



# A global network of marine protected areas for food

Reniel B. Cabral<sup>a,b,c,1</sup>, Darcy Bradley<sup>a,b,c</sup>, Juan Mayorga<sup>a,b,c,d</sup>, Whitney Goodell<sup>d</sup>, Alan M. Friedlander<sup>d,e</sup>,  
Eric Sala<sup>d</sup>, Christopher Costello<sup>a,b,c</sup>, and Steven D. Gaines<sup>a,b,c</sup>

<sup>a</sup>Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93117; <sup>b</sup>Marine Science Institute, University of California, Santa Barbara, CA 93117; <sup>c</sup>Environmental Market Solutions Lab, University of California, Santa Barbara, CA 93117; <sup>d</sup>Pristine Seas, National Geographic Society, Washington, DC 20036; and <sup>e</sup>Hawai'i Institute of Marine Biology, University of Hawai'i, Kāne'ohe, HI 96744

Edited by Jane Lubchenco, Oregon State University, Corvallis, OR, and approved September 15, 2020 (received for review January 6, 2020)

**Marine protected areas (MPAs) are conservation tools that are increasingly implemented, with growing national commitments for MPA expansion. Perhaps the greatest challenge to expanded use of MPAs is the perceived trade-off between protection and food production. Since MPAs can benefit both conservation and fisheries in areas experiencing overfishing and since overfishing is common in many coastal nations, we ask how MPAs can be designed specifically to improve fisheries yields. We assembled distribution, life history, and fisheries exploitation data for 1,338 commercially important stocks to derive an optimized network of MPAs globally. We show that strategically expanding the existing global MPA network to protect an additional 5% of the ocean could increase future catch by at least 20% via spillover, generating 9 to 12 million metric tons more food annually than in a business-as-usual world with no additional protection. Our results demonstrate how food provisioning can be a central driver of MPA design, offering a pathway to strategically conserve ocean areas while securing seafood for the future.**

marine protected areas | marine reserves | food security | sustainable fisheries | spillover benefits

Overfishing continues to be a significant challenge in many parts of the ocean, particularly in tropical developing nations, threatening food security, livelihoods, human health, and biodiversity conservation (1–3). While some countries have taken bold actions to address overfishing (4), a large fraction of global fisheries remains poorly managed (1, 5–8).

Marine protected areas (MPAs) are conservation tools that are increasingly implemented, and many coastal nations have committed to placing a substantial fraction of their marine areas in MPAs (9, 10). Although primarily designed to protect and recover marine biodiversity, MPAs also have implications for fisheries. While it is unlikely that MPAs can significantly increase yield in well-managed fisheries, it is widely agreed that strategically designed MPAs can increase yield in overfished fisheries. In this sense, well-designed MPAs can actually benefit fisheries (11–16). Theory suggests that the more overfished a fishery is, the greater the potential fisheries benefits from MPAs are via spillover of larvae and adults (17–20). Likewise, the optimal MPA size should scale in proportion with the level of overfishing such that larger MPAs will confer greater benefits in more overfished fisheries (21–23). Therefore, in regions where fisheries management is lacking, highly protected MPAs may simultaneously improve both fisheries catch and conservation if designed well (14, 24). Here, we ask how empirically relevant and geographically extensive such a yield-motivated MPA network could be. To address this question, we derive an optimized MPA network designed explicitly to improve fisheries catch at a global scale.

We define food provisioning as the projected change in catch of finfish and marine invertebrates (hereafter, “fish”) resulting from implementation of an MPA network, or  $\Delta H = H_{MPA} - H_{BAU}$ , where  $H_{MPA}$  and  $H_{BAU}$  are the future global catches with and without additional MPAs. To evaluate the effect of protection on catch, we build a spatially explicit population model of 1,338 commercially exploited fish stocks for which catch data have been

reported and species distributions are available. Spillover is modeled as a function of a species’ relative mobility, growth, and carrying capacity at a resolution of  $\sim 55 \text{ km} \times 55 \text{ km}$ . MPA effects on total catch are highly dependent on the management regime in the unprotected, fished area (25). Under this model and commensurate with previous papers, MPAs tend to increase catch in overexploited fisheries and tend to decrease catch in well-managed fisheries and those that are underexploited relative to maximum sustainable yield (26). Because any given region often contains stocks with diverse life histories, some of which may be overexploited and some underexploited, MPAs can have a range of consequences for overall yield. We account for fishery management using the spatial delineations of stocks for which assessments exist (27, 28), and we model exploitation rate and catch responses to MPA siting as a function of the current exploitation rate and MPA size, assuming a full transfer of fishing effort from areas designated as MPAs to the remaining fishing areas (see *Materials and Methods*). We generate maps of potential food provisioning by calculating changes in global food provisioning at 1) local scales (i.e., per pixel) that ignore interactions between protected pixels and 2) a global scale that renders a globally optimized MPA network. These two outputs identify specific areas around the world where MPAs could enhance food production by fisheries in addition to their conservation benefits.

## Results and Discussion

The 1,338 stocks included in this analysis collectively have a total global carrying capacity ( $K$ ) of 680 million metric tons (MMT), which could generate a maximum sustainable yield (MSY) of 61.4 MMT/yr [compared to  $K = 980$  MMT (29) and  $\text{MSY} = 80$  to

### Significance

**Strategically siting marine protected areas (MPAs) in overfished fisheries can have important conservation and food provisioning benefits. We use distribution data for 1,338 commercially important fisheries stocks around the world to model how MPAs in different locations would affect catch. We show that strategically expanding the existing global MPA network by just 5% can improve future catch by at least 20%. Our work demonstrates that a global network of MPAs designed to improve fisheries productivity can substantially increase future catch, enabling synergistic conservation and food provisioning.**

Author contributions: R.B.C., D.B., J.M., W.G., A.M.F., E.S., C.C., and S.D.G. designed research; R.B.C., D.B., J.M., C.C., and S.D.G. performed research; R.B.C., D.B., W.G., and A.M.F. contributed new reagents/analytic tools; R.B.C., D.B., J.M., and C.C. analyzed data; R.B.C., D.B., J.M., W.G., A.M.F., E.S., C.C., and S.D.G. wrote the paper; and R.B.C. and J.M. wrote the code.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

This open access article is distributed under [Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 \(CC BY-NC-ND\)](https://creativecommons.org/licenses/by-nc-nd/4.0/).

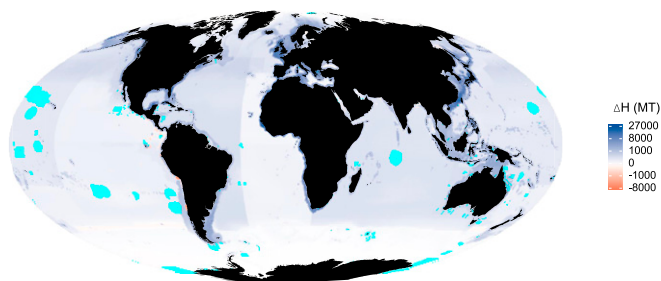
<sup>1</sup>To whom correspondence may be addressed. Email: rcabral@ucsb.edu.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2000174117/-DCSupplemental>.

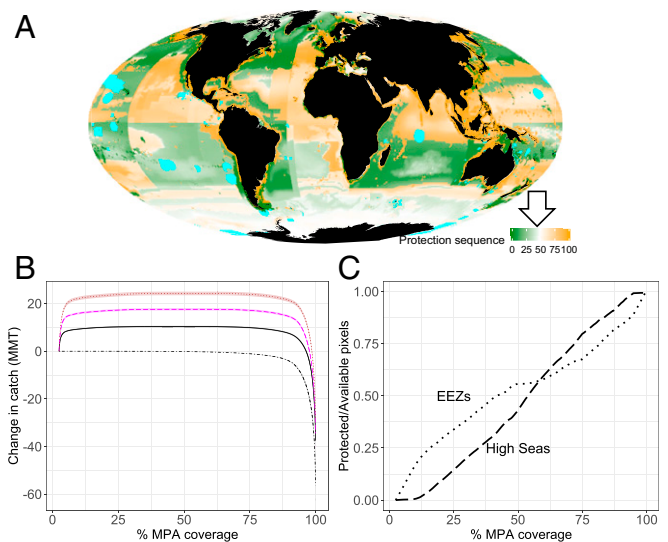
115 MMT/yr (1, 29–31) reported for all global stocks]. In a world without MPAs, our model forecasts a steady-state global fish catch of 41.8 MMT, or 68% of our working MSY. This is a consequence of overfishing on some stocks and underfishing (relative to MSY) on other stocks. Existing fully or highly protected MPAs (32), which cover 2.4% of the world's ocean (33), are projected to generate an additional 0.6 MMT of food per year via spillover. Hence, in our business-as-usual scenario (i.e., only existing MPAs and current fisheries management), total global fish catch is projected to be  $H_{BAU} = 42.4$  MMT/yr (69% of MSY). We then ask, How much more food could strategically sited additional MPAs generate?

The majority of ocean areas produce positive spillover benefits when MPA effects are evaluated for individual planning units (or per pixel) (Fig. 1), and pixels within the boundaries of exclusive economic zones (EEZs) produce an average of 12 times more biomass via spillover than the high seas (SI Appendix, Fig. S1). Forecasting the food provisioning potential of new MPA locations reveals important information about where individual MPAs could improve fisheries yield. However, scaling protection based on these values is suboptimal, because it ignores the nonlinear relationship between the area of a stock's range protected and the resulting change in catch. We therefore offer a solution that derives a global MPA network for food. We find that the marginal change in the food provisioning benefit ( $\Delta H$ ) becomes zero only after protecting the optimized 47% of the ocean (Fig. 2A). Abrupt changes in the spatial prioritization solution are due to the variation in stock status across different fisheries management areas. This globally coordinated MPA network highlights high-priority areas for protection within EEZs, the high seas, and several areas encompassing EEZ/high seas borders.

We find that the maximum amount of food provisioning benefits from an optimized global MPA network, under a conservative set of assumptions about future fishing effort and effort displacement, is 10.4 MMT. Although there are marginal benefits to fisheries catch that accrue up until a large fraction of the ocean is protected in MPAs, the bulk of these benefits accrue with a much smaller MPA network. We find that strategic protection of an additional 5% of the global ocean, beyond the current fully and highly protected MPAs, will generate 87% of the maximum possible spillover benefit from additional protection (i.e., 87% of 10.4 MMT) and produce  $9.0 \pm 0.3$  MMT/yr (mean  $\pm$  SD) more food—equivalent to 20 to 22% more catch—than a world without any additional protection (Fig. 2B, black solid line). The uncertainty bounds (SD) around our projections were derived by randomly drawing growth rate ( $r$ ) and  $K$  values per stock from uniformly distributed ranges of values. As a result, some stocks are assigned higher productivity values than average, while others are assigned lower productivity values than



**Fig. 1.** Individual-pixel change in catch. Colors indicate the spillover benefit or catch difference ( $\Delta H$ ) made by protecting each individual pixel (the value of each pixel is estimated independently). Areas in cyan represent current fully or highly protected marine protected areas. Blue = positive  $\Delta H$ , red = negative  $\Delta H$ , white = zero  $\Delta H$ . Each pixel is  $\sim 55$  km  $\times$  55 km.



**Fig. 2.** Global food provisioning potential. (A) The globally optimized MPA network for food. The color ramp indicates the relative importance of each pixel in an optimal, globally coordinated MPA network. Green indicates positive marginal change in  $\Delta H$ , and orange indicates negative marginal change in  $\Delta H$ , with white marking the transition from positive to negative marginal change in  $\Delta H$  (indicated by an arrow). It can also be interpreted as the optimal pixels to protect given a global MPA coverage target. The marginal change in catch as MPA coverage increases becomes negative after protecting 47% of the global ocean. Areas in cyan represent current fully or highly protected MPAs. (B) Change in catch ( $\Delta H$ ) as the proportion of the global ocean in MPAs increases following the optimal order of protection shown in A (black solid line); dashed and dotted lines display  $\Delta H$  trajectories for three additional fisheries exploitation scenarios (brown dotted line = collapse; magenta dashed line = BAU all stocks; black dot-dashed line = MSY; see SI Appendix, Figs. S2–S4 for the MPA network maps). The background shading represents SD from the mean generated from 100 model runs. (C) Protection within EEZs (dotted line) and high seas (dashed line) areas corresponding to the sequence of area protection in A. Each pixel is  $\sim 55$  km  $\times$  55 km.

average. The resulting variation in productivity at a stock level cancels out when we aggregate food provisioning benefits at the global level, as increased productivity of some stocks compensates for the reduced productivity of other stocks. If we assume that the unaccounted-for stocks, which have insufficient data to model directly, have the same characteristics as those included in the analysis (which is conservative, given that they tend to be disproportionately poorly managed), we can scale up our estimate by 30%, resulting in a future total catch of 67 MMT/year, with 12 MMT of food per year generated by additional protection. Assuming an average fish price of US\$1,625/MT (using the total first sale value of US\$130 billion for the 80 MMT global fish catch in 2016) (2), protecting this additional 5% of the ocean could generate US\$15 to US\$19 billion as spillover revenue annually, which significantly outweighs the US\$2 to US\$6 billion cost of managing the additional MPAs each year (34, 35).

The efficient placement of MPAs that cover both EEZ and high seas locations provides an opportunity to increase future global fisheries catch while closing more than 50% of the ocean to fishing (Fig. 2B and C). To put this in context, fishing occurs in between 4% [when calculated at a high resolution (36)] and 55% [at a lower resolution shared by our analysis (37)] of the global ocean. Taking Amoroso et al.'s (36) 4% number literally, over 90% of the ocean could be closed without constraining fishing. While our results suggest that you could close over 50% of the ocean at no cost to food production, most of the food benefits can likely be captured by strategically protecting a small

fraction of the global ocean. At the same time, we show that large spatial closures are unlikely to result in long-term fisheries losses, suggesting that substantial global MPA expansion is possible without compromising fisheries productivity.

In our projections, we adopt the business-as-usual (BAU “conservation concern”) scenario from Costello et al. (1), where assessed stocks retain current exploitation rates, unassessed conservation concern stocks (i.e., currently overfished stocks or those currently experiencing overfishing) are subject to open-access fishing dynamics, and unassessed nonconservation concern stocks have their exploitation rates set to maintain current biomass. Stocks in the first category tend to be managed around MSY, stocks in the second category are overfished relative to MSY, and stocks in the third category are underfished relative to MSY. Thus, the resulting optimal MPA network primarily benefits unassessed and often poorly managed fisheries, comprising 66% of our total MSY. To evaluate the impacts of these assumptions on future fish catch, we derive MPA networks given three other possible future fishery scenarios (results shown in Fig. 2B): 1) MSY, where all stocks are optimally managed at MSY; 2) BAU all stocks (1), where assessed stocks retain current exploitation rates and all unassessed stocks experience open-access fishing dynamics; and 3) collapse, where assessed stocks retain current exploitation rates and unassessed stocks have exploitation rates that will lead to their collapse [i.e., biomass set at 10% of its unfished level (6)]. In a world where all stocks are optimally managed at MSY, we find that MPAs would reduce global catch (Fig. 2B, black dot-dashed line)—this is consistent with most of the literature and highlights the importance of good fisheries management. If all unassessed stocks were to become overfished in the future, we estimate that the maximum potential catch benefits from MPAs increases by 70% relative to BAU conservation concern (Fig. 2B, magenta dashed line). Finally, if all unassessed fish stocks were to collapse in the future, then the maximum potential catch benefits from MPAs would increase by 134% relative to BAU conservation concern (Fig. 2B, brown dotted line). While many fisheries in developed nations are becoming increasingly better managed, the future of fisheries in the developing tropics—particularly for small-scale fisheries on which millions of people depend for food and livelihoods—remains highly uncertain (7, 8). Generally, the spillover benefit from the optimal MPA network decreases as global fisheries management improves (Fig. 3).

The spillover benefits of currently protected MPAs should be interpreted as future catches in the presence of those MPAs relative to a counterfactual where current MPAs are absent. While most of the large MPAs that are part of the 2.4% of the global ocean currently in fully or highly protected MPAs have been placed in remote locations, the possible expansion of global fishing effort could increase fishing in these isolated areas (38). Furthermore, while unaccounted for in our current model, large and remote MPAs may protect ecologically important areas that are vital for certain life history stages of even highly migratory species, which may result in fisheries benefits for target stocks. For example, tuna spawn inside the Phoenix Island Protected Area (39), and there is an increasing body of evidence demonstrating potential fisheries benefits from MPAs for pelagic populations in the Chagos Archipelago (40) and the Galápagos Marine Reserve (41).

We estimated  $K$  using MSY calculated from both the Food and Agriculture Organization of the United Nations (FAO) fish landings data and the RAM Legacy Stock Assessment database (1, 28, 42). Pauly and Zeller’s catch reconstruction (43) suggests that catches unreported to FAO constitute an average of 53% of the reported catch, mostly due to discarded bycatch from industrial fishing. FAO fish landings data likely also underreport catches from small-scale and subsistence fisheries, mainly in developing nations (43, 44). Stocks with a high volume of unreported catch tend to be poorly managed in general, and thus,

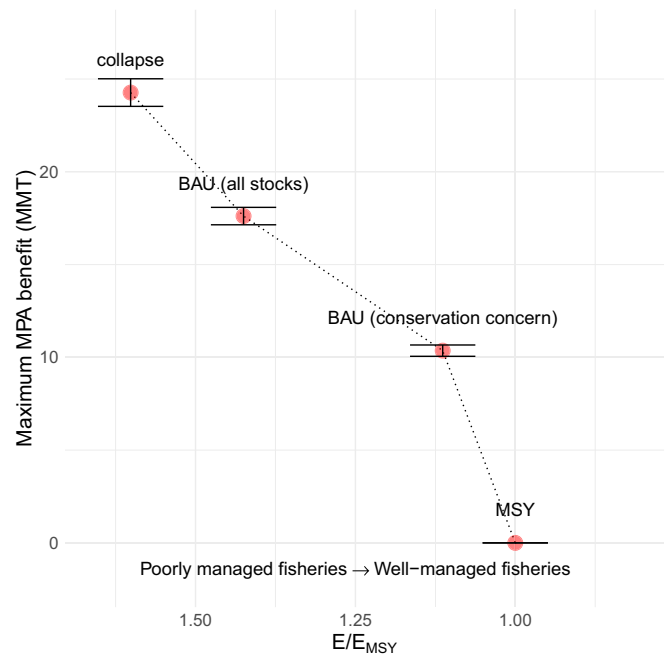


Fig. 3. Maximum global catch benefits from MPAs under alternative future fisheries management scenarios. MPA benefit is highest if mismanagement of fisheries continues. Future improvements in conventional fisheries management reduce the potential catch benefit from MPAs. The values on the horizontal axis that represent management pertain to the MSY-weighted mean value of the ratio of exploitation rate over exploitation rate at MSY, with values greater than 1 indicating overfishing. Error bars represent SD from the mean.

our estimate of the potential benefits of MPAs is likely conservative.

Other unaccounted-for factors that contribute to uncertainties in  $K$  include species interactions, food availability regulating growth, and future environmental impacts affecting habitat quality. While our computed  $K$  per stock implicitly accounts for current environmental impacts as it is based on actual catch data and stock assessments (1), it does not account for future impacts such as habitat destruction or climate change that could reduce or increase  $K$ , nor does it account for improvements in habitat that could increase  $K$  (45, 46). Furthermore, while we implicitly accounted for some of the constraints that bound the magnitude and spatial distribution of  $K$  by using actual catch data and modeled native species ranges to create spatial layers of  $K$  per stock, recovery of some species from protection may induce strong competitive or synergistic interactions with other species and may limit or enhance food availability for other species.

Beverton and Holt (23) and Hastings and Botsford (24) demonstrated theoretically that MPAs can have the same effect as conventional fisheries management that improves fisheries productivity by regulating fishing effort and that MPAs can improve catch in overfished fisheries through larval and adult spillover. However, the effect of MPAs for multiple overlapping species with different biological characteristics and geographic ranges remains unclear. While the placement of MPAs in overfished areas can improve food provisioning globally, other factors can affect food provisioning outcomes, such as the scale of the fishery and relative MPA placement (i.e., only a fraction of a species’ range should be protected, given that closing the entire geographic range of the species would result in zero catch). For fisheries that are expected to benefit from MPAs (i.e., overfished fisheries), we find that the median size of the protected area needed to optimize spillover benefits is 22.4% of the stock range

(mean = 23.0%, see *SI Appendix, Fig. S5*); less protection does not fully blunt the effects of overfishing, and more protection confers biomass benefits but leaves too small an area for fishing at current rates.

Our model of biomass export from MPAs to fished areas by adult spillover and larval subsidy is simple and deterministic. We assume a general larval pool model (24, 47) that ignores directional movement of larvae (48–54) but accounts for density-dependent movement of adults (19, 25, 55). Information about local habitat quality and availability—which affect larval settlement, recruitment, and adult movement directionality—is not available globally and therefore was not included in our analyses. We do not model larval contributions directly and instead assume that the population growth rate includes the effect of larval subsidy. All larval production (from MPAs and fished areas) is homogenized across the geographic range of the stock, and any biomass buildup in MPAs contributes uniformly to population growth in the fished area. We recognize that modeling larval export more explicitly and realistically could decrease the amount of larvae that end up in fished areas relative to the common larval pool model we use because of the Gaussian shape of the dispersal kernel (assuming that the dispersal kernel is centered inside the MPA) (48). Conversely, modeling larval export more explicitly could enhance the buildup of biomass inside MPAs and skew age structures to larger and older individuals, thus boosting both adult biomass spillover and larval export to fished areas (56). Tactical models of individual MPA design should attend to these spatial and dynamic idiosyncrasies.

While empirical studies have demonstrated spillover benefits for some species (13, 15, 16, 21, 50, 57–59) and provide support for fisheries benefits of both small (57–59) and large (39–41) MPAs, the majority of the species considered in our analyses lack empirical support (one way or the other) for spillover effects. Furthermore, while we rely only on MPA size as an important aspect of reserve design (25, 60–62), we recognize that other factors, such as MPA geometry, spacing, age, and habitat quality, also affect spillover (14, 63–65). Finally, we assume full compliance with MPA regulations. Nonetheless, our predictions can inform future studies looking into species-specific and area-specific spillover benefits from MPAs.

The size of our planning unit (~55 km × 55 km) is large compared to the median size of current MPAs of 1.6 km<sup>2</sup> (mean of 1,534 km<sup>2</sup>) (66). We recognize that few MPAs of this size are likely to be established in nearshore waters, where a number of ocean uses that support local economies exist. This is especially true in communities dominated by small-scale and subsistence fisheries, where establishing large MPAs in nearshore areas may have negative socioeconomic impacts on local livelihoods (e.g., fishers need to fish farther from their communities). However, our framework can serve as guidance for potential areas where protection could generate more food for the future, while a more strategic and surgical placement of smaller MPAs may be necessary in nearshore areas to avoid or reduce trade-offs with other ocean uses. Optimizing MPA network design within the high-priority areas identified by our model can improve the net benefit derived from marine protection, likely with a smaller total protected area required to maximize benefits to surrounding fisheries.

For model tractability and application at a global scale, we report changes to catch following protection as steady-state forecasted values that are not attached to specific time frames but note that fishery closures typically result in short-term reductions in catch (67–69) before achieving these benefits. Previous analyses suggest that stocks will take an average of 10 y to recover to their premanagement intervention state following conventional management reform (1) and MPA implementation (67, 68). It will take 35 y on average to recover a stock to a biologically healthy level (i.e., the ratio of in-water fish biomass to

the biomass that would provide maximum sustainable yield, or  $B/B_{MSY}$ , is greater than 0.8) when implementing fisheries management reform (1) or to 90% of unfished biomass inside fully protected MPAs (45). The long timescale necessary to recover fish stocks and capture fisheries benefits when implementing fisheries management reform and/or MPAs often creates political, social, and economic challenges. These challenges make it difficult for many communities, particularly those with a high dependence on fishing for livelihoods and nutrition, to implement conservation and fisheries management actions. Similar delayed benefits, however, also occur with other forms of management reform. While we limit the scope of our analysis to costs and benefits following protection in terms of fisheries catch, there are numerous other benefits of protection that we do not account for, such as tourism benefits from improved ecosystem health for coastal areas and biodiversity conservation that could mitigate short-term economic impacts following protection (70).

Our study suggests that when overfishing persists, MPAs can serve as a substitute for poor fishery management, thereby increasing yields even in the absence of fisheries reform (Fig. 3). Thus, the current interest expressed by many nations in expanding their MPAs provides an opportunity to not only protect biodiversity but also to improve fisheries productivity. This could help global efforts to rebuild and manage fish stocks, especially in areas where conventional fisheries management is challenging to implement but MPAs are feasible. Well-designed MPAs can provide additional benefits such as 1) buffering fisheries against uncertainty (24); 2) boosting larval production by protecting old and large individuals within the MPA borders, thus boosting biomass production in fished areas (56) and facilitating genetic flow (71); 3) reducing bycatch (72); and 4) protecting spawning grounds, nursery areas, and other biologically sensitive habitats that support fisheries productivity (73, 74).

Our analyses suggest large potential food benefits from strategic MPA implementation. Realizing the full spillover benefit would require that 1) MPAs have strong compliance to allow fish biomass buildup inside them (22) and 2) adequate habitat is available in fishing areas for larvae to settle and recruit and adults to move (14, 75). Achieving the full suite of benefits reported here will require global coordination, but significant benefits can also arise from national or regional efforts. Where rapid and lasting fisheries reform is challenging—often in places where food security is a major concern—MPAs can substantially boost fisheries productivity while simultaneously providing other ecosystem and conservation benefits.

## Materials and Methods

We define food provisioning as the ability of marine ecosystems to provide food for the future. We use changes in total catch due to protection as our food provisioning metric. This implies that the effect of a network of MPAs on fish catch is evaluated at the stock level, and the sum of the resulting changes in catch per stock represents the food provisioning potential of a network of MPAs.

In equation form, the change in total fish catch due to an MPA network ( $w$ ) is given by

$$\Delta H_w = H_{MPA} - H_{BAU}, \quad [1]$$

where  $H_{MPA} = \sum H_{w,i}$  and  $H_{BAU} = \sum H_{bau,i}$  are the total global catches with and without implementing additional MPAs, respectively.  $H_{w,i}$  and  $H_{bau,i}$  represent catches for stock  $i$ .

We model the effect of MPAs on 1,338 stocks as a function of species growth rate ( $r$ ), species mobility ( $m$ ), carrying capacity ( $K$ ), MPA size ( $R$ ), and fisheries management that drives future exploitation rates ( $E$ ) (76). The spatial distribution of  $K$  for each stock is derived by combining the maximum sustainable yield estimate per stock reported in Costello et al. (1) and growth rate per species from Thorson (77), FishBase (78), and SeaLifeBase (79) to calculate the total  $K$ . We distribute the total  $K$  in proportion to the relative probability of the species presence within its modeled native range (80).

The final equation for the food provisioning potential of a network of MPAs ( $w$ ) is

$$\Delta H_w = \left[ \sum_i E_{w,i} \left( \frac{m_i K_i (1 - R_{w,i})}{E_{w,i} R_{w,i} + m_i} \right) \left( 1 - \frac{E_{w,i} (1 - R_{w,i}) m_i}{(E_{w,i} R_{w,i} + m_i) r_i} \right) \right] - \left[ \sum_i E_{bau,i} \left( \frac{m_i K_i (1 - R_{bau,i})}{E_{bau,i} R_{bau,i} + m_i} \right) \left( 1 - \frac{E_{bau,i} (1 - R_{bau,i}) m_i}{(E_{bau,i} R_{bau,i} + m_i) r_i} \right) \right], \quad [2]$$

where  $R_{bau}$  represents the fraction of stock  $K$  in current fully or highly protected MPAs (33) (see *SI Appendix* for full details).

Our model requires stock-level estimates of future exploitation rates under the business-as-usual scenario ( $E_{bau,i}$ ) and with an MPA network ( $E_{w,i}$ ). To do this, we first estimate future fisheries with a no-MPA scenario. We adopt the business-as-usual (BAU conservation concern) future fisheries scenario of Costello et al. (1), which assumes that assessed stocks retain their current exploitation rates, unassessed conservation concern stocks (i.e., currently overfished stocks or those experiencing overfishing) are subject to open-access fishing dynamics, and unassessed nonconservation concern stocks have their exploitation rates set to maintain current biomass. Assessed stocks are assumed to retain their current exploitation rates because they are neither poorly managed nor necessarily optimally managed (1, 81). We use the RAM Legacy Stock Assessment database (28) to derive the most recent exploitation rates of assessed stocks. Applying these conditions gives us stock-level exploitation rates in the absence of MPAs ( $E_{base,i}$ ).

Establishing MPAs displaces fishing effort from the identified protected areas to the remaining fishing areas. We assume a full transfer of fishing effort, resulting in an increase in exploitation rate in the remaining fishing areas ( $E_{out,i}$ ) as MPA size ( $R_i$ ) increases:

$$E_{out,i} = 1 - (1 - E_{base,i})^{1/(1-R_i)}. \quad [3]$$

We use Eq. 3 to evaluate both changes in future exploitation rates given the current 2.4% of the global ocean in MPAs ( $E_{bau,i}$ ) and given an expanded network of MPAs ( $w$ ), i.e.,  $E_{w,i} = 1 - (1 - E_{base,i})^{1/(1-R_{w,i})}$  (*SI Appendix, Fig. S6*). This equation comes directly from the fishing effort redistribution model used by Beverton and Holt (23), Guénette and Pitcher (82), Apostolaki et al. (83), Walters et al. (84), and Hopf et al. (69), among others, which assumes that fishing mortality in fishing areas increases proportionally with MPA size, i.e.,  $F_{out} = \frac{F_{base}}{(1-R)}$  and substitutes the relationship between exploitation

rate and fishing mortality, i.e.,  $1 - E = e^{-F}$ . Under this effort redistribution assumption, the exploitation rate experienced by biomass in fishing areas increases as the size of the MPA network increases (*SI Appendix, Fig. S6*). A huge fraction of global fish catch (96%) is caught within EEZs (85), indicating that a majority of the commercially important fish stocks reside within EEZs. The slow increase in fishing effort when 10 to 80% of the global ocean is in protected areas indicates that high seas areas and areas within EEZs with low species overlap are being selected for protection (Fig. 2C). We limit the maximum value of  $E_{out,i}$  to 1 to prevent the case where catch at a given time exceeds the available biomass in fishing area.

We explore three alternative scenarios for future fisheries that change  $E_{base,i}$ : 1) MSY, where all fisheries are managed at MSY (i.e.,  $E_{base,i} = 0.5r_i$ ); 2) BAU all stocks (1), which assumes that assessed stocks retain their current exploitation rates in the future and that unassessed stocks experience open-access fishing dynamics; and 3) a collapse scenario, where assessed stocks retain their current exploitation rate in the future and unassessed stocks collapse. Here, we use Worm et al.'s (6) definition of collapse, i.e., biomass equals 10% of its unfished level. For the collapse scenario, we derive the exploitation rate by using *SI Appendix, Eq. S6* with  $B = 0.1K$ , i.e.,  $E_{base,i} = 0.9r_i$ . For cases where the current exploitation rate is sufficiently high to drive a stock to extinction, we cap the exploitation rate to a level that would drive the biomass to 10% of its unfished level.

For unassessed fisheries under open-access dynamics in Costello et al.'s (1) BAU scenarios, we set the exploitation rate to a level that will drive the equilibrium biomass depletion (i.e.,  $B/K$ ) to equal the 2050 values reported in Costello et al. (1) (*SI Appendix, Fig. S7*).

**Data Availability.** All study data are included in the article and *SI Appendix*. The code and data used in this paper can be accessed in Github (<https://github.com/rencabral/FoodProvision2019>) and have been deposited in the Dryad Digital Repository (DOI: [10.25349/D9C32R](https://doi.org/10.25349/D9C32R)).

**ACKNOWLEDGMENTS.** We thank the AquaMaps Project for data provisioning. C. Free for providing some of the parameter values used in this work, J. Palacios-Abrantes and W. Cheung for discussions about an early version of this work, Google for the computational resources for Cloud Computing, K. Siegel and E. O'Reilly for their comments, and two anonymous reviewers for their comments and suggestions that improved this work. This work received funding from the National Geographic Society.

1. C. Costello et al., Global fishery prospects under contrasting management regimes. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 5125–5129 (2016).
2. Food and Agriculture Organization of the United Nations, *The State of World Fisheries and Aquaculture: Meeting the Sustainable Development Goals*, (Food and Agriculture Organization of the United Nations, Rome, 2018).
3. C. C. Hicks et al., Harnessing global fisheries to tackle micronutrient deficiencies. *Nature* **574**, 95–98 (2019).
4. R. Hilborn et al., Effective fisheries management instrumental in improving fish stock status. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 2218–2224 (2020).
5. C. Mora et al., Management effectiveness of the world's marine fisheries. *PLoS Biol.* **7**, e1000131 (2009).
6. B. Worm et al., Rebuilding global fisheries. *Science* **325**, 578–585 (2009).
7. C. Costello et al., Status and solutions for the world's unassessed fisheries. *Science* **338**, 517–520 (2012).
8. Y. Ye, N. L. Gutierrez, Ending fishery overexploitation by expanding from local successes to globalized solutions. *Nat. Ecol. Evol.* **1**, 1–5 (2017).
9. K. Grorud-Colvert et al., High-profile international commitments for ocean protection: Empty promises or meaningful progress? *Mar. Policy* **105**, 52–66 (2019).
10. Conservation on Biological Diversity, Strategic plan for biodiversity 2011–2020: Provisional technical rationale, possible indicators and suggested milestones for the Aichi Biodiversity Targets. <http://www.cbd.int/doc/meetings/cop/cop-10/official/cop-10-27-add1-en.pdf>. Accessed 2 October 2020.
11. C. M. Roberts, J. A. Bohnsack, F. Gell, J. P. Hawkins, R. Goodridge, Effects of marine reserves on adjacent fisheries. *Science* **294**, 1920–1923 (2001).
12. G. R. Russ, A. C. Alcala, A. P. Maypa, H. P. Calumpong, A. T. White, Marine reserve benefits local fisheries. *Ecol. Appl.* **14**, 597–606 (2004).
13. R. Goñi, R. Hilborn, D. Diaz, S. Mallol, S. Adlerstein, Net contribution of spillover from a marine reserve to fishery catches. *Mar. Ecol. Prog. Ser.* **400**, 233–243 (2010).
14. S. D. Gaines, C. White, M. H. Carr, S. R. Palumbi, Designing marine reserve networks for both conservation and fisheries management. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 18286–18293 (2010).
15. S. E. Kerwath, H. Winker, A. Götz, C. G. Attwood, Marine protected area improves yield without disadvantaging fishers. *Nat. Commun.* **4**, 2347 (2013).
16. E. Moland et al., Lobster and cod benefit from small-scale northern marine protected areas: Inference from an empirical before-after control-impact study. *Proc. Biol. Sci.* **280**, 20122679 (2013).
17. D. S. Holland, R. J. Brazeel, Marine reserves for fisheries management. *Mar. Resour. Econ.* **11**, 157–171 (1996).
18. S. R. Palumbi, Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. *Annu. Rev. Environ. Resour.* **29**, 31–68 (2004).
19. C. D. Buxton, K. Hartmann, R. Kearney, C. Gardner, When is spillover from marine reserves likely to benefit fisheries? *PLoS One* **9**, e107032 (2014).
20. J. F. Quinn, S. R. Wing, L. W. Botsford, Harvest refugia in marine invertebrate fisheries: Models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *Integr. Comp. Biol.* **33**, 537–550 (1993).
21. F. Vandepierre et al., Effects of no-take area size and age of marine protected areas on fisheries yields: A meta-analytical approach. *Fish. Fish.* **12**, 412–426 (2011).
22. G. J. Edgar et al., Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216–220 (2014).
23. R. J. H. Beverton, S. J. Holt, *On the Dynamics of Exploited Fish Populations*, (Springer, Dordrecht, Netherlands, 1957).
24. A. Hastings, L. W. Botsford, Equivalence in yield from marine reserves and traditional fisheries management. *Science* **284**, 1537–1538 (1999).
25. R. B. Cabral et al., Designing MPAs for food security in open-access fisheries. *Sci. Rep.* **9**, 8033 (2019).
26. R. Hilborn, F. Micheli, G. A. De Leo, Integrating marine protected areas with catch regulation. *Can. J. Fish. Aquat. Sci.* **63**, 642–649 (2006).
27. C. M. Free et al., Impacts of historical warming on marine fisheries production. *Science* **363**, 979–983 (2019).
28. RAM Legacy Stock Assessment Database, version 4.44. <http://www.ramlegacy.org>. Accessed 22 September 2019.
29. World Bank, *The Sunken Billions Revisited: Progress and Challenges in Global Marine Fisheries*, (Environment and Development, World Bank, Washington, DC, 2017).
30. U. R. Sumaila et al., Benefits of rebuilding global marine fisheries outweigh costs. *PLoS One* **7**, e40542 (2012).
31. D. Alverson, K. Dunlop, *Status of World Marine Fish Stocks*, (Fisheries Research Institute, School of Fisheries, University of Washington, Seattle, 1998).
32. Oregon State University, IUCN World Commission on Protected Areas, Marine Conservation Institute, National Geographic Society, and UNEP World Conservation Monitoring Centre, An introduction to the MPA guide. <http://www.protectedplanet.net/cmpa-guide>. Accessed 22 October 2019.
33. Marine Conservation Institute, Atlas of marine protection. <https://mpatlas.org>. Accessed 22 October 2019.

34. A. Balmford, P. Gravestock, N. Hockley, C. J. McClean, C. M. Roberts, The worldwide costs of marine protected areas. *Proc. Natl. Acad. Sci. U.S.A.* **101**, 9694–9697 (2004).
35. S. Cullis-Suzuki, D. Pauly, Marine protected area costs as “beneficial” fisheries subsidies: A global evaluation. *Coast. Manage.* **38**, 113–121 (2010).
36. R. O. Amoroso, A. M. Parma, C. R. Pitcher, R. A. McConnaughey, S. Jennings, Comment on “Tracking the global footprint of fisheries”. *Science* **361**, eaat6713 (2018).
37. D. A. Kroodsmas *et al.*, Tracking the global footprint of fisheries. *Science* **359**, 904–908 (2018).
38. R. A. Watson, A. Tidd, Mapping nearly a century and a half of global marine fishing: 1869–2015. *Mar. Policy* **93**, 171–177 (2018).
39. C. M. Hernández *et al.*, Evidence and patterns of tuna spawning inside a large no-take marine protected area. *Sci. Rep.* **9**, 10772 (2019).
40. H. J. Koldewey, D. Curnick, S. Harding, L. R. Harrison, M. Gollock, Potential benefits to fisheries and biodiversity of the Chagos Archipelago/British Indian Ocean Territory as a no-take marine reserve. *Mar. Pollut. Bull.* **60**, 1906–1915 (2010).
41. K. Boerder, A. Bryndum-Buchholz, B. Worm, Interactions of tuna fisheries with the Galápagos marine reserve. *Mar. Ecol. Prog. Ser.* **585**, 1–15 (2017).
42. Food and Agriculture Organization of the United Nations (FAO), FAO Global Capture Production database. <http://www.fao.org/fishery/statistics/global-capture-production/en>. Accessed 18 April 2020.
43. D. Pauly, D. Zeller, Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat. Commun.* **7**, 10244 (2016).
44. D. Zeller, S. Harper, K. Zyllich, D. Pauly, Synthesis of underreported small-scale fisheries catch in Pacific island waters. *Coral Reefs* **34**, 25–39 (2015).
45. M. A. MacNeil *et al.*, Recovery potential of the world’s coral reef fishes. *Nature* **520**, 341–344 (2015).
46. T. R. McClanahan *et al.*, Global baselines and benchmarks for fish biomass: Comparing remote reefs and fisheries closures. *Mar. Ecol. Prog. Ser.* **612**, 167–192 (2019).
47. D. R. Hart, When do marine reserves increase fishery yield? *Can. J. Fish. Aquat. Sci.* **63**, 1445–1449 (2006).
48. R. A. Pelc, R. R. Warner, S. D. Gaines, C. B. Paris, Detecting larval export from marine reserves. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 18266–18271 (2010).
49. M. R. Christie *et al.*, Larval connectivity in an effective network of marine protected areas. *PLoS One* **5**, e15715 (2010).
50. H. B. Harrison *et al.*, Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr. Biol.* **22**, 1023–1028 (2012).
51. R. A. Abesamis *et al.*, Reef-fish larval dispersal patterns validate no-take marine reserve network connectivity that links human communities. *Coral Reefs* **36**, 791–801 (2017).
52. A. Le Port *et al.*, Temperate marine protected area provides recruitment subsidies to local fisheries. *Proc. Biol. Sci.* **284**, 20171300 (2017).
53. D. S. Baetscher *et al.*, Dispersal of a nearshore marine fish connects marine reserves and adjacent fished areas along an open coast. *Mol. Ecol.* **28**, 1611–1623 (2019).
54. D. H. Williamson *et al.*, Large-scale, multidirectional larval connectivity among coral reef fish populations in the Great Barrier Reef Marine Park. *Mol. Ecol.* **25**, 6039–6054 (2016).
55. B. S. Halpern, S. E. Lester, J. B. Kellner, Spillover from marine reserves and the replenishment of fished stocks. *Environ. Conserv.* **36**, 268–276 (2009).
56. D. J. Marshall, S. Gaines, R. Warner, D. R. Barneche, M. Bode, Underestimating the benefits of marine protected areas for the replenishment of fished populations. *Front. Ecol. Evol.* **17**, 407–413 (2019).
57. A. P. Maypa, G. R. Russ, A. C. Alcala, H. P. Calumpong, Long-term trends in yield and catch rates of the coral reef fishery at Apo Island, central Philippines. *Mar. Freshw. Res.* **53**, 207–213 (2002).
58. R. A. Abesamis, G. R. Russ, Density-dependent spillover from a marine reserve: Long-term evidence. *Ecol. Appl.* **15**, 1798–1812 (2005).
59. R. A. Abesamis, A. C. Alcala, G. R. Russ, How much does the fishery at Apo Island benefit from spillover of adult fish from the adjacent marine reserve? *Fish Bull.* **104**, 360–375 (2006).
60. N. C. Krueck *et al.*, Reserve sizes needed to protect coral reef fishes. *Conserv. Lett.* **11**, e12415 (2018).
61. J. Claudet *et al.*, Marine reserves: Size and age do matter. *Ecol. Lett.* **11**, 481–489 (2008).
62. B. S. Halpern, The impact of marine reserves: Do reserves work and does reserve size matter? *Ecol. Appl.* **13**, 117–137 (2003).
63. J. P. Kritzer, Effects of noncompliance on the success of alternative designs of marine protected-area networks for conservation and fisheries management. *Conserv. Biol.* **18**, 1021–1031 (2004).
64. A. Forcada *et al.*, Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Mar. Ecol. Prog. Ser.* **379**, 197–211 (2009).
65. K. A. Stamoulis, A. M. Friedlander, A seascape approach to investigating fish spillover across a marine protected area boundary in Hawai’i. *Fish. Res.* **144**, 2–14 (2013).
66. United Nations Environment World Conservation Monitoring Centre, International Union for Conservation of Nature, Marine Protected Planet. <http://www.protectedplanet.net>. Accessed 22 April 2020.
67. C. J. Brown, S. Abdullah, P. J. Mumby, Minimizing the short-term impacts of marine reserves on fisheries while meeting long-term goals for recovery. *Conserv. Lett.* **8**, 180–189 (2015).
68. D. Ovando, D. Dougherty, J. R. Wilson, Market and design solutions to the short-term economic impacts of marine reserves. *Fish Fish.* **17**, 939–954 (2016).
69. J. K. Hopf, G. P. Jones, D. H. Williamson, S. R. Connolly, Fishery consequences of marine reserves: Short-term pain for longer-term gain. *Ecol. Appl.* **26**, 818–829 (2016).
70. E. Sala *et al.*, Fish banks: An economic model to scale marine conservation. *Mar. Policy* **73**, 154–161 (2016).
71. S. R. Palumbi, Population genetics, demographic connectivity, and the design of marine reserves. *Ecol. Appl.* **13**, S146–S158 (2003).
72. A. Hastings, S. D. Gaines, C. Costello, Marine reserves solve an important bycatch problem in fisheries. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 8927–8934 (2017).
73. J. Beets, A. Friedlander, Evaluation of a conservation strategy: A spawning aggregation closure for red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. *Environ. Biol. Fishes* **55**, 91–98 (1999).
74. I. Nagelkerken, M. G. G. Grol, P. J. Mumby, Effects of marine reserves versus nursery habitat availability on structure of reef fish communities. *PLoS One* **7**, e36906 (2012).
75. R. B. Cabral *et al.*, Siting marine protected areas based on habitat quality and extent provides the greatest benefit to spatially structured metapopulations. *Ecosphere* **7**, e01533 (2016).
76. R. Cabral *et al.*, Data from: A global network of marine protected areas for food. *Dryad Digital Repository*. <https://doi.org/10.25349/D9C32R>. Accessed 6 October 2020.
77. J. T. Thorson, Predicting recruitment density dependence and intrinsic growth rate for all fishes worldwide using a data-integrated life-history model. *Fish Fish.* **21**, 237–251 (2020).
78. R. Froese, D. Pauly, FishBase, version 12/2019. <http://www.fishbase.org>. Accessed 2 October 2020.
79. M. L. D. Palomares, D. Pauly, SeaLifeBase, version 07/2020. <http://www.sealifebase.org>. Accessed 2 October 2020.
80. K. Kaschner *et al.*, AquaMaps: Predicted range maps for aquatic species, version 08/2016c. <http://www.aquamaps.org>. Accessed 22 April 2019.
81. S. D. Gaines *et al.*, Improved fisheries management could offset many negative effects of climate change. *Sci. Adv.* **4**, eaao1378 (2018).
82. S. Guénette, T. J. Pitcher, An age-structured model showing the benefits of marine reserves in controlling overexploitation. *Fish. Res.* **39**, 295–303 (1999).
83. P. Apostolaki, E. J. Milner-Gulland, M. K. McAllister, G. P. Kirkwood, Modelling the effects of establishing a marine reserve for mobile fish species. *Can. J. Fish. Aquat. Sci.* **59**, 405–415 (2002).
84. C. J. Walters, R. Hilborn, R. Parrish, An equilibrium model for predicting the efficacy of marine protected areas in coastal environments. *Can. J. Fish. Aquat. Sci.* **64**, 1009–1018 (2007).
85. L. Schiller, M. Bailey, J. Jacquet, E. Sala, High seas fisheries play a negligible role in addressing global food security. *Sci. Adv.* **4**, eaat8351 (2018).