

1 **Two decades of carbonate budget change on shifted coral reef assemblages:**
2 **are these reefs being locked into low net budget states?**

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13

14 **ABSTRACT**

15 The ecology of coral reefs is rapidly shifting from historical baselines. One key-question is
16 whether under these new, less favorable ecological conditions, coral reefs will be able to
17 sustain key geo-ecological processes such as the capacity to accumulate carbonate
18 structure. Here, we use data from 34 Caribbean reef sites to examine how the carbonate
19 production, net erosion, and net carbonate budgets, as well as the organisms underlying
20 these processes, have changed over the past 15 years in the absence of further severe
21 acute disturbances. We find that despite fundamental benthic ecological changes, these
22 ecologically shifted coral assemblages have exhibited a modest but significant increase in
23 their net carbonate budgets over the past 15 years. However, contrary to expectations this
24 trend was driven by a decrease in erosion pressure, largely resulting from changes in the
25 abundance and size-frequency distribution of parrotfishes, and not by an increase in rates
26 of coral carbonate production. Although in the short term the carbonate budgets seem to
27 have benefitted marginally from reduced parrotfish erosion, the absence of these key
28 substrate grazers, particularly of larger individuals, is unlikely to be conducive to reef
29 recovery and will thus likely lock these reefs into low budget states.

30

31 **Keywords:** geo-ecological functions, net carbonate balance, ecological trend analysis,
32 bioerosion, parrotfish, carbonate budgets state, feedback mechanisms.

33

34 INTRODUCTION

35 The physical structure of natural systems strongly influences ecological dynamics and their
36 capacity to provide ecosystem services. Examples of these ecosystems occur across
37 tropical and subtropical seas with different relative levels of complexity, such as mussel
38 beds, algal rims, and stromatolite reefs [1]. In coral reefs, sessile calcifying organisms
39 create a reef carbonate structure over hundreds to thousands of years. The resultant
40 three-dimensionality is a defining feature of most contemporary reefs and promotes high
41 species diversity: tropical reefs are home to one-third of marine biodiversity and support
42 the economy, safety and livelihoods of at least one-tenth of the world's human population
43 who inhabit tropical coastal areas [2]. Sustaining these ecosystem services over time
44 depends partly on reef growth potential, which is largely determined by the interaction
45 between carbonate production and erosion rates [3], in addition to the processes of
46 cementation, lithification, and physical material export [4]. The minimum requirement for a
47 coral reef to persist in the relatively short ecological term is for the resultant budgetary
48 state of the reef (the balance between production and erosion/loss) to be at least neutral
49 (i.e., in a state of approximate equilibrium between gross production and erosion);
50 whereas a relatively high net production rate is required to support sustained reef growth
51 at rates that can track sea-level rise [5,6].

52 Rates of gross production and erosion depend inherently on the abundance of
53 carbonate producing and eroding organisms. While accretion is classically driven by reef-
54 building coral species, in addition to the other scleractinian corals and crustose coralline
55 algae, bioerosion is driven by a diverse range of species of parrotfish, sea urchins,
56 encrusting sponges, and macro- and microborers [7]. The patterns of relative abundance
57 of species in many of these groups have however changed considerably across most reef-
58 building regions, leading in many cases to what are now termed 'shifted' coral reef
59 assemblages. The magnitude of change has, however, been most pervasive in the
60 Caribbean, this resulting from the low functional redundancy of its reef assemblages, and
61 the chronic and acute disturbances experienced in the last five decades, possibly
62 accentuated at the end of last century [6,8]. For instance, high gross carbonate production
63 rates that have historically relied on the monospecific dominance of species such as
64 *Acropora* spp. or *Orbicella* spp. in the region, have significantly decreased due to a series
65 of disease outbreaks, multiple bleaching events, and the loss of ecological resilience,
66 which has led to substantial declines in their populations of up to 80% [9]. Likewise, overall
67 erosion rates appear to have declined in the Caribbean, possibly by around 75%

68 compared with historical rates, although past data are sparse on this topic [10]. One
69 especially rapid decline occurred in tropical reefs immediately after the *Diadema antillarum*
70 die-off, which became functionally extinct throughout the Caribbean in the early 1980s
71 [10,11]. Parrotfish, the most important bioeroders on today's reefs, have shown biomass
72 reductions between 30 to 70% due to overfishing and habitat loss [12,13]. Encrusting
73 sponge erosion rates also probably declined considerably between the 1970s and the
74 2000s due to reductions in substrate availability [10], but have remained relatively stable
75 during the last two decades [14,15]. The described ecological changes occurred during a
76 short time period, at large scale and possibly with no parallel in the fossil record of modern
77 reefs [16,17]. As a result, major reductions in production of at least 50% compared to mid-
78 to late-Holocene rates, have been suggested [17]. Although this reduction is significant, it
79 is likely that the overall decrease in bioerosion rates has, to some extent buffered the
80 impact of net declines in carbonate production which otherwise would perhaps be more
81 marked [10].

82 An issue with undertaking such modern to historical comparisons in order to
83 understand the magnitudes of contemporary change is the paucity, and disaggregated
84 nature, of temporal bioerosion and carbonate production data sets. Where such temporal
85 records now exist they have mainly been collected as part of efforts to understand the
86 short-term impacts of coral bleaching, which results in near-instantaneous declines in
87 budget states due to both reduced live coral cover and/or declines in calcification rates
88 [18–20]. Longer term declines in net carbonate budgets in the Caribbean have also been
89 associated with shifts in coral assemblages [21,22]; whereas, at some sites in the Indo-
90 pacific, a lack of recovery in the carbonate budgets spanning a 16 year period, were linked
91 to an increase in bioerosion rates [23]. While these findings provide useful insights into net
92 budget changes, mostly in the context of punctuated perturbations, more time-series data
93 analyses are needed. This is particularly the case for assessing the impacts of longer-term
94 and seemingly persistent shifts in coral reef assemblages in order to: 1) better understand
95 whether contemporary low budget state reefs can recover; but also 2) to grasp how
96 producer and bioeroder rates might be interacting over time. Two recent studies have
97 suggested that bioerosion may play a key role in directing net carbonate budgets under
98 low production scenarios [4,10]; however, detailed analysis of how this might be occurring
99 remains to be explored. Here we use time-series data from 34 temporally replicated sites
100 spanning 15 years (2004 to 2018) to test these ideas through an investigation of the
101 temporal dynamics of carbonate budgets at sites along the Mexican Caribbean reef

102 system. Specifically, we use these data: 1) to determine how gross carbonate production,
103 net erosion, and net carbonate budgets have transitioned as coral reef assemblages have
104 shifted over recent decades; and 2) to identify how the abundance and/or size classes of
105 the organisms driving key elements of the budgets have changed over time.

106

107 **METHODS**

108 **Study Area**

109 The 34 reef sites are distributed across 400 km surrounding the mainland and two
110 major islands (Cozumel and Banco Chinchorro) in the Mexican Caribbean (Fig. 1A). Sites
111 span the three main geomorphological zones that define the reefs in the region, the back-
112 reef and crest zone, and the fore-reef, at a depth range between 1 and 15 meters. This
113 fringing reef system shows some variations in geomorphological development with latitude
114 [24]. However, the broad impact of natural and anthropogenic disturbances, such as the
115 aforementioned outbreak of diseases and thermal stress events, as well as the impact of
116 water quality associated with an unprecedented fast coastal development in this region
117 over the last five decades, has led to low coral cover and more homogeneous 'shifted
118 coral reef assemblages' [25,26]. These new community types are now relatively stable
119 ecologically, are dominated by what are often referred to as stress-tolerant or weedy
120 species, and which often have reduced calcification rates compared to fast-growing
121 competitive taxa [21,27].

122

123 **Data collection**

124 Historical data based on reef surveys or monitoring programs were obtained from
125 several sources, including scientific and monitoring reports from the Marine Park
126 authorities and researchers, as well as from non-governmental organizations such as the
127 Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program and the Healthy Reefs for
128 Healthy People Initiative. To complement these historical time-series data we conducted,
129 between 2017 and 2018, fieldwork following the ReefBudget methodology Version 2 [28].
130 Data was curated and integrated into the Caribbean Reef Information System, from the
131 Biodiversity and Reef Conservation Laboratory, UNAM, with records of more than 400
132 sites in the MRS and Gulf of Mexico. Due to the considerable number of variables
133 necessary to estimate both gross production and erosion, only 34 sites were selected
134 (Table S1), based on the following criteria: i) sites needed to have been systematically
135 monitored for at least a decade between 2004 and 2018; and ii) every temporal survey

136 needed to report both the abundance of carbonate producing taxa (i.e., CCA cover and
137 live coral cover) and the main eroding taxa (parrotfish, urchin, substrate available for
138 microbioerosion), and iii) for both historical and contemporary surveys, our target
139 organisms needed to have been identified to species level.

140 Regarding data from historical sources, benthic data were obtained by two main
141 methodologies: the Point Intercept Method (PIT) and Line Intercept Method (LIT). Both
142 methods have been shown to be comparable [29]. An average of six transects of 10 m
143 length were laid on the reef to obtain live coral cover, CCA cover, sponge cover, and other
144 benthic component data. Urchin and fish data were obtained in six and nine belt transects
145 respectively, of 10 m² for urchins and between 60 m² and 120 m² for fish.

146 For our recent surveys, we deployed an average of eight 10 m LIT transects to
147 estimate the live cover of scleractinian coral species, CCA, and other benthic organisms.
148 Along the same transects (1 m wide belts), the cover of all species of encrusting sponges
149 and the number and size (in 20 mm size classes) of all species of sea urchins were
150 recorded [28]; however, the number of transects was on average lower (i.e., six transects
151 for urchins and sponges). For parrotfish visual census, an average of eight belt transects
152 of 30 x 2 m were deployed, along which the number of individuals by species, life phase,
153 and size class were recorded based on total length (i.e., ≤ 5cm, 6-10 cm, and then in 10
154 cm bins).

155 Some adjustments were needed to calculate erosion rates with historical data.
156 First, because the size classes of sea urchins was not recorded in any of the historical
157 surveys, we assigned the average test-diameter obtained in contemporary surveys to
158 historical counts (i.e., a mean test-diameter of 60 mm was assigned to *Diadema*
159 *antillarum*) to be able to estimate the erosion potential of this group on historical surveys.
160 The rationale for this is that this size class represents the average as reported for different
161 reefs in the Caribbean over the last two decades [30,31]. Second, because the specific
162 record of eroding sponge species was not regularly annotated until recently (i.e., 2017 and
163 2018), we use the contemporary site-specific reported cover of encrusting sponges as a
164 site-specific constant during the study period. We considered this as a valid approximation
165 because: (i) recent evidence shows that the cover of this groups has been relatively stable
166 since the 2000s [14,15]; and (ii) in general encrusting sponges contribute relatively little to
167 the total erosion rate, although in some sites this number can be more significant [32].

168

169 **Carbonate budget estimations**

170 We estimated the net carbonate budgets for all sites during all surveys using the
171 ReefBudget methodology V2 [28], a census-based approach in which gross carbonate
172 production rate is estimated as follows: first, for each colony (corals and also CCA
173 patches) gross production is derived from species (or nearest equivalent species) specific
174 density (g cm^{-3}) and linear growth rate (cm yr^{-1}). This rate ($\text{kg CaCO}_3 \text{ yr}^{-1}$) is then
175 standardized per unit area according to the transect dimension and reported as kg CaCO_3
176 $\text{m}^{-2} \text{ yr}^{-1}$. For coral species, gross carbonate production rates are estimated considering the
177 species colony morphology (See [28] for details on equations and density and growth
178 rates), differentiated as massive, sub-massive, encrusting, foliose-and-plating, branching,
179 and columnar. Second, all estimated production rates are summarized at the transect
180 level, and finally, a site average rate is estimated from all surveyed transects (Table S2).
181 Bioerosion rates are estimated depending on the eroding organism recorded within each
182 transect. The parrotfish erosion rate is derived from the bite rate (bite hr^{-1} , which depends
183 on the total length and life-phase), bite volume (cm^3), the proportion of bites leaving scars
184 (%), and the species abundance. Then, the bioerosion rate ($\text{kg ind}^{-1} \text{ yr}^{-1}$) is multiplied by
185 365 (days in a year), standardized per unit area according to the transect dimension, and
186 reported as $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$. Urchin erosion rate is derived from the species, number
187 and size of urchins observed in each transect, and the already published species-specific
188 regression equation-constants (multiple and exponent), that were obtained from a
189 regression where X-axis values are test-size, and Y-axis values are bioerosion rates (g
190 $\text{urchin}^{-1} \text{ d}^{-1}$) reported for different sizes in a number of publications [28]. To yield the rate
191 per year, the total daily rate is multiplied by 365 and then divided by the transect area to
192 yield rate per unit area and reported as $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$. Sponge erosion rate is derived
193 from the species-specific substrate covered area (m^2) and the published erosion rates by
194 species ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$). Microbioerosion rate is estimated from the % cover of the
195 available hard-substrate that microborers can exploit and an average erosion rate (kg
196 $\text{CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) obtained from the published estimated rates of erosion by microendolithic
197 organisms per square meter. All erosion rates obtained per organism were summarized
198 per transect, and then an average of the total erosion rate reported per site (Table S2). An
199 estimate of the net carbonate budget can then be obtained from the mathematical
200 difference between the site's gross production and its erosion rate, reported in kg CaCO_3
201 $\text{m}^{-2} \text{ yr}^{-1}$, units recognized with a capital G.

202 To account for the difference between benthic cover estimations obtained from the
203 modified LIT-Reefbudget method and the earlier census using methods different from

204 Reefbudget, we multiplied the recorded species-specific cover (cm) for each transect by
205 the species-specific rugosity index [27], thus allowing us to estimate the true three-
206 dimensional length (cm) of each species and therefore, to make a more accurate estimate
207 of gross production [22]. Additionally, in the case of parrotfish data, the life phase was not
208 recorded in surveys before 2017. To account for this, we used an average between
209 juvenile and adult's published bite volume (cm³) and the proportion of bites leaving scars
210 (%). All of the species-specific rates used for producing and eroding organisms (e.g., bite
211 rates, bite volumes, and proportion of bites leaving scars) were obtained from the
212 ReefBudget database, which summarizes all data available to-date published in the
213 Caribbean [28].

214

215 **Data analysis**

216 Temporal carbonate budget dynamics were explored by means of Generalized
217 Linear Models (GLM), which unlike general linear models, allow for non-normal distribution
218 of the response variable (e.g., Gamma, Poisson). We used the function *glm* in R, with the
219 site average values of net budget, gross production, and erosion rate as separate
220 response variables and time as predictor. Site averages were used because differences in
221 the field methods impeded the estimation of carbonate production and erosion rates at
222 transect level. Uncertainty around site level estimates was generally low and consistent
223 through time (Fig. 1 B-D). Data was not transformed for analysis, but we used two different
224 distributions to account for non-normal distribution in one of the response variables, this is
225 gamma error distribution and log link function for erosion rate and gaussian distribution
226 with identity link function for net carbonate budget and gross production rate. Residual
227 plots were used to validate the model assumptions. To identify whether resultant net
228 budget trajectory was mostly pulled by the interaction of both producing and erosive
229 processes, or rather by one them, we compare GLM model resultant rates of change
230 direction and significance. Then, to identify to what extent specific producing and eroding
231 organisms had been responsible for observed changes in the net budget over time, we
232 adjust another set of GLM with gamma error distribution and log link function and non-
233 transformed data for producing and eroding organism specific rates. Three models for the
234 main carbonate producers were used, these were major reef framework builders such as:
235 i) Branching *Acropora* species; and ii) Massive species (including *Orbicella* species and
236 other hemispheric growth like species [27]; and iii) non-framework builders (including
237 foliose-digitiform species, milleporids, other encrusting coral species as well as crustose

238 coralline algae) [21,27]. Another four models were used for bioeroders, these were
239 parrotfish, sea urchins, encrusting sponges and microbioerosion. Residual plots were used
240 to validate the model assumptions.

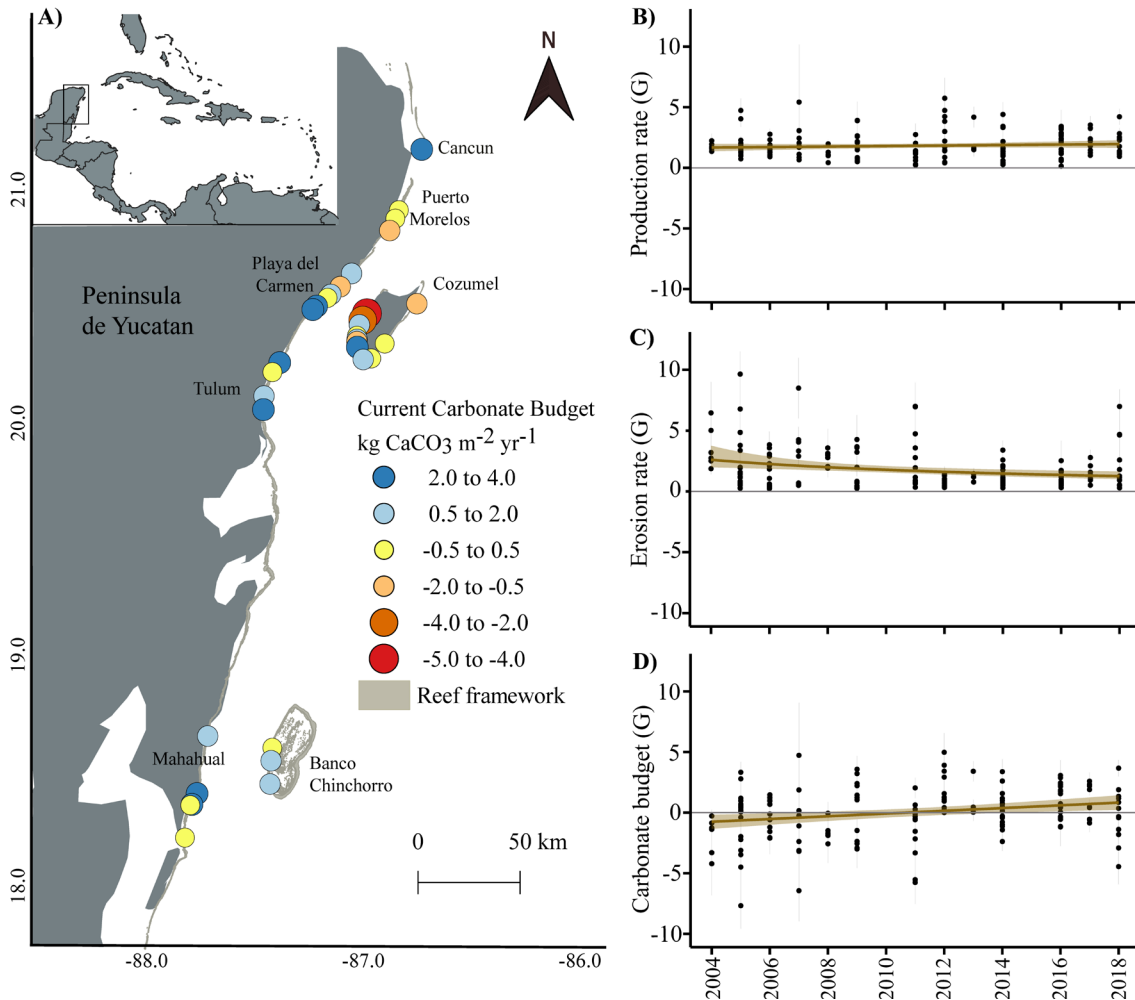
241 At this point in the analysis, only the parrotfish erosion rate showed a significant decline.
242 Therefore, to identify the specific parrotfish population metrics driving changes in their
243 erosion capacity (and consequently in the net budget trajectory), which is a function not
244 only of overall abundance but also of species and size, we performed two different
245 analyses. First, to explore total parrotfish frequency size distribution over time, we
246 performed a kernel density estimate, which represents the distribution of a numeric
247 variable as a smoothed version of a histogram. The kernel density estimate gives the
248 probability distribution from the data set so that the total area under the curve is equal to
249 one (i.e., normalization); a bin with a large number of observations will yield a higher
250 density value. This technique allows for easier comparison of the distributions among
251 years, particularly when comparing several groups [33]. Secondly, we adjusted a GLM,
252 setting parrotfish abundance as a response variable and time as the predictor, using a
253 gamma error distribution and log link function to account for non-normal distribution.
254 Because this last analysis result was indecisive, we decided to explore changes in
255 abundance of parrotfish as a function of differences in their foraging behavior and bite
256 type, which is related to their capacity to erode the substrate, as “excavating” parrotfish
257 (*Scarus guacamaia*, *Scarus coelestinus*, *Sparisoma viride*), “scraping” parrotfish (*Scarus*
258 *iseri*, *Scarus taeniopterus*, *Scarus vetula*, *Scarus coeruleus*) and “browsing” parrotfish
259 (*Sparisoma aurofrenatum*, *Sparisoma chrysopterus*, *Sparisoma rubripinne*) [34]. Similarly,
260 each group abundance was set as the response variable and time as the predictor, using a
261 gamma error distribution and log link function to account for non-normal distribution in all
262 the response variables.

263

264 **RESULTS**

265 Our data show that the net carbonate budgets of sites along the Mesoamerican reef
266 presently average 0.6 G, ranging from -4.4 G to 3.6 G (Fig. 1A). Consistent regional north-
267 to south trends are hard to discern but on average sites towards the southern end of our
268 survey area tended to have slightly higher contemporary net positive budgets. Our data do
269 show however, that net carbonate budgets on surveyed shifted coral reef assemblages
270 have changed in the past two decades (Fig. 1B). Estimates of gross carbonate production
271 suggest that rates have remained relatively stable across sites ($p > 0.05$), with a mean rate

272 remaining close to 1.8 G over the study period (Fig.1B). In contrast, erosion rates have
273 decreased significantly from an average rate of 2 G to 1.2 G ($p < 0.05$) over the past 15
274 years (Fig.1C). Consequently, the net carbonate budget showed a slight yet significant
275 increase over the surveyed period, increasing on average at an annual rate of ~ 0.1 kg
276 $\text{CaCO}_3 \text{ m}^{-2}$ ($p < 0.05$). Most significantly, we note that at the onset of the study period,
277 regional mean carbonate budget estimates were net negative (-0.8 G), that is, the erosion
278 rate exceeded the gross production rate. However, over time mean net budgets showed a
279 slight yet significant increase (+1.6 G in 15 years, $p < 0.05$), such that by the end of the
280 study period, the mean net carbonate budget was net positive (0.8 G; Fig. 1C).
281 Additionally, we also found that site-specific net budget estimates throughout the surveyed
282 period were high and more strongly correlated with site-specific erosion estimates ($R =$
283 0.61 , $p < 0.01$) than with estimated values of gross production ($R = 0.39$, $p < 0.01$; Figure S1).
284 These results suggest that erosion pressures on these phase-shifted reefs are now acting
285 as the main process driving net budget outcomes and recovery trajectories.
286



287

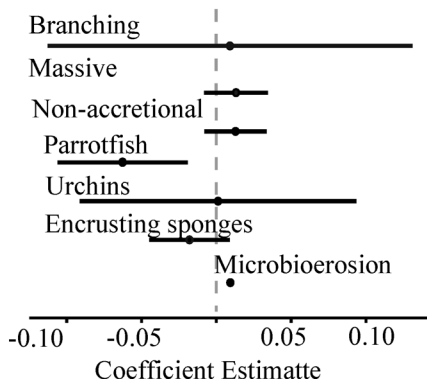
288 **Figure 1.** Temporal carbonate budget dynamics in the Mexican Caribbean. A) Current
 289 (2017-2018) net carbonate budgets of the 34 surveyed reefs; B) Model prediction of gross
 290 production from 2004 to 2018; C) Model prediction of erosion rate from 2004 to 2018; D)
 291 Model prediction of net carbonate production from 2004 to 2018. In panel B, C and D,
 292 mean site values are represented as black points; standard error for each mean estimated
 293 values are presented as vertical gray lines. Model effects are shown as lines and 95%
 294 confidence intervals colored in brown-like shadow. Units in kg CaCO₃ m⁻² yr⁻¹(G).

295

296 Consistent with the regional trend, gross production rates by different major reef
 297 framework builders (i.e., acroporids and massive corals) and non-framework builders
 298 showed no significant differences over time ($p > 0.05$ in all cases, Fig. 2). In the case of
 299 bioeroding organisms, as outlined above, the rate of erosion for encrusting sponges was
 300 already fixed as a constant value to account for its contribution to total erosion rate, given
 301 the lack of data in past years. Regarding sea urchins, the average rate of erosion did not

302 change over time ($p > 0.05$, Fig. 2); microbioerosion on the other hand showed a very
 303 slight but significant increase over time from 0.024 G to 0.027 G ($p < 0.05$). Only parrotfish
 304 erosion rate showed a significant decreasing trend (from 1.7 G to 0.7 G, $p < 0.05$) that is
 305 consistent with the regional trend of a decrease in the total erosion rate, and with the
 306 associated net carbonate budget recovery trend. This is strongly linked with the fact that
 307 parrotfish contribute the most (77%) to total estimated bioerosion rate.
 308

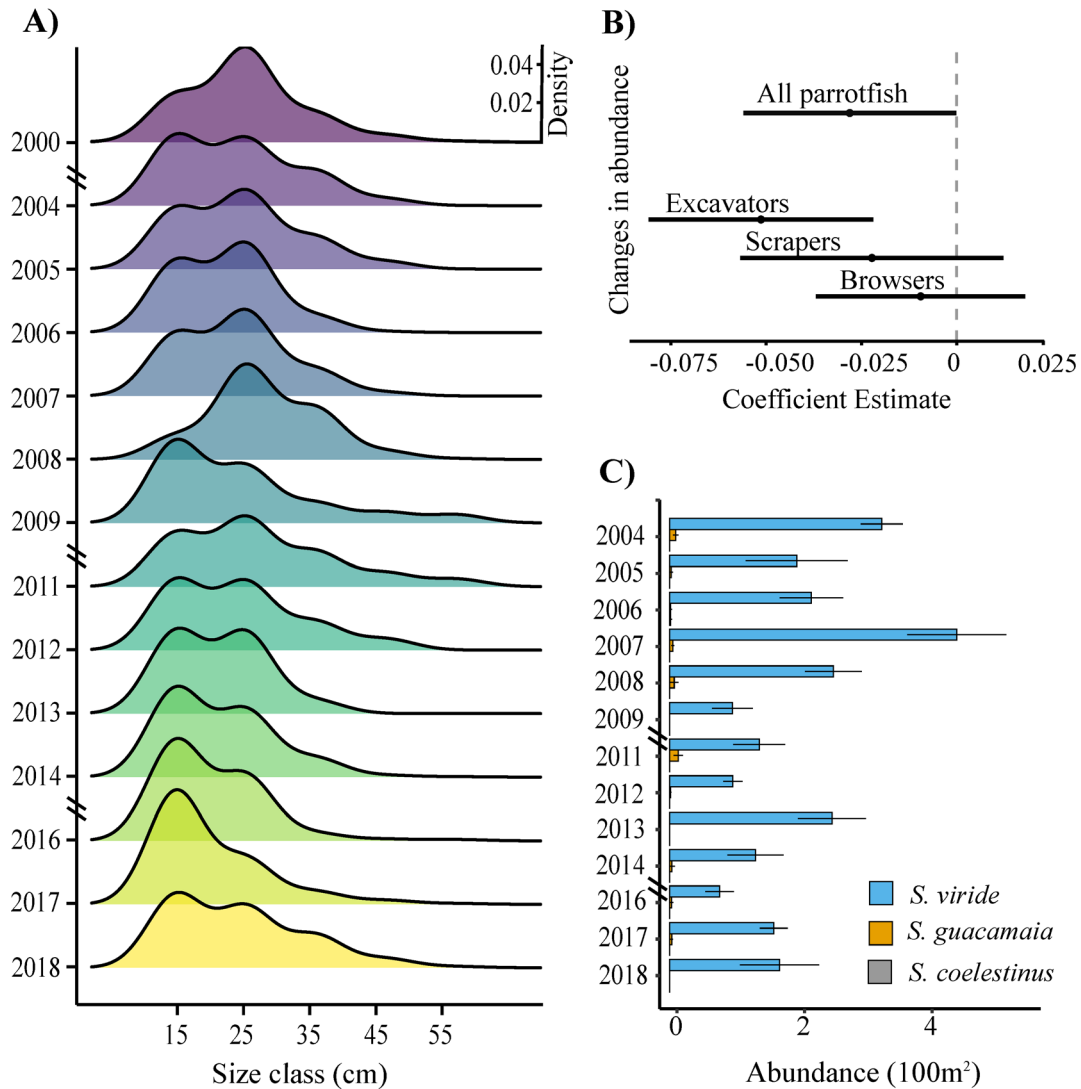
Producing and eroding organisms



309
 310 **Figure 2.** Producing and eroding organisms' coefficient estimates and confidence intervals
 311 of the fitted Generalized Linear Models for producers and eroders. Dots and lines
 312 represent each model coefficient and 95% confidence interval.

313
 314 Detailed analysis of the parrotfish data over the survey period also shows that the
 315 decrease in the parrotfish erosion rate was driven by changes in both the size structure
 316 and abundance of parrotfishes (Fig. 3A-B). Specifically, the size-frequency distribution of
 317 parrotfishes gradually moved towards a shorter body length. At the onset of the study
 318 period the modal length of parrotfishes was 25 cm (21 to 30 cm size class), whereas in
 319 recent years the modal length has reduced to the 11 to 20 cm size category (Fig. 3A). This
 320 implies a major reduction in the potential of individual fish to bite and erode the substrate
 321 while feeding ($\text{g CaCO}_3 \text{ ind}^{-1} \text{ dy}^{-1}$) because size is a major determinant of erosion rate [35].
 322 Regarding changes in parrotfish abundance, this did not significantly decrease for the
 323 whole group ($p = 0.0503$). However, when analyzing by specific feeding behaviour sub-
 324 groups (i.e., excavators, scrapers, browsers), there has been a significant reduction in the
 325 abundance of excavating parrotfishes ($p < 0.05$; Fig. 3B). This functional group is entirely
 326 dominated by *Sparisoma viride* (Fig. 3C).

327



328

329 **Figure 3.** Temporal changes in parrotfish size and abundance. A) Kernel density
 330 estimates for parrotfish size class (cm) distribution by year. Second y-axis in panel A
 331 shows the estimated density value, which is uniform for all curves as it gives the probability
 332 distribution from the data set so that the total area under each curve is equal to one. B)
 333 Coefficient estimates and confidence intervals of the fitted Generalized Linear Models for
 334 parrotfish abundance: lines represent each model coefficient and the 95% confidence
 335 interval for the overall parrotfishes, for excavating species, for scraping species, and for
 336 browsing species. C) Species-specific abundance (ind.100 m⁻²) of the excavating
 337 parrotfishes over time.

338

339 **DISCUSSION**

340 We found that shifted coral assemblages across our study sites have undergone a modest
341 but significant increase in their net carbonate budget states over the past 15 years,
342 increasing from a mean net rate of -0.8 G in 2004 to 0.8 G in 2018. However, whilst it
343 might be expected that such trends would be driven primarily by the recovery of the coral
344 assemblages, given that their decline induced in the first instance the transition to the
345 contemporary low budget states widely observed across the Caribbean [6,17], our data
346 show that coral carbonate production actually remained remarkably stable through the
347 survey period (see Fig. 1B). Instead, the main factor triggering the net positive budget
348 trajectory has been a decrease in biological erosion pressure, largely resulting from
349 ecological changes in the communities of associated parrotfishes. Specifically, we
350 observed both a change in the size-frequency distribution of parrotfishes towards small-
351 bodied individuals and a decline in the abundance of excavating parrotfishes.
352 Understanding how carbonate budgets on sites now dominated by non-framework building
353 corals are transitioning is crucial to predicting and assessing the geo-ecological responses
354 (*sensu* Perry & Alvarez-Filip [6]) of these ecosystems under currently rapid changing
355 environmental pressures.

356 Our findings suggest that reefs in the Mexican Caribbean now constitute shifted
357 coral reef assemblages as defined by low coral cover 17% (SD \pm 9%), a paucity of
358 historically important reef building species, and a low-and-stable carbonate production
359 rate. A series of acute and chronic disturbances led to these major declines in coral cover
360 and associated increases in the coverage of macroalgae and the loss of structural
361 complexity between the late 1970s and early 2000s [36]. Although coral cover has shown
362 some signs of recovery since [36], there are no clear signs that the capacity of the coral
363 communities to increase calcium carbonate accumulation rates have changed, at least at
364 equivalent rates [26,36]. This has been largely due to a lack of recovery by the most
365 important functional groups in the coral community. This is to say that whilst historical
366 losses of coral cover resulted mainly from losses of key reef-building species [22,37], what
367 recovery has occurred in terms of coral cover has been mainly associated with small
368 weedy corals such as *Agaricia agaricites* and *Porites astreoides*. These species may
369 protect to some extent the substrate from bioerosion [38,39], however, presently they are
370 not fulfilling the role of major reef framework builders [21,27]. The resultant assumption
371 therefore is that coral production rates are likely to remain relatively low, and thus that
372 biological eroding agents are likely to increase in importance as the main drivers of
373 contemporary carbonate budget states.

374 In this context, we found a decline of 0.8 kg CaCO₃ m⁻² in the erosion rate over the
375 study period, a decline sufficient to drive the positive shift in the net carbonate budget
376 states of these reefs (Fig. 1D). This means that while in the mid-2000s the rate at which
377 the carbonate structures were being eroded was higher than the rate at which they were
378 produced, by the mid to late 2010s this balance had changed, favoring the reef's
379 framework persistence. However, because the increase in net carbonate budget was not
380 related to an increase in the gross production, coral reef condition in the region has not
381 truly improved, but rather has been "stopped" from transitioning into states of more active
382 erosion and denudation. This has largely arisen as a function of the decline in biomass of
383 the main regional bioeroder group, the parrotfishes [10].

384 Supporting evidence for important reductions in parrotfishes' abundance and
385 biomass occurring in some Caribbean reefs over the past century have been reported by
386 other authors [13,40]. However, such trends have not been empirically related to an
387 increase in the amount of calcium carbonate accumulating on the region's reefs. According
388 to our findings, the reduced abundance of larger-sized parrotfishes and a decrease in the
389 number of the excavating parrotfishes specifically (*S. viride*, Fig. 3C), is now acting as an
390 ecological buffer that is for now compensating for the reduced ability of these reefs to
391 produce carbonate [10]. Although the change in the size-frequency distribution of
392 parrotfishes towards small-bodied individuals might not be so evident in terms of the total
393 size spectrum, the impact on the erosional potential of this group is significant because the
394 capacity of parrotfishes to erode substrate (i.e., as a function of bite rate and the amount of
395 mass removed per bite) is highly positively correlated with body size and life-phase
396 [34,41]. Furthermore, it is precisely at the smaller sizes (i.e., under 20 cm) that the
397 capacity of parrotfishes to erode substrate is severely reduced (i.e., the probability of
398 leaving a grazing scar decreases significantly) [34]. This has been exacerbated by the fact
399 that the decrease in abundance was specifically related to *S. viride*, the species, which
400 along with *Sc. vetula*, have historically been the major substrate eroding parrotfish species
401 in the Caribbean [35].

402 These observed changes in the parrotfish communities are likely to be a
403 consequence of several potentially interacting factors [40,42,43]. First, selective fishing on
404 larger individuals, not only indirectly increases the relative abundance of small-bodied
405 individuals, but also directly reduces the abundance of the organisms that, due to their
406 larger size, exert a greater effect on the ecosystem [35,41,44,45]. Although, in this region,
407 parrotfishes are not formally extracted for marketing, they can be caught as bycatch, and it

408 has been reported that self-consumption and sporadic commercialization can also occur
409 (e.g., by mislabeling), particularly as large piscivorous decline [46–48]. Second, long-term
410 habitat degradation, particularly following important losses in reef structural habitat
411 complexity, coral cover, and refuge availability, can negatively affect parrotfish and other
412 tropical fish populations (i.e., abundance and biomass), as these features mediate
413 productivity ($\text{g m}^{-3} \text{ yr}^{-1}$), recruitment, competition, predator-prey interactions, as well as the
414 fish size spectrum on reefs [12,43]. Additionally, because parrotfishes occur most
415 commonly in shallow reefal habitats, they are highly vulnerable to the impact of terrestrial
416 anthropogenic activities, including pollution, eutrophication and sedimentation [43]. These
417 can negatively impact not only the coral reefs, but also adjacent habitats such as seagrass
418 meadows and mangroves [49] where some parrotfish species occur, particularly during
419 their juvenile phases, as they search for food or nursery habitats [50,51].

420 Interestingly, the effect that the impaired parrotfish communities exerted on the
421 carbonate budget in this region, is the opposite to the effect described in some reefs in the
422 Indo-Pacific. In these cases, increases in parrotfish abundance and in their erosion rate
423 occurred after coral mass mortality events, stalling the recovery of the net carbonate
424 budgets even after an increase in the gross carbonate production rate [23]. Nevertheless,
425 several factors differ between these regions, for instance neither persistent habitat
426 degradation (i.e., critical losses in coral cover and generalized changes in coral
427 assemblages), widespread persistent transitions to macroalgal dominance, nor regional
428 depletion of herbivores in the Indo-Pacific, have been in general as pervasive as those that
429 have occurred across the wider Caribbean. This is very likely due to the Caribbean reefs'
430 higher vulnerability and lower functional redundancy [44,52]. They may help explain
431 different dynamics for producing and eroding communities between regions.

432 Other eroding organisms considered in this study (other than parrotfish) were not
433 related to the reduction in the overall erosion rate we observe. For instance, in the case of
434 sea urchins, although we only use density data to calculate rates of erosion, for this group
435 the observed trend was largely controlled by a consistent absence of these organisms
436 across sites and surveyed periods, as their populations have been depleted for decades
437 [53]. Furthermore, evidence suggests that despite slight recoveries in urchin populations
438 on some reefs, their population growth might be limited by low densities (i.e., by the Allee
439 effect [54]). In the case of encrusting sponges, because we use a constant coverage value
440 through time (see methods) the observed trend might have to be taken with some caution.
441 However, there is no evidence of important regional increases or declines in the coverage

442 of endolithic sponges over the last 20 years [14,15], and additionally encrusting sponges
443 contribute relatively little to total erosion rates, although in some sites this number can be
444 more significant [32].

445 Although in the short term the carbonate budget states of these sites, which are
446 dominated by non-framework building corals, seem to be favourable as a function of
447 recent declines in parrotfish populations, the absence of these organisms, particularly of
448 larger individuals, is likely to lock these reefs into low budget states. This is because
449 parrotfishes are also key herbivores that promote reef resilience and coral cover recovery
450 by regulating space competition between benthic organisms such as hermatypic corals
451 and algae [41,55]. A paradox in this context, is that any actions to promote increasing
452 parrotfish biomass on presently degraded reefs (especially excavating species; [56]) would
453 at least in the short term exacerbate the erosion of the reef carbonate framework. This is
454 particularly relevant because parrotfish protection seems to be effective in promoting coral
455 population resilience under some very narrow sets of environmental conditions such as
456 high coral cover, low algal productivity, or sufficient coral settlement [57], that are not met
457 in most of our study sites and elsewhere in the Caribbean [26,57,58]. For Caribbean reefs
458 to truly recover their capacity there is clearly a need for a recovery towards higher rates of
459 coral carbonate production. This will need to be underpinned by a return of both healthy
460 grazing and coral communities; a scenario that might only be achievable by adopting and
461 complying with management measures that directly address uncontrolled coastal
462 development and construction, poor regulated wastewater, and lack of the enforcement of
463 marine protection in addition to concerted efforts to reduce the rates of global
464 environmental change [25].

465 Our findings highlight the importance of the ecological-historical context in the
466 interpretation of current carbonate budgetary states and trajectories on now increasingly
467 common ecologically shifted-coral-reef assemblages [6,21], and the importance of
468 identifying those feedback mechanisms that may prevent low gross production rate reefs
469 transitioning to negative carbonate budget states. In order to predict potential paths of
470 coral reef recovery in the context of changing populations of major eroders (i.e.,
471 parrotfishes), further research could focus on describing the tradeoff between their
472 species-specific roles as herbivores and eroders. We also strongly recommend work on
473 model parametrization with local species-specific rates and further research into
474 understanding what factors might be driving different trends in eroders and producers'
475 abundance in highly perturbed reefs.

476

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