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The effect of catchment load reductions on water quality in the crown-of-thorn starfish outbreak initiation zone

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ABSTRACT

Crown-of-Thorns Starfish (CoTS) population outbreaks contribute to coral cover decline on Indo-Pacific reefs. On the Great Barrier Reef (GBR), enhanced catchment nutrient loads are hypothesised to increase phytoplankton food for CoTS larvae in the outbreak initiation zone. This study examines whether catchment load reductions will improve water quality in this zone during the larval period. We defined the i) initiation zone's spatial extent; ii) larval stage's temporal extent; and iii) water quality thresholds related to larval food, from published information. We applied these to model simulations, developed to quantify the effect of catchment load reductions on GBR water quality (Baird et al., 2021), and found a consistently weak response of chlorophyll-*a*, total organic nitrogen and large zooplankton concentrations in the initiation zone. Model results indicate marine and atmospheric forcing are more likely to control the planktonic biomass in this zone, even during major flooding events purported to precede CoTS outbreaks.

1. Introduction

Population outbreaks of Crown-of-Thorns Starfish (CoTS, *Acanthaster* spp.) are a major contributor to sustained declines in coral cover across the Indo-Pacific region (Bruno and Selig, 2007; De'ath et al., 2012; Pratchett et al., 2014). Outbreaks and their associated destructive impacts on coral reefs were first reported across the region in the 1950s and 1960s (Chesher, 1969; Endean, 1969; Endean and Chesher, 1973; Yamaguchi, 1986). Numerous hypotheses have been offered to explain the occurrence of CoTS population outbreaks either through natural causes or through human activities (Moran, 1986). Many of these hypotheses are not mutually exclusive, and it is unlikely that any single hypothesis can explain the initiation of all outbreaks (Babcock et al., 2016a; Pratchett et al., 2014). The role of nutrient enrichment, specifically the hypothesis that high nutrient availability increases phytoplankton biomass and enhances CoTS larval growth and survival leading to mass recruitment events and outbreaks, has been put forward several times (Brodie et al., 2005; Brodie, 1992; Fabricius et al., 2010; Lucas, 1973; Pearson and Endean, 1969; Wolfe et al., 2017). Indeed, the '*nutrient enrichment*' hypothesis, and specifically the role of nutrient enrichment from land-based run-off (i.e. the '*terrestrial run-off*' hypothesis) (Birkeland, 1982), is one of the main hypotheses proposed to account for an increased frequency of CoTS population outbreaks (Brodie et al., 2005; Fabricius et al., 2010; Wolfe et al., 2017).

On the Great Barrier Reef (GBR), four major waves of population outbreaks of the Pacific Crown-of-Thorns Starfish (CoTS, *Acanthaster* cf. *solaris*) have been recorded since the 1960s, starting in 1962 (Barnes, 1966; Endean, 1969), 1979 (Endean, 1982), 1993 (Wachenfeld et al., 1998) and 2010 (Pratchett et al., 2014). These four waves of outbreaks followed a similar pattern of initiation and spread (Pratchett et al., 2014; Vanhatalo et al., 2016), with each outbreak apparently originating in the Lizard Island - Cairns region (14.7°–16.7°S) (Barnes, 1966; Endean, 1969; Endean, 1982; Pratchett et al., 2014; Wachenfeld et al., 1998). This so-called 'initiation box' (Kenchington, 1977) has been corroborated by both hydrodynamic connectivity modelling and Bayesian spatiotemporal modelling (James and Scandol, 1992; Vanhatalo et al., 2016), confirming that waves of CoTS outbreaks originate near Lizard Island. The apparent initiation of the 1962 outbreak near the GBR continental coast contributed to the development of the '*terrestrial run-off*' hypothesis (Birkeland, 1982) and to scientific research examining its validity and likely mechanisms (Pratchett et al., 2017a; Pratchett et al., 2014; Wolfe et al., 2017). The potential link between elevated terrestrial runoff and CoTS outbreaks has become one of several arguments for policy and investment to improve GBR water quality (Anthony, 2016;

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Brodie et al., 2013; Roth et al., 2017; Waterhouse et al., 2017). At present, water quality improvement is one of three management approaches to reduce the detrimental impact of CoTS outbreaks on the GBR (Westcott et al., 2020), together with direct manual control (Rivera-Posada et al., 2014; Westcott et al., 2021), and Marine Protected Area (MPA) zoning (Kroon et al., 2021).

Several lines of evidence suggest that the frequency of primary CoTS population outbreaks on the GBR are influenced by nutrient-limited survival of the pelagic planktotrophic larvae (i.e. the '*terrestrial run-off*' hypothesis (Birkeland, 1982)). First, increased nutrient availability in the initiation zone is thought to be driven by considerable changes in catchment land use since the 1850 (Lewis et al., 2021), resulting in significant increases in terrestrial run-off discharged from these rivers into GBR waters (Bartley et al., 2017; Kroon et al., 2012; McCloskey et al., 2021). Recent catchment modelling estimates that, relative to their pre-colonization levels, mean GBR river pollutant loads have increased 3.7 times for fine sediment, 2.2 times for particulate nitrogen (PN) and 2.5 times for particulate phosphorous (PP) (McCloskey et al., 2021), and 3 times for dissolved inorganic nitrogen (DIN) and 4.8 times for dissolved inorganic phosphorous (DIP) (Kroon et al., 2012). Second, following major flooding events in the GBR catchment, in particular the Burdekin and Wet Tropics rivers, flood plumes reach the initiation zone during the summer-wet season (December to April) (Brinkman et al., 2014; Furnas et al., 2013; Wooldridge and Brodie, 2015). The timing and the size of these events appear to be critical for CoTS outbreak initiation, with combined discharges from these rivers exceeding 10 km^3 during the early wet season (November to February) two to five years prior to each of the four primary CoTS outbreaks (Furnas et al., 2013). Third, phytoplankton communities in the GBR exhibit a seasonal response to enhanced nutrient availability and freshwater inputs (Furnas et al., 2005; Richardson et al., 2021). During the summer-wet season, mean chlorophyl-*a* (Chl-*a*) concentrations in GBR surface waters are approximately 50 % greater than in the winter-dry season (May to November) (Brodie et al., 2007). Further, mean surface Chl-*a* concentrations from November to March are higher in the inner <25 km of the shelf of the central/northern GBR (15.1°–19.2°S), encompassing the CoTS initiation zone, compared to that in the far northern GBR (12.0°–15.0°S) (Fabricius et al., 2010). The composition of phytoplankton communities also changes after flood events, with a subsequent increase in zooplankton abundance in the nearshore region (Richardson et al., 2021). Whether these higher Chl-*a* levels reflect food sources favoured by CoTS larvae under experimental conditions, such as dinoflagellates and diatoms >2 μm (Ayukai, 1994; Henderson and Lucas, 1971; Lucas, 1973, 1982; Okaji et al., 1997a; Yamaguchi, 1973), remains unknown. It is also unclear whether elevated concentrations of nutrients and/or phytoplankton in the initiation zone drive CoTS larvae development and survival (Olson, 1985; Olson, 1987; Uthicke et al., 2018; Wolfe et al., 2017), and whether higher abundance of CoTS larvae in the plankton translate into increased settlement of juveniles on the reef (Endean and Cameron, 1985), and ultimately an increased frequency of primary CoTS outbreaks.

Since 2003, catchment and land management programs have been implemented to reduce river sediment and nutrient loads and improve GBR water quality (Commonwealth of Australia, 2018; The State of Queensland and Commonwealth of Australia, 2003), and reduce the exceedances of GBR water guideline values (Brodie et al., 2012; Great Barrier Reef Marine Park Authority, 2010). This includes a guideline for Chl-*a* established in 2010 using relationships between long-term Chl-*a* monitoring data and four groups of coral reef biota (De'ath and Fabricius, 2008), further supported by empirical data on enhanced CoTS larval survivorship at Chl *a* concentrations from 0.5 to 0.8 μg/L (Fabricius et al., 2010; Okaji, 1996). To date, however, there is little evidence that these programs have resulted in detectable long-term changes in GBR inshore water quality (Australian and Queensland governments, 2021, 2022; Waterhouse et al., 2021). This makes it unlikely that water quality improvement efforts to date would have affected CoTS population dynamics (Westcott et al., 2020). Hence, while catchment management efforts to improve water quality, especially during extremely wet years (Furnas et al., 2013), may ultimately influence CoTS larval survival and primary outbreak frequency, current CoTS management includes other approaches in addition to ongoing catchment management (Westcott et al., 2020). Improved water quality, particularly within river plumes, following reduction of anthropogenic catchment loads has been predicted in recent scenario simulations from catchment, hydrodynamic and biogeochemical models (the eReefs platform) (Baird et al., 2021; McCloskey et al., 2021; Waters et al., 2020), specifically developed for the GBR region (Steven et al., 2019). However, whether these improvements in water quality, including reduced Chl-*a* concentrations, are likely occur in the CoTS initiation zone during the months when CoTS larvae are present is currently unknown.

In this study, we ask whether modelled reductions of anthropogenic catchment loads would result in improved water quality in the CoTS outbreak initiation zone during the CoTS larval period. Specifically, we used published scenario simulations from the eReefs models (described briefly in the Methods section "Catchment and modelling scenarios" and in more detail by (Baird et al., 2021; McCloskey et al., 2021; Waters et al., 2020), to quantify likely changes in Chl-*a*, total organic nitrogen (TON) and zooplankton concentrations as a result of modelled catchment management and river load reductions in sediment and nutrients. To explicitly relate these changes in water quality to the CoTS life cycle and outbreak dynamics on the GBR, we defined on the basis of published literature for our assessment the i) spatial extent of the CoTS outbreak initiation zone; ii) seasonal presence and duration of the CoTS larval stage; and iii) water quality thresholds related to CoTS larval food. We then applied these definition to, and analysed the outputs from the existing eReefs scenario simulations (Baird et al., 2021) to assess changes in water quality within the CoTS initiation zone during the relevant season, with particular attention to changes in exceedance of the defined water quality thresholds for CoTS management. Our results show that the differences between the three catchment load reductions scenarios for spatially and temporally averaged terms relative to absolute Chl-*a*, TON and zooplankton concentrations were minor or negligible. Rather than riverine flood plumes, our model results support the overall dominance of marine and atmospheric forcing on water quality within the CoTS initiation zone during the months when CoTS larvae are present. We discuss our findings and discrepancies with previous studies on the '*terrestrial run-off*' hypothesis and provide research recommendations to inform future management of CoTS outbreaks.

2. Methods

2.1. Defining critical parameters for eReefs model analysis

To inform the interpretation of eReefs model outputs, we defined the following three critical parameters related to the spatio-temporal characteristics of primary CoTS outbreaks on the GBR, namely i) spatial extent of the outbreak initiation zone; ii) presence and duration of the larval stage; and iii) water quality thresholds related to larval food. We conducted comprehensive reviews of the published and available scientific and technical literature for reports that provide information relevant for all three critical parameters.

To define the spatial extent of the CoTS outbreak initiation zone for the analysis, we reviewed the literature for reports of CoTS presence and outbreaks on individual reefs from Green Island north since the 1960s (Vanhatalo et al., 2016). In addition, we used CoTS abundance data obtained from the Australian Institute of Marine Science's (AIMS) Long-Term Monitoring Program (LTMP) collected for individual reefs since 1983 (Australian Institute of Marine Science, 2020). CoTS data are based on field observations from manta tow surveys around the perimeter of each reef following AIMS's Standard Operational Procedure (Miller et al., 2019). Manta tows are conducted once per year but not all reefs are sampled every year. For each of the four major waves of recorded outbreaks (1962 (Barnes, 1966; Endean, 1969), 1979 (Endean, 1982), 1993 (Wachenfeld et al., 1998), 2010 (Pratchett et al., 2014)), CoTS presence and abundance records were reviewed over a four-year period: 1 year before the 'reported' start of the outbreak, the year of the start of the outbreak, and two years after. Thus, for the 1979 outbreak, records would be reviewed for the years 1978, 1979, 1980 and 1981. This enabled us to consider a larger body of records and observations as many individual reefs do not get monitored every year. For the 1962 outbreak, only presence or absence information was available from published records. For the remaining three outbreaks, we relied on the reports to confirm when populations of outbreak size were present on individual reefs (e.g., Moran et al., 1992). In addition, we used the CoTS abundance data from the AIMS LTMP data to determine whether CoTS densities were at or above population outbreak levels at an individual reef (i.e. CoTS population outbreak threshold of '>0.11 mean CoTS per manta tow') (Great Barrier Reef Marine Park Authority, 2020). In both cases, CoTS were noted as 'present' if CoTS were reported but not at or above population outbreak size. The annual data for each outbreak were aggregated by outbreak event, with the CoTS status of an individual reef defined as the highest level that occurred during the four year period examined for each outbreak. Once the CoTS status (absent, present, outbreak) for all individual reefs had been determined for all of the four outbreaks, the initiation zone was defined by drawing an equidistant boundary between reefs with CoTS and the mainland, and between reefs with CoTS and outer reefs. We used an equidistant boundary based on lack of current evidence of CoTS larvae being present in (Uthicke et al., 2015a), or dispersed into (James et al., 1990), coastal waters and most outer reefs between Cairns and Lizard Island. In cases where reefs close to the mainland or outer reefs had CoTS outbreaks, the mainland and/or the edge of the continental shelf were considered the boundary of the initiation zone. A smaller potential initiation zone around Lizard Island was also defined in the same manner, based on spatiotemporal modelling by Vanhatalo et al. (2016), who found that CoTS outbreaks appear to start around Lizard Island.

To determine the months when CoTS larvae are present in GBR waters, as well as the duration of the CoTS planktonic larval stage for the analysis, we reviewed the literature for reports on CoTS maturation, gonad development and indices, fertilization, and larval development and duration, as well as reports on CoTS spawning and detection of CoTS larvae in GBR waters. Finally, to define water quality threshold values related to CoTS larval food for the analysis, we reviewed the literature for reports on food and diet of CoTS larvae obtained from field observations as well as from controlled field and laboratory experiments.

2.2. Catchment and marine modelling scenarios

The eReefs platform, comprising a set of catchment models and marine hydrodynamic, sediment dynamic and biogeochemical ecosystem models, was developed to inform monitoring and management of the GBR (Steven et al., 2019). The catchment models, collectively termed GBR Dynamic SedNet and eWater Source, are used to simulate fine sediment and particulate and dissolved nutrient generation, loss, and transport processes across GBR catchments, and are calibrated with catchment-scale monitored data sets (McCloskey et al., 2021). The marine hydrodynamic, sediment dynamic and biogeochemical ecosystem models are driven by the CSIRO Environmental Modelling Suite (Baird et al., 2020), and extensively evaluated against observational data from the GBR Marine Park Authority Marine Monitoring Program (MMP) (Waterhouse et al., 2021) and from monitoring stations operated by Integrated Marine Observing System (IMOS) (Lynch et al., 2014). Recent evaluations of the marine models showed that results for phytoplankton and other key water quality variables are consistent with typical results for models of this complexity, and sufficient for the intended purposes of complementing in situ monitoring and projecting the likely effects of catchment management scenarios (Robson et al., 2020; Skerratt et al., 2019). Nonetheless, the development and application of simulation models of this scope and complexity require many assumptions and simplifications. Thus, the results of scenario simulations should be considered a guide to possible and likely outcomes of catchment interventions rather than specific predictions of future water quality conditions in the GBR.

To examine whether modelled reductions of anthropogenic catchment loads result in improved water quality in the CoTS outbreak initiation zone during the CoTS larval period, we used outputs from six recently published scenario simulations from the eReefs models (Baird et al., 2021; Waters et al., 2020) (Table 1). The original scenario simulations covering the period from December 2010 to 2019 were conducted to consider the likely effects of changes in catchment land use and management on near-surface GBR water quality (Baird et al., 2021; McCloskey et al., 2021; Waters et al., 2020). For these scenarios, models were run with a grid-resolution of approximately 4 km, allowing the computationally intensive, three-dimensional models to be run on the scale of the whole GBR over the multi-year simulation period. Over a subset of this period, an earlier version of the 4 km resolution model has been compared with a 1 km resolution version of the same model with respect to results at MMP water quality sampling sites, and has been found to yield similar results (Dr J. Skerratt, CSIRO, pers. comm.).

The period of the simulations encompasses both dry years, i.e., when GBR river discharge was well below average (i.e. in 2016), and (critical to our main question) extremely wet years (i.e., a one in a 100 year wet season in 2010/2011) (Baird et al., 2021). The six scenarios have identical meteorological, river freshwater and ocean conditions, but with different simulated catchment land use, land management, and sediment and nutrient loads (see (Waters et al., 2020) for full detail and assumptions). The first three scenarios (with configuration identified in between brackets, following (Baird et al., 2021)) represent (1) zero river pollutant loads (i.e. no sediment or nutrients in river flow) (q3O), (2) pre-industrial condition of the catchment (i.e. vegetation restored to predevelopment times) (q3p), and (3) present (i.e. 2019) catchment condition (q3b). The first scenario is included to assess the upper limit of the model's sensitivity to catchment loads and is not intended to represent a realistic scenario. The following three catchment management scenarios are compared against these three scenarios: (4) full adoption of minimal standard land management across all industries (q3C), (5) full adoption of best practice land management across all industries (q3B), and (6) full adoption of innovative land management practices across all industries innovative (q3A). For all scenarios, the models encompassed the whole GBR and were run over a continuous period from December 2010 through to April 2019 or later (Baird et al., 2021). For our analyses, we applied the scenario outputs to the spatial extent of the CoTS outbreak initiation zone, and to the temporal extent of the CoTS larval period in GBR waters. Following our definition of the initiation zone, we used the geographic centres of the (4 km resolution) eReefs marine model grid cells as the reference point to determine whether a cell was within the initiation zone or outside it.

The outputs of the six scenario simulations were used to quantify projected changes in Chl-*a*, total organic nitrogen (TON) and large zooplankton concentrations in the CoTS initiation zone for the time period when CoTS larvae are present. First, changes in Chl-*a* concentrations – a measure of phytoplankton abundance and biomass in coastal and marine waters (Davies et al., 2018) – were examined as it is the most widely used water quality indicator in studies of CoTS larval development and survival (Wolfe et al., 2017). For Chl-*a*, we quantified the reduction in mean concentration relative to the current Chl-*a* guideline value for open coastal and midshelf waters (0.45 μg/L) (Great Barrier Reef Marine Park Authority, 2010), as well as the frequency of daily exceedances of this guideline value. This Chl-*a* guideline value was derived based in part on supporting evidence that CoTS larvae survivorship becomes significantly enhanced at 0.5–0.8 μg/L Chl *a* and aims to ensure that CoTS outbreaks are minimised (Great Barrier Reef Marine Park Authority, 2010). Additional Chl-*a* thresholds were also examined

Table 1
Details of six catchment load scenarios (modified from Baird et al., 2021) used to examine water quality improvement in the outbreak initiation zone of the Pacific Crown-of-Thorns Starfish (CoTS, *Acanthaster* cf. *solaris*) on the Great Barrier Reef, Australia. The six scenarios have identical meteorological, river freshwater and ocean conditions, but with different catchment land use, land management, and sediment and nutrient loads (see (Baird et al., 2021; McCloskey et al., 2021; Waters et al., 2020) for more detail). DIN = dissolved inorganic nitrogen, PN = particulate nitrogen.

Number	Name	Catchment loads (Waters et al., 2020)	Catchment management	Configuration identifier
1	Zero river pollutant loads	No GBR catchment loads	River flow is unchanged but assumed to carry no sediment, nitrogen or phosphorus loads. This scenario is included to assess the upper limit of the model's sensitivity to catchment loads and is not intended to represent a realistic or achievable scenario	q3O
2	Pre-industrial	GBR catchment loads for the present water infrastructure but with vegetation restored to pre-development times	A best estimate of river sediment, nitrogen and phosphorus loads before land clearing and catchment development for agriculture, mining and urban land uses	q3p
3	Baseline conditions	Best estimate of current GBR catchment loads with present catchment condition	Current (i.e., 2019) catchment condition, land use and land management practices	q3b
4	Minimum standard	Reduction in GBR catchment loads of 4 % for sediment, 32 % for DIN, and 6 % for PN	Full adoption of minimal standard land management across all industries. This scenario represents the reduction in river loads if currently regulated minimum standards of land management are adopted throughout all GBR catchments.	q3C
5	Best-practice	Reduction in GBR catchment loads of 18 % for sediment, 50 % for DIN, and 30 % for PN	Full adoption of best practice land management across all industries. This scenario represents reduced river loads if currently recognised best practices in land management are adopted throughout all GBR catchments.	q3B
6	Innovative	Reduction in GBR catchment loads of 57 % for sediment, approximately 70 % for DIN, and 69 % for PN	Full adoption of innovative land management practices across all industries. This scenario represents the maximum achievable reduction of river loads of sediments and nutrients that may be realistically achievable using currently known land management approaches without changing land use.	q3A

based on the findings of our literature review on food and diet of CoTS larvae, and to take into account to some extent the tendency of the eReefs models to under-estimate Chl-*a* at all concentrations at most sites (Robson et al., 2020; Skerratt et al., 2019) (see 'Results and discussion'). Second, changes in TON were considered given that this encompasses most potential food sources for CoTS larvae including free amino acids, phytoplankton and organic detrital material (Lucas, 1982; Moran, 1986; Olson, 1987) (see 'Results and discussion'). Using TON rather than total organic carbon (TOC) excludes carbon sources that are likely to be of low nutritional value to CoTS larvae, such as marine chromotographic dissolved organic carbon (CDOM). For TON, we quantified the reduction in mean concentration relative to the current TON concentration. Third, we also considered changes in the concentrations of large zooplankton, with CoTS larvae being a component of this zooplankton community. Large zooplankton are simulated in the eReefs biogeochemical model as a functional group that graze on large phytoplankton such as diatoms and smaller zooplankton. While the behaviour of CoTS larvae is not specifically simulated, conceptually they may respond in a similar manner to other large zooplankton. For large zooplankton, we quantified the degree to which the models predict that changes in Chl-*a* will result in changes in zooplankton concentrations. Finally, the sensitivity of all results to the boundaries of the CoTS outbreak initiation zone was assessed by comparing the results obtained from the main and smaller initiation zones.

2.3. Critical assumptions and limitations

Our analysis was conducted to quantify the likely effects of changes in catchment land use and management on Chl-*a*, TON and zooplankton concentrations in the CoTS outbreak initiation zone during the CoTS larval period. To facilitate this, we made a number of simplifying assumptions. First, that the projected water quality changes simulated by the eReefs catchment and marine models are accurate (see Baird et al. (2021) and Robson et al. (2020) for discussions of some of the assumptions and limitations of the models). The following limitations bear particular emphasis:

- The "pre-industrial" scenario considers only changes in delivery of sediments and nutrients to rivers and not changes in hydrology (e.g., associated with large dams or flood mitigation works), or changes in run-off potentially associated with land clearing and development (Bartley et al., 2014; Waterhouse et al., 2016). Dams have likely reduced the delivery of small runoff-events to coastal waters while land clearing and flood mitigation have likely reduced the duration and increased the magnitude of large run-off events, possibly increasing the extent of flood plumes but reducing their duration. Not including these changes may lead to an under-estimation of the increase in delivery of nutrients to water further from river mouths (such as the CoTS initiation zone) between pre-industrial and baseline scenarios but should not affect the other scenarios considered here.
- All six scenarios assume the same marine initial conditions, including the same distribution of sediments and organic materials in the benthic sediments. Simulated water quality in shallow areas is often sensitive to sediment initial conditions (Robson, 2014), which may respond to changes in river loads on time-scales of years to decades (Robson et al., 2006). The marine models are very computationally intensive and rely on observed hydrological inputs and available modelled surface meteorological conditions, making a long spin-up difficult. It is likely that a spin-up period of at least a decade would magnify the differences between scenarios by changing the amount of nutrients stored in the sediments at the start of the period of comparison. We recommend that future land management scenarios run with the eReefs marine models consider this effect – though the effect is probably small for this analysis (if the effect were large, we would expect to see a greater difference between scenarios in the later years of the simulations).
- Reductions in anthropogenic river loads in response to changes in catchment management can take one or two decades (or more) to be fully realised (Kroon et al., 2014; Kroon et al., 2016; Lefcheck et al., 2018). The catchment modelling relied on here does not simulate the time-scale of catchment responses, so an instant response to changes in land management is assumed. This means that the analyses conducted here may over-estimate the immediate response of marine water quality to catchment land management changes and cannot be used to evaluate the time-scale over which such changes might occur. During the period of change, other changes, including climate change effects on hydrology, ground cover and ocean processes, will also come into play – these have not been included in the simulation.
- Simulated zooplankton concentrations must be considered speculation, as very limited zooplankton observational data are available to evaluate the performance of the models. The eReefs platform has been evaluated with respect to these limited zooplankton observations (Skerratt et al., 2019), as well as with respect to the relationship between zooplankton and Chl-*a* (Robson et al., 2020). This latter relationship has been found to be robust and consistent with expected results. Hence, we are confident that the feedback between simulated changes in Chl-*a* and grazing by zooplankton is well represented.
- The 4 km grid resolution of the biogeochemical model used in these scenario simulations does not allow simulation of small-scale spatial patchiness in Chl-*a* and other water quality variables, which may be important to the ability of CoTS larvae to take full advantage of food resources. Experimental work on CoTS larval survival in the presence of phytoplankton at different concentrations has also assumed uniform conditions, but this does not reflect real spatial patchiness. We do, however, directly compare model performance to observational data in the Results and discussion section (see Supplementary Materials).

Second, we assume that relevant changes in water quality are accurately reflected by simulated midday surface concentrations of Chl-*a*, TON and zooplankton. The eReefs marine models simulate water quality variables including Chl-*a* in three dimensions. We used the surface layer output from the three-dimensional model, the depth of which varies tidally but is typically about +0.5 to −0.5 m above Mean Sea Level. Model calibration and evaluation has been conducted primarily using surface (0.5 m depth) observations from the GBR Marine Park Authority MMP (Waterhouse et al., 2021) and from IMOS loggers (Lynch et al., 2014). Similarly, current Chl-*a* guideline values for the GBR Marine Park are applied to surface water monitoring data (Great Barrier Reef Marine Park Authority, 2010). The use of surface concentrations is supported by observational evidence from controlled field and laboratory experiments of CoTS larval behaviour that suggest they spend most of their time at the surface. Specifically, following hatching of embryos into gastrulae, CoTS larvae showed a photopositive swimming response (Lucas, 1982). Moran (1986) reported that observations from laboratory studies suggest that while in the plankton, larvae exhibit negative geotaxis and are photopositive actively swimming towards the water surface (e.g. Yamaguchi, 1973). This is supported by both laboratory observations (Moran, 1986) and the observed behaviour of larvae in in situ chambers (Olson, 1985). Towards the end of the brachiolaria stage, when the larvae are about 1–1.2 mm in size, they begin to drift downward and explore substrata to find a suitable surface on which to settle. Only towards the end of the brachiolaria stage, when a primordium is beginning to develop (typically around 12–14 days after fertilization but potentially up to 40 days after fertilization (Uthicke et al., 2015a), do the larvae become negatively buoyant and tend to sink (Birkeland and Lucas, 1990; Keesing et al., 1997; Olson, 1985).

Finally, we assume that changes in simulated surface Chl-*a* and TON concentrations are representative of changes in food availability for CoTS larvae (see Results and discussion). The current Chl-*a* guideline values are for total observed Chl-*a* and are informed by empirical data on CoTS larval growth and survivorship when provided with phytoplankton as a food source (Fabricius et al., 2010; Okaji, 1996). In reality, CoTS larvae feed selectively on more palatable or nutritious phytoplankton species (Mellin et al., 2017), though some other organic materials such as detrital particulate organic matter (included in TON) may also be viable food sources (see Results and discussion; (Lucas, 1982; Moran, 1986; Olson, 1987).

2.4. Resolving dominant environmental controls on the initiation zone

Comparison of eReefs model results between years of different climate forcing enables an assessment of the dominant controls, e.g., terrestrial/riverine, marine and atmospheric, on mean surface concentrations of Chl-*a*, TON and zooplankton in the CoTS initiation zone. Accordingly, the influence of riverine loads (Δx) relative to other drivers was determined by comparing the zero and baseline scenarios following Eq. (1)

$$\Delta \mathrm{x} = \frac{\mathrm{x}^{\mathrm{i}}_{\mathrm{zero}} - \overline{\mathrm{x}}_{\mathrm{zero}}}{\mathrm{x}^{\mathrm{i}}_{\mathrm{baseline}} - \overline{\mathrm{x}}_{\mathrm{baseline}}}$$

where x_s^i is the spatial mean of model term x in year i corresponding to scenario s, and $\overline{x}_s$ is the spatial and temporal mean of model term x in all other years during the study period. Note that this comparison is only valid when x_s^i is statistically different than the $\overline{x}_s$; during the study period this only occurred during 2011 (extremely wet year) and 2016 (dry year) (Baird et al., 2021), which corresponded to influence from the El Niño-Southern Oscillation (ENSO).

Riverine influence was further assessed at a highly aggregated scale by correlating eReefs model terms (December 2010–February 2019) within the CoTS initiation zone with nutrient loads from the baseline (q3b) GBR Dynamic SedNet model scenario. eReefs values for Chl-*a*, TON and large zooplankton consisted of the annual means for each study year for the months when CoTS larvae are present (December to February). GBR Dynamic SedNet values for total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) consisted of the cumulative riverine loads from GBR rivers south of Lizard Island for the same years and months. Within this geographic range, the Endeavour River represented the northernmost river resolved in GBR Dynamic SedNet and the Mary River the southernmost river.

3. Results and discussion

3.1. Definition of spatial extent of CoTS outbreak initiation zone

Since the 1960s, the GBR has recorded four major waves of CoTS population outbreaks with all four following a similar pattern of initiation and spread (Pratchett et al., 2014; Vanhatalo et al., 2016). Our review of CoTS presence and outbreaks on individual reefs from Green Island north corroborate previous findings that high densities are generally first reported in the north-central GBR (Table S1; Fig. 1) and that outbreaks initiate between Lizard Island and Cairns (i.e., the 'initiation box') (Kenchington, 1977). Recent spatiotemporal modelling applied to a 30-year CoTS survey of the GBR (Vanhatalo et al., 2016) also corroborates earlier hydrodynamic modelling (Scandol and James, 1992), which suggested that waves of CoTS outbreaks originate near Lizard Island (14.67°S). High connectivity between reefs in this region potentially exacerbates CoTS outbreaks (Hock et al., 2014; James et al., 1990).

The spread of each of the four major waves of outbreaks progressed in a south-easterly direction (Moran et al., 1992; Reichelt et al., 1990; Scandol and James, 1992; Vanhatalo et al., 2016), consistent with southward dispersal of CoTS larvae spawned at the outbreak front (Kenchington, 1977; Uthicke et al., 2015a). A simultaneous pattern of north-westerly spread may occur (Moran et al., 1992; Reichelt et al., 1990; Scandol and James, 1992; Vanhatalo et al., 2016), but this is less clear due to fewer surveys having been conducted in the northern GBR. The potential initiation of CoTS outbreaks north of Lizard Island is the topic of current research.

The first CoTS outbreak was reported from Green Island (16.8°S) and nearby reefs in 1962 (Barnes and Endean, 1964; Barnes, 1966; Endean, 1969; Pearson and Endean, 1969) (Table S1; Fig. 1). However, a lack of more wide-spread monitoring prior to 1966 means that it is possible that the outbreak started somewhere else (Pearson and Endean, 1969). The second outbreak, in 1979, was also first reported from Green Island (Endean, 1982; Kenchington and Pearson, 1981), with additional reports of outbreaks on other reefs between 14°S and 18°S in early 1980 (Moran et al., 1988; Moran et al., 1992; Nash and Zell, 1981). For some reefs in this second outbreak, the reef-ID (Lawrey and Stewart, 2016) could not be determined from the information provided in these references (Table S1): these reefs were not further considered in defining the initiation zone. The first stages of the third outbreak were detected on mid-shelf reefs between Lizard Island (14.7°S) and Cairns (16.9°S) in 1993–1995 (Australian Institute of Marine Science, 2020; Wachenfeld et al., 1998). The fourth and current outbreak was first reported on reefs near and south of Lizard Island in 2009–2010 (Australian Institute of Marine Science, 2020; Pratchett et al., 2014).

Combining these findings into a spatial map of the CoTS outbreak initiation zone resulted in an 8453 km^2 area encompassing most mid-shelf and some offshore reefs between Green Island in the south and Lizard Island to the north, with a boundary generally five to fifteen kilometres from the mainland and excluding most of the outer reefs (Fig. 1). Importantly, the initiation zone does not include any open

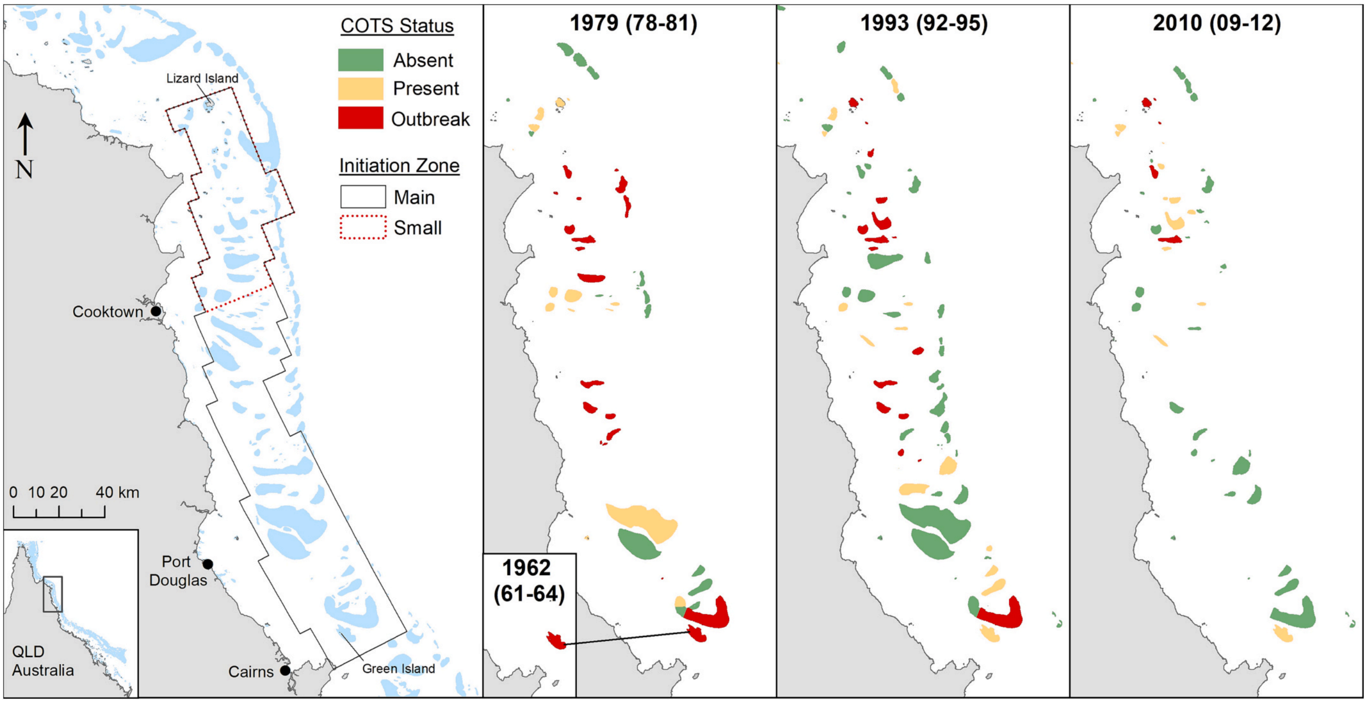

Fig. 1. Presence and outbreaks of the Pacific Crown-of-Thorns Starfish (CoTS, *Acanthaster* cf. *solaris*) on individual reefs north of Green Island on the Great Barrier Reef (GBR), Australia. For each of the major waves of outbreaks reported on the GBR since the 1960s, CoTS monitoring information was reviewed over a four year period: 1 year before the published start of the outbreak, the year the outbreak started, and two years after. See Table S1 for detailed information for each reef and each outbreak, and associated references. Annual data from Table S1 were aggregated by outbreak event for visualization, with the CoTS status of a reef displayed as the highest level that occurred during the four-year period examined. The main initiation zone encompasses all reefs where CoTS were present, including at outbreak levels, whereas the small initiation zone is based on the relatively higher number of reefs north of Cooktown with CoTS present, including at outbreak levels, combined with the findings that CoTS outbreaks initiate around Lizard Island (Vanhatalo et al., 2016).

coastal reefs and very little of the open coastal water body as defined for the GBR water quality guidelines (within 6 km from the Wet Tropics' coast; (Great Barrier Reef Marine Park Authority, 2010). Based on the relatively higher number of reefs north of Cooktown with CoTS present, including at outbreak levels, combined with the findings of spatiotemporal modelling by Vanhatalo et al., 2016 (Vanhatalo et al., 2016), we also defined a smaller initiation zone of an 2763 km^2 area around Lizard Island (Fig. 1). Ours is the first study to specifically define the spatial extent of the CoTS outbreak initiation zone (Table S1 and references therein). Previous studies referred to the initiation zone's location in more ambiguous terms (Brodie et al., 2017c; Fabricius et al., 2010; Kenchington, 1977), or only considered very small areas within the purported zone (i.e. Green Island, (Wooldridge and Brodie, 2015). The spatial boundaries of the main and the smaller initiation zones were subsequently applied to the eReefs model scenario outputs to assess the responses of Chl-*a*, TON and zooplankton concentrations within these zones.

3.2. Definition of seasonal presence and duration of CoTS larval stage

The life cycle of *Acanthaster* spp. consists of a planktonic stage (days to weeks) and a longer settled stage (5+ years) (Lucas, 1984; Pratchett et al., 2014). The planktonic stage begins with the release of oocytes and sperm, with estimates of immense gamete production (>100 million eggs; 1.1×10^{13} sperm) for larger individual starfish (Babcock et al., 2016b). Following fertilization, embryos develop into early bipinnaria larvae within 2 to 4 days and start feeding on suspended particulate matter (Henderson, 1969; Lucas, 1982; Yamaguchi, 1973). Development of CoTS larvae (0.5 to 1.5 mm long) then continues to the advanced bipinnaria stage and early, mid and late brachiolaria stages, with the latter stage achieving competency to settle (Lucas, 1984; Pratchett et al., 2014). Under laboratory experimental conditions, larval CoTS are able to clone themselves potentially extending their time in the plankton (Allen et al., 2019). Larval dispersal is thought to occur over large areas including 100 km south of reefs with current outbreaks (Uthicke et al., 2015a). The settled stage starts with CoTS larvae metamorphosising into a benthic juvenile starfish (0.5 mm ø) over a period of two days (Henderson and Lucas, 1971; Johnson et al., 1991; Lucas, 1973; Yamaguchi, 1973). This juvenile stage (1–10 mm ø) feeds on crustose coralline algae and generally lasts six months (Lucas, 1984; Pratchett et al., 2014), although can extend for 6.5 years in the laboratory if corals are not available (Deaker et al., 2020). Following a permanent shift to corallivory, laboratory studies show that juvenile and sub-adult stages (10–200 mm ø) develop into sexually mature adults (200–350 mm diameter) after approximately two years, and decline into senile adults (>350 mm ø) ceasing gametogenesis after 5+ years (Lucas, 1984; Pratchett et al., 2014).

On the GBR, observations of CoTS spawning (Babcock, 1990; Babcock and Mundy, 1992a; Babcock and Mundy, 1992b; Gladstone, 1987, 1992; Pearson and Endean, 1969; Pratchett et al., 2014) and CoTS gonadal development and maturation (Babcock and Mundy, 1992a; Babcock and Mundy, 1992b; Endean, 1969; Lucas, 1973; Pearson and Endean, 1969) indicate that spawning generally occurs from December to February (Table S2). This is corroborated by the detection of larval CoTS in reef waters from mid-November until late February, with highest larval densities recorded in late December and late January (Uthicke et al., 2015a; Uthicke et al., 2019). Results from controlled field and laboratory experiments show that the development and duration of the CoTS larval stage is strongly influenced by food quantity and quality (Fabricius et al., 2010; Lucas, 1982; Okaji et al., 1997a; Olson, 1987; Uthicke et al., 2018) as well as temperature and salinity (Clements et al., 2022; Henderson and Lucas, 1971; Keesing et al., 1997; Lamare et al., 2014; Lucas, 1973; Uthicke et al., 2015b; Yamaguchi, 1973) (Table S3). The minimum time reported for CoTS larvae development from fertilization to late-stage brachiolaria is 9 to 11 days (Birkeland and Lucas, 1990; Lucas, 1974). The minimum time reported for actual settlement, however, is 14 days in both laboratory (Johnson et al., 1991) and field (Olson, 1987) experiments. One other study reported settlement at 12 days based on unpublished data (Olson and Olson, 1989). Combined, we resolved that December, January and February were the most likely months for CoTS larvae to be present in GBR waters and defined the CoTS larvae period as December to February. These seasonal boundaries of the CoTS larval period were subsequently applied to the eReefs model scenario outputs to assess the responses of Chl-*a*, TON and zooplankton concentrations within this period. To conduct the analysis of the eReefs model outputs, we used the periods from the start of December each year within the range 2010 to 2018 through to the end of February the following year.

3.3. Definition of water quality thresholds related to CoTS larval food

Phytoplankton appears to be the main food source for CoTS larvae: in particular dinoflagellates and diatoms >2 μm (Ayukai, 1994; Henderson and Lucas, 1971; Lucas, 1973, 1982; Okaji et al., 1997a; Yamaguchi, 1973). Under controlled conditions, CoTS larvae have been reared successfully using natural phytoplankton and single or mixed species of cultured unicellular algae (Fabricius et al., 2010; Henderson and Lucas, 1971; Johnson et al., 1991; Keesing et al., 1997; Lucas, 1973, 1982; Mellin et al., 2017; Okaji, 1996; Olson, 1987; Uthicke et al., 2018; Uthicke et al., 2015b; Wolfe et al., 2015a, 2015b, 2017; Yamaguchi, 1973). Both phytoplankton abundance and composition influence development and survival of CoTS larvae (Fabricius et al., 2010; Lucas, 1982; Okaji et al., 1997a; Olson, 1987; Uthicke et al., 2018; Wolfe et al., 2015a, 2015b, 2017). Selective ingestion of phytoplankton by CoTS larvae has been reported, with preferred algal species having the highest energy content (Mellin et al., 2017) and having cell sizes in the range of 2–20 um (i.e., nanoplankton) (Ayukai, 1994; Lucas, 1982; Okaji et al., 1997a).

In addition to phytoplankton, other food sources such as detritus, dissolved organic matter (DOM), non-photosynthetic plankton and bacteria may also play an important role in providing nutrition to CoTS larvae (Carrier et al., 2018; Lucas, 1982; Moran, 1986; Olson, 1987). Amino acids are taken up by and may play a significant role in the energy supply and development of CoTS larvae (Hoegh-Guldberg, 1994; Okaji, 1996; Okaji et al., 1997b). However, mean summer concentrations of dissolved free amino acids are likely too low to support their nutrition without other sources (Ayukai et al., 1997). Whether other compounds of DOM, such as lipids and glycoproteins, may be important as a food source is currently unknown. Bacteria (<1 μm) were not ingested by CoTS larvae during controlled laboratory exposures (Ayukai, 1994) and gut content examination did not show any evidence of bacteria accumulation (R. Olson, unpublished data reported in (Olson and Olson, 1989)). Indeed, the large size of CoTS larvae (200 to 1500 μm) would suggest that free-floating bacteria and DOM are unlikely to be major food sources (Brodie et al., 2005; Brodie, 1992). Conversely, results from laboratory experiments suggest that particles >20 μm are not accessible to CoTS larvae (Lucas, 1982). Given that the inside diameter of the oesophagus is about 40–60 μm in CoTS larvae (Yamaguchi, 1973), their ability to ingest all known and potential food sources is likely to be restricted to certain sizes. A more recent report shows that CoTS larvae maintain a symbiosis with a diverse and dynamic bacterial community, distinct from the environmental microbiota (Carrier et al., 2018). We were unable to find any information on detritus or non-photosynthetic plankton as food sources for CoTS larvae. Overall, the potential importance of food sources other than phytoplankton for CoTS larvae development and survival in the field is still largely unknown. For this reason, we resolved to consider both Chl-*a* (as an indicator of phytoplankton food availability; the most likely and best-known food source for CoTS larvae) and total organic nitrogen (TON, as an indicator of the total availability of all known or potential food sources for CoTS larvae) in the eReefs model scenario outputs.

Chlorophyll-*a* concentration is the most studied water quality indicator for CoTS larval development, survival and settlement (Table S4). Despite this, Chl-*a* concentrations may not necessarily reflect food availability for CoTS larvae, as Chl-*a* does not distinguish between phytoplankton species and size classes (Brodie et al., 2005; Brodie, 1992; Olson and Olson, 1989; Pratchett et al., 2017a; Uthicke et al., 2018) nor does it include food sources other than phytoplankton. Successful CoTS larval development, survival and settlement occurs across a magnitude of Chl-*a* concentrations (0.5–5.0 μg/L; Table S4), irrespective of the experimental conditions (Wolfe et al., 2017). Most laboratory studies have reported critical lower and higher limits of Chl-*a* outside which development and survival is seriously impeded (Fabricius et al., 2010; Okaji, 1996; Pratchett et al., 2017b; Uthicke et al., 2015b; Wolfe et al., 2015a, 2015b, 2017) (Table S4). Within these extremes, a range of Chl-*a* concentrations appear to exist that maximise development, survival and settlement, with exact concentrations differing depending on the exact experimental conditions but reflecting those in GBR waters during summer wet-seasons (Wolfe et al., 2017). Notwithstanding, larvae do show phenotypic plasticity to low food and starvation food conditions in the laboratory (Wolfe et al., 2015a). The one controlled rearing experiment in situ, with Chl-*a* concentrations well below the minimum threshold established in the laboratory (0.4 μg/L), showed settlement after 14 days, with no evidence of starvation (Olson, 1987). A subsequent study using the in situ larval culture chambers reported a potential build-up of Chl-*a* concentrations (Okaji, 1993), although when initially tested such retention was not evident (Olson, 1985). The current guideline for Chl-*a* for open coastal and midshelf waters in the GBR Marine Park (0.45 μg/L) (Great Barrier Reef Marine Park Authority, 2010) still closely resembles concentrations at which larval development and survival is greatly enhanced in most recent studies (Pratchett et al., 2017b; Wolfe et al., 2015a, 2015b, 2017). Given that this guideline was derived based in part on supporting evidence that CoTS larvae survivorship becomes significantly enhanced at 0.5–0.8 μg/L Chl *a* (Great Barrier Reef Marine Park Authority, 2010), we first resolved that the minimum water quality threshold related to larval food to be used in our analysis is 0.45 μg/L for Chl-*a*. However, given that a clear Chl-*a* threshold for enhanced larval survival and settlement may not exist, with the exception that survival is low at oligotrophic conditions of 0.1 μg Ch-*a*/L (Wolfe et al., 2017), we also quantified the reduction in mean Chl-*a* concentration and frequency of daily exceedances of lower Chl-*a* thresholds, namely 0.30, 0.20 and 0.10 μg/L. Considering these lower Chl-*a* thresholds also allows us to take into account to some extent the tendency of the eReefs models to under-estimate Chl-*a* at all concentrations at most sites (Robson et al., 2020; Skerratt et al., 2019).

3.4. Analysis of catchment and marine modelling scenarios

The eReefs platform has been used in various applications to inform GBR water quality policy and management decisions (Steven et al., 2019). This includes (i) the establishment of pollutant load reduction targets for each catchment that discharges into the GBR (Australian and Queensland goverments, 2020; Brodie et al., 2017a; Brodie et al., 2017b), (ii) the evaluation of changes in catchment management and land use on GBR water quality (Baird et al., 2021; McCloskey et al., 2021; Waters et al., 2020), and (iii) the assessment of and annual reporting on GBR water quality (Australian and Queensland governments, 2022; Robillot et al., 2018). These applications include the area encompassing the initiation zone, such as pollutant load reduction targets for the Wet Tropics and Burdekin rivers hypothesised to influence water quality in the initiation zone (Furnas et al., 2013), and annual reporting on GBR water quality in the Wet Tropics and Cape York regions (Australian and Queensland governments, 2022). Here, we apply the scenario simulation outputs from the eReefs catchment and marine models (Baird et al., 2021) to assess projected changes in water quality within the CoTS initiation zone during the relevant season. Having specifically defined the CoTS outbreak initiation zone (Table S1, Fig. 1) and the seasonal presence (December–February) and duration (14 d) of the CoTS larval stage (Tables S2, S3), we applied these critical parameters to the eReefs' scenario simulation outputs (Baird et al., 2021; Waters et al., 2020). Next, we conducted three separate and independent evaluations of the results.

First, we examined the response of simulated surface Chl-*a*, TON and large zooplankton concentrations in coastal waters of the central and northern GBR from December to February following adoption of the strongest catchment management scenario (i.e., innovative land management, q3A; Table 1). Corroborating previous studies (Baird et al., 2021; Waters et al., 2020), the spatial extent where water quality improved included coastal waters south of Cairns, and to a lesser degree in waters inshore of the CoTS initiation zone (Fig. 2a–f). The relatively small reductions in Chl-*a* concentrations in our analysis are likely a result of constraining our analysis to only four months, with larger reductions predicted when the analysis is run over the full 12 months (Baird et al., 2021).

Second, we applied the scenario outputs to the spatial extent of the CoTS outbreak initiation zone specifically (Fig. 1) and examined the response of simulated surface Chl-*a*, TON and large zooplankton concentrations to the six different catchment management scenarios (Table 1), again from December to February. Comparison of spatially and temporally averaged model terms within the main and small initiation zones for each model scenario (Fig. 3a, b) provides a first-order check on whether the three water quality variables respond to altered riverine load scenarios as expected. Based on conventional understanding of GBR biogeochemical cycling (Brodie et al., 2007; Devlin et al., 2012; Furnas et al., 2005; Richardson et al., 2021), mean concentrations for Chl-*a*, TON and large zooplankton, and threshold exceedances for Chl-*a* would be expected to increase with higher riverine loads and decrease with lower riverine loads. Indeed, these mean terms in both the large and small initiation zones covaried with riverine loads across all six catchment management scenarios, showing intuitive directional trends amongst model scenarios (Fig. 3a, b). That is, all mean concentrations and threshold exceedances increased from the 'zero river pollutant loads' (q3O) to 'pre-industrial' (q3p) and then 'baseline' (q3b) scenarios, and subsequently decreased from the 'baseline' (q3b) to 'minimum' (q3C) to 'best-practice' (q3B) and then 'innovative' (q3A) catchment management scenarios. However, the differences between the six scenarios for mean concentrations and threshold exceedances were minor or negligible for all three water quality variables.

Finally, we compared our model results to two observational datasets to further evaluate the performance of the scenario simulation outputs from the eReefs modelling. Previous studies have evaluated the eReefs modelled Chl-*a* and other water quality variables against observations from the GBR Marine Park Authority MMP, the IMOS National Reference Stations and other IMOS sites (Robson et al., 2020; Skerratt et al., 2019). These evaluations have shown that although the models perform reasonably well in replicating seasonal and interannual fluctuations in coastal water quality (Baird et al., 2019), they systematically underestimate Chl-*a* concentrations observed at nearshore MMP sites and midshelf IMOS monitoring sites between 2010 and 2019 and the range over which these vary (Robson et al., 2020) (see https://research.csiro.au/ereefs/wp-content/uploads/sites/34/2015/08/gbr4-H2p0-B2p0-Chyd-Dcrt_vs_insitu_PartI.pdf, and https://research.csiro.au/ereefs/wp-content/uploads/sites/34/2015/08/gbr4-H2p0-B2p0-Chyd-Dcrt_vs_insitu_PartII.pdfs for a complete set of model evaluation metrics for each routine observation site).

Here, we compared our model results to two observational datasets obtained for the initiation zone during the relevant season, namely (i) discrete surface samples of Chl-*a* (pigment analysis) (Fig. S1a, b), and (ii) ocean glider (i.e. autonomous underwater vehicle) measurement of Chl-*a* fluorescence (Fig. S2a, b). Our comparison revealed results generally similar to previously reported eReefs model evaluation metrics for nearshore and mid-shelf waters (Supplementary Text) (Skerratt et al., 2019). Specifically, simulated Chl-*a* was well-correlated with

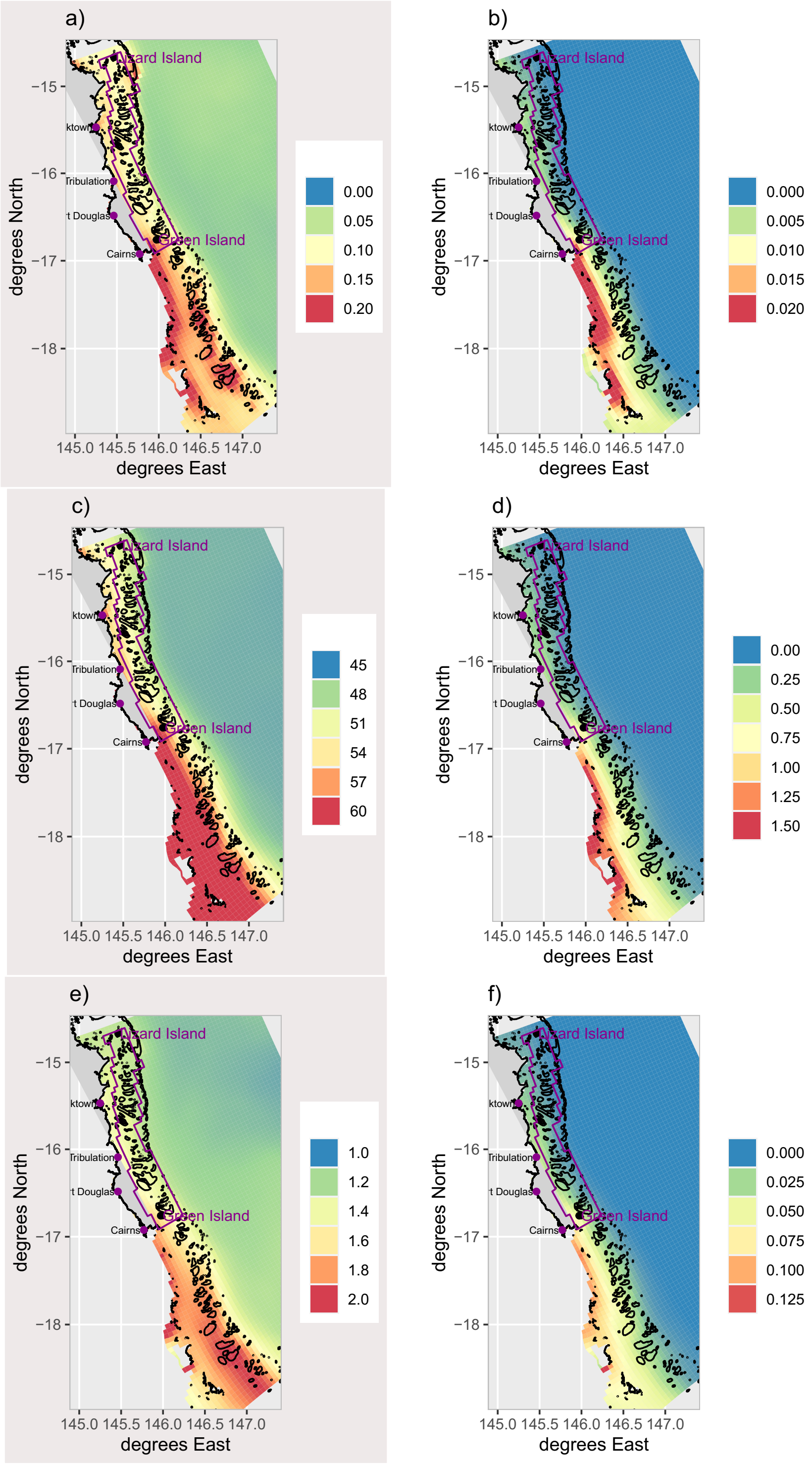

Fig. 2. Mean simulated baseline (q3b) surface concentrations (left; grey background) and reductions in mean simulated concentrations under innovative (q3A) land management (right; white background) of (**a, b**) chlorophyll-*a* (Chl-*a*, μg/L); (**c, d**) Total Organic Nitrogen (TON, μg N/L); and (**e, f**) large zooplankton (μg N/L), in coastal waters of the central and northern Great Barrier Reef, Australia, encompassing the CoTS outbreak initiation zone (main zone shown by magenta-bordered polygon) during the months when CoTS larvae are present (December to February). Mean simulated surface concentrations represent the 'baseline' scenario (q3b; 2019 catchment condition), with relative reductions following full adoption of the 'innovative land management' scenario (q3A). Details of the two catchment load scenarios are presented in Table 1. The most substantial changes occur south and inshore of the CoTS initiation zone. Colour scales are truncated to the range shown.

observed Chl-*a* for in situ samples and glider fluorescence in and near the CoTS initiation zone. Specifically, the comparison shows a statistically significant linear relationship between model results and observations, justifying our use of additional Chl-*a* thresholds (0.30, 0.20 and 0.10 μg/L). These results further indicate high model skill for a model of this type (Arhonditsis and Brett, 2004; Robson, 2014), and corroborate previous studies (Robson et al., 2020; Skerratt et al., 2019) that the eReefs models tend to under-estimate Chl-*a* at all concentrations at most sites. Despite these robust results, we do acknowledge the relative paucity of observational data in the CoTS initiation zone during the relevant season. Therefore, we strongly recommend data collection at relevant spatio-temporal scales to further examine potential links between water quality, food availability and CoTS larvae, as well as to evaluate and refine the eReefs model at these scales. Notwithstanding, the results of these three separate and independent evaluations provide confidence that the scenario outputs were performing as expected. Next, we apply these scenario outputs to specifically assess projected changes in water quality within the CoTS initiation zone during the relevant season.

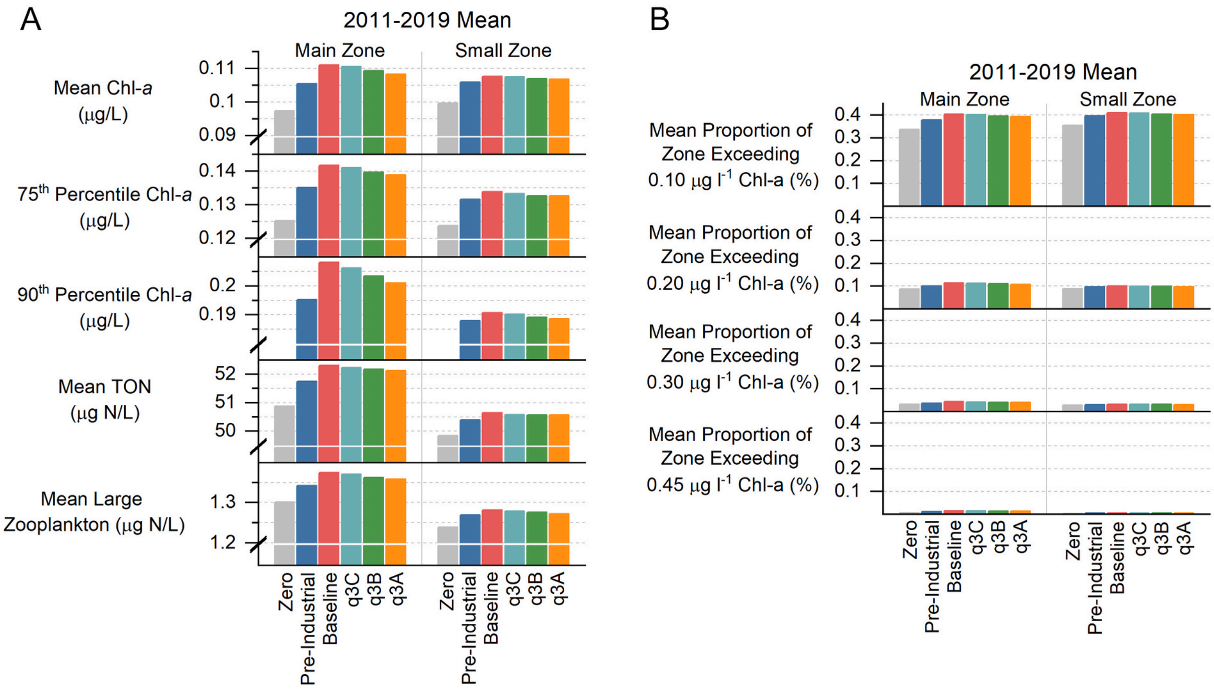

Fig. 3. Projected changes in (**A**) the simulated surface concentrations of chlorophyll-*a* (Chl-*a*, μg/L), total organic nitrogen (TON, μg N/L), and large zooplankton (μg N/L), and (**B**) the mean proportion of the initiation zone for which Chl-*a* concentrations exceed thresholds (0.1 to 0.45 μg/L), in the main and small CoTS initiation zones during the months when CoTS larvae are present (December to February). The mean proportion was calculated daily as a count of the number of model grid-cells in which the threshold is exceeded, and then averaged temporally over the simulation period (i.e., December to February of each water year from 2010/2011 through to 2018/2019). The six scenarios on the x-axis represent 'Zero river pollutant loads' (q3O), 'Pre-Industrial' (q3p), 'Baseline' (q3b), 'minimum' (q3C), 'best-practice' (q3B) and 'innovative' (q3A) catchment and land management scenarios (Table 1).

3.5. Projected changes in Chl-a, TON and large zooplankton concentrations

In sharp contrast to the water quality response south of Cairns (Fig. 2a–f) (Baird et al., 2021), the response of mean simulated surface concentrations of Chl-*a*, TON, and large zooplankton to the catchment management scenarios within the initiation zone during the CoTS larval season is weak (Figs. 4a–e, S3–S8). These results are consistent with previous eReefs simulations, showing that land-based run-off influences inshore reef waters in the Wet Tropics region, with minimal to no influence on midshelf and offshore waters, respectively (Skerratt et al., 2019). The greatest differences occurred between the pre-industrial (q3p) and the baseline (q3b) catchment management scenarios, ranging from a 1 % increase for TON and large zooplankton, to a 3 % increase for Chl-*a*. Even adoption of the strongest catchment management scenario (q3A) is predicted to result in only minimal reductions in mean simulated surface concentrations, with only small (2 % for Chl-*a*) to negligible (<1 % for TON and zooplankton) reductions relative to the baseline condition. Indeed, reductions across all three land management scenarios are either extremely small (i.e., 0.003 μg/L for Chl-*a*, 0.017 μg N/L for TON; and 0.189 μg N/L for large zooplankton) or non-existent (Figs. S6–S8). Further, most of these minimal changes in water quality are occurring in a small area inshore and south from Green Island (Figs. 4a–e, S3–S8). Even so, the reduction in mean simulated surface Chl-*a* concentration was still only 20 % at most in this area and was minor or negligible throughout the rest of the initiation zone (Figs. 4a, b; S6). When only considering the small initiation zone (Fig. 1), the predicted changes in mean simulated surface concentrations for Chl-*a*, TON and zooplankton were negligible for all three land management scenarios (i.e., <1 %) (Table S5).

Similarly, the frequency of daily exceedances of the 0.45 μg/L Chl-*a* water quality guideline over 14-day CoTS larval periods during the larval season within the main initiation zone was only marginally reduced following adoption of the strongest catchment management scenario (q3A) (Figs. 6a, S9). Similar results were obtained for the other three Chl-*a* thresholds examined, namely 0.30, 0.20 and 0.10 μg/L (Figs. 6b–d, S10–12). Importantly, applying the lower Chl-*a* thresholds also corrected for potential model bias in under-prediction of Chl-*a* concentrations. Even in the most strongly affected parts of the initiation zone, near Green Island, this reduction was on average fewer than one day per season for the Chl-*a* 0.45 μg/L threshold (Figs. 6a, S9), and 8 days for the 0.30 μg/L threshold (Figs. 6b, S10). Although exceedance probabilities were higher for the lower Chl-*a* thresholds, differences between catchment management scenarios were negligible regardless of the threshold applied. When only considering the small initiation zone (Fig. 1), the predicted reduction in the mean proportion of this area exceeding the different Chl-*a* threshold concentrations, were small for all three land management scenarios (i.e., ≤12 %) (Table S5).

Combined, these results strongly suggest that, in the CoTS initiation zone, the response of CoTS larval food sources (Chl-*a*, TON), and their abundance (large zooplankton) to changes in catchment management and riverine loads is minimal if not negligible. These findings appear to be inconsistent with previous studies reporting that, in the summer-wet season, flood plumes reach the initiation zone (Brinkman et al., 2014; Furnas et al., 2013; Wooldridge and Brodie, 2015), and mean surface Chl-*a* concentrations are higher in the inshore and midshelf waters compared to waters in the outer region encompassing the initiation zone (Fabricius et al., 2010). (Furnas et al., 2013) stressed the importance of the timing and size of major flooding events influencing the CoTS initiation zone and subsequent primary outbreaks. The two recent major flooding events, in 2011 and 2019, met both conditions with the combined discharges of the Burdekin and Wet Tropics rivers well exceeding 10 km^3 from December to February (Queensland Government, 2022). However, the likelihood that reef waters encompassed by the initiation zone, as spatially defined in our study, would have been exposed to flood plumes enriched in nutrients, sediment, phytoplankton and dissolved

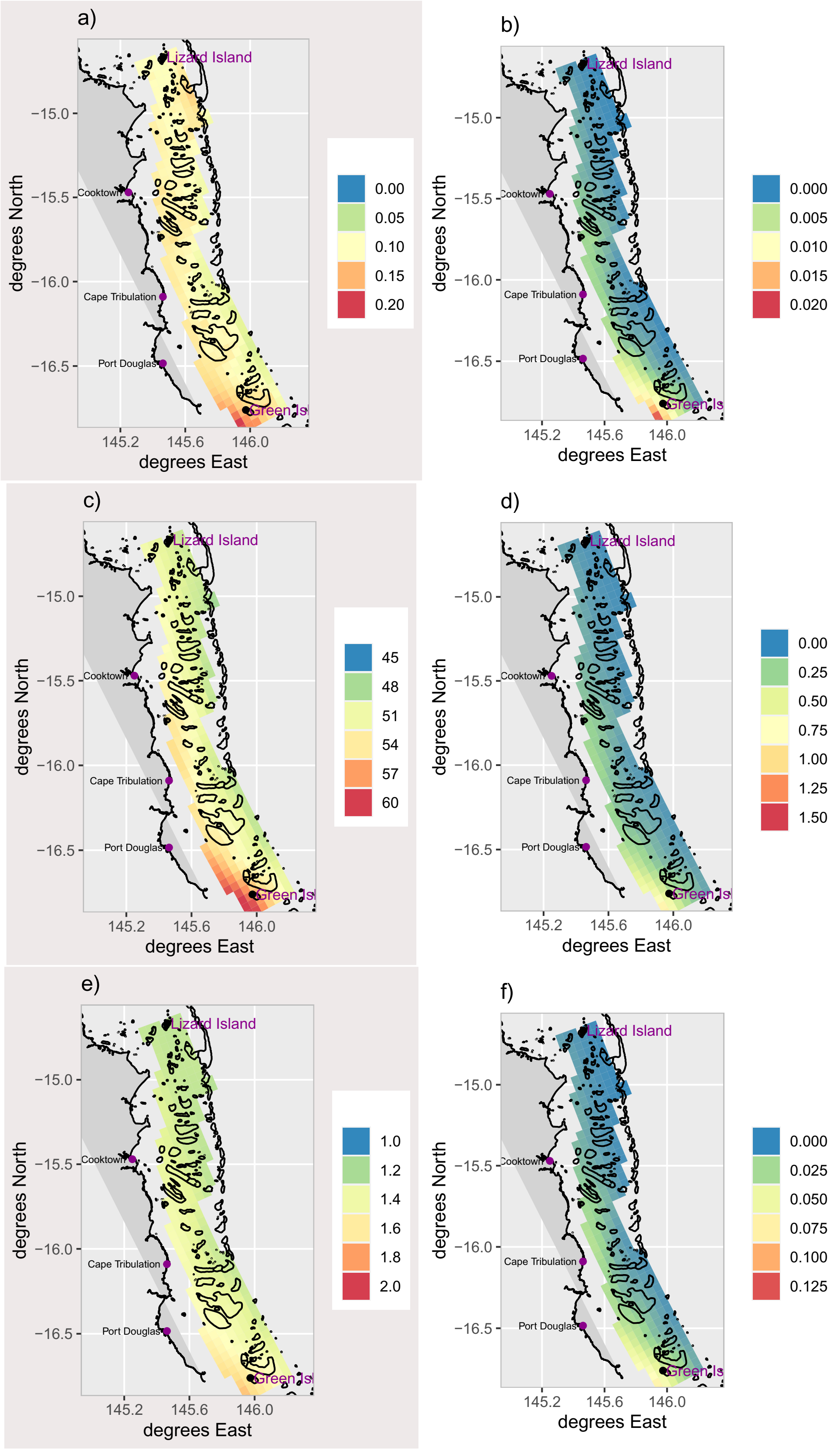

Fig. 4. Mean simulated baseline surface concentration (left; grey background) and reduction in mean simulated surface concentration under innovative land management (right; white background) of: (**a, b**) chlorophyll-*a* (Chl-*a*, μg/L; (**c, d**) Total Organic Nitrogen (TON, μg N/L); and (**e, f**) large zooplankton (μg N/L), in the CoTS initiation zone during the months when CoTS larvae are present (December to February). Mean simulated surface concentrations represent the 'baseline' scenario (q3b; 2019 catchment condition), with reductions following full adoption of the 'innovative land management' scenario (q3A). Details of all six catchment load scenarios are presented in Table 1, and results for all six scenarios in Supplementary Figs. S3–8.

organic matter (i.e. 'primary' and 'secondary' water types) would have been low for either flooding event (Devlin et al., 2013; Gruber et al., 2020). Further, reported mean surface Chl-*a* concentrations that are higher in the purported initiation zone are heavily influenced by samples collected in nearshore waters adjacent to (Brodie et al., 2007), and well south of (15.1°–19.2°S) (Fabricius et al., 2010) the initiation zone as defined here. Hence, the influence of riverine loads on water quality appears to be minimal in the CoTS outbreak initiation zone, even during major flooding events specifically purported to precede primary CoTS outbreaks. Previous eReefs simulation of the Wet Tropics region also showed that waters in the midshelf and outer regions were more affected by general oceanic processes (Skerratt et al., 2019).

3.6. *Resolving dominant environmental controls on the initiation zone*

In our final assessment, we aim to resolve the dominant environmental controls, e.g., terrestrial/riverine, marine and atmospheric, on mean surface concentrations of Chl-*a*, TON and zooplankton in the CoTS initiation zone. Within the main initiation zone, annual variability for the spatially averaged means of simulated surface concentrations of Chl-*a*, TON, and large zooplankton was generally low (Standard Deviation = 0.02 μg/L, 1.18 μg N/L and 0.13 μg N/L, or 18 %, 10 % and 2 %, respectively), irrespective of the catchment management scenario examined, except in 2011 and 2016 (Fig. 5). These two years coincided with strong climatic forcing associated with the ENSO. The Southern Oscillation Index (SOI) for December to February showed the strongest La Niña event on record in 2011 (1987–2021), and the fifth strongest El Niño event on record in 2016 (Bureau of Meteorology, 2021). Relative to the means for other years, mean Chl-*a* was over two-fold higher in 2011 (0.22 μg/L) and 50 % lower in 2016 (0.05 μg/L). TON and large zooplankton showed similar trends but much lower variability between years, with mean TON 17 % higher in 2011 and 6 % lower in 2016, mean large zooplankton 48 % higher in 2011 and 26 % lower in 2016, relative to other study years. Annual variability in the smaller initiation zone was comparable to or marginally lower than that observed in the large initiation zone.

Major climatic drivers such as the ENSO influence rainfall and therefore riverine loads from catchments discharging into the GBR (Dey et al., 2019; McCloskey et al., 2021). However, ENSO also directly influences the initiation zone by affecting sea temperature, wind patterns, tropical cyclone activity and nutrient input due to upwelling and ocean currents (Benthuysen et al., 2016; Wijeratne et al., 2018; Wooldridge and Brodie, 2015). Comparison of eReefs model results between years of different climate forcing following Eq.1 revealed large anomalies in mean Chl-*a* concentrations in 2011 and 2016, combined with low variability between model scenarios within these and all other years (Fig. 5). In 2011, the analogous positive anomaly in Chl-*a* for both the 'zero river pollutant load' (0.11 μg/L) and the baseline (0.12 μg/L) scenarios implies that only 8 % of the observed increase in Chl-*a* could possibly be attributed to riverine nutrient loads. The same comparison for 2016 shows that about 8 % of the negative anomaly in Chl-*a* could possibly be attributed to riverine nutrient loads. Anomalies for other model terms were similar to Chl-*a*; the proportion of TON and large zooplankton that could be attributed to riverine loads in 2011 was 18 % and 7 % respectively, and 12 % and 9 %, respectively, in 2016. These results suggests that marine and atmospheric forcing rather than riverine forcing are the dominant controls on planktonic biomass in the CoTS initiation zone. This apparent role of marine and atmospheric forcing is consistent with a prior assessment of nutrient and plankton dynamics using eReefs showing that dissolved organic nitrogen and Chl-*a* in the outer reefs and middle-to-outer lagoon reflected dominance of general oceanic processes, even during the strong La Niña in 2011 (Supplementary Text, Fig. S14) (Skerratt et al., 2019).

Finally, eReefs model terms (mean Chl-*a*, TON and large zooplankton) within the CoTS initiation zone showed good linear correlations with riverine nutrient loads (TDN, TDP) from the baseline (q3b) GBR Dynamic SedNet model scenario ($R^2 = 0.69$ to 0.84, Fig. S13) when all study years were considered. However, this correlation was highly dependent on extreme values in 2011 when covariance in marine and riverine forcing within the coastal zone would be expected due to large-scale climatic forcing associated with the strongest El Niño on record (Bureau of Meteorology, 2021). If 2011 is excluded, then mean simulated surface concentrations in the initiation zone showed poor correlations with riverine nutrient loads ($R^2 = 0.03$ to 0.21; Fig. S13), even without excluding the strong La Niña conditions in 2016. Riverine nutrient loads during these study years spanned from the 13th to 96th percentile of baseline loads (December to February) during GBR Dynamic SedNet years (1987 to 2018). It follows that mean simulated surface concentrations in the initiation zone are likely to be poorly correlated with riverine loads in all except the most extreme years. However, even during the extreme 2011 flood event, the modelled Chl-*a* response (0.22 μg/L) is still only half the concentration of the 0.45 μg/L water quality guideline for GBR midshelf waters (Great Barrier Reef Marine Park Authority, 2010), and is representative of a wet season water type with slightly above ambient water quality concentration (i.e. 'tertiary' water types (Devlin et al., 2013; Waterhouse et al., 2021). Mean salinity of >34 ‰ in the main initiation zone during the December–February period in 2011 further indicates the lack of direct influence of flood plumes during extreme wet years. Further, in these extreme years, e.g., with strong ENSO events, climatic forcing on scales

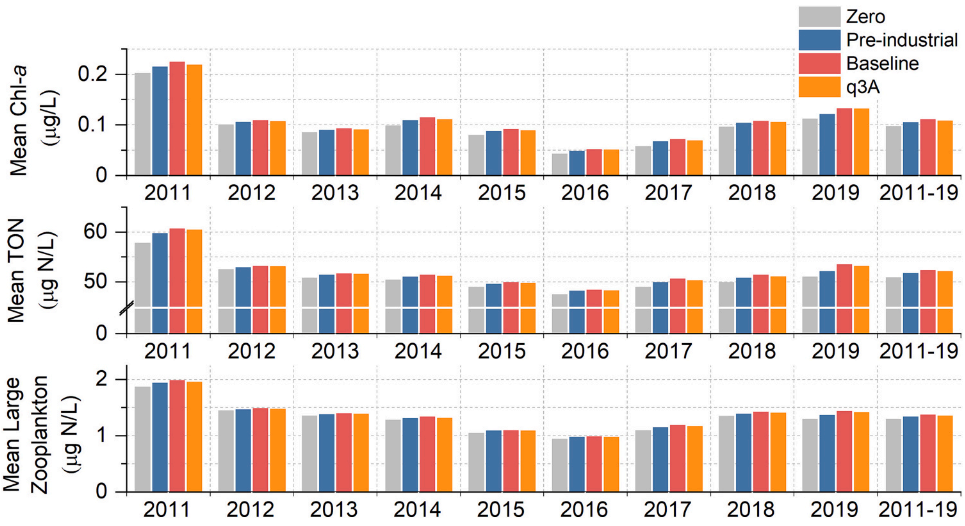

Fig. 5. Year-to-year variability in mean simulated surface concentrations of chlorophyll-*a* (Chl-*a*, μg/L), total organic nitrogen (TON, μg N/L), and large zooplankton (μg N/L), within the main CoTS initiation zone during the months when CoTS larvae are present (December to February), from 2010/2011 to 2018/2019. Multi-year (2011–2019) mean simulated surface concentrations are presented for comparison. The four colours represent (from left to right) 'zero river pollutant loads' (q3O), 'pre-industrial' (q3p), 'baseline' (q3b), and 'innovative' (q3A) catchment and land management scenarios (Table 1).

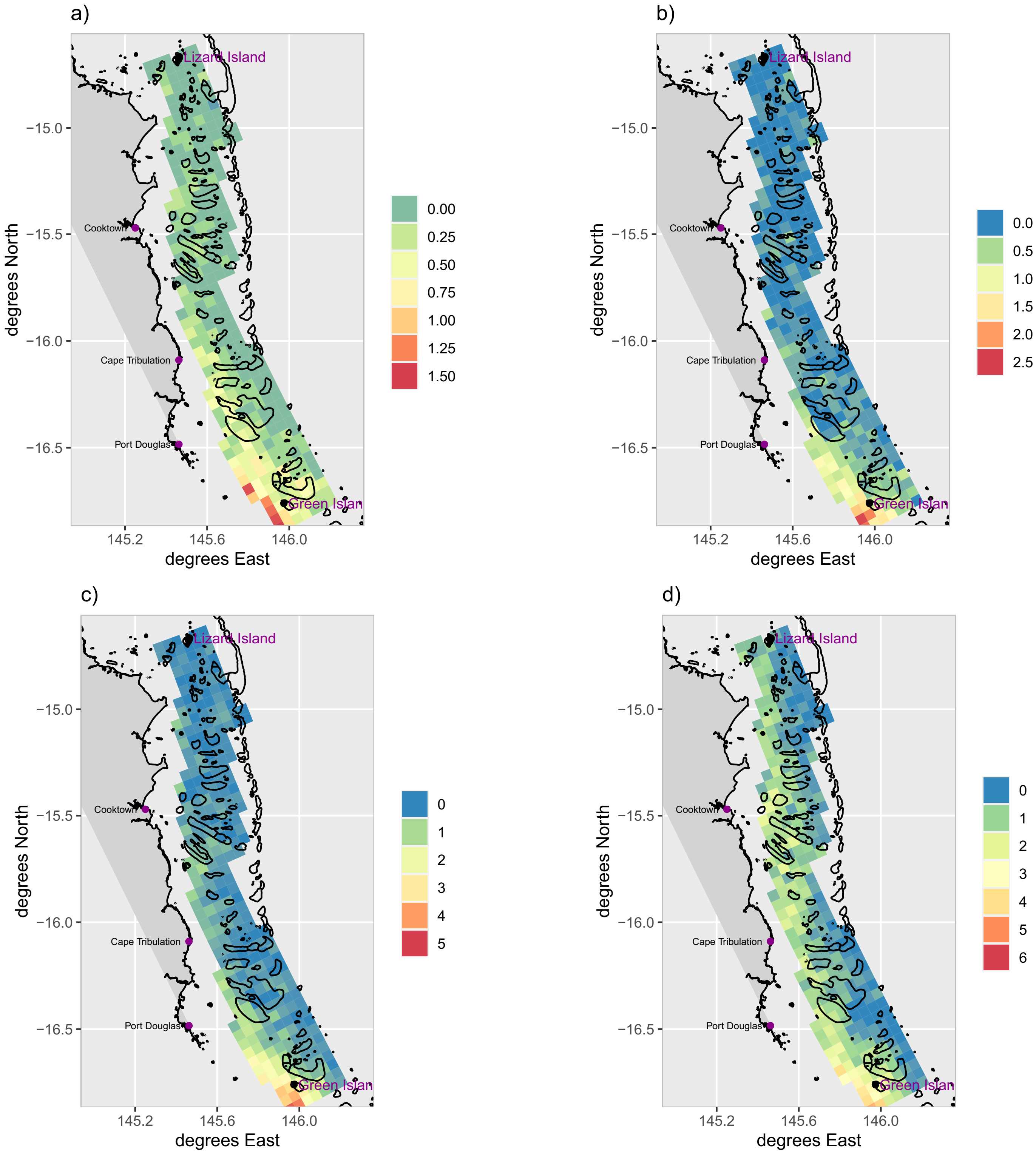

Fig. 6. Reduction in mean annual number of days that mean simulated surface concentrations of chlorophyll-a (Chl-*a*), during the months when CoTS larvae are present (December to February), exceed the (**a**) current 0.45 μg/L water quality guideline, and the additional thresholds examined, namely (**b**) 0.30 μg/L, (**c**) 0.20 μg/L, and (**d**) 0.10 μg/L. Reductions follow full adoption of the ‘innovative land management’ scenario (q3A), relative to the ‘baseline’ scenario (q3b; 2019 catchment condition). Details of all six catchment load scenarios are presented in Table 1, and results for all six scenarios in Supplementary Figs. S9–S12. Note that each panel uses a different colour scale to avoid obscuring spatial patterns.

much larger than the GBR region alone are likely to result in covariance of marine and riverine drivers in the coastal zone. While there is likely to be greater fine-scale spatial and temporal variability in GBR surface waters during stronger forcing, results from the models support the overall dominance of marine forcing on mean Chl-*a*, TON, and large zooplankton within the initiation zone.

4. Conclusion

In summary, our findings show that modelled reductions of catchment river loads result in only small to negligible improvements in water quality within a region that circumscribes the CoTS outbreak initiation zone during the months that CoTS larvae are present. The modelled response of Chl-*a*, TON and large zooplankton concentrations to catchment load reductions was consistently weak, even between the most contrasting catchment management and river load reduction scenarios (q3O, q3b), and during major flooding events purported to precede CoTS outbreaks (2011). Recent modelling studies found that proposed changes in catchment management will improve water quality in coastal waters south of Cairns, and to a lesser degree in waters inshore of the CoTS initiation zone (Baird et al., 2021; McCloskey et al., 2021; Waters et al., 2020). We applied these existing and published scenario simulations to the spatio-temporal characteristics of primary CoTS outbreaks on the GBR, following comprehensive reviews of the scientific and technical literature, including publicly available CoTS monitoring information (Australian Institute of Marine Science, 2020). Ours is the first study to specifically define the spatial extent of the CoTS outbreak initiation zone (Table S1 and references therein), enabling a more targeted analysis of current water quality conditions and the potential for further improvements within this zone. Second, we appraised the seasonal presence and duration of the CoTS larval period (Table S2, S3 and references therein), based on their detection in GBR waters using genetic markers (Uthicke et al., 2015a; Uthicke et al., 2019) and recent larval rearing experiments (Uthicke et al., 2018; Wolfe et al., 2017). Third, our summary of the reported effects of different Chl-*a* concentrations on CoTS larval development and survival (Table S4 and references therein) corroborates (Wolfe et al., 2017) that Chl-*a* thresholds may be lower than previously appreciated (Fabricius et al., 2010; Okaji, 1996), or may be a simplification that does not fully represent CoTS larval ecology (Pratchett et al., 2017b; Uthicke et al., 2018). Applying these lower Chl-*a* thresholds in our analyses, we still only found minimal to negligible changes in Chl-*a* concentrations, and in TON that captures additional potential food sources (Lucas, 1982; Moran, 1986; Olson, 1987). This suggests that food limitation for CoTS larvae, at least in the CoTS initiation zone and based on Chl-*a* and TON levels, may not be an issue (Carrier et al., 2018), unless nutrient sources other than land-based runoff are critical. While our use of surface concentrations is supported by CoTS larvae spending most of their planktonic stage at or near the surface (Birkeland and Lucas, 1990; Keesing et al., 1997; Lucas, 1982; Moran, 1986; Olson, 1985; Uthicke et al., 2015a; Yamaguchi, 1973), a 3-dimensional re-analysis is warranted to further examine the abundance and distribution of CoTS larvae, in combination with the role of nutrients from marine sources, such as upwelling and resuspension of remineralised material previously deposited in sediment stores (Benthuysen et al., 2016; Brodie, 1992; Wijeratne et al., 2018; Wooldridge and Brodie, 2015), influencing water quality in the CoTS initiation zone. Previous studies have posited a potential role of marine upwelling in driving persistent CoTS outbreaks on offshore reefs in the Swain section (22.0°S) of the GBR (Brodie et al., 2005; Pratchett et al., 2014).

Water quality improvement is one of the three management approaches to reduce the detrimental impacts of CoTS outbreaks on the GBR (Westcott et al., 2020), together with direct manual control (Rivera-Posada et al., 2014; Westcott et al., 2021) and MPA zoning (Kroon et al., 2021). Recent work has demonstrated that direct manual control is effective in protecting coral on the GBR when conducted within an integrated pest management control program (Westcott et al., 2021). Further, the significantly lower CoTS abundance on reefs closed to fishing compared to those open to fishing strongly supports targeted fisheries management to effectively reduce the detrimental impacts of CoTS outbreaks on the GBR and across the Indo-Pacific (Kroon et al., 2021; Kroon et al., 2020). The findings of our current study, however, do not appear to support a strong role of water quality improvement in effectively managing the initiation of primary CoTS population outbreaks on the GBR. Continued efforts to improve water quality remain nevertheless critical to reduce local pressures on the freshwater, coastal and marine ecosystems of the GBR region (Waterhouse et al., 2017). We acknowledge that our analysis omits aspects of CoTS larval development and distribution that may be relevant, and a more detailed analysis that considers spatio-temporal variations in CoTS larvae and phytoplankton abundance, including the cumulative impact of spatial and temporal variations in water quality over the full duration of the CoTS larval phase is warranted. Finally, water quality improvement in the central GBR is predicted to occur following reductions in catchment nutrient and sediment loads (Baird et al., 2021). Whether secondary CoTS outbreaks on the central mid-shelf reefs of the GBR would be influenced by such predicted water quality improvements (Brodie et al., 2017c), could be examined by applying the existing and published scenario simulations to the specific spatio-temporal characteristics of secondary outbreaks.

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Frederieke J. Kroon: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Joseph R. Crosswell:** Methodology, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Barbara J. Robson:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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