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Severe coral loss shifts energetic dynamics on a coral reef

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Abstract

1.   Declining coral cover and loss of structural complexity are widely reported on today's coral reefs. While coral loss frequently triggers changes in coral reef fish assemblage structure, the ecosystem-scale consequences of these changes are poorly known.
2.   Here we evaluate how four metrics of energy flow and storage that underscore a critical coral reef function, consumer biomass production, respond to severe coral loss on a coral reef in the northern Great Barrier Reef, Australia.
3.   We compared fish and benthic surveys at Lizard Island from 2003 to 2004 with surveys in 2018 using an individual-level modelling approach that integrates growth and mortality coefficients to estimate community-level standing biomass, productivity, consumed biomass and turnover.
4.   In the study period, coral cover declined by 72%–83% in forereef zones while turf cover increased by 18%–100% across all zones. Reef fish assemblages, in turn, responded with a 71% increase in standing biomass, 41% in productivity and 37% in consumed biomass, mainly driven by nominally-herbivorous fishes (Labridae—Scarini, Acanthuridae and Siganidae). By contrast, biomass turnover rates declined by 19%.
5.   Our findings suggest that coral loss can drive energetic shifts on coral reefs, leading to more productive, but slower paced reef fish assemblages. Although the observed build-up of biomass may appear positive, the decreased turnover rates indicate that the system is unable to maintain biomass replacement levels. This suggests that the

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enhanced productivity that accompanied coral loss may be driven by storage effects from the somatic growth of individuals already present, questioning the temporal stability of these changes to coral reef ecosystem functioning.

A free **Plain Language Summary** can be found within the Supporting Information of this article.

1 INTRODUCTION

The unprecedented, world-wide coral bleaching events of 2015–2017 sparked a re-evaluation of coral reef research, conservation goals and the role of corals in underpinning the services provided by coral reefs (Bellwood, Pratchett, et al., **2019**; Bruno, Côté, & Toth, **2019**; Hughes, Barnes, et al., **2017**; Williams et al., **2019**). There have been calls to accept this new low-coral state as an inevitable long-term situation, strengthened by ongoing coral degradation events (Bellwood, Pratchett, et al., **2019**; Hughes, Barnes, et al., **2017**). If we are to embrace this new reality, we need to understand the biological and ecological attributes of these new coral reef ecosystems (Bellwood, Streit, Brandl, & Tebbett, **2019**; Brandl, Rasher, et al., **2019**; Graham, Jennings, MacNeil, Mouillot, & Wilson, **2015**). For example, how will new reef configurations affect the energetic dynamics of coral reefs, and can they maintain their capacity to provide food resources for people?

Reduced coral cover and loss of structural complexity are the most widely reported contemporary changes in coral reef ecosystems (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, **2009**; Graham et al., **2015**; Hughes, Kerry, et al., **2017**). Such degradation is often exacerbated by other ecosystem stressors, such as increased benthic sediment loads (Tebbett, Streit, & Bellwood, **2019**) and reduced water quality (MacNeil et al., **2019**). The effect of these synergistic stressors on associated biota are often showcased by the responses of coral reef fishes (e.g. Pratchett, Thompson, Hoey, Cowman, & Wilson, **2018**; Stuart-Smith, Brown, Ceccarelli, & Edgar, **2018**) because of the critical services fishes provide in tropical ecosystems (e.g. fisheries resources, aesthetical value, Marshall et al., **2019**) and their potential role in mediating coral reef resilience (Bruno et al., **2019**; Hughes, Graham, Jackson, Mumby, & Steneck, **2010**; Hughes et al., **2007**).

Reef fish responses to coral reef degradation are often species-specific, depending on body size and the degree of dependence on live coral (e.g. Ceccarelli, Emslie, & Richards, **2016**; Cheal, MacNeil, Emslie, & Sweatman, **2017**; Graham et al., **2007**; Stuart-Smith et al., **2018**). Corallivorous, planktivorous and coral-dwelling fishes are reported to be particularly susceptible to coral loss while herbivores appear relatively resilient (Gilmour, Smith, Heyward, Baird, & Pratchett, **2013**; Graham et al., **2006**; Pratchett et al., **2018**; Stuart-Smith et al., **2018**). Because many of the species investigated initially respond negatively to coral loss (e.g. Bellwood, Hoey, Ackerman, & Depczynski, **2006**; Wilson, Graham, Pratchett, Jones, & Polunin, **2006**), it is generally expected that assemblage-level fish responses would also be negative. However, species-level responses to coral loss are neither linear nor additive at the ecosystem level, with evidence suggesting that post-coral loss stability in coarse fish assemblage metrics, such as abundance or biomass, is possible (Bellwood et al., **2006**; Ceccarelli et al., **2016**; Pratchett et al., **2018**). This apparent community stability may, however, overshadow major changes in species composition that result in alternate ecosystem states (Bellwood, Pratchett, et al., **2019**; Graham, Cinner, Norström, & Nyström, **2014**; Hughes, Barnes, et al., **2017**).

The energetic consequences of assemblage level responses to coral loss for fishes have relied predominantly on a single metric, standing biomass (e.g. Ceccarelli et al., **2016**; Pratchett et al., **2018**; Robinson, Wilson, Jennings, & Graham, **2019**; Stuart-Smith et al., **2018**). However, ecosystem functions operate through time and are, thus, more accurately assessed using dynamic, flow-based rates (Bellwood, Streit, et al., **2019**; Brandl, Tornabene, et al., **2019**; Hooper et al., **2005**). Indeed, reef fish biomass and the underlying rate of biomass production often show only limited correlation (Morais, Connolly, & Bellwood, **2020**). For example, small planktivores that comprise a small standing biomass are often important drivers of total biomass productivity (Morais & Bellwood, **2019**). Similarly, small cryptobenthic fishes contribute disproportionally to the biomass consumed by predators despite a negligible standing biomass, a result of their fast-paced lifestyle (i.e. short life span and high mortality rates, Brandl, Tornabene, et al., **2019**). This suggests that different ecosystem functions are likely to respond to coral reef degradation in fundamentally different ways (cf. Rogers, Blanchard, & Mumby, **2018**).

Here we focus on the impacts of coral loss on four metrics of energy flow and storage, which underpin consumer biomass production and thus, coral reef ecosystem functioning (Brandl, Rasher, et al., **2019**). We exploit a recently expanded approach to estimate fisheries-independent fish productivity, and other ecosystem functions, in high diversity communities such as coral reefs (Brandl, Tornabene, et al., **2019**; Depczynski, Fulton, Marnane, & Bellwood, **2007**; Morais, et al., **2020**). Because this approach is applied for each individual, it provides an ideal interface with underwater fish counts, the universal reef fish censusing method. By simultaneously quantifying multiple aspects of a key ecological process, we reinforce a pluralistic, process-oriented view of ecosystem research needed to decipher and better manage contemporary reef systems (Bellwood, Streit, et al., **2019**; Brandl, Rasher, et al., **2019**; Fulton et al., **2019**; Hughes, Barnes, et al., **2017**).

2 MATERIALS AND METHODS

2.1 Study locality and survey design

We carried out fish and benthic surveys at Lizard Island, on Australia's Great Barrier Reef (GBR, Figure **1**), in 2003–2004, and 14–15 years later, in 2018. Benthic surveys were used to quantify live coral and turf cover using point-intercepts and photoquadrats along transects in 2003/2004 and 2018 respectively. We randomly subsampled points to ensure a similar precision to be able to compare among these survey methods (Appendix **S1**). In both 2003/2004 and 2018, we surveyed 13 common reef fish families using visual surveys (belt transects) and enclosed clove oil stations. A detailed description of the field procedures is available in the Appendix **S1**. To combine the different fish survey methods into a single unit containing all surveyed fish families, we applied the resampling procedure described in Morais and Bellwood (**2019**).

FIGURE 1

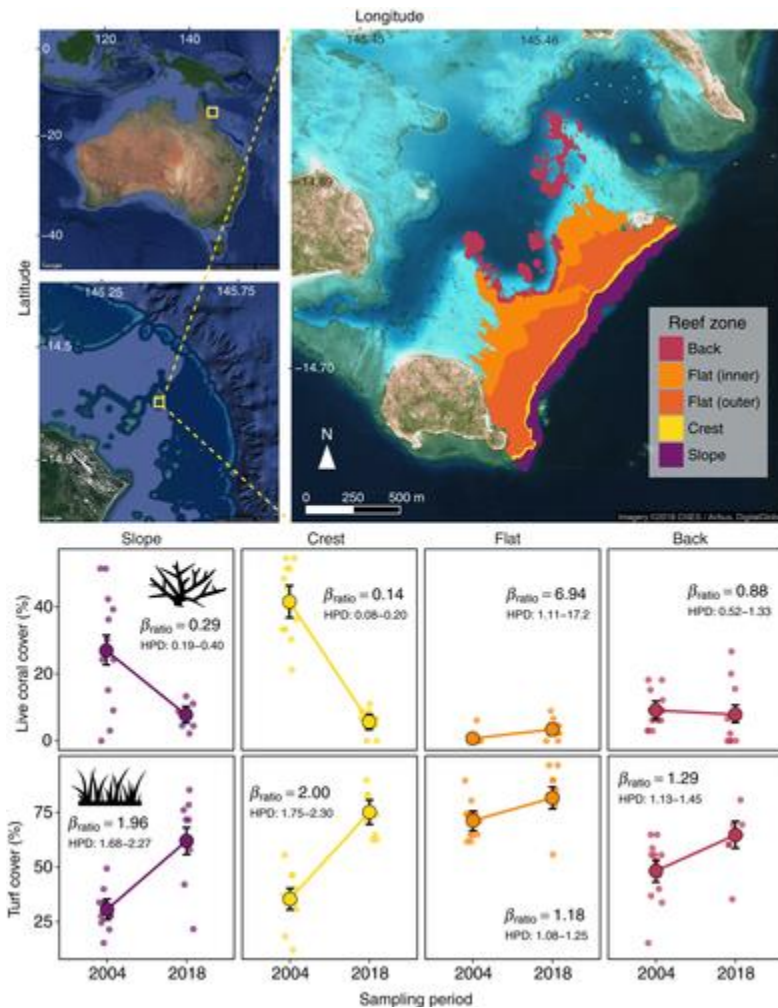The studied windward reef at Lizard Island, Great Barrier Reef. Coloured areas in the upper right panel represent the five mapped reef zones. Scatterplots show transect-level proportional live coral cover (upper panels) and turf cover (lower panels) in 2004 and 2018 (individual dots), model estimated median (larger dots), and 95% credibility interval (whiskers) for each reef zone. The inner and outer reef flats have been combined, together comprising the broader 'reef flat' zone. β_{ratio} is the ratio between the estimates in 2018 and 2004, high posterior density is the high posterior density interval of β_{ratio}

From 2014 to 2017, the reefs around the Lizard Island group were affected by four major coral degradation events which included two severe (category 5 and 4) cyclones in 2014 and 2015, closely followed by two major coral bleaching events in 2016 and 2017. These cumulative events resulted in up to 80% decline in coral cover throughout the island group, particularly at exposed sites (Ceccarelli et al., **2016**; Madin et al., **2018**). Our fish and benthic surveys were located in the southeast windward reef stretch between South Island and Bird Islet (Figure **1**) following Depczynski et al. (**2007**), and encompassed a spectrum of reef habitat zones: upper slope (7–9 m depth), forereef crest (3–4 m depth), flat (1–2 m depth) and lagoonal back reefs (2–3 m). We used satellite images to map each of these reef zones and estimate their area (Figure **1**, see Appendix **S1** for details).

2.2 Metrics of energy flow and storage

The procedures to obtain the four metrics used to evaluate energy flow and storage in this study followed Morais and Bellwood (**2019**) and Brandl, Tornabene, et al. (**2019**), and are described in detail in the Appendix **S1**. In brief, growth trajectories are predicted at the species/genus level based on traits and water temperature (Morais & Bellwood, **2018**). Then, the expected somatic growth, in g/day, is estimated by placing each individual in their predicted growth trajectory (Morais & Bellwood, **2019**). Daily mortality rates are obtained by combining species/genus mortality coefficients estimated from growth trajectories and water temperature with an exponential negative relationship with individual body size (see Appendix **S1**). These daily mortality rates are multiplied by the individual body mass to generate an 'expected per capita loss of biomass' due to mortality.

The total standing biomass and productivity of each resampled fish assemblage was derived from the combined weights and expected growth of all individuals respectively. Because productivity was estimated from the expected somatic productivity, it should be considered as a metric of potential productivity. See Appendix **S2** for a discussion on the relationship between individual weight and somatic growth. The term 'consumed biomass' is hereafter used broadly to indicate expected losses from standing biomass due to mortality, including losses that are not directly a result of predation (i.e. decomposition). These expected losses were estimated for each individual based on their likely mortality probabilities (see Appendix **S1**). While standing biomass measures an ecosystem pool of stored heterotrophic energy (scaled to t/ha), productivity and consumed biomass are dynamic ecosystem flow metrics (scaled to kg ha^{-1} day^{-1}; Hooper et al., **2005**).

We also calculated two derived rate measures: total turnover (%/year) and an instant biomass change metric (unitless). Turnover is classically defined as the ratio of production to biomass (Allen, **1971**; Odum & Odum, **1955**; Waters, **1969**). We expand on this concept by defining total turnover as the sum of net turnover (the quotient of productivity and standing biomass) and consumption turnover (the quotient of consumed and standing biomass; Brandl, Tornabene, et al., **2019**). Total turnover could be understood as the rate at which particles flow across the system, that is, are either incorporated into the food chain or released from it. Our instant biomass change metric was obtained by dividing consumed biomass by (net) productivity. This metric positions the fish assemblage along a gradient of immediate biomass response, from biomass erosion (values >1, when consumption exceeds production) to biomass accumulation (values <1, when production exceeds consumption).

To provide a system-level analysis of potential changes in the main reef habitat zones, we calculated the weighted average of the reef zone-specific standing biomass, productivity, consumed biomass and turnover. We used the area of each reef zone as obtained from satellite-based habitat mapping (see full description in the Appendix **S1**) as the averaging weights for all descriptors.

2.3 Data analyses

All data analyses were performed in R (R Core Team, **2019**). To evaluate family-level abundance and biomass patterns across reef zones, as well as potential changes from 2003/2004 to 2018, we used 100 bootstrap iterations of resampled

fish assemblages. These assemblages were aggregated by family and visualized in two dimensions using a non-metric multidimensional scaling (nMDS) ordination based on Bray–Curtis similarity of the square-root transformed community matrix. Because bootstrapped assemblages do not constitute replicates, instead of individualizing samples with dots, we depict their bi-dimensional variability using polygons. The magnitude of potential changes in each family was calculated as the $\log_{10}$ of the ratio of abundance (or biomass) in 2018 and 2003. We used the probability of an effect (decrease or increase) to guide interpretation of these potential changes.

We used a Bayesian analytical framework to test for differences in coral cover and ecosystem functioning metrics (fish standing biomass, productivity, consumed biomass and turnover) between sampling years for the different reef zones. We implemented MCMC chains using the No-U-Turn sampler algorithm in the Stan language with the RSTANARM interface to R (Goodrich, Gabry, Ali, & Brilleman, **2018**; Stan Development Team, **2018**). The full procedures, priors and model specifications can be found in the Appendix **S1**.

3 RESULTS

Between 2003/2004 and 2018, live coral cover declined from 27.0% to 7.3% on the forereef slope (72% decline, high posterior density interval [HPD] = 61%–82%) and from 41.6% to 5.7% on the reef crest (83% decline, HPD = 77%–90%; Figure **1**). There was no evidence of changing coral cover over the same time period in either the reef flat or back reef, with both HPDs including 1. The reef flat and back reef had low coral cover in 2003/2004 and remained unchanged in 2018 (Figure **1**). By contrast, turf cover increased substantially in the slope and crest (96% and 100% increase, respectively, HPD = 68%–127% and 75%–130%; Figure **1**), but less so in the reef flat and back reef (18% and 29% increase, respectively, HPD = 8%–25% and 13%–45%; Figure **1**). Turf cover had zone-specific minimum values of ~30% in 2003/2004, but did not comprise <60% in any zone in 2018.

There was a clear spatial mismatch between coral cover decline and the response of fish assemblages. While coral loss was greatest in exposed forereef habitats, fish assemblage structure changed markedly across all reef zones (Figure **2**). The direction of these changes was generally consistent among zones and was marked in terms of both abundance and biomass. Fish assemblages tended to move towards the origin of the abundance ordination, due in particular to family-level decreases in the Epinephelidae, Pomacanthidae and Chaetodontidae. A major shift towards positive MDS1 scores was largely driven by increases in Acanthuridae, Siganidae, Tripterygiidae and Pseudochromidae biomass.
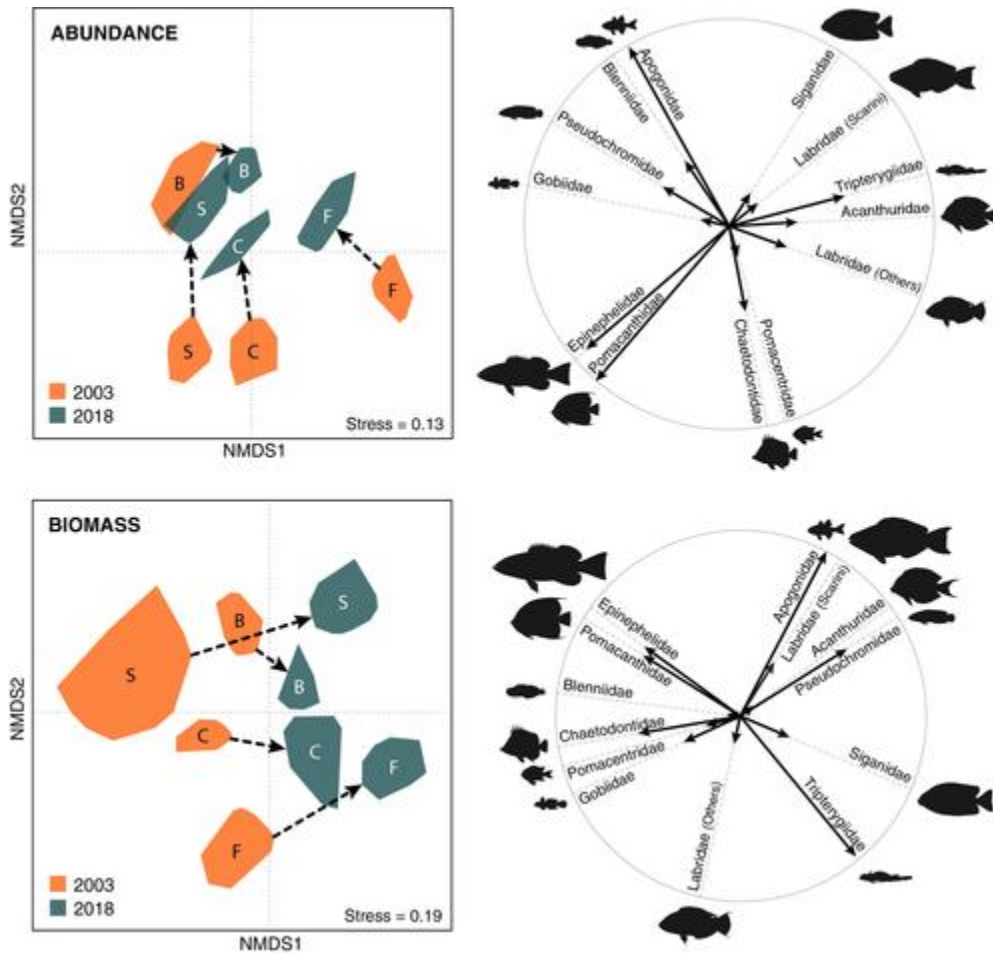
FIGURE 2

Patterns in the abundance and biomass of reef fish families among reef zones at Lizard Island in 2003 and 2018. Polygons on the left panels represent the space occupied by 100 resampling iterations of the fish assemblages for each reef zone on each non-metric multidimensional scaling, while arrows link reef zones in 2003 and 2018. Right panels exhibit the family vectors. S = slope, C = crest, F = flat, B = back reef

Changes in fish families showed a degree of consistency among habitat zones (Figures **S1** and **S2**). When family-level changes were normalized by the area of each reef zone, it became clear that the changes observed on Figure **2** were due to a combination of increases and decreases in the abundance and biomass of specific families (Figure **3**). The Chaetodontidae declined in both abundance and biomass, while the Pomacanthidae and Acanthuridae declined in abundance, but not in biomass. By contrast, the Gobiidae and Blenniidae declined in biomass, but not in abundance, whereas the Epinephelidae showed no clear reef-level change. However, most families increased in both abundance and biomass following coral loss. This includes mostly small-sized fishes, such as the Apogonidae and Pseudochromidae, but also larger body-sized groups, such as the Siganidae and parrotfishes (Labridae, Scarini). The Pomacentridae increased in both abundance and biomass, although these increases were small in magnitude (Figure **3**).

FIGURE 3
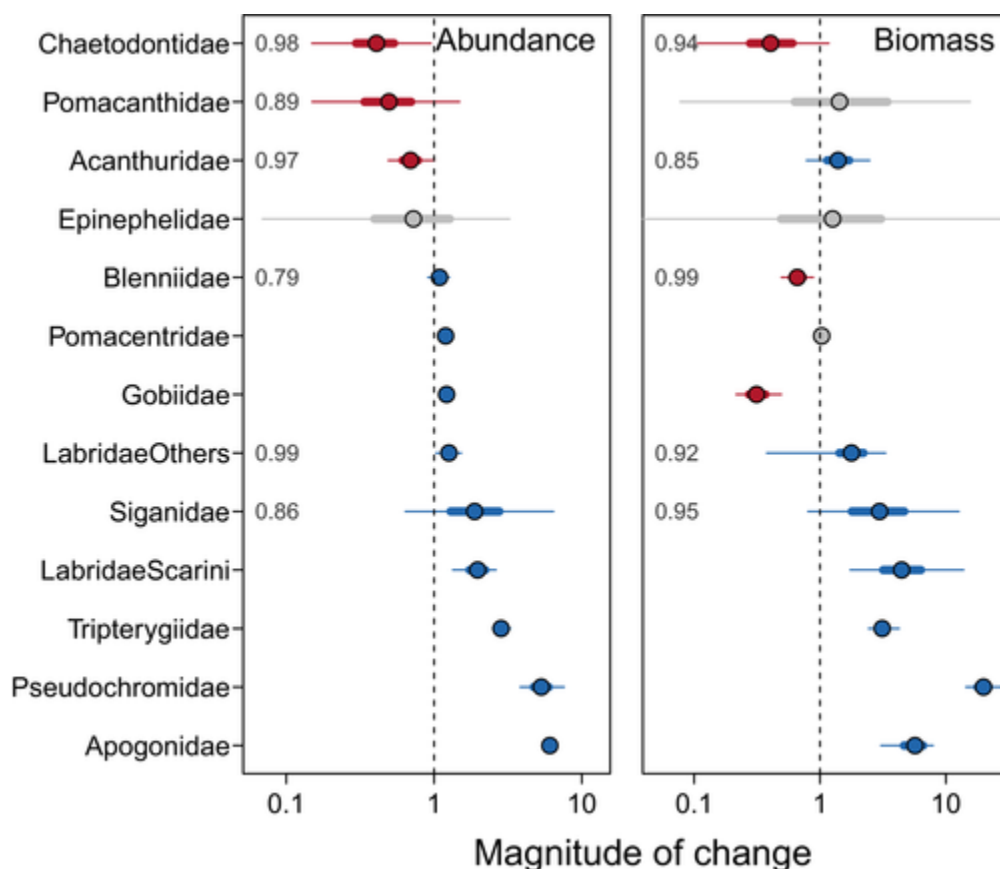Magnitude of change in the abundance and biomass of fish families on the studied windward reef at Lizard Island between 2003 and 2018. Circles represent medians across resampling iterations, wide bars the interquartile range and whiskers the 95% quantile range. Colours are proportional to the probability of an effect: grey = <70% probability of change; red > 70% probability of a decline; and blue > 70% probability of an increase. Numbers are the probabilities for all families with >70% and <100% probability (100% probabilities omitted)

Evaluating these reef-scale fish assemblage changes from an energetic standpoint revealed that total standing biomass and productivity increased by 71% (HPD = 64%–77%) and 41% (HPD = 39%–42%), respectively, while consumed biomass increased about 37% (HPD = 35%–38%; Figure **4**). This increase in standing biomass was driven by increases in parrotfishes, which were ranked fourth overall in 2003 and became second in 2018 (Figure **S3**), but also by surgeonfishes and rabbitfishes. These three families had higher abundance of moderately large individuals (100–1,000 g of body mass) and a lower abundance of relatively small individuals (with 10–100 g) in 2018 compared to 2003 (Figure **S4**). The increase in productivity in 2018 was mainly driven by surgeonfishes, parrotfishes and cardinalfishes and, to a lesser degree, rabbitfishes (Figure **S3**). Consumed biomass showed similar family-level changes to productivity (Figure **S3**).
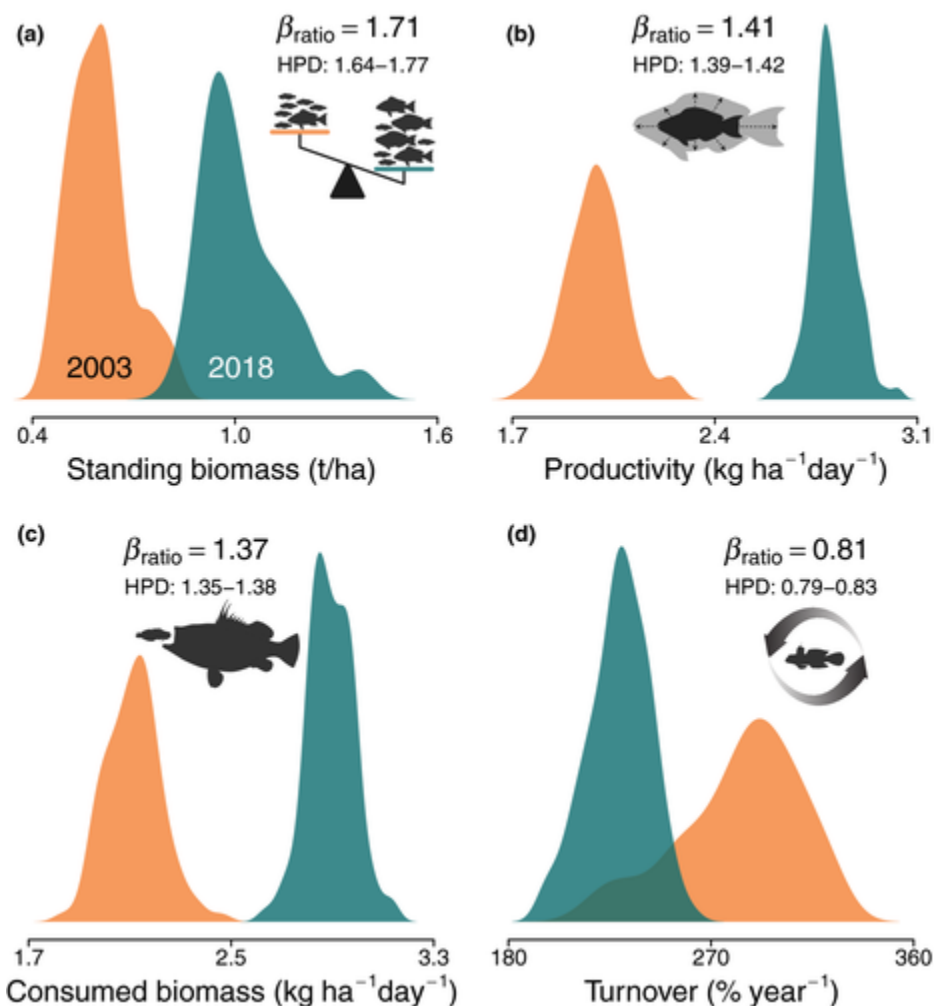
FIGURE 4

Differences in standing biomass, productivity, consumed biomass and total turnover of 13 reef fish families on a windward reef at Lizard Island between 2003 and 2018. Density curves are based on bootstrapped fish assemblages for each sampling year over 500 iterations. β_{ratio} is the ratio between the estimates in 2018 and 2003, high posterior density is the high posterior density interval of β_{ratio}

By contrast, the total turnover of this reef fish assemblage diminished by 19% (HPD = 17%–21%) between 2003/2004 and 2018 (Figure **4**). This happened irrespective of increased total abundance (from 1,275 to 1,817 individuals per 100 m^2), and of increased turnover in some small-body sized fish families (Figure **S3**). A closer look at the size structure of the fish assemblage in the two survey periods reveals that changes in biomass, productivity and consumed biomass followed similar size-related patterns (Figure **S5**). These three metrics clearly increased in the smallest sizes (from 0.1 to 1 g), and in moderately large sizes (~1,000 g, Figure **S5**). By contrast, the three showed similar values or even a small decline in the median size range (10–100 g) and very high variability in the largest sizes (>1,000 g).

Produced and consumed biomass increased at similar rates from 2003/2004 to 2018 in this fish assemblage (41% for produced and 37% for consumed biomass (Figures **4** and **5**). Consequently, there was only a small shift in the instant biomass change, that is, the ratio of consumed to produced biomass, of this assemblage in 2018 to about 96% relative to its value in 2003 (HPD = 96%–97%). In both cases, the total consumed biomass slightly exceeded the amount of

produced biomass (change >1, Figure **5**), and thus the magnitude of the instant biomass change was similar in both periods.

FIGURE 5
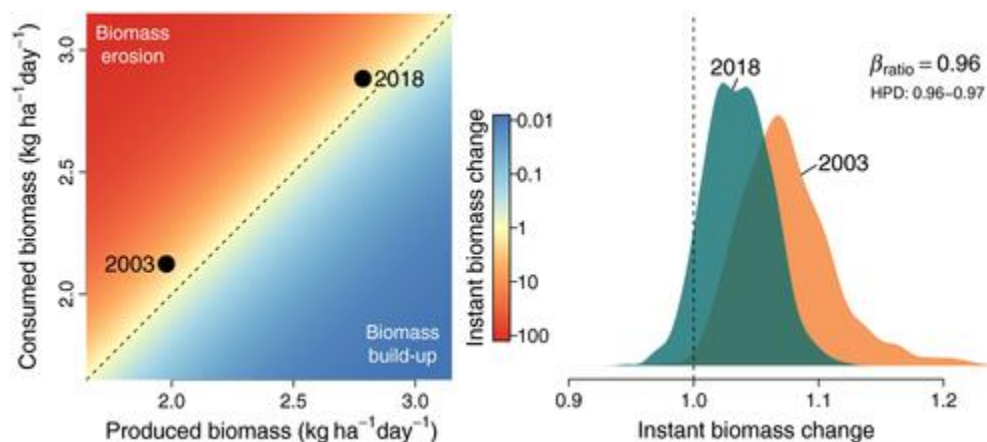The relationship between consumed and produced biomass on a windward coral reef at Lizard Island, northern Great Barrier Reef. The instant biomass change is the ratio of biomass consumption to production, with values <1 meaning biomass erosion, and values <1 meaning biomass accumulation. β_{ratio} is the ratio between the instant biomass change estimates in 2018 and 2003/2004, and HPD is the high posterior density interval of β_{ratio}

4 DISCUSSION

While the responses of coral reef fishes to coral reef degradation have attracted considerable attention (reviewed by Pratchett et al., **2008**, **2018**), most research to date has focused on species- and family-level responses and static aggregate metrics such as abundance, diversity and biomass. By estimating multiple dynamic metrics that portray consumer biomass production, a key component of ecosystem functioning, we reveal thus far overlooked ecosystem effects of coral loss that help explain previously documented assemblage responses. Most strikingly, coral loss was associated with substantial increases in total fish biomass, productivity and consumed biomass, but with decreased turnover. These findings imply a more productive but slower-paced reef fish assemblage following severe live coral loss.

4.1 Family-specific responses to coral degradation

Family-level responses were largely consistent with the literature. For example, chaetodontids exhibited the most extensive declines in abundance and biomass, a pattern repeatedly reported previously (e.g. Cheal et al., **2017**; Stuart-Smith et al., **2018**; Wilson, Graham, & Pratchett, **2013**). Similarly, although we did not observe a net decline of pomacentrids, most planktivorous damselfishes exhibited a strong decline on the reef crest (Figure **S6**) following an 86% coral loss in this zone. Such declines of planktivorous damselfishes are among the most widely reported responses of fishes after coral loss (e.g. Pratchett et al., **2008**, **2018**; Wilson et al., **2006**), potentially due to their reliance on branching coral structures for refuge (Wilson et al., **2008**; but see Wismer, Tebbett, Streit, & Bellwood, **2019**).

Positive responses were also consistent with previous studies, including increasing biomass of nominally herbivorous fishes (mainly Siganidae, Labridae—Scarini and Acanthuridae; Figure **2**). The vast majority of studies evaluating the responses of multiple coral reef fishes to coral degradation have found nominally herbivorous fishes to respond positively with increases in abundance and/or biomass (Adam et al., **2011**; Ceccarelli et al., **2016**; Cheal et al., **2017**; Pratchett et al., **2008**, **2018**; Robinson, Wilson, Jennings, et al., **2019**; Russ, Questel, Rizzari, & Alcala, **2015**; Wilson et al., **2006**). However, the families that displayed the strongest responses over the 15-year span of our study were small cryptobenthic reef fishes (sensu Brandl, Goatley, Bellwood, & Tornabene, **2018**). Pseudochromids, tripterygiids and apogonids all displayed over 10-fold increase in abundance and/or biomass (Figure **3**, Figures **S1** and **S2**), although the same pattern did not hold for gobies or blennies. Only one study has documented the response of cryptobenthic reef fishes to coral loss, likewise reporting increased abundance and a markedly different species composition following coral bleaching (Bellwood et al., **2006**, **2012**). It is possible that, because of their short generation times (Depczynski & Bellwood, **2006**), cryptobenthic fishes are more responsive to changes over medium-term timeframes than larger species.

4.2 Potential explanations for the observed energetic shifts

Our study, therefore, revealed responses of reef fishes to coral loss that reflect previous research, thus implying a typical assemblage-level response. The novelty of our findings, however, stems from an understanding of how these responses integrate with key elements of ecosystem function (Bellwood, Pratchett, et al., **2019**; Brandl, Rasher, et al., **2019**). The simultaneous increases in reef fish biomass, productivity and consumed biomass, alongside a decrease in turnover, imply higher productivity but slower-paced energetic flow in the fish assemblage of this new low-coral cover reef state. Although our study was restricted to a single locality, our results have broader implications for coral reefs because many of the key components of change (e.g. increases of nominally herbivorous fishes from the families Acanthuridae, Siganidae and Labridae—Scarini) are congruent with prior studies across the Indo-Pacific (see above).

Trophic models have suggested that reef fish productivity would follow a parabolic trajectory after coral loss (Rogers, Blanchard, & Mumby, **2018**; Rogers, Blanchard, Newman, Dryden, & Mumby, **2018**). Reduced live coral cover would initially trigger increased resource availability, favouring herbivores and invertivores; but the subsequent erosion of the reef structure would reduce the availability of predator refuges (Rogers, Blanchard, Newman, et al., **2018**). In our study, despite extensive reduction in structural complexity (as indicated by severe loss of corals, including branching ones; Figure **1** and Wismer et al., **2019**), we found no evidence of declining fish productivity. Rather, our results seem to corroborate long-term catch data that reported maintained, but increasingly variable, reef fishery yields in coral-degraded reefs that underwent phase shifts to structurally complex benthic macroalgae-dominated states (Robinson, Wilson, Robinson, et al., **2019**). However, no macroalgae-dominance shifts occurred in our site, suggesting that different mechanisms have underpinned this sustained productivity. Potential explanations for the observed ecosystem function responses in our study can be divided into two classes: (a) reduced resource limitation due to increased abundance, quality or accessibility of benthic resources; and (b) predator-release mechanisms, implying

increased fish survivorship. These mechanisms are not mutually exclusive and may reinforce one another (e.g. Carpenter, **1990**).

Nominally herbivorous fishes have been hypothesized to be resource-limited on coral reefs (Carpenter, **1990**; Hart, Klumpp, & Russ, **1996**; Hart & Russ, **1996**). Their major feeding substratum, algal turfs (Adam et al., **2018**; Bellwood & Choat, **1990**; Brandl & Bellwood, **2014**), is an important colonist of dead coral skeletons and is likely to increase in abundance following coral mortality (e.g. Diaz-Pulido & McCook, **2002**). Increased resource availability has been assumed to cause the strong correlation found between changes in coral and turf cover, and the abundance of nominally herbivorous fishes (Adam et al., **2011**; Hart et al., **1996**; Hart & Russ, **1996**; Russ et al., **2015**). Indeed, in our study, we detected algal turf cover increases of 18%–100%, depending on the reef zone, from an estimated cover of 32%–70% during 2003/2004 to 64%–83% in 2018. Some of this turf increase can be due to 'canopy-effects' from previously undetected turfs underneath structurally complex corals (Goatley & Bellwood, **2011**). However, increased energy yield of algal turfs to herbivores after coral loss is also possible if their accessibility, production or nutritional quality have improved, even if turf abundance remains unchanged. Increased accessibility can occur if larger herbivores are able to exploit algal turfs previously underneath branching corals (i.e., due to size constraints, Bennett, Vergés, & Bellwood, **2010**; Steneck, Arnold, & Mumby, **2014**) or vigorously defended by territorial damselfishes and surgeonfishes (Choat & Bellwood, **1985**; Robertson & Polunin, **1981**). Although territorial damselfishes, in particular, have been observed to decline following storm-induced coral loss (Ceccarelli et al., **2016**; Emslie et al., **2012**), these fishes were scarce in the forereef zones of our reef even before coral loss and showed no clear declining trend (Figure **S6**).

Increasingly productive algal turfs can arise, for example, through increased light irradiance from reduced coral canopy overshading or reduced sediment loads due to changes in water movements (Carpenter, **1985**; Goatley & Bellwood, **2013**; Klumpp & McKinnon, **1992**; Tebbett, Bellwood, & Purcell, **2018**). More productive algal turfs have been associated to increased herbivore biomass (Russ, **2003**). Additionally, other components of the epilithic algal matrix can be boosted under these circumstances, improving the nutritional quality of algal turfs (Clements, German, Piché, Tribollet, & Choat, **2016**; Kramer, Bellwood, & Bellwood, **2013**). Increases in turf abundance, productivity, accessibility or nutritional quality, in isolation or combination, could provide a causal explanation for the strong herbivore effect observed in our productivity metrics.

Finally, reduced predation could, in theory, contribute to the observed biomass and productivity increases through enhanced survivorship of juveniles settling from the pelagic realm or of adults migrating to forereef areas. It is unlikely that settlers would face decreased predation because of the substantial increases in the abundance of key mesopredators of juvenile reef fishes, such as labrids and pseudochromids (e.g. Connell, **1998**; Goatley, González-Cabello, & Bellwood, **2017**). However, large juveniles or adult reef fishes migrating to the area could face decreased predation risk from ambush predators that benefit from tabular coral structures for hunting (e.g. epinephelids such as *Plectropomus leopardus*, Samoilys, **1997**; Kerry & Bellwood, **2012**). Support for this hypothesis, however, is limited. Although there

was a trend of decreasing epinephelid abundance in the exposed forereef habitats (72% chance of a negative effect in the slope and crest, Figure **S1**), we did not detect clear reef-level responses of epinephelids to coral loss.

4.3 Temporal-stability and implications of energetic shifts for ecosystem functioning

Our findings suggest that cumulative coral loss can drive energetic shifts on coral reefs towards biomass accumulation. However, we did not detect a clear and consistent shift in the energetic balance (i.e. produced minus consumed biomass) of these fish assemblages between 2003/2004 and 2018, mainly because productivity and consumed biomass increased at similar rates (41% and 37% respectively). Nevertheless, the 71% increase in standing biomass during this period requires some mechanism of biomass accumulation. Two explanations appear plausible: either our two snapshot assessments obscured shifts in the balance between consumed and produced biomass that happened in between sampling periods, or the very small shift towards biomass accumulation (4%, depicted in Figure **5**) was sufficient over the 15-year time period to generate the observed biomass build-up. As noted above, the elements underpinning the observed energetic shift (i.e. increasing abundance and biomass of herbivores) are shared with other coral reefs, suggesting this may become a common feature of degraded coral reef systems. But what are the potential ecosystem consequences of the observed energetic shifts?

Superficially, the observed biomass accumulation may seem like a positive outcome of coral loss from a human perspective. The increase in fish productivity on our reef reinforces observations of stable reef fish catches after coral loss (Robinson, Wilson, Robinson, et al., **2019**), and suggests that the livelihoods of people that rely on food production on degraded coral reefs could be maintained. However, this superficial analysis conceals an important implication of another key finding of the present study: that the turnover of the fish assemblage decreased substantially despite the increased biomass and productivity.

On coral reefs, turnover has been shown to be dominated by small, fast-lived cryptobenthic reef fishes (Brandl, Tornabene, et al., **2019**; Depczynski & Bellwood, **2006**; Depczynski et al., **2007**) suggesting declines in this group could provide a primary driver for assemblage turnover. However, we observed increases in most families of cryptobenthic reef fishes including the highly abundant gobies (Figure **S3**). By contrast, we found evidence for reductions in the turnover of larger fish families (e.g. Labridae, Acanthuridae). Thus, it appears that the decline in turnover is due to a disproportional increase in the biomass relative to productivity or consumed biomass, for larger reef fishes. This is supported by a shift in the size structure of the three main nominally herbivorous fish families from 2003/2004 to 2018 (Figures **S4** and **S7**) that was not associated with an increase in overall abundance (see Figure **S3**). This size shift involved reduced biomass in small sizes (5–50 g) and increased in moderately large sizes (>500 g) for Acanthuridae and Labridae—Scarini, although these were less marked for the Siganidae (Figures **S4** and **S7**).

Decreased turnover, thus, indicates that the system is currently unable to replace biomass at the same rates as new biomass is generated. This suggests that, regardless of what mechanism underpinned the observed biomass

accumulation, the enhanced productivity might be due to storage effects from the somatic growth of individuals previously present (e.g. Hart et al., **1996**; Russ et al., **2015**). The somatic growth of individual herbivorous fishes has recently been found to increase after acute coral loss (Taylor et al., **2019**), further providing support for the role of storage effects in the enhanced productivity. Similar dynamics involving an initial increase of herbivore biomass following abrupt coral loss have been found to result in population crashes after recovery of coral cover (e.g. Gilmour et al., **2013**; Russ et al., **2015**). Even in the absence of coral recovery, sustained herbivore productivity would theoretically require sustained recruitment. However, so far, the recruitment dynamics of fishes on degraded coral reefs remain largely unknown. Finally, although our results are not entirely consistent with previous models forecasting declining fish productivity after the erosion of structural complexity (e.g. due to refuge loss, Pratchett et al., **2018**; Rogers, Blanchard, & Mumby, **2018**), it is not impossible that a low complexity threshold exists, which was not reached in our study. In this scenario, if complexity continues to decline past this 'refuge-threshold', fish populations would crash, and productivity would be bound to decline. Altogether, our findings warrant caution in interpreting the newly amassed biomass as temporally stable over extended timescales, especially where harvesting occurs.

5 CONCLUSIONS

Overall, our ecosystem-based functional evaluation of a coral reef fish assemblage after 15 years of cumulative coral loss provides evidence for nuanced but important shifts in the energetic pathways that underpin reef fish assemblages. Measuring, modelling or estimating functional attributes is gaining momentum in coral reef ecology, and can reveal key insights into the components that make or break these diverse marine ecosystems (Longo, Hay, Ferreira, Floeter, & Bates, **2019**; McWilliam et al., **2018**; Morais & Bellwood, **2019**; Ruttenberg, Adam, Duran, & Burkepile, **2019**; Streit, Cumming, & Bellwood, **2019**; Tebbett et al., **2019**). Our findings further underscore the utility of this approach and emphasize the need to investigate multiple metrics of ecosystem functioning simultaneously to reveal the complexity of functional shifts that can occur after major ecosystem shocks (Brandl, Rasher, et al., **2019**). For example, considering only standing biomass and productivity would not in itself reveal the full extent of the altered demographic dynamics unveiled by examining the turnover of this reef fish assemblage. Our results provide evidence that coral reefs facing extensive and cumulative coral loss likely undertake a number of energetic shifts. Furthermore, they suggest that, although some of these changes might be initially perceived as positive, their temporal stability is questionable.

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AUTHORS' CONTRIBUTIONS

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R.A.M., M.D., C.F., M.M., S.J.B. and D.R.B. conceived the ideas and designed methodology; R.A.M., M.D., C.F., M.M., P.N. and V.H. collected the data; R.A.M., M.D., P.N., V.H. and S.J.B. analysed the data; R.A.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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The only thing necessary for the triumph of evil is that good men do nothing"....Edmund Burke

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