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Directed conservation of the world's reef sharks and rays

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Many shark populations are in decline around the world, with severe ecological and economic consequences. Fisheries management and marine protected areas (MPAs) have both been heralded as solutions. However, the effectiveness of MPAs alone is questionable, particularly for globally threatened sharks and rays ('elasmobranchs'), with little known about how fisheries management and MPAs interact to conserve these species. Here we use a dedicated global survey of coral reef elasmobranchs to assess 66 fully protected areas embedded within a range of fisheries management regimes across 36 countries. We show that conservation benefits were primarily for reef-associated sharks, which were twice as abundant in fully protected areas compared with areas open to fishing. Conservation benefits were greatest in large protected areas that incorporate distinct reefs. However, the same benefits were not evident for rays or wide-ranging sharks that are both economically and ecologically important while also threatened with extinction. We show that conservation benefits from fully protected areas are close to doubled when embedded within areas of effective fisheries management, highlighting the importance of a mixed management approach of both effective fisheries management and well-designed fully protected areas to conserve tropical elasmobranch assemblages globally.

Shark and ray ('elasmobranch') populations are threatened by overexploitation, with potentially wide-reaching consequences for human livelihoods, food security and marine ecosystem function[1–3]. Elasmobranch management varies widely around the world[4–6] with fisheries management strategies such as catch limits, effort limits and restrictions on gear associated with higher shark abundance[7,8]. Marine protected areas (MPA) are often promoted as a solution to elasmobranch declines[9] and can provide conservation benefits for exploited species, especially when well designed[10] and fully protected[11].

The most recent global biodiversity framework includes targets for effective management of both fisheries and MPAs[12]. Although fisheries and protected area management rarely occur in isolation, there is little understanding of the benefits of a mixed management approach in which both are applied concurrently[13]. For elasmobranchs, there is some evidence of the benefits of effective fisheries management on a global scale and that large MPAs with high compliance contained a greater abundance of sharks[7]. However, the effectiveness of MPAs varies based on objectives that are often not designed for elasmobranchs[14,15], despite being among the most threatened vertebrates[2]. This discrepancy may occur because many elasmobranchs are highly mobile and less likely to benefit when protection from fishing is restricted to small protected areas[7,16,17]. However, the effectiveness of MPAs on rays and less mobile sharks has not been studied extensively[18]. Design principles of fully protected areas have primarily been based on teleosts[10,19–21], and it is unclear whether the same principles apply to elasmobranchs. Despite these knowledge gaps, management recommendations include the expansion of existing and establishment of new protected areas to increase protection for threatened elasmobranchs[9], without considering the potential of an approach that combines fisheries management and protected areas ('mixed management').

Here we use >18,000 baited remote underwater video stations (BRUVS), collected by a dedicated global survey of coral reef elasmobranchs ('Global FinPrint', https://globalfinprint.org), to assess the combined benefits of protected area and fisheries management for

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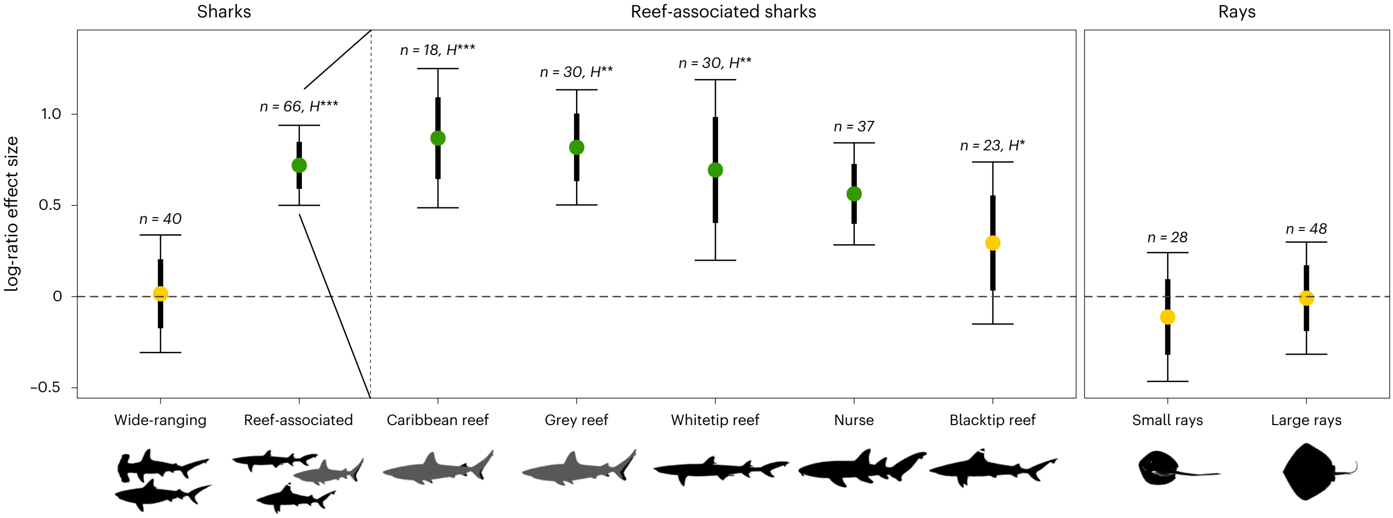

Fig. 1 | Effectiveness of fully protected areas in promoting shark and ray abundance. Effectiveness in promoting abundance of wide-ranging and reef-associated sharks (left), the most abundant species within the reef-associated group (middle), and small and large rays (right) based on log-ratio effect sizes inside/outside of fully protected areas. Green dots represent results where the 95% CI (upper and lower horizontal bounds) of the effect size does not overlap zero and yellow dots represent a null result overlapping zero. Also displayed are 75% CIs (bold portion of the vertical bar). For each category, the number of fully protected areas used to calculate the overall effect size is shown (*n*); an *H* indicates significant heterogeneity (*<0.05, ***<0.001) associated with the effect size.

elasmobranch conservation. Specifically, we quantify the relative abundance of elasmobranchs inside and outside of 66 fully protected areas, considering species characteristics, protected area design, habitat characteristics and human pressures. We also assess whether mixed management provided additional conservation benefits for reef sharks, by comparing fully protected areas and effective fisheries management benefits alone and when combined across 36 countries.

Results and Discussion

Benefits of fully protected areas

On average, fully protected areas had nearly twice the abundance of sharks compared with areas open to fishing (Extended Data Fig. 1), showing substantial conservation benefits. However, protected area benefits were confined to shark species that spend most of their life cycle on coral reefs. These reef-associated sharks were, together, over twice as abundant (105% ± 24%, 95% confidence interval (CI)) within fully protected areas relative to areas open to fishing (Fig. 1). The benefits for reef-associated sharks are likely derived from residency within protected area boundaries that closely matches their home range[22–24]. Conservation benefits for reef-associated sharks vary among species. Caribbean reef (*Carcharhinus perezi*), grey reef (*Carcharhinus amblyrhynchos*), whitetip reef (*Triaenodon obesus*) and nurse sharks (*Ginglymostoma cirratum* and *Nebrius ferrugineus* combined) were 138% (±46%), 127% (±37%), 100% (±64%) and 76% (±32%) more abundant in fully protected areas, respectively (Fig. 1). However, there was heterogeneity and a lower confidence in the effectiveness of fully protected areas for blacktip reef sharks (*Carcharhinus melanopterus*; 34% ± 31%). Blacktip reef sharks have broader habitat use than other reef sharks[25] and are more likely to occur outside of coral-reef-dominated MPAs during some parts of their life history. A reduced effect size may also be driven by larger-bodied grey reef sharks competitively excluding smaller-bodied blacktip reef sharks[26], making them less likely to approach BRUVS[27].

We demonstrate that fully protected areas can provide significant benefits to reef-associated sharks, but alone are unlikely to be an effective strategy for the conservation of tropical elasmobranch assemblages. We did not detect benefits for wide-ranging shark species that probably require management over much larger geographic areas than are typical of the world's existing MPAs. Our study also failed to detect conservation benefits of fully protected areas for rays (Extended Data Fig. 1), even when separated into large and small-bodied species (Fig. 1). Although many rays have small home ranges that would be encompassed by protected areas, they generally have a lower fisheries value and persist on reefs where sharks have been depleted[28]. The lack of conservation benefit is still surprising because substantial fishing pressure occurs on these species globally[1]. A lack of apparent protected area benefits for rays may also be driven by reduced detection on BRUVS, whereby rays are deterred from areas with higher shark abundance and/or exhibit more wary behaviours[29,30].

Variation in benefits of protected areas

Protected areas frequently aim to conserve a broad spectrum of biodiversity[31] and there has been considerable effort devoted to identifying optimal locations for elasmobranch protection[32]. Effect sizes from the 66 fully protected areas we sampled were plotted to show the location of the 18 significantly positive effects on sharks (Fig. 2 and Extended Data Fig. 2). Multiple effective protected areas were observed in Belize, Australia and the Philippines, with individual positive results observed at reefs in Antigua and Barbuda, Bahamas, Brazil, Colombia, Cuba, the Dutch Caribbean, Fiji, the United States (Hawaii), Indonesia and Malaysia. No negative effects were observed across the 66 fully protected areas sampled (Fig. 2; 95% CI). Variation in protected area effectiveness can be due to design principles and compliance[10], varying extent of human impacts (for example, human gravity[33,34]) and the effectiveness of fisheries management for elasmobranchs beyond protected areas[7]. We found that variation in the ability of fully protected areas to provide conservation benefits for reef-associated sharks was most strongly related to human gravity (Fig. 3), used as a proxy for the intensity of human impacts and measured as a function of the size of a population and its distance from each fully protected area[34] (see Methods). Where gravity and implied human impacts are low, abundances of top predators are high[7,33] and similar inside and outside of protected areas. As gravity increases, so too does the relative abundance of sharks within protected areas compared with outside, implying that the conservation benefits of protected areas are greatest for elasmobranchs in areas subject to human pressures. However, overall abundance of reef sharks

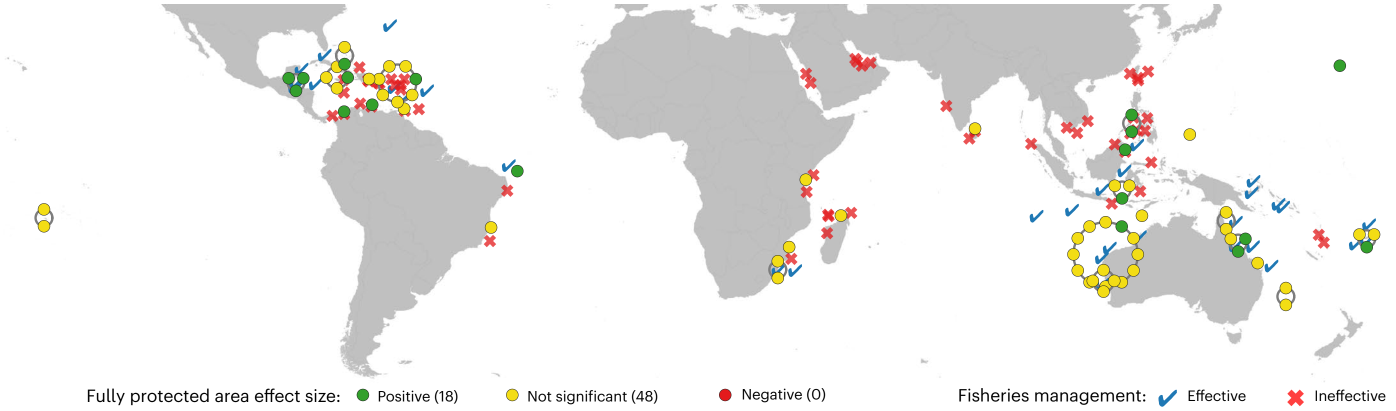

Fig. 2 | Effectiveness of fully protected areas and fisheries management for shark conservation. Green points represent a fully protected area with a greater abundance of sharks; yellow represents a protected area where 95% CIs overlap zero. Multiple fully protected areas were sampled at some locations, hence point displacement was used to distinguish between areas in clusters. Locations where fisheries management strategies for sharks were deemed effective are shown by blue ticks and ineffective with red crosses (see 'Fisheries management and fully protected areas' and Methods). Shark sanctuaries (a nationwide ban on shark fishing) and remote locations (total gravity of human impacts = 0) were excluded from the fisheries management analysis. For individual effect size results and fisheries management classifications by location, see Extended Data Fig. 2 and Supplementary Table 1.

is low at highest gravities[7], and studies of teleost biomass in locations with higher gravities than those sampled here suggest that conservation gains diminish where human impacts are intense[33].

Protected areas that encompassed distinct reefs (>20 km to the next reef) were more effective than those encompassing continuous or less distinct reefs (Fig. 3). By ensuring that protected areas cover whole reefs and are separated by deeper water or large expanses of non-reef habitat types (for example, sand), movement of sharks across boundaries into fished areas is likely reduced. The feasibility of protecting all suitable habitat will depend on the size of the reef, with the benefits for reef-associated sharks increasing as the size of fully protected areas increases (Fig. 3); this relationship is corroborated by studies on teleosts[7,8] and shark movement[22]. Protected areas that follow natural boundaries are better demarcated, conducive to improved compliance with regulations[10]. While compliance did not explain variation in the ability of protected areas to provide conservation benefits to reef-associated sharks, it is considered one of the most important drivers of conservation success for teleosts[10]. A lack of comparable quantitative data on enforcement (for example, patrol effort and infringements) across countries limited our study to a broad qualitative assessment that may not have captured finer scale variation in compliance.

We found that the presence of a shark sanctuary (a nationwide ban exclusively on shark fishing) was the fourth most important variable explaining variation in effectiveness of fully protected areas for reef-associated sharks. There was a clear positive effect of fully protected areas in shark-fishing nations (Fig. 3), reflecting higher fishing mortality outside of protected areas. Within shark sanctuaries, the effectiveness of protected areas is much more variable, reflecting the national ubiquity of sharks within some countries that have implemented effective bans[7,35]. Some positive reserve effects in shark sanctuary nations may be a legacy of past shark fishing or higher abundance of prey in fully protected areas attracting sharks[36].

Fisheries management and fully protected areas

Fisheries management that imposes catch limits and prohibits gillnets or longlines are associated with higher abundances of reef sharks globally[7], and locations with any of these measures in place were defined in this study as having 'effective' shark fisheries management. Locations that have no restrictions at all, or shark fisheries management that does not impose catch limits or prohibit gillnets and/or longlines, are associated with lower abundance of reef sharks[7] and were categorized as having 'ineffective' shark fisheries management. Fully protected areas embedded within locations where shark fisheries management was deemed effective provided close to double the conservation benefits compared with fully protected areas embedded within areas of ineffective fisheries management (90%, 64–120% CI; Fig. 4a(i)). This disparity corresponds to increased fishing mortality when sharks move beyond protected area boundaries in areas with limited or ineffective fisheries management. These results highlight the importance of regulations such as catch limits and gear restrictions for effective management of reef sharks[7,8] and indicates that these management approaches also effectively enhance conservation outcomes in fully protected areas.

Fully protected areas embedded within areas without effective fisheries management promote a greater abundance of reef sharks when compared with effective fisheries management by itself (39%, 19–62% CI; Fig. 4a(ii)). However, given that less than 10% of the world's coral reefs are currently incorporated within fully or highly protected zones[37], protected areas alone are unlikely to conserve reef sharks at the scale of populations. Importantly, even in areas with effective fisheries management, fully protected areas provide additional conservation benefits, with an average of 149% (122–179% CI) greater abundance of reef sharks within their boundaries compared with areas outside (Fig. 4a(iii)). These results demonstrate that a mixed management approach of embedding fully protected areas within areas of effective fisheries management will deliver the greatest conservation benefits for reef sharks globally.

High abundances of reef sharks were not exclusively linked to management regulations, with a greater than expected shark abundance at some outlier locations without effective fisheries management or fully protected areas (Fig. 4b, red dots). This pattern highlights that other factors such as cultural beliefs[38,39] or market availability[34] can play an important role in shark conservation in some locations. For example, there is no commercial shark fishery in the Cocos-Keeling Islands and limited historical take from local communities[40], while fisheries in Pedro Bank, Jamaica primarily target conch, lobster and teleosts rather than sharks[41]. Similarly, fishing in Marovo, Solomon Islands is primarily subsistence, with low numbers of sharks in community catch data, effective customary management and low technology fishing gears coupled with an exposed coastline[42,43]. In some parts of Solomon Islands, sharks also have high cultural importance, being regarded as embodiments of gods, guardians and protectors[44,45]. Outlier locations such as these may be candidates for shark protection legislation or continued effective

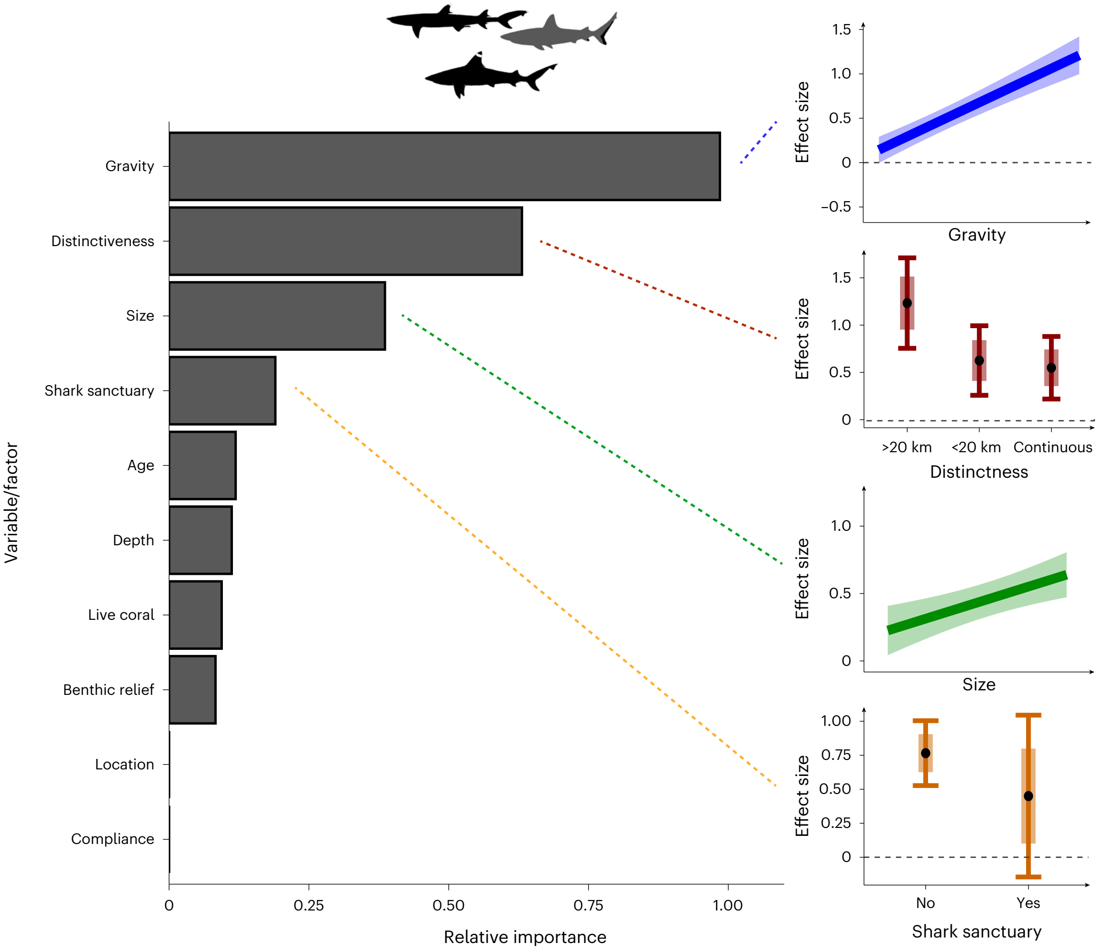

Fig. 3 | Relative importance of explanatory variables in predicting the effectiveness of fully protected areas in protecting reef-associated sharks. Variable scores are based on summed AIC weights (see Methods). The four most important variables that were also included in top models (see Methods) were plotted to demonstrate the direction and magnitude of their relationship with fully protected area effect sizes ($n = 66$). Shading indicates the standard error confidence bands, and error bars show both 95% and 75% CIs.

local management initiatives that fortify shark populations against potential changes in fishing pressure.

Conclusion

Our results show that fully protected areas provide conservation benefits to reef-associated sharks, and these benefits are greatest in large protected areas that incorporate distinct reefs. We provide evidence that effective fisheries management in the form of catch limits and restrictions on gillnets and longlines in conjunction with fully protected areas can almost double the conservation benefits of fully protected areas for reef sharks. This supports the recommended expansion of networks of highly protected areas to better conserve elasmobranchs[9], but importantly, it highlights the benefits of embedding them within effective fisheries management on a larger geographic scale. The large proportion of fully protected areas that did not provide significant benefits to elasmobranchs also highlights the importance of improving existing fully protected area management and design, particularly through increasing the size and incorporating whole reefs within boundaries. Further, since we did not observe conservation benefits for wide-ranging sharks or rays, which are often at high risk of extinction[2,46] and play an important role in structuring coral reef ecosystems[3,47], a focus on fisheries management at the national or regional scale would also benefit these species. A mixed management approach of appropriately large fully protected areas embedded within larger areas of effective fisheries management is essential to avoid projections of a global extinction crisis for elasmobranchs[1,2,28].

Methods

Global FinPrint dataset

We used a dedicated global survey (Global FinPrint; https://globalfinprint.org) of elasmobranch abundance collected by BRUVS across 58 countries, states and territories[7]. Most data were collected between 2015 and 2018, along with a small proportion of legacy data dating to 2009, following standardized procedures[48]. As a result, the methods used to estimate abundance (MaxN; the maximum number of sharks seen in a single video frame throughout the video), bait used (1 kg of oily fish primarily from the families Clupeidae and Scombridae), separation distance (at least 500 m between concurrent deployments), taxonomic resolution (species level where possible), depth (randomized between 1 and 40 m), soak time (60 min between 07:00–17:00) and broad-scale habitat sampled (coral reefs) were standardized. Variation in the bait plume dispersal and the sensitivity of different species to bait limit BRUVS to relative estimates of abundance such as MaxN. While MaxN has been criticized for hyperstability, the Global FinPrint dataset has been shown to provide an unbiased index of elasmobranch abundance[7] and BRUVS are considered one of the most effective methods for non-destructive sampling of sharks[49]. While surveys were completed during daytime, nocturnal sampling is unlikely to have changed results. Most reef-associated species were probably captured due to the use of bait and few elasmobranch species are exclusively nocturnal. Depth, visibility, substrate complexity and percentage of live coral were estimated for each deployment following standard procedures[48]

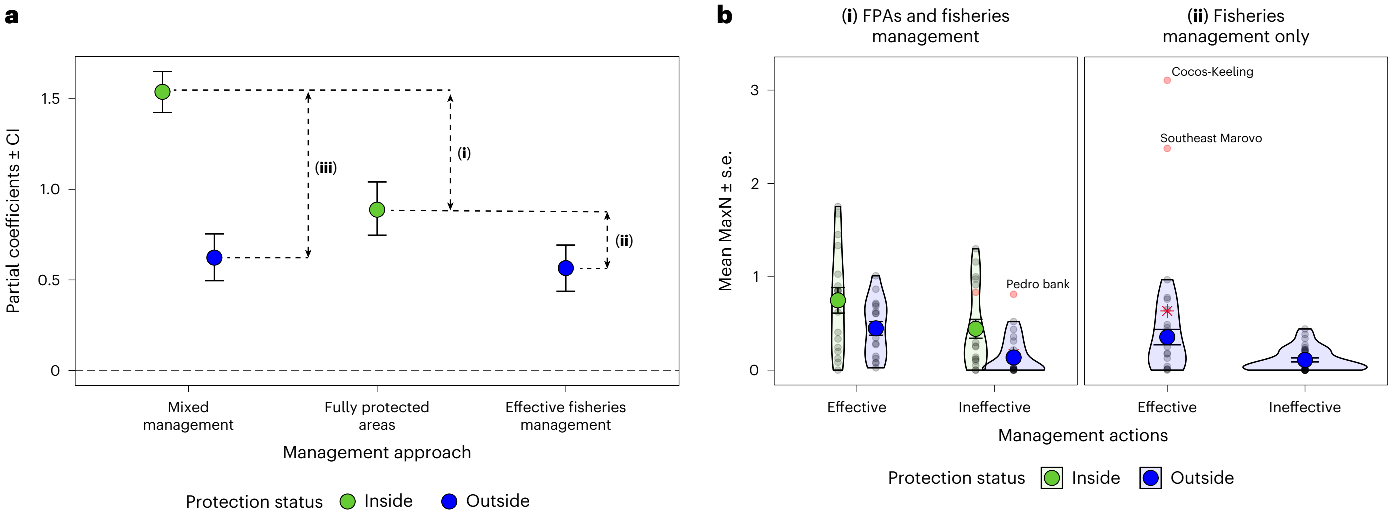

Fig. 4 | The effects of mixed management on shark abundance and fully protected area effectiveness. a, Partial effect coefficients derived from the abundance of sharks (mean MaxN) in areas with mixed management (both effective fisheries management and fully protected areas), areas with fully protected area and no effective fisheries management, and areas with effective fisheries management only. (**i**), The effect size used to calculate the benefits of embedding a fully protected area within areas of effective fisheries management vs ineffective. (**ii**), The effect of using fully protected areas without effective fisheries management compared to effective fisheries management on its own. (**iii**), The effect of a fully protected area compared to areas open to fishing when effective fisheries management is in place. Partial effects calculated inside protected areas are shown in green and outside in blue for each management approach. **b**(**i**), Abundance of sharks (mean MaxN) in areas with fully protected areas (FPAs) and effective (number of locations = 17)/ineffective fisheries management (number of locations = 18; see Methods). (**ii**), Areas with fisheries management only, number of locations with effective fisheries management = 15 and ineffective = 33. The mean abundance across all locations is shown inside protected areas (green circles) and outside (blue circles) for each management arrangement and individual sites (black dots). Shading represents the proportion of observations for each location. Outliers that were removed (see Methods) are shown in red, along with the original outlier affected mean (red asterisk).

in BenthoBox (https://benthobox.com/). We identified two subsets from these 18,348 BRUV replicates (1-h deployments): one subset that was appropriate for answering questions related to fully protected area effectiveness (4,281 replicates) and one that was used to assess the benefits of a mixed management approach of both fisheries and protected area management (10,400 replicates).

Fully protected area effectiveness

Selection criteria and data evaluation. Surveys had a minimum of four BRUVS replicates inside and four replicates outside of an area closed to fishing (fully protected area) for both teleosts and elasmobranchs (see Supplementary Table 1 for all sample sizes). Small sample sizes were generally associated with small fully protected area boundaries and were accounted for by weighting analysis by the inverse of the variance (see statistical analysis below). Fully protected areas and control pairs were within the same country/nation. Because the aim of this study was to assess a 'snapshot' of the effectiveness of fully protected areas, only the most recent inside/outside assessment was considered when a protected area was repeatedly sampled over time. To ensure that appropriate controls were assigned for each fully protected area, the spatial layout of data was overlaid on satellite imagery with protected area boundaries. The closest sites on either side of each protected area were used as controls, provided the broad-scale habitat was comparable (for example, fore-reef vs lagoon). A total of 66 assessments of fully protected areas met these criteria (4,281 replicates) and were used to assess benefits to reef sharks in terms of increased shark abundance (Supplementary Table 1).

Habitat variables. Sampling of fore-reef habitats was prioritized, with 89% of the fully protected area assessments including this habitat type and 31% including back-reef/lagoon (18% including both habitat types). If a different broad-scale habitat was sampled inside compared to outside, the protected area assessment was removed. Because visibility[50] and depth[42] can influence estimates of shark abundance from BRUVS, *t*-tests were used to compare the visibility and depth of replicates inside and outside of fully protected areas. Where depth was significantly different inside and outside protected areas ($P < 0.05$), outlying replicates that had significant leverage on test statistics were removed until no significant differences were found (Supplementary Table 2, $P > 0.05$, ~3.5% of deployments removed). Similarly, deployments with <5 m visibility were removed when sampling was unbalanced (1.5% of deployments removed). While it was not possible to balance benthic relief and live coral for each individual protected area assessment without jeopardizing the balance of depth or visibility, there was no significant difference inside and outside for overall tests based on a permutational analysis of variance (relief: pseudo-$F = 0.052$, $P = 0.813$; live coral: pseudo-$F = 0.574$, $P = 0.574$).

Response variables. We aggregated all shark species and all ray species observed on BRUVS to assess the broad-scale effect of fully protected areas on these two groups. While we observed a positive effect for sharks but not for rays, both results were heterogeneous (Extended Data Fig. 1) and the shark group was dominated by reef sharks (Supplementary Table 3). The shark group was therefore subdivided into wide-ranging and reef-associated species on the basis of movement studies[51], and when no studies were available, expert opinion from the authors. Rays were split into large (maximum length >75 cm) and small (maximum length <75 cm) species[52] due to a lack of detailed studies on movement (Supplementary Table 3) and on the basis of evidence that small rays are more impacted by predatory risk effects from sharks[29,30]. Finally, to assess species-specific benefits from fully protected areas, the five most frequently observed species that were present in at least 10 fully protected area/control pairs were examined: grey reef shark (*Carcharhinus amblyrhynchos*), blacktip reef shark (*Carcharhinus melanopterus*), Caribbean reef shark (*Carcharhinus perezi*), nurse sharks (*Ginglymostoma cirratum* and *Nebrius ferrugineus*) and whitetip reef shark (*Triaenodon obesus*).

Statistical analysis. Where sharks were completely absent either inside or outside a fully protected area (that is, one-sided zeros), the lowest mean across all inside/outside assessments for that group/

Table 1 | Potential variables influencing fully protected area effectiveness, their method of calculation, units, type of data and transformation before analysis

Factor	Method of calculation	Units/Levels	Data type	Transformation
Age of protected area	Time since establishment	Years (4–52)	Continuous	Square root
Size of protected area	Shapefiles or management plans	km^2 (0.84–36,000)	Continuous	log
Distinctiveness of protected area	Measured distance and visual examination via satellite imagery	<20 km; >20 km; Continuous	Categorical	NA
Compliance with protected area restrictions	Categorization by key stakeholders	Low; Medium; High	Categorical	NA
Gravity of human impacts for the location of the protected area	Population size for each 10×10 km cell within 500 km radius/travel time	Gravity (0.03–2,804)	Continuous	log + minimum value observed
Shark sanctuary presence	Is the fully protected area embedded within a shark sanctuary?	Yes; No	Dichotomous	NA
Depth of protected area	Average depth of the BRUVS within each fully protected area	M (1–40)	Continuous	Square root
Mean relief	Mean of a 0 to 5 estimate of benthic relief[72,73]	Mean of values between 0 and 5	Continuous	None
Live coral	The percentage of 20 grids placed over the field of view containing live coral as the dominant habitat type	%	Continuous	Square root
Location	The country where the fully protected area is located (countries covering multiple ocean basins split)	23 locations	Categorical	NA

species and its associated error were used instead of the zero and the same values added to the non-zero. This approach facilitated the inclusion of these effect sizes into the global analysis with minimal influence to the log-ratio given that the constant ranged between a mean of 0.06 and 0.008 (similar to constants used elsewhere[53]). An artificial global constant was not possible due to the creation of effect sizes with zero variance that would artificially inflate the weighting, and uneven sampling sizes prevented the addition of a 'dummy' shark to each assessment. A sensitivity analysis was performed using an alternative constant (the minimum value across all groups/2 = 0.004) and results were unaltered (Supplementary Table 4). For reef-associated sharks, the same approach was used for double-sided zeros (no sharks observed), which meant that the results from these fully protected areas did not influence the global effect size but could be incorporated within further analyses to explore variables that may be responsible for heterogeneity in effect sizes. log-ratio effect sizes were used to quantify differences in each metric inside and outside of each fully protected area:

$$E_{m,i} = \ln\left(\frac{\bar{X}_{m,P,i}}{\bar{X}_{m,F,i}}\right), \tag{1}$$

where $E_{m,i}$ is the log response ratio for each fully protected area i based on the metric m and $\bar{X}_{m,P,i}$ and $\bar{X}_{m,F,i}$ are the mean of each metric m in protected (P) and fished (F) areas, respectively.

Variances of the effect sizes were calculated as:

$$V_{Em,i} = \sum^{P,F} \sigma_i^2/(n_i \times \bar{X}_i^2), \tag{2}$$

where $v_{Em,i}$ is the variance associated with the effect size $E_{m,i}$, σ_i is the standard deviation associated with the mean and n_i is the number of replicates, summed for the protected (P) and fished areas (F).

We then used a mixed effects weighted effect size analysis where weights of each individual effect size incorporated these variances as follows:

$$w_{m,i} = \frac{1}{V_{Em,i} + V_{m,a}}, \tag{3}$$

where $w_{m,i}$ is the weight associated with each effect $E_{m,i}$, $v_{Em,i}$ is the within-study variance for each metric m and $v_{m,a}$ is the among-study variance for each metric. The among-study variance was obtained using the generalized equation[54]. Confidence intervals for group and overall effect sizes were derived from a Student's *t* statistic and both 95% and 75% confidence intervals were displayed to enable further interpretation when results were heterogeneous. Effect sizes and modelling were done using the metafor package[55] in the programme R[56] with the variance estimator set to the 'REML' restricted maximum likelihood estimator.

Full subsets analysis

Variables influencing fully protected area effectiveness. To explore heterogeneity in the effect size modelling, data on variables that are known or are likely to influence fully protected area efficacy were compiled (Table 1). Information on the age, size and distinctness of each fully protected area was collated (see Table 1 for details). In the absence of comparable empirical data, compliance with fishing restrictions within each fully protected area was categorized into three levels by local park authorities or researchers with substantial experience working in the area: high compliance indicated infrequent breaches of management rules; moderate compliance indicated occasional breaches of management rules; and low compliance indicated frequent breaches of management rules. The total gravity of human impacts was calculated as the summed human population size of each populated cell (10 km × 10 km) within a 500 km radius, divided by the squared travel time between that cell and the fully protected area surveyed[34]. Note that this measure of gravity does not account for foreign fishing fleets, which are more likely to be captured in compliance estimates.

The influences of fully protected area characteristics (size, age, compliance and distinctness), location/fishing pressure covariates (gravity, shark sanctuary presence and location) and habitat variables (depth, benthic relief and live coral; Table 1 and Supplementary Table 1) on the effect sizes for each metric were investigated using generalized additive models (GAMs[57]). The distribution of continuous predictors was examined and transformed appropriately to ensure that they were evenly distributed across their range (Table 1). No random effect was used as all location variables were highly correlated with other covariates of interest and regional differences in the data are largely attributable to differences in key human drivers of resource exploitation[58]. Because a large proportion of protected areas sampled were from Australia and the Caribbean, location in the form of the country or major region of a country (for example, east and west coasts of Australia) was included within the model as a fixed effect. A weighted (inverse of the variance) full subsets method was used to fit models of all possible combinations up to a maximum of three variables[59]. To avoid multicollinearity issues, predictor variables with Pearson correlations (or an equivalent approximation) greater than 0.36 were not included in the same model (Supplementary Table 5). The correlation cut-off value was increased from the recommended value of 0.28 (based on ref. 60) to allow simultaneous inclusion of the covariates compliance and age, which are known to influence fully protected area effectiveness[10,21].

In all models, the smoothing parameter was limited to a simple spline, allowing only monotonic relationships ($k = 3$). Model selection was based on Akaike's information criterion for small sample sizes (AICc[61]) and AICc weights (wAICc[62]), with models with AICc values differing by less than two units indicating weak evidence for favouring one over the other[63,64]. Relative support for each predictor variable was obtained by calculating the summed wAIC across all subsets of models containing that variable. Effect sizes were modelled with a Gaussian distribution using gam() in the mgcv package in R[65]. The R language for statistical computing[56] was used for all data manipulation and graphing[66].

Only reef-associated sharks were examined using full subsets analysis since this group represented the largest effect size with sufficient sample size to explore heterogeneity (Fig. 1). Although the null model was not selected, there was little evidence of a standout top model that explained a significantly higher proportion of variation in effect sizes, with gravity, protected area distinctness and size appearing in models within two AICc, and shark sanctuary in a model marginally greater than two AICc (Supplementary Table 6). We therefore used variables identified within all top models, as well as importance scores (the summed AICc weights), to interpret the most relevant variables influencing the effectiveness of fully protected areas for reef-associated sharks. Relationships between the variables and effect size were plotted to demonstrate the direction of each result.

Mixed management models. To assess the combined and individual benefits of fully protected areas and fisheries management, the MaxN of all sharks was summed for each BRUVS replicate using a subset of 10,400 replicates across 36 countries from the full Global FinPrint dataset[7]. At each site, a location where one or more reefs (a continuous reef tract of ~10 km in length) were surveyed, was classified into whether fisheries management actions were effective or ineffective for sharks. Gillnet and longlines have been identified as the most effective gears for catching reef sharks, and catch limits are associated with a higher abundance of reef sharks[7]. Therefore, locations were classified as having effective fisheries management actions for sharks if they used strategies that resulted in catch or effort limits (for example, bag or entrants), or gear restrictions that prohibited gillnets or longlines. Locations that had no restrictions at all, or fisheries management that did not include the methods above (for example, species/size restrictions or bans on other gears such as spearguns) were classified as having management actions that were deemed ineffective for sharks. We acknowledge that in some circumstances or locations, combinations of these strategies can be used to achieve management objectives and more detailed restrictions were not considered (for example, mesh size or number of hooks), but in this dataset they were identified as management interventions that influenced the relative abundance of sharks[7]. Assessments of management effectiveness were completed at the same time of sampling and may not reflect present or future management arrangements.

To compare management arrangement categories, the mean MaxN of sharks per site was calculated, visually examined for outliers using boxplots and then confirmed using a Rosner's test[67] in the package EnvStats[68]. Results were interpreted with and without outliers[69]. Outliers with greater than expected shark abundance included: the Cocos Islands in Western Australia and southeast Marovo in Solomon Islands for areas with effective fisheries management only, and Pedro Bank, Jamaica in areas with ineffective fisheries management and fully protected areas. Outliers, remote locations (total gravity of human impacts = 0) and shark sanctuaries were excluded from models to focus on locations where direct management actions were likely to influence shark abundance. To account for anthropogenic factors known to influence shark abundance, the human development index (HDI: a composite measure of life expectancy, income and education), voice accountability (the extent to which people in each nation are able to participate in governance, free expression, free media and free association) and total gravity were included in the model[7]. Depth, benthic relief, live coral and visibility were also included to account for variation across sites. When habitat information was not available for a BRUVS replicate (for example, was not visible in the field of view), the average for the site was used. Similar to the fully protected area analysis, continuous predictors were examined and transformed appropriately.

Shark abundance (MaxN) was modelled using a negative binomial distribution, with smooths for HDI, voice accountability, total gravity, depth, benthic relief, visibility and live coral, with mixed management included as a fixed factor. The negative binomial was used, as initial modelling using a Poisson distribution indicated overdispersion. A full subsets approach was used to identify the most important covariates in predicting shark abundance. This was achieved by first generating a model formula representing a complete set of all possible combinations of predictors using the generate.model.set() function in the FSSgam package in R[59] and then examining those models with the highest AICc weights[61]. Model weights were generated from the complete fitted model set using the model.sel() function in the MuMIn package in R[70]. Models were limited to a simple spline, allowing only monotonic relationships ($k = 3$), and the same correlation cut-off as the fully protected area modelling was used (0.36) to ensure that variables included in any one model had only limited collinearity.

The top model included mixed management, HDI, depth, visibility and live coral (weight = 0.67, Supplementary Table 7). The next top model (weight = 0.33, Supplementary Table 7) included the same variables except that benthic relief was favoured over live coral. As mixed management was in the top model, we explored the relative effect of different management scenarios in greater detail using a Bayesian framework, allowing an estimation of uncertainty in effects estimates. Partial effect coefficients (Supplementary Fig. 1) were used to calculate differences between management arrangements and quantify the benefits of mixed management compared to effective fisheries or fully protected area management in isolation (Fig. 4a). The mean MaxN for each category (ineffective/effective management and with/without fully protected areas) was also presented to show the spread of data and outliers (Fig. 4b). The top model with visibility fitted as a linear covariate was fitted under a Bayesian framework using the brms v.2.20.4 (ref. 71) package as follows:

$$\begin{aligned}&\text{Shark abundance (MaxN)} \sim \text{mixed management}\\&+s(\text{HDI}, \text{bs} = \text{“cs”}, k = 3) + \text{visibility} + s(\text{live coral}, \text{bs} = \text{“cs”}, k = 3)\\&+s(\text{depth}, \text{bs} = \text{“cs”}, k = 3).\end{aligned} \tag{4}$$

where s is the smooth terms and bs is the choice of smoother, cs, which is a shrinkage version of a cubic regression spline[57]. The posterior distributions of model parameters were estimated using No-U-Turn Sampler (NUTS) Hamiltonian Monte Carlo (HMC) by constructing four chains of 60,000 steps each, with 58,000 steps used as a warm-up and a thinning of 5, so a total of 1,600 steps were retained to estimate posterior distributions. All four independent chains reached convergence, that is, the Gelman–Rubin statistic $\hat{R}$ was ~1 for all parameters. We adopted a target average proposal acceptance probability of 0.95 and a maximum tree depth of 15. For the final model fit, no divergent transitions were observed. Default brms priors were adopted, which included flat priors on the fixed effects of management type and visibility, and Student's t (3, −2.3, 25) priors on the smoothing parameters. The fitted Bayesian model was used to estimate the effect of different management scenarios, using the posterior samples of the individual partial effects coefficients for each management category. Effects were presented as a median of the posterior sample, with 95% confidence intervals estimated using quantile().

Inclusion and ethics

Local researchers were included throughout the project and included as co-authors; research was both globally and locally relevant, and capacity building (for example, training in methodology to continue independent research) and two-way learning (for example, imparting local knowledge) were incorporated.

Reporting summary

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

Data availability

Data and code used to reproduce the analysis are available at https://github.com/JordanGoetze/MixedManagement.

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D.D.C., M. R. Heithaus, M. R. Heupel, C.A.S., M.A.M., M.M., E.H. and J.S.G. conceptualized the project. D.D.C., M. R. Heithaus, M. R. Heupel, C.A.S., M.A.M., M.M., E.H. and J.S.G. developed the methodology. All authors conducted the investigations. J.S.G. performed visualization. D.D.C. and M. R. Heithaus acquired funding. D.D.C., M. R. Heithaus, M. R. Heupel, C.A.S., M.A.M., M.M. and E.H. administered the project. J.S.G., S.W., C.A.S., D.D.C., M. R. Heithaus, M. R. Heupel, M.A.M., M.M. and E.H. wrote the original draft. All authors reviewed and edited the paper.

Competing interests

The authors declare no competing interests.

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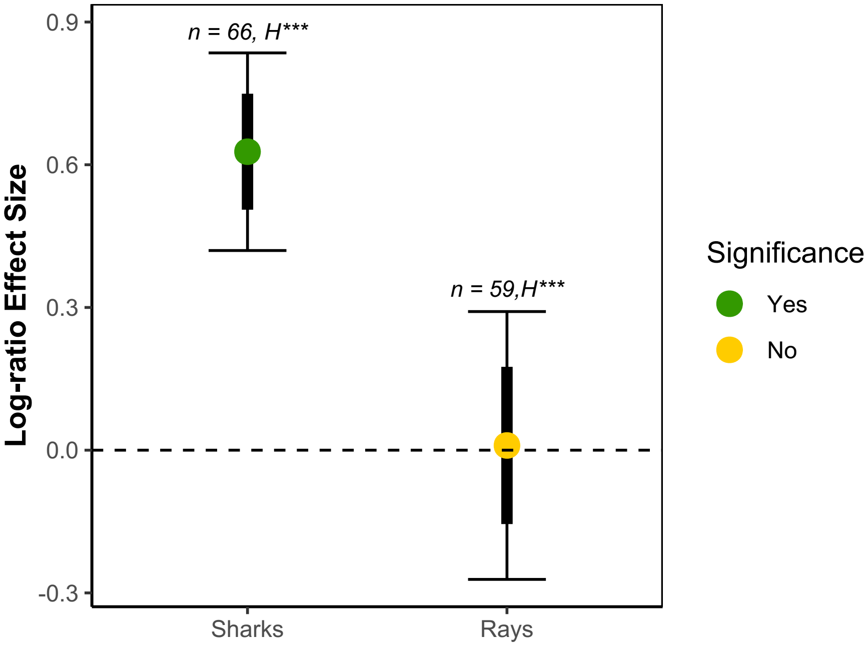
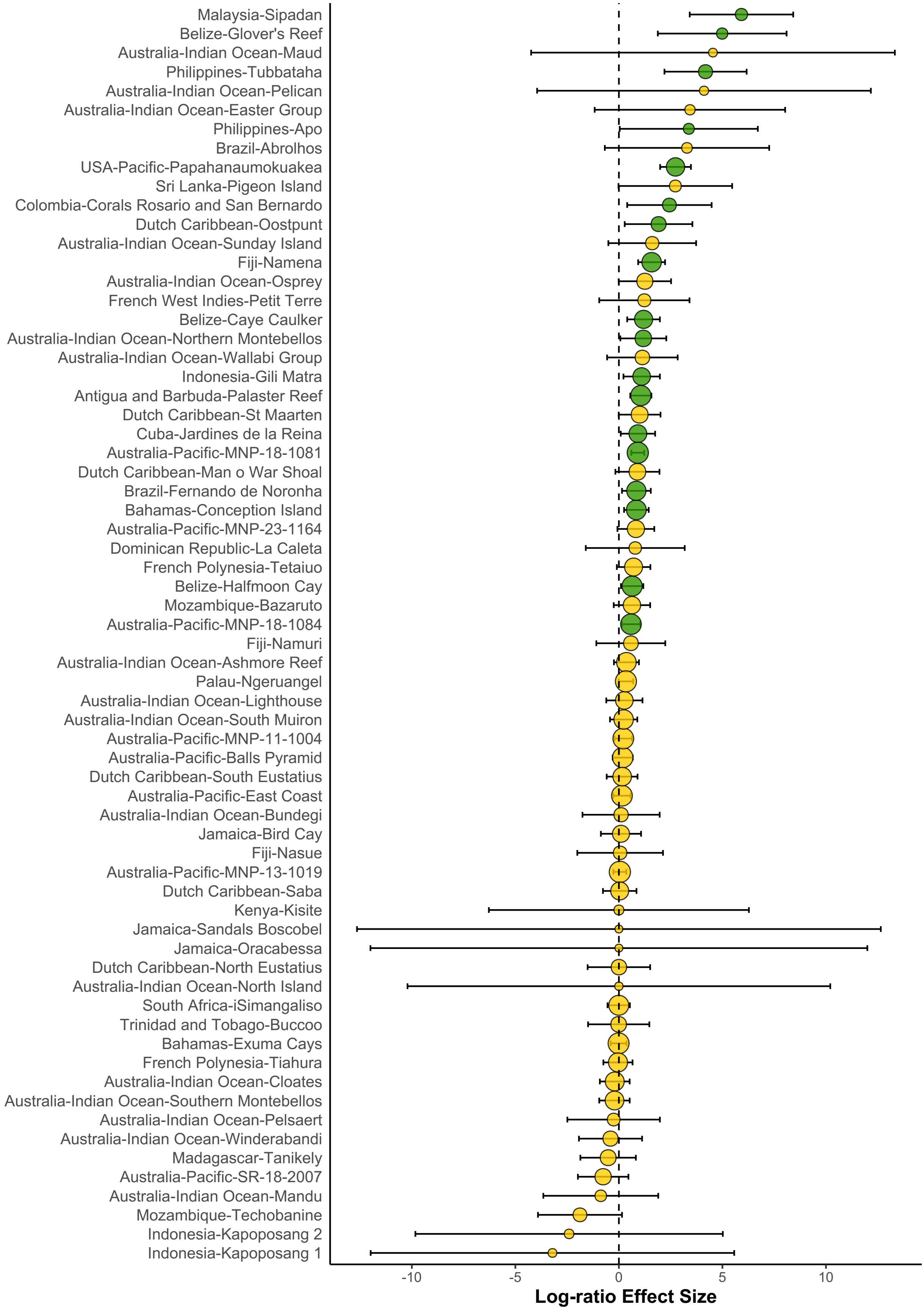


Extended Data Fig. 1 | The effectiveness of fully protected areas in promoting abundance of sharks and rays. Effectiveness of fully protected areas in promoting abundance of sharks and rays, based on log-ratio effect sizes inside/outside of fully protected areas (n = 66). Green dots represent positive results where the 95% confidence interval of the effect size does not overlap zero and yellow a null result. 75% confidence intervals are also displayed, and the superscript H indicates that significant heterogeneity (* < 0.05, *** < 0.001) was associated with the effect size, with n representing the number of fully protected areas used to calculate the overall effect size.



Extended Data Fig. 2 | The effectiveness of fully protected areas in promoting abundance of sharks. Green dots represent positive results where the 95% confidence interval of the effect size does not overlap zero and yellow where they do. Effect sizes were weighed based on the inverse of the variance with smaller points having a lower weighting.

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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	
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☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
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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	Videos were viewed and annotated in the FinPrint Annotator (v.1.1.44.0) or EventMeasure (www.seagis.com)
Data analysis	R was used for all data analysis and code will be available to reviewers in a zipped file and at https://github.com/JordanGoetze/MixedManagement before publication

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 Portfolio guidelines for submitting code & software for further information.

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Data used to reproduce the analysis—except for geolocations will be available at https://github.com/JordanGoetze/MixedManagement

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	NA
Reporting on race, ethnicity, or other socially relevant groupings	NA
Population characteristics	NA
Recruitment	NA
Ethics oversight	NA

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

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

Ecological, evolutionary & environmental sciences study design

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

Study description	We surveyed 371 coral reefs in 58 nations using 18,348 individual Baited Remote Underwater Video Stations, primarily between 2015 and 2018. The study was hierarchically structured, with sets made within reefs, reefs within nations, and nations within regions.
Research sample	Study reefs were selected to correspond as closely as possible to those surveyed by Cinner et al. 2018 Nature 535:416-419.
Sampling strategy	Nearly all (> 98%) BRUVS were deployed during daylight hours (07:00-17:00) and the initial deployment coordinates for each day were determined using a randomly generated position within the sampling area. The first BRUVS were then deployed as close as possible to these coordinates and the remainder were then set at least 500 m away from previous sets, at depths of 2-40 m. This spacing was designed to reduce the likelihood of individuals occurring on multiple cameras. Bottom depth was recorded for each deployment.
Data collection	Visibility, substrate complexity, and substrate type were estimated for each deployment using a still frame from the footage after the BRUVS settled to the bottom in the BenthoBox software (www.benthobox.com) BRUVS were retrieved after at least 60 minutes to ensure a standard 60 time. Videos were reviewed by at least two trained and independent readers at normal play speed and reviewed by a master annotator to ensure accuracy in species identification. Videos were viewed and scored in the FinPrint Annotator (v.1.1.44.0) or EventMeasure (www.seagis.com) to record species present and the number of individuals observed. Sharks were recorded as MaxN, which is the maximum number of individuals of each species seen on any given frame of a BRUVS video set.
Timing and spatial scale	Surveys were conducted haphazardly, as partner investigators became available and logistical constraints permitted, between July 20 15 and 2018
Data exclusions	We identified two subsets from these 18,348 BRUV replicates (1 hour deployments), one that was appropriate for answering questions related to fully protected area (FPA) effectiveness and one that was used to assess the benefits of a mixed management approach (fisheries and protected area management). For the FPA analysis surveys had a minimum of four BRUVS replicates inside and four replicates outside of an area closed to fishing (fully protected area) for both teleosts and elasmobranchs, resulting in assessments for 66 FPAs. Sample sizes for each individual assessment are included in a supplementary file. For the mixed management question, remote locations, locations with shark sanctuaries and locations were FPAs were present but not sampled were removed, resulting in a subset of 11,021 replicates across 36 countries.
Reproducibility	NA
Randomization	Sampling was systematic (50 target replicates per reef), covering most or large-swaths of survey reefs. Reefs were selected haphazardly due to location availability and correspondence with Cinner et al 2016 Nature 535:416-419.
Blinding	NA

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Field conditions were generally good, consistent, and had no-impact on remote samples made below the water surface. Replicates with poor visibility were removed from analysis.
Location	Global
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
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

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