

Human disruption of coral reef trophic structure

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24 **SUMMARY**

25 **The distribution of biomass among trophic levels provides a theoretical basis for**
26 **understanding energy flow and the hierarchical structure of animal communities. In the**
27 **absence of energy subsidies [1], bottom heavy trophic pyramids are expected to**
28 **predominate, based on energy transfer efficiency [2] and empirical evidence from**
29 **multiple ecosystems [3]. However, the predicted pyramid of biomass distribution among**
30 **trophic levels may be disrupted through trophic replacement by alternative organisms**
31 **in the ecosystem, trophic cascades, and humans preferentially impacting specific trophic**
32 **levels [4-6]. Using empirical data spanning >250 coral reefs, we show how trophic**
33 **pyramid shape varies given human-mediated gradients along two orders of magnitude**
34 **in reef fish biomass. Mean trophic level of the assemblage increased modestly with**
35 **decreasing biomass, contrary to predictions of fishing down the food web [7]. The mean**
36 **trophic level pattern is explained by trophic replacement of herbivorous fish by sea**
37 **urchins at low biomass and the accumulation of slow growing, large bodied,**
38 **herbivorous fish at high biomass. Further, at high biomass, particularly where fishers**
39 **are not selectively removing higher trophic level individuals, a concave trophic**
40 **distribution emerges. The concave trophic distribution implies a more direct link**
41 **between lower and upper trophic levels, which may confer greater energy efficiency.**
42 **This trophic distribution emerges when community biomass exceeds ~650 kg/ha,**
43 **suggesting that fisheries for upper trophic level species will only be supported under**
44 **lightly fished scenarios.**

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48 **KEYWORDS**

49 Trophic pyramids, coral reef ecology, trophic replacement, trophic cascades, fisheries
50 management, energetics, wilderness, coral reef fishes

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54 RESULTS AND DISCUSSION

55 We investigate trophic pyramid structures across a large gradient of coral reef fish biomass.
56 While differences in habitat condition can influence reef fish biomass, previous studies,
57 including some using large portions of the data we present here, have demonstrated that
58 humans are the dominant drivers of biomass [8, 9]. Our data span 253 coral reef sites across
59 nine countries or jurisdictions in the Indian Ocean, from heavily fished reefs in Kenya to
60 unfished reefs in the remote Chagos Archipelago. Across this gradient of two orders of
61 magnitude in reef fish biomass, we: 1) examine the relationship to mean trophic level of the
62 fish assemblages; 2) assess changes in trophic pyramid structure; 3) explore biomass-
63 dependent trophic replacement of fish by herbivorous sea urchins; and 4) characterize the
64 energetic impact of fishing based on biomass storage across trophic positions.

65 We found a weak negative relationship between total log-biomass and mean trophic level of
66 the fish assemblage (slope -0.057, confidence intervals -0.085 to -0.030), such that mean
67 trophic level was highest where fishing pressure was greatest (Figure 1). Our findings
68 contradict the ‘fishing down the food web’ paradigm, which predicts that mean trophic levels
69 of fish assemblages will decline with biomass as fishing pressure increases [7], supporting
70 critiques of this effect by others [*e.g.* 10]. Conversely, our patterns support recent findings by
71 Hatton et al. [3], suggesting trophic structures should become increasingly bottom heavy as
72 biomass increases. Although our relationship was statistically significant, there was
73 substantial variation in mean trophic level along the biomass continuum, suggesting that
74 trophic organization is influenced by many variables.

75 Upper trophic level fish biomass declined with reducing total biomass. However, overall
76 mean trophic level increased toward lower biomass levels due to increasing proportions of
77 mid trophic position individuals, while at higher biomass levels there were greater
78 proportions of lower trophic position individuals [3] (Figure 2). On a log scale, absolute
79 trophic structure appears as an undifferentiated stack at high biomass levels (Figure S1),
80 similar to expectations outlined by Trebilco et al. [2]. However, this obscures a concave
81 shape at high biomass, which is most apparent from the relative trophic structure (Figure 2).
82 Trophic-level biomass ratios of absolute community biomass highlight these concave
83 patterns, with less biomass at intermediate trophic positions (TP 2.5-3.5) than those above
84 (TP 3.5-4) or below (TP 2-2.5) (Table S1). This pattern is indicative of community-wide
85 trophic cascades [11], or related processes leading to biomass accumulation at the top and

86 bottom of the pyramid. This is the first large-scale demonstration of such community level
87 biomass distributions for coral reef fishes, supporting some smaller scale studies of strong
88 multi-level community structuring [12, 13], including examples of concave trophic
89 distributions (Midway atoll Hawaii) [14].

90 Sharks, falling in the upper trophic position (TP 4-4.5), are poached in even the large
91 unfished area in our analyses [15]. Further, although transient or nocturnal families excluded
92 from the analyses accounted for only 7% of the total biomass recorded in the large unfished
93 area, these fish predominantly (70%) fell in the top two trophic positions (TP 3.5-4.5).
94 Therefore, the biomass of upper trophic positions in the pyramid is under-represented, and
95 would be greater in the absence of poaching, or where sampling could consistently capture all
96 families. This may partly explain the differences between our results and those showing
97 inverse biomass pyramids in remote Pacific atolls with no shark poaching [16]. Nevertheless,
98 the substantial accumulation of biomass at the bottom of the pyramid on lightly fished Indian
99 Ocean reefs would make an inverted structure unlikely.

100 Under optimal foraging, reef predators are expected to encounter a greater density and variety
101 of fish prey at high biomass levels [17, 18]. This should provide a competitive advantage to
102 piscivores (e.g. many species with TPs >3.5) relative to generalist carnivores as biomass
103 increases, leading to a peak in top predators at the highest biomass levels [19]. In turn, mid
104 trophic level generalists often have smaller body size that renders them vulnerable to
105 predation, and their relative biomass is expected to decline as total and upper trophic level
106 biomass increases [13, 20]. This relative increase in higher trophic positions at the expense of
107 middle trophic positions is expected to contribute to the concave pattern we observe at high
108 biomass. Accumulation of upper trophic level biomass is likely also subsidised by feeding on
109 non-reef energy pathways such as pulses of oceanic productivity in the form of small pelagic
110 fish [21, 22]. Further, species with more efficient consumption rates and slow life histories
111 characterize mature communities that promote the accumulation of biomass [23, 24]. Unlike
112 temperate marine food webs [25], many of the lower trophic level fish in coral reefs are large
113 bodied species of parrotfish, surgeonfish, and rabbitfish that are not commonly consumed by
114 mid-tier species as adults. The large base of the trophic pyramids is therefore expected to be
115 maintained, even at high biomass, by consumption of highly productive algae and detritus
116 among large bodied herbivores and detritivores [26].

117 The energetic consequences of concave trophic pyramids imply that top-level piscivores,
118 which can represent fish of varying body size, draw energy from multiple levels of the
119 pyramid, including primary consumers. This interpretation is supported by dietary studies
120 that show top trophic position fish on coral reefs typically have diverse fish prey drawn from
121 all trophic levels, including the bottom of the pyramid [27]. Indeed, transfer of energy to top
122 predators via multiple pathways, or multichannel feeding [11, 28, 29], is supported by
123 energy-balanced ecosystem models of coral reefs [30]. This means reef pyramids are not
124 simply linear food chains, but have a high potential for energy to pass directly from lower to
125 upper trophic levels. As such, primary production can be channelled to upper trophic levels,
126 minimising loss of energy by metabolism at intermediate tiers.

127 A key consequence of large body size among many coral reef herbivores and detritivores is
128 that they are frequent targets for fisheries, leading to declines in biomass under heavy fishing
129 [31], as seen at low total biomass in our data. Here, an alternative energy pathway emerges,
130 with the trophic replacement of herbivorous fish (TP 2-2.5) by herbivorous sea urchins within
131 the reef community ($p < 0.001$; Figure 3). This leads to a higher proportion of smaller-bodied
132 mid-level fishes (TP 3-3.5; $p < 0.001$) that are often invertebrate feeders (e.g. species of wrasse
133 and triggerfish) able to feed directly or scavenge on juvenile sea urchins [32]. These fish
134 species are less targeted in conventional or artisanal fisheries and may be under weaker
135 predation pressure when total biomass is low [6]. Sea urchins are thus providing both a
136 trophic replacement in terms of energetics, and a functional replacement in terms of some
137 herbivore functions.

138 Given the pervasiveness of fishing, differentiating natural underlying variability versus
139 human impacts due to fishing is challenging [33]. Therefore, we separated unfished versus
140 fished pyramid structures by directly comparing remote unfished reefs to fished seascapes
141 across a comparable biomass gradient (6.5-8.5 log total biomass). In unfished locations
142 greater biomass accumulated in the upper trophic levels, while mid trophic levels dominated
143 in fished locations (Figure 4). Therefore, while the concave pyramid structure still emerges in
144 fished seascapes with greater biomass in upper trophic levels compared to 1.0 trophic level
145 below (Figure S2), fishing dampens the accumulation of biomass in upper trophic levels.

146 A key assumption of trophic pyramid analyses is that community members share a common
147 and explicitly defined resource base [2]. Here, we examined fish communities belonging to
148 individual coral reefs - defined as continuous associations of hard corals that are separated

149 from neighbouring reefs by a channel [34] - with transects assumed to be representative
150 samples from within each reef. Species known to move among reefs, such as large non-reef
151 associated sharks and other pelagic fish, were excluded because they frequently source
152 energy from beyond reefs. This definition aims to bound energy input for each trophic
153 pyramid to a discrete unit, although energy subsidies from non-reef environments, including
154 from pelagic pathways, are likely to occur [21, 22]. Our sampling design also assumed that
155 the within-reef home ranges of individual community members are sufficiently random that
156 our sampling methods would not favour particular trophic groups.

157 Our findings illustrate the effects of fishing on energy flux and the high feeding flexibility
158 within these highly diverse coral reef food webs. At the lower end of the biomass gradient,
159 where heavy fishing pressure has reduced biomass of all trophic levels, sea urchins provide a
160 trophic replacement and a step from primary production to mid trophic position organisms.
161 At the other end of the biomass gradient, trophic structure is concave and upper trophic level
162 fish are likely to increasingly feed on fish from the bottom of the pyramid. This pathway
163 infers a more direct link from primary production to upper trophic levels and reduced
164 metabolic losses at intermediate trophic levels. It is also possible, however, that fast turnover
165 species at mid trophic positions are supporting upper trophic levels; high predation pressure
166 can lead to composition shifts toward species with faster life history traits [23, 35].

167 Coral reef fisheries management utilizing an energetics perspective will benefit from our
168 findings. Upper trophic position species, such as groupers, are economically valuable [36],
169 but are easily overfished, leaving fisheries dependent on lower value species [37]. Once total
170 log biomass exceeds 6.5 (665 kg/ha) along our gradient, coral reef trophic pyramids become
171 concave and support biomass in upper trophic positions (Figure 2). Therefore, ensuring total
172 biomass remains above this level should help maintain piscivore fisheries on coral reefs. For
173 example, the valuable coral trout fisheries on the Great Barrier Reef, Australia, exist in an
174 otherwise lightly fished system with high overall biomass [19, 38]. Multispecies maximum
175 sustainable yield (B_{MMSY}) estimates for the Indian Ocean have been proposed at 300-600
176 kg/ha of fishable biomass, which suggests that upper trophic position fish will be diminished
177 by the time yields are maximized [20, 39]. While fishing at these B_{MMSY} targets will likely
178 maintain several key ecosystem processes and produce a diverse capture [19, 39], fisheries
179 aimed at upper trophic positions will need to set a higher target, >665 kg/ha. Our results
180 inform ecosystem-based decision making for reef fisheries based on energy transfer through

181 multiple trophic levels, filling an important gap in our understanding of fisheries targets on
182 coral reefs.

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184 **EXPERIMENTAL PROCEDURES**

185 **Field surveys and trophic categorisation**

186 Coral reef fish biomass estimates were based on underwater visual surveys from 253
187 individual reefs across 9 countries or jurisdictions in the Indian Ocean, spanning
188 approximately 35° latitude and 52° longitude. Reefs were surveyed in the Chagos
189 archipelago, the Comoros, Kenya, Madagascar, Mayotte, Mozambique, the Maldives,
190 Seychelles, and Tanzania. Data were collected from 2005 to 2013, resulting in a database of
191 342 reef/time combinations. Of these data points, 209 are from reefs that allow fishing, 109
192 are from unfished reefs in marine reserves surrounded by fished seascapes, and 24 are on
193 unfished reefs in large remote unfished wilderness [20, 40]. Sea urchin biomass data was
194 collected from 97 of these sites. Details of survey methods and fish families included in the
195 analyses can be found in the Supplemental Experimental Procedures.

196 **Data handling and analysis**

197 Mean trophic level was calculated as a biomass-weighted community average, based on the
198 composition and biomass distribution of the fish community at each reef. Families were
199 assigned to trophic level categories based on the average trophic level of the species found in
200 each family in the Indian Ocean region. The analyses needed to be performed at the family
201 level as this is the taxonomic resolution at which the data were collected at many sites.
202 However, it should be borne in mind that some families have substantial variation in trophic
203 level among their constituent species, for example the Labridae. Therefore, we examined the
204 relationship between mean trophic level calculated at the family level versus the species level
205 for the 89 samples where we had species level information (covering three countries). This
206 showed very comparable information, with a tight correlation, closely fit to a 1:1 line, with an
207 R^2 of 0.96 (Figure S3A).

208 To assess the change in mean trophic level ($MTL_{c,s,t}$) of coral reef fish communities across
209 the biomass gradient (Figure 1), we developed a Bayesian hierarchical linear model that
210 accounted for both sites nested within countries, and repeat observations through time:

211 $MTL_{c,s,t} \sim N(\beta_{c,s} + \beta_1 \log Biomass, \sigma_t)$

212 $\beta_{c,s} \sim N(\beta_c, \sigma_s)$

213 $\beta_c, \beta_1 \sim N(0, 100)$

214 $\sigma_t, \sigma_s \sim U(0, 100)$

215 Where c is country, s is site, and t is time. Assumptions of the model were assessed by
216 examining the residuals for goodness of fit and plotting the estimated model against the data.
217 The country level random effect enables the model to average over variation associated with
218 differing disturbance histories or coral cover. Because method (and thus observer) is collinear
219 with country (Figure S4), to test for any influence of method on our results, we re-ran the
220 model with method used in place of country. This provided a worse fit (>50 units based on
221 DIC values), indicating that there is no evidence for method having a strong influence on our
222 findings.

223 To visualise the changes in the relative (Figure 2) and log (Figure S1) biomass of trophic
224 positions across the biomass gradient, we fit first order polynomial trend lines to the data, and
225 constructed trophic pyramid shapes (based on 0.5 trophic position categories) for 1.0 log total
226 biomass bins across the gradient. To examine changes in pyramid shape across the biomass
227 gradient, we adapted the predator:prey mass ratio, to calculate a trophic-level biomass ratio as
228 the community biomass at trophic position n, divided by the biomass at trophic position n-1
229 [2]. We examined the relationship between family versus species level categorisation of
230 trophic positions for the 89 samples where species level information was available.
231 Correlations had R² values ranging from 0.45-0.98, with the best fits to the 1:1 line at lower
232 trophic positions (Figure S3B-F), indicating there would be some subtle differences among
233 upper trophic positions if run at a species level.

234 Relationships between the biomass of specific trophic positions of the fish community and
235 sea urchin biomass were assessed using generalised linear models with a quasipoisson
236 distribution due to over dispersion. All fits, except TP 2.5-3 were significant, with the
237 strongest relationships and steepest slopes for TP 3-3.5 and 2-2.5 (Figure 3).

238 We plotted the difference in each trophic position in the pyramid (Figure 4) and pyramid
239 structure (Figure S2) between fished (n=50) and unfished (n=17) reefs for the log biomass
240 range 6.5-8.5, representing the range that the concave trophic distribution was observed.
241 Unfished reefs were from the large unfished wilderness areas of the Chagos archipelago,

242 where local human impacts are minimal [40]. We compared the differences between relative
243 biomass at each trophic position using a Bayesian hierarchical multinomial (softmax) model.

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245 **SUPPLEMENTAL INFORMATION**

246 Supplemental Information includes supplemental experimental procedures, four figures, and
247 one table, and can be found with this article online.

248

249 **AUTHOR CONTRIBUTIONS**

250 N.A.J.G, T.R.M, M.A.M, J.E.C., and S.K.W. conceived the idea for the study. N.A.J.G. and
251 T.R.M collected the data. C.H. and M.A.M. performed the analyses. N.A.J.G., M.A.M.,
252 S.K.W., and T.H.H. wrote the first draft of the manuscript, and all authors wrote and / or
253 substantially edited portions of the paper.

254

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263 **REFERENCES**

- 264 1. Mourier, J., Maynard, J., Parravicini, V., Ballesta, L., Clua, E., Domeier, M.L., and
265 Planes, S. (2016). Extreme inverted trophic pyramid of reef sharks supported by
266 spawning groupers. *Curr. Biol.* 26, 2011–2016.
- 267 2. Trebilco, R., Baum, J.K., Salomon, A.K., and Dulvy, N.K. (2013). Ecosystem
268 ecology: size-based constraints on the pyramids of life. *Trends Ecol. Evol.* 28, 423–
269 431.
- 270 3. Hatton, I.A., McCann, K.S., Fryxell, J.M., Davies, T.J., Smerlak, M., Sinclair, A.R.E.,
271 and Loreau, M. (2015). The predator-prey power law: Biomass scaling across
272 terrestrial and aquatic biomes. *Science* 349, aac6284.
- 273 4. Pace, M.L., Cole, J.J., Carpenter, S.R., and Kitchell, J.F. (1999). Trophic cascades

- 274 revealed in diverse ecosystems. *Trends Ecol. Evol.* *14*, 483–488.
- 275 5. Darimont, C.T., Fox, C.H., Bryan, H.M., and Reimchen, T.E. (2015). Human impacts.
- 276 The unique ecology of human predators. *Science* *349*, 858–860.
- 277 6. McClanahan, T.R., and Muthiga, N.A. (2016). Geographic extent and variation of a
- 278 coral reef trophic cascade. *Ecology* *97*, 1862–1872.
- 279 7. Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. (1998). Fishing
- 280 down marine food webs. *Science* *279*, 860–863.
- 281 8. Cinner, J.E. McClanahan, T.R., Daw, T.M., Graham, N.A.J., Maina, J., Wilson, S.K.,
- 282 and Hughes, T.P. (2015). Linking social and ecological systems to sustain coral reef
- 283 fisheries. *Curr. Biol.* *19*, 206–212.
- 284 9. Cinner, J.E., Huchery, C., MacNeil, M.A., Graham, N.A.J., McClanahan, T.R.,
- 285 Maina, J., Maire, E., Kittinger, J.N., Hicks, C.C., Mora, C., et al. (2016). Bright spots
- 286 among the world’s coral reefs. *Nature* *535*, 416–419.
- 287 10. Branch, T.A., Watson, R., Fulton, E.A., Jennings, S., McGilliard, C.R., Pablico, G.T.,
- 288 Ricard, D., and Tracey, S.R. (2010). The trophic fingerprint of marine fisheries.
- 289 *Nature* *468*, 431–435.
- 290 11. Polis, G.A. (1999). Why are parts of the world green? Multiple factors control
- 291 productivity and the distribution of biomass. *Oikos* *86*, 3–15.
- 292 12. Mumby, P., Steneck, R., Edwards, A., Ferrari, R., Coleman, R., Harborne, A., and
- 293 Gibson, J. (2012). Fishing down a Caribbean food web relaxes trophic cascades. *Mar.*
- 294 *Ecol. Prog. Ser.* *445*, 13–24.
- 295 13. Ruppert, J.L.W., Travers, M.J., Smith, L.L., Fortin, M.-J., and Meekan, M.G. (2013).
- 296 Caught in the middle: combined impacts of shark removal and coral loss on the fish
- 297 communities of coral reefs. *PLoS One* *8*, e74648.
- 298 14. Sandin, S.A., and Zgliczynski, B.J. (2015) Inverted trophic pyramids. In *Ecology of*
- 299 *Fishes on Coral Reefs*, C. Mora, ed. (Cambridge University Press), pp. 247-251.
- 300 15. Graham, N.A.J., Spalding, M.D., and Sheppard, C.R.C. (2010). Reef shark declines in
- 301 remote atolls highlight the need for multi-faceted conservation action. *Aquat.*
- 302 *Conserv. Mar. Freshw. Ecosyst.* *20*, 543–548.
- 303 16. Sandin, S.A., Smith, J.E., DeMartini, E.E., Dinsdale, E.A., Donner, S.D., Friedlander,
- 304 A.M., Konotchick, T., Malay, M., Maragos, J.E., Obura, D., et al. (2008). Baselines
- 305 and degradation of coral reefs in the northern Line Islands. *PLOS ONE* *3*, e1548.
- 306 17. MacArthur, R.H., and Pianka, E.R. (1966). On optimal use of a patchy environment.
- 307 *Am. Nat.* *100*, 603–609.
- 308 18. Hughes, R. N. (1980). Optimal foraging theory in the marine context. *Oceanogr. Mar.*
- 309 *Biol. Ann. Rev.* *18*, 423-481.
- 310 19. MacNeil, M.A., Graham, N.A.J., Cinner, J.E., Wilson, S.K., Williams, I.D., Maina, J.,
- 311 Newman, S., Friedlander, A.M., Jupiter, S., Polunin, N.V.C., et al. (2015). Recovery
- 312 potential of the world’s coral reef fishes. *Nature* *520*, 341–344.
- 313 20. McClanahan, T.R., Graham, N.A.J., MacNeil, M.A., and Cinner, J.E. (2015).
- 314 Biomass-based targets and the management of multispecies coral reef fisheries.
- 315 *Conserv. Biol.* *29*, 409–417.
- 316 21. McCauley, D.J., Young, H.S., Dunbar, R.B., Estes, J.A., Semmens, B.X., and
- 317 Micheli, F. (2012). Assessing the effects of large mobile predators on ecosystem
- 318 connectivity. *Ecol. Appl.* *22*, 1711–1717.
- 319 22. Trebilco, R., Dulvy, N.K., Anderson, S.C., and Salomon, A.K. (2016). The paradox of
- 320 inverted biomass pyramids in kelp forest fish communities. *Proc. Roy. Soc. B.* *283*,
- 321 *20160816*.
- 322 23. McClanahan, T.R. (1992). Resource utilization, competition, and predation: a model
- 323 and example from coral reef grazers. *Ecol. Model.* *61*, 195-215.

- 324 24. DeMartini, E.E., Friedlander, A.M., Sandin, S.A., and Sala, E. (2008). Differences in
325 fish-assemblage structure between fished and unfished atolls in the northern Line
326 Islands, central Pacific. *Mar. Ecol. Prog. Ser.* 365, 199-215.
- 327 25. Jennings, S., and Mackinson, S. (2003). Abundance-body mass relationships in size-
328 structured food webs. *Ecol. Lett.* 6, 971–974.
- 329 26. Hatcher, B.G. (1988). Coral reef primary productivity: A beggar’s banquet. *Trends*
330 *Ecol. Evol.* 3, 106–111.
- 331 27. Farmer, B.M., and Wilson, S.K. (2011). Diet of finfish targeted by fishers in North
332 West Australia and the implications for trophic cascades. *Environ. Biol. Fishes* 91,
333 71–85.
- 334 28. Polis, G.A., and Strong, D.R. (1996). Food web complexity and community
335 dynamics. *Am. Nat.* 147, 813–846.
- 336 29. Vadeboncoeur, Y., McCann, K.S., Zanden, M.J. Vander, and Rasmussen, J.B. (2005).
337 Effects of multi-chain omnivory on the strength of trophic control in lakes.
338 *Ecosystems* 8, 682–693.
- 339 30. Ruiz Sebastian, C., and McClanahan., T. R. (2013). Description and validation of
340 production processes in the coral reef ecosystem model CAFFEE (Coral-Algae-Fish-
341 Fisheries Ecosystem Energetics) with a fisheries closure and climatic disturbance.
342 *Ecol. Model.* 263, 326-348.
- 343 31. Edwards, C.B., Friedlander, A.M., Green, A.G., Hardt, M.J., Sala, E., Sweatman,
344 H.P., Williams, I.D., Zgliczynski, B., Sandin, S.A., and Smith, J.E. (2014). Global
345 assessment of the status of coral reef herbivorous fishes: evidence for fishing effects.
346 *Proc. R. Soc. B.* 281, 20131835.
- 347 32. McClanahan, T.R. (1998). Predation and the distribution and abundance of tropical
348 sea urchin populations. *J. Exp. Mar. Bio. Ecol.* 221, 231–255.
- 349 33. Williams, G.J., Gove, J.M., Eynaud, Y., Zgliczynski, B.J., and Sandin, S.A. (2015).
350 Local human impacts decouple natural biophysical relationships on Pacific coral
351 reefs. *Ecography* 38, 751–761.
- 352 34. MacNeil, M.A., and Connolly, S.R., (2015). Multi-scale patterns and processes in reef
353 fish abundance. In *Ecology of Fishes on Coral Reefs*, C. Mora, ed. (Cambridge
354 University Press), pp.116-124.
- 355 35. Jennings, S., Greenstreet, S.P.R., and Reynolds, J.D. (1999). Structural change in an
356 exploited fish community: a consequence of differential fishing effects on species
357 with contrasting life histories. *J. Anim. Ecol.* 68, 617-627.
- 358 36. Thyresson, M., Crona, B., Nyström, M., de la Torre-Castro, M., and Jiddawi, N.
359 (2013). Tracing value chains to understand effects of trade on coral reef fish in
360 Zanzibar, Tanzania. *Mar. Policy* 38, 246–256.
- 361 37. Hicks, C.C., and McClanahan, T.R. (2012). Assessing gear modifications needed to
362 optimize yields in a heavily exploited, multi-species, seagrass and coral reef fishery.
363 *PLoS One* 7, e36022.
- 364 38. Hopf, J.K., Jones, G.P., Williamson, D.H., and Connolly, S.R. (2016). Synergistic
365 effects of marine reserves and harvest controls on the abundance and catch dynamics
366 of a coral reef fishery. *Curr. Biol.* 26, 1543-1548.
- 367 39. McClanahan, T.R., Graham, N.A.J., Macneil, M.A., Muthiga, N.A., Cinner, J.E.,
368 Bruggemann, J.H., and Wilson, S.K. (2011). Critical thresholds and tangible targets
369 for ecosystem-based management of coral reef fisheries. *Proc. Natl. Acad. Sci. U. S.*
370 *A.* 108, 17230–17233.
- 371 40. Graham, N.A.J., and McClanahan, T.R. (2013). The last call for marine wilderness?
372 *Bioscience* 63, 397–402.

373 **Figure 1. Change in mean trophic level of coral reef fish assemblages across a large biomass**
374 **gradient**

375 The credible (dark grey) and predictive (light grey) intervals are shown around the linear fit. See also
376 Figure S3 which shows the influence of calculating mean trophic level based on family versus species
377 level information, and Figure S4 which shows how biomass by survey method (and observer) are
378 related to countries.

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381 **Figure 2. Change in relative trophic structure of coral reef fish communities across a biomass**
382 **gradient**

383 The proportion of each trophic position category is modelled. Mean trophic pyramid shape is
384 depicted based on the relative difference in biomass among trophic positions for 1.0 log total
385 biomass units along the biomass gradient. See also Figure S1 which shows the absolute (log) trophic
386 structure, Table S1 which contains the trophic-level biomass ratios, and Figure S3 which compares
387 species versus family level calculation of each trophic position.

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390 **Figure 3. Relationships between the biomass of different trophic positions of the fish community**
391 **and biomass of sea urchins**

392 Sea urchin biomass increases at low fish biomass, and particularly with low biomass of trophic
393 positions 2-2.5 and 3-3.5. Data represent 97 sites where sea urchins were surveyed. Trophic pyramid
394 graphics indicate trophic position represented in each panel.

395 (A) TP 2-2.5, slope = -0.44.

396 (B) TP 2.5-3, slope = -0.23.

397 (C) TP 3-3.5, slope = -0.61.

398 (D) TP 3.5-4, slope = -0.34.

399 (E) TP 4-4.5, slope = -0.39.

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401

402 **Figure 4. Disparity in trophic pyramid structure between fished and unfished seascapes**

403 Difference in relative biomass distribution (6.5-8.5 log biomass) between fished and unfished
404 locations for each trophic position. Bayesian multinomial model 95% uncertainty intervals did not
405 overlap zero for all trophic positions relative to a 2-2.5 TP baseline, suggesting substantial
406 differences in trophic structure between fished and unfished reefs. See also Figure S2 which displays
407 the biomass distribution among trophic positions separately for fished and unfished locations.

408

Figure 1







