTS larvae [22] in experimental aquarium conditions but the extent of predation in reefal waters is not known.

3. Conceptual understanding of the nutrient enrichment-CoTS link

In the 1970s Charles Birkeland formulated the hypothesis that CoTS population outbreaks were more common on high islands in the Pacific islands due to terrestrial runoff of nutrients (nitrogen and phosphorus) than they were on atoll islands were there is no natural runoff [23]. This hypothesis was founded on the fact that CoTS have a planktonic larval stage (of a few weeks) which needs to feed on a certain amount of phytoplankton to reach a level of viability such that they can settle on a reef. Nutrient runoff in river discharge from high islands can provide the conditions needed for

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 7 December 2016 doi:10.20944/preprints201612.0041.v1

Peer-reviewed version available at Diversity 2017, 9, 17; doi:10.3390/d9010017

phytoplankton to bloom and hence provide the food source for this larval stage to develop [6,24]. In "normal" nutrient conditions the larvae have insufficient phytoplankton food to reach competence [10] and thus cannot provide the conditions required for the survival of high population numbers.

The anthropogenic causation theory of nutrient enrichment is strongly linked to the increase in human activities such as sewage discharge, fertiliser runoff and increased erosion of nutrient-rich soil. These activities lead to the enrichment of adjacent coastal waters [25], higher phytoplankton biomass, a shift to larger species of phytoplankton which are more suitable as CoTS larval food [26] resulting in better survivorship of CoTS larvae ultimately leading to more frequent outbreaks [6,11].

Analysis of larval growth, the effects of environmental factors and the experimental testing of the nutrient enrichment hypothesis was first carried out in the 1970s [10,27,28,29] and showed that COTS larvae were food limited and did not develop well in low nutrient and phytoplankton biomass conditions. In contrast, experimental testing using more sophisticated apparatus [30,31] tested the growth of larvae in a range of nutrient conditions with results suggesting no nutrient effect. However the experiments were repeated, this time with more care given to strict protocols regarding nutrient supply, with results supporting the nutrient enrichment hypothesis [12,20,21,32]. CoTS outbreaks associated with anthropogenic nutrient enrichment are now seen as one of the "signals" of partial eutrophication of the GBR [25,33]. Recently, refinements of the experiments have further supported the hypothesis [34,35,36] to an agreement that larval survivorship increases with increased food supply of phytoplankton biomass, represented by chlorophyll a concentrations of about 1 μgL^{-1} [35a,36] or at algal food densities above 1000 cells mL^{-1} [34] but with development is being inhibited at low chlorophyll a concentrations of 0.1 μgL^{-1}. Higher chlorophyll a concentrations close to 10 μgL^{-1} appear to retard development [35,36,37], indicating an optimum range of phytoplankton biomass or cell counts for larval survivorship.

Concentrations of chlorophyll a in the GBR lagoon are generally less than 0.5 μgL^{-1} in non-river discharge conditions [38] but can be in the range 0.5 – 3 μgL^{-1} where influenced by major river discharge, in particular in the Burdekin - Wet Tropics regions, where flood plumes reach the mid- and outer shelf reefal areas [39,40,41,42]. Conditions measured during these peak and post flow condition are able to support high larval survivorship of CoTS juveniles if the high nutrient conditions intersect with periods of high larval counts.

4. Crown of thorns starfish and the Great Barrier Reef

The cycles (waves) of outbreaks on the GBR have occurred from 1962 to 1976, 1979 to 1991, 1993 to 2005 [11,12] and 2009 – current [5,43]. Each wave has severely reduced coral cover on the GBR especially in the mid-shelf reefs of the central section [44]. CoTS outbreaks have been less frequent on inner and outer shelf reefs for not-well understood reasons. There is evidence that CoTS outbreaks have occurred on the GBR over the past 7000 years [45], although historical records suggest that the waves of outbreaks post 1962 appear to be a unusual phenomenon and outbreaks have become more frequent in recent times (see below) [11,12].

Outbreaks on the GBR have been traditionally divided into primary outbreaks and secondary outbreaks. Primary outbreaks originate in the "initiation area" between Cairns and Lizard Island. Conditions believed necessary for the initiation of an outbreak wave include sufficient coral biomass for food [12], nutrient enrichment and a high biomass of phytoplankton to sustain larval survivorship [11] and suitable oceanographic conditions so as to retain high connectivity [43,46]. Following the initiation of a primary outbreak, massive larval production [47] leads to secondary outbreaks to the north and south of the initiation area with a wave of secondary outbreaks occurring to the south of the initiation area from Cairns towards Townsville over approximately 8-9 years after the primary outbreak and then offshore from Mackay (12 years) after which the outbreaks appear to diminish [5].

 doi:10.20944/preprints201612.0041.v1

Peer-reviewed version available at *Diversity* **2017**, *9*, 17; doi:10.3390/d9010017

Oceanographic conditions associated with the ENSO cycle [46] also play a part in initiating CoTS outbreaks in the Cairns area of the GBR with nutrient enrichment from river runoff and increased connectivity due to ENSO conditions both providing conditions that result in the initiation of waves of outbreaks 43]. Indeed this new climate association suggests that the 'natural' frequency of CoTS outbreaks may have also been highly variable on the GBR over the past 7000 years given changes in the strength of ENSO forcing during this period. However, the modern conditions of strong ENSO coupled with increased nutrient sources likely creates a scenario where CoTS outbreaks become an almost continuous feature on the GBR.

It is also important to note that CoTS outbreaks can occur at sites with no obvious nutrient enrichment [48] but where in reality upwelling may be present but not documented and at sites with possible nutrient enrichment associated with natural upwelling systems (e.g. in the Chagos archipelago – [49]) or at oceanic nutrient/productivity fronts [50,51]. There has also been a persistent outbreaks area in the Swains but this is not considered to be associated with the outbreaks to the north and to the cycle of anthropogenic drivers and higher larval survivorship.

The long-standing CoTS outbreaks in the Swains reefs in the southern GBR have been associated with the known upwelling systems in that region [11]. This has been identified as an area of upwelling associated with the Capricorn Eddy [52,53,54] and that the resultant phytoplankton blooms are associated with other enrichment phenomenon such as manta ray feeding aggregations [55] and plankton enrichment [56]. It is likely that these factors can help to explain the outbreaks in the Swains and Capricorn-Bunker Group reefs of the southern GBR [48]. In addition the recent outbreaks in the southern Capricorn Bunker Group [48] may be associated with record river discharge from the Burnett and Mary Rivers in early 2011 and 2013 [57].

Miller et al. [48] did consider the role of one large southern river, the Fitzroy, but did not show that the discharge from this river had a significant effect on the outbreaks. However, work on the extent of all southern rivers, i.e. Mary, Burrum, Burnet, Kolan and Baffle) clearly shows the discharge plume extent of these rivers did reach into the southern Capricorn Bunkers [57]. While the Fitzroy River discharge only influences the northern section of the Capricorn-Bunker Group reefs during rare large flood events that are coupled with favourable wind conditions [39,58], the five rivers to the south of the Fitzroy are known to influence phytoplankton dynamics in the southern Capricorn-Bunker group [55] and may influence the survivorship of CoTS larvae.

5. Nutrient enrichment and secondary outbreaks

While it often assumed that nutrient enrichment is primarily involved in producing "primary" outbreaks in the initiation area (Cairns – Lizard Island) there is now evidence that nutrient enrichment can be enhancing "secondary" outbreaks, especially in the offshore Wet Tropics region. Nutrient loading from these rivers have greatly increased with the proliferation of agriculture and associated fertiliser use in the region [59,60]. In the period where

Peer-reviewed version available at Diversity 2017, 9, 17; doi:10.3390/d9010017

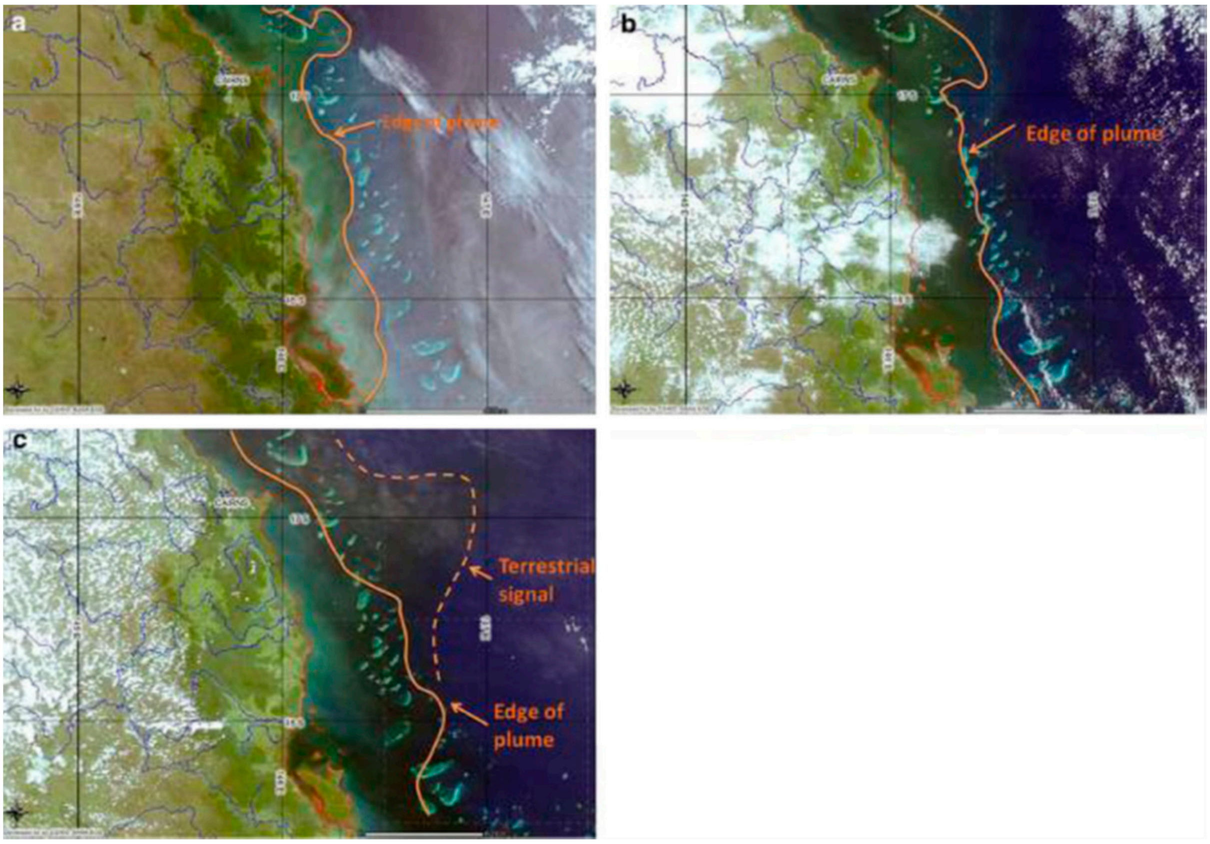
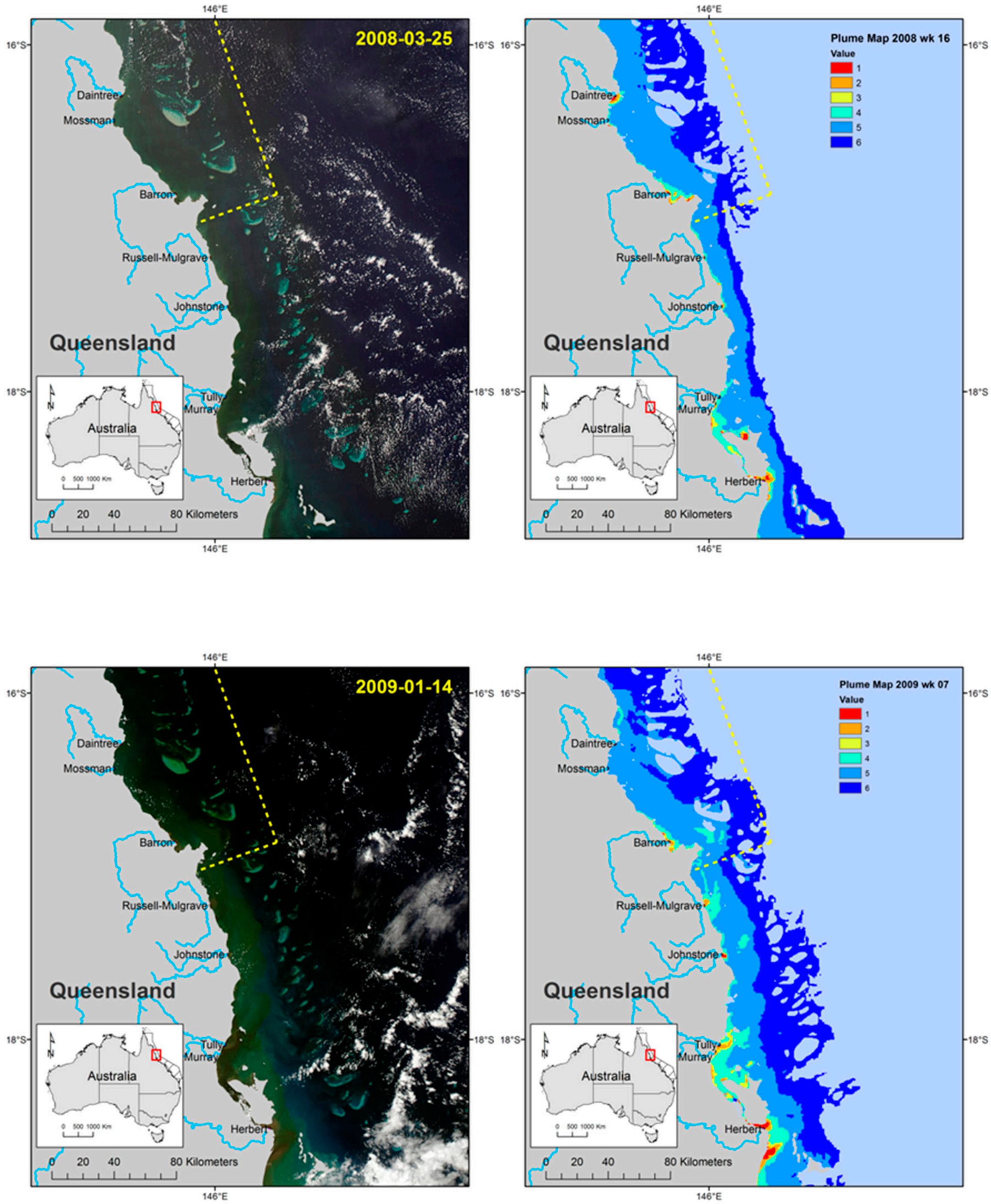


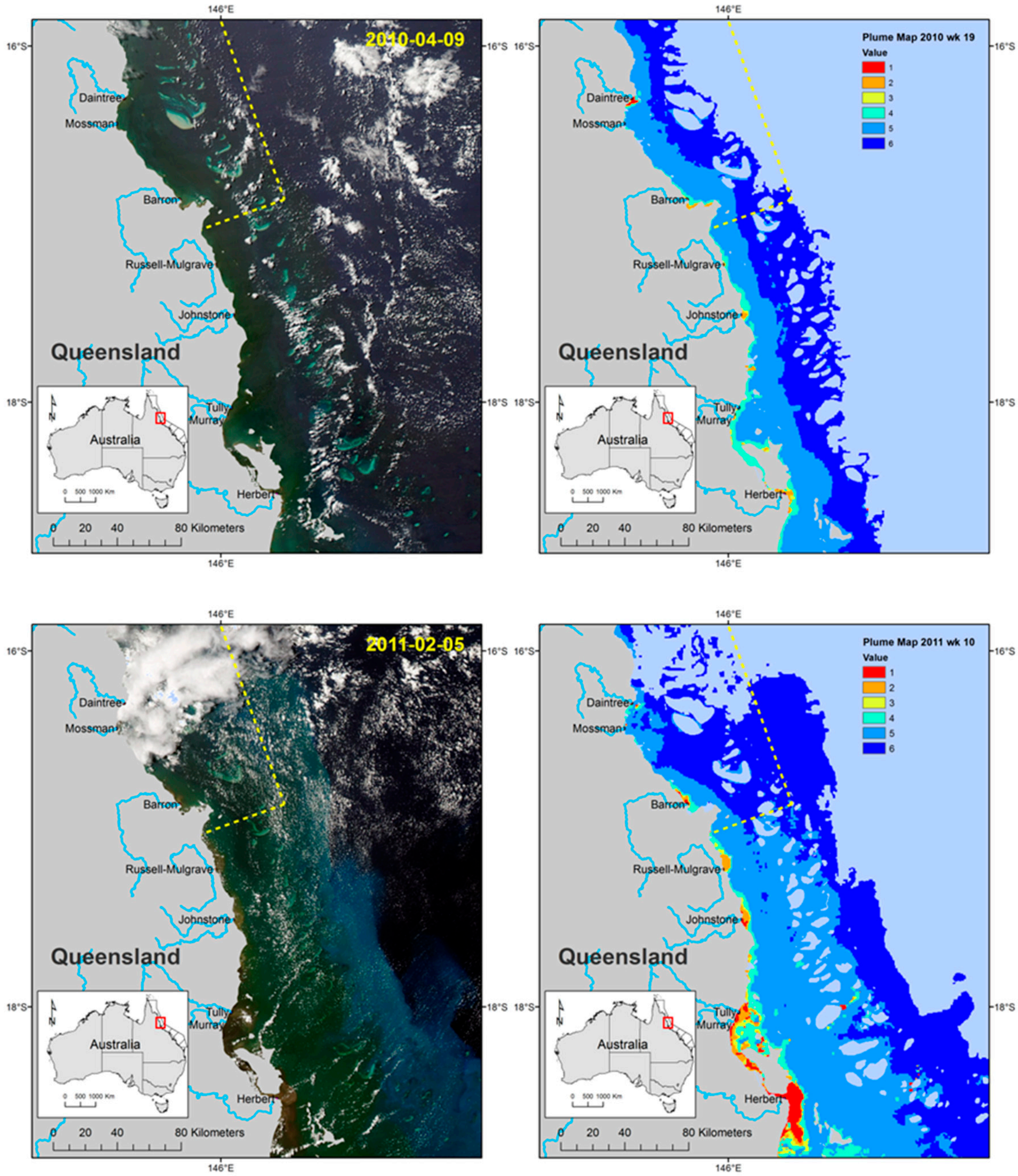
Figure 1. Progression (a–c) of multiple river plumes in the Wet Tropics (9, 11, 13 February 2007, respectively) extending from the coast to beyond the outer reef. The lines show the outer edge of the plume made visible due to Coloured Dissolved Organic Matter and phytoplankton. Images (a–c) show the transformation from a plume dominated by terrestrial particulate matter (brown colour near river mouths) into a plume dominated by a dissolved nutrient driven phytoplankton bloom (green colour). A proportion of the contained nutrients in the plume may be seen 'escaping' to the Coral Sea in part c. Image courtesy of CSIRO.

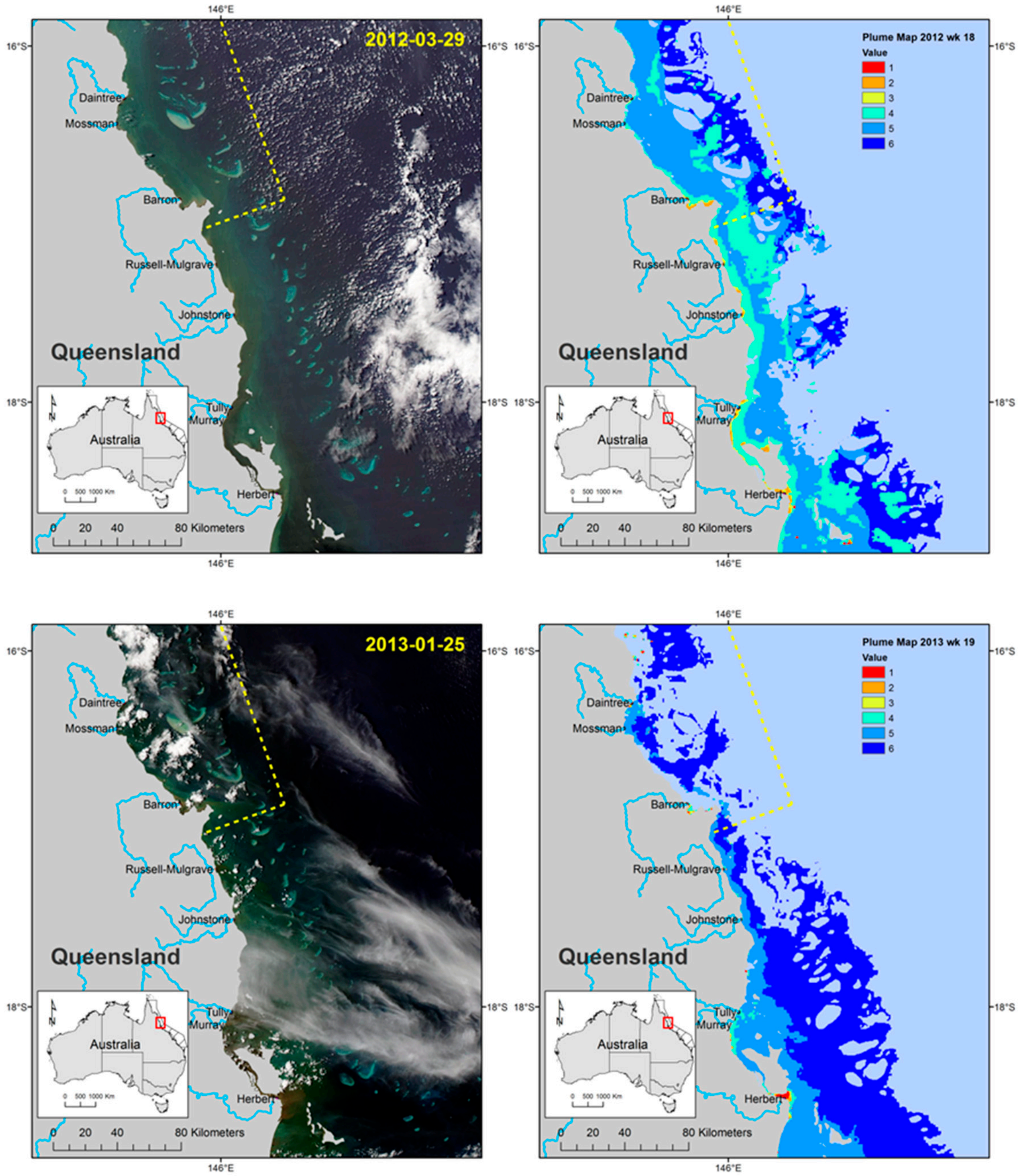
CoTS larvae are in the plankton stages during November to February when Wet Tropics rivers are in high discharge every year and regularly produce phytoplankton blooms on the GBR shelf in this region [39,40,61,62,63,64]. Measurements of high chlorophyll concentrations during this periods represent an extended period of time in which conditions of high phytoplankton biomass are optimal (see also [35,65]).

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 7 December 2016 doi:10.20944/preprints201612.0041.v1

Peer-reviewed version available at *Diversity* **2017**, *9*, 17; doi:10.3390/d9010017




2010-04-09
Plume Map 2010 wk 19
Value
1
2
3
4
5
6
2011-02-05
Plume Map 2011 wk 10
Value
1
2
3
4
5
6
146°E
16°S
18°S
Daintree
Mossman
Barron
Russell-Mulgrave
Johnstone
Tully
Murray
Herbert
Queensland
Australia
0 500 1000 Km
0 20 40 80 Kilometers


2012-03-29
Plume Map 2012 wk 18
Value
1
2
3
4
5
6
2013-01-25
Plume Map 2013 wk 19
Daintree
Mossman
Barron
Russell-Mulgrave
Johnstone
Tully
Murray
Herbert
Queensland
Australia
0 20 40 80 Kilometers
146°E
16°S
18°S

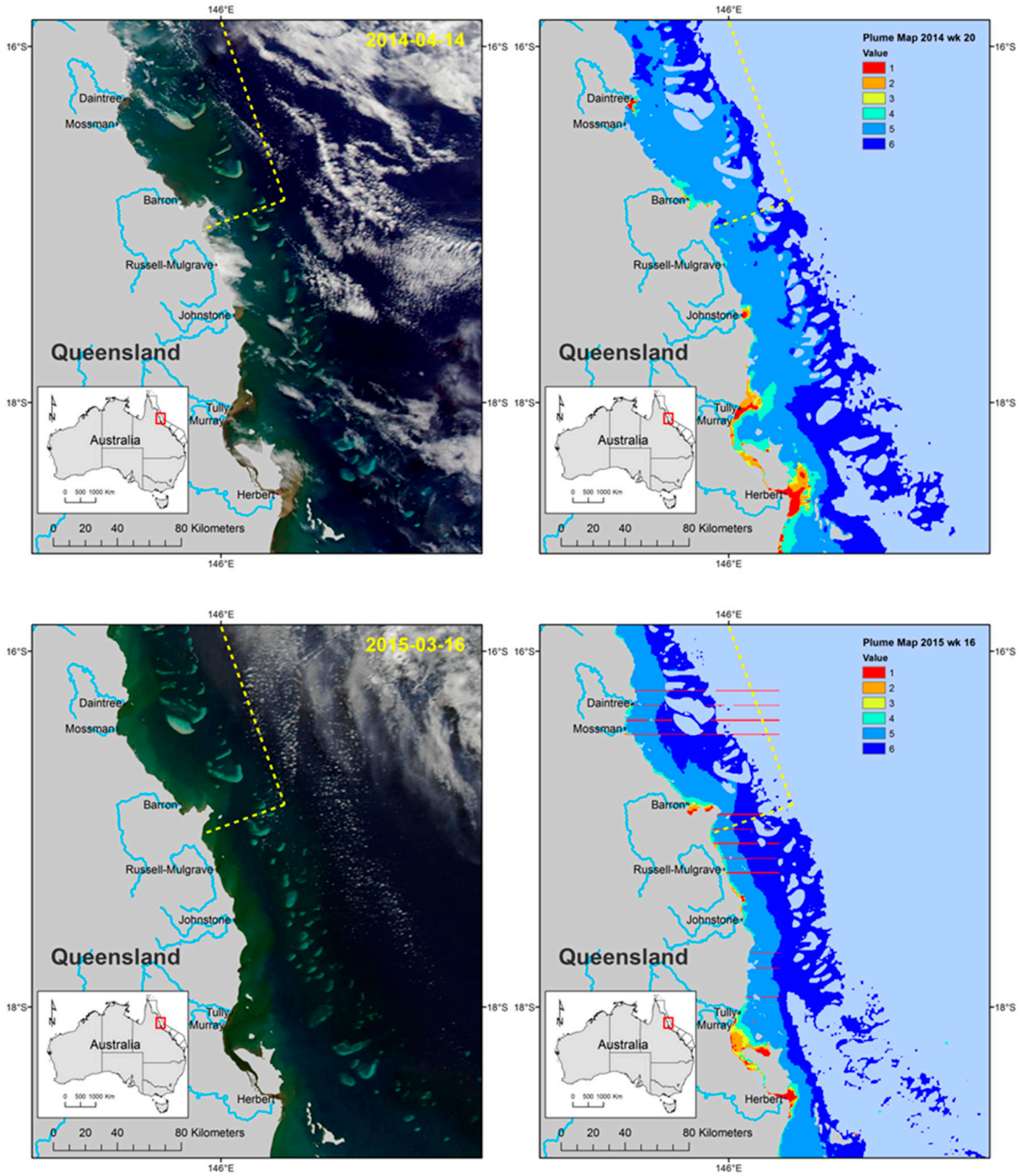


Figure 2. Selected satellite images showing plume water intrusion into the CoTS initiation zone (south) and the region south to the Palms over several years (left column) and the corresponding weekly plume colour class map. Dashed yellow lines on maps stand for the south delimitation of the CoTS initiation zone. Plume colour classes vary from 1 to 6, being 1 for more riverine water and 6 for marine water with some riverine influence. The stage of river discharge on each occasion is shown in Figure 3.

Images of river discharge are easily identifiable using remote sensed imagery, where the brown turbid, coastal waters are clearly contrasted with the greener offshore waters associated with increased phytoplankton production (see Figure 1). In Figure 1 we show a series of MODIS images in true colour from 2007 demonstrating the formation and dispersal of a phytoplankton bloom driven by high discharge from Wet Tropics rivers over a four day period. By the 13 February the plume/bloom has extended across the outer-shelf reefs of this area and into the Coral Sea.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 7 December 2016 doi:10.20944/preprints201612.0041.v1

Peer-reviewed version available at Diversity 2017, 9, 17; doi:10.3390/d9010017

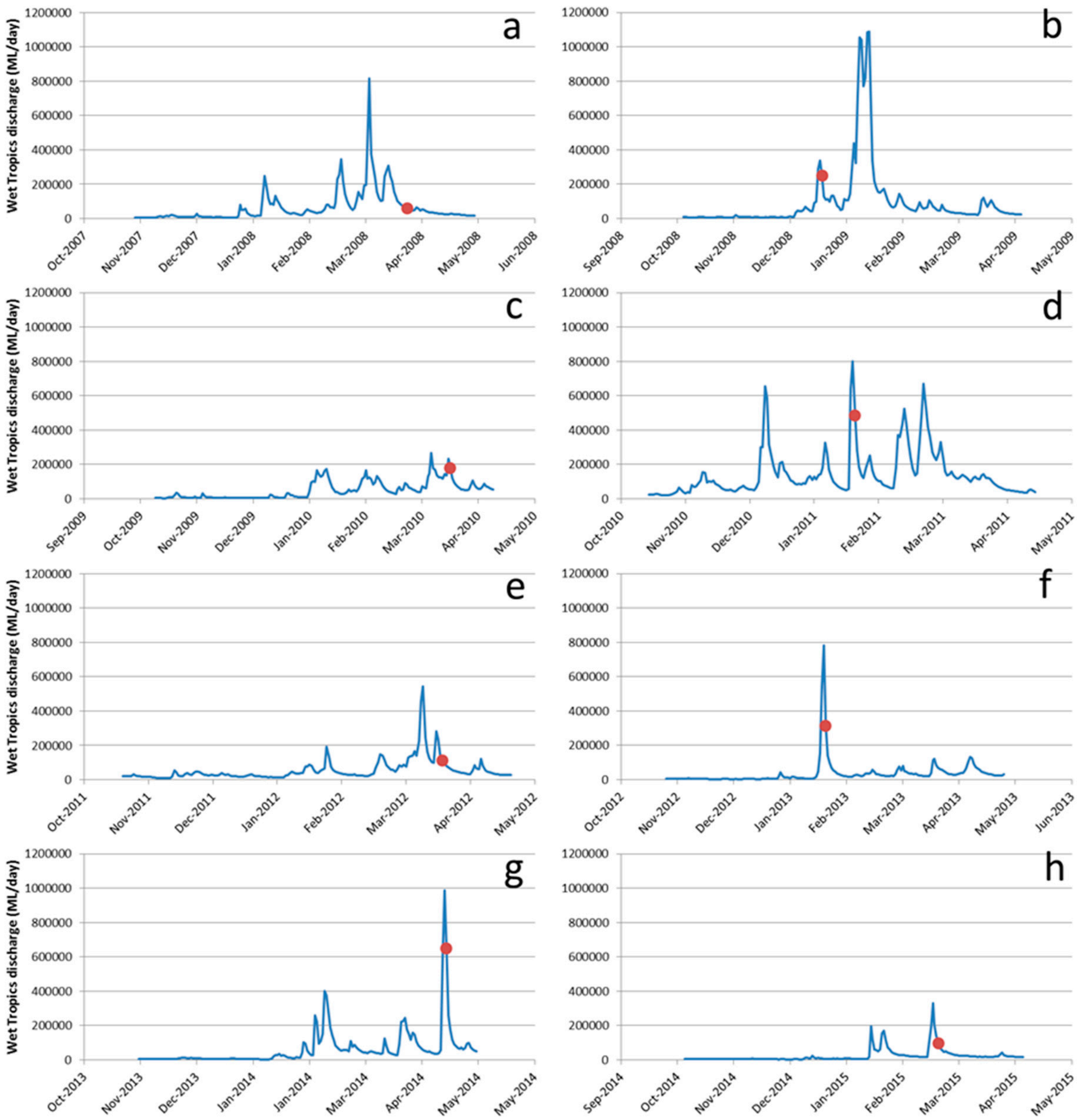


Figure 3. Total daily wet season discharge (November to April, inclusive, ML/day) for the Wet Tropics rivers from 2007-2008 to 2014-2015. Red dots stand for the day where the satellite images shown on Fig 2 were taken.

A daily image of flood plumes was selected from remote sensed imagery (MODIS, Aqua, 250m) (Figure 2), at a period of high discharge (Figure 3) and at periods of low clouds to ensure that the plume was visible. These images from plumes associated with the Wet Tropics rivers show elevated phytoplankton biomass on the mid-shelf reefal area of the GBR between Cairns and Townsville generally in the period when CoTS may be spawning, with examples presented for the period between November to March (Figure 3) for each year.

These conditions of elevated phytoplankton biomass are seen both visually and by water type analysis [41,62,63] where the colour classes of 2 to 5 represent secondary waters, corresponding to elevated phytoplankton biomass (Figure 2b).

Each image represents a period of time of optimal conditions for high phytoplankton biomass, and potentially a source of increased larval survivorship. Chlorophyll a concentrations measured on the Cairns – Townsville mid-shelf area during major river discharge periods (December to March) are

Peer-reviewed version available at Diversity 2017, 9, 17; doi:10.3390/d9010017

0.5 – 3 µgL-1 at salinities in the range 30 – 35 [39,66,62]. These concentrations are in the range at which CoTS larval development is most favourable. The remote sensed imagery only examines a single day during the high discharge period and a further analysis to extend the period over the primary four months associated with CoTS spawning i.e. November to March inclusive would be needed to further advance this speculative hypothesis. However it is worth noting that the river flow conditions for all images were variable, and represent period of flow from 80 to 99th percentile conditions. Optimal growth conditions can still occur at the lower flow rates, indicating that high phytoplankton biomass can be stimulated in first flush, medium to high flow conditions, and may represent a period of time from days to weeks. Extended periods of high biomass conditions can increase the probability of time that a larval bloom and enhanced plume conditions can intersect and increase survivorship, and support growth associated with secondary outbreaks.

6. Conclusions

The range of phytoplankton biomass as measured via a chlorophyll a concentration, for favourable development of CoTS, is 0.6 – 2 µgL-1. This range has been shown to occur commonly in the wet season on the mid-shelf waters of the GBR between Cairns and Townsville where secondary CoTS outbreaks occur. As such it is possible that enhanced survivorship of CoTS larvae is occurring in this region on a regular basis as a result of increased nutrient delivery during periods of high discharge from the Wet Tropics rivers [39] and also during the much more irregular high discharge periods from the Burdekin River (e.g. [67]). Thus these secondary outbreaks of CoTS, while mainly driven by massive larval supply, may also be accelerated by suitable phytoplankton conditions provided by increased nutrient discharges from the relevant rivers [59].

Further studies will be required to assess the strength of the nutrient enrichment element in secondary outbreaks of CoTS especially in the mid-shelf area between Townsville and Cairns where river plumes reach this area on a regular basis. Further south from Townsville river plumes (from rivers south of the Burdekin) rarely reach the mid-shelf of the GBR and it may be speculated that this effect does not play a part in enhancing CoTS outbreaks. An exception may be associated with very large discharge events from the Mary and Burnett Rivers and CoTS outbreaks in the southern Capricorn Bunker Group reefs, but to confirm this connection needs further research.

Acknowledgements

We would like to acknowledge the help of Dieter Tracey and Eduardo da Silva in preparing Figures 2 and 3.

Author Contributions: Jon Brodie conceived the intent and structure of the paper while all authors contributed to writing the text.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Birkeland, C., Lucas J.S. *Acanthaster planci*: Major Management Problem of Coral Reefs. 1990. Boca Raton: CRC Press, Inc.
2. Moran. P.J. The Acanthaster phenomenon. 1986. Oceanography and Marine Biology Annual Review, 24, 379–480.
3. Zann, L., Brodie, J., Berryman, C., Naqasima, M. Recruitment, ecology, growth and behavior of juvenile *Acanthaster planci* (L.)(Echinodermata: Asteroidea). 1987. Bulletin of Marine Science 41, 561–575.
4. Zann, L., Brodie, J., Vuki, V. History and dynamics of the crown-of-thorns starfish *Acanthaster planci* (L.) in the Suva area, Fiji. 1990. Coral Reefs 9 (3), 135-144

5. Pratchett, M.S., Caballes, C.F., Rivera-Posada, J.A., Sweatman, H.P.A. Limits to understanding and managing outbreaks of crown-of-thorns starfish (Acanthaster spp.). 2014. Oceanography and Marine Biology Annual Review, 52, 133-200.
6. Brodie, J.E. Enhancement of larval and juvenile survival and recruitment in Acanthaster planci from the effects of terrestrial runoff: a review. 1992. Australian Journal of Marine & Freshwater Research, 43 (3), 539-554.
7. Caballes, C. F., Pratchett, M. S. Reproductive biology and early life history of the crown-of-thorns starfish. 2014. In: Whitmore, Eric, (ed.) Echinoderms: Ecology, Habitats and Reproductive Biology. Nova Science Publishers, New York, USA, pp. 101-146.
8. Sweatman, H.P.A. A field study of fish predation on juvenile crown of- thorns starfish. 1995. Coral Reefs, 14, 47–53.
9. Mendonça, V.M., Al Jabri, M.M., Al Ajmi, I., Al Muharrami, M., Al Areimi, M., Al Aghbari, H.A. Starfish *Acanthaster planci* in the Northwestern Indian Ocean: are they really a consequence of unsustainable starfish predator removal through overfishing in coral reefs, or a response to a changing environment? 2010. Zoological Studies 49 (1), 108–123.
10. Lucas, J.S. Quantitative studies of feeding and nutrition during larval development of the coral reef asteroid *Acanthaster planci* (L.). 1982. Journal of Experimental Marine Biology and Ecology, 65, 173–193.
11. Brodie, J., Fabricius, K., De'ath, G., Okaji, K. Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. 2005. Marine Pollution Bulletin, 51, 266–278.
12. Fabricius, K.E., Okaji, K., De'ath, G. Three lines of evidence to link outbreaks of the crown-of-thorns seastar *Acanthaster planci* to the release of larval food limitation. 2010. Coral Reefs, 29, 593–605.
13. Potts, D.C., Crown-of-thorns starfish—man-induced pest or natural phenomenon. 1981. The ecology of pests. CSIRO, Melbourne, pp.55-86.
14. Chesher, R.H. Destruction of the Pacific Corals by the Sea Star *Acanthaster planci*. 1969. Science, 165, 280–283.
15. Randall, J. E. Chemical pollution in the sea and the crown-of-thorns starfish (*Acanthaster planci*). 1972. Biotropica 4, 132-44.
16. Keesing, J.K., Halford, A.R. Importance of post settlement processes for the population dynamics of *Acanthaster planci* (L.). 1992a. Marine and Freshwater Research, 43, 635–651.
17. Keesing, J.K., Halford, A.R. Field measurement of survival rates of juvenile *Acanthaster planci*: Techniques and preliminary results. 1992b. Marine Ecology Progress Series, 85, 107–114.
18. Keesing, J.K., Wiedermeyer, W.L., Okaji, K., Halford, A.R., Hall, K.C., Cartwright, C.M. Mortality rates of juvenile starfish *Acanthaster planci* and *Nardoa* spp. measured on the Great Barrier Reef, Australia and in Okinawa, Japan. 1996. Oceanologica Acta, 19, 441–448.
19. Ayukai, T. Ingestion of ultraplankton by the planktonic larvae of the crown-of-thorns starfish *Acanthaster planci*. 1994. Biological Bulletin 186, 90–100.
20. Okaji, K., Ayukai, T., Lucas, J. Selective feeding by larvae of the crown-of-thorns starfish, *Acanthaster planci* (L.). 1997a. Coral Reefs, 16, 47–50.
21. Okaji, K, Ayukai, T., Lucas, J., Are *Acanthaster planci* larvae food limited in the Great Barrier Reef waters. 1997b. In: Proceedings of the 8th International Coral Reef Symposium, Panama, 1996.
22. Cowan, Z.L., Dworjanyn, S.A., Caballes, C.F., Pratchett, M.S. Predation on crown-of-thorns starfish larvae by damselfishes. 2016. Coral Reefs, 35(4), 1253-1262.
23. Birkeland, C. Acanthaster in the cultures of high islands. 1981. Atoll Research Bulletin 255, 55-8.
24. Birkeland, C. Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). 1982. Marine Biology, 69, 175–185.
25. Brodie, J.E., Devlin, M., Haynes, D., Waterhouse, J. Assessment of the eutrophication status of the Great Barrier Reef lagoon (Australia). 2011. Biogeochemistry, 106 (2), 281-302.
26. Mellin, C., Lugrin, C., Okaji, K., Francis, D.S., Uthicke, S. Selective feeding and microalgal consumption rates by Crown-of-Thorns Seastar (Acanthaster cf. solaris) larvae. 2016. Preprints 2016, 2016110124 (doi: 10.20944/preprints201611.0124.v1).
27. Henderson, J.A., Lucas, J.S. Larval development and metamorphosis of *Acanthaster planci* (Asteroidea). 1971. Nature 232, 655–657.
28. Lucas, J.S. Reproductive and larval biology of *Acanthaster planci* (L.) in Great Barrier Reef waters. 1973. Micronesica 9, 197–203.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 7 December 2016 doi:10.20944/preprints201612.0041.v1

Peer-reviewed version available at *Diversity* **2017**, *9*, 17; doi:10.3390/d9010017

29. Lucas, J.S. Growth, maturation and effects of diet in *Acanthaster planci* (L.)(Asteroidea) and hybrids reared in the laboratory. 1984. Journal of Experimental Marine Biology and Ecology, 79, 129–147.
30. Olson, R. R. In situ culturing as a test of the larval starvation hypothesis for the crown-of -thorns starfish, *Acanthaster planci.* 1987. Limnology and Oceanography 32, 895-904.
31. Olson, R. R., Olson, M. H. Food limitation of planktotrophic marine invertebrate larvae: does it control recruitment success?. 1989. Annual Review of Ecology and Systematics, 20, 225–247.
32. Ayukai, T., Okaji, K., Lucas, J.S. Food limitation in the growth and development of crown-of-thorns starfish in the Great Barrier Reef. 1997. In: Proceedings of the 8th International Coral Reef Symposium, Panama, 1996. pp. 621–626.
33. Fabricius, K.E. Factors determining the resilience of coral reefs to eutrophication: a review and conceptual model. 2011. In: Dubinski Z, Stambler N (eds) Coral Reefs: An Ecosystem in Transition. Springer, New York, pp 493–509
34. Uthicke, S., Logan, M., Liddy, M., Francis, D., Hardy, N., Lamare, M. Climate change as an unexpected co-factor promoting coral eating seastar (*Acanthaster planci*) outbreaks. 2015a. Scientific Reports, 5.
35. Wolfe, K., Graba-Landry, A., Dworjanyn, S.A., Byrne, M. Larval starvation to satiation: Influence of nutrient regime on the success of *Acanthaster planci.* 2015a. PloS one, 10(3), p.e0122010.
36. Pratchett, M.S., Dworjanyn, S., Mos, B., Caballes, C.F., Thompson, C.A. Blowes, S. Larval Survivorship and Settlement of Crown-of-Thorns Starfish (*Acanthaster cf. solaris*) at Varying Chlorophyll Concentrations. 2016. Preprints (www.preprints.org) doi:10.20944/preprints201611.0074.v1
37. Wolfe, K., Graba-Landry, A., Dworjanyn, S.A., Byrne, M. Larval phenotypic plasticity in the boom-and-bust crown-of-thorns seastar, *Acanthaster planci*. 2015b. Marine Ecology Progress Series, 539, 179-189.
38. Brodie, J., De'ath, G., Devlin, M., Furnas, M., Wright, M. Spatial and temporal patterns of near-surface chlorophyll a in the Great Barrier Reef lagoon. 2007. Marine and Freshwater Research, 58 (4), 342-353.
39. Devlin, M.J., Brodie, J. Terrestrial discharge into the Great Barrier Reef Lagoon: Nutrient behaviour in coastal waters. 2005. Marine Pollution Bulletin, 51 (1-4), 9-22.
40. Devlin, M., Schaffelke, B. Spatial extent of riverine flood plumes and exposure of marine ecosystems in the Tully coastal region, Great Barrier Reef. 2009. Marine and Freshwater Research, 60(11), 1109-1122.
41. Devlin, M.J., Da Silva, E.T., Petus, C., Wenger, A., Zeh, D., Tracey, D., Álvarez-Romero, J.G., Brodie, J. Combining in-situ water quality and remotely sensed data across spatial and temporal scales to measure variability in wet season chlorophyll-a: Great Barrier Reef lagoon (Queensland, Australia). 2013. Ecological Processes, 2(1), 1-22.
42. Schroeder, T., Devlin, M.J., Brando, V.E., Dekker, A.G., Brodie, J.E., Clementson, L.A., McKinna, L. Inter-annual variability of wet season freshwater plume extent into the Great Barrier Reef lagoon based on satellite coastal ocean colour observations. 2012. Marine Pollution Bulletin, 65 (4-9), 210-223.
43. Wooldridge, S., Brodie, J. Environmental triggers for primary outbreaks of crown-of-thorns starfish on the Great Barrier Reef, Australia. 2015. Marine Pollution Bulletin 101, 805 – 815.
44. De'ath, G., Fabricius, K.E., Sweatman, H., Puotinen, M. The 27-year decline of coral cover on the Great Barrier Reef and its causes. 2012. Proceedings National Academy Science U. S. A. 109 (44), 17734e17735. http://dx.doi.org/10.1073/pnas.1208909109.
45. Walbran, P.D. Henderson, R.A. Faithful, J.W. Polach, H.A. Sparks, R.J. Wallace, G. Lowe, D.C. Crown of thorns starfish outbreaks on the Great Barrier Reef: a geological perspective based upon the geological record. 1989. Coral Reefs, 8, 67-78.
46. Hock, K., Wolff, N.H., Condie, S.A., Anthony, K., Mumby, P.J. Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. 2014. Journal of Applied Ecology, 51(5), 1188-1196.
47. Uthicke, S., Doyle, J., Duggan, S., Yasuda, N., McKinnon, A.D. Outbreak of coral-eating Crown-of-Thorns creates continuous cloud of larvae over 320 km of the Great Barrier Reef. 2015b. Scientific Reports, 5.
48. Miller, I., Sweatman, H., Cheal, A., Emslie, M., Johns, K., Jonker, M., Osborne, K. Origins and implications of a primary crown-of-thorns starfish outbreak in the southern Great Barrier Reef. 2015. Journal of Marine Biology, 2015.
49. Roche, R.C., Pratchett, M.S., Carr, P., Turner, J.R., Wagner, D., Head, C., Sheppard, C.R.C. Localized outbreaks of *Acanthaster planci* at an isolated and unpopulated reef atoll in the Chagos Archipelago. 2015. Marine Biology, 162(8), 1695-1704.

50. Houk, P., Raubani, J. *Acanthaster planci* outbreaks in Vanuatu coincide with ocean productivity, furthering trends throughout the Pacific Ocean. 2010. Journal of Oceanography, 66, 435–438.
51. Houk, P., Bograd, S., van Woesik, R. The transition zone chlorophyll front can trigger *Acanthaster planci* outbreaks in the Pacific Ocean: Historical confirmation. 2007. Journal of Oceanography, 63, 149–154.
52. Weeks, S., Bakun, A., Steinberg, C., Brinkman, R., Hoegh-Guldberg, O. The Capricorn Eddy: A prominent driver of the ecology and future of the southern Great Barrier Reef. 2010. Coral Reefs 29, 975–985.
53. Mao, Y., Luick, J.L. Circulation in the southern Great Barrier Reef studied through an integration of multiple remote sensing and in situ measurements. 2014. Journal of Geophysical Research: Oceans, 119(3), 1621-1643.
54. Condie, S., Condie, R., Retention of plankton within ocean eddies. 2016. Global Ecology and Biogeography, 25(10), 1264-1277.
55. Weeks, S.J., Magno-Canto, M.M., Jaine, F.R.A., Brodie, J., Richardson, A.J. Unique sequence of events triggers manta ray feeding frenzy in the southern Great Barrier Reef, Australia. 2015. Remote Sensing 7, 3138-3152. doi:10.3390/rs70303138
56. Alongi, D.M., Patten, N.L., McKinnon, D., Köstner, N., Bourne, D.G., Brinkman, R. Phytoplankton, bacterioplankton and virioplankton structure and function across the southern Great Barrier Reef shelf. 2015. Journal of Marine Systems, 142, 25-39.
57. Da Silva, E.T., Devlin, M., Wenger, A., Petus, C. Burnett-Mary Wet Season 2012–2013: Water Quality Data Sampling, Analysis and Comparison against Wet Season 2010–2011 Data. 2013. Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER) Publication, James Cook University, Townsville, 31pp.
58. Brodie, J.E., Mitchell, A.W. Nutrient composition of the January (1991) Fitzroy River flood plume. 1992. In: Byron, G.T. (Ed.), Workshop on the Impacts of Flooding. GBRMPA Workshop Series No. 17, Great Barrier Reef Marine Park Authority, Townsville, Australia, pp. 56–74.
59. Kroon, F.J., Kuhnert, P.M., Henderson, B.L., Wilkinson, S.N., Kinsey-Henderson, A., Abbott, B., Brodie, J.E., Turner, R.D.R. River loads of suspended solids, nitrogen, phosphorus and herbicides delivered to the Great Barrier Reef lagoon. 2012. Marine Pollution Bulletin, 65 (4-9), 167-181.
60. Waterhouse, J., Brodie, J., Lewis, S., Mitchell, A. Quantifying the sources of pollutants in the Great Barrier Reef catchments and the relative risk to reef ecosystems. 2012. Marine Pollution Bulletin, 65 (4-9), 394-406.
61. Furnas, M., Mitchell, A., Skuza, M., Brodie, J. In the other 90%: Phytoplankton responses to enhanced nutrient availability in the Great Barrier Reef Lagoon. 2005. Marine Pollution Bulletin, 51 (1-4), 253-265.
62. Devlin, M.J., McKinna, L.W., Álvarez-Romero, J.G., Petus, C., Abott, B., Harkness, P., Brodie, J. Mapping the pollutants in surface riverine flood plume waters in the Great Barrier Reef, Australia. 2012. Marine Pollution Bulletin, 65 (4-9), 224-235.
63. Álvarez-Romero, J.G., Devlin, M., Teixeira da Silva, E., Petus, C., Ban, N.C., Pressey, R.L., Kool, J., Roberts, J.J., Cerdeira-Estrada, S., Wenger, A.S., Brodie, J. A novel approach to model exposure of coastal-marine ecosystems to riverine flood plumes based on remote sensing techniques. 2013. Journal of Environmental Management, 119, 194-207.
64. Blondeau-Patissier, D., Schroeder, T., Brando, V.E., Maier, S.W., Dekker, A.G., Phinn, S. ESA-MERIS 10-year mission reveals contrasting phytoplankton bloom dynamics in two tropical regions of Northern Australia. 2014. Remote Sensing, 6(4), 2963-2988.
65. Devlin, M., Petus, C., da Silva, E., Tracey, D., Wolff, N., Waterhouse, J., Brodie, J. 2015. Water quality and river plume monitoring in the Great Barrier Reef: an overview of methods based on ocean colour satellite data. Remote Sensing, 7, 12909-12941. doi:10.3390/rs71012909
66. Devlin, M., Waterhouse, J., Taylor, J., Brodie, J. Flood plumes in the Great Barrier Reef: spatial and temporal patterns in composition and distribution. 2001. GBRMPA Research Publication No. 68, Great Barrier Reef Marine Park Authority, Townsville, Australia.
67. Bainbridge, Z.T. Wolanski, E. Álvarez-Romero, J.G. Lewis, S.E. Brodie, J.E. Fine sediment and nutrient dynamics related to particle size and floc formation in a Burdekin River flood plume, Australia. 2012. Marine Pollution Bulletin, 65, 236-248.