RESEARCH ARTICLE

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Multi-decadal stability of fish productivity despite increasing coral reef degradation

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Abstract

1. Under current trajectories, it is unlikely that the coral reefs of the future will resemble those of the past. As multiple stressors, such as climate change and coastal development, continue to impact coral reefs, understanding the changes in ecosystem functioning is imperative to protect key ecosystem services.

2. We used a 26-year dataset of benthic reef fishes (including cryptobenthic fishes) to identify multi-decadal trends in fish biomass production on a degraded coral reef. We converted fish abundances into estimates of community productivity to track the long-term trend of fish biomass production through time.

3. Following the first mass coral bleaching event in 1998, the abundance, standing biomass and productivity of fish communities remained remarkably constant through time, despite the occurrence of multiple stressors, including extreme sedimentation, cyclones and mass coral bleaching events. Species richness declined following the 1998 bleaching event, but rebounded to prebleaching levels and also remained relatively stable.

4. Although the species composition of the communities changed over time, these new community configurations still maintain a steady level of fish biomass production. While these highly dynamic and increasingly degraded systems can still provide some critical ecosystem functions, it is unclear whether these patterns will remain stable over future decades.

KEYWORDS
bleaching, cryptobenthic fishes, cyclones, productivity, resilience, rfishprod, stability

1 | INTRODUCTION

Anthropogenic pressures, such as climate change and overexploitation, are reshaping biological systems across various scales (Johnson et al., 2017). The effects of these stressors can occur in isolation or act synergistically with other co-occurring stressors (Côté et al., 2016); therefore, the impacts of multiple stressors may manifest differently across different levels of community organisation (Darling & Côté, 2008). Although high-diversity systems may be able to resist some of these impacts (Craven et al., 2018; Shurin et al., 2007), it is unclear whether biodiversity can bolster the functioning of degraded systems (e.g. Yan et al., 2022). Given the magnitude at which we are transforming ecosystem structures (Halpern et al., 2008; Sala et al., 2000), understanding the flow-on effects

of changes in habitat configurations on critical ecosystem functions and services should be at the forefront of modern-day conservation and management actions.

Of all ecosystems, Anthropocene coral reefs are among the most threatened, with many in a state of transition (Bellwood et al., 2019; Hughes et al., 2017). Various benthic components, such as macroalgae (Graham et al., 2006; Graham et al., 2015), sessile epifauna (Norström et al., 2009; Tebbett et al., 2019) and especially algal turfs (Smith et al., 2016; Tebbett et al., 2021, 2023), are increasing in prevalence as coral cover declines globally. Although climate change is undoubtedly one of the largest drivers of coral mortality, coral reefs are also experiencing a multitude of other, localised stressors (Bellwood et al., 2019; Bruno et al., 2018; Nyström et al., 2000). For example, increased coastal development and agricultural activity has increased sedimentation and eutrophication on coastal reefs (Fabricius, 2005; Kroon et al., 2016), while intensive fishing practices have depleted herbivorous fish stocks and changed ecosystem trophodynamics (Hughes et al., 2007; Jackson et al., 2001). Area-based protection measures (i.e. marine protected areas, MPAs) currently dominate the coral reef management discourse; however, there is a mismatch between the scale of protection and the scale of the stressors (Bellwood et al., 2019; Bruno et al., 2018). Mainly, local coral reef management strategies (e.g. MPA establishment) are unable to fully mitigate stressors that occur at regional or global levels (Côté & Darling, 2010). To circumvent this mismatch in scale, future coral reef management regimes could instead target their actions towards both understanding and protecting the critical ecosystem functions and services provided by coral reefs transitioning to altered states (Hughes et al., 2018).

Although most previous work has focused on traits or derived parameters as proxies for function (e.g. standing stock biomass, total abundance, diversity), advances in the quantification of critical coral reef ecosystem functions have enabled scientists to approximate energy fluxes on transitioning reefs (Morais & Bellwood, 2020; Schiettekatte et al., 2020). While our abilities to evaluate these impacts are increasing rapidly, the magnitude and direction of these energy fluxes in response to various stressors is uncertain, especially when they are assessed at different ecological scales. Specific fish groups tend to react negatively to the loss of corals; for example, increases in the sediment load on reefs coincided with a decrease in herbivorous fish biomass production (Tebbett et al., 2021) and a loss of brightly coloured fishes (Hemingson et al., 2022). Conversely, when the entire communities are sampled across several years, fish biomass production can increase following both mass coral cover decline (Morais et al., 2020) and coral cover recovery (Hamilton et al., 2022). This discrepancy in functional responses raises the question: how will the energy fluxes of entire communities be affected over longer time-scales?

Here, we use a long-term dataset, spanning nearly 30 years, to examine changes in a key ecosystem function (i.e. consumer biomass production) of benthic reef fish assemblages through time. The assemblage incorporates a wide range of small, epibenthic fishes, including damselfishes (family Pomacentridae), wrasses (Labridae),

butterflyfishes (Chaetodontidae) and various species of cryptobenthic reef fishes, which are small, bottom-dwelling fishes that are behaviourally and morphologically cryptic (Brandl et al., 2018; Depczynski & Bellwood, 2003). The physiological constraints associated with small body sizes (e.g. limited respiratory surface area, high mass-specific metabolic rates; Nilsson et al., 2009), paired with the high habitat or microhabitat specialisation (Brandl et al., 2018; Depczynski & Bellwood, 2004), are likely to make cryptobenthic reef fishes more susceptible to extreme environmental conditions than larger reef fishes (Brandl et al., 2020). By using a novel approach to calculate fish biomass production at the community level, we quantify the changes in benthic reef fish productivity through multiple stressor events, including mass coral bleaching and extreme sedimentation.

2 | MATERIALS AND METHODS

All sampling was conducted in Pioneer Bay on the leeward side of Orpheus Island on Australia's Great Barrier Reef (GBR; 18°35′S, 146°28′E). Although protected from fishing, over the last three decades, Orpheus Island has been exposed to a wide range of environmental stressors, including multiple coral bleaching events, extreme sedimentation and cyclones (Bellwood et al., 2019; Tebbett et al., 2021; Torda et al., 2018). Orpheus Island was particularly impacted by the 1998 and 2016–2017 bleaching events on the GBR, and the inorganic sediment load in Pioneer Bay has increased by over 2000% in the last 15 years (Bellwood et al., 2006, 2012; Tebbett et al., 2021). Consequently, Orpheus Island presents an ideal model system to investigate the potential for multiple stressor events to impact the energy fluxes in benthic reef fish communities.

We investigated two different approaches to calculating the changes in energy fluxes of benthic fish communities: (i) a process-based quantification of the biomass production and (ii) the static use of abundance and standing stock biomass as proxies for biomass production. The former estimates productivity as a rate of biomass accumulation in the system by combining somatic growth and probabilities of mortality to estimate the productivity of the community per unit time per unit area (Morais & Bellwood, 2020). The latter is easily measured in the field and, although has been correlated with various human processes like fishing (e.g. Cinner et al., 2020), is not necessarily indicative of the true underlying energy fluxes of the system, which is mainly driven by nonlinear scaling relationships between energetic fluxes and biomass (Barneche et al., 2014). Consequently, we included both process-based (i.e. productivity) and static proxies (i.e. abundance and standing stock biomass) of biomass production in our analyses.

2.1 | Sampling protocol

We sampled benthic reef fishes annually from 1993 to 2021 (excluding 2014, 2017 and 2020) at approximately 3–5 m depth.

Sampling always occurred during the Austral winter to avoid sampling during the peak summer recruitment (Bellwood et al., 2006, 2012). Each year, two to four coral outcrops (hereon referred to as stations) of roughly equal sizes were sampled (approximately 2 m³; Bellwood et al., 2006, 2012). We chose stations that were isolated from continuous reef structures, could be entirely contained within the netting (see below), and had some form of structural complexity; stations were not chosen based on the status of the coral colonies present (i.e. both healthy and dead coral structures were included). Due to the extremely fast turnover and short lifespan of cryptobenthic fishes, which is typically shorter than one year (Brandl et al., 2018), mortality due to sampling likely had no impact on the productivity or community structure of the subsequent year. Because cryptobenthic reef fishes cannot be surveyed adequately using visual surveys, we used enclosed ichthyocide stations to sample the entire small benthic fish communities (e.g. Ackerman & Bellwood, 2000; Brandl et al., 2019; Morais & Bellwood, 2019). Each station was enclosed in a 2 mm mesh mosquito net (double bed), weighed along the perimeter by a 2.3 m long steel chain. The net was sown over the chain to avoid coral abrasion. The net was then enclosed in a two-man tent, again weighed down by a chain. All fishes within the net were euthanized with rotenone or (after 2000) anaesthetised with clove oil (cf. Ackerman & Bellwood, 2000); both rotenone and clove oil equally sample benthic fishes (Ackerman & Bellwood, 2002). After 5 min, the divers slowly removed the tent and net, searching for anaesthetised fishes. All fishes were collected in plastic bags and placed on ice. In the laboratory, the fishes were identified to species, where possible, and counted. All collections were done in compliance with approved permits (Great Barrier Reef Marine Park Authority G23/46994.1) and ethics (James Cook University A2752).

2.2 | Productivity calculations

To calculate productivity, we followed Morais and Bellwood (2020) using the corresponding R package RFISHPROD, which incorporates somatic growth and mortality into estimates of biomass production. Using 1000 bootstrapped boosted regression tree iterations from the *predKmax* function, we were able to calculate the standardised growth parameter K_{max} for all species. In short, K_{max} is a standardisation of the Von Bertalanffy growth parameter K (Von Bertalanffy, 1949) and can be interpreted as the rate at which fishes would reach their asymptotic size if they grew to the species' maximum recorded size (cf. Morais & Bellwood, 2018). For each surveyed species, we recorded the maximum body size ever recorded for each species, dietary preference (i.e. herbivore/detritivore, herbivore/macroalgivore, planktivore, omnivore, mobile invertivore, sessile invertivore and fish and cephalopod predator), and position in the water column (i.e. benthic, benthopelagic, pelagic) from the literature or from FishBase (Froese & Pauly, 2016).

Following the framework set forth by Morais and Bellwood (2018, 2020), we then combined these ecological traits with annual estimates of sea surface temperature using boosted regression trees, bootstrapped for 1000 iterations, to generate estimates of K_{max} (Morais & Bellwood, 2018, 2020). We collated annual mean estimates of sea surface temperature from weekly means for the same coordinate (18°35′35.412″S, 146°28′59.934″E) in Pioneer Bay for each year that was sampled from the National Ocean and Atmospheric Administration's Optimum Interpolation Sea Surface Temperature V2 (https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.html). The mean sea surface temperature over the entire survey period was 26.4°C: the temperature was lowest in 1994, 1997, 2000 and 2011 (25.9°C) and highest in 1998 (27.3°C; Table S1). For each species, we recorded the median and the 95% confidence interval of the predicted K_{max} values.

At the community or population level, mortality can be expressed as a rate and is largely dependent on the age and size of each fish (Brown et al., 2004; Gislason et al., 2010; Morais & Bellwood, 2020). To calculate the natural mortality rates (i.e. where fishing mortality is zero), we used a subsample of preserved individuals to generate size frequencies of all sampled benthic fish species. Specifically, we recorded the identity and measured the total length of all individuals collected in 2006 and 2011–2013 (Table S2). Using these measurements, we were able to generate local size distributions for all surveyed species. When there was not an adequate sample available to generate a size distribution at the species level, we used the distribution at the genus or family level. For each observation, we drew a total of 1000 random samples from a truncated normal distribution with a lower limit of zero, centred and shaped based on the corresponding species' mean and standard deviation respectively. We then used the *predM* function with a Gislason mortality equation (Gislason et al., 2010) to calculate the instantaneous mortality rate of each bootstrapped body size estimate for each observation.

We followed Morais and Bellwood (2018, 2020) to incorporate growth and mortality rates with benthic fish surveys to calculate the productivity of each species. We used the Bayesian length–weight regression coefficients (Froese et al., 2014) to convert all bootstrapped estimates of body size into standing stock biomass (g). We then used the *applyMstoch* function to apply a probability of mortality for each individual by using a Bernoulli distribution based on the instantaneous mortality rate predicted from the *predM* function (see above) to determine the fate of each individual. The *somaGain* function was then used to calculate the somatic growth expected for each surviving individual, which was determined by the instantaneous mortality rate, over the course of one day. To calculate somatic growth, we drew values of K_{max} from a truncated normal distribution bound by the 95% confidence interval of predicted K_{max} values from the above-mentioned *predKmax* function. The total productivity (g day⁻¹) was then calculated as the sum of the somatic growth after 1 day of all surviving individuals over 1000 bootstrapped iterations (Morais & Bellwood, 2020).

2.3 | Analysis

We used Bayesian generalised additive models (GAMs) to model the nonlinear changes in abundance, standing biomass, species richness and productivity of the benthic fish communities through time. We specified a negative binomial distribution with a log link to independently model the changes in abundances and richness, and a gamma distribution with a log link to independently model the changes in productivity and standing stock biomass through time. We generated individual GAMs to assess the changes of the entire fish communities. We also fit additional GAM models, fitting individual splines separately for cryptobenthic fishes and noncryptic families. Because damselfishes (family Pomacentridae) can form relatively large schools around individual coral colonies, which can have disproportionally large impacts on biomass estimates, we further separated noncryptic families into Pomacentridae and all other fishes. Distributions were chosen based on the residual error structure of the response variable and by using leave-one-out information criterion (*looic*; see Supporting Information). All models used 10,000 iterations with an initial burn-in phase of 2000 iterations and a thinning rate of five. We used the default, weakly informative priors and the thin plate regression splines as part of the BRMS package (Bürkner, 2017). To validate the models, we ran posterior predictive checks, visually inspected simulated residuals from the DHARMA package (Hartig, 2022), and used leave-one-out cross-validation to ensure that all Pareto-k diagnostic values were less than 0.7. We did not detect any temporal autocorrelation among any of the simulated residuals and achieved chain convergence on all estimated parameters for all models (rhat = 1.00).

To determine whether temporal changes in the abundance, richness, standing stock biomass and productivity of benthic fishes coincided with disturbance years, we also tested for ecological thresholds in each nonlinear time series. Here, ecological thresholds are defined as relatively large changes in the ecosystem state (i.e. abundance, standing biomass, species richness or productivity) as a response to environmental stressors (Samhouri et al., 2017), such as mass bleaching events or tropical storms. Following Samhouri et al. (2017) and Fewster et al. (2000), we quantified ecological thresholds by calculating the curvature of each time series using its respective second-order derivative of each fitted GAM. Positive second-order derivatives indicate U-shaped valleys in the time series, whereas negative second-order derivatives indicate peaks in the time series; second-order derivatives around zero indicate relatively linear patterns (Fewster et al., 2000). We calculated the second-order derivatives of each posterior draw for the smoothing term $s(year)$ for the whole-community model and $s(year, by = crypto)$ for the cryptobenthic model, and determined the strength of the threshold by assessing the median and the 95% credible interval across all posterior draws.

Finally, for all identified ecological thresholds, we assessed the changes in community composition before and after the threshold year. We performed a nonmetric multidimensional scaling ordination (NMDS) using a Bray–Curtis dissimilarity matrix based on species'

abundances or standing biomass (see Section 3). We used a fourth root and a Wisconsin double transformation on the abundance/biomass data before using a PERMANOVA to assess the difference in communities before and after the threshold. We also conducted similarity percentage (SIMPER) analyses to assess the contribution of each species to the separation of each community. All multivariate analyses were conducted using the VEGAN package (Oksanen et al., 2020); all models and figures were generated in R v 4.1.0 (R Core Team, 2021).

3 | RESULTS

Approximately half of all fishes were cryptobenthic fishes (sensu Brandl et al., 2018), mainly gobies; the remainder were mainly planktivorous damselfishes and a range of small-bodied species belonging to large-bodied families (e.g. *Pteragogus cryptus* of the family Labridae; see Brandl et al., 2018). The mean number of cryptobenthic fishes sampled per year ranged from 20.5 in 1997 to 103 in 2015, whereas the mean number of fishes from the family Pomacentridae ranged from 11.5 in 2013 to 109 in 2005. On average, only three individuals were recorded from noncryptic fishes (excluding Pomacentridae) in 1993, 1997 and 2009; in 2004, mean abundance was 11.2. We recorded the fewest number of individuals per station in 1998 ($n = 38$) and the highest in 2009 ($n = 404$).

3.1 | Changes in productivity and proxies

We found a distinct shift in the energetic dynamics between the pre- and post-1998 bleaching benthic fish communities. Despite multiple disturbances, we found an overwhelming pattern of stasis in the productivity of the postbleaching fish assemblage (i.e. 2001 onwards), with no evidence of any change between 2001 and 2021, despite multiple stressor events (median per cent change [95% credible interval]: −24% [−59% to 21%]; Figure 1a). These patterns of stasis were similarly mirrored in cryptobenthic fishes (−17.3% [−67.1% to 61.5%]; Figure 1b), pomacentrids (−39.6% [−70.6% to 5.95%]) and noncryptic fishes (19.0% [−42.2% to 100.0%]; Figure 1c). The prebleaching assemblage, however, exhibited a strong increase in the productivity of the entire benthic reef fish communities between 1993 and 2001 by 110% [3% to 284%]. This increase was not likely driven by any particular group, as there was no evidence of an increase across cryptobenthic fishes (130% [−14.4% to 401%]), pomacentrids (111% [−20.8% to 297%]) nor noncryptic fishes (58.3% [−21.4% to 268%]).

We found slightly different patterns in the proxies of productivity between the entire community responses compared to the responses of individual fish groups (i.e. cryptobenthic fishes, pomacentrids and noncryptic fishes). The abundance of the community followed a similar pattern to the productivity of the community and increased 100% [23%–198%] from 1993 to 2001, and then stabilised from 2001 to 2021 (−17% [−45% to 19%]; Figure 2a). From
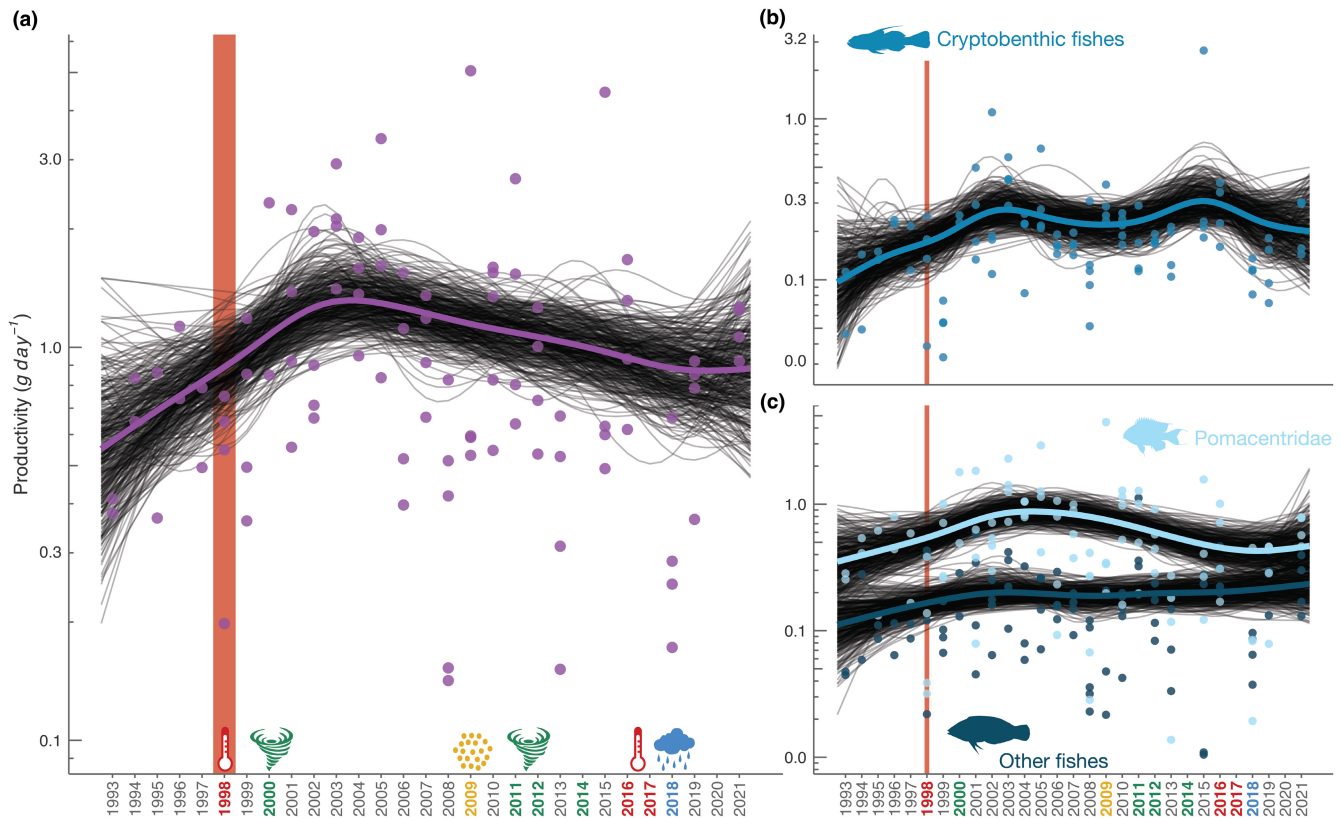
FIGURE 1 Patterns of benthic reef fish productivity ($g\,day^{-1}$) through time of (a) the entire fish community, (b) cryptobenthic fishes and (c) noncryptic fishes. The thin black lines are 400 randomly sampled draws from the posterior distribution and the thick coloured lines show the median trends. The coloured points denote the raw data points. Note the y-axes are different and on the log_{10} scale. The red bars indicate the 1998 mass coral bleaching event. The coloured axis labels along the bottom illustrate the major stressors that have impacted Orpheus Island along the timeline, including coral bleaching events (red), cyclones (green), sedimentation (yellow) and floods (blue).

1993 to 2001, there was no change in the abundance of pomacentrids (79.9% [−10.5% to 202%]) nor noncryptic fishes (54.2% [−30.3% to 211%]; Figure 2b); however, the abundance of cryptobenthic fishes increased 109% [11%–237%]. The abundance of cryptobenthic and noncryptic fishes had remained stable from 2001 to 2021 (6.82% [−39.9% to 64.5%] and 38.6% [−23.1% to 125%] respectively; Figure 2b). During this time, however, the abundance of pomacentrids had declined by 44% [−69.8% to −11.2%].

The standing stock biomass of the entire fish community had remained relatively stable between 1993 and 2001 (−73.2% [−11.9% to 189.0%]) and between 2001 and 2021 (−33.4% [−62.9% to 6.1%]; Figure 2c). We found no evidence for changes in the standing stock biomass between 1993 and 2001 for cryptobenthic fishes (193% [−33.4% to 587%]), pomacentrids (59.3% [−30.9% to 214%]) nor noncryptic fishes (40.4% [−26.5% to 223%]; Figure 2d). Similarly, between 2001 and 2021, we detected no changes in the biomass of pomacentrids (−42.9% [−73.7% to 2.99%]) nor noncryptic fishes (−4.9% [−55.2% to 62.5%]; Figure 2d). Conversely, the biomass of cryptobenthic fishes had declined by 54.3% [−83.5% to −0.63%].

We found a strong change in the species richness of the community surrounding the 1998 mass bleaching event. Prior to 1999, species richness had strongly declined by −27% [−48 to −3%], then shifted and increased 35% [10% to 63%] over the following 4 years to

near prebleaching levels (Figure 2e). Species richness then fluctuated but remained relatively stable from 2003 onwards, only changing −9% [−30.3% to 13%]. We found no change in the richness of cryptobenthic fishes (−9.0% [−33.8% to 23.7%]), pomacentrids (−23.2% [−61.0% to 14.9%]) nor noncryptic fishes from 1993 to 2001 (3.5% [−36.2% to 40.0%]; Figure 2f), nor from 2001 to 2021 (cryptobenthic fishes: 3.4% [−23.4% to 34.1%]; pomacentrids: −6.5% [−41.4% to 43%]; non-cryptic fishes: 23.3% [−15.7% to 77.2%]; Figure 2f).

3.2 | Ecological thresholds

By assessing the second-order derivatives at the community level, we found no evidence for ecological thresholds in the productivity, abundance nor the standing biomass of benthic fishes through time (Figure 3a–c). We found a single ecological threshold in species richness in 1999, only one year after the 1998 mass bleaching (median second-order derivative [95% credible interval]: 0.051 [0.0026 to 0.11]; Figure 3d). This ecological threshold surrounding the 1998 mass bleaching event resulted in a distinct shift in community composition. The PERMANOVA explained 80.9% of the variation in species' abundances and used 999 permutations (Figure 4a). The centroids of the prebleaching and postbleaching benthic fish assemblages were significantly
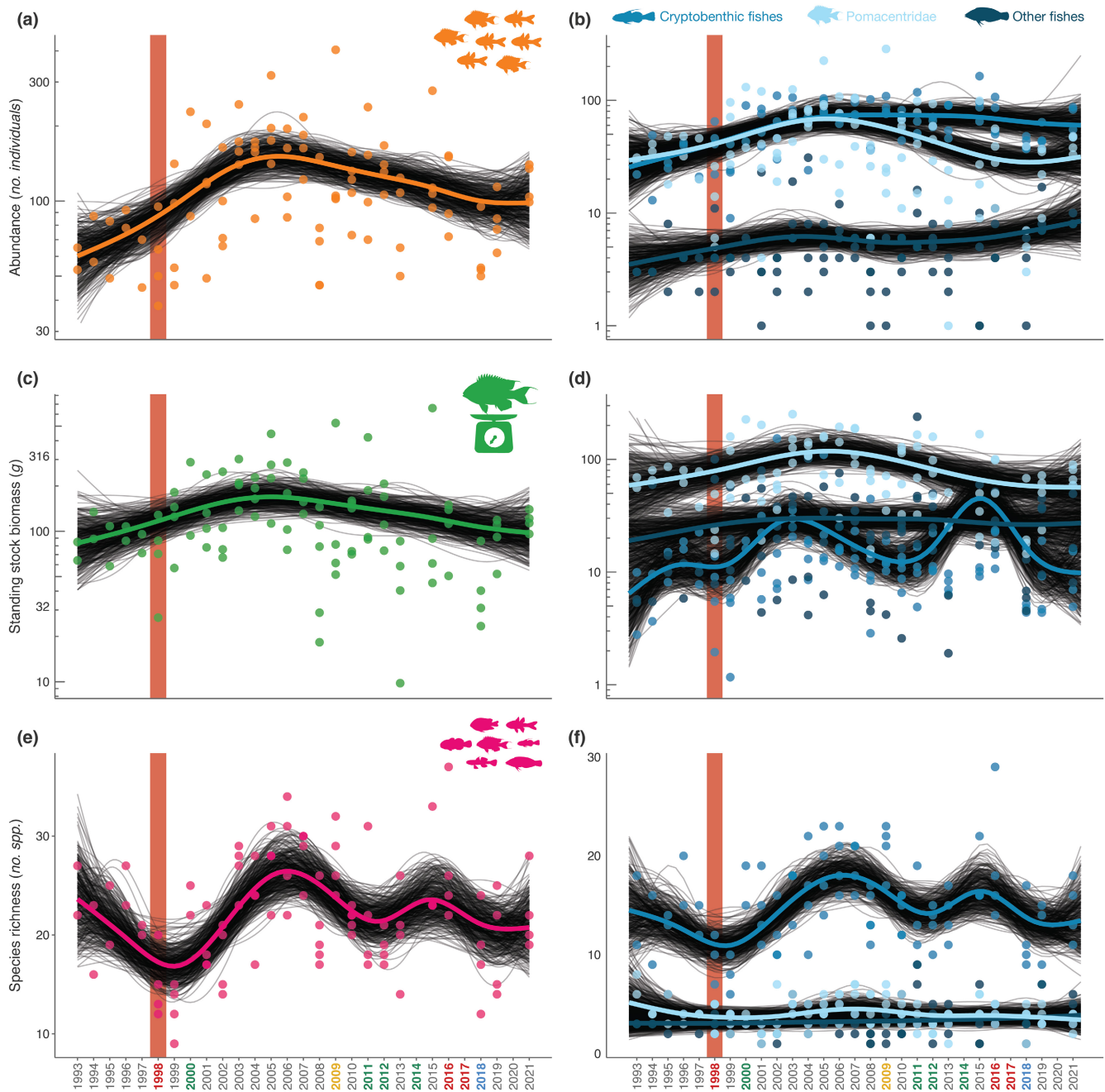
FIGURE 2 Patterns of $\log_{10}$ abundance (a, b), $\log_{10}$ standing stock biomass (c, d) and species richness (e, f) of entire benthic reef fish communities (a, c, e) through time. Panels (b, d, f) show the respective patterns, separated by cryptobenthic fishes (medium blue), damselfishes (family Pomacentridae; light blue) and other noncryptic fishes (dark blue). The thin black lines show 400 random draws sampled from the posterior distribution, while the thick coloured lines denote the median trends. The red bars indicate the 1998 mass coral bleaching event and the coloured points are showing the raw data points. The axis text colours along the bottom denote the stressors as shown in Figure 1.

different from one another ($df=1$, $F=5.3$, $p<0.01$), as illustrated by completely separate community clusters (Figure 4a). The 10 most influential species show a distinct shift in coral feeding fishes and carnivores loading towards the prebleaching assemblage (Figure 4b).

We found a single, negative ecological threshold in the time series assessing the standing stock biomass of cryptobenthic fishes in 2015 (−3.29 [−5.89 to −0.933]; Figure S1). Using 999 permutations,

the PERMANOVA on the biomass of cryptobenthic fishes explained 81.7% of the variation and showed a significant deviation from the centroid between the two communities ($df=1$, $F=2.1$, $p=0.03$; Figure S2). Although there is overlap between the two community convex hulls, we also found significant dispersion between the two communities, whereby the community of cryptobenthic fishes became less variable after 2015 ($df=1$, $F=6.0$, $p=0.02$; Figure S2).

FIGURE 3 Second-order derivatives calculated for (a) productivity, (b) abundance, (c) standing stock biomass and (d) species richness of the entire benthic fish assemblage. The coloured ribbons denote the 95% credible intervals and the thick black lines denote the median trend lines. Ribbons crossing zero indicate relatively linear patterns; positive values indicate U-shaped valleys and negative values indicate peaks in the time series. The red line indicates the 1998 mass coral bleaching events and the coloured axis text along the bottom denotes the stressors as shown in Figures 1 and 2.

4 | DISCUSSION

By applying a novel assessment of fish biomass production to a long-term monitoring dataset of high spatial and temporal resolution, we were able to assess the changes in benthic fish productivity through time. Despite the magnitude of coral loss and disturbance over the last three decades at Orpheus Island, we only detected a discernable shift in the productivity, total abundance and richness of benthic reef fish assemblages after the first mass coral bleaching event in 1998, where roughly 65% of the corals near Pioneer Bay were affected by bleaching and between 5% and 10% died (Marshall & Baird, 2000). Before 2001, we found increases in both the productivity and abundance of benthic fishes coinciding with a decrease in species richness, which was mirrored by an increase in the abundance of cryptobenthic fishes. However, the productivity and abundance of benthic reef fishes began stabilising around 2001, with species richness returning to prebleaching levels in 2003 and fluctuating only slightly during the remainder of the time series. From 2001 onwards, we found a decline in the abundance of pomacentrids and a decline in the standing stock biomass of cryptobenthic fishes. Despite changes in productivity, abundance and species richness, we found no discernable change in standing stock biomass

over the entire sampling period. Overall, although there has been a considerable reshuffling of the benthic fishes following the first mass coral bleaching event in 1998, the key ecosystem function of fish biomass production was maintained by this altered system, despite major ongoing stressors.

The 1998 mass coral bleaching event experienced on the GBR has undeniably reshaped the community composition of benthic reef fishes at Orpheus Island (Bellwood et al., 2006, 2012; Hemingson et al., 2022); consequently, specific species or families have exhibited a range of responses in productivity through time. Such variation in productivity has been reported in specific groups of fishes across various reef systems, including studies on the GBR (e.g. Morais et al., 2020; Tebbett et al., 2021) and the Seychelles (Hamilton et al., 2022). Interestingly, despite this relatively high species turnover, the functioning of the benthic fish communities after the first mass bleaching event has remained remarkably stable, which was consistent in both process-based and static proxies of productivity. This is likely driven by the specific life-history traits and mortality rates expressed by small benthic reef fishes, including cryptobenthics, which are epitomised by their high-turnover–high-productivity lifestyles. Their small body sizes and subsequent extremely high mortality rates drive shorter lifespans
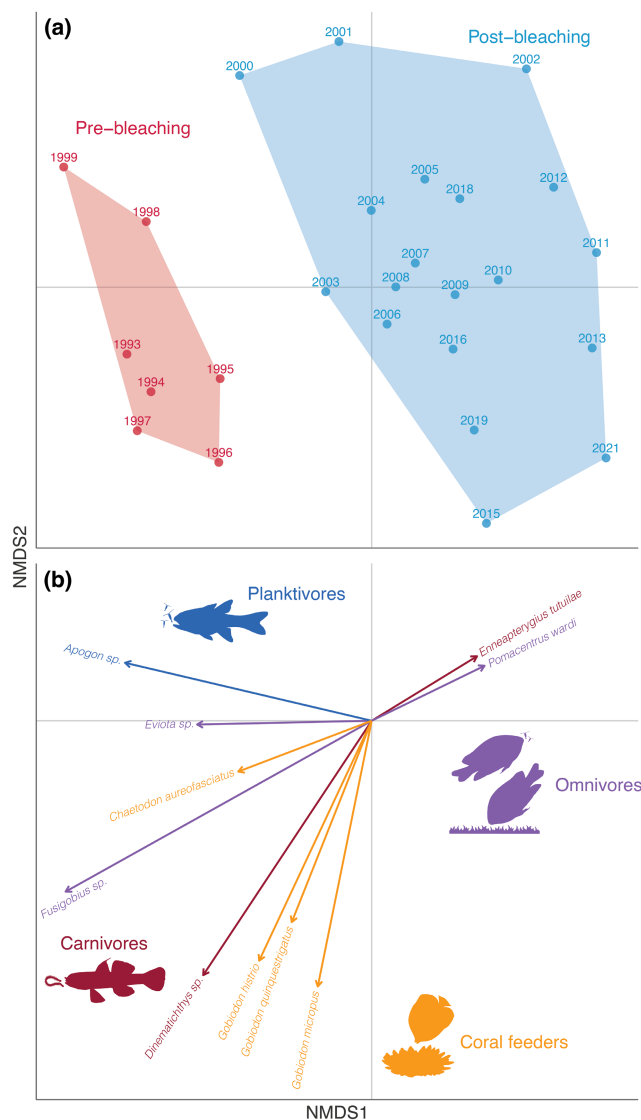
FIGURE 4 (a) Nonmetric multidimensional scaling (NMDS) ordination of benthic fish communities before (i.e. prebleaching; red) and after (i.e. postbleaching; blue) the 1998 mass coral bleaching event on the Great Barrier Reef. Sample years are labelled above their respective points and polygons encapsulate all points for a given sample period (i.e. before or after bleaching). (b) The relative contribution of the 10 most important species contributing to the separation of the pre- and postbleaching assemblages, coloured by dietary preferences.

in cryptobenthic fishes, while high abundances and constant reproduction result in a steady supply of nearshore cryptobenthic reef fish larvae (Brandl et al., 2018, 2019). Consequently, the loss of corals and coral-associated fishes creates new niches that can be quickly colonised by the nearby larvae of cryptobenthic fishes that prefer degraded reef configurations (e.g. detritivores; Bellwood et al., 2012).

The extent and intensity of the first mass bleaching event on the GBR marked a clear shift in the energetic dynamics of small benthic fishes. Indeed, this shift from coral-associated fishes towards species that are less dependent on corals is well documented by Bellwood

et al., (2006, 2012). Similarly, brightly coloured benthic fishes, which are associated with high coral cover, declined drastically immediately after the 1998 bleaching event and shifted towards communities comprising duller colours, a characteristic of degraded reef habitats (Hemingson et al., 2022). We found similar shifts in the benthic fish communities: species richness declined before the bleaching event, which coincided with an increase in total abundance and productivity (see Figures 1 and 2). Additionally, the community composition immediately following the bleaching event was significantly different from the prebleaching assemblage (see Figure 4). Eighty-seven per cent of inshore reefs, such as those found near Orpheus Island, experienced bleaching during the 1998 mass bleaching event on the GBR (Berkelmans & Oliver, 1999). The subsequent coral mortality (~5% near Pioneer Bay; Baird & Marshall, 2002; Marshall & Baird, 2000) may have shifted the community composition from comprising slower-growing, coral-associated fishes, including a loss of coral-associated damselfishes, to highly productive detritivores and planktivores. Indeed, despite the decline in standing stock biomass of cryptobenthic fishes (and a peak-shaped threshold around 2015), their stable productivity likely represents a shift from larger-bodied, coral-associated gobies (e.g. *Gobiodon* spp.) to smaller-bodied, detritivorous gobies (e.g. *Eviota* spp.).

While environmental stressors are shifting the composition of fish communities, they may also be generating communities that can withstand subsequent disturbance events. Although species richness may not buffer communities against large-scale habitat changes per se (Yan et al., 2022), communities comprising species with diverse habitat/diet *preferences* may contribute to the stability in ecosystem functioning via the 'portfolio effect' (Schindler et al., 2010, 2015). For example, the loss of corals has been associated with a shift in fisheries catch composition (Robinson et al., 2019) and trophic-specific community size structuring (Rogers et al., 2018), yet the total biomass yield in both instances has remained relatively stable (or increasing). These altered communities, which are capitalising on newly available resources, may be positively cotolerant to subsequent stressor events (i.e. more functionally resilient) and can sustain consistent levels of biomass production and abundance.

This constancy of small benthic reef fish productivity may provide a glimpse into the future functioning of coral reefs impacted by multiple stressors. Although specific families and the functions they supply likely declined following the first mass bleaching event in 1998, the altered, postbleaching community as a whole may be able to maintain functioning at a consistent level. Cryptobenthic reef fishes contribute disproportionally more to the consumed biomass on coral reefs (Brandl et al., 2019); therefore, their ability to maintain high levels of productivity indicates that these bottom-up processes on degraded reefs may be resilient to large-scale perturbations, regardless of the species composition of the community. Consequently, the productivity of benthic reef fishes may provide a strong foundation to fuel the productivity of higher trophic levels on transitioning coral reefs. Given that millions of people globally are reliant on the productivity of coral reef fishes for food and financial security through fisheries (Teh et al., 2013; Wilkinson, 2004),

understanding the resilience of the key ecosystem functions and services of degraded coral reefs will be pivotal to the effective conservation of reefs in the Anthropocene.

AUTHOR CONTRIBUTIONS

Helen F. Yan was involved in conceptualisation, formal analysis, writing—original draft and visualisation. David R. Bellwood was involved in conceptualisation, resources, methodology, data curation, investigation, resources, writing—review and editing, supervision and funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code are available on Dryad (https://doi.org/10.5061/dryad.dr7sqvb36) and Zenodo (https://doi.org/10.5281/zenodo.7700441) respectively.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Second order derivatives from the time series models for (a) productivity, (b) abundance, (c) standing stock biomass, and (d) species richness separated for cryptobenthic fishes (top, medium blue), non-cryptic fishes (middle; dark blue), and pomacentrids (bottom, light blue). The coloured ribbons denote the 95% credible intervals and the thick coloured lines denote the median trend lines.

Figure S2. Non-metric multidimensional scaling (NMDS) ordination of cryptobenthic fishes before (blue) and after (orange) the 2015 ecological threshold. Polygons depict convex hulls, which is the smallest polygon that encapsulates all points for a given sample period. Arrows and labels denote the magnitude and direction of the 10 most influential species from a SIMPER analysis.

Table S1. Annual mean sea surface temperature taken from Pioneer Bay in Orpheus Island (18°35′35.412″S, 146°28′59.934″E) from 1993 to 2021 (excl. 2014, 2017, and 2020).

Table S2. Summary of total length (cm) size distributions for subsampled fishes.