

Synchronous biological feedbacks in parrotfishes associated with pantropical 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 are entraining the biological responses of disparate communities to respond in synchrony. This may fundamentally alter feedbacks in the relationships between parrotfishes and reef systems.

KEYWORDS

climate change, coral reefs, growth, herbivory, production, resilience

1 | INTRODUCTION

Climate change impacts are altering ecosystems across the globe (Hoegh-Guldberg & Bruno, 2010; Walther, 2010; Walther et al.,

2002). 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

(Camac, Williams, Wahren, Hoffman, & Vesik, 2017; Seidl, Schelhaas, & Lexer, 2011), 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 kick-start negative biological feedbacks that confer resistance to changes in trajectory and may maintain the potential for regeneration after disturbance (Chapin, Torn, & Tateno, 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, Folke, & Moberg, 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 (Bruno, Cote, & Toth, 2019; Hughes, Anderson, et al., 2018; Hughes, Kerry, et al., 2018). 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 to 2017 (Hughes, Anderson, et al., 2018). The temporal alignment and magnitude of geographically disparate bleaching events in recent years suggest 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, Hughes, Nes, & Scheffer, 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 & Choat, 2018; Clements, German, Piché, Tribollet, & Choat, 2017). 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., Emslie & Pratchett, 2018; Questel & Russ, 2018; Russ, Questel, Rizzari, & Alcalá, 2015). However, direct evidence linking disturbance events to demographic responses by parrotfish populations remains lacking (Taylor, Trip, & Choat, 2018). 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. A hypothesis that incorporates disturbance-mediated feedback loops between parrotfishes and coral communities suggests a more nuanced and complex system than the traditional view of constant top-down control might imply (Bruno et al., 2019). Resolving this relationship is a critical goal if we are to understand the organization and resilience of coral reef ecosystems in the Anthropocene, and most importantly, the ability of reefs to support human livelihoods in the future (Brandl et al., 2019; Woodhead, Hicks, Norström, Williams, & Graham, 2019).

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

2 | METHODS

2.1 | Study sites and fish sampling

This study sampled coral reefs of the Chagos Archipelago (CA; central Indian Ocean) and the northern Great Barrier Reef (GBR; western Pacific Ocean; Figure 1). The northern atolls of the CA have been uninhabited for over four decades and have been under full protection from fishing since 2010; the outer reefs of the Lizard Island region of the GBR have been managed using a well-enforced network of marine protected areas, and herbivorous species are not targeted by fishers in the region. Hence, both locations support relatively pristine and diverse parrotfish assemblages (Johnson et al., 2019; Samoilys, Roche, Koldewey, & Turner, 2018). Coral reefs of the CA and the GBR have experienced severe

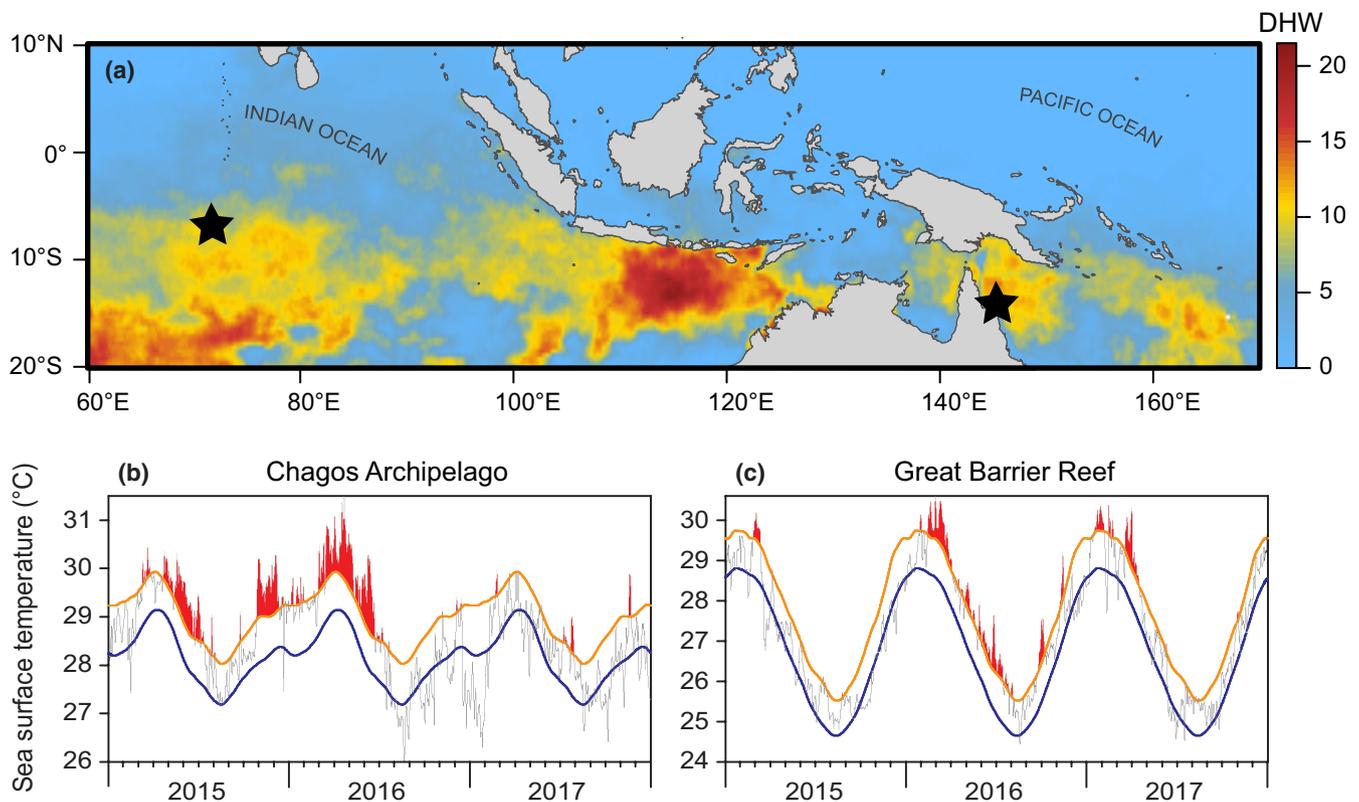


FIGURE 1 Heat exposure in the tropical Indo-Pacific during 2015–2017. Black star symbols (a) show locations of study sites in the Indian (Chagos Archipelago) and Pacific Oceans (northern Great Barrier Reef) where widespread coral bleaching occurred during 2015–2017. The color scale in (a) displays Degree Heating Weeks (DHW, °C-weeks) during March–April 2016, when both regions faced the greatest thermal stress. Bottom panels (b, c) highlight thermal anomalies during 2015–2017 at each location (blue line, seasonal expected temperature; orange line, seasonal threshold temperature [90th percentile, following Hobday et al., 2016]; gray line, observed temperature. Source: Schlegel, 2018)

heat stress and consequent coral bleaching during 2015–2016 and 2016–2017, respectively, resulting in drastic losses of living coral cover (Head et al., 2019; Hughes, Kerry, et al., 2018; Sheppard et al., 2017).

We sampled adult parrotfishes from reefs that experienced high mortality of coral due to bleaching in each region on two occasions (GBR: December 2017 and March 2019; CA: May 2018 and March 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 color 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 1,200 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 transverse section <200 μm thick and a coverslip was applied using thermoplastic glue. Otolith cross sections were photographed using an Olympus DP27 digital camera on an Olympus SZ61TR stereo microscope with a transmitted light source.

The widths of annual increments were measured three times for each individual along parallel transects on the ventral side of the otolith cross section using ImageJ (version 1.52; National Institutes of Health; Supporting Information). Mean estimates across the three replicate series were used to represent each year's otolith growth at the corresponding fish age. Increments were measured from the center of an opaque zone to the center of the

following opaque zone, representing the annual growth between austral spring seasons (Choat, Axe, & Lou, 1996). Because growth increments naturally decrease in width as fishes age, individual series for the shorter lived parrotfishes and surgeonfishes were standardized by detrending as follows. A growth index for the first year of life was estimated by dividing the increment width by the grand mean Year 1 increment width from all fish within a given species. Subsequent annual growth performance for individuals is relative to the growth pattern of that fish, rather than compared to the performance of others. For example, a strong year of growth for a small individual may produce an increment width of only average size for a given age compared with that of other members of the population. Therefore, the remaining growth series was detrended by fitting a power function (Increment width = $a[\text{age}]^b$) to the increment width by age data for each specimen and dividing the observed width by the predicted width (Figure S1). To ensure sufficient data points to appropriately fit the power curve within specimens, only specimens ≥ 5 years old were included in the analysis. The detrended series were aligned by calendar year and a mean index chronology for each species was developed across years with ≥ 5 individuals. Because the two snapper species were considerably longer lived and therefore subject to changes in growth on decadal scales, these species were detrended using a double detrending method detailed in the Supporting Information. A Pearson correlation matrix was used to compare annual growth responses across all species. Population signal strength for all species (i.e., common variance among individuals) was assessed by calculating the interseries correlation, represented by the mean correlation of each detrended individual series with the mean of all others.

2.3 | Decoupling thermal growth responses from bleaching

Thermal performance curves for ectothermic species demonstrate that physiological performance, and therefore growth rate, increases with temperature until an optimum is reached; beyond this point, performance declines (Huey & Kingsolver, 2019). We set out to determine whether coral bleaching (which occurs at the highest water temperatures) is associated with enhanced growth in parrotfishes irrespective of trends in thermal response. To decouple the potential influence of coral bleaching on otolith growth from the standard thermal growth response, we fitted linear regressions to the population-level growth index predicted by sea surface temperature from the warmest annual 3 month period (the "growing season"; SST_{hi}). SST_{hi} data were extracted and summarized from the HadISST database (Met Office Hadley Centre's Sea Surface Temperature dataset; available from <https://coastwatch.pfeg.noaa.gov/erddap/griddap/erdHadISST.graph>); March–May for CA and January–March for GBR. This analysis excluded data from 2016, the year for which chronologies indicated a spike across multiple populations. We then examined the difference between the observed and predicted (based on

linear regressions) 2016 growth index to test for an increase in the post-bleaching growth index beyond what is predicted based on the relationship between temperature and growth. Although full performance curves are inherently nonlinear, we used linear fits to summarize responses because our observations spanned only slightly less than 1°C, a range over which strongly nonlinear trends are unexpected. Additional six specimens of *C. microrhinos* from January 2012 collections at the GBR (representing all those available from this collection period that were ≥ 5 years old, following the criterion described above) were included in this analysis to extend the number of annual growth index/SST_{hi} pairs. We also fitted linear regression models to all data for each species and evaluated the influence of post-bleaching responses using Cook's distance (Cook, 1977).

2.4 | Drivers of individual growth response

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

3 | RESULTS

3.1 | Growth chronologies

For eight of the nine parrotfish species we sampled, the highest annual growth index for the past decade occurred during 2016. The exception was the phylogenetically distinct *H. longiceps* from GBR (Figure 2). The increase in increment width was most pronounced for *S. altipinnis* (GBR) and the three *Chlorurus* spp. from the CA. All parrotfish species from CA had 2016 growth indices with 95% confidence intervals (CI) that did not overlap with the expected (value = 1.0), indicating significant departure from expected patterns of growth (Figure S3). The trend of increased growth was also apparent for GBR parrotfishes, but *S. altipinnis* was the only species for which the growth index 95% CI did not overlap 1.0 (Figure S3). For some of these species, this may reflect the lower sample sizes obtained from the GBR reefs. The surgeonfishes *A. lineatus* and *N. unicornis* (both locations), the two snappers *L. bohar* and *L. gibbus*, and the parrotfish *H. longiceps* showed unique annual patterns of growth with little, if any, commonalities among species. Overall, parrotfishes generally had higher interspecies as well as interseries (within species) correlations (Table S1; Figure S2) than other

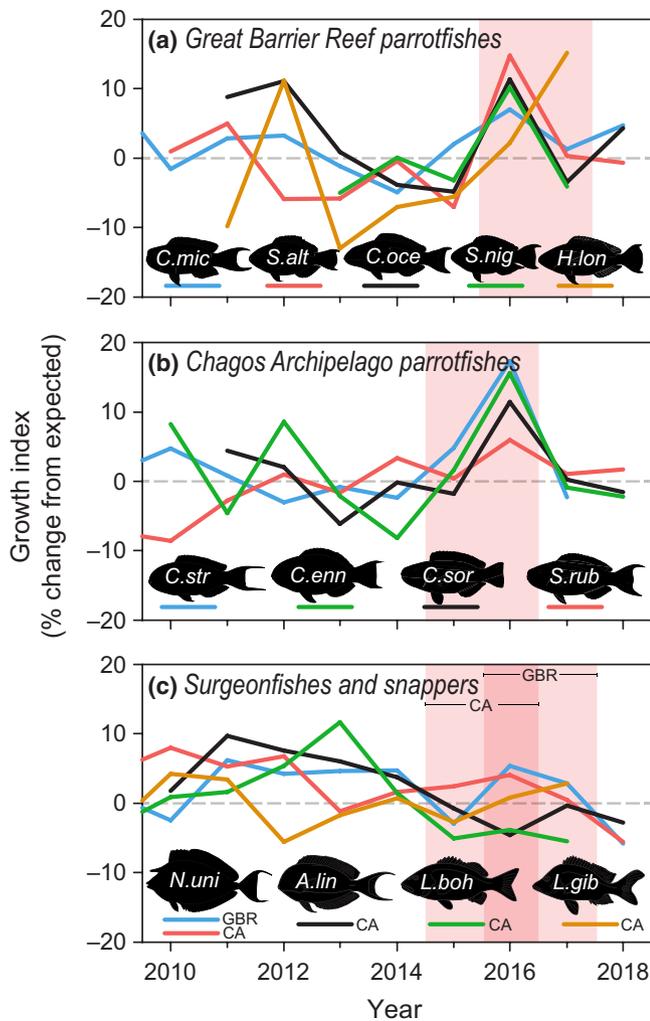


FIGURE 2 Otolith growth-increment chronologies for parrotfishes from the Great Barrier Reef (a) and the Chagos Archipelago (b), as well as for surgeonfishes and snappers from both locations (c). Lines represent the mean population-level growth response through time for each respective species. Shaded 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 Figure S3

species, with both metrics positively influenced by the synchronous signal during 2016. This result implies temporal synchrony in growth patterns within and among parrotfishes between ocean basins.

3.2 | Thermal growth response versus bleaching response

Otolith growth in 2016 (post bleaching) greatly exceeded thermal performance expectations for parrotfishes that had peak growth indices in that year (Figure 3). Post-bleaching growth indices for these species greatly influenced their respective SST_{hi} -growth response relationships, with an average Cook's distance value of 4.84 (± 1.31 SD) times greater than the mean, versus 1.53 (± 1.92 SD) for species that

showed no bleaching response (Table S2). We note that *N. unicornis* from GBR had a high Cook's distance value for 2016 (5.33, Table S2), although the growth index value for that year did not exceed what was expected (Figures S3 and S4). On average, the eight parrotfishes (excluding *H. longiceps*) had post-bleaching growth indices that were 10%–20% greater than expected (mean = $13.25 \pm 4.69\%$ SD; Figure 3b), with five of these species exhibiting 2016 indices well outside the 95% confidence bands derived from relationships with SST_{hi} (Figure S4). Only *C. microrhinos* had an observed index reasonably close to predicted values (3.6% higher). In contrast, the surgeonfishes, snappers, and the parrotfish *H. longiceps* had observed growth indices that did not differ from expected ($M = -0.97 \pm 5.24\%$ SD; Figure 3). Across all species, observed relationships between growth indices and SST_{hi} reflected both positive and negative trends, suggesting these species are collectively straddling the peak of their thermal performance curves in the recent decade. Notably, half of the parrotfishes (*Cet. ocellatus* and *S. niger* in GBR, *Chl. sordidus* and *S. rubroviolaceus* in CA) had decreasing growth index values associated with increasing SST_{hi} , whereas post-bleaching growth index values (during the hottest year) were far greater than the expected trend.

3.3 | Individual growth responses after bleaching

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

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—were 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 & Choat, 2018; Clements et al., 2017) that posits that parrotfishes benefit

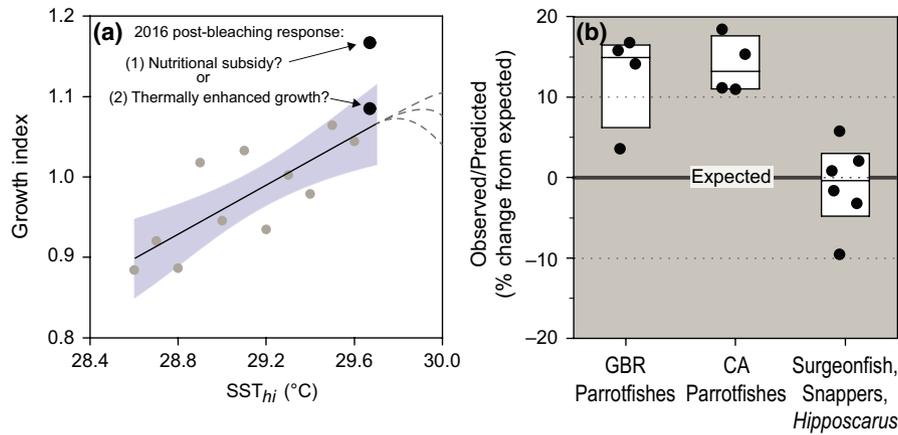


FIGURE 3 Post-bleaching growth response in the context of thermal performance. (a) Growth performance in ectotherms increases with temperature up to a particular threshold, thereby generating thermal performance curves. Increased metabolic demands associated with higher temperatures require greater food intake. We used thermal response relationships (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% and 20% greater than expectations based on thermal performance. Species not hypothesized to have enhanced growth associated with coral bleaching responded as predicted

(a) ANOVA table

Factor	df	Coefficient	SE	F	p
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	AIC _c	BIC	log-likelihood	p
2016GI ~ age	4	534.4	547.1	-263.1	0.106
2016GI ~ 1 (null)	3	534.9	544.5	-264.4	

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

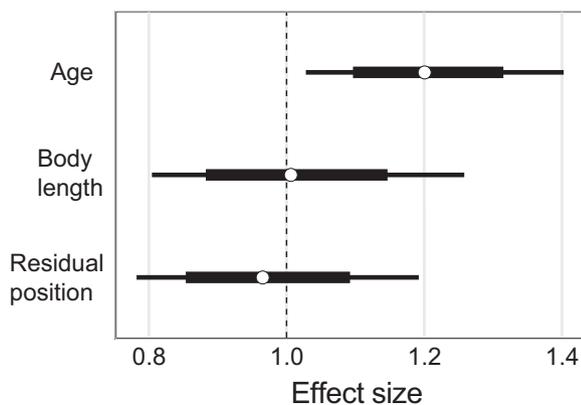


FIGURE 4 Estimated effect sizes from the linear mixed-effects model predicting the magnitude of post-bleaching growth response across eight parrotfish species. Thick and thin bars represent 75% and 95% confidence intervals, respectively. Dashed line indicates no estimated effect

from disturbance to corals and the resultant expansion of nutritional resources through succession of microbial photoautotrophs on or in carbonate substrata. Furthermore, a mode of life that benefits from successional change implies a fundamentally different and more nuanced set of ecological feedbacks between parrotfishes and benthic substrates than previously considered—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., Adam et al., 2011; Gilmour, Smith, Heyward, Baird, & Pratchett, 2013; Lamy, Legendre, Chancerelle, Siu, & Claudet, 2015; Lindahl, Öhman, & Schelten, 2001; Russ et al., 2015; Wilson, Graham, Pratchett, Jones, & Polunin, 2006), 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 CA (Sheppard, Spalding, Bradshaw, & Wilson, 2002) and on the GBR (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 leaving the underlying skeleton still intact, at least initially (e.g., bleaching, crown-of-thorns). Increased densities of successional photoautotrophic microbial communities that are a nutritional resource for parrotfishes then follow. Our review of the literature suggests that parrotfishes typically respond to disturbance by increasing in numbers with a peak occurring approximately 2 years after the event. Numerical densities at this time are a factor of two to eight times the predisturbance densities (e.g., Adam et al., 2011; Gilmour et al., 2013; Russ et al., 2015). Longer term (decadal) datasets demonstrate a return to predisturbance densities following coral recovery across a wider range of timescales (up to a decade or more; e.g., Russ et al., 2015). A lagged effect at this scale implies not only an initial expansion of resources following disturbance-related coral mortality but also a significant augmentation of nutritional resources at a level that enhances somatic and subsequent population growth. The ubiquitous pattern we observed of spikes in growth immediately following bleaching across the multiple species of parrotfishes provides strong evidence that the expansion and enhancement of nutritional resources by the proliferation of photoautotrophic microbial communities underpin the demographic responses commonly observed across species and locations. This appears to be particularly true for bleaching events versus other forms of disturbance as the heat-driven proliferation of photoautotrophic microbes following mortality enhances dissolution of coral skeletons (Leggat et al., 2019), providing ideal nutritional gains for microphages. Our observation that individual traits (e.g., body size, age, sex) were not good predictors of the magnitude of the otolith growth response in parrotfishes is not surprising, as we would not expect either density-dependent or size-dependent competition to be strong following resource expansion.

There was a strikingly consistent temporal alignment in annual growth responses between ocean basins, whereby eight of nine parrotfish species had their highest growth index value in 2016. This consistency was initially unexpected given that there was a slight offset in the timing of maximum thermal stress and consequent bleaching between the CA and GBR. Reefs of the CA experienced widespread bleaching in 2015 and 2016, with stark declines in relative coral cover observed following both annual events (Head et al., 2019; Sheppard et al., 2017). 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, Kerry, et al., 2018; Hughes et al., 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 animal material and is thus distinct from that of most other parrotfishes (de la Torre-Castro, Eklöf, Rönnbäck, & Björk, 2008).

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

The contrasting patterns of parrotfish abundance and coral cover on disturbed reefs suggest a negative feedback system whereby removal of living coral benefits somatic growth and ultimately demography of parrotfishes. This increase in size and density of parrotfishes leads to increased rates of grazing and reworked sediment by at least the same magnitude as observed increases in density, thereby potentially enhancing the role parrotfishes play in coral recovery. Finally, recovery of coral cover eventually reduces abundance of parrotfishes to predisturbance levels

(cf. Cramer, O'Dea, Clark, Zhao, & Norris, 2017). Presumably, lack of coral recovery and the successional dominance of algae on coral skeletons may have the same effect on parrotfish abundance over time by reducing endolithic and early successional epilithic photoautotrophs. This view integrates the context of disturbance dynamics and cycles of succession on coral reefs and, as such, posits a more nuanced framework of interaction compared with the classical notion in which coral reef herbivores, including parrotfishes, simply exert constant top-down control on the structure of the reef. We note that the latter viewpoint (previously considered a positive feedback loop; van de Leemput et al., 2016) largely ignores the influence of disturbance cycles and has not been met with robust empirical support (Bruno et al., 2019; Questel & Russ, 2018), likely because of the complex interactions of a myriad of stressors affecting coral reefs (Hughes & Connell, 1999). Robust analysis of ecosystem recoveries after severe coral bleaching has demonstrated that herbivore biomass can predict the recovery potential of coral reefs, but other factors such as reef structural complexity, juvenile coral density, and depth are far better predictors (Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015). Many studies suggest parrotfishes indirectly facilitate coral recovery by increasing suitable settlement substratum through feeding (Birkeland, 1977; Burkepile & Hay, 2008; Mumby & Steneck, 2008); however, this interaction appears to be dependent on the demographic composition of both juvenile corals and parrotfishes, since incidental mortality from feeding on the reef substrate may limit post-settlement survivorship of corals (Mumby, 2009; Trapon, Pratchett, & Hoey, 2013). Ultimately, the evidence suggests that interactions between parrotfishes and benthic communities are not straightforward—especially in the highly diverse fish assemblages of the Indo-Pacific—and are likely dependent on many external factors (Bruno et al., 2019). If this system represents a true negative feedback process (i.e., one that enhances system stability by diminishing fluctuations of processes involved), then evidence from this study and others suggests that influences from the benthic communities on parrotfishes (i.e., bottom-up forces) are more pronounced and consistent than top-down processes. Furthermore, such a feedback system would have previously manifested at small spatial scales, given the historically patchy nature and lower severity of the disturbance events described above. However, these events are now emerging more frequently and at global scales (Hughes, Anderson, et al., 2018; Oliver et al., 2018).

Temporal synchrony in biological processes (e.g., abundance patterns of species, demographic rates of individuals, or functional composition of communities) represents the level of common variance over time in a biological system (Loreau & de Mazancourt, 2008). An increased frequency of extreme climatic events (such as thermally induced coral bleaching) is expected to enhance synchrony within ecosystems, as extreme events often disproportionately influence biological processes and may change ecosystem functions (Jentsch, Kreyling, & Beierkuhlein, 2007). High biological synchrony may also indicate low response diversity, implying an ecosystem with low resilience to change (Mori, Furukawa, & Sasaki, 2013). Recent climate

histories are driving synchronous biological and physical patterns across multiple ecosystems (e.g., Black et al., 2018). The patchiness and high level of demographic diversity across small areas within coral reef systems (Gust, Choat, & Ackerman, 2002; Kingsford, Welch, & O'Callaghan, 2019; Taylor, Brandl, et al., 2018) imply that population dynamics of organisms within coral reefs are heavily influenced by individual microhabitats, perhaps to an extent greater than most other ecosystems. Hence, the temporal synchronization of growth responses across spatially disjunct populations spanning two ocean basins following pantropical bleaching highlights the severity and pervasiveness of the effects of contemporary climate change.

The recent decline of coral reef ecosystems has brought the role of ecosystem functioning to the forefront (Bellwood, Hughes, Folke, & Nyström, 2004). Bellwood, Streit, Brandl, and Tebbett (2019) defined “function” as the movement or storage of energy or material, which implies that the key to understanding functions is through rate-based ecological processes (Brandl et al., 2019). However, many long-established functional classifications commonly used in the context of coral reefs were derived from observations of “pre-bleaching, 20th-century reefs” (Bellwood et al., 2019). The view presented here emphasizes the strong feedback linkages on coral reefs between (a) carbonate dynamics, that is, coral-mediated carbonate production and parrotfish-mediated bioerosion; and (b) plant-herbivore interactions, that is, primary production by microscopic photoautotrophs and parrotfish herbivory. Clearly, understanding the interactions between these rate processes will be as important as measuring the processes themselves. The present study and others demonstrate that disturbance is a key process that mediates ecological functions on coral reefs by having a profound influence on the rates of movement and storage of nutrients and material. Parrotfishes are considered a major functional group on coral reefs and here we demonstrate that disturbance can influence the capacity for nutrient harvesting that fuels growth processes and provides storage products that underwrite the investment in reproduction, thereby stimulating change in demographic and grazing rates over time that will interact with carbonate dynamics and ultimately influence reef geomorphology. Unfortunately, the natural states of ecosystems are changing over ecological timescales, with increased frequency and severity of disturbance cycles engendering an uncertain future for the responses of communities.

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SUPPORTING INFORMATION

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