Potential yield and food provisioning gains from rebuilding the world's coral reef fish stocks

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Many coral reefs have fish stocks that are depleted below the level at which sustainable production is maximized. Lower production means that millions of people are losing out on potential food, income, and livelihoods. Rebuilding these stocks to maximize sustainable production can contribute toward ending hunger and malnutrition but requires active and effective fisheries management. Yet, for fish stock recovery plans to be implemented, recovery benefits, targets, and timeframes need to be quantified. Here, using 1,211 individual reef sites and 23 jurisdictions identified globally as being below maximum sustainable production levels, we show that reefs have the potential to increase sustainable yields by nearly 50% if allowed to recover toward their maximum production levels. For individual jurisdictions, this recovery represents from 20,000 up to 162 million additional sustainable servings of reef fish per year in comparison to current sustainable production, meeting recommended seafood intake for up to 1.4 million additional people a year. However, such growth and food provisioning will require fish stocks to double their standing biomass (increase by a median of 32 t/km^2). Recovery timeframes range from 6.4 y under the most stringent scenario (a moratorium) to 49.7 y under the maximum harvest scenario that results in recovery. We find that locations with the greatest potential for sustainable gains in yield are among those with the greatest food and micronutrient deficiencies, underscoring both the challenges and opportunities in recovering fish assemblages to achieve their maximum sustainable potential.

food security | multispecies fisheries | coral reef fish | sustainable yield | recovery potential

Multispecies coral reef fisheries often operate in locations with compromised food security, employment, and income (1–3). In such locations, reef resources can be a readily accessible (4) source of food and nutrients, contributing to nutritional intake both directly, as key sources of vitamin B_{12}, heme iron, retinol, niacin, and protein (5), and indirectly by generating income that allows people to purchase other nutrient-dense foods (6). Thus, managing reef resources to maximize sustainable food provisioning is a path toward meeting key sustainable development goals such as "Zero Hunger" (7). However, recent global assessments of coral reef fisheries have shown that most reefs have fish biomass values below those that would maximize sustainable production and are not delivering their full yield potential (8, 9). For example, 64% of 1,903 exploited reef sites and 47% of 49 tropical jurisdictions assessed globally had reef fish stocks that were below 50% of their estimated unfished biomass (9), a common reference point at which yields are expected to be maximized (10). Having assemblages below reference point values increases the risk of stock collapse (10), decreases economic returns (11), imperils ecosystem functioning (8, 12, 13), and can jeopardize fishery yields and food security (14–16). Low fish biomass levels means that the millions of people who depend on reef ecosystems (17) are losing out on potential sustainable food supplies, income, and livelihood opportunities.

If fished populations become depleted below reference point levels aimed at maximizing sustainable production, the main goal of fisheries management is often to recover populations back to those levels (10, 18). For multispecies fisheries, key reference points can include those that produce "multispecies maximum sustainable yields" [MMSY (19)] or "pretty good multispecies yields" [PGMY; defined as a catch that is ≥0.8 of MMSY (20, 21)]. However, in many locations, such as those where multispecies coral reef fisheries operate, managing fish stocks to achieve recovery remains a major challenge (18). Recovery costs (22), together with socioeconomic and management constraints (1, 23), and a lack of defined context-specific recovery targets and timeframes (8), tend to outweigh the unknown or uncertain benefits from recovery, hindering the design of, and compliance with, effective fisheries management plans (24, 25).

Significance

Coral reef fisheries are a critical food source for people throughout the tropics. However, most reefs around the globe have fish biomass values below those enabling maximal sustainable production, risking food availability, income, and livelihoods. Rebuilding fish assemblages can increase sustainable food supplies and, if these are well distributed, directly contribute toward enhanced food security. We show that recovering fish stocks on coral reefs can significantly increase the number of sustainable fish servings produced per year and the number of people meeting fish intake recommendations, particularly for countries with high malnutrition. Our study highlights the sustainable food provisioning potential of recovering reef fisheries and quantifies how much recovery would be needed and the time such recovery would take.

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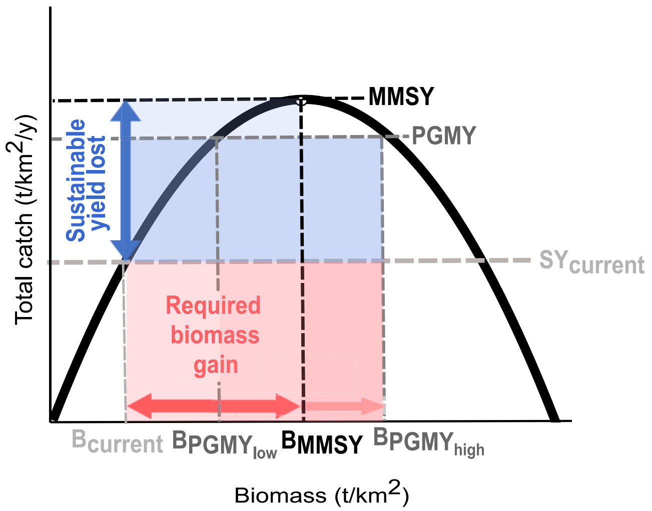

Fig. 1. Theoretical relationship between sustainable yield losses and required biomass gains in coral reef fisheries. Conceptual surplus production curve diagram exemplifying how to quantify i) the sustainable yield lost from having fish assemblages below biomass levels aimed at maximizing sustainable production B_{MMSY} ($B_{current} < B_{MMSY}$) and ii) the required biomass increases to recover assemblages to either maximum production values (MMSY) or PGMY. The *x* axis represents the standing fish assemblage biomass and the *y* axis the sustainable total catch or estimated surplus production for the whole multispecies assemblage. The solid line represents the expected surplus production along a gradient of biomass (assuming a Graham-Schaefer surplus curve for the multispecies assemblage, according to which MMSY is achieved at biomass levels corresponding to 50% of unfished biomass). $SY_{current}$ is the expected long-term yield (i.e., surplus) from a hypothetical multispecies assemblage given its standing biomass ($B_{current}$); B_{MMSY} is the estimated biomass at which MMSY is achieved; and B_{PGMY} are the estimated biomass at which PGMY are attained (below and above B_{MMSY}: $B_{PGMY,low}$ and $B_{PGMY,high}$, respectively). Note that we are not comparing current yields (i.e., how much is being caught on a reef) with potential maximum sustainable yields (i.e., how much could be caught sustainably if assemblages were managed to maximize production) but instead how much sustainable yields could increase from their current hypothetical sustainable levels.

Quantifying recovery targets and timeframes is necessary to effectively implement recovery management plans (10, 26). Additionally, quantifying foregone sustainable yields presents a means to evaluate costs of recovery plans against potential yield and food provisioning gains from recovered stocks (27). Recent frameworks developing context-specific reference points for reef fish using environmental conditions and assessing reef fisheries globally (e.g., ref. 9) provide an opportunity to quantify the potential food-security benefits of rebuilding fish stocks, as well as quantifying recovery timeframes and required biomass increases to achieve such benefits. Here, using data from 1,211 coral reef sites and 23 jurisdictions identified globally as having fish assemblages below 50% of their unfished biomass [*Materials and Methods* (9)], we i) quantify the sustainable yield lost due to having fish stocks below levels aimed at maximizing sustainable production (Fig. 1); ii) highlight the benefits of recovering fish assemblages in terms of food provisioning; iii) estimate the standing biomass increases required to recover assemblages to MMSY (i.e., B_{MMSY}) and biomass levels that produce PGMY (i.e., $B_{PGMY,low}$ and $B_{PGMY,high}$); and iv) estimate the time it would take to recover multispecies fish assemblages to those levels.

Results

Sustainable Yield Lost from Stocks Below B_{MMSY}. We quantified the sustainable yield lost from depleted coral reef fish assemblages for each site and jurisdiction classified below B_{MMSY} as the difference between the estimated MMSY and the estimated surplus production from the standing fish biomass (Fig. 1)–based on location-specific sustainable reference points estimated from a multispecies Graham-Schaefer surplus production model [*Materials and Methods*; (9)]. We found that, globally and based on median values, reefs classified as below B_{MMSY} are provisioning 68% of their maximum [*SI Appendix*, Fig. S1; (28)] and have a sustainable production deficit of 1.9 t/km^2/y, but with substantial among site variation (from 0.1 to 18.8 t/km^2/y; site-specific posterior medians; Fig. 2 *A*–*C*). This deficit represents a potential increase of ~47 [2 – 14,574]% (median [min-max] across sites) in long-term yields compared to current surplus levels if stocks were allowed to recover to maximum production (B_{MMSY}). Converting these yields to 100 g fish servings and to the number of people potentially meeting fish intake recommendations for cardiovascular health [*Materials and Methods*; (29)], we show that an additional 9,088 [276 – 93,255] reef fish servings could be produced yearly per square kilometer of coral reef, or 77 [2 – 791] additional people per square kilometer of reef could meet their yearly fish intake recommendations. A smaller increase of 0.7 [–1.8 – 14.7] t/km^2/y or 17 [–18 – 11,791]% would be possible if stocks were allowed to recover to PGMY values (e.g., $B_{PGMY,low}$), which translates into 3,361 [–9,160 – 69,446] fish servings/km^2/y or 29 [–78 – 621] people meeting yearly fish intake recommendations (with negative values indicating such sites are already between $B_{PGMY,low}$ and B_{MMSY}, and thus producing > PGMY).

Lost sustainable yields and food supplies are widespread among all geographic basins (Fig. 2*C*). However, the greatest estimated yield losses occur in locations where fish assemblages are most depleted (Fig. 2*B*), meaning they have the greatest potential long-term gains in yield. For example, at a jurisdiction scale, Kenya, Mauritius, or Oman—which have median biomass values below 10% of their estimated unfished biomass (9)–could increase their median per-unit-area sustainable catches by 418, 330, and 193%, respectively, if stocks were allowed to recover to levels that produce MMSY, with slightly lower, but still substantial, increases with recovery to PGMY (314, 244, and 134%; Fig. 2*D*). For these specific jurisdictions, increased yields to MMSY could translate into >23,000 additional sustainable reef fish servings (each 100 g) produced per year per square kilometer of reef or >198 additional people meeting yearly fish intake recommendations per square kilometer of coral reef in comparison to what would be sustainable given current estimated biomass levels (Fig. 2*E*).

Jurisdiction-Specific Food and Potential Nutrition Benefits of Recovering Reef Fish Stocks. By scaling per-unit-area sustainable yield gains and fish servings to the total reef area open to fishing within each jurisdiction (*Materials and Methods*), we found that jurisdictions are missing out on between 3.9 to 32,389.6 t/y (jurisdiction-specific medians) due to fish assemblages being below MMSY values, and thus jurisdictions have the potential to produce from 0.02 to 161.95 million additional fish servings a year compared to their current estimated production (*SI Appendix*, Fig. S2). These numbers mean that, dependent on the jurisdiction, from 166 to 1,373,208 additional people could meet yearly fish intake recommendations from coral reef fish recovery (Fig. 3*A*). For nations such as French Polynesia people meeting fish intake recommendations from gained yields represents 97% of the coastal population, and for others such as Tanzania, Maldives, and Mauritius, >20% of the coastal population could meet yearly fish intake recommendations from gained yields (Fig. 3*A* and *SI Appendix*, Table S1).

Based on the current status of fish stocks, jurisdictions can provide from 0.3 (Reunion) to 483.6 (Indonesia) million sustainable reef fish servings per year, meeting the yearly fish intake

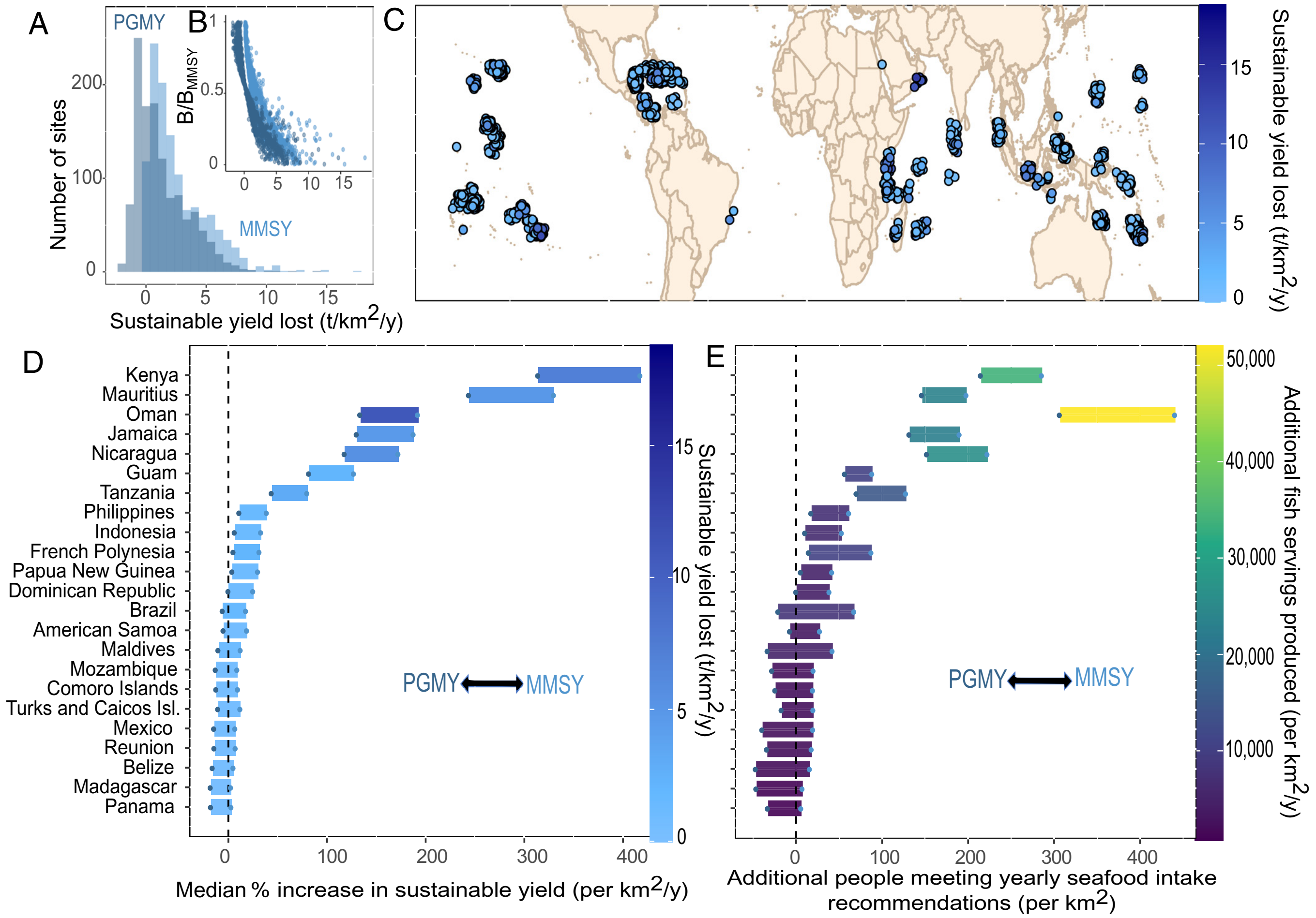

Fig. 2. Per unit area sustainable yield lost from coral reef assemblages. (*A*) Posterior median sustainable yield loss for coral reef sites open to fishing classified as being below B_{MMSY}. Colors represent losses based on MMSY (light blue) or PGMY (dark blue). Negative values in the PGMY distribution means those sites are already within PGMY values (i.e., between $B_{PGMY,low}$ and B_{MMSY}). (*B*) Relationship between expected sustainable yield lost and site-specific biomass status (B/B_{MMSY}). Points are posterior medians for each exploited site classified as below B_{MMSY}. Different colors are the same sites but for MMSY and PGMY. (*C*) Map of sampled fished sites below B_{MMSY}, color-coded by the median sustainable yield lost based on MMSY. Points are jittered to add clarity. (*D*) Median % increase in sustainable yields expected per jurisdiction if recovered to MMSY (upper limit of horizontal bar) or PGMY (lower limit of horizontal bar) in comparison to current estimated sustainable production. Only jurisdictions which have median estimated biomass values below B_{MMSY} are included (biomass values are weighted optimistically assuming the proportion of marine protected areas in a jurisdiction are at unfished biomass values; *Materials and Methods*). Bars are colored by the median sustainable yield lost based on MMSY. (*E*) Additional people potentially meeting yearly seafood intake recommendations per square kilometer for each jurisdiction based on median values. Bars are colored by the potential additional number of fish servings produced per km^2 if reef assemblages are recovered to MMSY. Note that in *D* and *E* if bars overlap the horizontal dashed line (~0% increase) it means that jurisdictions median biomass for exploited reefs is estimated to be within $B_{PGMY,low}$ and B_{MMSY} (i.e., they are already estimated to be producing >80% of MMSY, so meeting 80% can result in negative numbers).

recommendations for up to 4.1 million people (i.e., Indonesia; *SI Appendix*, Table S1). For jurisdictions such as French Polynesia, their estimated sustainable production already meets the seafood intake recommendations for >100% of the coastal population. However, for others (i.e., Jamaica, Philippines, Dominican Republic, Indonesia, Panama, Reunion, Mexico, Brazil, and Kenya) current estimated sustainable production covers much lower percentages of the coastal population (<5%; *SI Appendix*, Table S1). Allowing fish stocks to recover to MMSY can significantly benefit jurisdictions. Indonesia, for example, could provide enough yearly seafood intake recommendations for a total of ~5.5 million people if their reef fish stocks were managed at MMSY. Similarly, >50% of the coastal population from Tanzania, Turks and Caicos, Madagascar, Belize, and Maldives could meet yearly intake recommendations from recovered stocks. Recovering fish stocks to MMSY could allow some jurisdictions to double (Guam), triple (Jamaica, Nicaragua, and Oman), or increase above fourfold and fivefold (Mauritius and Kenya, respectively) the percent of coastal population meeting yearly fish intake recommendations (*SI Appendix*, Table S1).

By matching the number of additional people meeting intake recommendations to jurisdiction-specific hunger and hidden-hunger indexes (*Materials and Methods*), we found that places with higher human hunger [i.e., hunger and undernourishment (30, 31)] and hidden hunger [i.e., micronutrient deficiencies (32, 33)] are within jurisdictions with the greatest potential sustainable yield and food supply gains (Fig. 3; Spearman's correlation of ~0.5 and 0.3, respectively). For example, jurisdictions with "Alarming" and "Severe" hunger values (i.e., Madagascar, Mozambique, Tanzania, Kenya, Indonesia, and Philippines), which have inadequate food supplies, high child undernutrition, and mortality (30, 31), are missing out on 2,545 to 32,390 t/y of sustainable reef fish production by having reef stocks below maximum sustainable production values, equivalent to 12.7 to 161.9 million additional 100 g reef fish servings per year or 107,914 to 1,373,208 additional people potentially meeting yearly fish intake recommendations (Fig. 3*B*). Similar conclusions apply to jurisdictions with Alarming and Severe micronutrient deficiencies in preschool children [i.e., Madagascar, Mozambique, Tanzania, and Kenya; (32)], which are losing 2,545 to 15,814 tonnes of sustainably sourced reef fish, 12.7 to 79.1

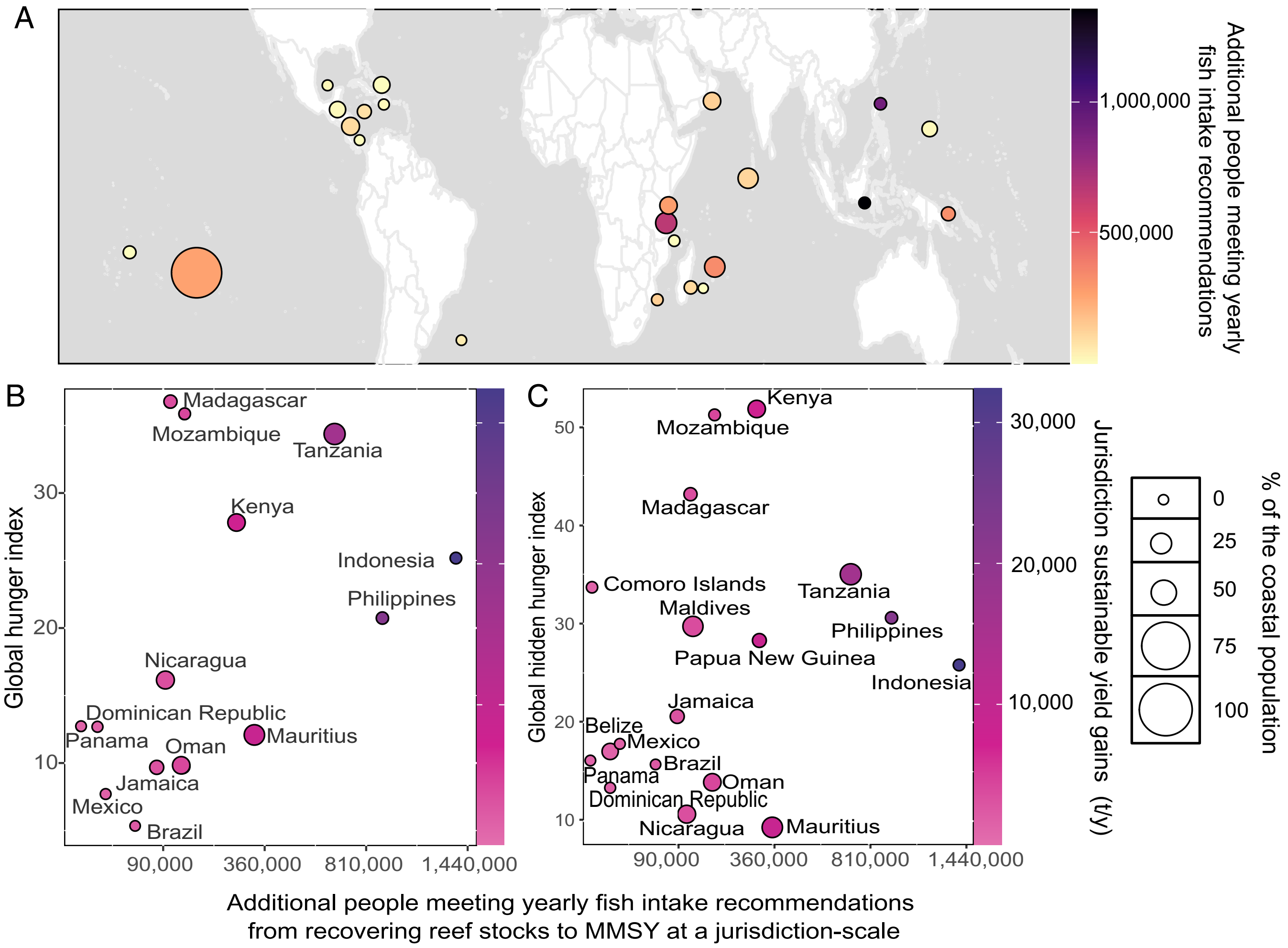

Fig. 3. Tackling hunger and micronutrient deficiencies by rebuilding reef fish stocks to maximum production levels. (*A*) Jurisdiction-specific estimated number of additional people who could meet yearly fish intake recommendations from the sustainable yields generated from recovering fish assemblages to MMSY values. (*B* and *C*) Relationship between the estimated number of people that could meet yearly fish intake recommendations from recovering reef fish assemblages to MMSY values and (*B*) global hunger and (*C*) hidden hunger indices. Each point is a jurisdiction classified as below B_{MMSY} with available index information (i.e., jurisdictions in panel *A* that are not highlighted in panels *B* and *C* did not have these indices available, *Materials and Methods*). Points are color-coded by the estimated yield gains based on jurisdiction-specific per-unit-area yield gains to MMSY extrapolated to the estimated reef area open to fishing (excluding the percentage of area estimated to be protected; *Materials and Methods*). Point size in *A*–*C* is scaled based on the % of the coastal population that could meet yearly fish intake recommendations from gained yields (i.e., additional people who would benefit from recovering fisheries as a percentage of the coastal population). See *SI Appendix*, Table S1 for actual numbers.

million reef fish servings per year, and foregoing the opportunity to meet fish intake recommendations for 107,914 to 670,473 additional people (Fig. 3*C*).

Recovery Targets and Timeframes. Sustainable yield gains and their benefits can only be realized if depleted fish stocks are allowed to recover, which in turn requires temporary reductions in catch to below current production levels, with larger reductions typically facilitating faster recovery. Consequently, we estimated the site-specific and jurisdiction-level standing biomass increases that would be required to obtain i) the biomass at which MMSY is expected under a Graham-Schaefer surplus production model (i.e., B_{MMSY}; Fig. 1), and ii) corresponding PGMY biomass levels (i.e., $B_{PGMY,low}$ and $B_{PGMY,high}$). We found that, to reach maximum production levels at B_{MMSY}, reef sites would have to double their standing biomass by a median of 32 t/km^2, but with substantial among-site variation depending on the state of depletion [from 0.4 to 192.9 t/km^2]. Lower biomass increases (6 [−45.2 – 102.2] t/km^2) would be required to reach PGMY levels below B_{MMSY} and larger biomass increases (62 [17.2 – 283.7] t/km^2) would be required to reach PGMY levels above B_{MMSY}—a target that entails less risk of imposing catches that overshoot true maximum sustainable yields (20) and is associated with increased biodiversity and ecosystem benefits (e.g., refs. 8 and 9). Jurisdictions like Oman, Kenya, or Mauritius, for example, are among those with less current surplus production and major potential benefits per unit area but also require substantial standing biomass recovery to achieve them: 132.9, 78.4, and 55.4 t/km^2 to reach B_{MMSY} and ~0.5 or 1.5 times that to reach $B_{PGMY,low}$ and $B_{PGMY,high}$, respectively (Fig. 4*C*).

The key impediment to rebuilding stocks toward target biomass values lies in the near to medium-term costs (e.g., loss of catch) to be borne by resource users. We estimated that, when fishing for recovery, reef sites can take from 6.4 to 49.7 y to reach maximum production biomass levels (*SI Appendix*, Fig. S3). More specifically, in the most stringent and fastest recovery scenario (10), where fishing moratoria are in place covering the entire reef fish metacommunity, locations estimated to be below B_{MMSY} would take a median of 6.4 y [0.03 – 33.1; dependent on site] to

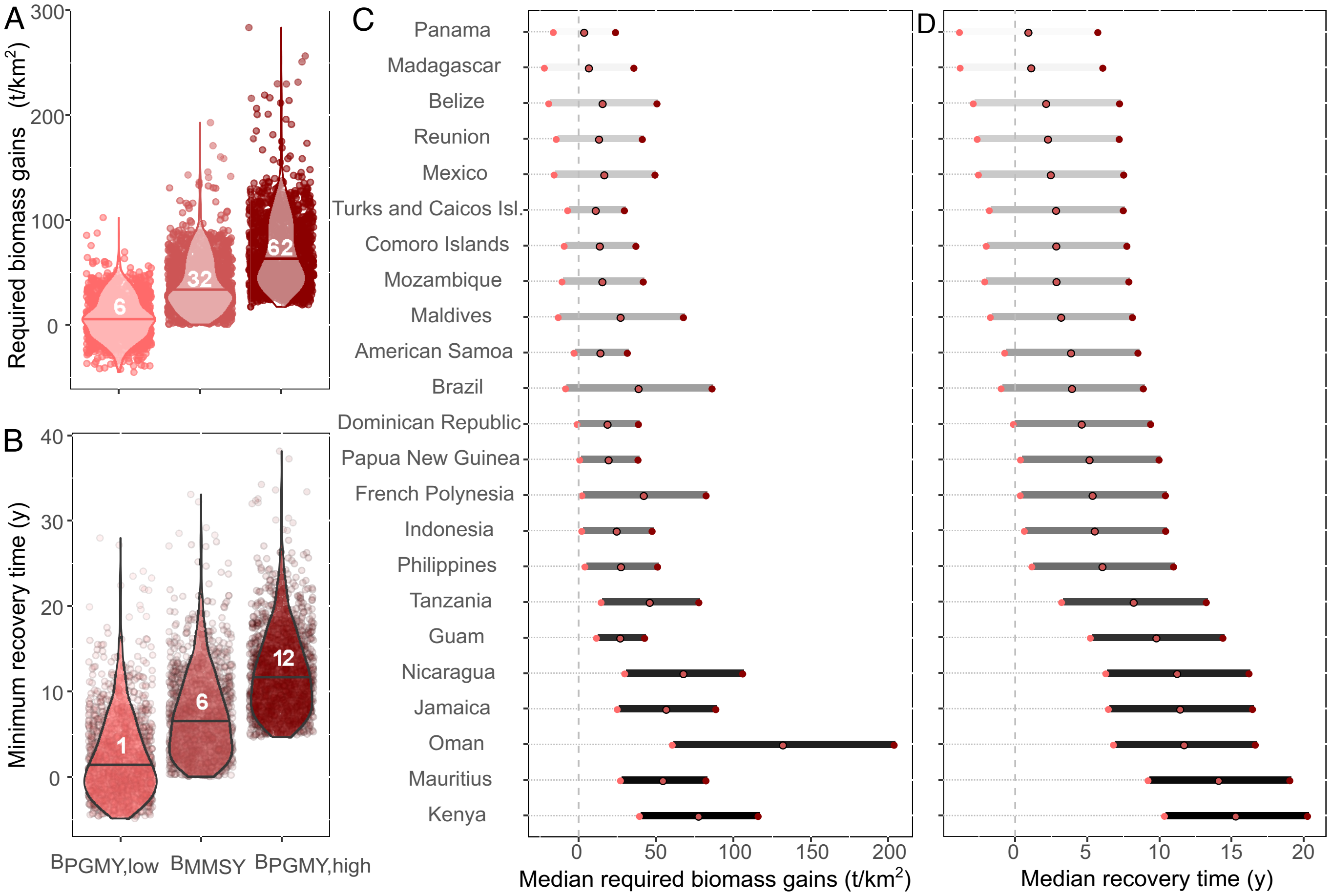

Fig. 4. Median required biomass recovery and timeframes. (*A*) Distributions of posterior median site-specific biomass increases required to achieve site-specific $B_{PGMY,low}$, B_{MMSY}, and $B_{PGMY,high}$ levels, respectively. (*B*) Distributions of site-specific recovery timeframes (posterior medians) under the most stringent moratorium scenario (i.e., minimum recovery time assuming the entire reef fish metacommunity is closed to fishing) to recover stocks below B_{MMSY} to their estimated site-specific $B_{PGMY,low}$, B_{MMSY}, and $B_{PGMY,high}$ levels, respectively. Numbers in (*A* and *B*) are median values for all sites. (*C*) Median required biomass gains per jurisdiction. (*D*) Estimated jurisdiction-specific recovery timeframes under the most stringent moratorium scenario (i.e., minimum recovery times). Horizontal bars in (*C* and *D*) represent the biomass gains or recovery times required to reach $B_{PGMY,low}$ (left limit) and $B_{PGMY,high}$ (right limit) given a jurisdiction's current sustainable surplus and standing stock biomass, whereas the middle point represents B_{MMSY} conditions. Colors in (*C* and *D*) are based on the biomass status (B/B_{MMSY}), with darker meaning worse (more below B_{MMSY}). See *SI Appendix*, Fig. S3 for recovery timeframes with harvesting.

recover toward assemblage-level maximum production (B_{MMSY}), 1.3 [−4.9 – 27.9] years to reach $B_{PGMY,low}$ values and 11.6 [4.7 – 38.2] years to reach the PGMY targets above B_{MMSY} (Fig. 4*B*). However, the estimated recovery timeframes increase as a larger proportion of the standing stock is harvested (e.g., *SI Appendix*, Fig. S3), with recovery times reaching up to 49.7 [3.7 – 106.7] years under the maximum harvesting regime that allows for recovery to B_{MMSY} (*SI Appendix*, Fig. S3). For heavily depleted jurisdictions like Oman, Mauritius, or Kenya, we estimate that recovering stocks to B_{MMSY} can take up to 70 y under the maximum harvesting regime that allows for recovery (*SI Appendix*, Fig. S3), with a minimum of 11 y in a scenario where the entire reef fish metacommunity is assumed to be within the area closed to fishing (Fig. 4*D*)–an approach that contrasts with the current practice of single reserve patches within interconnected fished seascapes that likely export biomass (e.g., refs. 8 and 34). Such moratoria are not socially desirable, feasible, or economically viable (11) for most reef fishery locations, especially where dependence on fisheries for food and nutrition security is high. Consequently, our fishing moratoria are not intended as a policy goal, but rather an estimation of minimum recovery timeframes to help inform alternative rebuilding actions.

Discussion

Management of wild fisheries to maximum sustainable production values is one of the main pathways to increase food supplies from the sea (16) and a direct way to tackle global micronutrient deficiencies (3, 14). We build upon past work assessing the status of coral reef fish (9) to quantify the potential sustainable yield and food provisioning benefits from coral reef fish recovery. We show that rebuilding coral reef fish stocks on coral reefs can significantly increase the number of sustainable fish servings produced per year and the number of people meeting fish intake recommendations, particularly for countries with high malnutrition. Thus, our study highlights the potential of fisheries recovery plans to contribute toward policies that aim to tackle pervasive food insecurity in tropical developing regions.

Challenges and Opportunities of Realizing Recovery. In contrast to many well-studied fish stocks where fisheries management strategies have been implemented to exploit stocks at sustainable levels (18, 19, 35), most coral reef multispecies fisheries lack information about the ecological, social, and economic costs and benefits of different recovery pathways and their trade-offs. Management measures such as networks of high-compliance no-take marine reserves (36–38) have the potential to allow reef assemblages to recover and realize their sustainable yield and food supply gains. Yet, the most-effective pathways to recovery will be context-specific to metapopulation structure, species composition, resource user preferences, and other features of the socioecological system (19, 38–40).

Ecologically, the lack of spatiotemporal data on recovery limits the extent to which we understand the functional form of the surplus production curve for whole assemblage biomass in different locations (9) and how this is impacted by environmental change, species composition [e.g., trophic turnover (41, 42)], or novel reef assemblages (43). For example, here we estimated recovery timeframes for the multispecies assemblage using community growth rates inferred from different reserve sites of different ages [i.e., a space-for-time substitution (9)] and assuming production peaks at 50% of unfished biomass values of a symmetric production curve. However, timeframes and biomass recovery targets to achieve maximum production could differ if the fish assemblage recovers at a different rate or the assemblage production function peaks at different biomass values.

Recovery and its timelines can be influenced by a range of factors, including trophodynamics (42), habitat impacts (26, 36), the state of depletion (35), and changing environmental contexts (26, 35, 44). For coral reef fish, in particular, how biomass recovers is not solely correlated with metrics related to fishing intensity (45), suggesting that cumulative impacts on the seascape will likely affect recovery (46). Furthermore, biomass on reefs is predicted to decrease with increased projected thermal stress (47, 48), but given that most fisheries are not effectively managed to maximize production, how such expected decreases will impact recovery to maximum production targets, or the targets themselves, is not straightforward (49). Rebuilding assemblages to levels that correspond to 50% of unfished biomass (e.g., B_{MMSY}) or higher (e.g., $B_{PGMY,high}$) is associated with stock and ecosystem benefits such as increased mean fish length and species richness, and enhanced ecosystem functioning (8, 9, 12), which are likely to feedback as long-term socioeconomic gains (50). Yet, a better understanding of recovery in terms of how community growth rates vary spatially and temporally (44) or how the species available for harvest vary at different recovery phases (41, 42) will help fine-tune these benefits and allow dynamic adjustment of targets and timelines under different contexts (51).

By rebuilding reef assemblages and retaining the increased catches locally, one can increase sustainable food quantities and, if distributed equitably, partially or fully address nutrient deficiencies using local fish stocks. Tropical marine fish are rich in calcium, iron, vitamin A, and zinc in comparison to other marine fish species (3), and reef fish, in particular, can be the main source of vitamin B_{12}, iron, niacin, and vitamin A in the diet of tropical coastal communities (5). However, food provisioning benefits will only contribute to food and nutrition security if sustainable reef fish production is accessible to those who need it most. For example, benefits of recovery may be jeopardized if locations have social, economic, or institutional barriers preventing equitable access to them (4, 52–54). While stock recovery is the first step toward enhanced sustainable food supplies, pausing or reducing fishing to promote recovery will impact people's reef fish supplies and will require alternate food sources from agriculture, mariculture, or offshore resources (14) that ensure people have access to adequate amounts of nutritious foods. Reef fish are an important source of food and nutrients for people who depend on reef-based food systems (5), so promoting a reduction in reef fish consumption to enhance recovery will require active food-system interventions that are able to overcome established cultural and supply links to reef fish. This is especially the case for locations currently overfishing their reef fish stocks beyond sustainable levels (9), where current yields being harvested surpass the estimated surplus production or MMSY, and where maximum sustainable production actually results in a decrease in the yearly number of humans meeting fish intake recommendations in comparison to unsustainable yields (e.g., Indonesia, Philippines, Mexico, Dominican Republic, Jamaica, Nicaragua, Oman, and Panama; *SI Appendix*, Fig. S4). Locations with large and fertile arable lands and diverse food sources might be compatible with temporary or well-placed sea closures, but many small island states without arable land may require ocean (16) or trade-based solutions besides gradual decreases in fishing effort to realize their potential reef-fish benefits.

Recovering coral reef fish populations to maximum production biomass also requires considerations of multiple time horizons that impact projected returns on investment (2). For instance, successfully realizing recovery requires active fisheries management, monitoring, and enforcement (10). This will generate economic gains in the long-term (55), however establishing fisheries reforms and monitoring their effectiveness will also require short to medium-term economic investments, and evaluating the trade-offs of implementing different management measures (56). Reductions in fishing, even if temporally, will require alternative innovative livelihood options such as tourism, agriculture, or mariculture (37, 57) and institutional systems that provide the right incentives (e.g., economic) to displaced resource users (58). Their success will be context-specific. For example, locations with high tourism potential might be compatible with fishing bans where tourism is not reliant on reef fisheries (59) and tourism benefits are distributed among those affected by recovery plans. For places with low tourism potential a transition to sustainable agriculture or mariculture might be more advantageous if conditions and infrastructure permit it (57). Economic incentives for individual operators to recover their fish assemblages might be possible for some high development countries. However, given the lack of strong institutions in most locations where reef fisheries operate (1), many reef locations may require international support systems that support recovery and their complex socioecological landscape (e.g., ref. 60).

Another social dimension to consider is employment and the social cost of employment displacement. For locations that have high percentage of fishers within the population, recovery might translate into excessive employment costs, whereas for others employment displacements might be relatively minimal and feasible with incentives. However, reefs and their resources are important to communities in a number of ways beyond food, income, and employment (61), supporting deep cultural values, identity, and well-being (62–64). Having healthy resources is likely to benefit fishers multiple ways, but cessation of fishing to promote recovery will bring context-specific costs that will have to be considered at relevant scales to successfully achieve recovery (65).

Conclusions

Two key, interdependent United Nations Sustainable Development Goals are to "conserve and sustainably use marine resources for sustainable development", as well as to "end hunger" (https://sustainabledevelopment.un.org; 66). Here, we have quantified the sustainable fish yields lost as a consequence of reef fish assemblages being below maximum production levels and the potential sustainable long-term food provisioning gains that can be achieved from their recovery. Yet to realize those potential benefits, reef fish assemblages need to be substantially recovered. Locations that most suffer from hunger and micronutrient deficiencies are within those with the greatest potential for sustainable yield gains, yet they are also where assemblages are most depleted, where more and longer recovery will be required, and thus where it is probably hardest to implement fisheries management plans to promote recovery. We provide benchmark recovery targets and timeframes against which to judge alternative recovery scenarios. The challenge now is finding effective pathways to recovery for each context even under climate change, ensuring people have access to nutritious foods. This will likely require effective reef fisheries management that builds upon increased local knowledge and participation, creation of alternative livelihood and food supplies, long-term planning, continuous monitoring, and financial and other support mechanisms that allow tropical communities to recover their lost potential yields.

Materials and Methods

Overview of Approach. Site-specific and jurisdiction-scale standardized reef fish biomass estimates and sustainable production curves were obtained for coral reef fish assemblages using the same fisheries-independent approach as a recent global reef fisheries assessment that calculated site-specific multispecies sustainable reference points for coral reef fish assemblages (*SI Appendix*, Table S2) based on environmental conditions (9). Using a total of 2,053 sampled reef sites (i.e., reef communities) worldwide, that study estimated site and jurisdiction-specific sustainable reference points for coral reef fish globally. The study used a joint modeling approach which combined several types of data. Remote uninhabited reefs and high compliance marine reserve sites of different ages (N = 150) informed estimates of unfished biomass for reef fish assemblages, how the unfished biomass varies with environmental context (i.e., coral cover, ocean productivity, sea surface temperature, and whether the reef is an atoll), and how reef fish populations grow in the absence of fishing toward unfished biomass (i.e., community biomass growth rate). The remaining 1,903 fished reefs also informed sampling parameters (e.g., related to census method, sampling area, habitat type, and depth of survey), and were used to assess the status of exploited fish assemblages at site and jurisdiction levels [i.e., expressing the biomass per unit area and/or annual catch per unit area relative to the corresponding estimated reference points aimed at maximizing sustainable production (9)]. Site level assessments for each of the 1,903 sites were performed assuming sampled reefs are representative of the conditions at the scale of metapopulation closure. Jurisdiction level assessments were performed for 49 individual jurisdictions. These analyses incorporated information from reef sites within the jurisdiction but were separately assessed at the jurisdiction level.

To estimate site and jurisdiction-level reference points, the study tested alternative model structures through leave-one-out cross-validation (i.e., null model excluding covariates vs. full model including covariates such as environmental variables) finding the full model was significantly preferred. The study also used different aggregate surplus production curves (e.g., Gompertz–Fox, Graham–Schaefer, and other versions of the Pella-Tomlinson model), all of which fit the recovery data relatively well (i.e., residual patterns among models looked identical and the expected log-predictive density differences from leave-out-one cross-validation model comparisons were similar). Here, we build upon that work and used site and jurisdiction-specific sustainable reference point estimates based on an aggregate Graham–Schaefer surplus growth model in which the whole multispecies assemblage is treated as a single population (67, 68), and a symmetric (logistic) population growth curve whose productivity (and thus sustainable yields) peaks at 50% of unfished biomass is assumed (69, 70). See the *SI Appendix*, *Supporting Text* file and ref. 9 for further details.

Yield Lost. As the aim of the present study was to quantify the expected sustainable yield lost from exploited assemblages below levels aimed at maximizing sustainable production, from the 1,903 exploited reef sites assessed (i.e., defined as openly fished and restricted), we only included 1,211 (64%) sites that, based on median estimates, had reef fish biomass values below 50% of their estimated unfished biomass (i.e., those where biomass was estimated to be below the biomass at which multispecies maximum sustainable yields or B_{MMSY} is expected to be achieved). Similarly, from all jurisdictions with biomass data available that were assessed (N = 49), in this study, we only included jurisdictions that had median biomass values (weighted by the reported percentage of territorial waters protected) also considered to be below B_{MMSY} (N = 23). These weighted biomass values per jurisdiction optimistically assume that the percentage of territorial waters that are protected from fishing are at unfished biomass values and exploited individual reef sites sampled within a jurisdiction are representative of jurisdiction-level conditions (9). If jurisdictions have lower overall biomass values than assumed by our weighting approach, recovery would translate into larger yield and food provisioning benefits, and longer recovery timeframes. In summary, the sample size and unit of analyses of the present study was 23 for jurisdiction-level observations and 1,211 for site-level observations.

For each location *i* (i.e., site or jurisdiction), we extracted i) the median estimated posterior biomass (estimated standing stock biomass standardized for methodological effects; $B_{current,i}$), and ii) associated reference points (i.e., B_{MMSYi}, $MMSY_i$, $B_{PGMY,lowi}$, $B_{PGMY,highi}$, $PGMY_i$, and the estimated surplus $SY_{current,i}$; *SI Appendix*, *Supporting Text*). Location-specific yield losses were calculated as the difference between the estimated site-specific MMSY ($MMSY_i$) or PGMY (i.e., $PGMY_i$), hereafter yield target $Y_{target,i}$, and the site-specific estimated surplus ($SY_{current,i;}$e.g., Fig. 1).

$$YL_i = Y_{target,i} - SY_{current,i}. \qquad [\mathbf{1}]$$

For each location (i), we also calculated proportions ($SY_{current,i}/Y_{target,i}$), equivalent to the food provision index in ref. 28 (*SI Appendix*, Fig. S1).

To estimate jurisdiction-level yearly potential yield gains (YG_i), jurisdiction per-unit-area sustainable yield losses (i.e., potential gains) were extrapolated to the reef area open to fishing (71, 72), assuming the proportion of territorial waters protected within a jurisdiction (73, 74) was equal to the proportion of reef area within a jurisdiction closed to fishing:

$$YG_i = YL_i * \left(R_i * \left(1 - p_{mpa,i}\right)\right), \qquad [\mathbf{2}]$$

where R_i is the estimated reef area for jurisdiction *i* and $p_{mpa,i}$ is the estimated proportion of waters protected in jurisdiction i. Note that this is not comparing current yields (i.e., how much is harvested) to potential maximum sustainable yields (i.e., the maximum that can be harvested sustainably based on surplus production models), but instead current estimated sustainable yields (i.e., how much could be harvested sustainably based on the estimated current biomass of a site or jurisdiction and surplus production models) to potential maximum sustainable yields. A jurisdiction or site can be subject to overfishing, and in such a case, actual yields can surpass sustainable yields and even maximum sustainable yields. See *SI Appendix*, Fig. S4 for a comparison to actual yields estimated over coral reefs (9) based on reconstructed reef fish landings.

Fish Servings and Fish Intake Recommendations. Per-unit-area yearly expected yield losses of reef fish (which are also the yearly per-unit-area potential yield gains from recovery) at both site and jurisdiction level (i.e., YL_i) were converted to 100 g fish servings by converting live weight estimated production to edible weights, conservatively assuming 50% of reef fish live weight produced (in metric tonnes) are edible (48, 75). We also calculated the number of people potentially meeting yearly recommended seafood intake from estimated yield gains by combining edible weights with per capita weekly seafood intake recommendations of 8 oz [i.e., 226.796 g (29)], assuming 52 wks in a year and that weekly intake recommendations are met throughout the year. These weekly intake seafood recommendations are based on long-chain omega 3 fatty acids concentrations in seafood and recommended intake to minimize the risk of cardiovascular disease (29). At a jurisdiction scale, additional servings and people meeting recommended intake values per year were also estimated using jurisdiction-level yearly potential yield gains that account for jurisdiction-specific coral reef areas potentially open to fishing (i.e., YG_i). Additional people meeting recommended fish intakes were then converted to percents of the coastal population using the estimated coastal population size within 30 km of the coastline [calculated from Grided Population of the World for 2019; (76, 77)].

Global Hunger and Hidden Hunger Indexes. Available jurisdiction-level global hunger and global hidden hunger in preschool children indices were obtained from Our World in Data [https://ourworldindata.org/; (30–33)]. The global hunger index was obtained for 2010 [consistent with most reef fish assemblage data (9)] and combined four indicators: undernourishment, child wasting, child stunting, and child mortality (30). The global hidden hunger in preschool (age <5 y) index was obtained for the period 1999 to 2009 and is calculated as the average of three deficiency prevalence estimates weighted equally: preschool children affected by stunting, anemia due to iron deficiency, and vitamin-A deficiency (32). Note that these indices were not calculated for some jurisdictions in the selected time periods so these were excluded for this part of the analyses (e.g., French Polynesia). For the hidden hunger index, scores between 0 and 19.9 are considered mild, 20 to 34.9 moderate, 35 to 44.9 severe, and 45 to 100 are considered alarmingly high (33). For the hunger index, scores between 0 and 10 are considered low, 10 to 20 moderate, 20 to 35 serious, 35 to 50 alarming, and >50 extremely alarming (31). To categorize indexes consistently, we renamed "alarmingly high" to alarming, "Serious" to severe, and "Low" to mild in the hidden-hunger index.

Required Biomass Gains and Recovery Timeframes. Location-specific required biomass gains to achieve B_{MMSY} or B_{PGMY}, hereafter $B_{target,i}$, were calculated for each location (i.e., site or jurisdiction) as the difference between the estimated biomass target ($B_{PGMY,low}$, $B_{MMSY,}$ or $B_{PGMY,high}$) and the estimated biomass ($B_{current,i}$; e.g., Fig. 1). Although $B_{PGMY,low}$ should not be considered a target (because it is below B_{MMSY} and imposes a higher risk of driving stocks to collapse), it may be useful from a food security perspective (e.g., minimum biomass required to get 80% of MMSY):

$$B_{gains,i} = B_{target,i} - B_{current,i}. \qquad [3]$$

Location-specific recovery timeframes (**Rt_i**) under a moratorium scenario (i.e., minimum time for recovery to $B_{PGMY,low,}$ B_{MMSY}, and $B_{PGMY,high}$ based solely on fishing assuming the entire reef fish metacommunity is protected) were calculated by combining the posterior community growth rates (*SI Appendix, Supporting Text*) with the location-specific standing stock biomass, unfished biomass, and biomass target (i.e., $B_{PGMY,low}$, $B_{MMSY,}$ or $B_{PGMY,high}$) estimates (78). Following the logistic growth curve of biomass through time and assuming zero exports, we calculated the recovery time (**Rt**) for a given location i (i.e., site or jurisdiction) as:

$$Rt_i = \frac{-\log\left(\frac{B_{current,i} * \left(\frac{B_{0,i}}{B_{target,i}} - 1\right)}{\left(B_{0,i} - B_{current,i}\right)}\right)}{r}, \qquad [4]$$

where r is the posterior biomass community growth rate, and $B_{current,i}$, $B_{0,i}$, and $B_{target,i}$ are the posterior location-specific standing reef fish assemblage biomass, unfished biomass, or target to be achieved (i.e., B_{MMSY} or B_{PGMY}), respectively. Details on how parameters such as the biomass community growth rate and unfished biomass were estimated, as well as their estimated values, can be found in the *SI Appendix, Supporting Text*. Note that recovery targets and timeframes could yield negative results for $B_{PGMY,low}$ if the estimated biomass for a site or jurisdiction was below B_{MMSY} but above $B_{PGMY,low}$.

We also estimated site-specific recovery times to B_{MMSY} using density-dependent harvesting scenarios (79), adding to the recovery time equation the harvest proportionality h (effort). We used a sequence of 10 harvesting values that varied from 0 (no fishing) to the sustainable exploitation rate that yields the multispecies surplus production (~0.097), representing the minimum and maximum recovery times when harvesting for recovery (i.e., below the estimated surplus production).

$$Rt\_harvest_i = \frac{\log\left(\left(\frac{B_{current,i} * ((B_{0,i} * h) - (B_{0,i} * r) + (B_{target,i} * r))}{B_{target,i} * ((B_{0,i} * h) - (B_{0,i} * r) + (B_{current,i} * r))}\right)\right)}{(h - r)}. \qquad [5]$$

Data, Materials, and Software Availability. Reef fish assemblage data from tropical coral reefs with associated attributes as well as code to replicate the analyses have been deposited in Zenodo (10.5281/zenodo.16276103) (80).

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