



Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence

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Abstract

The cause(s) of primary outbreaks of the coral-eating crown-of-thorns starfish (*Acanthaster planci*) are still subject to scientific controversy. The possibility of primary outbreaks being linked to terrestrial runoff has been postulated a number of times, suggesting that enhanced nutrient supply is critical for enhanced *A. planci* larval development. This paper examines the evidence for such a cause, focussing particularly on the Great Barrier Reef (GBR). Nutrient discharges from rivers have increased at least four-fold in the central GBR over the last century, and concentrations of large phyto-plankton (>2 µm) of the inshore central GBR shelf in the wet season when *A. planci* larvae develop, is double that of other places and times. Larval development, growth and survival increase almost ten-fold with doubled concentrations of large phyto-plankton. This and other lines of evidence suggest that frequent *A. planci* outbreaks on the GBR may indeed be a result of increased nutrient delivery from the land.

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1. Introduction

Coral-eating crown-of-thorns starfish (*Acanthaster planci*) have caused widespread damage to many coral reefs in the Indo-Pacific over the past four decades (Birkeland and Lucas, 1990). On the Great Barrier Reef a third observed outbreak cycle is now in progress. The cycles have occurred from 1962 to 1976, 1979 to 1991 and 1993 to present. Each cycle appears to have begun in an area off Cairns between 16° and 17°S, the first outbreak being 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) (Fig. 1). Outbreaks may have occurred before 1962 but were not observed or reported.

The cause (or causes) of the outbreaks has been a controversial issue (Engelhardt and Lassig, 1997) and there are two opposing views as to the origin of the outbreaks. The first one, proposed by Vine (1973) and partially by Potts (1981), postulates that population outbreaks are a 'natural phenomenon'. It is based on the inherently unstable population sizes of highly fecund organisms such as *A. planci*, which can produce >10⁶ fertilised eggs annually per mature female under good conditions (Mundy et al., 1994). Natural fluctuations in temperature, salinity or food for the planktonic larvae could all increase larval survival. Examination of *A. planci* spines in sediment cores has been used to suggest

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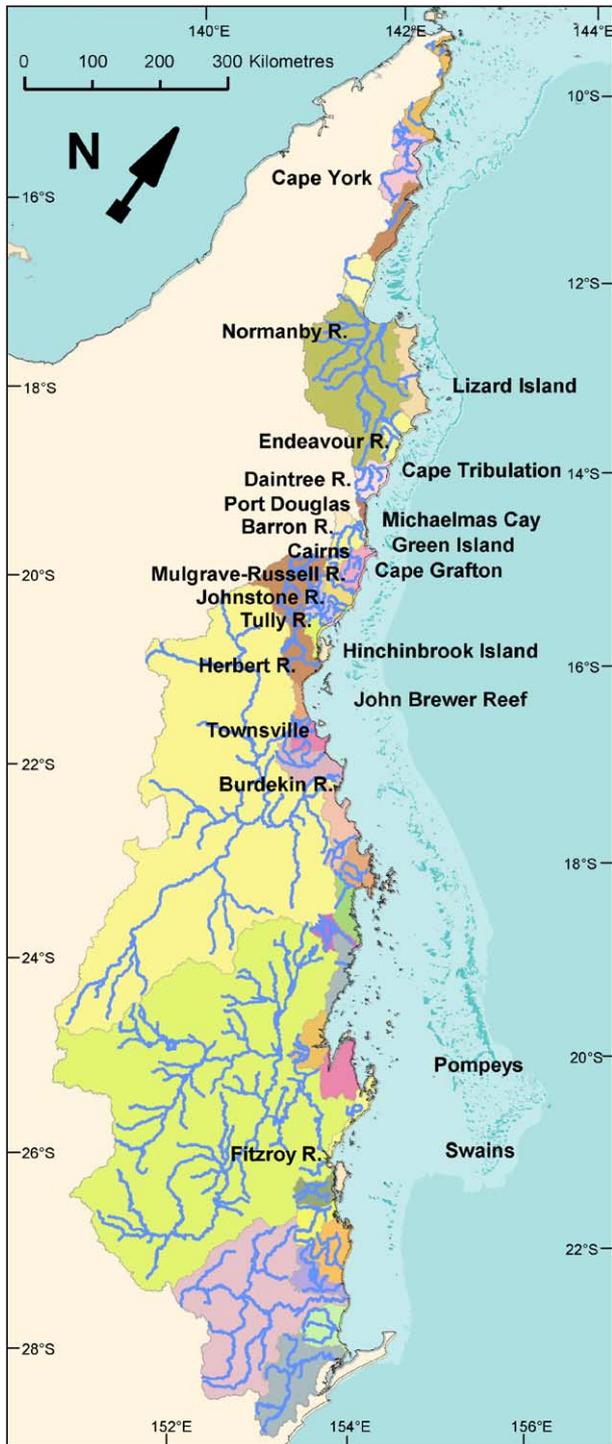


Fig. 1. Great Barrier Reef and catchment locations.

that considerable populations of the starfish may have existed on Green Island and John Brewer Reef over many thousands of years (Walbran et al., 1989a; Walbran et al., 1989b), however the assumptions of that work have been challenged, due to a number of difficulties in using sedimentary records to estimate outbreak frequencies (Keesing et al., 1992). Fabricius and Fabricius (1992) showed that the sclerite peaks interpreted

as signs of "earlier outbreaks" disappeared when data were standardised by sediment age, whereas the recent outbreak peaks remained. Feeding scars on massive corals by *A. planci* have also been used to provide historic records of outbreak frequencies, and such scars appear to have substantially increased in frequency within the last half century compared to earlier decades (Devantier and Done, in press). Other data also raise doubts whether present frequencies and intensities of outbreaks could have been sustained over long periods of time throughout the history of coral reefs. In particular, full recovery of reef areas other than fore-reef crests takes several decades (centuries to replace large and old massive colonies), and the present outbreak interval on the GBR of 15 years does not allow full recovery between outbreaks. Therefore the possibility that outbreaks are occurring far more frequently in recent times and that this is caused by anthropogenic activity cannot be discounted.

The second view states that outbreaks are due to anthropogenic changes to the environment of the starfish, naming various possible anthropogenic causal hypotheses, including: removal of adult predators (particularly fish and gastropods) (Endean, 1977); changes to population structures of predators on larval and juvenile stages, caused by pesticide pollution (Randall, 1972); destruction of larval predators, particularly corals, by construction activities on reefs (Chesher, 1969); and larval food supply (phyto-plankton) enhancement from nutrient enriched terrestrial run-off (Birkeland, 1982; Lucas, 1982; Brodie, 1992).

The 'predator removal' hypothesis is based on the assumption that the starfish population is largely controlled by predation, and thus the number of starfish to survive to maturity would increase in response to the commercial exploitation of predatory fish. While large starfish appear to escape predation due to their poisonous spines and large size, predation pressure on small crown-of-thorns could be high. The cryptic behaviour of small starfish during the day indicates avoidance of visually searching predators during the day, i.e., fish. However, the only known commercially exploited natural predator of *A. planci* is the giant triton snail (*Charonia tritonis*). The stars and stripes pufferfish (*Arothron hispidus*), humphead maori wrasse (*Cheilinus undulatus*) and titan triggerfish (*Balistoides viridescens*) have all been suggested as predators but neither *A. hispidus* or *B. viridescens* are exploited commercially or for pleasure on the GBR. Evidence that *C. undulatus* is a significant natural predator is weak. The most extensive study of the diet of this species on the GBR found no COTS eaten on a number of reefs with COTS outbreaks (Sweatman, 1995). All of the proposed predators occur at low abundances at present. Other more abundant fish such as emperors (Lethrinidae) and snappers (Lutjanidae) may have also contributed to predation on juvenile

starfish (Ormond et al., 1990), although these fish take juvenile *A. planci* only reluctantly and often reject them (Sweatman, 1995). As mortality is ca. 99% in the first year of the starfish after settlement (Zann et al., 1987; Keesing and Halford, 1992), it is likely that a wide range of small invertebrates living in coral rubble also eat juvenile starfish. If some small, as yet unidentified invertebrate species were responsible for controlling starfish numbers, they would need to be widely distributed, and potentially would have to have undergone a global decline in numbers to account for the presently observed outbreaks. The framework of every coral reef is riddled with numerous species of small crabs and shrimp—all omnivores or carnivores and it is inconceivable that all these species or one critical species have suddenly declined in numbers. Therefore, existing data do not support the hypothesis that predation on juveniles by large fish or invertebrate predators can fully explain the population dynamics of *A. planci*.

Lucas (1982) suggested that the critical stage of the life cycle at which large changes in adult population could be initiated was the larval stage, forming the *larval survival hypothesis*. The possibility of outbreaks being linked to terrestrially derived pollutants was postulated a number of times. Pearson and Endean (1969) noted that the reefs damaged in the initial outbreaks north of Cairns in the early 1960s were also those parts of the main reef body that lie closest to the Australian mainland and were therefore most likely to be affected by river runoff. These ideas were combined with the work of Henderson (1969) and Lucas (1972, 1973, 1975) that low salinities and high temperatures enhanced larval survival and growth. Pearson (1975) also reported reduced salinities near the coast between Ingham and Mossman in summer, coincident with the period suggested as the breeding period for *A. planci*. Another larval and/or juvenile survival hypothesis invoked the widespread presence of pesticide residues (particularly DDT and dieldrin) in marine ecosystems as a factor in reducing predation on *A. planci* larvae or juveniles (Fisher, 1969; Randall, 1972). While considerable flux of persistent pesticides to the oceans occurs via atmospheric transport, river runoff is also a route especially in coastal areas. Outbreak populations would therefore be expected to be most common in areas where rivers, flowing through agricultural areas, discharge directly into waters containing reefal systems.

The most developed of the larval survival hypotheses linking terrestrial runoff with planktonic survival is the *terrestrial runoff hypothesis* by Birkeland (1982) which suggests that enhanced nutrient supply in river runoff is critical for enhanced *A. planci* larval survival. Tsuda (1971) and Pearson (1975) noted that most outbreaks occurred on reefs near high islands or continental edges. Birkeland (1981) also noted that indigenous people from high islands in the Pacific had specific names for *A.*

planci while those from the atoll islands did not, using a general name for 'starfish' to describe the animal. His explanation was that *A. planci* outbreaks only occur on high islands, thus becoming conspicuous enough to warrant a local 'specific' name (Birkeland, 1987). On atolls, while the starfish occurred in low numbers, it did not form outbreak populations. Birkeland (1982) demonstrated that starfish outbreaks tend to occur 2–3 years after periods of high (especially drought-breaking) rainfall around high continental land masses but not around low coral atolls. The two years delay was explained by its development period into a visible, mature starfish. The spatial pattern was explained by the fact that nutrients and sediments only run off high continental land masses, but not off low-lying coral atolls free of rivers and deep soils. The elevated nutrient levels discharged from the land then caused phyto-plankton blooms in coastal waters during the starfish larval period. Unusually high survival of the larvae ensued, whereas under 'normal' conditions most larvae starved. This terrestrial runoff hypothesis is linked to the scenario proposed by Lucas (1982) that *A. planci* suffers high levels of larval starvation in the absence of phyto-plankton blooms or in the 'normal' phyto-plankton concentrations found in oceanic waters. One source of phyto-plankton blooms may be river runoff, although a number of other possible causes also exist (e.g. upwellings and sediment resuspension during storms, see Furnas and Mitchell, 1986; Furnas, 1989).

Flood plumes modify not only water column nutrients but also salinity, a factor that also affects the survival of *A. planci* larvae. Larval survival is optimal at 30 ppt salinity and 28°C water temperature (Lucas, 1973, 1975). Salinities of 30 ppt only occur on the north Queensland coast during periods of terrestrial runoff in the wet season. Lucas found that survival of larvae was enhanced up to threefold at a salinity of 30 ppt, an increase in survival that is, on its own, insufficient to account for the postulated increase in larval survival preceding a primary outbreak. The optimal survival temperature is close to that normally found in North Queensland waters (e.g. 27–31°C in December and January; Walker, 1981) and not normally affected by river runoff in this period (Wolanski and van Senden, 1983; Brodie et al., 1997).

The larval survival hypotheses are generally put forward to explain so called *primary* outbreaks (Endean, 1973) whereas *secondary* outbreaks are seen as the result of massive larval production from a primary outbreak impacting on 'down current' reefs (Kenchington, 1977). In the outbreak episodes on the GBR large populations appeared on individual reefs in a southward progressing wave over a period of approximately 15 years for the first episode over 12 years for the second and now at least 10 years for the third. Such progressive secondary outbreaks have been explained by hydrodynamic

modelling of larval transport (Dight et al., 1990a; Dight et al., 1990b). The waves, separated by ca. 15 years, are generally explained by the ability of coral to recover after outbreaks to a stage able to provide food for another outbreak. Various predator (fish) removal hypotheses (McCallum, 1987; Ormond et al., 1990) also lead to waves of *A. planci* outbreaks (Bradbury and Seymour, 1997).

For the terrestrial runoff hypotheses to explain the frequent outbreaks in recent times, a mechanism for increased nutrient loads in river runoff in the last 100 years is required. The obvious mechanisms are increased nutrients from fertilisers and sewage discharge combined with increased soil erosion and river sediment load (with its nutrient content) from deforestation and agricultural usage. These mechanisms operate throughout the Indo-Pacific, not least on the northeastern Australian coast (Brodie et al., 2001a; Brodie, 2002). A number of recent studies have verified the elevated nutrient concentration and loads in north Queensland rivers (Bramley and Roth, 2002; Mitchell et al., 1997; Furnas and Mitchell, 2001; Mitchell et al., 2001; Hunter et al., 1996; Hunter, 1997; Mitchell et al., 1996; Furnas, 2003). Estimates of the change in nutrient loads from the pre-development period to the present for GBR Catchment Area rivers have been made in a number of studies. The increase for rivers with substantially developed catchments is of the order of three to six times for both N and P (Furnas, 2003; Brodie et al., 2003). The increases are greatest in rivers to the south of Port Douglas (Fig. 1) where catchment development has been most intense, compared to rivers to the north on Cape York where development is minimal. Brodie (1992) and Engelhardt and Lassig (1997) reviewed the potential links between crown-of-thorns outbreaks on the GBR and increased terrestrial runoff of nutrients. Recent work by Day (2000) has also suggested a potential link between Burdekin River discharge patterns and the patterns of starfish outbreaks in the central GBR.

There are few suitable evidential systems to draw conclusions about a complex ecological hypothesis such as that linking terrestrial nutrient runoff to crown of thorns outbreaks. Fabricius and De'ath (2004) have recently devised a method based on epidemiological models, that were previously used to link cancer to smoking, to draw conclusions about the general issue of terrestrial runoff and impacts on ecosystems of the GBR. We also use this method to analyse the evidence for increased nutrient runoff causing increased frequency of crown of thorns outbreaks. To explain the evidence for the individual links in the complete chain of evidence, we pose a series of questions that relate to each link and then present the case to confirm the link. In a companion paper a model using the results from the evidential chain show that the observed frequency and pattern of crown of thorns outbreaks in the GBR can be explained using nutrient

enrichment data from a chlorophyll monitoring program (De'ath et al., unpublished data).

2. Evidence for each causal link

(1) *Are higher loads of nutrients (N and P), particularly completely bioavailable nutrients such as nitrate, ammonia and phosphate, being discharged from GBR rivers now than pre-1900?*

Yes.

On a global scale, riverine fluxes of nutrients to the oceans have increased markedly this century (Smith et al., 2003). Anthropogenic fluxes of nitrogen and phosphorus are now considered to be at least comparable to, and probably significantly greater than, natural fluxes (Vitousek et al., 1997). For the GBR, input of nutrients from farming comes from a large number of rivers that flow into the GBR lagoon. These range in size from the two large systems, the Burdekin and Fitzroy, to about twenty medium sized coastal rivers e.g. the Proserpine and Herbert, to a large number of coastal streams. The annual runoff of freshwater from the GBR Catchment carries eroded soils and nutrients (both from natural soils and agricultural fertilisers) into the GBR. This runoff also carries a variety of agricultural and industrial chemicals. The first estimates of sediment runoff to the reef (e.g. Belperio, 1983) were based upon estimates of the volume of terrigenous sediment along the coast over the last 5000 years. Since then, improved estimates have been made using a variety of flow/export relationships derived from a number of rivers (Neil and Yu, 1996; Furnas et al., 1995; Furnas, 2003). Models that extrapolate measured soil erosion and nutrient loss rates from paddocks and catchments indicate that land-sourced inputs of sediment and nutrients to the GBRWHA have increased several-fold since the commencement of European land use practices in the mid-19th century (Moss et al., 1992; Neil and Yu, 1996; Prosser et al., 2001; Brodie et al., 2003). It is now estimated that rivers transport an average of 16 million tonnes of sediment, 63,000 tonnes of nitrogen and 11,000 tonnes of phosphorus each year into the GBRWHA (Brodie et al., 2003). The best available estimates of pre-1850 sediment and nutrient runoff indicate that mean suspended sediment exports have increased 8-fold (2 million tonnes per year (Mt/y) to 16Mt/y), total nitrogen exports have increased ca. 4-fold (14,500t/y to 63,000t/y) and total phosphorus has increased 6-fold (1800t/y to 11,000t/y) relative to current runoff (Brodie et al., 2003).

River discharge during early summer flood events from catchments with significant cropping area is characterised by dissolved inorganic nitrogen (nitrate and ammonia) concentrations up to 30 times concentrations occurring in rivers with undeveloped catchments (140–

1400 $\mu\text{gN l}^{-1}$ compared to 14–70 $\mu\text{gN l}^{-1}$) (Brodie, 2002). In rivers where the upper catchment is undeveloped or lightly developed, flood waters from pristine or relatively undisturbed parts of the catchment typically have lower concentrations of dissolved inorganic nutrients (e.g. 14–140 $\mu\text{gN l}^{-1}$). The same waters, after passing through the cropping-dominated lower catchment and floodplain, have higher concentrations of dissolved inorganic nutrients, particularly of nitrogen (e.g. 140–1400 $\mu\text{gN l}^{-1}$). Furnas (2003) presents data which allows comparison of the Normanby River on Cape York (Fig. 1), with low intensity grazing (about two animals per km^2), with the Burdekin River, with moderate to high intensity rangeland grazing (about 10 animals per km^2) and the Tully River, with a substantial area of fertilised cropping (sugarcane and bananas). Median and mean concentrations in the rivers show the elevation of nitrate in the rivers with more intensive grazing regimes, i.e. more cattle per ha or fertilised cropping (median and mean nitrate concentrations near 150 $\mu\text{gN l}^{-1}$) compared to the Normanby (median and mean 10 $\mu\text{gN l}^{-1}$).

(2) *Are there increased concentrations of nutrients (and/or nutrient indicators) compared with pre-1900 on the Wet Tropics shelf especially in periods during November–February?*

Yes, probably.

Rivers draining into the GBR have highly variable flow regimes, both between and within years. Discharge of both water and sediment is dominated by large flood events associated with tropical cyclones and monsoonal rainfall (Mitchell and Furnas, 1997; Furnas and Mitchell, 2001).

The areal extent of direct river discharge influence in the GBR has been quantified through mapping of flood plumes (Devlin et al., 2001; Devlin et al., 2002), water quality monitoring in coastal waters (Devlin et al., 2001), benthic sediment analysis (Lembeck and Woolfe, 2000), measurements of terrestrial marker chemicals in corals (McCulloch et al., 2003; Lough et al., 2002) and sediment cores (Walker and Brunskill, 1997) and hydrodynamic modelling (King et al., 2001). Direct terrestrial influence is largely restricted to the inner shelf. Some inner shelf systems, particularly those bordering the Wet Tropics region of the central GBR, experience runoff events on an annual basis. Significant runoff events occur less frequently in southern GBR rivers, with major events occurring on a decadal basis. Mid and outer shelf reefs of the central GBR are directly affected by runoff plumes on a far less frequent basis, typically every three to five years, and only in a highly diluted form (Brodie and Furnas, 1996; Devlin et al., 2001). Nutrient concentrations show weak gradients across the shelf, with higher values inshore, in non-flood conditions (Furnas and

Brodie, 1996; Furnas, 2003). There are strong gradients in flood conditions (Devlin et al., 2001). The combined effects of the prevailing southeasterly wind conditions and forces caused by the earth's rotation (Coriolis) cause flood plumes to flow northward from the river mouth for distances of up to 200 km, but usually not more than 20 km from the coast (Devlin et al., 2001). Major floods from large rivers such as the Burdekin may extend northward to Cairns (ca. 450 km) (Wolanski and van Senden, 1983). Plumes from Wet Tropics rivers generally only intersect mid and outer shelf reefs (as distinct from inner-shelf reefs) in the area north of Cape Grafton, off Cairns (Fig. 1), where the reef is close to the coast. Less frequently, Burdekin plumes reach the main reef from Townsville north (Wolanski and van Senden, 1983; King et al., 2001). At Green Island, off Cairns, the recent large expansion of seagrass meadows on reefal areas normally without seagrass is attributed to increased nutrient supply from the mainland (Udy et al., 1999).

The area of the GBR shelf between Cape Grafton and Cape Tribulation (Fig. 1) is unique as it is the only section of the GBR shelf where the middle and outer shelf is exposed to river runoff on a virtually annual basis. Devlin et al. (2001, 2002) showed that river plumes from the Russell–Mulgrave and Johnstone Rivers, steered offshore in their northward movement by Cape Grafton, cover the area of the outer shelf from Green Island north. This occurs due to the combined effects of the proximity of the outer shelf to the land in the Cape Grafton–Cape Tribulation area (<50 km) and the steering effect of Cape Grafton and Cape Kimberley (Ayukai et al., 1997b). In the 10 years between 1991 and 2000 when plumes were studied in this area, plume water impinged into this outer shelf area in most years (Devlin et al., 2001; Devlin et al., 2002). The rivers which discharge into this area, the Johnstone, Russell–Mulgrave, Barron, Mossman–Mowbray and Daintree, all have areas of fertilised cropping on their catchments (19%, 12%, 7%, 12%, and 2%, respectively) (Brodie et al., 2001b). They thus discharge considerable quantities of nutrients and large proportions of the dissolved inorganic nutrient forms, mostly nitrate and orthophosphate (Furnas, 2003; Brodie et al., 2003). Nitrate and orthophosphate are able to be transported large distances in plume water (Devlin and Brodie, 2004) and promote the formation of phyto-plankton blooms completely across the shelf in this area. Thus, the Cape Grafton–Cape Tribulation area is unique in experiencing near annual phyto-plankton blooms across the shelf with chlorophyll concentrations above $2 \mu\text{g l}^{-1}$. Chlorophyll in other areas of the GBR falls in the range 0.2–0.8 $\mu\text{g l}^{-1}$ (Haynes et al., 2001). This area, off and to the north of Cairns, is where all three *A. planici* outbreak waves were first detected (in 1962, 1979, 1993) and were believed to have commenced. It is often called the 'initia-

tion' area for this reason. Birkeland (1982) noted the importance of both water residence time and nutrient supply for the build-up of a phyto-plankton standing crop sufficient to enhance larval survival of *A. planci*. Nutrient concentrations in river plumes from developed catchments can be as much as 50 times higher than ambient seawater concentrations in non-flood periods (Brodie and Furnas, 1996; Devlin et al., 2001), though in most cases, plume nutrient concentrations are about five times non-flood concentrations.

(3) Compared with pre-1900 is there elevated biomass of phyto-plankton (as measured by chlorophyll concentrations) on the Wet Tropics shelf in periods during November–February?

Yes, probably.

Results from GBR-wide chlorophyll monitoring show that inner shelf waters in the Port Douglas to Townsville coastal area, adjacent to catchments with substantial agricultural activity, have higher concentrations (an indicator of nutrient availability) than adjacent offshore waters or coastal waters bordering remote Cape York Peninsula, where there is little land clearing and negligible fertiliser use (Haynes et al., 2001; GBR long-term chlorophyll monitoring program, 2004). Long-term mean chlorophyll values on the central GBR inner-shelf region from a chlorophyll monitoring program are $0.55 \mu\text{g l}^{-1}$ compared to mean values of $0.25 \mu\text{g l}^{-1}$ on Cape York inner, middle and outer shelves and the central GBR middle and outer shelves (Haynes et al., 2001). Regional-scale changes in phyto-plankton biomass (and hence chlorophyll concentrations) occur slowly due to the size of the system. On the middle and outer shelf of the GBR between Townsville and Cairns no upward trend in chlorophyll concentrations was observed in chlorophyll data collected between 1975 and 1996 (Brodie et al., 1997).

In flood plume conditions, chlorophyll concentrations on the Wet Tropics coast shelf are much higher than in the 'ambient' conditions reported above. Samples taken in the plumes of the Tully, Johnstone, Russell–Mulgrave and Barron Rivers during the floods associated with Cyclone Justin (March, 1997) had chlorophyll concentrations in the range 0.2 – $4.6 \mu\text{g l}^{-1}$ with a mean of $1.5 \mu\text{g l}^{-1}$ (Devlin et al., 2001). Maximum values of chlorophyll (in $\mu\text{g l}^{-1}$) measured in flood plumes in the Wet Tropics area with the month recorded include: 2.2 (Cyclone Sadie, February, 1994); 4.6 (Cyclone Violet, March, 1995); 2.0 (Cyclone Ethel, March, 1996); 4.6 (Cyclone Justin, March, 1997); 2.5 (Cyclone Sid, Jan., 1998); 2.2 (Cyclone Rona, February, 1999) (Devlin et al., 2001). It is important to note, however, that these extreme values have probably only coincided with the larval stage of *A. planci* occasionally in the last 10 years, e.g. in Cyclone Joy of December, 1990. However con-

centrations $>0.6 \mu\text{g l}^{-1}$ are more common and have occurred in the inner and middle shelf off Cairns regularly during November to January in the last ten years (GBR long-term chlorophyll monitoring program, 2004).

(4) Is there a higher proportion of larger phyto-plankton (nano- and micro-plankton, $>2 \mu\text{m}$, diatoms and dinoflagellates) compared to smaller phyto-plankton ($<2 \mu\text{m}$, phototrophic picoplankters, *Prochlorococcus*, *Synechococcus*) on the Wet Tropics coast shelf in periods during November to February compared to 'normal' GBR shelf water?

Yes, probably.

Feeding experiments have demonstrated that *A. planci* larvae feed predominantly on phyto-plankton in the $>2 \mu\text{m}$ size class, whereas pico-plankton does not constitute a large part of their diet (Okaji, 1996). Photosynthetic pico-plankton (0.2 to $2 \mu\text{m}$) are the dominant component of phyto-plankton assemblages in tropical waters in normal low nutrient conditions (Stockner and Antia, 1986) and in the GBR (Furnas and Mitchell, 1997). However, as phyto-plankton biomass increases in response to nutrient enrichment from events such as terrestrial runoff and upwelling, the composition of the phyto-plankton also shifts towards larger size classes (Revelante and Gilmartin, 1982; Furnas and Mitchell, 1986; Furnas and Mitchell, 1987; Furnas, 1989; Ayukai, 1992). Beers and Stewart (1969) have shown the importance of nano- and pico-plankton (0.2 – $20 \mu\text{m}$) in the overall phyto-plankton community and that higher populations of micro-plankton (20 – $200 \mu\text{m}$), the 'classical' plankton (Fenchel, 1988), are associated with more nutrient rich conditions, while in oligotrophic waters pico- (0.2 – $2 \mu\text{m}$) and nanoplankters (2 – $20 \mu\text{m}$) predominate. Nutrient depleted areas of the tropical oceans are largely dominated by prochlorophytes, particularly *Prochlorococcus* sp. (Campbell et al., 1994). In slightly more nutrient enriched conditions, such as in coral reef lagoonal environments, picocyanobacteria such as *Synechococcus* sp. increase in abundance (Blanchot and Charpy, 1997). Larger phyto-plankton such as diatoms, dinoflagellates and chlorophytes are also more abundant in nutrient-enriched waters (Higgins and Mackey, 2000) associated with El Nino conditions in the western Equatorial Pacific. Diatoms in shelf waters of the GBR are capable of growth in the range of 2–5 doublings per day compared to rates of <2 doublings per day for microflagellates and pico-plankton (Furnas, 1991) and may preferentially grow in nutrient-enriched conditions. Diatoms are known to show a strong response to nutrient addition in Gulf of Mexico waters off the Mississippi River (Strom and Strom, 1996; Qian et al., 2003). Discharges from the Mississippi and Apalachicola Rivers are the major factors in controlling the spatial distribu-

tion of water-column chlorophyll in northeastern Gulf of Mexico (Lohrenz et al., 1999; Qian et al., 2003). On the GBR shelf, chlorophyll from species $>10\mu\text{m}$ showed the greatest increase in concentration at the front of a flood plume from the Burdekin River (McKinnon and Thorrold, 1993), which would have been associated with a large pulse of nutrient rich water (Devlin et al., 2001). In the GBR, Furnas and Mitchell (1986, 1987) have shown that pico-plankton may comprise 20–100% of the phyto-plankton biomass but that, particularly inshore, diatoms and to a lesser extent dinoflagellates (in the nano- and micro-plankton) are more responsive to nutrient inputs and may increase their relative biomass in periods of nutrient enrichment.

Thus, on the Wet Tropics coast shelf in non-flood plume conditions, pico-plankton, particularly cyanobacteria dominate (Furnas and Mitchell, 1997; Liston et al., 1992; Crosbie and Furnas, 2001). In the wet season under the influence of high nutrient river discharges, a shift to nano-plankton, particularly dinoflagellates and diatoms (in the size class $>2\mu\text{m}$), occurs. Similarly, zoo-plankton biomass is also enhanced in river plume fronts on the GBR shelf (McKinnon and Thorrold, 1993; Thorrold and McKinnon, 1995). A general higher level in phyto-plankton biomass in the Cairns area compared to other parts of the GBR is also observable from chlorophyll monitoring data (Haynes et al., 2001). This appears to be the case for the far southern Swains GBR sector, where outbreaks are chronic as well. Satellite images show high chlorophyll concentrations in the Swains/southern outer shelf GBR, possibly associated with upwelling (Kuchler and Jupp, 1988).

(5) *Does the known planktonic period for A. planci coincide with periods of high biomass of large phytoplankters in the same area on some occasions?*

Yes.

A. planci appears to have a peak spawning period in December (Babcock, 1990; Babcock and Mundy, 1992), although there may also be spawning in November and January. The animals are believed to aggregate at this time (Sloan, 1980) to enhance fertilisation success. For successful recruitment larval cohorts must encounter a suitable settling substratum within their competency period. The settlement competence period begins about 11 days after fertilisation (Birkeland and Lucas, 1990). At 12–22 days after fertilisation the larvae become negatively buoyant and then, when they come into contact with a surface, begin a searching behaviour (Johnson et al., 1991; Okaji, 1996). How long larvae can remain in the plankton, without encountering a surface, and remain competent is not known. *A. planci* is a widely dispersed animal in the Indo-Pacific and genetic differences between geographically separated populations are relatively small (Benzie and Stoddart, 1988; Nishida and

Lucas, 1988). This suggests that larvae are able to recruit over considerable distances and that a relatively long competency period (of more than three weeks) is likely.

Very high chlorophyll concentrations in flood plumes, reflecting high phyto-plankton biomass and increased proportions of nano-plankton, has occurred in the spawning period of *A. planci* (Devlin et al., 2001; Haynes et al., 2001), but not frequently; i.e. this is an irregular coincidence. Even in non-flood conditions, chlorophyll concentrations are higher in summer (say November–April) than winter by a factor of 1.5 (GBR long-term chlorophyll monitoring program, 2004). This factor, along with the higher chlorophyll concentrations in the inner-shelf Cairns area (Haynes et al., 2001), is likely to substantially enhance larval survival in this area.

(6) (a) *Do A. planci larvae survive, grow, and reach competency earlier and in higher numbers in conditions of elevated biomass of large phytoplankters.* (b) *Are A. planci larvae food-limited in ambient GBR shelf phytoplankton conditions?*

(a) Yes. (b) Yes.

A. planci larvae cannot utilise pico-plankton efficiently due to the small size of such plankton (Fenchel, 1988; Okaji et al., 1997a). Plankton found suitable for larval growth ranged in size from 6 to $15\mu\text{m}$ (Lucas, 1982). It is thus possible that food suitable for *A. planci* larvae only becomes available in periods of nutrient-enrichment when nano- and micro-plankton become more common. Chlorophyll-*a* measurements alone do not distinguish the various photosynthetic phyto-plankton size classes and may give a false impression of the food available to the larvae. Furnas and Mitchell's work (1986, 1987) in the GBR has shown that the variability in nano- and micro-plankton biomass is greater than for the pico-plankton.

The links in the hypothesis that larvae were normally 'starved' and that this affected their mortality and/or speed of development were tested in *in situ* culturing experiments (Olson, 1985; Olson, 1987; Olson et al., 1988; Olson and Olson, 1989). Larvae developing in *in situ* flow-through culture chambers were treated with either natural local seawater or sea water enriched with *Dunaliella primolecta*, the phyto-plankton shown by Lucas (1982) to support the highest larval survivorship and development in laboratory rearing. No significant difference in survivorship between the two treatment groups and only a minor decrease in development time for the larvae fed the enriched diet were found. Olson and Olson (1989) therefore concluded that there was no evidence that food limitation of larvae was an important factor controlling recruitment success. However, when this work was repeated with better control over chamber fouling by algae, it became obvious that larvae were unable to meet even half of their basic energy requirements

in ambient concentrations of phyto-plankton (Okaji, 1996; Okaji et al., 1997a; Okaji et al., 1997b; Ayukai et al., 1997a). Larval development rate and survival were near zero in water with the $>2\mu\text{m}$ fraction filtered out, but increased with increasing chlorophyll concentrations when water was enriched with cultured microalgae or nutrients. The proportion of larvae that completed their development was still low at $0.5\mu\text{g l}^{-1}$ chlorophyll, but for every doubling in chlorophyll concentration, the rate of larvae completing development increased nine-fold. For example, at concentrations of 0.8, 0.4 and $0.2\mu\text{g l}^{-1}$, development completion rates were 25%, 3.5% and 0.4% respectively. Typical chlorophyll a concentrations found in ambient GBR shelf waters are in the range $0.1\text{--}0.4\mu\text{g l}^{-1}$, suggesting that larvae are usually food limited.

A number of other food sources for *A. planici* larvae besides nano- and micro-plankton have been suggested, including bacteria and dissolved organic matter (DOM) (Lucas, 1982; Olson, 1987). While it has been shown that DOM can be utilised by echinoderm larvae (Manahan et al., 1983), it is improbable that organisms as large as *A. planici* larvae gain a substantial energy input from this source (Fenchel, 1988). Hoegh-Guldberg (1994) and Ayukai et al. (1996) showed that dissolved free amino acids (an important bioavailable component of DOM), at the concentrations found in GBR shelf waters at the *A. planici* spawning season, cannot play a significant role in larval nutrition. Similarly, Fenchel (1988) concluded that, in general, typical length ratios between prey and predator are 1:10 and are rarely less than 1:100 in the plankton community. It is therefore unlikely that bacteria in the size range $0.2\text{--}2\mu\text{m}$ form an important food source for *A. planici* larvae, which range in size from 200 to $1500\mu\text{m}$ (Birkeland and Lucas, 1990). Examination of the gut contents of *A. planici* larvae in natural and experimental conditions also showed that bacteria and pico-plankton were an unimportant part of the nutritional requirements of the larvae (Ayukai and Hoegh-Guldberg, 1992; Ayukai, 1994; Okaji et al., 1997a).

Thus, growth and survival of *A. planici* larvae is low at $<0.5\mu\text{g l}^{-1}$ and increases with increasing phyto-plankton biomass, and with increasing proportions of nano- and micro-plankton compared to pico-plankton. In contrast, DOM, dissolved free amino acids and bacteria are not significant sources of nutrition.

(7) Are chlorophyll concentrations in the GBR normally (a) $<0.5\mu\text{g l}^{-1}$, but (b) $>0.5\mu\text{g l}^{-1}$ on the shelf between Hinchinbrook Island and Cape Tribulation (Wet Tropics coast) in the November–February period regularly?

(a) Yes

(b) Yes

Median chlorophyll concentrations have been calculated for large sections of the GBR from a long-term mon-

itoring program (Haynes et al., 2001; GBR long-term chlorophyll monitoring program, 2004). The areas chosen for comparison are inshore ($<25\text{km}$ from coast) versus offshore and northern (north of Port Douglas), central (between Port Douglas and Townsville) and southern (south of Townsville) giving six regions (Fig. 1). Chlorophyll concentrations typically range from 0.1 to $0.3\mu\text{g l}^{-1}$ for offshore northern, central and southern GBR, $0.2\mu\text{g l}^{-1}$ for northern inshore and $0.3\text{--}0.7\mu\text{g l}^{-1}$ for central and southern inshore. Unusual values are found in the Shoalwater Bay and Torres Strait regions due to persistent strong tidal currents driving resuspension and nutrient cycling between the sediment and the water column (Brodie and Furnas, 1996; Furnas and Brodie, 1996; Brodie et al., 1997). Chlorophyll concentrations in summer (November–May) are approximately 1.6 times those in winter. Overall, chlorophyll is $>0.5\mu\text{g l}^{-1}$ in summer on the Wet Tropics shelf but more generally $<0.5\mu\text{g l}^{-1}$ in most other conditions in the GBR. The higher concentrations on the Wet Tropics shelf cannot be explained by a higher sediment resuspension probability (e.g., due to strong tidal flow, windy conditions or particularly shallow sea floor), and therefore appear to be a result of recent anthropogenic nutrient inputs to this region.

Some forms of phyto-plankton, specifically *Trichodesmium* spp., diatoms and dinoflagellates have increased in concentration near Low Isles (off Port Douglas) in the period 1928–1992 (Bell et al., 1999). Measurements in the period 1992/1993 compared those taken in the 1928/1929 Great Barrier Reef Expedition (Marshall, 1933) showed a large increase in *Trichodesmium* abundance (Bell et al., 1999). Similar large increases between 1928/29 and 1992/1993 were shown for diatoms and dinoflagellates (Bell and Elmetri, 1995).

(8) Are there good records of flood events being followed by *A. planici* outbreaks in the Wet Tropics area ca. 3 years later?

Some

The 1962 and 1979 outbreaks of *A. planici* in the GBR occurred 3–5 years after major floods of the large Burdekin River (Day, 2000), and this is also true for the 1993 outbreak that followed a major Burdekin flood from cyclone Joy in December 1990. This correlation agrees with the observations of flood-related outbreak occurrences in other parts of the Indo-Pacific (Birkeland, 1982). It can however not be concluded that Burdekin floods on their own are responsible for triggering *A. planici* outbreaks, since floods of Wet Tropical rivers often co-occur with floods of the Burdekin River. It is therefore possible that a large flood plume of the Burdekin, travelling past the Wet Tropics towards Cairns, is joined (and enriched) by the smaller, but less diluted flood plumes from the Wet Tropics Rivers. In addition, areas of the northern Wet Tropics coast experience flood

plumes every year (Devlin et al., 2001) and this produces a situation of annual phyto-plankton blooms in this area with occasional (at intervals of a few years) additional inputs from the Burdekin River. The signal connecting *A. planci* outbreaks to specific river discharge is likely to be complex.

(9) *Is there evidence of 'chronic' A. planci outbreaks in conditions of chronic nutrient loading?*

Yes.

A number of reefal areas in the Indo-Pacific now appear to be chronically infested with *A. planci*. The best documented of these are the Suva area, Fiji (Zann et al., 1987; Zann et al., 1990) and islands in the Ryukyus, Japan (Muzik, 1985; Nishihira and Yamazato, 1974; Nishihira, 1987). Heavy terrestrial runoff occurs in both cases (Nishihira, 1987; Naidu et al., 1991). While there could be a connection between runoff and chronic *A. planci* outbreaks, the reefs in question are also subject to a number of other stresses, such as overfishing, destructive fishing and coral destruction from construction and dredging.

Naturally high chlorophyll concentrations are found in the Southern GBR (in particular, the Pompeys and Swains) (Fig. 1), due to differences in water column productivity related to latitude, upwelling and strong tidal currents. This area is characterised by chronic *A. planci* outbreaks (Sweatman et al., 2000). The chlorophyll levels on these Southern offshore areas of the GBR are likely to be little altered by human activities. Nevertheless, this observation contributes weight to the link between high chlorophyll levels and *A. planci* outbreaks.

3. Conclusions

Overall, each of the links in the evidential chain has been clearly established. The case can be summarised:

1. Greatly increased nutrient discharge, and specifically dissolved inorganic nutrient discharge, has occurred from north Queensland rivers associated with agricultural development on the catchments.
2. The rivers, with their nutrient load, discharge into the Wet Tropics section of the GBR lagoon on an annual basis in periods of monsoon and cyclone driven floods.
3. The river discharge spreads completely across the shelf in the section between Cape Grafton and Cape Tribulation.
4. The elevated nutrient content of the river discharges causes phyto-plankton blooms in the period of plumes with chlorophyll concentrations above $2\mu\text{g l}^{-1}$ and throughout the rest of the year with chlorophyll concentrations often above $0.5\mu\text{g l}^{-1}$.
5. The increased above-natural discharge also shifts phyto-plankton species composition from a natural dominance by pico-plankton to a situation with a greater proportion of nano- and micro-plankton.
6. On occasions, nutrient enrichment driven phyto-plankton blooms will coincide in the 'initiation' area with *A. planci* spawning.
7. On these occasions, *A. planci* larval survival will be strongly enhanced with increasing phyto-plankton biomass and a substantial proportion of nano- and micro-plankton. In conditions of chlorophyll $<0.5\mu\text{g l}^{-1}$ and a predominance of pico-plankton, most *A. planci* larvae starve.
8. With high larval survivorship, recruitment to the benthos is likely to be enhanced and an outbreak population of adult *A. planci* results.
9. With outbreaking *A. planci* populations on a number of reefs in the initiation area a wave of outbreaks can be driven by massive larval production and transport to down-current reefs, both to the north and south of the initiation area. Nutrient enrichment of these areas from terrestrial runoff may also increase outbreak intensity throughout the outbreak cycle.

4. Causal attribution

Determination of causality in ecosystems is difficult, both philosophically and practically, and these difficulties increase with the scale and complexity of ecosystems. A framework to address these problems based on the use of epidemiological causal criteria (Fabricius and De'ath, 2004) can be used to assess causality of the relationship between *A. planci* and terrestrial runoff. The six criteria and their interpretation for this debate follow:

1. *The relationship between the dose (the putative cause) and the response(s) should be monotonic.* Increased chlorophyll leads to increased *A. planci* larval survival. This in turn increased numbers of adults, and increased numbers of outbreaks.
2. *The association between the dose and the response should be strong.* Doubling of chlorophyll levels results in ca.10-fold higher larval survival.
3. *The response should be specific to the cause.* This is not the case, since reduced predation can also enhance *A. planci* juvenile survival, however empirical evidence for this is weak.
4. *There should be a logical time sequence of events; i.e. the response should occur after the dose has been applied.* Laboratory experiments, observational studies and historical data all suggest that increases in *A. planci* populations follow increases in terrestrial runoff.

5. *There should be consistency both across populations within a study, and with results from other studies.* We have observations and studies from the GBR and the Pacific islands that agree with the terrestrial run-off theory.
6. *The observations should agree with known biological facts.* Laboratory studies show increased larval development and survival with increased levels of chlorophyll and increased proportions of nano- and micro-plankton.

Five of the six criteria are clearly met, the exception being the third criterion for which the evidence is less clear-cut. This outcome can be considered as strong evidence for a causal link between nutrient enrichment and increased outbreak frequencies of *A. planici*. The magnitude of change in larval survival is great enough, when coupled with observed spatial and temporal differences in chlorophyll, to initiate primary population outbreaks of *A. planici*, and to account for substantial long-term changes in *A. planici* populations. Unless the problem of increasing nutrient enrichment of the inshore waters in the central GBR is addressed, we can expect ongoing outbreaks of *A. planici* of increased frequency with reduced levels of hard coral cover.

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