# Productive instability of coral reef fisheries after climate-driven regime shifts 

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#### Abstract

Tropical coastal communities are highly reliant on coral reefs, which provide nutrition and employment for millions of people. Climate-driven coral bleaching events are fundamentally changing coral reef ecosystems and are predicted to reduce productivity of coral reef fish and fisheries, with significant implications for food security and livelihoods. Yet evidence of long-term bleaching impacts on coral reef fishery productivity is lacking. Here, we analyse over 20 years of fish abundance, catch and habitat data to assess long-term impacts of climate-driven coral mass mortality and regime shifts on nearshore artisanal coral reef fisheries in the Seychelles. Contrary to expectations, total catch and mean catch rates were maintained or increased after coral bleaching, consistent with increasing abundance of herbivorous target species in underwater surveys, particularly on macroalgal-dominated reefs. Catch instability increased as habitats followed divergent post-disturbance trajectories and the distribution of target species became more spatially variable, potentially impacting fisher incomes and local market supply chains. Although coral bleaching increased fishery dependence on herbivore species, our results show that climate-impacted reefs can still provide livelihoods and fish protein for coastal communities.


Around 6 million people fish on coral reefs, and their estimated annual catches of 1.4-4.2 million tonnes provide critical sources of protein, micronutrients and income for many millions more ${ }^{1-3}$. Coral reef ecosystems are highly vulnerable to a changing climate, with extreme thermal events increasing in frequency and severity across the tropics ${ }^{4}$. Prolonged heat stress can trigger extensive coral bleaching and mortality, which, through subsequent loss of habitat structure, may cause local extinctions of coral-dependent fish species such as corallivores ${ }^{5}$, reduce taxonomic and functional fish diversity ${ }^{6}$ and, in some cases, initiate macroalgal regime shifts ${ }^{7}$. Bleaching-induced structural collapse of reefs is expected to cause recruitment failures of reef-dependent species and thus reduce the productivity of reef fisheries ${ }^{8}$. Projections of fisheries stocks under recurrent bleaching scenarios suggest that fisheries yields will decline as coral habitat decreases ${ }^{9}$, impacting livelihoods in fishery-dependent communities ${ }^{10}$. Yet evidence of benthic recovery ${ }^{7,11}$ and high response diversity of functionally important fishes ${ }^{6}$ point to contrasting responses of species to bleaching, with the potential to ameliorate losses of fisheries yield among reef-dependent species. Empirical tests of such changes are challenged by ecological lags that unfold over decadal time scales ${ }^{12}$ and by the paucity of long-term coral reef fisheries and ecological datasets from regions where the timing and scale of severe climate disturbances and the differential responses of reefs are fully documented.

Here, we investigate long-term changes in reef fishery catches, catch rates and catch composition over a 23 -year period that spanned a mass coral mortality event in 1998 when $>90 \%$ losses of live coral were followed by macroalgal regime shifts on some reefs ${ }^{7}$. To assess the evidence for indirect and lagged responses to this bleaching event, we analyse fishery-dependent observations from trap fishers ( 44,945 daily fisheries landing records from 41 landings
sites; 1994-2016) and fishery-independent fish and habitat observations on the fishing grounds in the Seychelles (960 underwater surveys at 12 sites; 1994-2014). Traps are used to target reef-associated species in shallow nearshore habitats and are widely used by coastal fishers in the tropics, including the Western Indian Ocean ${ }^{13}$, Pacific Island states ${ }^{14}$ and the Caribbean ${ }^{15}$. By focusing on a commonly deployed gear and reef-associated fishery in Seychelles, where longterm benthic changes are representative of bleaching impacts across Indo-Pacific reefs ${ }^{7}$, our findings are expected to provide insights into climate impacts on reef-associated fisheries in other regions.

## Results

Monthly, seasonal and interannual changes in the fishery were described with catch rates, catches and catch composition. In the Seychelles, trap gears are defined by duration of fishing deployment, with sturdier 'fixed' traps that catch fish passively and are deployed for one to three days and lighter 'active' traps that target spawning aggregations and are deployed for several hours ${ }^{16,17}$. Fishers group catches into 'packets' of several related species for sale at local markets ${ }^{16}$. These packets were weighed in fishery surveys and classed into three major groups, comprising (1) siganids, (2) a mixed species group of scarids and mullids and (3) lethrinids. Between 1994 and 2016, catch per unit effort (CPUE) for both fixed and active traps was higher for siganid and mixed species groups than lethrinid species (median observed CPUE $\pm$ s.e.m.: siganid $=3.49 \pm 0.11 \mathrm{~kg} \mathrm{trap}^{-1}, \quad 1.05 \pm 0.06 \mathrm{~kg} \mathrm{trap}^{-1} \operatorname{set}^{-1} \mathrm{~h}^{-1} ;$ mixed species $=3.10 \pm 0.08 \mathrm{~kg} \mathrm{trap}^{-1}, \quad 0.75 \pm 0.05 \mathrm{~kg} \mathrm{trap}^{-1}$ set $^{-1} \mathrm{~h}^{-1} ;$ lethrinid $=2.25 \pm 0.11 \mathrm{~kg} \mathrm{trap}^{-1}, \quad 0.73 \pm 0.07 \mathrm{~kg} \mathrm{trap}^{-1}$ set $\left.^{-1} \mathrm{~h}^{-1}\right)$. For all target species groups, fixed trap CPUE remained constant (siganid) or declined slightly through time (mixed species, lethrinid), which resulted in relatively stable long-term trends in overall CPUE across all species (Fig. 1a-d). For active traps, CPUE trends for mixed

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Fig. 1 | Temporal change in mean CPUE (1994-2016) for each target species group. a-h, CPUE estimates are shown for siganids (a,e), mixed species (b,f), lethrinids ( $\mathbf{c}, \mathbf{g}$ ) and across all catches combined ( $\mathbf{d}, \mathbf{h}$ ) with fixed traps ( $\mathrm{kg} \mathrm{trap}^{-1}$, top row) and active traps ( $\mathrm{kg} \mathrm{trap}^{-1}$ set $^{-1} \mathrm{~h}^{-1}$, bottom row). Estimates are predicted CPUE in each sampling month, holding seasonal, oceanographic and fleet size covariates to their means ( 0 ) for sampling strata on each island (thin solid and dashed lines, Mahé in light colours and Praslin in dark colours) and the mean effect across strata (thick solid and dashed lines).
species were weakly positive, although from 2010 to 2016 CPUE increased sharply for both siganid ( $\sim 1$ to $2 \mathrm{~kg}^{\operatorname{trap}}{ }^{-1} \operatorname{set}^{-1} \mathrm{~h}^{-1}$ ) and lethrinid ( $\sim 0.6$ to $1.2 \mathrm{~kg} \mathrm{trap}^{-1} \operatorname{set}^{-1} \mathrm{~h}^{-1}$ ) groups, driving similar increases in overall CPUE across all species (Fig. 1e-h).

Despite maintaining or increasing average catch rates, there was greater instability in fixed trap CPUE of siganids and mixed species after the bleaching event. Between 1994 and 2016, variation in daily CPUE within months (coefficient of variation of CPUE, $\mathrm{CV}_{\text {CPUE }}$ ) increased from $\sim 51$ to 65 for siganids (Fig. 2a) and $\sim 47$ to 58 for mixed species (Fig. 2b). For lethrinids, $\mathrm{CV}_{\text {CPue }}$ patterns were non-linear, declining from $\sim 80$ to 61 between 1994 and 2007 before increasing to ~75 by 2016 (Fig. 2c). CV $_{\text {CPUE }}$ trends were robust to background oceanographic and seasonal changes (Supplementary Fig. 1) and still apparent when we generated estimates solely from strata with high numbers of recorded catches (Supplementary Fig. 2), although we were unable to assess $\mathrm{CV}_{\text {CPUE }}$ for active traps that were less frequently deployed. Increased catch variability was partly explained by temporal changes in the frequency of very low and very high catches, defined as the $10 \%$ and $90 \%$ quantiles of observed CPUE, respectively. Subsampling from observed catches revealed declines in minimum CPUE for mixed species from 1994 to 2016 and lethrinid targets from 2008 to 2016 (Supplementary Fig. 3), which probably contributed to greater catch variability of these groups.

Despite greater instability of catch rates, increased fishing fleet size and maintenance of average CPUE combined to maintain or increase total catches across the post-bleaching period. From 1994 to 2016, total catches from fixed traps (average $=\sim 11$ metric tonnes ( t ) per month) exceeded active traps ( $\sim 4.8 \mathrm{t}$ per month) at both Mahé and Praslin islands, although catch compositions varied between gears and locations. Catches of siganid species generally exceeded catches of other species, except at Praslin Island where mixed species dominated fixed trap catches (Fig. 3). Catches displayed considerable interannual variability and, although trends were predicted with high certainty (deviance explained $=42-90 \%$
for all species $\times$ gear combinations, Supplementary Table 1), we found no evidence of consistent long-term changes in catch composition (Fig. 3; Supplementary Fig. 4). In the Mahé region there were long-term increases in siganid catches from $\sim 6$ to 16 t per month for fixed traps (Fig. 3a), coinciding with steady increases in fixed trap fleet size (Supplementary Fig. 5a). Mahé fixed trap catches did decline after bleaching (1998-2007) for mixed species (6-2.5t per month) and lethrinids ( $3-1.5 \mathrm{t}$ per month) but recovered to pre-bleaching levels between 2008 and 2014. In the Praslin region, catches were relatively stable for all species groups and both gears, and were consistently high from 2000 to 2010 , while mixed species catches doubled from 1 to 2 t per month between 2010 and 2014. For the siganid active trap fishery on Praslin, stability of catches after bleaching contrasted with CPUE increases between 2010 and 2016, although this was probably due to high uncertainty in catch predictions (Fig. 3d).

We investigated mechanisms underlying long-term fishery changes with fishery-independent monitoring data from the fishing grounds. Relative to pre-bleaching surveys in 1994, greater mean and spatial variance of siganid and mixed species biomass between 2005 and 2014 (Fig. 4a) corresponded with greater multivariate dispersion of these groups (Supplementary Fig. 6a-c,e). Increasing dispersion in species composition indicates that target species biomass was more variable among sites within survey years, and thus biomass availability to fishers would have been more spatially variable following bleaching. This was probably a response to greater spatial variation in habitat structural complexity, macroalgal cover and hard coral cover following bleaching (Fig. 4b and Supplementary Fig. 6d,f). Although we were unable to examine short-term ecological responses to bleaching (1998-2004), the spatial divergence of benthic community composition through time can be attributed to contrasting long-term post-bleaching trajectories, with structural complexity and coral recovering on some reefs, while other reefs shifted to macroalgaldominated states ${ }^{7}$.


Fig. 2 | Temporal change in CPUE variability (1994-2016) for target species groups landed by fixed trap gears. a-c, Model predictions of $\mathrm{CV}_{\text {CPuE }}$ shown for siganids (a), mixed species (b) and lethrinids (c). Lines are mean $\mathrm{CV}_{\text {CPUE }}$ predictions with seasonal, oceanographic and fleet size covariates held to their means (0) for sampling strata on each island (thin lines, Mahé in light colours and Praslin in dark colours) and the mean effect across strata (thick lines). Underlying $\mathrm{CV}_{\text {CPUE }}$ estimates were generated from a minimum catch threshold of five.

Regime-shifted sites with $10-50 \%$ macroalgal cover supported a greater biomass of siganid species (2005-2014, post-bleaching) (Fig. 4c), whereas mixed species biomass was greater at recovering sites with higher structural complexity (Fig. 4d). Such accumulation of herbivore biomass is consistent with a shift towards bottom-heavy trophic structures at shifted and recovering reefs ${ }^{18}$, but the different biomass patterns probably reflect differing habitat associations of these groups. Many siganid species browse on macroalgae ${ }^{19}$ and recruit to macroalgal habitats ${ }^{20}$, and thus appear to benefit from moderate macroalgal growth on regime-shifted reefs (Supplementary Fig. 7c). Low siganid biomass at two sites with $>70 \%$ macroalgal cover suggests that siganid availability may decrease on some regime-shifted reefs, possibly due to fish avoidance of dense macroalgal habitats ${ }^{21}$, which may explain why median siganid biomass was similar between 1994 and 2014. Conversely, the mixed species group were most abundant on recovering reefs, owing to growth of scraper populations (Supplementary Fig. 7a) that can respond positively to increased availability of dead coral substrate ${ }^{22,23}$. Invertivore and mixed-diet species in the mixed species group, such as species in the family Mullidae, are habitat generalists and thus may have been least impacted by habitat shifts ${ }^{24}$. For lethrinid species, we detected biomass reductions at sites with high macroalgal cover (Fig. 4e). Reef-associated lethrinid species can be long-lived (15-24 years) and some species undergo ontogenetic
habitat shifts from macroalgal nurseries to adult reef habitats ${ }^{25}$, implying that rapid habitat change may have lagged and diffuse effects on population regulation. Thus, extensive areas of regimeshifted reef with high macroalgal cover may improve resources for juveniles, but limit habitat availability and abundance of adults ${ }^{26}$.

Increased spatial dispersion of target fish biomass coincided with greater catch variability $\left(\mathrm{CV}_{\text {CPUE }}\right)$, particularly of siganid species (Fig. 2a). Our data suggest that the link between increased spatial variance in siganid abundance (Fig. 4a) and increased temporal variation in siganid catches ( $\mathrm{CV}_{\text {CPUE }}$ ) was driven by increases in school sizes on regime-shifted reefs (Supplementary Fig. 8a). High CPUE is expected when larger schools encounter traps and, on regime-shifted reefs, mean siganid school sizes increased from 12 to 20 individuals between 2005 and 2014, whereas schools were rarely encountered on recovering reefs (Supplementary Fig. 8a). Subsampling from observed catches also revealed increases in maximum CPUE for siganids from 2007 to 2016, although maximum CPUE was highly variable post-bleaching through 2006 (Supplementary Fig. 3). This lagged response post-bleaching, which was strongly apparent in active trap CPUE (Fig. 1e) coincided with a rapid post-2005 increase in macroalgal cover on regime-shifted reefs ${ }^{7}$. Collectively, these sources of evidence imply that increases in siganid recruitment and thus school size, which drive the high $\mathrm{CV}_{\text {CPUE }}$ in the current fishery, were linked to the increase in macroalgal cover on shifted reefs.

For mixed species, greater $\mathrm{CV}_{\text {CPUE }}$ and decreasing minimum catch sizes occurred despite increased biomass on recovering reefs. Inference of mechanisms underlying variability in mixed species catches were confounded by the high number of species targeted $(n=27)$ and the differential responses of invertivore, grazer, browser and scraper groups to habitat change (Supplementary Fig. 7). However, greater variability in mixed species biomass ( $>60 \%$ unexplained deviance, Supplementary Table 3) and CPUE may be partially attributed to differences in habitat quality among recovering reefs, where mixed species biomass exceeded prebleaching levels at some sites and was depleted at others (Fig. 4d).

Sensitivity of fish population biomass, and hence CPUE, to environmental variation may also increase with fishing pressure owing to truncated age structures and changes in demographic parameters ${ }^{27}$. Although full population assessments are not currently feasible for the species in the groups we consider, the catch and effort data do not suggest substantial changes in fishing impact on siganids, which retained sufficient productivity to sustain catches after bleaching (Fig. 3). There is also no consistent evidence that siganid CPUE is maintained at low biomass as a result of hyperstability (Supplementary Fig. 8b,c), and the size structure of all species groups does not indicate overfishing of large individuals but instead suggests strong recruitment of small siganid size classes in 2008 and 2011, and greater biomass of large-bodied individuals in the mixed species group following bleaching (Supplementary Fig. 9). Finally, given its relevance to continuity of protein supply and income, we considered CPUE variation at the level of days within months rather than directly among years, and thus the majority of CPUE measurements in any given year are not impacted by substantial changes in population structures resulting from episodic or seasonal processes such as recruitment. Consequently, we conclude that the spatial differentiation of habitats, as driven by alternate benthic recovery trajectories ${ }^{7}$, coupled with larger school sizes on the regime-shifted reefs, account for the increased $\mathrm{CV}_{\text {CPUE }}$.

## Discussion

Contrary to the predicted declines in fisheries for coral reef-associated species following bleaching events and associated regime shifts ${ }^{6,8,9}$, our results show that changes in the structure of fish assemblages can help to maintain total catches. For example, increases in siganid abundance on regime-shifted reefs have helped to maintain


Fig. 3 | Temporal change in total catches (1994-2016) for each target species group in each region. a-d, Catch estimates for fixed (a,b) and active trap gears ( $\mathbf{c}, \mathbf{d}$ ), for siganids, mixed species and lethrinids around Mahé Island (top row) and Praslin Island (bottom row). Estimates are model predictions ( $\pm 2$ s.e.m.) for each sampling month holding seasonal and oceanographic covariates to their means (0).
catch rates and total catches across trap fisheries (Fig. 3), most notably for active traps, which selectively target spawning aggregations such as those formed by siganids ${ }^{17}$. Siganid species are typically short-lived and fast-growing. For example, Siganus sutor, a dominant species in the Seychelles trap catches, reproduce and recruit to fishery sizes within one year ${ }^{28}$ and can sustain high yields in algal-dominated systems despite intense exploitation rates ${ }^{13}$. Consequently, the siganid fishery is likely to be sustainable and provide effective buffering of the effects of the 1998 bleaching event. The increased fishery dependency on this small group of species, and evidence of interannual fluctuations in siganid availability (Fig. 3a-c), implies that fishery managers will need to focus strongly on maintaining the sustainability of the siganid fishery, informed by ongoing monitoring of biomass and catch rates. Furthermore, increased catch instability may impact individual livelihoods in any situation where there is strong short-term dependency on the fishery for food and income ${ }^{29}$, such as low-income artisanal sectors where poorer fishers are likely to be most vulnerable to changes in resource availability ${ }^{30}$. In the Seychelles, greater frequency of low catches (Supplementary Fig. 3) expose fishers to unstable incomes and local fish markets to fluctuations in the type and weight of landed species.

The paucity of long-term fishery-dependent data for coral reef systems restricts our findings to a case study of a single country. The reef ecology of the Seychelles and its trap fisheries are, however, expected to be representative of other exploited coral reefs. For example, average herbivore biomass levels and benthic conditions documented here are typical for Indian Ocean reefs, to the extent that the Seychelles' benthic trajectories accurately predicted postbleaching benthic states of other Indo-Pacific systems ${ }^{7}$. Trap gears similar to those used in the Seychelles typically target low trophic level fishes, such as Siganus sutor in Kenya ${ }^{13}$ and Scaridae throughout the Caribbean ${ }^{31}$, and so gear selectivities are comparable across
small-scale fisheries of Indo-Pacific ${ }^{13,14}$ and Caribbean nations ${ }^{15}$. Thus, given its representative reef ecology, gear usage and fishery selectivity, the Seychelles is a model system for understanding bleaching impacts on small-scale trap fisheries.

Since catch rates in trap fisheries increase when species become more abundant, and there are no specific restrictions on catch rates or target species, the increases in browser and scraper biomass directly benefit fishers. However, because reef ecosystems will be subjected to repeated and more intense thermal disturbances in the future ${ }^{32}$, the patterns we observe on reefs and in fisheries may be modified by additional impacts on recovering reefs. These will alter the relative proportion of shifted to recovering habitats and the extent of suitable habitat for browser, scraper and invertivore target species. Furthermore, given that the presence of browsing, grazing and scraping fishes can increase the capacity for reefs to recover to coraldominated states ${ }^{33}$, fishing mortality on these species may need to be limited to maintain biomass and diversity at levels that are sufficient to preserve their functional role ${ }^{34,35}$. Although information on fisher movements and habitat targeting were unavailable for Seychelles, comparison of catch rates on recovering and regime-shifted reefs would help to define appropriate catch limits for reef fishes.

Our results demonstrate that catches from nearshore reef-associated fisheries can be maintained following climate-driven coral mortality. Fishery changes were underpinned by species' differential responses to the post-bleaching benthic trajectories, suggesting that projections for reef fisheries that are based on habitat-driven loss of fish biomass (for example ref.') have overlooked the potential for increased productivity of low trophic levels ${ }^{22}$, particularly browsing herbivores on regime-shifted reefs. Given our focus on a representative gear and a reef-associated fishery, our findings are applicable to other regions where bleaching events have occurred, but we caution that effective and ongoing fisheries management remains essential


Fig. 4 | Spatial heterogeneity in resource biomass and benthic habitat from 1994 to 2014. a, Boxplots of $\log _{10}\left[\right.$ biomass $\left.+1\left(\mathrm{~kg} \mathrm{ha}^{-1}\right)\right]$ for siganid (green), mixed species (orange) and lethrinid (blue) species groups from 1994 to 2014, boxes are 1st and 3rd quantiles with solid median line, whiskers extend to $1.5 \times$ interquantile range. $\mathbf{b}$, Functional dispersion of fish biomass and benthic composition. Euclidean distance of each site to its group centroid (groups = all sites in one year) for biomass of trap target groups ( $y$ axis) and benthic composition of hard coral, macroalgae and structural complexity ( $x$ axis). Points are distance to group centroids coloured by year, with mean values as large points $\pm 2$ s.e.m. Lines are fitted linear regression of fish dispersion-benthic dispersion, with dashed $95 \%$ confidence intervals (slope coefficient $=0.23 ; P<0.05$ ). $\mathbf{c - e}$, Model predictions for each target species group $\log _{10}[$ biomass $+1(\mathrm{~kg}$ ha-1)] from 1994 to 2014 against the habitat covariate that explained the highest proportion of deviance explained (Supplementary Table 3). Panels show siganids (c) (macroalgae, 23\% deviance explained), mixed species (d) (structural complexity, 10\%) and lethrinids (e) (macroalgae, 14\%). Fitted lines are the predicted smooth effects of each focal benthic covariate on fish biomass holding all other covariates constant, and points are partial residuals for recovering (triangles) and shifted (points) regime states as defined in ref. ${ }^{7}$. Shaded intervals are 2 s.e.m. from the fitted smooth line and rugs indicate distribution of data along each $x$ axis.
to sustain yields in any reef fishery and that projected increases in the intensity and frequency of bleaching will influence impact and recovery trajectories.

## Methods

Reef ecosystems of the Inner Seychelles support a diverse artisanal fishery that targets herbivorous, invertivorous and piscivorous fishes in shallow nearshore habitats ${ }^{35}$. The nearshore fishery predominantly uses bamboo traps that are either set on the reef floor and left to soak for one to three days ('fixed traps') or deployed at different depths for shorter soak times ('active traps') ${ }^{16}$. Trap fishery target species are primarily browsing Siganidae and scraping Scaridae species, although catches of Lethrinidae, Mullidae and Lutjanidae are also important contributions to annual total catches ${ }^{16}$. Other gears such as handlines and gillnets also contribute substantially to artisanal catches and employment but because these typically target pelagic or deep water species ${ }^{36,37}$ for which abundance is not assessed by fishery-independent surveys, we focus here on the shallow, nearshore trap fishery only. First, we analysed fishery-dependent data of daily catches to examine temporal trends in fishery catch rates, fleet size and effort between 1994 and 2016. Ecological changes underlying fishery trends were then investigated using fishery-independent underwater monitoring data of fish biomass and benthic composition to examine potential mechanisms underlying changes in fishery resources before (1994) and after (2005-2014) mass bleaching.

Fishery-dependent datasets. Catch estimates were extracted from the Seychelles Fishing Authority (SFA) database of standardized catch assessment surveys. From 1988 to 2016 (except 1996), SFA conducted monthly surveys at 41 landings sites distributed across the Seychelles' two main islands (Mahé and Praslin) (Supplementary Fig. 10) in which fish catches were categorized by boat type (pirogue, outboard motor, schooner and whaler) and gear (fixed and active traps, handlines, gillnets). Catches were recorded by coarse species groups, which were defined by SFA according to how fish are packaged for sale and consumption into 'packets' of several species ${ }^{16,38}$. To ensure that surveys were representative of catch and effort of each fishing sector, landings sites were grouped according to their geographic location, and then stratified by the number of boat types and survey locations randomly allocated in each month. Thus, the number of surveys conducted each month were proportional to the number of active fishing boats in each landings site (between 1 and 22 surveys, with a median of 3). In each survey, observers subsampled landed catches to estimate landed weight by species and gear, as well as fishing effort in terms of the number of traps set (fixed gears), number of traps, hours and sets (active gears) and total number of active boats (by gear type). To ensure catch data came from shallow reef habitats we examined catches from pirogues (unpowered or boats with up to 15 horsepower outboard engines) and low-powered motorboats ( $15-40$ horsepower) that are limited to inshore fishing grounds ${ }^{16}$. We selected reef-associated species groups, Siganidae (five species), Lethrinidae ( 12 species) and a mixed species group of Acanthuridae, Scaridae, Mullidae, Labridae and Haemulidae (27 species), which together comprise $>95 \%$ of total trap fishery catches ${ }^{38}$ (Supplementary Table 4). The mixed
species group was dominated by grazers and scrapers ( $n=20$ species), but also contained several invertivorous and mixed-diet species $(n=7)$. The SFA trap catch database consisted of 44,945 catch records spanning 41 sites in six strata across Mahé and Praslin from January 1994 to December 2016. Because catch surveys were compiled from landed catches, CPUE estimates do not account for fishing trips with zero total catches, but do include trips where individual traps did not catch fish. Thus, our analyses describe temporal changes in successful fishing trips rather than in catch success rates.

For each survey, we estimated the mean CPUE of each landed species group by gear type (fixed or active traps). Effort was defined separately for fixed (kg trap ${ }^{-1}$ ) and active gears (kg trap $\left.{ }^{-1} \operatorname{set}^{-1} \mathrm{~h}^{-1}\right)$, and we corrected large catches that may have been incorrectly reported by capping CPUE outliers at their $95 \%$ quantile. These daily catch estimates were then used to estimate the mean and coefficient of variation of CPUE (equation (1)) in each month for each landings stratum:

$$
\begin{equation*}
\mathrm{CV}_{\mathrm{CPUE}}=\frac{\text { standard deviation }(\mathrm{CPUE})}{\operatorname{mean}(\mathrm{CPUE})} \tag{1}
\end{equation*}
$$

To ensure $\mathrm{CV}_{\mathrm{CPUE}}$ estimates would not be biased by months with few catches, we constrained estimates to strata with $\geq 5$ landed catches per month (for each gear $\times$ species group in each stratum). Our minimum catch threshold reduced the catch dataset to 27,936 records ( $62.2 \%$ of the full dataset) and prevented regular $\mathrm{CV}_{\text {CPUE }}$ estimation for active traps, which were deployed far less frequently $(7,127$ records). We examined the sensitivity of $\mathrm{CV}_{\mathrm{CPUE}}$ estimates to sample size by also estimating $C V_{\text {CPUE }}$ for a minimum catch threshold of $\geq 10$ catches (per month, for each gear $\times$ species group in each stratum). Lethrinid catches were also rarer than those for both siganid and mixed species groups, such that our fixed gear $\mathrm{CV}_{\mathrm{CPUE}}$ estimates for lethrinids with a ten-catch threshold were limited to four strata in irregular months from 1995 to 2016.

To link observed $\mathrm{CV}_{\mathrm{CPUE}}$ trends with expected fishery catch weights, we measured temporal change in the value of very low and very high catch weights, represented by the $10 \%$ and $90 \%$ quantiles of observed CPUE, respectively. We ensured that quantiles were robust to catch differences among landings sites and potential outliers across years by subsampling from observed CPUEs. For each species group, we randomly sampled 100 (siganid and mixed species) or 50 (lethrinid) observed CPUEs and extracted the $10 \%$ and $90 \%$ quantile, repeating subsampling for 1,000 replicates. Temporal change in very low and very high catches was visualized using the median and $5 \%$ and $95 \%$ percentiles of the bootstrap distribution across years.

In addition to sampled catch and effort data, SFA provided total monthly catch estimates for each stratum, species group and gear type. SFA converted daily sampled catch weights to stratum-level monthly landed weights (metric tonnes) by accounting for the number of boats fishing during each survey that were not sampled, the registered number of boats per landings site and the number of fishing days in each month ${ }^{39}$. Daily catches were extrapolated to monthly total catches for each landings site and calculated across all sites on each island for each month between 1994 and 2016. We also considered shifts in overall fishery composition by extracting catches of non-target species groups, for which data were available between 2000 and 2016. Mean catches were $\log _{10}$ transformed to ensure normality prior to statistical modelling.

We considered several oceanographic and seasonal explanatory covariates that might explain temporal variation in catches. Within years, seasonal monsoon patterns influence nearshore fishing activity of small boats, whereby trap fishing activity is limited by adverse sea conditions during the southeast monsoon (June-September) and catches are higher during the calmer northwest monsoon (October-May) ${ }^{16}$. Between years, variability in temperature and productivity of the Indian Ocean is driven by the El Niño/Southern Oscillation (ENSO) and Indian Ocean dipole (IOD) ${ }^{40}$, which may influence fish catches by altering both resource availability and gear effectiveness. For example, recruitment of siganid and lethrinid species to macroalgal habitats in western Australia has been linked to oceanographic processes that, through periodic temperature changes, may influence both larval supply and habitat quality ${ }^{41}$. Furthermore, trap gear effectiveness has been linked to fine-scale variation in ocean current strength ${ }^{42}$, although associations between ENSO, IOD and trap fishery CPUE remain untested. We extracted two oceanographic covariates that represented ENSO and IOD strength for each month sampled in the catch dataset (1994-2016). The Bivariate ENSO Timeseries (BEST; https://www.esrl.noaa.gov/psd/people/ cathy.smith/best/\#years) combines atmospheric pressure variation (the Southern Oscillation index) with mean oceanic temperature (HadSST Niño 3.4) differences across the Indian Ocean, standardized by each month across the time series 1988 to $2017^{43}$. Positive values indicate a strong ENSO phase of warm climate conditions (that is, El Niño) and negative values indicate weak, cooler ENSO phases (that is, La Niña). The dipole mode index (DMI; https://www.esrl.noaa.gov/psd/ gcos_wgsp/Timeseries/DMI/) measures the strength of the IOD using a gradient of sea surface temperature values between the western and southeastern zones of the equatorial Indian Ocean, with positive values associated with anomalous oceanic warming and negative values with anomalous oceanic cooling ${ }^{44,45}$.

In addition to oceanographic and seasonal effects, we considered the effect of long-term changes in fleet size and individual fisher effort on temporal catch
patterns. We developed a proxy of monthly fishing activity at each island that represents the total fleet size in the trap fishery and accounts for incomplete sampling of sites and fishing days (that is, not all active fishing boats were censused). For each landings site in each month, we averaged the survey-level estimates of the number of active fishing boats by gear type (fixed or active trap) and then calculated these monthly averages across all sites on each island (Mahé or Praslin). In this way, 'fleet size' represents the average daily number of active fishing boats on each island for each gear type in each surveyed month. We also examined temporal trends in individual fisher effort, represented by average trap deployment time per fishing trip. Gear use was defined separately for each gear type, whereby fixed trap effort was the mean number of traps deployed and active trap effort was the mean number of trap deployment hours, across all fishing trips in each month, per stratum.

Fishery-independent datasets. Changes in fish resource availability and benthic habitat composition were assessed with fishery-independent survey data. Underwater visual censuses (UVC) were conducted at 12 locations on the reef slope of the Inner Seychelles in five survey years between 1994 and 2014 (Supplementary Fig. 10). Surveyed locations were distributed equally among patch reefs ( $n=4$ ), fringing carbonate reefs $(n=4)$ and granitic rocky reefs $(n=4)$, and were all located in or adjacent to trap fishing grounds ${ }^{16}$. We assigned UVC sites the same strata categories as in the catch dataset, excluding Mahé NE for which no visual surveys were conducted in trap fishing grounds. Fish communities were censused in $7-\mathrm{m}$ radius survey areas $\left(154 \mathrm{~m}^{2}\right)$ by one scientific diver (S.J. or N.A.J.G.) at 4.5-9.5 m depth. In each count, the diver recorded the abundance, size and species identity of individuals $\geq 8 \mathrm{~cm}$ total length from a list of 134 diurnally active reef-associated species ${ }^{7}$. Large mobile species were censused before smaller reef-dwelling species to minimize diver avoidance or attraction. Following each fish survey, a second scientific diver (S.J. or S.K.W.) conducted a visual assessment of reef topography and benthic community composition. Percent cover of habitatforming groups (hard corals, soft corals, macroalgae), rubble, sand and rock were recorded in each point count survey area. Structural complexity was assessed on a six-point scale from 0 (reefs of no vertical relief) to 5 (highly complex overhangs and caves ${ }^{46}$. As with the fish observations, estimates were averaged across replicates to produce site-level benthic cover values.

Counts were replicated within locations at 16 sites in 1994, 2005 and 2008, and eight sites in 2011 and 2014. To avoid introducing biases associated with unequal sampling effort among replicates, we restricted our analysis to the first eight site replicates of 1994, 2005 and 2008, such that every site was represented by eight surveys in each year. Although the UVC observer changed between 1994 (S.J.) and 2005-2014 (N.A.J.G. and S.K.W.), survey methods were identical between years and observer bias is minimal for UVC surveys of Indian Ocean reefs ${ }^{47}$. Biomass estimates were produced by converting lengths to masses using published length-weight relationships ${ }^{48}$, adding biomass of each species within each replicate and averaging across replicates within each site. Species were assigned functional feeding groups based on diet and behaviour ${ }^{7}$. We matched UVC data to catch surveys and thus focused on siganids (three of five target species observed in UVC), the mixed species group ( 24 of 27 species) and lethrinids ( 7 of 12 species) (Supplementary Table 4). Surveys were designed to census reef-associated fishes and, as such, provided reliable insights into the availability of herbivorous and invertivorous species to trap fishers. We note that Lethrinidae are often poorly sampled by underwater visual surveys ${ }^{49}$, which may have confounded our interpretation of habitat and fishing effects on these populations.

Temporal trends in catches from fishery analyses. We examined trends in mean CPUE, $\mathrm{CV}_{\text {CPUE }}$ and total monthly catches using generalized additive models (GAM) fitted with oceanographic, seasonal and fleet size covariates, and autocorrelation structures that accounted for catches landed within sampling strata. In this way, we used GAMs to standardize CPUE and total catches to oceanographic, seasonal and fleet size influences, and thus isolate the temporal catch trends. In all GAMs, main effects were cubic regression smooths for sampling month (1994-2016), ENSO, DMI and mean number of active boats. Seasonality was captured in a cyclic month term that was independent of year (that is, January-December) and fitted with 12 knots, and autocorrelation structures were captured by allowing random temporal smooths for catches within strata. The degree of model smoothing was assessed by fitting each cubic regression smooth to different knot values $(k)$ and selecting the model with lowest Akaike's information criterion (AIC). For competing models that were not distinguished by AIC values (that is, AIC difference in models <2), we selected the simpler model (that is, lower smoother value) ${ }^{50}$ (Supplementary Tables 1 and 2). We further checked that smooths were defined appropriately by ensuring that the effective degrees of freedom were sufficiently lower than $k$ (gam.check in $m g c v$ ) ${ }^{51}$. For each final model, we assessed fitted residuals for normality and measured model performance with deviance explained values. We inferred temporal changes by visualizing predictions of mean standardized CPUE and $\mathrm{CV}_{\text {CPUE }}$ for each gear and species group across all landing sites (that is, mean temporal trend) and separately for each stratum (that is, random smooth predictions) from 1994 to 2016. Stratum-level catch estimates were unavailable, and therefore catch GAMs were fitted with random smooths for each island (Mahé or Praslin) and temporal trends were predicted at the island scale. All explanatory
covariates were scaled and centred to a mean of 0 and standard deviation of 1 . CPUE and CV $_{\text {CPUE }}$ models were fitted with gamma distributed errors.

We assessed temporal catch trends in the context of changing fishing effort. Following the same GAM fitting procedure in the catch analysis, we fitted GAMs to estimates of fleet size and average gear use through time. Main effects were cubic regression smooths for sampling month (1994-2016), ENSO, DMI and month (cyclic smooth). Autocorrelation structures were captured with random temporal smooths for island region (fleet size) or strata (average gear use). Models were fitted separately for fixed and active traps.

Spatio-temporal variability of fish and benthic communities from UVC analyses. We used fishery-independent UVC data to assess whether fishery resource availability, habitat composition and fish-habitat associations had changed through time and space. First, we examined the spatial variability of target species biomass and benthic composition with a multivariate, abundance-based dissimilarity metric. Multivariate dispersion quantifies the dissimilarity in species composition among sampling units ${ }^{52}$ and was employed here to quantify withinsurvey spatial variability in (1) relative biomass of target species and (2) benthic composition of habitat-forming groups. For fish, we computed distance to centroid values of mean site-level estimates of $\log _{10}\left[\right.$ biomass $\left.+1\left(\mathrm{~kg} \mathrm{ha}^{-1}\right)\right]$ for each target species group (Siganidae, mixed species and Lethrinidae) in each survey year. Biomass estimates were scaled and centred, and then converted into a Euclidean distance matrix. Compositional dissimilarity in each year was the mean distance of all sites to the group (that is, survey year) centroid. For benthos, we measured dispersion in the relative abundances of dominant benthic taxa (hard coral and macroalgae) and in reef topography across survey years. Multivariate dispersions were computed using the percentage cover of hard coral and macroalgae, and structural complexity (six-point scale) was computed by grouping sites by survey year. As for fish biomass, we $\log _{10}(x+1)$ transformed cover and complexity values, scaled and centred each covariate, converted into Euclidean distances and estimated the mean distance to group centroids. Temporal change in spatial variability was assessed by linearly regressing fish-benthic dispersion distances, and with permutational multivariate analysis of variance (PERMANOVA) to assess year effects for fish and benthic dispersion distances separately ${ }^{52}$.

We examined fish-habitat associations through time by fitting GAMs to $\log _{10}$ transformed site-level biomass estimates for each target group. Survey year $(n=5)$, structural complexity, hard coral cover and macroalgal cover were fitted as cubic regression smoothers, each with 5 knots. Possible autocorrelation between sites within strata was modelled as random smooths, and model fits were assessed using residual plots and deviance explained estimates. The strength of predicted relationships was assessed by estimating the variance uniquely explained for each smoothing term, using deviance measures of global and reduced models ${ }^{53}$. We extracted the deviance explained by the global model $(G)$, a null model $(y \sim 1)$ $(N)$ and a series of reduced models with each explanatory covariate removed but constrained to fit the original smoothing terms (from the global model) for each remaining parameter ( $X_{i}$, where $i$ is the explanatory covariate of interest). Deviance uniquely explained by each explanatory covariate ( $i$ ) was:

$$
\begin{equation*}
\frac{\text { deviance }\left(X_{i}\right)-\text { deviance }(G)}{\text { deviance }(N)} \times 100 \tag{2}
\end{equation*}
$$

Fish-habitat relationships were visualized using partial residual plots and the robustness of those relationships to pre-bleaching observations was tested by refitting GAMs without 1994 surveys.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## Data availability

All analyses were conducted in R 3.4.2 ${ }^{54}$ using $m g c v^{51}$ and $v e g a n^{55}$. Model predictions and R analysis scripts are provided at github.com/jpwrobinson/prodinstability. The fishery-dependent dataset is not publicly available but may be requested from the authors with permission of SFA.

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## Author contributions

J.P.W.R., S.K.W. and N.A.J.G. conceived the study and wrote the first draft of the manuscript, with substantial input from S.J. Underwater ecological data were collected by S.K.W., S.J. and N.A.J.G. C.G., J.R., J.L., C.A. and R.G. designed and managed the Seychelles fisheries monitoring programme. J.P.W.R. conducted all statistical analyses.

## Competing interests

The authors declare no competing interests.

## Additional information

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Clearly defined error bars
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## Software and code

Policy information about availability of computer code
Data collection
Fisheries data were collected in ARTFISH database (see Mees, C. C.. Seychelles Artisanal Catch Assessment Survey: Notes for
Implementation. Seychelles Fishing Authority, 1990).
Data analysis

| All analyses were conducted in R (version 3.4.2) and we provide all R code required for statistical models and figure creation at https:// |
| :--- |
| github.com/jpwrobinson/prod-instability |

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## Data

[^1]
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# Ecological, evolutionary \& environmental sciences study design 

| Study description | Fisheries data ( 44,945 catch records from 41 landings sites): temporal trends over 1994-2016 in the 1) monthly mean and monthly coefficient of variation of catch-per-unit-effort and 2) fishery catches were analyzed with general additive models, with date, oceanographic and seasonal covariates as explanatory factors, and random fisheries landings site correlation structures to account for non-independence of fishers catches through time. Models were fitted separately to 3 fish target groups. Underwater data (12 sites each with 8 replicate surveys in each year): spatial variation in the mean biomass of target fish groups and mean benthic cover of habitat-forming taxa were analysed over time (5 years in 1994-2014) using multivariate dispersion methods. Temporal trends in fish biomass were also fitted with general additive models, with time and benthic cover (coral, macroalgae, complexity) as explanatory covariates and survey location as random correlation structures, separately for each fish target group ( $n=3$ ). |
| :---: | :---: |
| Research sample | Fisheries data were the identity and weight of reef-associated fishes caught by trap fishers in Seychelles, collected as part of a longterm monitoring program by the Seychelles Fishing Authority over 1994-2016. Underwater data were the identity, size and abundance of reef-associated fishes and benthic composition (percent cover) at shallow, hardbottom reef habitats in the inner Seychelles, collected by coauthors Shaun Wilson, Simon Jennings and Nick Graham over 1994-2014. |
| Sampling strategy | Fisheries data: daily catches of individual fishers were randomly surveyed by observers, with survey site location and survey frequency allocated according to fishing effort across Seychelles landings sites. Underwater data: fish and benthic survey locations were replicated at 12 sites in fishing grounds across the inner Seychelles, including 3 reef habitat types. Surveys were repeated at each site in each year for 8 or 16 replicates, though we only analyzed the first 8 replicates to maintain consistent sampling effort through time. |
| Data collection | Fisheries data were collected by trained fisheries observers using standardized catch assessment surveys (Seychelles Fishing Authority). Underwater data were collected by coauthors Shaun Wilson, Simon Jennings and Nick Graham by visual observation. |
| Timing and spatial scale | Fisheries data: surveys were conducted from January 1st 1994 to December 31st 2016, excluding 1996. Surveys were conducted daily but, as landings sites were stratified by fishing effort, not all landings sites were surveyed in every day. The spatial scale encompassed all of Mahe and Praslin islands. Underwater surveys were conducted in April of 1994, 2005, 2008, 2011 and 2014, encompassing 12 sites adjacent to the coastlines of Mahe and Praslin islands. |
| Data exclusions | We excluded fisheries landings of species that were rarely caught by trap fishers, and excluded these species from underwater observations. Where appropriate, we excluded underwater replicates 9-16, thus ensuring consistent sampling effort through time, |
| Reproducibility | The study was conducted with observational data and was not repeatable. We provide analysis code scripts and model predictions to replicate statistical analyses. |
| Randomization | Fisheries survey locations were stratified among Seychelles' fishing ports according to levels of fishing activity, whereby heavily-fished locations were surveyed more frequently. Underwater surveys were stratified to equitably survey granitic, carbonate and patch reef habitat types. Target fish species were grouped according to genus (e.g. Siganid) or to their grouping at fish markets (e.g. mixed species). |
| Blinding | Blinding was not possible because fisheries observers repeatedly sampled fishers through time, and were familiar to the fishing community. |

Did the study involve field work? $\quad \square$ Yes $\quad \square$ No

## Field work, collection and transport

Field conditions

Location

Access and import/export

Fishery surveys were conducted daily in every year from 1994-2016. Underwater surveys were conducted in April of 1994, 2005, 2008, 2011 and 2014 during the North-West monsoon period of calm ocean conditions, warm weather (average daily minimum $=25 \mathrm{C}$, average daily maximum $=31 \mathrm{C}$ ), and low rainfall (average daily precipitation $=175 \mathrm{~mm}$ ).

Nearshore coral reef habitats and trap fishing grounds of the inner Seychelles ( $4^{\circ} 30^{\prime} 16.4^{\prime \prime} \mathrm{S}, 55^{\circ} 32^{\prime} 38.5^{\prime \prime} \mathrm{E}$ ). Fishery surveys were conducted on land at fishing ports and underwater surveys were conducted at shallow depths ( $5-10 \mathrm{~m}$ ) on hard-bottom habitats.

Fisheries surveys were conducted by Seychelles Fishing Authority with permission from trap fishers and Seychelles' government.

## Reporting for specific materials，systems and methods

| Materials \＆experimental systems |  |
| :--- | :--- |
| $\mathrm{n} / \mathrm{a}$ | Involved in the study |
| $\searrow$ | $\square$ Unique biological materials |
| $\searrow$ | $\square$ Antibodies |
| $\searrow$ | $\square$ Eukaryotic cell lines |
| $\searrow$ | $\square$ Palaeontology |
| $\searrow$ | $\square$ Animals and other organisms |
| $\searrow$ | $\square$ Human research participants |


| Methods |  |
| :---: | :---: |
| n／a | Involved in the study |
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| 】 | $\square$ Flow cytometry |
| 】 | $\square$ MRI－based neuroimaging |


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