1   **Synchronous biological feedbacks in parrotfishes associated with pantropical**

2   **coral bleaching**

3   Running title: Parrotfish responses to coral bleaching

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Abstract

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

1 | Introduction

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

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

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

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

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

2.2 | Chronological reconstructions of otolith growth
We used annual otolith growth to derive a proxy of somatic growth index across calendar years. Otoliths were sectioned in the laboratory using a standard grinding technique. One otolith from each pair was affixed to a glass slide using thermoplastic glue with the primordium (core) positioned just inside the slide edge, with the sulcal ridge perpendicular to the slide edge. The otolith was ground to the slide edge using a 1200-grit diamond lapping disc with continuous water flow. The newly sectioned 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[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

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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

10

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 ~ *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
intercept	1,175	0.057	0.133	0.000	1.000
age	1,175	0.183	0.080	5.990	0.015
body length	1,175	0.006	0.115	0.199	0.656
residual position	1,175	-0.035	0.109	0.157	0.693
sex (male)	2,175	-0.084	0.165	0.130	0.878

b) Comparison with null

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

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297   **Figures and figure legends**
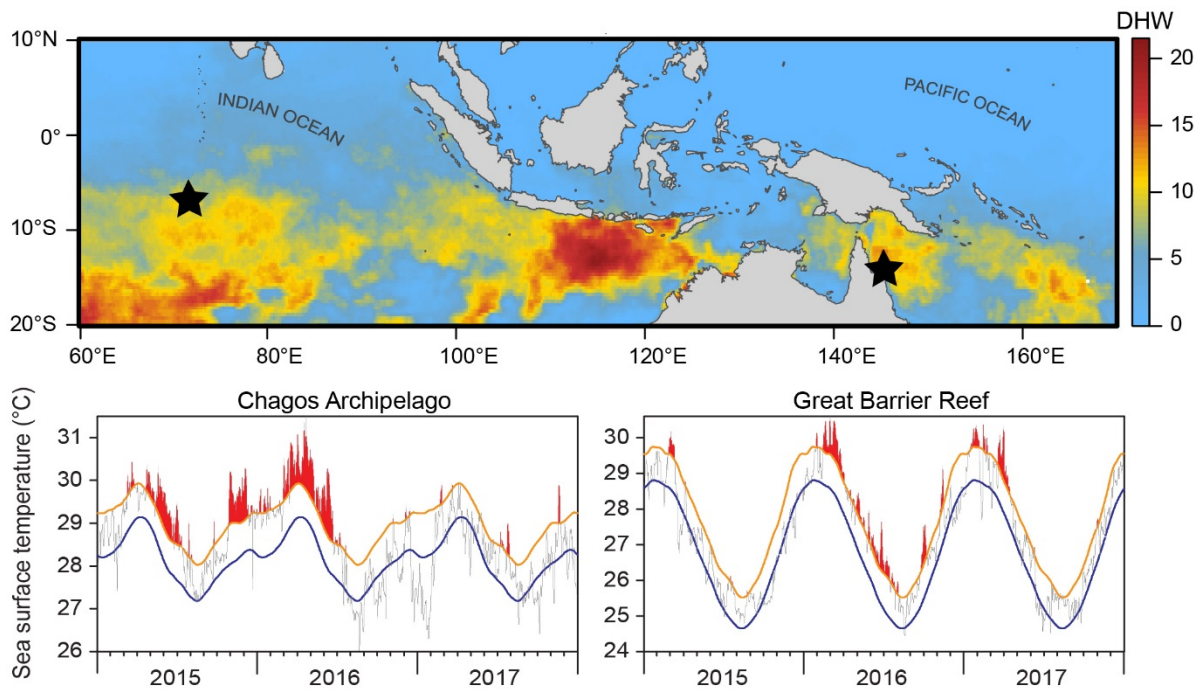
298

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).

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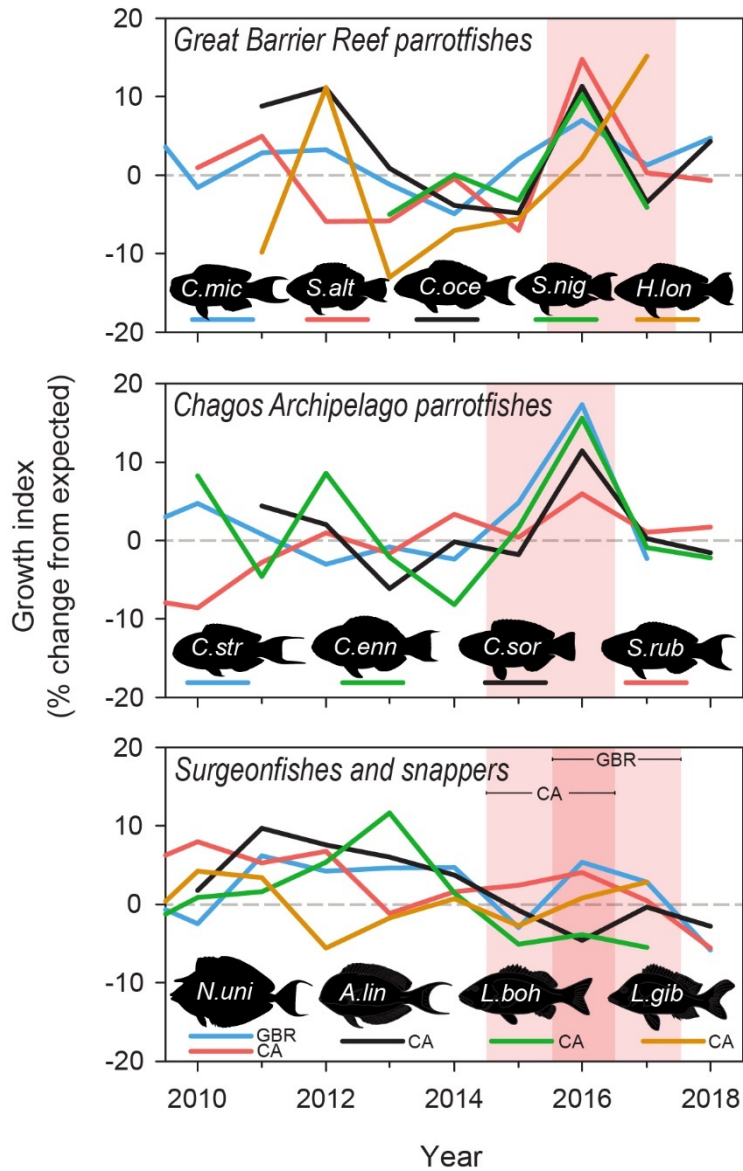
Figure 2. Otolith growth-increment chronologies for parrotfishes, surgeonfishes, and snappers from the Great Barrier Reef and the Chagos Archipelago. Lines represent the mean population-level growth response through time for each respective species. Shaded regions delineate annual periods of mass coral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

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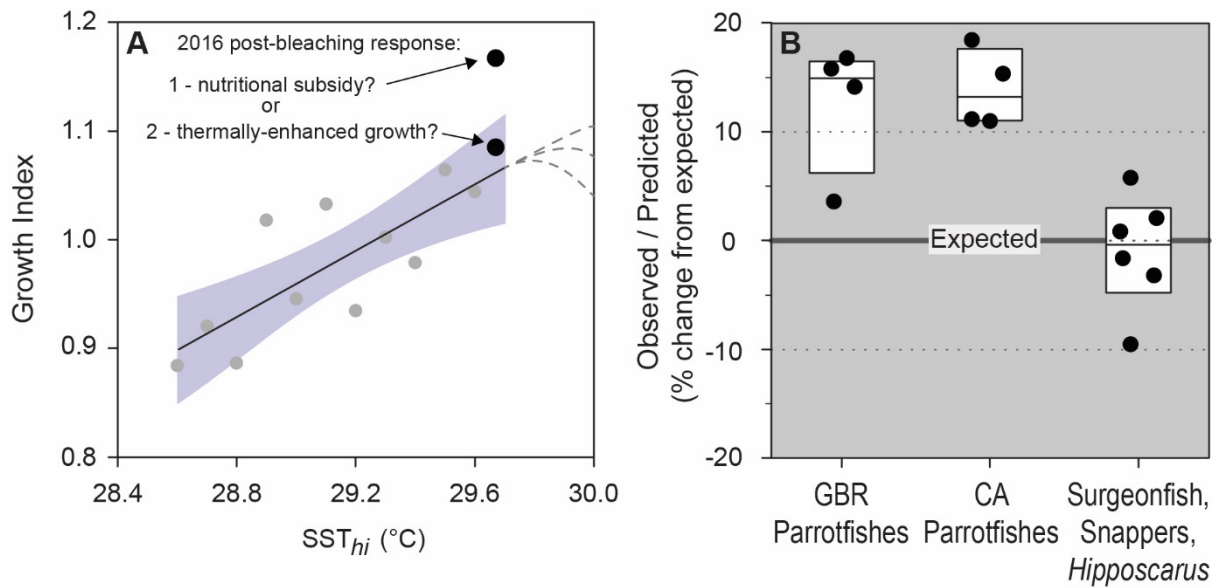
Figure 3. Post-bleaching growth response in the context of thermal performance.
(A) Growth performance in ectotherms increases with temperature up to a particular
threshold, thereby generating thermal performance curves. Increased metabolic
demands associated with higher temperatures require greater food intake. We used
thermal response relationships (Supplementary Material; Figure S4) to assess
whether increased growth of parrotfish after bleaching (hypothetically represented
by the black dots) results from enhanced nutritional resources (yielding greater than
expected growth indices) or simply reflects higher growth rates within a range
expected from thermal performance relationships. (B) Overall, parrotfishes from
both regions exhibited post-bleaching growth responses between 10-20% greater
than expectations based on thermal performance. Species not hypothesized to have
enhanced growth associated with coral bleaching responded as predicted.

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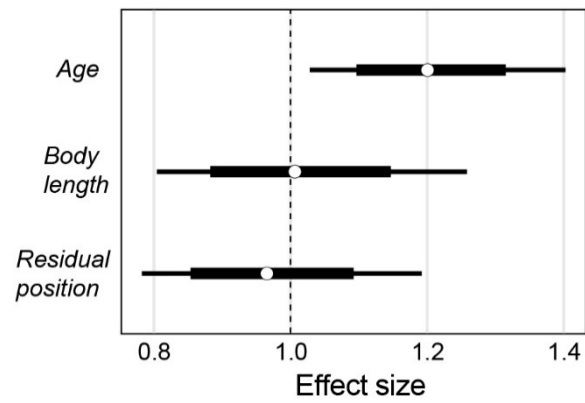
Figure 4. Estimated effect sizes from the linear mixed-effects model predicting the magnitude of post-bleaching growth response across eight parrotfish species. Thick and thin bars represent 75% and 95% confidence intervals, respectively. Dashed line indicates no estimated effect.

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4 | Discussion

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

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

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

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