

## Global Status and Conservation Potential of Reef Sharks

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145 **Decades of overexploitation have devastated shark populations, leaving considerable**  
146 **doubt as to their ecological status. Yet much of what is known has been inferred**  
147 **from catch records in industrial fisheries, with little information about sharks in**  
148 **coastal habitats. Here we address this knowledge gap using data from more than**  
149 **15,000 standardized baited remote underwater video stations deployed on 371 reefs**  
150 **in 58 nations to estimate the conservation status of reef sharks globally. Our results**  
151 **reveal the profound impact that fishing has had on reef shark populations, with no**

sharks observed on close to twenty percent of reefs surveyed. Reef sharks were almost completely absent from reefs in several nations, and shark depletion was strongly related to socioeconomic conditions such as the size and proximity of the nearest market, poor governance, and human population density. Yet opportunities for reef shark conservation remain: shark sanctuaries, closed areas, catch limits, and an absence of gillnets and longlines were associated with substantially higher relative abundance. These results reveal multiple policy pathways for restoring and managing reef shark populations, from direct top-down management of fishing to indirect improvement of governance conditions. Only by engaging with socioeconomic aspects of tropical fisheries will reef shark populations have the best chance of recovery.

Global demand for shark products, such as fins and meat, as well as high levels of bycatch have caused widespread declines in shark populations globally<sup>1-3</sup>, likely impacting the function of ocean ecosystems<sup>4</sup> and jeopardizing associated fishing and tourism sectors<sup>5,6</sup>. However, there are large knowledge gaps concerning the population status of sharks in coastal environments such as coral reefs, where the majority of threatened species occur<sup>1</sup>. Scientific surveys for reef fish typically utilize underwater visual census by divers, which can lead to under- or over-estimates of the abundance of large roving animals such as sharks<sup>7</sup>. Although a handful of studies from remote, uninhabited, or no-access reefs have recorded exceptionally-high reef shark biomass<sup>8,9</sup> and evidence of declines<sup>9,10</sup>, there are large differences in environmental features<sup>11</sup> and sampling<sup>7</sup> that undermine the use of pristine remote areas as conservation baselines for inhabited coastal environments<sup>12</sup>. In practice, shark conservation targets for

most reefs should reflect levels of abundance found in the best managed places where people are present, acknowledging the environmental and social contexts under which people utilize ocean resources<sup>13</sup>.

We used baited remote underwater video stations (BRUVS) in a dedicated global survey ('Global FinPrint', <https://globalfinprint.org>) to quantify the status of reef sharks in 58 countries, states, and territories (hereafter 'nations'). BRUVS footage was analysed to provide a standardized index of relative shark abundance – given as the maximum number of sharks seen in a single frame of each video set (MaxN; see Methods) – that has been shown to compare well with alternative methods of estimating the relative abundance of sharks<sup>14</sup> (Extended Data Fig 1). Global FinPrint surveys included sightings of 59 shark species, the vast majority of sightings (93%) comprising species that complete their life cycle on coral reefs or frequently visit them (see Methods). Despite our assumption that sharks would be present on all the world's coral reefs<sup>15</sup>, they were not observed at 19% (69/371) of reefs surveyed and 63% of the 15,165 BRUVS sets in our survey did not record a shark, indicating that there has been widespread depletion of reef sharks across much the world's tropical oceans (Figure 1a,b).

We developed a set of Bayesian hierarchical models to quantify the relative abundance of reef sharks across a range of management regimes and understand how reef shark abundance varies globally. We used a zero-inflated modeling approach that allowed us to examine factors influencing both the shark presence/absence (the occurrence of excess zeros) and the relative abundance of sharks among reefs, nations, and regions (see



Methods). While the conditional mode of regional-level random effects for reef sharks was 40% higher in the Central Pacific than other regions (Figure 1c – null model), these differences disappeared under our full model, suggesting the observed inter-regional disparities were largely due to reef and national scale effects captured by the covariates we included (Figure 1c – full model). In other words, although we observed strong regional differences in our data, these were largely attributable to differences in key human drivers of resource exploitation.

Our results show that declines in reef sharks from the coastal tropical oceans correlate with key socio-economic differences among reefs and nations (Figure 1d). Our civil society metric (voice and accountability; *VOICE*) was associated with a higher likelihood of sharks being observed, whereas nations with larger coastal populations (*POP*) coincided with sharks not being observed; we found little evidence for an effect of increased national wealth (human development index; *HDI*). We also found that the relative abundance of reef sharks had a negative relationship with the ‘gravitational pull’ of i) the closest human settlement and ii) markets within 500 km of each BRUVS set (our gravity metric was calculated as the size of human populations divided by their squared distance from surveyed reefs; see Methods)<sup>13</sup>. Given that shark fins are effectively non-perishable and it is common for fishers to travel long distances and for fin-traders to regularly visit remote communities<sup>16</sup>, we expected some decoupling of our gravity metrics and shark relative abundance. In contrast, these results suggest that there may be high levels of local consumption in many areas<sup>13</sup>, supporting recent findings that markets for shark meat have followed the increase in catches for the global fin trade<sup>6</sup>, making

local market-interventions aimed at reducing shark meat consumption a potentially valuable conservation investment in some areas. Our results also suggest that long-term, socio-economic disparities have very likely led to the functional extinction of sharks from survey reefs in up to eight nations (*i.e.* where the probability of sharks being observed was <0.1%; see Methods and Extended Data Figure 2). This emphasizes that, for many places, there are no clear solutions to advancing reef shark recovery without addressing the socioeconomic challenges that indirectly lead to overexploitation.

Prevalence of impoverished countries, weak governance, and the high economic value of wildlife products is a fundamental driver of overexploitation in many of the world's marine and terrestrial ecosystems<sup>17</sup>. Although there are some notable successes in moving communities away from shark fishing and into tourism or other less-destructive sectors<sup>16,18</sup>, livelihood diversification requires substantial, long-term investment and capacity-building efforts suited to local contexts<sup>19</sup>. Therefore, to understand how top down management alternatives relate to reef shark abundance, we estimated relative effect sizes for a range of direct management actions globally (Figure 2a). At the national level, the presence of a shark sanctuary (*i.e.* no targeted catch or trade in shark or shark products) supported 50% [20%, 68%] (Median [90% Highest Posterior Density Uncertainty Intervals]) higher relative abundance than nations without sanctuary status (Figure 2b). Legislation establishing shark sanctuaries has generally been introduced in nations where local communities did not heavily fish sharks for cultural or economic reasons (*e.g.* shark eco-tourism)<sup>20</sup>, which makes their potential effectiveness difficult to predict in jurisdictions where people currently fish for sharks. Despite this, our survey

shows that the nine shark sanctuary nations we surveyed are globally and regionally important refuges for reef sharks.

In places where people engage in shark fishing, we found clear benefits of top-down fisheries management interventions and closed areas (*i.e.* no-take reserves; Fig 2). The use of gillnets and longlines had the most negative influence on relative reef shark abundance, with an average reduction in relative abundance of 36% [11%, 54%] in jurisdictions where one or both gears were used, reflecting their widespread efficiency in capturing sharks, often as bycatch<sup>21,22</sup>. We also found evidence that the use of catch limits (*i.e.* caps on the number of sharks permitted to be caught per day per vessel or fisher or season) were associated with higher reef shark abundance. However, the effect of catch limits on relative abundance was inconsistent across jurisdictions (36% [0%, 58%]), possibly due to the greater difficulty in enforcing catch-based, rather than gear-based, regulations<sup>23</sup>. Banning drumlines (29% [-13%, 52%]) or moving toward more selective hook and line fishing (25% [-8%, 48%]) were estimated to be less effective but may be more acceptable management alternatives in some contexts. Gear restrictions were found to be more effective than closed areas in supporting higher numbers of reef sharks (28% [0%, 50%]; Figure 2a,b), however the benefits increased 2-fold among the largest (~20,000 km<sup>2</sup>) closed areas (49% [11%, 71%]).

Identifying the most appropriate direct management strategies for conservation depends heavily on the nature of local fisheries, social norms, and cultures, as well as some understanding of relative stock status. Therefore, to evaluate relative status of reef shark

abundance among nations, we developed an abundance status score, given by the posterior probability of national expected MaxN being greater than the regional average under our null model (see Methods). This placed each nation in its observed regional context, scoring it relative to its neighbors and reflecting levels of recovery that do not rely on achieving global maxima.

The best performing nations relative to regional expectations included the Bahamas, continental Australia, Solomon Islands, the Federated States of Micronesia and French Polynesia (Figure 3). These nations had many of the effects of key attributes we found to be associated with increased abundances of reef sharks, including being well-governed, and/or remote, and having strong, directed shark fisheries management or shark sanctuaries (Figure 2). In contrast, the worst-ranked nations for reef sharks include Qatar, the Dominican Republic, continental Colombia, Sri Lanka, and Guam, which have suffered from varying levels of poor governance<sup>13</sup> and extreme overfishing. Overall, 59% of nations (34/58) had abundance scores below 50% of their regional expectation, suggesting loss of reef sharks is pervasive among reefs globally.

Given this level of depletion, restoration of reef shark populations will require dedicated and effective management of some form. To evaluate the potential conservation benefits of the most promising management alternatives, we estimated the relative impact of gillnet/longline bans, closures, catch limits, and shark sanctuaries via the expected change in national abundance scores given implementation under our model. Our results show that fisheries management actions are likely to be most effective at conserving reef sharks

overall, with the average regional score increase for catch limits (15%) and gillnet/longline bans (9%) exceeding the benefits of average-sized closed areas (8%) in places where such regulations are currently absent. Although closed areas that are large, old, isolated, and well-enforced have been shown to be among the most successful conservation measures for reef fishes<sup>24</sup>, only very large (~20,000 km<sup>2</sup>) closures outperformed these other measures ('Large closures' in Figure 3a,b).

The apparent difference in the effectiveness of average-sized closed areas for sharks relative to reef fish is likely due to the smaller home range sizes of reef-associated fish, which tend to remain within the bounds of a given closed area, while sharks range more widely and are therefore likely to stray outside<sup>25</sup>. In many places, fisheries management has the potential to be applied across a much larger area than fully closed areas, which are difficult to implement at very large scales as people are typically unwilling or unable to stop fishing entirely<sup>25</sup>. As a result, many closed areas are simply not designed to protect sharks<sup>26</sup>. Yet if measures to stop catches and trade in sharks and shark products could be implemented at the national scale, shark sanctuaries could have the greatest potential benefit (a 25% increase on average) for reef sharks (Figure 3). Again, the economic feasibility and cultural acceptance of this approach is expected to be limited in most places that currently catch and trade shark products.

Given the clear conservation benefits of a range of direct top-down management actions for sharks, a key question lies in asking where the greatest conservation gains could be made if regulations were well-enforced. To address this question, we calculated a total

conservation potential score for each nation, given as the maximum of the sum of estimated conservation benefits from gillnet/longline bans, MPAs, and catch limits or implementation of a shark sanctuary (Supplementary Information). Nations with the highest conservation potential included Madagascar, Mayotte, Indonesia, Vanuatu, Bermuda, and Barbados among others (Figure 3a), all of which lack established management schemes for sharks and have some level of degradation in relative reef shark abundance. As with any fishery, realizing the conservation potential of these nations will require strong engagement and buy-in from judicial systems, fisheries managers, and local fishers to ensure compliance, monitoring, and enforcement of regulations.

Without an absolute estimate of abundance for sharks, it is difficult to know how effective estimated levels of conservation potential might be in restoring shark populations in reef ecosystems that have been degraded by overfishing. Although research has shown that fully recovered reef fish communities have biomasses between 1000 kg/ha<sup>27</sup> and 1500 kg/ha<sup>12</sup>, we have no current estimate of the size of the forage base that is required by a recovered shark population, or how the bottom-up effects of prey biomass might influence the recovery potential of reef sharks. A key question remains as to whether management strategies that only pursue shark conservation can make substantive or limited gains, relative to those that include restoration of the wider reef ecosystem. If whole ecosystem restoration is necessary to fully restore shark populations, our results support those for teleost reef fish that underscore the need for managers to engage with the wider social, economic, and cultural drivers of marine exploitation<sup>28</sup>.

Our study makes clear that concern over the global status of reef sharks is warranted, especially in the Western Pacific, Indian Ocean, and Western Atlantic regions where multiple nations are characterized by dense coastal populations and poor governance. Further, our results identify two management pathways –socioeconomic policy (indirect) and direct management (top-down) – that could yield positive conservation outcomes for sharks when implemented and enforced. From national bans on targeting and trade of sharks, to reef level gear restrictions and closed areas, the societal contexts in which management actions are used will substantially influence where they are likely to be accepted and achieve meaningful conservation gains. Fishery and marine area managers are faced with a daunting problem and, although there is no panacea that will succeed everywhere, these results provide new insights into a portfolio of approaches that could begin to restore reef shark populations throughout the world.

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## Figure Legends

**Figure 1 | Distribution of reef sharks from Global FinPrint.** a. observed proportion of sets containing reef sharks from baited remote underwater video stations (BRUVS) among 371 study reefs; regions are Indian Ocean (squares), Western Pacific (diamonds), Central Pacific (circles), and Western Atlantic (triangles); b. observed distribution of MaxN from n=15,165 individual BRUVS sets, with model-estimated ‘excess’ zeros (n=1481) indicated in red that correspond to the proportion of observed zeros that are inconsistent with the observed distribution of counts (x-axis truncated at 8, which includes >99% of observations); c. conditional modes of regional-level random effects for MaxN per BRUVS set from both null (spatial hierarchy and nuisance parameters only) and full (null + additional management and socio-economic covariates included) models, illustrating the degree to which the full model accounts for inter-regional disparity; vertical white lines are global median expected MaxN values. Regional estimates under the null model were: Western Atlantic: 0.23 [0.14, 0.37] sharks/hr; Central Pacific: 0.59 [0.36, 0.97]; Indian Ocean: 0.29 [0.16, 0.48]; Western Pacific: 0.18 [0.09, 0.35]. Regional estimates under the full model were: Western Atlantic: 0.24 [0.15, 0.39]; Central Pacific: 0.29 [0.18, 0.49]; Indian Ocean: 0.24 [0.15, 0.38]; Western Pacific: 0.23 [0.14, 0.38]; d. Estimated relative effect sizes for the influence of national socio-economic conditions (including the Human Development Index, HDI) on the expected proportion of

negative binomial (NB) variates on BRUVS sets or, for gravity metrics, on expected MaxN/hr; reported values are highest posterior density median values (circles), with 50% (thick lines) and 90% (thin lines) uncertainty intervals. Black symbols indicate 90% UI did not overlap zero; grey symbols indicate 50% UI did not overlap zero; and white symbols indicate 50% UI did overlap zero.

**Figure 2 | Management action effect sizes for reef sharks.** a. Standardized effect sizes of the presence of various management alternatives on the average relative abundance of sharks (expected MaxN). Density plots show the posterior distributions of the estimated effect sizes (Cohen's d scores plotted on the logit scale). The values on the left- and right-hand side of zero (vertical white line) indicate the posterior probability of a negative or positive effect of each management alternative (as percentages). b. Expected change in MaxN given the presence or absence of management alternatives; shading indicates posterior uncertainty intervals from 50 to 90%.

**Figure 3 | Conservation potential for reef sharks.** a. regionally-scaled abundance scores (colors, corresponding to abundance scores in [b]) and conservation potential (circle sizes) for 58 nations surveyed by Global FinPrint (nations with conservation potential >0.9 are labeled); b. net abundance scores (circles without border), relative to region-scale expected values (Figure 1c, null model), and expected change in abundance score (black horizontal lines, net abundance score gain,  $\Delta_{gain,m}$ ) given implementation of potential management options (circles with black border) and estimated average effect sizes from the full model. Line lengths vary by the shape of the estimated posterior average for each nation and are scaled by the percentage of reefs currently not under each management alternative; average percent abundance score increase greater than zero are given in parentheses at top of each panel. Note the capacity to increase conservation scores is limited in many of the lowest-scored sites due to exceptionally low probabilities of shark presence; where management options are already implemented, the conservation potential remains the same.

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#### **Author Contributions**

DDC and MHEI conceived of the study with assistance from MHEU, CAS, MM, EH, and MAM. DDC, MHEI, MHEU, CAS, MM, and EH directed field work run by JG, JK, MB, LCR, CS, KF, JV, GC, and CSS. Database management was by TG. MAM and DDC drafted the manuscript, with help from MHEI, MHEU, CAS, JEC, MM, EH, JG, JK, MB, LCR, CS, CSS, MJR, VU, and TG. All other authors contributed equally, having made substantial contributions to data collection, having provided input and approved the text in the manuscript.

#### **Competing interests**

The authors declare no competing interests.

#### **Author Information**

Reprints and permissions information is available at [www.nature.com/reprints](http://www.nature.com/reprints). The authors declare no competing interests. Correspondence and requests for materials should be addressed to [a.macneil@dal.ca](mailto:a.macneil@dal.ca).

#### **Data Availability Statement**

Data and code used to reproduce the analysis – except for geolocations – can be accessed at <https://github.com/mamacneil/FinPrint>.

## **Methods**

### *Surveys*

Our study began in July 2015 but also incorporated a minority of BRUVS deployed prior to 2015, collected according to the standard methodology described below (6% of all sets were deployed prior to June 2015). Sampling ended in June 2018. Each sampling site (hereafter referred to as a “reef”;  $n=371$ ) consisted of a continuous reef tract ~10 km in length. Reefs were selected for sampling based on access through a local collaborator and the operational range of the vessel used for sampling. Within nations, we generally attempted to sample at least one reef that was “closed” to fishing and one reef that was “open” to fishing and/or had “restricted” fishing. When larger numbers of reefs were sampled within a nation, as far as practicable, sampling included reefs across a range of distances from urban centers. Each deployment of a BRUVS was considered a ‘set’ (which are referred to as a ‘drop’).

BRUVS were comprised of a video camera (primarily GoPro HERO2, GoPro HERO3, GoPro Hero4 Silver, <https://www.gopro.com>, or Sony CX7, but also Sony Legria HF10, and Sony Handycam DCR-HC52 in sets made prior to July 2015) fixed on a stainless steel, aluminum or rebar frame with bait mounted on a 1.5 m long pole in the camera's

field of view, with a rope and float tied to the top of the frame to facilitate deployment, relocation, and retrieval<sup>14</sup>. Each BRUVS set was baited with approximately 1 kg of oily fish (e.g. primarily from families *Clupeidae* and *Scombridae*). Metal cages prevented baits from being eaten although plastic was used in some cases. Nearly all reefs were sampled with replicate BRUVS sets over a single period of < 10 days (mean BRUVS per reef = 39; range = [9, 71]).

Nearly all (> 98%) BRUVS sets 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 sets were then deployed as close as possible to these coordinates and the remainder were then set at least 500 m away from previous sets<sup>14,29</sup>, at depths of 2-40 m. This spacing was designed to reduce the likelihood of individuals occurring on multiple cameras. Bottom depth and sea surface temperature were recorded at deployment. Visibility, substrate complexity, and substrate type were estimated for each deployment using a still frame from the footage after the BRUVS set settled to the bottom in the Benthobox software ([www.benthobox.com](http://www.benthobox.com)). BRUVS sets were retrieved after at least 70 minutes to ensure a standard 60 minutes of data collection from the time of settlement. 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. Where images were ambiguous (4.82% of cases), the lowest taxa to which it could be confidently assigned (genus, family, etc) was used. As such we assumed there was no ambiguity in assignment of species as being 'reef sharks' (see below).

543

544 Videos were viewed and scored in the FinPrint Annotator (v.1.1.44.0) or EventMeasure  
545 ([www.seagis.com](http://www.seagis.com)) to record species present and the number of individuals observed.

546

547

548 *MaxN*

549

550 By convention, the quantity reported from BRUVS data is an index of relative abundance  
551 known as MaxN, which is the maximum number of individuals of each species seen on  
552 any given frame of a BRUVS video set. MaxN has become the standard metric for  
553 reporting due to concerns by researchers that they will re-count the same individual  
554 should they leave the field of view and return<sup>30</sup>. Here we define MaxN as the maximum  
555 number of individual reef sharks seen on any one frame of a single BRUVS video set.

556

557 Note that we defined ‘reef sharks’ as being those species that spend the majority of their  
558 life-history on or around reef habitats or species that regularly visit reefs. The most  
559 common species observed included grey reef (*Carcharhinus amblyrhynchos*), whitetip reef  
560 (*Triaenodon obesus*), blacktip reef (*C. melanopterus*), Caribbean reef (*C. perezi*),  
561 silvertip (*C. albimarginatus*), Galapagos (*C. galapagensis*), nurse (*Ginglymostoma*  
562 *cirratum*), tiger (*Galeocerdo cuvier*), great hammerhead (*Sphyrna mokarran*) and lemon  
563 sharks (*Negaprion acutidens*, *N. brevirostris*). We calculated MaxN as the collective  
564 MaxN across all species of shark, calculated as the sum of the MaxN values for all reef  
565 shark species observed on a single BRUVS set.

*Potential MaxN Bias*

As MaxN has been criticized for hyperstability (i.e. counts remaining high as true abundance decreases)<sup>31</sup>, we examined the relationship between MaxN and MeanCount – the average number of sharks observed in video frames at regular intervals – which has been shown to be linearly-related to absolute abundance<sup>32</sup>. For a subset of 62 reefs, spanning MaxN ranges from zero to 24 (within the top 0.001% of observed values), we examined the relationship between MaxN and average MeanCount, taken as the average number of sharks observed across 360 still images (i.e. 10 sec intervals over an hour). For our data, MaxN was linearly related to MeanCount (Extended Data Fig 1), suggesting that MaxN is an unbiased index of abundance within the context of our study. This result is consistent with those of Schobernd et al. (2014), who found hyperstability in MaxN values at true abundances beyond 20 individuals<sup>31</sup>. Given that this study is quantifying relative abundance of sharks, which occur in low numbers, there is no evidence of the video ‘saturation’ effect by which hyperstability occurs.

However, in response to Referee comments, we conducted three additional analyses to support our original conclusions regarding the MaxN vs MeanCount relationship. First, we calculated an MeanCount for an additional 20 BRUVS and again estimated the slope of the relationship with MaxN, finding a similar slope to our original analysis (2.30 [1.65, 3.30]). Second, we conducted a bootstrap resampling procedure, sampling 5 observations 1000 times at random without replacement



from our original dataset and estimating the slope of the relationship between MaxN and MeanCount, also finding a similar slope to our original analysis (3.17 [1.89, 6.49]). Lastly, we conducted a bootstrap-based power analysis, whereby we sampled from 3 to 11 observations, 1000 times each at random with replacement from our original dataset and calculated, at each step, the proportion of bootstrap replicates for which the 95% confidence intervals of the estimated slope do not overlap zero. Our results show that 7 samples are sufficient to have >95% probability of observing a positive slope between MaxN and MeanCount (Extended Data Figure 1).

#### *Variable selection*

Extensive work by the Social-Ecological Research Frontiers (SERF) working group has explored relationships between numerous social-ecological factors and the reef fish exploitation<sup>13,27,33,34</sup>. However, due to the data limitations of surveying sharks<sup>7</sup> – which are inconsistently observed and recorded – relationships between many of the factors affecting reef fish have not been explored for sharks. Therefore, we built on this previous work, selecting a set of variables that have been shown to impact reef fish or have other theoretical support.

As social and ecological processes operate at various spatial scales, the variables we selected occurred at one of four scales: *region* – either Western Atlantic, Indian Ocean, Western Pacific, or Central Pacific; *national* – the major jurisdiction, encompassing country, territory, or large-scale division (e.g. continental Australia was divided into the

Pacific and Indian Ocean coasts given distinctive state jurisdictions). Australia, Jamaica and Colombia were also divided into the core sampling area along the nation's main coastline and offshore locations (Australia Indian Ocean Territories, Jamaica Pedro Bank and Colombia Seaflower Biosphere Reserve, respectively) given differences in governance, population density, and remoteness of these jurisdictions; *reef* – each continuous association of hard corals, ranging from hundreds of meters to tens of kilometers across, separated by a deep channel, within which BRUVS were deployed<sup>35</sup>; *set* – each individual BRUVS deployment, consisting of a single baited drop recording a continuous hour of standardized video. All variables were checked for problematic collinearity (Pearson's correlations >0.9)<sup>36</sup>; none were removed aside from Gross Domestic Product (*GDP*) – which was collinear with *HDI* – and our longline/gillnet issues reported below.

National-scale variables were primarily related to socio-cultural, economic, and political conditions, within each nation, that have been associated with rates of environmental degradation<sup>13</sup>.

*HDI* – Human Development Index: a composite measure (0 to 100) of life-expectancy, income, and education factors developed by the UN Development Programme; <http://hdr.undp.org/en/content/human-development-index-hdi>

*VOICE* – Voice and accountability: a composite metric (-2.5 to 2.5) developed by the World Bank that represents the extent to which people in each nation are able to

participate in governance, free expression, free media, and free association;

<https://info.worldbank.org/governance/wgi/pdf/va.pdf>

*POP* – Size of the coastal population within 50 km of the sampled reef;

<https://sedac.ciesin.columbia.edu/data/collection/gpw-v4/sets/browse>

*BAN* – Shark sanctuary: a dummy variable (0/1) indicating if nation is a designated ‘shark sanctuary’ that ‘prohibit targeted commercial shark fishing at a minimum, and intend to make it unlawful to possess, sell, or trade sharks or their parts’<sup>20</sup>. Note that Palau is widely-regarded as the world’s first shark sanctuary, both domestically and internationally, however this has only recently been passed into law; we regarded it as a *de-facto* shark sanctuary in our data.

*CLN* – Coast length: length of the national marine coastline in km.

Reef-scale variables were primarily concerned with the shark-related management scheme in place at the sampling location.

*PRO* – Shark protection status: mutually-exclusive dummy variables indicating if reefs include fishing restrictions (*Restricted*) or are closed to fishing (*Closed*). Note ‘dummy’ variables below consist of 0/1 values indicating presence/absence

*MPS* – The size ( $\log(\text{km}^2)$ ) of the closed area (where present)

658

659            *HIG* – Dummy variable indicating if the closed area is high compliance, i.e. that  
660 there is likely little to no poaching occurring.

661

662            *GEAR* – Dummy variables for each shark-related fishing gear in use, including  
663 *Gillnets/longlines (GIL)*, *Drumlines (DRU)*, and *Hook & line (HLN)* fishing. Gillnets and  
664 longlines were analyzed as one variable due to strong co-linearity in our dataset.  
665 Drumlines were defined as single baited hooks anchored to the substrate and left alone,  
666 while Hook & line was defined as fishers from vessels deploying baited hand lines.

667

668            *REM* – Dummy variable indicating if reef is more than 200km from human  
669 settlement<sup>13,27</sup>.

670

671            *GRAV* – We developed two gravity metrics: 1) the nearest population, equal to the  
672 population of the nearest human settlement divided by the squared travel time between  
673 the reef site and the settlement; and 2) the nearest market, equal to the population of the  
674 nearest market (defined as a port, provincial capital, or major city) divided by the squared  
675 travel time between the reef site and the market. see Methods in Cinner et al. 2016<sup>13</sup> for  
676 details.

677

678            *BAG* – Dummy variable indicating if catch limits are in place for sharks

679

680            *TEM* – Dummy variable indicating if temporal limits are in place for sharks

681

682           *SPP* – Dummy variable indicating if species limits are in place for sharks

683

684           *RTY* – Reef type; mutually exclusive dummy variable indicating if the surveyed

685 reef was from a reef *slope*, *lagoon*, *flat*, or *other* reef type.

686

687

688   Set-scale variables were primarily concerned with alleviating bias in potential BRUVS

689 deployments within each nation.

690

691           *DEPTH* – depth of BRUVS deployment (m)

692

693           *VIS* – estimated visibility in the water column (m)

694

695           *HC* – percentage of hard coral cover present in the field of view (%)

696

697           *RUG* – 0 to 5 ranked score for structural complexity of the surrounding reef (in

698 field of view)<sup>37</sup>.

699

700           *BAIT* – a mutually-exclusive dummy variable indicating the fish family group

701 used for bait; one of *Clupeidae*, *Scombridae*, *Sphyraenidae*, *Mixed*, or *Other* (one-

702 off/rare).

703

TIME – number of minutes away from noon at the start of the BRUVS set (min)  
to account for diurnal activity

Note that all variables were standardized prior to analysis (mean centered, divided by 2x  
standard deviation) to make them broadly comparable in relative impact.

### *Bayesian hierarchical model*

To quantify the relationship between candidate variables of interest and observed reef-  
shark MaxN we developed a Bayesian hierarchical model that encompassed regional ( $r$ ),  
national ( $k$ ), reef ( $j$ ), and set ( $i$ ) spatial scales. Note that while more reefs were observed  
from jurisdictions such as Australia, this hierarchical model structure explicitly accounts  
for such imbalances. In addition, as more than 60% of BRUVS did not observe a single  
shark, we compared the model fit of a conventional negative binomial (NB) likelihood  
model for counts with that of a zero-inflated negative binomial (ZINB) model, which  
allows for ‘excess’ zeros that exceed those expected given an NB model (Extended Data  
Table 1). Note also that, in terms of selecting an NB model, we had initially fit Poisson  
(which has theoretical support due to MaxN being derived from a collection of individual  
shark arrivals at the BRUVS station) and zero-inflated Poisson models to the data, but the  
presence of substantial overdispersion led to poor model fit and our adoption of the NB  
(which can be equivalent to the Poisson as a special case).

Based on Referee comments, we developed a set of alternative model structures beyond our zero-inflated full model, for null (intercept-only), partial null (hierarchical model with nuisance parameters relating to sampling), and full model (hierarchical model with all covariates) approaches, both with and without zero-inflation. Using this set, we implemented a weighted-model approach to inference, using the Pareto Smoothed Importance Sampling Leave-one-out (PSIP-LOO) cross validation methods recommended by Vehtari et al. (2017)<sup>38</sup> to calculate individual model weights, which are provided by convenience functions within PyMC3 (see <https://docs.pymc.io/api/stats.html?highlight=compare#pymc3.stats.compare> for documentation). The weighted-model method proceeds by summing posterior parameter estimates from each model that have been multiplied by their PSIS-LOO model weights, thereby integrating the relative support for each model in the final weighted model used for inference, conditional on the data. Note this places the national-scale variables of *HDI*, *VOICE*, and *POP* in both the zero and count parts of the final weighted ZINB model (see parameter estimates in Extended Data Figure 3).

Under the weighted ZINB model we estimated excess zeros occurring in 10% of BRUVS sets (n=1481; Figure 1b), which, by placing posterior weight (77%, via PSIP-LOO) on having key national-scale covariates in the zero component of the ZINB model, we assumed reflects long-term degradation that has led to shark presence/absence among reefs. Conversely, under the ZINB count-only model (16% PSIP-LOO weight) these national-scale covariates were part of the count component, which we assume represents contemporary conditions amenable to management. Lastly, the PSIP-LOO results

revealed 11 high-leverage observations for which the observation-wise Pareto  $\hat{k}$  estimate was  $>0.7^{38}$  (Supplementary Information), which we removed prior to final model comparison.

The observation model for each BRUVS set assumed that BRUVS counts occurred as a mixture of presence/absence (the ‘zeros model’) and counts (the ‘count model’), each of which contained a hierarchical component that were jointly ZINB distributed for set ( $i$ ), reef ( $j$ ), nation ( $k$ ), and region ( $r$ ):

$$Max N_{ijkr} \sim ZINB(\phi_{ikr}, \mu_{ijkr}, \alpha)$$

where  $\phi$  is the probability of an excess zero,  $\mu$  is the mean count conditional on an excess zero not occurring, and  $\alpha$  is the dispersion parameter of the negative binomial, given a  $\sim \Gamma(0.001, 0.001)$  prior. For the full ZINB model, the log-odds of an excess-zero ( $\eta_{z0kr}$ ) was modelled as a linear function of three national-level covariates, using a non-centered parameterization<sup>39</sup> to handle divergent transitions that we detected in the process of peer review (Extended Data Figure 7):

$$\begin{aligned} \text{logit}(\phi_{ikr}) &= \eta_{z0kr} \\ \eta_{z0kr} &\sim N(\eta_{z0r} + \eta_{z1}HDI_k + \eta_{z2}VOICE_k + \eta_{z3}POP_k, \sigma_{z0\eta}) \\ \sigma_{z0\eta} &\sim \text{Exp}(1) \\ \eta_{z0r} &= \pi_{z0} + \sigma_{z0v}\widetilde{\pi_{z0r}} \\ \widetilde{\pi_{z0r}} &\sim N(0,1) \end{aligned}$$



$$\sigma_{z0v} \sim \text{Exp}(1)$$

$$\pi_{z0} \sim \text{Cauchy}(0,10)$$

$$\eta_{z1}, \eta_{z2}, \eta_{z3} \sim \text{Cauchy}(0,3)$$

767

768 For the ZINB count-only model, parameters  $\eta_{z1}$  to  $\eta_{z3}$  were passed to the count  
 769 component (as additional parameters  $v_3, v_4$ , and  $v_5$  in the national-scale model below –  
 770 not shown), leaving only the intercepts in the hierarchical structure of the zeros-model.  
 771 For both models, the log of the conditional mean count was modelled as a linear function  
 772 of multiple covariates at the three smaller scales:

773

$$\log(\mu_{ijk_r}) = \kappa_{0jkr} + \rho_1 \text{DEPTH}_i + \rho_2 \text{VIS}_i + \rho_3 \text{HC}_i + \rho_4 \text{RUG}_i + \rho_5 \text{BAIT}_i$$

$$\kappa_{0jkr} \sim N(\mu_{0jkr}, \sigma_{0jkr})$$

$$\begin{aligned} \mu_{0jkr} = & \eta_{0kr} + \kappa_1 \text{RTY}_j + \kappa_2 \text{CLO}_j + \kappa_3 \text{MPS}_j + \kappa_4 \text{HIG}_j + \kappa_5 \text{GIL}_j + \kappa_6 \text{DRU}_j + \kappa_7 \text{HLN}_j \\ & + \kappa_8 \text{REM}_j + \kappa_9 \text{GRAV}_j + \kappa_{10} \text{GRAV}_{\text{NC},j} + \kappa_{11} \text{BAG}_j + \kappa_{12} \text{TEM}_j + \kappa_{13} \text{SPP}_j \end{aligned}$$

$$\eta_{0kr} \sim N(\mu_{0kr}, \sigma_{0kr})$$

$$\mu_{0kr} = v_{0r} + v_1 \text{BAN}_k + v_2 \text{CLN}_k$$

$$v_{0r} = \pi_0 + \sigma_{0v} \widetilde{\pi_{0r}}$$

$$\widetilde{\pi_{0r}} \sim N(0,1)$$

$$\sigma_{0jkr}, \sigma_{0kr}, \sigma_{0v} \sim U(0,100)$$

$$\pi_0 \sim N(0,3)$$

774

775 We chose priors that allowed for a wide range of parameter values before consideration  
 776 of the data, representing our relative ignorance about the parameters in our model prior to

analysis, but also within realistic ranges. We checked our choice of prior across realistic ranges from  $N(0,1)$  to  $N(0,8)$  for the count model parameters, and over  $Cauchy(0, 1)$  to  $Cauchy(0,8)$  for the zero model parameters. Results show our posterior parameter estimates had low sensitivity to the choices of prior across these ranges, with the greatest effects seen among larger-scale parameters including *HDI*, *VOICE*, *POP*, and the overall MaxN rate (Extended Data Figure 5). While these effects were evident, they did not substantively affect the inferences made in our analysis.

We implemented all our models using the PyMC3 package<sup>40</sup> for the Python programming language, and assessed model convergence by Gelman-Rubin statistics (R-hat), whereby values very near one are deemed to have converged, and by examining posterior traces. We also assessed model fit using posterior predictive distributions, whereby observed values are compared to the posterior distribution for each observation (Extended Data Figure 6). Well calibrated models will include the observation within higher-density regions, rather than out on the tails of the posterior distribution. The highest posterior density of the  $\alpha$  parameter of the ZINB was 6.64 [5.79, 7.73]. Note we also found important sampling effects (i.e. locally-varying conditions) among our nuisance parameters related to depth (0.08 [0.04, 0.13]), rugosity (0.07 [0.02, 0.12]), visibility (0.32 [0.27, 0.39]), season (winter=-0.21 [-0.33, -0.08], shoulder=-0.03 [-0.16, 0.08]) and bait type (Scombridae=0.23 [0.05, 0.42], Mixed=-0.12 [-0.32, 0.07], Other=-0.27, [-0.48, -0.05], Sphyraenidae=1.07 [0.65, 1.47]) that constituted potential sampling bias and necessitated inclusion in our partial null model (Extended Data Fig 3).

*No sharks observed*

The zero density portion of ZINB model we used allows for an 'excess' of zeros (no sharks observed) at the reef and national levels such that, if no sharks were observed in the data, this can arise naturally by random chance (given by the NB likelihood component, given the distribution of the counts) or due to a zero-inflation process that may be unknown. This does not mean that sharks are necessarily locally extinct from any nation we surveyed; rather it is a statistical result that most likely means that sharks are at such low local densities that they are unlikely to be observed among the reefs we surveyed. In general, we regard these locations as places where sharks are functionally extinct, meaning they likely play little to no role in the function of the ecosystem, rather than locally extinct, meaning they do not occur. In addition, readers may note that places with near zero-probability of presence (Extended Data Fig 2), nonetheless have a positive expected MaxN, conditional on an excess zero not occurring (Extended Data Fig 7), in places such as for example the Dominican Republic. This seeming paradox is often present in zero-inflated models and stems from the observed data assuming to have arisen from a mixture of two processes: one for excess zeros, and one for counts when excess zeros do not occur. The near-zero probability of presence was because no sharks were observed across 120 BRUVS sets in the Dominican Republic (0/120). Yet nearby nations, such as Puerto Rico (4/77), Cuba (30/241), and Turks and Cacaos (3/37) all observed sharks to varying levels. So, in the absence of any counts, the expected MaxN given presence increases toward an expected value given Caribbean-wide average and the national-level covariates in the count portion of the model. Yet for the data we observe,

the estimated values are given by the product of this large average and the near-zero estimate, meaning the unconditional expected counts in the Dominican Republic are near zero.

#### *Abundance scores*

Given the complete lack of baselines for reef sharks globally, we developed a national-scale scoring system to evaluate the national conservation status of reef sharks relative to the expected average MaxN within each region under our null ZINB model.

$$\Pr(E(\eta_{0kr}) > v_{0r} | \eta_{z0kr})$$

In doing so, it is important to recognize that we explicitly ranked national performance under something akin to a bell curve, assigning ‘winners’ and ‘losers’. Yet our scoring system is more nuanced than this – the abundance score for each nation is the proportion of their posterior density of the nation’s expected MaxN that was greater than their regional expected MaxN (i.e. regional posterior median). If all nations within a region had the same posterior expected MaxN then they would all have abundance scores of 0.5 (i.e. their expected MaxN would be the same as their regional expected MaxN, leading to 50% of their posterior density above and below their posterior regional median). What this means in practice is that our abundance scores represent national-scale performance being evaluated as greater or less than average (0.5), with high (>0.9) and low (<0.1) scores indicating relatively high and low conservation status, respectively.

845

846 The null model was used to evaluate current status conditional only on nuisance  
847 parameters (i.e. parameters that have the potential to bias sampling but are not of direct  
848 interest) to alleviate sampling bias, rather than model-adjusted status given by the  
849 national-scale intercepts under our full model, which would not include realized benefits  
850 from closed areas or losses from destructive gears. The null-model national estimates  
851 reflect the observed data while still accounting for sampling, while the full-model  
852 national estimates would reflect remaining national-scale differences given the covariates  
853 in our model. In other words, we calculated national abundance scores based on their  
854 observed (but bias-corrected) data, rather than model-derived estimates based on average  
855 conditions globally. Note that while national-scale estimates are our best-available data  
856 for the relative abundance of reef sharks and resultant abundance scores, the number of  
857 reefs sampled varies in proportion to the total coastline. For example, among the lowest-  
858 performing nations, the four reefs surveyed along the 1,288 km-long coast of Dominican  
859 Republic are likely more representative than the two reefs surveyed from the 7,516 km-  
860 long coast of India and we did find evidence of slightly lower MaxN values on longer  
861 coastlines (Extended Data Fig 3). Ultimately additional reefs from a representative  
862 sample within each nation will provide more precise, and potentially more accurate,  
863 estimates than those we report here.

864

865 *Benchmarking BRUVS with other approaches*

866

While it is difficult to compare relative shark abundance estimates among studies that use different abundance indices (all methods are biased to an often-unknown degree), we found our results are broadly comparable to smaller-scale surveys among subsets of our survey nations. For example, recreational SCUBA diver surveys found very similar spatial patterns to what we observed with BRUVS in the greater Caribbean, reporting an absence or very few sharks observed at sites where we did not observe sharks (Mainland Jamaica, Dominican Republic and French West Indies) and reporting that sharks were commonly observed in our highest abundance locations such as the Bahamas and Florida Keys<sup>7</sup>. Furthermore, similar species richness and seasonal abundance trends have been observed for sharks surveyed with BRUVS and longlines in the Bahamas<sup>41</sup>. Lastly, recent work has shown that Bahamas/Turks and Caicos had greater shark diversities and abundances than Belize/Jamaica when compared using eDNA<sup>42</sup>.

### *Conservation potential*

To represent the conservation potential of management alternatives under average conditions in our model, we first estimated the individual conservation gains expected within each nation, given their successful implementation. We estimated conservation gain as the expected difference between the current abundance score under the null model (*i.e.* current, sampling corrected estimated relative abundance  $\eta_{0kr}$ ) and the expected abundance score given implementation of each management effect ( $\kappa_m$ ), weighted by the proportion of reefs where they are not currently in place ( $P_m$ ):

890

$$\Delta_{\text{gain},m} = \Pr(E(\eta_{0kr} + \kappa_m P_m) > u_{0r} | \eta_{z0kr}) - \Pr(E(\eta_{0kr}) > u_{0r} | \eta_{z0kr})$$

891

892 In essence, these scores represent the marginal gains that remain to be made given each  
893 management action ( $m$ ) and current conditions, and are the horizontal black lines seen in  
894 Fig 3. Conservation gains were calculated by adding (or subtracting) posterior effect  
895 sizes, conditional on our model.

896

897 We calculated total conservation potential as being the maximum abundance score  
898 change from either: a) implementing a shark sanctuary or b) the sum of abundance score  
899 changes for implementing a gillnet/longline ban, catch limits, and large-scale closed areas  
900 (shark bans being mutually exclusive to the other measures). Note this summation  
901 assumes benefits can be accrued additively, as specified by our statistical model. Note  
902 that in practice, we expect local cultural features to impact conservation outcomes in  
903 ways that deviate from the globally averaged conditions presented here.

904

## 905 **Additional References**

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**Extended Data Fig 1 | MaxN vs MeanCount relationships** a. for 82 BRUVS sets across the range of MaxN values observed by Global FinPrint. Linear model estimates are 1.56 [1.09, 2.05] (intercept) and 3.03 [2.75, 3.26] (slope) (median [95% uncertainty intervals of highest posterior density]). Red line is the highest posterior density model fit; grey lines are 100 realizations of possible model fits given random samples from the model posteriors, showing a tight relationship to the estimated red line. b. 1000 Bootstrap-based linear model estimates from samples of 5 BRUVS sets (with

replacement) from the sample of 62 BRUVS in a., with estimates of 1.26 [0.29, 2.67] (intercept) and 3.17 [1.89, 6.49] (slope), using the OLS function from the *scipy statsmodels* package in Python. Wider variability in b. due to estimating lines from 5 datapoints with replacement. c. Bootstrap-based power analysis results showing the number of observations required to have a 95% probability of the estimated linear slope being  $> 0$ ; probability on the y-axis are the proportion of bootstrap replicates (with replacement) for which the 95% confidence intervals of the estimated slope do not overlap zero.

**Extended Data Fig 2 | Expected probability of sharks being observed** on BRUVS sets from 58 national jurisdictions surveyed by Global FinPrint; number of reefs surveyed in parentheses. Among the eight lowest-ranked nations there is estimated to be less than 0.1% chance of a shark being present any time a BRUVS is deployed, suggesting sharks are functionally extinct on these survey reefs. Functional extinction here means that reef sharks are essentially absent from the ecosystem, playing little to no functional role in structuring the surrounding reef fish community via predation or fear-based effects<sup>43</sup>. Symbols are median (circles), 50% (wide horizontal lines), and 95% (thin horizontal lines) highest posterior density (credible) intervals. Note that while there are more reefs observed from jurisdictions such as Australia, the hierarchical model used explicitly accounts for such imbalance.

**Extended Data Fig 3 | Forrest plot of ZINB posterior distribution effect sizes for candidate models** including a. count covariates, and b. zero-inflation covariates, showing

median (circles), and 95% (thin horizontal lines) highest posterior density (credible) intervals for four independent MCMC chains (left panel). Models with PSIS-LOO-based weights  $>0$  include the ZINB full model (77% weight; squares), the ZINB full count model (16% weight; up triangle), and ZINB partial null (7% weight; down triangle); circles indicate model-weighted estimates used for inference. R-hat values for all parameters were all between 1.01 and 1, suggesting no evidence that models failed to converge. Note differences in the scale along x-axes.

**Extended Data Fig 4 | Diagnostic plots for Hamiltonian Monte Carlo:** bivariate plots of posterior traces (red dots) of **a, b.** global zero slopes and region-level zero variances and **c,d** global count slopes and region-level count variances. Green dots highlight potentially divergent transitions in NUTS samples. Left column (**a, c**) shows a high number of clustered divergent transitions clustered indicative of pathological parameter space; right column (**b,d**) shows elimination of these problems using a non-centered, re-parameterization<sup>39</sup> of the original full zero-inflated hierarchical model, which had 77% of posterior PSIS-LOO model weight.

**Extended Data Fig 5 | Sensitivity plot for the effects of  $N(0,\sigma)$  or  $C(0,\gamma)$  prior standard deviations ( $\sigma$ ) and scales ( $\gamma$ ) on selected posterior parameter estimates using the full zero-inflated negative binomial model (77% of PSIS-LOO weight) of reef shark MaxN observations in Global Fingerprint.** Symbols are median (circles), 50% (wide horizontal lines), and 95% (thin horizontal lines) highest posterior density (credible)

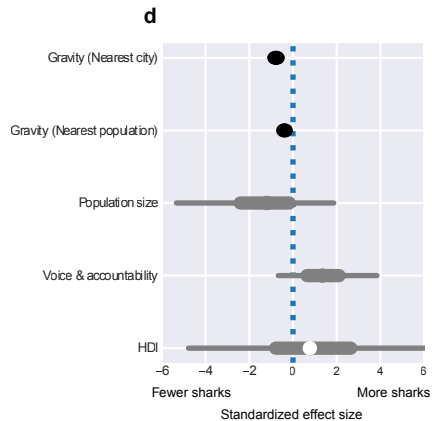
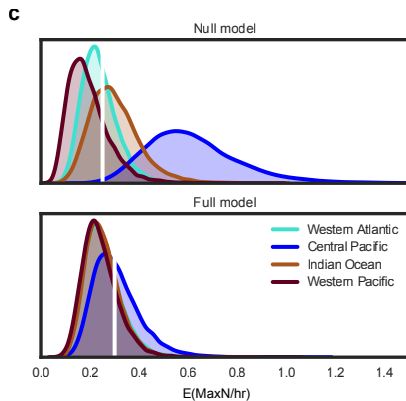
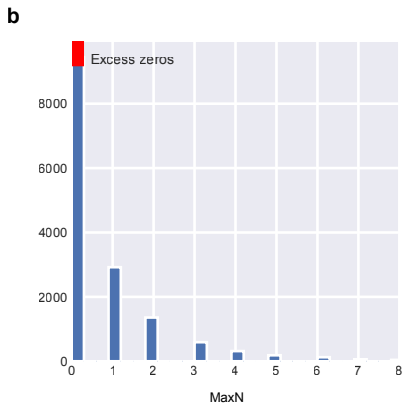
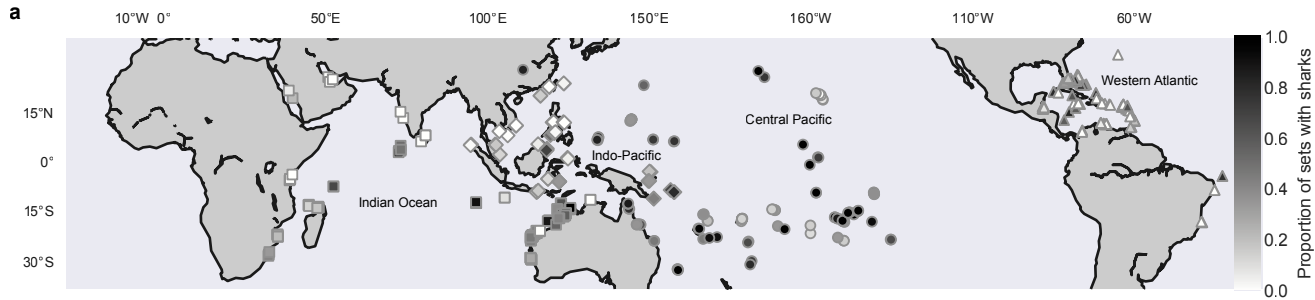
intervals. Results show minor effects of prior specification on the global rate, with small changes to Cauchy prior scale values for HDI, VOICE, and POP.

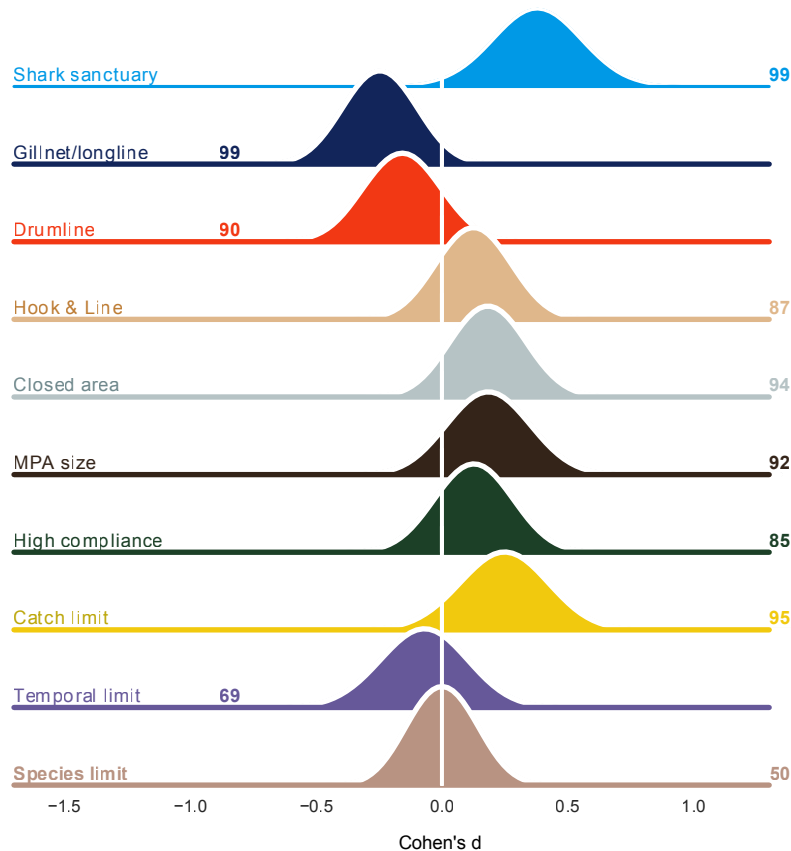
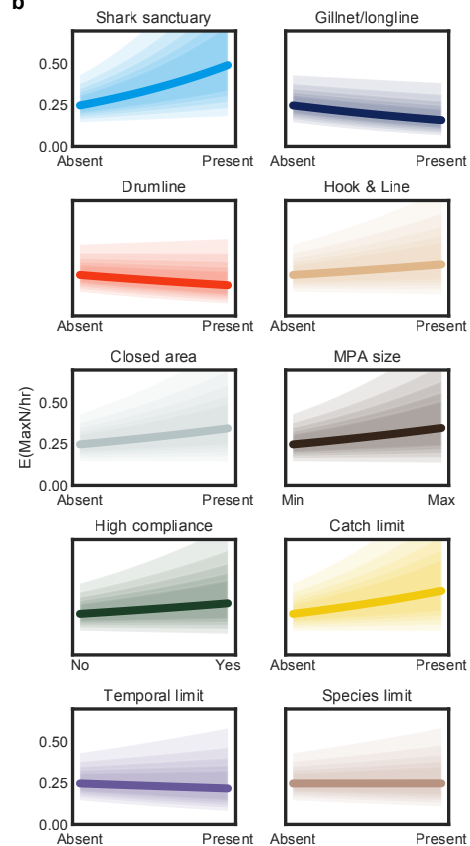
**Extended Data Fig 6 | Posterior predictive distributions** (blue distributions) for the full model, which had the majority (77%) of posterior model weight, of a) observed MaxN (vertical red lines) for 25 (of >15,000) randomly-selected BRUVS sets from Global FinPrint, and b) the observed overall mean MaxN (vertical blue line); distributions consistently overlapping observed values are taken as evidence of the full ZINB model being consistent with the observed data; c) frequency distribution of posterior predictive densities (boxplots) and observed mean MaxN values (red dots) for 15,176 BRUVS observed as part of Global FinPrint; d) Note in a) only 4.3% of observations were outside their 95% highest posterior predictive density (HPPD), suggesting there is no evidence that the full model is inconsistent with the observed data. Note plot c) was truncated at MaxN = 10 (representing >99% of observed MaxN) for clarity.

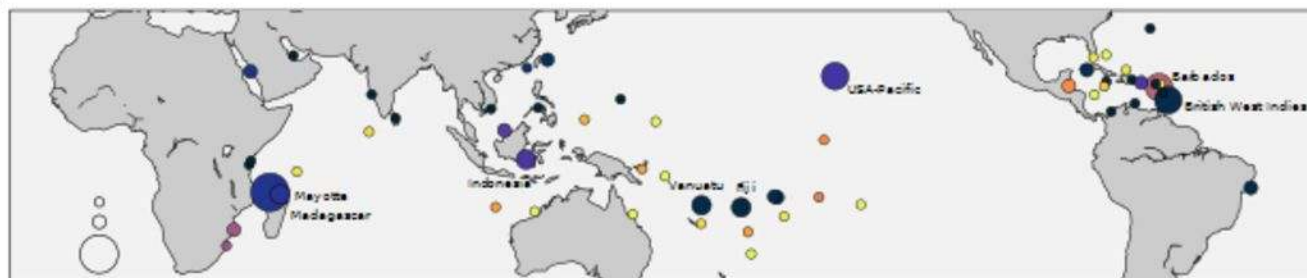
**Extended Data Fig 7 | Expected relative abundance (MaxN) conditional on an excess zero not occurring**, on BRUVS sets from 58 national jurisdictions surveyed by Global FinPrint; number of reefs surveyed in parentheses. Symbols are median (circles), 50% (wide horizontal lines), and 95% (thin horizontal lines) highest posterior density (credible) intervals.

**Extended Data Table 1 | Model selection** for candidate Negative Binomial (NB) models for estimating relative reef shark abundance (MaxN) within the Global FinPrint dataset.

1026 The NB model used was parameterized as a Poisson random variable whose rate  
1027 parameter is gamma distributed. ZI stands for zero-inflated; LOO is leave-one-out cross-  
1028 validation and SE is the standard error of LOO;  $\Delta$ LOO is the net difference in LOO  
1029 scores relative to LOO for the lowest-scored model. Weight is the probability of each  
1030 model being equivalent to the lowest-ranked LOO model (ZI full), based on the standard  
1031 error of the difference in LOO scores (See methods).



**a****b**

**a****b**