Bright spots among the world's coral reefs

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Ongoing declines among the world's coral reefs[1,2] require novel approaches to sustain these ecosystems and the millions of people who depend on them[3]. A presently untapped approach that draws on theory and practice in human health and rural development[4,5] is systematically identifying and learning from the 'outliers'- places where ecosystems are substantially better ('bright spots') or worse ('dark spots') than expected, given the environmental conditions and socioeconomic drivers they are exposed to. Here, we compile data from more than 2,500 reefs worldwide and develop a Bayesian hierarchical model to generate expectations of how standing stocks of reef fish biomass are related to 18 socioeconomic drivers and environmental conditions. We then identified 15 bright spots and 35 dark spots among our global survey of coral reefs, defined as sites that had biomass levels more than two standard deviations from expectations. Importantly, bright spots were not simply comprised of remote areas with low fishing pressure- they include localities where human populations and use of ecosystem resources is high, potentially providing novel insights into how communities have successfully confronted strong drivers of change. Alternatively, dark spots were not necessarily the sites with the lowest absolute biomass and even included some remote, uninhabited locations often considered near-pristine[6]. We surveyed local experts about social, institutional, and environmental conditions at these sites to reveal that bright spots were characterised by strong sociocultural institutions such as customary taboos and marine tenure, high levels of local engagement in management, high dependence on marine resources, and beneficial environmental conditions such as deep-water refuges. Alternatively, dark spots were characterised by intensive capture and storage technology and a recent history of environmental shocks. Our

results suggest that investments in strengthening fisheries governance, particularly aspects such as participation and property rights, could facilitate innovative conservation actions that help communities defy expectations of global reef degradation.

Main text

Despite substantial international conservation efforts, many of the world's ecosystems continue to decline[1,7]. Most conservation approaches aim to identify and protect places of high ecological integrity under minimal threat[8]. Yet, with escalating social and environmental drivers of change, conservation actions are also needed where people and nature coexist, especially where human impacts are already severe[9]. Here, we highlight an approach for implementing conservation in coupled human-natural systems focused on identifying and learning from outliers - places that are performing substantially better than expected, given the socioeconomic and environmental conditions they are exposed to. By their very nature, outliers deviate from expectations, and consequently can provide novel insights on confronting complex problems where conventional solutions have failed. This type of positive deviance, or 'bright spot' analysis has been used in fields such as business, health, and human development to uncover local actions and governance systems that work in the context of widespread failure[10,11], and holds much promise in informing conservation.

To demonstrate this approach, we compiled data from 2,514 coral reefs in 46 countries, states, and territories (hereafter 'nation/states') and developed a Bayesian hierarchical model to generate expected conditions of how standing reef fish biomass (a key indicator of resource availability and ecosystem functions[12]) was related to 18 key environmental variables and socioeconomic drivers (Fig. 1; Extended Data Tables 1-4; Extended Data Figures 1-3; Methods). Drawing on a broad body of theoretical and empirical research in the social sciences[13-15] and ecology[2,6,16] on coupled human-natural systems, we quantified how reef fish biomass (Fig. 1a) was related to distal social drivers such as markets, affluence, governance, and population (Fig. 1b,c), while controlling for well-known environmental conditions such as depth, habitat, and productivity (Fig. 1d) (Extended Data Table 1, Methods). In contrast to many global studies of reef systems that are focused on demonstrating the severity of human impacts[6], our examination seeks to uncover potential policy levers by highlighting the relative role of specific social drivers. A key and significant finding from our global analysis is that our metric of potential interactions with urban centres, called market gravity[17] (Methods), more so than local or national population pressure, management, environmental conditions, or national socioeconomic context, had the strongest relationship with reef fish biomass (Fig.1). Specifically, we found that reef fish biomass decreased as the size and accessibility of markets increased (Extended Data Fig. 1b). Somewhat counter-intuitively, fish biomass was higher in places with high local human population growth rates, likely reflecting human migration to areas of better environmental quality[18]-a phenomenon that could result in increased degradation at these sites over time. We found a strong positive, but less certain relationship (*i.e.* a high standardized effect size, but only >75% of the posterior distribution above zero) with the Human Development Index, meaning that reefs tended to be in better condition in wealthier nation/states (Fig. 1c). Our analysis also confirmed the role that marine reserves can play in sustaining biomass on coral reefs, but only when compliance is high (Fig.1b), reinforcing the importance of fostering compliance for reserves to be successful.

Next, we identified 15 ‘bright spots’ and 35 ‘dark spots’ among the world's coral reefs, defined as sites with biomass levels more than two standard deviations higher or lower than expectations from our global model, respectively (Fig. 2; Methods; Extended Data Table 5). Rather than simply identifying places in the best or worst condition, our bright spots approach reveals the places that most strongly defy expectations. Using them to inform the conservation discourse will certainly challenge established ideas of where and how conservation efforts should be focused. For example, remote places far from human impacts are conventionally considered near-pristine areas of high conservation value[6], yet most of the bright spots we identified occur in fished, populated areas (Extended Data Table 5), some with biomass values below the global average. Alternatively, some remote places such as parts of the NW Hawaiian Islands underperform (i.e. were identified as dark spots).

Detailed analysis of why bright spots can evade the fate of similar areas facing equivalent stresses will require a new research agenda gathering detailed site-level information on social and institutional conditions, technological innovations, external influences, and ecological processes[19] that are simply not available in a global-scale analysis. As a hypothesis-generating exploration to begin uncovering why bright and dark spots may diverge from expectations, we surveyed data providers who sampled the sites and other experts with first-hand knowledge about the presence or absence of 10 key social and environmental conditions at the 15 bright spots, 35 dark spots, and 14 average sites with biomass values closest to model expectations (see Methods and SI for details). Our initial exploration revealed that bright spots were more likely to have high levels of local engagement in the management process, high dependence on coastal resources, and the presence of sociocultural governance institutions such as customary tenure or taboos (Fig. 3, Methods). For example, in one bright spot, Karkar Island, Papua New Guinea, resource use is restricted through an adaptive rotational harvest system based on ecological feedbacks, marine tenure that allows for the exclusion of fishers from outside the local village, and initiation rights that limit individuals' entry into certain fisheries[20]. Bright spots were also generally proximate to deep water, which may help provide a refuge from disturbance for corals and fish[21] (Fig. 3, Extended Data Fig. 4). Conversely, dark spots were distinguished by having fishing technologies allowing for more intensive exploitation, such as fish freezers and potentially destructive netting, as well as a recent history of environmental shocks (*e.g.* coral bleaching or cyclone; Fig. 3). The latter is particularly worrisome in the context of climate change, which is likely to lead to increased coral bleaching and more intense cyclones[22].

Our global analyses highlight two novel opportunities to inform coral reef governance. The first is to use bright spots as agents of change to expand the conservation discourse from the current focus on protecting places under minimal threat[8], toward harnessing lessons from places that have successfully confronted high pressures. Our bright spots approach can be used to inform the types of investments and governance structures that may help to create more sustainable pathways for impacted coral reefs. Specifically, our initial investigation highlights how investments that strengthen fisheries governance, particularly issues such as participation and property rights, could help communities to innovate in ways that allow them to defy expectations. Conversely, the more typical efforts to provide capture and storage infrastructure, particularly where there are environmental shocks and local-scale governance is weak, may lead to social-ecological traps[23] that reinforce resource degradation beyond expectations. Effectively harnessing the potential to learn from both bright and dark spots will require scientists to increase research efforts in these places, NGOs to catalyze lessons from other areas, donors to start investing in novel solutions, and policy makers to ensure that governance structures foster flexible learning and experimentation. Indeed, both bright and dark spots may have much to offer in terms of how to creatively confront drivers of change, identify paths to avoid and those offering novel management solutions, and to prioritize conservation actions. Critically, the bright spots we identified span the development spectrum from low to high income (e.g., Solomon Islands and territories of the USA, respectively; Fig. 2), showing that lessons about effective reef management can emerge from diverse places.

A second opportunity stems from a renewed focus on managing the socioeconomic drivers that shape reef conditions. Many social drivers are amenable to governance interventions, and our comprehensive analysis (Fig. 1) suggests that an increased policy focus on social drivers such as markets and development could result in improvements to reef fish biomass. For example, given the important influence of markets in our analysis, reef managers, donor organisations, conservation groups, and coastal communities could improve sustainability by developing interventions that dampen the negative influence of markets on reef systems. A portfolio of market interventions, including eco-labelling and sustainable harvesting certifications, fisheries improvement projects, and value chain interventions have been developed within large-scale industrial fisheries to condition access to markets based on sustainable harvesting[24,25]. Although there is considerable scope for adapting these interventions to artisanal coral reef fisheries in both local and regional markets, effectively dampening the negative influence of markets may also require developing novel interventions that address the range of ways in which markets can lead to overexploitation. Existing research suggests that markets create incentives for overexploitation not only by affecting price and price variability for reef products[26], but also by influencing people's behavior[27,28], including their willingness to cooperate in the collective management of natural resources[29].

The long-term viability of coral reefs will ultimately depend on international action to reduce carbon emissions[22]. However, fisheries remain a pervasive source of reef degradation, and effective local-level fisheries governance is crucial to sustaining ecological processes that give reefs the best chance of coping with global environmental change[30]. Seeking out and learning from bright spots is a novel approach to conservation that may offer insights into confronting the complex governance problems facing coupled human-natural systems such as coral reefs.

Figure Legends

Figure 1| Global patterns and drivers of reef fish biomass. (a) Reef fish biomass [(log)kg/ha] among 918 study sites. Points vary in size and colour proportional to the amount of fish biomass. b-d) Standardised effect size of local scale social drivers, nation/state scale social drivers, and environmental covariates, respectively. Parameter estimates are Bayesian posterior median values, 95% uncertainty intervals (UI; thin lines), and 50% UI (thick lines). Black dots indicate that the 95%UI does not overlap 0; Grey closed circles indicates that 75% of the posterior distribution lies to one side of 0; and grey open circles indicate that the 50%UI overlaps 0.

Figure 2 | Bright and dark spots among the world's coral reefs. (a) Each site's deviation from expected biomass (y-axis) along a gradient of nation/state mean biomass (x-axis). The 50 sites with biomass values >2 standard deviations above or below expected values were considered bright (yellow) and dark (black) spots, respectively. Each grey vertical line represents a nation/state; those with bright or dark spots are labelled and numbered. There can be multiple bright or dark spots in each nation/state. (b) Map highlighting bright and dark spots with large circles, and other sites in small circles. Numbers correspond to panel a.

Figure 3 | Differences in key social and environmental conditions between bright spots, dark spots, and 'average' sites. *=p<0.05, **=p<0.01, ***=p<0.001. P values are determined using Fisher's Exact test. Intensive netting includes beach seine nets, surround gill nets, and muro-ami.

Methods

Scales of data

Our data were organized at three spatial scales: reef (n=2514), site (n=918), and nation/state (n=46).

i) reef (the smallest scale, which had an average of 2.4 surveys/transects - hereafter 'reef').

ii) site (a cluster of reefs). We clustered reefs together that were within 4km of each other, and used the centroid of these clusters (hereafter ‘sites’) to estimate site-level social and site-level environmental covariates (Extended Data Table 1). To make these clusters, we first estimated the linear distance between all reefs, then used a hierarchical analysis with the complete-linkage clustering technique based on the maximum distance between reefs. We set the cut-off at 4km to select mutually exclusive sites where reefs cannot be more distant than 4km. The choice of 4km was informed by a 3-year study of the spatial movement patterns of artisanal coral reef fishers, corresponding to the highest density of fishing activities on reefs based on GPS-derived effort density maps of artisanal coral reef fishing activities[31]. This clustering analysis was carried out using the R functions ‘hclust’ and ‘cutree’, resulting in an average of 2.7 reefs/site.

iii) Nation/state (nation, state, or territory). A larger scale in our analysis was ‘nation/state’, which are jurisdictions that generally correspond to individual nations (but could also include states, territories, overseas regions, or extremely remote areas within a state such as the northwest

Hawaiian Islands; Extended Data Table 2), within which sites and reefs were nested for analysis.

Estimating Biomass

Reef fish biomass can reflect a broad selection of reef fish functioning and benthic conditions[12,32-34], and is a key metric of resource availability for reef fisheries. Reef fish biomass estimates were based on instantaneous visual counts from 6,088 surveys collected from 2,514 reefs. All surveys used standard belt-transects, distance sampling, or point-counts, and were conducted between 2004 and 2013. Where data from multiple years were available from a single reef, we included only data from the year closest to 2010. Within each survey area, reef associated fishes were identified to species level, abundance counted, and total length (TL) estimated, with the exception of one data provider who measured biomass at the family level. To make estimates of biomass from these transect-level data comparable among studies, we:

i) Retained families that were consistently studied and were above a minimum size cut-off. Thus, we retained counts of >10cm diurnally-active, non-cryptic reef fish that are resident on the reef (20 families, 774 species), excluding sharks and semi-pelagic species. We also excluded three groups of fishes that are strongly associated with coral habitat conditions and are rarely targets for fisheries (Anthiinae, Chaetodontidae, and Cirrhitidae). Families included are: Acanthuridae, Balistidae, Diodontidae, Ephippidae, Haemulidae, Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Monacanthidae, Mullidae, Nemipteridae, Pinguipedidae, Pomacanthidae, Serranidae, Siganidae, Sparidae, Synodontidae, Tetraodontidae, Zanclidae. We calculated total biomass of fishes on each reef using standard published species-level length-weight relationship parameters or those available on FishBase[35]. When length-weight relationship parameters were not available for a species, we used the parameters for a closely related species or genus.

ii) Directly accounted for depth and habitat as covariates in the model (see "environmental conditions" section below);

iii) Accounted for any potential bias among data providers (capturing information on both inter-observer differences, and census methods) by including each data provider as a random effect in our model.

Biomass means, medians, and standard deviations were calculated at the reef-scale. All reported log values are the natural log.

Social Drivers

1. Local Population Growth: We created a 100km buffer around each site and used this to calculate human population within the buffer in 2000 and 2010 based on the Socioeconomic Data and Application Centre (SEDAC) gridded population of the world database[36]. Population growth was the proportional difference between the population in 2000 and 2010. We chose a 100km buffer as a reasonable range at which many key human impacts from population (e.g., land-use and nutrients) might affect reefs[37].

2. Management: For each site, we determined if it was: i) unfished- whether it fell within the borders of a no-take marine reserve. We asked data providers to further classify whether the reserve had high or low levels of compliance; ii) restricted - whether there were active restrictions on gears (e.g. bans on the use of nets, spearguns, or traps) or fishing effort (which could have included areas inside marine parks that were not necessarily no take); or iii) fished - regularly fished without effective restrictions. To determine these classifications, we used the expert opinion of the data providers, and triangulated this with a global database of marine reserve boundaries[38].

3. Gravity: We adapted the economic geography concept of *gravity*[17,39-41], also called interactance[42], to examine potential interactions between reefs and: i) major urban centres/markets (defined as provincial capital cities, major population centres, landmark cities, national capitals, and ports); and ii) the nearest human settlements. This application of the gravity concept infers that potential interactions increase with population size, but decay exponentially with the effective distance between two points. Thus, we gathered data on both population estimates and a surrogate for distance: travel time.

Population estimations

We gathered population estimates for: 1) the nearest major markets (which includes national capitals, provincial capitals, major population centres, ports, and landmark cities) using the World Cities base map from ESRI™; and 2) the nearest human settlement within a 500km radius using LandScan™ 2011 database. The different datasets were required because the latter is available in raster format while the former is available as point data. We chose a 500km radius from the nearest settlement as the maximum distance any non-market fishing activities for fresh reef fish are likely to occur.

Travel time calculation

Travel time was computed using a cost-distance algorithm that computes the least 'cost' (in minutes) of travelling between two locations on a regular raster grid. In our case, the two locations were either: 1) the centroid of the site (i.e. reef cluster) and the nearest settlement, or 2) the centroid of the site and the major market. The cost (i.e. time) of travelling between the two locations was determined by using a raster grid of land cover and road networks with the cells containing values that represent the time required to travel across them[43]:

- Tree Cover, broadleaved, deciduous & evergreen, closed; regularly flooded Tree Cover, Shrub, or Herbaceous Cover (fresh, saline, & brackish water) = speed of 1 km/h
- Tree Cover, broadleaved, deciduous, open (open= 15-40% tree cover) = speed of 1.25 km/h
- Tree Cover, needle-leaved, deciduous & evergreen, mixed leaf type; Shrub Cover, closed-open, deciduous & evergreen; Herbaceous Cover, closed-open; Cultivated and managed areas; Mosaic: Cropland / Tree Cover / Other natural vegetation, Cropland / Shrub or Grass Cover = speed of 1.5 km/h
- Mosaic: Tree cover / Other natural vegetation; Tree Cover, burnt = speed of 1.25 km/h
- Sparse Herbaceous or sparse Shrub Cover = speed of 2.5 km/h
- Water = speed of 20 km/h
- Roads = speed of 60 km/h
- Track = speed of 30 km/h
- Artificial surfaces and associated areas = speed of 30 km/h
- Missing values = speed of 1.4 km/h

We termed this raster grid a *friction-surface* (with the time required to travel across different types of surfaces analogous to different levels of friction). To develop the friction-surface, we used global datasets of road networks, land cover, and shorelines:

- Road network data was extracted from the Vector Map Level 0 (VMap0) from the National Imagery and Mapping Agency's (NIMA) Digital Chart of the World (DCW®). We converted vector data from VMap0 to 1km resolution raster.
- Land cover data were extracted from the Global Land Cover 2000[44].
- To define the shorelines, we used the GSHHS (Global Self-consistent, Hierarchical, High-resolution Shoreline) database version 2.2.2.

These three friction components (road networks, land cover, and water bodies) were combined into a single friction surface with a Behrmann map projection. We calculated our cost-distance models in R[45] using the *accCost* function of the *'gdistance'* package. The function uses Dijkstra's algorithm to calculate least-cost distance between two cells on the grid and the associated distance taking into account obstacles and the local friction of the landscape[46]. Travel time estimates over a particular surface could be affected by the infrastructure (e.g. road quality) and types of technology used (e.g. types of boats). These types of data were not available at a global scale but could be important modifications in more localised studies.

Gravity computation

i) To compute the gravity to the nearest market, we calculated the population of the nearest major market and divided that by the squared travel time between the market and the site. Although other exponents can be used[47], we used the squared distance (or in our case, travel time), which is relatively common in geography and economics. This decay function could be influenced by local considerations, such as infrastructure quality (e.g. roads), the types of transport technology (i.e. vessels being used), and fuel prices, which were not available in a comparable format for this global analysis, but could be important considerations in more localised adaptations of this study.

ii) To determine the gravity of the nearest settlement, we located the nearest populated pixel within 500kms, determined the population of that pixel, and divided that by the squared travel time between that cell and the reef site.

As is standard practice in many agricultural economics studies[48], an assumption in our study is that the nearest major capital or landmark city represents a market. Ideally we would have used a global database of all local and regional markets for coral reef fish, but this type of database is not available at a global scale. As a sensitivity analysis to help justify our assumption that capital and landmark cities were a reasonable proxy for reef fish markets, we tested a series of candidate models that predicted biomass based on: 1) cumulative gravity of all cities within 500km; 2) gravity of the nearest city; 3) travel time to the nearest city; 4) population of the nearest city; 5) gravity to the nearest human population above 40 people/km^2 (assumed to be a small peri-urban area and potential local market); 6) the travel time between the reef and a small peri-urban area; 7) the population size of the small peri-urban population; 8) gravity to the nearest human population above 75 people/km^2 (assumed to be a large peri-urban area and potential market);

9) the travel time between the reef and this large peri-urban population; 10) the population size of this large peri-urban population; and 11) the total population size within a 500km radius. Model selection revealed that the best two models were gravity of the nearest city and gravity of all cities within 500km (with a 3 AIC value difference between them; Extended Data Table 3). Importantly, when looking at the individual components of gravity models, the travel time components all had a much lower AIC value than the population components, which is broadly consistent with previous systematic review studies[49]. Similarly, travel time to the nearest city had a lower AIC score than any aspect of either the peri-urban or urban measures. This suggests our use of capital and landmark cities is likely to better capture exploitation drivers from markets rather than simple population pressures. This may be because market dynamics are difficult to capture by population threshold estimates; for example some small provincial capitals where fish markets are located have very low population densities, while some larger population centres may not have a market. Downscaled regional or local analyses could attempt to use more detailed knowledge about fish markets, but we used the best proxy available at a global scale.

4. Human Development Index (HDI): HDI is a summary measure of human development encompassing: a long and healthy life, being knowledgeable, and having a decent standard of living. In cases where HDI values were not available specific to the State (e.g. Florida and Hawaii), we used the national (e.g. USA) HDI value.

5. Population Size: For each Nation/state, we determined the size of the human population. Data were derived mainly from census reports, the CIA fact book, and Wikipedia.

6. Tourism: We examined tourist arrivals relative to the nation/state population size (above). Tourism arrivals were gathered primarily from the World Tourism Organization's Compendium of Tourism Statistics.

7. National Reef Fish Landings: Catch data were obtained from the Sea Around Us Project (SAUP) catch database (www.seaaroundus.org), except for Florida, which was not reported separately in the database. We identified 200 reef fish species and taxon groups in the SAUP catch database[50]. Note that reef-associated pelagics such as scombrids and carangids normally form part of reef fish catches. However, we chose not to include these species because they are also targeted and caught in large amounts by large-scale, non-reef operations.

8. Voice and Accountability: This metric, from the World Bank survey on governance, reflects the perceptions of the extent to which a country's citizens are able to participate in selecting their government, as well as freedom of expression, freedom of association, and a free media. In cases where governance values were not available specific to the Nation/state (e.g. Florida and Hawaii), we used national (e.g. USA) values.

Environmental Drivers

1. Depth: The depth of reef surveys were grouped into the following categories: <4m, 4-10m, >10m to account for broad differences in reef fish community structure attributable to a number of inter-linked depth-related factors. Categories were necessary to standardise methods used by data providers and were determined by pre-existing categories used by several data providers.

2. Habitat: We included the following habitat categories: i) Slope: The reef slope habitat is typically on the ocean side of a reef, where the reef slopes down into deeper water; ii) Crest: The reef crest habitat is the section that joins a reef slope to the reef flat. The zone is typified by high wave energy (i.e. where the waves break). It is also typified by a change in the angle of the reef from an inclined slope to a horizontal reef flat; iii) Flat: The reef flat habitat is typically horizontal and extends back from the reef crest for 10’s to 100’s of metres; iv) Lagoon / back reef: Lagoonal reef habitats are where the continuous reef flat breaks up into more patchy reef environments sheltered from wave energy. These habitats can be behind barrier / fringing reefs or within atolls. Back reef habitats are similar broken habitats where the wave energy does not typically reach the reefs and thus forms a less continuous 'lagoon style' reef habitat. Due to minimal representation among our sample, we excluded other less prevalent habitat types, such as channels and banks. To verify the sites’ habitat information, we used the Millennium Coral Reef Mapping Project (MCRMP) hierarchical data[51], Google Earth, and site depth information.

3. Productivity: We examined ocean productivity for each of our sites in mg C / m2 / day (http://www.science.oregonstate.edu/ocean.productivity/). Using the monthly data for years 2005 to 2010 (in hdf format), we imported and converted those data into

ArcGIS. We then calculated yearly average and finally an average for all these years. We used a 100km buffer around each of our sites and examined the average productivity within that radius. Note that ocean productivity estimates are less accurate for nearshore environments, but we used the best available data.

Analyses

We first looked for collinearity among our covariates using bivariate correlations and variance inflation factor estimates (Extended Data Fig. 2, Extended Data Table 4). This led to the exclusion of several covariates (not described above): i) *Geographic Basin* (Tropical Atlantic, western Indo-Pacific, Central Indo-Pacific, or eastern Indo-Pacific); ii) *Gross Domestic Product* (purchasing power parity); iii) *Rule of Law* (World Bank governance index); iv) *Control of Corruption* (World Bank governance index); and v*) Sedimentation*. Additionally, we removed an index of climate stress, developed by Maina et al.[52], which incorporated 11 different environmental conditions, such as the mean and variability of sea surface temperature due to repeated lack of convergence for this parameter in the model, likely indicative of unidentified multi-collinearity. All other covariates had correlation coefficients 0.7 or less and Variance Inflation Factor scores less than 5 (indicating multicolinearity was not a serious concern). Care must be taken in causal attribution of covariates that were significant in our model, but demonstrated colinearity with candidate covariates that were removed during the aforementioned process. Importantly, the covariate that exhibited the largest effect size in our model, market gravity, was not strongly collinear with other candidate covariates.

To quantify the multi-scale social, environmental, and economic factors affecting reef fish biomass we adopted a Bayesian hierarchical modelling approach that explicitly recognized the three scales of spatial organization: reef (j), site (k), and nation/state (s).

In adopting the Bayesian approach we developed two models for inference: a null model, consisting only of the hierarchical units of observation (i.e. intercepts-only) and a full model that included all of our covariates (drivers) of interest. Covariates were entered into the model at the relevant scale, leading to a hierarchical model whereby lower-level intercepts (averages) were placed in the context of higher-level covariates in which they were nested. We used the null model as a baseline against which we could ensure that our full model performed better than a model with no covariate information. We did not remove 'non-significant' covariates from the model because each covariate was carefully considered for inclusion and could therefore reasonably be considered as having an effect, even if small or uncertain; removing factors from the model is equivalent to fixing parameter estimates at exactly zero - a highly-subjective modelling decision after covariates have already been selected as potentially important[53].

The full model assumed the observed, reef-scale observations of fish biomass (y_{ijks}) were modelled using a noncentral-t distribution, allowing for fatter tails than typical log-normal models of reef fish biomass[32]. We chose the noncentral-t after having initially used a log-normal model because our model diagnostics suggested that several model parameters had not converged. We ran a supplemental analysis to support our use of the noncentral t-distribution with 3.5 degrees of freedom (See Supplementary Information). Therefore our model was:

$$log(y_{ijks}) \sim NoncentralT(\mu_{ijks}, \tau_{reef}, 3.5)$$

$$\mu_{ijks} = \beta_{0jks} + \beta_{reef} X_{reef}$$

$$\tau_{reef} \sim U(0,100)^{-2}$$

with X_{reef} representing the matrix of observed reef-scale covariates and βreef array of estimated reef-scale parameters. The τ_{reef} (and all subsequent τ's) were assumed common across observations in the final model and were minimally informative53. Using a similar structure, the reef-scale intercepts (β_{0jks}) were structured as a function of site-scale covariates (X_{sit}):

$$\beta_{0jks} \sim N(\mu_{jks}, \tau_{sit})$$

$$\mu_{jks} = \gamma_{0ks} + \gamma_{sit} X_{sit}$$

$$\tau_{sit} \sim U(0,100)^{-2}$$

with γ_{sit} representing an array of site-scale parameters. Building upon the hierarchy, the site-scale intercepts (γ_{0ks}) were structured as a function of state-scale covariates (X_{sta}):

$$\gamma_{0ks} \sim N(\mu_{ks}, \tau_{sta})$$

$$\mu_{ks} = \gamma_{0s} + \gamma_{sta} X_{sta}$$

$$\tau_{sta} \sim U(0,100)^{-2}$$

Finally, at the top scale of the analysis we allowed for a global (overall) estimate of average log-biomass (μ_0):

$\gamma_{0s} \sim N(\mu_0, \tau_{glo})$

$\mu_0 \sim N(0.0, 1000)$

$\tau_{glo} \sim U(0,100)^{-2}$

The relationships between fish biomass and reef, site, and state scale drivers was carried out using the PyMC package[54] for the Python programming language, using a Metropolis-Hastings (MH) sampler run for 10^6 iterations, with a 900,000 iteration burn in thinned by 10, leaving 10,000 samples in the posterior distribution of each parameter; these long burn-in times are often required with a complex model using the MH algorithm. Convergence was monitored by examining posterior chains and distributions for stability and by running multiple chains from different starting points and checking for convergence using Gelman-Rubin statistics[55] for parameters across multiple chains; all were at or close to 1, indicating good convergence of parameters across multiple chains.

Overall model fit

We conducted posterior predictive checks for goodness of fit (GoF) using Bayesian p-values[43] (BpV), whereby fit was assessed by the discrepancy between observed or simulated data and their expected values. To do this we simulated new data (y_i^{new}) by sampling from the joint posterior of our model (θ) and calculated the Freeman-Tukey measure of discrepancy for the observed (y_i^{obs}) or simulated data, given their expected values (μ_i):

$$D(y|\theta) = \Sigma_i(\sqrt{y_i} - \sqrt{\mu_i})^2$$

yielding two arrays of median discrepancies $D(y^{obs}|\theta)$ and $D(y^{new}|\theta)$ that were then used to calculate a BpV for our model by recording the proportion of times $D(y^{obs}|\theta)$ was greater than $D(y^{new}|\theta)$ (Extended Data Fig. 3a). A BpV above 0.975 or under 0.025 provides substantial evidence for lack of model fit. Evaluated by the Deviance Information Criterion (DIC), the full model greatly outperformed the null model (ΔDIC=472).

To examine homoscedasticity, we checked residuals against fitted values. We also checked the residuals against all covariates included in the model, and several covariates that were not included in the model (primarily due to collinearity), including: 1) *Atoll* - A binary metric of whether the reef was on an atoll or not; 2) *Control of Corruption:* Perceptions of the extent to which public power is exercised for private gain, including both petty and grand forms of corruption, as well as 'capture' of the state by elites and private interests. Derived from the World Bank survey on governance; 3) *Geographic Basin*- whether the site was in the Tropical Atlantic, western Indo-Pacific, Central Indo-Pacific, or eastern Indo-Pacific; 4) *Connectivity* – we examined 3 measures based on the area of coral reef within a 30km, 100km, and 600km radius of the site; 5) *Sedimentation*; 6) *Coral Cover* (which was only available for a subset of the sites); 7) *Climate stress*[52]; and 8) *Census method*.

The model residuals showed no patterns with these eight additional covariates, suggesting they would not explain additional information in our model.

Bright and dark spot estimates

Because the performance of site scale locations are of substantial interest in uncovering novel solutions for reef conservation, we defined bright and dark spots at the site scale. To this end, we defined bright (or dark) spots as locations where expected site-scale intercepts (γ_{0ks}) differed by more than two standard deviations from their nation/state-scale expected value (μ_{ks}), given all the covariates present in the full hierarchical model:

$$SS_{spot} = |(\mu_{ks} - \gamma_{0ks})| > 2[SD(\mu_{ks} - \gamma_{0ks})]$$

This, in effect, probabilistically identified the most deviant sites, given the model, while shrinking sites toward their group-level means, thereby allowing us to overcome potential bias due to low and varying sample sizes that can lead to extreme values from chance alone. After an initial log-Normal model formulation, where we were not confident in model convergence, we employed a noncentral-t distribution at the observation scale, which facilitated model convergence and dampened any effects of potentially extreme reef-scale observations on the bright and dark spot estimates. Further, we did not consider a site a bright or dark spot if the group-level (i.e. nation/state) mean included fewer than 5 sites.

Analysing conditions at bright spots

For our preliminary exploration into why bright and dark spots may diverge from expectations, we surveyed data providers and other experts about key social, institutional, and environmental conditions at the 15 bright spots, 35 dark spots, and 14 sites that performed most closely to model specifications. Specifically, we developed an online survey (SI) using Survey Monkey (www.surveymonkey.com) software, which we asked data providers who sampled those sites to complete with input from local experts, where necessary. Data providers generally filled in the survey in consultation with nationally-based field team members who had detailed local knowledge of the socioeconomic and environmental conditions at each of the sites. Research on bright spots in agricultural development[19] highlights several types of social and environmental conditions that may lead to bright spots, which we adapted and developed proxies for as the basis of our survey into why our bright and dark spots may diverge from expectations. These include:

i) *Social and institutional conditions*. We examined the presence of customary management institutions such as taboos and marine tenure institutions, whether there was significant engagement by local people in management (specifically defined as there being substantial active engagement by local people in reef management decisions. Token involvement and consultation were not considered significant engagement), and whether there were high levels of dependence on marine resources (specifically, whether a majority of local residents depend on reef fish as a primary source of food or income). All social and institutional conditions were converted to presence/absence data. Dependence on resources and engagement were limited to sites that had adjacent human populations. All other conditions were recorded regardless of whether there is an adjacent community;

ii) *Technological use/innovation*. We examined the presence of motorised vessels, intensive capture equipment (such as beach seine nets, surround gill nets, and muro-ami nets), and storage capacity (i.e. freezers);

iii) *External influences* (such as donor-driven projects). We examined the presence of NGOs, fishery development projects, development initiatives (such as alternative livelihoods), and fisheries improvement projects. All external influences were recorded as present/absent then summarised into a single index of whether external projects were occurring at the site;

iv) *Environmental/ecological processes* (e.g. recruitment & connectivity). We examined whether sites were within 5km of mangroves and deep-water refuges, and whether there had been any major environmental disturbances such as coral bleaching, tsunami, and cyclones within the past 5 years. All environmental conditions were recorded as present/absent.

As an exploratory analysis of associations between these conditions and whether sites diverged more or less from expectations, we used two complementary approaches. The link between the presence/absence of the aforementioned conditions and whether a site was bright, average, or dark was assessed using a Fisher's Exact Test. Then we tested whether the mean deviation in fish biomass from expected was similar between sites with presence or absence of the mechanisms in question (i.e. the presence or absence of marine tenure/taboos) using an ANOVA assuming unequal variance. The two tests yielded similar results, but provide slightly different ways to conceptualise the issue, the former is correlative while the latter explains deviation from expectations based on conditions, so we provide both (Fig. 3, Extended Data Fig. 4). It is important to note that some of these social and environmental conditions were significantly associated (i.e. Fisher's Exact probabilities <0.05), and further research is required to uncover how these and other conditions may make sites bright or dark.

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End Notes

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions

J.E.C. conceived of the study with support from M.A.M, N.A.J.G, T.R.M, J.K, C.H, D.M, C.M, E.A, and C.C.H; C.H. managed the database; M.A.M., J.E.C., and D.M. developed and implemented the analyses; J.E.C. led the manuscript with M.A.M, and N.A.J.G. All other authors contributed data and made substantive contributions to the text.

Author Information

Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Correspondence and request for materials should be addressed to J.E.C. (Joshua.cinner@jcu.edu.au). This is the Social-Ecological Research Frontiers (SERF) working group contribution #11.

Extended Data Tables

Extended Data Table 1 | Summary of social and environmental covariates. Further details can be found in the Supplemental Online Methods. The smallest scale is the individual reef. Sites consist of clusters of reefs within 4km of each other. Nation/states generally correspond to country, but can also include or territories or states, particularly when geographically isolated (e.g. Hawaii).

Extended Data Table 2 | List of 'Nation/states' covered in study and their respective average biomass (plus or minus standard error) In most cases, nation/state refers to an individual country, but can also include states (e.g. Hawaii or Florida), territories (e.g. British Indian Ocean Territory), or other jurisdictions. We treated the NW Hawaiian Islands and Farquhar as separate 'nation/states' from Hawaii and Seychelles, respectively, because they are extremely isolated and have little or no human population. In practical terms, this meant different values for a few nation/state scale indicators that ended up having relatively small effect sizes, anyway (Fig. 1b): Population, tourism visitations, and in the case of NW Hawaiian Island, fish landings.

Extended Data Table 3| Model selection of potential gravity indicators and components.

Extended Data Table 4 | Variance Inflation Factor Scores (VIF) for continuous data before and after removing variables due to colinearity. X = covariate removed.

Extended Data Table 5| List of Bright and Dark Spot locations, population status, and protection status.

Extended Data Figure Legends

Extended Data Figure 1 | Marginal relationships between reef fish biomass and social drivers. a) local population growth, b) market gravity, c) nearest settlement gravity, d) tourism, e) nation/state population size, f) Human development Index, g) high compliance marine reserve (0 is fished baseline), h) restricted fishing (0 is fished baseline), i) low compliance marine reserve (0 is fished baseline), j) voice and accountability, k) reef fish landings, l) ocean productivity; m) depth (-1= 0-4m, 0= 4-10m, 1=>10m), n) reef flat (0 is reef slope baseline), o) reef crest flat (0 is reef slope baseline), p) lagoon/back reef flat (0 is reef slope baseline). All X variables are standardized. Red lines are the marginal trend line for each parameter as estimated by the full model. Grey lines are 100 simulations of the marginal trend line sampled from the posterior distributions of the intercept and parameter slope, analogous to conventional confidence intervals. ** 95% of the posterior density is either a positive or negative direction (Fig. 1b-d); * 75% of the posterior density is either a positive or negative direction.

Extended Data Figure 2| Correlation plot of candidate continuous covariates before accounting for colinearity (Extended Data Table 4). Colinearity between continuous and categorical covariates (including biogeographic region, habitat, protection status, and depth) were analysed using boxplots.

Extended Data Figure 3 | Model fit statistics. a) Bayesian p Values (BpV) for the full model indicating goodness of fit, based on posterior discrepancy. Points are Freeman-Tukey differences between observed and expected values, and simulated and expected values. Plot shows no evidence for lack of fit between the model and the data. b) Posterior distribution for the degrees of freedom parameter (ν) in our supplemental analysis of candidate distributions. The highest posterior density of 3.46, with 97.5% of the total posterior density below 4, provides strong evidence in favour of a noncentral t-distribution relative to a normal distribution and supports the use of 3.5 for ν.

Extended Data Figure 4| Box plot of deviation from expected as a function of the presence or absence of key social and environmental conditions expected to produce bright spots. Boxes range from the first to third quartile and whiskers extend to the highest value that is within 1.5 * the inter-quartile range (i.e., distance between the first and third quartiles). Data beyond the end of the whiskers are outliers, which are plotted as points.