

1 **Synchronous biological feedbacks in parrotfishes associated with pantropical**
2 **coral bleaching**

3 Running title: Parrotfish responses to coral bleaching
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13

14 **Abstract**

15 Biological feedbacks generated through patterns of disturbance are vital for
16 sustaining ecosystem states. Recent ocean warming and thermal anomalies have
17 caused pantropical episodes of coral bleaching, which has led to widespread coral
18 mortality and a range of subsequent effects on coral reef communities. Although the
19 response of many reef-associated fishes to major disturbance events on coral reefs is
20 negative (e.g., reduced abundance and condition), parrotfishes show strong
21 feedbacks after disturbance to living reef structure manifesting as increases in
22 abundance. However, the mechanisms underlying this response are poorly
23 understood. Using biochronological reconstructions of annual otolith (ear stone)
24 growth from two ocean basins, we tested whether parrotfish growth was enhanced
25 following bleaching-related coral mortality, thus providing an organismal
26 mechanism for demographic changes in populations. Both major feeding guilds of
27 parrotfishes (scrapers and excavators) exhibited enhanced growth of individuals
28 after bleaching that was decoupled from expected thermal performance, a pattern
29 that was not evident in other reef fish taxa from the same environment. These results
30 provide evidence for a more nuanced ecological feedback system—one where
31 disturbance plays a key role in mediating parrotfish-benthos interactions. By
32 influencing the biology of assemblages, disturbance can thereby stimulate change in
33 parrotfish grazing intensity and ultimately reef geomorphology over time. This
34 feedback cycle operated historically at within-reef scales; however, our results
35 demonstrate that the scale, magnitude, and severity of recent thermal events is
36 entraining the biological responses of disparate communities to respond in
37 synchrony. This may fundamentally alter feedbacks in the relationships between
38 parrotfishes and reef systems.

39

40

41 Keywords: coral reefs, growth, herbivory, resilience, production, climate change

42

43 **1 | Introduction**

44 Climate change impacts are altering ecosystems across the globe (Walther et al.,
45 2002; Hoegh-Guldberg & Bruno, 2010; Walther, 2010). Many of the changes observed
46 to date have resulted from an amplification of the frequency and severity of
47 otherwise natural cycles of disturbance. For example, increased frequency of fires is
48 changing plant distributions in a variety of forest communities (Seidl et al., 2011;
49 Camac et al., 2017), whereas rapid sea surface warming and oceanographic changes
50 are restructuring assemblages of marine fishes in both temperate and tropical
51 ecosystems (McLean et al., 2019). Normal cycles of disturbance are thought to play a
52 significant role in the stability of ecosystem states over time, as they kickstart
53 negative biological feedbacks that confer resistance to changes in trajectory and may
54 maintain the potential for regeneration after disturbance (Chapin et al., 1996).
55 However, rates of disturbance and recovery are now becoming increasingly
56 mismatched, and are inducing permanent changes in the structure and function of
57 many ecosystems.

58 Coral reef ecosystems are no exception; these systems are temporally dynamic
59 owing to regular cycles of hydrodynamic (e.g., seasonal storm surge, intermittent
60 cyclones), thermal (e.g., heat stress, coral bleaching) and biotic (e.g., crown-of-thorns
61 starfish outbreaks) disturbances (Nyström et al., 2000). Climate change has increased
62 the frequency and severity of physical stressors on a global scale, so that the
63 trajectory of disturbance has now radically departed from historical cycles (Hughes
64 et al., 2018a; 2018b; Bruno et al., 2019). This was first documented nearly three
65 decades ago (Glynn, 1993), but has been highlighted in recent years by several
66 pantropical thermal anomalies that, coupled with baseline warming trends, caused
67 unprecedented mass bleaching of corals across the globe from 2015 through 2017
68 (Hughes et al., 2018a). The temporal alignment and magnitude of geographically
69 disparate bleaching events in recent years suggests that global climate change is now
70 triggering synchronous biological responses at the largest spatial scales.

71 The primary effect of coral bleaching events is mass mortality of coral colonies
72 (Glynn, 1993)—the dominant producers of benthic structure in these ecosystems—
73 with a wide range of flow-on effects to associated fish communities that rely on this
74 structure (Pratchett et al., 2008). A prominent feedback widely investigated in coral
75 reef systems concerns the interaction between the reef and parrotfishes (Scarinae,
76 Labridae)—an abundant group of fishes with modified jaws (including teeth that
77 represent one of the hardest biominerals known; Marcus et al., 2017) that allow them
78 to modify the benthic biota through feeding (Bellwood & Choat, 1990). Traditionally,
79 studies of this interaction have focused on the top-down influence of parrotfishes,
80 whose feeding limits the growth of turf algae and macroalgae and thereby has an
81 indirect and positive effect on coral recovery by reducing algae-coral competition.
82 Numerous studies have argued that this feedback loop has consequences for reef
83 resilience at ecosystem scales (reviewed in Mumby & Steneck, 2008; van de Leemput
84 et al., 2016). However, insights from nutritional ecology now identify parrotfishes as
85 microphages that target protein-rich epilithic and euendolithic photoautotrophic
86 microbes—pioneering microorganisms that dominate early successional stages in
87 bare substrata (Clements et al., 2017; Clements & Choat, 2018). These dietary targets
88 imply that parrotfishes benefit nutritionally following disturbances such as cyclones
89 and bleaching events, as the loss of coral and proliferation of microbial communities
90 offer a major expansion and enhancement of targeted food resources for both
91 scraping and excavating species (Clements & Choat, 2018). Such a scenario is
92 supported by correlative evidence from long-term (decadal) monitoring surveys that
93 typically record a proliferation of parrotfish communities after disturbance followed
94 by a subsequent decline in their abundance with recovery of corals (e.g., Russ et al.,
95 2015; Questel & Russ, 2018; Emslie & Pratchett, 2018). However, direct evidence
96 linking disturbance events to demographic responses by parrotfish populations
97 remains lacking (Taylor et al., 2018a). Analysis of organismal responses to
98 disturbance may clarify the extent to which potential nutritional subsidies stemming
99 from successional change scale up from individuals to populations and assemblages.

100 A hypothesis that incorporates disturbance-mediated feedback loops between
101 parrotfishes and coral communities suggests a more nuanced and complex system
102 than the traditional view of constant top-down control might imply (Bruno et al.,
103 2019). Resolving this relationship is a critical goal if we are to understand the
104 organisation and resilience of coral reef ecosystems in the Anthropocene and most
105 importantly, the ability of reefs to support human livelihoods in the future (Brandl et
106 al., 2019; Woodhead et al., 2019).

107 Here, we sampled assemblages of reef fishes across two ocean basins from
108 coral reef systems that were recently subjected to intense coral bleaching. We tested
109 for somatic growth responses at population levels related to bleaching-induced coral
110 mortality across multiple families using biochronological reconstructions of
111 individual growth histories of fishes. Following lines of evidence for microphagy
112 and population responses to disturbance, we hypothesized that parrotfishes exhibit
113 unique positive growth responses to coral mortality that are decoupled from regular
114 thermal response relationships, thereby revealing a biological mechanism that
115 underpins previously documented but poorly understood population- and
116 community-scale responses. This study advances our understanding of important
117 feedback systems related to disturbance events on coral reefs through the integration
118 of species' biology with climate change effects across ocean-basin scales.

119

120 **2 | Methods**

121 *2.1 | Study sites and fish sampling*

122 This study sampled coral reefs of the Chagos Archipelago (central Indian Ocean)
123 and the northern Great Barrier Reef (western Pacific Ocean; Figure 1). The northern
124 atolls of the Chagos Archipelago (CA) have been uninhabited for over 4 decades and
125 have been under full protection from fishing since 2010; the outer reefs of the Lizard
126 Island region of the Great Barrier Reef (GBR) have been managed using a well-
127 enforced network of marine protected areas, and herbivorous species are not
128 targeted by fishers in the region. Hence, both locations support relatively pristine

129 and diverse parrotfish assemblages (Samoilys et al., 2018; Johnson et al., 2019). Coral
130 reefs of the CA and the GBR have experienced severe heat stress and consequent
131 coral bleaching during 2015-2016 and 2016-2017, respectively, resulting in drastic
132 losses of living coral cover (Sheppard et al., 2017; Hughes et al., 2018b; Head et al.,
133 2019).

134 We sampled adult parrotfishes twice from reefs that experienced high
135 mortality of coral due to bleaching in each region (GBR: Dec 2017 and Mar 2019; CA:
136 May 2018 and Mar 2019). On the GBR, sampling targeted *Chlorurus microrhinos*,
137 *Scarus altipinnis*, *Cetoscarus ocellatus*, *Scarus niger* and *Hipposcarus longiceps*, whereas
138 in the CA, sampling targeted *Chlorurus strongylocephalus*, *Chlorurus enneacanthus*,
139 *Chlorurus sordidus* and *Scarus rubroviolaceus* (Table S1). For comparison, we also
140 sampled the herbivorous surgeonfishes *Naso unicornis* from both locations and
141 *Acanthurus lineatus* from CA—species that feed on macroalgae and turfing algae,
142 respectively—as well as two longer-lived mesopredator snapper species, *Lutjanus*
143 *bohar* and *Lutjanus gibbus*, from CA. We hypothesized that these non-parrotfish
144 species would show no post-bleaching growth response as their food resources
145 would not proliferate at the same magnitude or rate as those of parrotfishes
146 immediately after coral mortality. For each specimen, we recorded body length, sex,
147 and colour phase (generally associated with sex in parrotfishes). We surgically
148 removed the sagittal otoliths and stored these dry for laboratory analysis.

149

150 2.2 | Chronological reconstructions of otolith growth

151 We used annual otolith growth to derive a proxy of somatic growth index across
152 calendar years. Otoliths were sectioned in the laboratory using a standard grinding
153 technique. One otolith from each pair was affixed to a glass slide using thermoplastic
154 glue with the primordium (core) positioned just inside the slide edge, with the sulcal
155 ridge perpendicular to the slide edge. The otolith was ground to the slide edge using
156 a 1200-grit diamond lapping disc with continuous water flow. The newly sectioned
157 surface was then reaffixed flat against the slide and ground to produce a thin

158 transverse section <200 μm thick and a coverslip was applied using thermoplastic
159 glue. Otolith cross-sections were photographed using an Olympus DP27 digital
160 camera on an Olympus SZ61TR stereo microscope with a transmitted light source.

161 The widths of annual increments were measured three times for each
162 individual along parallel transects on the ventral side of the otolith cross-section
163 using ImageJ (version 1.52, National Institutes of Health, USA; Supplemental
164 Material). Mean estimates across the three replicate series were used to represent
165 each year's otolith growth at the corresponding fish age. Increments were measured
166 from the centre of an opaque zone to the centre of the following opaque zone,
167 representing the annual growth between austral spring seasons (Choat et al., 1996).
168 Because growth increments naturally decrease in width as fishes age, individual
169 series for the shorter-lived parrotfishes and surgeonfishes were standardised by
170 detrending as follows. A growth index for the first year of life was estimated by
171 dividing the increment width by the grand mean Year 1 increment width from all
172 fish within a given species. Subsequent annual growth performance for individuals
173 is relative to the growth pattern of that fish, rather than compared to the
174 performance of others. For example, a strong year of growth for a small individual
175 may produce an increment width of only average size for a given age compared with
176 that of other members of the population. Therefore, the remaining growth series was
177 detrended by fitting a power function (Increment width = $a[\text{age}]^b$) to the increment
178 width by age data for each specimen and dividing the observed width by the
179 predicted width (Figure S1, Supplemental Material). To ensure sufficient data points
180 to appropriately fit the power curve within specimens, only specimens ≥ 5 years old
181 were included in the analysis. The detrended series were aligned by calendar year
182 and a mean index chronology for each species was developed across years with ≥ 5
183 individuals. Because the two snapper species were considerably longer-lived and
184 therefore subject to changes in growth on decadal scales, these species were
185 detrended using a double detrending method detailed in Taylor et al., (*under review*).
186 A Pearson correlation matrix was used to compare annual growth responses across

187 all species. Population signal strength for all species (i.e., common variance among
188 individuals) was assessed by calculating the interseries correlation, represented by
189 the mean correlation of each detrended individual series with the mean of all others.

190

191 2.3 | *Decoupling thermal growth responses from bleaching*

192 Thermal performance curves for ectothermic species demonstrate that physiological
193 performance, and therefore growth rate, increases with temperature until an
194 optimum is reached; beyond this point, performance declines (Huey & Kingsolver,
195 2019). We set out to determine whether coral bleaching (which occurs at the highest
196 water temperatures) is associated with enhanced growth in parrotfishes irrespective
197 of trends in thermal response. To decouple the potential influence of coral bleaching
198 on otolith growth from the standard thermal growth response, we fitted linear
199 regressions to the population-level growth index predicted by sea surface
200 temperature from the warmest annual three-month period (the 'growing season';
201 SST_{hi}). SST_{hi} data were extracted and summarised from the HadISST database (Met
202 Office Hadley Centre's Sea Surface Temperature data set; available from
203 <https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdHadISST.graph>); Mar-May for
204 CA and Jan-Mar for GBR. This analysis excluded data from 2016, the year for which
205 chronologies indicated a spike across multiple populations. We then examined the
206 difference between the observed and predicted (based on linear regressions) 2016
207 growth index to test for an increase in the post-bleaching growth index beyond what
208 is predicted based on the relationship between temperature and growth. Although
209 full performance curves are inherently non-linear, we used linear fits to summarize
210 responses because our observations spanned only slightly less than 1°C, a range over
211 which strongly non-linear trends are unexpected. An additional six specimens of *C.*
212 *microrhinos* from Jan 2012 collections at the GBR (representing all those available
213 from this collection period that were ≥ 5 years old, following the criterion described
214 above) were included in this analysis to extend the number of annual growth
215 index/ SST_{hi} pairs. We also fitted linear regression models to all data for each species

216 and evaluated the influence of post-bleaching responses using Cook's distance
217 (Cook, 1977).

218

219 2.4 | Drivers of individual growth response

220 Otolith-growth responses during 2016 varied among individuals within species, so
221 we developed a linear mixed-effects model to examine whether certain traits
222 predicted the magnitude of growth index value across species for which 2016 had
223 the highest index value. In this model, post-bleaching growth index was predicted
224 by fixed factors *age* (during 2016 [backcalculated from age at capture]), *body length* (at
225 capture), *sex*, and *residual position* on the growth curve (i.e., size of an individual
226 relative to the mean for their respective age). *Species* was included as a random factor
227 and all numerical factors (2016 growth index, *age*, *body length*, and *residual position*)
228 were centred and scaled by *species*. We examined the relative effect size of each
229 predictor variable and compared models of significant variables against a null
230 model.

231

232 3 | Results

233 3.1 | Growth chronologies

234 For eight of the nine parrotfish species we sampled, the highest annual growth index
235 for the past decade occurred during 2016. The exception was the phylogenetically
236 distinct *H. longiceps* from GBR (Figure 2). The increase in increment width was most
237 pronounced for *S. altipinnis* (GBR) and the three *Chlorurus* spp. from the CA. All
238 parrotfish species from CA had 2016 growth indices with 95% confidence intervals
239 that did not overlap with the expected (value = 1.0), indicating significant departure
240 from expected patterns of growth (Figure S3, Supplemental Material). The trend of
241 increased growth was also apparent for GBR parrotfishes, but *S. altipinnis* was the
242 only species for which the growth index 95% confidence interval did not overlap 1.0
243 (Figure S3, Supplemental Material). For some of these species, this may reflect the
244 lower sample sizes obtained from the GBR reefs. The surgeonfishes *A. lineatus* and

245 *N. unicornis* (both locations), the two snappers *L. bohar* and *L. gibbus*, and the
246 parrotfish *H. longiceps* showed unique annual patterns of growth with little, if any,
247 commonalities among species. Overall, parrotfishes generally had higher
248 interspecies as well as interseries (within species) correlations (Table S1, Figure S2,
249 Supplemental Material) than other species, with both metrics positively influenced
250 by the synchronous signal during 2016. This result implies temporal synchrony in
251 growth patterns within and among parrotfishes between ocean basins.

252

253 3.2 | Thermal growth response versus bleaching response

254 Otolith growth in 2016 (post bleaching) greatly exceeded thermal performance
255 expectations for parrotfishes that had peak growth indices in that year (Figure 3).
256 Post-bleaching growth indices for these species greatly influenced their respective
257 SST_{hi} -growth response relationships, with an average Cook's distance value of 4.84
258 (± 1.31 S.D.) times greater than the mean, versus 1.53 (± 1.92 S.D.) for species that
259 showed no bleaching response (Table S2, Supplemental Material). We note that *N.*
260 *unicornis* from GBR had a high Cook's distance value for 2016 (5.33, Table S2),
261 although the growth index value for that year did not exceed what was expected
262 (Figures S3 and S4, Supplemental Material). On average, the eight parrotfishes
263 (excluding *H. longiceps*) had post-bleaching growth indices that were 10-20% greater
264 than expected (mean = 13.25% ± 4.69 S.D.; Figure 3b), with five of these species
265 exhibiting 2016 indices well outside the 95% confidence bands derived from
266 relationships with SST_{hi} (Figure S4, Supplemental Material). Only *C. microrhinos* had
267 an observed index reasonably close to predicted values (3.6% higher). In contrast, the
268 surgeonfishes, snappers and the parrotfish *H. longiceps* had observed growth indices
269 that did not differ from expected (mean = -0.97% ± 5.24 S.D.; Figure 3). Across all
270 species, observed relationships between growth indices and SST_{hi} reflected both
271 positive and negative trends, suggesting these species are collectively straddling the
272 peak of their thermal performance curves in the recent decade. Notably, half of the
273 parrotfishes (*Cet. ocellatus* and *S. niger* in GBR, *Chl. sordidus* and *S. rubroviolaceus* in

274 CA) had decreasing growth index values associated with increasing SST_{hi} , whereas
275 post-bleaching growth index values (during the hottest year) were far greater than
276 the expected trend.

277

278 3.3 | *Individual growth responses after bleaching*

279 Our linear mixed-effects model that tested for an effect of individual traits on the
280 magnitude of growth response to bleaching included 2016 growth index information
281 of the eight parrotfishes (GBR: *Chl. microrhinos*, *S. altipinnis*, *Cet. ocellatus*, and *S.*
282 *niger*; CA: *Chl. strongylocephalus*, *Chl. enneacanthus*, *Chl. sordidus*, and *S. rubroviolaceus*)
283 that showed post-bleaching growth responses that were strongly positive. Overall,
284 age was the only significant predictor variable, suggesting that older individuals
285 conferred a slightly greater benefit to otolith growth across species (Table 1, Figure
286 4). However, a growth index \sim age model was not significantly different to a null
287 model with no predictor variables (Table 1), implying that otolith growth responses
288 across individuals were largely equivalent (Figure S5, Supplemental Material).

289

290

291 **Tables**

292 Table 1. Summary of linear mixed-effects model predicting the magnitude of post-
 293 bleaching otolith growth response across eight parrotfish species from the Great
 294 Barrier Reef and the Chagos Archipelago. *Species* included as a random factor.

a) Anova table

Factor	df	Coefficient	St. Err.	F-value	P-value
<i>intercept</i>	1,175	0.057	0.133	0.000	1.000
<i>age</i>	1,175	0.183	0.080	5.990	0.015
<i>body length</i>	1,175	0.006	0.115	0.199	0.656
<i>residual position</i>	1,175	-0.035	0.109	0.157	0.693
<i>sex (male)</i>	2,175	-0.084	0.165	0.130	0.878

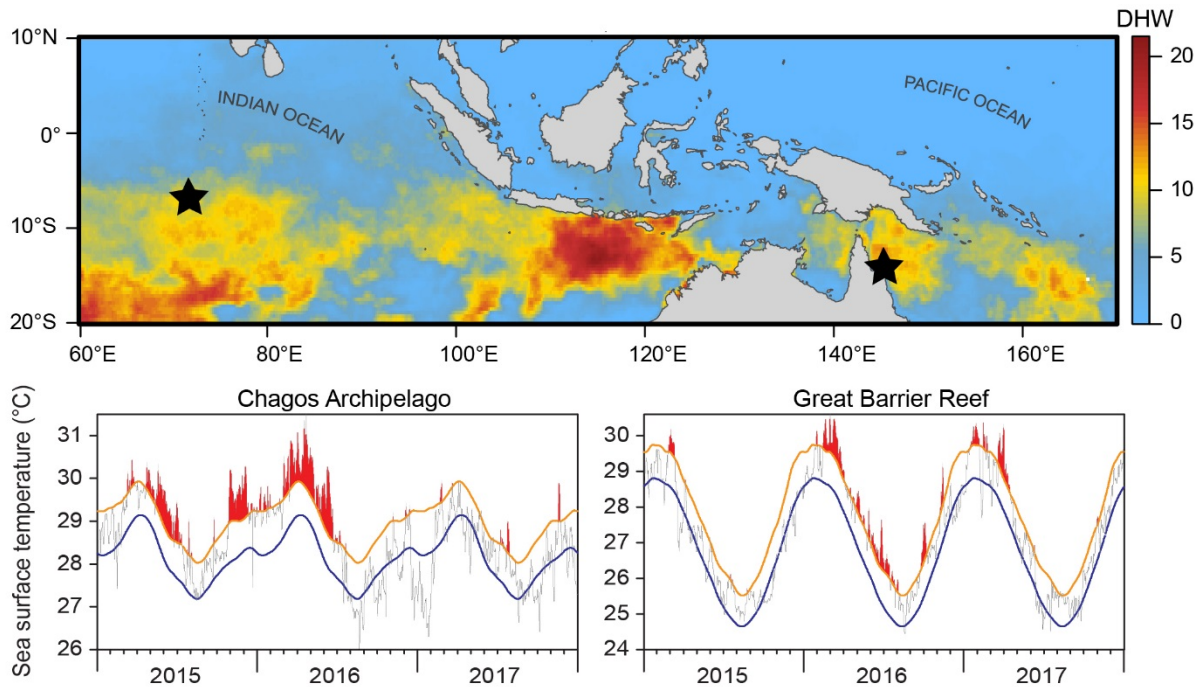
b) Comparison with null

Model	df	AICc	BIC	log-likelihood	P-value
2016GI ~ <i>age</i>	4	534.4	547.1	-263.1	0.106
2016GI ~ 1 (null)	3	534.9	544.5	-264.4	

295

296

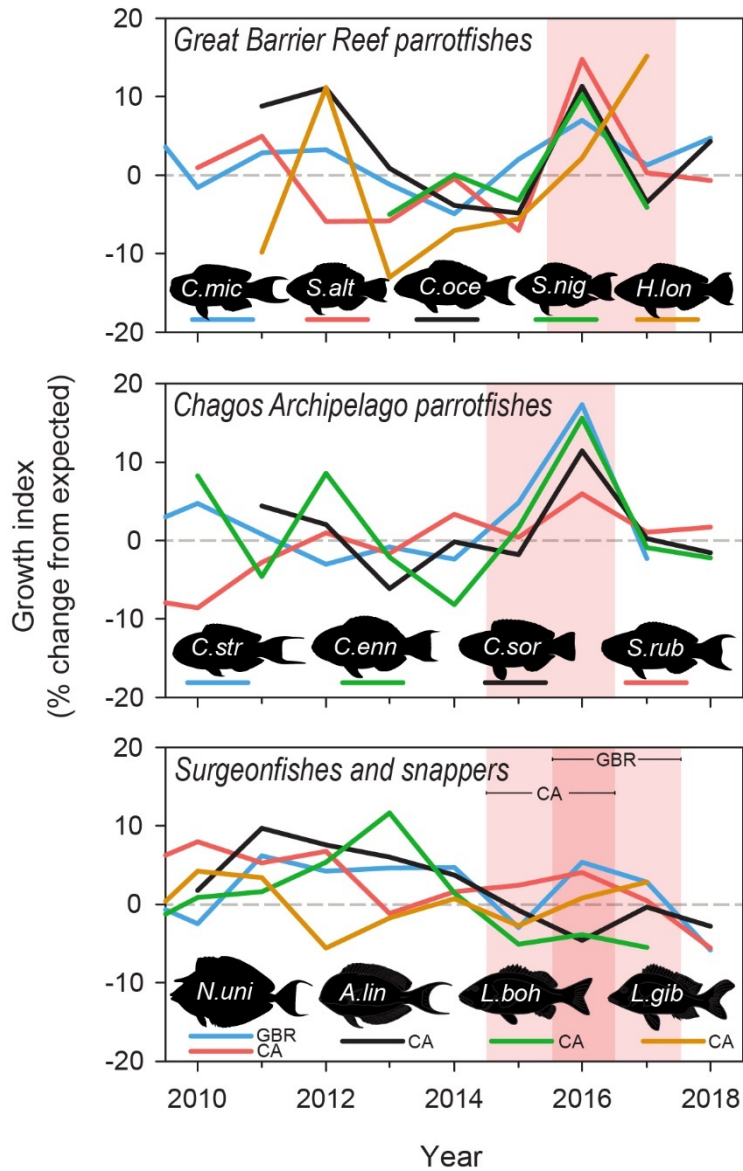
297 **Figures and figure legends**



298

299 **Figure 1. Heat-exposure in the tropical Indo-Pacific during 2015-2017.** Symbols
300 show study sites in the Indian (Chagos Archipelago) and Pacific Oceans (northern
301 Great Barrier Reef) where widespread coral bleaching occurred during 2015-2017.
302 The colour-scale in the top panel displays Degree Heating Weeks (DHW, °C-weeks)
303 during March-April 2016, when both regions faced the greatest thermal stress.
304 Bottom panels highlight thermal anomalies during 2015-2017 at each location (blue
305 line, seasonal expected temperature; orange line, seasonal threshold temperature
306 (90th percentile, following Hobday et al., 2016); grey line, observed temperature;
307 source: Schlegel, 2018).

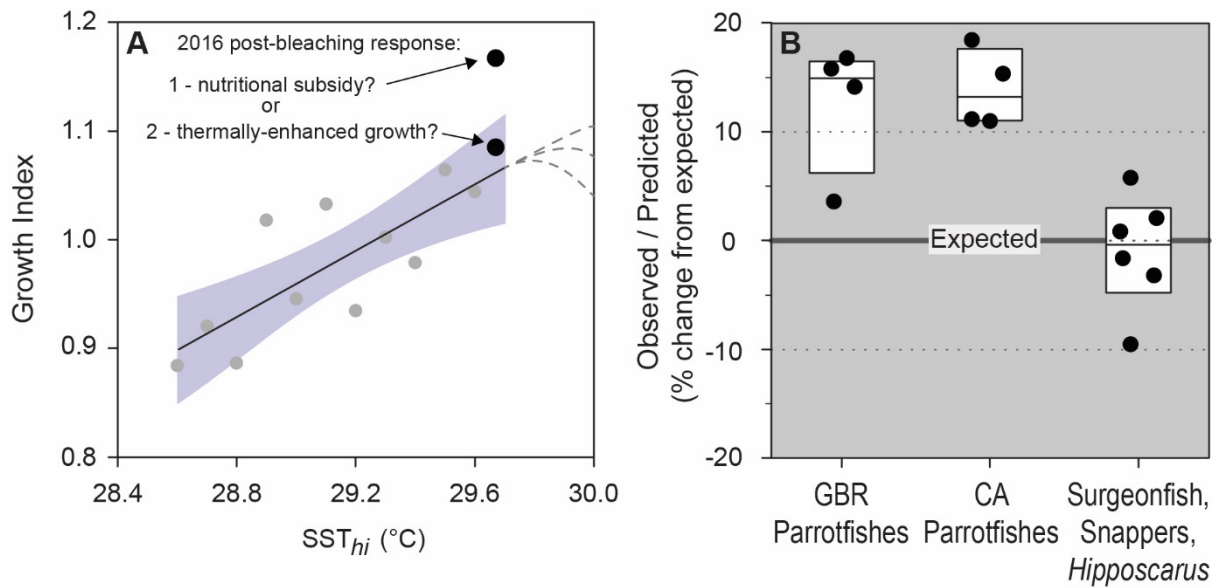
308



309

310 **Figure 2. Otolith growth-increment chronologies for parrotfishes, surgeonfishes,**
 311 **and snappers from the Great Barrier Reef and the Chagos Archipelago. Lines**
 312 **represent the mean population-level growth response through time for each**
 313 **respective species. Shaded regions delineate annual periods of mass coral bleaching**
 314 **for each region. 95 % confidence intervals for each chronology, demonstrating**
 315 **significant departures from expected growth indices across years, are presented in**
 316 **the Supplemental Material (Figure S3).**

317

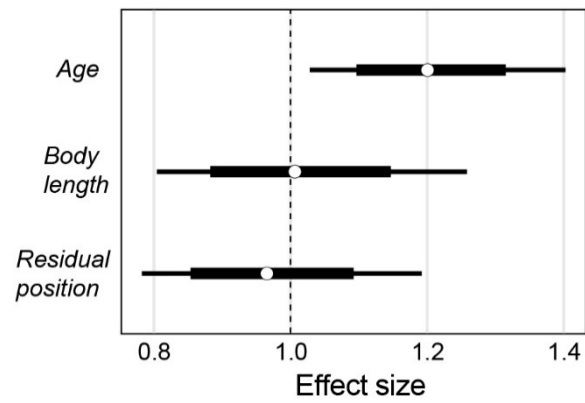


318

319 **Figure 3. Post-bleaching growth response in the context of thermal performance.**

320 (A) Growth performance in ectotherms increases with temperature up to a particular
 321 threshold, thereby generating thermal performance curves. Increased metabolic
 322 demands associated with higher temperatures require greater food intake. We used
 323 thermal response relationships (Supplementary Material; Figure S4) to assess
 324 whether increased growth of parrotfish after bleaching (hypothetically represented
 325 by the black dots) results from enhanced nutritional resources (yielding greater than
 326 expected growth indices) or simply reflects higher growth rates within a range
 327 expected from thermal performance relationships. (B) Overall, parrotfishes from
 328 both regions exhibited post-bleaching growth responses between 10-20% greater
 329 than expectations based on thermal performance. Species not hypothesized to have
 330 enhanced growth associated with coral bleaching responded as predicted.

331



332

333 **Figure 4. Estimated effect sizes from the linear mixed-effects model predicting the**
 334 **magnitude of post-bleaching growth response across eight parrotfish species.**

335 Thick and thin bars represent 75% and 95% confidence intervals, respectively.

336 Dashed line indicates no estimated effect.

337

338 4 | Discussion

339 We found that parrotfishes on reefs with extensive bleaching mortality of corals
340 responded with positive individual growth rates that manifested at both the
341 population and assemblage levels. Other families of reef fishes displayed no
342 common growth response after bleaching events, beyond that expected from thermal
343 performance relationships. The magnitude and ubiquity of the observed growth
344 response—both across species and between ocean basins—was compelling, and
345 undoubtedly reflected the scale and severity of the 2015-2017 pantropical coral
346 bleaching event. These findings have several implications for our understanding of
347 energetic pathways and post-disturbance dynamics on coral reefs. Our results
348 strongly support the microphagy-disturbance hypothesis (Clements et al., 2017;
349 Clements & Choat, 2018) that posits that parrotfishes benefit from disturbance to
350 corals and the resultant expansion of nutritional resources through succession of
351 microbial photoautotrophs in bleached coral substratum. Further, a mode of life that
352 benefits from successional change implies a fundamentally different and more
353 nuanced set of ecological feedbacks between parrotfishes and the reef than has been
354 considered in the past—one where disturbance plays a key role in mediating
355 parrotfish-benthos interactions. The temporal synchronization of a biological process
356 as intricate as individual fish growth across ocean basins represents a troubling
357 signal of the scale of climate change impacts in the Anthropocene.

358 Many studies have shown positive short-term responses of parrotfish
359 demography (notably abundance) to a variety of disturbances on coral reefs (e.g.,
360 Lindahl et al., 2001; Wilson et al., 2006; Adam et al., 2011; Gilmour et al., 2013; Russ
361 et al., 2015; Lamy et al., 2015), including coral bleaching events, destructive blast
362 fishing, storms, cyclones, and predation by crown-of-thorns starfish. These studies
363 also include bleaching events in our localities in the Chagos Archipelago (Sheppard
364 et al., 2002) and on the Great Barrier Reef (Emslie & Pratchett, 2018). All disturbances
365 have the common effect of reducing live coral cover either through physical
366 destruction of habitat (e.g., cyclones) or by causing the death of coral colonies while

367 leaving the underlying skeleton still intact, at least initially (e.g., bleaching, crown-
368 of-thorns). Increased densities of successional photoautotrophic microbial
369 communities that are a nutritional resource for parrotfishes then follow. Our review
370 of the literature suggests that parrotfishes typically respond to disturbance by
371 increasing in numbers with a peak occurring approximately two years after the
372 event. Numerical densities at this time are a factor of two to eight times the pre-
373 disturbance densities (e.g., Adam et al., 2011; Gilmour et al., 2013; Russ et al., 2015).
374 Longer-term (decadal) data sets demonstrate a return to pre-disturbance densities
375 following coral recovery across a wider range of time scales (up to a decade or more;
376 e.g., Russ et al., 2015). A lagged effect at this scale implies not only an initial
377 expansion of resources following disturbance-related coral mortality, but also a
378 significant augmentation of nutritional resources at a level that enhances somatic
379 and subsequent population growth. The ubiquitous pattern we observed of spikes in
380 growth immediately following bleaching across the multiple species of parrotfishes
381 provides strong evidence that the expansion and enhancement of nutritional
382 resources by the proliferation of photoautotrophic microbial communities underpins
383 the demographic responses commonly observed across species and locations. This
384 appears to be particularly true for bleaching events versus other forms of
385 disturbance as the heat-driven proliferation of photoautotrophic microbes following
386 mortality enhances dissolution of coral skeletons (Leggat et al., 2019), providing
387 ideal nutritional gains for microphages. Our observation that individual traits (e.g.,
388 body size, age, sex) were not good predictors of the magnitude of the otolith growth
389 response in parrotfishes is not surprising, as we would not expect either density-
390 dependent or size-dependent competition to be strong following resource expansion.

391 There was a strikingly consistent temporal alignment in annual growth
392 responses between ocean basins, whereby eight of nine parrotfish species had their
393 highest growth index value in 2016. This consistency was initially unexpected given
394 that there was a slight offset in the timing of maximum thermal stress and
395 consequent bleaching between the CA and GBR. Reefs of the CA experienced

396 widespread bleaching in 2015 and 2016, with stark declines in relative coral cover
397 observed following both annual events (Sheppard et al., 2017; Head et al., 2019). The
398 decline of coral cover was greater following the initial 2015 event, but thermal stress
399 was more intense in 2016 (Head et al., 2019). This general interannual pattern also
400 occurred on the northern GBR but was spread across 2016 and 2017 (Hughes et al.,
401 2018b; 2019). Hence, we expected disturbance-related benefits to parrotfish growth
402 to appear in 2015 for the CA and 2016 for the GBR. However, the temporal
403 resolution of our method (i.e., biochronological reconstructions from annual bands
404 in otoliths) is coarse, and annual growth bands are deposited in the austral spring,
405 rather than the beginning/end of the calendar year (Choat et al., 1996). Because
406 thermally-induced coral bleaching occurred later in the year at CA (~May, with
407 lagged coral mortality and successional proliferation of the microbial community),
408 increases in growth rates of parrotfishes related to enhanced nutritional resources
409 would likely not have occurred until approximately three quarters of the way
410 through the period of increment deposition. In comparison, GBR coral reefs bleached
411 in February, allowing more time for enhanced growth to be reflected in that year's
412 increments, thus accounting for the temporal alignment of enhanced growth from
413 both locations during 2016 (representing austral spring 2015 through austral spring
414 2016). Only one parrotfish, *H. longiceps* (GBR), did not display peak growth in 2016,
415 but instead peaked the following year. Repeating the analysis from Figure S4 but
416 considering 2017 as the key post-bleaching year yielded an observed/predicted value
417 for *H. longiceps* of 1.17, which is on par with the post-bleaching responses from other
418 parrotfish species, implying it may benefit similarly but target later stages of
419 succession. However, the thermal relationship was weak, and thus whether this 2017
420 peak reflected a delayed response to disturbance is unclear. The genus *Hipposcarus* is
421 sister to the clade containing *Chlorurus* and *Scarus*, and is thus phylogenetically
422 distinct from the remaining parrotfishes examined here. Research on the stomach
423 contents of the sister species (*H. harid*) suggests that its diet includes substantial

424 animal material and is thus distinct from that of most other parrotfishes (de la Torre-
425 Castro et al., 2008).

426 Recent histories of disturbance have differed between reefs of the northern
427 GBR and the CA. Although both experienced recent widespread coral bleaching in
428 successive years, the northern GBR has endured a greater frequency of localised
429 disturbances in the form of cyclones, episodes of coral disease, crown-of-thorns
430 outbreaks and severe storms (Emslie & Pratchett, 2018). Such disturbances have had
431 severe and spatially-restricted impacts on coral cover (Hughes et al., 2018b) that
432 have collectively reduced coral abundance throughout the region. In contrast, the
433 CA experienced a long period of relatively low disturbance since recovering from
434 the mass bleaching event in 1998. This might explain why post-bleaching growth
435 responses were generally more pronounced across species from the CA than those
436 from the GBR. Although responses of individual parrotfishes are subject to
437 environmental changes occurring within their home ranges, the widespread and
438 extreme nature of the 2015-2017 coral bleaching event has driven a collective
439 response across species and regions. The nature of individual responses is shown in
440 the timing of peaks within each otolith time series; however when pooled to the level
441 of location, a very clear trend for the population emerges.

442 The contrasting patterns of parrotfish abundance and coral cover on
443 disturbed reefs suggests a negative feedback system whereby removal of living coral
444 benefits somatic growth and ultimately demography of parrotfishes. This increase in
445 size and density of parrotfishes leads to increased rates of grazing and reworked
446 sediment by at least the same magnitude as observed increases in density, thereby
447 potentially enhancing the role parrotfishes play in coral recovery. Finally, recovery
448 of coral cover eventually reduces abundance of parrotfishes to pre-disturbance levels
449 (cf. Cramer et al., 2017). Presumably, lack of coral recovery and the successional
450 dominance of algae on coral skeletons may have the same effect on parrotfish
451 abundance over time by reducing endolithic photoautotrophs. This view integrates
452 the context of disturbance dynamics and cycles of succession on coral reefs and, as

453 such, posits a more nuanced framework of interaction compared with the classical
454 notion in which coral reef herbivores, including parrotfishes, simply exert constant
455 top-down control on the structure of the reef. We note that the latter viewpoint
456 (previously considered a positive feedback loop; van de Leemput et al., 2016) largely
457 ignores the influence of disturbance cycles and has not been met with robust
458 empirical support (Questel & Russ, 2018; Bruno et al., 2019), likely because of the
459 complex interactions of a myriad of stressors affecting coral reefs (Hughes &
460 Connell, 1999). Robust analysis of ecosystem recoveries after severe coral bleaching
461 has demonstrated that herbivore biomass can predict the recovery potential of coral
462 reefs, but other factors such as reef structural complexity, juvenile coral density, and
463 depth are far better predictors (Graham et al., 2015). Many studies suggest
464 parrotfishes indirectly facilitate coral recovery by increasing suitable settlement
465 substratum through feeding (Birkeland, 1977; Burkepile & Hay, 2008; Mumby &
466 Steneck, 2008); however, this interaction appears to be dependent on the
467 demographic composition of both juvenile corals as well as parrotfishes, since
468 incidental mortality from feeding on the reef substrate may limit post-settlement
469 survivorship of corals (Mumby, 2009; Traçon et al., 2013). Ultimately, the evidence
470 suggests that interactions between parrotfishes and benthic communities are not
471 straightforward—especially in the highly diverse fish assemblages of the Indo-
472 Pacific—and are likely dependent on many external factors (Bruno et al., 2019). If
473 this system represents a true negative feedback process (i.e., one that enhances
474 system stability by diminishing fluctuations of processes involved), then evidence
475 from this study and others suggests that influences from the benthic communities on
476 parrotfishes (i.e., bottom-up forces) are more pronounced and consistent than top-
477 down processes. Further, such a feedback system would have previously manifested
478 at small spatial scales, given the historically patchy nature and lower severity of the
479 disturbance events described above. However, these events are now emerging more
480 frequently and at global scales (Oliver et al., 2018; Hughes et al., 2018a).

481 Temporal synchrony in biological processes (e.g., abundance patterns of
482 species, demographic rates of individuals, or functional composition of
483 communities) represents the level of common variance over time in a biological
484 system (Loreau & de Mazancourt, 2008). An increased frequency of extreme climatic
485 events (such as thermally-induced coral bleaching) is expected to enhance synchrony
486 within ecosystems, as extreme events often disproportionately influence biological
487 processes and may change ecosystem functions (Jentsch et al., 2007). High biological
488 synchrony may also indicate low response diversity, implying an ecosystem with
489 low resilience to change (Mori et al., 2013). Recent climate histories are driving
490 synchronous biological and physical patterns across multiple ecosystems (e.g., Black
491 et al., 2018). The patchiness and high level of demographic diversity across small
492 areas within coral reef systems (Gust et al., 2002; Taylor et al., 2018b; Kingsford et al.,
493 2019) implies that population dynamics of organisms within coral reefs are heavily
494 influenced by individual microhabitats, perhaps to an extent greater than most other
495 ecosystems. Hence, the temporal synchronization of growth responses across
496 spatially disjunct populations spanning two ocean basins following pantropical
497 bleaching highlights the severity and pervasiveness of the effects of contemporary
498 climate change.

499 The recent decline of coral reef ecosystems has brought the role of ecosystem
500 functioning to the forefront (Bellwood et al., 2004). Bellwood et al. (2019) defined
501 ‘function’ as the movement or storage of energy or material, which implies that the
502 key to understanding functions is through rate-based ecological processes (Brandl et
503 al., 2019). However, many long-established functional classifications commonly used
504 in the context of coral reefs were derived from observations of “pre-bleaching, 20th-
505 century reefs” (Bellwood et al., 2019). The view presented here emphasises the
506 strong feedback linkages on coral reefs between (i) carbonate dynamics, i.e., coral-
507 mediated carbonate production and parrotfish-mediated bioerosion, and (ii) plant-
508 herbivore interactions, i.e. primary production by microscopic photoautotrophs and
509 parrotfish herbivory. Clearly, understanding the interactions between these rate

510 processes will be as important as measuring the processes themselves. The present
511 study and others demonstrate that disturbance is a key process that mediates
512 ecological functions on coral reefs by having a profound influence on the rates of
513 movement and storage of nutrients and material. Parrotfishes are considered a major
514 functional group on coral reefs and here we demonstrate that disturbance can
515 influence the capacity for nutrient harvesting that fuels growth processes and
516 provides storage products that underwrite the investment in reproduction, thereby
517 stimulating change in demographic and grazing rates over time that will interact
518 with carbonate dynamics and ultimately influence reef geomorphology.
519 Unfortunately, the natural states of ecosystems are changing over ecological time
520 scales, with increased frequency and severity of disturbance cycles engendering an
521 uncertain future for the responses of communities.

522

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