

On the fate of dead coral colonies

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Abstract

- Carbonate budgets dynamically balance production and loss of calcium carbonate (CaCO_3) on coral reefs. To sustain or expand the coral reef framework, CaCO_3 production by calcifying organisms must be higher than erosion. However, global climate change has been negatively impacting carbonate production, with bleaching events causing widespread coral mortality. Although bleaching and coral mortality are well documented, the fate of coral colonies after their death, including their erosion rates, are still poorly known.
- We followed the fate of 143 recently dead individual coral colonies with complex growth forms (arborescent, caespitose, corymbose, digitate and tabular), whose mortality was triggered by two consecutive bleaching events. These colonies, spread over 16 km² of the Lizard Island reef complex, were tracked for up to 5 years, allowing detailed examination of erosion rates and post-mortality structural persistence. We also tested how variables that are commonly used in coral reef erosion studies relate to spatial and temporal variability in the erosion rates of dead coral colonies.
- We revealed rapid erosion of dead coral colonies, with an average of 79.7% of dead colonies completely disintegrating within 60 months. The predicted half-life of a dead coral colony was 40 months, with limited variation among wave exposure levels. Remarkably, we found no effect of estimated parrotfish bioerosion, wave exposure, nor coral growth form, on observed erosion rates.
- Our results suggest that our understanding of the erosion of dead corals may be more limited than previously thought. The rapid loss of coral colonies on our study sites calls for a re-evaluation of the role of corals with complex growth forms in reef growth and of parrotfishes in reef erosion.

KEY WORDS

bioerosion, coral erosion, dead coral colony, ecosystem function, parrotfish

1 | INTRODUCTION

The physical structure of coral reefs is dependent on the dynamic balance between the production and loss of calcium carbonate

(CaCO_3). In this 'carbonate budget', production by calcifying organisms must be higher than erosion to sustain or expand the coral reef framework (Cornwall et al., 2021; Kleypas et al., 2001). Sustaining the physical structure of reefs is vital for maintaining the abundance,

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diversity and ecosystem functioning of reef-associated communities (Coker et al., 2014; Graham & Nash, 2013) and key services to people, such as coastal protection from inundation during storms (Elliff & Silva, 2017; Reguero et al., 2018). However, the persistence of positive carbonate budgets and reef structures may be at risk due to the increasing impact of climate change on coral reefs (Cornwall et al., 2021; Hughes et al., 2017; Perry et al., 2018).

On coral reefs, there are three main types of natural carbonate erosion: chemical, physical and biological. Chemical erosion occurs via carbonate dissolution. This process is slow but has been forecast to increase due to acidification (Eyre et al., 2018; Eyre et al., 2014; Schönberg, Fang, Carreiro-Silva, et al., 2017). Physical erosion is mostly caused by storms, including cyclones, which are often localized and short in duration (Puotinen et al., 2020). Biological erosion or 'bioerosion' refers to the removal of carbonate from the consolidated reef structure or from the skeletons of reef-building taxa (e.g., hard corals) by organisms (Hutchings et al., 2005; Kiene & Hutchings, 1994). Bioerosion is the most widespread and consistent form of carbonate removal and is the primary form of erosion on most reefs (Scoffin et al., 1977). Of all bioeroding taxa, parrotfish are arguably the most important, delivering rates of bioerosion that may approach total calcification (Bellwood et al., 2003; Morgan & Kench, 2016). It is well known that estimated bioerosion rates, and the organisms that underpin this process, exhibit marked spatial variability across depths, habitats and exposure levels (Bellwood et al., 2003; Brown et al., 2021; Yarlett et al., 2020). However, this is based on estimates of removal, primarily using proxies e.g. fish abundances. Our understanding of the links between potential bioeroders and the disappearance of dead coral skeletons is in its infancy.

Given the context of ongoing, widespread coral bleaching events, it is important to quantify how long coral colony structure remains following mortality, and how the loss of coral structure relates to estimated erosion rates. To fill this knowledge gap, we tracked the fate of 143 individual coral colonies of complex growth forms spread across 16 km² on the Lizard Island reef complex for 5 years (2016–2021), following their bleaching-induced mortality. In addition, we investigate the effect of variables that are commonly used in bioerosion studies, to assess how these may help to explain spatial and temporal variability in dead coral colony erosion around Lizard Island.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

Data collection was based on a comprehensive series of photo-quadrat censuses at Lizard Island (14°40'S, 145°28'E), in the northern Great Barrier Reef (GBR) (Figure 1). In 2016, a severe marine heatwave affected the GBR, including Lizard Island, triggering the most severe coral bleaching event recorded on the GBR (Hughes et al., 2021). In 2017 and 2020 the area experienced less intense bleaching events (Hughes et al., 2021). In February

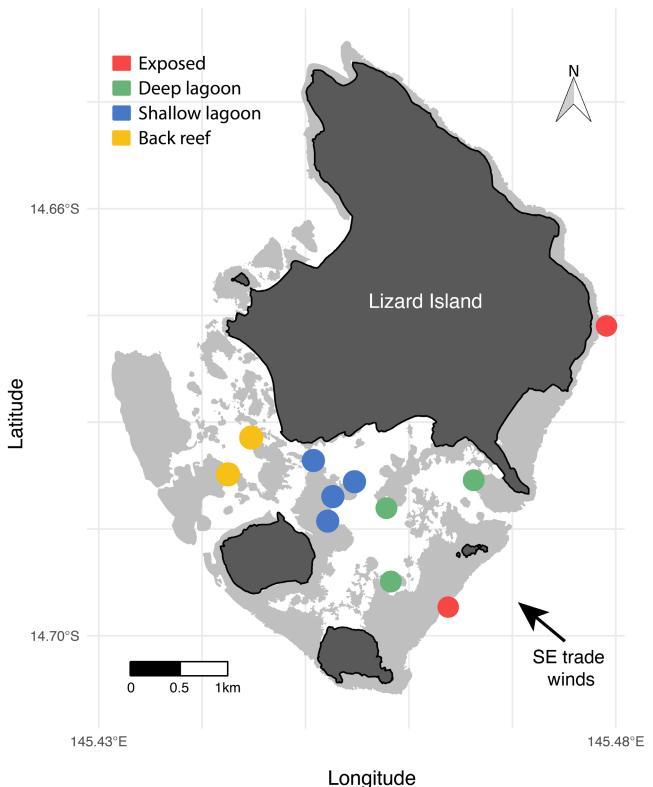


FIGURE 1 A map of Lizard Island showing the 11 sampling locations and their depth/exposure categories. (relative to the prevailing south-east trade winds).

2016, immediately prior to the major bleaching event, a series of 19 permanent transects, between 50 and 210 m in length (constrained by the nature of the reef) were established along the reef crest/edge (0–4 m below chart-datum) around Lizard Island. Each transect comprised between 12 and 38 quadrats (1 m² area) placed approximately 5 m apart. These quadrats were photographed initially and on five additional field trips: in April 2016 (3 months since first sampling), October 2016 (9 months), January 2018 (24 months), January 2020 (48 months) and January/February 2021 (60 months). Using SCUBA, a bird's-eye-view photograph of each quadrat was taken in each of the six sampling periods using a Nikon Coolpix W300 camera. Note that the quadrat frames were not fixed in place. Instead, we used a second camera containing previous images of each quadrat, ordered from the start to the end of the transect, as a guide to enable quadrat frames to be placed in the same position on each sampling trip (see Wismer et al., 2019 for sensitivity analysis of this method). For this study, we only used transects that included initially (in 2016) more than two visually trackable coral colonies, with the prerequisite that these colonies died at some point during the following five field surveys. This resulted in 11 transects in total, distributed among exposure regimes according to their position relative to the prevailing south-east trade winds (Fulton & Bellwood, 2005). Two transects were in exposed locations, three on the windward side of the lagoon (henceforth 'deep lagoon'), four in the protected

lagoon ('shallow lagoon') and two on the back reef (Figure 1). Research was conducted under Great Barrier Reef Marine Park Authority (GBRMPA) permit G17/38142.1.

2.2 | Erosion metrics

To investigate coral erosion of individual colonies, we tracked the fate of all corals with complex growth forms (i.e., arborescent, caespitose, corymbose, digitate, and tabular), that died during our sampling period (most died after the 2016 bleaching event). Massive corals were not tracked due to low mortality rates (Morais et al., 2021). We did not consider colonies that were already dead in the first sampling period, selecting only living colonies that could be tracked until their mortality to ensure we examined the entire post-mortality period (Figure 2).

To quantify erosion, estimates of individual coral colony volume are required. However, although there are now methods such as 3D photogrammetric approaches via Structure-from-Motion available that can facilitate this process (Aston et al., 2022; Bayley & Mogg, 2020; Pizarro et al., 2017), such processes have a number

of limitations, especially in terms of processing times and light requirements (House et al., 2018). Moreover, it is impossible to utilize this method post-hoc (i.e., after the corals have already died and begun to erode), limiting our capacity to understand how processes on the reef could have changed. However, it has now been repeatedly shown that 2D estimates of colony surface area are inextricably linked to 3D volume for corals of the same morphology (House et al., 2018; Husband et al., 2022; Urbina-Barreto et al., 2021). Therefore, by deriving relationships between 2D surface area and 3D volume, one can estimate colony volume from data on surface area alone. We utilized such an approach herein. Specifically, we used the software ImageJ (Abràmoff et al., 2004) to measure planar area (in cm^2) from the photographs of each colony in each sampling period (following Morais et al., 2021). We then applied the relationships between planar area and colony volume provided in Urbina-Barreto et al. (2021) to convert estimates of coral planar surface area from our photoquadrats to predict 3D colony volume (see Appendix S1 for further details and potential limitations of this method).

To comprehensively address all the comparisons and models in our study, the loss of calcium carbonate ('erosion') was expressed in five different ways.

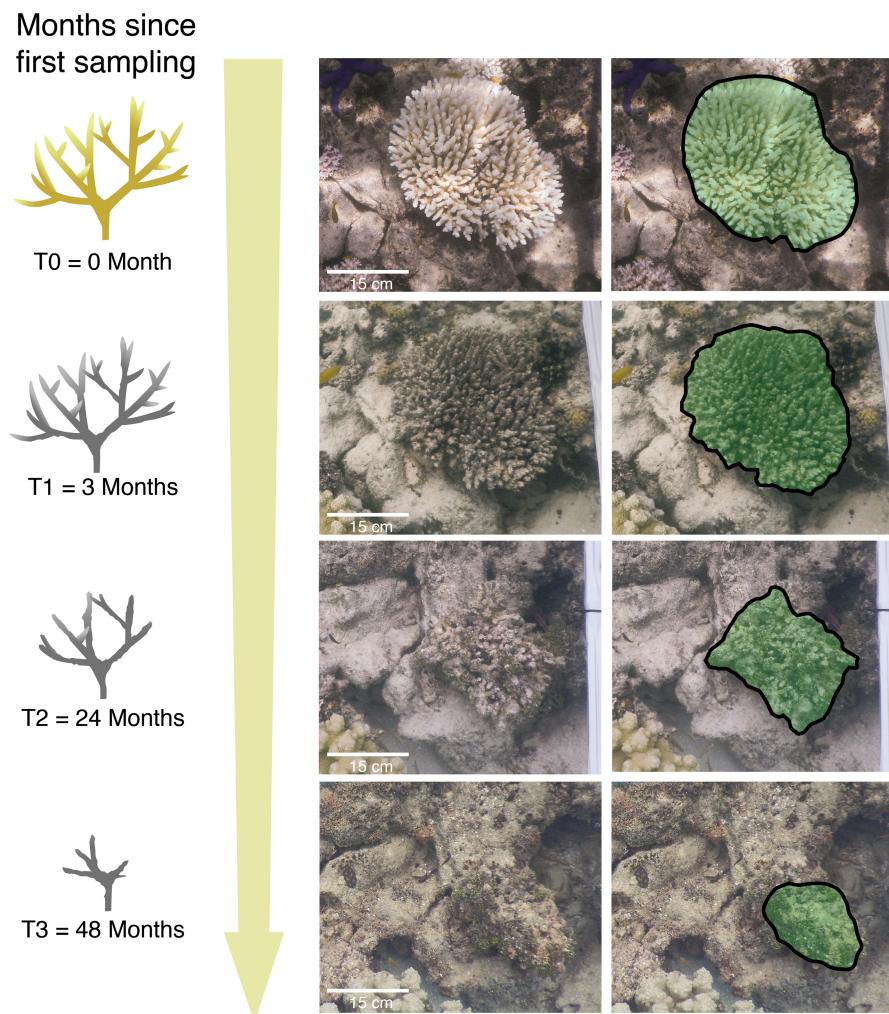


FIGURE 2 Sequence of photos showing an example of an *Acropora* coral colony eroding over time. Left image, right showing the digitalized area.

1. The changing volume of each colony (in cm^3) was predicted from its planar area based on the relationships in Urbina-Barreto et al. (2021) (Appendix S1).
2. To calculate the loss of CaCO_3 in grams per colony per year, we first calculated the mass of calcium carbonate in each colony by multiplying the estimated volume by species or genera-specific skeletal densities from the coral traits database (<http://coraltraits.org>; Madin et al., 2016). Where multiple density values were available for a species, these were averaged. For coral species with no density data, data from the closest related species with the same growth form were used. Then we calculated the difference in estimated calcium carbonate (g) between the largest size recorded for each colony and its size at the last sampling (i.e., the end of the study or when colony was undetectable, planar area = 0). Dividing the mass lost per colony (g) by the time in years (between the largest recorded size and the last sampling or when the colony was undetectable) provided the average carbonate loss in g per colony per year (this was calculated for each colony then averaged for each transect).
3. To model erosion rates per colony we took the colony specific mass lost from (2) and standardized it by the initial colony size, to account for variation in initial colony sizes. Erosion rates in this case are therefore the loss of g carbonate per cm^2 of initial colony area, per year.
4. To calculate total carbonate mass lost per unit area of reef (i.e. the loss of CaCO_3 in $\text{kg m}^{-2} \text{ year}^{-1}$), as in (2), we first calculated the mass of calcium carbonate in each colony by multiplying the estimated volume by species skeletal densities. Then, we calculated the differences in the mass of calcium carbonate (in kg) between the largest size recorded for each colony and its size at the last sampling period. To calculate carbonate loss per unit area (i.e. average carbonate lost per m^{-2} surveyed in each transect), the total loss of mass across all colonies, per transect, was divided by the area of the total number of quadrats in that transect (including quadrats that did not host colonies). This resulted in the total loss of CaCO_3 in kg m^{-2} (in each transect) over the 5 years, which was then divided by 5 to provide an annual rate of erosion per unit area of reef.
5. To estimate the average erosion rates per unit area across all transects in $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$, we simply averaged the values in (4) across all transects in the study.

2.3 | Explanatory variables

In addition to erosion, we quantified a number of key explanatory variables. Specifically, we calculated potential parrotfish erosion at each transect location based on two 50×5 m transect surveying all parrotfishes larger than 10 cm total length (TL). We specifically chose surveys of this size (covering an area of 500 m^2 at each location) because this is reflective of methods commonly used in the literature on parrotfish bioerosion (e.g. $240\text{--}720 \text{ m}^2$ per site; Alwany et al., 2009; Graham et al., 2018; Kuffner et al., 2019; Morgan & Kench, 2016; Perry et al., 2015). This was important because it ensured our results aligned

with the methods commonly used in this research field, thus allowing our results to be placed into the context of this past research more directly. Our surveys included data on species identity, abundance, and size (total length, in cm) and were undertaken by the same experienced SCUBA diver (last author) between January and February 2021. We considered only excavating parrotfishes, which disproportionately dominate fish bioerosion (Bellwood & Choat, 1990). Only three excavating species were observed: *Chlorurus microrhinos*, *Chlorurus spilurus*, and *Chlorurus bleekeri*. All counts were conducted between 0930 and 1600 h. From the counts, potential bioerosion (in kilograms of CaCO_3 per m^2 of reef per year) for each transect was estimated by multiplying individual fish size by the proportion of bites that leave scars (from Hoey, 2018), bite volume ($\text{mm}^3 \text{ bite}^{-1}$) (from Bellwood, 1995), feeding day length (in minutes; from Bellwood, 1995, averaged across winter and summer), bite rate (bites per minute; Bellwood & Choat, 1990 values for Lizard Island), and the abundance of each fish species, as well as an overall estimate of the carbonate density of the 'reef matrix' (following Bellwood, 1995). It is important to note that these methods for quantifying the process of bioerosion by parrotfishes from one-off surveys, inherently assumes that this process is consistent both spatially and temporally (e.g., Bellwood, 1995; Kuffner et al., 2019; Morgan & Kench, 2016; Perry et al., 2012).

In addition to potential parrotfish bioerosion, potential wave exposure and coral growth form, we also incorporated geometric and environmental factors: skeleton density, local coral cover, colony size (planar area), colony volume and colony density (number of colonies per transect), which allowed us to control for potential morphological and environmental variation in our model. As per above, coral skeletal density was obtained from (Madin et al., 2016). Colony size was considered to be the largest size of the colony during our sampling period, which in all cases coincided with the last time the colony was seen alive or the first time it was recorded dead. Colony volume was the same as used above in metric #1. Colony density was the count of the number of colonies per transect. Finally, coral cover was determined from the photographs and was calculated by determining the cover under 40 randomly positioned points per quadrat using the software Photoquad v.1.4 (Trygonis & Sini, 2012).

2.4 | Data analyses

To estimate the rates of loss of individual coral colonies and the predicted 'half-life' of coral colonies as a recognizable physical structure following mortality, we used a Bayesian generalized linear mixed effects model with a binomial distribution and logit link. The fate of the colony at each survey occasion (i.e. if completely eroded or retaining visible signs of colony structure) was used as the response variable and time (difference in months between last time seen alive and the end of the study or when the colony was undetectable, planar area = 0), exposure level and their interaction were treated as predictors. Transect identity was included as a random effect to account for the lack of spatial independence in the sampling design. The model was based on three chains with 5000 iterations, including

3000 iterations to warm-up and a thinning interval of 2, with weakly informative priors. Model fit and assumptions were evaluated using residual and autocorrelation plots, accompanied by metrics of sampling efficiency (*rhat*) and effective sample size (*neff*) scores, all of which were satisfactory and suggested that the MCMC chains were well mixed and converged. All Bayesian models were performed in Stan (Stan Development Team, 2021) via the 'rstan' interface using the package 'rstanarm' (Goodrich et al., 2020) in R (R Core Team, 2020).

We tested the hypothesis that parrotfish erosion, level of wave exposure and coral growth form influenced the rates of calcium carbonate loss in coral colonies at Lizard Island using a Bayesian generalized linear mixed effects model with a gamma distribution and a log link function. Loss of calcium carbonate (erosion metric #3) was the response variable, while estimated parrotfish erosion, wave exposure, and growth form were used as predictor variables. Potential geometric and environmental factors, such as: skeleton density, local coral cover, colony size (planar area), colony volume and colony density (number of colonies per transect) were also included as control for potential morphological and environmental variation in our model. Again, we included transect as a random effect to account for the lack of spatial independence. The model fit and assumptions were as above.

3 | RESULTS

3.1 | Rates of colony loss

After 24 months, 42% of the initial 143 colonies were completely eroded. After 48 months, this stood at 103 colonies, or 72%. By the end of the study, 60 months after first sampling, a total of 114 colonies or 79.7% of all colonies had been totally eroded. Thus, from

the initial 143 colonies, only 29 maintained some visually discernible evidence of physical structure at the end of the study period. Our model suggested that the predicted 'half-life' of coral colonies as a recognizable physical structure following mortality at Lizard Island was on average 3.3 years (or 40 months), ranging from 2.6 years (31.3 months) in the exposed locations to 4.1 (50 months) in the deep lagoon (Figure 3).

Furthermore, there was little variation in colony disappearance rates across exposure levels, with almost no effect on differences across habitats (except between deep lagoon vs. exposed and deep lagoon vs. shallow lagoon, Table S1). Indeed, locations in all exposure types presented relatively similar rates of colony disappearance based on volume (erosion metric #1) over the 60 months of the study, ranging from over 80% in the shallow lagoon and exposed locations to around 64% in the back reef and 61% in the deeper part of the lagoon (Figure 4).

3.2 | Explanatory variables

To investigate the likely drivers of dead coral erosion at Lizard Island, we compared observed coral erosion in each transect (erosion metric #4) to the predicted erosion caused by parrotfishes estimated from fish counts at the same sites. If parrotfishes are the main source of bioerosion of dead corals, we would expect to find a clear match between observed coral erosion and predicted parrotfish erosion. Instead, there was a clear spatial mismatch between the two rates. Only four transects were estimated to experience sufficient parrotfish-driven bioerosion to explain coral erosion, with the majority of the transects having little or no predicted parrotfish erosion. Interestingly, in the shallow lagoon, which had both the

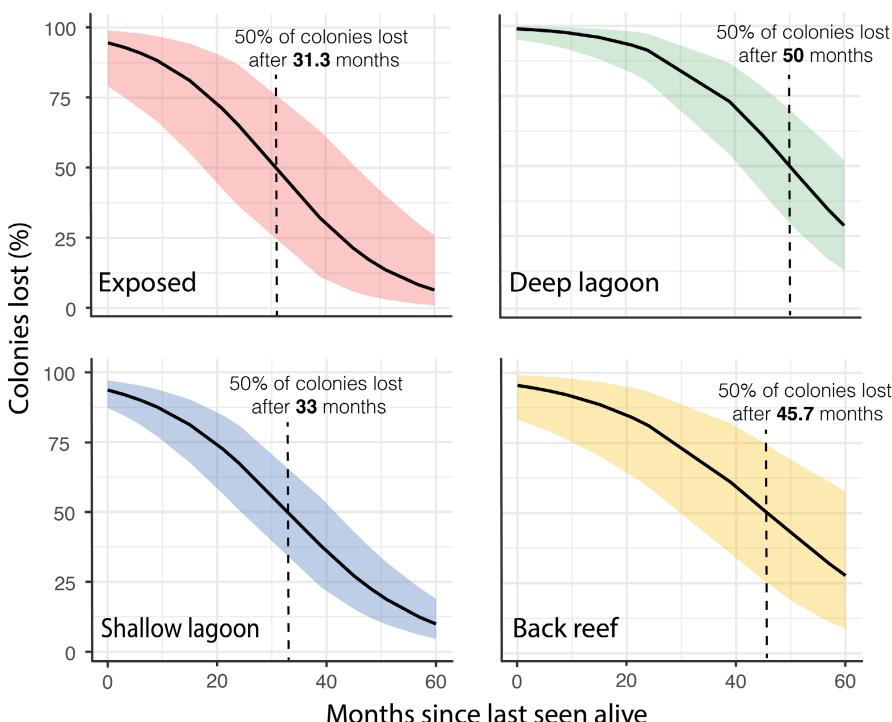
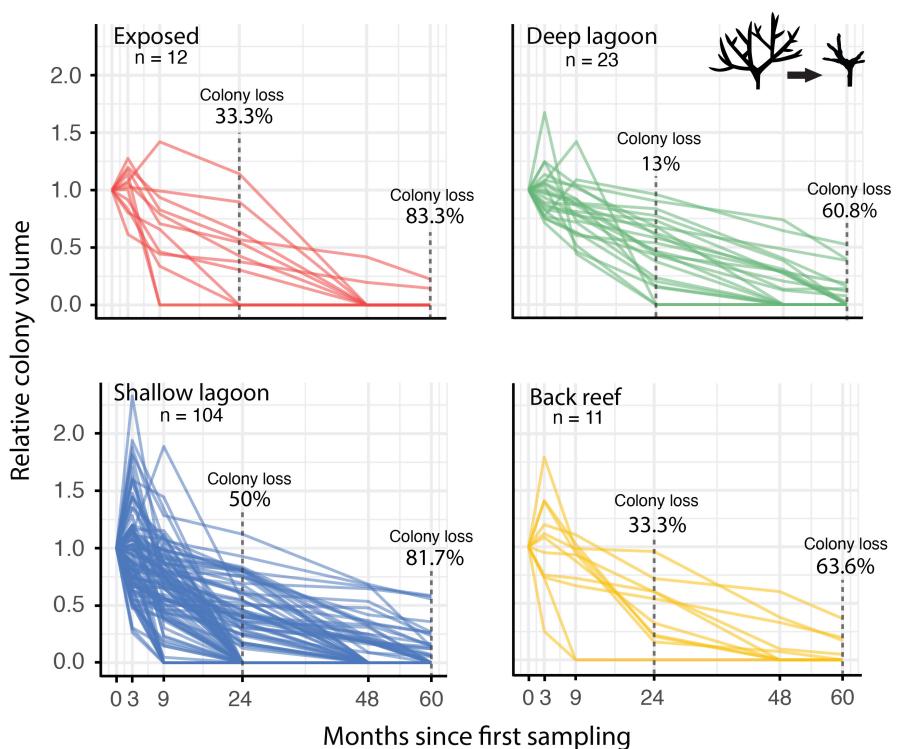


FIGURE 3 Predicted rate of coral structure loss at each exposure level following bleaching-induced mortality at Lizard Island, northern Great Barrier Reef. A generalized linear mixed model was used to estimate the logistic regression line (black line) and 95% high posterior density intervals (coloured ribbons).

FIGURE 4 Relative volume of complex growth form coral colonies tracked over 60 months. Each line represents a single colony, with colours representing the wave exposure categories from Figure 1. Relative volume (cm^3) is the predicted volume based on the planar area of the colony relative to the value at first detection. Vertical dashed lines represent the proportion of colonies that completely disappeared at that point in time.



highest number of colonies tracked and the highest rates of coral colony loss (Figure 4), parrotfish erosion was estimated to be close to zero (Figure 5). The same pattern was observed for both transect level erosion (metric #4) and colony level erosion (metric #2) (Figure 5). This was also reflected in our model, which showed no effect of predicted parrotfish erosion at the quadrat level or for coral colony estimated erosion (Figure 6). This suggests that other factors may be driving dead coral colony erosion at Lizard Island.

After this preliminary investigation, we looked more broadly at other potential explanatory variables. Surprisingly, we found that erosion (per colony, standardized, metric #3) was constant across wave exposures levels, with no effect on erosion rates across habitats (Table S1). The same was observed for growth forms, where erosion was constant across all categories (Figure 6).

4 | DISCUSSION

The potential impacts of global climate change on carbonate accretion on coral reefs has been widely reported (Bozec et al., 2015; Cornwall et al., 2021), largely because of widespread coral bleaching and mortality events triggered by severe heatwaves. Although coral mortality during and after bleaching events is well documented (Hughes et al., 2017; Madin et al., 2018; Morais et al., 2021; Sully et al., 2019), the fate of coral colonies after their death, including their rates of erosion, has received limited attention (but see Kuffner et al., 2019; Roff et al., 2015). We addressed this knowledge gap by using a novel dataset that allowed us to track the fate of dead coral colonies over 5 years. This enabled us to investigate dead coral colonies individually and thus examine a range

of environmental factors that have been hypothesized to drive their erosion, including their growth form and exposure to waves (Madin & Connolly, 2006) and parrotfish erosion (Bellwood, 1995; Morgan & Kench, 2016; Perry, Murphy, et al., 2013). Importantly, it is believed that dead coral colonies are an integral component in the formation of the reef matrix (Cornwall, 2019; Stanley, 1981). However, contrary to these expectations, we found intense dead coral colony erosion with an average of 79.7% of dead colonies completely disintegrating within 60 months. Furthermore, the predicted half-life of a dead coral colony was on average only 40 months, ranging from 31 to 50 months among wave exposure levels (Figure 3). We also found that neither estimated parrotfish erosion nor exposure level or coral growth form, were capable of explaining observed variation in coral erosion rates. These results suggest we may need to reevaluate the role of corals in reef building and associated processes.

4.1 | Coral structure loss

Our study revealed that even relatively large colonies (up to 40 cm wide) were completely eroded within just 9 months (Figure 4). Indeed, regardless of the location, after 5 years, between 60.8 and 83.3% of all dead coral colonies were completely eroded (Figure 4). This is a relatively fast rate of disappearance and raises questions about the contributions of complex growth form corals to reef growth. If corals are an integral part of reef matrix growth, we would have expected a considerable degree of coral colony structure to remain. However, the loss of a relatively high number of coral colonies in only a few months suggests that corals with branching or tabular growth forms

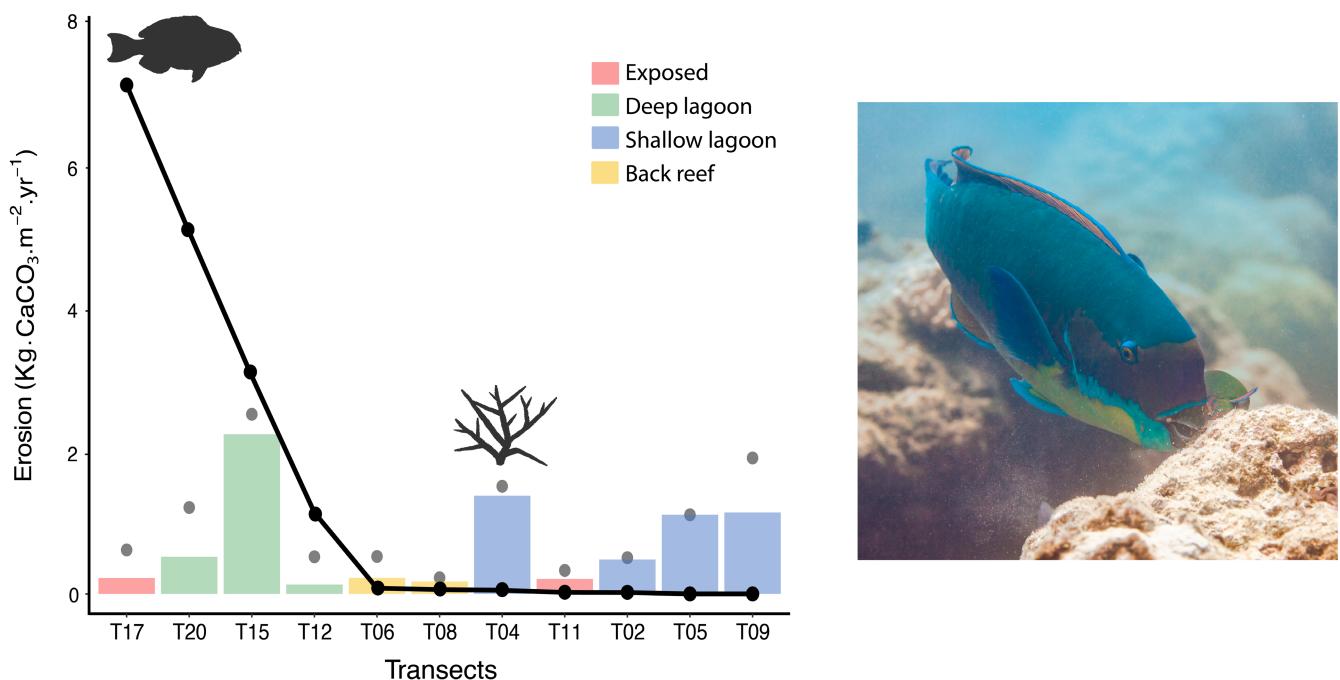


FIGURE 5 Dead coral colony erosion and estimated parrotfish erosion on 11 transects around Lizard Island. Y-axis applies to the bars, which indicate total estimated coral erosion with colours showing exposure levels, to the black dots and line which represent predicted parrotfish erosion on each transect, and to the grey dots (erosion metric #2), which represent overall carbonate lost per colony ($\text{kg.CaCO}_3 \cdot \text{Colony} \cdot \text{year}^{-1}$). On average, coral erosion was $0.6 \text{ kg.m}^{-2} \cdot \text{year}^{-1}$ [metric #5]. Note that this figure is used exclusively to illustrate the distinct spatial patterns of these variables. Photograph: Victor Huertas.

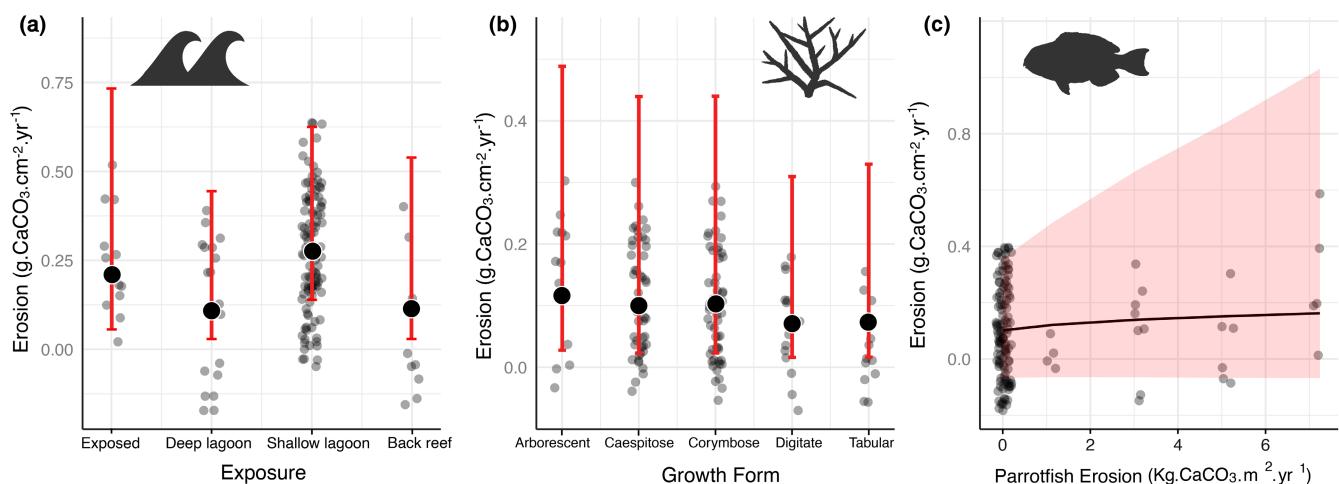


FIGURE 6 Effects and partial residual plots of the relationship between erosion of individual coral colonies and the response variables: (a) exposure level, (b) coral colony growth form and (c) predicted parrotfish erosion. Model fits pertain to a gamma Bayesian generalized linear mixed model (with transect as a random effect). The erosion on the y-axis is the differences in the mass of calcium carbonate (in grams) between the largest size recorded for each colony and its size at the last sampling per year (expressed as a rate per cm^2 of initial colony area, to account for variation in initial colony sizes). Black point represents estimated marginal means and red lines and ribbon represents 95% high posterior density intervals (HPD).

may play a limited role in reef growth. This phenomenon may be particularly important in the absence of coral recovery after a mortality event. If high rates of coral erosion are a widespread phenomenon in complex growth form corals on Indo-Pacific coral reefs, then it is possible that the major role of these corals may lay in rubble formation (Hughes, 1999) and reef infilling (Perry, Kench, et al., 2013,

Perry, Murphy, et al., 2013) rather than growth via the deposition of in situ coral skeletons.

Coral rubble is generated and further broken down through a variety of biological, chemical and mechanical processes such as bioerosion and storms that deposit fragmented dead coral skeletons onto the fore-reef slope (Rasser & Riegl, 2002). Hughes (1999)

documented a high rate of coral fragment export at Lizard Island from the reef slope down to the reef base, with an average of 132 fragments, weighing 1.87 kg, per horizontal meter of slope-base interface per year, or $\sim 0.2 \text{ kg.m}^{-2}.\text{year}^{-1}$ if divided by the slope depth (8–12 m). However, this is still far from the observed erosion rates of dead coral colonies in our study. Hughes' values of $\sim 0.2 \text{ kg.m}^{-2}.\text{year}^{-1}$ are approximately 3-fold lower than the $\sim 0.6 \text{ kg.m}^{-2}.\text{year}^{-1}$ erosion rates herein (erosion metric #5). Additionally, there was limited evidence of fallen coral branches among the remaining colonies, suggesting that the branches are being broken into finer sediment fractions (see Figure S4 for coral rubble cover). Clearly a large proportion of the dead coral colony structure is 'disappearing'.

4.2 | Drivers of coral erosion

4.2.1 | Physical erosion

Coral loss is not just about the loss of colony structure and the services it provides to fishes and invertebrates. Coral loss also represents a major loss of calcium carbonate from the reef structure (Bozec et al., 2015; Gvirtzman, 1994). Therefore, it needs to be interpreted from a functional perspective, which requires knowledge of both rates of material movement and potential drivers. The primary potential drivers of erosion tested herein included the location (as a proxy for wave energy) and the morphology of the coral colony (i.e. growth form).

While estimated bioerosion has been found to correlate with exposure (i.e., higher bioerosion in exposed compared to lagoonal habitats; Hoey & Bellwood, 2008; Hutchings et al., 1992), these patterns were linked with biological agents (parrotfishes or sponges etc.) not the physical action of waves. Waves could be a direct primary driver of erosion, particularly in the face of severe storms (Puotinen et al., 2020). However, if wave energy was important, we would expect that exposure levels would have shaped the erosion rates in our study, with more exposed habitats exhibiting higher erosion than more sheltered ones. Similarly, the vulnerability of colonies to physical erosion will likely depend on their size, shape and growth form (Madin et al., 2014; Madin & Connolly, 2006), which are highly variable at very local scales. However, we found no clear effects of either exposure or coral morphology/growth form in our analyses. Given the absence of major storms and cyclones during the study period, there is, thus, limited evidence to support the suggestion that physical disturbance was a key driver of coral erosion of complex growth forms at Lizard Island during our study period (during which no major storms occurred; Figure 6).

4.2.2 | Bioerosion

Internal

Internal bioerosion is a process which can substantially remove calcium carbonate from recently dead coral colonies (Glynn, 1997; Aline

Tribollet & Golubic, 2011). This process comprises microbioerosion, which is often caused by chemical dissolution driven by microborers (Garcia-Pichel, 2006; Grange et al., 2015), and macrobioerosion, caused most by polychaetes, bivalves and sponges (Schönberg, Fang, & Carballo, 2017; Schönberg, Fang, Carreiro-Silva, et al., 2017). Despite being a natural process on coral reefs, future scenarios of ocean warming and acidification are predicted to cause an increase in internal erosion rates by accelerating CaCO_3 dissolution (Cornwall et al., 2021; Leggat et al., 2019; Reyes-Nivia et al., 2013).

However, internal bioerosion has relatively low rates of CaCO_3 removal if compared to external bioerosion. Indeed, extensive studies of the process of erosion at our study location (Lizard Island) have suggested that this process is relatively minor compared to erosion by parrotfishes. For example, Kiene and Hutchings (1994) found internal erosion rates ranging from 0.058 to $0.2 \text{ kg m}^{-2}.\text{year}^{-1}$ while the average rates of grazing erosion ranged from 0.30 to $1.96 \text{ kg m}^{-2}.\text{year}^{-1}$. Similarly, Osorno et al. (2005) showed internal erosion (by macrobores, sponges, polychaetes, and molluscs) accounted for just $0.035 \text{ kg m}^{-2}.\text{year}^{-1}$. These examples from Lizard Island also appear to be mirrored in other studies in other areas. For example, Yeung et al. (2021) found that in Hong Kong, total internal erosion ranged from 0.02 to $0.36 \text{ kg m}^{-2}.\text{year}^{-1}$, while total erosion (i.e. internal and external) ranged from 0.72 to $3.09 \text{ kg m}^{-2}.\text{year}^{-1}$. Similarly, Kuffner et al. (2019) found that in the Florida Keys the average contributions of sponge erosion and microbioerosion was up to 0.1 and $0.2 \text{ kg m}^{-2}.\text{year}^{-1}$, respectively, while parrotfish bioerosion represented $1.6 \text{ kg m}^{-2}.\text{year}^{-1}$. Taken together, these results all suggest that, internal erosion is likely to account for only a small fraction of the total loss of calcium carbonate observed in our study.

It should be noted, however, that different kinds of erosion are not isolated and may interact with each other (Grange et al., 2015; Schönberg, Fang, Carreiro-Silva, et al., 2017). Internal erosion can weaken the structure of dead corals, particularly complex growth form colonies, by rapidly increasing its porosity and making them more susceptible to wave action or biological activity (Leggat et al., 2019). Internal erosion may also make corals more susceptible to external erosion (Chazottes et al., 1995; Tribollet & Golubic, 2005). However, the lack of an effect of location or estimated external erosion on coral loss, suggests that internal erosion, if present, had only a limited impact, directly or indirectly.

External

There is an extensive body of literature that identifies parrotfishes as the primary reef bioeroders (Bruggemann et al., 1996; Gygi, 1969; Kuffner et al., 2019; Morgan & Kench, 2016; Ong & Holland, 2010; Perry et al., 2012; Scoffin et al., 1977). Indeed, one of the key locations for the development of this work was Lizard Island, where the role of excavating parrotfish were first documented in the Indo-Pacific (Bellwood, 1995, 1996; Bellwood & Choat, 1990). However, our analyses did not find a clear correlation between predicted parrotfish erosion and the rates of coral colony erosion. This raises the question: why do our observations contrast so markedly with these past studies?

One of the first factors to consider in explaining our results is the context of the reef in question. Our study examined coral erosion on a heavily disturbed reef system where the selected habitats had significant coral cover (>10%), due to past cyclones (Madin et al., 2018) and crown-of-thorns starfish outbreaks (Pratchett, 2010) prior to our study beginning in 2016. These altered conditions may not be comparable to the relatively high coral cover reefs of the past, although they may be more representative of, and particularly relevant to, the frequently disturbed reefs of the future.

In addition, in terms of context, it is important to discount the role of sea urchins at our location as these are the other primary external bio-eroding organism on coral reefs (Glynn, 1988; Griffin et al., 2003). While these organisms may contribute substantially to this process in some areas (Dumont et al., 2013; Peyrot-Clausade et al., 2000), the role of sea urchins in bioerosion at Lizard Island is extremely limited ($\sim 0.011 \text{ kg m}^{-2} \text{ year}^{-1}$) as their abundances are low (Tebbett & Bellwood, 2018; Young & Bellwood, 2011). Therefore, parrotfishes are the chief external bioeroders in this location (Bellwood, 1995; Kiene & Hutchings, 1994; Tebbett & Bellwood, 2018).

After this process of elimination, which suggests other factors only have a limited capacity to account for the coral colony erosion rates in our study, this leaves parrotfish bioerosion as the chief explanatory factor with the capacity to account for the observed erosion rates. Therefore, the most parsimonious explanation for the mismatch in parrotfish erosion versus coral colony erosion herein, could be that the most common current approach used to quantify parrotfish bioerosion on coral reefs are inadequate. Below we detail several potential limitations that could shape our understanding of parrotfish bioerosion. Importantly, we followed methods that aligned closely with those commonly used in this research field, therefore, these limitations may apply beyond our study. They suggest that our current understanding of parrotfish bioerosion is incomplete.

The first issue is that most estimates of parrotfish bioerosion are based on static, one-off surveys of fish abundance to calculate a dynamic process (bioerosion). In other words, these estimates are underpinned by the assumption that 'presence = function', with estimated functions assumed to occur homogenously through space and time (discussed in Bellwood et al., 2019). While such a simplifying assumption may offer insights into the potential for functions to be delivered, it does not provide any information on the actual delivery of function by fishes. This point was previously highlighted as a major limitation in our understanding reef functions more generally (Bellwood et al., 2019) and a growing number of studies are now documenting a substantial disconnect between fish presence and their capacity to deliver functions (Carlson et al., 2017; Longo et al., 2014; Streit et al., 2019; Tebbett et al., 2020; Welsh & Bellwood, 2012). The results of our study support this earlier work. Our estimates of coral colony erosion represents the measurement of an actual process, accounting for variation in space and time, while the estimates of parrotfish bioerosion merely represents an estimate of a potential process. As there was no clear alignment between the two, this suggests that current approaches to estimating parrotfish bioerosion may not accurately reflect ecosystem processes documented herein.

One of the primary reasons why the assumption that presence = function may not apply to parrotfish bioerosion is the fact that one-off surveys do not account for temporal variation in parrotfish presence, that is, in movement. As bioeroding parrotfishes such as *Chlorurus microrhinos* have home ranges in the order of nearly 8000 m^2 , and use space within this home range in a heterogenous manner (Welsh & Bellwood, 2012), the abundance of parrotfishes at the spatial scale of our surveys per site (i.e., 500 m^2) could vary over relatively short temporal scales. Indeed, parrotfish home-range can vary considerably depending on the spatial and temporal scales of measurement (Davis et al., 2017), with these patterns being tightly connected to different aspects of their life history and ecology (Afonso et al., 2008). Therefore, one-off surveys may not accurately capture temporal variability (although how many times surveys would have to be replicated to capture this variability is currently unclear). It is important to note, however, that while parrotfish presence may vary over short temporal scales, average parrotfish abundance at this location has remained relatively consistent across years despite major disturbances (Huertas et al., 2021; Morais et al., 2020).

Given the size of parrotfish home ranges compared to the size of the surveys used in our study, and in most other studies on parrotfish bioerosion around the world, there is also the potential that we could have underestimated the abundance of key parrotfishes. In this respect, the size of surveys commonly used are unlikely to have captured the effect of the largest of all bioeroding parrotfishes, *Bolbometopon muricatum* (Bellwood, 1994). Rarely seen on, or recorded in, short transects, this rare species feeds on erect coral growth forms (Bellwood et al., 2003), removing corals at the rate of 5 tonnes per individual fish per year. On the crests of outer reefs of the GBR, they can remove nearly $30 \text{ kg m}^{-2} \text{ year}^{-1}$ of carbonate (Bellwood et al., 2003). Thus, only a few individuals would be required to completely clear the study sites and account for the erosion rates documented herein. While not observed in our surveys, *B. muricatum* have been seen in small groups at all our study locations around Lizard Island (on multiple occasions from 2016–2021) and are probably part of a larger group of ~50 individuals that rove around the Lizard Island complex (authors pers. obs. Figure S3). However, given their rarity, and very large home ranges (with individuals like to roam over several kilometres in a day, Hamilton, 2005), *B. muricatum* are highly unlikely to be detected in small-scale transects. Indeed, specific survey designs (that cover $4000\text{--}5000 \text{ m}^2$) per site are required to have a good chance of documenting *B. muricatum* abundances (Bellwood et al., 2003). Therefore, the traditional transects used to study parrotfish bioerosion may overlook one of the most relevant bioeroders in the Indo-Pacific.

It must be noted, however, that Lizard Island may be atypical relative to many other modern reefs in the Indo-Pacific, as relatively healthy *B. muricatum* populations are still present (Bellwood et al., 2012). Across the Indo-Pacific, from Mauritius to French Polynesian, where *Bolbometopon*, in particular, have been heavily fished, external bioerosion by parrotfishes is now negligible (Bellwood et al., 2012). Moreover, in other coral reef realms such as the Western Atlantic, there are no bioeroding parrotfishes

comparable to *B. muricatum*, with reefs in this realm functioning in a different manner to Indo-Pacific reefs (Siqueira et al., 2019). Therefore, the rapid loss of coral colonies recorded on Lizard Island may represent an anomaly for most Anthropocene coral reefs. On reefs where *Bolbometopon* have been severely overfished, erosion rates of coral colonies may be far lower, warranting attention in future research.

Overall, it appears that the most parsimonious explanation for the mismatch between predicted parrotfish erosion and coral colony erosion is a combination of a spatial mismatch in functions and limitations with the current method of estimating parrotfish erosion, which may not effectively account for the largest of all bioeroders, *B. muricatum*. Indeed, while frequently used, current methods for estimating parrotfish bioerosion had not previously been 'ground-truthed' against actual measurements of coral colony erosion on the reef. Given the mismatch we documented, and the fact that similar methods for estimating parrotfish erosion are widely applied across this entire research field, this suggest our current understanding of parrotfish bioerosion on coral reefs could be severely limited, especially in terms of the erosion of recently killed complex coral colonies.

5 | CONCLUSION

By individually tracking the fate of dead coral colonies around Lizard Island, we revealed that corals with complex growth forms rapidly erode and, in most cases, completely disappear within 5 years. Such rapid erosion rates suggest that the calcium carbonate laid down by these corals may not be incorporated into the reef matrix. At most, these corals are likely to perform a role in reef growth that is more aligned to rubble or sand formation and infilling. Furthermore, among the potential physical and biological drivers investigated, we found no clear explanation for the rapid erosion observed, including no correlation with estimated rates of parrotfish erosion, the major reported bioeroders. This suggests that there is a gap in our understanding of how bioerosion of dead corals occurs on coral reefs. We hypothesise that, at Lizard Island, this may be accounted for by roving schools of *Bolbometopon*, but the evidence is circumstantial. Clearly, our understanding of reef growth and erosion is far from complete, especially under intensifying drivers of coral mortality from global climate change.

AUTHOR CONTRIBUTIONS

Juliano Morais, Renato Morais and David R. Bellwood conceived the ideas and designed methodology; Juliano Morais and Sterling B. Tebbett collected the data; Juliano Morais, Renato Morais and Sterling B. Tebbett analysed the data; Juliano Morais and David R. Bellwood led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at the Zenodo repository <https://doi.org/10.5281/zenodo.7071166> (Morais et al., 2022).

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SUPPORTING INFORMATION

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