



REPORT

Climate impacts alter fisheries productivity and turnover on coral reefs

Mark Hamilton¹ · James P. W. Robinson¹ · Cassandra E. Benkwitt¹ · Shaun K. Wilson^{2,3} · M. Aaron MacNeil⁴ · Ameer Ebrahim⁵ · Nicholas A. J. Graham¹

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Abstract Alteration of benthic reef habitat after coral bleaching and mortality induces changes in fish assemblages, with implications for fisheries. Our understanding of climate impacts to coral reef fisheries is largely based on fish abundance and biomass. The rates at which biomass is produced and replenished (productivity and turnover) are also important to sustaining fisheries, yet the responses of these metrics following bleaching are largely unknown. Here, we examine changes in fish productivity and turnover after mass coral bleaching events in Seychelles, on reefs that were recovering to coral-dominated habitats and those that shifted to macroalgae-dominated regimes. Productivity of fish assemblages increased on all recovering reefs, particularly on fished reefs resulting in levels similar to protected reefs 19 years after bleaching. Herbivore-detritivores, such as scraping and excavating parrotfish, appeared to drive biomass production through increased abundance on recovering

reefs. Productivity on regime-shifted reefs remained stable at 1994 levels in fished areas, with increases observed on protected reefs. Large increases in browser productivity (particularly on protected reefs), combined with increases for invertivores, maintained post-bleaching productivity on macroalgal reefs. For all diet groups, net turnover was generally higher on fished regime-shifted reefs than on recovering reefs, suggesting fish biomass is more readily replenished on macroalgal reefs. Reef structural complexity was a positive predictor of productivity for all diet groups. These findings indicate that post-bleaching reef fish productivity is strongly influenced by benthic recovery trajectories, and demonstrates the importance of herbivore and invertivore species in sustaining small-scale inshore fisheries following climatic disturbances.

Keywords Coral bleaching · Reef degradation · Small-scale fisheries · Reef recovery · Regime shifts · Reef fish

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✉ Mark Hamilton
mark.hamilton@lancaster.ac.uk

¹ Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

² Department of Biodiversity, Conservation and Attractions, Perth, WA 6151, Australia

³ Oceans Institute, University of Western Australia, Crawley, WA 6009, Australia

⁴ Department of Biology, Dalhousie University, Halifax, NS B3H 4R2, Canada

⁵ Seychelles Fishing Authority, Fishing Port, Victoria, Mahé, Seychelles

Introduction

Mass coral bleaching events often cause extensive coral mortality and reef degradation (Hughes et al. 2018) that can influence reef fish populations and associated fisheries (Cinner et al. 2012; Pratchett et al. 2014). Approximately six million fishers are employed in reef fisheries (Teh et al. 2013) that supply hundreds of millions of people in tropical nations with livelihoods and nutrition (Johnson et al. 2013). Yet, ongoing climate-induced habitat degradation and overfishing threaten the food provisioning services provided by coral reefs worldwide (Allison et al. 2009; MacNeil et al. 2015).

A key factor that determines the response of reef fish assemblages to coral bleaching is the recovery trajectory of corals following climate disturbances. Reefs where live

corals recover tend to be associated with higher fish biodiversity, whereas those that shift to a macroalgal state with lower structural complexity are likely to have lower overall abundance and species richness of reef fishes (Roth et al. 2018; Fulton et al. 2019; Graham et al. 2020). Both recovery trajectories can induce long-term changes in fish species composition and abundance across multiple trophic groups (Bellwood et al. 2012; Robinson et al. 2019a), and some fish species may benefit from altered reef states (Pratchett et al. 2014). For example, the hunting efficiency of predators can increase as prey become more exposed on degraded reefs (Rogers et al. 2018a), while increases in algal growth as coral cover declines can benefit herbivorous fishes (Wilson et al. 2006) and may favour the juvenile recruitment of some taxa (Fulton et al. 2020). These changes in fish assemblages on post-bleaching reef habitats impact species biomass and the resources available to fisheries (Graham et al. 2007; Karr et al. 2015).

Standing biomass is a useful indicator in reef fisheries management (MacNeil et al. 2015; McClanahan et al. 2015), but does not necessarily reflect how productive fish stocks are or how well they may sustain fishery yields (Morais et al. 2020a). Predatory fish may grow large and have high biomass on reefs with high coral cover and structural complexity, yet growth rates, which underpin productivity, may be relatively low due to reduced hunting efficiency (Rogers et al. 2018a; Rogers and Mumby 2019). Conversely, species with low biomass may still be able to sustain fisheries on reefs with reduced coral cover if increased resources result in enhanced productivity of individuals (McClanahan 2018). For example, herbivore growth can be enhanced by improved food quality or quantity following coral mortality (Taylor et al. 2019). However, the enhanced productivity that some species initially experience can weaken over time, particularly if reef structure becomes severely degraded (Rogers et al. 2018b). Changes to fisheries productivity following coral bleaching will therefore be determined by shifts in species abundances and growth rates that are linked to the availability and quality of resources (Brandl et al. 2016; Taylor et al. 2019), and long-term shifts in species composition will dictate assemblage-level productivity. However, the long-term productivity responses of fish assemblages, trophic groups and individual species in post-bleaching reef states, as well as the stability of increased productivity, are poorly understood (Morais et al. 2020b).

Productivity has been a major focus in the management of exploited fish stocks (Conn et al. 2010) but, due to data deficiency and complexity of reef systems, has been understudied in mixed-species coral reef fisheries. Fish biomass has been found to accumulate on some post-bleaching coral reefs (Graham et al. 2020), leading to increases in fisheries yields (Robinson et al. 2019b). However, the rates at which biomass is produced and stored as standing biomass (i.e.

biomass turnover) are unknown, thus limiting our understanding of the long-term stability of fisheries yields (Morais et al. 2020b). Newly available methods for estimating fish productivity on coral reefs (Morais and Bellwood 2020) suggest that high fish biomass and productivity corresponds with low turnover and may indicate low recruitment rates of individuals to fish populations (Brandl et al. 2019; Morais et al. 2020b). Fast-growing and short-lived species with higher turnover rates, such as siganids (Grandcourt 2002), may be important fishery targets on post-bleaching reefs (Robinson et al. 2019b) and more adaptable to changing reef environments than long-lived species with longer generation times (Bellwood et al. 2012). With the increasing frequency of coral bleaching events (Hughes et al. 2018), it is important to understand bleaching impacts on the productivity of fish species and subsequent implications for reef fisheries.

In this study, we determine how the productivity and turnover of fish assemblages have responded to post-bleaching habitat degradation on coral reefs in Seychelles. Following a severe bleaching event in 1998 that caused > 90% mortality of hard corals on inner Seychelles reefs (Graham et al. 2006), benthic habitats reorganised into two novel reef states: recovering reefs dominated by branching corals and reefs that regime-shifted to macroalgae-dominated states (Graham et al. 2015). We investigate the long-term productivity and turnover responses of fish on these post-bleaching reef states, as well as short-term effects from a second bleaching event in 2016 that caused 70% coral mortality on recovering reefs (Wilson et al. 2019), and highlight the implications of climate-induced reef degradation for small-scale reef fisheries. Specifically, we ask the following questions: (1) how are productivity and turnover of whole fish assemblages affected on post-bleaching reefs, (2) which trophic groups of fish and key fisheries target species are responsible for driving these trends, and (3) can productivity trends be explained by benthic reef variables?

Methods

Reef survey data

Surveys of fish communities and benthic composition were carried out at 21 inshore sites on shallow fringing reefs in the Seychelles (Graham et al. 2015), stratified across carbonate and granitic reef habitats (Fig. S1). Nine sites were within four marine reserves (established in the 1970s) where no fishing took place, although poaching was a known issue according to expert knowledge at Seychelles Fishing Authority. Twelve sites were regularly fished by artisanal fisheries (Fig. S1).

Artisanal fisheries are of high importance in Seychelles as they provide food to the local population and tourism sector,

as well as exports of high-value fish that generate earnings to support local fishers and their livelihoods (Robinson and Shroff 2004). Seychellois fishers deploy traps and handlines from both motorised and unmotorised vessels (Christ et al. 2020), to target fish such as siganids, scarids, lethrinids, lutjanids and mullids within inshore reef habitats (Robinson et al. 2019b). These gears and fishing approaches are common in coral reef fisheries throughout the tropics.

Surveys were first completed in 1994 prior to a major coral bleaching event in 1998 and then every three years from 2005 to 2017. A second bleaching event occurred in 2016, which caused declines in hard corals (particularly branching) that had been recovering from the 1998 event (Fig. 1; Wilson et al. 2019). Surveys took place between March and April at all 21 sites, with the exception of 2017 when three sites within a protected area were not surveyed. Replicate sites were classified as “recovering coral” ($n = 12$) or “regime-shifted” ($n = 9$) based on their benthic trajectory to either a coral-dominated or macroalgae-dominated state, respectively, following the 1998 bleaching event (Graham et al. 2015). Recovering sites were defined as those where hard coral cover was greater than that of macroalgae following bleaching in 1998 and remained higher than macroalgae for the remainder of the time series (Fig. 1a). Regime-shifted sites were defined as those where macroalgae cover increased after 1998 and remained higher than coral cover (Fig. 1b). Although coral cover on recovering reefs declined

notably in 2017 following bleaching in 2016, coral cover was still higher than on regime-shifted reefs (Fig. 1).

At each survey site, eight replicate point counts of non-cryptic reef fishes (≥ 8 cm in length) were carried out by underwater visual census (UVC) along the base of the reef slope. Abundance and the lengths (nearest cm) of all species were estimated within a 7 m radius (154 m^2) point count area (Polunin and Roberts 1993). One diver (Simon Jennings) conducted fish point counts in 1994 and a second diver (Nicholas Graham) conducted all other counts from 2005 to 2017. Fish length estimation was validated by divers estimating the lengths of randomly selected PVC pipes prior to the first point count at each site (as described by Graham et al. 2007), with no evidence that bias among divers influenced fish counts. Replicates at each site were at least 15 m apart and divers swam for approximately one minute between point counts (Graham et al. 2006).

Visual estimates and transects of reef structural complexity and benthic composition were also carried out within each point count area after fish counts were completed. The overall structural complexity of each point count area was scored from 0 (sand or rubble with no vertical relief) to 5 (exceptionally complex) (Polunin and Roberts 1993). Coral and macroalgae cover were estimated using the plan view technique, where a diver hovered 1 to 2 m above the reef to estimate the percentage cover within each point count area. Both techniques are correlated with

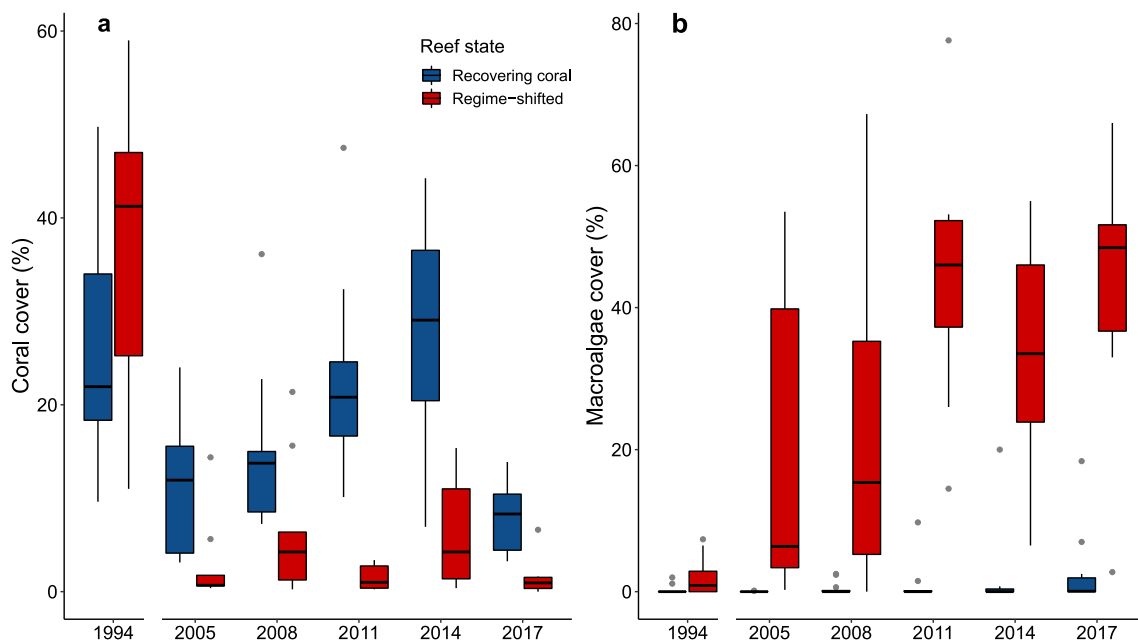


Fig. 1 Comparisons of hard coral **a** and macroalgae **b** cover on each reef state (recovering coral in blue, regime-shifted in red) before and after a major coral bleaching event in 1998. Thick horizontal lines display medians and coloured sections of each box represents the

interquartile range. Reef sites considered to be outliers are shown as points. The break in the x axis represents an eleven-year gap between surveys, during which the 1998 coral bleaching event occurred. A second bleaching event occurred in 2016

other methods of measuring reef cover and complexity (Wilson et al. 2007).

Productivity calculations

We used a trait-based approach to calculate productivity, as described by Morais and Bellwood (2020), using details of diet, position on the reef and maximum total length for each species. Species were grouped by diet (Table S1) and reef position, according to Morais and Bellwood (2018), using information from published sources (Morais and Bellwood 2018, 2019; Benkwitt et al. 2020; FishBase (and references therein; Froese and Pauly 2020); Jennings et al. 1995). Maximum total lengths for each species were obtained from FishBase (Froese and Pauly 2020) and Morais and Bellwood (2018). Any individual fish with an estimated length greater than or equal to the maximum length for the species (0.8 and 0.9% of observations, respectively) had its length reduced to 0.1 cm below the maximum, with the assumption it was overestimated in the field; this avoided numerical issues in productivity calculations.

The productivity of every individual fish was calculated using the “*rfishprod*” package (Morais and Bellwood 2020) in R (version 4.0.3; R Core Team, 2021). First, the growth coefficient at the maximum theoretical size for each species, K_{\max} (described by Morais and Bellwood 2018), was calculated at the population level using species traits (diet, reef position, maximum length) and the mean sea surface temperature over the study period (28 °C for Seychelles; Liu et al. 2014). Traditionally, the growth coefficient of a population (K) as it approaches the population asymptotic size (L_{∞}) is used in models of fish growth; however, K_{\max} combines K and L_{∞} for a species population into a single parameter, standardised to the maximum reported size for the species, L_{\max} , by assuming $L_{\infty} = L_{\max}$ (Morais and Bellwood 2018). Consequently, K_{\max} , but not K , allows comparisons between growth rates of fish from different geographies and habitats by constraining estimates to each species’ L_{\max} (Morais and Bellwood 2018). As such, we assumed all individuals of the same species belonged to the same population with identical species-specific K_{\max} estimates after bootstrapping over 1,000 iterations, regardless of individual lengths.

The estimated daily growth in length was calculated per fish over one year by incorporating age estimates into the Von Bertalanffy Growth Function (VBGF):

$$L_{t+1} = L_{\max}(1 - \exp(-K_{\max} \times t)) \quad (1)$$

where L = total length (cm) and t is the estimated age in days (simulated as being derived from otolith rings using *rfishprod*; Morais and Bellwood 2020). Length–weight relationships were used to convert the daily growth in length into daily accumulation of somatic mass, using the formula:

$$W = aL^b \quad (2)$$

where W = mass (grams), L = total length (cm) and a and b are species-specific length–weight parameters (Froese 2006). Daily productivity estimates for each individual were simulated over 365 days, accounting for the growth of individuals as the year progressed. That is, growth on any day resulted in a small change in length that affected the productivity estimate of the following day.

Natural mortality was estimated using the *rfishprod* package (Morais and Bellwood 2020), to simulate fish being removed from the system (e.g. through predation). The instantaneous rate of mortality (M) was calculated per fish based on its observed length estimate, species maximum size and K_{\max} value, giving the probability of survival to the next day. Individual survival was then simulated over one year by calculating the cumulative survival rate over 365 days from the date surveyed, and multiplying the survival probability at time t by survival at $t - 1$ (i.e. the previous day), resulting in the survival probability gradually decreasing as the year simulation progressed. Once a fish was removed, it did not contribute to productivity for the remaining days in the year, therefore productivity represented the growth (mass produced) of individuals present on the reef each day (Morais and Bellwood 2020). This probabilistic stochastic removal of individuals was iterated 100 times. After each iteration, the estimated mass produced per day per individual was summed over the year to obtain annual estimates of net productivity. We calculated the mean annual net productivity from all iterations and used these values in all analyses.

Fish below 8 cm in length were not surveyed and therefore productivity estimates within the size range of juvenile recruits to reefs and their subsequent growth over a year could not be estimated. However, contributions of juvenile fish to the production of biomass are assumed to be negligible (Morais et al. 2020a). It should be noted that the productivity of each individual fish was dependent on the traits and parameters stated above. The productivity of predatory fish was not adjusted in relation to the length-based removal of smaller individuals through natural mortality or variation in prey availability. Similarly, the productivity of herbivores was not adjusted based on variation in macroalgae or live coral cover between reef sites. This trait-based approach standardised by species is consistent with previous studies into the productivity of reef fishes (Morais et al. 2020a, 2020b; Benkwitt et al. 2020).

Simulating fishing selectivity

Next, we simulated fishing mortality on target species to account for the effects of trap fisheries on fish productivity. Although fish landings from handlines have historically dominated the Seychelles artisanal fishery (67% by weight

in 2017, compared to 13% for traps; Seychelles Fishing Authority, 2018), fish traps were the dominant fishing gear used in the inshore reef areas surveyed and were therefore chosen as the basis for estimating fishing selectivity. Target species were defined as primary, important and occasional targets, according to Grandcourt (1999) and expert knowledge at Seychelles Fishing Authority (see online supplementary information). The average size at first capture across all target species from inshore fish trap catches (mean = median = 18 cm) was used to represent the approximate size at which individuals were recruited to the trap fishery, using catch data from Seychelles (Graham et al. 2007). A fishing probability distribution developed by Morais et al. (2020a) was used to simulate size-selective fishing susceptibility of individuals at each cm length (Fig. S2). This involved applying a power-Gompertz sigmoidal curve that sharply increased probability of capture at lengths above the target length of 18 cm before plateauing as it approached a set maximum length (100 cm).

For each cm length class, instantaneous fishing mortality (F) values were obtained by multiplying the susceptibility to fisheries capture (between 0 and 1) by a fishery capture rate representing fishing intensity. A capture rate of 0.2 was chosen to account for fishing pressure on all fished reefs (found to result in biomass depletion; Morais et al. 2020a) and we ran sensitivity tests to examine the effect of varying capture rates on whole fish assemblages for each reef state (Fig. S3). The length-specific F values were used to proportionally reduce the annual net productivity estimates of individuals considered a fisheries target. Productivity of non-target species, individuals below the target size and all individuals on protected reefs was unaffected. Although the size of the fishing fleet around the two study islands of Mahé and Praslin increased from 1994 to 2017 (Robinson et al. 2019b), long-term data on fishing mortality were not available. We therefore calculated fish productivity assuming fishing pressure remained constant from 1994 to 2017.

Data analyses

All data analyses and visualisation were conducted in R (version 4.0.3; R Core Team, 2021). Fish biomass and productivity estimates were summed for every point count each year, for different taxonomic groupings (whole assemblage, diet groups and individual species), and then averaged across equal numbers of point counts to give site-level estimates. Net turnover (%) was also calculated at each site, by dividing net productivity ($\text{kg ha}^{-1} \text{yr}^{-1}$) by the standing biomass (kg ha^{-1}) and multiplying by 100. Site-level values were further aggregated to give means and standard errors (SEM) for each reef state and management type.

Of the seven primary target species in the inshore Seychelles trap fishery (Graham et al. 2007), the two most productive species per reef state over the post-1998 bleaching time series were chosen to represent species that are of importance to the fishery (Fig S4). These were *Chlorurus sordidus* and *Scarus rubroviolaceus* on recovering coral reefs and *Siganus sutor* and *C. sordidus* on regime-shifted reefs.

Generalised linear models (GLM) were used to assess differences in fish biomass, net productivity and net turnover between fished and protected reefs in 1994. *Management* was a categorical covariate (“fished” or “protected”). Models were constructed as shown in Eq. 3, where Y represents fish biomass, productivity or turnover (all log-transformed).

$$Y \sim \alpha + \text{Management}_i \quad (3)$$

The effects of reef and management characteristics on the net productivity of each diet group following the 1998 bleaching event were quantified with generalised linear mixed models (GLMM) using the “lme4” package (Bates et al. 2015) in R. Observations from protected regime-shifted reefs in 2017 were not included in analyses, as only one of four survey sites were sampled that year. To model net productivity as a function of the covariates, a GLMM (Eq. 4) was used for each of four focal fish diet groups important to fisheries: macroalgal browsers, herbivore-detritivores, mobile invertivores and piscivores. Site-level data were analysed for all diet groups to reduce the effect of zero values in the response from individual point counts. As observations were made at the same sites over multiple years, *Site* was included as a random intercept to account for temporal correlations within each site. *Year* was also included as a random intercept to account for correlations within each survey year.

$$\begin{aligned} \text{NetP}_i \sim & \alpha + \beta_1 \times \text{Structural Complexity}_i + \beta_2 \times \text{Depth}_i \\ & + \beta_3 \times \text{Live Coral Cover}_i + \beta_4 \times \text{Dead Coral Cover}_i \\ & + \beta_5 \times \text{Macroalgae Cover}_i + \text{Reef State}_i \\ & + \text{Management}_i + \text{Habitat}_i + \text{Site}_j \\ & + \text{Year}_k \text{Site}_j \sim N(0, \sigma_{\text{Site}}^2) \text{Year}_k \sim N(0, \sigma_{\text{Year}}^2) \end{aligned} \quad (4)$$

where NetP was log-transformed net productivity ($\text{kg ha}^{-1} \text{yr}^{-1}$) and i represents a given reef site in a given survey year. *ReefState* (“recovering coral”, “regime-shifted”), *Management* (“fished”, “protected”), *Habitat* (“carbonate”, “granitic”), *Year* ($n = 5$) and *Site* ($n = 21$) were all categorical. Continuous covariates (structural complexity, depth, live coral cover, dead coral cover and macroalgae cover) were scaled with mean = 0 and standard deviation = 1 ($(x - \text{mean}(x))/\text{sd}(x)$). Standardised covariates allowed the relative effect sizes of explanatory variables to be examined, with

higher t values of predictors indicative of having a greater influence on net productivity (Cade 2015). Model assumptions of all GLM and GLMM were verified using the protocol described by Zuur and Ieno (2016), by plotting residuals against fitted values, each covariate in the model, and covariates not in the model. Residuals were assessed to confirm there were no temporal or spatial dependencies.

Results

Whole assemblage biomass, productivity and turnover

Pre-1998 bleaching (1994) estimates on protected reefs were higher than fished reefs for fish biomass (protected: 555.1 ± 101.7 kg ha⁻¹, fished: 307.9 ± 31.5 kg ha⁻¹; GLM: effect size = 0.55, $t = 7.7$) and productivity (153.3 ± 10.9 kg ha⁻¹ yr⁻¹, 98.6 ± 9.3 kg ha⁻¹ yr⁻¹; GLM: effect size = 0.44, $t = 6.0$) (Fig. 2 a–d; Table S2). Conversely, net turnover in 1994 was slightly lower on protected reefs ($28.0 \pm 1.7\%$, GLM: effect size = -0.03 , $t = -2.9$) than fished reefs ($32.2 \pm 1.7\%$) (Fig. 2 e, f; Table S2).

Seven years after the 1998 coral bleaching event, biomass and productivity on fished recovering coral reefs were slightly lower than 1994 values, then increased over the time series to be above 1994 levels and reach values seen on protected reefs by 2017 (biomass: 593.6 ± 61.0 kg ha⁻¹, productivity: 199.4 ± 61.0 kg ha⁻¹ yr⁻¹) (Fig. 2 c, d). Turnover on fished reefs in 2005 was lower than 1994 ($24.8 \pm 1.5\%$) and steadily increased until 2017, returning close to 1994 levels by 2011 ($30.0 \pm 1.9\%$). Biomass, productivity and turnover on protected recovering reefs remained similar to 1994 until 2017, when productivity and turnover slightly exceeded 1994 levels (productivity: 224.9 ± 41.3 kg ha⁻¹ yr⁻¹, turnover: $33.0 \pm 2.2\%$) (Fig. 2 b, d, f). Assemblage biomass, productivity and turnover were at their highest levels in 2017 on all recovering reefs, shortly after the 2016 bleaching event.

On reefs that regime-shifted to a macroalgal state, smaller increases in biomass and productivity compared to recovering reefs were observed on fished sites. Estimates exceeded 1994 values by 2017 but with higher variability (biomass: 394.8 ± 90.3 kg ha⁻¹, productivity: 131.5 ± 29.1 kg ha⁻¹ yr⁻¹) (Fig. 2 a, c). Turnover on fished regime-shifted reefs in 2005 was similar to 1994, then increased to reach the highest levels observed on any reef by 2011 ($44.8 \pm 7.5\%$), before decreasing back to the 1994 level in 2017, with high variability in all years. On protected reefs, clear productivity and turnover increases were observed, from slightly below 1994 levels in 2005 to exceeding 1994 levels by 2014 (productivity: 246.2 ± 25.3 kg ha⁻¹ yr⁻¹, turnover: $37.8 \pm 2.0\%$) (Fig. 2 d, f).

Productivity and turnover trends by diet group

Recovering coral reefs

Similar to the whole assemblage trend on recovering coral reefs, net productivity of all diet groups on fished reefs increased over post-bleaching years and exceeded 1994 levels, particularly herbivore-detritivores which reached approximately 235% of pre-bleaching productivity by 2017 (112.2 ± 12.9 kg ha⁻¹ yr⁻¹) (Fig. 3). All diet groups decreased in productivity from 1994 to 2005 on fished reefs, most notably for herbivore-detritivores and piscivores (with no overlap of standard errors with 1994 values; herbivore-detritivore: 28.6 ± 5.8 kg ha⁻¹ yr⁻¹, piscivore: 4.0 ± 1.0 kg ha⁻¹ yr⁻¹). Net turnover of all diet groups remained below or at 1994 levels in most years on fished reefs but increased for invertivores in 2014 and 2017 and for piscivores in 2005 (Fig. 3). Herbivore-detritivore turnover was around half the 1994 value by 2005 and increased to almost pre-bleaching levels by 2017 ($31.6 \pm 1.4\%$). The highest productivity estimates on recovering reefs generally occurred when turnover was low, particularly for herbivore-detritivores and piscivores (Fig. S5).

Productivity was also enhanced on protected reefs, with the exception of piscivores which fluctuated generally below 1994 levels (Fig. S6). Post-bleaching turnover was at or above 1994 levels for all diet groups on protected reefs, except herbivore-detritivore turnover which was at or below 1994 levels (Fig. S6).

Regime-shifted reefs

On fished regime-shifted reefs, productivity was more variable between diet groups than on recovering reefs (Fig. 3). Browser productivity generally exceeded 1994 levels, particularly from 2011 onwards, peaking in 2014 (27.8 ± 17.6 kg ha⁻¹ yr⁻¹). Invertivore productivity exceeded 1994 levels by 2008 and peaked in 2017 with high variability (50.8 ± 13.6 kg ha⁻¹ yr⁻¹). Herbivore-detritivore and piscivore productivity generally stayed similar to pre-1998 bleaching levels although decreased below 1994 levels in 2005 for herbivore-detritivores (37.7 ± 4.7 kg ha⁻¹ yr⁻¹) and in 2011 for piscivores (2.8 ± 0.8 kg ha⁻¹ yr⁻¹) (Fig. 3). Net turnover tended to be higher and more variable each year than on recovering reefs for all diet groups (Fig. 3) and was often higher when productivity was low (Fig. S5). Turnover peaked in 2011 for herbivore-detritivores (with high variability; $49.9 \pm 16.3\%$), invertivores ($53.0 \pm 3.1\%$) and piscivores ($91.4 \pm 17.9\%$). Browser turnover peaked in 2008, but had high variability ($101.0 \pm 55.6\%$) due to the absence

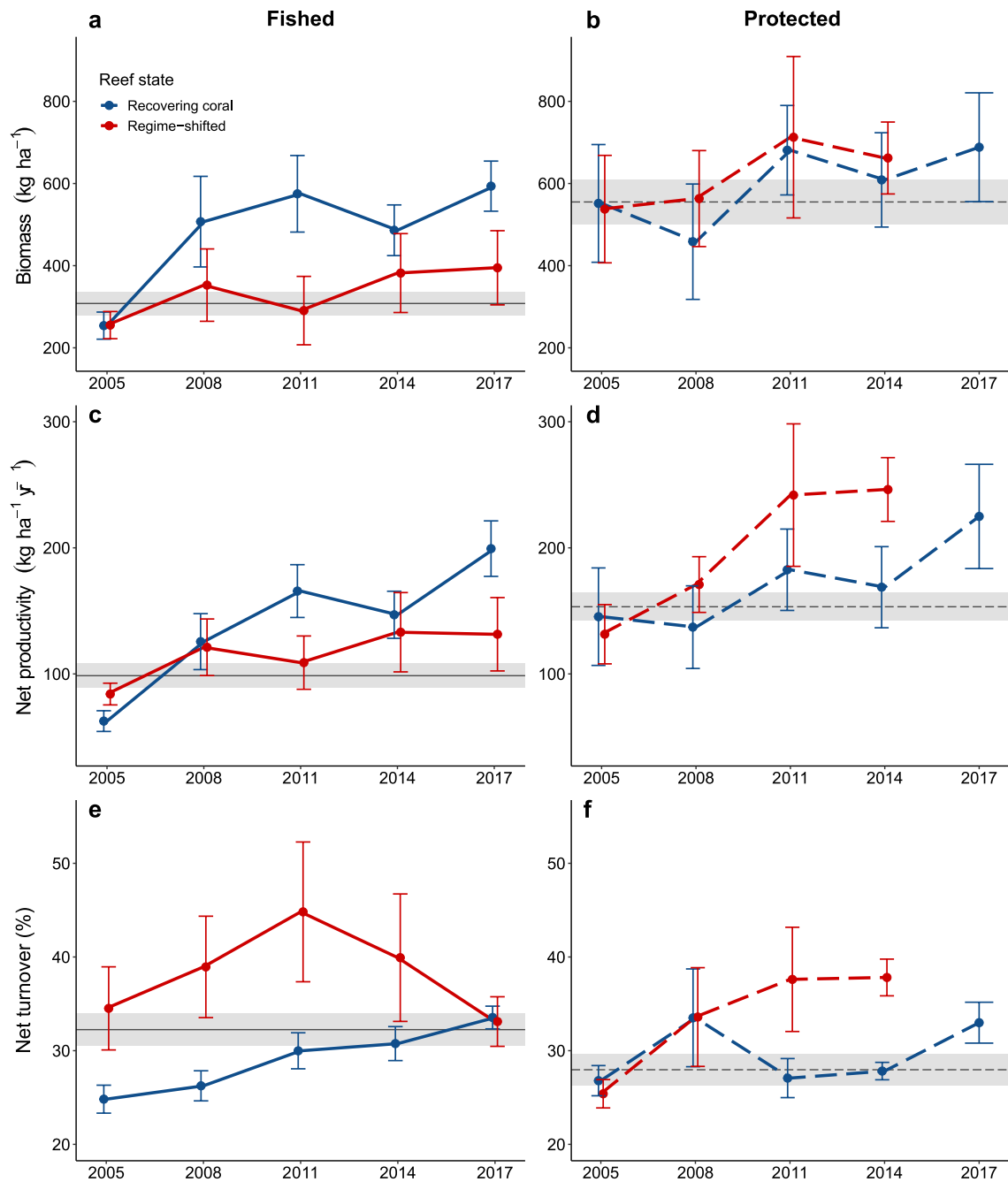


Fig. 2 Mean biomass, net productivity and net turnover of fish assemblages on reefs following recovering (blue) and regime-shifted (red) trajectories after a major coral bleaching event in 1998, on fished (left) and protected (right) reefs. A second bleaching event occurred in 2016. Error bars represent the standard error of the mean

across all reef locations surveyed each year. Pre-bleaching estimates from 1994 are shown as grey horizontal lines (with shading for ± 1 standard error of the mean). Protected regime-shifted reefs are not presented for 2017 as three of four reef locations (Cousin Island) were not sampled

of browsers in most point counts (87.5%), then decreased below the 1994 level in 2017 ($26.8 \pm 7.4\%$).

On protected reefs, both browser and herbivore-detritivore productivity rose sharply over post-bleaching years, exceeding 1994 levels by 2014, with browser productivity

distinctly higher and more variable compared to protected recovering reefs (Fig. S6). Post-bleaching piscivore productivity on protected reefs was lower than 1994 levels in all years (Fig. S6). Differences in turnover between regime-shifted and recovering reefs were less clear on

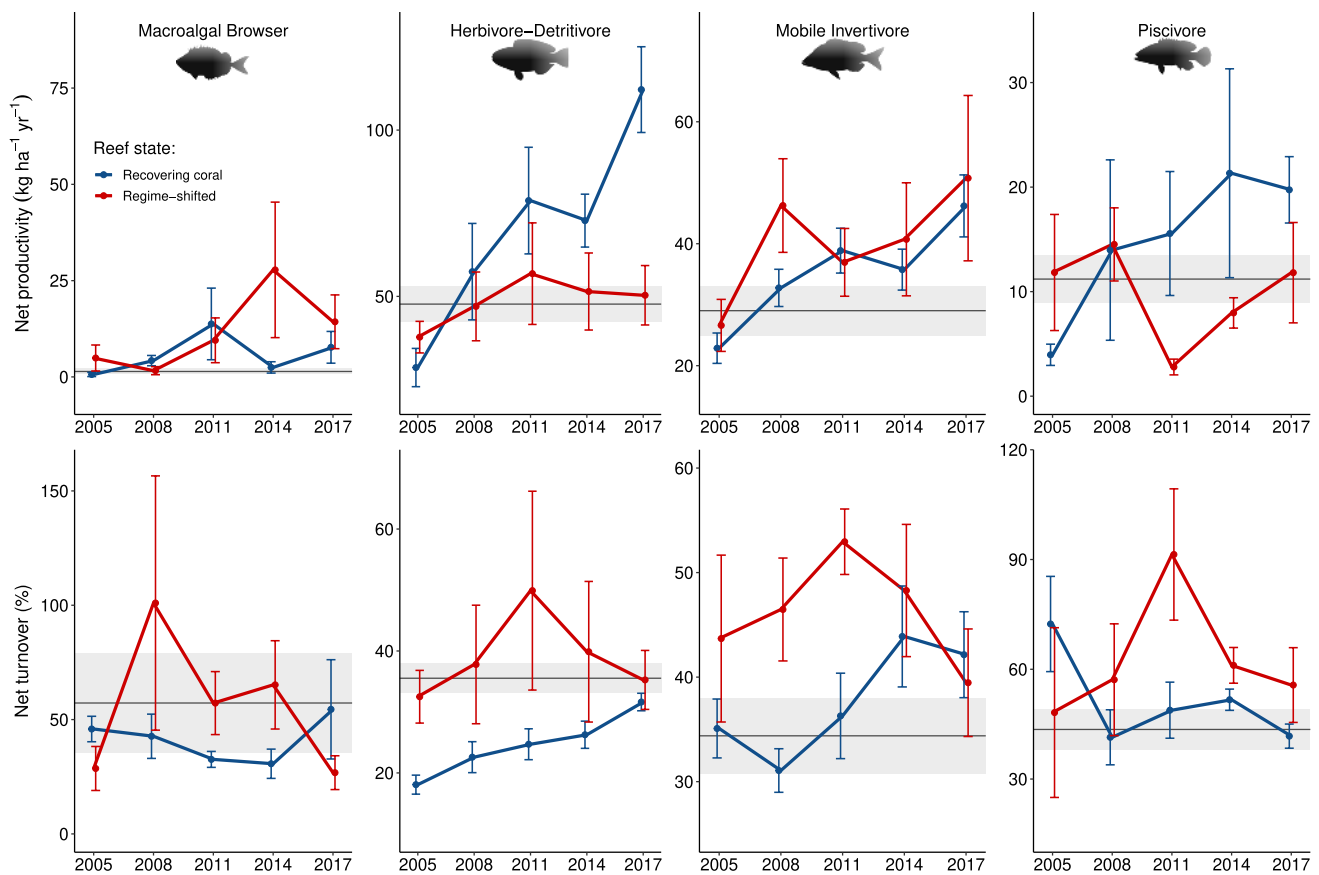


Fig. 3 Mean net productivity (top) and net turnover (bottom) for selected fish diet groups on fished reefs following recovering (blue) and regime-shifted (red) trajectories after a major coral bleaching event in 1998. A second bleaching event occurred in 2016. Error bars represent ± 1 standard error of the mean across all reef locations surveyed each year. Pre-bleaching estimates are shown as grey horizon-

tal lines (with shading for ± 1 standard error of the mean). Standard error for macroalgal browser productivity estimates in 1994 is narrow due to low abundance of this group that year. Note that y-axis scales differ between diet groups. Fish silhouettes are from the R package “fishualize” (Schiettekatte et al. 2019)

protected compared to fished reefs; however, invertivore turnover was consistently higher than 1994 on protected reefs (Fig. S6).

Effects of reef characteristics on fish productivity

Reef structural complexity had a positive effect on fish productivity for all diet groups, particularly for browsers (effect size = 0.68 ± 0.16 , $t = 4.3$) and piscivores (0.34 ± 0.12 , $t = 2.9$). Depth had no strong effect on any group, although browser productivity was lower on deeper reefs (Fig. 4; Table S3). Live coral cover had a negative effect on browser productivity (-0.48 ± 0.19 , $t = -2.6$) and weak positive effects for all other groups, while dead coral cover had a slight positive effect on the productivity of all groups, especially piscivores (0.19 ± 0.10 , $t = 2.0$; Fig. 4; Table S3). The effect of macroalgae cover was variable, with a strong positive effect on browser productivity

(0.67 ± 0.17 , $t = 4.0$) and weak negative effects for all other groups (Table S3). Productivity tended to be higher on regime-shifted reefs, however, this did not apply to browsers (Fig. 4). Protection from fishing had a consistently positive effect on productivity of all diet groups, with a particularly strong effect for invertivores (0.37 ± 0.09 , $t = 3.9$; Table S3). Productivity was higher on granitic reefs than carbonate reefs, especially for browsers (0.70 ± 0.31 , $t = 2.3$).

Target species

Changes in the net productivity of primary target species on fished reefs were estimated over 2005–2017 for the two most productive species on both recovering coral (*Chlorurus sordidus* and *Scarus rubroviolaceus*) and regime-shifted (*Siganus sutor* and *C. sordidus*) reefs (Fig. 5 a,d).

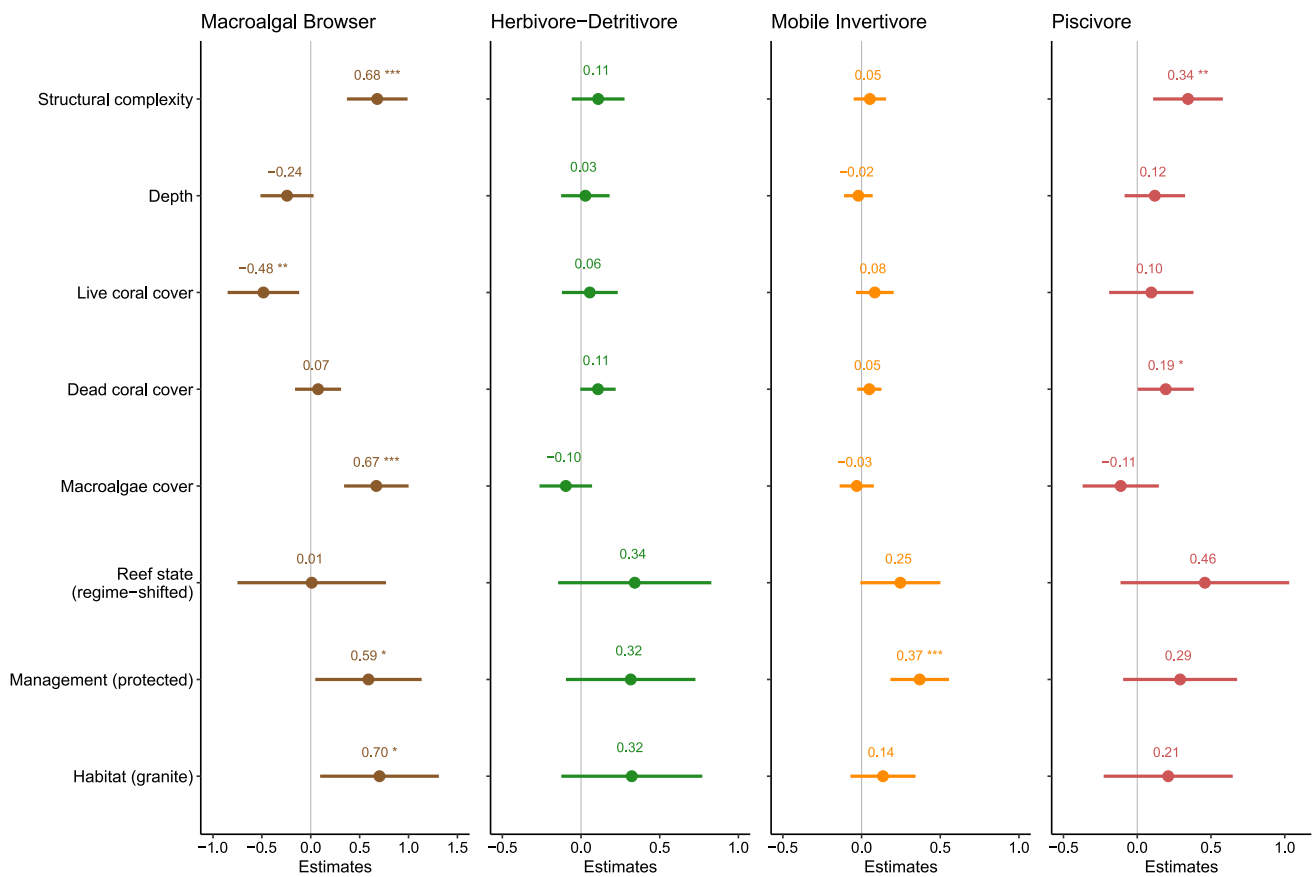


Fig. 4 GLMM results for select diet groups, showing effect size estimates of predictors on net productivity (the response) in years after the 1998 bleaching event. Effect sizes for each covariate are labelled on each panel, with the level of significance shown (***= $p \leq 0.001$, **= $p \leq 0.01$, *= $p \leq 0.05$). Separate models were used for each diet group. Note the x-axis scale for macroalgal browsers differs

from other diet groups. Numerical covariates (structural complexity, depth, live coral cover, dead coral cover, macroalgae cover) were scaled from raw values. Factor levels represented by model intercepts (vertical grey lines) were reef state = recovering coral, management = fished and habitat = carbonate

Recovering coral reefs

On recovering reefs, 1994 *C. sordidus* productivity was higher ($10.2 \pm 3.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$) than *S. rubroviolaceus* ($1.9 \pm 0.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$). Both species increased in productivity after bleaching, reaching their highest values in 2017 (*C. sordidus*: $37.7 \pm 8.6 \text{ kg ha}^{-1} \text{ yr}^{-1}$, *S. rubroviolaceus*: $17.16 \pm 7.3 \text{ kg ha}^{-1} \text{ yr}^{-1}$) which coincided with declines in hard coral cover (Fig. 1). *C. sordidus* abundance followed a similar trend to productivity, initially decreasing from 1994 to 2005 (from 89 to 43 individuals ha^{-1}) before increasing over post-bleaching years to its highest level in 2017 (154 individuals ha^{-1}) (Fig. 5 b). More large *C. sordidus* individuals (30 – 40 cm, closest to the length of maximum daily productivity; Fig. 6) were observed in post-bleaching years compared to 1994, while the abundance of smaller size classes (10 – 20 cm) also increased after bleaching and exceeded 1994 abundance by 2017. *S. rubroviolaceus* abundance also increased over

post-bleaching years to a maximum in 2017 (34 individuals ha^{-1}), particularly for smaller size classes (<40 cm), but also with greater representation of larger (40 to 60 cm), highly productive individuals (Fig. 6). *S. rubroviolaceus* total abundances and abundances per size class were lower than *C. sordidus* in all years (Fig. 5c). The net turnover of both *C. sordidus* and *S. rubroviolaceus* was also relatively high on recovering reefs following the 1998 bleaching event (Fig. S4).

Regime-shifted reefs

On regime-shifted reefs, *S. sutor* productivity remained at 1994 levels until peaking at $21.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in 2014, though this was highly variable ($\pm 18.3 \text{ kg ha}^{-1} \text{ yr}^{-1}$) (Fig. 5 d). *S. sutor* productivity decreased in 2017 but remained higher than 1994 levels ($8.9 \pm 7.0 \text{ kg ha}^{-1} \text{ yr}^{-1}$). *C. sordidus* productivity decreased in 2005 ($11.4 \pm 1.3 \text{ kg ha}^{-1} \text{ yr}^{-1}$), before recovering to 1994 levels between 2008 and 2017

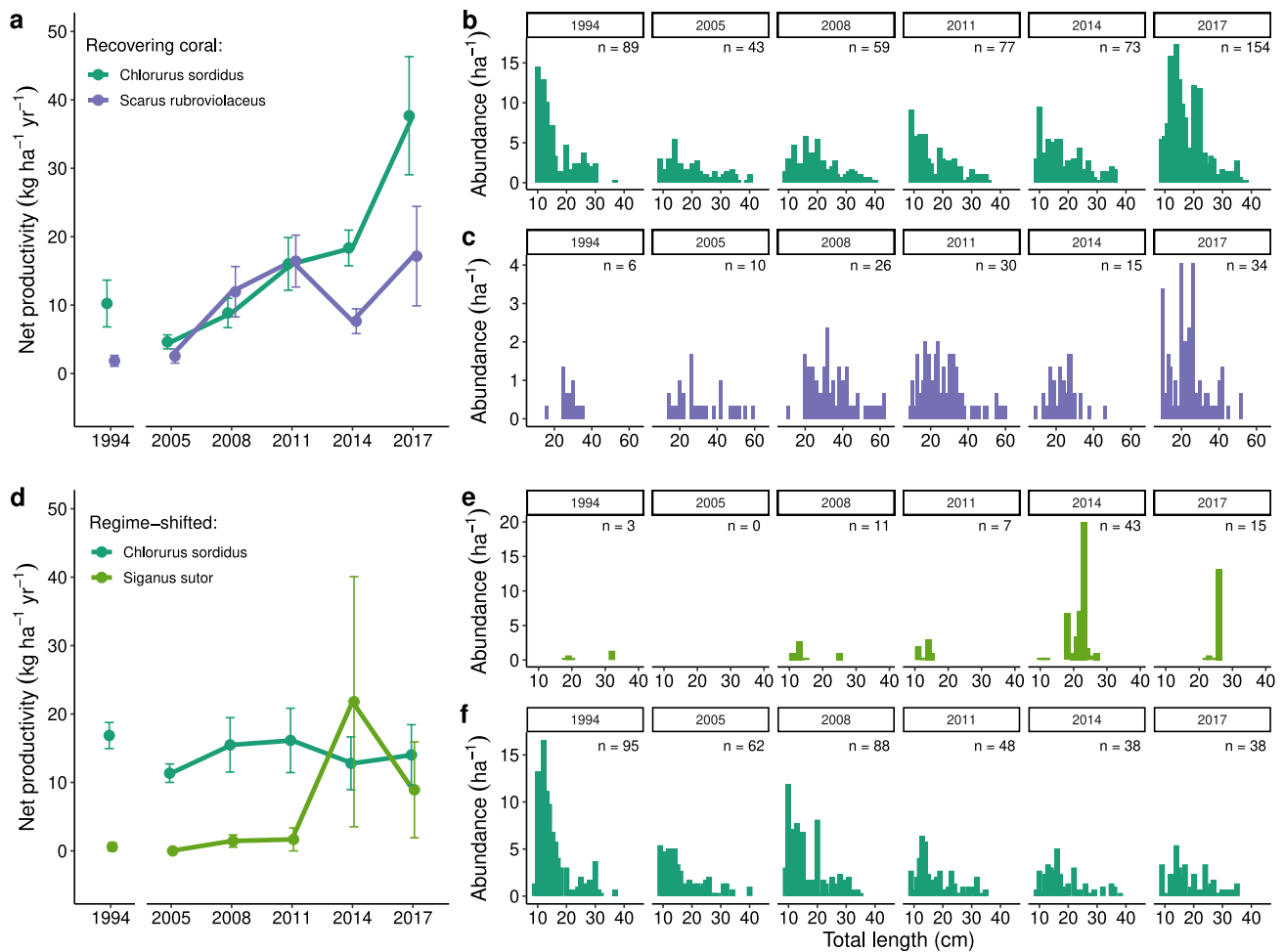


Fig. 5 Net productivity of primary target species in the inshore Seychelles trap fishery for the two most productive species on fished recovering coral reefs (*Chlorurus sordidus* and *Scarus rubroviolaceus*; top left) and regime-shifted macroalgal reefs (*Siganus sutor* and *Chlorurus sordidus*; bottom left) over the time series (no other species exceeded $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$). Error bars are \pm one standard error of the mean. Note the eleven-year gap in the time series between 1994

and 2005, during which the 1998 coral bleaching event occurred. Length-frequency histograms for each species from UVC data are displayed on the right, in line with the corresponding reef state plots, using the mean abundance of each length across all fished recovering or regime-shifted reefs. Total abundance across all lengths is displayed on each panel

(mean = $14.6 \pm 4.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$) (Fig. 5d). Post-bleaching *S. sutor* abundance reflected the productivity trend (though no individuals were observed in 2005) (Fig. 5e). *S. sutor* populations were mostly comprised of small individuals (< 20 cm) between 2005 and 2011, before increasing to 43 individuals ha^{-1} and shifting towards larger fish (> 20 cm) with higher daily productivity in 2014 (Fig. 6). *C. sordidus* abundance dropped from 1994 to 2005 (from 95 to 62 individuals ha^{-1}) following bleaching (particularly the smallest sizes) and remained close to that level over post-bleaching years (Fig. 5f), similar to the productivity trend. Net turnover of primary fishery target species tended to be dominated by herbivorous species on fished reefs (Fig S4).

Discussion

Our results demonstrate that benthic habitat states and fishery restrictions influence the long-term production of fish biomass on coral reefs following mass coral bleaching. Post-bleaching fish productivity at the assemblage level increased on recovering coral reefs in both fished and protected areas, but only on regime-shifted reefs that were protected from fishing. Productivity increases were largely driven by herbivore-detritivores (except on fished regime-shifted reefs), and invertivores and macroalgal browsers on all fished reefs, indicating these species groups will be of high importance for climate-disturbed coral reef fisheries. Net turnover of all diet groups on fished regime-shifted reefs generally exceeded that of recovering reefs, indicating that

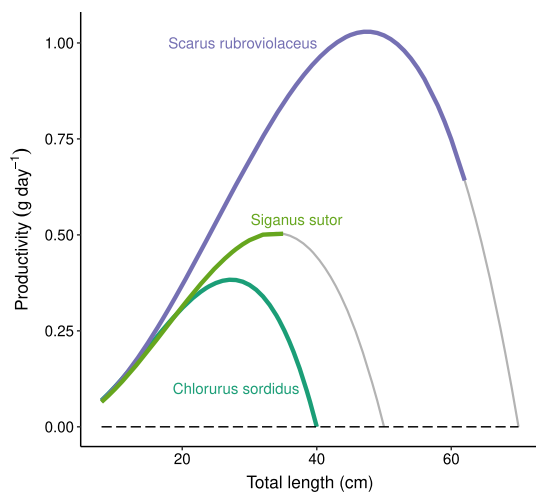


Fig. 6 The relationship between total body length and individual mass produced per day (in grams) for three highly productive herbivorous fish species on fished reefs (shown in Fig. 4). Relationships are plotted from 8 cm (minimum fish length recorded during surveys) to the maximum total length for each species. Thicker, coloured sections of each line represent the range of fish lengths observed during surveys. The dashed line indicates zero productivity

the replenishment of biomass occurs more readily on macroalgal reefs, and may provide a mechanism for fisheries yields to be maintained after climate-driven regime shifts.

Increases in productivity and turnover of fish assemblages on both fished and protected reefs indicate that biomass production does not appear to be hindered by fishing on reefs that are recovering from bleaching. The weak influence of fishing activity on productivity and turnover after bleaching may explain why fish biomass was able to accumulate on recovering reefs (Graham et al. 2020), although calls into question the effectiveness of marine reserves for enhancing biomass production following severe coral bleaching. Productivity and turnover increases on recovering reefs following bleaching suggests enhanced growth rates of individuals coincided with increasing replenishment of standing biomass. Simultaneous increases in assemblage biomass and productivity have previously been documented on reefs following mass coral loss, but in conjunction with lower turnover owing to storage effects in larger individuals (Morais et al. 2020a, 2020b). The return of turnover to pre-bleaching (1994) levels seen on recovering reefs here suggests ample recruitment of smaller individuals, consistent with the length frequencies observed for *C. sordidus*. Recovering coral reefs appeared to provide favourable habitat conditions that enhanced fish productivity regardless of fishing activity, especially after further coral loss following the 2016 bleaching event. This supports evidence from other tropical reefs that shifts in habitat can have a greater impact on fish assemblages than fishing pressure (Russ et al. 2021).

The increased productivity of herbivore-detritivores on recovering reefs suggests low trophic levels are driving the biomass accumulation of whole fish assemblages on these reefs, as has been found elsewhere following climatic disturbances (Adam et al. 2011; Hempson et al. 2018; Morais et al. 2020b; Russ et al. 2021). An increasing abundance of small excavating and scraping parrotfish individuals (*C. sordidus* and *S. rubroviolaceus*, respectively) suggests high recruitment on reefs recovering from bleaching, which will also contribute to increased herbivore-detritivore turnover. In addition to increasing abundance and turnover, the large body size of some herbivore-detritivore individuals such as *S. rubroviolaceus* resulted in large *per capita* contributions to fish productivity. The combination of increased abundance, individual growth rates and turnover of herbivore-detritivores would have contributed substantially to the biomass accumulation on recovering reefs.

Elevated assemblage productivity on regime-shifted reefs protected from fishing suggests the positive reserve effects on biomass production is maintained on post-bleaching macroalgal reefs. Higher fish biomass within marine reserves following disturbances has been documented elsewhere (McClure et al. 2020); however, our results indicate that this effect can be influenced by benthic state following coral bleaching. Biomass and productivity were maintained at 1994 levels on fished macroalgal reefs, despite an extreme change in benthic habitat that reduced fish species richness (Robinson et al. 2019a), likely sustaining fisheries production. The elevated turnover on fished macroalgal reefs may have initiated a “buffering productivity” effect (Morais et al. 2020a), where fisheries-induced decreases in productivity are less than decreases in biomass, perhaps acting as a compensatory mechanism allowing the production of biomass to be maintained. However, turnover also increased on reefs protected from fishing, therefore changes in fish assemblage composition on macroalgal reefs is likely the main driver of increased turnover, as species more suited to these habitats become more prominent. Our results suggest macroalgal reefs can support fish assemblages that sustain fishery catches, albeit without the elevated biomass seen on protected and recovering reefs.

Enhanced productivity and turnover of invertivores on fished macroalgal reefs suggest these species will become increasingly important for fisheries. Higher invertivore biomass on reefs following habitat disturbances is likely driven by increased productivity and availability of invertebrate prey on dead coral substrate (Rogers et al. 2018a, b; Fraser et al. 2021). In the inner Seychelles, the contribution of invertivores, such as lethrinids (e.g. “kaptenn”), to artisanal catches has increased in recent years (Seychelles Fishing Authority, 2018) and may form substantial components of catches on regime-shifted reefs. Herbivorous fish are also a major target for fish traps on reef habitat, with browser

species such as *S. sutor* sustaining catch rates on Seychelles' macroalgal reefs (Robinson et al. 2019b). The dominance of smaller-bodied, productive species, such as *S. sutor*, is linked to reef topography and regime. Macroalgal reefs act as nursery and foraging habitats for reef fish species, including productive fisheries targets that undertake ontogenetic shifts in their use of reef habitats (Macreadie et al. 2017; Fulton et al. 2020). *S. sutor*, for example, are associated with regime-shifted reefs but also travel between coral reef and seagrass habitats (Ebrahim et al. 2020a). Enhanced fish productivity on protected macroalgal reefs could result in a spillover effect of some species from these reserves to fished reefs and may benefit inshore fisheries in Seychelles.

The substantial contributions of herbivorous species to fish productivity were likely influenced by the quantity, accessibility and nutritional quality of benthic food resources (Morais et al. 2020b). Enhanced primary productivity following bleaching and reductions in live coral cover benefit large-bodied herbivores, including scraping and excavating parrotfish (Han et al. 2016; Rogers et al. 2018a, b; Arias-Godínez et al. 2019). This increase in algal and microbial food resources likely underpins the increased parrotfish abundance and productivity on recovering Seychelles reefs by enhancing individual growth rates (Taylor et al. 2019; Nicholson and Clements 2020), particularly in 2017 when coral cover was severely reduced after the 2016 bleaching event. The high abundance of macroalgae, such as *Sargassum*, on regime-shifted reefs in Seychelles provide a reliable food source for browsers (Ebrahim et al. 2020b). Increased nutrient content of macroalgae has been found up to a year after bleaching-induced coral mortality in Seychelles (Vaughan et al. 2021), potentially enhancing the productivity of browser species. Enhanced primary productivity also likely benefited invertivores feeding on herbivorous and detritivorous invertebrates (Fulton et al. 2019). Reef structural complexity appeared to promote fish productivity, especially for browsers, although availability of benthic feeding resources has been predicted to be a greater determinant of herbivorous fish biomass than structural complexity (Oakley-Cogan et al. 2020). The relationship between fish productivity and reef structural complexity was consistent with other modelling suggesting reduced reef structure lowers fisheries productivity (Rogers et al. 2014). As such, maintaining reef complexity seems to be important for maintaining fisheries productivity and yields.

Although enhanced fish productivity appeared to be influenced by the benthic state of reefs, it should be acknowledged that other potential causes were not accounted for. For example, other energy sources that fuel trophic pathways include cryptobenthic fish species that are vital for ecosystem functioning due to their high productivity and turnover rates (Brandl et al. 2019), as well as pelagic inputs that are transferred to reefs through small planktivorous fishes (Morais and Bellwood 2019). Fish < 8 cm were not surveyed on reefs and so were not accounted for in this study which

focused on fish groups targeted by fisheries. Inclusion of these small species may have revealed linkages between low and high trophic levels, for example productive prey species that may sustain larger piscivores that are of relevance to fisheries. Fishery effects on fish productivity also require further research in Seychelles, as accurate estimates of fishing mortality were unavailable. A fishing mortality estimate greater than that included in our study may have resulted in larger disparities between fish biomass and productivity due to increased net turnover maintaining higher productivity (Morais et al. 2020a). Connectivity between fished and protected reefs was unaccounted for, and likely contributed to high post-bleaching fisheries productivity (Hopf et al. 2019).

The herbivore and invertivore fish species that sustain Seychelles inshore reef fisheries are likely to remain important on reefs impacted by climate change. Herbivore-detritivores with high productivity, such as parrotfish, will be particularly key to sustaining catch rates on recovering coral reefs. While our results show this group was highly productive regardless of fishing pressure, fisheries management should aim to maintain the biomass required to perform critical herbivory functions (Hughes et al. 2007; MacNeil et al. 2015). The elevated turnover of different trophic groups on macroalgal reefs suggest they may better withstand fishing pressure, as higher turnover rates provide more resilience to exploitation (McClanahan and Hicks 2011; Russ et al. 2021), although turnover dropped in 2017 following bleaching in 2016. The trophic structure of fish assemblages is skewed towards herbivores on climate-impacted reefs (more so on regime-shifted than recovering reefs; Hempson et al. 2018), such that fisheries management may need to account for greater dependency on fewer species.

Future projections of global fisheries under climate change scenarios indicate stock biomass and yields in tropical fisheries are more likely to be negatively impacted compared to elsewhere (Gaines et al. 2018). The enhanced productivity and biomass accumulation seen on Seychelles' reefs following coral bleaching suggests reef fish assemblages may be able to maintain fisheries yields several years after climatic disturbance. The particularly high biomass and productivity of herbivores could indicate these reefs may be able to resist future regime-shifts to algal habitats (McClanahan et al. 2011), while also providing benefits to fisheries. However, it remains to be seen what longer term impacts the 2016 bleaching may have on fish assemblages in Seychelles. Increasing intensity and frequency of bleaching events (Hughes et al. 2018) are expected to result in further regime shifts. Transitions from recovering to macroalgal reefs would likely alter fish assemblages and lead to higher fisheries dependence on macroalgal-associated species. Tropical coastal communities that rely on reef fisheries must adapt to species distribution and productivity changes caused by climate change to offset

potential negative effects on food security and livelihoods (Cheung et al. 2013; Gaines et al. 2018).

Our analyses of fisheries productivity and turnover highlights how these growth metrics respond over long time-scales in fish assemblages on two differing post-bleaching reef states. The accumulation and maintenance of biomass observed here was driven by highly productive species that prosper in post-bleaching habitats: herbivore-detritivores on recovering reefs and browsers and invertivores on macroalgal reefs. Our results build on previous work on coral reef fish productivity (Morais et al. 2020b) to reveal the influence of post-bleaching habitat regimes, providing evidence that fishery production can be sustained on reefs that have experienced severe bleaching. This sustained productivity is promising for tropical coastal fisheries that rely on reefs for food and income security. However, further coral bleaching and macroalgal dominance are likely to increase the contribution of low trophic level fishes to fisheries catches and may increase dependency on those species.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data and code availability We provide data and code associated with this study at an open source repository (<https://github.com/Mark-H-22/sey-fish-prod.git>). The source data underlying all Figures (including Supplementary Figures) are provided as a Source Data file.

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