

1 **Carbonate budgets as indicators of functional reef “health”: a** 2 **critical review of data underpinning census-based methods and** 3 **current knowledge gaps**

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15 **Abstract**

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

32 **Keywords**

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

34

35 **1. Introduction**

36 1.1 What are reef carbonate budgets?

37 Coral reefs are major focal points of benthic carbonate production across tropical and sub-tropical
38 marine environments (Milliman 1993, Montaggioni and Braithwaite 2009). Depending on the
39 environmental conditions at a given site, this carbonate can accumulate over millennia to form
40 extensive reef structures (Kleypas et al. 2001). The net accumulation rate of framework carbonate is
41 thereby controlled by a range of biologically-, physically- and chemically-driven production and
42 erosion processes (Scoffin 1993, Perry et al. 2008, Montaggioni and Braithwaite 2009). Scleractinian
43 corals are typically the primary reef framework producers (Chave et al. 1972), with additional
44 biologically-derived carbonate being deposited by a range of calcareous encrusters. The predominant
45 encrusters are usually crustose coralline algae (CCA) (Payri 1997) which, in very shallow, high energy
46 settings, can even dominate biological carbonate production e.g., within algal ridge systems (Adey
47 1978, Grigg 1998). Additional carbonate from sediment import and skeletal cementation can also
48 contribute to reef framework construction, helping to bind reef material and thereby promoting the
49 stability of the reef framework (Scoffin 1992, Perry and Hepburn 2008). Offsetting the production of
50 framework carbonate are processes that biologically or mechanically erode the reef structure. For
51 example, extensive biological erosion (or bioerosion) occurs as a by-product of the feeding activities
52 of many species of parrotfish (Bellwood and Choat 1990, Bruggemann et al. 1996) and sea urchins
53 (Bak 1994), and through the boring activities of endolithic macro- and microboring organisms (Vogel
54 et al. 2000, Tribollet and Golubic 2005). Episodic physical disturbances associated with cyclones and
55 storms can also influence reef development through the import/export of sedimentary materials and
56 the generation of coral rubble (Scoffin 1993). In addition, reef-derived carbonate, especially sediment,
57 may dissolve chemically, at a rate correlated with the aragonite saturation state of the overlying
58 seawater (Eyre et al. 2018).

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60 The relative rates at which these production and erosion processes operate strongly influence net
61 rates of carbonate production, also expressed as a reef's carbonate budget, i.e., the sum of gross
62 carbonate production, less the amount of carbonate lost through dissolution and erosion (Chave et al.
63 1972). The carbonate budget of a coral reef can be considered as a quantitative measure of the
64 functional state of a reef at a given point in time (Perry et al. 2008, Kuffner and Toth 2016) and is an
65 important metric for several reasons. First, it indicates whether coral communities at a given site have
66 the capacity to build and accrete reef structures over time, i.e. providing an estimate of a reef's growth
67 potential (Kleypas et al. 2001). Second, it describes the complexity and maintenance of the reef
68 framework, which essentially controls many of the functions and ecosystem services provided by
69 reefs (Perry and Alvarez-Filip 2018). These functions include the provision of shelter and habitat for
70 fish and invertebrate species (Friedlander and Parrish 1998, Graham and Nash 2013), coastal
71 protection through the dissipation of wave energy (Ferrario et al. 2014, Beetham et al. 2017), and the
72 generation of sediments to sustain adjacent beaches and shorelines (Perry et al. 2011, Kuffner and
73 Toth 2016). Thus, a single metric, the carbonate budget, serves as a proxy for the maintenance of
74 biodiversity and much of the function of an entire ecosystem (Mace et al. 2014).

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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.

112 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	<ul style="list-style-type: none"> Includes total precipitation and chemical dissolution of carbonates Highlights temporal variability and allows investigation of daily and seasonal differences 	<ul style="list-style-type: none"> 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	<ul style="list-style-type: none"> Allows determination of the relative contribution of different carbonate producers/eroders Allows spatial comparisons of different reef environments Supports other indices of reef functionality 	<ul style="list-style-type: none"> 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	<ul style="list-style-type: none"> Integrates post-depositional carbonate dissolution and erosion Enables comparisons with historical rates 	<ul style="list-style-type: none"> Does not differentiate between production/erosion processes Resolution not fine enough to differentiate between individual years

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 114 Whilst many of the earliest studies on carbonate budgets followed the hydrochemical approach,
 115 census-based methodologies have been employed with increasing frequency in the past two
 116 decades. The primary reason for this is probably that census-based approaches quantify contributions
 117 from different functional groups and taxa, and thus provide an opportunity to directly link data from
 118 standardised reef ecological monitoring approaches (e.g. [AGRRA](#)) and budget state assessments. In
 119 light of the rapidly changing ecological states of many reef communities, this also offers the potential
 120 to predict and model future budget states (e.g., Alvarez-Filip et al. 2013, Kennedy et al. 2013) and to
 121 link these to changes in ecosystem services. Census-based budget state assessments thus provide a
 122 measure of reef “health” that moves beyond more simplistic assessments of ecological status (as
 123 defined by measures of coral cover and community composition alone), and allow questions around
 124 the functional performance of a reef (as defined by reef structural complexity and integrity, carbonate
 125 production, and reef growth potential) to be explored (Alvarez-Filip et al. 2011, Graham and Nash
 126 2013, González-Barrios and Álvarez-Filip 2018).

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 128 Two recent examples of indices exploring the functional metrics of reef structures are: i) the
 129 BioConstruction Potential (BCP) index, which groups carbonate producers into five bioconstructional
 130 guilds, whose cover is multiplied with assigned importance scores to yield a BCP value. This index
 131 defines reefs as accreting or eroding, is positively correlated with carbonate deposition rate and reef
 132 accretion rate, and has been used to illustrate long-term, bleaching-related changes in reef states at
 133 sites in the Maldives (Bianchi et al. 2016, Bianchi et al. 2017, Montefalcone et al. 2018); and ii) the
 134 Reef Functional Index (RFI), which uses a combination of survey data on coral cover and published
 135 species trait information (calcification rate, rugosity and colony height, integrated into a ‘Functional
 136 Coefficient’) to estimate the functional contribution of each coral species to reef-building capacity and
 137 structural complexity at a given reef site. This methodology has been used to compare reef states at
 138 170 sites along the Mesoamerican Barrier Reef (González-Barrios and Álvarez-Filip 2018).

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140 These emerging functional assessment indices are both underpinned by the ReefBudget
141 methodology, which follows the framework production states approach discussed by Perry et al.
142 (2008), and focuses on quantifying the relative contributions made by different carbonate
143 producer/eroder groups to net biologically driven carbonate production (Perry et al. 2012a).
144 Production and erosion rates of each group are calculated using survey data on organism cover and
145 abundance, combined with available extension, production or erosion rate data. Calculations generate
146 estimates of net carbonate production (in $G = \text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$). The protocols and data entry
147 spreadsheets are available online and are pre-set with Caribbean or Indo-Pacific relevant datasets to
148 support estimates of carbonate budget states from site-specific survey data
149 (<http://www.exeter.ac.uk/geography/reefbudget>). Importantly, however, all pre-set rates can be
150 substituted for regional-, site- or environment-specific values as deemed most appropriate by the
151 user. In recent years the ReefBudget method has been employed in the Caribbean (Perry et al.
152 2012a, Perry et al. 2013, Perry et al. 2015b, Courtney et al. 2016, Manzello et al. 2018, Perry et al.
153 2018a), the central Indian Ocean (Perry et al. 2015a, Perry and Morgan 2017a, b, Perry et al. 2018a,
154 Lange and Perry 2019, Ryan et al. 2019), the western Indian Ocean (Herrán et al. 2017,
155 Januchowski-Hartley et al. 2017), and the Red Sea (Roik et al. 2018), and thereby represents the
156 most extensive set of comparable budget estimates made thus far.

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158 1.3 Aim of this review

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

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177 **2. Current status and gaps in reef carbonate budget research**

178 We performed an extensive review of available literature on reef carbonate budgets using the search
179 terms “reef budget”, “carbonate budget” and “community calcification” as well as following up

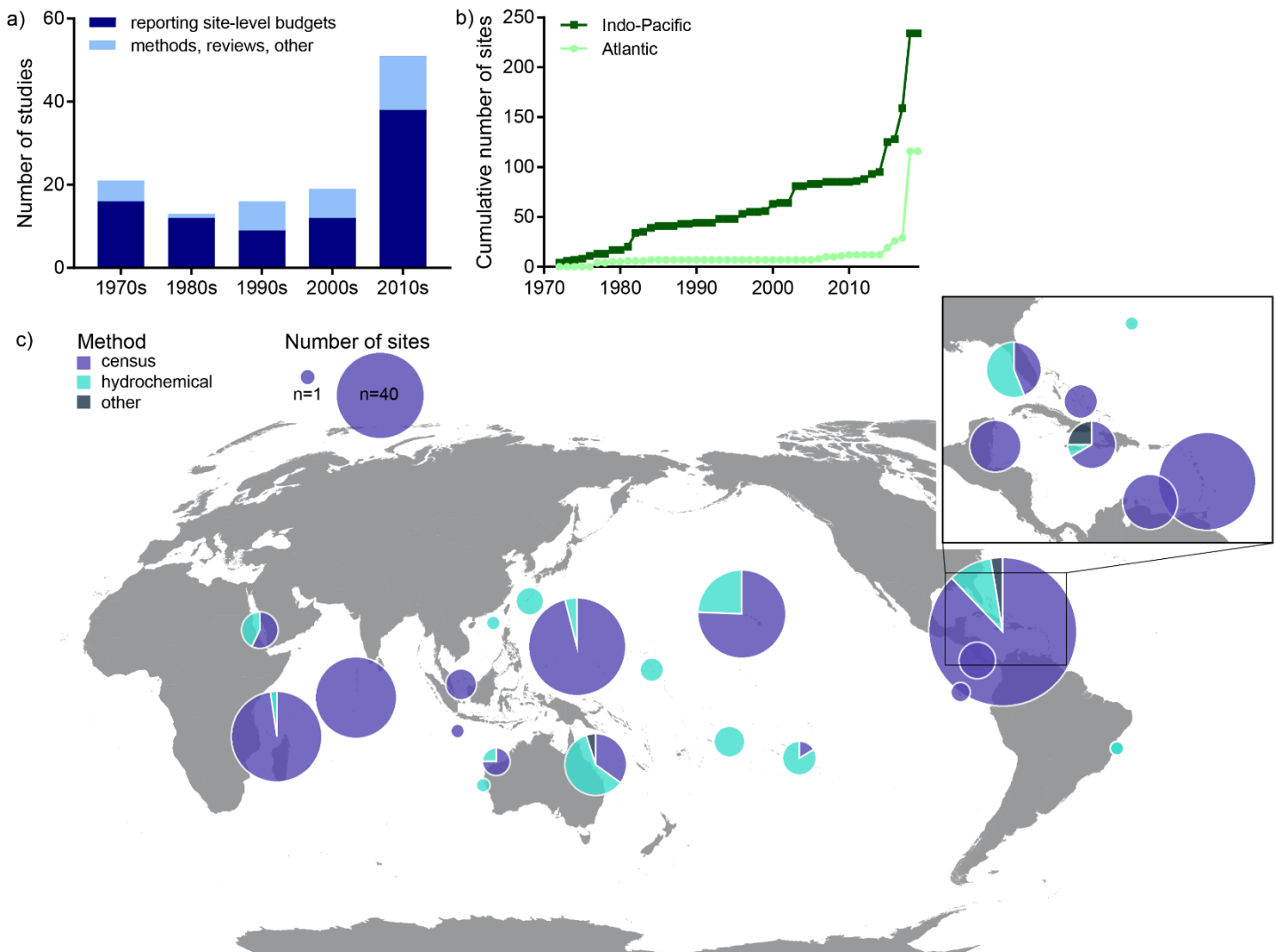
180 references within relevant articles. In total we found 91 studies reporting carbonate budgets for 338
181 reef sites (116 in the Atlantic, 222 in the Indo-Pacific), applying both census- and hydrochemical
182 methodologies. Additionally, regional budgets were reported in 3 studies, global estimates in 7
183 studies, and further papers have described methodological developments or reviewed the current
184 state of knowledge on reef carbonate budgets, reef architecture and vertical accretion rates (all
185 studies listed in Table S1a). From this analysis we observe that although the concept of reef budgets
186 developed quite early in the context of coral reef science (Chave et al. 1972, Kinsey 1972), the
187 number of studies on this topic and investigated sites remained relatively low and constant for almost
188 40 years until the 2010s, when numbers tripled (Fig. 1a, b). However, despite this increased interest
189 the reef budget state approach is still underrepresented in studies and monitoring efforts if compared
190 with more traditional “health” indicators such as coral cover.

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192 2.1 Geographic status

193 Geographic coverage of budget state assessments is spatially very heterogeneous both between and
194 within the major reef-building regions (Fig. 1c). On a province scale, the Tropical Northwestern
195 Atlantic has been the focus of the largest number of carbonate budget studies (19 studies reporting
196 rates for 115 sites), likely reflecting the simplified challenge of modelling reef dynamics in an area with
197 relatively low species diversity, good accessibility of sites, and a high socio-economic interest in
198 understanding the long-term degradation of Caribbean reefs. Almost half of these budget estimates
199 have been determined for islands in the Eastern Caribbean (50 sites), although there is also a rapidly
200 expanding body of data from the Mesoamerican reef and Florida. In the Indo-Pacific region, the
201 Western and Central Indian Ocean are reasonably well represented as a result of recent research
202 efforts and encompass studies investigating the impacts of bleaching events on carbonate budgets
203 (Januchowski-Hartley et al. 2017, Perry and Morgan 2017a, Lange and Perry 2019). The central Indo-
204 Pacific is also well represented concerning the number of sites assessed, although these mostly
205 derive from one study reporting data from 48 sites in Palau and Yap (van Woerik and Cacciapaglia
206 2018) and thus overall coverage of reef types and habitats in this area remains relatively low. The
207 Great Barrier Reef region is relatively well represented concerning the number of studies (24 studies,
208 half of these resulting from the early research efforts of Kinsey and colleagues 1972-1983) but not the
209 number of sites (19 sites including 1 in Torres Strait). In the Eastern Tropical Pacific, relatively few
210 sites have been studied regarding carbonate budgets, but existing studies have been very detailed,
211 discussing the effects of marginal reef conditions, thermal stress and bioerosion over time (Glynn et
212 al. 1979, Glynn 1988, Eakin 1996, Reaka-Kudla et al. 1996, Eakin 2001, Manzello et al. 2017).
213 It is perhaps most striking that only one study has, to-date, been conducted in the Coral Triangle and
214 Sunda Shelf region (5 sites on Java, Edinger et al. 2000), despite this area being the epicentre of
215 marine diversity and a global priority for conservation (Roberts et al. 2002, Veron et al. 2009). We
216 thus suggest an urgent need for budget studies in a range of provinces and habitats within the Coral
217 Triangle and Tropical Southwestern Pacific region, both because of its high biodiversity, and because
218 it is a region that is experiencing rapid population growth and extensive land use changes (e.g., Jantz
219 et al. 2015, Neumann et al. 2015). Due to their remoteness, the numerous reef systems across

220 Polynesia and other central Pacific island groups have also had relatively little attention, especially
 221 considering the diversity of settings and reef types that exist there. Further areas currently
 222 underrepresented in budget estimates are Western Australia, the Red Sea and the Arabian Gulf.
 223



224 Figure 1: Temporal and spatial distribution of reef carbonate budget studies. Number of a) studies on carbonate budgets and b)
 225 sites with budget states over time; and c) geographic range of published carbonate budgets. Bubble size indicates the number
 226 of sites in biogeographical provinces (world map) and ecoregions (inset, Caribbean) after Spalding et al. (2007). Colours
 227 indicate the methodology used for calculations. All studies and respective budget ranges are listed in Table S1.
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229 2.2 Predictors of reef budget states

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

235 To investigate possible regional and temporal patterns in carbonate budget states we performed
 236 preliminary analyses on site-level net carbonate budget data (Table S1b), testing the effects of
 237 method (hydrochemical, census, other), ocean (Indian Ocean, Atlantic, Pacific), biogeographical

238 province (17 provinces after Spalding et al (2007)), reef habitat (fore reef, reef flat, back reef, lagoon,
239 patch reef), water depth (in m) and time (year of data collection) (Fig. 2a-g). Factorial data was tested
240 using One-Way ANOVAs and TukeyHSD-tests, and numerical data was tested using linear model
241 fitting in R 3.5.1 (RCoreTeam 2016).

242

243 The methodological approach used for calculations does not have a significant impact on the
244 magnitude of published carbonate budget states (Fig. 2a). Supportively, at the few sites where
245 several methods were used in tandem, budget states were in good agreement (Montaggioni and
246 Braithwaite 2009, Hamylton et al. 2013, Courtney et al. 2016). Geographically, carbonate budgets on
247 Indian Ocean reefs are significantly lower than on Atlantic reefs (Fig. 2b, $F_{2,325}=7.807$, $p<0.001$,
248 TukeyHSD: IO-A<0.001, P-A=0.321, P-IO=0.051), likely because available data in the Seychelles and
249 Maldives include a relatively large number of post-bleaching data points. Province has a significant
250 influence on published budget states ($F_{16,311}=4.387$, $p<0.001$) and the plot shows a wide range both
251 across and within regions (Fig. 2d). Concerning habitats, early studies suggested a predictable
252 distribution of carbonate production across reef zones in both Atlantic and Indo-Pacific (reef-flats = 4
253 G, lagoons = 0.8 G, Kinsey 1981). In our analysis, reef habitat did not show a significant impact on
254 reef budget states (“entire reef” and “reef base” excluded from analysis, Fig. 2c). Water depth did not
255 have a significant influence on budget state variability either, but 97% of investigated sites were
256 located in ≤ 10 m depth (Fig. 2e). Such broad regional assessments over a heterogenous dataset are
257 problematic, because the variability for a given habitat type across study locations with a range of
258 environmental conditions is naturally very high. Indeed, it is reasonable to assume that there are likely
259 to be very significant differences in budget states across individual reefs as the taxa driving
260 production and bioerosion processes vary between habitats and depth zones (Smith and Kinsey
261 1976, Kinsey and Hopley 1991, Perry and Hepburn 2008). We therefore suggest that there is an
262 urgent need not only to address some of the major geographic and reef type data gaps, but also to
263 improve our understanding of how budget states vary across reef habitats and depths. This would
264 help with analyses of spatial heterogeneity in habitat forming and reef building potential, and to
265 increase understanding of spatial (and bathymetric) consequences of ecological change. For
266 example, whilst the budgets of shallow reefs may decline markedly under bleaching-driven stress
267 (Perry and Morgan 2017a), the budgets of proximal intermediate and deeper water habitats may be
268 far less impacted. Along the same line, given the growing research interest in mesophotic reefs (>30
269 m depth) as a thermal refugia under future conditions, assessments of their budget states would be a
270 valuable focus of research efforts.

271

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

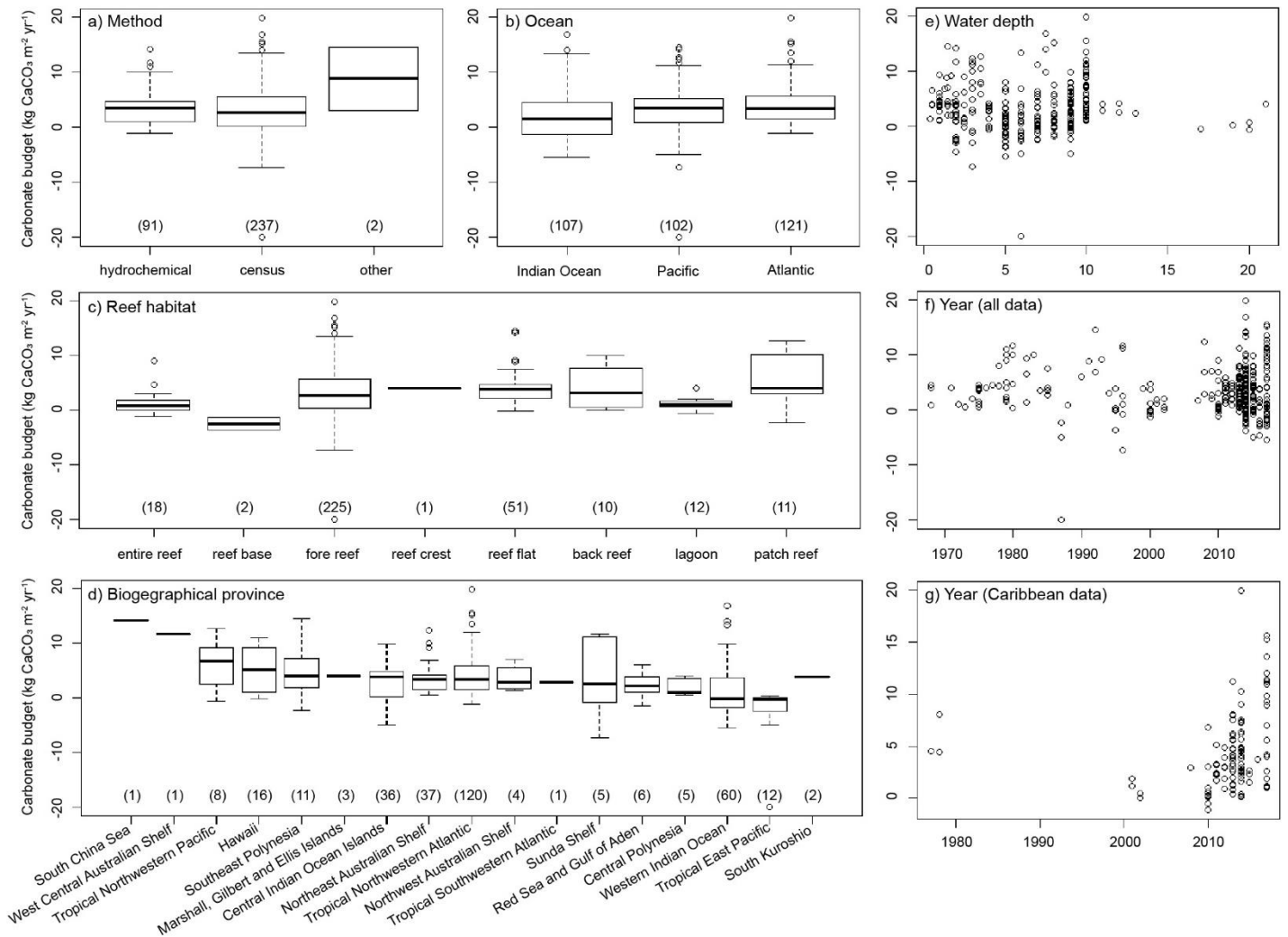
278 highlights the need for more time-series data from consistent sites and depths to fully understand
279 temporal dynamics of budget states through disturbance and recovery cycles.

280 In the context of this discussion, an important focus of recent research has been on whether and how
281 quickly budget states may recover from major disturbance events such as coral bleaching
282 (Januchowski-Hartley et al. 2017, Perry and Morgan 2017a, Manzello et al. 2018, Lange and Perry
283 2019). These studies are proving particularly useful for understanding how relative contributions of
284 different taxa change over time, and which communities are more resilient to disturbance. For
285 example, reefs dominated by branching and tabular *Acropora* spp. in the Indian Ocean changed
286 significantly following the 2016 bleaching event, re-setting budgets from highly positive to net negative
287 states (Perry and Morgan 2017a, Lange and Perry 2019). In contrast, sites dominated by the stress-
288 tolerant coral *Orbicella faveolata* in the Florida Keys have generally low budget states but did not
289 experience a significant decrease in carbonate budgets after bleaching in 2014 and 2015 (Manzello et
290 al. 2018).

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

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



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

312

313 2.3 Marginal reefs

314 Another obvious gap with respect to the current coverage of budget state assessments relates to
 315 marginal reef-building settings, which include those at high latitudes and those exposed to naturally
 316 high turbidity or upwelling influence. Marginal reefs can be highly diverse and are probably far more
 317 extensive than currently assumed, but many are defined by low or absent framework development
 318 (Perry and Larcombe 2003 and references therein). The effects of “non-optimal” environmental
 319 conditions on contemporary carbonate budget states remains poorly quantified. Notable exceptions
 320 include work undertaken on upwelling- and ENSO-influenced sites in the Eastern Pacific, which
 321 showed a permanent loss of reef framework structures in Galapagos after the 1982–83 El Niño
 322 warming event, while reefs in Panama recovered to slightly positive net carbonate budgets (Manzello
 323 et al. 2017 and references therein). In contrast, high carbonate budgets (>7 G; Browne et al. 2013)
 324 and rapid vertical reef accretion (8.3 mm yr⁻¹; Perry et al. 2012c) has been reported on highly turbid
 325 reefs on the inshore Great Barrier Reef. In either situation, marginal reefs may provide a critical

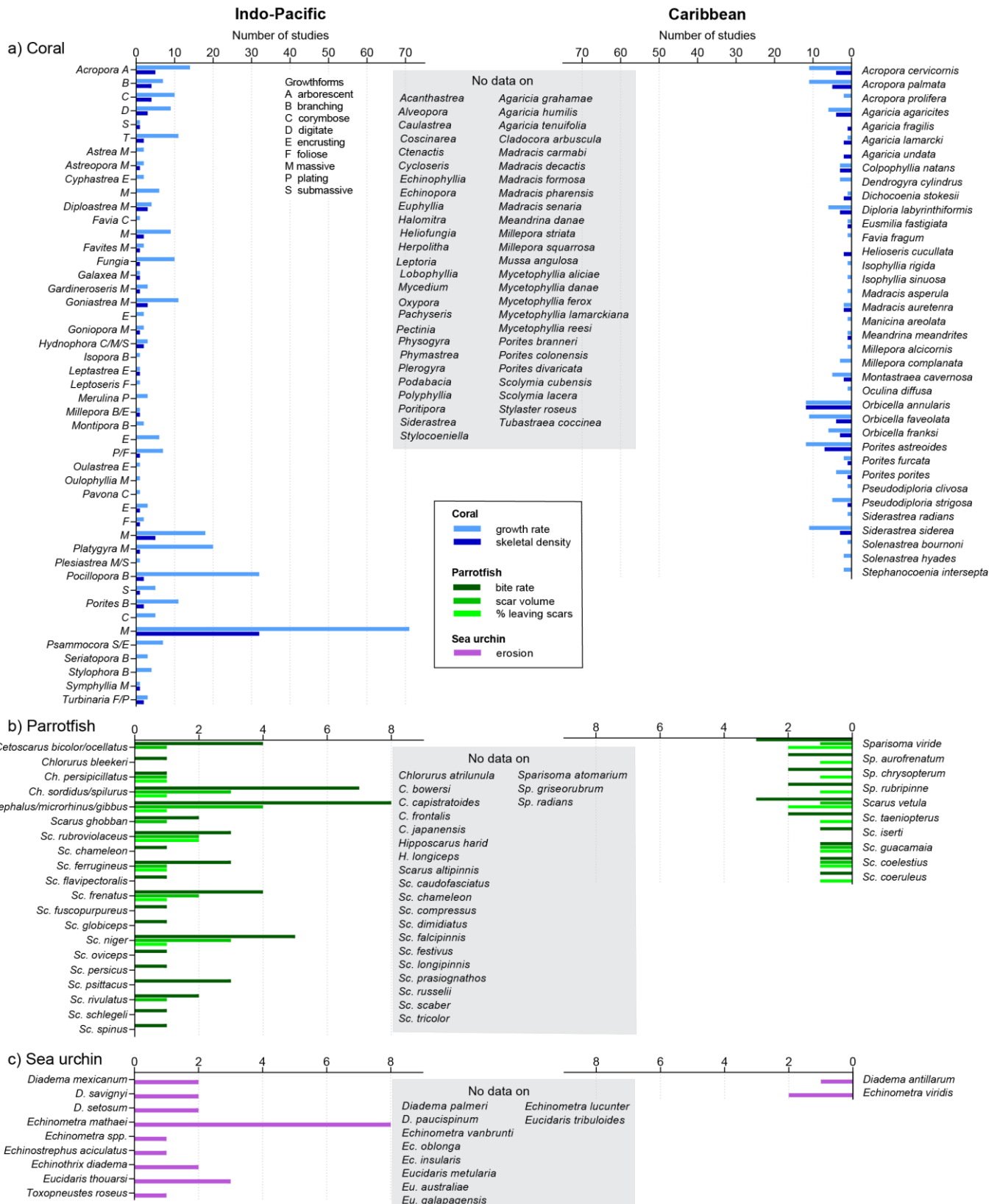
326 habitat and important refugia for numerous species under future environmental conditions
327 (Cacciapaglia and Van Woesik 2016, Morgan et al. 2017). Further work in such marginal settings and
328 high latitudes should therefore be a focus of future research efforts, as it is not yet understood how,
329 for example, ocean warming and the subsequent expansion of species ranges will affect the
330 carbonate budgets of these coral communities. It has been hypothesized that in most high latitude
331 regions lower aragonite saturation states and light availability will compensate for any positive growth
332 effects from sea surface warming (Couce et al. 2013, Muir et al. 2015), while marginal reefs in the
333 Eastern Pacific and along the northern Brazilian coast might actually increase in suitability for reef
334 development (Couce et al. 2013). Additional work in these systems would clearly be invaluable to
335 understand the dynamics of future reef development.

336

337 **3. Available data on underpinning metrics and major knowledge gaps**

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

354



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

359

360 3.1 Coral growth rates and skeletal density

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

380
381 In the Caribbean, there is relatively extensive data for the major reef framework builder *Orbicella* spp.,
382 and extension rate data from several sites exist for both *Acropora cervicornis* and *A. palmata*
383 (although both are numerically rare on many reefs now). But even for these well-studied species,
384 geographic or environmental variability is poorly constrained. Of the increasingly spatially dominant
385 “weedy” or opportunistic taxa, only *Porites astreoides* and *Siderastrea siderea* are reasonably well
386 represented in studies from multiple sites, whilst rates for the genera *Agaricia*, *Diploria* and
387 *Pseudodiploria* are sparse (Fig. 3a). For the Indo-Pacific region we grouped species into genera and
388 growth forms due to the larger number of species. Some genera are relatively well represented
389 (*Acropora*, *Favia*, *Fungia*, *Goniastrea*, *Montipora*, *Pavona*, *Platygyra*, *Pocillopora*, *Porites*), but growth
390 rates are often restricted to one dominant growth form of the respective taxa (except *Acropora* which
391 has a good range over its different growth forms). For most coral taxa only very few rates are
392 available, and for many other coral taxa no growth data exists at all (Fig. 3a). The amount of data on
393 skeletal densities in both oceans is even scarcer, with only very few columnar, submassive and
394 encrusting taxa represented, despite the relatively easy and fast determination of density via buoyant
395 weight/Archimedes bath techniques (Bucher et al. 1998). Densities of massive taxa are more often
396 reported, possibly because these are often measureable from x-radiography.

397
398 The paucity of data means that coral carbonate production estimates at a specific site often have to
399 rely on calcification rates from other regions. Problematically, growth rate and density gathered on

400 one species in the Eastern Pacific may not accurately represent the same species in the Red Sea or
401 Western Indian Ocean, as coral growth rates tend to vary considerably in response to light and water
402 quality, temperature, and aragonite saturation state (Pratchett et al. 2015). Where not even taxa-
403 specific rates from other regions are available, mean values for all hard corals of a specific
404 morphology are currently a necessary substitute for missing rates in budget estimations, as colony
405 morphology has been shown to be a major control on coral growth (Dornelas et al. 2017).
406 The above synthesis point to the urgent need for growth and density data from an increased number
407 of coral species and taxa across the Indo-Pacific region, and for those taxa that are becoming
408 increasingly abundant on degraded Caribbean reefs. Additionally, detailed studies are needed to
409 better understand how calcification rates vary with depth, temperature and water quality in order to
410 reduce uncertainties in budget estimates. For instance, growth responses to depth can be highly
411 variable in different species (*Pseudodiploria strigosa*: 2.5-4.2 mm yr⁻¹ at 3-32 m depth with highest
412 growth rates at 3-6 m (Logan et al. 1994); *Montastrea cavernosa*: 2.0-10.9 mm yr⁻¹ at 10-30 m depth
413 with highest rates at 20 m (Huston 1985)) despite similar average growth rates (4.9±2.3 and 4.2±1.6
414 mm yr⁻¹, respectively (Table S2b).
415 While skeletal density measurements still require the extraction of small coral samples for buoyant
416 weight/Archimedes bath techniques (Bucher et al. 1998), growth rates can be quantified *in situ* using
417 recent non-invasive Structure-from-Motion (SfM) techniques, which use stereophotogrammetry and
418 the comparison of 3-dimensional models over time to calculate annual growth rates (Ferrari et al.
419 2017). When calculating coral calcification rates from extension and density data, coral morphology
420 should be taken into account in order to avoid overestimation of calcification, e.g. massive colonies
421 experience dome shaped growth, but branching colonies require a conversion factor to account for
422 growth of branch tips only (González-Barrios and Álvarez-Filip 2018, Perry et al. 2018b). Furthermore,
423 as the growth of different parts or branches within a colony can differ depending on position, age or
424 size, these calculations have to be seen as an approximation and could possibly be improved by
425 insights from emerging SfM methods.

426

427 3.2 CCA calcification rates

428 Very few published data are available on *in situ* annual CCA calcification, adversely affecting
429 quantitative estimates of total carbonate production. While there is some data from controlled
430 physiological measurements (e.g., Gao and Zheng 2010, Johnson and Carpenter 2012, Vásquez-
431 Elizondo and Enríquez 2016), these rates are not included in Table S3 due to conversion difficulties
432 from algal mass to algal cover and uncertainties associated with upscaling hourly to annual
433 calcification rates. However, controlled experiments testing the effects of different light, thermal or
434 pCO₂ regimes on CCA calcification open up the potential for modifying field-derived rates and factor
435 for changing depth, ocean chemistry and temperatures.

436 Geographically, data coverage on *in situ* CCA calcification in the Caribbean is poor and, to our
437 knowledge, no studies at all exist in the Coral Triangle and the Eastern Pacific (Table S3). Where
438 data does exist, studies typically deployed *Porites* spp. blocks, ceramic tiles or PVC substrates in reef
439 settings over six months to five years and analysed them for lateral and vertical growth of algal

440 patches or directly for annual calcium carbonate production rates of encruster communities. Most of
441 these studies have been conducted at very shallow (1-6 m depth) sites, with only 2 studies reporting
442 values at 8-10 m depth (Osorno et al. 2005, Chazottes et al. 2017). Strikingly, published calcification
443 rates in the Indo-Pacific are on average five times higher in studies that deployed substrates for less
444 than one year, indicating much faster growth of encrusting organisms in the initial settling period. As
445 an easy approach for determining local rates of CCA calcification, we thus suggest the deployment of
446 simple experimental substrates such as lightly sanded PVC cards for 12-24 months, as these are
447 easy to analyse and have been shown to develop natural CCA communities (Kuffner et al. 2013,
448 Kennedy et al. 2017). Calcification by unit area is then quantified by weighing the substrate before
449 and after dissolving the CCA crust in 10% HCl and dividing the difference by the surface area and
450 deployment time.

451

452 3.3 Parrotfish erosion rates

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

462

463 While each functional group of parrotfish (grazers, scrapers, excavators) is important to the resilience
464 and long-term maintenance of coral reefs, only the latter two have significant impacts on reef
465 bioerosion, and excavators contribute to a much larger extent than scrapers (Bellwood and Choat
466 1990, Bonaldo et al. 2014). Both groups mainly feed on the epilithic algal matrix on reefs, with
467 occasional bites on live coral and CCA (Hoey et al. 2016b, Morgan and Kench 2016). Most scrapers
468 in both the Atlantic and Indo-Pacific belong to the genus *Scarus*. Excavating parrotfish on Caribbean
469 reefs are of the genus *Sparisoma* spp. (Bruggemann et al. 1996), while the dominant genus on Indian
470 and Pacific Ocean reefs is *Chlorurus* spp., although *Cetoscarus ocellatus/bicolor* and larger
471 individuals of both *Scarus rubroviolaceus* and *Sc. ghobban* are also considered to have excavating
472 modes of feeding (Bellwood and Choat 1990, Ong and Holland 2010). Numerous authors have
473 reported much higher bioerosion rates for larger fish (Bellwood 1995, Bruggemann et al. 1996, Ong
474 and Holland 2010) and some studies found higher feeding rates in initial phase than in terminal phase
475 fish (Bruggemann et al. 1994a, Bruggemann et al. 1994b, Mumby 2006, Lokrantz et al. 2008, but see
476 Afeworki et al. 2013, Yarlett et al. 2018). Thus, the method used most frequently for calculating
477 parrotfish bioerosion is based on size- and life-phase specific bite rates (bites d⁻¹), bite volume (cm³)
478 and proportion of bites leaving scars (%) for each parrotfish species. Currently, data on these metrics
479 is very patchy and exists for only a subset of species (Fig. 3b).

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

492

493 An additional uncertainty that has to be recognized in estimates of bioerosion is that, as with
494 calcification, rates may be strongly influenced by environmental conditions. For instance, there is
495 evidence to suggest that feeding rates may differ across zones and locations (Hoey and Bellwood
496 2008) and with season and temperature (Ong and Holland 2010, Afeworki et al. 2013). Additionally,
497 bite volume has been shown to be affected by food type and water depth (Ong and Holland 2010) as
498 well as by microtopography (convex, flat, concave surfaces) (Bellwood and Choat 1990). In order to
499 increase the accuracy of models used to predict bite rates and volumes from parrotfish size, more
500 data on feeding rates and bite scars for a larger range of species, sites and environments is urgently
501 needed. Such metrics can be collected by following an individual parrotfish for 5 min, counting its
502 bites, and percentage of bites leaving scars, and measuring the dimensions of bite scars with callipers
503 (Bellwood 1995), although the latter remains an issue of considerable uncertainty due to the very
504 shallow depth of bites and variable substrate morphology (Yarlett et al. 2018). There is thus a need
505 for consideration of more effective ways to estimate bite volumes or parrotfish erosion.

506

507 3.4 Urchin erosion rates

508 Sea urchins of the family Diadematidae (*Diadema* spp., and *Echinothrix* spp.), and of the genera
509 *Echinometra*, *Echinostrephus* and *Eucidaris* are a group of major bioeroding grazers (Bak 1994). In
510 the Caribbean they have been shown to be of higher importance for algal removal and ecological reef
511 functioning than parrotfish (Mumby et al. 2007). Sea urchins erode coral reef substratum either by
512 burrowing behaviour, which weakens the reef structure and increases a reef's susceptibility to storm
513 damage, or directly through abrading the reef substrate during grazing. The rate of erosion through
514 grazing is a function of species and size, with larger individuals causing significantly higher reef
515 erosion (Bak 1994). A variety of techniques have been used to estimate bioerosion rates by urchins,
516 including quantifying the CaCO₃ content of the gut (e.g., Bak 1990, Conand 1997, Carreiro-Silva and
517 McClanahan 2001) or faecal pellets (e.g., Glynn et al. 1979, Mokady et al. 1996, Griffin et al. 2003),
518 both with or without estimations of reworked sediment, spine abrasion and gut turnover (Table S5a).
519 This makes it difficult to compare urchin bioerosion rates derived from different studies. In addition,

520 the number of species for which data exists is limited, and from the few species observed, only
521 *Echinometra mathaei* is represented in more than 3 studies (Fig. 2c). Whilst plots of available data
522 suggest a reasonably strong correlation between test size and erosion rate for both Diadematidae and
523 *Echinometra* spp. (Table S5b), we strongly encourage further research into size- and species-specific
524 urchin erosion rates using adequately planned experiments and analyses. This data need applies
525 especially to the Caribbean and the wider Western Pacific region where data are extremely scarce.

526

527 3.5 Endolithic macro- and microbioerosion rates

528 Endolithic macroborers are defined as those eroders which produce boreholes with diameters >1 mm
529 and include endolithic sponges, polychaete and sipunculid worms, bivalves, decapods and cirripeds
530 (Perry and Hepburn 2008, Glynn and Manzello 2015). Across the Caribbean region, sponges have
531 received the greatest attention because they typically dominate the macroboring community,
532 comprising 75-90% of substrate infestation (e.g., Highsmith 1981, Kiene and Hutchings 1994,
533 Schönberg et al. 2017). Across the Indo-Pacific, evidence suggests a more diverse range of
534 macroendolithic taxa, with worms making a relatively larger contribution to microbioerosion,
535 especially in the first few years that substrate is available for colonisation (Pari et al. 2002, Tribollet
536 and Golubic 2005, Carreiro-Silva and McClanahan 2012). Remarkably high microbioerosion intensity
537 caused by high abundances and fast growth of lithophagine bivalves have been reported from the
538 upwelling-influenced Eastern Pacific (Reaka-Kudla et al. 1996, Fonseca et al. 2006, Alvarado et al.
539 2017, Wizemann et al. 2018) and at high latitudes (Chen et al. 2013).

540 Microendolithic bioerosion describes the activities of photosynthetic cyanobacteria, chlorophytes and
541 rhodophytes, and heterotrophic fungi and bacteria (Golubic et al. 1981) and has the potential to
542 contribute to a significant amount of bioerosion on coral reefs, with published rates of similar
543 magnitude to those of macroborers (Table S6). In addition, microbioerosion could make the substrate
544 surface more easily eroded by grazers and physical destruction. Similar to microbioerosion, rates
545 may increase with enhanced nutrient availability (but see Vogel et al. 2000, Carreiro-Silva et al. 2009),
546 and show a considerable range across sites.

547

548 The amount of data on endolithic erosion, specifically microbioerosion rates, is very low and major
549 geographic gaps are obvious in the Caribbean, the Indian Ocean and the Red Sea (Table S6). We
550 therefore encourage increased research into endolithic erosion rates, including for a variety of
551 ecosystems and habitats. Assessments of both macro- and microbioerosion rates have tended to rely
552 on deploying experimental substrates, predominately dead *Porites* spp. blocks, and subsequent
553 analyses of relative weight or volume loss. Another approach is to quantify boring cavities in coral
554 cores (e.g., DeCarlo et al. 2015) or collected coral fragments (e.g., Carreiro-Silva and McClanahan
555 2012), which has the advantage of observing an established bioeroder community, but complicates
556 quantification of the length of time that substrates have been exposed to erosion. In the Caribbean,
557 rates of microbioerosion are typically based on sponge erosion studies, of which only a few report
558 erosion rates per m² reef (Table S6). However, there are a number of recent datasets that can assist
559 calculations of sponge erosion in a given reef by combining erosion rates per m² sponge tissue

560 (supplementary table Schönberg et al. 2017, de Bakker et al. 2018) with sponge tissue surveys at the
561 study site (Perry et al. 2012b, Murphy et al. 2016). Sponge bioerosion rates may vary with density of
562 the reef substrate (Hernández-Ballesteros et al. 2013), but again detailed datasets to allow these
563 variations to be factored for in erosion rate calculations are presently limited.

564

565 3.6 Concluding thoughts on current data availability

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

578

579 **4. Future challenges and opportunities**

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

588

589 4.1 Temporal coverage

590 The first challenge of using census-based methodologies for budget estimates is that the use of
591 snapshots in time concerning producer/eroder abundances (especially parrotfish as these are mobile)
592 may not accurately reflect long-term rates of production/erosion. One option to reduce this bias is to
593 average parrotfish abundances over time or for closely located sites assuming they are connected by
594 roaming fish. However, home ranges of parrotfish have been found to be limited and positively related
595 to body mass, so care has to be taken to pool data in an appropriate manner (e.g. 150-300m² for
596 adult *Scarus* spp., 7,800m² for larger *Chlorurus* spp. and up to 24km² for schooling *Scarus* spp.;
597 Welsh and Bellwood (2012b, 2012a), Welsh et al. (2013)). Alternatively, total external erosion rates
598 can be quantified over extended periods of time, although these do not allow the differentiation of
599 taxa-specific contributions. Roff et al. (2015), for example, used high precision U/Th dating and CT

600 scan analysis to estimate average vertical erosion rates of dead coral ramets over a 13 year period,
601 which was in good alignment with a parallel quantification of erosion from parrotfish surveys. Kuffner
602 et al. (2019) measured reef-elevation loss around permanent markers fitted on dead *Orbicella*
603 colonies in 1998, suggesting erosion rates may be higher than obtained from census-based
604 approaches. These methods mainly quantify external parrotfish erosion which commonly
605 compromises the largest fraction of bioerosion on a reef. A third emerging approach for quantifying
606 net rates of erosion or production over a longer time period and spatial scale is to measure changes
607 in reef height or volume, either based on seafloor elevation data (from historical soundings or Lidar
608 digital elevation models; Yates et al. (2017)), or using diver-based underwater photogrammetry and
609 the construction of scaled, digital 3-D models of reef areas using Structure-from-Motion (SfM)
610 techniques (Bailey 2019, Rossi et al. 2019). Change in net reef volume over time (decades in the
611 former example, years in the latter), can then be multiplied with framework density data to give an
612 estimate of the total net reef carbonate production/erosion rate. A comparison of census-based and
613 volume-based methods at the same study sites would be very useful to highlight the merits and
614 increase the accuracy of each approach.

615

616 4.2 Spatial coverage

617 Another challenge in carbonate budget assessments is spatial coverage, as the replication and area
618 that can be surveyed during a dive is often small due to time and depth constraints. In this context,
619 photographing a reef and quantifying benthic cover and reef structure metrics from digital 3-D models
620 allows greater spatial coverage in less dive time (e.g., Burns et al. 2015, Ferrari et al. 2016, Bailey
621 2019). However, challenges remain in terms of accounting for cryptic substrate cover in visual
622 models, especially on structurally complex reefs, and for different substrate densities. SCUBA diving
623 limitations have also tended to limit carbonate budget state assessments and the collection of taxa-
624 specific data on calcification and erosion rates to sites <15 m depth. One option to enable surveys in
625 deeper reef areas is to use SfM techniques in combination with camera equipped autonomous
626 underwater vehicles (AUVs) or remotely operated vehicles (ROVs), which are evolving rapidly in
627 quality and affordability. However, major disadvantages of AUV/ROV use are the lower accuracy of
628 organism identification from photographic/video material due to poor lightning and motion blur (Turner
629 et al. 2018), and again difficulties in quantifying true 3-D cover along the reef profile due to complex
630 overgrowth. Both factors would affect the accuracy of carbonate budget estimations. Additionally,
631 beside a general acceptance that coral growth rates (e.g., Fricke et al. 1987, Anthony and Hoegh-
632 Guldberg 2003, Grigg 2006, Weinstein et al. 2016) and the abundance of internal and external
633 bioeroders (Nemeth and Appeldoorn 2009, Weinstein et al. 2014) decrease with increasing depth,
634 taxa-specific growth and erosion rate data at greater depth is very limited.

635

636 A further area of development in a spatial data context is in the use of remote and near-remote
637 sensing methods to support quantification of reef area and benthic community type across entire
638 lagoon systems or reef tracks. This areal up-scaling has been used in several studies to extrapolate
639 published or determined carbonate production values of different benthic cover types to larger reef

640 environments (Andréfouët and Payri 2000, Brock et al. 2006, Moses et al. 2009, Hamylton et al. 2013,
641 Leon and Woodroffe 2013, Hamylton et al. 2017). Although this results in relatively crude estimates at
642 present, satellite imagery and drones are rapidly improving, becoming more affordable and algorithms
643 are constantly increasing in quality, meaning that the detail of benthic cover estimates will likely
644 improve considerably and allow a more detailed extrapolation of locally derived carbonate budgets to
645 whole reef systems (e.g., Hedley et al. 2018).

646

647 4.3 Environmental change

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

658

659 **Statement of competing interests**

660 The authors have no competing interests to declare.

661

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666

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670

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