

## SCIENCE POLICY

# Diversification insulates fisher catch and revenue in heavily exploited tropical fisheries

James P. W. Robinson<sup>1\*</sup>, Jan Robinson<sup>2</sup>, Calvin Gerry<sup>3</sup>, Rodney Govinden<sup>3</sup>, Cameron Freshwater<sup>4</sup>, Nicholas A. J. Graham<sup>1</sup>

Declines in commercial landings and increases in fishing fleet power have raised concerns over the continued provisioning of nutritional and economic services by tropical wild fisheries. Yet, because tropical fisheries are often data-poor, mechanisms that might buffer fishers to declines are not understood. This data scarcity undermines fisheries management, making tropical fishing livelihoods particularly vulnerable to changes in marine resources. We use high-resolution fisheries data from Seychelles to understand how fishing strategy (catch diversification) influences catch rates and revenues of individual fishing vessels. We show that average catch weight decreased by 65% over 27 years, with declines in all nine species groups coinciding with increases in fishing effort. However, for individual vessels, catch diversity was associated with larger catches and higher fishing revenues and with slower catch declines from 1990 to 2016. Management strategies should maximize catch diversity in data-poor tropical fisheries to help secure nutritional security while protecting fishing livelihoods.

## INTRODUCTION

Tropical fisheries composed of diverse fleets, from low-technology artisanal fishers to large commercial vessels, contribute a large proportion of domestic wild fish and dietary nutrition for tropical nations (1) and provide employment for millions of people (2, 3). Recent national-scale catch reconstructions, however, have indicated that many tropical fisheries are declining (4, 5) as artisanal fishing effort accelerates (6), raising concerns over food security in tropical regions where growing human populations will require greater nutritional returns from marine resources (1, 7). Yet, analyses of national-scale databases mask changes in the status of specific fisheries (e.g., by gear or species) and are unable to identify differences in catch rates and fishing strategies among individual fishers and vessel types. Data deficiency in tropical fisheries is compounded by the diversity within tropical socioecological systems, where fishers typically target multiple habitats (demersal, pelagic, and coral reef) using various gears (lines, traps, and nets) to exploit hundreds of fish species (8–10). Without fine-scale information about catch composition, fishing effort, and catch rates, it remains unclear which fishers may be most affected by the depletion of fish populations and which management strategies can achieve sustainability in fisheries (11) while minimizing costs to fishing communities (12).

Fishers may minimize economic risk during periods of environmental change by pursuing catch strategies that balance exploitation across several populations (13). When populations fluctuate asynchronously, this catch diversification can stabilize incomes to changes in catch rates of single stocks that might occur following ecological regime shifts (14) or spatial shifts in species distributions (15), and diversification has been proposed as a framework for promoting socioeconomic resilience by buffering fishing revenues against species-specific declines associated with overfishing (13, 16). Diversification effects, however, are largely understood in the context of highly regulated commercial fisheries in the United States (15, 17, 18), leaving

tropical systems understudied. Dynamics of data-rich temperate fisheries may be unreliable indicators of dynamics in tropical fisheries, which typically involve far higher numbers of fishers, use unconventional governance systems, and may have greater standing stock biomass (19, 20). As a result, catch diversification may operate differently in systems where marine resources are both unmanaged and heavily exploited. Diversification is frequently proposed as an adaptation strategy to increase the resilience of tropical nations to changes in fishery resources (7, 21, 22), and yet, our empirical understanding of current levels of catch diversification practiced by tropical fishers is limited, while the effect of diversification on catch rates and fishing revenues is unknown.

In this study, we test how catch diversification affects the catch success of individual fishers participating in declining tropical fisheries. We use a rare data-rich tropical fishery in Seychelles, an archipelago nation in the Indian Ocean. In Seychelles' exclusive economic zone of 1.37 million km<sup>2</sup>, offshore artisanal fisheries target over 100 fish species in pelagic and demersal habitats. These fisheries are unmanaged but routinely monitored and account for 40% of artisanal landings with 80% of the catch sold and consumed domestically. The fishers exclusively use handlines but target different fish groups by altering the number of hooks, bait type, and line deployment strategy (vertical droplines, floated lines for midwater, and bottom set lines). Fishers may also supplement their typical catches by targeting seasonal spawning aggregations (23), night fishing, or fishing cooperatively to stimulate feeding by semipelagic species. Recent stock assessments indicate that several economically valuable species are at high risk of overexploitation (24) but the landed seafood sustains an increasing local population, a growing international demand for tropical products, and a large tourism sector (25). Using daily catch data spanning 1990–2016, we quantify the magnitude of catch declines across different species groups. By tracking vessel-specific catch rates over 10 years, we model data on vessel size and effort, catch diversity, market value of species, and fishing ground size to understand how diversification influences catch rates and fishing revenues. Given the paucity of high-resolution catch data in tropical coastal nations, these data can provide an important empirical basis for investigating diversification effects in unmanaged artisanal fisheries in the tropics.

<sup>1</sup>Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK. <sup>2</sup>Ministry of Finance, Trade and Economic Planning, Victoria, Seychelles. <sup>3</sup>Seychelles Fishing Authority, Fishing Port, P.O. Box 449, Mahe, Seychelles. <sup>4</sup>Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia, Canada.

\*Corresponding author. Email: james.robinson@lancaster.ac.uk

## RESULTS

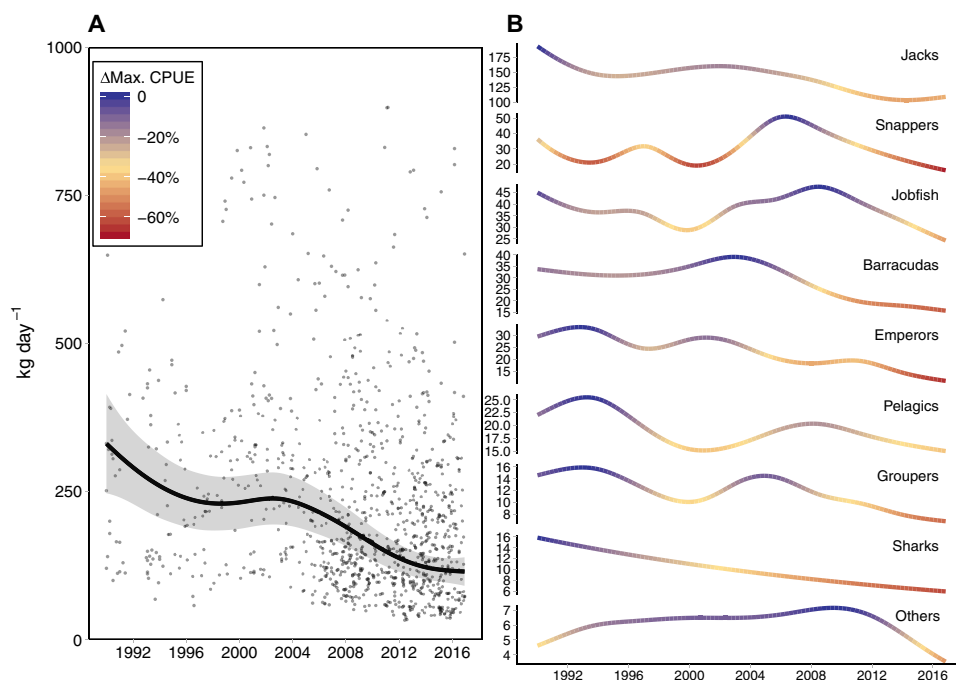
Total catch per unit effort (CPUE) decreased substantially from 1990 to 2016 across the fishery, with declines in all nine species groups contributing to an overall 65% decline from 330 to 115 kg day<sup>-1</sup> (Fig. 1A). The largest declines occurred for groups with the highest landed weights. For example, jacks (Carangidae; 193 to 109 kg day<sup>-1</sup>), snappers (Lutjanidae; 36 to 16 kg day<sup>-1</sup>), jobfish (*Aprion virescens*; 45 to 24 kg day<sup>-1</sup>), and barracuda (Sphyraenidae; 34 to 16 kg day<sup>-1</sup>) all declined by over 40% from 1990 to 2016 (Fig. 1B). Other target groups also declined at similar rates, but these were typically lower catch weights and thus contributed less to overall CPUE. Many species groups were characterized by nonlinear behavior with short periods of increasing CPUE (2 to 6 years), and catches of jobfish, snappers, and barracudas were highest during the middle of the time series. Sharks, in contrast, were characterized by steady linear decline in CPUE from 16 to 6 kg day<sup>-1</sup>. For all species, the lowest catch rates observed in the time series occurred in the most recently surveyed year (2016), and these CPUE declines contributed to a ~50% reduction in total landed weight over 2000–2016 (from ~200 to 100 metric tons month<sup>-1</sup>; fig. S2).

Long-term declines in fishery CPUE occurred during a spatial expansion of fishing grounds, a shift toward longer fishing trips, and increase in fleet size. For the 57 vessel monitoring data (VMS)-tracked vessels that were active in at least 5 years between 2006 and 2015, fishing vessels covered a greater area within the Mahé plateau fishing ground, with the average fishing area covered annually by one vessel increasing from 2300 to 3100 km<sup>2</sup> (fig. S3A) and the total area covered by fishing vessels each year increasing from 28,000 to 32,000 km<sup>2</sup> (fig. S3B). Effort data from catch surveys were consistent with a fleet-wide fishing ground expansion, with vessels using more fuel and un-

dertaking longer fishing trips over 1990–2016 (fig. S3, C and D). Over the same time period, the active fishing fleet increased fivefold, from 16 to 82 active vessels year<sup>-1</sup> (fig. S3E).

For a focal fleet of 41 vessels tracked from 2006 to 2015, the magnitude and rate of catch declines varied among vessels (fig. S4), suggesting that fishing strategy and vessel capacity might moderate fishing success (Table 1). Differences in vessel capacity were also strong predictors of catch success (Fig. 2, A, B, and E). CPUE increased fivefold from the smallest (3 m, 50 kg day<sup>-1</sup>) to largest boats (13 m, 270 kg day<sup>-1</sup>) and from 130 to 260 kg day<sup>-1</sup> as engine power increased from 2 to 195 horsepower. Vessels that expended more effort had lower catch rates, with CPUE declining as fishing trip length increased from 1 to 7 days (225 to 70 kg day<sup>-1</sup>; Fig. 2C). Vessels fishing in eastward locations also had marginally greater catch rates than those in westward locations, although most vessels operated between 55° and 56° (Fig. 2D).

With these vessel and spatial characteristics accounted for, we detected an effect of fishing strategy, with a strong positive effect of catch diversification on catch rates (Fig. 2E). For individual fishing trips, vessels targeting a more diverse range of fish species could increase their catch rate by up to ~50 kg day<sup>-1</sup>, relative to catches of single species groups (Fig. 3A). For the entire fleet across the entire monitoring time series, catch diversity provided some buffering of catches from long-term declines in CPUE (Fig. 3B), whereby CPUE of high diversity catches declined at a slower rate than did CPUE of low diversity catches. These effects did not coincide with temporal changes in catch diversity, which remained relatively constant from 1990 to 2016 (mean diversity, 0.64 ± 0.012; mean turnover, 0.74 ± 0.013), and were not caused by differences in catch diversity between the focal fleet and the full fleet (fig. S5) or correlations with vessel size (fig. S6). Catch turnover



**Fig. 1. Catch-per-unit-effort (kilograms per day) per fishing trip from 1990 to 2016. (A)** Total catches, where line is predicted generalized additive model (GAM) temporal smooth excluding seasonal, oceanographic, and vessel effects ( $\pm 2$  SEM), overlaid with points showing the partial effect of all other model covariates. **(B)** Catches by species group, where species are ordered by the relative contribution to overall catches. Lines are GAM temporal smooth predictions excluding seasonal, oceanographic and vessel effects, colored according to the percent change in CPUE relative to its maximum value (see fig. S1 for SEM of species-level trends).

**Table 1. Covariates for predictive models fitted to focal fleet datasets (2006–2015).** CAS, catch assessment surveys; SFA, Seychelles Fishing Authority vessel database collected in 2017; VMS, vessel monitoring data. Scale indicates the resolution of data collection. CAS covariates were averaged across surveys to give annual estimates.

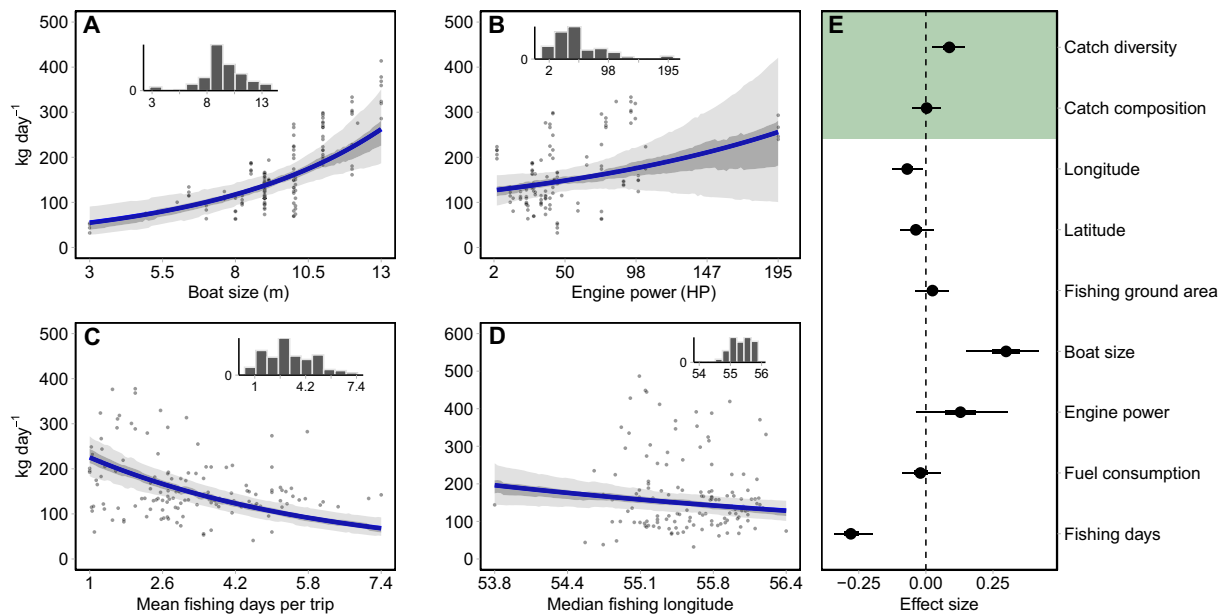
Covariate	Definition	Scale	Source	Vessel trait
<i>Fishing strategy</i>				
Catch diversity	Simpson's index of catch diversity	Individual fishing trip	CAS	Ability to target multiple species buffers catches to declines in single species groups (within fishing trips)
Catch composition	Bray-Curtis index of catch dissimilarity	Annual	CAS	Ability to switch target species buffers catches to declines in single species groups (among fishing trips)
<i>Vessel capacity</i>				
Longitude	Longitude of fishing activity	Annual	VMS	Location of fishing grounds
Latitude	Latitude of fishing activity	Annual	VMS	Location of fishing grounds
Fishing ground area	Area of fishing activity (square kilometers)	Annual	VMS	Ability to explore large and/or distant fishing grounds where fish populations may be less exploited or access areas of seasonal abundance (e.g., fish aggregations) buffers catches to local declines
Boat size	Length of boat (meters)		SFA	Influences fishing trip duration, fishing ground area, capacity to store fish, size of crew, impact of sea condition, amount of gear; enables vessels to target distant fisheries
Engine power	Engine size (horsepower)		SFA	Determines time spent fishing versus traveling to fishing grounds
Fuel	Fuel consumed (metric tons and USD)	Individual fishing trip	CAS	Financial capacity for distant and/or multiday fishing trips that may provide larger catches
Fishing trip duration	Days spent at sea	Individual fishing trip	CAS	Longer fishing trips may enable fishers to reach distant and less-exploited fishing grounds, increasing catch rates

over longer time periods (i.e., within years) was only weakly associated with catch rates (Fig. 2E).

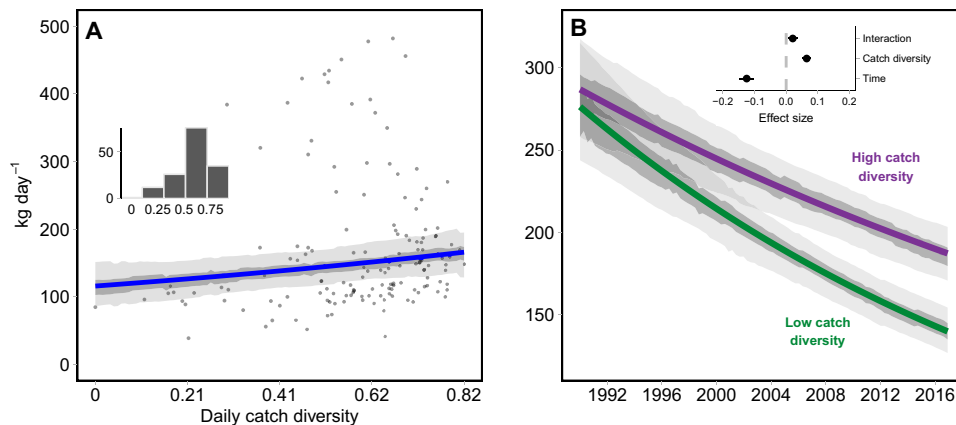
Vessel revenue also increased with catch diversification (Fig. 4, A and B). At the scale of individual fishers, revenue was partially associated with catch rates (for CPUE and USD per fisher per day, Pearson's correlation  $r = 0.33$ ) and, as a result, increased with catch diversity from 160 to 280 USD (per fisher per day; Fig. 4A). Even if correcting revenue by catch weight (USD per kilogram per fisher per day), strong catch diversification effects on revenue were only detected in 5 of 11 years, based on catch composition alone (Fig. 4C). These years coincided with high market values of rarer species such as red snappers, jobfish, and grouper, which had relatively low catch rates (CPUE, 17.5 to 84.5 kg day<sup>-1</sup>) but, from 2013 to 2016, were over double the market value of the most commonly caught species (jacks: CPUE, 260 kg day<sup>-1</sup>) (Fig. 4D).

## DISCUSSION

By distributing effort across a diverse stock portfolio, catch diversification across fisheries can help fishers to maintain catch rates during periods of variable abundance in fished populations (14). Yet, for tropical fisheries, which typically target high diversity ecosystems, the portfolio of strategies used by different fishers and effects of diversification on fishing success are unknown. Our study demonstrates that catch diversification raises the size and market value of catches and somewhat buffers individual vessels to long-term declines across multiple species groups. In addition to variation in catch rates caused by differences in vessel capacity, these analyses highlight mechanisms by which small-scale fishers may vary in their vulnerability to declining resources. The long-term declines in catch rates and total landed weight were concurrent with a quadrupling of fleet size, suggesting that exploitation pressure on pelagic and demersal fisheries has increased



**Fig. 2. Catch diversification and vessel capacity effects on mean CPUE from 2006 to 2016.** (A to D) Selected fishing capacity covariates with moderate or strong effects on CPUE. Lines are the median effect from 1000 posterior samples excluding the effect of all other model covariates (fixed and random), with 50% (dark) and 95% (light) credible interval (CI), overlaid with partial effect points accounting for all other model covariates. Insets are histograms of the observed data for each covariate. HP, horsepowers. (E) Fixed covariate effect sizes, showing posterior median and 95% (thin) and 50% (thick) CI.

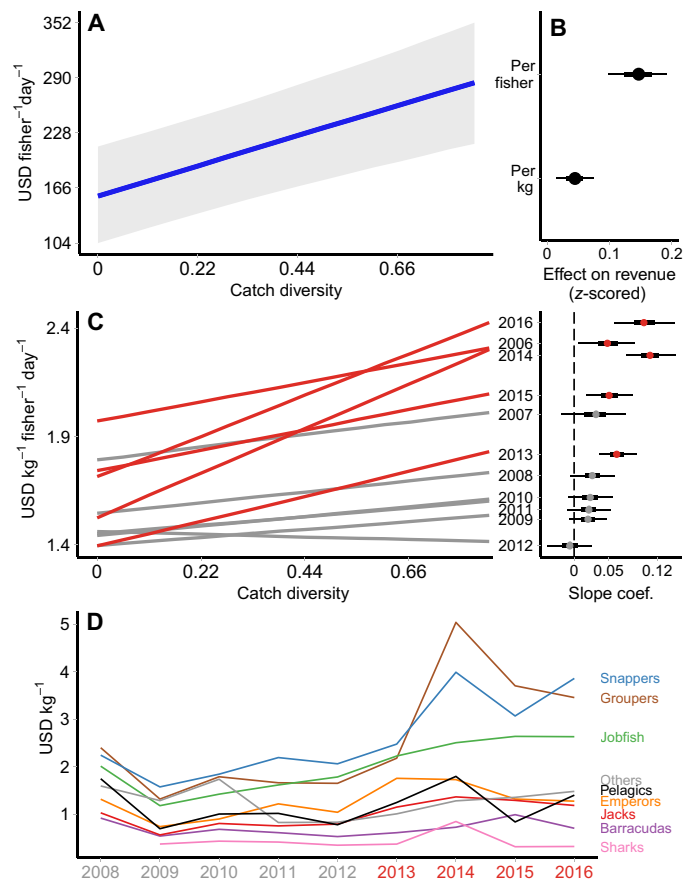


**Fig. 3. Diversification effects on CPUE.** (A) Effect of catch diversity for the focal fleet over 2006–2015. (B) Effect of catch diversity on temporal catch trends for the full fleet over 1990–2016, predicted for high (90% quantile of observed diversity values; purple) and low (10% quantile; green) catch diversity. Catch diversity is the Simpson index of each fishing trip averaged across each year. Lines are the median effect from 1000 posterior samples excluding the effect of all other model covariates (fixed and random), with 50% (dark) and 95% (light) CI, overlaid with partial effect points accounting for all other model covariates. Standardized effect sizes ( $\pm 95\%$  CI) for the full fleet model are inset in (B).

substantially. Given the magnitude of catch declines, these findings indicate that recent calls for diversifying tropical fisheries to safeguard food security in the tropics (7) will be constrained by the exploitation status of coastal fishing stocks.

Our focus on heavily exploited fisheries reveals that catch diversity can partially insulate fishers against long-term declines in catch rates. Fishing vessels that targeted multiple species in one fishing trip using several gear strategies (e.g., depth, bait, and line deployment; see Materials and Methods) had greater success than those who specialized on fewer groups. At this scale, diversification may raise CPUE simply by minimizing the inherent uncertainty associated with tar-

geting specific species in wild fisheries (13). Integrating CPUE with market price data indicated that more diverse catches were also more valuable and returned greater revenues. Because overall catches were dominated by relatively low-value Carangidae species, diversification likely promoted the potential market value of catches through both greater catch rates and inclusion of rarer and high-value species such as red snapper, grouper, and jobfish. These findings for unmanaged and declining tropical fisheries are consistent with those from highly regulated temperate commercial fisheries, which show that fishers with diverse catch portfolios have greater revenues (18). Turnover in catch composition (Bray-Curtis dissimilarity among catches per year)



**Fig. 4. Effect of catch diversity on fishing revenue.** (A) Change in daily fishing revenue (USD per fisher per day) across the range of observed catch diversity values, with fitted line (median) shaded with 50% (dark) and 95% (light) CI. (B) Standardized parameter coefficients indicating catch diversification effect on revenue per fisher and per kilogram (posterior median, 50 and 95% CI). (C) Change in daily fishing revenue corrected for catch weight (USD per kilogram per fisher per day) in each year, with posterior median ( $\pm 50$  and 95% CI) of slope coefficients. Diversification relationships with slopes that do not overlap 0 are colored red (see fig. S7 for year effects on daily fishing revenue). (D) Market value of each target group for 2008–2016 (USD per kilogram). Years with strong effects in (B) are colored red on x-axis labels (see fig. S8 for intra-annual variation in values).

was a weak influence on CPUE, indicating that fishers who changed targeted species between fishing trips had similar catch rates to those who specialized on certain species groups. Turnover of catch composition may help buffer fishers to declines over longer time periods (e.g., interannual or decadal) (14, 26), which span the considerable interannual variability in CPUE of multiple species groups (Fig. 1B) (24).

In managed commercial fisheries, the ability to diversify is constrained by individual fishing capacity and by fisheries regulations. For example, in fisheries regulated with individual fishing quotas, holding catch portfolios can be prohibitively expensive (18), and if distant fishing grounds are only accessible to fishers with large vessels, then portfolio strategies may be limited by vessel size or the proximity of fisheries to ports (17). In Seychelles, despite larger and more powerful boats returning the highest catch rates, portfolio strategies were not linked to boat size, and diversification effects on catch revenue were independent of catch size. This lack of economic constraint on catch diversity may arise because the offshore fisheries are exploited

by one gear type (handlines) and most vessels are constrained to a comparatively small shallow plateau (41,000 km<sup>2</sup>, <100 m deep; fig. S9). Fishing is unmanaged, which allows all fishers to target all stocks, and thus, diversification strategies are likely to be equally available to all vessels. It is unclear why only some fishers successfully pursued diverse catch portfolios (fig. S5), although the knowledge and skills required to target multiple species may be linked to fishers' age and experience (27, 28). Variation in fishing capacity does, however, indicate differences among fishers in vulnerability to changes in resource availability. For example, catch size is an indicator of a fishers' (hypothetical) readiness to exit a declining fishery (29), which suggests that small boat fishers are most likely to leave these fisheries. Alternatively, fishing crews of large vessels may be more vulnerable if fishing costs (e.g., fuel and crew size) are not offset by their greater fishing capacity.

In other catch diversification studies, the availability of highly resolved catch and revenue data has been used to understand how fishing specialization changes over time for individual vessels (30, 31). Here, catch surveys were composed of random subsamples of the offshore fleet. Although we increased the temporal resolution of our diversification analysis by selecting vessels that were most active and surveyed frequently (focal fleet vessels were ~70% of the full fleet from 2006 to 2015), these snapshot surveys required us to average predictor covariates at the scale of years rather than daily or monthly catches. As a result, we were unable to model seasonal shifts in catch diversity that might arise from vessels targeting spawning aggregations (23) or from ocean conditions constraining the availability of certain fishing grounds (32). Similarly, Seychelles' fishers diversified their catches by changing fishing depth, hook number, and line deployment strategies, which contrasts with other diversified fisheries where catch portfolios typically hold multiple gear types (18). Nevertheless, tropical fisheries are among the most data-deficient fishing sectors (4), meaning that the long-term catch and vessel monitoring datasets analyzed here are unusually highly resolved.

Collectively, the declining CPUE and landed weights of multiple-species groups and overall increase in number of fishing vessels suggest that targeted fish populations have declined. Because available fishing areas are largely restricted to the 41,000-km<sup>2</sup> Mahé plateau, and mostly at 5- to 65-m depth (fig. S9) (24), the spatial expansion of fishing grounds within this area and increase in fuel consumption further indicate that fishers expended greater effort without generating higher catches. Although industrial tuna fisheries operating out of Seychelles are well developed, these vessels operate beyond the Mahé plateau including in international waters (24, 33) and are unlikely to contribute to the declining catches reported here. Fuel subsidies have been provided since 1991 and may have stimulated the increase in fishing effort. With the offshore fisheries analyzed here contributing >40% of domestic landings in Seychelles (33), the effects of long-term declines in pelagic and demersal fisheries on fishing livelihoods and local food supplies require further investigation.

For tropical island nations, proposed adaptations to maintain food security in the face of climate-driven declines in coastal fisheries (34, 35) have focused on increasing the exploitation of offshore fish stocks, such as tuna and small pelagic species (21, 36). These strategies, however, assume that all fishers have the capacity to exploit offshore resources and that tuna and pelagic fisheries are more resilient to ocean warming than coastal fisheries. Our findings suggest that offshore locations are more successfully targeted by larger vessels and, therefore, the shorter range and storage capacity of smaller vessels may limit poorer fishers to coastal fisheries that are more heavily exploited

(32). In addition, while this offshore fishery is in decline, the coastal coral reef fisheries have maintained or increased their catch levels despite ocean warming causing widespread loss of coral habitat and ecological regime shifts (37). Given the scarcity of data in other tropical nations, it is critical that strategies for adapting tropical fisheries to climate impacts incorporate information about the availability of emerging fisheries resources to small-scale fishers (e.g., offshore stocks), as well as changes to coastal fisheries arising from ocean warming (e.g., coral bleaching).

Here, we have identified two major factors that determined catch rates in heavily exploited and unmanaged fisheries in Seychelles. First, vessels with diverse catch portfolios recorded larger catches and experienced slower declines in catch rates during a period of substantial declines in multiple-species groups. Because diverse catches were larger and rarer species had high market values, catch diversification also produced greater fishing revenues. Second, smaller low-powered vessels had the lowest catch rates, and so those fishers may be most vulnerable to declines in fish populations and to future environmental changes (38). Because the effects of vessel capacity and catch diversity are not well understood for most tropical nations, analyses such as ours can be used to help transition tropical fisheries toward management strategies that maintain seafood supply and protect fisher incomes when marine resources are depleted. Diversification strategies must also be balanced against the need to limit fishing of rare or long-lived species that may be particularly vulnerable to heavy exploitation. For unmanaged tropical fisheries where effort is accelerating (6) and landings are declining (5), such as those in Seychelles, the introduction of effort controls alongside considerations of how diversification strategy and vessel capacity (e.g., size) influence catch rates will be paramount.

## MATERIALS AND METHODS

### Seychelles' offshore fisheries

The sampled fishery targets pelagic- and demersal-associated species between 0- and 60-m depth and contributes ~40% of landed weight (959 metric tons in 2016; table S1) of all domestic artisanal fisheries in Seychelles (33, 39). Catches are consumed locally (80%) or exported (20%) and are primarily composed of species in the Carangidae, Lutjanidae, Serranidae, and Sphyraenidae families (table S1) (33). Fishing grounds are primarily located on a shallow shelf ("the Mahé plateau", ~ 41,000 km<sup>2</sup>, <100-m depth) and exploited by a diverse fleet ranging from low-powered outboards to vessels with inboard motors, capable of fishing for up to 8 days with a 100-km range. All fishers use handlines, but the number of hooks, bait type, and line deployment strategy (vertical droplines, floated lines for midwater, and bottom set lines) is altered according to target species. Fishers may also supplement their typical catches by targeting seasonal spawning aggregations (23), night fishing for barracuda, or fishing cooperatively to stimulate feeding by semipelagic species. These fisheries are regulated through fishing licenses, but there are no management controls on fishing effort.

### Catch assessment surveys

Catch and effort data were collected by catch assessment surveys conducted from 1990 to 2016 by Seychelles Fishing Authority (SFA). Surveys included major fish landing sites in the inner Seychelles, and survey effort was stratified by the number of registered vessels per site. In each survey, SFA staff interviewed fishers immediately after

fishing trips to assess trip effort and measured the weight of the landed catch. Catches were categorized into 32 groups according to how species are sold at local markets. Because survey groups contained different numbers of species and some closely related species were assigned to multiple groups, we further combined these into eight groups of related species and one group of target species typically associated with coastal habitats (table S1). For the purposes of this study, we treated each species group as a distinct fishery. Effort data included the number of days fished, cost of fuel, bait and gear, number of lines deployed, and size of fishing crew. Fuel costs were corrected for inflation for revenue analysis and also converted to volume of fuel used as a measure of fishing trip distance. After excluding surveys with missing effort data, the SFA database was composed of 18,458 fishing trips (mean number of surveys, 683 year<sup>-1</sup> and 60 month<sup>-1</sup>) collected from 224 fishing vessels. Corresponding estimates of fisheries landings (metric tons per month) were developed by SFA for 2000–2016.

### Modeling catch and effort trends

Catch weights were standardized by fishing trip effort to give catch per day fishing (kilograms per day; CPUE) for all species combined and for each species group. We presented CPUE in terms of catch per day fishing rather than per line per day fishing because the number of handlines deployed did not vary strongly among years (mean = 3.8 and SD = 0.65), such that kilograms per handline per day was strongly correlated with kilograms per day (Pearson's correlation  $r = 0.93$ ) (fig. S10). We noted that CPUE estimates were derived from species groups containing multiple species and thus may mask changes in the catchability or abundance of single species within groups.

For effort, we measured individual vessel effort as the average number of fishing days and fuel consumption per fishing trip and measured fleet size as the number of unique registered vessels surveyed in each year. For each of the 13 response variables (total CPUE, CPUE of each of the nine species groups, number of fishing days, fuel consumption, and fleet size), we fitted generalized additive models (GAMs) to identify temporal patterns that were standardized by seasonal and oceanographic influences. In Seychelles, seasonal monsoon patterns can influence fishing activity through its effect under sea condition (40). Offshore fishing activity is reduced during exposed, stormy conditions of the Southeast monsoon from June to September and highest during the calmer Northwest monsoon from December to March. To account for potential oceanographic effects on catch rates, we extracted monthly indices for the El Niño/Southern Oscillation (ENSO; BEST; www.esrl.noaa.gov/psd/people/cathy.smith/best/#years) and Indian Ocean dipole [dipole mode index (DMI); www.esrl.noaa.gov/psd/gcos\_wgsp/Timeseries/DMI/] indices from remote sensing datasets, which capture intra- and interannual variation in sea surface temperatures whereby positive ENSO (El Niño) and DMI phases correspond with ocean warming, and negative ENSO (La Niña) and DMI phases correspond with ocean cooling (41, 42).

All GAMs were fitted with sequential month-year (2004–2016), Julian month (1 to 12), ENSO index, and DMI index as fixed effects with smoothers ( $f$ ), and vessel ID as a random intercept term

$$\text{CPUE}_i = \alpha + f(\text{monthyear}_i) + f(\text{month}_i) + f(\text{ENSO}_i) + f(\text{DMI}_i) + \alpha_{\text{vessel}[i]} \quad (1)$$

for Gamma-distributed errors. Month-year, ENSO, and DMI terms were fitted as cubic regression splines, and the Julian month term was cyclic (37). The degree of smoothing (i.e., knot value) was determined

by generalized cross-validation (43), models were diagnosed for normality with residual plots, and model fits were assessed with deviance explained values. We visualized temporal trends by predicting each response covariate over time, excluding seasonal, oceanographic, and vessel effects by setting those covariates to their mean value.

### Catch diversification and vessel capacity analysis

We examined how catch diversification and vessel capacity influenced CPUE in a focal fleet of 41 vessels. Although catch surveys were available from 1990 to 2016, we focused on CPUE trends from 2006 to 2015 when VMS were available. To ensure boats were regularly fishing across this time period and thus had opportunities to change behavior in response to catch declines, we selected vessels where recorded catches were in at least 5 years between 2006 and 2015. CPUE trends were analyzed with the same GAM structure as for the full CAS dataset but including a random smooth term that modeled temporal trends for each vessel (44).

$$\text{CPUE}_i = \alpha + f(\text{month year}_i) + f(\text{month}_i) + f(\text{ENSO}_i) + f(\text{DMI}_i) + f_{\text{vessel}_i}(\text{month year}_i) \quad (2)$$

We extracted individual vessel catch trends from the fitted model by predicting the monthly CPUE for each vessel, holding seasonal and oceanographic covariates to their means (0). Using these model predictions, we quantified catch trends using the average annual CPUE for each focal vessel.

We examined variation in predicted catch trends using mixed effects models fitted with covariates on catch diversification and vessel capacity (Table 1). Larger vessels with greater engine power likely have the highest catch rates due to their ability to exploit distant fishing grounds, lower impact of adverse sea conditions, and greater capacity for ice and catch storage. In addition to vessel capacity, fishers who spend more time at sea (fishing days) or cover larger fishing grounds may have larger catches than those limited to single-day trips in fewer fishing locations. We extracted the duration (number of days) and fuel cost of each fishing trip recorded in catch surveys and averaged for each year. Boat size (length in meters) and engine power (horsepower) were provided by an SFA census of fishing fleets that was conducted in 2017.

We used VMS data to estimate the area of operation of each focal vessel from 2006 to 2015 (45). We extracted the Global Positioning System coordinates of all registered vessels fishing offshore (i.e., on the Mahé plateau) and examined movement patterns of vessels which were actively fishing by filtering the dataset to tracks with a recorded speed of <2 knots. Potential fishing activity in shallow coastal habitats was excluded by removing all points within 1 km of coastline (45), and incomplete fishing movements when sequential points were over 4 hours apart were removed. Each point was assigned a cell in a 10-min grid (cell area of ~340 km<sup>2</sup> at -4.5°S). We defined fishing activity in each year using point summation (45) where proportional fishing activity (%) was the number of points in each cell divided by the total number of points. From this spatial dataset, we filtered cells to those containing 90% of cumulative fishing activity, which focused our analysis on the core fishing grounds and excluded marginal fishing areas (46). Model covariates derived from VMS data were the total area covered at fishing speeds (square kilometers) in each year and, as indicators of average fishing location, the median latitude and longitude per fishing trip averaged for each year (Table 1). Although the coarse spatial resolution likely overestimates the true fishing ground

area (47), the resolution is consistent in time, and we used these estimates as proxies for the potential area of operation in the fishery rather than quantifying the spatial footprint of Seychelles' fisheries. Because we excluded incomplete VMS data and catch surveys subsampled fishing vessels and fishing trips, we were unable to match spatial movement data to catch records at the scale of individual fishing trips. Thus, VMS covariates estimate the fishing movement pattern of each vessel in each year.

We measured catch diversification at two scales: individual fishing trips and across all fishing trips in each year. We selected vessels with at least 10 recorded catches year<sup>-1</sup> to ensure that surveys captured potential variation in the catch composition of each vessel. For individual fishing trips, catch diversity of each vessel  $v$  was the annual average Simpson index  $D$  of each catch, where  $p$  is the proportional catch weight of each species  $a$  for total species catch groups  $S$  (Eq. 3). High values indicate diverse catch portfolios, and low values indicate catches specialized to fewer species groups. For fishing trips in each year, the annual turnover in catch composition was the Bray-Curtis dissimilarity across all catches (1, 2, 3 ...  $N$ ;  $T$  = total annual catch; one trip = one catch) for each vessel in each year ("multisite  $\beta$ -dissimilarity") (48), where high values indicate a greater degree of turnover among multiple catches within 1 year (Eq. 4). To reduce the dependence of diversity metrics on high biomass carangid catches, we estimated diversity metrics using  $\log_{10}(x + 1)$ -transformed catch weights.

$$D_v = 1 - \sum_{a=1}^S p_a^2 \quad (3)$$

$$\beta_v = \frac{[N \sum_a^S \max(x_{ab}, x_{ac}, x_{ad}, x_{ae}, \dots)] - T}{(N - 1) T} \quad (4)$$

We fitted Bayesian linear mixed-effects models with standardized explanatory covariates (mean = 0 and SD = 1) and random intercept terms which accounted for temporal correlations in catch trends of individual vessels and within years. To examine the relative influences of diversification and fishing capacity on catch rates, we fitted the model

$$\mu_i = \alpha + \beta_1 \text{daysfishing}_i + \beta_2 \text{fishedarea}_i + \beta_3 \text{latitude}_i + \beta_4 \text{longitude}_i + \beta_5 \text{fuelconsumed}_i + \beta_6 \text{enginesize}_i + \beta_7 \text{boatsize}_i + \beta_8 \text{diversity}_i + \beta_9 \text{turnover}_i + \alpha_{\text{vessel}[i]} + \alpha_{\text{year}[i]} \quad (5)$$

for each vessel ~ year combination  $I$  and Gamma-distributed annual mean CPUE (log link)

$$\text{CPUE}_i \sim \text{Gamma}(\mu_i, k) \quad (6)$$

Model priors were drawn from normal distributions with mean = 0 and SD = 10 [i.e.  $N(0, 10)$ ] for  $\beta$  covariates, Cauchy(0, 2) for variance terms vessel and year, and Exp(2) for Gamma shape parameter  $k$  (table S2). Model parameters were estimated by Markov chain Monte Carlo (MCMC) sampling of 7000 iterations across three chains, and model convergence was assessed with posterior predictive checks and inspecting  $\hat{R}$  and the number of effective samples. Covariate effect sizes were visualized by sampling 1000 values from the posterior distribution and estimating 50% (weak inference) and 95% (strong inference) credible intervals (CIs). For covariates with 50% CIs, which did not overlap zero, we visualized predicted effects by computing

posterior predictions along the range of that covariate, excluding effects of other fixed covariates and variance terms.

### Long-term effects of diversification

We examined the potential for diversification to buffer fishers against long-term declines in CPUE by extending the focal fleet model to the full catch time series. For all vessels with at least five recorded catches in each year from 1992 to 2016, we estimated the daily catch diversity of each landed catch. We examined the effect of catch diversity in moderating the linear rate of temporal CPUE declines by fitting a Bayesian model with time and catch diversity as interacting fixed effects

$$\mu_i = \alpha + \beta_{10} \text{time}_i + \beta_{11} \text{diversity}_i + \beta_{12} \text{time}_i * \text{diversity}_i + \beta_{13} \text{boatsize}_i + \alpha_{\text{vessel}[i]} \quad (7)$$

for Gamma-distributed CPUE (Eq. 6), following the same MCMC sampling procedure, diagnostic tests, and data visualization approach used for the focal fleet model. Correlations in CPUE of individual vessels were accounted for using a random-varying intercept term, and vessel size (the strongest predictor in the focal fleet model) was included as a fixed-effect term. Model priors were weakly informative [fixed effects,  $N(0, 10)$ ; intercept,  $N(5.1, 10)$ ; vessel term,  $\text{Cauchy}(0, 2)$ ; Gamma shape parameter  $k$ ,  $\text{Exp}(2)$ ] (table S2).

### Catch price analysis

We examined how catch diversification might affect the revenue collected by individual fishing vessels using a price database, which indicated the market value of fishery targets between 2008 and 2017. SFA generated the database from market prices of commonly caught pelagic and demersal species sold by wholesalers or direct purchases from offshore fishers. We estimated the potential market value of each surveyed catch group, corrected to unit weights (per kilogram) and adjusted to 2010 prices using the World Bank's Consumer Price Index (<https://data.worldbank.org/indicator/FP.CPI.TOTL.ZG?locations=SC>). By combining price data with the focal fleet data (2006–2015, fitted to Eq. 5), we then estimated the potential catch value of each surveyed catch, corrected for effort and catch weight. Revenue of each fishing trip was the catch value minus fuel, bait, and gear costs, which we corrected for effort (USD per fisher per day) and for catch weight (USD per kilogram per fisher per day) and averaged across trips per year to give average daily revenues per vessel. Price data were unavailable for 2006–2007, and these years were estimated using prices in 2008.

We modeled revenue as a function of diversity, fitting random intercepts for vessels, as well as random slopes and intercepts for year (Eq. 9). This structure accounted for vessel- and year-specific deviations in mean values, as well as year-specific deviations in the relationship between diversity and revenue. We assumed that revenue followed a Student  $t$  distribution (Eq. 8), which, as a heavy-tailed distribution, accounts for an increased probability of extreme events (49), and capped extreme revenues above 99% and below 1% of the revenue distribution. The Student  $t$  distribution includes an additional parameter  $\nu$  representing the degrees of freedom and controlling the weight of the distribution's tails—as  $\nu$  approaches infinity, the  $t$  distribution converges on the normal. Revenue models were fit with four chains and 3000 iterations, and chain convergence was assessed by inspecting  $\hat{R}$  and the number of effective samples.

$$\text{revenue}_i \sim \text{Student } t(\nu, \mu_i, \sigma) \quad (8)$$

$$\mu_i = \alpha + (\beta + \beta_{\text{year}[i]}) \text{diversity}_i + \alpha_{\text{vessel}[i]} + \alpha_{\text{year}[i]} \quad (9)$$

All analyses were conducted in R 3.6.0 (50). GAMs were fitted in `mgcv` (43), catch diversity metrics were estimated using `vegan` (51) and `betapart` (52), and Bayesian hierarchical models were implemented in Stan 2.18.1 using `rethinking` (53) and `RStan` (54). We provided data and R code at an open source repository ([github.com/jpwrobinson/tropical-catch-div](https://github.com/jpwrobinson/tropical-catch-div)).

### SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/8/eaaz0587/DC1>

- Fig. S1. Change in CPUE from 1990 to 2016 for eight species groups.
- Fig. S2. Total landed weight from offshore fisheries over 2000–2016.
- Fig. S3. Fishing grounds of the focal fleet (2006–2015) and effort of the full fleet (1992–2016).
- Fig. S4. Vessel catch trends for the 41 vessels in the focal fleet over 2005–2016.
- Fig. S5. Catch diversification from 1990–2016 for full and focal fleets.
- Fig. S6. Catch diversification according to boat length.
- Fig. S7. Effect of catch diversity on daily fishing revenue (USD per fisher per day) across years.
- Fig. S8. Market value of each target group for 2008–2016 (USD per kilogram).
- Fig. S9. Spatial movement and fishing grounds of focal fleet from 2006 to 2015.
- Fig. S10. Correlation between CPUE metrics.
- Table S1. Species caught in Seychelles' offshore small-scale fisheries, categorized into groups of closely related species or species that share similar habitats (i.e., the fisheries analyzed).
- Table S2. Prior distributions for Bayesian models.

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## Diversification insulates fisher catch and revenue in heavily exploited tropical fisheries

James P. W. Robinson, Jan Robinson, Calvin Gerry, Rodney Govinden, Cameron Freshwater and Nicholas A. J. Graham

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