

MacNeil MA, Graham NAJ, Cinner JE, Wilson SK, Williams ID, Maina J,  
Newman SP, Friedlander A, Jupiter S, Polunin NVC, McClanahan TR.

[Recovery potential of the world's coral reef fishes.](#)

*Nature* 2015, 520(7547), 341-344

**Copyright:**

© The authors 2016

**DOI link to article:**

<http://dx.doi.org/10.1038/nature14358>

**Date deposited:**

30/03/2016

**Embargo release date:**

08 October 2015



This work is licensed under a [Creative Commons Attribution-NonCommercial 3.0 Unported License](#)

## 1 Recovery potential of the world's coral reef fishes

2  
3 M. Aaron MacNeil<sup>1\*</sup>, Nicholas A.J. Graham<sup>2</sup>, Joshua E. Cinner<sup>2</sup>, Shaun K. Wilson<sup>3</sup>, Ivor D.  
4 Williams<sup>4</sup>, Joseph Maina<sup>5,6</sup>, Steven Newman<sup>7</sup>, Alan M. Friedlander<sup>8</sup>, Stacy Jupiter<sup>6</sup>, Nicholas  
5 V.C. Polunin<sup>7</sup>, and Tim R. McClanahan<sup>6</sup>

6  
7 <sup>1</sup>Australian Institute of Marine Science, PMB 3 Townsville MC, Townsville, QLD 4810  
8 Australia

9 <sup>2</sup>Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook  
10 University, Townsville, QLD 4811 Australia

11 <sup>3</sup>Department of Parks and Wildlife, Kensington, Perth WA 6151 Australia

12 <sup>4</sup>Coral Reef Ecosystems Division, NOAA Pacific Islands Fisheries Science Center, Honolulu, HI  
13 96818 USA

14 <sup>5</sup>Australian Research Council Centre of Excellence for Environmental Decisions (CEED),  
15 University of Queensland, Brisbane St Lucia QLD 4074 Australia

16 <sup>6</sup>Wildlife Conservation Society, Marine Programs, Bronx, NY 10460 USA

17 <sup>7</sup>School of Marine Science and Technology, Newcastle University, Newcastle upon Tyne NE1  
18 7RU UK

19 <sup>8</sup>Fisheries Ecology Research Lab, Department of Biology, University of Hawaii, Honolulu, HI  
20 96822 USA

21 \*Correspondence to: [a.macneil@aims.gov.au](mailto:a.macneil@aims.gov.au)

22  
23  
24 **Ongoing degradation of coral reef ecosystems has generated substantial interest in how**  
25 **management can support reef resilience<sup>1,2</sup>. Fishing is the primary source of diminished reef**  
26 **function globally<sup>3-5</sup>, leading to widespread calls for additional marine reserves to recover**  
27 **fish biomass and restore key ecosystem functions<sup>6</sup>. Yet there are no established baselines for**  
28 **determining when these conservation objectives have been met or whether alternative**  
29 **management strategies provide similar ecosystem benefits. Here we establish empirical**  
30 **conservation benchmarks and fish biomass recovery timelines against which coral reefs can**  
31 **be assessed and managed by studying the recovery potential of more than 800 coral reefs**  
32 **along an exploitation gradient. We found that resident reef fish biomass in the absence of**  
33 **fishing ( $B_0$ ) averages ~1000 kg/ha and that the vast majority (83%) of fished reefs are**  
34 **missing more than half their expected biomass, with severe consequences for key ecosystem**  
35 **functions such as predation. Given protection from fishing in both open and restricted**  
36 **areas, reef fish biomass has the potential to recover within 35 years on average and within**  
37 **59 years when heavily depleted. Importantly, alternative fisheries restrictions are largely**  
38 **(64%) successful at maintaining biomass above 50% of  $B_0$ , sustaining key functions such as**  
39 **herbivory. Our results demonstrate that critical ecosystem functions can be maintained**  
40 **through a range of fisheries restrictions, allowing coral reef managers to develop recovery**

41 **plans that meet conservation and livelihood objectives in areas where marine reserves are**  
42 **not socially or politically feasible solutions.**

43

44 There is widespread agreement that local and global drivers need to be addressed to reduce the  
45 degradation of coral reef ecosystems worldwide<sup>1,2</sup>. Numerous reef fisheries are so severely  
46 overexploited that critical ecosystem functions such as herbivory and predation are at risk<sup>3-5</sup>.  
47 Attempts to rebuild reef fish abundances and associated functions require clear timeframes over  
48 which assemblages can be restored, and viable management alternatives, such as marine reserves  
49 or gear restrictions, that promote recovery. Here we develop the first empirical estimate of coral  
50 reef fisheries recovery potential, compiling data from 832 coral reefs across 64 localities  
51 (countries and territories; Fig. 1a) to: i) estimate a global unfished biomass ( $B_0$ ) baseline – *i.e.* the  
52 expected density of reef fish on unfished reefs (kg/ha); ii) quantify the rate of reef fish biomass  
53 recovery in well-enforced marine reserves using space-for-time substitution; iii) characterize the  
54 state of reef fish communities within fished and managed areas in terms of depletion against a  $B_0$   
55 baseline; iv) predict the time required to recover biomass and ecosystem functions across the  
56 localities studied; and v) explore the potential returns in biomass and function using off-reserve  
57 management throughout the broader reefscape.

58

59 We used a Bayesian approach to jointly estimate  $B_0$  as the recovery asymptote from well-  
60 enforced marine reserves (where fishing is effectively prohibited; Fig. 1b) and the average  
61 standing biomass of unfished remote areas more than 200 km from human settlements (Fig. 1c).  
62 We first used a space-for-time analysis of recovery in well-enforced marine reserves that varied  
63 in age and controlled for available factors known to influence observed fish biomass, including  
64 local net primary productivity, the percentage of hard coral cover, water depth, and reserve size<sup>6</sup>  
65 (Fig. 1b). We then modelled  $B_0$  by linking this recovery data with prior information<sup>4</sup> on  $B_0$  and  
66 biomass from remote reefs (Fig 2c), an approach that explicitly assumes that marine reserves  
67 have the potential to recover to such levels in the absence of complicating factors, such as  
68 poaching or disturbance, and are of appropriate size<sup>6</sup>. Globally, expected  $B_0$  for diurnally active,  
69 resident reef fish was 1013 [963, 1469] kg/ha (posterior median [95% highest posterior density  
70 intervals]), with a biomass growth rate ( $r_0$ ) of 0.054 [0.01, 0.11] from an estimated initial biomass  
71 in heavily fished reefs of 158 [43, 324] kg/ha (Fig. 1). The wide uncertainty in absolute  $B_0$   
72 reflected variability in average biomass among remote localities (from ~500 to 4400 kg/ha; log-  
73 scale coefficient of variation (CV)=0.08; geometric CV=0.61) as well as differences in  
74 productivity, hard coral cover, and atoll presence among reefs (Extended Data Fig. 1). We found  
75 no evidence of data provider bias (Extended Data Fig. 2) and model goodness-of-fit was high  
76 (Bayesian p-value=0.521; Extended Data Fig. 3).

77

78 The status of reef fish assemblages on fished reefs against a  $B_0$  baseline varied considerably by  
79 locality and whether there were management restrictions on fishing activities. Fished reefs (those  
80 that lacked management restrictions) spanned a wide range of exploitation states, from heavily  
81 degraded in the Caribbean and Western Pacific, to high-biomass in the remote but inhabited

82 Pitcairn and Easter Islands (Fig. 2a). While previous studies have assessed how global reef fish  
83 yields relate to human population density<sup>7</sup>, we characterise, for the first time, the state of fished  
84 reefs against an empirical baseline. Of concern was that more than a third of the fished reefs  
85 sampled had biomass below  $0.25 B_0$ , a point below which multiple negative ecosystem effects of  
86 overfishing have been shown to occur in the Western Indian Ocean<sup>7</sup>. Only two localities, in  
87 Papua New Guinea and Guam, were at or near  $0.1 B_0$ , a fisheries reference point assumed to  
88 indicate collapse<sup>8</sup>. Reef fish assemblages fared far better when fishing activities were restricted in  
89 some way, including limitations on the species that could be caught, the gears that could be used,  
90 and controlled access rights (Fig. 2b). None of the localities with fisheries restrictions had  
91 average biomass levels below  $0.25 B_0$  and 65% were above  $0.5 B_0$ , although some individual  
92 reefs within localities were below this level (Fig. 2b).

93  
94 Despite extensive research into the benefits and planning of marine reserves, there is limited  
95 understanding of how long it takes reef fishes to recover once protected from fishing, limiting the  
96 ability of decision makers to navigate management tradeoffs. To estimate recovery times for  
97 fished and restricted reefs under hypothetical protection from fishing, we used the empirical  
98 recovery curve from marine reserves to back-calculate posterior virtual reserve ages ( $VA_i$ ) for  
99 each locality, given their estimated level of fish biomass. We estimated the expected age of  
100 reserves at 90% recovery ( $AR_{0.9}$ ) and subtracted the virtual reserve ages to calculate reef-specific  
101 expected recovery times ( $TR_{0.9,i}$ ) under full closure (*i.e.*  $TR_{0.9,i} = AR_{0.9} - VA_i$ ). By sampling these  
102 quantities from the posteriors of our Bayesian model, we were able to develop probabilistic time  
103 frames for management along an expected path to recovery. Consistent with other studies on  
104 recovery benchmarks<sup>9</sup>, and the United Nations Food and Agricultural Organization's (FAO)  
105 definition of underexploited fisheries being between 0.8 and  $1.0^{(10)}$ , we defined recovered at 0.9  
106 of  $B_0$ , but also estimated median recovery timeframes for a range of other recovery benchmarks  
107 and rates of increase (Methods).

108  
109 On average, the fished and fishing-restricted reefs surveyed within localities would require 35  
110 years of protection from fishing to recover to  $0.9 B_0$ , while the most depleted reefs would require  
111 59 years (Fig. 2c; Extended Data Fig. 4). Recovery times depended critically on the estimated  
112 rate of biomass recovery and the recovery benchmark used (Extended Data Fig. 5). Although the  
113 influence of marine reserves can be detected within several years<sup>11</sup>, our global analysis supports  
114 previous case studies<sup>12,13</sup> and a meta-analysis<sup>14</sup> showing comprehensive recovery of reef fish  
115 biomass likely takes decades to achieve. This suggests that the majority of marine reserves,  
116 having been implemented in the past 10 to 20 years, will require many more years to achieve  
117 their recovery potential, underscoring the need for continued, effective protection and  
118 consideration of other viable management options.

119  
120 To understand how the ecosystem functions provided by fishes change with protection from  
121 fishing, we examined relative changes in functional group biomass along the gradient from  
122 collapsed (101 [68, 144] kg/ha) to recovered (908 [614, 1293] kg/ha), using generalized additive

123 models to characterise trends. Despite substantial variability in the proportion of each functional  
124 group among reefs, clear non-linear trends were present in relative function (Extended Data Fig.  
125 6). During initial recovery, functional returns of key low trophic level species increased rapidly,  
126 including browsers, scraper/excavators, grazers, and planktivores (Fig. 2d; Extended Data Fig. 7).  
127 These are some of the most important ecosystem functions on coral reefs, as browsers and  
128 scraper/excavators promote coral dominance by controlling algae and clearing reef substrate for  
129 coral settlement and growth<sup>15</sup>; grazers help to limit the establishment of macroalgae by intense  
130 feeding on algal turfs<sup>16</sup>; and planktivores capture water-borne nutrients and sequester them to the  
131 reef food web<sup>17</sup>. Critically, the relative functions of grazers and scrapers/excavators reached 80 to  
132 100% of their maximum biomass by 0.5  $B_0$ , while browsers, planktivores, and the three top  
133 predator groups (macro-invertivores, pisci-invertivores, and piscivores) increased steadily as  
134 standing biomass increased toward  $B_0$ . This overall pattern of functional change shows that key  
135 herbivore functions can be fulfilled at intermediate biomass levels, rather than solely among  
136 pristine areas.

137  
138 Studies across gradients of human population and fishing densities have previously found the  
139 highest absolute losses of herbivores<sup>5</sup> and predators<sup>18,19</sup> can occur with relatively low fishing  
140 pressure; in contrast, our results show that the greatest functional changes occur when more than  
141 half of total biomass has been removed, supporting previous non-linear relationships between  
142 biomass and function<sup>4,16</sup>. This disparity likely reflects differences in studying the effects of  
143 fishing on pristine versus altered reefs - where the apex predators not included in our analysis are  
144 readily removed<sup>20</sup> - and differences in socioeconomic conditions that influence reef exploitation  
145 at specific locations<sup>21</sup>.

146  
147 Although marine reserves have been widely advocated conservation tools<sup>4</sup>, they can be untenable  
148 where people depend heavily on reef-based resources, highlighting the need for management  
149 alternatives to regulate fisheries on reefs. Therefore to complement the use of effective marine  
150 reserves, we estimated expected biomass given alternative fishing restrictions (Fig. 2e), which  
151 typically receive less resistance from fishers than marine reserves<sup>22</sup>. On average, reefs with some  
152 form of fisheries restriction had biomass 27% higher than reefs open to fishing (Fig. 2a,b).  
153 Critically, on reefs with bans on specific fishing gears, such as beach seines, or restrictions on the  
154 types of fish that can be caught, such as herbivores, biomass levels were between 0.3 and 0.4  $B_0$ ,  
155 the point at which up to 80% of herbivore function was retained (Fig. 2e). Thus, even simple  
156 fisheries restrictions can have substantial impacts on fish functional groups that support important  
157 reef processes. Still greater biomass and functional returns were observed on reefs with access-  
158 restrictions limiting the number of people allowed to fish a reef, such as family relations, or  
159 where other forms of established local marine tenure enable exclusion of external fishers<sup>21</sup>.  
160 Although these management alternatives clearly promote important functional gains relative to  
161 openly-fished reefs, it is only among well-enforced, long-established marine reserves that  
162 predation is maximized, more than tripling the function of piscivory present on collapsed reefs.

163

164 The continuing degradation of the world's coral reefs underscores the need for tangible solutions  
165 that promote recovery and enhance ecosystem functions<sup>4,23</sup>. Our results demonstrate that well-  
166 enforced marine reserves can support a full suite of reef fish functions given enough time to  
167 recover. However, for reefs where marine reserves cannot be implemented, we find that  
168 ecosystem functions can be enhanced through various forms of fisheries management.  
169 Addressing the coral reef crisis ultimately demands long-term, international action on global-  
170 scale issues such as ocean warming and acidification<sup>24</sup>, factors that may diminish recovery  
171 potential by ~6% over the coming decades (Extended Data Fig. 8). Despite these challenges, a  
172 range of fisheries management options are available to support reef resilience and it is likely that  
173 some combination of approaches will be necessary for success. Having benchmarks and timelines  
174 within an explicit biomass context, such as those provided here, increase the chances of agreeing  
175 on, and complying with, a mix of management strategies that will achieve conservation  
176 objectives while sustaining reef-based livelihoods.  
177  
178  
179

## 180 **References**

- 181  
182 <sup>1</sup>Hughes, T.P. *et al.* Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.*  
183 **25**, 633–642 (2010).  
184  
185 <sup>2</sup>Graham, N.A.J. *et al.* Managing resilience to reverse phase shifts in coral reefs. *Front. Ecol.*  
186 *Environ.* **11**, 541–548 (2013).  
187  
188 <sup>3</sup>Dulvy, N.K., Freckleton, R.P. & Polunin, N.V.C. Coral reef cascades and the indirect effects of  
189 predator removal by exploitation. *Ecol. Lett.* **7**, 410–416 (2004).  
190  
191 <sup>4</sup>McClanahan, T.R. *et al.* Critical thresholds and tangible targets for ecosystem-based  
192 management of coral reefs. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 17230–17233 (2011).  
193  
194 <sup>5</sup>Bellwood, D.R. *et al.* Human activity selectively impacts the ecosystem roles of parrotfishes on  
195 coral reefs. *Proc. R. Soc. B* **279**, 1621–1629 (2012).  
196  
197 <sup>6</sup>Edgar, G.J. *et al.* Global conservation outcomes depend on marine protected areas with five key  
198 features. *Nature* **506**, 216–220 (2014).  
199  
200 <sup>7</sup>Newton, K. *et al.* Current and future sustainability of island coral reef fisheries. *Curr. Biol.* **17**,  
201 655–658 (2007).  
202  
203 <sup>8</sup>Worm, B. *et al.* Rebuilding global fisheries. *Science* **325**, 578–585 (2009).  
204

205 <sup>9</sup>Lambert, G.I. *et al.* Quantifying recovery rates and resilience of seabed habitats impacted by  
206 bottom fishing. *J. Appl. Ecol.* DOI: 10.1111/1365-2664.12277 (2014).  
207

208 <sup>10</sup>Worm, B. & Branch, T.A. The future of fish. *Trends Ecol. Evol.* **27**, 594-599 (2012).  
209

210 <sup>11</sup>Babcock, R.C. *et al.* Decadal trends in marine reserves reveal differential rates of change in  
211 direct and indirect effects. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 18256-18261 (2010).  
212

213 <sup>12</sup>McClanahan, T.R., Graham, N.A.J., Calnan, J. & MacNeil, M.A. Towards pristine biomass:  
214 reef fish recovery in coral reef marine protected areas in Kenya. *Ecol. Appl.* **17**, 1055-1067  
215 (2007).  
216

217 <sup>13</sup>Russ, G.C. & Alcala, A.C. Decadal-scale rebuilding of predator biomass in Philippine marine  
218 reserves. *Oecologia* **163**, 1103-1106 (2010).  
219

220 <sup>14</sup>Molloy, P.P., McLean, I.B. & Côté, M. Effects of marine reserve age on fish populations: a  
221 global meta-analysis. *J. Anim. Ecol.* **46**, 743-751 (2009).  
222

223 <sup>15</sup>Rasher, D.B. *et al.* Consumer diversity interacts with prey defenses to drive ecosystem function.  
224 *Ecology* **94**, 1347-1358 (2013).  
225

226 <sup>16</sup>Mumby, P.J. *et al.* Empirical relationships among resilience indicators on Micronesian reefs.  
227 *Coral Reefs* **32**, 213-226 (2013).  
228

229 <sup>17</sup>Hamner, W.H. *et al.* Export-import dynamics of zooplankton on a coral reef in Palau. *Mar.*  
230 *Ecol. Prog. Ser.* **334**, 83-92 (2007).  
231

232 <sup>18</sup>Jennings, S. *et al.* Effects of fishing effort and catch rate upon the structure and biomass of  
233 Fijian reef fish communities. *J. Appl. Ecol.* **33**, 400-412 (1996).  
234

235 <sup>19</sup>Dulvy, N.K. *et al.* Size structural change in lightly exploited coral reef fish communities:  
236 evidence for weak indirect effects. *Can. J. Fish. Aquat. Sci.* **61**, 466-475 (2004).  
237

238 <sup>20</sup>Robbins, W.D., Hisano, M., Connolly, S.R. & Choat, J.H. Ongoing collapse of coral-reef shark  
239 populations. *Curr. Biol.* **16**, 2314-2319 (2006).  
240

241 <sup>21</sup>Cinner, J.E. *et al.* Co-management of coral reef social-ecological systems. *Proc. Natl. Acad.*  
242 *Sci. U.S.A.* **109**, 5219-5222 (2012).  
243

244 <sup>22</sup>McClanahan, T.R., Abunge, C.A. & Cinner, J.E. Heterogeneity in fishers' and managers'  
245 preferences towards management restrictions and benefits in Kenya. *Environ. Conserv.* **39**, 357-  
246 369 (2012).

247  
248 <sup>23</sup>Bellwood, D.R., Hughes, T.P., Folke, C. & Nyström, M. Confronting the coral reef crisis.  
249 *Nature* **429**, 827-833 (2004).

250  
251 <sup>24</sup>Hoegh-Guldberg, O. *et al.* Coral reefs under rapid climate change and ocean acidification.  
252 *Science* **318**, 1737-1742 (2007).

253  
254

### 255 **Supplementary Information**

256 Is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

257  
258

### 258 **Acknowledgments**

259 We thank M. Emslie, A. Cheal, J. Wetherall, C. Hutchery, and K. Anthony for comments on  
260 early drafts of the manuscript and three anonymous reviewers for insightful comments in  
261 reviewing the manuscript. The Australian Institute of Marine Science, the ARC Centre of  
262 Excellence for Coral Reef Studies, and the John D and Catherine T McArthur Foundation  
263 supported this research.

264  
265

### 265 **Author Contributions**

266 M.A.M. conceived of the study with N.A.J.G, T.R.M, S.K.W., and J.E.C; M.A.M. developed and  
267 implemented the analysis; M.A.M. led the manuscript with N.A.J.G, J.E.C, and S.K.W. All other  
268 authors contributed data and made substantive contributions to the text.

269  
270

### 270 **Author Information**

271 Reprints and permissions information is available at [www.nature.com/reprints](http://www.nature.com/reprints). The authors  
272 declare no competing financial interests. Correspondence and request for materials should be  
273 addressed to M.A.M. ([a.macneil@aims.gov.au](mailto:a.macneil@aims.gov.au)). This is SERF working group contribution #10.

274  
275  
276



277 **Figure 1 | Global reef fish biomass among management categories.** **a.** Study (n=832) and  
278 prior (n=157) sites, with numbers matching panel **c.**; **b.** posterior median recovery trajectory  
279 (black line) of reef fish biomass among reserve locations (n=45), with 95% uncertainty intervals  
280 (UI; grey), 95% prediction intervals (PI; dotted line), estimated initial biomass (white circle with  
281 50% (thick line), and 95% (thin line) highest posterior densities), and observed UVC data (green  
282 symbols); **c.** posterior biomass for remote locations (n=22; boxplots; 50% quantiles) with data  
283 (grey circles), median  $B_0$  (black line), 95% UI (grey shading), and 95% PI (dotted line) from  $B_0$   
284 in **d.**; **d.** prior (violet), joint informed (dark blue), and uninformed posterior (black line) densities  
285 for  $B_0$ .

286  
287 **Figure 2 | Coral reef fish responses across the spectrum of potential recovery.** Posterior  
288 density proportion of  $B_0$  for **a.** fished (n=23) and **b.** fishing-restricted (n=17) coral reef locations,  
289 shaded from red (collapsed = 0.1  $B_0$ ) to green (recovered = 0.9  $B_0$ ). **c.** expected times to recovery  
290 (0.9  $B_0$ ) for fished (circles) and restricted (squares) reefs given full, effective closure. **d.** average  
291 reef fish functional returns from collapsed to recovered; **e.** median estimated proportion of  $B_0$   
292 among reef fishery management alternatives (black circles) with 50% (thick line) and 95% (thin  
293 line) uncertainty intervals.  
294

295 **Methods**

296

297 Reef fish biomass estimates were based on instantaneous visual counts (UVC) from 2096 surveys  
298 collected from coral reef slopes (*i.e.* the sloping, windward outer reef, selected specifically to  
299 standardize the reef habitat and remove potential bias associated with habitat type) on 832  
300 individual reef sites (hereafter 'reef'). All data were collected using standard belt-transects  
301 (50\*5m or 30\*4m) or point-counts (7m radius) between 2002 and 2013, with the bulk of the data  
302 (92%) collected since 2006 (Supplementary Table 1). Data from belt transects and point counts  
303 have repeatedly been shown to be comparable in estimating fish abundance<sup>25</sup> and biomass<sup>26</sup>.

304 Within each survey area, reef associated fishes were identified to species level, abundance  
305 counted, and length (TL) estimated to the nearest 5 cm. A single experienced observer collected  
306 data for each dataset except the NOAA data from the Pacific where multiple observers operate on  
307 every sampling mission. However NOAA has extensive protocols in place to ensure their  
308 observers are well trained and follow consistent protocols, ensuring the data are consistent and  
309 unbiased. We tested for any bias among data providers (capturing information on both inter-  
310 observer differences, and census methods) by including each data provider as a random effect in  
311 our model (see below), which assumes that there are inherent correlations within datasets that  
312 affect the means and associated errors estimated from their data. This analysis showed that there  
313 was no bias among data providers and that there is little information present in data provider  
314 identities (Extended Data Fig. 2). From these transect-level data we retained counts of diurnally-  
315 active, non-cryptic reef fish that are resident on the reef slope, excluding sharks and semi-  
316 pelagics (Supplementary Table 2). Metadata for the surveys are within the James Cook  
317 University research data repository, the Tropical Data Hub (<https://eresearch.jcu.edu.au/tdh>).

318

319 Total biomass of fishes on each transect was calculated using published length-weight  
320 relationships or those available on FishBase (<http://fishbase.org>). During this process we removed  
321 35 transects where divers were mobbed by behaviourally-aggregating species (*e.g.* *Acanthurus*  
322 *coeruleus*; n=34) or high biomass aggregating species (*i.e.* *Bolbometopon muricatum*; n=1) that  
323 led to potentially unreliable estimates of standing biomass according to the data provider. This  
324 truncated dataset was averaged to the reef level (*i.e.* transects within the same section of  
325 continuous reef)<sup>27</sup> forming 832 distinct reefs that formed the basic data for our study. The data  
326 were sampled from key coral regions around the world; however, the coral triangle, Brazil, West  
327 Africa, and the Red Sea/Arabian Sea regions are not represented. Fish species were assigned to  
328 functional groups based on trophic guilds and dietary information from the literature and  
329 FishBase. A key scale in our analysis was 'locality', defined as reef areas from 10's to 100's of km  
330 that generally correspond to individual nations and map closely onto ranges of human  
331 influence<sup>27</sup>, within which reefs were nested for analysis. In this way our analysis consisted of  
332 three spatial scales: reef, locality, and global. This dataset can be obtained from the senior author  
333 upon request (MAM; [a.macneil@aims.gov.au](mailto:a.macneil@aims.gov.au)) and combined with PyMC code in the  
334 Supplementary Methods to replicate our Bayesian hierarchical analysis.

335

336 We used the PyMC package<sup>28</sup> for the Python programming language to conduct our analysis,  
 337 running the (Metropolis-Hastings; MH) MCMC sampler for  $10^6$  iterations, with a 900,000  
 338 iteration burn in and a thinning rate of 100, leaving 1000 samples in the posterior of each  
 339 parameter; these long (relative to say, Gibbs sampling) burn-in times are often required with a  
 340 MH algorithm. Convergence was monitored by examining posterior chains and distributions for  
 341 stability and by running 5 chains from different starting points and checking for convergence  
 342 using Gelman-Rubin statistics<sup>29</sup> for parameters across multiple chains, all of which were at or  
 343 close to 1, indicating good convergence of parameters across multiple chains.

344  
 345 We used multiple data sources, including remote areas, asymptotes of well enforced marine  
 346 reserves, and prior information, to estimate unfished biomass ( $B_0$ ) and time for recovery. Remote  
 347 areas - defined as having no recent history of fishing and being more than 200 km from human  
 348 settlement - informed local  $B_{0l}$  and global  $B_0$ , given reef-specific covariates  $x_{nj}$  thought to  
 349 influence standing biomass that were available at the majority of localities. These covariates  
 350 included local net primary production (NPP)<sup>30</sup>, average proportion of hard coral cover<sup>31</sup>, depth of  
 351 survey (m)<sup>32</sup>, and having been collected on an atoll (0/1 dummy variable)<sup>33</sup>. NPP was calculated  
 352 as ensemble mean of estimates based on two NPP algorithms applied on MODIS and SeaWiFS  
 353 data (*i.e.* *Carbon-based Production Model-2 (CbPM2)*<sup>34</sup> and *Vertically Generalized Production*  
 354 *Model (VGPM)*<sup>35</sup>: <http://orca.science.oregonstate.edu>; mg C / m<sup>2</sup> / day. Each of these reef-  
 355 specific nuisance parameters were mean centred to offset the reef level observations relative to  
 356 the main focus of our model - the  $B_{0l}$  estimates.

357  
 358 To ensure an appropriate sub-model structure was used, we evaluated fits of three potential linear  
 359 and non-linear relationships (linear, second-order polynomial, and third-order polynomial) for  
 360 each continuous nuisance parameter. We selected the best-fitting relationship for each nuisance  
 361 parameter individually based on having the lowest deviance information criteria (DIC) value  
 362 (Extended Data Table 1) and then compared DIC values of a candidate model set having all  
 363 combinations of each nuisance parameter to select a final model (Extended Data Table 2). We  
 364 also examined the posterior residuals for each nuisance parameter sub-model to ensure no  
 365 heteroskedascity was present and that errors were normally-distributed (Extended Data Fig. 9).

366  
 367 To recognize potential data provider methodological effects, we incorporated data-provider status  
 368 in our  $B_0$  estimates by adding a random effect  $\rho_j$  for data provider  $j$  in our Bayesian hierarchical  
 369 model. These factors were included in a log-Normal hierarchical model for  $B_0$ , given reef-scale  
 370 observations  $y_{il,r}$ :

$$\begin{aligned}
 y_{il,r} & \sim N(\mu_{il,r}, \sigma_l) \\
 \mu_{il,r} & = B_{0l} + \beta_1 x_{coral,i} + \beta_2 x_{coral,i}^2 + \beta_3 x_{coral,i}^3 + \beta_4 x_{atoll,i} + \beta_5 x_{production,i} + \beta_6 x_{production,i}^2 + \beta_7 x_{production,i}^3 + \rho_j \\
 B_{0l} & \sim N(B_0, \sigma_b),
 \end{aligned}$$

[1,2,3]

373  
 374  
 375

376 and weakly-informative priors  
 377

$$\beta_{1,\dots,7} \sim N(0.0,100)$$

$$378 \quad \sigma_{l,b} \sim U(0.0,100) \quad [4,5,6]$$

$$\rho_j \sim N(0.0,100).$$

379  
 380 Because this study built upon previous research conducted in the Western Indian Ocean<sup>7</sup> we used  
 381 the posterior  $B_\theta$  estimate from that study as the prior for our analysis:

$$382 \quad B_0 \sim LN(7.08,0.46) \quad [7]$$

383  
 384 allowing us to build on existing knowledge by directly integrating information between studies.  
 385 As a check for those averse to building upon previous research in this way, we also ran the full  
 386 model using an uninformative  $B_\theta$  prior, resulting in highly similar inferences, albeit with  
 387 marginally greater uncertainty than the informed estimates (6.92 [6.52, 7.27] log(kg/ha)  
 388 informed; 6.82 [6.45, 7.23] log(kg/ha) uninformed), demonstrating that the observed data  
 389 dominated the prior in our analysis.

390  
 391 To estimate times to biomass recovery we relied on data from well-enforced, previously fished  
 392 marine reserves from around the world (Fig. 1a) and used a space-for-time substitution approach,  
 393 assuming the relationship between reserve age and standing biomass follows a standard logistic  
 394 regression model and the same reef-scale offset terms as above:

$$395 \quad y_{i,a} \sim N(\mu_a, \sigma_m)$$

$$396 \quad \mu_a = \frac{B_0}{1+(B_0=\mu_0)/\mu_0} e^{-ra} + \beta_1 x_{coral,i} + \beta_2 x_{coral,i}^2 + \beta_3 x_{coral,i}^3 + \beta_4 x_{atoll,i} + \beta_5 x_{production,i} + \beta_6 x_{production,i}^2 + \beta_7 x_{production,i}^3 + \rho_j$$

397  
 398  
 399  
 400  
 401  
 402  
 403  
 404  
 405  
 406  
 407  
 408  
 409  
 410  
 411  
 412

403 Here  $a$  is the age of the marine reserve in years;  $\mu_0$  is the average initial reserve biomass; and  $r$   
 404 the average rate of biomass increase. This model is somewhat less hierarchically-explicit than  
 405 equation [2] due to the scarcity of global marine reserve biomass data, and relies on the key  
 406 assumption that average reserve potential recovery is consistent, absent the reef-scale effects in  
 407 the model. Importantly,  $B_0$  is the same as in equation [3] and the linear offsets  $\beta_{1,\dots,7}$  the same as  
 408 in [2], meaning their effects were jointly estimated from both remote and marine reserve data.  
 409 Therefore  $B_0$  is estimated from both the trajectory of marine reserves through time and from the  
 410 average biomass of all areas defined *a priori* as being remote:  $B_0$  is the asymptote in the reserve  
 411 component of the model and the global mean in the remote component of the model.  $\mu_0$ , the  
 412 minimum biomass at reserve age zero, was given an uninformative  $\sim U(1,10)$  prior that spanned

413 the range of the data; the standard deviation  $\sigma_m$  was as in [5];  $x_{size,i}$  was set to allow for potential  
 414 effects of reserve size, thought to be an important component of reserve success<sup>6</sup>.

415  
 416 Next we estimated standing reef fish biomass across a range of fished locations, again  
 417 hierarchically, given observer effects and reef-level observations within each location:  
 418

$$\begin{aligned}
 y_{il,f} & \sim N(\mu_{il,f}, \sigma_f) \\
 \mu_{il,f} & = B_{l,f} + \beta_1 x_{coral,i} + \beta_2 x_{coral,i}^2 + \beta_3 x_{coral,i}^3 + \beta_4 x_{atoll,i} + \beta_5 x_{production,i} + \beta_6 x_{production,i}^2 + \beta_7 x_{production,i}^3 + \rho_j \\
 B_{l,f} & \sim N(0.0, 100)
 \end{aligned}$$

[10,11,12]

419  
 420 Here the  $B_{l,f}$  terms denote independent log-biomass priors per location as we did not assume any  
 421 parent (hierarchical) structure among locations other than potential data-provider effects; the  
 422 standard deviation prior for  $\sigma_f$  was as in [5]. Note that fishing pressure is a continuous variable  
 423 that implicitly underlies the observed differences in exploitation state outside of the factors  
 424 included in our analysis.  
 425

426  
 427 To estimate the standing biomass across a range of management categories,  $z$ , we applied similar  
 428 methods:  
 429

$$\begin{aligned}
 y_{il,z} & \sim N(\mu_{il,z}, \sigma_z) \\
 \mu_{il,z} & = B_{l,z} + \beta_1 x_{coral,i} + \beta_2 x_{coral,i}^2 + \beta_3 x_{coral,i}^3 + \beta_4 x_{atoll,i} + \beta_5 x_{production,i} + \beta_6 x_{production,i}^2 + \beta_7 x_{production,i}^3 + \rho_j \\
 B_{l,z} & \sim N(0.0, 100).
 \end{aligned}$$

[13,14,15]

430  
 431 As for the fished locations, the  $B_{l,z}$  terms denote independent log-biomass priors per location and  
 432 the standard deviation prior for  $\sigma_z$  was as in [5]. Management alternative effects were calculated  
 433 as the average of the location-level posteriors for each group. Note that some locations in the data  
 434 (Agrihan, Alamagan, Asuncion, Farallon de Pajaros, Guguan, Maug, Pagan, Rose, and Sarigan)  
 435 were passively fishery-restricted due to isolation limiting effort that could be directed at the  
 436 resource and, as a trait that cannot be actively managed, we excluded these locations from this  
 437 section of our analysis.  
 438

439  
 440  
 441 *Overall model fit*

442  
 443 We conducted posterior predictive checks for goodness of fit (GoF) using Bayesian p-values<sup>36</sup>,  
 444 whereby fit was assessed by the discrepancy between observed or simulated data and their  
 445 expected values. To do this we simulated new data ( $y_i^{new}$ ) by sampling from the joint posterior of

446 our model ( $\theta$ ) and calculated the Freeman-Tukey measure of discrepancy for the observed ( $y_i^{obs}$ )  
 447 or simulated data, given their expected values ( $\mu_i$ ):

$$449 \quad D(y|\theta) = \sum_i (\sqrt{y_i} - \sqrt{\mu_i})^2 \quad [16]$$

450  
 451 yielding two arrays of median discrepancies  $D(y^{obs}|\theta)$  and  $D(y^{new}|\theta)$  that were then used to  
 452 calculate a Bayesian p-value for our model by recording the proportion of times  $D(y^{obs}|\theta)$  was  
 453 greater than  $D(y^{new}|\theta)$  (Extended Data Fig. 3). For models not showing evidence of being  
 454 inconsistent with the observed data,  $D(y^{obs}|\theta)$  will greater than  $D(y^{new}|\theta)$  50% of the time, giving  
 455 a p-value = 0.5; for models that showing evidence of being inconsistent with the observed data,  
 456  $D(y^{obs}|\theta)$  will, by specification, be greater than (or less than)  $D(y^{new}|\theta)$  95% of the time.

#### 458 *Times to recovery*

461 We capitalized on our integrated Bayesian model to estimate location-specific recovery times for  
 462 fished and fishery-restricted reefs within the Bayesian MCMC scheme. First we calculated the  
 463 average reserve age at recovery (*i.e.*  $0.9 B_0: B_{0.9}$ ), given the posterior biomass rate of growth  $r$  and  
 464 initial biomass of  $\mu_0$  (see posterior parameter estimates in Supplementary Table 3):

$$466 \quad AR_{0.9} = \frac{\log\left[\left(\frac{B_0}{B_{0.9}} - 1\right) / \left(\frac{B_0 - \mu_0}{\mu_0}\right)\right]}{-r} \quad [17]$$

467  
 468 Next we calculated location-specific virtual reserve ages, given their estimated level of log-  
 469 biomass:

$$470 \quad VA_i = \frac{\log\left[\left(\frac{B_0}{B_{l,f/z}} - 1\right) / \left(\frac{B_0 - \mu_0}{\mu_0}\right)\right]}{-r}, \quad [18]$$

471  
 472 and subtracted this from  $AR_{0.9}$  to give an expected time to recovery for each location:

$$474 \quad TR_{0.9,i} = AR_{0.9} - VA_i. \quad [19]$$

475  
 476 Because these calculations were conducted within our MCMC scheme they included posterior  
 477 uncertainties, given the data and our model.

#### 480 *Variable recovery targets*

481  
 482 Our choice to define recovery at  $0.9B_0$  was based on recent work on recovery in the North Sea<sup>9</sup>  
 483 and being the midpoint at which individual fish stocks are considered underexploited by the

484 United Nations Food and Agricultural Organization<sup>10</sup>. However, to explore how expected time to  
485 recovery was dependent on this choice and the estimated rate of biomass growth, we calculated  
486 average reserve ages at recovery ( $AR_{x,y}$ ) using the median posterior  $B_0$  and  $\mu_0$  values (in [17])  
487 while systematically varying the proportion of  $B_0$  defined as recovered (between 0.8 to 1.0) and  
488 the rate of biomass growth (between posterior 95% UI range of 0.012 and 0.11). The resulting  
489 surface plot showed exponential increases in reserve ages at recovery for slower biomass growth  
490 rates and higher values of defined recovery due to the asymptotic nature of the logistic growth  
491 model used. (Extended Data Fig. 5)

492  
493

#### 494 *Potential effects of climate change on $B_0$*

495

496 A key assumption of the conclusions drawn from our results is that factors affecting total  
497 potential  $B_0$  will remain stable through time. Climate projections have been equivocal as to what  
498 might happen to tropical fisheries over the coming decades<sup>37</sup>, primarily due to uncertainty in how  
499 production<sup>38</sup> and hard coral habitat<sup>39</sup> is expected to change, as well as difficulty in modelling  
500 tropical coastal habitats<sup>37</sup>. Nonetheless we used the estimated relationships of log-biomass to  
501 productivity and hard coral cover (Extended Data Fig. 1) to explore changes in  $B_0$  due to declines  
502 in both environmental conditions, using the median posterior estimates from our Bayesian  
503 hierarchical model. Results showed that by 2040, given an expected 4% loss of primary  
504 productivity<sup>38</sup> and a 2% annual loss of coral cover<sup>39</sup>, we would expect to see a 6% drop in  $B_0$ , to  
505 953 kg/ha (Extended Data Fig. 8).

506

507

#### 508 *Log vs. arithmetic scales of estimation*

509

510 By adopting a hierarchical approach we, in effect, chose to average over location-specific  
511 differences in order to make global-scale inferences. We elected to model our data on the log-  
512 scale, as per fisheries convention<sup>40</sup>, because it normalized the variance around our hierarchical  
513 model, greatly improving the precision of model estimates and the convergence of our model fits.

514

515 A key related point in our analysis is that our posterior calculations for fractions of  $B_0$  were all on  
516 the arithmetic scale, by exponentiating each location-scale estimate and dividing by  $e^{B_0}$ . To see  
517 why this makes sense, taking the posterior estimates for log-biomass from Ahus, PNG (4.54) and  
518  $B_0$  (6.92), Ahus would have retained  $4.54/6.92 = 0.66$  unfished log-biomass but only  $e^{4.54}/e^{6.92} =$   
519  $0.09$  absolute biomass. Given that this is the most heavily exploited reef in our database and that  
520 fisheries conventions for defining collapsed and recovered are arithmetic, we retained the  
521 arithmetic for our posterior calculations.

522

523

#### 524 *Functional returns*

525  
526  
527  
528  
529  
530  
531  
532  
533  
534  
535  
536  
537  
538  
539

To understand how relative reef fish function would be expected to vary over the recovery range from collapsed (101 [68, 143] kg/ha) through to recovery (908 [614, 1293] kg/ha), we modelled the average biomass of each functional group across this range (*i.e.* log(101) to log(908) kg/ha) relative to their initial biomass values (*i.e.* average biomass of each functional group at log(101) kg/ha). We deemed these relative changes in biomass 'functional returns' because they express relative increases in function that could be expected given log-scale increases in the total biomass of a given functional group on a coral reef. To do this, and allow for expected non-linearities in functional group responses (due to *e.g.* community interactions, resource dynamics etc., the shape of response to which is currently unknown for most functional groups) we fit a series of generalized additive models (GAMs) to the proportion of each functional group over the community recovery range (Extended Data Fig. 6) in models that included the same covariates as our Bayesian hierarchical model (NPP, average proportion of hard coral cover, depth of survey, and having been collected on an atoll). The form of the model was, for each functional group  $k$ :

$$y_{il,k} \sim N(\mu_{il,k}, \sigma_k)$$
$$\mu_{il,k} = \beta_{0l} + f_1(x_{\log\text{-biomass},i}) + \beta_1 x_{\text{coral},i} + \beta_2 x_{\text{atoll},i} + \beta_3 x_{\text{production},i}$$
$$\beta_{0l} \sim N(0.0, 100).$$

541  
542  
543  
544  
545  
546  
547  
548  
549  
550  
551  
552  
553  
554

[20,21,22]

with the smooth function  $f_1(x_{\log\text{-biomass},i})$  describing the non-linear relationship between observed functional group proportions and total log-biomass. Dividing the fitted GAMs for each functional group by the proportion at collapse provided a measure of expected functional return for each group, where a functional return of 2.0 would mean there is twice the log-biomass of a given functional group present compared to initial conditions. The rationale for this approach was that, as our data span the full range from 0.1 to 0.9  $B_0$ , we did not need to predict outside of the data, but rather uncover the potentially non-linear changes in relative function for each group over this range. All GAMs were run using in the *GAMM* package in R (<http://www.r-project.org>), using default smooth parameters that provided consistent fits to a per 0.1 log-kg moving average.

### 555 **Additional references**

556 <sup>25</sup>Samoilys, M.A. & Carlos, G. Determining methods of underwater visual census for estimating  
557 the abundance of coral reef fishes. *Environ. Biol. Fish.* **57**, 289-304 (2000).

558 <sup>26</sup>Watson, R.A. & Quinn, T.J. Performance of transect and point count underwater visual census  
559 methods. *Ecol. Model.* **104**, 103-112 (1997).

560 <sup>27</sup>MacNeil, M.A. & Connolly, S.R. in *Ecology of Fishes on Coral Reefs: The Functioning of and*  
561 *Ecosystem in a Changing World*, C. Mora, Ed. (Cambridge Univ. Press, Cambridge, 2014), chap  
562 12.



- 563 <sup>28</sup>Patil A., Huard, D. & Fonnesbeck, C.J. PyMC: Bayesian stochastic modelling in Python. *J.*  
564 *Stat. Softw.* **35**, 1-81 (2000).
- 565 <sup>29</sup>Gelman, A. & Rubin, D.B. Inference from iterative simulation using multiple sequences. *Stat.*  
566 *Sci.* **7**, 457-511 (1992).
- 567 <sup>30</sup>Chasot, E. *et al.* Global marine primary production constrains fisheries catches. *Ecol. Lett.* **13**,  
568 495-505 (2010).
- 569 <sup>31</sup>Graham N.A.J. *et al.* Climate warming, marine protected areas and the ocean-scale integrity of  
570 coral reef ecosystems. *PLoS ONE* **3**, e3039 1-9 (2008).
- 571 <sup>32</sup>Newman, M.J.H., Paredes, G.A., Sala, E. & Jackson, J.B.C. Structure of Caribbean coral reef  
572 communities across a large gradient of fish biomass. *Ecol. Lett.* **9**, 1216-1227 (2006).
- 573 <sup>33</sup>Cinner, J.E., Graham, N.A.J., Huchery, C. & MacNeil M.A. Global effects of local human  
574 population density and distance to markets on the condition of coral reef fisheries. *Conserv. Biol.*  
575 **27**, 453-458 (2013).
- 576 <sup>34</sup>Westberry, T., Bherenfeld, M.J., Siegel, D.A., & Boss, E. Carbon-based primary productivity  
577 modeling with vertically resolved photoacclimation. *Global Biogeochem. Cy.* **22**, GB2024  
578 (2008).
- 579 <sup>35</sup>Bherenfeld, M.J. & Falkowski, P.G. Photosynthetic rates derived from satellite-based  
580 chlorophyll concentration. *Limnol. Oceanogr.* **42**, 1-20 (1997).
- 581 <sup>36</sup>Brooks, S.P., Catchpole, E.A. & Morgan, B.J.T. Bayesian animal survival estimation. *Stat. Sci.*  
582 **15**, 357-376 (2000).
- 583 <sup>37</sup>Cheung, W.W.L. *et al.* Large-scale redistribution of maximum fisheries potential in the global  
584 ocean under climate change. *Glob. Change Biol.* **16**, 24-35 (2010).
- 585 <sup>38</sup>Sarmiento, J.L. *et al.* Response of ocean ecosystems to climate warming. *Global Biogeochem.*  
586 *Cycles* **18**, GB3003 1-24 (2004).
- 587 <sup>39</sup>Bruno, J.F. & Selig, E.R. Regional Decline of Coral Cover in the Indo-Pacific: Timing, Extent,  
588 and Subregional Comparisons. *PLoS ONE* **3**, e711 1-8 (2007).
- 589 <sup>40</sup>Walters, C.J. & Martell, S.J.D. *Fisheries Ecology and Management*. (Princeton Univ. Press,  
590 Princeton, 2004).

591 **Extended Data Figure 1 | Nuisance parameter posterior estimates for modelled recovery.**  
592 Joint Bayesian hierarchical recovery model **a.** prior (flat black line) and posterior (histograms)  
593 nuisance parameter densities (vertical dotted line at zero) for factors influencing total reef fish  
594 biomass (kg/ha), including three parameters for a third order polynomial for hard coral cover [*i.e.*  
595 Hard coral (1) , (2) , (3)], an offset for atoll vs. non-atoll, and three parameters for a third order  
596 polynomial for productivity [*i.e.* Productivity (1) , (2) , (3)]; **b.** estimated relationship between  
597 percent hard coral cover and total biomass using posterior median values (blue line), with 99  
598 samples from the posterior distribution of the parameters in **a.** (thick grey lines) and marginal  
599 data (black dots; n=832 reefs); **c.** plot of observed depth and marginal total biomass given the full  
600 model (no depth effect present); **d.** estimated relationship between atoll (1) vs. non-atoll (0) and  
601 total biomass, with marginal data (boxplot and black squares); **e.** plot of reserve size and marginal  
602 total fish biomass given the full model (no reserve size effect present); **f.** estimated relationship  
603 between productivity and total biomass, with marginal data.  
604

605 **Extended Data Figure 2 | Data provider random effect posteriors.** Bayesian hierarchical  
606 model posterior estimated effects of data provider identity, including 95% posterior densities  
607 (thin lines), 50% posterior densities (thin lines), and posterior median values (black circles).  
608 Results show no apparent bias among data providers, with little information present in provider  
609 identities.  
610

611 **Extended Data Figure 3 | Bayesian p-values for goodness of fit.** Discrepancy-based posterior  
612 predictive checks for Bayesian hierarchical model goodness of fit. Points represent Freeman-  
613 Tukey discrepancy measures between observed and expected values,  $D(y^{obs}|\theta)$ , and simulated and  
614 expected values,  $D(y^{new}|\theta)$ . Plot shows high level of agreement between observed and simulated  
615 discrepancies ( $p=0.521$ ), indicating the model is not inconsistent with the observed data. Labelled  
616 clusters of distinct points reflect various components of the joint model.  
617

618 **Extended Data Figure 4 | Posterior expected times to recovery among localities.** Bayesian  
619 hierarchical model posterior estimated times to recovery ( $0.9B_0$ ) for fished (green circles) and  
620 restricted (amber squares) localities around the world. Black lines are 50% highest posterior  
621 densities and symbols are posterior median values.  
622

623 **Extended Data Figure 5 | Change in expected reserve age at recovery given specified**  
624 **recovery target.** Change in expected reserve age at recovery (contour lines; in years) given  
625 specified values for recovery (as a proportion of  $B_0$ ) and the 95% highest posterior density range  
626 for the rate of biomass growth ( $r_0$ ) estimated from a joint Bayesian hierarchical model of  
627 recovery. Expected recovery time from the most degraded locality (Ahus, PNG; posterior  
628 median: 94 kg/ha) given  $r_0$  (posterior median: 0.054) is 59 years when recovery is defined at  
629  $0.9B_0^9$  (blue dot).  
630

631 **Extended Data Figure 6 | Average reef fish functional group across a biomass gradient.**  
632 Generalized additive model (GAM) fits to the relative proportion of **a.** excavators/scrapers, **b.**  
633 browsers, **c.** grazers, **d.** detritivores, **e.** planktivores, **f.** micro-invertivores, **g.** macro-invertivores,  
634 **h.** pisci-invertivores, and **i.** piscivores in community log-biomass for 832 reef slope sites from  
635 around the world. Grey dots are reef-level observations; blue dots are a 0.1 log-kg interval  
636 moving average; GAM fits are represented by mean (solid black line) and 95% confidence  
637 intervals (dashed line) across the full data range. Mean model fits between initial reserve biomass  
638 and recovered log-biomass (vertical dotted lines) were scaled relative to their values at  $0.1B_0$  to  
639 characterise reef fish functional responses in Fig. 2.

640  
641 **Extended Data Figure 7 | Generalized additive model (GAM) functional returns with**  
642 **uncertainty.** Average relative reef fish functional returns in log-biomass across the range from  
643 collapsed to recovered given the GAM fits in Fig. 2d; lines are GAM fits for log-biomass per  
644 functional group relative to their average biomasses at marine reserve age zero (estimated initial  
645 log-biomass) in Fig. 1; dashed lines are approximate 95% confidence intervals. Data include 832  
646 individual reefs.

647  
648 **Extended Data Figure 8 | Potential long term changes in  $B_0$  under climate change.** Response  
649 surface (contour lines) for potential change in  $B_0$  (kg/ha) given a plausible range of decline in  
650 average primary productivity (from current 4.7 kg C/ha/day) and coral cover (from current 26%  
651 average hard coral cover). Response surface based on model estimated effects of productivity and  
652 hard coral cover on  $B_0$  (Extended Data Fig. 1). Current conditions are in the upper right of the  
653 panel (blue dot); a plausible scenario for 2040 given a 4% loss of primary productivity and a 2%  
654 annual loss of coral cover would lead to a 6% drop in expected  $B_0$ , down to 953 kg/ha (dot-  
655 triangle).

656  
657 **Extended Data Figure 9 | Nuisance parameter residual error plots.** Joint Bayesian  
658 hierarchical recovery model nuisance parameter absolute residuals and residual histograms for **a.**  
659 percentage of hard coral cover; **b.** having been collected on an atoll; and **c.** average productivity  
660 in kg C/ha/day. Dashed red lines indicate non-significant linear trends in absolute residuals  
661 showing no heteroskedasticity was present; blue solid lines show a normal probability  
662 distribution fit to the residuals, demonstrating appropriate normal sub-model fit.

663  
664  
665  
666  
667  
668  
669  
670  
671

672 **Extended Data Table 1 | DIC-based model selection for individual nuisance parameter sub-**  
673 **models.** Joint Bayesian hierarchical recovery model selection for covariates thought to influence  
674 standing biomass. Candidate models include linear, second-order polynomial (2) and third-order  
675 polynomial (3) models for each nuisance parameter fit individually (*i.e.* other nuisance  
676 parameters absent from full model). Models M1-M12 were used to select the best model form for  
677 each parameter given the lowest DIC value (bold) for each.

678  
679 **Extended Data Table 2 | DIC-based model selection for combined nuisance parameter sub-**  
681 **models.** Joint Bayesian hierarchical recovery model selection for covariates thought to influence  
682 standing biomass. Candidate models include varying combinations of linear, second-order  
683 polynomial (2) and third-order polynomial (3) models for each nuisance parameter selected as the  
684 lowest DIC-valued model in Extended Data Table 1. Models M13-M34 were used to select  
685 parameters included in the final model given the lowest DIC value (bold). Atoll 1 indicates atoll  
686 offset was included in the model.



