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Protection efforts have resulted in ~10% of existing fish biomass on coral reefs

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The amount of ocean protected from fishing and other human impacts has often been used as a metric of conservation progress. However, protection efforts have highly variable outcomes that depend on local conditions, which makes it difficult to quantify what coral reef protection efforts to date have actually achieved at a global scale. Here, we develop a predictive model of how local conditions influence conservation outcomes on ~2,600 coral reef sites across 44 ecoregions, which we used to quantify how much more fish biomass there is on coral reefs compared to a modeled scenario with no protection. Under the assumptions of our model, our study reveals that without existing protection efforts there would be ~10% less fish biomass on coral reefs. Thus, we estimate that coral reef protection efforts have led to approximately 1 in every 10 kg of existing fish biomass.

marine conservation | marine protected area | coral reef | fisheries | social-ecological

Significance

As nations strive to fulfill their commitments to protect 30% of the planet by 2030 (what is often referred to as "30 × 30"), it will be critical to understand what conservation efforts to date have actually achieved and what could be achieved by further protection. Our modeling of ~2,600 global coral reef sites suggests that 1) coral reef management efforts (including both fishing restrictions and outright fishing prohibitions) to date have led to ~10% of existing fish biomass on coral reefs; and 2) if fishing restrictions were implemented on all remaining unmanaged reefs, we predict that it would increase fish biomass by an additional 10.5% of existing fish biomass.

Anthropogenic impacts, including climate change, pollution, sedimentation, and overfishing have led to severe degradation of coral reefs, affecting millions of people worldwide (1). One key approach used to mitigate the latter of these impacts includes protection efforts that either restrict fishing (e.g., through effort, gear, or species limits) (2–4) or prohibit fishing altogether in fully protected Marine Protected Areas (5–7) (hereafter "fully protected MPAs"). Recently, 196 nations agreed to protect 30% of the earth's land and sea by 2030 (what is referred to as 30 × 30) (8). Global ocean coverage of all MPAs is currently 8.4%, with fully protected MPAs estimated to be only 2.9% (9), and we estimate similar coverage for coral reefs in fully protected MPAs (3%; *SI Appendix*, Table S1). Yet, simply tallying the extent of area protected tells us little about the difference these protection efforts have made (or will make) to the global condition of coral reefs because key outcomes from protection (e.g., increasing the biomass of fish) also depend on the type of protection applied (i.e., fully protected MPAs or fishing restrictions), how well people comply with protection efforts, and the socioeconomic, environmental, and ecological context in which protection is implemented (2, 5, 10–15). To date, the actual outcomes achieved by existing coral reef protection efforts have yet to be quantified at a global scale. Here, we address this gap by developing a predictive model to quantify the outcomes of protection efforts (including both fully protected MPAs and fisheries restrictions), relative to predictions of what would have happened without these protections (15–17).

Using linear mixed-effects models with spatial random effects (spaMMs), we estimate fish biomass gains that have been realized through partial or full protection at 1,244 of 2,599 surveyed coral reef sites from 44 marine ecoregions (*Methods*). We use fish biomass as a key ecological outcome since it is a crucial indicator of many potential coral reef contributions to people (e.g., potential fish stocks available to harvest) and to nature (e.g., nutrient cycling and herbivory) (18–20). We first tested which combinations of socioeconomic, environmental, and ecological predictors best predicted observed fish biomass within five protection categories (Table 1), while also accounting for geographic effects (*Methods* and *SI Appendix*, Table S2). We then used the most predictive uncorrelated models (i.e., combining lowest root mean squared errors and least correlation among predictions; *SI Appendix*, Table S3) to estimate expected fish biomass within each surveyed site under an extreme scenario with no protection (fished scenario), given that site's local context. Finally, we calculated "realized gains" as the difference between the fished scenario biomass and the original (status quo) biomass for each site. The advantage of using this modeling-based approach is that it allows us to predict location-specific shifts in fishing (i.e., counterfactuals) by explicitly accounting for each location's socioeconomic and environmental conditions. We use this approach to answer three key questions: 1) "What difference have existing

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The authors declare no competing interest.

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Table. 1. Proportional representation and descriptions for protection categories

Protection category	# Sites (%)	Extent (area/age)	Fishing allowed
Big and old high compliance fully protected MPA	200 (7.7%)	>10 km^2 and >10 y	None (fully protected)
Small or new high compliance fully protected MPA	158 (6.1%)	≤10 km^2 or ≤10 y	None (fully protected)
Low compliance fully protected MPA	301 (11.6%)	All	None (fully protected, but rules not well followed)
Restricted fishing	585 (22.5%)	All	Some (partially protected; access, gear, or species limits)
Open to fishing	1,355 (52.1%)	N/A	Unrestricted

coral reef protection efforts made to the amount of fish biomass on global coral reefs?," 2) "What is the role of context in coral reef protection outcomes?," and 3) "What are the expected gains from further coral reef protection?"

Results

The Difference Made by Existing Coral Reef Protection Efforts. In our fully fished scenario, where the 1,244 sites in fully protected MPAs or restricted fishing areas were instead simulated as open to fishing, we estimate that there would be 21.4% less fish biomass (95% quantiles = 20.5 to 22.3%; Fig. 1*A*) across all of our sites, suggesting that approximately 1 in every 5 kg of current coral reef fish at our sites is attributable to protection efforts. Most realized gains (67%) were from the 358 sites in high compliance fully protected MPAs (all sizes and ages combined), without which the total biomass in all 2,599 sites would be 14.2% lower (95% quantiles = 13.5 to 15.0%; Fig. 1*A*). However, since we surveyed a greater proportion of fully protected MPAs (25.4% of our sites) than are represented globally on coral reefs, we randomly subsampled from all our fully protected MPA sites to recalculate a more globally representative estimate for total realized gains (Fig. 1*B*). Including only 3% fully protected areas (to match our estimates of global coral reef coverage; *SI Appendix*, Table S1), we estimate that there would be 10.2% less reef fish biomass (95% quantiles = 9.4 to 11.1%) without current protection. Thus, one interpretation of our findings, under some key limiting assumptions (e.g., our sites are representative, the fish families we sampled are representative of other families, and our model adequately captured localized environmental effects), is that the outcomes from all protection efforts to date (including both fully protected MPAs and fisheries restrictions) have led to ~10% of the fish biomass on coral reefs. Our results also indicate that fisheries restrictions are having a positive impact—we estimate that there would be 5.7% less fish biomass (95% quantiles = 5.2 to 6.3%) among our surveyed sites without such restrictions.

The Importance of Context. Importantly, local socioeconomic and environmental context led to a variation of up to two orders of magnitude in biomass among sites within the same protection category (Fig. 2*A*). For example, the relationship between market gravity (a proxy for fishing and other human impacts) and protection status in the models (*SI Appendix*, Fig. S1 and Table S3) meant that realized gains among big and old high-compliance fully protected MPAs were not uniform (Fig. 2*B*). In each of the most predictive models, the highest realized gains occurred where human impacts were low (Fig. 2*B*). Other conditions that were favorable to producing high biomass gains included specific habitat types (slopes, crests, and lagoons were associated with higher biomass than reef flats), depth (>10 m), less extreme primary productivity (lower maximum chlorophyll-*a*), and sea surface temperatures that were warmer most of the time (lower SST skewness) (*SI Appendix*, Fig. S1). Thus, the most favorable sites were those that had lower levels of human gravity, were reef slopes, crests, or lagoons, and had lower maximum chlorophyll-*a* and SST skewness.

While high compliance fully protected MPAs generated the greatest average realized biomass gains within each site (pairwise Wilcoxon Rank Sum Tests; all $P < 0.001$), our global study revealed that the context-driven range in payoffs among reefs (Fig. 2*A*) means that fisheries restrictions implemented in more favorable locations can produce greater absolute gains than well complied with big and old fully protected MPAs implemented in less favorable locations. Likewise, although some small or new high compliance fully protected MPAs had greater realized gains than other big and old high compliance fully protected MPAs (Fig. 2*A*), this does not indicate that small or new MPAs would be less effective if they were big and old. Rather, this pattern is driven by some small or new fully protected areas being located in more favorable socioeconomic and environmental contexts (*SI Appendix*, Fig. S1).

Scope for Further Gains. Understanding what has been achieved by existing coral reef protection efforts also requires benchmarking the status quo against the potential for further gains. Consequently, we calculated "potential gains" by comparing status quo fish biomass with a second "full protection" scenario (21), where all reefs are in big and old high compliance fully protected MPAs (potential gains = full protection scenario − status quo). This extreme scenario is not intended as a policy goal, as we recognize prohibiting fishing on 100% of coral reefs would be economically, culturally, and nutritionally devastating to coastal societies (1). However, including this scenario allows us to gauge the status of coral reef fish biomass along a gradient from no fishing to full fishing (Fig. 3*A*), and to identify which sites would benefit most from fully protected MPAs (Fig. 3*B*). In this extreme "full protection" scenario (where all surveyed sites were in big and old high compliance fully protected MPAs), we predict that the median biomass among surveyed locations would be 956 kg/ha (95% quantiles = 404 to 2,766 kg/ha), and that there would be 78.1% more fish biomass compared to status quo (95% quantiles = 75.1 to 81.1%; Fig. 3*A*). However, if we simulate a 30% coverage of fully protected MPAs, we estimate biomass would be ~17 to 28% higher, depending on whether additional sites were protected at random (median = 16.6%; 95% quantiles = 15.2 to 18.1%) or selected to maximize biomass gains (median = 28.2%; 95% quantiles = 26.1 to 30.4%; Fig. 3*A*). In other words, variation in outcomes based on local conditions means that strategically selecting sites for protection results in >50% more fish biomass gains than haphazardly selecting sites (Fig. 3*A*). Since we recognize that "full protection" would mean removing fishing opportunities, we also contrasted that scenario with a "restricted fishing" scenario and find that there would

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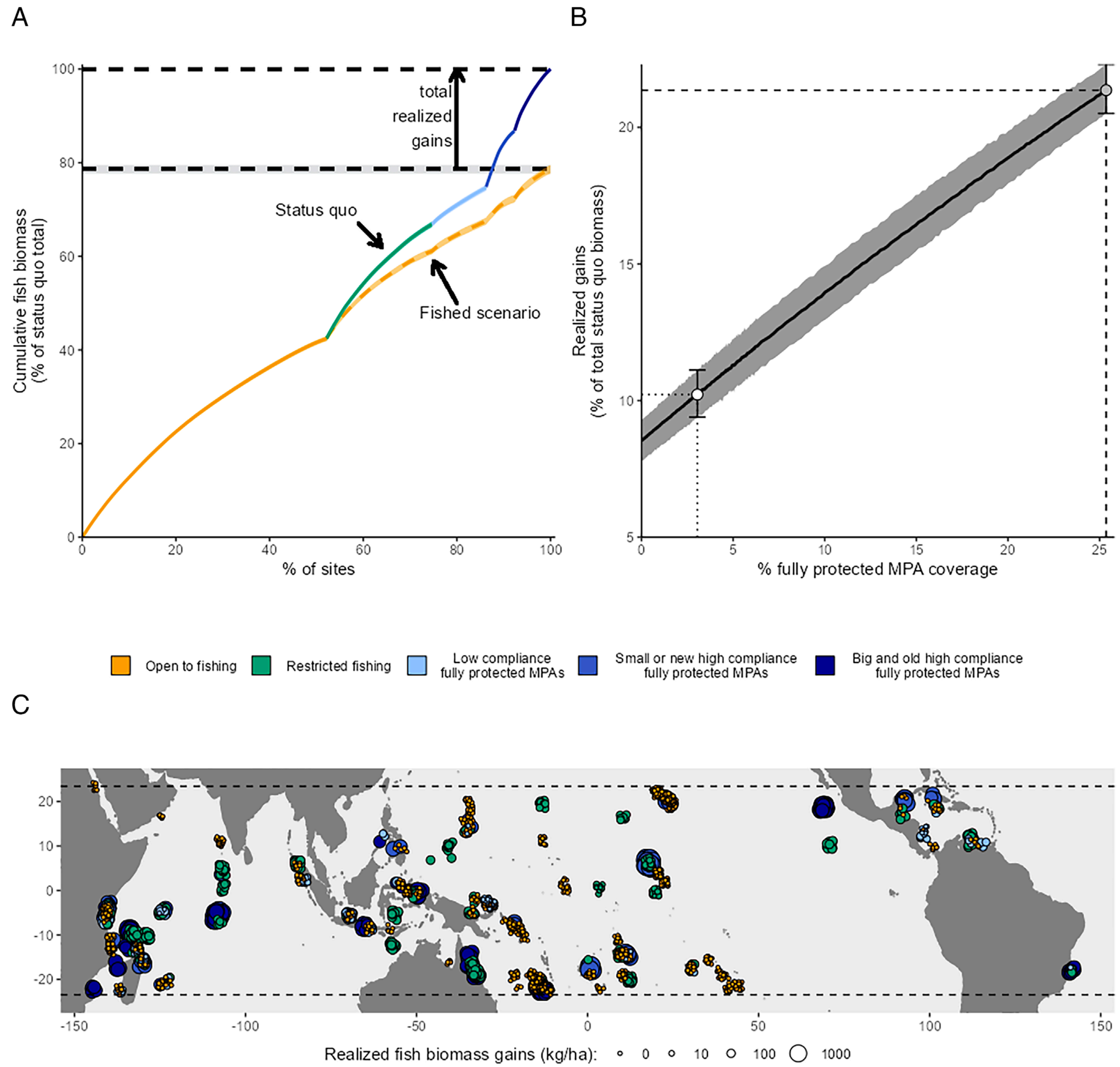

Fig. 1. Realized fish biomass gains from coral reef protection. (*A*) Medians (lines) and 95% quantiles (ribbons) for cumulative status quo fish biomass (solid line colored by protection category) and cumulative predicted biomass if all surveyed sites were open to fishing (orange dashed line), showing that most gains come from a minority of high compliance fully protected MPAs. Note that 95% quantiles are small, making them difficult to discern from the lines. (*B*) Medians (line) and 95% quantiles (ribbon) of recalculated total realized gains after successively subsampling fewer fully protected MPAs than were surveyed to more closely represent global estimates. The dotted lines and white point represent the gains from a subsample approximating a 3% estimate for current global coverage of fully protected MPAs on tropical coral reefs (*SI Appendix*, Table S1), whereas the dashed line and gray point are the gains from the surveyed coverage of fully protected MPAs. (*C*) Map of realized gains, with points sized by median gain, colored by protection category, and jittered to visualize overlapping sites.

be 10.5% more fish biomass (95% quantiles = 9.9 to 11.1%) if all fished sites were in restricted fishing areas.

Discussion

We quantified the outcomes of coral reef protection efforts by simulating fish biomass under different alternative scenarios of protection for a globally distributed sample of ~2,600 coral reef sites. Our study has three key results.

First, we used our model to simulate what would have happened if all reefs were open to fishing, revealing that there would be ~10% less fish biomass on coral reefs globally without current fully protected MPAs and fisheries restrictions (based on our study sites corrected for oversampling within MPAs) (Fig. 1). Of course, this is a global estimate and individual sites that are currently in fully protected MPAs would lose much more than the ~10% decrease estimated across all our sites if they were openly fished. Our modeling approach differed from the existing body of literature on the efficacy of coral reef MPAs and fisheries restrictions (7, 10, 15, 22–24) by enabling us to simulate what would have happened across a global sample without these protection efforts. Doing so was an important step in moving beyond simply adding up the area protected and toward quantifying global outcomes of coral reef protection efforts.

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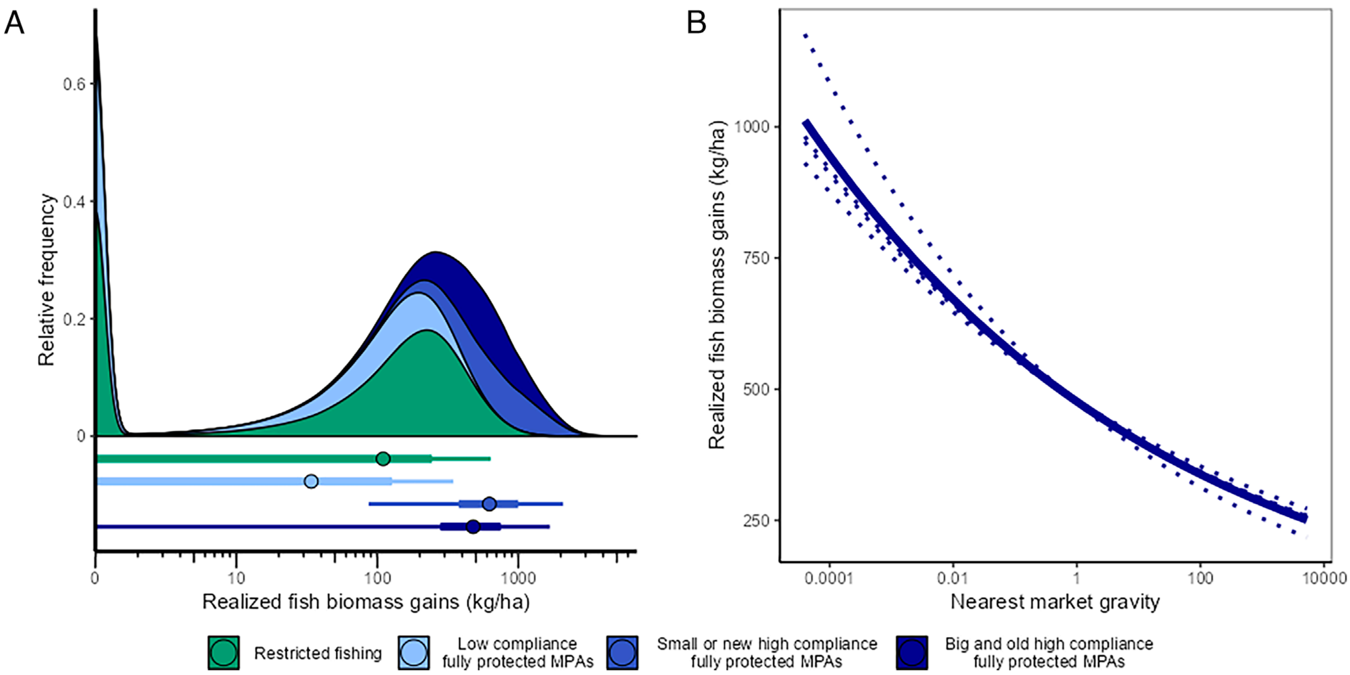

Fig. 2. Variation in realized reef fish biomass gains within protection categories. (*A*) Stacked frequency distributions of realized gains colored by management category, with medians (points), 50% quantiles (thick lines), and 95% quantiles (thin lines) shown for each category below the origin line. (*B*) Marginal mean realized gains predicted from each of the four selected spatial GLMMs (dotted lines) and the multimodel median prediction (solid line) for all represented nearest market gravities. Marginal mean gains are calculated from the difference between marginal mean fish biomass predictions if a site was in a big and old high compliance fully protected MPA vs. if it were open to fishing.

Our second key result was quantifying the context-driven range in payoffs among coral reefs (Fig. 2). We revealed that context can result in more than two orders of magnitude difference in fish biomass gains from the same strategy (Fig. 2*A*). We also showed how strategically selecting sites for protection based on favorable context could result in >50% more biomass gains than haphazardly selecting sites for a hypothetical target of 30% of coral reefs in fully protected MPAs (Fig. 3). Consistent with other studies, we found that, on average, fully protected MPAs had greater biomass gains than locations with fisheries restrictions (4, 25). However, a key finding from our study is that fisheries restrictions implemented in more favorable locations can produce as much or more biomass gains than well complied with fully protected MPAs implemented in less favorable locations. This finding provides empirical evidence on the important contributions that partially protected areas can make to global 30 × 30 conservation outcomes (26), particularly when implemented in favorable locations. Indeed, we found that there would still be 10.5% more fish biomass if all of the fished surveyed locations were in restricted fishing areas. In cases where partial protection is less controversial and/or less costly to implement (McClanahan and Abunge 2020), conservationists may leave potential conservation gains on the table if they push exclusively for full protection.

Our third key result was that by simulating no fishing on all reefs, we estimated that there could be 78% more fish biomass within our global coral reef sample compared to the current status quo. While clearly not a desirable policy goal, this extreme scenario contributes to efforts defining reference points for how much fish we might expect on coral reefs in the absence of fishing activities. Our modeling approach complements an emerging body of research examining unfished benchmarks and reference points on coral reef fisheries (27–31). A key contribution of our approach is that we were able to generate site-specific estimates that reflect the local context (also see ref. 29), whereas much of the previous work has focused on generating a single global or regional unfished biomass reference point (32). It is important to keep in mind that we used a hindcasting approach, which explores what would have happened under the extreme scenario of being fully unfished (or fully fished). This approach should not be interpreted as a forecast of future conditions for any particular location.

Although our study incorporated a proxy of human impacts (market gravity) into our model, we were unable to directly measure fishing effort at the local scale for our globally distributed study sites. Since MPAs can displace fishing effort into adjacent areas (thereby increasing exploitation there) (33–35), it is plausible that the realized gains in biomass we predicted are overestimated because the biomass in fished areas are actually lower than they would be without protection. Consequently, the difference in fish biomass between fished and fully protected MPAs may appear greater than it should be. Conversely, we were also unable to directly account for spillover of adult fish and larvae from fully protected MPAs toward fished areas, which could potentially have the opposite effect (i.e., underestimating the potential gains from fully protected MPAs since the difference between fully protected and fished areas appears less than it should be) (36–39). Although our data and methodology could not account for fishing effort or spillover directly, we ran a sensitivity analysis showing that the residuals from our models did not vary with distance from MPAs for fully fished sites within 50 km of an MPA (adjusted $R^2 = -0.00118$; *SI Appendix*, Fig. S2). In other words, although we were unable to directly account for processes like effort redistribution and spillover, these omissions did not appear to bias our estimates of the gains from protection efforts.

Our study has key caveats that should be kept in mind when drawing inference. First, our results on ecological outcomes of protection efforts depend at least in part on the degree to which species' home ranges are covered by protection. Numerous studies have found that coral reef fishes have relatively limited home ranges compared to other marine and terrestrial systems (40–42), and,

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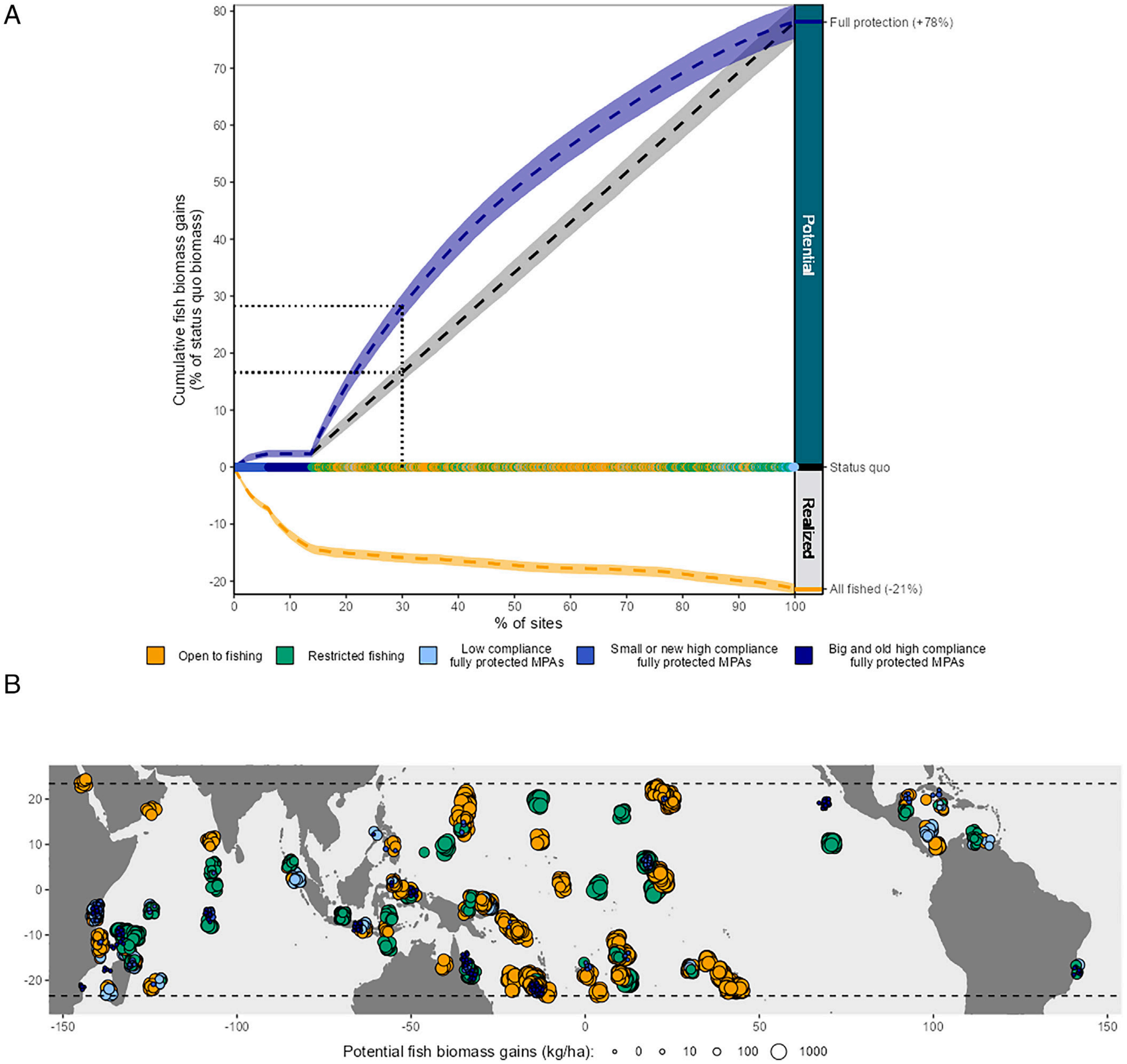

Fig. 3. Potential fish biomass gains from full protection on coral reefs. (*A*) Cumulative potential gains if all sites were in big and old high compliance fully protected MPAs (dashed dark blue line [median] and ribbon [95% quantiles]; ordered from highest to lowest gains for sites that are not already in high compliance MPAs), and realized gains that would be lost if corresponding sites were open to fishing (dashed orange line [median] and ribbon [95% quantiles]). The y-axis represents the percentage gain (potential) or loss (realized) compared to status quo fish biomass (horizontal line at 0, colored by protection status). Dashed black line and gray ribbon are the median, and 95% quantiles of potential gains from randomly reordering sites that are not already fully protected MPAs (1,000 times) and recalculating cumulative gains. Dotted lines indicate the expected potential gains if 30% of the sites were fully protected MPAs. (*B*) Map of potential gains, with points sized by median gain, jittered to visualize overlapping sites, and colored by protection category.

consequently, our results may not be directly applicable to other systems. Second, we used a modeling approach to predict site-specific effects of protection efforts because the data required for the gold standard measurement of conservation impacts (i.e., before-after-control-impact studies which are randomized across the world's coral reefs) (16, 43, 44) simply do not exist at the global scale (43). Our study sites and their protection were not randomly assigned (*Methods*). Thus, caution should be taken when making inferences beyond our ~2,600 globally distributed study sites.

Here, we quantified fish biomass gains that have been realized through existing coral reef protection efforts, highlighted the important role of context in reef protection outcomes, and estimated the scope for further gains. Together, our results provide cause for cautious optimism about what conservation efforts have achieved to date—marine protection efforts ranging from fisheries restrictions to fully protected MPAs have made a modest difference to the global biomass of coral reef fishes—our models suggest that approximately 10% of the fish biomass on reefs is attributable to these efforts. As governments pursue the 30 × 30 target of increasing global MPA coverage, maximizing further conservation gains will require balancing strategy and context. For example, although strategies such as fisheries restrictions are less effective on average than fully protected MPAs, fisheries restrictions located in more favorable locations can produce better outcomes than fully protected MPAs implemented in less favorable locations. Although we focused our analysis on a single ecological outcome (fish

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biomass), in future analyses our approach could be applied to numerous other potentially important ecological outcomes from protection [e.g., productivity (45), ecosystem functioning (46), biodiversity (4)].

Methods

Reef Fish Surveys. We compiled 2,599 underwater visual census (UVC) fish surveys from tropical reef locations (i.e., within 23.5 latitude degrees of the equator; *SI Appendix*, Fig. S1*A*), representing 44 unique marine ecoregions from 20 marine provinces (47). All sites were surveyed between 2004 and 2019. If data were available for multiple years at the same location, we used only the most recent year. All UVC surveys used standard belt transect, distance sampling, or point count methods. These methods were included as parameters in the analyses to control for any differences in survey methodology (*SI Appendix*, Fig. S1), and in the main text all data presented have been standardized for the different approaches used (Figs. 1–3). In addition to the census method, location (latitude and longitude), habitat type (slope, lagoon/back reef, flat, or crest), and depth category (0 to 4 m, 4 to 10 m, or >10 m) were recorded for each site and used in the models. In each survey, diurnal reef-associated noncryptic fishes were identified (to species or family level), and their sizes (total lengths) were estimated. To convert total lengths to biomass estimates, we used length-weight conversions from FishBase (48). When length-weight conversion parameters were not available for a species, we used parameters for a closely related species or genus. We then calculated total reef fish biomass for each site by combining the biomasses of all fishes >10 cm from 22 fish families consistently censused by observers (i.e., Acanthuridae, Balistidae, Carangidae, Diodontidae, Ephippidae, Haemulidae, Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Monacanthidae, Mullidae, Nemipteridae, Pinguipedidae, Pomacanthidae, Serranidae, Siganidae, Scaridae, Sparidae, Synodontidae, Tetraodontidae, and Zanclidae). Transient, strictly plankton-feeding groups, and species that are difficult to accurately estimate, such as Caesionidae, Pomacentridae, and sharks, respectively, were removed (see ref. 49 for the methods of establishing fishable biomass). We limited our analysis to fish >10 cm within these 22 fish families to more closely represent fish available for human consumption.

Marine Spatial Protection Categories. The UVC fish surveys included a range of spatial protection types which we used to assess the impact of management on fish biomass, including fully protected (i.e., no-take) MPAs, other fisheries restrictions, and sites open to fishing. We assigned each survey site to one of five protection status categories: 1) big and old high compliance fully protected MPAs, 2) small or new high compliance fully protected MPAs, 3) low compliance fully protected MPAs, 4) restricted fishing areas, and 5) areas open to fishing (Table 1). The three fully protected MPA categories include all sites that fall within borders of MPAs where no fishing is allowed. We asked data providers to assign each fully protected MPA site to either a high or low compliance category, based on their expert opinion surveying those sites. To account for potential differences in biomass associated with MPA age and size, we then further subdivided the high compliance locations into those that were big and old (MPAs with no-take zones >10 km^2 and >10 y old) and those that were either small or new (no-take zones ≤10 km^2 or ≤10 y old). This "small or new" category thus includes high compliance fully protected MPAs that are any of the following: big and new, small and old, or small and new. We did not further subdivide the small or new category into others (e.g., small and new, etc.) due to the small sample sizes that would have resulted and because we were most interested in predicting big and old fully protected MPAs rather than exploring the differential effects of MPA age and size. We chose the 10 y and 10 km^2 cutoffs as break points because they are within ranges that should represent adequate ages and sizes to protect many coral reef fish species according to empirical evidence (12, 23, 50, 51), and a preliminary analysis showed that those breaks resulted in a split that balanced maximizing the difference in observed coral reef fish biomass between the two groups with creating two groups of fairly equal sample sizes (*SI Appendix*, Fig. S3). Although some past analyses (15) and the MPA Atlas use a threshold of 100 km^2 as a cutoff for "large" MPAs, the vast majority of MPAs are smaller than that threshold (9) and we wanted to be more conservative to include smaller, community-driven MPAs that can still be effective. The restricted fishing category includes all sites that had active restrictions on either access (e.g., customary tenure; periodic closures), gear (e.g., bans on use of nets, spear guns, or traps), or species (including MPAs that were not no-take). We assigned the final, "open to fishing" category to sites with no fishing restrictions.

Social and Environmental Predictors. To account for the effects of potential social, environmental, and ecological variables on fish biomass, we examined which of a suite of variables best predict fish biomass (*SI Appendix*, Table S2). In addition to management, candidate social predictor variables included two proxies for human pressure: market and population gravity (4, 11, 52–54). In addition to the habitat type and depth categories assigned during each reef fish survey, we extracted publicly available data for a variety of remotely sensed environmental factors: sea surface temperature, two metrics of temperature stress (sea surface temperature anomalies and degree heating weeks), a proxy for primary productivity (chlorophyll-*a*), light availability (photosynthetically active radiation), and wave energy (*SI Appendix*, Table S2 for full descriptions, sources, and rationale/support). We chose each of these potential social and environmental predictors because each has been linked to either reef fish or their coral habitats in past studies. Global representativeness of these predictors is shown in *SI Appendix*, Figs. S6 and S7. To account for regional differences in expected fish biomass, we also assigned each survey location to their marine ecoregions and provinces (47).

Gravity. Both gravity metrics we examined are based on the same calculation between reef sites and nearby populations (gravity = population size/travel time^2) but use different populated locations. In each case, travel time was calculated using a cost-distance algorithm that computes the least cost (in minutes) it would take to travel between reef sites and human populations, while taking into account that the cost of travel will differ over water and different land surfaces (11). For population and market gravity, we used the population sizes and travel times to the nearest populated settlement (of any size), or nearest major urban center (i.e., provincial capital cities, major population centers, landmark cities, national capitals, and ports), respectively (52–54). While market gravity is an indicator of the market-driven influences on reef fish, population gravity can indicate both direct impacts of fishing (due to easier access) and other human impacts (e.g., sedimentation, pollution, coastal development).

Remotely sensed environmental data. We extracted the following remotely sensed environmental variables from freely available online data sources: wave energy, sea surface temperature (SST), sea surface temperature anomalies (SSTa), degree heating weeks (DHW), chlorophyll-*a* (Chl-*a*), and photosynthetically active radiation (PAR). For wave energy, we used mean values obtained for each survey location from the Marine Socio-Environmental Covariates platform (55). For each of the other remotely sensed predictors, we extracted the closest available daily mean values within 10 km of each surveyed location from either Coral Reef Watch (SST, SSTa, DHW) (56) or the GlobColour Project (Chl-*a* and PAR) (57). If the nearest available data were ≥ 10 km from the survey site, we did not include that site, reasoning that the environmental conditions were not estimated close enough to be representative for that site. For each survey, we extracted all available daily values for the two years prior to the survey date and then calculated summary statistics that reflect either central tendency (mean), variation (SD), distribution (skewness, kurtosis), or extremes (minimum and maximum) for that period at that location (*SI Appendix*, Table S2 for rationale/support from previous studies). However, in the models, we only included summary statistics for each variable that has previously been linked to either reef fish or their coral habitats in past studies (*SI Appendix*, Table S2 for rationale/support).

Model Selection. We developed and compared a series of candidate spatial mixed-effects models (spaMMs) that predicted fish biomass using noncorrelated combinations of the above predictors (as fixed effects) and accounted for regional differences and spatial autocorrelation (as random effects). Each model predicted fish biomass using a Gamma response family (log link) since fish biomass tends to be normally distributed in log space. To account for skewed distributions in the predictors, we log transformed both gravity metrics, SST kurtosis, both DHW metrics, both Chl-*a* metrics, PAR kurtosis, and mean wave energy before including them in the models. We assessed collinearity among the predictors using variance inflation factors (VIF). We then built a series of spaMMs that represented the longest models that included at least one instance of each predictor variable with VIF < 3. All models included the same four surveyed categorical predictors (management, habitat, depth, and census method) and at least one of the gravity predictors (nearest market or nearest population). Since there is evidence that the effect of gravity differs among management types (11), we also included an interaction between

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gravity and management (either nearest market or nearest population in any one model). Significant correlations among many of the remotely sensed environmental variables meant that we could only combine subsets of each of the predictor variables. In addition to these fixed effects, we included a nested random effect of marine ecoregion within marine province to account for regional differences in expected fish biomass. We extracted ecoregions and provinces for each survey location from Marine Ecoregions of the World (47) data available online from Data Basin (58). To further account for spatial autocorrelation in fish biomass (i.e., nearby locations are more likely to have more similar fish biomass), we included a Matérn covariance function that uses the projected latitude and longitude coordinates (i.e., Northing and Easting) of each site as another random effect in each model (59). We used the R package spaMM (59) to fit all models.

Among our candidate spAMMs, we selected those that were best at predicting test data and were least correlated with each other using a 20-fold, spatially blocked cross-validation process. To account for spatial structure in the data in our cross validation, we used hierarchical clustering to split the dataset into 20-folds where each fold was spatially clustered (60). For each of the 20-folds, we fit each candidate model to a dataset without the fold (training dataset) and then used the fitted model to predict fish biomass at the sites represented within the fold (test dataset). We then compared those predictions with the observed (surveyed) fish biomass in the test dataset using root mean squared error (RMSE). Once we had completed the 20-fold cross validation for all candidate models, we identified the model that was best at predicting among all folds (i.e., lowest mean RMSE). We then used a modification of the one-standard-error rule (61) to identify models that had similar predictive power and did not result in the same predictions as the best model. To apply that modification, we first calculated the correlation between the predictions from each model and the best model ($\rho_{best,m}$). We then calculated an adjusted SE by multiplying the SE of the RMSE values of the best model (σ_{best}) with the square root of (1-$\rho_{best,m}$), thus penalizing any models that were closely correlated with the best model. In addition to the model with the lowest mean RMSE (i.e., best-predicting model), we selected any models whose adjusted error interval included the RMSE of the best model. We then used those selected models to predict counterfactual biomasses and calculate biomass gains.

We selected four models that either best predicted observed (surveyed) fish biomass or had comparable predictive performance after accounting for correlation in their predictions (*SI Appendix*, Table S3). After correcting for differences among surveys (census method, depth, and habitat), median observed fish biomasses (i.e., "status quo") ranged from 191 to 2,387 kg/ha across all 2,599 surveyed tropical reef locations (*SI Appendix*, Fig. S1 *A*, *B*). The effect sizes of the variables in the four models we selected illustrate both the effect of management and the importance of other social and environmental variables on fish biomass (*SI Appendix*, Fig. S1*C*). In addition to census method, depth, habitat, and an interaction between nearest market gravity and management, the four models we selected included five of the same environmental predictors: two ocean productivity metrics (Chl-*a* mean and maximum), two metrics of light availability (PAR mean and SD), and mean wave energy (*SI Appendix*, Table S3). Seven other environmental predictors were included in at least one (but not all) of the models we selected: three sea surface temperature metrics (SST mean, maximum, and skewness), two metrics of light availability (PAR skewness and kurtosis), a metric of accumulated temperature stress (DHW maximum), and nearest population gravity. However, only two of the environmental predictors (Chl-*a* max and SST skewness) had effect sizes whose 95% CI did not overlap with zero (*SI Appendix*, Fig. S1*C*). Accounting for geographical patterns (by including spatial autocorrelation and marine ecoregion nested within province as random effects) substantially increased the amount of variance explained by the models we selected (marginal $R^2 = 0.240$ to 0.251; conditional $R^2 = 0.713$ to 0.715; *SI Appendix*, Table S3).

Calculating Realized and Potential Reef Fish Biomass Gains. Using the four selected spaMMs, we calculated a corrected "status quo biomass" and predicted three counterfactual scenarios for each of our surveyed sites: 1) if all locations were open to fishing ("fully fished scenario"), 2) if all locations were in big and old high compliance MPAs ("full protection scenario"), and 3) if all fished locations were in restricted fishing areas ("restricted scenario"). To account for differences across surveys, we first corrected for those differences by predicting the expected fish biomasses at each survey location if all surveys had used the most common census method ("belt transect"), depth category ("4 to 10 m"), and habitat ("slope"), but with the remaining predictors unchanged. We refer to this reference biomass as the "status quo biomass" and use the same census method, depth category, and habitat categories for the counterfactual scenarios. For each counterfactual scenario, we then predicted expected biomasses by additionally setting the management for all survey locations to either "open to fishing," "big and old high compliance fully protected MPAs," or "restricted fishing." We used the "predict" function in spaMM (59) with each of the four selected models to estimate mean log(biomass) values and the "get_predVar" function to estimate uncertainties around the means from the linear predictors (prediction variance) for each surveyed location for the status quo and two counterfactual scenarios. We then calculated multimodel means and propagated uncertainty across all four models for each point prediction (i.e., for each survey location). To calculate the multimodel error, we first calculated SD from the prediction variance and then propagated those within model uncertainties by calculating the square roots of the means of the squared SD. We then calculated among model uncertainties as the SD of the multimodel means for each point prediction. Finally, we combined the within and among model uncertainties in quadrature to calculate a total error (SD) for each multimodel mean.

To calculate what has already been accomplished from current spatial management (realized gains) and what could still be accomplished from changes in management (potential gains), we compared predictions of "status quo biomass" with predictions of the counterfactual scenario biomasses. Since these comparisons are in biomass rather than log(biomass), and we wanted to accurately represent the uncertainty around the comparisons, we simulated sample distributions using the multimodel means and propagated uncertainties before backtransforming the predictions. For each surveyed location and each scenario (status quo and counterfactual scenarios), we generated 1,000 samples of log(biomass) from a normal distribution, given the predicted multimodel means and SD for each survey location. We then backtransformed the sample values into biomass (in kg/ha) to calculate gains. To calculate realized fish biomass gains, we subtracted the 1,000 predicted "fully fished scenario" biomasses from the 1,000 "status quo" biomasses for each site. To calculate potential gains and restricted gains, we subtracted the 1,000 "status quo" biomasses from either the 1,000 "full protection scenario" biomasses or the 1,000 "restricted fishing" biomasses. For all gains, we truncated the data at zero, reassigning any negative values to that minimum value (i.e., no negative gains). We then calculated median and quantile values for the respective gains for each surveyed location. Since we predicted status quo biomass (and counterfactual biomasses) using the actual conditions at each site, there is substantially more overlap among management categories in those biomasses than there would be if all locations had the same conditions (e.g., *SI Appendix*, Fig. S1*B*).

To account for the higher proportion of fully protected MPAs (where no fishing is allowed) in our surveys compared to global coverage estimates, we randomly subsampled the surveyed fully protected MPAs so they represented successively lower proportions. We then recalculated total realized gains from those subsamples (Fig. 1*B*). Since global estimates of the extent of fishing restrictions are lacking, we assumed the proportion of restricted fishing sites among our surveys was broadly representative in this analysis. However, future studies could update this analysis as better data on the global extent of fishing restrictions become available.

To visualize how realized fish biomass gains vary along a gradient of nearest market gravity (Fig. 2*B*), we subtracted the marginal mean model predictions if sites were in big and old high compliance fully protected MPAs from the marginal mean predictions if sites were open to fishing. We used the "predict" function in the "spaMM" R package (59) to calculate marginal mean values along the full gradient of market gravities found in the fish surveys for each of the four spaMMs we selected. We then backtransformed the log(biomass) results to biomass before calculating the realized gains. Finally, we calculated the multimodel median values across the gradient of nearest market gravity (solid line in Fig. 2*B*) from the marginal mean realized gains of the four selected models (dotted lines in Fig. 2*B*).

Data, Materials, and Software Availability. Data and R code have been deposited in Zenodo (62).

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