nature sustainability

Article

https://doi.org/10.1038/s41893-023-01150-4

Co-benefits of marine protected areas for nature and people

Received: 26 April 2022

Accepted: 22 May 2023

Published online: 22 June 2023

Check for updates

A. Justin Nowakowski[1,2,3], Steven W. J. Canty[1,2,4], Nathan J. Bennett[5,6,7], Courtney E. Cox[8], Abel Valdivia[9], Jessica L. Deichmann[2,10,11], Thomas S. Akre[2,10], Sara E. Bonilla-Anariba[12], Sebastien Costedoat[3] & Melanie McField[2,4]

Conservation interventions are central strategies for achieving sustainable development goals given the inextricable dependence of humanity on nature. Current debate centres on whether interventions such as marine protected areas (MPAs) promote co-benefits or trade-offs among multiple goals such as poverty alleviation, food security and protection of marine resources. Resolving this question is hindered by a lack of quantitative impact evaluations of concurrent ecological and social co-benefits of MPAs. Here we use a statistical matching approach to examine whether MPAs are associated with co-benefits or trade-offs between reef fish abundances and measures of human well-being, including income, diet and food security in the Mesoamerican region. We find that highly protected areas (HPAs) with stringent fishing restrictions tend to support high mean abundances and stable or increasing trends in fish abundances compared with unprotected sites and 'general use zones' of MPAs. At the same time, indicators of income and food security were elevated in communities near MPAs, especially HPAs, compared with communities far from MPAs. Finally, proximity to MPAs and to reefs with high fish abundance were both positively associated with well-being across space. Together, these results provide quantitative evidence of co-benefits for fish and people associated with MPAs, highlighting the potential value of MPAs in achieving multiple sustainable development goals.

The global community has adopted a broad set of Sustainable Development Goals (SDGs) aimed at increasing the prosperity of humanity while protecting the ecosystems on which it depends[1]. These goals include alleviating poverty (SDG 1), increasing food security (SDG 2), and protecting and sustainably using marine resources (SDG 14, Aichi Targets 11). However, there is debate over whether these goals are compatible—can one be achieved without unintended negative consequences for another or are co-benefits possible[2–5]? There is limited empirical evidence that demonstrates synergies among multiple SDGs or the ability of conservation interventions to produce co-benefits for nature and people[6–9].

One of the intended benefits of marine protected areas (MPAs) is to slow the declines of marine fisheries, a natural resource important

[1]Smithsonian Environmental Research Center, Edgewater, MD, USA. [2]Working Land and Seascapes, Smithsonian Institution, Washington, DC, USA. [3]Conservation International, Arlington, VA, USA. [4]Smithsonian Marine Station, Fort Pierce, FL, USA. [5]Global Science, WWF, Washington, DC, USA. [6]People and the Ocean Specialist Group, Commission on Environmental, Economic and Social Policy, International Union for the Conservation of Nature, Gland, Switzerland. [7]School of Public Policy and Global Affairs, University of British Columbia, Vancouver, British Columbia, Canada. [8]Barefoot Ocean, Houston, TX, USA. [9]Oceans, WWF, Washington, DC, USA. [10]Smithsonian's National Zoo and Conservation Biology Institute, Front Royal, VA, USA. [11]Liz Claiborne and Art Ortenberg Foundation, New York, NY, USA. [12]Department of Agricultural Economics, Sociology, and Education, Pennsylvania State University, University Park, PA, USA. e-mail: Nowakowskia@si.edu

 https://doi.org/10.1038/s41893-023-01150-4

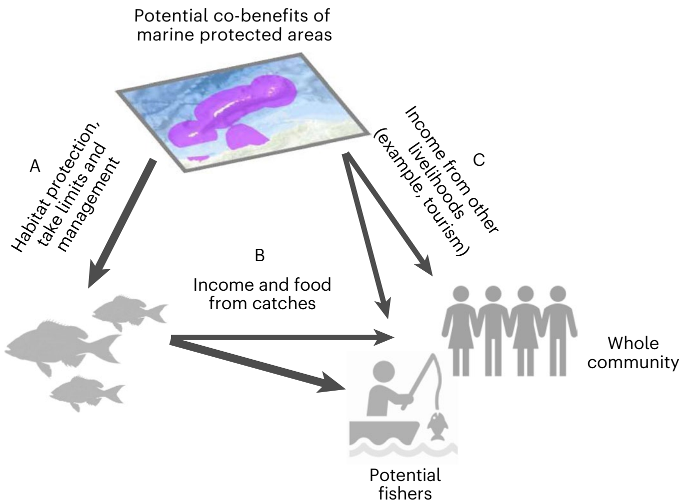


Fig. 1 | Conceptual diagram illustrating potential co-benefits for fisheries and local communities from MPAs. A primary objective of many MPAs is to maintain marine ecosystems, including fish assemblages, through habitat protection and fishing restrictions (A). However, the effectiveness of MPAs for maintaining fisheries is context dependent, with evidence supporting the importance of well enforced, no-take regulations and larger, older MPAs[15–17]. MPAs may also affect food security and income of nearby communities through at least two general, non-mutually exclusive pathways, A+B and C[21–24]. First, fishing is a primary source of income and food security for many coastal communities (A+ B). If MPAs effectively replenish adjacent fishing grounds, recruitment and spillover may increase income and subsistence through increased catches near MPAs, especially those with no or limited take. If benefits of MPAs are primarily through enhancing fisheries, we expect households of fishers to benefit more than non-fishers. Second, MPAs can generate access to alternative livelihood opportunities such as tourism, which may benefit a broad cross-section of the local community (C). Conversely, loss of access rights in MPAs can have negative consequences for livelihoods in some cases. If loss of access is not compensated through spillover and alternative livelihoods, proximity to MPAs may be associated with decreased income and food security in fisheries-dependent communities. Through our analyses, we assessed the impacts of MPAs on reef fish abundances (A), the effect of proximity to MPAs on income and food security in local communities (A + B + C) and the spatial association between fish abundance and human well-being indicators (B). The current data allow for assessment of potential co-benefits associated with MPAs (pathways A+B+C) but not for fully disentangling the contributions of pathways A+B versus C. Map data are from open sources in refs. 54,55.

for sustainable development[10]. Countries have rapidly expanded their MPA networks to cover >7% of oceans in pursuit of the 10% target set by the Convention on Biological Diversity and SDG 14[11], as well as the more recent commitment to 30% coverage by 2030[12]. Achieving the underlying goals of these targets depends not only on increasing area but also on the ability of MPAs to generate co-benefits for fish and people (Fig. 1). There is substantial evidence that MPAs can help sustain fish assemblages[13–17]. However, MPA effectiveness depends on the complex interplay among contextual conditions that can include the level of human pressure[14], MPA size and age[15], fishing restrictions[16,18,19], enforcement[16,17] and community engagement[20]. Marine protected areas also have potential to benefit people, for example, by improving fisheries catches and providing livelihood alternatives related to tourism[21,22]. Conversely, MPAs can disempower and displace local communities through loss of access or tenure rights, which may decrease livelihoods and food security[23,24]. However, quantitative evidence of MPA effects on human well-being (HWB) is limited—few studies have used counterfactual designs—and most research has focused on economic outcomes while effects on health, nutrition and food security remain understudied[7,21,25,26]. Furthermore, quantitative impact evaluations of MPAs have typically examined ecological and social outcomes separately, limiting direct evidence of trade-offs or co-benefits associated with MPAs[22].

Here we examine the nexus of MPAs, fish assemblages and HWB outcomes in the Mesoamerican Reef (MAR) region. This region represents an important potential proof-of-concept because it has a well-developed network of 47 MPAs and a substantial coastal population of over 2 million people with a high dependence on fisheries for livelihoods and food security[27]. We use a long-term dataset of underwater visual surveys to characterize reef fish abundance[28] and USAID Demographic and Health Surveys (DHS) data[29] to characterize dimensions of HWB in nearby coastal communities, including income, fish as a dietary component and stunting as an indicator of food insecurity.

Through our analysis, we address the overarching question of whether MPAs lead to trade-offs or co-benefits for fisheries and coastal communities. To do so, we examined three underlying questions. First, we asked what are the impacts of MPAs with different levels of fishing restriction on fish abundances in the region? Second, what are the effects of proximity to MPAs on income, fish as a dietary component and probability of stunting in nearby communities? And third, looking across coastal areas, does well-being of local communities covary with the condition of fish assemblages at nearby reefs? Because locations of MPAs are often biased toward areas with lower human pressure, we statistically matched sites inside and outside of (or near and far from) MPAs on the basis of site characteristics to reduce the influence of location bias and thereby strengthen inferences about MPA impacts (questions one and two; see methods). We then quantified associations between fish and HWB outcomes across pairs of nearest-neighbour communities and reef sites (question three).

We expected that proximity of communities to MPAs may be associated with income and nutrition benefits, either directly through the natural resources they aim to protect, primarily increased catches near or within the MPAs[22], or indirectly through alternative income streams, such as those associated with tourism[21] (Fig. 1). If the potential benefits of MPAs occur primarily through increased catches, we expected these effects to be observed disproportionately in households of fishers compared with non-fishers. In contrast, if spillover and alternative livelihoods are insufficient, communities near MPAs may experience reduced income and food security resulting from fishing restrictions[22–24]. In both cases, we tested whether income and food security outcomes near MPAs are influenced by the level of fishing restrictions that can determine both the maintenance of local fisheries and level of access to those resources.

Outcomes for fish assemblages in MPAs

To determine whether MPAs are associated with co-benefits in a region, it is necessary to concurrently assess the effects of MPAs on both fisheries and HWB. Therefore, we first examined whether MPAs and their attributes (fishing restrictions, size, age and level of enforcement) affect means and trends of fish abundance across the region. We compared fish abundance outcomes among levels of fishing restrictions, which included 'open-access' areas and MPAs subdivided into 'general use zones' (GUZs) and highly protected areas (HPAs) (Methods). The HPAs have complete prohibition of commercial fishing on reefs, while some sites in this region allow for limited traditional and recreational catch and release fishing. In contrast, GUZs have variable levels of fishing restrictions that include catch limits or bans on certain fishing gear. We used statistical matching to select a subsample of GUZ sites (as these were most prevalent in the dataset) that reduced the average covariate imbalance among the different levels of fishing restriction (Methods)[17,30]. The aim of matching was to limit bias in the estimation of MPA effects on fish biomass by reducing the potential influence of differences in site characteristics among groups, including coastal development, sea surface temperature anomalies and reef type, among others. We further controlled for these potential confounders by including matching variables as covariates in our models. The fish dataset, post matching,

 https://doi.org/10.1038/s41893-023-01150-4

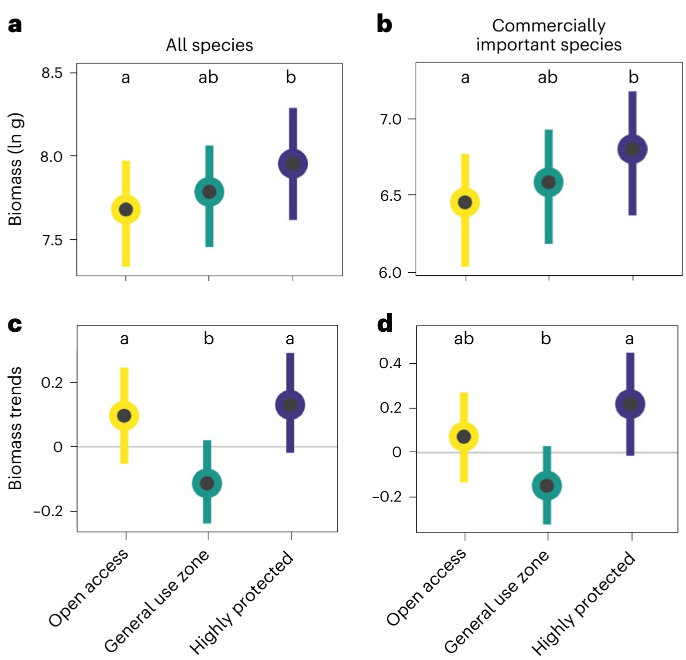


Fig. 2 | Mean abundance and trends of reef fish in open-access sites and marine protected areas (MPAs), including general use zones (GUZs) and highly protected areas (HPAs). To assess the effects of fishing restrictions associated with MPAs on assemblages, we used a statistical matching approach wherein we first matched survey sites on the basis of site characteristics and then quantified effects of fishing restrictions (GUZs versus HPAs) while controlling for remaining variation in matching variables in Bayesian hierarchical models (all covariate estimates provided in Supplementary Tables 1–4). **a**–**d**, Plots show estimated effects of fishing restrictions on means (**a**,**b**) and trends (**c**,**d**) in total biomass of all species (**a**,**c**) and commercially important species (**b**,**d**) (n = 4,336 transects sampled at 87 sites). Biomass trends represent model coefficients for the effect of year; the units of these trends are change in log biomass per s.d. of the year variable. Error bars represent 95% BCIs and different letters indicate differences among groups that have statistical support, that is, 95% BCIs for contrasts excluding zero.

included observations of 83 finfish species from 4,336 transects sampled at 87 sites in the Caribbean coastal waters of Mexico, Belize, Guatemala and Honduras (Extended Data Fig. 1a and Methods). Each site was sampled during at least three different years from 2005 to 2018.

We found evidence that strict fishing restrictions within MPAs (HPAs) helped maintain local fish abundance in the Mesoamerican region and for some groups, these effects were strengthened by increasing reserve age, size and level of enforcement (Fig. 2 and Extended Data Figs. 2–5). When evaluating effects of fishing restrictions, we examined both variation in mean abundance across sites (states) and linear rates of change in fish abundance over time (trends), as these represent two complementary indicators of the relative condition of local fish assemblages. We defined well-performing sites as those that have both high mean fish abundance relative to the region, and stable or increasing trends. In contrast, poorly performing sites exhibit low mean abundance and decreasing trends. Sites that have low mean abundance but increasing trends may be indicative of assemblages undergoing recovery. We examined these potential abundance outcomes by analysing the total biomass of all surveyed fish species, the biomass of all commercially important species and counts of three commercially important families—snapper (Lutjanidae), grouper (Serranidae) and grunts (Haemulidae)—as response variables.

Across fish groups, HPAs tended to support higher mean abundance than open-access sites, as well as stable or increasing trends (Fig. 2 and Supplementary Tables 1–4). The mean estimate of total fish biomass was 27% (95% Bayesian credible interval (BCI) = 3–51%) greater in HPAs than in open-access sites, with intermediate biomass in GUZs (Fig. 2a and Supplementary Table 1). Similarly, biomass of commercially important species was 35% (BCI = 2–71%) greater in HPAs than in open-access sites while not significantly different from that in GUZs (Fig. 2b and Supplementary Table 3). For total and commercial biomass, HPA sites supported trends that were significantly more positive than those in GUZs (95% BCIs for contrasts exclude 0; Fig. 2c,d, and Supplementary Tables 2 and 4). Commercially important families varied in their response to fishing restrictions. For example, snapper and grunts reached highest mean counts and had increasing trends in HPAs (Extended Data Fig. 2; 95% BCI for significant trend estimates excludes 0), whereas grouper had highest mean counts and stable trends (95% BCI for trend estimates includes 0) in both GUZs and HPAs. This variation in responses among taxa may be mediated by different life history traits and levels of fishing pressure across groups[31]. Our results indicate that across groups (Fig. 2), full protection from fishing within HPAs was more effective at maintaining high fish abundances than the multi-use restrictions associated with GUZs, which constitute the vast majority of current MPA coverage.

We then examined the effects of MPA age, size and enforcement on fish assemblages. The effects of MPA age on total and commercially important fish biomass depended on the level of fishing restrictions (HPA or GUZ), such that mean biomass increased across sites with increasing age of HPAs while decreasing with increasing age of GUZs (95% BCIs for interaction terms exclude 0; Extended Data Fig. 3 and Supplementary Table 5). When examining trends, biomass declined within older GUZs, while MPA age had negligible influence on trends in HPAs (Extended Data Fig. 4 and Supplementary Table 6). MPA size had no effect on mean total biomass but trends in biomass tended to be more stable in larger MPAs regardless of level of fishing restrictions (Extended Data Fig. 5 and Supplementary Table 7). For most groups, inclusion of enforcement levels as a covariate did not improve model fit over level of fishing restrictions alone (Supplementary Table 8), suggesting that even underenforced HPAs—those with limited patrols and potentially higher levels of poaching—can reduce fishing impacts on local assemblages[10]. Importantly, all HPAs in the analysis had some level of enforcement. Long-standing prohibitions on fishing (that is, older HPAs) appear to be the most important characteristics of MPAs for maintaining high local biomass in the MAR. Although there was remaining covariate imbalance after matching, these results are consistent with a growing understanding that MPA effectiveness is highly context dependent[13–18]. Therefore, confirming the specific conditions that lead to benefits for fish—here, HPAs, especially old, large HPAs—is a requisite for assessing potential co-benefits or trade-offs with HWB.

The nexus of MPAs, human well-being and fish assemblages

Are the ecological benefits of MPAs, HPAs in particular, accompanied by costs or benefits to people in terms of livelihoods and food security in coastal communities? We examined whether proximity to MPAs affects the DHS wealth index as an indicator of household assets and income, and probability of stunting of children as an index of food insecurity. Stunting is defined as height-for-age scores less than two standard deviations below the Child Growth Standards median[32]. We also assessed the effect of MPA proximity on probability of fish consumption as one potential mechanistic link between fisheries and food security outcomes. We used statistical matching of DHS survey clusters near (≤10 km from) MPAs to those far (>10 km) from MPAs. Matching was based on characteristics of clusters that are likely to be correlated with multiple dimensions of HWB, including education level, distance to markets and population density, among others (Methods). After matching, our dataset of HWB indicators contained survey responses for up to 2,117 individuals from 222 survey clusters along the coasts of Guatemala and Honduras (depending on outcome variable; Supplementary

https://doi.org/10.1038/s41893-023-01150-4

Table 9 and Extended Data Fig. 1b). We fit models to compare HWB in communities near and far from MPAs with different levels of fishing restrictions (GUZs versus HPAs) while again controlling for possible confounders by including matching variables in our models[33,34].

Among coastal communities of Honduras and Guatemala, we found that proximity to MPAs was associated with lower incidence of stunting. The overall probability of stunting in the surveyed population was 0.15 (BCI = 0.13–0.17; mean = 0.18 in Guatemala and 0.14 in Honduras). Probability of stunting was 40–47% lower in communities near MPAs than those that were far from MPAs (Fig. 3a and Supplementary Table 10). There was statistical support for the negative effects of both GUZs and HPAs on stunting (β_{GUZ} = −0.57, 95% BCI = (−1.05, −0.01), β_{HPA} = −0.72, 95% BCI = (−1.46, −0.08)). However, the mean effects of GUZs and HPAs on stunting were statistically indistinguishable (95% BCI of contrast between GUZ and HPA effect includes 0), suggesting that incidence of stunting tends to be lower near MPAs regardless of fishing restrictions. To test whether households of potential fishers benefit disproportionately from MPAs (Fig. 1), we examined the interactions between proximity to MPAs and occupation, here coded as potential fisher versus non-fishers. Although rates of stunting were greater in households with potential fishers, the lack of significant interaction indicates that stunting was similarly reduced near MPAs in households of fishers and non-fishers. Because food security and income are often tightly coupled, we then refit models with wealth index as an additional covariate to assess effects of MPAs on stunting after controlling for income. The inclusion of wealth index resulted in a modest decrease in the effect of HPAs but not of GUZs (Extended Data Fig. 6), suggesting that the influence of HPAs on stunting is at least partially driven by income. For all HWB outcomes, we examined model sensitivity to the matching approach (use of calipers) and the choice of distance thresholds for defining clusters near and far from MPAs, finding that results were qualitatively similar under these different analytical decisions (Methods and Extended Data Fig. 7).

We assessed fish consumption as a potential mechanistic link between maintenance of fisheries within MPAs and food security in local communities. The probability of fish consumption was negatively associated with proximity to HPAs (β_{HPA} = −1.54, 95% BCI = (−2.79, −0.30); Supplementary Table 11), further indicating that reduced stunting near HPAs probably occurs through other dietary sources that may become more accessible as income increases. In many regions, small-scale fisheries provide an important food source that has potential to increase food security in coastal communities[35,36]. For example, the majority of landed catches of small-scale fisheries is sold at local markets and used for direct local consumption[37], and diverse artisanal fisheries have potential to supply critical micronutrients, with up to 50–90% of animal protein in diets of some coastal communities coming from fish consumption[36,37]. In the MAR region, however, subsistence fishing and reliance on fish as a dietary component may be most prevalent in lower-income communities that are far from HPAs. Further, increases in food security in communities near MPAs may be more closely linked with income and levels of wealth from non-fisheries livelihoods.

We then considered the impacts of proximity to MPAs on household wealth index[38]. We found no effect of GUZs on the wealth index. In contrast, the average wealth index of households near HPAs was 33% greater than that of households far from MPAs (Fig. 3b; β_{HPA} = 0.29, 95% BCI = (0.15, 0.41); Supplementary Table 12). Proximity to MPAs had similar effects on the wealth index for households of potential fishers and non-fishers. For all HWB outcomes, considering other MPA characteristics such as age and size did not improve model fit (Supplementary Table 13). In resource-dependent populations such as small-scale fishing communities, livelihoods are tightly linked to food security, giving rise to positive or negative synergies between these HWB dimensions[7,39]. For example, loss of access rights or gear confiscation can reduce income and have cascading effects on nutrition. Studies have documented both positive and negative effects of MPAs on income and food security, impeding generalizations. As with fish outcomes, HWB outcomes appear heavily dependent on geographic, social and ecological contexts. In coastal communities in Guatemala and Honduras, proximity of households to MPAs, especially HPAs, was associated with elevated indicators of both food security and income within local communities.

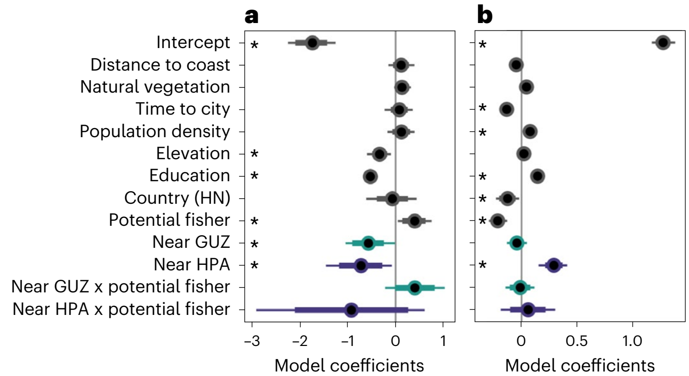


Fig. 3 | The probability of stunting is lower near marine protected areas (MPAs), and the mean wealth index is greater near highly protected areas (HPAs) than in areas far from MPAs. To assess the effects of MPA proximity on dimensions of human well-being, we used a quasi-experimental approach wherein we first matched survey clusters near (≤10 km) and far (>10 km) from MPAs on the basis of site characteristics and then quantified effects of MPA proximity on well-being outcomes using Bayesian hierarchical models. We controlled for remaining variation in matching variables by including them as covariates in our models. Plots show model coefficients that represent the effects of MPA proximity on the probability of (**a**) stunting (n = 1,919 individuals) and (**b**) mean wealth index (n = 2,117 respondents). Error bars represent 80% (thick) and 95% (thin) BCIs, and asterisks indicate mean effects with statistical support (95% BCIs excluding zero).

Lastly, where there was geographic overlap in fish and HWB datasets, we examined whether HWB of coastal communities covaries with fish abundance at the nearest sampled reef, to determine whether trade-offs or co-benefits in these outcomes exist across space. This analysis provides a complementary line of evidence to the separate analyses of MPA impacts on fish abundance and HWB. On average, the probability of stunting decreased while the probability of fish consumption increased with increasing fish biomass at nearby reef sites; however, estimated mean slopes were statistically indistinguishable from 0 (Extended Data Fig. 8). There was a significant positive association between fish biomass and household wealth index across coastal communities (Fig. 4 and Supplementary Table 14). When examining this overlapping subset of the data along the northern coasts of Guatemala and Honduras, proximity to both GUZs and HPAs had a significant positive effect on the wealth index (β_{GUZ} = 0.19, 95% BCI = (0.01, 0.36); β_{HPA} = 0.25, 95% BCI = (0.07, 0.43)). Coastal communities in Guatemala and Honduras are heavily dependent on both subsistence and commercial fisheries for their livelihoods and food security[40]. Fishers typically venture 5–15 km from ports[41] and navigate a mosaic of open-access waters interspersed among MPAs with multiple levels of restriction. The spatial association among fish biomass, MPAs and HWB indicators emphasizes the importance of verifying the ecological and social outcomes of conservation interventions beyond just area- and process-based indicators. Identifying contexts that have produced co-benefits in the past is necessary for promoting future synergies among SDGs related to food security, poverty alleviation and sustainable use of marine resources.

Discussion

Achieving the SDGs depends on the potential for interventions such as MPAs to improve HWB and ecological sustainability. Resolving the question of whether MPAs can simultaneously contribute to poverty

https://doi.org/10.1038/s41893-023-01150-4

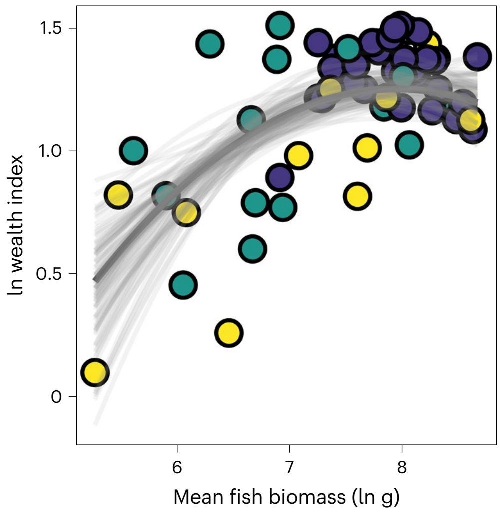


Fig. 4 | Fish biomass is positively associated with the wealth index of nearby communities. Communities near marine protected areas (MPAs), both general use zones (green) and highly protected areas (purple), had significantly higher income, as measured by a multivariate wealth index, compared with communities far from MPAs (yellow) (n = 58 pairs of reef sites and survey clusters). Heavy grey line represents the mean posterior effect of fish biomass on the wealth index, and light grey lines are 100 random samples from the posterior distribution.

alleviation (SDG 1), food security (SDG 2) and sustainable fisheries (SDG 14) requires evidence from impact evaluations that explicitly examine these co-benefits. Even within ecological and social domains, studies of MPA impacts on fish have only recently employed counterfactual-based methods of impact evaluation to strengthen causal inferences[17,30]. Likewise, systematic reviews have found that assessments of MPA effects on HWB infrequently used counterfactual designs[7,21]. Using a statistical matching approach to assess MPA impacts on both ecological and HWB outcomes, we find evidence of potential co-benefits for nature and people associated with MPAs, especially long-standing HPAs.

While there were positive HWB and fisheries outcomes associated with MPAs on average, we interpret these results cautiously in light of data limitations and future research needs. First, fish monitoring sites were non-randomly located with respect to environmental gradients and we were able to only partially mitigate spatial biases through statistical matching, requiring that we also control for post-matching variation in potential confounders in the models. Second, DHS data represent a snapshot of HWB in the region, allowing for control–impact comparisons but not before–after comparisons, limiting our ability to make strong inferences about the direction of causality. For example, it is uncertain whether local income remained high following establishment of HPAs or if it increased over time following MPA establishment. Third, the scope and resolution of the DHS data did not allow us to fully address nuances that probably underlie MPA effects on HWB, such as whether members of different social groups (for example, those engaged in fisheries versus tourism or business owners versus staff) experienced unequal benefits of MPAs[7,22]. Although there were apparent co-benefits between fish abundance and indicators of food security and income associated with MPAs, there may be trade-offs with other social dimensions such as equity and cultural dimensions[7]. Finally, there is also a need to further untangle the enabling conditions, policies and management approaches that have allowed for apparent synergies between fish assemblages and HWB in the region[4,42]. For example, examining the contributions of community-managed HPAs to socio-ecological outcomes as well as the gender equality of social outcomes are priorities. Increased integration of ecological and social outcomes into quantitative impact analyses[6] will be vital for determining the conditions under which continued expansion of MPAs will be successful in contributing to multiple SDGs globally.

As countries expand MPA coverage to meet area-based targets of the Post-2020 Biodiversity Framework and SDGs, numerous coastal communities will be affected by these interventions. Expanded MPA networks are unlikely to be effective and equitable without first determining the potential for co-benefits and the specific contexts under which MPAs can maintain marine resources while benefiting local communities. Here we find that (1) HPAs in the Mesoamerican region tend to support high fish abundance and stable or increasing trends. (2) Rather than experiencing reduced livelihoods and food security, for example through access restrictions, communities had greater food security near MPAs and higher incomes near HPAs specifically, mirroring a recent finding for terrestrial protected areas[43]. (3) Finally, MPAs themselves and the fisheries they support were both positively associated with HWB across coastal areas. Taken together, these results highlight the potential for synergies among SDGs at the nexus of MPAs, marine resources and local communities.

Methods

Fish assemblage and MPA data

We characterized means and trends in fish abundance using coral reef monitoring data collected through the Healthy Reefs Initiative (HRI), a multi-institutional collaboration that monitors the status of reef ecosystems and management efforts in the MAR region. Since 2005, underwater visual surveys (UVS) have been conducted at reef sites from the northern Yucatan Peninsula of Mexico southward to Belize and Guatemala and eastward along the northern coast of Honduras (Extended Data Fig. 1a). These UVS followed standard protocols developed by the Atlantic and Gulf Rapid Reef Assessment (AGRRA)[28]. Briefly, dive teams counted individuals of 83 monitored fish species (Supplementary Table 15) along 30 × 2 m belt transects. The focal species are a subset of fish assemblages found on Caribbean coral reefs and were chosen due to their ecological and commercial roles. The size class of each fish was recorded and biomass was estimated using species-specific allometric equations. Dive teams concurrently measured benthic variables at each site, including coral cover estimated as the proportion of 100 evenly spaced points along 10 m transects that intersect live coral.

We limited the pre-matching dataset to 139 sites that have been sampled during at least three different years (median of 5 years and maximum of 6 years) over the monitoring period (2005–2018). Sites were sampled once on a given year with at least 10 transects typically sampled per site on a given sampling occasion. Sites were categorized according to three broad levels of fishing restrictions that exist in the region: (1) 'open-access' fishing grounds wherein fishers adhere to national fisheries regulations to enter the fishery and MPAs, which are subdivided into (2) 'general use zones' (GUZs) and (3) 'highly protected areas' (HPAs). General use zones have variable levels of fishing restrictions that include a mixture of catch limits (for example, moratoriums) and bans on certain fishing gears (for example, fish traps). Highly protected areas have complete prohibition of commercial fishing on reefs (no-take zones), although some HPAs allow for traditional fishing practices and recreational catch and release. Most MPAs (HPAs and GUZs) are co-managed by a department within a national government and a non-government organization (NGO); however, community-led implementation of HPAs is increasing in the region, which is a fisher-led response to declines in landed catches and perceived associated benefits of HPAs. We used the World Database of Protected Areas (which excludes other area-based conservation measures) and shapefiles maintained by the Healthy Reefs Initiative to delineate MPAs. We derived two MPA variables: a static variable indicating whether a site was recognized as an MPA at any time during the monitoring period and a dynamic variable that reflected changes in site status (for example, open access to GUZ) at some sites during the

https://doi.org/10.1038/s41893-023-01150-4

monitoring period (see analyses). Enforcement of fishing restrictions in GUZs and HPAs was scored as part of an audit conducted by HRI, using standardized ratings based on surveys of NGOs, local managers and government agencies[44].

Demographic and health survey data

We quantified income and food security indicators from USAID Demographic and Health Surveys (DHS), a programme aimed at generating data for planning and evaluating nutrition and health programmes[29]. These data are collected in over 90 countries with 5,000–30,000 households surveyed per country during a survey year. Sampled households are spatially aggregated into survey clusters with up to 25 households sampled per cluster. At each household, interviewers administer household-level and individual-level questionnaires. We obtained survey responses for Guatemala and Honduras for the years 2011, 2012, 2014 and 2015 (Extended Data Fig. 1; surveys were not implemented in Mexico and Belize within the 2005–2018 timeframe of our analysis). We extracted responses from the DHS Standard Survey, which gathers information on education, housing conditions, wealth, nutrition and health indicators, among other topics.

To derive and analyse indicators of relative income and food security, we extracted responses from individual women and children surveys on child age, years of education attainment of women, an index of fish as a dietary component, height-for-age scores of children 6 months to 5 years old and a household wealth index. We also characterized broad occupational categories of 'potential fishers' and 'other occupations' from 32 possible occupation responses, such as 'teachers', 'health workers' and 'agriculture and fishery worker'. We compared households with 'potential fishers' to households with adult males (as surveyed) from other occupations to determine whether effects of MPAs are greater for fishers; although the category 'potential fishers' may also include agricultural workers, fishing is a predominant occupation in the coastal region of the study[27]. The wealth index is calculated by USAID as a linearized metric of multiple survey responses meant to characterize relative income on the basis of the presence at the household of a standardized suite of material items, such as a television, motorcycle and other items. Fish as a dietary component was quantified using a binary variable indicating whether a child had received fish/shellfish in the last 24 h or not. Height-for-age scores were reported as standard deviations (z-scores) calculated using the World Health Organization's (WHO) Child Growth Standards. From these scores, we derived a binary variable indicating whether a child was stunted using the WHO definition of stunting as height-for-age less than two standard deviations below the Child Growth Standards median[32].

Covariates

We characterized environmental variables associated with each site for pre-analysis matching and to further control for these variables in our models (Supplementary Tables 16 and 17). For analyses examining MPA impacts on reef fish abundance, we extracted three remotely sensed variables: human impact, ocean productivity and local climate change. Human modification of coastal areas around each site was quantified using the human footprint index, which is a composite of population densities, land use and infrastructure[45] and here serves as a proxy for direct human pressures on reefs, such as siltation and fishing. We extracted near-surface concentrations of chlorophyll a (mg m^{-3}) from NASA's MODIS product at each site, for each month between 2005–2018. Mean chlorophyll a concentrations were then calculated across the entire monitoring period (2005–2018) to capture variation in long-term average conditions among sites. These values largely reflect geographic variation in phytoplankton biomass, which can serve as an indicator of ocean productivity and at high values, eutrophication[46]. We characterized local climate changes as means of sea surface temperature (SST) anomalies from NOAA's Coral Reef Watch[47]. The SST anomaly data provide deviations of daily temperature from 28-year averages (from 1985–2012) of SST for each month. At each site, we calculated a mean of the maximum annual SST anomalies from 2005 to 2018. Positive values, therefore, represent increased frequency of temperatures above the long-term average at a given site. We also characterized depth, reef habitat type and mean live coral cover at each site from transect surveys (all covariates and hypothesized effects are listed in Supplementary Table 16).

For analyses examining MPA impacts on human well-being metrics, we measured spatial covariates within a 10 km radius centred around the GPS coordinates for each DHS survey cluster. These variables describe demographic and biophysical characteristics of sites that broadly characterize communities' placement along urban–rural gradients. These variables can influence dimensions of HWB, as access to employment and services are generally greater in developed, densely populated areas[33] (all covariates and hypothesized effects are listed in Supplementary Table 17). We characterized the amount of natural landcover for 2012 as derived from the European Space Agencies' CCI product[48] to align with the years of the DHS. Elevation of each cluster was measured using a digital elevation model derived from NASA's STRM data because elevation can constrain property values, suitability for agriculture and associated livelihoods, as well as ease of access to services[34,49]. We also characterized population densities using data from NASA's SERDAC v.4 2015 product and travel time to cities, which is heavily determined by proximity to urban centres and the least-cost path afforded by local road networks[33]. We measured the distance of each cluster to the nearest coast. Lastly, we characterized the mean education level and wealth index of DHS clusters for site matching.

Pre-analysis matching for fish abundance outcomes

The locations of MPAs are non-random and often biased toward ecologically intact areas, farther from population centres and with relatively low levels of fishing pressure[50]. When assessing the impacts of MPAs on fish assemblages (question and analysis 1 below), it is important to account for site characteristics that may affect fish abundances and can be biased with respect to MPA locations, including diffuse stressors such as climate change and coastal land use[50]. To account for these stressors and other observable confounding factors, we matched sites on the basis of SST anomalies, chlorophyll a concentrations, human footprint in nearby coastal areas, live coral cover, site depth and reef habitat type (Supplementary Tables 16 and 18).

We matched sites with the nearest multivariate Mahalanobis distance, thereby minimizing multivariate differences between sets of matching variables for each sample group. Sites were matched without replacement, achieving a 1:1 ratio of sites between pairs of sample groups. Because the majority of HRI sites are within GUZs (90 of 139 sites; Extended Data Fig. 1a), we separately matched GUZs as reference sites to 26 open-access and 23 HPA sites, using the static MPA variable. This approach was necessary to retain adequate sample sizes of open-access and HPA sites in the database while increasing balance of these samples with a reference category, here GUZ sites. Some variables remained moderately imbalanced post matching (Supplementary Table 18), and we controlled for this remaining variation by including matching variables as covariates in models (below). Post matching, we obtained 87 sites that were used in the analyses (26 open-access, 38 GUZ and 23 HPA sites; post-matching sample sizes are also provided in Supplementary Table 9). Unmatched GUZ samples were discarded from further analysis.

Pre-analysis matching for HWB outcomes

When assessing the impacts of MPAs on human well-being (question and analysis 2 below), we again used pre-analysis matching to pair DHS survey clusters near MPAs to those far from MPAs. We first subset survey clusters to those <30 km from a coast. We then calculated the distance of coastal clusters to the nearest MPA using polygons from the World Database of Protected Areas for GUZs and those from the Healthy Reefs

Initiative for HPAs. We excluded MPAs that were designated after the surveys were conducted. Survey clusters were then categorized as 'near to' or 'far from' an MPA using 10 km as a threshold distance. This threshold represents the scale at which we expect diminished impacts of MPAs, considering spillover of fish populations, distances typically travelled daily to fishing grounds and proximity of tourism[41,51], and it allows direct comparisons to a previous study of terrestrial protected areas[43]. We assessed the sensitivity of our results to the choice of distance thresholds by refitting models with thresholds of 5, 10, 15 and 20 km, finding that results were qualitatively similar (Extended Data Fig. 7).

We matched near and far survey clusters on the basis of geographic covariates that may influence HWB metrics, including natural land cover, elevation, population density, travel time to cities, distance to nearest coast, country, Caribbean versus Pacific coasts and education level of respondent (Supplementary Tables 17 and 19). Matched samples were again selected using Mahalanobis distances, here minimizing the sum of all pairwise distances and selecting one control (far from MPAs) for every treatment (near MPA) cluster without replacement. Unmatched survey clusters were not included in analyses. Because there was moderate imbalance in some covariates post matching, we again controlled for matching variables as covariates in all models. All matching was performed using the MatchIt package in R (ref. 52).

Sensitivity of HWB results

We further assessed the influence of covariate imbalance on HWB results by repeating the matching process using calipers. We set calipers that resulted in post-matching standardized mean differences in all covariates (between near and far clusters) that were <0.25 (Supplementary Table 20). The use of calipers resulted in loss of treatment sites (near MPAs) for which matches did not meet the threshold and therefore yielded a post-matching dataset with lower sample sizes. Nevertheless, the effects of MPA proximity on HWB indicators were qualitatively similar when using calipers, suggesting that the results are robust to decisions made about the matching approach (Supplementary Tables 21–23). See Supplementary Methods for analyses of sensitivity of results to potential hidden bias (and Supplementary Table 24).

Site pairing for associations between biomass and HWB outcomes

To examine associations between fish biomass and HWB indicators (question and analysis 3 below), we paired DHS clusters with the nearest-neighbour reef site in the HRI dataset (Extended Data Fig. 1c) for the region where there was spatial overlap in HWB and fish datasets along the Caribbean coasts of Guatemala and Honduras. In pairing nearest-neighbour survey clusters with reef sites, the order of sites was randomized and pairing was conducted without replacement.

Statistical analyses

To address our three overarching questions, we conducted three sets of analyses that quantified: (1) the effects of MPAs and their attributes on fish abundance in the region after statistical matching of sites (above), (2) the effect of proximity to MPAs on HWB using indicators of income, diet and stunting, after statistical matching of survey clusters (above) and (3) whether the condition of reef fish assemblages covaries with measures of HWB in nearby communities across pairs of nearest-neighbour reef sites and survey clusters (above).

Analyses of effects of MPAs on reef fish abundance

To evaluate potential co-benefits of MPAs for fish and HWB, we first examined the impacts of MPAs on fish assemblages. We estimated states and trends in fish abundance using Bayesian implementations of generalized linear mixed models (GLMMs). Models included environmental covariates—coral cover, chlorophyll, SST anomalies, human footprint and depth—to control for remaining variation post matching, while assessing the impacts of fishing restrictions (MPA type) and level of enforcement on fish abundance (see Supplementary Methods for the full model structure). For all analyses, we centred and scaled covariates and examined pairwise correlations among covariates (for all pairwise correlations, $r < 0.7$).

For analyses of total fish biomass and biomass of all commercially important species as the response, we fit models with a gamma probability distribution. This distribution was chosen because it accommodated the positive continuous outcome variables as well as the right-skewed distribution of commercially important biomass. Models of biomass trends included varying intercepts and slopes for the effect of year among individual sites to allow for spatial variation in estimates and account for spatial structure of the dataset (Supplementary Methods). Models of mean biomass across sites included varying intercepts among sites and years. For models of commercially important families, including snapper, grouper and grunts, we fit the same covariate and random effect structure as for biomass but instead used zero-inflated Poisson GLMMs to model counts and accommodate excess zeroes in the data for these groups.

To analyse variation in mean fish abundances (both biomass and counts) across sites, we fit models with a dynamic MPA variable that reflected changes in site status at some sites across survey years (primarily sites where GUZs were established in open-access areas during the monitoring period). When analysing variation in trends, to avoid confounding year and MPA effects in the model, we fit models with the static MPA variable that indicates whether a site was an MPA at any point during the monitoring period. To examine the effects of enforcement of fishing restrictions, we fit the same model structures as above but with a composite factor that combined fishing restrictions (open access, GUZ and HPA) and level of enforcement (inadequate, moderate or good). For example, HPA sites were categorized into three factor levels representing the level of enforcement at each site. On the basis of leave-one-out information criterion (LOOIC), we evaluated whether the inclusion of enforcement of fishing restrictions improved model fit over models that did not include enforcement level. To examine the effects of MPA age and area on mean abundance and trends, we subset the data to MPA sites and refit the base models above while including these MPA characteristics. Each of these models was run using two Markov chain Monte Carlo (MCMC) chains with a total of 5,000 iterations sampled at a thin rate of 20 iterations, 500 of which were discarded as burnin. We examined Gelman–Rubin statistics and traceplots to assess adequate mixing and convergence, and evaluated model fit using standard posterior predictive checks. All models addressing questions 1 and 2 were fit in Stan using the Brms package (v.2.16) to interface with the R environment (v.4.10)[53].

Analysis of effect of proximity to MPAs on HWB

We again used Bayesian GLMMs to analyse the effects of MPA proximity on HWB metrics from DHS data. We fit three main models, one for each outcome variable. When analysing indicators of stunting and fish diet as binary responses, we specified a binomial probability distribution in the likelihood function. We included DHS cluster as a varying intercept in the model to account for spatial non-independence of survey responses from the same cluster. All models were fit with additive covariates of distance to coast, natural land cover, time to city, population density, elevation, education and country, as well as the interaction between MPA proximity and occupation (Supplementary Methods).

When analysing stunting and fish diet as outcomes, we refit models with and without wealth index included as both a matching variable and model covariate to examine the partial effects of MPAs after controlling for wealth index. When analysing wealth index as the response variable, we fit models with the same general structure, except that we instead specified a negative binomial probability distribution appropriate for integers. To examine the contributions of additional covariates to all HWB outcome variables while being cautious to not overfit models, we then fit and compared a second set of models with an expanded covariate structure that included characteristics of MPAs, including MPA area and age as well as their interactions with MPA proximity. We compared the fit of base and expanded models using LOOIC. Each model was again run using two MCMC chains with a total of 5,000 iterations sampled at a thin rate of 20 iterations, 500 of which were discarded as burnin.

Analysis of associations between fish biomass and HWB

To examine covariation in total fish biomass and HWB metrics for pairs of nearest-neighbour reef sites and survey clusters, we conducted two-stage analyses. In the first stage, we estimated means of HWB metrics for each survey cluster using GLMMs. In the second stage, we fit models that simultaneously estimated mean fish biomass for each site while also modelling HWB estimates (the response) as a function of biomass estimates and fishing restrictions as covariates in linear models. We thereby integrated uncertainty in estimates of fish biomass estimates into each stage of the analyses.

In the first stage of the analysis, we estimated mean wealth index (quartiles) for each survey cluster as a varying intercept in a GLMM with a negative binomial likelihood function to accommodate integers and potential overdispersion (see Supplementary Methods for the full model structure). Similarly, we estimated the mean probability of stunting and fish consumption at each cluster as a varying intercept in a GLMM with a binomial probability distribution in the likelihood function. Then, in the second stage, we fit a submodel to estimate biomass for each reef site as a varying intercept. Here, focusing on total biomass, we fit a model with a Gaussian error distribution, as total biomass was normally distributed. At the same time, we fit a submodel of variation in estimated wealth index for each survey cluster as a linear function of mean total fish biomass of the nearest-neighbour reef site and whether clusters are near GUZs or HPAs. As the relationship between wealth index and fish biomass was curvilinear, we included a polynomial term in the model (Supplementary Table 14). To model variation in the probability of stunting and fish consumption in response to fish biomass and MPAs, we specified a beta probability distribution in the likelihood function, as the responses varied between 0 and 1. We fit two-stage models in JAGS and used the jagsUI package to implement models from the R environment. To sample the posterior from adequately converged chains, models were ultimately run with four chains for 10,000 iterations at a sampling rate of 20 iterations, discarding 5,000 iterations as burnin.

Reporting summary

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

Data availability

All data used in this study were obtained from open sources listed in Supplementary Tables 16 and 17. Ecological data are available on www.agrra.org, with some years also displayed in healthyreefs.org. Human well-being indicators are freely available from www.dhsprogram.com/data.

Code availability

The R and JAGS code used for analyses are available upon reasonable request to the corresponding author.

References

1. *Transforming Our World: the 2030 Agenda for Sustainable Development* (United Nations, 2015).
2. Hopkins, S. R. et al. How to identify win–win interventions that benefit human health and conservation. *Nat. Sustain.* **4**, 298–304 (2021).
3. Nilsson, M., Griggs, D. & Visbeck, M. Policy: map the interactions between Sustainable Development Goals. *Nature* **534**, 320–322 (2016).
4. Singh, G. G. et al. A rapid assessment of co-benefits and trade-offs among Sustainable Development Goals. *Mar. Policy* **93**, 223–231 (2018).
5. McElwee, P. et al. The impact of interventions in the global land and agri-food sectors on Nature's Contributions to People and the UN Sustainable Development Goals. *Glob. Change Biol.* **26**, 4691–4721 (2020).
6. Baylis, K. et al. Mainstreaming impact evaluation in nature conservation. *Conserv. Lett.* **9**, 58–64 (2016).
7. Gill, D. A. et al. Social synergies, tradeoffs, and equity in marine conservation impacts. *Annu. Rev. Environ. Resour.* **44**, 347–372 (2019).
8. Sims, K. R. E. & Alix-Garcia, J. M. Parks versus PES: evaluating direct and incentive-based land conservation in Mexico. *J. Environ. Econ. Manage.* **86**, 8–28 (2017).
9. Ferraro, P. J. et al. Estimating the impacts of conservation on ecosystem services and poverty by integrating modeling and evaluation. *Proc. Natl Acad. Sci. USA* **112**, 7420–7425 (2015).
10. *Global Indicator Framework for the Sustainable Development Goals and Targets of the 2030 Agenda for Sustainable Development* (United Nations, 2018).
11. *Protected Planet Live Report* (UNEP-WCMC, IUCN and NGS, 2021).
12. *Kunming-Montreal Global biodiversity Framework: Draft Decision Submitted by the President* (Convention on Biological Diversity, 2022).
13. Halpern, B. S. & Warner, R. R. Marine reserves have rapid and lasting effects. *Ecol. Lett.* **5**, 361–366 (2002).
14. Cinner, J. E. et al. Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science* **368**, 307–311 (2020).
15. Claudet, J. et al. Marine reserves: size and age do matter. *Ecol. Lett.* **11**, 481–489 (2008).
16. Edgar, G. J. et al. Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216–220 (2014).
17. Gill, D. A. et al. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* **543**, 665–669 (2017).
18. Turnbull, J. W., Johnston, E. L. & Clark, G. F. Evaluating the social and ecological effectiveness of partially protected marine areas. *Conserv. Biol.* **35**, 921–932 (2021).
19. Costello, M. J. & Ballantine, B. Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. *Trends Ecol. Evol.* **30**, 507–509 (2015).
20. Pollnac, R. & Seara, T. Factors influencing success of marine protected areas in the Visayas, Philippines as related to increasing protected area coverage. *Environ. Manage.* **47**, 584–592 (2011).
21. Ban, N. C. et al. Well-being outcomes of marine protected areas. *Nat. Sustain.* **2**, 524–532 (2019).
22. Mascia, M. B., Claus, C. A. & Naidoo, R. Impacts of marine protected areas on fishing communities. *Conserv. Biol.* **24**, 1424–1429 (2010).
23. Bennett, N. J. & Dearden, P. From measuring outcomes to providing inputs: governance, management, and local development for more effective marine protected areas. *Mar. Policy* **50**, 96–110 (2014).
24. Mascia, M. B. & Claus, C. A. A property rights approach to understanding human displacement from protected areas: the case of marine protected areas. *Conserv. Biol.* **23**, 16–23 (2009).
25. McKinnon, M. C. et al. What are the effects of nature conservation on human well-being? A systematic map of empirical evidence from developing countries. *Environ. Evid.* **5**, 8 (2016).
26. Conservation Effectiveness. *Visualizing the Effectiveness of Conservation Strategies* https://www.conservationeffectiveness.org/ (2021).

27. Kramer, P. A. & Kramer, P. R. *Ecoregional Conservation Planning for the Mesoamerican Caribbean Reef* (WWF, 2002).
28. Lang, J. C., Marks, K. W., Kramer, P. A., Kramer, P. R. & Ginsburg, R. N. *AGRRA Protocols Version 5.4* (Atlantic and Gulf Rapid Reef Assessment Program, 2010).
29. *Demographic and Health Survey Interviewer's Manual* (ICF, 2020).
30. Ahmadia, G. N. et al. Integrating impact evaluation in the design and implementation of monitoring marine protected areas. *Phil. Trans. R. Soc. B* **370**, 20140275 (2015).
31. Babcock, R. C. et al. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proc. Natl Acad. Sci. USA* **107**, 18256–18261 (2010).
32. *Reducing Stunting in Children: Equity Considerations for Achieving the Global Nutrition Targets 2025* (World Health Organization, 2018).
33. Weiss, D. J. et al. A global map of travel time to cities to assess inequalities in accessibility in 2015. *Nature* **553**, 333–336 (2018).
34. Okwi, P. O. et al. Spatial determinants of poverty in rural Kenya. *Proc. Natl Acad. Sci. USA* **104**, 16769–16774 (2007).
35. Canty, S. W. J. & Deichmann, J. L. Do small-scale fisheries have the capacity to provide food security to coastal populations? *Fish Fish.* **23**, 708–718 (2022).
36. Hicks, C. C. et al. Harnessing global fisheries to tackle micronutrient deficiencies. *Nature* **574**, 95–98 (2019).
37. *The State of World Fisheries and Aquaculture 2018*: *Meeting the Sustainable Development Goals* (FAO, 2018).
38. Hruschka, D. J., Gerkey, D. & Hadley, C. Estimating the absolute wealth of households. *Bull. World Health Organ.* **93**, 483–490 (2015).
39. Garcia, S. M., Charles, A., Sanders, J. & Westlund, L. in *Marine Protected Areas: Interactions with Fishery Livelihoods and Food Security* (FAO, 2018).
40. Canty, S. et al. The hidden value of artisanal fisheries in Honduras. *Fish. Manage. Ecol.* **26**, 249–259 (2019).
41. Chollett, I., Canty, S. W. J., Box, S. J. & Mumby, P. J. Adapting to the impacts of global change on an artisanal coral reef fishery. *Ecol. Econ.* **102**, 118–125 (2014).
42. Grorud-Colvert, K. et al. The MPA Guide: a framework to achieve global goals for the ocean. *Science* **373**, eabf0861 (2021).
43. Naidoo, R. et al. Evaluating the impacts of protected areas on human well-being across the developing world. *Sci. Adv.* **5**, eaav3006 (2019).
44. Healthy Reefs Initiative. *Eco-audit 2021* https://eco-audits.healthyreefs.org/ (2021).
45. Venter, O. et al. Global terrestrial Human Footprint maps for 1993 and 2009. *Sci. Data* **3**, 160067 (2016).
46. Ha, N. T. T., Koike, K. & Nhuan, M. T. Improved accuracy of chlorophyll-a concentration estimates from MODIS imagery using a two-band ratio algorithm and geostatistics: as applied to the monitoring of eutrophication processes over Tien Yen Bay (Northern Vietnam). *Remote Sens.* **6**, 421–442 (2014).
47. Skirving, W. et al. CoralTemp and the Coral Reef Watch Coral Bleaching Heat Stress Product Suite Version 3.1. *Remote Sens.* **12**, 3856 (2020).
48. ESA. *Land Cover CCI Product User Guide Version 2* maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf (2017).
49. Muyanga, M. & Jayne, T. S. Effects of rising rural population density on smallholder agriculture in Kenya. *Food Policy* **48**, 98–113 (2014).
50. Kuempel, C. D., Jones, K. R., Watson, J. E. M. & Possingham, H. P. Quantifying biases in marine-protected-area placement relative to abatable threats. *Conserv. Biol.* **33**, 1350–1359 (2019).
51. Hallpern, B. S., Lester, S. E. & Kellner, J. B. Spillover from marine reserves and the replenishment of fished stocks. *Environ. Conserv.* **36**, 268–276 (2009).
52. Stuart, E. A., King, G., Imai, K. & Ho, D. MatchIt: nonparametric preprocessing for parametric causal inference. *J. Stat. Softw.* **42**, 1–28 (2011).
53. Bürkner, P.-C. brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).
54. Protected Planet. *The World Database on Protected Areas (WDPA)* www.protectedplanet.net (UNEP-WCMC and IUCN, 2020).
55. Esri. *Oceans Basemap* https://www.arcgis.com/home/item.html?id=5ae9e138a17842688b0b79283a4353f6 (2020).
56. Esri. *World Countries* https://hub.arcgis.com/maps/esri::world-countries-generalized/about (2020).

Acknowledgements

We thank the many people who collected, processed, collated and made available the data underlying this study, particularly the 74 partner organizations within the Healthy Reefs Initiative (www.healthyreefs.org/partners). Primary funding for reef surveys was provided by Summit Foundation and Oak Foundation. S.W.J.C. and M.M. were supported by Summit Foundation. S.C. thanks the generous support received from Betty and Gordon Moore. A.J.N. was supported by a Smithsonian SI-CI Postdoctoral Fellowship. This is Smithsonian Marine Station contribution number 1191.

Author contributions

A.J.N., S.W.J.C. and N.B. designed the study. S.W.J.C., C.C., A.V. and M.M. contributed to field data collection on reefs. M.M. oversaw ecological data acquisition, compilation., and funding. A.J.N. collated data, conducted analyses., and led manuscript preparation. A.J.N., S.W.J.C., N.B., C.C., A.V., J.L.D., T.S.A., S.E.B.-A., S.C. and M.M. all contributed to substantive revisions and edits.

Competing interests

The authors declare no competing interests.

Additional information

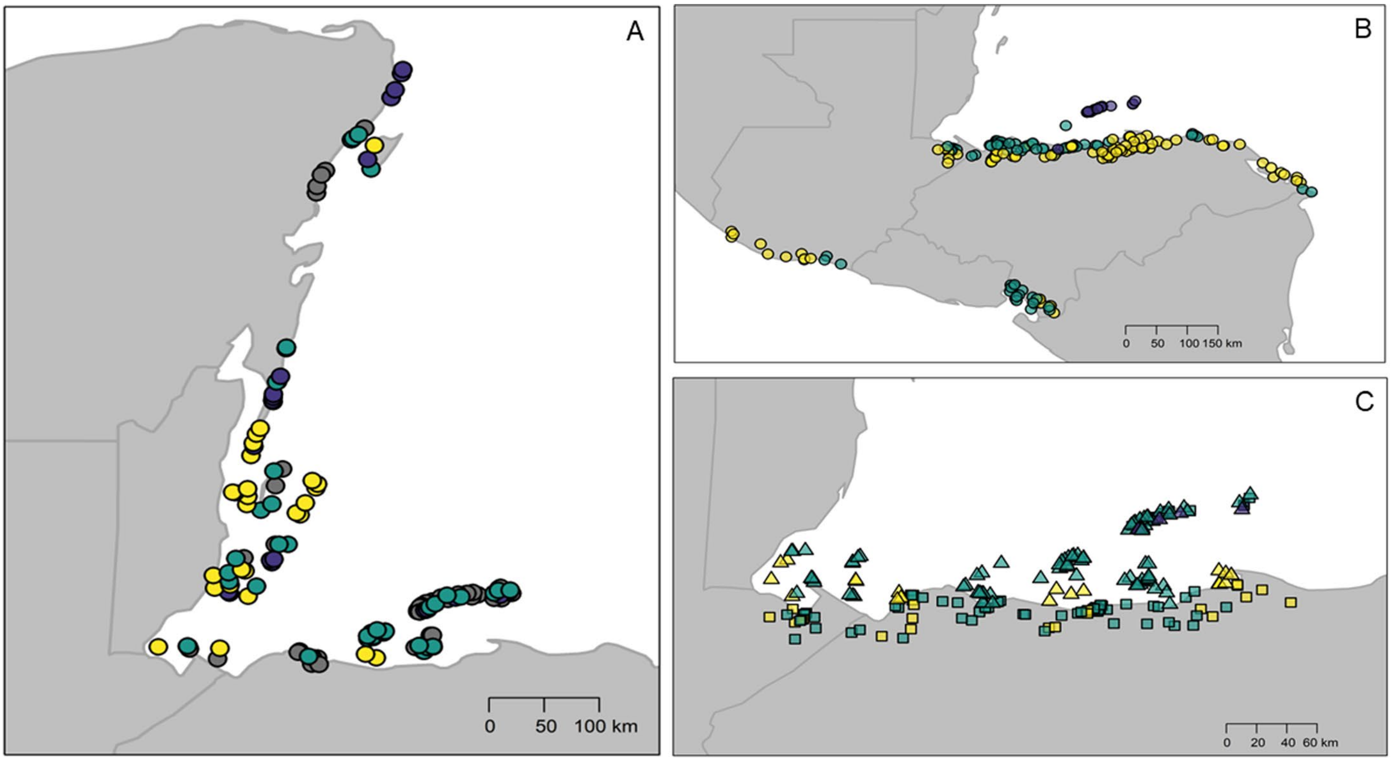
Extended data is available for this paper at https://doi.org/10.1038/s41893-023-01150-4.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41893-023-01150-4.

Correspondence and requests for materials should be addressed to A. Justin Nowakowski.

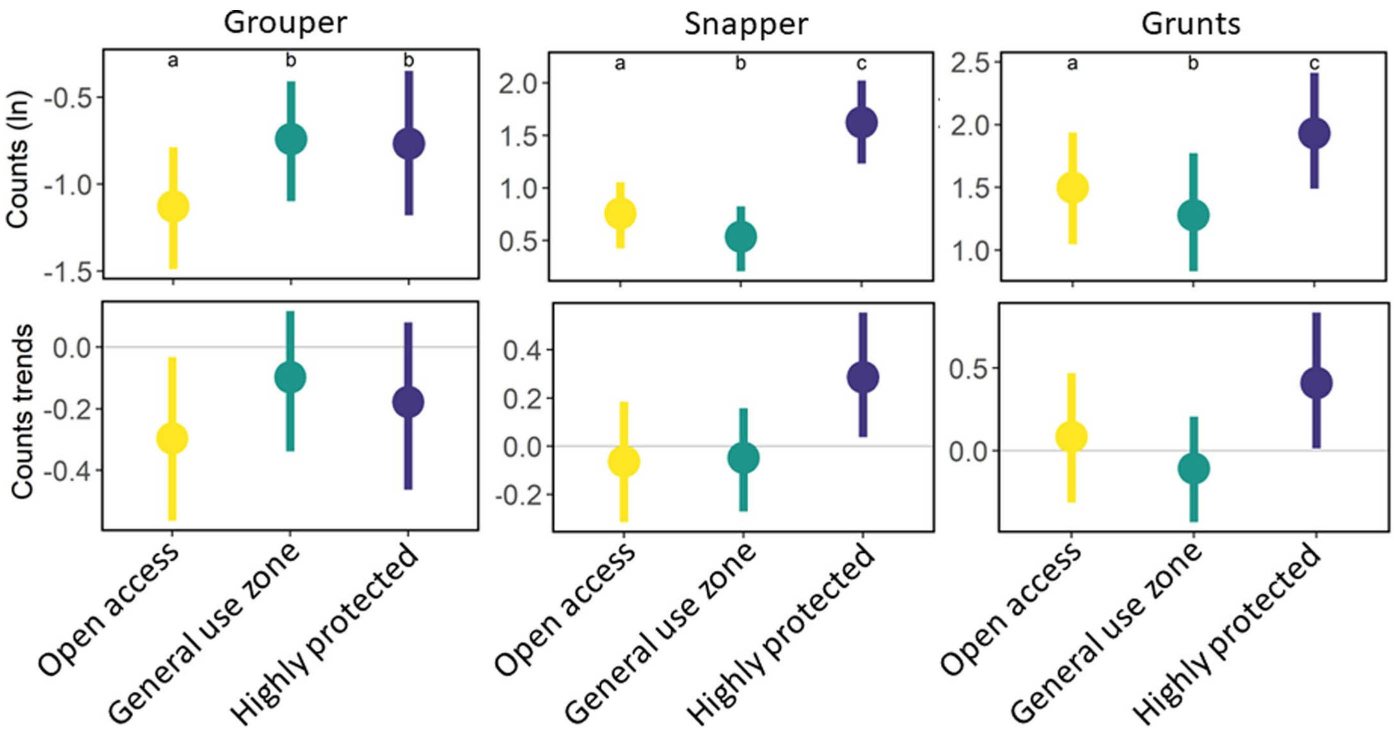
Peer review information *Nature Sustainability* thanks Elliott Hazen, M. Aaron MacNeil and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

 https://doi.org/10.1038/s41893-023-01150-4



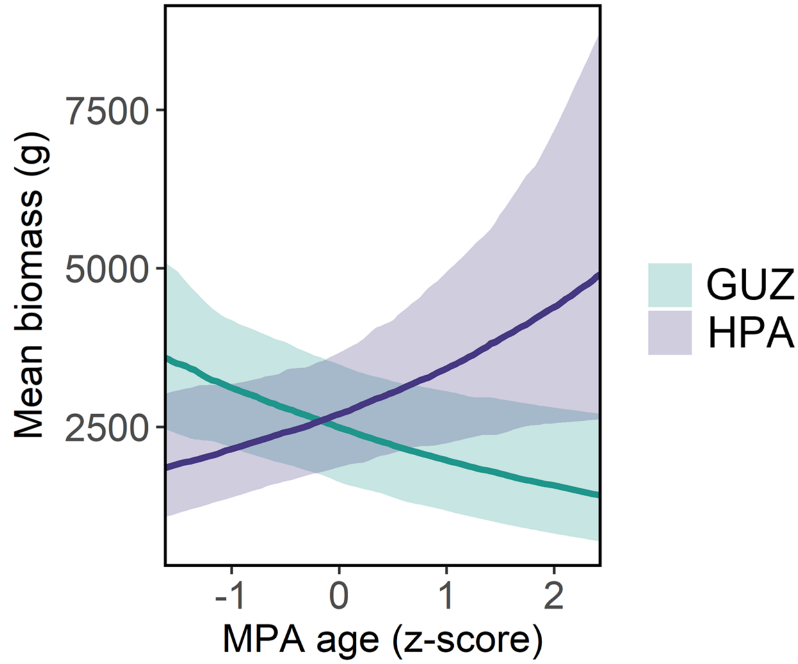
Extended Data Fig. 1 | Maps of monitored reef sites and Demographic and Health Survey (DHS) clusters in coastal areas. (**A**) To examine the effects of marine protected areas (MPAs) on fish abundance, we analysed monitoring data from reef sites (n = 87) along coastal waters of Mexico, Belize, Guatemala and Honduras in open access waters (yellow) and in general use (GUZs; green) and highly protected areas (HPAs; purple) of MPAs. Unmatched sites are shown in grey. (**B**) To determine whether MPAs affect indicators of human well-being, we analysed survey responses for up to 2,117 individuals from 222 matched DHS clusters along coasts of Guatemala and Honduras that were far from MPAs (>10 km; yellow) or near GUZs (≤10 km; green) or HPAs (purple). (**C**) To evaluate potential tradeoffs or synergies between human well-being and fish assemblages across space, we analysed fish biomass and indicators of food security and income from nearest neighbour reef sites (triangles) and DHS clusters (squares) along the Atlantic coast of Guatemala and Honduras. Map data are from sources in refs. 28,29,56.

https://doi.org/10.1038/s41893-023-01150-4



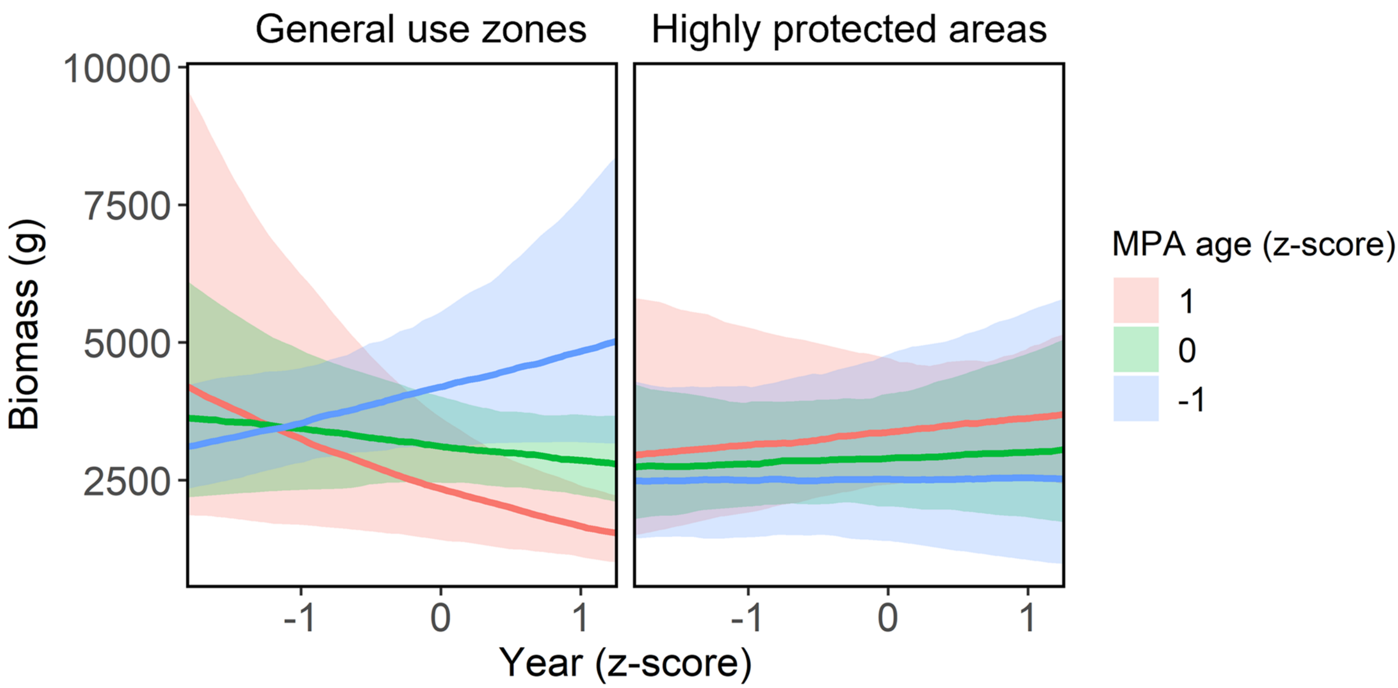
Extended Data Fig. 2 | Mean abundance and trends in open access sites and general use (GUZs) and highly protected areas (HPAs) of marine protected areas (MPAs) (n = 4,336 transects sampled at 87 sites). To assess the effects of fishing restrictions associated with MPAs on assemblages, we used a quasi-experimental approach wherein we first matched survey sites based on site characteristics and then quantified effects of fishing restrictions (GUZs versus HPAs) while controlling for remaining variation in matching variables in Bayesian hierarchical models. Plots show estimated effects of fishing restrictions on means and trends in counts for three commercially important fish families. Error bars represent 95% Bayesian credible intervals, and letters indicate difference among groups that have statistical support – that is, 95% BCIs for contrasts exclude zero.

https://doi.org/10.1038/s41893-023-01150-4



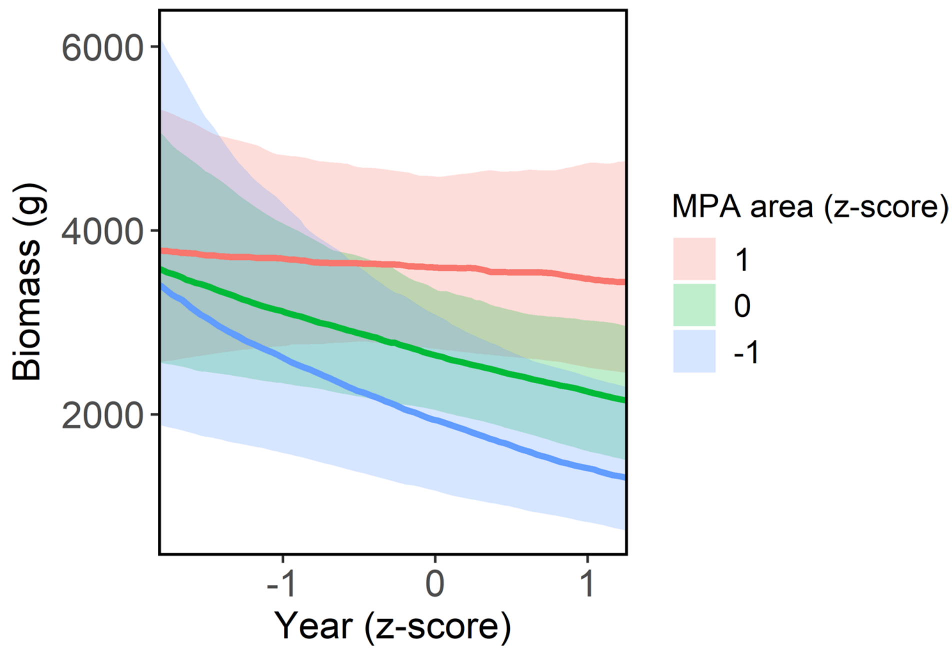
Extended Data Fig. 3 | Interactive effects of fishing restrictions and age of marine protected areas (MPAs) on mean total fish biomass (n = 2,596 transects sampled at 61 sites). Mean predictions (lines) and 95% credible bands (shaded areas) are from Bayesian hierarchical models fit with interaction terms for MPA age and fishing restrictions while controlling for leftover variation in matching variables. MPA age is centreed and scaled (z-score).

https://doi.org/10.1038/s41893-023-01150-4

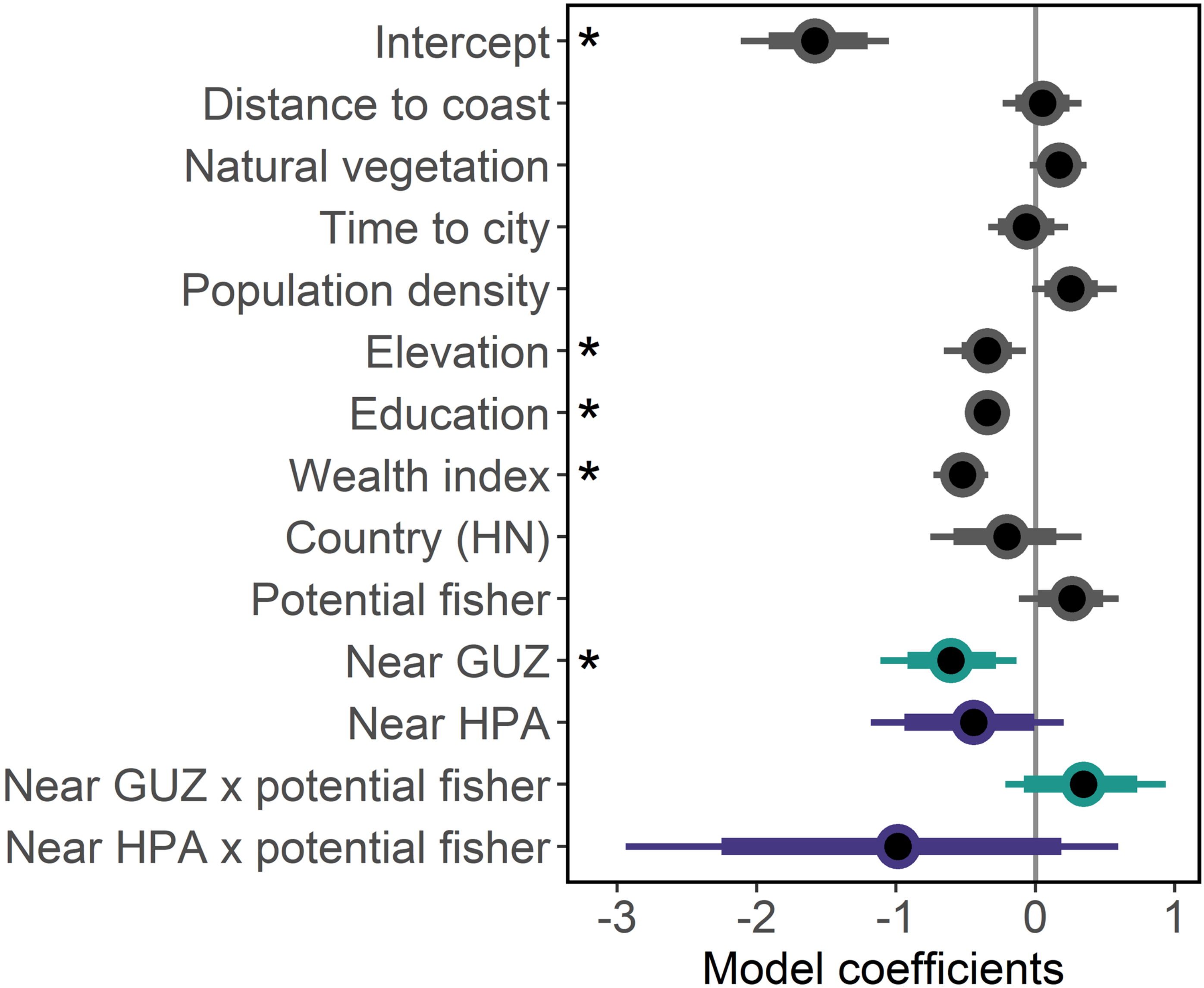


Extended Data Fig. 4 | Interactive effects of fishing restrictions and age of marine protected areas (MPAs) on trends in total fish biomass (n = 3,102 transects sampled at 61 sites). Mean predictions (lines) and 95% credible bands (shaded areas) are from Bayesian hierarchical models fit with interaction terms among MPA age, fishing restrictions, and year while controlling for leftover variation in matching variables. Year is centred and scaled (z-score).

https://doi.org/10.1038/s41893-023-01150-4

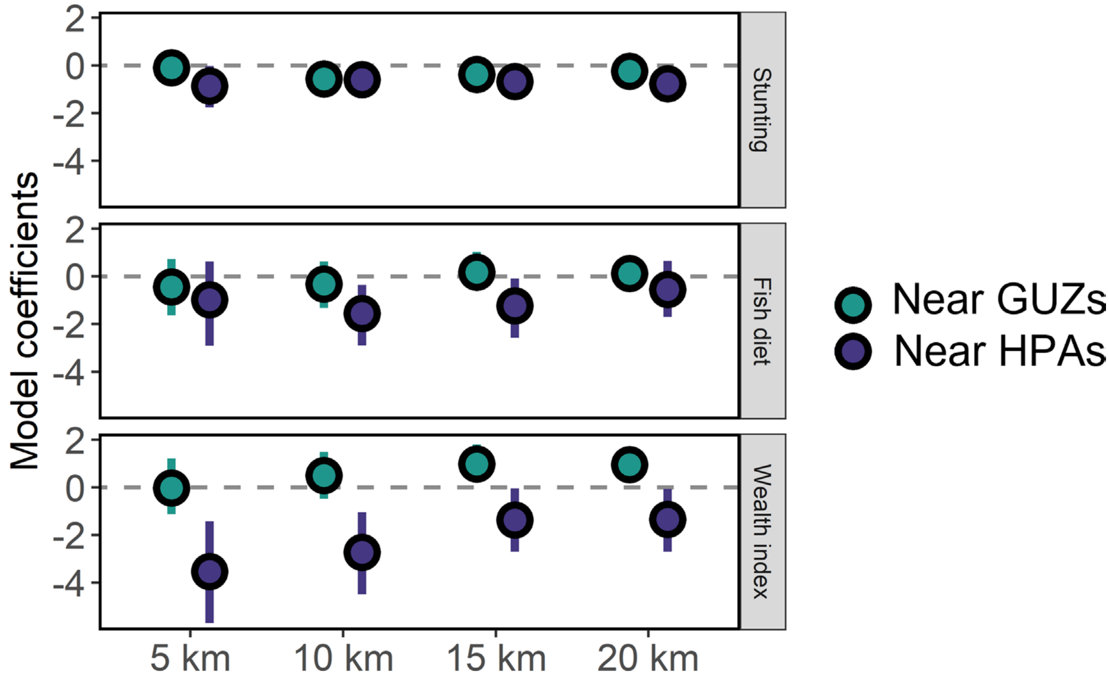


Extended Data Fig. 5 | Effects of size of marine protected areas (MPAs) on trends in total fish biomass (n = 3,102 transects sampled at 61 sites). Mean predictions (lines) and 95% credible bands (shaded areas) are from Bayesian hierarchical models fit with interaction terms for MPA area and year while controlling for leftover variation in matching variables. Year is centred and scaled (z-score).



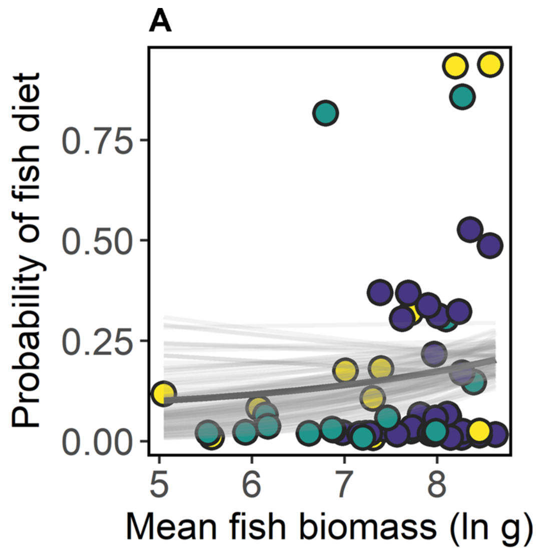
Extended Data Fig. 6 | The probability of stunting (n = 1,880 individuals) is lower near marine protected areas (MPAs) than areas far from MPAs. Plot shows model coefficients that represent the effects of MPA proximity on probability of stunting, here while controlling for wealth index. To assess the effects of MPA proximity on dimensions of human wellbeing, we used a quasi-experimental approach wherein we first matched survey clusters near and far from MPAs based on site characteristics and then quantified effects of MPA proximity while controlling for remaining variation in matching variables using Bayesian hierarchical models. Error bars represent 80% (thick) and 95% (thin) Bayesian credible intervals (BCI), and asterisks indicate mean effects with statistical support – 95% BCIs exclude zero.

 https://doi.org/10.1038/s41893-023-01150-4



Extended Data Fig. 7 | Effects of proximity to general use zones (GUZ) and highly protected areas (HPA) on well-being indicators are qualitatively similar under different choices of threshold distances for defining clusters near and far from these zones of marine protected areas (MPAs). Model coefficients are from Bayesian hierarchical models fit as in Fig. 3, while defining threshold distance as 5, 10, 15, or 20 km. Coefficients represent mean differences relative to the reference category of clusters far from MPAs. Error bars represent 95% Bayesian credible intervals. Sample sizes varied across datasets when applying different distance thresholds. For the stunting outcome, n for 5 km = 1251, 10 km = 1919, 15 km = 2611, and 20 km = 2843. For the fish diet outcome, n for 5 km = 796, 10 km = 1305, 15 km = 1801, and 20 km = 2012. For the wealth index outcome, n for 5 km = 1382, 10 km = 2117, 15 km = 2866, and 20 km = 3121.

 https://doi.org/10.1038/s41893-023-01150-4



Extended Data Fig. 8 | Association between fish biomass and probability of fish consumption (A) and stunting (B) in nearby communities. Colours indicate communities near general use zones (green) and highly protected areas (purple) of marine protected areas (MPAs) and those far from MPAs (yellow). Heavy grey line represents the mean posterior effect of fish biomass on human well-being indicators, and light grey lines are 100 random samples from the posterior distribution. For the fish diet outcome, n = 56 pairs of reef sites and survey clusters. For the stunting outcome, n = 58 pairs of reef sites and survey clusters.

nature research

Corresponding author(s): Aaron Justin Nowakowski

Last updated by author(s): May 6, 2022

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☐	☒	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used
Data analysis	All analyses were conducted using the R open source statistical platform (v4.10). R packages used for analyses included MatchIt (v4.4.0), Brms (v2.16), and jagsUI (v1.5.2). The R and JAGS code used for analyses are available upon request to the corresponding author.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

All data are available through open sources listed in the manuscript. Reef monitoring data are available on www.agrra.org, with some years also displayed in healthyreefs.org/dataexplorer. USAID Demographic and Health Surveys data are available upon request at dhsprogram.com/data/.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	*Describe how sample size was determined, detailing any statistical methods used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient.*
Data exclusions	*Describe any data exclusions. If no data were excluded from the analyses, state so OR if data were excluded, describe the exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.*
Replication	*Describe the measures taken to verify the reproducibility of the experimental findings. If all attempts at replication were successful, confirm this OR if there are any findings that were not replicated or cannot be reproduced, note this and describe why.*
Randomization	*Describe how samples/organisms/participants were allocated into experimental groups. If allocation was not random, describe how covariates were controlled OR if this is not relevant to your study, explain why.*
Blinding	*Describe whether the investigators were blinded to group allocation during data collection and/or analysis. If blinding was not possible, describe why OR explain why blinding was not relevant to your study.*

Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	*Briefly describe the study type including whether data are quantitative, qualitative, or mixed-methods (e.g. qualitative cross-sectional, quantitative experimental, mixed-methods case study).*
Research sample	*State the research sample (e.g. Harvard university undergraduates, villagers in rural India) and provide relevant demographic information (e.g. age, sex) and indicate whether the sample is representative. Provide a rationale for the study sample chosen. For studies involving existing datasets, please describe the dataset and source.*
Sampling strategy	*Describe the sampling procedure (e.g. random, snowball, stratified, convenience). Describe the statistical methods that were used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient. For qualitative data, please indicate whether data saturation was considered, and what criteria were used to decide that no further sampling was needed.*
Data collection	*Provide details about the data collection procedure, including the instruments or devices used to record the data (e.g. pen and paper, computer, eye tracker, video or audio equipment) whether anyone was present besides the participant(s) and the researcher, and whether the researcher was blind to experimental condition and/or the study hypothesis during data collection.*
Timing	*Indicate the start and stop dates of data collection. If there is a gap between collection periods, state the dates for each sample cohort.*
Data exclusions	*If no data were excluded from the analyses, state so OR if data were excluded, provide the exact number of exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.*
Non-participation	*State how many participants dropped out/declined participation and the reason(s) given OR provide response rate OR state that no participants dropped out/declined participation.*
Randomization	*If participants were not allocated into experimental groups, state so OR describe how participants were allocated to groups, and if allocation was not random, describe how covariates were controlled.*

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We assessed the ability of marine protected areas (MPAs) to induce co-benefits for fisheries and nearby coastal communities. We examined three underlying questions: (1) What are the impacts of MPAs with different attributes on fish assemblages in the region? (2) What are the effects of MPAs on income, diet, and food security of nearby communities? And (3), looking across coastal areas, does HWB of local communities covary with the condition of fish assemblages at nearby reefs? We use a long-term dataset of

	underwater visual surveys to characterize fish assemblages and USAID Demographic and Health Surveys (DHS) data to characterize dimensions of HWB in nearby coastal communities, including income, diet, and food security. To reduce potential confounding effect of environmental variables, we used statistical matching of trends inside and outside MPAs (fish data) and survey clusters near and far from MPAs (human well-being data). We then applied a Bayesian multilevel modeling framework to examine the effects of MPAs on fish asssemblages and measures of human well-being. All models were fit with matching variables as covariates to control for remaining variation post-matching.
Research sample	The fish dataset, post-matching, included observations of 83 fish species along 4,336 transects sampled at 87 sites in the Caribbean coastal waters of Mexico, Belize, Guatemala, and Honduras. Each site was sampled during at least three different years from 2005-2018. We quantified income and food security metrics from USAID Demographic and Health Surveys (DHS). This dataset contained survey responses for 2,201 individuals at 219 survey clusters along the coasts of Guatemala and Honduras, from 2011, 2012, 2014, and 2015.
Sampling strategy	Sample sizes reflect the largest number of sites that were available after harmonizing open datasets, quality control, applying inclusion criteria, and statistical matching.
Data collection	All data used in this study were obtained from open sources. Reef monitoring data are available on www.agrra.org, with some years also displayed in healthyreefs.org/dataexplorer. USAID Demographic and Health Surveys data are available upon request at dhsprogram.com/data/
Timing and spatial scale	The spatial scale of the analysis is across multiple countries in Mesoamerica. Fish assemblages data consisted of repeated abundance observations at discrete sampling locations in the coastal waters of Mexico, Belize, Guatemala, and Honduras. Each reef site was sampled during at least three different years from 2005-2018. Poverty and food security data were from coastal communities of Guatemala and Honduras and were generated from surveys that were conducted in 2011, 2012, 2014, and 2015.
Data exclusions	For fish assemblage data, we excluded reef sites that were sampled during fewer than three different years, resulting in 139 reef sites available pre-matching. We then conducted statistical matching yielding 87 matched sites for analyses. For poverty and food security data, we excluded all USAID survey clusters that were > 30 km from a coast and then matched sites far from MPAs to those near MPAS, resulting in 2,201 survey responses from 219 clusters (communities). Unmatched samples were discarded from further analysis.
Reproducibility	While not a true experiment, we analyzed multiple subsets of the data and applied multiple analytical approaches (reported in methods), finding that our results were robust to these assessments. Data are open access and analysis code will be available on Figshare.
Randomization	Data were not randomized but represent a large sample analyzed within a quasi-experimental framework. In large scale, retrospective impact assessments of conservation interventions, true randomization is often not possible. We identified appropriate controls using statistical matching, whereby control sties were selected from a larger pool of potential controls by matching with treatment sites (those in or near MPAs) on the basis of potentially confounding covariates (e.g., population density, natural habitat cover, etc.). We matched treatment sites and potential controls using multivariate Mahalanobis distances, based on sets matching variables, resulting in a 1:1 ratio of samples in and outside of MPAs (or near and far from MPAs).
Blinding	Blinding was not used or necessary as no experimental procedures were used that could be prone to observer biases.

Did the study involve field work? ☐ Yes ☒ No

Field work, collection and transport

Field conditions	NA
Location	NA
Access & import/export	NA
Disturbance	NA

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Antibodies

Antibodies used

Describe all antibodies used in the study; as applicable, provide supplier name, catalog number, clone name, and lot number.

Validation

Describe the validation of each primary antibody for the species and application, noting any validation statements on the manufacturer's website, relevant citations, antibody profiles in online databases, or data provided in the manuscript.

Eukaryotic cell lines

Policy information about cell lines

Cell line source(s)

State the source of each cell line used.

Authentication

Describe the authentication procedures for each cell line used OR declare that none of the cell lines used were authenticated.

Mycoplasma contamination

Confirm that all cell lines tested negative for mycoplasma contamination OR describe the results of the testing for mycoplasma contamination OR declare that the cell lines were not tested for mycoplasma contamination.

Commonly misidentified lines
(See ICLAC register)

Name any commonly misidentified cell lines used in the study and provide a rationale for their use.

Palaeontology and Archaeology

Specimen provenance

Provide provenance information for specimens and describe permits that were obtained for the work (including the name of the issuing authority, the date of issue, and any identifying information).

Specimen deposition

Indicate where the specimens have been deposited to permit free access by other researchers.

Dating methods

If new dates are provided, describe how they were obtained (e.g. collection, storage, sample pretreatment and measurement), where they were obtained (i.e. lab name), the calibration program and the protocol for quality assurance OR state that no new dates are provided.

☐ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

Ethics oversight

Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals

NA

Wild animals

Provide details on animals observed in or captured in the field; report species, sex and age where possible. Describe how animals were caught and transported and what happened to captive animals after the study (if killed, explain why and describe method; if released, say where and when) OR state that the study did not involve wild animals.

Field-collected samples

For laboratory work with field-collected samples, describe all relevant parameters such as housing, maintenance, temperature, photoperiod and end-of-experiment protocol OR state that the study did not involve samples collected from the field.

Ethics oversight

Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Human research participants

Policy information about studies involving human research participants

Population characteristics	*Describe the covariate-relevant population characteristics of the human research participants (e.g. age, gender, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."*
Recruitment	*Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.*
Ethics oversight	*Identify the organization(s) that approved the study protocol.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Clinical data

Policy information about clinical studies

All manuscripts should comply with the ICMJE guidelines for publication of clinical research and a completed CONSORT checklist must be included with all submissions.

Clinical trial registration	*Provide the trial registration number from ClinicalTrials.gov or an equivalent agency.*
Study protocol	*Note where the full trial protocol can be accessed OR if not available, explain why.*
Data collection	*Describe the settings and locales of data collection, noting the time periods of recruitment and data collection.*
Outcomes	*Describe how you pre-defined primary and secondary outcome measures and how you assessed these measures.*

Dual use research of concern

Policy information about dual use research of concern

Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes	
☐	☐	Public health
☐	☐	National security
☐	☐	Crops and/or livestock
☐	☐	Ecosystems
☐	☐	Any other significant area

Experiments of concern

Does the work involve any of these experiments of concern:

No	Yes	
☐	☐	Demonstrate how to render a vaccine ineffective
☐	☐	Confer resistance to therapeutically useful antibiotics or antiviral agents
☐	☐	Enhance the virulence of a pathogen or render a nonpathogen virulent
☐	☐	Increase transmissibility of a pathogen
☐	☐	Alter the host range of a pathogen
☐	☐	Enable evasion of diagnostic/detection modalities
☐	☐	Enable the weaponization of a biological agent or toxin
☐	☐	Any other potentially harmful combination of experiments and agents

ChIP-seq

Data deposition

☐ Confirm that both raw and final processed data have been deposited in a public database such as GEO.

☐ Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

Data access links *May remain private before publication.*	*For "Initial submission" or "Revised version" documents, provide reviewer access links. For your "Final submission" document, provide a link to the deposited data.*
Files in database submission	*Provide a list of all files available in the database submission.*
Genome browser session (e.g. UCSC)	*Provide a link to an anonymized genome browser session for "Initial submission" and "Revised version" documents only, to enable peer review. Write "no longer applicable" for "Final submission" documents.*

Methodology

Replicates	*Describe the experimental replicates, specifying number, type and replicate agreement.*
Sequencing depth	*Describe the sequencing depth for each experiment, providing the total number of reads, uniquely mapped reads, length of reads and whether they were paired- or single-end.*
Antibodies	*Describe the antibodies used for the ChIP-seq experiments; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Peak calling parameters	*Specify the command line program and parameters used for read mapping and peak calling, including the ChIP, control and index files used.*
Data quality	*Describe the methods used to ensure data quality in full detail, including how many peaks are at FDR 5% and above 5-fold enrichment.*
Software	*Describe the software used to collect and analyze the ChIP-seq data. For custom code that has been deposited into a community repository, provide accession details.*

Flow Cytometry

Plots

Confirm that:

☐ The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).

☐ The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).

☐ All plots are contour plots with outliers or pseudocolor plots.

☐ A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparation	*Describe the sample preparation, detailing the biological source of the cells and any tissue processing steps used.*
Instrument	*Identify the instrument used for data collection, specifying make and model number.*
Software	*Describe the software used to collect and analyze the flow cytometry data. For custom code that has been deposited into a community repository, provide accession details.*
Cell population abundance	*Describe the abundance of the relevant cell populations within post-sort fractions, providing details on the purity of the samples and how it was determined.*
Gating strategy	*Describe the gating strategy used for all relevant experiments, specifying the preliminary FSC/SSC gates of the starting cell population, indicating where boundaries between "positive" and "negative" staining cell populations are defined.*

☐ Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

Magnetic resonance imaging

Experimental design

Design type	*Indicate task or resting state; event-related or block design.*
Design specifications	*Specify the number of blocks, trials or experimental units per session and/or subject, and specify the length of each trial or block (if trials are blocked) and interval between trials.*
Behavioral performance measures	*State number and/or type of variables recorded (e.g. correct button press, response time) and what statistics were used to establish that the subjects were performing the task as expected (e.g. mean, range, and/or standard deviation across subjects).*

Acquisition

Imaging type(s) — *Specify: functional, structural, diffusion, perfusion.*

Field strength — *Specify in Tesla*

Sequence & imaging parameters — *Specify the pulse sequence type (gradient echo, spin echo, etc.), imaging type (EPI, spiral, etc.), field of view, matrix size, slice thickness, orientation and TE/TR/flip angle.*

Area of acquisition — *State whether a whole brain scan was used OR define the area of acquisition, describing how the region was determined.*

Diffusion MRI ☐ Used ☐ Not used

Preprocessing

Preprocessing software — *Provide detail on software version and revision number and on specific parameters (model/functions, brain extraction, segmentation, smoothing kernel size, etc.).*

Normalization — *If data were normalized/standardized, describe the approach(es): specify linear or non-linear and define image types used for transformation OR indicate that data were not normalized and explain rationale for lack of normalization.*

Normalization template — *Describe the template used for normalization/transformation, specifying subject space or group standardized space (e.g. original Talairach, MNI305, ICBM152) OR indicate that the data were not normalized.*

Noise and artifact removal — *Describe your procedure(s) for artifact and structured noise removal, specifying motion parameters, tissue signals and physiological signals (heart rate, respiration).*

Volume censoring — *Define your software and/or method and criteria for volume censoring, and state the extent of such censoring.*

Statistical modeling & inference

Model type and settings — *Specify type (mass univariate, multivariate, RSA, predictive, etc.) and describe essential details of the model at the first and second levels (e.g. fixed, random or mixed effects; drift or auto-correlation).*

Effect(s) tested — *Define precise effect in terms of the task or stimulus conditions instead of psychological concepts and indicate whether ANOVA or factorial designs were used.*

Specify type of analysis: ☐ Whole brain ☐ ROI-based ☐ Both

Statistic type for inference (See Eklund et al. 2016) — *Specify voxel-wise or cluster-wise and report all relevant parameters for cluster-wise methods.*

Correction — *Describe the type of correction and how it is obtained for multiple comparisons (e.g. FWE, FDR, permutation or Monte Carlo).*

Models & analysis

n/a	Involved in the study
☐	☐ Functional and/or effective connectivity
☐	☐ Graph analysis
☐	☐ Multivariate modeling or predictive analysis

Functional and/or effective connectivity — *Report the measures of dependence used and the model details (e.g. Pearson correlation, partial correlation, mutual information).*

Graph analysis — *Report the dependent variable and connectivity measure, specifying weighted graph or binarized graph, subject- or group-level, and the global and/or node summaries used (e.g. clustering coefficient, efficiency, etc.).*

Multivariate modeling and predictive analysis — *Specify independent variables, features extraction and dimension reduction, model, training and evaluation metrics.*