Carbonate budgets as indicators of functional reef “health”: a critical review of data underpinning census-based methods and current knowledge gaps

Ines D Lange[1]*, Chris T Perry[1], Lorenzo Alvarez-Filip[2]

[1]Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK
[2]Biodiversity and Reef Conservation Laboratory, Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Mexico

*i.lange@exeter.ac.uk, University of Exeter, Geography, Amory Building, Rennes Drive, Exeter EX4 4RJ, United Kingdom

Abstract

The carbonate budget of a reef describes the net rate of carbonate production resulting from various biologically-, physically- and chemically-driven production and erosion processes. Thus, budget state metrics can provide important information on a reef’s growth potential and on the capacity of reefs to sustain key geo-ecological services such as habitat provision and coastal protection. Whilst various approaches for estimating carbonate budgets exist, census-based methods have gained recent interest because they quantify the contribution of different functional groups and taxa, and allow assessments of the links between changing reef ecology and budget states. However, the present paucity of supporting data on growth and erosion rates for the majority of coral species and reef-associated taxa represents a constraint on these budget estimates and limits meaningful between-site comparisons. In light of the growing interest in using carbonate budgets as a functional reef “health” assessment tool, this review thus considers our current state of knowledge regarding the geographic coverage of existing reef budget states and the availability of relevant supporting data. We use this to highlight current knowledge gaps, future challenges, and opportunities that emerging techniques may offer. The primary aim of this review is to encourage increased research efforts on budget states and underlying metrics in order to better constrain reef carbonate budget estimates from across a broad range of sites and environments.

Keywords

calcium carbonate budget – reef budget state – community calcification – reef growth – reef accretion

1. Introduction

1.1 What are reef carbonate budgets?

Coral reefs are major focal points of benthic carbonate production across tropical and sub-tropical marine environments (Milliman 1993, Montaggioni and Braithwaite 2009). Depending on the environmental conditions at a given site, this carbonate can accumulate over millennia to form extensive reef structures (Kleypas et al. 2001). The net accumulation rate of framework carbonate is thereby controlled by a range of biologically-, physically- and chemically-driven production and erosion processes (Scoffin 1993, Perry et al. 2008, Montaggioni and Braithwaite 2009). Scleractinian corals are typically the primary reef framework producers (Chave et al. 1972), with additional biologically-derived carbonate being deposited by a range of calcareous encrusters. The predominant encrusters are usually crustose coralline algae (CCA) (Payri 1997) which, in very shallow, high energy settings, can even dominate biological carbonate production e.g., within algal ridge systems (Adey 1978, Grigg 1998). Additional carbonate from sediment import and skeletal cementation can also contribute to reef framework construction, helping to bind reef material and thereby promoting the stability of the reef framework (Scoffin 1992, Perry and Hepburn 2008). Offsetting the production of framework carbonate are processes that biologically or mechanically erode the reef structure. For example, extensive biological erosion (or bioerosion) occurs as a by-product of the feeding activities of many species of parrotfish (Bellwood and Choat 1990, Bruggemann et al. 1996) and sea urchins (Bak 1994), and through the boring activities of endolithic macro- and microboring organisms (Vogel et al. 2000, Tribollet and Golubic 2005). Episodic physical disturbances associated with cyclones and storms can also influence reef development through the import/export of sedimentary materials and the generation of coral rubble (Scoffin 1993). In addition, reef-derived carbonate, especially sediment, may dissolve chemically, at a rate correlated with the aragonite saturation state of the overlying seawater (Eyre et al. 2018).

The relative rates at which these production and erosion processes operate strongly influence net rates of carbonate production, also expressed as a reef's carbonate budget, i.e., the sum of gross carbonate production, less the amount of carbonate lost through dissolution and erosion (Chave et al. 1972). The carbonate budget of a coral reef can be considered as a quantitative measure of the functional state of a reef at a given point in time (Perry et al. 2008, Kuffner and Toth 2016) and is an important metric for several reasons. First, it indicates whether coral communities at a given site have the capacity to build and accrete reef structures over time, i.e. providing an estimate of a reef's growth potential (Kleypas et al. 2001). Second, it describes the complexity and maintenance of the reef framework, which essentially controls many of the functions and ecosystem services provided by reefs (Perry and Alvarez-Filip 2018). These functions include the provision of shelter and habitat for fish and invertebrate species (Friedlander and Parrish 1998, Graham and Nash 2013), coastal protection through the dissipation of wave energy (Ferrario et al. 2014, Beetham et al. 2017), and the generation of sediments to sustain adjacent beaches and shorelines (Perry et al. 2011, Kuffner and Toth 2016). Thus, a single metric, the carbonate budget, serves as a proxy for the maintenance of biodiversity and much of the function of an entire ecosystem (Mace et al. 2014).

As the composition of reef assemblages has an inherent influence on a reef's budget (e.g., abundance of coral species and bioeroding taxa), it is reasonable to assume that budget states are temporally variable (Kleypas et al. 2001, Perry et al. 2008) and can respond to both short-term high magnitude stress events, and to on-going gradual changes in reef ecology. For example, large and rapid reductions in carbonate budget states have been observed following episodic coral bleaching events in the Indian Ocean (Perry and Morgan 2017a, Lange and Perry 2019) and the Eastern Tropical Pacific (Eakin 1996) as a direct response to changes in the abundance of species that locally drive carbonate production and erosion. In the Caribbean, a combination of disease, overfishing and pollution over the past few decades has led to progressive shifts in coral communities towards non-framework building taxa, critically reducing local budget states (Perry et al. 2015b). More generally, where the balance between production and erosion shifts in favour of erosional processes, the budgets of reefs will become progressively net negative, leading to structural complexity declines and the loss of reef structures (Glynn 1988, Alvarez-Filip et al. 2009). Such changes are critical because they have negative consequences not only for many reef-associated species, but also for numerous ecological and geomorphological services essential to human well-being (Jackson et al. 2014, Newman et al. 2015, Quataert et al. 2015, Richardson et al. 2017). Given that direct anthropogenic disturbances and climate impacts are rapidly expanding the "footprint" of ecological change on reefs globally (e.g., Hoey et al. 2016a, Hughes et al. 2018), there has been a growing interest in understanding how and at what rates the carbonate budgets of reefs in different regions may be changing.

1.2 How are reef carbonate budgets measured?

Quantifying reef carbonate budget states is a methodologically complex process and can be approached from different perspectives, but two main approaches have been most commonly used: 1) hydrochemical methodologies, which measure net community calcification by integrating calcification and dissolution rates, and which are based on measured changes in pH and total alkalinity or oxygen in the water above a reef (e.g., Kinsey 1972, Smith 1981, Takeshita et al. 2016); and 2) census-based approaches, which quantify rates of carbonate production and erosion by individual reef taxa, and to which measures of sediment production and physical export rates can be added (e.g., Chave et al. 1972, Scoffin 1980, Perry et al. 2012a). Less commonly employed methods are based on 3) the quantification of carbonate accumulation in geological cores (Hubbard et al. 1990, Ryan et al. 2001). Each of these methods provides different insights into the processes and rates of carbonate production, differ in the spatial and temporal scales over which they can be applied, and yield different types of data (see Box 1 for advantages and disadvantages). Resulting data are thus complementary rather than directly comparable.

Box 1: Comparison of different approaches to estimate reef carbonate budgets

Approach	Resultant data	Advantages	Disadvantages
Hydrochemical estimate: derived from measured changes in pH and total alkalinity in the water above a reef	Provides measures of net carbonate production by specific benthic communities	• Includes total precipitation and chemical dissolution of carbonates • Highlights temporal variability and allows investigation of daily and seasonal differences	• Does not allow differentiation of production processes by different calcifiers • Does not take into account biological/physical erosion processes • Complex to apply where significant water mixing occurs
Census-based estimate: calculated from biota cover/abundance and taxa- or species-specific rates of growth/erosion	Sums up the individual contributions made by biological producers and eroders	• Allows determination of the relative contribution of different carbonate producers/eroders • Allows spatial comparisons of different reef environments • Supports other indices of reef functionality	• Does not account for carbonate added or removed through lithification or dissolution • Potential error from using abundance snapshots • Time consuming and thus limited in spatial scale and depth
Net accumulation rate: calculated from long-term framework and sediment accumulation rates in cores	Reflects long-term rates of net carbonate accumulation	• Integrates post-depositional carbonate dissolution and erosion • Enables comparisons with historical rates	• Does not differentiate between production/erosion processes • Resolution not fine enough to differentiate between individual years

Whilst many of the earliest studies on carbonate budgets followed the hydrochemical approach, census-based methodologies have been employed with increasing frequency in the past two decades. The primary reason for this is probably that census-based approaches quantify contributions from different functional groups and taxa, and thus provide an opportunity to directly link data from standardised reef ecological monitoring approaches (e.g. AGRRA) and budget state assessments. In light of the rapidly changing ecological states of many reef communities, this also offers the potential to predict and model future budget states (e.g., Alvarez-Filip et al. 2013, Kennedy et al. 2013) and to link these to changes in ecosystem services. Census-based budget state assessments thus provide a measure of reef "health" that moves beyond more simplistic assessments of ecological status (as defined by measures of coral cover and community composition alone), and allow questions around the functional performance of a reef (as defined by reef structural complexity and integrity, carbonate production, and reef growth potential) to be explored (Alvarez-Filip et al. 2011, Graham and Nash 2013, González-Barrios and Álvarez-Filip 2018).

Two recent examples of indices exploring the functional metrics of reef structures are: i) the BioConstruction Potential (BCP) index, which groups carbonate producers into five bioconstructional guilds, whose cover is multiplied with assigned importance scores to yield a BCP value. This index defines reefs as accreting or eroding, is positively correlated with carbonate deposition rate and reef accretion rate, and has been used to illustrate long-term, bleaching-related changes in reef states at sites in the Maldives (Bianchi et al. 2016, Bianchi et al. 2017, Montefalcone et al. 2018); and ii) the Reef Functional Index (RFI), which uses a combination of survey data on coral cover and published species trait information (calcification rate, rugosity and colony height, integrated into a 'Functional Coefficient') to estimate the functional contribution of each coral species to reef-building capacity and structural complexity at a given reef site. This methodology has been used to compare reef states at 170 sites along the Mesoamerican Barrier Reef (González-Barrios and Álvarez-Filip 2018).

These emerging functional assessment indices are both underpinned by the ReefBudget methodology, which follows the framework production states approach discussed by Perry et al. (2008), and focuses on quantifying the relative contributions made by different carbonate producer/eroder groups to net biologically driven carbonate production (Perry et al. 2012a). Production and erosion rates of each group are calculated using survey data on organism cover and abundance, combined with available extension, production or erosion rate data. Calculations generate estimates of net carbonate production (in G = kg $CaCO_3$ m^{-2} $year^{-1}$). The protocols and data entry spreadsheets are available online and are pre-set with Caribbean or Indo-Pacific relevant datasets to support estimates of carbonate budget states from site-specific survey data (http://www.exeter.ac.uk/geography/reefbudget). Importantly, however, all pre-set rates can be substituted for regional-, site- or environment-specific values as deemed most appropriate by the user. In recent years the ReefBudget method has been employed in the Caribbean (Perry et al. 2012a, Perry et al. 2013, Perry et al. 2015b, Courtney et al. 2016, Manzello et al. 2018, Perry et al. 2018a), the central Indian Ocean (Perry et al. 2015a, Perry and Morgan 2017a, b, Perry et al. 2018a, Lange and Perry 2019, Ryan et al. 2019), the western Indian Ocean (Herrán et al. 2017, Januchowski-Hartley et al. 2017), and the Red Sea (Roik et al. 2018), and thereby represents the most extensive set of comparable budget estimates made thus far.

1.3 Aim of this review

As outlined above there are different approaches to quantifying carbonate budgets on reefs. This review focuses on the census-based approach and provides a critical perspective on the state of knowledge regarding empirical data on calcification and bioerosion rates that are essential elements of the underlying calculations. This is a timely contribution given the growing interest in using budget states as a functional reef “health” assessment tool, and as awareness of the potential for rapid changes in budget states following anthropogenic and climatic stressors has increased. This review therefore aims to: i) consider the current status of published carbonate budget estimates in terms of global coverage, and to identify specific data poor regions and habitat types; ii) summarise the current state of knowledge regarding taxa-specific rates that underpin estimates of carbonate production and erosion in census-based approaches, and again highlight major taxa or geographic gaps with the aim of guiding future research efforts; and iii) consider future challenges and opportunities in reef carbonate budget research. The review is accompanied by expansive datasets on published budget states and underpinning metrics. We hope that the synthesis of available data will encourage research that will address the most pressing research needs in this field, specifically the need to expand the range and variety of locations and reef settings from which carbonate budget states exists, and to increase the breadth of data that supports census-based budget estimates, i.e. species- and environment-specific rates of carbonate production and erosion.

2. Current status and gaps in reef carbonate budget research

We performed an extensive review of available literature on reef carbonate budgets using the search terms “reef budget”, “carbonate budget” and “community calcification” as well as following up references within relevant articles. In total we found 91 studies reporting carbonate budgets for 338 reef sites (116 in the Atlantic, 222 in the Indo-Pacific), applying both census- and hydrochemical methodologies. Additionally, regional budgets were reported in 3 studies, global estimates in 7 studies, and further papers have described methodological developments or reviewed the current state of knowledge on reef carbonate budgets, reef architecture and vertical accretion rates (all studies listed in Table S1a). From this analysis we observe that although the concept of reef budgets developed quite early in the context of coral reef science (Chave et al. 1972, Kinsey 1972), the number of studies on this topic and investigated sites remained relatively low and constant for almost 40 years until the 2010s, when numbers tripled (Fig. 1a, b). However, despite this increased interest the reef budget state approach is still underrepresented in studies and monitoring efforts if compared with more traditional "health" indicators such as coral cover.

2.1 Geographic status

Geographic coverage of budget state assessments is spatially very heterogeneous both between and within the major reef-building regions (Fig. 1c). On a province scale, the Tropical Northwestern Atlantic has been the focus of the largest number of carbonate budget studies (19 studies reporting rates for 115 sites), likely reflecting the simplified challenge of modelling reef dynamics in an area with relatively low species diversity, good accessibility of sites, and a high socio-economic interest in understanding the long-term degradation of Caribbean reefs. Almost half of these budget estimates have been determined for islands in the Eastern Caribbean (50 sites), although there is also a rapidly expanding body of data from the Mesoamerican reef and Florida. In the Indo-Pacific region, the Western and Central Indian Ocean are reasonably well represented as a result of recent research efforts and encompass studies investigating the impacts of bleaching events on carbonate budgets (Januchowski-Hartley et al. 2017, Perry and Morgan 2017a, Lange and Perry 2019). The central Indo-Pacific is also well represented concerning the number of sites assessed, although these mostly derive from one study reporting data from 48 sites in Palau and Yap (van Woesik and Cacciapaglia 2018) and thus overall coverage of reef types and habitats in this area remains relatively low. The Great Barrier Reef region is relatively well represented concerning the number of studies (24 studies, half of these resulting from the early research efforts of Kinsey and colleagues 1972-1983) but not the number of sites (19 sites including 1 in Torres Strait). In the Eastern Tropical Pacific, relatively few sites have been studied regarding carbonate budgets, but existing studies have been very detailed, discussing the effects of marginal reef conditions, thermal stress and bioerosion over time (Glynn et al. 1979, Glynn 1988, Eakin 1996, Reaka-Kudla et al. 1996, Eakin 2001, Manzello et al. 2017).
It is perhaps most striking that only one study has, to-date, been conducted in the Coral Triangle and Sunda Shelf region (5 sites on Java, Edinger et al. 2000), despite this area being the epicentre of marine diversity and a global priority for conservation (Roberts et al. 2002, Veron et al. 2009). We thus suggest an urgent need for budget studies in a range of provinces and habitats within the Coral Triangle and Tropical Southwestern Pacific region, both because of its high biodiversity, and because it is a region that is experiencing rapid population growth and extensive land use changes (e.g., Jantz et al. 2015, Neumann et al. 2015). Due to their remoteness, the numerous reef systems across

Polynesia and other central Pacific island groups have also had relatively little attention, especially considering the diversity of settings and reef types that exist there. Further areas currently underrepresented in budget estimates are Western Australia, the Red Sea and the Arabian Gulf.

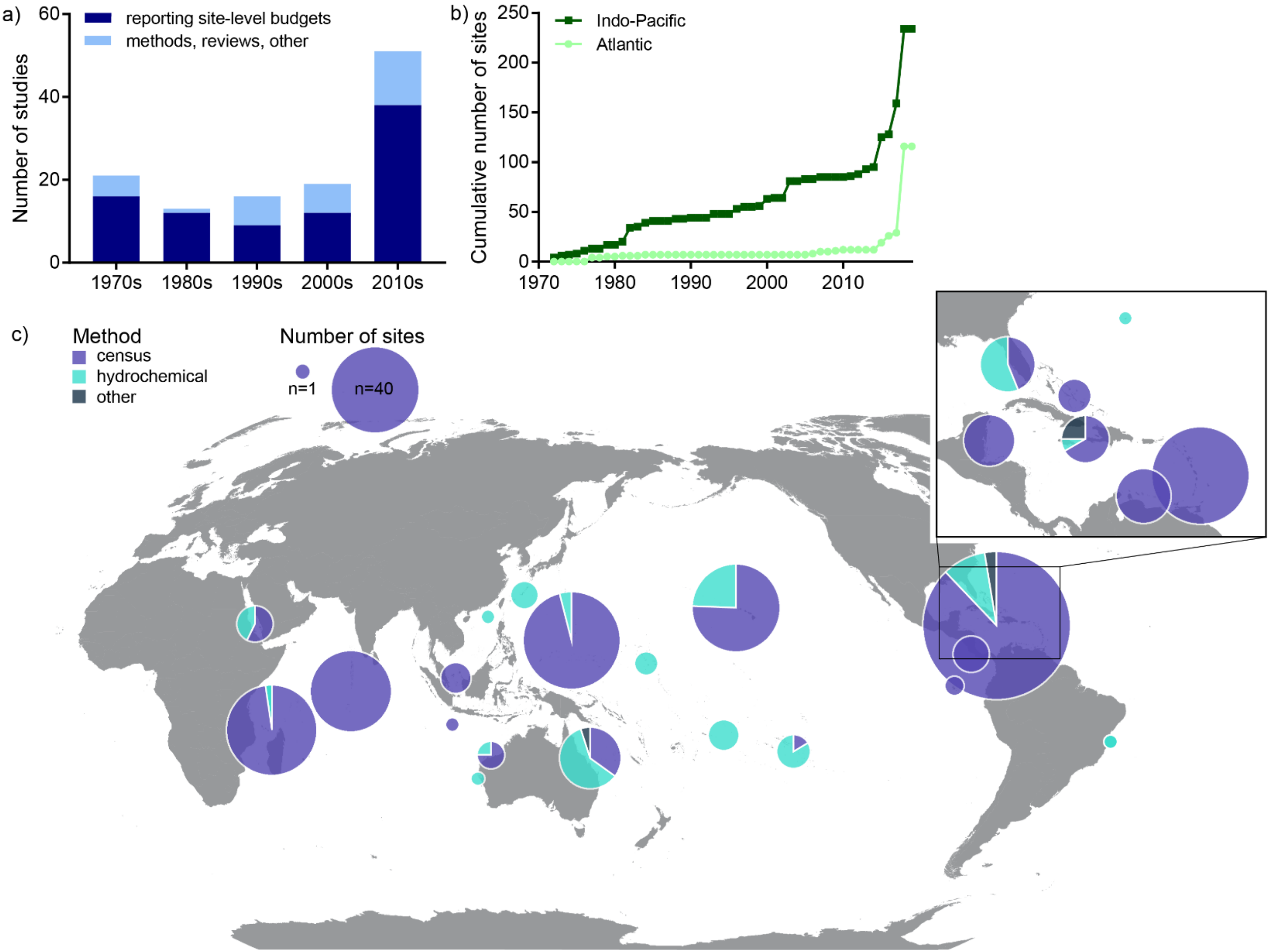

Figure 1: Temporal and spatial distribution of reef carbonate budget studies. Number of a) studies on carbonate budgets and b) sites with budget states over time; and c) geographic range of published carbonate budgets. Bubble size indicates the number of sites in biogeographical provinces (world map) and ecoregions (inset, Caribbean) after Spalding et al. (2007). Colours indicate the methodology used for calculations. All studies and respective budget ranges are listed in Table S1.

2.2 Predictors of reef budget states

Whilst the global coverage and the diversity of sites for which detailed data exists remains relatively small, these studies provide a basis for understanding the range of budget states that define contemporary reefs (Table S1a). In this context, available data point to widely divergent budgets on reefs, reflecting marked natural spatial heterogeneity in reef community composition and differential impacts of ecological changes, but probably also the use of different methods and metrics.

To investigate possible regional and temporal patterns in carbonate budget states we performed preliminary analyses on site-level net carbonate budget data (Table S1b), testing the effects of method (hydrochemical, census, other), ocean (Indian Ocean, Atlantic, Pacific), biogeographical province (17 provinces after Spalding et al (2007)), reef habitat (fore reef, reef flat, back reef, lagoon, patch reef), water depth (in m) and time (year of data collection) (Fig. 2a-g). Factorial data was tested using One-Way ANOVAs and TukeyHSD-tests, and numerical data was tested using linear model fitting in R 3.5.1 (RCoreTeam 2016).

The methodological approach used for calculations does not have a significant impact on the magnitude of published carbonate budget states (Fig. 2a). Supportively, at the few sites where several methods were used in tandem, budget states were in good agreement (Montaggioni and Braithwaite 2009, Hamylton et al. 2013, Courtney et al. 2016). Geographically, carbonate budgets on Indian Ocean reefs are significantly lower than on Atlantic reefs (Fig. 2b, $F_{2,325}=7.807$, $p<0.001$, TukeyHSD: IO-A<0.001, P-A=0.321, P-IO=0.051), likely because available data in the Seychelles and Maldives include a relatively large number of post-bleaching data points. Province has a significant influence on published budget states ($F_{16,311}=4.387$, $p<0.001$) and the plot shows a wide range both across and within regions (Fig. 2d). Concerning habitats, early studies suggested a predictable distribution of carbonate production across reef zones in both Atlantic and Indo-Pacific (reef-flats = 4 G, lagoons = 0.8 G, Kinsey 1981). In our analysis, reef habitat did not show a significant impact on reef budget states (“entire reef” and “reef base” excluded from analysis, Fig. 2c). Water depth did not have a significant influence on budget state variability either, but 97% of investigated sites were located in ≤10 m depth (Fig. 2e). Such broad regional assessments over a heterogenous dataset are problematic, because the variability for a given habitat type across study locations with a range of environmental conditions is naturally very high. Indeed, it is reasonable to assume that there are likely to be very significant differences in budget states across individual reefs as the taxa driving production and bioerosion processes vary between habitats and depth zones (Smith and Kinsey 1976, Kinsey and Hopley 1991, Perry and Hepburn 2008). We therefore suggest that there is an urgent need not only to address some of the major geographic and reef type data gaps, but also to improve our understanding of how budget states vary across reef habitats and depths. This would help with analyses of spatial heterogeneity in habitat forming and reef building potential, and to increase understanding of spatial (and bathymetric) consequences of ecological change. For example, whilst the budgets of shallow reefs may decline markedly under bleaching-driven stress (Perry and Morgan 2017a), the budgets of proximal intermediate and deeper water habitats may be far less impacted. Along the same line, given the growing research interest in mesophotic reefs (>30 m depth) as a thermal refugia under future conditions, assessments of their budget states would be a valuable focus of research efforts.

Concerning temporal patterns in carbonate budgets, a region-wide decline in the Caribbean has been documented in terms of coral cover (Gardner et al. 2003), reef complexity (Alvarez-Filip et al. 2009) and carbonate budgets (Perry et al. 2013, Perry et al. 2015b). However, the analysis of all available budget states or for Caribbean subsets did not show significant temporal declines (Fig 2f,g). This is most likely because early data on net budgets are scarce, there are very few time-series data from the same sites, and recently studied sites display widely divergent budgets. This analysis thus really highlights the need for more time-series data from consistent sites and depths to fully understand temporal dynamics of budget states through disturbance and recovery cycles.

In the context of this discussion, an important focus of recent research has been on whether and how quickly budget states may recover from major disturbance events such as coral bleaching (Januchowski-Hartley et al. 2017, Perry and Morgan 2017a, Manzello et al. 2018, Lange and Perry 2019). These studies are proving particularly useful for understanding how relative contributions of different taxa change over time, and which communities are more resilient to disturbance. For example, reefs dominated by branching and tabular *Acropora* spp. in the Indian Ocean changed significantly following the 2016 bleaching event, re-setting budgets from highly positive to net negative states (Perry and Morgan 2017a, Lange and Perry 2019). In contrast, sites dominated by the stress-tolerant coral *Orbicella faveolata* in the Florida Keys have generally low budget states but did not experience a significant decrease in carbonate budgets after bleaching in 2014 and 2015 (Manzello et al. 2018).

An additional element of climate-driven change is that reef budget states not only depend on the abundance of species, but also on the physiological response of those species to changing environmental conditions. For example, reduced calcification in response to *in situ* thermal stress has been documented for a range of coral species and regions (e.g., Carricart-Ganivet et al. 2012, Tanzil et al. 2013, Manzello et al. 2015, Manzello et al. 2018), and for coralline algae (Johnson and Carpenter 2012, Vásquez-Elizondo and Enríquez 2016). This emerging data provides important opportunities for parameterising budget estimates to factor for changing environmental conditions or disturbance events.

The above synthesis points to an urgent need for further research into the budgetary response of different reef communities to environmental change, which will help answer questions about which and how reefs will continue to provide geo-ecological services under projected warming and sea level rise (Kennedy et al. 2013). In addition to evaluating reef budget states over time, there is a pressing need to improve our understanding of long-term changes in coral and coralline algal calcification rates across a broad range of species and environments, especially for those corals that are important habitat forming species, but which do not allow for retrospective measures of growth using cores and banding (e.g. *Acropora*, *Pocillopora*) (Pratchett et al. 2015, Manzello et al. 2017).

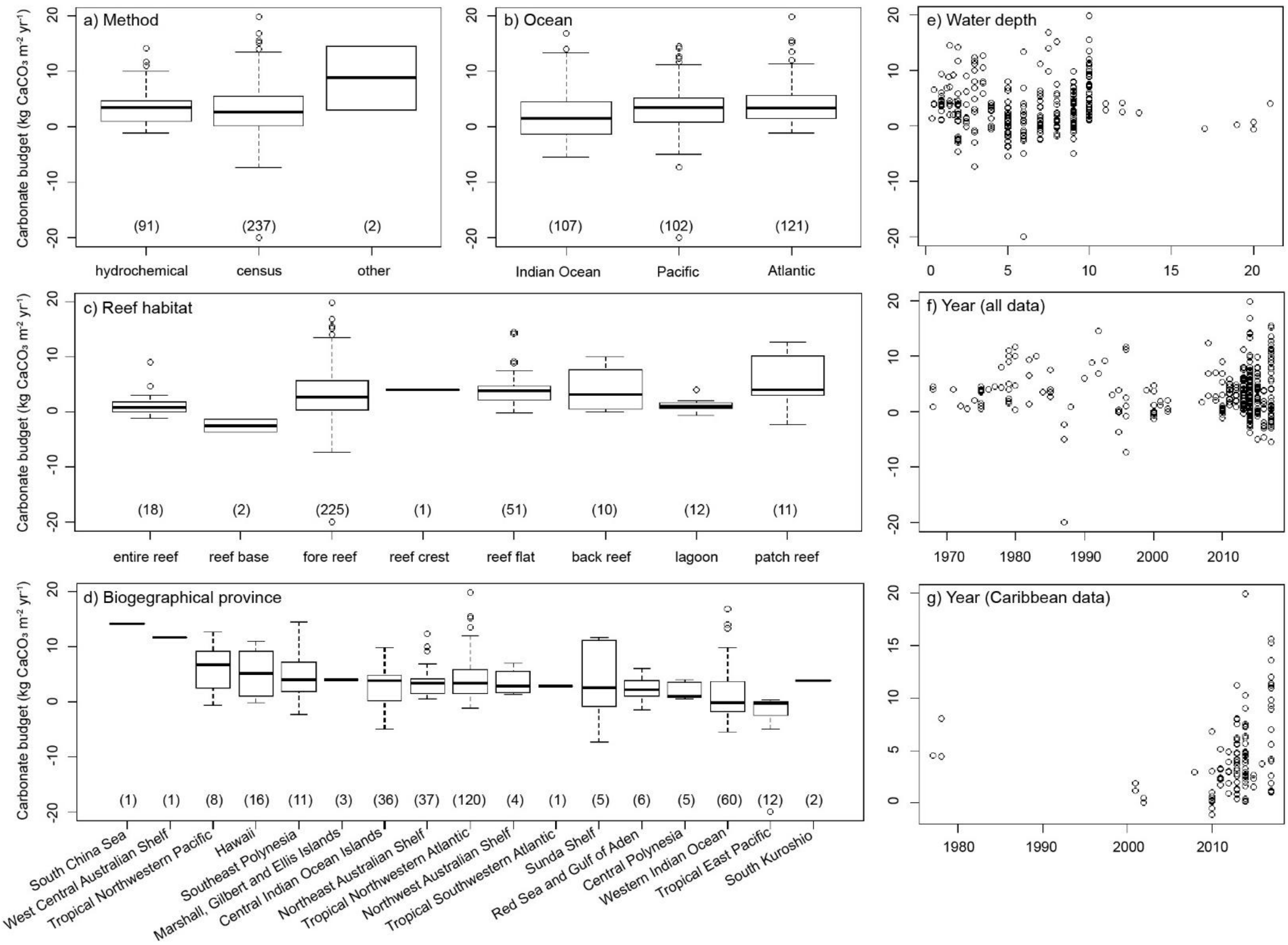

Figure 2: Predictors of reef carbonate budget states. Published site-level net carbonate budgets (listed in Table S1b) grouped into a) methodological approach used for calculations, b) ocean, c) reef habitat/zone, d) biogeographical province after Spalding et al. (2007), e) water depth, and year of data collection for f) all carbonate budget states or g) Caribbean budget states. Numbers in brackets indicate number of budget states in each group.

2.3 Marginal reefs

Another obvious gap with respect to the current coverage of budget state assessments relates to marginal reef-building settings, which include those at high latitudes and those exposed to naturally high turbidity or upwelling influence. Marginal reefs can be highly diverse and are probably far more extensive that currently assumed, but many are defined by low or absent framework development (Perry and Larcombe 2003 and references therein). The effects of “non-optimal” environmental conditions on contemporary carbonate budget states remains poorly quantified. Notable exceptions include work undertaken on upwelling- and ENSO-influenced sites in the Eastern Pacific, which showed a permanent loss of reef framework structures in Galapagos after the 1982–83 El Niño warming event, while reefs in Panama recovered to slightly positive net carbonate budgets (Manzello et al. 2017 and references therein). In contrast, high carbonate budgets (>7 G; Browne et al. 2013) and rapid vertical reef accretion (8.3 mm yr-1; Perry et al. 2012c) has been reported on highly turbid reefs on the inshore Great Barrier Reef. In either situation, marginal reefs may provide a critical habitat and important refugia for numerous species under future environmental conditions (Cacciapaglia and Van Woesik 2016, Morgan et al. 2017). Further work in such marginal settings and high latitudes should therefore be a focus of future research efforts, as it is not yet understood how, for example, ocean warming and the subsequent expansion of species ranges will affect the carbonate budgets of these coral communities. It has been hypothesized that in most high latitude regions lower aragonite saturation states and light availability will compensate for any positive growth effects from sea surface warming (Couce et al. 2013, Muir et al. 2015), while marginal reefs in the Eastern Pacific and along the northern Brazilian coast might actually increase in suitability for reef development (Couce et al. 2013). Additional work in these systems would clearly be invaluable to understand the dynamics of future reef development.

3. Available data on underpinning metrics and major knowledge gaps

The use of standardized census-based methodologies offers the opportunity to compare carbonate budgets states across local and regional scales, or over time. However, budget estimates are only as good as the quality and quantity of supporting data on carbonate production and erosion rates, which necessarily underpin budget calculations. The collection of such taxa-specific supporting data (i.e. coral growth rates and density, CCA calcification, parrotfish erosion, urchin grazing and endolithic erosion) requires significant amounts of sampling, analysis, and time – and whilst fundamental to quantifying budget states, and indeed for understanding reef functions and processes generally, do not readily sit as high priorities for reef scientists and funding agencies. Consequently, regional data on these processes is often scarce, necessitating carbonate budget estimates to be based on data from different biogeographic regions or utilising rates for “most closely related” organisms. These constraints need to be acknowledged in any assessments of carbonate budgets and should be minimized, wherever possible, by the collection of meaningful local data on calcification and erosion rates. Where data from the literature is supporting budget estimates, rates from the same region and similar environments should be used if available. Below we provide a summary of the relevant data that, to our knowledge, is currently available and highlight existing knowledge gaps. All of this information is compiled and referenced in Tables S2-S6 to make it readily available for use.

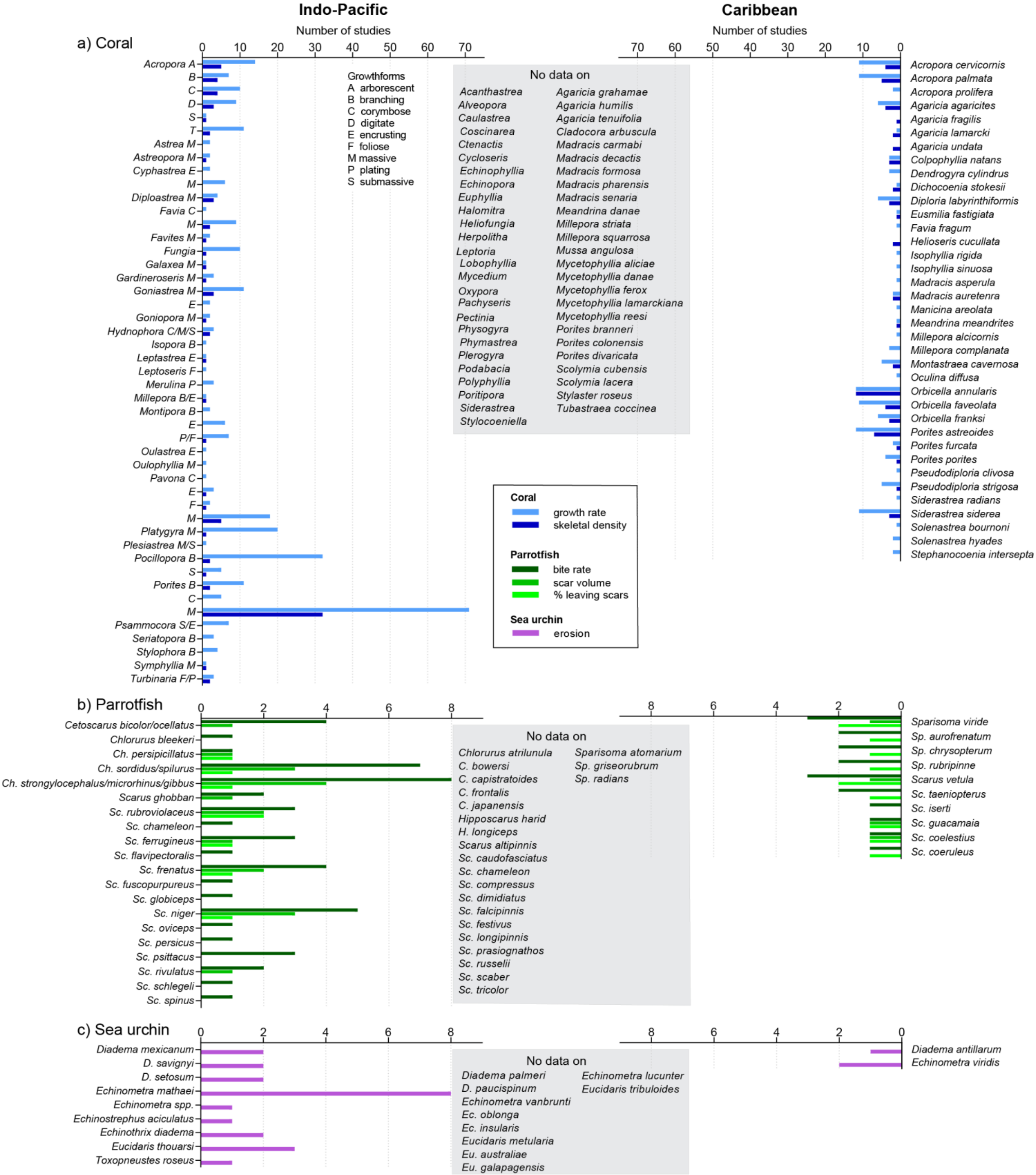

Figure 3: Calcification and erosion rates. Number of studies reporting taxa/species-specific metrics underpinning the quantification of a) coral calcification, b) parrotfish erosion and c) sea urchin erosion in the Indo-Pacific (left column) and the Caribbean (right column). Please note different ranges on x-axes. Grey boxes in the centre report taxa/species for which, to our knowledge, no data is available.

3.1 Coral growth rates and skeletal density

Whilst significant amounts of data on coral growth and skeletal density have been collected over the past few decades, analysis of this information suggests considerable variability in data availability in different biogeographic provinces and a paucity of data for many important taxa. The Caribbean harbours a relatively low diversity of reef-building corals (~62 species; Veron (2000)) within a restricted geographical area, which (alongside easier site access and a relatively high density of marine research stations) has facilitated the development of relatively extensive datasets on both coral growth rates and skeletal densities. In contrast, the Indo-Pacific has a much higher biodiversity of reef-building stony corals (~753 species; Veron (2000)), with reefs developed over much wider longitudinal and latitudinal gradients, and which thus experiences an arguably broader range of environmental conditions. Unsurprisingly, the relative number of species for which there are well-replicated data across the Indo-Pacific is therefore very small compared to the Caribbean. The massive corals *Porites lobata* and *lutea* are exceptions, because they are often used in paleoclimate studies. New platforms such as coraltraits.org (Madin et al. 2016) offer an excellent source to find species-specific coral growth rates, but associated metadata is often not readily apparent, e.g. if observations stem from manipulative experiments or if environmental conditions were locally disturbed. Table S2 therefore collates currently available data on linear extension rates and skeletal density from coral colonies that were not manipulated across depth or other environmental factors for both the Indo-Pacific (Table S2a) and the Caribbean (Table S2b,c). Figure 3a provides an overview of the number of these studies for each species (Caribbean) or genera (Indo-Pacific).

In the Caribbean, there is relatively extensive data for the major reef framework builder *Orbicella* spp., and extension rate data from several sites exist for both *Acropora cervicornis* and *A. palmata* (although both are numerically rare on many reefs now). But even for these well-studied species, geographic or environmental variability is poorly constrained. Of the increasingly spatially dominant “weedy” or opportunistic taxa, only *Porites astreoides* and *Siderastrea siderea* are reasonably well represented in studies from multiple sites, whilst rates for the genera *Agaricia*, *Diploria* and *Pseudodiploria* are sparse (Fig. 3a). For the Indo-Pacific region we grouped species into genera and growth forms due to the larger number of species. Some genera are relatively well represented (*Acropora, Favia, Fungia, Goniastrea, Montipora, Pavona, Platygyra, Pocillopora, Porites*), but growth rates are often restricted to one dominant growth form of the respective taxa (except *Acropora* which has a good range over its different growth forms). For most coral taxa only very few rates are available, and for many other coral taxa no growth data exists at all (Fig. 3a). The amount of data on skeletal densities in both oceans is even scarcer, with only very few columnar, submassive and encrusting taxa represented, despite the relatively easy and fast determination of density via buoyant weight/Archimedes bath techniques (Bucher et al. 1998). Densities of massive taxa are more often reported, possibly because these are often measureable from x-radiography.

The paucity of data means that coral carbonate production estimates at a specific site often have to rely on calcification rates from other regions. Problematically, growth rate and density gathered on one species in the Eastern Pacific may not accurately represent the same species in the Red Sea or Western Indian Ocean, as coral growth rates tend to vary considerably in response to light and water quality, temperature, and aragonite saturation state (Pratchett et al. 2015). Where not even taxa-specific rates from other regions are available, mean values for all hard corals of a specific morphology are currently a necessary substitute for missing rates in budget estimations, as colony morphology has been shown to be a major control on coral growth (Dornelas et al. 2017).

The above synthesis point to the urgent need for growth and density data from an increased number of coral species and taxa across the Indo-Pacific region, and for those taxa that are becoming increasingly abundant on degraded Caribbean reefs. Additionally, detailed studies are needed to better understand how calcification rates vary with depth, temperature and water quality in order to reduce uncertainties in budget estimates. For instance, growth responses to depth can be highly variable in different species (*Pseudodiploria strigosa*: 2.5-4.2 mm yr^{-1} at 3-32 m depth with highest growth rates at 3-6 m (Logan et al. 1994); *Montastrea cavernosa*: 2.0-10.9 mm yr^{-1} at 10-30 m depth with highest rates at 20 m (Huston 1985)) despite similar average growth rates (4.9±2.3 and 4.2±1.6 mm yr^{-1}, respectively (Table S2b).

While skeletal density measurements still require the extraction of small coral samples for buoyant weight/Archimedes bath techniques (Bucher et al. 1998), growth rates can be quantified *in situ* using recent non-invasive Structure-from-Motion (SfM) techniques, which use stereophotogrammetry and the comparison of 3-dimensional models over time to calculate annual growth rates (Ferrari et al. 2017). When calculating coral calcification rates from extension and density data, coral morphology should be taken into account in order to avoid overestimation of calcification, e.g. massive colonies experience dome shaped growth, but branching colonies require a conversion factor to account for growth of branch tips only (González-Barrios and Álvarez-Filip 2018, Perry et al. 2018b). Furthermore, as the growth of different parts or branches within a colony can differ depending on position, age or size, these calculations have to be seen as an approximation and could possibly be improved by insights from emerging SfM methods.

3.2 CCA calcification rates

Very few published data are available on *in situ* annual CCA calcification, adversely affecting quantitative estimates of total carbonate production. While there is some data from controlled physiological measurements (e.g., Gao and Zheng 2010, Johnson and Carpenter 2012, Vásquez-Elizondo and Enríquez 2016), these rates are not included in Table S3 due to conversion difficulties from algal mass to algal cover and uncertainties associated with upscaling hourly to annual calcification rates. However, controlled experiments testing the effects of different light, thermal or pCO_2 regimes on CCA calcification open up the potential for modifying field-derived rates and factor for changing depth, ocean chemistry and temperatures.

Geographically, data coverage on *in situ* CCA calcification in the Caribbean is poor and, to our knowledge, no studies at all exist in the Coral Triangle and the Eastern Pacific (Table S3). Where data does exist, studies typically deployed *Porites* spp. blocks, ceramic tiles or PVC substrates in reef settings over six months to five years and analysed them for lateral and vertical growth of algal patches or directly for annual calcium carbonate production rates of encruster communities. Most of these studies have been conducted at very shallow (1-6 m depth) sites, with only 2 studies reporting values at 8-10 m depth (Osorno et al. 2005, Chazottes et al. 2017). Strikingly, published calcification rates in the Indo-Pacific are on average five times higher in studies that deployed substrates for less than one year, indicating much faster growth of encrusting organisms in the initial settling period. As an easy approach for determining local rates of CCA calcification, we thus suggest the deployment of simple experimental substrates such as lightly sanded PVC cards for 12-24 months, as these are easy to analyse and have been shown to develop natural CCA communities (Kuffner et al. 2013, Kennedy et al. 2017). Calcification by unit area is then quantified by weighing the substrate before and after dissolving the CCA crust in 10% HCl and dividing the difference by the surface area and deployment time.

3.3 Parrotfish erosion rates

Several fish species contribute to the erosion of reef substrate while grazing on algae or feeding on coral tissue or internal bioeroders (Randall 1974). Surgeonfishes (Acanthuridae) and parrotfishes (Scaridae) are the principal grazers, with most species in the latter family capable of scraping and excavating substantial amounts of carbonate. Triggerfishes (Balistidae), filefishes (Monacanthidae) and puffers (Tetraodontidae, Canthigasteridae) are largely carnivorous and responsible for fragmenting live coral colonies. The latter usually contribute small amounts to overall carbonate erosion, although recent research has shown that in the Eastern Tropical Pacific corallivory by the pufferfish *Arothron meleagris* can remove up to 16% of the annual carbonate produced by local coral communities (Palacios et al. 2014).

While each functional group of parrotfish (grazers, scrapers, excavators) is important to the resilience and long-term maintenance of coral reefs, only the latter two have significant impacts on reef bioerosion, and excavators contribute to a much larger extent than scrapers (Bellwood and Choat 1990, Bonaldo et al. 2014). Both groups mainly feed on the epilithic algal matrix on reefs, with occasional bites on live coral and CCA (Hoey et al. 2016b, Morgan and Kench 2016). Most scrapers in both the Atlantic and Indo-Pacific belong to the genus *Scarus*. Excavating parrotfish on Caribbean reefs are of the genus *Sparisoma* spp. (Bruggemann et al. 1996), while the dominant genus on Indian and Pacific Ocean reefs is *Chlorurus* spp., although *Cetoscarus ocellatus*/*bicolor* and larger individuals of both *Scarus rubroviolaceus* and *Sc. ghobban* are also considered to have excavating modes of feeding (Bellwood and Choat 1990, Ong and Holland 2010). Numerous authors have reported much higher bioerosion rates for larger fish (Bellwood 1995, Bruggemann et al. 1996, Ong and Holland 2010) and some studies found higher feeding rates in initial phase than in terminal phase fish (Bruggemann et al. 1994a, Bruggemann et al. 1994b, Mumby 2006, Lokrantz et al. 2008, but see Afeworki et al. 2013, Yarlett et al. 2018). Thus, the method used most frequently for calculating parrotfish bioerosion is based on size- and life-phase specific bite rates (bites d^{-1}), bite volume (cm^3) and proportion of bites leaving scars (%) for each parrotfish species. Currently, data on these metrics is very patchy and exists for only a subset of species (Fig. 3b).

Geographically, few data are available for the Caribbean, and of the species studied *Sparisoma aurofrenatum*, *Sp. chrysopterum*, *Sp. rubripinne* and *Scarus coeruleus* actually do not contribute to erosion of reef carbonates (Adam et al. 2018). In the Indo-Pacific, eight studies reporting bite rates were conducted in the Indian Ocean or Red Sea, three on the Great Barrier Reef and one in Hawaii (Table S4a). Geographic coverage is therefore very low, with extensive knowledge gaps in the Coral Triangle, the Central Pacific and the Eastern Pacific. While the most common excavators *Chlorurus sordidus, C. strongylocephalus* and *Sparisoma viride* are relatively well represented in existing bite rate studies, most *Scarus* species have very low coverage or are generally ignored (*Scarus niger*, *Sc. frenatus* and *Sc. vetula* are an exception). Data on scar volume and proportion of bites leaving scars are even scarcer despite being equally important to quantify contributions to bioerosion. Due to the paucity of species-specific data, metrics for most species currently have to be substituted with genera-level data.

An additional uncertainty that has to be recognized in estimates of bioerosion is that, as with calcification, rates may be strongly influenced by environmental conditions. For instance, there is evidence to suggest that feeding rates may differ across zones and locations (Hoey and Bellwood 2008) and with season and temperature (Ong and Holland 2010, Afeworki et al. 2013). Additionally, bite volume has been shown to be affected by food type and water depth (Ong and Holland 2010) as well as by microtopography (convex, flat, concave surfaces) (Bellwood and Choat 1990). In order to increase the accuracy of models used to predict bite rates and volumes from parrotfish size, more data on feeding rates and bite scars for a larger range of species, sites and environments is urgently needed. Such metrics can be collected by following an individual parrotfish for 5 min, counting its bites, and percentage of bites leaving scars, and measuring the dimensions of bite scars with callipers (Bellwood 1995), although the latter remains an issue of considerable uncertainty due to the very shallow depth of bites and variable substrate morphology (Yarlett et al. 2018). There is thus a need for consideration of more effective ways to estimate bite volumes or parrotfish erosion.

3.4 Urchin erosion rates

Sea urchins of the family Diadematidae (*Diadema* spp., and *Echinothrix* spp.), and of the genera *Echinometra*, *Echinostrephus* and *Eucidaris* are a group of major bioeroding grazers (Bak 1994). In the Caribbean they have been shown to be of higher importance for algal removal and ecological reef functioning than parrotfish (Mumby et al. 2007). Sea urchins erode coral reef substratum either by burrowing behaviour, which weakens the reef structure and increases a reef's susceptibility to storm damage, or directly through abrading the reef substrate during grazing. The rate of erosion through grazing is a function of species and size, with larger individuals causing significantly higher reef erosion (Bak 1994). A variety of techniques have been used to estimate bioerosion rates by urchins, including quantifying the $CaCO_3$ content of the gut (e.g., Bak 1990, Conand 1997, Carreiro-Silva and McClanahan 2001) or faecal pellets (e.g., Glynn et al. 1979, Mokady et al. 1996, Griffin et al. 2003), both with or without estimations of reworked sediment, spine abrasion and gut turnover (Table S5a). This makes it difficult to compare urchin bioerosion rates derived from different studies. In addition, the number of species for which data exists is limited, and from the few species observed, only *Echinometra mathaei* is represented in more than 3 studies (Fig. 2c). Whilst plots of available data suggest a reasonably strong correlation between test size and erosion rate for both Diadematidae and *Echinometra* spp. (Table S5b), we strongly encourage further research into size- and species-specific urchin erosion rates using adequately planned experiments and analyses. This data need applies especially to the Caribbean and the wider Western Pacific region where data are extremely scarce.

3.5 Endolithic macro- and microbioerosion rates

Endolithic macroborers are defined as those eroders which produce boreholes with diameters >1 mm and include endolithic sponges, polychaete and sipunculid worms, bivalves, decapods and cirripeds (Perry and Hepburn 2008, Glynn and Manzello 2015). Across the Caribbean region, sponges have received the greatest attention because they typically dominate the macroboring community, comprising 75-90% of substrate infestation (e.g., Highsmith 1981, Kiene and Hutchings 1994, Schönberg et al. 2017). Across the Indo-Pacific, evidence suggests a more diverse range of macroendolithic taxa, with worms making a relatively larger contribution to macrobioerosion, especially in the first few years that substrate is available for colonisation (Pari et al. 2002, Tribollet and Golubic 2005, Carreiro-Silva and McClanahan 2012). Remarkably high macrobioerosion intensity caused by high abundances and fast growth of lithophagine bivalves have been reported from the upwelling-influenced Eastern Pacific (Reaka-Kudla et al. 1996, Fonseca et al. 2006, Alvarado et al. 2017, Wizemann et al. 2018) and at high latitudes (Chen et al. 2013).
Microendolithic bioerosion describes the activities of photosynthetic cyanobacteria, chlorophytes and rhodophytes, and heterotrophic fungi and bacteria (Golubic et al. 1981) and has the potential to contribute to a significant amount of bioerosion on coral reefs, with published rates of similar magnitude to those of macroborers (Table S6). In addition, microbioerosion could make the substrate surface more easily eroded by grazers and physical destruction. Similar to macrobioerosion, rates may increase with enhanced nutrient availability (but see Vogel et al. 2000, Carreiro-Silva et al. 2009), and show a considerable range across sites.

The amount of data on endolithic erosion, specifically microbioerosion rates, is very low and major geographic gaps are obvious in the Caribbean, the Indian Ocean and the Red Sea (Table S6). We therefore encourage increased research into endolithic erosion rates, including for a variety of ecosystems and habitats. Assessments of both macro- and microbioerosion rates have tended to rely on deploying experimental substrates, predominately dead *Porites* spp. blocks, and subsequent analyses of relative weight or volume loss. Another approach is to quantify boring cavities in coral cores (e.g., DeCarlo et al. 2015) or collected coral fragments (e.g., Carreiro-Silva and McClanahan 2012), which has the advantage of observing an established bioeroder community, but complicates quantification of the length of time that substrates have been exposed to erosion. In the Caribbean, rates of macrobioerosion are typically based on sponge erosion studies, of which only a few report erosion rates per m^2 reef (Table S6). However, there are a number of recent datasets that can assist calculations of sponge erosion in a given reef by combining erosion rates per m^2 sponge tissue (supplementary table Schönberg et al. 2017, de Bakker et al. 2018) with sponge tissue surveys at the study site (Perry et al. 2012b, Murphy et al. 2016). Sponge bioerosion rates may vary with density of the reef substrate (Hernández-Ballesteros et al. 2013), but again detailed datasets to allow these variations to be factored for in erosion rate calculations are presently limited.

3.6 Concluding thoughts on current data availability

The above sections highlight current data availability but also the key knowledge gaps that remain, and which are significant for many areas. In general, it is recommended that local growth and erosion rates of dominant taxa are collected for the area of budget state assessments, especially in the Indo-Pacific with its wide range of environmental conditions. If published rates are used to underpin calculations, we emphasize the use of rates from the same geographic region, and from similar environments and depths. Another option to address the issues of geographic variability may be to develop predictive models of environmentally controlled variations in calcification and erosion rates for those taxa where sufficient data presently exists, or to apply appropriate conversion factors derived from experimentally determined species-specific responses to variations in depth, temperature, water chemistry or nutrient regime. Publications should always provide the rates which have been used for calculations (e.g. attached as supplementary tables) to facilitate comparison of carbonate budgets, and methodologies have to stay flexible to adjust to new or more local rates when available.

4. Future challenges and opportunities

To increase our understanding of spatial variability in reef geo-ecological functioning now and in the future there is a need for the quantification of reef carbonate budgets in different regions and reef settings, and for the expansion of supporting datasets which are necessary to calculate accurate census-based carbonate budget states. Future studies should ideally include an assessment of confidence based on the quality of underlying data, and comparisons would benefit from a confidence analysis of existing studies. Existing methodologies, as outlined in the sections above, can help address many of these current limitations, but there are also a number of interesting future challenges and opportunities that are pertinent to highlight here.

4.1 Temporal coverage

The first challenge of using census-based methodologies for budget estimates is that the use of snapshots in time concerning producer/eroder abundances (especially parrotfish as these are mobile) may not accurately reflect long-term rates of production/erosion. One option to reduce this bias is to average parrotfish abundances over time or for closely located sites assuming they are connected by roaming fish. However, home ranges of parrotfish have been found to be limited and positively related to body mass, so care has to be taken to pool data in an appropriate manner (e.g. 150-300m^2 for adult *Scarus* spp., 7,800m^2 for larger *Chlorurus* spp. and up to 24km^2 for schooling *Scarus* spp.; Welsh and Bellwood (2012b, 2012a), Welsh et al. (2013)). Alternatively, total external erosion rates can be quantified over extended periods of time, although these do not allow the differentiation of taxa-specific contributions. Roff et al. (2015), for example, used high precision U/Th dating and CT scan analysis to estimate average vertical erosion rates of dead coral ramets over a 13 year period, which was in good alignment with a parallel quantification of erosion from parrotfish surveys. Kuffner et al. (2019) measured reef-elevation loss around permanent markers fitted on dead *Orbicella* colonies in 1998, suggesting erosion rates may be higher than obtained from census-based approaches. These methods mainly quantify external parrotfish erosion which commonly compromises the largest fraction of bioerosion on a reef. A third emerging approach for quantifying net rates of erosion or production over a longer time period and spatial scale is to measure changes in reef height or volume, either based on seafloor elevation data (from historical soundings or Lidar digital elevation models; Yates et al. (2017)), or using diver-based underwater photogrammetry and the construction of scaled, digital 3-D models of reef areas using Structure-from-Motion (SfM) techniques (Bailey 2019, Rossi et al. 2019). Change in net reef volume over time (decades in the former example, years in the latter), can then be multiplied with framework density data to give an estimate of the total net reef carbonate production/erosion rate. A comparison of census-based and volume-based methods at the same study sites would be very useful to highlight the merits and increase the accuracy of each approach.

4.2 Spatial coverage

Another challenge in carbonate budget assessments is spatial coverage, as the replication and area that can be surveyed during a dive is often small due to time and depth constraints. In this context, photographing a reef and quantifying benthic cover and reef structure metrics from digital 3-D models allows greater spatial coverage in less dive time (e.g., Burns et al. 2015, Ferrari et al. 2016, Bailey 2019). However, challenges remain in terms of accounting for cryptic substrate cover in visual models, especially on structurally complex reefs, and for different substrate densities. SCUBA diving limitations have also tended to limit carbonate budget state assessments and the collection of taxa-specific data on calcification and erosion rates to sites <15 m depth. One option to enable surveys in deeper reef areas is to use SfM techniques in combination with camera equipped autonomous underwater vehicles (AUVs) or remotely operated vehicles (ROVs), which are evolving rapidly in quality and affordability. However, major disadvantages of AUV/ROV use are the lower accuracy of organism identification from photographic/video material due to poor lightning and motion blur (Turner et al. 2018), and again difficulties in quantifying true 3-D cover along the reef profile due to complex overgrowth. Both factors would affect the accuracy of carbonate budget estimations. Additionally, beside a general acceptance that coral growth rates (e.g., Fricke et al. 1987, Anthony and Hoegh-Guldberg 2003, Grigg 2006, Weinstein et al. 2016) and the abundance of internal and external bioeroders (Nemeth and Appeldoorn 2009, Weinstein et al. 2014) decrease with increasing depth, taxa-specific growth and erosion rate data at greater depth is very limited.

A further area of development in a spatial data context is in the use of remote and near-remote sensing methods to support quantification of reef area and benthic community type across entire lagoon systems or reef tracks. This areal up-scaling has been used in several studies to extrapolate published or determined carbonate production values of different benthic cover types to larger reef environments (Andréfouët and Payri 2000, Brock et al. 2006, Moses et al. 2009, Hamylton et al. 2013, Leon and Woodroffe 2013, Hamylton et al. 2017). Although this results in relatively crude estimates at present, satellite imagery and drones are rapidly improving, becoming more affordable and algorithms are constantly increasing in quality, meaning that the detail of benthic cover estimates will likely improve considerably and allow a more detailed extrapolation of locally derived carbonate budgets to whole reef systems (e.g., Hedley et al. 2018).

4.3 Environmental change

A third challenge for the calculation of carbonate budgets are ongoing changes in environmental conditions due to climate change (i.e., elevated temperature, increased solar irradiance and reduced seawater pH), which highlight the need to address associated fluctuations in production and erosion processes. Declines in coral linear extension and calcification over the last decades are already apparent for some species (Edmunds 2005, Bak et al. 2009, De'ath et al. 2009, Tanzil et al. 2009, Cantin et al. 2010, Manzello 2010, Tanzil et al. 2013) and are likely to decrease further as environmental conditions become more marginal. Future effects of climate change will vary spatially (e.g., with latitude) and taxonomically (Cooper et al. 2008, Anderson et al. 2015), emphasizing the importance of further studies on carbonate budget states and underpinning processes to discern these differences, and to estimate the impacts on geo-ecological services provided by coral reefs.

Statement of competing interests

The authors have no competing interests to declare.

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References

Adam, T.C., Duran, A., Fuchs, C.E., Roycroft, M.V., Rojas, M.C., Ruttenberg, B.I., Burkepile, D.E., 2018. Comparative analysis of foraging behavior and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. Marine Ecology Progress Series 597, 207-220

Adey, W.H., 1978. Coral reef morphogenesis: a multidimensional model. Science 202, 831-837

Afeworki, Y., Zekeria, Z.A., Videler, J.J., Bruggemann, J.H., 2013. Food intake by the parrotfish Scarus ferrugineus varies seasonally and is determined by temperature, size and territoriality. Marine Ecology Progress Series 489, 213-224.10.3354/meps10379

Alvarado, J.J., Grassian, B., Cantera-Kintz, J.R., Carballo, J.L., Londoño-Cruz, E., 2017. Coral reef bioerosion in the eastern tropical Pacific, Coral reefs of the eastern tropical Pacific. Springer, pp. 369-403.

Alvarez-Filip, L., Carricart-Ganivet, J.P., Horta-Puga, G., Iglesias-Prieto, R., 2013. Shifts in coral-assemblage composition do not ensure persistence of reef functionality. Sci Rep-Uk 3, 3486.10.1038/srep03486

Alvarez-Filip, L., Côté, I.M., Gill, J.A., Watkinson, A.R., Dulvy, N.K., 2011. Region-wide temporal and spatial variation in Caribbean reef architecture: is coral cover the whole story? Global Change Biol 17, 2470-2477.10.1111/j.1365-2486.2010.02385.x

Alvarez-Filip, L., Dulvy, N.K., Gill, J.A., Côté, I.M., Watkinson, A.R., 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proceedings of the Royal Society of London B: Biological Sciences 276, 3019-3025

Anderson, K.D., Heron, S.F., Pratchett, M.S., 2015. Species-specific declines in the linear extension of branching corals at a subtropical reef, Lord Howe Island. Coral Reefs 34, 479-490

Andréfouët, S., Payri, C., 2000. Scaling-up carbon and carbonate metabolism of coral reefs using in-situ data and remote sensing. Coral Reefs 19, 259-269

Anthony, K., Hoegh-Guldberg, O., 2003. Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and understoreys? Functional Ecology 17, 246-259

Bailey, D.T., 2019. Empirical and mechanistic approaches to understanding and projecting change in coastal marine communities. PhD thesis. University College London.

Bak, R., 1990. Patterns of echinoid bioerosion in two Pacific coral reef lagoons. Mar Ecol Prog Ser 66, 272

Bak, R., 1994. Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables. Coral Reefs 13, 99-103

Bak, R.P., Nieuwland, G., Meesters, E.H., 2009. Coral growth rates revisited after 31 years: what is causing lower extension rates in Acropora palmata? Bulletin of Marine Science 84, 287-294

Beetham, E., Kench, P.S., Popinet, S., 2017. Future reef growth can mitigate physical impacts of sea-level rise on atoll islands. Earth's Future 5, 1002-1014.10.1002/2017ef000589

Bellwood, D.R., 1995. Direct estimate of bioerosion by two parrotfish species, Chlorurus gibbus and C. sordidus, on the Great Barrier Reef, Australia. Mar Biol 121, 419-429.10.1007/bf00349451

Bellwood, D.R., Choat, J.H., 1990. A functional analysis of grazing in parrotfishes (family scaridae) - the ecological implications. Environ Biol Fish 28, 189-214.Doi 10.1007/Bf00751035

Bianchi, C., Morri, C., Montefalcone, M., 2016. Bioconstructor Guild Analysis to Assess Maldivian Reefs Following Ocean Warming and Coral Bleaching, American Geophysical Union, Ocean Sciences Meeting 2016, abstract# PC52A-02.

Bianchi, C.N., Morri, C., Lasagna, R., Montefalcone, M., Gatti, G., Parravicini, V., Rovere, A., 2017. Resilience of the marine animal forest: lessons from Maldivian coral reefs after the mass mortality of 1998. Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, 1241-1269

Bonaldo, R.M., Hoey, A.S., Bellwood, D.R., 2014. The ecosystem roles of parrotfishes on tropical reefs. Oceanography and Marine Biology: An Annual Review 52, 81-132

Brock, J.C., Yates, K.K., Halley, R.B., Kuffner, I.B., Wright, C.W., Hatcher, B.G., 2006. Northern Florida reef tract benthic metabolism scaled by remote sensing. Marine Ecology Progress Series 312, 123-139

Browne, N.K., Smithers, S.G., Perry, C.T., 2013. Carbonate and terrigenous sediment budgets for two inshore turbid reefs on the central Great Barrier Reef. Marine Geology 346, 101-123.10.1016/j.margeo.2013.08.011

Bruggemann, J.H., Begeman, J., Bosma, E.M., Verburg, P., Breeman, A.M., 1994a. Foraging by the stoplight parrotfish Sparisoma viride. II. Intake and assimilation of food, protein and energy. Marine Ecology-Progress Series 106, 57-71

Bruggemann, J.H., Van Oppen, M.J., Breeman, A.M., 1994b. Foraging by the stoplight parrotfish Sparisoma viride. I. Food selection in different, socially determined habitats. Marine Ecology-Progress Series 106, 41-55

Bruggemann, J.H., vanKessel, A.M., van Rooij, J.M., Breeman, A.M., 1996. Bioerosion and sediment ingestion by the Caribbean parrotfish Scarus vetula and Sparisoma viride: Implications of fish size, feeding mode and habitat use. Marine Ecology Progress Series 134, 59-71.DOI 10.3354/meps134059

Burns, J., Delparte, D., Gates, R.D., Takabayashi, M., 2015. Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. PeerJ 3, e1077.10.7717/peerj.1077

Cacciapaglia, C., Van Woesik, R., 2016. Climate-change refugia: shading reef corals by turbidity. Global Change Biol 22, 1145-1154

Cantin, N.E., Cohen, A.L., Karnauskas, K.B., Tarrant, A.M., McCorkle, D.C., 2010. Ocean warming slows coral growth in the central Red Sea. Science 329, 322-325

Carreiro-Silva, M., McClanahan, T., 2001. Echinoid bioerosion and herbivory on Kenyan coral reefs: the role of protection from fishing. Journal of Experimental Marine Biology and Ecology 262, 133-153

Carreiro-Silva, M., McClanahan, T.R., 2012. Macrobioerosion of dead branching Porites, 4 and 6 years after coral mass mortality. Marine Ecology Progress Series 458, 103-122.10.3354/meps09726

Carreiro-Silva, M., McClanahan, T.R., Kiene, W.E., 2009. Effects of inorganic nutrients and organic matter on microbial euendolithic community composition and microbioerosion rates. Marine Ecology Progress Series 392, 1-15.10.3354/meps08251

Carricart-Ganivet, J.P., Cabanillas-Teran, N., Cruz-Ortega, I., Blanchon, P., 2012. Sensitivity of calcification to thermal stress varies among genera of massive reef-building corals. PLoS One 7, e32859

Chave, K.E., Smith, S.V., Roy, K.J., 1972. Carbonate production by coral reefs. Marine Geology 12, 123-140

Chazottes, V., Hutchings, P., Osorno, A., 2017. Impact of an experimental eutrophication on the processes of bioerosion on the reef: One Tree Island, Great Barrier Reef, Australia. Mar Pollut Bull 118, 125-130.10.1016/j.marpolbul.2017.02.047

Chen, T., Li, S., Yu, K., 2013. Macrobioerosion in Porites corals in subtropical northern South China Sea: a limiting factor for high-latitude reef framework development. Coral Reefs 32, 101-108.10.1007/s00338-012-0946-4

Conand, C., 1997. The carbonate budget of a fringing reef in La Reunion Island (Indian Ocean); sea urchin and fish bioerosion and net calcification, Proceedings of the 8th International Coral Reef Symposium, 1997, pp. 953-958.

Cooper, T.F., De'Ath, G., Fabricius, K.E., Lough, J.M., 2008. Declining coral calcification in massive Porites in two nearshore regions of the northern Great Barrier Reef. Global Change Biol 14, 529-538

Couce, E., Ridgwell, A., Hendy, E.J., 2013. Future habitat suitability for coral reef ecosystems under global warming and ocean acidification. Glob Chang Biol 19, 3592-3606.10.1111/gcb.12335

Courtney, T.A., Andersson, A.J., Bates, N.R., Collins, A., Cyronak, T., de Putron, S.J., . . . Tribollet, A., 2016. Comparing Chemistry and Census-Based Estimates of Net Ecosystem Calcification on a Rim Reef in Bermuda. Frontiers in Marine Science 3, 181.10.3389/fmars.2016.00181

De'ath, G., Lough, J.M., Fabricius, K.E., 2009. Declining coral calcification on the Great Barrier Reef. Science 323, 116-119

de Bakker, D.M., Webb, A.E., van den Bogaart, L.A., van Heuven, S., Meesters, E.H., van Duyl, F.C., 2018. Quantification of chemical and mechanical bioerosion rates of six Caribbean excavating sponge species found on the coral reefs of Curacao. PLoS One 13, e0197824.10.1371/journal.pone.0197824

DeCarlo, T.M., Cohen, A.L., Barkley, H.C., Cobban, Q., Young, C., Shamberger, K.E., . . . Golbuu, Y., 2015. Coral macrobioerosion is accelerated by ocean acidification and nutrients. Geology 43, 7-10.10.1130/g36147.1

Dornelas, M., Madin, J.S., Baird, A.H., Connolly, S.R., 2017. Allometric growth in reef-building corals. Proc. R. Soc. B 284, 20170053

Eakin, C., 1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Nino at Uva Island in the eastern Pacific. Coral Reefs 15, 109-119

Eakin, C.M., 2001. A tale of two ENSO events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. Bulletin of Marine Science 69, 171-186

Edinger, E.N., Limmon, G.V., Jompa, J., Widjatmoko, W., Heikoop, J.M., Risk, M.J., 2000. Normal coral growth rates on dying reefs: are coral growth rates good indicators of reef health? Mar Pollut Bull 40, 404-425

Edmunds, P.J., 2005. The effect of sub-lethal increases in temperature on the growth and population trajectories of three scleractinian corals on the southern Great Barrier Reef. Oecologia 146, 350-364

Eyre, B.D., Cyronak, T., Drupp, P., De Carlo, E.H., Sachs, J.P., Andersson, A.J., 2018. Coral reefs will transition to net dissolving before end of century. Science 359, 908-911

Ferrari, R., Figueira, W.F., Pratchett, M.S., Boube, T., Adam, A., Kobelkowsky-Vidrio, T., . . . Byrne, M., 2017. 3D photogrammetry quantifies growth and external erosion of individual coral colonies and skeletons. Sci Rep 7, 16737.10.1038/s41598-017-16408-z

Ferrari, R., McKinnon, D., He, H., Smith, R., Corke, P., González-Rivero, M., . . . Upcroft, B., 2016. Quantifying multiscale habitat structural complexity: A cost-effective framework for underwater 3D modelling. Remote Sensing 8, 113.10.3390/rs8020113

Ferrario, F., Beck, M.W., Storlazzi, C.D., Micheli, F., Shepard, C.C., Airoldi, L., 2014. The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. Nat Commun 5, 3794.10.1038/ncomms4794

Fonseca, A., Dean, H.K., Cortés, J., 2006. Non-colonial coral macro-borers as indicators of coral reef status in the south Pacific of Costa Rica. Revista de biología tropical 54, 101-115

Fricke, H., Vareschi, E., Schlichter, D., 1987. Photoecology of the coral Leptoseris fragilis in the Red Sea twilight zone (an experimental study by submersible). Oecologia 73, 371-381

Friedlander, A.M., Parrish, J.D., 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology 224, 1-30

Gao, K., Zheng, Y., 2010. Combined effects of ocean acidification and solar UV radiation on photosynthesis, growth, pigmentation and calcification of the coralline alga *Corallina sessilis* (Rhodophyta). Global Change Biol 16, 2388-2398

Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A., Watkinson, A.R., 2003. Long-term region-wide declines in Caribbean corals. Science 301, 958-960

Glynn, P.W., 1988. El Nifio warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. Galaxea 7, 129-160

Glynn, P.W., Manzello, D.P., 2015. Bioerosion and Coral Reef Growth: A Dynamic Balance, Coral Reefs in the Anthropocene. Springer, Dordrecht, pp. 67-97.

Glynn, P.W., Wellington, G.M., Birkeland, C., 1979. Coral reef growth in the Galapagos: limitation by sea urchins. Science 203, 47-49

Golubic, S., Friedmann, E.I., Schneider, J., 1981. The lithobiontic ecological niche, with special reference to microorganisms. Journal of Sedimentary Research 51, 475-478

González-Barrios, F.J., Álvarez-Filip, L., 2018. A framework for measuring coral species-specific contribution to reef functioning in the Caribbean. Ecological Indicators 95, 877-886.10.1016/j.ecolind.2018.08.038

Graham, N.A.J., Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. Coral Reefs 32, 315-326.10.1007/s00338-012-0984-y

Griffin, S.P., García, R.P., Weil, E., 2003. Bioerosion in coral reef communities in southwest Puerto Rico by the sea urchin Echinometra viridis. Mar Biol 143, 79-84.10.1007/s00227-003-1056-1

Grigg, R., 1998. Holocene coral reef accretion in Hawaii: a function of wave exposure and sea level history. Coral Reefs 17, 263-272

Grigg, R.W., 2006. Depth limit for reef building corals in the Au'au Channel, SE Hawaii. Coral Reefs 25, 77-84

Hamylton, S., Silverman, J., Shaw, E., 2013. The use of remote sensing to scale up measures of carbonate production on reef systems: a comparison of hydrochemical and census-based estimation methods. International Journal of Remote Sensing 34, 6451-6465.10.1080/01431161.2013.800654

Hamylton, S.M., Duce, S., Vila-Concejo, A., Roelfsema, C.M., Phinn, S.R., Carvalho, R.C., . . . Joyce, K.E., 2017. Estimating regional coral reef calcium carbonate production from remotely sensed seafloor maps. Remote Sensing of Environment 201, 88-98.10.1016/j.rse.2017.08.034

Hedley, J.D., Roelfsema, C., Brando, V., Giardino, C., Kutser, T., Phinn, S., . . . Koetz, B., 2018. Coral reef applications of Sentinel-2: Coverage, characteristics, bathymetry and benthic mapping with comparison to Landsat 8. Remote Sensing of Environment 216, 598-614.10.1016/j.rse.2018.07.014

Hernández-Ballesteros, L.M., Elizalde-Rendón, E.M., Carballo, J.L., Carricart-Ganivet, J.P., 2013. Sponge bioerosion on reef-building corals: Dependent on the environment or on skeletal density? Journal of Experimental Marine Biology and Ecology 441, 23-27.https://doi.org/10.1016/j.jembe.2013.01.016

Herrán, N., Narayan, G.R., Reymond, C.E., Westphal, H., 2017. Calcium carbonate production, coral cover and diversity along a distance gradient from stone town: A case study from Zanzibar, Tanzania. Frontiers in Marine Science 4, 412.10.3389/fmars.2017.00412

Highsmith, R.C., 1981. Coral bioerosion at Enewetak: agents and dynamics. Internationale Revue der gesamten Hydrobiologie und Hydrographie 66, 335-375

Hoey, A., Howells, E., Johansen, J., Hobbs, J.-P., Messmer, V., McCowan, D., . . . Pratchett, M., 2016a. Recent Advances in Understanding the Effects of Climate Change on Coral Reefs. Diversity 8, 1-22.10.3390/d8020012

Hoey, A.S., Bellwood, D.R., 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. Coral Reefs 27, 37-47.10.1007/s00338-007-0287-x

Hoey, A.S., Feary, D.A., Burt, J.A., Vaughan, G., Pratchett, M.S., Berumen, M.L., 2016b. Regional variation in the structure and function of parrotfishes on Arabian reefs. Mar Pollut Bull 105, 524-531.10.1016/j.marpolbul.2015.11.035

Hubbard, D.K., Miller, A.I., Scaturo, D., 1990. Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, US Virgin Islands); applications to the nature of reef systems in the fossil record. Journal of Sedimentary Research 60, 335-360

Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., . . . Wilson, S.K., 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359, 80-83.10.1126/science.aan8048

Huston, M., 1985. Variation in coral growth rates with depth at Discovery Bay, Jamaica. Coral Reefs 4, 19-25

Jackson, J., Donovan, M., Cramer, K., Lam, V., 2014. Status and trends of Caribbean coral reefs, Global Coral Reef Monitoring Network. IUCN, Gland, Switzerland.

Jantz, S.M., Barker, B., Brooks, T.M., Chini, L.P., Huang, Q., Moore, R.M., . . . Hurtt, G.C., 2015. Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. Conservation Biology 29, 1122-1131

Januchowski-Hartley, F.A., Graham, N.A.J., Wilson, S.K., Jennings, S., Perry, C.T., 2017. Drivers and predictions of coral reef carbonate budget trajectories. P Roy Soc B-Biol Sci 284, 20162533.ARTN 20162533 10.1098/rspb.2016.2533

Johnson, M.D., Carpenter, R.C., 2012. Ocean acidification and warming decrease calcification in the crustose coralline alga *Hydrolithon onkodes* and increase susceptibility to grazing. Journal of Experimental Marine Biology and Ecology 434, 94-101

Kennedy, E.V., Ordoñez, A., Lewis, B.E., Diaz-Pulido, G., 2017. Comparison of recruitment tile materials for monitoring coralline algae responses to a changing climate. Marine Ecology Progress Series 569, 129-144.10.3354/meps12076

Kennedy, E.V., Perry, C.T., Halloran, P.R., Iglesias-Prieto, R., Schonberg, C.H., Wisshak, M., . . . Mumby, P.J., 2013. Avoiding coral reef functional collapse requires local and global action. Current Biology 23, 912-918.10.1016/j.cub.2013.04.020

Kiene, W.E., Hutchings, P.A., 1994. Bioerosion experiments at Lizard Island, Great Barrier Reef. Coral Reefs 13, 91-98.10.1007/bf00300767

Kinsey, D., 1972. Preliminary observations on community metabolism and primary productivity of the pseudo-atoll reef at One Tree Island, Great Barrier Reef, Proceedings of the Symposium on Corals and Coral Reefs, Cochin, India, pp. 13-32.

Kinsey, D., Hopley, D., 1991. The significance of coral reefs as global carbon sinks—response to greenhouse. Palaeogeography, Palaeoclimatology, Palaeoecology 89, 363-377

Kleypas, J.A., 1997. Modeled estimates of global reef habitat and carbonate production since the Last Glacial Maximum. Paleoceanography 12, 533-545.10.1029/97pa01134

Kleypas, J.A., Anthony, K.R.N., Gattuso, J.-P., 2011. Coral reefs modify their seawater carbon chemistry - case study from a barrier reef (Moorea, French Polynesia). Global Change Biol 17, 3667-3678.10.1111/j.1365-2486.2011.02530.x

Kleypas, J.A., Buddemeier, R.W., Gattuso, J.-P., 2001. The future of coral reefs in an age of global change. International Journal of Earth Sciences 90, 426-437.10.1007/s005310000125

Kuffner, I.B., Hickey, T.D., Morrison, J.M., 2013. Calcification rates of the massive coral Siderastrea siderea and crustose coralline algae along the Florida Keys (USA) outer-reef tract. Coral Reefs 32, 987-997.10.1007/s00338-013-1047-8

Kuffner, I.B., Toth, L.T., 2016. A geological perspective on the degradation and conservation of western Atlantic coral reefs. Conservation Biology 30, 706-715.10.1111/cobi.12725

Kuffner, I.B., Toth, L.T., Hudson, J.H., Goodwin, W.B., Stathakopoulos, A., Bartlett, L.A., & Whitcher, E.M., 2019. Improving estimates of coral reef construction and erosion with in situ measurements. Limnology and Oceanography 9999, 1-12. https://doi.org/10.1002/lno.11184

Lange, I.D., Perry, C.T., 2019. Bleaching impacts on carbonate production in the Chagos Archipelago: influence of functional coral groups on carbonate budget trajectories Coral Reefs https://doi.org/10.1007/s00338-019-01784-x.

Leon, J.X., Woodroffe, C.D., 2013. Morphological characterisation of reef types in Torres Strait and an assessment of their carbonate production. Marine Geology 338, 64-75.10.1016/j.margeo.2012.12.009

Logan, A., Yang, L., Tomascik, T., 1994. Linear skeletal extension rates in two species of Diploria from high-latitude reefs in Bermuda. Coral Reefs 13, 225-230.10.1007/bf00303636

Lokrantz, J., Nyström, M., Thyresson, M., Johansson, C., 2008. The non-linear relationship between body size and function in parrotfishes. Coral Reefs 27, 967-974.10.1007/s00338-008-0394-3

Mace, G. M., Reyers, B., Alkemade, R., Biggs, R., Chapin III, F. S., Cornell, S. E., ... & Purvis, A., 2014. Approaches to defining a planetary boundary for biodiversity. Glob Environ Change, 28, 289-297. https://doi.org/10.1016/j.gloenvcha.2014.07.009

Madin, J.S., Anderson, K.D., Andreasen, M.H., Bridge, T.C.L., Cairns, S.D., Connolly, S.R., . . . Baird, A.H., 2016. The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Sci Data 3, 160017.DOI: 10.1038/sdata.2016.17

Manzello, D., 2010. Coral growth with thermal stress and ocean acidification: lessons from the eastern tropical Pacific. Coral Reefs 29, 749-758

Manzello, D.P., Eakin, C.M., Glynn, P.W., 2017. Effects of global warming and ocean acidification on carbonate budgets of Eastern Pacific coral reefs, Coral reefs of the eastern tropical Pacific. Springer, Dordrecht, pp. 517-533.

Manzello, D.P., Enochs, I.C., Kolodziej, G., Carlton, R., 2015. Coral growth patterns of Montastraea cavernosa and Porites astreoides in the Florida Keys: The importance of thermal stress and inimical waters. Journal of Experimental Marine Biology and Ecology 471, 198-207.https://doi.org/10.1016/j.jembe.2015.06.010

Manzello, D.P., Enochs, I.C., Kolodziej, G., Carlton, R., Valentino, L., 2018. Resilience in carbonate production despite three coral bleaching events in 5 years on an inshore patch reef in the Florida Keys. Mar Biol 165, 99.ARTN 9910.1007/s00227-018-3354-7

Milliman, J.D., 1993. Production and accumulation of calcium carbonate in the ocean: budget of a nonsteady state. Global Biogeochemical Cycles 7, 927-957

Mokady, O., Lazar, B., Loya, Y., 1996. Echinoid bioerosion as a major structuring force of Red Sea coral reefs. The Biological Bulletin 190, 367-372

Montaggioni, L., Braithwaite, C., 2009. Patterns of carbonate production and deposition on reefs. Developments in marine geology. Elsevier, Amsterdam, 171-222

Montefalcone, M., Morri, C., Bianchi, C.N., 2018. Long-term change in bioconstruction potential of Maldivian coral reefs following extreme climate anomalies. Global Change Biol 24, 5629-5641.10.1111/gcb.14439

Morgan, K.M., Kench, P.S., 2016. Parrotfish erosion underpins reef growth, sand talus development and island building in the Maldives. Sediment Geol 341, 50-57.10.1016/j.sedgeo.2016.05.011

Morgan, K.M., Perry, C.T., Johnson, J.A., Smithers, S.G., 2017. Nearshore Turbid-Zone Corals Exhibit High Bleaching Tolerance on the Great Barrier Reef Following the 2016 Ocean Warming Event. Frontiers in Marine Science 4.10.3389/fmars.2017.00224

Moses, C.S., Andréfouët, S., Kranenburg, C.J., Muller-Karger, F.E., 2009. Regional estimates of reef carbonate dynamics and productivity using Landsat 7 ETM+, and potential impacts from ocean acidification. Marine Ecology Progress Series 380, 103-115.10.3354/meps07920

Muir, P.R., Wallace, C.C., Done, T., Aguirre, J.D., 2015. Limited scope for latitudinal extension of reef corals. Science 348, 1135-1138

Mumby, P.J., 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecological Applications 16, 747-769

Mumby, P.J., Hastings, A., Edwards, H.J., 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450, 98-101.10.1038/nature06252

Murphy, G.N., Perry, C.T., Chin, P., McCoy, C., 2016. New approaches to quantifying bioerosion by endolithic sponge populations: applications to the coral reefs of Grand Cayman. Coral Reefs 35, 1109-1121.10.1007/s00338-016-1442-z

Nemeth, M., Appeldoorn, R., 2009. The distribution of herbivorous coral reef fishes within fore-reef habitats: the role of depth, light and rugosity. Caribbean Journal of Science 45, 247-253

Neumann, B., Vafeidis, A.T., Zimmermann, J., Nicholls, R.J., 2015. Future coastal population growth and exposure to sea-level rise and coastal flooding-a global assessment. PloS one 10, e0118571

Newman, S.P., Meesters, E.H., Dryden, C.S., Williams, S.M., Sanchez, C., Mumby, P.J., Polunin, N.V., 2015. Reef flattening effects on total richness and species responses in the Caribbean. Journal of Animal Ecology 84, 1678-1689.10.1111/1365-2656.12429

Ong, L., Holland, K.N., 2010. Bioerosion of coral reefs by two Hawaiian parrotfishes: species, size differences and fishery implications. Mar Biol 157, 1313-1323.10.1007/s00227-010-1411-y

Osorno, A., Peyrot-Clausade, M., Hutchings, P.A., 2005. Patterns and rates of erosion in dead Porites across the Great Barrier Reef (Australia) after 2 years and 4 years of exposure. Coral Reefs 24, 292-303.10.1007/s00338-005-0478-2

Palacios, M., Muñoz, C., Zapata, F., 2014. Fish corallivory on a pocilloporid reef and experimental coral responses to predation. Coral Reefs 33, 625-636

Pari, N., Peyrot-Clausade, M., Hutchings, P.A., 2002. Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) during 5 years of exposure. Journal of Experimental Marine Biology and Ecology 276, 109-127

Payri, C., 1997. Hydrolithon reinboldii rhodolith distribution, growth and carbon production of a French Polynesian reef, Proceedings of the 8th international coral reef symposium, pp. 755-760.

Perry, C.T., Alvarez-Filip, L., Graham, N.A.J., Mumby, P.J., Wilson, S.K., Kench, P.S., . . . Macdonald, C., 2018a. Loss of coral reef growth capacity to track future increases in sea level. Nature 558, 396-400.10.1038/s41586-018-0194-z

Perry, C.T., Alvarez-Filip, L., 2018. Changing geo-ecological functions of coral reefs in the Anthropocene. Functional Ecology https://doi.org/10.1111/1365-2435.13247, 1-13.https://doi.org/10.1111/1365-2435.13247

Perry, C.T., Edinger, E.N., Kench, P.S., Murphy, G.N., Smithers, S.G., Steneck, R.S., Mumby, P.J., 2012a. Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire. Coral Reefs 31, 853-868.10.1007/s00338-012-0901-4

Perry, C.T., Hepburn, L.J., 2008. Syn-depositional alteration of coral reef framework through bioerosion, encrustation and cementation: Taphonomic signatures of reef accretion and reef depositional events. Earth-Science Reviews 86, 106-144.10.1016/j.earscirev.2007.08.006

Perry, C.T., Kench, P.S., Smithers, S.G., Riegl, B., Yamano, H., O'Leary, M.J., 2011. Implications of reef ecosystem change for the stability and maintenance of coral reef islands. Global Change Biol 17, 3679-3696.10.1111/j.1365-2486.2011.02523.x

Perry, C.T., Lange, I.D., Januchowski-Hartley, F.A., 2018b. ReefBudget Indo-Pacific: online resource and methodology., http://geography.exeter.ac.uk/reefbudget/.

Perry, C.T., Larcombe, P., 2003. Marginal and non-reef-building coral environments. Coral Reefs 22, 427-432.10.1007/s00338-003-0330-5

Perry, C.T., Morgan, K.M., 2017a. Bleaching drives collapse in reef carbonate budgets and reef growth potential on southern Maldives reefs. Sci Rep-Uk 7, 40581.10.1038/srep40581

Perry, C.T., Morgan, K.M., 2017b. Post-bleaching coral community change on southern Maldivian reefs: is there potential for rapid recovery? Coral Reefs 36, 1189-1194.10.1007/s00338-017-1610-9

Perry, C.T., Murphy, G., Edinger, E.N., Kench, P.S., Mumby, P.J., Smithers, S.G., Steneck, R.S., 2012b. ReefBudget Caribbean: online resource and methodology, Retrieved from http://geography.exeter.ac.uk/reefbudget/.

Perry, C.T., Murphy, G.N., Graham, N.A., Wilson, S.K., Januchowski-Hartley, F.A., East, H.K., 2015a. Remote coral reefs can sustain high growth potential and may match future sea-level trends. Sci Rep-Uk 5, 18289.10.1038/srep18289

Perry, C.T., Murphy, G.N., Kench, P.S., Smithers, S.G., Edinger, E.N., Steneck, R.S., Mumby, P.J., 2013. Caribbean-wide decline in carbonate production threatens coral reef growth. Nat Commun 4, 1402.ARTN 1402 10.1038/ncomms2409

Perry, C.T., Smithers, S.G., Gulliver, P., Browne, N.K., 2012c. Evidence of very rapid reef accretion and reef growth under high turbidity and terrigenous sedimentation. Geology 40, 719-722.10.1130/g33261.1

Perry, C.T., Spencer, T., Kench, P.S., 2008. Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. Coral Reefs 27, 853-866.10.1007/s00338-008-0418-z

Perry, C.T., Steneck, R.S., Murphy, G.N., Kench, P.S., Edinger, E.N., Smithers, S.G., Mumby, P.J., 2015b. Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. Global Change Biol 21, 1153-1164.10.1111/gcb.12792

Pratchett, M.S., Anderson, K.D., Hoogenboom, M.O., Widman, E., Baird, A.H., Pandolfi, J.M., . . . Lough, J.M., 2015. Spatial, temporal and taxonomic variation in coral growth-implications for the structure and function of coral reef ecosystems. Oceanography and Marine Biology: An Annual Review 53, 215-295

Quataert, E., Storlazzi, C., van Rooijen, A., Cheriton, O., van Dongeren, A., 2015. The influence of coral reefs and climate change on wave-driven flooding of tropical coastlines. Geophysical Research Letters 42, 6407-6415.10.1002/2015gl064861

Randall, J., 1974. The effect of fishes on coral reefs, in: Cameron, A., et al. (Eds.), Proceedings of the Second International Coral Reef Symposium, Brisbane, Australia, pp. 159-166.

RCoreTeam, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Last accessed 25/04/2019

Reaka-Kudla, M.L., Feingold, J.S., Glynn, W., 1996. Experimental studies of rapid bioerosion of coral reefs in the Galápagos Islands. Coral Reefs 15, 101-107.10.1007/bf01771898

Richardson, L.E., Graham, N.A.J., Pratchett, M.S., Hoey, A.S., 2017. Structural complexity mediates functional structure of reef fish assemblages among coral habitats. Environ Biol Fish 100, 193-207.10.1007/s10641-016-0571-0

Roberts, C.M., McClean, C.J., Veron, J.E., Hawkins, J.P., Allen, G.R., McAllister, D.E., . . . Wells, F., 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295, 1280-1284

Roff, G., Zhao, J.X., Mumby, P.J., 2015. Decadal-scale rates of reef erosion following El Nino-related mass coral mortality. Global Change Biol 21, 4415-4424.10.1111/gcb.13006

Roik, A., Roethig, T., Pogoreutz, C., Saderne, V., Voolstra, C.R., 2018. Coral reef carbonate budgets and ecological drivers in the naturally high temperature and high total alkalinity environment of the Red Sea. Biogeosciences Discussions 10.5194/bg-2018-57, 1-34.10.5194/bg-2018-57

Rossi, P., Castagnetti, C., Capra, A., Brooks, A.J., & Mancini, F. 2019. Detecting change in coral reef 3D structure using underwater photogrammetry: critical issues and performance metrics. Applied Geomatics, 1-15, 10.1007/s12518-019-00263-w

Ryan, D.A., Opdyke, B.N., Jell, J.S., 2001. Holocene sediments of Wistari Reef: towards a global quantification of coral reef related neritic sedimentation in the Holocene. Palaeogeography, Palaeoclimatology, Palaeoecology 175, 173-184

Ryan, E.J., Hanmer, K., & Kench, P.S., 2019. Massive corals maintain a positive carbonate budget of a Maldivian upper reef platform despite major bleaching event. Scientific reports, 9(1), 6515

Schönberg, C.H.L., Fang, J.K.H., Carreiro-Silva, M., Tribollet, A., Wisshak, M., 2017. Bioerosion: the other ocean acidification problem. ICES Journal of Marine Science 74, 895-925.10.1093/icesjms/fsw254

Scoffin, T., 1980. Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part II-Erosion, sediments and internal structure. Bulletin of Marine Science 30, 475-508

Scoffin, T., 1993. The geological effects of hurricanes on coral reefs and the interpretation of storm deposits. Coral Reefs 12, 203-221

Scoffin, T.P., 1992. Taphonomy of coral reefs: a review. Coral Reefs 11, 57-77.10.1007/bf00357423

Smith, S., 1981. The Houtman Abrolhos Islands: Carbon metabolism of coral reefs at high latitude. Limnology and Oceanography 26, 612-621

Smith, S., Kinsey, D., 1976. Calcium carbonate production, coral reef growth, and sea level change. Science 194, 937-939

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., . . . Lourie, S.A., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. AIBS Bulletin 57, 573-583

Takeshita, Y., McGillis, W., Briggs, E.M., Carter, A.L., Donham, E.M., Martz, T.R., . . . Smith, J.E., 2016. Assessment of net community production and calcification of a coral reef using a boundary layer approach. Journal of Geophysical Research: Oceans 121, 5655-5671

Tanzil, J., Brown, B., Tudhope, A., Dunne, R., 2009. Decline in skeletal growth of the coral Porites lutea from the Andaman Sea, South Thailand between 1984 and 2005. Coral Reefs 28, 519-528

Tanzil, J.T., Brown, B.E., Dunne, R.P., Lee, J.N., Kaandorp, J.A., Todd, P.A., 2013. Regional decline in growth rates of massive Porites corals in Southeast Asia. Global Change Biol 19, 3011-3023

Tribollet, A., Golubic, S., 2005. Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia. Coral Reefs 24, 422-434.10.1007/s00338-005-0003-7

Turner, J.A., Babcock, R.C., Hovey, R., Kendrick, G.A., 2018. AUV-based classification of benthic communities of the Ningaloo shelf and mesophotic areas. Coral Reefs 37, 763-778.10.1007/s00338-018-1700-3

van Woesik, R., Cacciapaglia, C.W., 2018. Keeping up with sea-level rise: Carbonate production rates in Palau and Yap, western Pacific Ocean. PLoS One 13, e0197077.10.1371/journal.pone.0197077

Vásquez-Elizondo, R.M., Enríquez, S., 2016. Coralline algal physiology is more adversely affected by elevated temperature than reduced pH. Sci Rep-Uk 6, 19030.10.1038/srep19030

Veron, J., 2000. Corals of the world. Australian Institute of Marine Science, Townsville.

Veron, J., Devantier, L.M., Turak, E., Green, A.L., Kininmonth, S., Stafford-Smith, M., Peterson, N., 2009. Delineating the coral triangle. Galaxea, Journal of Coral Reef Studies 11, 91-100

Vogel, K., Gektidis, M., Golubic, S., Kiene, W.E., Radtke, G., 2000. Experimental studies on microbial bioerosion at Lee Stocking Island, Bahamas and One Tree Island, Great Barrier Reef, Australia: implications for paleoecological reconstructions. Lethaia 33, 190-204.doi:10.1080/00241160025100053

Weinstein, D., Sharifi, A., Klaus, J., Smith, T., Giri, S., Helmle, K., 2016. Coral growth, bioerosion, and secondary accretion of living orbicellid corals from mesophotic reefs in the US Virgin Islands. Marine Ecology Progress Series 559, 45-63

Weinstein, D.K., Smith, T.B., Klaus, J.S., 2014. Mesophotic bioerosion: Variability and structural impact on U.S. Virgin Island deep reefs. Geomorphology 222, 14-24.10.1016/j.geomorph.2014.03.005

Welsh, J., Bellwood, D., 2012a. How far do schools of roving herbivores rove? A case study using Scarus rivulatus. Coral Reefs 31, 991-1003

Welsh, J., Bellwood, D., 2012b. Spatial ecology of the steephead parrotfish (Chlorurus microrhinos): an evaluation using acoustic telemetry. Coral Reefs 31, 55-65

Welsh, J., Goatley, C., Bellwood, D., 2013. The ontogeny of home ranges: evidence from coral reef fishes. Proceedings of the Royal Society of London B: Biological Sciences 280, 20132066

Wizemann, A., Nandini, S.D., Stuhldreier, I., Sánchez-Noguera, C., Wisshak, M., Westphal, H., . . . Reymond, C.E., 2018. Rapid bioerosion in a tropical upwelling coral reef. PloS one 13, e0202887

Yarlett, R.T., Perry, C.T., Wilson, R.W., Philpot, K.E., 2018. Constraining species-size class variability in rates of parrotfish bioerosion on Maldivian coral reefs: implications for regional-scale bioerosion estimates. Marine Ecology Progress Series 590, 155-169.10.3354/meps12480

Yates, K.K., Zawada, D.G., Smiley, N.A., Tiling-Range, G., 2017. Divergence of seafloor elevation and sea level rise in coral reef ecosystems. Biogeosciences 14, 1739-1772.10.5194/bg-14-1739-2017