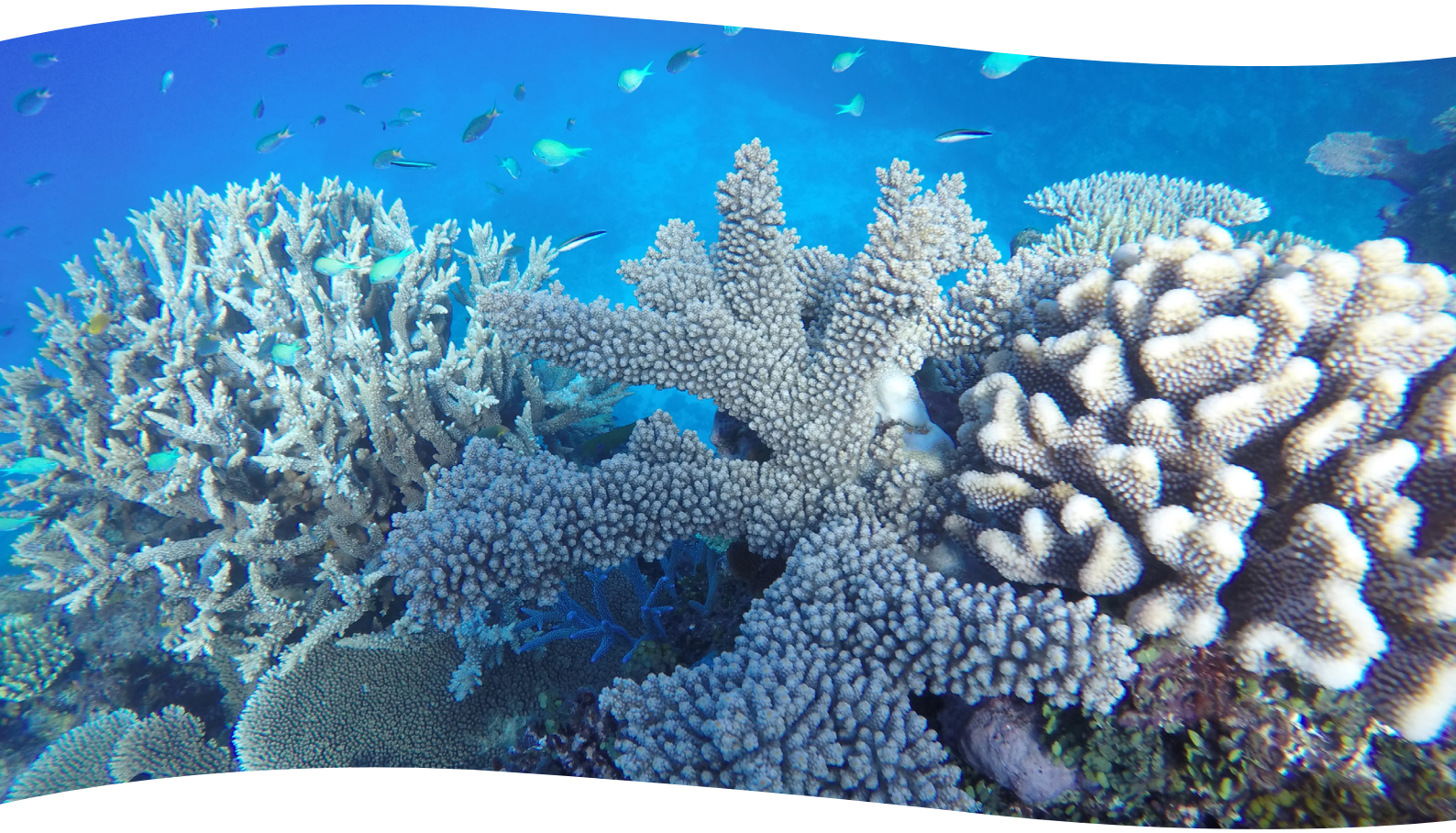
Tropical Water Quality Hub

National Environmental Science Programme

Technical Report

Integrative carbonate budget model of the Great Barrier Reef

Amelia Desbiens, George Roff, Tries B. Razak, Kennedy Wolfe, Michael J. Emslie, Andrew Hoey, Emma V. Kennedy, Angus Thompson, Matthew P. Adams, Mark Baird, Milani Chaloupka, Guillermo Diaz-Pulido, Mathieu Mongin, Peter J. Mumby



The University Of Queensland
AUSTRALIA

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ACRONYMS

AIMS..... Australian Institute of Marine Science
CCA ..... Crustose Coralline Algae
GBR..... Great Barrier Reef
LTMP ..... Long-Term Monitoring Program
NESP ..... National Environmental Science Program
SD..... Standard Deviation
SST..... Sea Surface Temperatures
TWQ..... Tropical Water Quality

EXECUTIVE SUMMARY

This project synthesizes and refines the carbonate budget produced for the Great Barrier Reef (GBR) in Wolfe et al. (2019). Here, we present robust methodological advances to facilitate the calculation of carbonate budgets for the GBR, including:

1. The first method to quantify carbonate budgets using percent-cover data, alleviating the requirement for detailed *in-situ* census-based approaches to quantifying structural complexity and carbonate production (e.g., rugosity).
2. Development of a carbonate budget model for the GBR that allows for site-specific conversions of coral cover to produce estimates of carbonate production.
3. Inclusion of ecologically-relevant parameterisation of parrotfish bioerosion using an integrative modelling approach and GBR-specific parameter estimates.
4. Explicit consideration of uncertainty surrounding production and erosion processes across spatial and temporal dimensions.
5. A consequent R package ("*caRbs*") for use by scientists and managers.

Using the Australian Institute of Marine Science's (AIMS) Long-Term Monitoring Program (LTMP) data on coral cover and fish biomass between 2016–2020 to parameterise the *caRbs* package, we quantified spatial and temporal patterns in carbonate production and bioerosion and identified the thresholds in coral cover required to maintain a positive carbonate budget for the GBR. Results highlighted the importance of *Acropora* sp. as the primary contributor to the carbonate budget, although massive *Porites* sp. were identified as key framework builders to maintain carbonate production. Carbonate production varied latitudinally, with higher calcification rates at low latitudes, while there were no clear spatial or temporal trends in primary bioerosion on the GBR. Parrotfish (*Chlororus microrhinus*) was the primary driver of bioerosion on fore-reef habitats. The study concluded that overall estimates of the carbonate budget on the GBR ranged between -4.9 and 28.4 kg m^{-2} yr^{-1} (~73% of sites had net positive budgets), and the threshold of coral cover to maintain a positive carbonate budget on the GBR were estimated at ~17%.

Key take home messages from a management perspective are:

1. For mid and outer shelf reef slope communities, overall coral cover needs to exceed 17% for reefs to have a positive carbonate budget.
2. We do not yet have a corresponding threshold for inshore reefs where a number of processes, including bioerosion and biogeochemistry, can be quite different.
3. The fact that an individual reef may sit below the 17% threshold does not necessarily indicate that there is a problem; it may just be in an early stage of recovery.
4. The *caRbs* package presents an important tool to evaluate trends of reef state over time, asking how the proportion of reefs sitting below and above the 17% threshold is changing and to ask whether one region has a higher proportion of 'positive reefs' than another.
5. A positive carbonate budget is a pre-requisite for many reef services but does not necessarily imply that all services, including accretion with sea-level rise and provision of high-quality habitat for fish and coastal protection, will occur at historical rates. Further work is needed to link carbonate budget trends explicitly to ecosystem functions. This work has started by linking carbonate budgets to reef accretion (Perry et al. 2018) but there is more to do.

1.0 INTRODUCTION

Coral reefs globally are in decline, with increasing frequency and intensity of disturbance events resulting in losses of coral cover and ecosystem function (Bruno and Selig 2007; De'ath et al. 2012; Hughes et al. 2017). Over the last two decades, the Great Barrier Reef (GBR) has been impacted by cyclone disturbances (Cheal et al. 2017), crown-of-thorns starfish outbreaks (De'ath et al. 2012; Babcock et al. 2016; MacNeil et al. 2016), and successive mass coral bleaching events (Hughes et al. 2019), resulting in regional declines in coral cover and shifts in the population structure of coral communities (Hughes et al. 2018; Dietzel et al. 2020). Worldwide, most studies and monitoring programs quantify the impact of disturbances on coral reefs by documenting changes in coral cover as an indicator of reef "health" (Jonker et al. 2008; Hughes et al. 2017). While this metric is important in quantifying long-term change and shifts in coral assemblages, coral cover alone is unable to provide insight into ecological processes or changes in ecosystem function.

From a geological perspective, coral reefs accrete expansive framework over millennia through the growth of biologically derived carbonate (Scoffin 1993; Montaggioni 2005). Scleractinian corals act as primary framework builders, with additional accretion by secondary producers such as crustose coralline algae and other calcifying algal species (Stearn et al. 1977; Hubbard et al. 1990; Scoffin 1993) The production of carbonate frameworks is balanced by erosional processes, which can be either biological, physical or chemical (Lange et al. 2020). Bioerosion (the biologically mediated removal of carbonate) occurs primary through the grazing of parrotfish and other reef organisms (e.g. urchins), and secondarily through microbioerosion (e.g. algae, fungi) and macrobioerosion (bivalves, sponges) of reef frameworks by endolithic species (Hutchings 1986; Hoey and Bellwood 2008). The net outcome of this balance is termed the "carbonate budget" (Stearn et al. 1977; Perry et al. 2018).

Carbonate budgets represents a quantitative measure of the functional state of a reef at any given point in time (Lange et al. 2020). Over time, carbonate budgets can indicate the growth potential of coral reefs by quantifying whether coral reefs can build or maintain reef framework (i.e., accretional state) or carbonates are being lost from the reef framework (i.e., net erosional state). By quantifying ecosystem processes, carbonate budgets can also provide key insight into the complexity and maintenance of the reef framework (Januchowski-Hartley et al. 2017; González-Barrios and Álvarez-Filip 2018) and the provisioning of ecosystem functions such as coastal protection (e.g. Perry et al. 2018), dissipation of wave energy (e.g. Harris et al. 2018), framework for fish habitat and diversity (e.g. Alvarez-Filip et al. 2013), and sediment production for coastlines (e.g. Perry et al. 2015).

While the principle of carbonate budgets and the balance of production and erosion have remained largely unchanged since their inception (Stearn et al. 1977), carbonate budgets have been quantified using a range of different methodological approaches (Lange et al. 2020). The use of carbonate budgets to quantify ecosystem functions has grown exponentially over the past few decades and expanded to reefs throughout the world (Lange et al. 2020), yet non-standardised approaches to quantifying carbonate budgets and differences in methodologies render comparisons between regions and among time periods problematic. To overcome this limitation, standardised census-based approaches have been successfully implemented at global scales (e.g. ReefBudget, Perry et al. 2018), which have recently been applied to reefs

in the Caribbean (e.g. Perry et al. 2013) and more recently the Indian Ocean (e.g. Lange and Perry 2019). Here we build on these approaches by developing a method to quantify three-dimensional structures and carbonate production for reefs on the GBR. The application of a standardised methodology that allows for conversion of percent coral cover data to carbonate budgets would expand comparative research in the region and allow for retrospective hindcasting of carbonate budgets.

Here, we outline the development of a model of carbonate budgets for the GBR (*caRbs*) that allows for site-specific conversions of coral cover to produce estimates of carbonate production. The model provides a revision of parameters on parrotfish feeding to ensure carbonate budget calculations are ecologically relevant. We summarise development of the model and the resulting R package (*caRbs*). Using the Australian Institute of Marine Science's (AIMS) Long Term Monitoring Program (LTMP) data, and GBR specific parameter estimates, we used the model to quantify carbonate budgets for 94 reefs over a four-year period (2016–2020). We quantified spatial and temporal patterns in carbonate production and bioerosion across the AIMS LTMP reefs and identified thresholds in coral cover required to maintain a positive carbonate budget on the GBR.

2.0 THE *CARBS* PACKAGE

To facilitate data sharing and create a standardised methodology, calculations of carbonate production and bioerosion were operationalised through the creation of an open-source R package (caRbs). The functions contained within caRbs take user-input data from standard monitoring surveys, such as the AIMS LTMP data, to estimate four distinct processes contributing to carbonate budgets on coral reefs (Figure 1). These functions balance coral growth (primary production) and other benthic calcifiers (secondary production) against parrotfish feeding (primary erosion) and micro- and macro-bioerosion (secondary erosion). We addressed carbonate dynamics in a biological and ecological context. Greater consideration would be needed to parameterise geophysical processes (e.g. sediment production, hydrodynamics, microbial lithification, etc.) whose influences are better understood across timeframes that exceed the scope of this study.

The package *caRbs* is available via github (https://github.com/aadesbiens/caRbs) for use by scientists and managers and allows for future model development through changes to the production and erosion functions. By using a simulation-based approach, the output of the model explicitly incorporates uncertainty around estimates of production and erosion that better inform management decisions. Incorporating GBR specific functions of coral growth (skeletal density, accretion rates), coral geometric shapes (branch spacing, colony structure), primary bioerosion (bite rate, bite volume, proportion of bites), and secondary bioerosion (microborers and macroborers) (Figure 1), the model allows for explicit parameterisation to GBR reefs. The model also provides a foundation for incorporating spatial variability in functions (e.g., latitudinal variability in growth rate, cross-shelf variability in secondary bioerosion) that can be improved in future iterations.

While specific to the GBR, the *caRbs* package can be adapted for coral reefs throughout the Pacific through modification of the base parameters. By developing the primary production function, the model overcomes previous limitations of carbonate budgets that require field-specific census-based approaches to quantifying structural complexity and individual colony size. These functions are readily transferable to any Pacific coral cover data and provide a foundation for quantifying carbonate production potential among studies. This represents a substantial methodological advancement as current differences in methodologies and non-standardised approaches to quantifying carbonate budgets render comparisons among regions and time periods problematic (Lange et al. 2020).

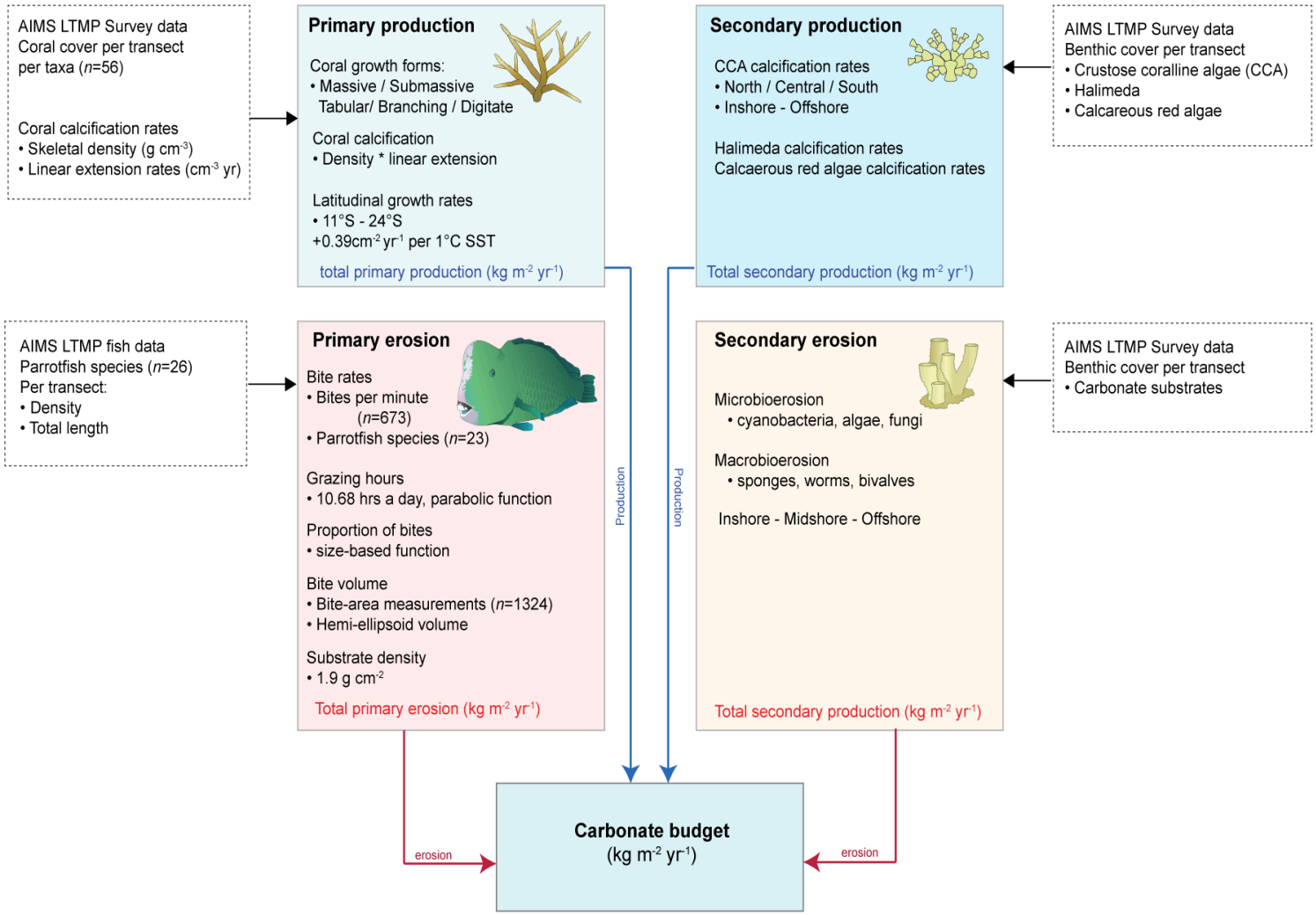


Figure 1: Overview of the main model functions (primary production, secondary production, primary erosion and secondary erosion) and ecological parameterisation underlying the *caRbs* model.

2.1 Carbonate production

Rates of total carbonate production (kg m^{-2} yr^{-1}) were estimated as the sum of primary (hard corals) and secondary (calcareous algae) production. Primary production (*pproduction* function*)* is calculated as a function of mean % cover of each coral at a given site multiplied by their estimated calcification rate at a specified latitude. Secondary production (*sproduction* function) is calculated as a function of mean % cover of each algae group multiplied by their region- and shelf-specific calcification rate and correction for rugosity.

$$\text{Total Carbonate production}_{lbv}(\text{kg m}^{-2}\ \text{yr}^{-1}) = \sum_{i=1}^{56} \beta_{il} C_i \ \text{(primary)} + \sum_{x=1}^{4} \partial_{xbv} A_x \ R \ \text{(secondary)}$$

Where:

β_{il} = calcification rate of the ith coral species at the lth degree of latitude (kg m^{-2} yr^{-1})

C_i = mean % cover of the ith coral taxa

∂_{xbv} = calcification rate of the xth algal species in the bth region (north, central, south) at the vth shelf position (inner, mid, outer) (kg m^{-2} yr^{-1})

A_x = mean % cover of the xth algal taxa

R = rugosity

2.1.1 Hard corals

Coral taxa categories were derived from the AIMS LTMP survey data, which included 50 genera of scleractinian coral of which the dominant coral (*Acropora* sp.) has seven distinct growth forms (56 groups total). As the AIMS LTMP dataset does not distinguish species-specific growth forms within each genera, we used the most common growth form within each genera. Calcification rates (β_{il}) of coral taxa were estimated by simulating colony growth in single species assemblages of varying size distributions across a gradient in total cover to estimate the relationship between carbonate production and gross planar coral cover.

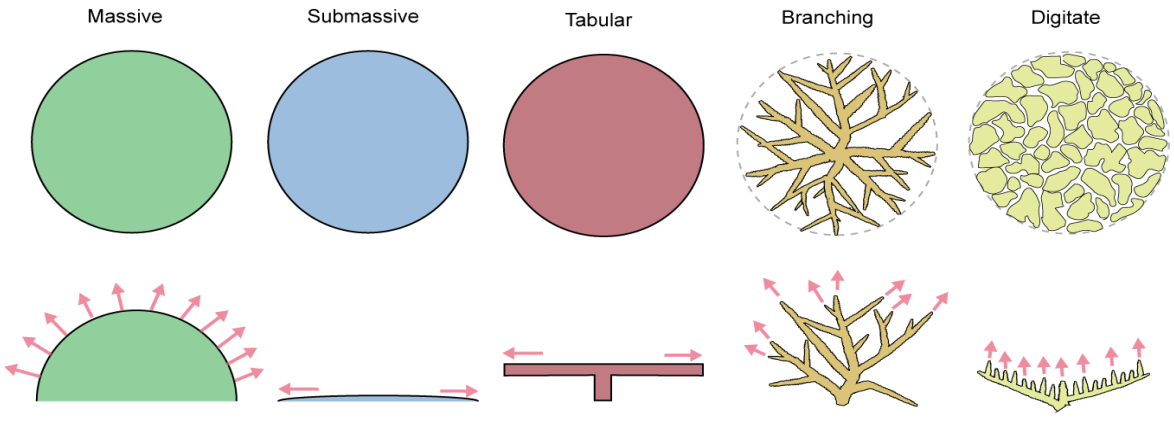


Figure 2: Illustrations of geometric shapes and dominant growth patterns used to determine 3-dimensional carbonate production from 2-dimensional coral cover data.

We began by defining an arbitrary available reef area of 20m x 20m ($400m^2$) and then randomly selecting coral cover between 0 – 80%. We then generated a set of coral colonies of random size distribution whose planar area summed to the selected cover area. Maximum colony sizes for each coral taxon was determined from published literature. Species-specific extension rate and skeletal density of these colonies were randomly drawn from a normal distribution defined by a mean and standard deviation (SD). Estimates of extension rate and skeletal density for each taxon was extracted from the published literature and unpublished data for Pacific coral reefs within the same latitude as the GBR. The production of each colony is then estimated based on a geometric equation (Table 1) that relates 3-dimensional growth to changes in planar cover (Figure 2). This process was iterated 1000 times for each species to obtain a calibration curve that estimates mean±SD of annual carbonate production (kg m^{-2} yr^{-1}) as a function of total cover (Figure 3).

Table 1: Growth of distinct coral geometric shapes for carbonate production.

Growth form	Geometric equation
Massive	(2*pi*((sqrt(((area))/pi))^2))*density*extension
Plating	(2*sqrt(pi*area)*extension*density*thickness)+(0.1*(area*extension*density))
Submassive	area*density*extension
Digitate	(area*conversionfactor*extension*density) + (area (conversionfactor*area)*0.1*extension*density)
Branching	((((radial*bthick*extension*density)*0.1)*(axial* bthick*extension*density)*100)/100000)*area

(thickness = colony thickness, conversionfactor = proportion of growing tips to non-growing regions within colonies [i.e. interbranch areas], bthick = branch thickness, density = number of axial and radial branches)

2.1.2 Calcareous algae

Calcification rates of algal taxa were compiled from published literature (Figure 4). Estimates of calcification for crustose coralline algae (CCA) were obtained from field experiments on the GBR (Kennedy & Diaz-Pulido, unpublished data). Rates of calcification for upright calcareous red macroalgae used data from *Amphiroa* from temperate eastern Australia (McCormack 2014), while for the green macroalgae *Halimeda* we used published data from the southern GBR (Castro-Sanguino et al. 2016). There are no estimates of calcification rates for *Peyssonnelia* in the literature, therefore we used expert opinion to estimate that calcification of this algae could be half of that of CCA as their encrusting tissues are only partially calcified. While the primary production model relies on three-dimensional models to quantify carbonate production, secondary production by calcareous algae requires estimates of rugosity to quantify the three-dimensional structure of the reef. The AIMS LTMP quantifies “substrate complexity” as the total complexity of the underlying substrate without coral structure on an ordinal scale of 0 – 5. To convert this to standard rugosity metric, i.e. the linear distance covered by a 10 m length of chain fitted to the reef contour (Risk 1972), we used a conversion between the visual assessment and rugosity, which are closely correlated (Wilson et al. 2007).

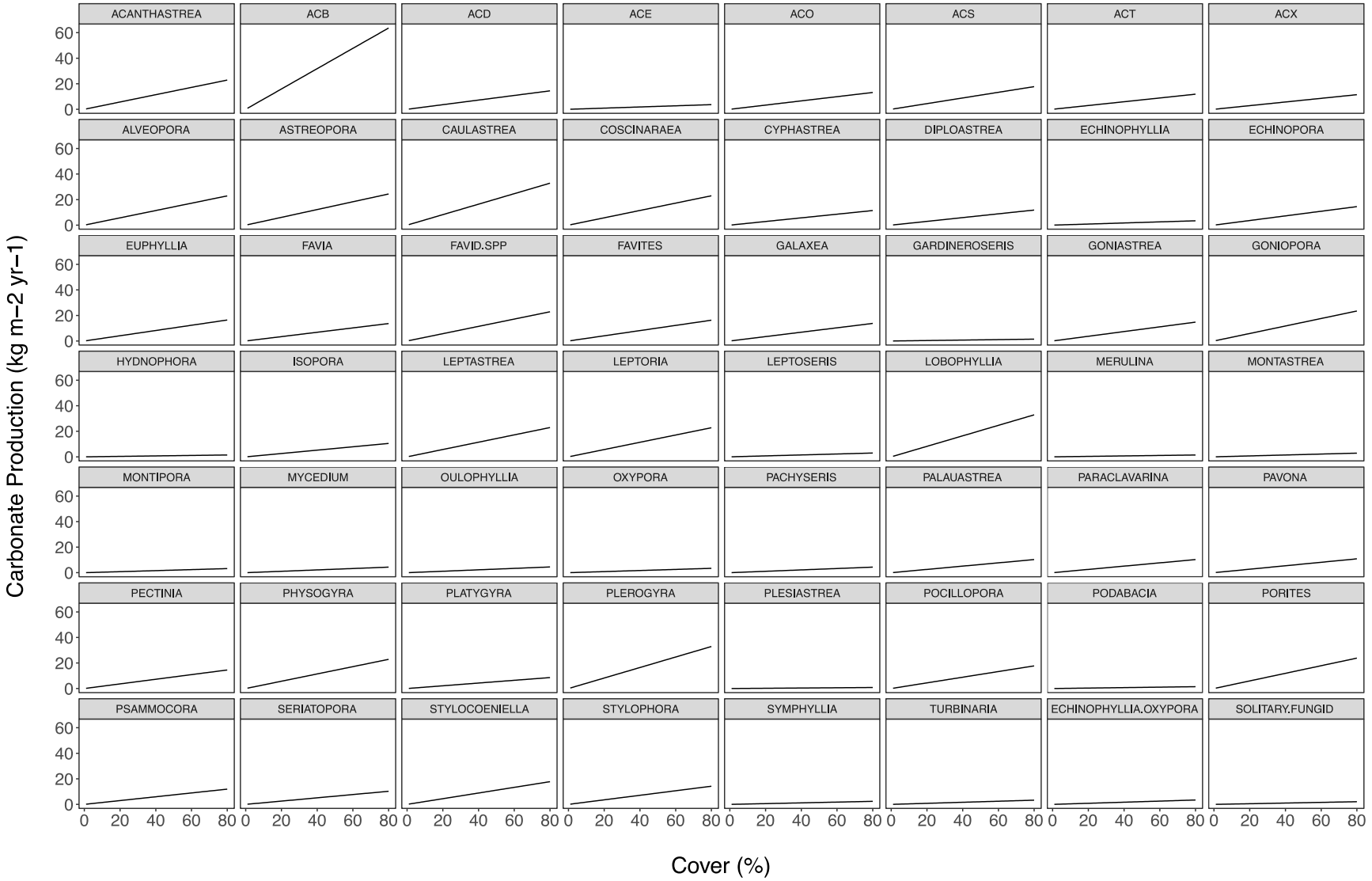


Figure 3: Carbonate production for 50 genera of corals within the AIMS LTMP dataset according to levels of coral cover. *Acropora* groups divided by growth form: ACB = branching, ACD = digitate, ACE = encrusting, ACO = corymbose, ACS = submassive, ACT = tabular, ACX = bottlebrush.

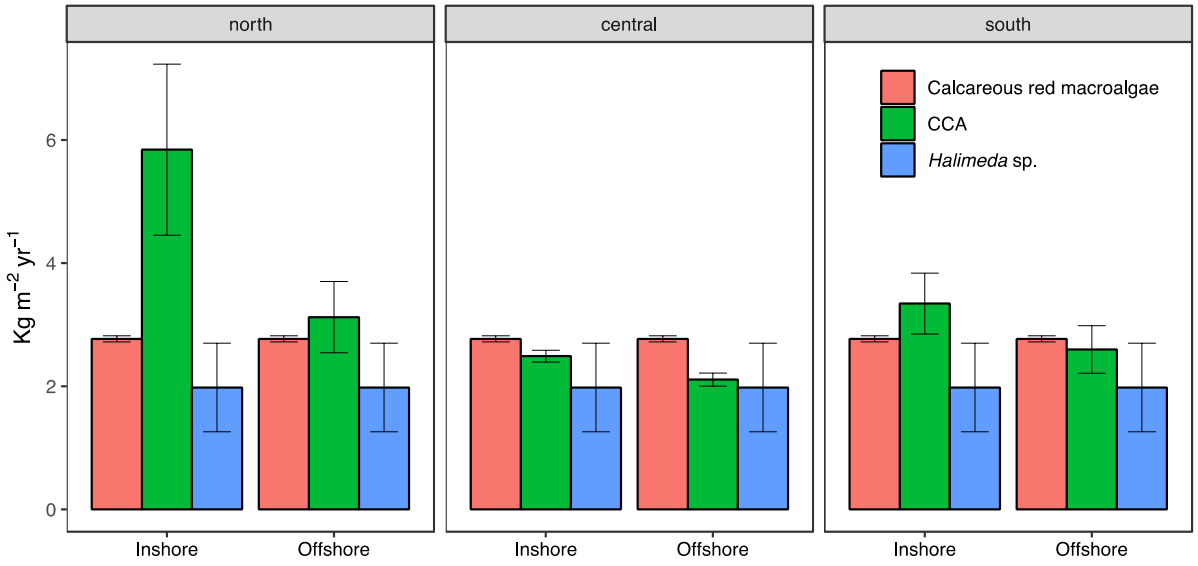


Figure 4: Cross shelf and latitudinal trends of carbonate production from secondary producers on the GBR.

2.2 Bioerosion

Rates of gross bioerosion (kg m^{-2} yr^{-1}) were estimated as the sum of primary (parrotfish) and secondary (micro- and macro-boring) erosion. Primary bioerosion (*perosion* function) was calculated as a function of species-specific parrotfish densities of known body size multiplied by their erosion rate. Secondary bioerosion (*serosion* function) was calculated as a function of mean % cover of available (non-coral) substrate multiplied by mean shelf-specific micro- and macro-scale erosion rates and a visual assessment of rugosity (ordinal scale 0 – 5).

$$\text{Total Bierosion}_v\ (\text{kg m}^{-2}\ \text{yr}^{-1}) = \sum_{i,t} \alpha_{it}\ F_{it}\ (\text{primary}) + \sum_{x=1}^{2} \theta_{xv}\ SR\ \ (\text{secondary})$$

Where:

$\alpha_{it} = \text{erosion rate of the } i\text{th species of length } t$ (kg yr^{-1})

$F_{it} = \text{density } (\text{m}^{-2}) \text{ of the } i\text{th fish species of length } t$ (cm)

$\theta_{xv} = \text{erosion rate at the } x\text{th scale } (\text{micro}, \text{macro}) \text{ at } v\text{th shelf position } (\text{inner}, \text{mid}, \text{outer})$ (kg m^{-2} yr^{-1})

$S = \text{mean \% cover of non} - \text{coral substrate}$

$R = \text{rugosity } (0 - 5)$

2.2.1 Parrotfish feeding

Parrotfish bioerosion rates were estimated as the product of species-specific feeding characteristics dependent on individual body size. Specifically, erosion of individual fish was calculated as the product of total number of bites taken, proportion of bites leaving scars, bite volume and substrate density. Each of these parameters was characterised with feeding data collected from Lizard Island (Hoey, unpublished data), and bioerosion calculated using the following equation:

$$\alpha_{it} = (\sum_{z=1}^{365} bn_{zit}\,)p_{it}ba_{it}d_{it}s$$

Where:

$bn_{zit} = \int_{360}^{1000.8} \frac{-br}{230400}(x-780)^2 + br\,\mathrm{d}x$ (where x = time (min) and br = max bite rate (bites min^{-1}))

$p_{it} =$ proportion of bites leaving scars of the ith species of length t

$ba_{it} =$ bite area of the ith species of length t (m^2)

$d_{it} =$ bite depth of the the ith species of length t (m)

$s =$ substrate density (1.75e-06 kg m^{-3})

The total number of bites taken by an individual was characterised in two steps. First, relationships were established between bite rate and body length for each species. Bite rate (bites min^{-1}) as a function of body length (cm) was best characterised with exponential decay curves. Estimates of bite rate (bites min^{-1}) of each fish was obtained with these equations and then scaled to daily number of bites. Parrotfish feed for an average of 10.68 hours per day (~6am – 5pm, Alwany et al. 2009; Ong and Holland 2010) and bite rates vary substantially throughout this period (Alwany et al. 2009), increasing through the morning, reaching a peak around 1pm and then declining through the afternoon. This pattern can be described with a parabolic function whose vertex is defined by the maximum daily bite rate, usually occurring around 1pm (780 minutes from midnight) and its x-intercept as 5am (based on visual inspection of Alwany et al. 2009; Ong and Holland 2010). Maximum bite rate in this case is taken from the species-specific exponential decay curve. The integral of the parabolic function between the hours of 6am and 4.41pm (360 and 1000.8 minutes from midnight) then gives the total number of bites in a day (bn_{zit}). For *Chlorurus microrhinos* individuals, whose feeding is concentrated on the reef crest (~3m) but foray into deeper water throughout the day, the total number of bites taken was scaled to the ratio between bites taken at 10m vs 3m, i.e. divided by 7 as per Bellwood 1995.

Total number of bites is scaled by the proportion of bites actually leaving scars, also computed as a function of body length using field data from Lizard Island. Proportion of bites leaving scars was averaged across broad size categories (10cm bins) of each species. The area of each bite, modelled as an oval shape, was also determined from field data as a function of body size. Bite volume was then calculated as half of an ellipsoid whose depth was held constant for all excavators (1.72 mm) and varied by body size for all *Scarus* spp. To then estimate total carbonate removal, bite volume was multiplied by substrate density, estimated as 1.75e-06 kg m^{-3} (average skeletal density for coral taxa). Total contribution of parrotfish to primary bioerosion was calculated for the 24 species captured in the AIMS LTMP data (Figure 5).

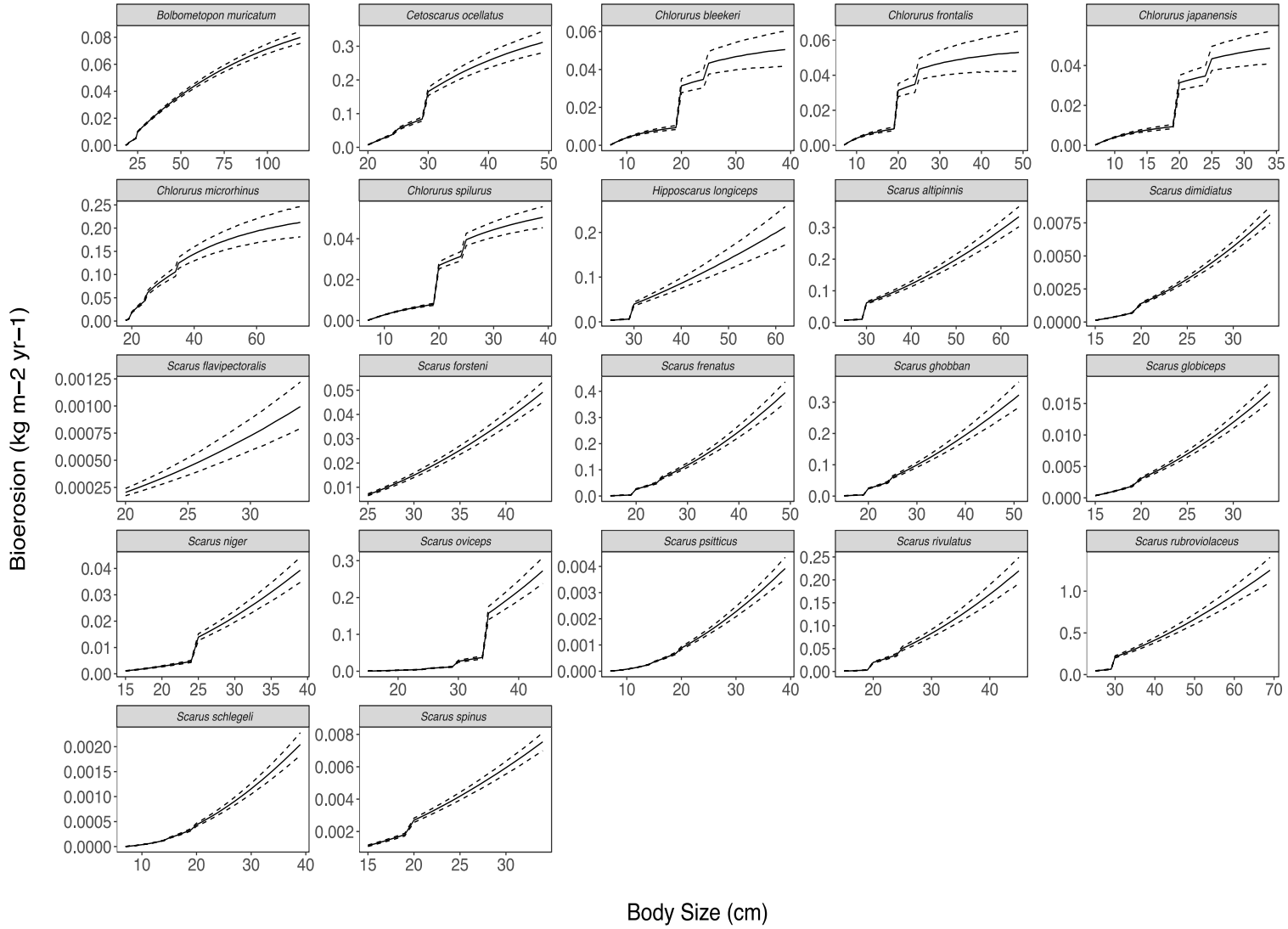


Figure 5: Bioerosion (kg m^{-2} yr^{-1}) ± 95% credible interval (CI) of parrotfish species as a function of total body size (cm). Two species (*Scarus chameleon* and *Calotomus carolinus*) did not generate any bites during observation period (Hoey, unpublished data) and were omitted on the plot.

2.2.2 Secondary bioerosion

Erosion rates of micro- and macro- borers were established from published work that tracked changes in density and volume of carbonate blocks across locations of the GBR (Osorno et al. 2005; Tribollet and Golubic 2005). Microbioerosion follows a cross-shelf trend by which erosion is highest in offshore reefs, and lowest in inshore reefs, as low light levels inhibit microbioerosion in inshore environments (Figure 6). Macrobioerosion follows an inverse cross-shelf trend to microbioerosion, by which erosion is lowest in offshore reefs, and highest in inshore reefs, as inshore reefs have greater particulate matter for heterotrophic feeding (Figure 6). Combined as secondary erosion (Figure 6), the inverse trends in micro and macrobioerosion resulted in comparable erosion rates on mid-shelf and off-shelf reefs, with higher erosion on inshore reefs due to elevated macrobioerosion rates (Figure 6). To scale secondary erosion to a reef level, erosion rates (kg m^{-2} yr^{-1}) were multiplied across the "reef matrix" (i.e., space not occupied by corals or algae), and multiplied by rugosity to provide 3-dimensional estimates of bioerosion potential.

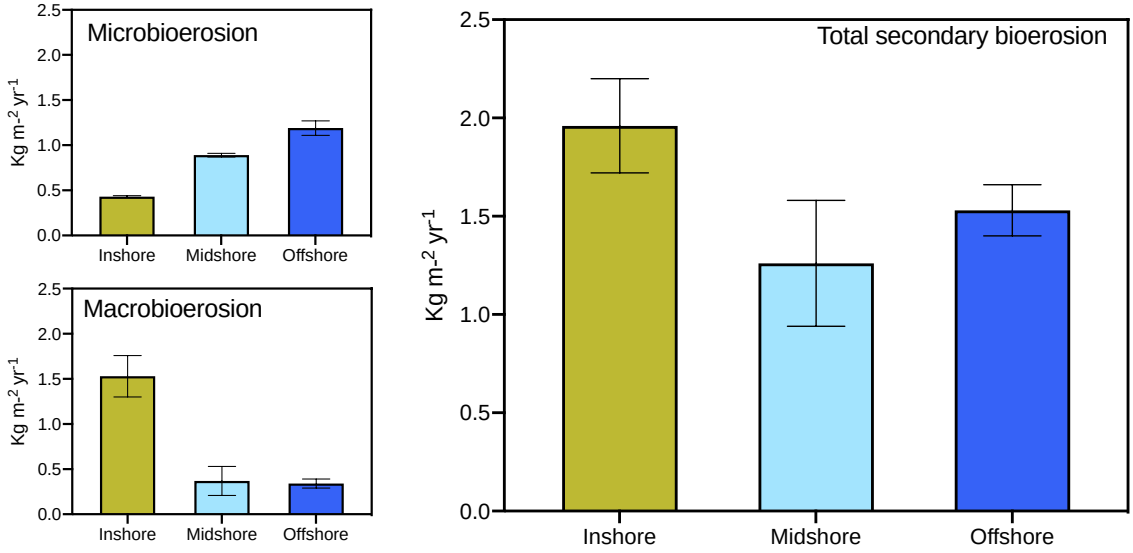


Figure 6: Cross-shelf patterns of microbioerosion, macrobioerosion and total secondary bioerosion on the GBR.

2.3 Incorporating uncertainty

Models of ecosystem function and processes are inherently uncertain across spatial and temporal dimensions. Here, we attempt to directly account for this uncertainty using a Monte Carlo simulation approach. Within each function, production and erosion parameters are randomly drawn from Normal distributions (mean +- SD) across 10,000 simulations. The resulting outputs are defined as posterior probability distributions (median ± 95% credible intervals). The distributions of each distinct function can be summed to obtain an overall estimate of the carbonate budget for each location (*cbudget* function).

3.0 RESULTS AND DISCUSSION

To quantify spatial and temporal patterns in carbonate budgets on the GBR, we used the AIMS LTMP data for 99 reefs on the GBR. While long-term densities in fish abundance are available from the LTMP, fish length was not counted prior to 2016, so biomass (and therefore primary bioerosion rates) are unavailable, and the dataset was constrained between 2016 and 2020. We highlight here that the following results pertain primarily to mid and offshore reef slopes occurring at ~10m where AIMS LTMP survey sites are concentrated. For this reason, carbonate budget dynamics for inshore locations, where benthic community and fish assemblage composition are quite different, are not addressed.

3.1 Carbonate production

Rates of primary production from coral communities across the GBR varied both within and between years and regions (Figure 7), ranging from 0 to 29 kg m^{-2} y^{-1}. Primary production generally declined through time, especially in the central and southern regions (Figure 7). In terms of carbonate production, the model identifies high rates of carbonate production from the dominant reef-building acroporid corals, particularly branching *Acropora* (Figure 3). Through rapid linear extension and indeterminate colony structure, branching *Acropora* can generate exceptionally high rates of carbonate production, and provide critical habitat for reef fish and cryptic reef organisms. Despite lower growth rates, massive corals such as *Porites* that are key framework builders in the Pacific maintain high rates of carbonate production and are key components of carbonate budgets on the GBR. While rarer taxa such as *Lobophyllia* are capable of producing substantial volumes of carbonate, they are numerically less dominant on the GBR and infrequently encountered in surveys meaning their contribution to the carbonate budget on the GBR are marginal.

The results of the model indicate a latitudinal trend in carbonate production, primarily driven by explicit parameterisation of higher calcification rates in warmer sea surface temperatures (SST) at low latitudes. The lower carbonate production rates in 2016/2017 in the Northern GBR are due to low coral cover resulting from the mass bleaching events (Hughes et al. 2017). The resurveying of AIMS monitoring sites in 2019 with high levels of coral cover (e.g., Lagoon Reef, 39% coral cover in 2019) that appear unimpacted by the regional mass bleaching may explain the sudden apparent increase in carbonate production in the North region between 2017 and 2019 (Figure 7).

Total coral cover was strongly linked to both primary production and overall carbonate budgets, especially for sites dominated by fast-growing *Acropora*. Coral assemblages with lower *Acropora* cover exhibited the lowest carbonate budgets (Figure 8). We explored the potential for coral cover as a metric for predicting site-level carbonate budgets. We used a metric of confidence wherein 80% of sites had median budget + CI higher than 0 as threshold. Across all offshore sites, we identified that a minimum of 17% coral cover ensured that carbonate budgets are reliably maintained in a positive state (Figure 8).

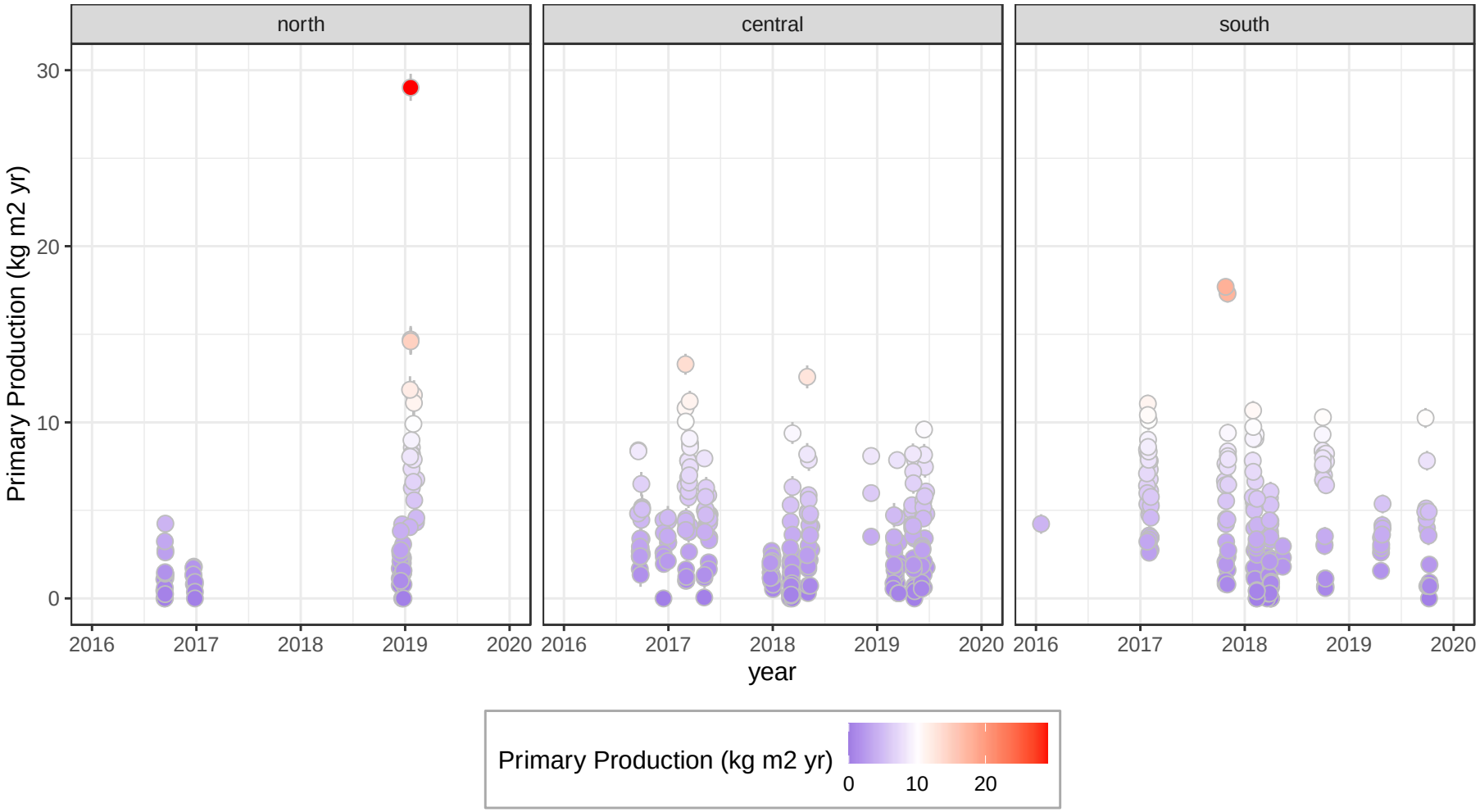


Figure 7: Primary production on the GBR derived from the AIMS LTMP monitoring sites (2016-2020).

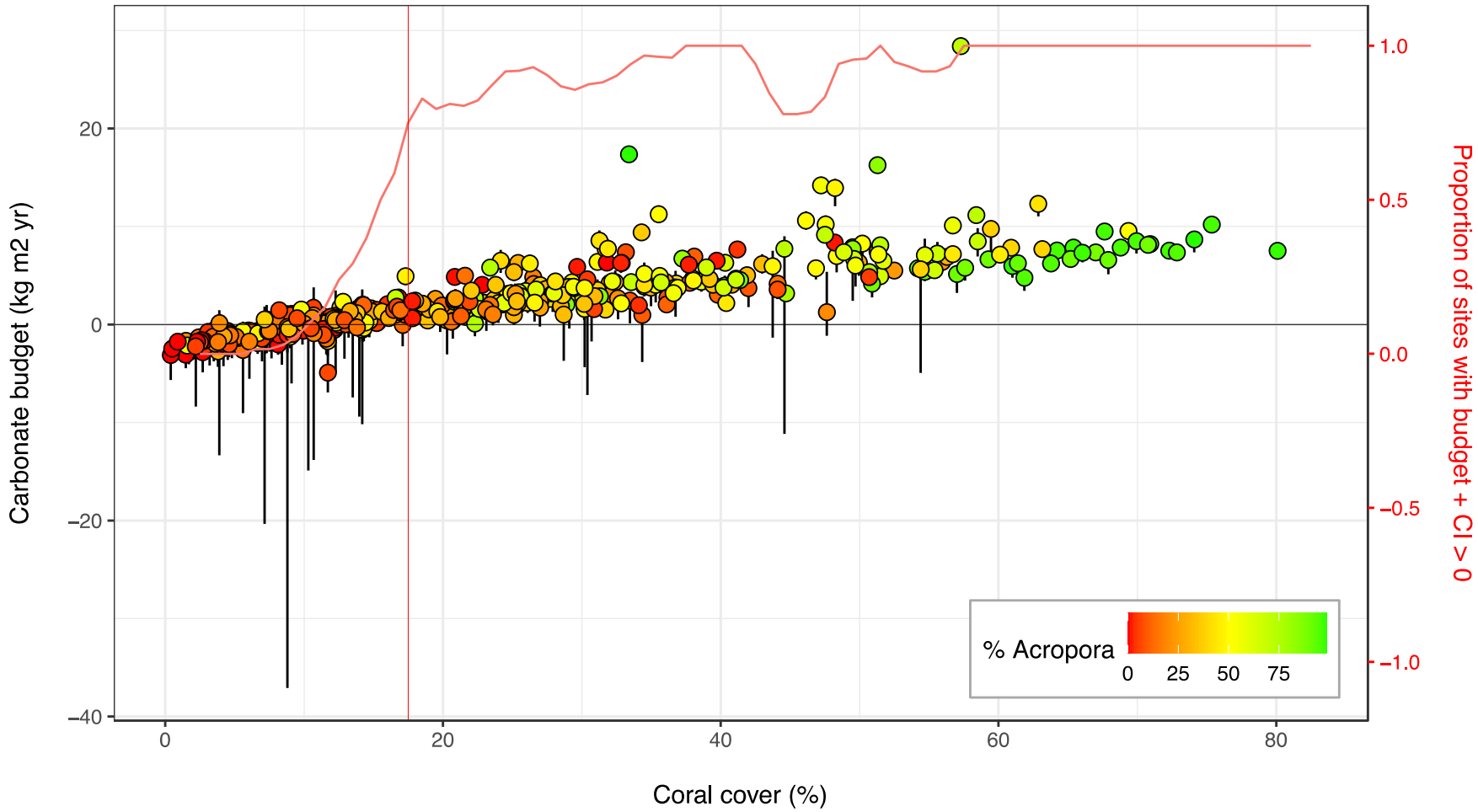


Figure 8: Relationship between coral cover and carbonate budget for AIMS LTMP sites (2016-2020) (n = 99). Red vertical line shows threshold in % coral cover below which carbonate budget become negative.

3.2 Bioerosion

By including ecologically realistic parameterisation of bioerosion, the model allows for species-specific bioerosion rates for 24 parrotfish species on the GBR (Figure 5). Rates of bioerosion were variable through space and time (range: 0 to -7.3 kg m^{-2} y^{-1}) and did not display any clear patterns across regions or years (Figure 9).

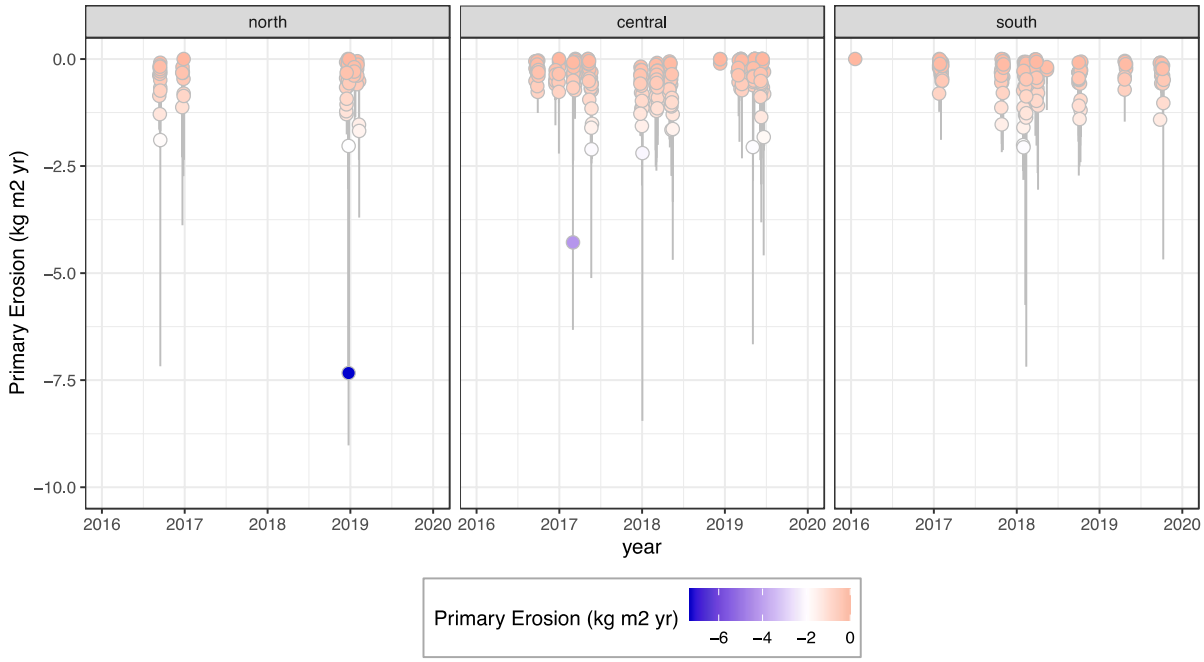


Figure 9: Spatial patterns of primary erosion from the AIMS LTMP survey data (2016-2020).

Variation in parrotfish biomass did not necessarily explain patterns in overall budgets, even when explicitly considering the contributions of large excavators (Figure 10). Coupling the model with survey data from AIMS LTMP indicates that the excavating parrotfish *Chlororus microrhinus* was the primary driver of bioerosion on fore-reef habitats on the GBR, while *Scarus* species contributed less to overall rates of bioerosion at reef scales. These results are consistent with previous studies of bioerosion on the GBR (e.g. Hoey and Bellwood 2008). While individuals of *Bolbometopon muricatum* are key drivers of bioerosion on GBR reefs (Figure 5), they were infrequently encountered on AIMS LTMP surveys, in part due to their schooling behaviour and preference for feeding in shallow reef-crest habitats. Analysis of primary bioerosion rates from the AIMS LTMP data (2016-2020) indicates no clear spatial or temporal trends in primary bioerosion on the GBR. As parrotfish biomass increases following coral disturbance due to an increase in substrate for grazing (Taylor et al. 2020), longer-time series of parrotfish numbers may indicate an increase in bioerosion following losses of coral production that may negatively impact net carbonate budgets on the GBR.

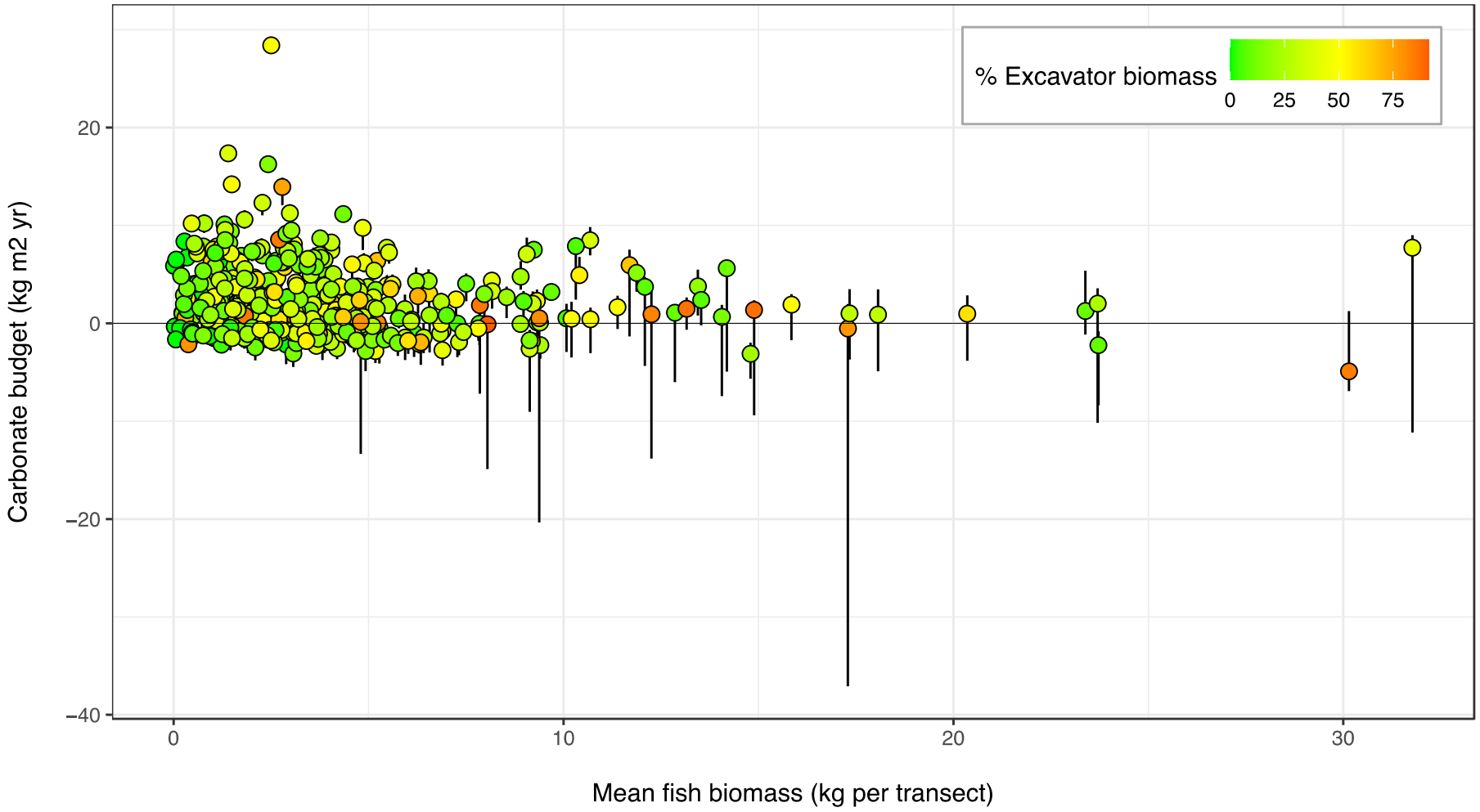


Figure 10: Relationship between fish biomass and carbonate budget for GBR reefs (2016-2020).

3.3 Carbonate budgets

Across sites, net carbonate budgets ranged from a median of -4.9 to 28.4 kg m^{-2} yr^{-1} (Figure 11 & 12), driven mostly by changes in coral cover. Modest declines in budgets were observed across central and southern sites (Figure 11), largely reflecting changes in primary production (Figure 7). Overall estimates were within the range of values calculated using carbonate budget models and census-based methods at other locations (e.g. ReefBudget, Perry et al. 2018). Based upon surveys of 19 coral reefs throughout the Caribbean, a previous study identified a live coral cover threshold of ~10% that is critical in maintaining positive production states for Caribbean reefs (Perry et al. 2013). By incorporating estimates of uncertainty in model parameters, we identified a threshold of coral cover on offshore reef slopes of the GBR of ~17% that will reliably ensure a positive carbonate budget. Below this coral cover level, carbonate budgets usually become net negative, and may impact upon reef accretion and ecosystem function. Approximately 73% of sites had net positive budgets (median > 0 kg m^{-2} yr^{-1}) (Figure 12).

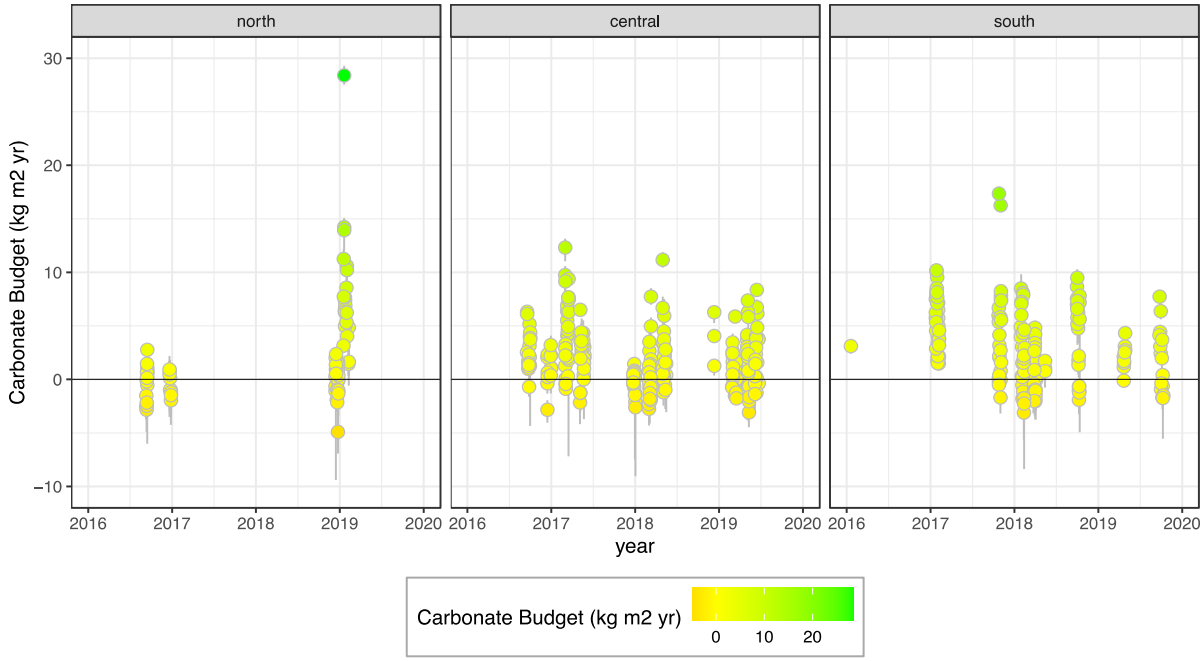


Figure 11: Spatial and temporal patterns for carbonate budgets on the GBR (2016-2020).

From a management perspective, while reefs below this coral cover threshold are net negative, this does not preclude recovery of corals following disturbance and a transition from a negative balance of erosion to a positive balance of carbonate production. Recent disturbances in the far Northern region have resulted in reefs that are close to this threshold, yet recovery of corals through recruitment and regeneration is likely to drive carbonate budgets into a positive state. Future studies should focus on exploring the potential for ecological feedbacks that may maintain reefs in a net negative erosional state on the GBR.

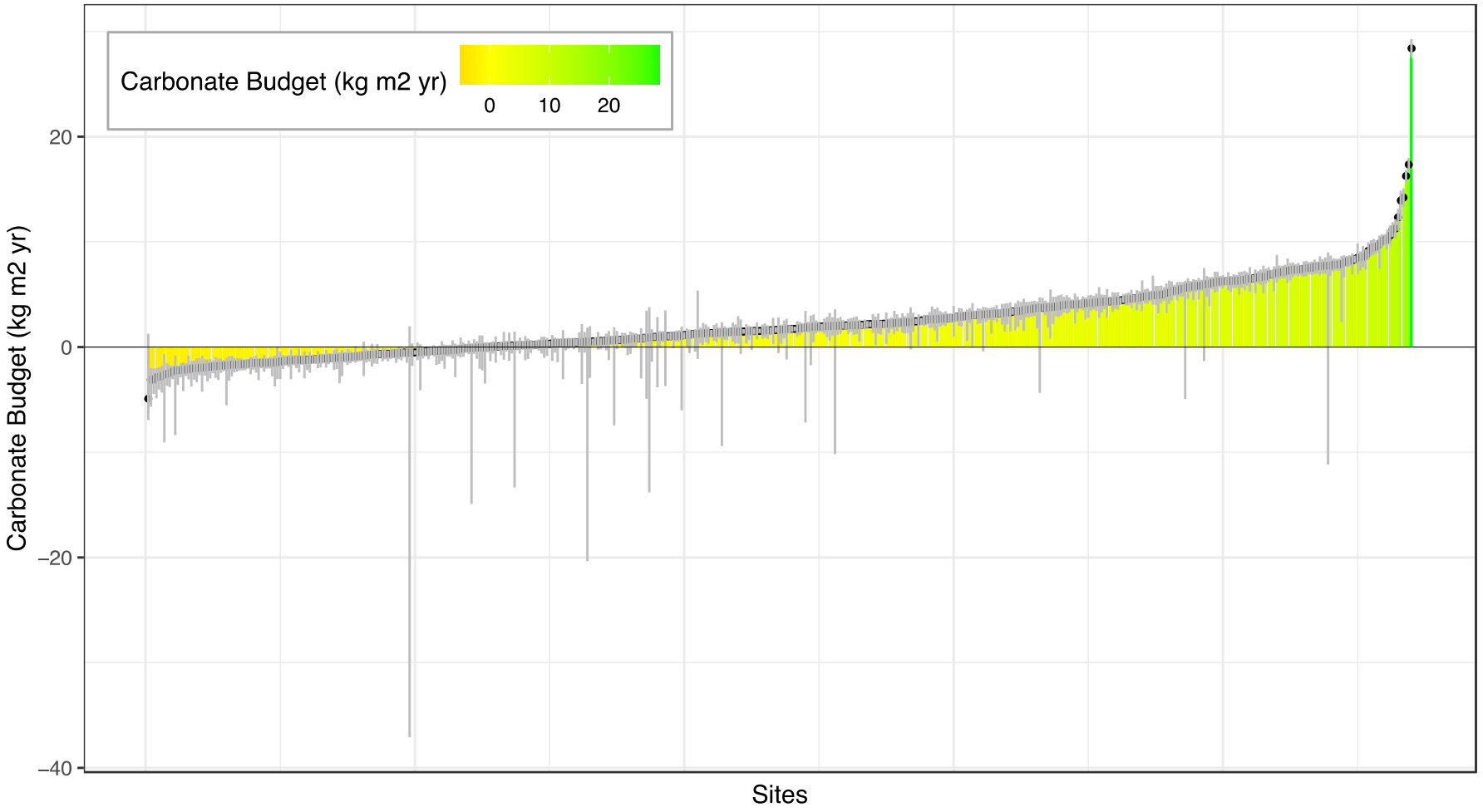


Figure 12: Carbonate budget and uncertainty estimates for 99 reefs (2016-2020) on the Great Barrier Reef.

3.4 Inclusion of ocean acidification

Development of this carbonate budget model into the *caRbs* package enables on-going model development and refinement. This ensures that significant advances in knowledge can be incorporated to make carbonate budget calculations and outputs more ecologically realistic and relevant. For example, broad-scale alterations to seawater chemistry will impair net calcification processes on coral reefs (Albright et al. 2016, 2018). Incorporation of ocean acidification into the *caRbs* model will likely reduce total carbonate production. However, there are likely to be spatial and temporal differences in the extent to which ocean acidification impacts the carbonate budget, as changes in seawater chemistry are not homogeneous across the GBR (Uthicke et al. 2014; Mongin et al. 2016). Thus, *caRbs* could be modified to parameterise findings by Mason et al. (2020) on the effects of ocean acidification on net calcification, using spatial and temporal data provided by eReefs on seawater chemistry parameters (e.g., pH, saturation states (Ω), pCO_2) for the GBR.

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