Modelling Global Coral Reef Fisheries

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Introduction

Coral reef fisheries are of critical importance to coastal peoples world-wide, generating food, employment and income both for fishers and across communities and wider societal networks (Teh et al. 2013, Cinner 2014). Over time they also provide food security, an important consideration in the face of global change and political uncertainty.

Despite their importance, coral reefs have been subject to degradation for several decades, arising from the impacts of overfishing, destructive fishing, pollution, sedimentation, direct destruction from coastal development, surges in disease and the influence of invasive species. For over two decades the dramatic consequences of ocean warming have generated pulsed but coral bleaching events, often associated mass coral mortalities. Ocean acidification and de-oxygenation are likely to exacerbate these pressures in coming decades (Spalding and Brown 2015).

There is evidence that sound reef management can not only reduce many local pressures, but in doing so it can increase coral reef resilience, enabling a more robust response to, or recovery from, unmanageable impacts such as coral bleaching and disease outbreaks (Ortiz et al. 2018, Darling et al. 2019).

An understanding of reef fisheries, especially in the context of sustainability, provides a critical resource for coral reef management, with considerable social, economic and ecological benefits. Giving a broader spatial scale to such understanding, whether at regional or even global scales, can further support national, regional and global policy approaches in areas ranging from conservation prioritisation to development programming to climate change adaptation investments.

To date, two broad approaches have been taken to track coral reef fisheries: catch monitoring and fisheries independent surveys, which in coral reefs are typically in-water surveys. Both approaches have been used at local or small scales, but also in larger review and synthesis papers and modelling approaches.

Fisheries dependent assessments rely on representative sampling, however the multi-species nature of coral reef fisheries, and the predominance of small-scale, artisanal and even opportunistic fishers can lead to under-reporting. National level reporting to the FAO has been estimated to capture only 5-25% of coral reef fisheries and may also be failing to capture overall trends (Zeller et al. 2007, Pauly and Zeller 2014). Where more comprehensive data, such as creel surveys, can be utilised reporting may be more complete e.g. (Cuetos-Bueno and Houk 2015, Weijerman et al. 2016). Fishery-independent surveys offer the advantage of direct ecological observation and the potential for systematic sampling, but they do not directly provide catch data, and are usually used to describe catch impact (Harborne et al. 2018).

These same broad approaches also translate into regional and global models and syntheses. For example, (Teh et al. 2013) used reef fish catches alongside modelled estimates of overall fisher numbers, and the proportion of reef in total fishing grounds, to generate an estimate of 6 million reef fishers in 99 countries world-wide. (Cinner et al. 2018, McClanahan et al. 2019) have both utilised fishery-independent survey data in large-scale assessments to build models of biomass and fishery impacts.

In the current work, we construct a model of projected fish catch for the shallow, structural coral reefs of the world, informed by fisheries-independent data and by a number of proxy indicators of reef condition and likely fishing pressure. Our aim was to develop a systematic and transparent model which incorporated key elements of ecological and fisheries thinking, but could also provide a starting point for future discussion or improved modelling.

Methods

As a base map and study extent for this work we utilised the global map that was compiled in 2010 for *Reefs at Risk Revisited* (Burke et al. 2011). This map is largely based on standardised maps developed under the Millennium Coral Reef Mapping Project Coral from 30m Landsat data, but 20% of the coverage is derived from other sources and so, as with the previous products using this source, we utilised a 500m gridded version of the map. Under this work, coral reefs are thought to approximate to the working definition of “physical structures which have been built up, and continue to grow over decadal time scales, as a result of the accumulation of calcium carbonate laid down by hermatypic corals and other organisms” (Spalding et al. 2001). The gridding of this layer has the effect of adding a 250m buffer to the outer edges of these reefs, but this is considered a reasonable expansion, given the likely ecological reach of many reefs and their extension, in many places, into deeper water below the reach of most mapping efforts. The total area of reefs from such a mapping exercise is 250,000km^{-2}, a figure similar to that of 284,000km^{-2} estimated ten years earlier from a separate mapping exercise (Spalding et al. 2001). It is felt that this map also correlates relatively well with the ecological structures that have formed the basis of many field studies, an important consideration for the extrapolations which follow.

The broad outline of our methods is laid out in Figure 1. A key element was the development of a dataset of biomass estimates from reef fish surveys world-wide, alongside associated data on reef condition and management: these were used to generate estimates of multispecies maximum sustainable yield (MMSY) for unfished sites. Using data on condition for these sites, we developed a simple model of the relationship between reef condition and MMSY. Separately, a global map of reef condition was developed. Using the relationships derived from the field data, the reef condition map provided a direct proxy for potential MMSY for all reefs world-wide. A global map of reef gravity (a function of human population size and reef accessibility) (Cinner et al. 2018) provided a basis for estimating a likely proportion of MMSY that would be caught on reefs world-wide. This was then used to generate a base-map of likely catch. In a final step, these numbers were modified by the presence of known and effective no-take marine reserves which both halt fishing within their boundaries, but may enhance fishing in surrounding areas. Further details are provided below.

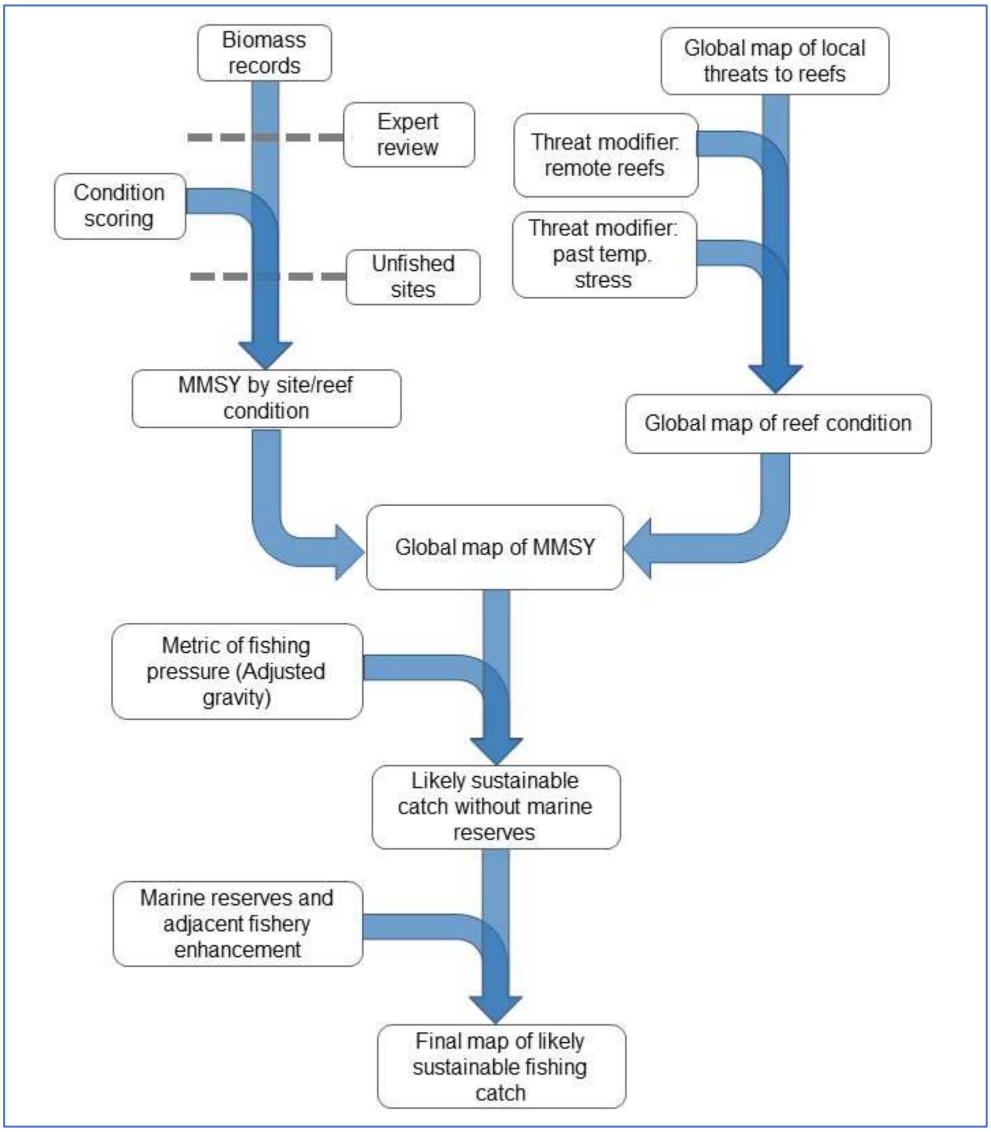

Figure 1: Visual summary of the methods

Step 1 – Estimating Maximum Sustainable Yield+

A literature review was conducted using *Web of Science* to extract data from field studies on coral reef fisheries productivity (see Supplementary Material). Searches were undertaken in July and August 2021. In the initial search, 207 papers were identified as potentially relevant. Where appropriate, references were snowballed, which resulted in a further 66 papers to be examined. It should be noted that several of the snowballed references could not be located online, so some secondary referencing was included. Additional sources recommended by expert contributors (Tim McClanahan and Mark Spalding) were also examined for useful data and concepts, giving a total of 294 papers, reports and other data sources which were searched for relevant data (see Supplementary Material).

All papers were reviewed for numerical data which might be useful in understanding fisheries or fisheries potential, notably: on-reef fish biomass, fisheries yield, and multispecies maximum sustainable yield (MMSY). Such data was extracted alongside information on location, reef condition, conservation status and study methods. Reef condition scored between 1 (near-pristine) and 5 (degraded) based on overall ecological condition observations (such as coral cover, rugosity, water quality, fishing impacts). Such scores were based on expert judgement, informed by the source publication, alongside independent data, including:

- Reefs at Risk Revisited (Burke et al. 2011)
- Global Coral Reef Monitoring Network publications e.g. (Wilkinson 2008)
- NOAA coral reef data (Waddell and Clarke 2008, Boyle et al. 2017) and online resources https://coralreef.noaa.gov/
- sppast bleaching models (Beyer et al. 2018) and data from https://coralreefwatch.noaa.gov/
- Reef "gravity" metrics (Cinner et al. 2018)
- Other national and regional sources (Lang 2003, Souter and Lindén 2005)

Where relevant, it was attempted to ensure that condition estimates were tied to the same approximate time period as the fish census data. These condition scores are shared along with the biomass values in Annex 1. In our final dataset our top condition (near pristine) class was confined to data from remote reefs in large, old, and high compliance no-take marine reserves located far from human populations. These were confined to the Indian and Pacific Oceans (13 locations distributed across the Chagos Archipelago, Phoenix Islands, Line Islands, Northwest Hawaiian Islands and Easter Island).

In reviewing the findings, neither yield data nor estimates of MMSY were sufficiently abundant for meaningful analyses. By contrast, biomass data was widely gathered. From the original pool, 150 biomass values were extracted that were linked to underwater visual census surveys and which could be linked to specific locations and field studies. These were taken from 22 sources and were further enhanced by data contributions from Alastair Harborne from studies on Atlantic reefs. Of these values some 68 were in unfished sites.

The link between biomass and MMSY has previously been explored by several authors, most notably Tim McClanahan (McClanahan 2018, McClanahan and Azali 2020). McClanahan and others have worked with standard fisheries models to link biomass and MMSY and it was decided that for this work a simple form of the logistic population growth equation, would suffice. This has close parallels to the Schaefer model (Schaefer 1954) which is still widely used in fisheries (Pauly and Froese 2020):

$$MMSY = K \times r/4$$

Where K is unfished biomass (B_0) or carrying capacity

Where r is the intrinsic growth rate of the fish population or recovery rate

Across the literature there is general agreement that fishing at MSY typically equates to a biomass equilibrium at 0.25-0.5 of B_0 (Hilborn and Stokes 2010, McClanahan 2011, Thorson et al. 2012, McClanahan 2018). Given the complexity and variability of *multispecies* systems in general, and the inherent complexity of coral reef ecosystems, we felt it was appropriate to assume that Multispecies MSY (ie. MMSY) would be achieved at 0.5 B_0 or half carrying capacity (K).

Intrinsic growth rate *r* varies between species, but is rarely calculated for exploited reef fish stocks (Abesamis et al. 2014). For multispecies syntheses, intrinsic growth rates can only be estimated to capture an averaged biomass growth rate. It has further been suggested that such rates may vary depending on reef condition. For example, Neubauer et al (2013) showed a clear relationship between intrinsic growth rate and overexploitation, with *r* increasing in more heavily exploited populations.

Other factors may also influence intrinsic growth rates. Jiao drew attention to the impact of regime shifts in marine ecosystems and how these ought to be considered in fisheries management (Jiao 2009). From a coral reef perspective, McClanahan and Graham (McClanahan and Graham 2015), showed clear differences in recovery rates linked to reef condition, even between unfished sites. Relatively unimpacted reef systems typically have an abundance of slow-growing species such as sharks, giving these reefs a relatively low *r* value. By contrast, as reef systems are impacted by multiple factors, such species are often lost and reefs become dominated by short-lived species with faster growth rates (McClanahan et al. 2021b). Typical pressures include long-term and large-scale fishing impacts, pollution, destructive fishing, solid waste, and recent history of bleaching mortality and disease. The results of such impacts are reflected in many ecological changes alongside changes in fish abundance, biomass and species composition, including losses of coral cover and declines surface complexity.

Values of *r* for coral reef fish communities have been used elsewhere (McClanahan 2018, McClanahan 2021), and for the current work we used values of $r = 0.3$ for degraded reefs and $r = 0.12$ for 'baseline' or pristine reefs (McClanahan and Graham 2015 and Tim McClanahan, pers. comm. 21/09/2021). These numbers were built into a range to match our 5-levels of reef condition as shown:

Condition category	**r value**
1 (near-pristine)	0.12
2	0.165
3	0.21
4	0.255
5 (degraded)	0.30

McClanahan and co-authors have also shown that protected areas can be important in driving seascape level influences on peak (unfished) biomass, essentially by enhancing condition (McClanahan et al. 2021a, McClanahan et al. 2021b). While we do not include such metrics directly into our scores of reef condition in this model, we do allow the influence of protection in a final stage of the model (Step 5, below)

Step 2 – Relating MMSY to reef condition

To determine values for MMSY, we utilised the biomass values from unfished reefs (n=68) as metrics for carrying capacity, combined with the estimates for intrinsic growth rates based on reef condition (above). (The spread of sites covered each of the five condition classes, with sites in poor condition typically equating to well enforced marine reserves, that were nonetheless degraded due to adjacent threats or past impacts).

A linear mixed-effects (LME) model was used to determine the effect of condition ranking on MMSY in unfished sites. Data was assessed for normality using a Shapiro-Wilk test. A non-normal distribution was found, so the MMSY data was $\log_{10}$ transformed to meet the assumption of normality. An initial LME containing all explanatory variables ("condition rank" and "study") was fitted using the logged MMSY data.

While biomass data were all derived from visual census surveys, the methods were still variable (notably between fixed point and transect based surveys), while observer differences can often driver further differences. Given this, it was postulated that study might have some influence on overall MMSY estimates. Boxplots of the initial model residuals against the “study” variable supported this disparity. As the effect of “study” was not the focus of this analysis, the inclusion of a random effect allowed findings to be generalised, by controlling for the variance which is attributable to different studies.

Residuals were extracted and model fit was assessed using visual inspection of various residual plots, as recommended by Zuur *et al.* (2009). The same authors further suggest that three plots are needed to validate a linear model: (1) residuals versus fitted values to verify homogeneity, (2) a QQ-plot or histogram of the residuals for normality, and (3) residuals versus each explanatory variable to check independence. All of these graphs were plotted, and assumptions verified for all cases.

The LME model was built and fitted in R Studio (R Core Team 2021) using the “nlme” package (Pinheiro et al. 2020). The “lmerTest” package was then used to extract *p* values associated with the LME (Kuznetsova et al. 2017). The slope identified using this linear model was used to predict MMSY values at each condition rank. Plots were generated in R Studio using the “ggplot” package (Wickham et al. 2021).

The variation driven by individual studies was found to mask a clear underlying pattern. As can be seen in Figure 2, by incorporating study as a random variable a clear pattern emerges. The model estimates were greater than the error for MMSY all 5 condition categories, which means the effect (or slope) can be distinguished from zero. A *p* value of **0.00169** indicates that there is a statistically significant effect of condition rank on MMSY.

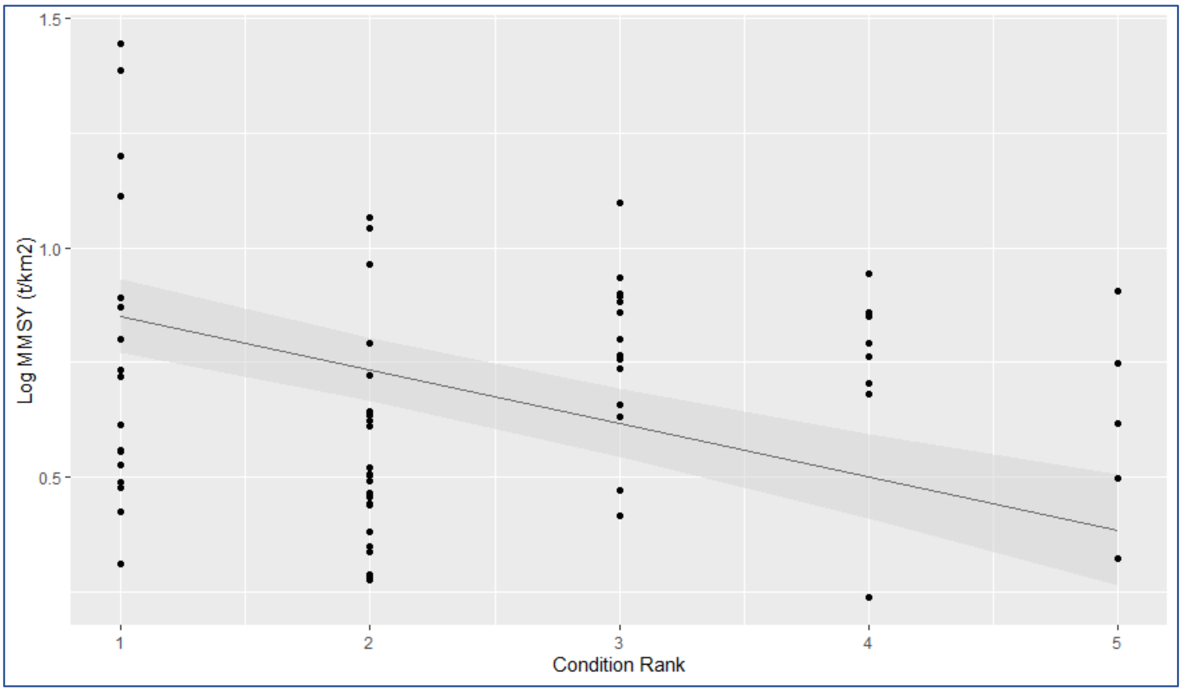

Figure 2: Estimated MMSY data from unfished sites against condition rank. The raw data show no clear corelation, however using a linear mixed effects model (LME) allowing study as a random effect shows a clear correlation, as plotted, with standard errors.

From this mixed linear model, the following MMSY predictions were generated for each condition rank.

Condition rank	**MMSY prediction** **(**mt km^{-2} yr^{-1}**)**
1	7.10
2	5.43
3	4.15
4	3.18
5	2.43

These MMSY predictions formed the basis of subsequent steps to build a global map of potential reef fish MMSY.

One unexpected outcome from this review work was that the differences in MMSY between Ocean basins was negligible. Initially we had intended to incorporate regional variation in MMSY across a number of biogeographic regions, and by latitude, based on prior assumptions of both biogeographic and oceanographic drivers (McClanahan et al. 2019). On investigation, however, it was clear with our limited data inputs, regional differences were not detectable. This may have been due, in part, to a small sample size, but also perhaps some influence of the very high biomass data from high latitude remote reefs in the North Pacific. It was therefore decided to build a simple model for all reefs, an approach that has been taken by others (MacNeil et al. 2015).

Step 3 – Estimating reef condition

There is no global and consistent map of coral reef condition. The closest proxy for such a map is Reefs at Risk Revisited (Burke et al. 2011), a threat map built up from proxy metrics, which have likely already generated impacts on coral reef condition in most areas. We used the "local drivers" of threat from this map, which capture coastal development impacts, watershed-based pollution, marine-based pollution, and fishing impacts. This source recognises 4 classes of threat: "low", "medium", "high" and "very high" and these provided a starting point for our condition scores.

Under the Reefs at Risk Model some 39% of reefs were classed as low threat globally. It was apparent from the fish biomass data and our own scores that the proportion of truly good condition reefs is far lower than this. To highlight areas of very low human impact and near-pristine condition, we used the gravity scores from (Cinner et al. 2018), placing all reefs which had both a Reefs at Risk score of "low threat" and a gravity score of zero (defined aa being more than 12 hours travel time from human populations) into a new class of "very low" threat. Two exceptions were made to this modification – the reefs of the South China Sea and the reefs of Diego Garcia in the Chagos Archipelago. While not having permanent populations, both of these have considerable military developments which are likely impacting coral reefs through fishing and the impacts of coastal development, sedimentation and pollution (McManus 2017, Samoilys et al. 2018).

A second modification was made to account for climate impacts, notably ocean warming. Although Reefs at Risk also included a map that factored in climate related threats, we opted to update this component using a simple assessment of cumulative warmwater stress anomalies over the past 35 years (NOAA Coral Reef Watch 2021). Although others have attempted to develop more accurate models of bleaching thresholds and thus to more accurately predict known past bleaching events (e.g. Beyer et al. 2018), we felt that the local and regional variation in such thresholds (McClanahan et al. 2020, Muir et al. 2021) would be hard to capture and a simple map of anomalies would better capture the general patterns of change. For our purposes, we simply took the top decile of reefs showing the highest cumulative SST anomalies as indicative of likely high impact on reef condition. All reefs not already classed as high-threat under local metrics were thus "degraded" to the next class if they had a high cumulative temperature anomaly. One modification was made to this approach which was to remove the past bleaching impact from the reefs of the northern Red Sea: although many of these reefs are recorded in the top decile, there appears to be a very high regional resistance to bleaching (Osman et al. 2017, Kleinhaus et al. 2020).

The resulting map (Figure 3A) uses 5 categories of condition from 1 (near-pristine or baseline) to 5 (degraded). By linking the MMSY score to the reef condition map we generated a global map of potential MMSY for the world's coral reefs, see inset, Figure 4A.

Step 4 – Estimating fishing pressure

Fishing pressure on any reef is driven by an array of demand from local and subsistence needs, to small markets, to very large markets influencing international trade. A number of studies have helped to focus our understanding of these demands, computing travel times rather than simple distance metrics (Maire et al. 2016, Cinner et al. 2018, McClanahan 2020). From these, we utilised the global model of Cinner et al (2018) showing reef "gravity" as a single score for each reef unit derived from a composite of the size of population modulated by travel time to that reef. This metric allows for large populations (and markets) to have a longer reach (gravitational pull), while allowing small populations to have a more localised influence. The metric sets a limit of 12 hours travel time, beyond which reefs are considered to have a score of zero gravity. Broadly, these are equivalent to the "baseline" reefs of McClanahan (who sets travel time at 9 hours).

Initially, gravity scores were fitted to our base-map of reefs. These scores, however, do not take account of available fishing area, or the fact that many fishers will fish across multiple adjacent habitats. The gravity scores were therefore modified, to account for adjacent fishing opportunity (AFO) from nearby reef, mangrove and shallow shelf areas, following a similar approach used by zu Ermgassen et al (zu Ermgassen et al. 2020). The total area of coral reef, mangrove and shallow shelf was estimated within a 5km radius of each reef pixel. The fishery value of reefs and mangroves were considered equal, while shallow shelf was weighted at one-tenth of that value. Thus, for each reef pixel we calculated a score:

AFO = sum extent (mangrove + coral reef + shallow shelf/10)

We then divided the gravity score of each reef cell by its AFO, generating an adjusted gravity score, reducing original gravity scores in proportion to the likely adjacent fishing opportunity. Adjusted gravity is our metric for fishing effort or pressure.

Step 5 – Estimating catch

Catch for any location will be a function of fishing effort and available fish biomass. In most reef settings MMSY is unknown, but such a figure nonetheless represents a useful indicator of possible sustainable catch in areas of peak effort. Elsewhere, fishing effort and resultant catch will be below that required to reach MMSY, declining towards zero pressure and zero catch for a small number of very remote baseline reefs.

With no direct data to indicate the relationship between fishing pressure (adjusted gravity) and catch, or to relate these to MMSY, we selected a number of reefs that we believed would be harvested at full fishing pressure, together with others that we expected would be fished below this point. These reefs were selected utilising information on populations and markets, measured biomass, and an understanding of AFO. From these sites we estimated full fishing pressure would be reached when $\log_{10}$ Adjusted Gravity > 3.0.

As already stated, zero fishing pressure was assumed when gravity was zero. We assumed a simple linear relationship between fishing pressure from $\log_{10}$ Adjusted Gravity scores 0-3 and from this derived a score for likely catch as a proportion of total MMSY for reefs with these intermediate fishing pressures such that:

$$\text{Estimated catch} = \text{MMSY} \times 0.33\text{Log}_{10}\text{AdjGrav}$$

Our model does not allow for overfishing to depressing overall catch, except through the long-term impacts of reef degradation (which lower MMSY in the model). In reality, the impact of overfishing on catch is highly time dependent, and it can lead to short-term catch enhancement, but with subsequent population losses, or even collapse. The shape of such a curve, however, is poorly understood and there have been some suggestions that the multi-species nature of our fishery gives a level of resilience such that catch rates decline only slightly as fishing pressure increases (Halls et al. 2006).

Step 6 - incorporating management

The effect of fisheries regulations on catch and sustainability can be considerable, but the most dramatic impacts are through the full closure of areas to all fishing. Within such marine reserves or no-take zones, there can be dramatic changes in fish abundance and size structure, net biomass and species diversity (Halpern 2003, PISCO 2007). An extensive literature exists on the benefits of marine reserve to fish catches in adjacent areas, derived from both adult spillover and larval enhancement (Kerwath et al. 2013, De Leo and Micheli 2015, Green et al. 2015). We included marine reserves into our model, both by removing any fishing from these areas, and by allowing an influence of the reserves on likely MMSY in surrounding areas via spillover. This reserve adjacent influence is explained here:

Adult spillover: The most powerful influence of spillover is felt in the immediate vicinity (Kaunda-Arara and Rose 2004, Halpern et al. 2010, Russ and Alcala 2010, Di Lorenzo et al. 2020). Most authors agree that the likely influence of spillover will vary with the mobility of individual species. Green et al (2015) plot this for numerous species, linking potential spillover distances to home-range sizes, and in some cases to ontogenetic shifts, spawning migrations or other factors.

The influence of adult spillover on fishing yields is typically local, with the highest gains in the immediate vicinity of the boundary and rapid declines in this gain/benefit at distances over ~3km (Kaunda-Arara and Rose 2004). Other authors, however, have detected fishery gains out to 30km from reserve boundaries (Kerwath et al. 2013). Informed by these and other studies, we built a simple framework to allow potential yield increases of up to 25% in the immediate vicinity, diminishing rapidly with distance. We also allowed for larger reserves, which are host to increased numbers of wide-ranging species such as larger predators, to have a broader reach in their fishery enhancement, out to 10km (see Table 1).

Larval export. The influence of larval export to reserve-adjacent areas is long-term, as recruits can take one to several years to reach fishable sizes. As with adult spillover, there is likely to be some species specificity to the distance of reserve-influence, largely driven by the longevity of larval phases (almost all fished reef species have pelagic larval stages). A number of studies have explored the relative proportion of reserve-derived fish in reserve-adjacent areas (Harrison et al. 2012, Almany et al. 2013). The relationship between recruitment and catchable stock (the recruitment subsidy) is less clear, although in one study it was reported as contributing to a doubling in Catch Per Unit Effort (CPUE) on temperate reefs in South Africa (Kerwath et al. 2013).

The distances involved in larval dispersal are greater than in adult spillover: in a large meta-analysis, the median demographic dispersal distance for marine reserves was estimated at 42km (Manel et al. 2019), but with high variability between species. The influence of reserve size is also likely to be important, with larger reserves, hosting highly fecund individuals, having a larger influence over wider areas (Pelc et al. 2010).

Based on these considerations, we adopted what we believe to be a conservative approach to the influence of larval dispersal in reserve adjacent reefs, with a maximum influence of a 5% increase in MMSY, declining with distance, albeit more slowly than with adult overspill, out to a maximum distance of 40km (see Table 1).

For this work, we used data for fully no-take marine protected areas (MPAs) from the Marine Protection Atlas (MPAtlas 2020) (Figure 3B), which represents the most comprehensive global dataset of functioning no-take areas available. Buffers were created around all marine reserves for 0.5, 1, 3, 10, 40km. All reefs within these buffer areas were linked to the combined MMSY percentage adjustments shown in Table 1. Where reefs were influenced by two or more marine reserves the percentage adjustments were summed – in reality this was rare and the maximum summed multiplier was 62%.

We further allowed catches to be raised in these reserve-adjacent reefs, by raising the MMSY to the next highest condition rank where they were not already in the highest rank. This had the effect of allowing the benefits to be brought up to, but no higher than this higher MMSY level.

Table 1: estimates of the influence of effective no-take reserves on adjacent fisheries. Percentage figures represent our estimates of the likely impact of the reserve on MMSY, which includes separate estimates for both adult spillover and larval exports, with the impact affected both by reserve size and diminishing with distance from reserve boundary. The combined impacts used in the model are presented at the bottom of the table.

		Distance from boundary:				
	Reserve size	0.5km	1km	3km	10km	40km
Adult Spillover	>100 km^{-2}	25%	18%	12%	5%	0%
	10-100km^{-2}	25%	15%	8%	3%	0%
	1-10km^{-2}	12%	8%	4%	1%	0%
	<1km^{-2}	8%	4%	1%	0%	0%
Larval Export	>100 km^{-2}	6%	6%	4%	3%	2%
	10-100km^{-2}	6%	6%	4%	3%	2%
	1-10km^{-2}	3%	3%	2%	1%	0%
	<1km^{-2}	2%	2%	1%	0%	0%
Combined	>100 km^{-2}	31%	24%	16%	8%	2%
	10-100km^{-2}	31%	21%	12%	6%	2%
	1-10km^{-2}	15%	11%	6%	2%	0%
	<1km^{-2}	10%	6%	2%	0%	0%

Results

Total global catches from mapped shallow reefs are modelled at 460,000 mt yr^{-1}, with a mean catch of 1.84 mt km^{-2} yr^{-1} (or 2.27 mt km^{-2} yr^{-1} for fished reefs only). Under this model, approximately 16% of reefs are unfished due to their distance from populations and markets, while some 9% meet the requirement in our model for full exploitation, based on the adjusted gravity scores. Further consideration regarding the accuracy or applicability of these numbers is given in the discussion, but an important component of this work is the spatial breakdown.

Global maps are presented in Figure 3. In our condition classification, some 13% of coral reefs are classified as being in good condition (near pristine, score = 1) and some 10% in the lowest condition category (5). The map of catch, Figure 3C, shows the diverse range in projected catches globally, with variation driven by the combination of reef condition, available fishing area, fishing pressure and human management (fisheries closures and associated spillover).

Figure 4 provides further detail showing the intense fishing effort in more highly populated areas, and the small but clearly visible influence of marine reserves. These higher resolution figures, and those in Figure 5, also show how reef degradation is limiting total catches in areas closest to human population centres, with increased catches often occurring slightly away where improved reef health is generating higher potential MMSY .

Regional breakdowns in Table 2 show the considerable variance in management, fishing effort and total catch. Further detail can be seen for the ten largest coral reef countries in Table 3, which also shows how the drivers of condition and gravity vary quite considerably between countries.

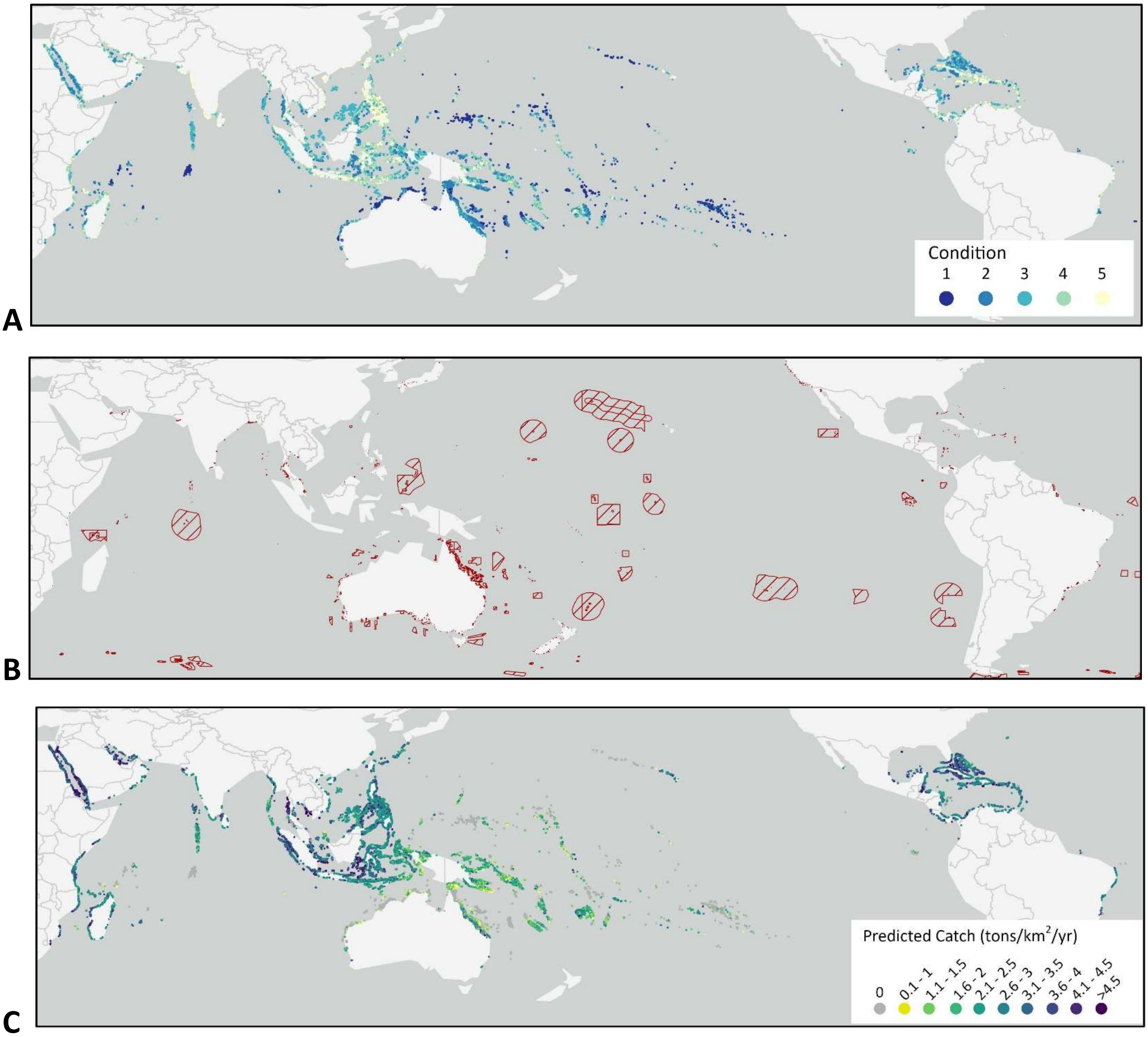

Figure 3: Global data layers. A – Revised map of reef condition with five classes. Based on (Burke et al. 2011), with amendments to incorporate the most remote reefs, occupied military bases (not classed as inhabited, but impacted), and likely coral bleaching impacts. B - global distribution of effective no-take marine reserves from MPAtlas. (Red are no-take, green are sites which may incorporate some no-take, but not included in this study as the exact extent and location of no-take is not available). C – projected mixed species catches from the world's coral reefs, dark green is zero, based either on remote reefs or effective fisheries closure, deep blue is >4 mt km^{-2} yr^{-1}per year, which requires a combination of relatively good reef condition and sufficient fishing pressure to drive towards MMSY.

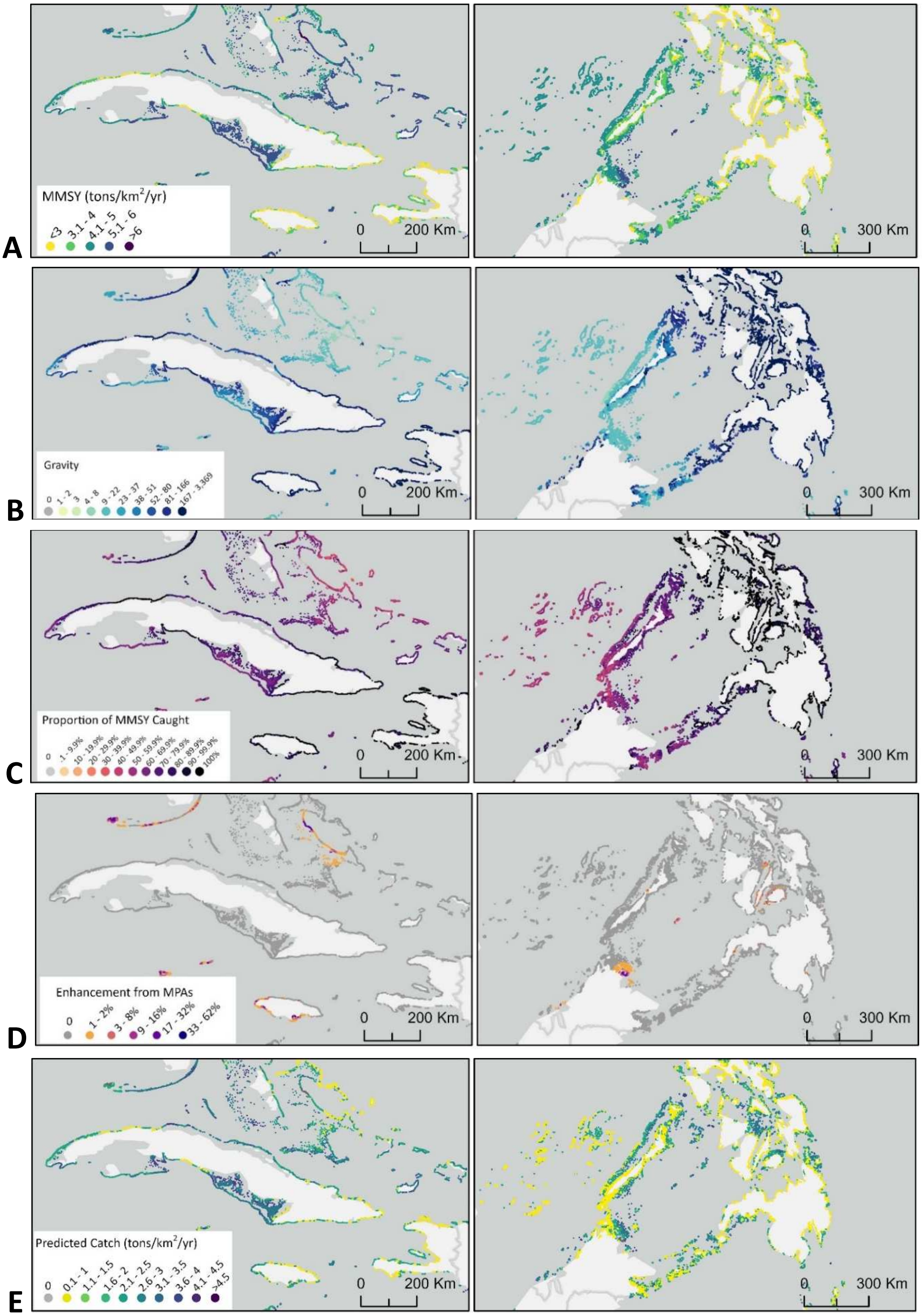
MMSY (tons/km²/yr)
<3
3.1 - 4
4.1 - 5
5.1 - 6
>6
0 200 Km
0 300 Km
A
Gravity
0
1 - 2
3
4 - 8
9 - 22
23 - 37
38 - 51
52 - 80
81 - 166
167 - 3,369
B
Proportion of MMSY Caught
0
.1 - 9.9%
10 - 19.9%
20 - 29.9%
30 - 39.9%
40 - 49.9%
50 - 59.9%
60 - 69.9%
70 - 79.9%
80 - 89.9%
90 - 99.9%
100%
C
Enhancement from MPAs
0
1 - 2%
3 - 8%
9 - 16%
17 - 32%
33 - 62%
D
Predicted Catch (tons/km²/yr)
0
0.1 - 1
1.1 - 1.5
1.6 - 2
2.1 - 2.5
2.6 - 3
3.1 - 3.5
3.6 - 4
4.1 - 4.5
>4.5
E

Figure 4: Regional insets showing the components (A-D) and output from the model for two regions: Central Caribbean (Lefthand maps – Cuba, Southern Bahamas, Cayman Islands, Haiti and Turks and Caicos) and Central Southeast Asia (Righthand maps – Southern Philippines, Spratly Islands (disputed), Sabah (Malaysia) and Brunei Darussalam). **A -** MMSY estimates of 2.43-7.1 tonnes /km2, directly equated to reef condition (see Figure x); **B -** Gravity scores, unadjusted (0-19000) based on (Cinner et al. 2018); **C -** Proportion of MMSY being targeted (deep red = 100%): a function of gravity modified by adjacent fishing opportunity from other reefs, mangrove forests and shallow shelf within 5km of target reefs; **D -** Modelled fisheries enhancement adjacent to marine reserves. Most effects are highly localised, but our model attempts to account for both adult and larval spillover, with the latter contributing minor enhancement as far as 40km from the largest marine reserves. **E -** Predicted catch, a function of fishing effort and location-specific MMSY and management influences from marine reserves.

Table 2: Regional summaries

Region	**Reef area km²**	**Proportion of global reefs**	**No-take reef area km²**	**Proportion of regional**	**Fully fished area km²**	**Proportion of regional**	**Total catch (mt yr⁻¹)**	**Proportion of global**
Americas	26,730	10.7%	1,470	5.5%	3,642	13.6%	73,064	15.9%
Australia	42,111	16.9%	10,787	25.6%	61	0.1%	23,878	5.2%
East and Southeast Asia	72,972	29.2%	582	0.8%	11,905	16.3%	180,652	39.3%
Indian Ocean	27,924	11.2%	3,361	12.0%	2,802	10.0%	58,445	12.7%
Middle East	14,249	5.7%	23	0.2%	2,726	19.1%	49,864	10.8%
Pacific	65,893	26.4%	7,079	10.7%	1,544	2.3%	74,155	16.1%
Grand Total	**249,878**		**23,301**	**9.3%**	**22,679**	**9.1%**	**460,059**	**100.0%**

Table 3: summary statistics for the ten countries and territories with the largest coral reef extents.

Country	**Reef area km²**	**Average Condition**	**Average gravity**	**No-take area km²**	**Total catch (mt yr⁻¹)**
Australia	41,871	1.91	3.53	43,106	23,669
Indonesia	39,782	3.30	190.90	70	96,843
Philippines	22,553	3.93	495.76	79	59,598
Papua New Guinea	14,523	2.98	23.82	2	20,324
New Caledonia	7,450	2.43	7.50	10,322	6,996
Solomon Islands	6,752	2.95	13.85	257	8,971
Fiji	6,704	3.03	34.38	57	11,212
French Polynesia	5,983	1.81	39.66	0	4,462
Saudi Arabia	5,291	2.72	474.63	0	19,117
Maldives	5,281	2.96	32.13	637	11,426

Indonesia and the Philippines dominate the catch statistics, with estimated catches of ~97,000 and ~60,000 mt yr^{-1}tonnes per year, respectively. Below these two, total catches drop considerably, particularly for those countries and territories with extensive offshore reefs remote from dense human populations, such as French Polynesia, New Caledonia and the Solomon Islands.

World-wide, approximately 9% of reefs are within effective no-take protected areas where our models predict no fishing, however it is notable that over half of these areas are actually in remote and naturally unfished areas, which leaves only about 3.7% of reefs in no-take areas that would be under significant fishing pressure without protection. Our model predicts a lost catch from the closure of these areas of almost 13,000 mt yr^{-1}, however associated gains from enhanced fishing in adjacent areas amount to almost 4,000 mt yr^{-1}. At the national level, a small number of countries show net positive gains from their marine reserves, notably Belize and the Philippines.

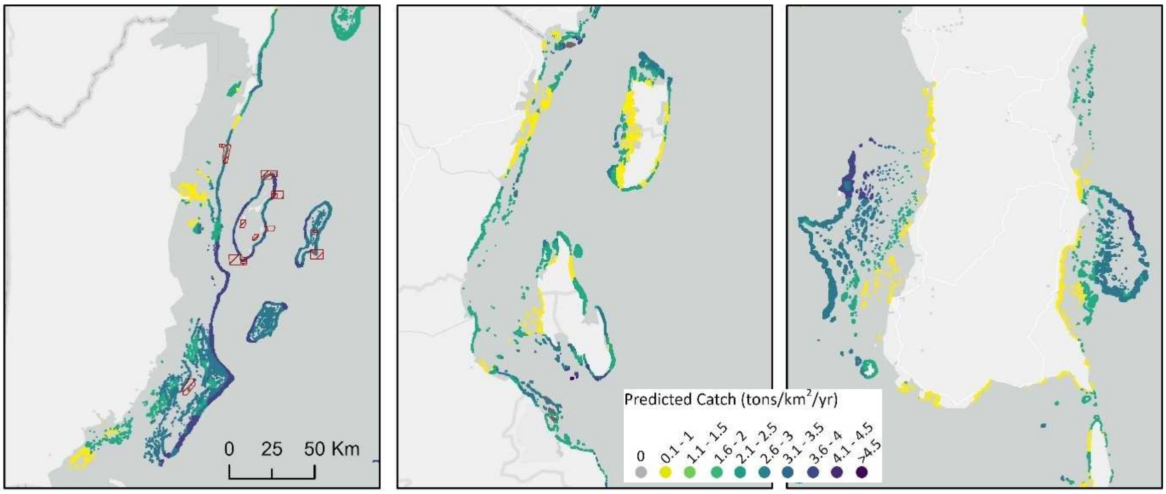

Figure 5: details from our catch models at higher resolution for Belize (left), Northern Tanzania (centre) and South Sulawesi (right), showing the gradients of catch, which are broadly linked to coastal populations. Nearshore and near human areas are often lower condition, which limits potential catches. Fishing pressure remains high further offshore leading to higher catches as reef condition improves. Fishing pressure, and catches, begin to drop off with greater distance from human populations. In Belize the influence of no-take marine reserves can also be clearly seen.

Discussion

Coral reef fisheries are vital for coastal people around the world, providing food security, employment and income to millions. Our study provides a first attempt at a global map of coral reef fisheries, focussing on shallow structural coral reefs where productivity and fishing opportunity are maximised. Our work builds upon the known close relationship between coastal populations and markets as well as the expected impact that reef degradation can have on productivity. We also build some of the likely benefits of no-take marine reserves into our model.

From the maps we clearly see patterns highlighting three broad-scale and often interacting processes. Reef condition, and hence MMSY in our model, typically improves with distance from population, especially larger population centres. In many places, this is matched by declining fishing pressure. The result of this is that the modelled catch often peaks at some intermediate distance from population centres, where reef condition is improved, but where fishing pressure remains sufficient to utilise the increased MMSY. The third influence on pattern comes from marine reserves, which clearly interrupt fishing, but also generate haloes of increased catches around their periphery.

Our data also enable the estimation of catch size. Such numbers must of course be treated with caution – they are derived from a model, and are focused on catches from shallow structural reef, which are likely to be only part of the catch of coastal reef fisheries (see below). Even so, the numbers are informative, especially in developing an understanding of distribution and relative importance of fisheries in different settings and locations. Both the maps and numbers presented in this report should be of utility for policy and management, especially in the face of global threats, not only to coral reefs, but also to human lives and livelihoods in the face of climate change. They model present benefits, but can also be used to consider future scenarios, from improvements in management to the potential impacts of increased fishing pressure.

The apparent role of no-take marine reserves in our model is clearly visible. While they represent areas of no fishing, they show potential stock enhancement, albeit often small, to adjacent areas which cover over 16% of the world's reefs. In terms of catch enhancement, benefits are most widely reflected around the small marine reserves in otherwise fished areas. By contrast, many of the very large and remote marine reserves offer minimal benefits to fisheries: such sites are primarily designated for biodiversity benefits, however their role both as refugia and in supporting low-level, long-distance recruitment enhancement should not be discounted (Manel et al. 2019). Although we restricted the positive influence of protected areas to no-take areas, there is evidence that other forms of protection, where fishing is permitted but limited and regulated, can offer additional catch advantages (Muallil et al. 2019, Osuka et al. 2021).

Coral reef fisheries, like all multi-species fisheries, present considerable challenges for sustainable management, not least because of the variance in vulnerability between species, and the complex and diverse nature of both fishing communities and fishing methods. Although some have questioned the feasibility of obtaining a metric for a multi-species MSY (Fenner 2012), many others have used such an approach and our estimates of MMSY match well with those of Dalzell of 5 mt km^{-2} yr^{-1} (Dalzell 1996, Kimberley et al. 2003), and 1-10 mt km^{-2} yr^{-1} (Newton et al. 2007). Other authors have suggested higher rates: from 10 to 20 mt km^{-2} yr^{-1} (Russ 1991, Halls et al. 2006), however our belief is that the conservative numbers in our model are probably appropriate given the very broad scale extrapolation we are undertaking, and the variety of reef habitats incorporated into the global map (see below). It is also noted that some of the very high yields from earlier studies may have been driven by somewhat unusual fisheries such as those in the Philippines which have included a very high proportion of schooling planktivorous species that do not feature in reef fisheries more widely (Russ 1991).

One important influence on any study that seeks to build out catch estimates at large scales is the definition and mapped extent of habitat (Russ 1991). From a socio-ecological perspective, "reef" fishing may extend across wide areas of reef associated habitats. In catch-return studies, reported catches may include catches from many different settings, including seagrass, hardbottom and non-reef structural habitats across wide areas of shelf. While such areas would have lower net productivity than the shallow reef slopes, they could be extensive. This may explain the very high reef fish catches reported in some studies (Newton et al. 2007, Pauly and Zeller 2014). In the same way, it is likely that the figure of 6 million reef fishers worldwide (Teh et al. 2013) would include those fishers working in a wider habitat range. By contrast, many fishery independent surveys of fish communities focus on shallow reef slopes where biomass or productivity are often high and might suggest very high potential yields, however such habitats have a limited spatial extent, so total catch extrapolated across such habitat will tend to be small.

Our base-map of reefs is that used in previous studies (Burke et al. 2011), derived in large part from a globally consistent map of shallow structural reefs, gridded to a 500m cell-size. We are aware that this gridding may buffer, or exaggerate the apparent extent of reefs, but at the same time, the base-map tends to underestimate the location and extent of deeper reefs or non-structural reef systems (for example on the leeward coasts of the islands in the Eastern Caribbean). The use of another base-map would profoundly affect our estimate of catch, but we believe that this map is broadly representative of the habitats which are the focus of in-water fish surveys and is therefore still provides a good approximation of likely catch on these habitats.

Many authors have pointed to the widespread problem of over-exploitation on coral reefs (Newton et al. 2007, MacNeil et al. 2015), however it has also been pointed out that fisheries collapse is actually relatively rare and that species compensation can lead to more robust populations, dominated by smaller, fast-growing species (often lower value) which can bear higher fishing pressure with a more gradual decline in catches in the face of overfishing above MMSY (Halls et al. 2006). While our maps do not provide a direct metric of overfishing it is important to note that they do clearly give some indication of fisheries-related impacts from the combination of reef condition impacts on MMSY and number of reefs fished to current MMSY. Given the growing understanding of the need for community structure, and particularly the important role of large grazers, it is also important to consider that over-exploitation may drive other ecological vulnerability before the MMSY of degraded reefs is reached.

There may still be some concern that our model could be exaggerating the total area of "unfished" reefs. As mentioned, we did make modifications to gravity scores for "unpopulated" military bases, however we note (but did not incorporate) other remote locations exist where fishing is recorded, including in the Coral Sea (Young et al. 2016), the more remote atolls of the Seychelles (Robinson et al. 2020) and Micronesia (Harborne et al. 2018). Such locations offer rich fishing grounds for very high value target species (Berkes et al. 2006) and there may be some value in adjusting the 12-hour travel distance limit in the gravity model to capture such multi-day fishing enterprises, or indeed to build other metrics for the harvest of highest value species which in some cases are being air-freighted to distant markets (Cuetos-Bueno et al. 2018). Likewise, the assumption that no-take areas are fully no-take is clearly inaccurate – the very high value of certain species is a powerful driver of illegal fishing, even in well-resourced locations such as Australia and the Chagos Archipelago (Hays et al. 2020, Vince et al. 2021). Other improvements might be made to models of this sort, for example by incorporating national or other modifiers to fishing pressure to account for socio-economic dependence of reefs (McClanahan 2020). Such an approach might, for example, reduce apparent catches for some countries where seafood dependency may be lower such as Saudi Arabia.

Coral reef fisheries are too important to ignore and yet the absence of a global, consistent map of this importance may be hindering crucial policy developments, management interventions and investment decisions. By providing a model of catch we believe we have provided a starting point. While we recognise that some flaws remain, we believe that the models have relevance and enable a move from a simplistic assumption of importance to a map that highlights some of the key drivers of value – reef condition, the role of populations and markets, and the role that marine reserves are playing. Such maps enable a more nuanced discussion about present values and can inform future planning.

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Supplementary material

Table S1: Summary of search strings used to find fisheries relevant data. Each search term was entered into *Web of Science* exactly as seen in this table.

Search term	**Hit rate (no. relevant / no. irrelevant)**
coral+reef+fish+product*	6.2
coral+reef+sustainable+fish*+yield	1.1
coral+reef+fish*+maximum+sustainable+yield	0.5
coral+reef+fish*+potential*sustainable*yield	0.9
degraded+coral+reef+fish*+product*	6.2
healthy+coral+reef+fish*+product*	7.3
coral+reef+fish*+pressure	7.5
coral+reef+fish*+catch+effort	2.3
coral+reef+fish*+market	2.7
coral+reef+fish*+market+proximity	0.4
coral+reef+apex+predator+biomass	0.8
coral+reef+apex+predator+product*	0.7
coral+reef+product*+no+take	3.4
coral+reef+product*+marine+reserve	6.9
coral+reef+fish*+standing+stock	10.0
coral+reef+fish*+spillover	3.3

Table S2: Biomass data, condition scores and MMSY estimates. The following is the list of datasets used to inform biomass statistics. The estimates of MMSY are derived from the Schaefer model described in the text for no-take sites only, based on the assumption that these sites are at carrying capacity, B_0. Source references are provided below the table.

Country/location	Location detail	Unfished	Source reference	Biomass mt km^{-2}	Condition	r value	MMSY mt km^{-2} yr^{-1}
American Samoa			Craig, Green & Tuilagi, 2008	260.0	3	0.21	
Antigua		Y	Karr et al 2015	28.0	5	0.3	2.10
Australia	NE Australian Shelf	Y	McClanahan et al 2019	71.1	2	0.165	2.93
Australia	NW Australian Shelf		McClanahan et al 2019	108.3	2	0.165	
Bahamas	Abaco		Harborne 2021, in lit.	94.0	3	0.21	
Bahamas	Andros_central		Harborne 2021, in lit.	27.0	3	0.21	
Bahamas	Andros_north		Harborne 2021, in lit.	26.0	3	0.21	
Bahamas	Andros_south		Harborne 2021, in lit.	31.0	3	0.21	
Bahamas	Conception		Harborne 2021, in lit.	27.0	3	0.21	
Bahamas	Eleuthera		Harborne 2021, in lit.	163.0	3	0.21	
Bahamas	Exuma Cays Land and Sea Park	Y	Harborne 2021, in lit.	149.0	3	0.21	7.82
Bahamas	Exuma Cays N		Harborne 2021, in lit.	47.0	3	0.21	
Bahamas	Freeport		Harborne 2021, in lit.	85.0	4	0.255	
Bahamas	Lee Stocking		Harborne 2021, in lit.	67.0	3	0.21	
Bahamas	San Salvador		Harborne 2021, in lit.	59.0	3	0.21	
Barbados		Y	Karr et al 2015	55.1	5	0.3	4.13
Belize	Ambergis Cay	Y	Newman et al 2006	110.0	3	0.21	5.78
Belize	Ambergris Cay		Newman et al 2006	160.0	3	0.21	
Belize	Glovers Reef	Y	Newman et al 2006	104.0	3	0.21	5.46
Belize	Glovers Reef		Newman et al 2006	69.0	3	0.21	
Belize		Y	Karr et al 2015	110.9	4	0.255	7.07
British Virgin Islands		Y	Karr et al 2015	90.8	4	0.255	5.79
Cayman Islands		Y	Karr et al 2015	41.9	5	0.3	3.14
Central Polynesia		Y	McClanahan et al 2019	104.4	2	0.165	4.31
Chagos Archipelago	Diego Garcia	Y	Graham et al 2013	128.2	2	0.165	5.29
Chagos Archipelago	Great Chagos Bank	Y	Graham et al 2013	810.0	1	0.12	24.30
Chagos Archipelago	Peros Banhos	Y	Graham et al 2013	930.0	1	0.12	27.90
Chagos Archipelago	Salomon	Y	Graham et al 2013	433.6	1	0.12	13.01
Chile	Easter Island		McClanahan et al 2019	79.2	2	0.165	
Chile	Easter Island		Friedlander et al 2013	45.0	2	0.165	
Chile	Salas y Gomez Motu Motiro Hiva Marine Park	Y	Friedlander et al 2013	120.0	2	0.165	4.95
Cuba	Jardines de la Reina	Y	Newman et al 2006	283.0	2	0.165	11.67
Cuba		Y	Karr et al 2015	192.5	3	0.21	10.11
Dominican Republic		Y	Karr et al 2015	74.5	5	0.3	5.59
Florida	Dry Tortugas	Y	CORIS 2021	120.6	3	0.21	6.33
Florida	Dry Tortugas		CORIS 2021	118.7	3	0.21	
Florida	Dry Tortugas		Newman et al 2006	104.0	3	0.21	
Florida	Lower Keys	Y	CORIS 2021	79.6	4	0.255	5.07
Florida	Lower Keys		CORIS 2021	68.8	4	0.255	
Florida	Marquesas	Y	CORIS 2021	113.1	4	0.255	7.21
Florida	Marquesas		CORIS 2021	71.9	4	0.255	
Florida	Middle Keys	Y	CORIS 2021	75.2	4	0.255	4.79
Florida	Middle Keys		CORIS 2021	71.3	4	0.255	
Florida	SE Florida		CORIS 2021	78.5	5	0.3	
Florida	Southern Florida Keys		Newman et al 2006	135.0	4	0.255	
Florida	Southern Florida Keys NTZ	Y	Newman et al 2006	138.0	4	0.255	8.80
Florida	Upper Keys	Y	CORIS 2021	97.4	4	0.255	6.21

Country/location	Location detail	Unfished	Source reference	Biomass mt km^{-2}	Condition	r value	MMSY mt km^{-2} yr^{-1}
Florida	Upper Keys		CORIS 2021	66.7	4	0.255	
Hawaii			McClanahan et al 2019	92.6	2	0.165	
Hawai'i	French Frigate	Y	Boyle et al 2017	88.9	2	0.165	3.67
Hawai'i	Hawaii		Boyle et al 2017	30.6	3	0.21	
Hawai'i	Kauai		Boyle et al 2017	22.2	3	0.21	
Hawai'i	Kure	Y	Boyle et al 2017	120.8	2	0.165	4.98
Hawai'i	Lanai		Boyle et al 2017	26.4	2	0.165	
Hawai'i	Laysan	Y	Boyle et al 2017	68.1	2	0.165	2.81
Hawai'i	Lisianski	Y	Boyle et al 2017	175.0	2	0.165	7.22
Hawai'i	Maro	Y	Boyle et al 2017	112.5	2	0.165	4.64
Hawai'i	Maui		Boyle et al 2017	26.4	2	0.165	
Hawai'i	Midway	Y	Boyle et al 2017	150.0	2	0.165	6.19
Hawai'i	Molokai		Boyle et al 2017	26.4	3	0.21	
Hawai'i	Niihau		Boyle et al 2017	54.2	2	0.165	
Hawai'i	Oahu		Boyle et al 2017	11.1	3	0.21	
Hawai'i	Pearl & Hermes	Y	Boyle et al 2017	211.1	2	0.165	8.71
Hawai'i	West Hawaii		Foo et al 2021	49.3	2	0.165	
Honduras		Y	Karr et al 2015	238.2	3	0.21	12.51
Indonesia	Cenderawasih Bay	Y	Purwanto et al 2021	46.7	2	0.165	1.93
Indonesia	Cenderawasih Bay		Purwanto et al 2021	25.4	2	0.165	
Indonesia	Falfak		Purwanto et al 2021	35.7	2	0.165	
Indonesia	Kaimana	Y	Purwanto et al 2021	222.8	2	0.165	9.19
Indonesia	Kaimana		Purwanto et al 2021	60.3	2	0.165	
Indonesia	Lombok		Carvalho et al 2021	3.6	3	0.21	
Indonesia	North Raja Ampat	Y	Purwanto et al 2021	77.5	2	0.165	3.20
Indonesia	North Raja Ampat		Purwanto et al 2021	100.1	2	0.165	
Indonesia	Raja Ampat		Carvalho et al 2021	237.1	2	0.165	
Indonesia	South Raja Ampat	Y	Purwanto et al 2021	58.4	2	0.165	2.41
Indonesia	South Raja Ampat		Purwanto et al 2021	70.9	2	0.165	
Indonesia	South Sulawesi		Rogers et al 2018b	35.0	4	0.255	
Indonesia	South Sulawesi		Rogers et al 2018b	117.0	2	0.165	
Jamaica	Discovery Bay		Newman et al 2006	32.0	5	0.3	
Jamaica	Jamaica		Bruckner et al 2014	94.3	5	0.3	
Jamaica	Montego Bay		Newman et al 2006	42.0	5	0.3	
Jamaica		Y	Karr et al 2015	107.0	5	0.3	8.03
Kenya	Kenya closures		McClanahan 2011	120.0	3	0.21	
Kenya	Kenya fished		McClanahan 2011	11.0	3	0.21	
Kenya		Y	Graham & McClanahan 2013	111.4	3	0.21	5.85
Kenya			Graham & McClanahan 2013	39.6	3	0.21	
Kenya			McClanahan & Graham 2005	15.0	3	0.21	
Kenya			McClanahan & Graham 2005	120.0	3	0.21	
Kiribati	Kiritimati (Christmas Island)		Sandin et al 2008	130.0	2	0.165	
Kiribati	Tabuaeran (Fanning Island)		Sandin et al 2008	170.0	2	0.165	
Madagascar			Graham & McClanahan 2013	44.6	3	0.21	
Madagascar			Graham & McClanahan 2013	49.5	3	0.21	
Maldives			Graham & McClanahan 2013	143.6	2	0.165	
Maldives			McClanahan 2011	150.0	2	0.165	
Marshall Islands	Ailuk		Martin et al 2017	91.0	3	0.21	
Marshall Islands	Majuro Atoll		Martin et al 2017	126.0	2	0.165	
Marshall Islands	Rongelap	Y	Martin et al 2017	67.0	2	0.165	2.76
Mauritius		Y	Graham & McClanahan 2013	81.7	3	0.21	4.29
Mauritius			Graham & McClanahan 2013	34.7	3	0.21	
Mayotte		Y	Graham & McClanahan 2013	108.9	3	0.21	5.72
Mayotte			Graham & McClanahan 2013	99.0	3	0.21	

Country/location	Location detail	Unfished	Source reference	Biomass mt km^{-2}	Condition	r value	MMSY mt km^{-2} yr^{-1}
Mexico	Cozumel		Newman et al 2006	242.0	3	0.21	
Mozambique		Y	Graham & McClanahan 2013	101.5	2	0.165	4.19
Mozambique			Graham & McClanahan 2013	79.2	2	0.165	
Netherlands Antilles		Y	Karr et al 2015	163.6	3	0.21	8.59
Northern Mariana Islands	Agrihan	Y	Boyle et al 2017	75.0	2	0.165	3.09
Northern Mariana Islands	Alaman, Guguam, Sarigan	Y	Boyle et al 2017	80.6	2	0.165	3.32
Northern Mariana Islands	Asuncion	Y	Boyle et al 2017	77.8	2	0.165	3.21
Northern Mariana Islands	Farallon de Pajaros	Y	Boyle et al 2017	69.4	2	0.165	2.86
Northern Mariana Islands	Maug	Y	Boyle et al 2017	45.8	2	0.165	1.89
Northern Mariana Islands	Pagan	Y	Boyle et al 2017	58.3	2	0.165	2.40
Philippines	Tubbataha Reefs National Marine Park	Y	Muallil et al 2019	106.5	2	0.165	4.39
Philippines			Muallil et al 2019	10.9	3	0.21	
Philippines			Muallil et al 2019	20.1	3	0.21	
Samoa	Ofu & Olosega		Boyle et al 2017	59.7	2	0.165	
Samoa	Rose		Boyle et al 2017	41.7	2	0.165	
Samoa	Swains		Boyle et al 2017	44.4	1	0.12	
Samoa	Tau		Boyle et al 2017	40.3	2	0.165	
Samoa	Tutuila		Boyle et al 2017	38.9	3	0.21	
Saudi Arabia			Kattan et al 2017	406.0	2	0.165	
SE Polynesia		Y	McClanahan et al 2019	99.1	2	0.165	4.09
Seychelles		Y	Graham & McClanahan 2013	49.5	3	0.21	2.60
Seychelles			Graham & McClanahan 2013	39.6	3	0.21	
South Mariana Islands	Aguijan		Boyle et al 2017	25.0	3	0.21	
South Mariana Islands	Guam		Boyle et al 2017	19.4	3	0.21	
South Mariana Islands	Rota		Boyle et al 2017	20.8	3	0.21	
South Mariana Islands	Saipan		Boyle et al 2017	16.7	3	0.21	
South Mariana Islands	Tinian		Boyle et al 2017	16.7	3	0.21	
St Lucia		Y	Karr et al 2015	145.2	3	0.21	7.62
St Vincent and Grenadines		Y	Karr et al 2015	27.1	4	0.255	1.73
Sudan			Kattan et al 2017	495.8	2	0.165	
Tanzania		Y	Graham & McClanahan 2013	86.6	3	0.21	4.55
Tanzania			Graham & McClanahan 2013	47.0	3	0.21	
Tonga		Y	Smallhorn-West et al 2020	47.0	2	0.165	1.94
Tonga			Smallhorn-West et al 2020	14.4	2	0.165	
Tropical NW Pacific		Y	McClanahan et al 2019	66.7	2	0.165	2.75
Turks and Caicos	TCI_central		Al Harborne et al 2021	60.0	3	0.21	
Turks and Caicos	TCI_north		Al Harborne et al 2021	123.0	3	0.21	
Turks and Caicos	TCI_south		Al Harborne et al 2021	63.0	3	0.21	
Turks and Caicos		Y	Karr et al 2015	137.7	3	0.21	7.23
US Remote Pacific Islands	Baker	Y	Boyle et al 2017	102.8	1	0.12	3.08
US Remote Pacific Islands	Howland	Y	Boyle et al 2017	100.0	1	0.12	3.00
US Remote Pacific Islands	Jarvis	Y	Boyle et al 2017	180.6	1	0.12	5.42
US Remote Pacific Islands	Johnston	Y	Boyle et al 2017	54.2	2	0.165	2.24
US Remote Pacific Islands	Kingman	Y	Boyle et al 2017	247.2	1	0.12	7.42
US Remote Pacific Islands	Kingman	Y	Sandin et al 2008	530.0	1	0.12	15.90
US Remote Pacific Islands	Palmyra	Y	Boyle et al 2017	137.5	1	0.12	4.13
US Remote Pacific Islands	Palmyra	Y	Sandin et al 2008	260.0	1	0.12	7.80
US Remote Pacific Islands	Wake	Y	Boyle et al 2017	52.8	2	0.165	2.18
USA	Flower Garden Banks	Y	Munoz et al 2017	267.3	2	0.165	11.03

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Table S3: National results for countries with >500km2 of coral reefs

Country or Territory	Reef area (km²)	Av Condition	Av gravity	Area fully fished (km²)	Proportion reefs fully fished	Area no-take reef (km²)	Total Catch (mt yr^{-1})	Average MMSY (mt km^{-2} yr^{-1})
Australia	41,871	1.9	3.5	61	0%	10,777	23,669	6.1
Bahamas, The	4,081	2.6	35.4	8	0%	60	11,276	4.8
Belize	1,794	2.7	111.4	10	1%	39	6,229	4.8
Bermuda	672	4.4	319.2	53	8%	-	1,109	2.9
Brazil	1,173	2.9	473.3	251	21%	457	2,249	5.1
Chagos Archipelago (disputed)	2,697	1.1	0.4	-	0%	2,697	-	7.1
China	602	4.6	816.3	494	82%	-	1,615	2.7
Colombia	1,417	2.5	99.3	114	8%	491	2,537	5.6
Cook Islands	528	2.1	21.7	9	2%	3	278	5.5
Cuba	4,931	2.8	171.3	515	10%	-	16,594	4.5
Disputed - South China Sea	3,856	3.0	10.0	-	0%	-	8,078	4.1
Dominican Republic	838	4.1	680.6	358	43%	-	2,529	3.2
Egypt, Arab Republic of	3,153	2.9	261.6	762	24%	-	10,280	4.4
Eritrea	1,879	2.6	187.1	190	10%	-	7,170	4.8
Fiji	6,704	3.0	34.4	85	1%	14	11,212	4.3
French Polynesia	5,983	1.8	39.7	81	1%	-	4,462	5.9
Haiti	848	4.5	917.5	657	77%	-	2,315	2.8
Honduras	1,060	3.3	55.0	27	3%	-	2,257	3.9
India	3,507	3.2	706.6	733	21%	210	8,295	4.2
Indonesia	39,782	3.3	190.9	3,711	9%	18	96,843	3.9
Jamaica	734	3.7	337.1	267	36%	14	2,061	3.7
Japan	1,771	4.0	561.9	436	25%	3	4,577	3.3
Kenya	700	4.0	1787.9	239	34%	22	1,928	3.4
Kiribati	3,041	3.5	23.4	38	1%	153	3,408	3.8
Madagascar	3,934	3.5	98.8	174	4%	-	10,117	3.7
Malaysia	2,865	3.5	139.2	173	6%	159	6,168	3.8
Maldives	5,281	3.0	32.1	55	1%	159	11,426	4.4
Marshall Islands	3,558	1.9	10.7	21	1%	530	3,132	5.8
Mauritius	976	2.9	368.5	213	22%	2	1,680	4.6
Mayotte	512	3.7	208.9	108	21%	-	1,403	3.5
Mexico	1,481	2.5	383.5	114	8%	7	3,886	4.8
Micronesia, Federated States of	4,925	1.7	8.8	17	0%	0	3,047	6.0
Mozambique	2,436	3.4	97.1	122	5%	-	6,143	3.9
Myanmar	1,364	3.1	107.8	54	4%	12	4,271	4.2
New Caledonia	7,450	2.4	7.5	30	0%	2,581	6,996	5.4
Nicaragua	758	3.0	21.2	-	0%	-	1,815	4.2
Palau	966	2.0	3.2	-	0%	129	719	5.8
Panama	1,521	3.4	65.5	37	2%	35	3,959	3.9
Papua New Guinea	14,523	3.0	23.8	204	1%	1	20,324	4.3

Country or Territory	Reef area (km²)	Av Condition	Av gravity	Area fully fished (km²)	Proportion reefs fully fished	Area no-take reef (km²)	Total Catch (mt yr^{-1})	Average MMSY (mt km^{-2} yr^{-1})
Philippines	22,553	3.9	495.8	6,619	29%	20	59,746	3.3
Saudi Arabia	5,291	2.7	474.6	799	15%	-	19,117	4.6
Seychelles	1,904	1.5	27.2	37	2%	233	676	6.5
Solomon Islands	6,752	3.0	13.9	41	1%	64	8,971	4.4
Somalia	589	3.3	986.2	174	30%	-	1,925	3.9
Sudan	1,069	2.5	77.4	43	4%	-	3,915	4.8
Taiwan, Province of China	629	4.3	456.8	232	37%	217	1,174	3.2
Tanzania	3,009	3.8	651.6	430	14%	27	8,133	3.4
Thailand	510	3.5	252.9	125	25%	166	1,092	4.3
Tonga	1,662	2.6	24.7	34	2%	-	2,088	4.8
Tuvalu	1,231	1.4	4.2	-	0%	68	337	6.7
United States - Florida	1,179	3.5	1631.4	325	28%	168	3,135	4.0
United States - Hawaii	3,834	1.7	362.7	389	10%	3,084	1,755	6.4
Vanuatu	1,803	3.6	32.6	50	3%	-	3,108	3.6
Venezuela	728	3.6	180.5	94	13%	-	1,911	3.7
Vietnam	691	4.0	396.2	418	60%	-	2,041	3.4
Wallis and Futuna	626	1.9	3.8	-	0%	-	323	5.9
Yemen	915	3.4	283.4	240	26%	-	3,252	3.9