

Global effects of marine protected areas on food security are unknown

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Marine protected areas (MPAs) can be a powerful conservation tool and can positively or negatively affect food security. Sala et al.¹ estimate the effects of a global network of MPAs designed for biodiversity, carbon sequestration and food security. However, the model used to project these benefits depends on a series of unrealistic and insufficiently tested assumptions that are inconsistent with its source material; using a more realistic model markedly changes the map of priority MPAs and reduces potential food benefits by 62%. This extreme sensitivity in the outcomes of MPA networks to highly uncertain parameters and modelling assumptions means that the true global effects of MPAs on food security remain unknown.

We agree with Sala et al.¹ that MPAs can have an important role in managing and conserving marine ecosystems. But we are concerned that the model used by the authors does not present a reliable assessment of the effect of MPAs on the yields of fisheries and, by extension, that it is not a reliable foundation for the broader assessment of the role of MPAs in achieving multiple objectives of marine conservation, food security and climate action¹. The results of Sala et al.¹ depend on the same model as those of a previously published study² (see also ref. 3), which assumes that density dependence is a function of total pooled population size, independent of how fish are distributed in space, and that unassessed fish stocks (that is, stocks not included in the RAM Legacy Stock Assessment Database) of a given species are a single global interconnected population. These two assumptions generate results that are neither consistent with their source material⁴ nor ecologically reasonable. The global distribution assumed for unassessed stocks implies that MPAs around Australia can increase catches along the shores of North America³, or that a single fish population can be affected both by MPAs in the Caribbean and in the waters off of China (Supplementary Fig. 2). When movement rates are low under their assumption of pooled density dependence, fishing more outside an MPA can produce higher biomass inside the MPA than there would have been in the absence of any fishing at all (Supplementary Fig. 5).

The food projections made by Sala et al.¹ are based on estimates of fishing mortality rates and life history values provided by a previous study⁴. In that study, a Pella–Tomlinson⁵ population model was used and it was assumed that separate stock units exist inside the waters of a specific country within a major statistical area designated by the Food and Agriculture Organization (FAO) for each unassessed taxonomic group, except for highly mobile unassessed stocks, which are assumed to be well-mixed within FAO major statistical areas. Sala et al.¹ aggregated all the individual unassessed stocks assumed by the previous

study⁴ into one global stock per species and converted the underlying population-dynamics model to a logistic growth equation. We call these assumptions made by Sala et al.¹ the ‘global’ scenario.

To assess the effect of these strong choices, we ran a version of the analysis by Sala et al.¹ changing three key assumptions to be consistent with those of the previously published study⁴: the spatial resolution of the simulated populations, the population-dynamics model used and the nature of the density dependence. For our base results, we assume that density dependence (such as the competition for food or habitat) occurs at a local scale, with MPAs providing a spill-over of fish biomass to fished areas through the movement dynamics in the model. We call this alternative group of assumptions the ‘regional’ scenario.

Under the global assumptions, global food production is maximized with an MPA network covering 22% of the carrying capacity, which can be achieved by protecting 24% of the ocean surface. Under the regional assumptions, the maximum yield benefits were much lower; 38% of the maximum benefits of the global assumptions could be achieved by protecting 14% of the carrying capacity (29% of ocean surface) (Fig. 1). The flatter form of the curve for the regional model in Fig. 1a suggests that a greater portion of carrying capacity could be protected without substantially reducing global fishery catches. The global results place much of the west coast of North America in the top 30% of areas for protection, but omit much of the coastal Indian Ocean and the Coral Triangle. These results are flipped under our regional assumptions. The global assumptions of Sala et al.¹ suggest that 46% of the exclusive economic zone of the USA could be placed in MPAs while increasing or maintaining food production, whereas under our regional assumptions that number drops to 13% (Fig. 2).

The assumption that density dependence occurs at the local scales used in our regional results is common in the MPA modelling literature, including in studies^{6–11} authored by authors of the study by Sala et al.¹. We tested the sensitivity of our regional results to using the same approximation of larvae commonly dispersing outside the MPA to fished areas as Sala et al.¹ did; the stark contrast in both the magnitude and design of a global MPA network for food provision remains (see the pooled assumption results in Supplementary Figs. 3 and 4).

Fish often disperse vast distances at one or more phases of their life cycle. However, even for the most mobile species, dispersal and complete mixing across entire ocean or planetary scales is rare¹². Sala et al.¹ used the spatial stock structure described previously¹³ for the assessed fisheries; the footprints of these stocks are generally much smaller than the entire exclusive economic zone of a country, and of

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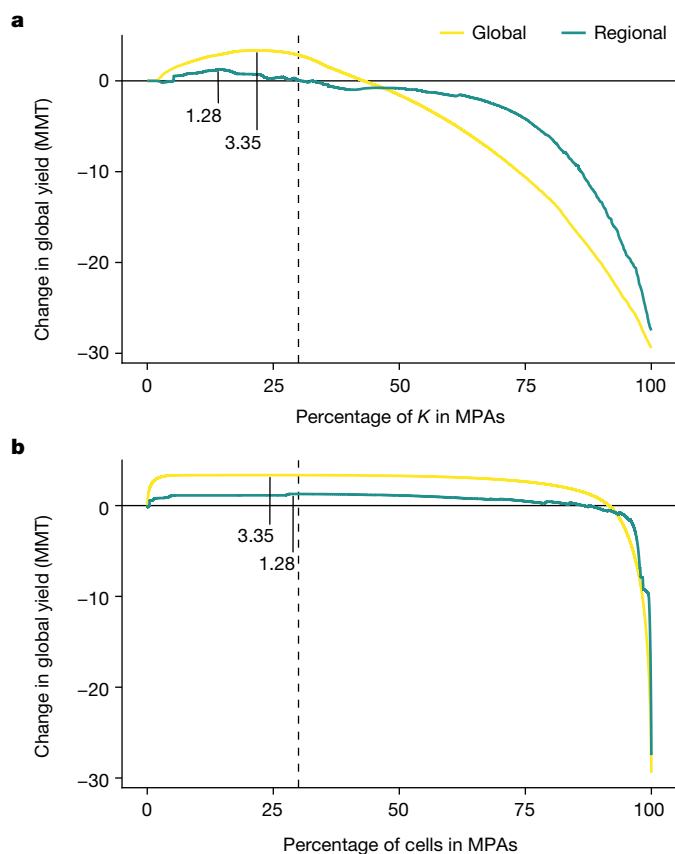


Fig. 1 | The change in global fishery yields and the percentage of global ocean in MPAs. **a**, The change in global fishery yields in millions of tonnes (MMT) as a function of the percentage of global carrying capacity (K) in MPAs. **b**, The percentage of global ocean surface in MPAs. Numbers and solid lines point to values at the peak of each curve. Vertical dashed line indicates the location of 30% on the x axis. Global assumes one global stock per unassessed species and a pooled density dependence, following Sala et al.¹ Regional indicates that stocks are modelled as described previously⁴ with a local density dependence. Using the regional rather than the global assumptions results in a 62% decrease in maximum yield.

the unassessed fisheries (Supplementary Fig. 6). It is inconsistent to use the smaller footprints¹³ for the assessed stocks, as Sala et al.¹ have done, but then skip past the regional stock structure to the much larger single global stock distribution for unassessed species, as assumed in the global results. The alternative assumption made previously⁴ that stocks of species that are not highly mobile are contained within country borders is not perfect, but it is more in line with the best available evidence of stock sizes¹³.

We are not suggesting that the regional results are the ‘right’ findings. Instead, we are demonstrating that the central results of Sala et al.¹ are not robust to changes to their core assumptions. Other shortcomings remain in both the global and regional scenarios. The spatial complexity of MPAs is simplified to a two-patch surplus production model. The models assume that displacing fishing effort for one species outside an MPA has no effect on other species or habitats in the remaining fished area; these dynamics must be taken into consideration when assessing not only the yield but also the biodiversity and carbon impacts of MPAs.

There are places on Earth where MPAs can benefit food production, particularly where stocks are heavily overfished. However, these locations and the resulting effects on food provision cannot be reliably identified using the global-scale model and data used by Sala et al.¹. Refinements to their assumptions, in accordance with their own references, do not just alter the results at the margin, but fundamentally change their conclusions at multiple scales. Assessments of the role of MPAs in food provision should be wary of these issues, and clearly evaluate and communicate key sensitivities and potential trade-offs between conservation and food provision arising from alternative sets of plausible assumptions, so that communities can make decisions on MPAs with the full knowledge of both the potential and uncertainty of the effects of MPAs on food security.

Methods

Methods are provided in the Supplementary Information. Owing to discrepancies in values between Sala et al.¹ and the dataset of ref. 4, we restricted our analysis to stocks found in both analyses (1,011 stocks as defined by Sala et al.¹ out of 1,150 total stocks). We then adjusted the maximum sustainable yield for each stock to match the generally lower values reported previously⁴, leaving a set of stocks with the same total maximum sustainable yield in both the regional and global analyses. As a consequence of these adjustments, the global results are not exactly the same as those reported by Sala et al.¹, although they are very similar.

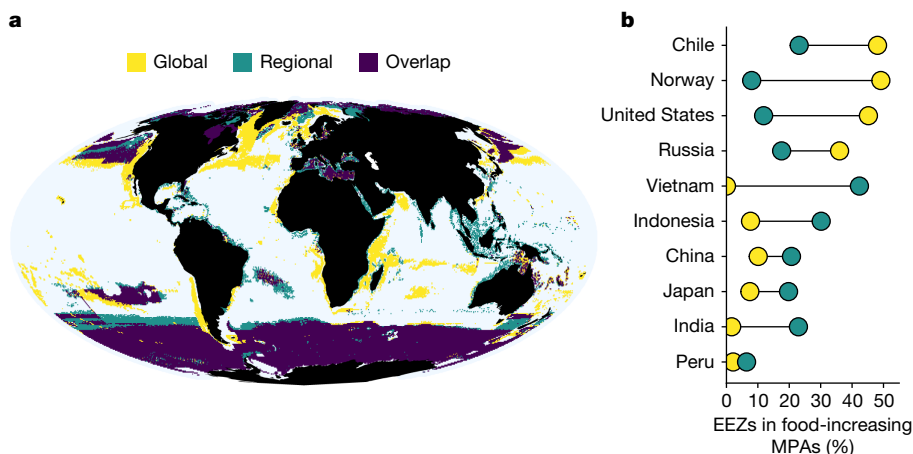


Fig. 2 | Spatial differences in MPA outcomes between alternative assumptions. **a**, The map shows cells identified in the top 30% by food provision of MPAs, where the colour indicates which set of assumptions produced which cells, with overlapping cells indicated by the ‘Overlap’ colour. **b**, The points indicate the percentage of the exclusive economic zone (EEZ) of the top-ten countries (based on recent FAO reported catches) that could be placed inside

food-increasing MPAs under each set of assumptions. Existing MPAs are omitted because these are automatically included by the model. Global assumes one global stock per unassessed species and a pooled density dependence, following Sala et al.¹. Regional indicates that stocks are modelled as described previously⁴ with local density dependence.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data and materials needed to fully reproduce the results in this paper are publicly available at GitHub (<https://github.com/DanOvando/mpas-and-food-unknown>) and Figshare (<https://doi.org/10.6084/m9.figshare.16709362.v5>).

Code availability

All code needed to fully reproduce the results in this paper are publicly available at GitHub (<https://github.com/DanOvando/mpas-and-food-unknown>) and Figshare (<https://doi.org/10.6084/m9.figshare.16709362.v5>). All analyses were conducted in R (v.4.3.1)¹⁴.

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Author contributions Analyses were performed by D.O. and A.P. All of the authors contributed to the conceptualization and writing of the paper.

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Additional information

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Reply to: Global effects of marine protected areas on food security are unknown

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REPLYING TO D. Ovando et al. *Nature* <https://doi.org/10.1038/s41586-023-06493-8> (2023)

The main goal of our study was to develop a flexible conservation-planning framework to prioritize marine protected areas (MPAs) in places that would result in multiple benefits today and in the future¹. Every model has assumptions that will affect its results to varying degrees. In the accompanying Comment, Ovando et al.² challenge two important assumptions of our food provision model: (1) the scale of spatial connectivity of unassessed stocks and (2) the nature of the density dependence. Here, we isolate and test for the effect of reducing the scale of spatial connectivity and provide arguments for why assuming a global density dependence is justified.

Our model estimated the global food-provision benefits of MPAs for 1,150 fish stocks. For stocks that have formal assessments, we used the spatial delineation of each stock to constrain adult and larval dispersal. For those stocks without assessment, we used the geographical range of the species as the envelope for spatial connectivity. For all stocks, we assumed that the contribution of larvae from MPAs distributes homogeneously within the range of a stock. We vary adult movement according to a categorical movement parameter derived from a literature review that results in relatively low, medium or high levels of movement across the range of the stock. The estimated MPA effects are then the changes to equilibrium catch that result from protection accounting for adult movement and larval dispersal across stock ranges. By contrast, Ovando et al.² propose a model in which the ecological connectivity of unassessed stocks is constrained by the political jurisdictions of countries (with an exception for migratory tunas). We tested the sensitivity of our results to this alternative approach and find modest reductions in global food-provision benefits.

We re-ran our original model changing only the extent of ecological connectivity for unassessed stocks to the intersection of geographical ranges and exclusive economic zones (EEZs)—often resulting in a smaller spatial footprint than the EEZ spatial constraints used by Ovando et al.²—for adult movement, larval connectivity and fisher redistribution. The result of this change is a substantial increase in the number of modelled stocks from 1,150 in our original model to around 32,000 distinct stocks. We find that the maximum food-provisioning benefits produced under this new model specification are similar to our original estimates, and the results hold across both fishing effort redistribution scenarios considered (complete effort redistribution and

no effort redistribution after MPA implementation). Under the assumption of complete effort redistribution, our original model estimated 5.9 million tonnes (MMT) of additional catch (90% of which could be obtained by strategically protecting 5.1% of the ocean), whereas the EEZ-constrained model yields a net gain of 5 MMT (90% of this can be obtained with 5.5% of the ocean protected). Under the assumption of no effort redistribution, our original model estimated 5.2 MMT of additional catch (90% of which could be obtained by strategically protecting 3.8% of the ocean), whereas the EEZ-constrained model yields a net gain of 4.4 MMT (90% of which can be obtained by protecting 4.5% of the ocean) (Figs. 1–3).

Constraining ecological connectivity to EEZs is not only ecologically dubious, but it is analytically inappropriate in that it forces the prioritization algorithm to maximize pixels for protection within EEZs, defeating our goal of producing a true global prioritization. However, it further reinforces the robustness of our approach in that it is relatively insensitive to even this substantial spatial constraint proposed by Ovando et al.², resulting in a modest decrease (15%) in maximum potential benefits and a small increase in the area needed to achieve them (Figs. 1–3). Relative to the original model, the EEZ-constrained model identifies priorities in all countries, and it reduces the effect that the global spatial patterns of marine productivity have on potential food provision benefits, as shown in Fig. 2 of Ovando et al.².

The second critique of Ovando et al.² focuses on our choice to model density dependence as a global process, with larval production distributed across the range of individual stocks. They instead propose that density dependence should be applied at the local scale, which they operationalize in section 1.3.2 of their Supplementary Information by constraining the distribution of larvae produced inside MPA borders to remain within the MPA. Ovando et al.² further clarify their definition of the local assumption in the caption of their Supplementary Fig. 5 as “Local” implies that the growth inside the MPA is a function of biomass inside the MPA.” Density-dependent processes in the local case can be applied either to the spawning or reproduction stage or to the settlement stage; in both cases, larvae produced inside the MPA all remain within the MPA.

Density dependence in spawning or reproduction implies that larval production tapers off as the population inside the MPA approaches

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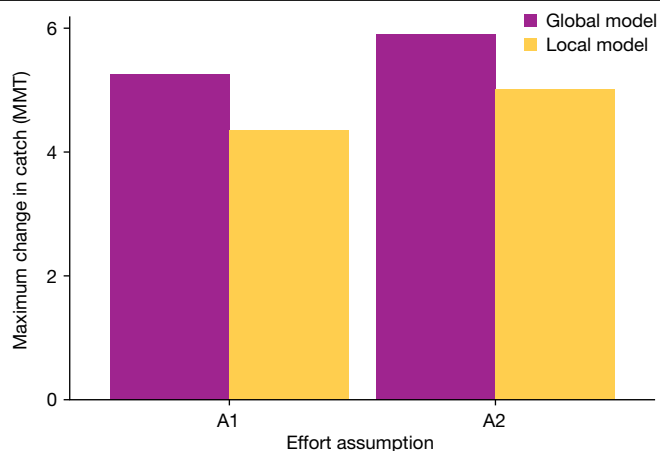


Fig. 1 | Maximum food-provisioning benefits generated from global versus local models under two fishing effort redistribution assumptions. The ‘global’ model represents the results reported in Sala et al.¹ and the ‘local’ model is a version in which larval dispersal distance and adult movement are constrained within the EEZ of the countries, but allows for the dispersal of larvae outside MPAs. The two fishing effort redistribution assumptions are the same as those reported in Sala et al.¹ in which A1 assumes no effort redistribution (that is, fishing effort in the remaining fished areas will remain the same) and A2 assumes complete effort redistribution (that is, fishing effort from MPAs relocates to the remaining fishing areas outside MPAs). Only the unassessed stocks were partitioned by EEZ, as all other stocks have spatially defined management boundaries.

carrying capacity (which is likely to happen for low-mobility species). Density dependence in the settlement stage implies higher competition between recruits and adults as biomass builds up inside the MPA compared with the lower competition for larvae that can disperse and settle in fished areas where biomass is lower. Assuming that all larvae from an MPA would be self-seeded and experience increased competition for food and space at settlement as the biomass inside the MPA builds up, and assuming that larval production tapers off to zero as the population rebuilds, would both substantially reduce fisheries benefits from MPAs. This also neglects the recruitment subsidy commonly attributed in the literature as a mechanism for MPAs to benefit fisheries^{3–5}. We posit that these assumptions are driving the large sensitivities reported by Ovando et al.², as we have shown that the scale of spatial connectivity does not substantially alter our results.

That leaves the question as to which set of assumptions (local versus global) would be more ecologically defensible. Naturally, neither assumption is correct for all fish stocks, and reality probably falls somewhere in between. Density-dependent effects on larval production and settlement are relevant to the food benefits of MPAs, because they determine changes to the production function as a population rebuilds inside an MPA and approaches carrying capacity⁶. Studies demonstrate that larval production typically grows faster than biomass within MPAs^{4,7,8}. In other words, most species increase larval production as the fish populations inside the MPA approach carrying capacity; larval production does not typically taper off as populations rebuild in MPAs. In fact, larval production scales hyperallometrically with fish mass at the spawning stage, and because larger fish tend to be found in higher abundance in highly protected MPAs than in unprotected areas, our model probably underestimates larval subsidies from MPAs⁷. Thus, we believe our density-dependence assumption is well supported by the scientific literature.

Regarding larval dispersal, several studies have suggested that the scales of larval transport typically far exceed MPA size^{3,5,8,9}. The larger the population inside the MPA, the more larvae it can produce, and these larvae can contribute to fisheries productivity hundreds of kilometres

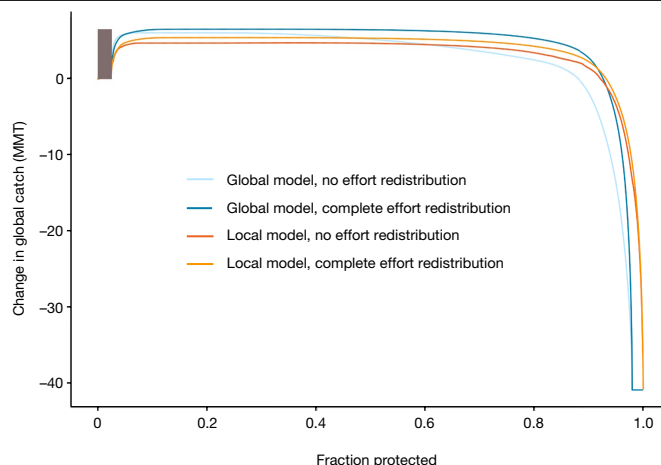


Fig. 2 | Global food benefit accumulation curves. The blue curves represent the change in global catch as more area of the ocean is protected using the original model under the no effort redistribution assumption and complete effort redistribution. The red and orange curves represent the net change in global catch if individual fish stocks are constrained to the EEZs.

away, even for populations with sessile adults. For example, genetic studies of species on the Great Barrier Reef have found that adults within long-established MPAs that cover 28% of the reef are the parents of more than half of the recruits to fished areas outside the MPAs⁸. In fact, recent evidence has shown that many species have extremely long dispersal distances and fish larvae and adults cross multiple political jurisdictions^{10,11}, although we agree with Ovando et al.² that assuming truly global dispersal is inaccurate (as we stated in our original paper¹). However, the alternative scenario proposed by Ovando et al.² of no dispersal outside MPAs and no exchange of larvae and adult biomass among countries is also incorrect for most marine species. As long as one assumes that larvae commonly disperse outside the MPAs, regardless of how far outside, our overall food provision benefits will be similar, as we have shown. However, the details of actual dispersal distances will greatly affect the specific locations that receive those benefits, so better estimates of larval connectivity and hydrodynamically influenced source–sink dynamics will be very helpful in determining the true extent of spillover and pinpointing the spatial distribution of food provision beneficiaries of MPAs. Furthermore, ignoring the spatial connectivity of species results in a globally optimal MPA network in which all countries have some area protected, but overall more MPAs are prioritized in low-productivity areas, and fewer MPAs are prioritized in highly productive areas relative to our original result¹.

Methods

We model fish population dynamics in the presence of an MPA as a two-patch system composed of a fished area and an MPA. We model the biomass transitions of each individual stock j inside ($B_{in,j}$) and outside ($B_{out,j}$) an MPA as follows for biomass transition inside the MPA:

$$B_{in,j,t+1} = B_{in,j,t} + f_{in,j,t}(\cdot) - B_{trans,j,t}$$

and for biomass transition outside the MPA (or in the fished area)

$$B_{out,j,t+1} = (1 - E_{out,j,t})B_{out,j,t} + f_{out,j,t}(\cdot) + B_{trans,j,t}$$

where t is the time in years, $f_{in}(\cdot)$ and $f_{out}(\cdot)$ are the added biomass inside the MPA and in the fished area through larval production and dispersal, B_{trans} is the exchange of biomass between the MPA and the fished area through adult movement, and E_{out} is the exploitation rate

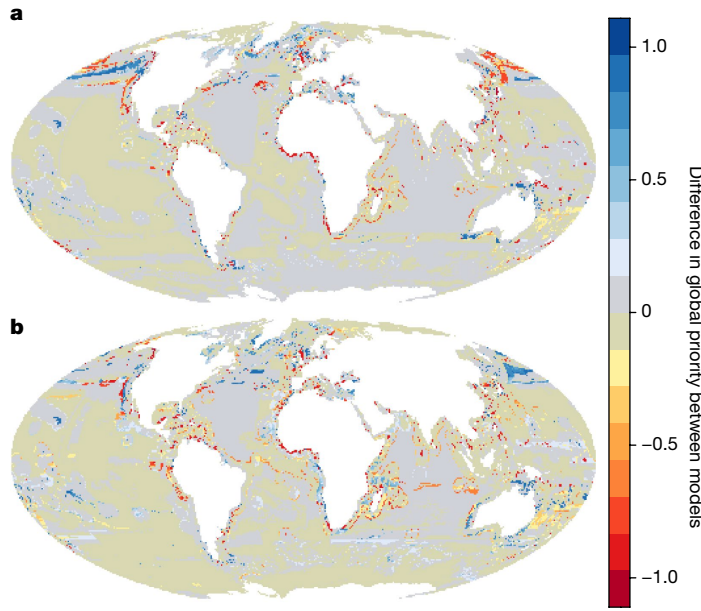


Fig. 3 | Differences in global conservation priorities between the global and the EEZ-constrained models. a, b. Differences in global conservation priorities between the global and the EEZ-constrained models under no effort redistribution (a) and complete effort redistribution (b) assumptions. The red areas correspond to those that increase in priority with the EEZ-constrained model relative to the global model.

experienced by the stock in the fished area. The transfer of biomass between the MPA and the fished area through adult movement is given by:

$$B_{\text{trans},j,t} = m_j(1 - R_j) \left(B_{\text{in},j,t} - \frac{R_j}{1 - R_j} B_{\text{out},j,t} \right)$$

where m is the adult mobility (parameterized using categorical adult mobility information for each species that considers low ($m = 0.1$) medium ($m = 0.3$) and high ($m = 0.9$) movement capacities based on a literature review) and R is the MPA size defined as the proportion of the geographical range of a species in the MPA (see ‘Adult movement’ for the derivation of the biomass transfer equation).

Fish that are located inside and outside the MPA contribute to the population growth inside and outside MPA through larval exchanges. We model larval production and transport as a common larval pool. This means that larval productions inside and outside the MPA are pooled and then distribute homogeneously inside and outside the MPA (within the range of a stock) proportional to the size of MPA and the remaining fished area according to:

$$f_{\text{in},j,t}(\cdot) = R_j r_j (B_{\text{in},j,t} + B_{\text{out},j,t}) \left(1 - \frac{B_{\text{in},j,t} + B_{\text{out},j,t}}{K_j} \right)$$

$$f_{\text{out},j,t}(\cdot) = (1 - R_j) r_j (B_{\text{in},j,t} + B_{\text{out},j,t}) \left(1 - \frac{B_{\text{in},j,t} + B_{\text{out},j,t}}{K_j} \right)$$

Our model fundamentally differs from that of Ovando et al.² as they assumed that fish populations in the MPA and the fished area are connected only through adult movement, that is by B_{trans} . Ovando et al.² defined their local assumption in Supplementary Fig. 5 as follows: ‘Local’ implies that growth inside the MPA is a function of biomass inside the MPA. This means that $f_{\text{in},j,t}$ is a function of biomass inside the MPA ($B_{\text{in},j,t}$) and $f_{\text{out},j,t}$ is a function of the biomass in the fished area ($B_{\text{out},j,t}$). Under the assumption by Ovando et al.², there will be no larval subsidies from the MPA to the fished area.

We agree with Ovando et al.² that under the boundary condition of $m = 0$, which is equivalent to true zero adult movement and not ecologically relevant to the fished species considered in our approach, our model can exhibit bizarre behaviour in which the biomass inside the MPA can increase as fishing pressure outside the MPA increases. Although biomass has not been used as an output in our model, caution must be taken when using our model to track biomass inside the MPA under the boundary condition of $m = 0$.

Adult movement

The transfer of biomass between the MPA and the fished area through adult movement (B_{trans}) was derived using the following logic.

Under full biomass transfer (FT) between the MPA and the fished area, in which this transfer results in the biomass density inside and outside the MPA being equal, we have:

$$\frac{B_{\text{in},j} - B_{\text{trans},j/\text{FT}}}{R} = \frac{B_{\text{out},j} + B_{\text{trans},j/\text{FT}}}{1 - R}$$

Solving for $B_{\text{trans},j/\text{FT}}$, we have:

$$B_{\text{trans},j/\text{FT}} = (1 - R_j) B_{\text{in},j} - R B_{\text{out},j}$$

Species movement rates influence the exchange of biomass between the MPA and the fished area. The exchange will be minimal for species with low adult mobility and large for species with high adult mobility. Using m as a parameter describing species mobility, we can generalize the transfer of biomass as:

$$B_{\text{trans},j} = m_j((1 - R_j) B_{\text{in},j} - R_j B_{\text{out},j}) \text{ or } B_{\text{trans},j,t} = m_j(1 - R_j) \left(B_{\text{in},j,t} - \frac{R_j}{1 - R_j} B_{\text{out},j,t} \right)$$

Sensitivity analysis

In addition to the assumption by Ovando et al.² that larvae will not disperse out of an MPA, the authors also propose that the scale of movement by adult fish should be constrained within the surrounding EEZ. We test the sensitivity of our model to this idea by constraining the distribution of larvae and adult movement to the surrounding EEZs, but use the same population model as in our original paper¹ and keep all other parameters unchanged to isolate the effect of the approach proposed by Ovando et al.². We test our results under both effort redistribution scenarios (that is, complete effort redistribution and no effort redistribution).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The underlying data used in this study are available from the sources listed in the supplementary information of the original paper¹.

Code availability

The code supporting the findings of this additional analysis is available at GitHub (<https://github.com/emlab-ucsb/ocean-conservation-priorities>).

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Competing interests The authors declare no competing interests.

Additional information

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Data collection

No software was used to collect data in this study. All data came from different existing sources listed in the Methods section of the original paper by Sala et al. (2021)

Data analysis

All data processing was done in R using the raster, sf, and rasterVis libraries.

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Research sample	We used data on: Fisheries - RAM Legacy Database, Global Fishing Watch Marine Protected Areas - Atlas of Marine Protection
Sampling strategy	N/A - This is a modeling study using available data
Data collection	Data were obtained from online repositories and directly from colleagues
Timing and spatial scale	Our data range from 2006 (marine ecoregion classification) to present
Data exclusions	No data were excluded from our modeling study.
Reproducibility	N/A - No experiments were performed
Randomization	N/A - No experiments were performed
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