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# Reef state and performance as indicators of cumulative impacts on coral reefs

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ABSTRACT

Coral bleaching, cyclones, outbreaks of crown-of-thorns seastar, and reduced water quality (WQ) threaten the health and resilience of coral reefs. The cumulative impacts from multiple acute and chronic stressors on "reef *State*" (i.e., total coral cover) and "reef *Performance*" (i.e., the deviation from expected rate of total coral cover increase) have rarely been assessed simultaneously, despite their management relevance. We evaluated the dynamics of coral cover (total and per morphological groups) in the Central and Southern Great Barrier Reef over 25 years, and identified and compared the main environmental drivers of *State* and *Performance* at the reef level (i.e. based on total coral cover) and per coral group. Using a combination of 25 environmental metrics that consider both the frequency and magnitude of impacts and their lagged effects, we find that the stressors that correlate with *State* differed from those correlating with *Performance*. Importantly, we demonstrate that WQ metrics better predict *Performance* than *State*. Further, inter-annual dynamics in WQ (here available for a subset of the data) improved the explanatory power of WQ metrics on *Performance* over long-term WQ averages. The lagged effects of cumulative acute stressors, and to a lesser extent poor water quality, correlated negatively with the *Performance* of some but not all coral groups. Tabular *Acropora* and branching non-*Acropora* were the most affected by water quality demonstrating that group-specific approaches aid in the interpretation of monitoring data and can be crucial for the detection of the impact of chronic pressures. We highlight the complexity of coral reef dynamics and the need of evaluating *Performance* metrics in order to prioritise local management interventions.

## 1. Introduction

Coral reefs in all tropical oceans are under pressure from a variety of local (e.g., runoff, fishing) and global (global warming, cyclones) pressures leading to progressive coral loss, the so-called 'coral reef crisis' (Pandolfi et al., 2003). Understanding cumulative impacts from multiple stressors is critical for successful management of coral reefs (Anthony et al., 2013). Although cumulative impacts have been identified as key drivers of reef health, there are still large knowledge gaps in our understanding of both the effects of individual stressors and the interplay of local and global stressors on the health and resilience of reef ecosystems (Ban et al., 2014; Harborne et al., 2017). Coral cover as a proxy for *State* is the most common metric used to evaluate reef health, however reef resilience largely depends on reef recovery potential after disturbance (Osborne et al., 2017). Measuring how reef recovery compares with the expected reef growth potential (i.e., expected in the absence of stressors) can provide information about changes in *Performance* over time. The impact of multiple stressors on both indicators of reef health, measured as *State* and *Performance,* has rarely been assessed simultaneously (Thompson et al., 2020).

The frequency and magnitude of stressors are critical for evaluating impacts on ecosystem responses (Connell et al., 1997; Hall et al., 2012;

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Mellin et al., 2019b). Contrasting sensitivities of coral communities further contribute to variation in: i) magnitude of impacts (Madin et al., 2014; Hughes et al., 2018b; Mellin et al., 2019b), ii) coral recovery potential (Osborne et al., 2017; Ortiz et al., 2018; Mellin et al., 2019a) and iii) the interactions among global-acute stressors (Ban et al., 2014; Vercelloni et al., 2017) and local stressors (Fabricius et al., 2010; Oxenford and Vallès, 2016; Sully and Woesik, 2020; Wooldridge and Done, 2009). The increased frequency of intense cyclones and mass bleaching events due to heat stress are also threatening the persistence of coral reef communities (Emanuel, 2005; Hughes et al., 2018a). Specifically, on the Great Barrier Reef (GBR), the world's largest coral reef ecosystem and a World Heritage site these two acute stressors, as well as the outbreaks of crown-of-thorns starfish (CoTS) have caused simultaneously massive impacts along and across the entire extent of the ecosystem. However, these impacts vary spatially and temporally (Osborne et al., 2011; Mellin et al., 2019b) due to variations in impact intensity, spatial extent, and frequency (e.g. De'ath et al., 2012; Puotinen et al., 2016, 2020). The overall decline in total coral cover in the GBR Marine Park due to multiple stressors has been well documented (De'ath et al., 2012). However, cumulative impacts on the *Performance* of specific coral groups has been less explored.

Measuring the contribution of water quality (WQ) to the *State* and *Performance* of the GBR at a regional scale has proven challenging, with studies reporting contrasting conclusions regarding the relative importance of different WQ parameters on the GBR (Lam et al., 2018; Ceccarelli et al., 2019; MacNeil et al., 2019; Mellin et al., 2019a). Reduced water quality in inshore areas of the GBR Marine Park is a result of the increased loads of fine sediment, nutrients, and pesticides discharged from land use changes in the GBR catchment (Brodie and Fabricius, 2008; Kroon et al., 2012). Specifically, terrestrially-sourced dissolved inorganic nitrogen (DIN) may be linked to increased frequency of CoTS through proliferation of phytoplankton as larval food (Fabricius et al., 2010; Wooldridge and Brodie, 2015; Brodie et al., 2017), and to increased susceptibility of scleractinian coral to bleaching and disease prevalence (Wooldridge and Done, 2009; Wiedenmann et al., 2013; Morris et al., 2019). River runoff reduces WQ by affecting parameters such as light availability and salinity, which are drivers of reef health (De'ath and Fabricius, 2008; Fabricius et al., 2013, 2016). While there is empirical data linking poor WQ to decreasing coral health (Berkelmans et al., 2012; Humanes et al., 2017a, 2017b), the link to reductions of coral cover on the GBR is less clear (Fabricius et al., 2012). For example, while the abundance of juvenile corals is negatively affected by increases in Chlorophyll-a and total suspended solids, adult populations are unaffected (Thompson et al., 2014). In addition, challenges for evaluating WQ include the availability of data at relevant spatial and temporal scales, the use of different metrics, and the fact that multiple WQ variables are highly correlated with each other. As a result, the effect of WQ on the GBR has often been assessed using proxies such as Secchi depth (Lam et al., 2018) or a single compound metric (MacNeil et al., 2019; Mellin et al., 2019a). However, because impacts likely differ among taxonomic groups (De'ath and Fabricius, 2008; Fabricius et al., 2012) given differences in traits such as growth rate, depth range, and colony morphology among others (Madin et al., 2016) the evaluation of a single compound WQ variable may be of limited use to identify the most likely mechanisms of regional coral degradation. Assessment of impacts from specific WQ variables aids with identification of key environmental parameters for monitoring and targeted management.

Here, we applied a comprehensive approach to improve our understanding of cumulative impacts of multiple stressors on reef ecosystems by using state-of-the-art data characterizing the abiotic environment and disturbance regime from two regions of the GBR. We combined i) 25 years of coral cover data evaluated at the level of four morphologically different coral groups (i.e., *Acropora* tabular, *Acropora* branching, other branching corals, and massive/submassive/encrusting corals), ii) the exposure of 122 reefs to acute disturbances using intensity and frequency metrics and iii) multiple environmental drivers and indicators of water quality. Importantly, we compare cumulative impacts of acute disturbances and WQ on two reef metrics: *State* (i.e., coral cover) and *Performance* (an index based on growth model predictions introduced by Thompson et al., (2020)). We assessed these responses separately on the total coral community and per each coral group. We specifically assess Acroporids (tabular vs branching) because they are among the most sensitive species to the impacts of coral bleaching (Hughes et al., 2018b), cyclones (Adjeroud et al., 2009) and CoTS (Pratchett et al., 2017).

Our study aimed to assess 1) whether *Performance* is a better indicator of cumulative impacts than the commonly used *State* metric or whether both metrics together can provide a more meaningful measure of impacts from multiple stressors and 2) whether divergent responses to multiple stressors by different coral groups are being masked, when metrics encompass the total coral community (as most frequently done for the GBR). We also explicitly test the importance of improved temporal resolution in WQ data by comparing models with long-term averages vs. yearly WQ data which at the scale of individual reefs is often limited for long-term studies. Considering two indicators of reef health (*State* and *Performance*), and many possible combinations of stressors (acute + several metrics describing different aspects of water quality), we identify and quantify the contribution of stressors that jointly have the best explanatory value for the *State* and *Performance* of GBR reefs, to inform better targeted management options.

## 2. Methods

### 2.1. Reef responses

The impact of multiple stressors on corals was evaluated using two reef metrics: '*State*' i.e., observed coral cover, and '*Performance*', an index reflecting deviation from expected change in cover provided no acute disturbances occurred. Absolute percentage coral cover data were obtained on an annual or biannual basis for 122 reefs (335 reef sites) by the AIMS Long-Term Monitoring Program (LTMP) and Marine Monitoring Program (MMP) between 1992 and 2017. Reef specific time series vary in length depending on the starting date of monitoring programs. Coral cover was estimated at 5–9 m depth from replicated permanent photo- and video belt transects at each site using photo-point intercept methods (see Abdo et al., 2004; Jonker et al., 2008 for methods). Total coral cover and cover of four specific coral groupings, namely *Acropora* tabular, *Acropora* branching, other (non-*Acropora*) branching, and non-*Acropora* massive/submassive and encrusting species (MSE) were used for this study. We identified the most common taxa which were then grouped based on taxonomy and colony morphology (relevant for growth rate estimates). Free-living growth forms and foliose species with low abundance were only included in total coral cover estimates (Table S1). Reefs were separated in two main regions for analyses: Central [16–21°S] and South [21–25°S] GBR.

Here "*Performance*" is interpreted as an index of reef functioning that evaluates, within each region (Central and South), the observed *State* (i.e. for total coral cover and that of each coral group) relative to the expected *State* based on model predicted rates of coral cover increase (Thompson et al., 2020). Predicted rates of coral cover increase where derived by fitting Bayesian Gompertz equations to a subset of the monitoring time-series between 1992 and 2001. The same form of equation was applied for each coral group:

$$lnCGroup_t = r_{CGroup} + lnCGroup_{t-1} + \left(-r_{CGroup}/lnK\right) \times ln(HC_{t-1} + SC_{t-1}) + \varepsilon$$

where, $CGroup_t$ is the group-specific cover at time $t$, SC = soft corals, HC = all hard corals and $K$ is the community size at equilibrium (100 – the cover of loose silt and sand substrate). Prior to model fitting, the observed changes in coral cover at each reef were standardised to 1 year intervals (i.e. 365 days) since the previous observation to account for variability in the time spanned between consecutive surveys.

Observations directly following a known acute disturbance were excluded, as per Thompson and Dolman (2010). The use of pre-2002 data for model parameterization was based on previous work showing large reductions in GBR reef recovery rates after the mass bleaching event that took place in 2002 (Osborne et al., 2017; Ortiz et al., 2018). This approach allowed us to retain enough data to include in the models assessing impacts on *Performance* because only years not used in the parameterisation of expected cover (i.e., from 2002 onwards) and with no acute disturbance were used for modelling *Performance* (Central = 885 observations, South = 747 observations). Importantly, while only a small portion of inshore reefs were sampled during the early part of the study period (Central = 330 observations, South = 311 observations) we did not find any bias in the calculation of *Performance* due to shelf position that could limit the interpretation of results (Fig. S1).

Specific modelled rates of coral cover increase for each coral group within regions were estimated for each site using the observed coral cover in year $x$ to calculate the expected coral cover in year $x + 1$ to obtain the group-specific expected coral cover over the evaluated period. For total *Performance* (i.e., including all surveyed coral species), a separate parameterisation of the Gompertz model was obtained differentiating the rates of coral cover increase for Acroporidae vs. all other hard coral families, which were then combined for predicting the total cover population growth rate (as per Osborne et al., 2017; Thompson et al., 2020). The location of the observed coral cover relative to the distribution of expected cover was used to scale reef *Performance* for the total coral community and per coral group using a quantitative score system (0–1) (as per Thompson et al., 2020, Table 1). Due to low growth rates for MSE, the distribution of expected changes in cover for this group had a low median and narrow range, meaning that the relative variability in scores due to sampling error rather than change is higher for this group. To reduce variability in scores for MSE the thresholds for scoring where broadened (Table 1). For years where there was no survey, each reef was scored based on the mean score value of the previous year(s) (lag-1 or lag-2 if necessary), i.e. assumes consistent growth since the last observation.

### 2.2. Acute disturbance data

Temporally and spatially explicit acute disturbance data was either collated from existing sources or generated for this study (Table 2). Metrics of acute disturbances include measures of the magnitude and frequency (i.e. presence/absence) of exposure. CoTS densities were collected along the coral cover transects (MMP) and during AIMS manta-tow surveys (LTMP reefs). Data from each survey technique was combined by standardising transect CoTS densities to manta tow area and correcting for sampling bias due to higher detectability (by a factor of 9.3) on transects compared to manta tows (AIMS, unpublished data). To

**Table 1**
Criteria to scale *Performance* based on the location of observed cover relative to the distribution of expected cover (based on Thompson et al. 2020). MSE = massive/submassive/encrusting corals. Upper and lower boundaries include 95% of the distribution of predicted changes in cover.

| *Performance* score | | Observed cover change between surveys |
|---|---|---|
| Better than expected | 1 | Greater than double (or triple for MSE) the upper boundary of expected distribution |
| | 0.9 | At double (or triple for MSE) the upper boundary of expected change |
| | 0.8 | Between upper and double (or triple for MSE) the upper |
| | 0.7 | boundary of expected change |
| Expected | 0.6 | Equal to upper boundary of expected change |
| | 0.5 | At the median of expected change |
| | 0.4 | Equal to lower boundary of expected change |
| Worse than expected | 0.3 | Below lower boundary of expected change |
| | 0.2 | |
| | 0.1 | No change |
| | 0 | Decline |

predict CoTS on reefs and years with no survey data, we used spatio-temporal Inverse Distance Weighting analysis with the function *idwST* from the R-package *geosptdb* which considers the value of a point from the weighted (with power value = 2) averages of values of the nearest neighbours (n = 3) in terms of the spatio-temporal locations (time factor = 1) (Melo and Melo 2015). Frequency of CoTS outbreaks was determined as a factor additional to CoTS density, with an outbreak defined as CoTS densities > 0.22 individuals per tow (Moran and De'Ath 1992).

Site-level frequency of storms and bleaching-risk events were derived from GBR-wide models of cyclone and heat stress (Degree Heating Week, DHW) exposure as presence/absence data (Table 2). GBR-wide model predictions may not capture disturbance observed at the scale of sites, for what frequency data was adjusted with field observations to better represent true disturbances. For example, cyclone exposure which measures hours of damaging waves based on wave height thresholds (Puotinen et al., 2016) can sometimes understimate the true wave climate when swell waves track beyond the storm or non-cyclone winds help build waves. 'Frequency of storm impacts' therefore includes the AIMS *in situ* observation of storms as agents of coral mortality that were not captured in cyclone layers. Frequency of bleaching or bleaching-risk mortality events was considered for DHW above 3 (Hughes et al., 2018b), but because satellite-derived data may fail in capturing *in situ* conditions and coral bleaching can also be caused by other environmental stressors, our bleaching-risk metric was complemented by AIMS *in situ* records of bleaching causing coral mortality even at DHW below 3.

Exposure to acute disturbances was assigned to each reef site and year relative to the date of benthic surveys. If the disturbance occurred before the survey on a given year, that disturbance was assigned to the year of the survey; if the disturbance occurred after the survey that same year, the disturbance was assigned to the following year. The frequency of each acute disturbance and its cumulative lagged effects were evaluated using windows of 1, 3 or 5 years (Table 2). Time windows were chosen given the average temporal gap between consecutive surveys for a given reef and the availability of historical data for testing lagged effects. Cumulative effects of all disturbances combined (i.e., CoTS outbreaks + storms + bleaching) were also evaluated. The rationale for this metric is to represent the combined effects of recurrent acute disturbances and the critical role of recent history for the *State* and *Performance* of coral reefs.

### 2.3. Environmental and local disturbance data

Thresholds of water quality that correlate to negative impact on corals may depend on the time window evaluated (i.e., annual vs. seasonal average) (De'ath and Fabricius, 2008). Therefore, we focused on the WQ environment associated with the wet-season (i.e., Dec-April) to better assess the influence of pollutants from catchment run-off and its importance in predicting *State* and *Performance* at the scale of GBR regions (Fig. 1). The selected WQ variables (Table 2) are known to have a direct and strong effect on coral health and have been targeted for management (Brodie et al., 2016). For example, Chlorophyll-a, provides an estimate of phytoplankton biomass associated to river discharge (Brodie et al 2016). Reductions in coral recruitment and loss of species diversity have been associated with elevated sedimentation and eutrophication whereas light reduction from turbidity reduces calcification and shifts in coral community structure (Fabricius, 2005). Salinity was represented as a cumulative index based on the number of days of exposure to low (<30 PSU) salinity by adding the salinity units below 30 for every day that salinity was below this threshold (i.e., $\sum$ (30 − salinity) × days) following Berkelmans et al., (2012) and Brinkman et al., (unpublished data). Metrics of environmental DIN are likely poor representatives of terrestrially-sourced DIN as DIN is rapidly bio-assimilated (Brodie et al., 2016). Therefore, we explored an additional metric of nutrients, river DIN (as per Wolff et al., 2018), which reflects the total river DIN load that enters the system in runoff and

**Table 2**

Summary of acute disturbances and environmental variables selected for modelling. Shaded columns indicate the years of available data. Metric descriptions correspond to each available (i.e., shaded) year. In the absence of yearly WQ data (i.e., non-shaded years), long-term averages were used for the first set of analyses (1992–2017). Yearly data for all drivers was used for the second set of analyses (2010–2017).

| Time-series | Year | 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 |
|---|---|---|
| | Variables | metrics |
| Acute disturbances | [a]Heat stress (DHW) | Annual maxima and that of the previous year (i.e., 1yr-lag) |
| | [*a-b] Bleaching risk (Occurrence of bleaching in-situ and DHW >3) | Annual, 1-yr lag, 3yr and 5yr-cumulative sum |
| | [*a] Cyclones (hours of waves >4m height) | Annual, 1-yr lag and 5yr-cumulative sum |
| | [*a-b] Storm events (Ocurrence of Cyclones + storms evidenced in-situ) | 5yr-cumulative sum |
| | [*b] CoTS density (Individuals per manta tow) | Annual average and 1yr-lag |
| | [*b] CoTS Outbreaks (>0.22 Ind. per manta tow) | Annual, 1-yr lag and 5yr-cumulative sum |
| | [*a-b] Total Acute events (bleaching-risk events + Storm events + CoTS outbreaks) | Annual, 1-yr lag and 5yr-cumulative sum |
| Water quality (WQ) | [c] Daily light PAR mol photons $m^{-2}$ $d^{-1}$ | Annual wet-season (Dec-April) average, 8m depth |
| | [d] Chlorophyll a (Chla) $mg.m^{-3}$ | Annual wet-season (Dec-April) average, 5m depth |
| | [d] Fine Suspended Sediments $kg.m^{-3}$ | |
| | [d,*e-f] Salinity Index Cumulative exposure to salinity <30 PSU (PSU $Days^{-1}$) | |
| | [d] Environmental DIN (DINe) $mg.m^{-3}$ | |
| | [*g] Total DIN in river discharge runoff (River DIN) $mg.m^{-3}$ | Annual wet-season (Dec-April) average |
| Zoning | [*h] Fisheries management status (Zone) | Before /after re-zoning in 2004: OO: always open to fishing, CC: always closed, OC: open, then closed , CO: closed, then open |
| Spatial | [a] Distance to coast (degrees) | Minimum distance to the coast |

*This study, based on; [a]Mathews et.al. 2019; [b]AIMS LTMP/MMP surveys; [c]Magno-Canto et.al. 2019; [d]eReefs BGC v 2.0 (Steven et al. 2019, Baird et al. in press); [e]Berkelmans et al. 2012; [f]Brinkman et al. unpublished; [g]Wolff et al. 2018; [h]GBRMPA 2019

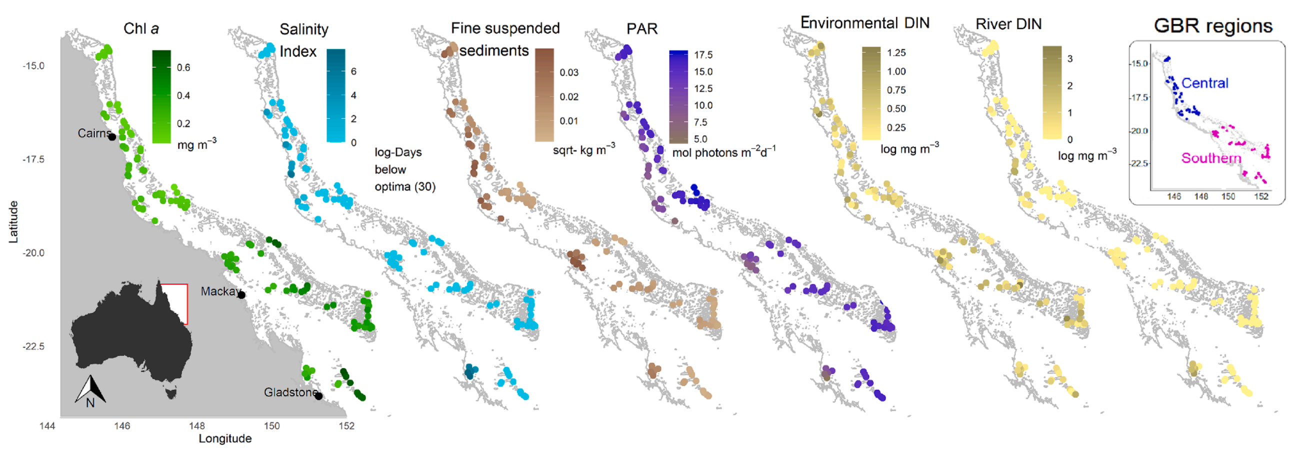


**Fig. 1.** Spatial variability in WQ metrics. Values represent reef-level long-term means from 2010 to 2017 except for River DIN available from 1992 to 2017. Chlorophyll *a* (mg $m^{-3}$ Chl *a*), Salinity Index (days below optima), Fine suspended sediments (kg $m^{-3}$) and environmental DIN (mg $m^{-3}$) were extracted at 5 m depth from GBR4 eReefs models. PAR (mol photons $m^{-2}$ $d^{-1}$) corresponds to light at 8 m depth based on Magno-Canto et al. (2019). River DIN (mg $m^{-3}$) represents the total concentration of N derived from river discharge DIN (based on Wolff et al. 2018). Reef location per region indicated in top right inset map. Some scales are transformed for visualization.

reaches each reef in any form (Fig. 1). River DIN is based on the yearly (wet-season) volume of discharge of all the rivers (from 1992 to 2017) that influences each reef based on circulation models and estimated DIN concentrations at each river mouth (Wolff et al., 2018) and it is the only WQ metric used here with yearly data available throughout the whole time-series (Table 2). Minimum distance to the coast (selected among other distance metrics based on correlation coefficients, Fig. S2) accounts for inherent geomorphological characteristics that may affect the reef response to disturbances. Categorization of reef management status accounts for the relative importance of fishing management in explaining *State* and *Performance* (Table 2).

## *2.4. Statistical analyses*

The relative importance of multiple stressors on the *State* and *Performance* of the GBR was analysed separately per coral group within each region (i.e., 5 coral groups × 2 regions × 2 response metrics = 20 models). Two sets of data were considered for analyses: The first set which includes long-term wet-season averages for most WQ metrics except river DIN, was used for modelling *State* (from 1992 to 2017) and *Performance* (from 2002 to 2017) (Table 1, Fig. 1). The second set which includes yearly data for all WQ variables was only used for modelling *Performance* from 2010 to 2017 (Table 1). This shorter dataset consisted in 123 and 117 observations for Central and Southern GBR respectively. The intention of this set of models was to test the potential limitations in evaluating the relative importance of WQ metrics for *Performance* in long-term cumulative impact assessments, where year to year variability in environmental data was often lacking. Models comparing WQ data were restricted to the same period (i.e. 2010–2017).

We used a full-subset model selection approach that allows testing all possible combinations of the predictor variables with generalised additive mixed models (GAMMS) (Fisher et al., 2018). *State* and *Performance* were modelled independently for each coral group and region due to the strong regional differences in disturbance patterns and water quality. Site-level (the lowest replication unit) *State* was modelled as absolute proportional cover of each coral group. Both *State* and *Performance* metrics were bounded between > 0 and < 1 and fitted with Beta distribution. We identified the predictors considered for modelling based on the correlation coefficients among all variables (Fig. S2). A conservative correlation value of 0.7 (Fisher et al., 2018) was chosen above which the most meaningful variable of each pair was selected based on ecological knowledge about their likely effects of coral population dynamics. Data transformations (e.g., log or square-root) were applied when necessary to improve the distribution of predictors. To account for spatial and temporal covariance among observations, a random term for sites nested within reefs, a smooth term of reef latitude coordinates (in kilometres using the Universal Transverse Mercator (UTM) coordinate system), and a smooth term of time (date of survey) were included in the model. This spatio-temporal structure was used as the null model, against which all possible models were built. Longitude was not included in the null model to avoid masking effects of WQ variables most of which show a gradient with distance to the coast. Given the amount of data available for model fitting, the maximum number of fixed predictors was restricted to 5 in any one model. The basis dimension used to represent the smooth terms was restricted to k = 3 to reduce overfitting. Further restrictions in multicollinearity (<0.28) were applied during model runs for excluding collinear models (Fisher et al., 2018). Penalized-likelihood criteria estimates (AIC) using model weights were used to evaluate competing models by comparing model *delta* values ($_{\Delta}AIC_c < 2$) (Burnham and Anderson 2002).

Two outputs were derived from this approach: First, we measured the relative importance of each modelled predictor based on model weights summed across all the models where any given predictor was present (Fisher et al., 2018). Because sums of AIC model weights are really a measure of relative importance of models and provide little information about contribution of predictors to variance reduction, the second output was the identification of the strongest predictors for explaining *State* and *Performance*. The best predictors were evaluated from selected candidate models (within $_{\Delta}AIC_c < 2$) based on the most parsimonious model (i.e., with the lowest number of variables), and the variable contribution to deviance explained among competing models (i.e., with similar number of predictors). Final models were refitted using Restricted Maximum Likelihood (REML) to get best fitted curves and evaluated visually using diagnostic plots (Fig. S3). All statistical analyses were performed in R version 3.4.3 (R Core Team 2017) using the R packages *mgcv* (Wood 2017) and *FSSgam* (Fisher et al., 2018).

## 3. Results

The state of GBR reefs has been variable over the 1992–2017 period, but the permanent transect data studied here show that the overall mean in total coral cover at 5–9 m depth is greater in the Southern than Central GBR (31.2% ± 16.8% Standard Deviation-SD vs. 24% ± 14.0% SD) (Fig. S4). On average, the proportion of MSE corals (i.e. relative to total coral cover) was the highest in both regions (0.28–0.31). Acroporids contributed more to Southern (Tabular: 0.24, branching: 0.17) than Central cover (Tabular: 0.17, branching: 0.07) whereas other branching species contributed significantly more to Central (0.20) than Southern cover (0.07).

Visual inspection of the *Performance* metric (Fig. 2) for total coral and MSE showed a clear reduction from the expected rate of cover increase since 2002: the distribution of *Performance* scores were predominantly below 0.5, which represents the rate of increase observed prior to 2002 during periods of no acute disturbances. Importantly, low performance was not driven by the reduced sampling of inshore reefs during parametrization (Fig. S1). Tabular *Acropora* underperformed (i.e., cover increase was below the lower boundary of expected change) 51–54% of the time in both regions, whereas branching corals (*Acropora* and non-*Acropora*) underperformed slightly more often in the Central region compared to the Southern region (~55% vs. ~ 45% of the time respectively).

## 4. Drivers of state

In the Central GBR, models of *State* for the 1992–2017 period showed high level of agreement in identifying the most important predictors of *State* among all coral groups (i.e., total cover and each of the four coral groups). In the Southern GBR, coral groups differed in their responses to these predictors (Fig. 3), hence there was less agreement in the relative importance of predictors for total *State* and that of specific coral groups (Fig. S5).

Based on the 'best' models for the Central GBR (with $R^2$ ranging from 0.33 to 0.68, Table S2, Fig. S6) the strongest predictors correlated negatively with each *State* metric, but explained different amounts of variance among coral groups (Tabular *Acropora* > Total cover > MSE > branching *Acropora* > other branching, Fig. 3). Reefs experiencing two or more years of CoTS outbreaks in the previous 5 years (exposure level at the 95th percentile of data, Fig. 3) showed 30% less total coral cover (58% less tabular *Acropora,* 28% less branching *Acropora* and 19% less MSE cover) than reefs without an outbreak within the same period. A single storm impact in the previous 5 years (exposure level at the 50th

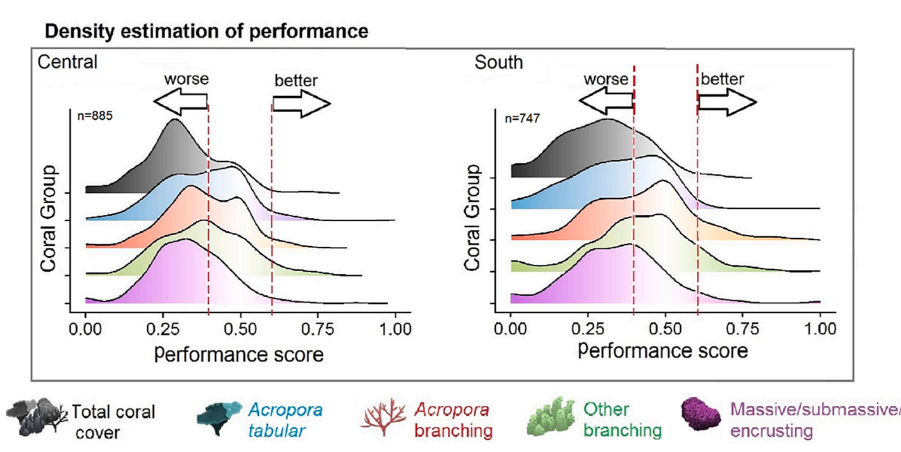


**Fig. 2.** Distribution of *Performance* scores (i.e. deviation from expected growth rates in the absence of acute disturbances) obtained for the period 2002–2017 for each coral group in Central and Southern GBR (n = observations). Reef sites showing the expected growth scored values within red dashed lines (scores ~ 0.5). Coral groups: Total coral cover (black), *Acropora* tabular (blue), *Acropora* branching (red), other non-*Acropora* branching (green), massive-submassive-encrusting species (purple). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

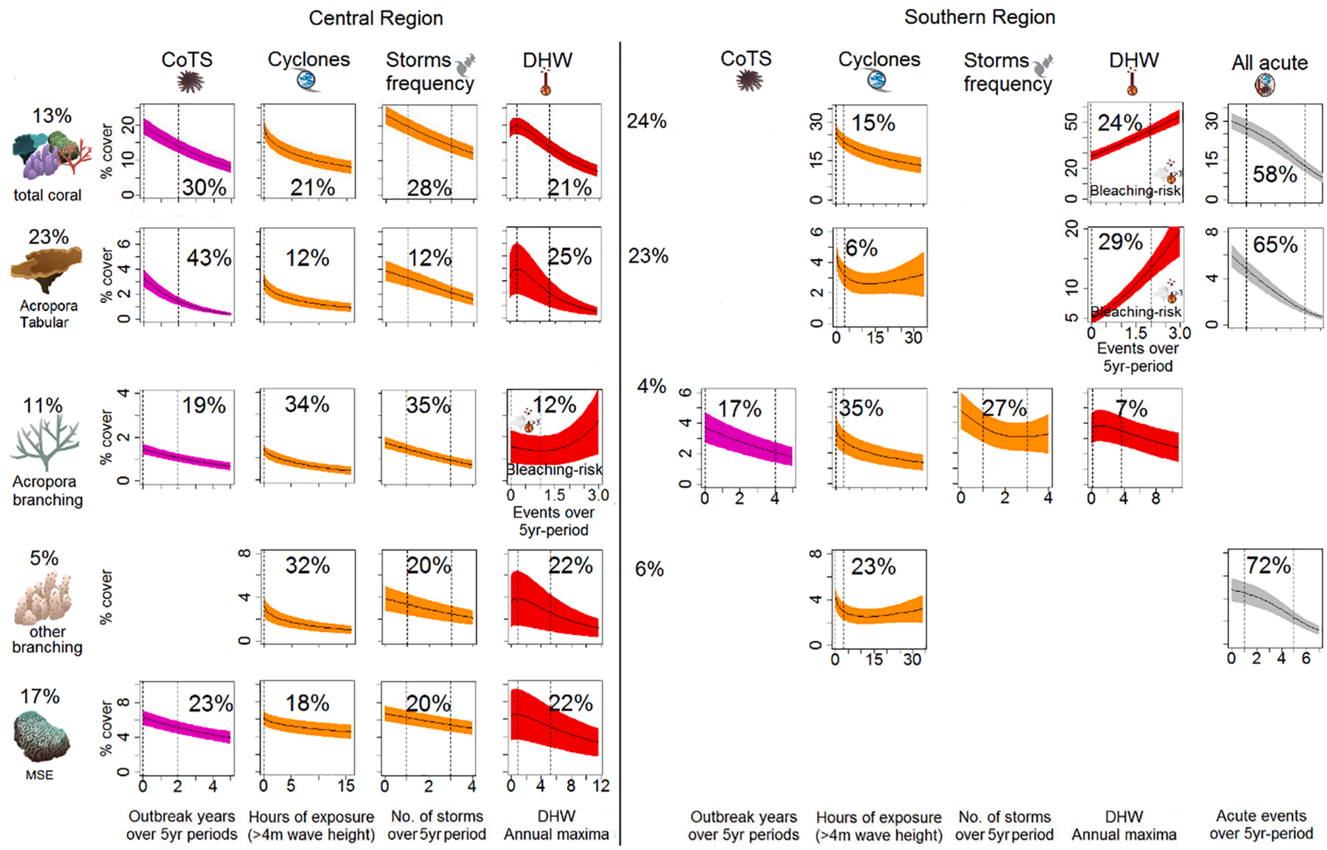


**Fig. 3.** Effect of the strongest predictors (columns) for each *State* metric (rows) for the Central and Southern GBR (1992–2017 dataset). Solid lines are the partial effects attributable to each of the variables on 'best' GAMMs ± 95% confidence. Dashed vertical lines indicate data at 50th and 95th percentiles. Only predictors contributing to explaining variance are shown. Percentages indicate total variance explained by predictors (% outside the plots) in the 'best' model and the relative contribution of each predictor (% inside plots) to the total variance. Common axes at the base of each column unless indicated with icon on each plot. Fig. S6 shows partial residual plots for all predictors and best models.

percentile of data) related to an average 15% decline in *State* of most coral groups except tabular *Acropora*. Exposure to heat stress above 2.3 DHW was detrimental for the *State* of most coral groups except branching *Acropora* corals which were also unaffected by the 5 yr-cumulative frequency of bleaching-risk events (i.e., Occurrence of bleaching in-situ and DHW > 3 over 5-year period).

The 'best' models for the Southern region (with $R^2$ ranging from 0.47 to 0.68, Table S2, Fig. S6) explained a similar amount of variance in the *State* of total coral cover and the cover of tabular *Acropora* (24% and 23%, respectively) with the same combination of stressors (Fig. 3). Variability in the *State* of branching *Acropora* and non-*Acropora*, and MSE was mostly explained by reef location and time and poorly explained by the best predictors (4%, 6% and 1% variance explained, respectively). Therefore, their effect is not discussed in detail here. A single metric combining the cumulative frequency of all acute disturbances (i.e., total number of disturbance events over a 5 yr period) explained most of the variability of the *State* of tabular *Acropora* and total coral cover on Southern GBR. Total coral cover was up to 40% lower with 3 disturbances over a 5 yr period whereas the cover of tabular *Acropora* was 38% lower with 2 disturbances over a 5 yr period. The frequency of bleaching or bleaching-risk events were associated with greater total coral cover and tabular *Acropora* coral cover (Fig. 3) suggesting the negative impacts of the single 'all acute' metric are most likely related to the combined impact of CoTS outbreaks and storms. Salinity and sediments were the only WQ metrics in selected 'best' models for Southern *State* of *Acropora* tabular and MSE (Table S2, Fig. S5) but with no significant contribution to variance explained.

## 5. Drivers of performance

For comparison, we modelled impacts on *Performance* on the same exposure dataset as *State*. However, to further explore the importance of more detailed WQ data we also used a shorter dataset with higher resolution in WQ data. For the long dataset, models show that in the absence of acute disturbances, the lagged effect of cyclones (i.e., metric of exposure to cyclone magnitude in previous year) was the most common predictor for *Performance*. Some metrics of importance for total *Performance* were uninformative at the level of specific coral groups and vice versa (Fig. 4 and Fig. S7 for Relative importance scores). Specifically, WQ metrics (mainly environmental and river sourced DIN) were less important for total *Performance* compared to that of other branching corals (in Central) and MSE in the Southern GBR where river DIN correlated positively to MSE *Performance* contributing to 25% of explained variance (Figs. 4, S8).

Although WQ metrics appeared more often in final models of *Performance* compared to *State*, the strongest predictors of *Performance* were the lagged effects of acute disturbances. Total *Performance* was also negatively correlated to the lag of all acute impacts combined in Central GBR and specifically to lag CoTS densities in Southern GBR, where it also correlated positively with the previous exposure to heat stress (lag-DHW). Our models on specific coral groups show that previous prolonged CoTS outbreak conditions (5 yr-outbreaks) in Central GBR were consistently the most important driver of low *Performance* for tabular *Acropora* and branching corals (*Acropora* and non-*Acropora*) during non-disturbance years. Interestingly, while the recovery of tabular *Acropora* was negatively affected by the lagged effects of intense cyclones, it was higher with greater past storm frequency in Central GBR. Positive

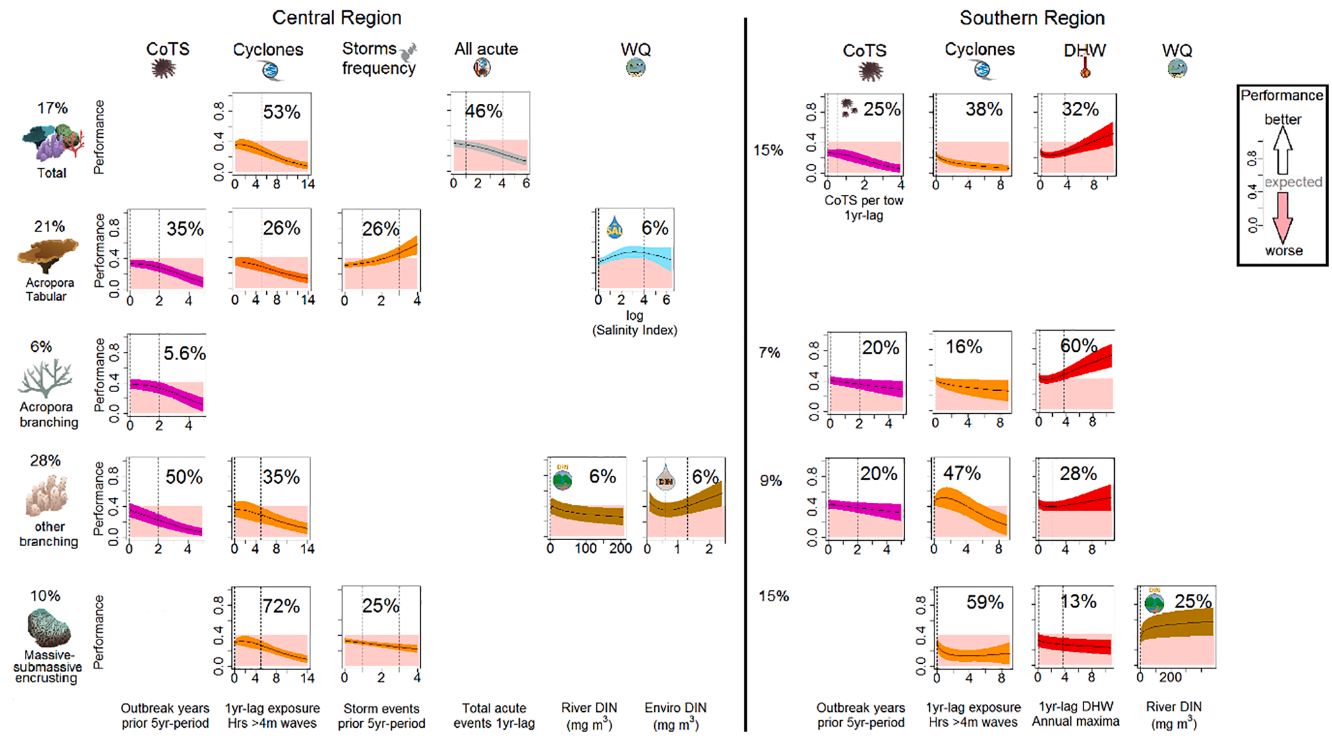


**Fig. 4.** Predicted effects of acute and chronic stressors (columns) on *Performance* for the period 2002–2017 per coral group (rows) for the Central and Southern GBR. Percentages indicate total variance explained by predictors (% outside the plots) in the 'best' model and the relative contribution of each predictor (% inside plots) to the total variance. Metrics other than those at the base of each column are indicated with icon on each plot. Solid lines are the partial effects attributable to each of the variables based on GAMMs ± 95% confidence. Dashed vertical lines indicate data at 50th and 95th percentiles. Pink and white areas on plots indicate worse and better than expected *Performance,* respectively. Only predictors contributing to explain variance are shown. Fig. S8 shows partial residual plots for all predictors and best models. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

correlations with lag-DHW were also obtained for the *Performance* of branching corals (*Acropora* and non-*Acropora*) but not MSE corals in Southern GBR.

While models of *Performance* showed overall lower explanatory power ($R^2$ ranging from 0.19 to 0.29; Table S3) and lower consistency across coral groups than *State* models, several competing models were obtained for *Performance* differing mostly by the presence of WQ metrics (Table S3). River DIN, environmental DIN, and salinity appeared in final models for branching non-*Acropora* (DIN metrics) and tabular *Acropora* (Salinity) explaining a small proportion of the variability in *Performance* (Fig. 4). Based on these results, we explored further the impact of WQ metrics on *Performance* using a shorter time-series (2010–2017) where the annual values for all WQ variables were available. Analyses were limited by the small sample size, and further restricted by dropping many years with acute disturbances. The remaining data points (123 and 117 in Central and South respectively) make model selection ineffective given the large number of predictors included in the models (up to 7 continuous predictors: 5 fixed + 2 covariates, each with k = 3). Therefore, only the relative importance scores of WQ metrics were evaluated (Fig. S9). The difference in importance score values between models with and without yearly variability in WQ (i.e., subtracting the score obtained with long-term averages from the score values obtained with yearly data) showed an increase in relative importance of Chl *a*, salinity, and river DIN on Southern GBR but not on Central WQ where only PAR show an increase in importance when year-to-year variability in WQ was explicitly modelled (Fig. 5). We chose a difference >0.8 units as meaningful changes in variable importance scores considering our results from the complete data set showing that variables with importance scores >0.8 had some explanatory power in the 'best' models (Figs. 4, S9).

## 6. Discussion

The cumulative impact of multiple stressors but in particular acute

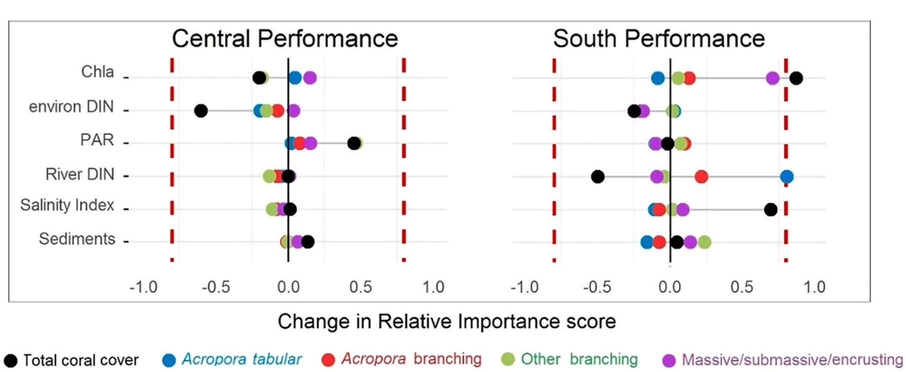


**Fig. 5.** Change in WQ importance score for predicting *Performance* (total and by coral groups) per region (Central and Southern GBR). Change is measured as the difference in score value obtained in models with yearly (Yr) variability in WQ metrics minus values obtained with long-term averaged (Av) WQ values (Change = Yr-Av). Scores based on GAMMs with full-subsets approach using 2010–2017 dataset (see each model heatmap in Fig. S9). Only changes beyond red dotted lines (difference in scores >0.8) are considered meaningful. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stressors and their long-lasting effects are the greatest contributors to the overall degradation of the GBR. We show that *Performance* (i.e., the rate of coral cover increase) on the GBR is susceptible to both acute and chronic stressors. Accordingly, *Performance* scored worse than expected in comparison with pre-2002 data. More than half of the reefs underperformed between 2002 and 2017. Our results are consistent with previous studies detecting reductions in recovery rates on the GBR (Osborne et al., 2017; Ortiz et al., 2018). Low *Performance* on the GBR is driven mainly by the cumulative impacts of acute stressors and to a lesser extent, by the effect that poor water quality has on specific coral groups. Our results highlight that metrics based on total coral cover are insufficient when evaluating the impact of multiple stressors given corals respond differently to variation in environmental conditions. Particularly for *State* metrics, group-specific impacts associated to heat stress were masked using total coral cover. For *Performance*, group-specific water quality effects were masked with the reef-level metric based on total cover growth. Importantly, we show that a lack of historical data for water quality may limit our ability to detect water quality (WQ) effects at regional scales. By comparing two metrics of reef health (*State* and *Performance*) we also demonstrated that WQ effects are stronger predictors of *Performance* than *State*.

The prolonged exposure of reefs to multiple acute disturbances affect reef *State* and reef recovery (*Performance*). However, modelling the *State* and *Performance* of specific coral groups show that corals responded differently to acute stressors. *State* decline is mostly attributed to reductions in tabular *Acropora* which correlated negatively to all acute disturbances in Central GBR but not Southern GBR where it correlated positively to bleaching-risk events (in the period covered here). Low or sub-optimal *Performance* is mostly attributed to low recovery of branching non-*Acropora* corals in Central GBR due to the prolonged lagged effects of CoTS outbreaks and low recovery of MSE after recurrent cyclones in Southern GBR. Differential responses between the Central and Southern regions and between measures of intensity versus frequency of disturbances highlight the complex dynamics of coral reef ecosystems and the importance of evaluating different exposure metrics on structurally-different coral communities to understand overall impacts on reefs. These results may help understand why some regions of the GBR perform better than others in the face of repeated acute and chronic stressors.

*Performance* of tabular *Acropora* responded positively to frequency of storms. One explanation for this positive effect is the time spanned between recurrent disturbances and benthic surveys which was not captured with our frequency metric over a 5 year period. Only 4 of the 19 reefs exposed to three storm events within the previous 5 year period experienced a storm in the year previous to surveys. Hence, time allowed for tabular *Acropora* to recover on most reefs. While coral loses after cyclones tend to be higher on reefs dominated by fragile morphologies such as branching and plate corals (Madin and Connolly, 2006; Foster et al., 2011), Acroporids in particular tend to show greater recovery after physical disturbance from cyclones (Halford et al., 2004; Adjeroud et al., 2009).

Crown of thorns Seastar (CoTS) densities alone was a poor predictor of reef health (i.e., *State* and *Performance*). Instead, a cumulative metric of CoTS based on prolonged exposure to densities above 0.22 per manta tow (i.e. above threshold for incipient outbreaks) was the best predictor of CoTS impact on *State* and *Performance*. Despite that some Southern reefs experience CoTS outbreaks more frequently than in Central GBR (e.g., in the Swains region), CoTS alone were a weak predictor of *State* in the Southern GBR. The most likely explanation for this result is the fact that the metric of all acute disturbances combined was the strongest predictor and already incorporates frequency of CoTS outbreaks. Similarly, during periods of no disturbance, the legacy effect of CoTS contributes to overall reef degradation by limiting *Performance* in Southern GBR. The legacy effect of CoTS is likely to affect periods of recovery after outbreaks as the remaining individuals (also with densities that are below the outbreak threshold) continue to feed on the surviving corals. The contribution of CoTS as leading causes of coral loss and poor recovery of *Acropora* populations on the GBR has been previously documented (Osborne et al., 2011; De'ath et al., 2012; Vercelloni et al., 2017). Here we provide further evidence of CoTS undermining the *Performance* of branching non-*Acropora* corals and the cover status of non-branching coral communities (i.e., MSE which include *Montipora* spp). While *Acropora* and *Montipora* are the preferred prey of *Acanthaster* spp., their feeding preferences are flexible and depend on the abundance and distribution of prey (Pratchett et al., 2017).

Until 2018, the Southern GBR had experienced less widespread heating stress (95 percentile below 3.66 DHW) compared to northern and Central GBR (95 percentile below 5.29 DHW annual maxima). The Southern GBR escaped the devastating impacts of heat stress that cause massive bleaching and coral mortality in the northern and Central GBR during 2016 and 2017 (Hughes et al., 2018b). Our model results support these patterns showing that 1) exposure to DHW above 2.3 was an important predictor of reduced coral cover in Central GBR where reefs experienced DHW up to 5.29, 2) DHW was a poor predictor of regional reef degradation (low cover and low rates of cover increase) in the Southern GBR where most reefs experienced DHW below 3.7 during the same period, and 3) the frequency of bleaching and bleaching-risk events have no detectable impact on corals in the Southern GBR. Our findings with impacts being measurable at $>$ 2.3 DHW are consistent with recent analysis of the GBR bleaching data from 2016 which show substantial mortality occurring at 3–4 DHW (Hughes et al., 2018b). An apparent positive impact of bleaching-risk events on Southern GBR may indicate that our threshold of DHW is still below thermal threshold for corals in the Southern region or simply that very few reefs experienced levels much higher than this threshold. As heat stress was lower in the Southern GBR, the positive correlation with *Performance* may be an indicator that the temperature optimum in Southern reefs is higher than the historic summer average, and that mild marine heat waves may accelerate colony growth. Our threshold of 2.3 DHW for cover decline of different coral groups in Central GBR coincides with that estimated by Ceccarelli et al., (2019) for total coral cover of inshore GBR reefs alone. Unfortunately, with the latest marine heat wave delivering DHW in excess of 3 over much of the GBR in 2020 (NOAA 2018, updated daily) it is likely that the spatial patterns observed in our models with respect to the response of corals to DHW and bleaching-risk events will change.

Relative to some acute disturbances, modelled or remotely sensed WQ variables explained little of the variability in reef health (i.e., *State* and *Performance*). The strong explanatory power detected for acute disturbances, and the lack of long time-series in WQ data are likely contributing to these results. Ceccarelli et al., (2019) obtained similar results while evaluating the effect of chlorophyll *a*, turbidity and the frequency of exposure to highly turbid flood plumes (the "primary" water type) on total coral cover (here, reef *State*) of inshore GBR reefs. In their study, negative effects of reduced WQ variables were measurable, but the effect size was smaller than that of acute disturbances. This is despite the fact that inshore reefs are much more exposed to changes in WQ that the overall area investigated here (comprising both inshore and offshore reefs). We only detected negative impacts of WQ (low salinity and elevated River DIN) in *Performance* metrics affecting only few coral groups in Central GBR when WQ metrics were evaluated as long-term averages. While we assess a very comprehensive dataset for WQ metrics for the GBR, these are modelled products rather than in-situ observations, which limits their accuracy and potential explanatory power as some metrics may under-estimate real concentrations as well as under-estimating WQ variability (Skerratt et al., 2019; Robson et al., 2020). Despite this, WQ metrics appeared in competing models evaluating *Performance* (albeit low explanatory power), suggesting they are likely to be better metrics for assessing the rate of cover increase potential than *State* (i.e., cover). The frequency of flood plumes encompassing multiple WQ variables was recently identified as an important predictor of reef resilience (Mellin et al., 2019a). Lack of strong spatial influence of individual WQ metrics across the continental shelf can also limit the evaluation of their importance in our study. Despite not having large explanatory power as drivers, our analysis suggested several WQ parameters as important contributors to the final models. Greater temporal resolution (as shown with the reduced dataset with yearly variability) in variables such as Chl *a,* and river DIN, resulted in these being more important predictors of *Performance* in southern reefs albeit having a more localised impact of poor WQ compared to central reefs. During the period we evaluated *Performance*, southern reefs had shown fast recovery offshore (faster than in the Central region). This lead to a greater difference in recovery between areas affected by poor WQ versus those with no water quality issues. The results of this analysis however, need to be interpreted with caution given there is debate around the use of summed Akaike weights as a metric to quantifying relative variable importance (Galipaud et al., 2014, but see Giam and Olden, 2016).

River DIN with yearly historical values along the entire dataset had better explanatory power compared to all other WQ metrics, particularly in Central GBR where its relative importance was comparable to that of acute stressors. With the exception of some inshore reefs in the dataset, southern reefs are further removed from the coast and therefore less likely to suffer WQ impact from land runoff. Here, central mid shelf reefs experienced on average five-fold greater river DIN than southern mid shelf reefs. Negative WQ impacts associated with river runoff on coral reef communities have also been demonstrated at smaller scale studies along water quality gradients (Fabricius and De'ath, 2004; Thompson et al., 2020).

Water quality can have indirect effects on coral health and *Performance* not captured in our analyses. Although still under debate (Pratchett et al., 2017) WQ decline (increased nutrients) may increase phytoplankton food for CoTS larvae thus increasing numbers of surviving larvae for settlement (Fabricius et al., 2010), an effect which is further enhanced by elevated temperatures (Uthicke et al., 2015). Increased imbalances in dissolved inorganic nutrients may also increase bleaching susceptibility and coral disease risk (Wiedenmann et al., 2013), whereas corals adapted to turbid waters may exhibit higher bleaching tolerance (Sully and Woesik, 2020). The reason our analyses were not able to tease apart these effects are: i) Lack of historical data as shown with our shorter term analyses, ii) spatial resolution not being adequate (i.e., data derived from 1 km and 4 km models may not be representative of environmental conditions experienced at the scale of surveys for biological data), iii) limited accuracy of modelled variations in WQ, and iv) interactive effects not having been explicitly tested in our models. However, data presented here and in previous studies suggest that WQ at least has a modulating effect on coral *State* and *Performance*. Improved future monitoring designs should ensure that in addition to monitoring of biota sufficient data on abiotic parameters is collected to allow teasing apart the role of WQ variables on the *State* and *Performance* of coral reefs in the future.

Coral reefs have experienced more intense and more frequent climate-related disturbances over the last few years (Hughes et al., 2018b). Our models show that lagged effects of cumulative acute impacts are impairing reef recovery by slowing down coral cover increase. The accelerated pace at which reefs are experiencing disturbance that also impede reef recovery may lead to the loss of the ecosystem functioning and resilience. Typical metrics of coral reef health based on total coral cover may be insufficient to capture changes in the coral community structure which is key to understanding and predicting how reefs can cope with recurrent disturbance regimes. Metrics capturing dynamics of coral growth and recovery processes (here, *Performance*) add valuable information to state metrics particularly when seeking guidance for prioritization of management actions. Local actions centred in controlling CoTS outbreaks on some reefs including reductions in WQ pressures are needed along with global efforts to reduce global warming and ocean acidification. Differentiating key components of the coral community (i.e., coral types) and regular monitoring of WQ can provide a better understanding of the relative importance of acute vs. chronic stressors on the GBR at regional scales.

## 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.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107335. R-code generated for this study can be found at https://github.com/carcasan/CImpacts.

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