



## Local human impacts disrupt depth-dependent zonation of tropical reef fish communities

Richardson, Laura; Heenan, Adel; Delargy, Adam; Neubauer, Philipp; Lecky, Joey; Gove, Jamison M. ; Green, Mattias; Kindinger, Tye; Ingeman, Kurt; Williams, Gareth J.

### Nature Ecology and Evolution

DOI:

[10.1038/s41559-023-02201-x](https://doi.org/10.1038/s41559-023-02201-x)

E-pub ahead of print: 25/09/2023

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*

Richardson, L., Heenan, A., Delargy, A., Neubauer, P., Lecky, J., Gove, J. M., Green, M., Kindinger, T., Ingeman, K., & Williams, G. J. (2023). Local human impacts disrupt depth-dependent zonation of tropical reef fish communities. *Nature Ecology and Evolution*. <https://doi.org/10.1038/s41559-023-02201-x>

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1 **TITLE**

2 Local human impacts disrupt depth-dependent zonation of tropical reef fish communities

3 **AUTHOR LIST**

4 Laura E. Richardson<sup>1</sup>, Adel Heenan<sup>1</sup>, Adam J. Delargy<sup>1,2</sup>, Philip Neubauer<sup>3</sup>, Joey Lecky<sup>4,5</sup>, Jamison M.  
5 Gove<sup>4</sup>, J. A. Mattias Green<sup>1</sup>, Tye L. Kindinger<sup>4</sup>, Kurt E. Ingeman<sup>4,6</sup>, Gareth J. Williams<sup>1</sup>

6 **AFFILIATIONS**

7 <sup>1</sup> *School of Ocean Sciences, Bangor University, Menai Bridge, Wales, UK*

8 <sup>2</sup> *School for Marine Science & Technology, University of Massachusetts Dartmouth, MA, USA*

9 <sup>3</sup> *Dragonfly Data Science, Wellington, New Zealand*

10 <sup>4</sup> *Pacific Islands Fisheries Science Center, National Oceanic Atmospheric Administration, Honolulu, HI,*  
11 *USA*

12 <sup>5</sup> *IBSS Corporation, Silver Spring, MD, USA*

13 <sup>6</sup> *Department of Environmental Studies, Linfield University, McMinnville, OR, USA*

14

15 *Corresponding author*

16 Laura E. Richardson ([l.richardson@bangor.ac.uk](mailto:l.richardson@bangor.ac.uk)): <https://orcid.org/0000-0002-1284-4011>.

17

18 **AUTHOR INFORMATION**

19 *Affiliations*

20 **School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, UK**

21 Laura E. Richardson, Adam J. Delargy, J.A. Mattias Green, Adel Heenan, Gareth J. Williams

22 **Ecosystem Sciences Division, Pacific Islands Fisheries Science Center, National Oceanic and**  
23 **Atmospheric Administration, Honolulu, HI, USA**

24 Tye L. Kindinger, Jamison M. Gove, Kurt E. Ingeman, Joey Lecky

25 **Dragonfly Data Science, Wellington, NZ**

26 Phillip Neubauer

27 **School for Marine Science & Technology, University of Massachusetts Dartmouth, MA, USA**

28 Adam J. Delargy

29 **IBSS Corporation, Silver Spring, MD, USA**

30 Joey Lecky

31 **Department of Environmental Studies, Linfield University, McMinnville, OR, USA**

32 Kurt E. Ingeman

33 **ABSTRACT**

34 The influence of depth and associated gradients in light, nutrients, and plankton on the ecological  
35 organisation of tropical reef communities was first described over six decades ago but remains  
36 untested across broad geographies. During this time humans have become the dominant driver of  
37 planetary change, requiring we re-visit historic ecological paradigms to ensure they capture the  
38 dynamics of contemporary ecological systems. Analysing >5,500 in-water reef fish surveys between  
39 0–30 m depth on reef slopes at 35 islands across the Pacific, we assess whether a depth gradient  
40 consistently predicts variation in reef fish biomass. We reveal predictable ecological organisation at  
41 unpopulated locations, with increased biomass of planktivores and piscivores, and decreased  
42 primary consumer biomass with increasing depth. Bathymetric steepness also had a striking  
43 influence on biomass patterns, primarily for planktivores, emphasising potential links between local  
44 hydrodynamics and the upslope propagation of pelagic subsidies to the shallows. However, signals  
45 of resource-driven change in fish biomass with depth were altered or lost at populated islands, likely  
46 due to depleted fish biomass baselines. While principles of depth zonation broadly held, our findings  
47 expose limitations of the paradigm for predicting ecological dynamics where human impacts  
48 confound connections between ecological communities and their surrounding environment.

49

50 **KEYWORDS**

51 *Ecological zonation; paradigm; spatial scales; biophysical gradients; depth; bathymetric steepness;*  
52 *fish biomass; macroecology; coral reefs; human impacts*

53

54 **MAIN TEXT**

55 Ecological paradigms inform the understanding and management of natural systems but are limited  
56 by two fundamental issues. First, biophysical processes governing ecological organisation often  
57 occur at regional and continental scales<sup>1–3</sup>, inherently introducing scale-dependent patterns and  
58 heterogeneity in observed local community structure<sup>4–6</sup>. To understand ecological generality, a large  
59 enough lens across a land- or seascape is required to encompass these processes<sup>7</sup>. However, many  
60 influential paradigms were developed from single-point studies in the mid-20<sup>th</sup> century (e.g. <sup>6–8</sup>).  
61 Until recently our ability to test generalisable predictions on ecological organisation in hierarchically  
62 structured ecosystems has been limited by a lack of spatially comprehensive data and accessible  
63 statistical tools<sup>7,11</sup>. Second, escalating anthropogenic impacts confound natural drivers of ecological  
64 organisation<sup>12–14</sup> such that humans are now considered the dominant force of planetary change<sup>15</sup>.  
65 Where theories are founded on a premise that ecological organisation occurs in isolation of  
66 anthropogenic forcing<sup>16,17</sup>, the predictive capacity of historical paradigms can breakdown (e.g. island  
67 biogeography theory<sup>18</sup>), requiring thorough reassessment of their applicability in this era of rapid  
68 change<sup>16,19</sup>.

69 Ecological zonation—the distribution of organisms across space—represents one of the oldest  
70 ecological concepts<sup>8,9,20</sup>. Here we revisit this basic principle in the context of resource driven depth  
71 zonation of tropical coral reef communities—the distribution of reef fish biomass among distinct  
72 trophic groups. Depth was recognised as a fundamental structuring force over six decades ago<sup>10,21–23</sup>,  
73 and recently shown to be an important predictor of fish diversity<sup>24</sup>. Ocean-facing reefs are formed  
74 along a bathymetric depth gradient with covarying gradients in availability of sunlight, water  
75 temperature, surface wave energy, and nutrients<sup>21,25–27</sup>. With increasing depth, there are predictable  
76 changes in energetic resource supply. Light for primary producers diminishes<sup>25</sup> but particulate foods  
77 and nutrients derived from deeper water that support higher trophic levels such as planktivorous  
78 predators, secondary consumers, and piscivores<sup>28–30</sup>, increase with depth with increased proximity  
79 to sources of upwelling<sup>26,31,32</sup>. The degree to which upwelling can boost shallow-water (<30 m  
80 depth<sup>33</sup>) primary production is, in turn, determined by the steepness of the reef slope—either  
81 facilitating or impeding the upslope propagation of deeper nutrient-rich waters to the  
82 shallows<sup>26,31,32</sup>. Where bathymetry mediates local hydrodynamics around islands, upwelling  
83 processes can concentrate in specific areas<sup>34,35</sup>, creating intra-island variation in pelagic resource  
84 supply<sup>36</sup>. At larger spatial scales, cross-regional gradients in primary production<sup>3</sup> likely underscore  
85 background levels of local depth-dependent resource supply. However, despite these important  
86 structuring forces and a general acceptance of an effect of depth, we have maintained a limited  
87 understanding of resource driven depth zonation on shallow coral reefs. Early observations were  
88 born of single-location point studies and to date the applicability of the theory remains untested  
89 across broad geographies, limiting our understanding of how this ubiquitous physical characteristic  
90 of tropical reefs influences natural ecological biomass baselines<sup>37</sup>. Modern-day island reefs span vast  
91 ocean expanses and are among some of the most biodiverse, socio-economically important, but also  
92 human-impacted ecosystems on our planet<sup>19,38</sup>. Traversing numerous biophysical gradients that  
93 mediate ecological organisation across scales<sup>6</sup>, they provide a unique focal system to explicitly test  
94 early ecological theories across scales, and assess whether classic paradigm-based science and  
95 management of contemporary coral reefs should be adapted<sup>16,19,39</sup>. Reefs are exposed to ocean  
96 warming and acidification, and a suite of local human impacts that deplete biological communities  
97 and degrade habitats<sup>16,19</sup>. Some of these human activities are also stratified by depth. Fishing, for  
98 example, tends to concentrate in shallower depths and disproportionately targets distinct trophic  
99 groups of reef fishes such as large-bodied piscivores, herbivores, and planktivores<sup>40–42</sup>. With human

100 impacts on coral reefs globally widespread<sup>38</sup>, it is unknown how anthropogenic forcing interacts with  
101 natural energetic resource-supply across depth, and therefore whether a classic depth zonation  
102 model is effective for predicting the ecological organisation of modern reefs.

103 Establishing meaningful baselines from which to effectively measure change requires spatially  
104 comprehensive replication at the un-impacted end of the intact-to-degraded spectrum<sup>37</sup>. Using a  
105 standardised Pacific-wide set of reef fish surveys<sup>43</sup>, composite data on bathymetric steepness, and  
106 hierarchical statistical models, we test whether depth zonation patterns in fish biomass are  
107 generalisable on tropical coral reefs across broad geographies, and compare patterns in locations  
108 with and without local human populations. To explicitly assess generality, we isolate the study focus  
109 to test a framework of *a-priori* defined hypotheses of the effects of depth, bathymetric steepness,  
110 and human population status on the biomass of reef fishes across a broad spatial extent  
111 characterised by known environmental and anthropogenic variation<sup>3,44</sup>. In doing so, we intentionally  
112 exclude other known influential biophysical and anthropogenic covariates on reef fish biomass (e.g.  
113 <sup>44,45</sup>) to test the predictive capacity of depth at an ocean-basin scale on the biomass of fishes  
114 grouped by their major dietary sources<sup>46</sup> – primary consumers, planktivores, secondary consumers,  
115 and piscivores. We link data from 5,525 visual surveys at 35 islands and atolls (hereafter ‘islands’)  
116 across five distinct ecoregions<sup>47</sup> spanning approximately 4,600 km latitude and 6,800 km longitude in  
117 the Pacific (Supplementary Table 1) with prior information on unfished biomass baseline estimates  
118 to integrate existing global-scale research<sup>48</sup>. We do this to (1) quantify gradients in fish biomass  
119 across shallow reef depths (1–30 m) and steepness; (2) compare depth zonation patterns at  
120 unpopulated versus human populated locations; and (3) estimate the scale-dependency of observed  
121 patterns by quantifying variability in fish biomass across reefs, islands, and ecoregions.

## 122 RESULTS

123 Hierarchical Bayesian regression estimates showed that at unpopulated islands there was evident  
124 depth zonation in the biomass of all trophic groups of reef fish across or within the 0–30 m depth  
125 range (Fig. 1 and 2; Table 1; Extended Data Fig. 1; Supplementary Tables 4 and 5). However, the  
126 effect of depth on fish varied by trophic group (Fig. 2), evidenced by differences in estimated effect  
127 sizes (Fig. 1; Supplementary Table 4) and probability from model posterior draws (Table 1;  
128 Supplementary Table 5). The biomass of planktivores and piscivores increased across the 0–30 m  
129 depth gradient with high probability ( $P(\beta_{depth}>0) = 0.98$ , both), while primary consumer biomass  
130 decreased with increasing depth from 0–30 m ( $P(\beta_{depth}>0) = 0.93$ ; Fig. 2; Table 1; Supplementary  
131 Table 4). The biomass of secondary consumers increased from 0–10 m depth, plateaued from 10–20  
132 m, and then decreased from 20–30 m (Table 1; Fig. 2). Combining all trophic groups, total fish  
133 biomass increased from 0–20 m depth ( $P(\beta_{depth}>0) = 0.75$ ; Supplementary Table 5), and plateaued  
134 from 20–30 m (Table 1). Overall, human population status had a negative effect on the biomass of all  
135 trophic groups (all:  $P(\beta_{population\ status}<0) = 1.00$ ; Fig. 1; Supplementary Table 5), with posterior  
136 estimates of fish biomass at populated islands consistently lower than at unpopulated islands across  
137 0–30 m depth (Fig. 2). The greatest negative effect of human population status was on the biomass  
138 of piscivore reef fish (Fig. 1 and 2; Supplementary Table 4).

139 After establishing the direction of change in fish biomass per trophic group over an increasing depth  
140 range (Fig. 2; Table 1; Supplementary Table 4), we next sought to determine the magnitude of  
141 change in fish biomass across the study depth range, across nominally shallow (0–10 m), mid-depth  
142 (10–20 m), and deep (20–30 m) sites. We examined the density distributions from the model  
143 posteriors of predicted biomass changes across each depth bin and for each trophic group (Fig. 3A),  
144 and compared the difference in depth zonation measured as absolute change in biomass at

145 populated versus unpopulated islands (Fig. 3B). At populated islands, the magnitude of change in  
146 fish biomass across depth was reduced (total biomass, planktivores, piscivores, and secondary  
147 consumers) or not observed (primary consumers) relative to patterns observed at unpopulated  
148 islands (Fig. 2, Fig. 3A and B; Supplementary Table 7). Total biomass increase was predominantly  
149 lower at populated locations across 0–20 m, piscivore and planktivore biomass increases were lower  
150 across 0–30 m, and secondary consumer biomass increase was reduced within the shallow 0–10 m  
151 range (Fig. 3A and B; Supplementary Table 7). We observed little change in primary consumer  
152 biomass across depth at populated islands (Fig. 3A and B; Supplementary Table 7). Examining  
153 zonation as a function of proportionate change in biomass across depth, there was greater observed  
154 depth zonation at populated islands in the biomass of secondary consumers and piscivores than at  
155 unpopulated islands (Fig. 3C; Extended Data Fig. 2; Supplementary Table 8). These inverse trends in  
156 zonation, indicating greater proportionate change with depth at populated islands, were likely  
157 driven by lower biomass baselines and higher incidences of zero-count observations across all fish  
158 groups, but most notably for piscivores, at populated islands and in shallower depths than at  
159 unpopulated islands (Supplementary Table 9).

160 Incorporating site-level derived estimates of mean bathymetric steepness ( $^{\circ}$ ) from within a 400 m  
161 buffer radius into fish biomass models revealed confounding and variable effects of forereef  
162 steepness on the biomass of planktivores, primary consumers, and total fish biomass  
163 ( $P(\beta_{steepness} > 0) \geq 0.92$ ; Fig. 4; Extended Data Fig. 1; Supplementary Tables 4 and 5). Increased reef  
164 steepness between 0 to an initial threshold of approximately 5–10 $^{\circ}$  strongly correlated with a two-  
165 fold increase in biomass of planktivores, 25% increase in biomass of primary consumers, and 50%  
166 increase in total fish biomass (Fig. 4). Planktivore biomass increased between 0–30 $^{\circ}$  with the  
167 sharpest increase between 0 to 5–10 $^{\circ}$ , and plateauing around 30 $^{\circ}$ . Conversely, total biomass and  
168 primary consumer biomass plateaued around 10 $^{\circ}$ , then declined from 30 $^{\circ}$  (Fig. 4).

169 The proportion of variation in fish biomass explained by each spatial scale, quantified by extracting  
170 the posterior standard deviations of these modelled random effects, varied among trophic fish  
171 groups (Fig. 5; Supplementary Tables 10 and 11; see Extended Data Fig. 3 for variation in island-level  
172 depth effects among ecoregions). For all trophic groups except secondary consumers, there was  
173 greater variation in biomass at the site-scale (25–52% variance) and ecoregion-scale (25–66%) than  
174 at the island-scale (8–22%), suggesting that intra-island and inter-regional processes are more  
175 influential on fish biomass distributions than those occurring among islands (Fig. 5; Supplementary  
176 Table 10). The biomass of secondary consumers was most variable at the site scale (63%), relative to  
177 the island and ecoregion scales (20%, 17% respectively; Fig. 5; Supplementary Table 10). There were  
178 high probabilities across all fish groups that variation was greater at the site-scale than island-scale  
179 ( $P(sds_{SITE} > sds_{ISLAND}) \geq 0.99$ ; Supplementary Table 11). For planktivores, variation in biomass was  
180 proportionately greatest at the ecoregion-scale (66% variance). For all other groups except  
181 planktivores and piscivores, site-scale variance was greater than at the ecoregion-scale ( $P(sds_{SITE} >$   
182  $sds_{ECOREGION}) \geq 0.85$ ) (Fig. 5, Supplementary Tables 10 and 11).

183

## 184 **DISCUSSION**

185 While the structuring force of depth on reef ecology featured among the earliest descriptions of  
186 tropical coral reefs (for example, zonation in species composition)<sup>10,22,23</sup>, these observations were  
187 restricted to single-point locations. To date, the generality of resource driven depth zonation in fish  
188 biomass remains untested across broad geographies. Here, we show that in the absence of local

189 human populations there are predictable changes in tropical fish biomass with depth that track  
190 expected gradients in energetic resource supply to reefs<sup>25,28</sup>. These patterns hold true across the  
191 study area which spans distinct biogeographic regions, with high spatial consistency across islands  
192 and ecoregions (Extended Data Fig. 3) despite varying spatial heterogeneity in fish biomass among  
193 trophic groups, suggesting the role of distinct scale-dependent drivers. Recent work details declining  
194 patterns of reef fish diversity with increasing depth from the shallows to the mesophotic zone (max  
195 150 m depth)<sup>24</sup>. We build on these findings by revealing a common degree of ecological organisation  
196 in relation to both depth and bathymetric steepness across geographically distinct reefs. However,  
197 while there was evidence of resource-driven depth zonation in some groups at human-populated  
198 islands, the absolute change in biomass with depth relative to unpopulated islands was much  
199 reduced (planktivores, secondary consumers, piscivores) or was absent (primary consumers). Where  
200 humans have fundamentally re-set standing biomass baselines<sup>48</sup>, changes to naturally observed  
201 zonation may signal biological depletion confounding the predictive capacity of depth-dependent  
202 gradients in resource supply. These findings support calls for revisiting and potentially updating  
203 twentieth century ecological paradigms (e.g. island biogeography theory<sup>18</sup>) that may no longer  
204 capture ecological patterns and processes in a human-dominated world<sup>16</sup>.

205 At geographically distinct unpopulated islands, we show that reef fish biomass of all broad trophic  
206 groups correlated predictably and relatively consistently across depth despite underlying variation in  
207 biophysical drivers known to affect standing reef fish biomass<sup>3,29,45</sup>. Focussing on the shallowest 0–30  
208 m, we show that secondary consumer biomass increased between 0–15 m then plateaued. This  
209 diverse trophic group includes macro- and sessile invertivores and omnivores whose biomass can  
210 vary differentially with depth at local scales<sup>33,49</sup>. However, broad energetic pathways are governed  
211 by primary productivity, generally with nutrient limitations in the shallows<sup>32</sup> but greater productivity  
212 with depth, which at broader scales may cause the more consistent zonation pattern of this  
213 group<sup>25,50</sup>. Planktivore and piscivore biomass increased across 0–30 m depth, likely reflecting the  
214 increased proximity to pelagic energetic subsidies<sup>25,26,32</sup> delivered by upwelling that support the  
215 growth of planktonic prey for planktivorous fishes<sup>51,52</sup>. These planktivorous fishes are in turn prey for  
216 higher trophic level piscivores<sup>28</sup>, such that the distribution of piscivores can be indirectly governed  
217 by the availability of pelagic energetic subsidies<sup>29,44,53</sup>. Notably, we observed an approximate two-  
218 fold increase in the biomass of planktivores and piscivores between 0–10 m depth. If the biomass of  
219 these groups tracks the availability of their dietary targets, then this trend might be driven by the  
220 limited subsidies reaching the shallows. The upslope delivery of pelagic subsidies from deeper  
221 waters can be highly variable and upwelled waters are often depth-restricted to below 10 m depth<sup>25</sup>.  
222 This can be due to friction caused by the reef topography slowing the propagation of these nutrient-  
223 rich waters up the reef slope<sup>54</sup> and limiting their positive benefits on the concentration of  
224 zooplankton to greater depths<sup>25</sup>. In contrast, primary consumer biomass decreased with increasing  
225 depth, likely limited by the rapid attenuation of light available for photosynthetic algal production  
226 with depth<sup>25</sup>. Across latitudinal gradients, primary consumer biomass is higher in areas of greater  
227 irradiance<sup>29</sup>. Their distribution across depth is therefore also likely driven by the enhanced benthic  
228 primary production that occurs in shallower well-lit waters.

229 Reef fish biomass also exhibited a striking and varied relationship with bathymetric steepness,  
230 primarily in planktivores and primary consumers. For this study, we measured average steepness at  
231 the site-scale using a 400 m radial-buffer. The correlation between steepness at this scale and fish  
232 biomass may reflect the role of localized hydrodynamics<sup>34</sup> and physical hydrodynamic interactions  
233 with the benthos<sup>54</sup> in determining the delivery of nutrient-rich subthermocline water up onto  
234 shallow reefs<sup>26</sup>. While the presence of a depth gradient is a fundamental physical feature of every  
235 tropical coral reef island and atoll in the world, the steepness of this gradient can vary. As such, the

236 two can combine to determine the influx of pelagic subsidies to otherwise nutrient-poor tropical  
237 waters<sup>31</sup> and likely set natural limits on the distribution and productivity of reef fishes<sup>55–58</sup>. Previous  
238 studies employing estimates of reef steepness derived at broader spatial scales (e.g. 10 km site  
239 buffer radius) have found inconsistent effects of reef steepness on fish productivity<sup>52</sup>, possibly  
240 highlighting critical scale-dependency in localised upwelling processes created by physical features  
241 like internal waves<sup>36</sup>. Planktivores and primary consumers are strongly influenced by energetic  
242 subsidies to coral reefs<sup>29,44,59</sup>, and their biomass is naturally higher in areas of higher oceanic primary  
243 production<sup>45,52</sup>. Our results show that planktivore biomass increased between 0–30° with the  
244 sharpest increase observed within the initial 0 to 5–10°. Indeed, an increase in reef steepness from  
245 just 0 to 5–10° yielded twice the biomass of planktivores and a 25% increase in the biomass of  
246 primary consumers. Notably, a threshold of approximately 0–10° steepness is required for  
247 enhanced nearshore primary production around these islands and atolls<sup>31</sup>. At steepness levels of 30–  
248 44°, planktivore biomass plateaued, and primary consumer biomass declined. This may indicate a  
249 threshold of critical slope steepness where internal waves rich in deep-water pelagic nutrients  
250 become more likely to be reflected back offshore than to propagate upslope and/or break at steeper  
251 topography<sup>35,60,61</sup>. We thereby provide novel ocean-basin scale evidence quantifying the influence of  
252 local-scale reef steepness on patterns of reef fish biomass. Combined, the results suggest the  
253 existence of lower and upper local-scale thresholds in critical reef steepness in mediating delivery of  
254 allochthonous subsidies into the shallows and that these effects propagate through to determine the  
255 natural carrying capacity of specific trophic groups of reef fishes. Previous studies document variable  
256 peaks in planktivorous and piscivorous fishes at mesophotic depths beyond the 30 m limit of this  
257 study<sup>49,62</sup>. These variable peaks may be indicative of spatial variation in upwelling, potentially linked  
258 to—among other oceanographic factors and associated changes in benthic composition<sup>33</sup>—differences  
259 in local bathymetric steepness among those study locations.

260 Despite marked bathymetric gradients in fish biomass at unpopulated islands, we show that depth  
261 related changes in biomass were altered by depleted biomass baselines at islands inhabited by  
262 people. There was overall lower fish biomass across the depth gradient for all trophic groups at  
263 populated locations. Further, the change in absolute biomass of planktivores, piscivores, and  
264 secondary consumers across depth was substantially reduced at populated islands, and depth  
265 zonation in primary consumers was lost. Conversely, when measured as percent change in biomass,  
266 depth zonation was greater on populated islands for secondary consumers and especially piscivores.  
267 However, at populated islands overall lower biomass baselines of all groups and frequent absence of  
268 piscivores in shallow water surveys (i.e. zero-count survey observations) likely served to artificially  
269 inflate proportionate change across depth. These findings add to mounting global evidence of  
270 humans changing fundamental ecological organisation on tropical reefs<sup>16,19</sup>. Human-driven declines  
271 in reef fish biomass even at relatively low levels of human exploitation are well documented in the  
272 Pacific<sup>44,63</sup>. Fishing reduces the overall standing biomass of reef fishes across trophic groups<sup>44</sup>, often  
273 with marked losses of piscivores and herbivores<sup>42,64–66</sup>. Our findings of diminished biomass of  
274 primary consumers from shallow depths and piscivores and planktivores between 0–30 m on  
275 populated reefs does not exclude the possibility of mesophotic refugia for depth-generalists<sup>33,42,49,67</sup>.  
276 It does, though, underscore the vulnerability of herbivorous fishes that are largely restricted to  
277 shallow reef zones<sup>68</sup>. We note that human impacts on reef fish assemblages are not limited to the  
278 effects of fishing<sup>16,63</sup>. Global warming interacts with local threats such as land-use related  
279 sedimentation and nutrient loading into watersheds, dredging, plastic pollution, and invasive  
280 species<sup>16,69</sup>. As a result of these multiple stressors, underlying relationships between reef organisms  
281 and their surrounding environmental settings have been blurred across the region<sup>14,39</sup>. Our findings  
282 show that by using human population presence/absence as a simple binary predictor of these



283 impacts, natural zonation signals of absolute fish biomass change across depth are substantially  
284 reduced or are lost at populated islands, with variable responses among trophic groups. Such  
285 evidence emphasises the critical need for greater protection for reef ecosystems from a suite of  
286 human impacts<sup>16,38</sup>, and in particular for depth-constrained trophic groups that perform distinct and  
287 important functions.

288 Natural resource management is most effective when applied at scales aligning with (or broader  
289 than) scales of ecological variance<sup>70</sup>. This is because ecological communities exist in relation to their  
290 environment at spatial scales where structuring biophysical processes dominate to limit or promote  
291 the abundance of competitive organisms<sup>1,2,50</sup>. For example, intra-island gradients in surface wave  
292 energy and localised upwelling can determine the abundance and spatial-clustering of benthic  
293 organisms on coral reefs<sup>36,71</sup>. For reef fish assemblages, inter-island variability in oceanic productivity  
294 and island geomorphology can mediate levels of species richness and functional redundancy<sup>5</sup>.  
295 Conversely, finer-scale habitat quality (i.e. complexity and cover) can be more influential in  
296 determining other aspects of fish assemblage diversity and the abundance of particular groups and  
297 species<sup>5,6</sup>. As a result, variation in these biophysical processes through space can create inherent  
298 ecological heterogeneity across those spatial scales<sup>4,70</sup>.

299 While there was minimal observed deviation from the global depth effect across the study islands  
300 and ecoregions, our results show that spatial variation in fish biomass—across site, island, and  
301 ecoregion scales—was differentially and unevenly distributed among trophic groups, underscoring  
302 the importance of scale of observation in ecological enquiry<sup>1,72</sup>. The 35 islands and atolls in this study  
303 span much of the western and central Pacific and encompass substantial biophysical gradients that  
304 influence ecological organisation—ranging from local variation in live coral habitat availability among  
305 reefs for example, to regional disparities in temperature, irradiance, and primary production<sup>3,14,29,44</sup>.  
306 These scale-dependent gradients can influence the biomass of herbivorous, planktivorous, and  
307 piscivorous reef fishes observed across the region<sup>44,45,52</sup>. We found that the greatest spatial variance  
308 was at the site-scale for primary and secondary consumers, piscivores, and total biomass. We note  
309 that unmeasured temporal stochasticity at the site-level due to factors like fish recruitment,  
310 mobility, or behaviour can influence small-scale single time point observations and their associated  
311 variability at that scale<sup>6</sup>. Nonetheless, the importance of site-scale characteristics, indicated by this  
312 intra-island heterogeneity, supports numerous studies that identify habitat availability<sup>73</sup>, local  
313 hydrodynamics<sup>5</sup>, and local disturbances<sup>16,63,74</sup> as predominant mediators of the biomass of those  
314 groups<sup>6</sup>. Spatial variance at the site-level was particularly high (63%) for secondary consumers,  
315 emphasising trends in location-specific variability in their biomass-depth relationships described in  
316 previous studies<sup>33,49</sup>. Conversely, spatial variance in planktivore biomass was greatest at the  
317 ecoregion-scale, pointing towards regional disparities in primary production<sup>3</sup> and the availability of  
318 pelagic subsidies as a primary correlate in the distribution of planktivorous fish biomass<sup>30,52</sup>. These  
319 findings align with previous studies that describe habitat composition at the site-level to be the likely  
320 dominant driver of reef fish metacommunity structure, including diversity and the biomass of most  
321 trophic groups, while attributing greater prevalence of planktivores to larger-scale gradients in  
322 overall ocean productivity<sup>6</sup>. That we observed lower variation at the island-scale than site and  
323 ecoregion scales may be due, in part, to a dominant influence of local variation in habitat,  
324 hydrodynamics, or disturbances and variable background levels of productivity across ecoregions,  
325 over processes occurring at the island-scale. In this context, our findings suggest that management  
326 of primary consumers, piscivores, and especially secondary consumers might achieve satisfactory  
327 outcomes at local within-island scales with no-take areas<sup>75</sup> (assuming a source of larval supply),  
328 habitat restoration, or better regulated destructive human activities<sup>74</sup>. Local management of  
329 planktivores is no doubt also important<sup>30</sup>, but given the potential influence of regional-scale drivers

330 on planktivore biomass production and the importance of this group as the prey base for higher  
331 trophic levels<sup>28</sup>, more nuanced, region-specific targets for recovery<sup>76</sup> or catch of planktivores may be  
332 advisable in areas of naturally lower primary production.

333 In revisiting one of the oldest ecological theories—energetic resource-driven depth zonation of  
334 tropical coral reef communities, to date untested at scale<sup>10,21–23</sup>—we provide evidence of  
335 generalisable depth zonation spanning islands across the Pacific. While the principle of resource-  
336 driven depth zonation held at both unpopulated and populated islands for some trophic groups (e.g.  
337 direction of change for planktivores, piscivores, secondary consumers), their magnitude of change  
338 with depth (i.e. absolute biomass) was substantially reduced at populated islands. For functionally  
339 important primary consumers, the depth zonation signal was conspicuously absent at populated  
340 islands. Therefore, while we broadly evidence sustained depth zonation in these contemporary reef  
341 systems, our findings expose limitations of the energetic resource-driven zonation paradigm for  
342 predicting ecological dynamics where human impacts increasingly confound connections between  
343 ecological communities and their surrounding environment<sup>12,14,39</sup>.

344

## 345 **METHODS**

### 346 **Study location**

347 To examine the fish zonation across depths and investigate how humans may impact natural  
348 zonation on coral reefs, we used monitoring data from a standardized dataset that spans the central  
349 and western Pacific<sup>43</sup>. Specifically, 5,525 distinct surveys from 2,253 forereef sites ( $\leq 30$  m depth)  
350 conducted on 35 US and US-affiliated islands and atolls across 42 degrees ( $^{\circ}$ ) of latitude ( $14^{\circ}$  S to  
351  $28^{\circ}$  N), and  $62^{\circ}$  of longitude ( $178^{\circ}$  W to  $145^{\circ}$  E). The data were collected between 2010–2014 for the  
352 National Oceanic and Atmospheric Administration (NOAA) Pacific Reef Assessment and Monitoring  
353 Program (RAMP; 2010–2012) and NOAA’s National Coral Reef Monitoring Program (NCRMP; 2013–  
354 2019), conducted by the Ecosystem Sciences Division (ESD) of NOAA’s Pacific Islands Fisheries  
355 Science Center (PIFSC)<sup>43</sup>. We classified sites around islands and atolls (hereafter ‘islands’) as  
356 ‘populated’ or ‘unpopulated’ based on unpopulated islands having  $<50$  residents and located  $>100$   
357 km from the nearest larger human settlement using the 2010 US census  
358 ([www.census.gov/2010census](http://www.census.gov/2010census)) (*sensu*<sup>14,63</sup>). Of the 35 study islands, 21 were classified as  
359 unpopulated ( $n = 2,321$  surveys, across 923 sites) and 14 as populated ( $n = 3,204$  surveys, across  
360 1,330 sites) (Supplementary Table 1). Islands were also classified by their location within ecoregions:  
361 Hawaii Islands; Line Islands; Mariana Islands; Phoenix, Tokelau, Northern Cook Islands; and Samoa  
362 Islands<sup>47</sup>. The location of each replicate site was pre-selected by randomised stratified design per  
363 sampling units of the Pacific RAMP/NCRMP protocol (island, group of small islands, or subsections of  
364 larger islands). The target sampling domain was hard-bottom substrate, with sampling effort  
365 stratified by reef zone and depth (0–6 m; 6–18 m; 18–30 m)<sup>43</sup>. We constrained the dataset to  
366 forereef habitat only to remove any possible confounding effects of habitat type on reef fish  
367 assemblages. Reef depth (m) was recorded by divers *in situ* at survey sites. An online map viewer of  
368 the study sites is available:  
369 [http://noaa.maps.arcgis.com/apps/webappviewer/index.html?id=da5c18ea60d049588fca5feecb82f](http://noaa.maps.arcgis.com/apps/webappviewer/index.html?id=da5c18ea60d049588fca5feecb82fe07)  
370 [e07](http://noaa.maps.arcgis.com/apps/webappviewer/index.html?id=da5c18ea60d049588fca5feecb82fe07)

### 371 **Reef fish survey data**

372 The abundance and body-size of all diurnal, non-cryptic reef fishes were estimated using stationary  
373 point count (SPC) surveys (*sensu*<sup>5,43,44,77-79</sup>). At each site, divers conducted simultaneous visual fish  
374 counts within 1–4 adjacent, visually-estimated 15-m diameter cylindrical plots, extending from the  
375 substrate to the limit of vertical visibility<sup>43</sup>. First, divers compiled lists of all species observed within  
376 the survey area over a 5-min period, then counted and estimated the size (total length, TL, to the  
377 nearest cm) of listed species present within the cylinder over approximately 30-mins. Surveys were  
378 conducted by multiple observers across the study ecoregions and years. NOAA employs extensive  
379 training and technical validation protocols to ensure consistency and avoid bias in survey technique,  
380 fish species identification, and size estimation<sup>43</sup>. Full details on SPC survey methods and technical  
381 validation steps are available in [43]. To further mitigate any confounding effect of observer bias  
382 among fish surveys, we included ‘diver identity’ as a random intercept in all statistical models  
383 (described below) (*sensu*<sup>48</sup>). We calculated individual species biomass from the SPC counts using the  
384 allometric conversion as  $W = aL^b$ , where  $W$  is the biomass for individual fishes,  $L$  is the estimated  
385 body length of each individual, and parameters  $a$  and  $b$  are constants for each species (from<sup>80</sup>). Fish  
386 biomass ( $\text{g m}^{-2}$ ) was pooled into total fish biomass and four trophic groups: ‘Primary Consumers’  
387 (herbivores and detritivores), ‘Planktivores’, ‘Secondary Consumers’ (omnivores and benthic  
388 invertivores), and ‘Piscivores’<sup>46</sup>. Taxa that are not typically reef-associated were excluded from the  
389 analyses, including tuna, bonito, and milkfish (families *Chanidae*, *Myliobatidae*, *Scombridae*;  
390 Supplementary Table 12). Sixteen species of shark, jack, and barracuda (families *Carcharhinidae*,  
391 *Carangidae*, *Sphyrnidae*) were also excluded from the analyses as these highly mobile, large-bodied,  
392 roving piscivores are known to be affected by the presence of stationary divers, typically resulting in  
393 systematic over-inflation of visual survey density estimates<sup>81</sup> (*sensu*<sup>44,48</sup>; Supplementary Table 12).  
394 Further, the presence of divers among study locations also likely introduces a potential source of  
395 differential bias of biomass estimates of these fishes, with ‘mobbing’ behaviour by jacks, sharks, and  
396 barracuda known to occur particularly in remote, unpopulated areas such as the northwestern  
397 Hawaiian Islands<sup>44,45</sup>. Zonation patterns in piscivore biomass were comparable with and without this  
398 filtering approach. This suggests that the reported patterns were not an artifact of the data handling  
399 choice to exclude some species known to be affected and systematically overestimated by divers  
400 (Extended Data Fig. 4). However, model outputs of population level effects of depth and bathymetric  
401 steepness showed much greater biomass estimates at unpopulated than populated islands,  
402 indicating that conservative exclusion of these species mitigated potential systematic bias associated  
403 with the survey method among locations (Extended Data Fig. 4).

#### 404 **Bathymetric reef steepness**

405 We derived site-level estimates of bathymetric steepness ( $^{\circ}$ ) from depth mosaics created from  
406 multibeam SONAR, bathymetric LiDAR, and imagery derived depths in ArcGIS Pro v2.7 using the  
407 ‘Slope’ tool (Spatial Analyst) (Supplementary Table 2). Resulting mosaics ranged in spatial resolution  
408 from 5–50 m. Steepness estimates were calculated by averaging steepness values within a 400 m  
409 radial buffer around each replicate SPC site, and manually excluding backreef and lagoon areas and  
410 land-mass elevation using NOAA PIFSC ESD habitat map information. All analyses were done in the  
411 appropriate Universal Transverse Mercator zone for each island. A radial buffer-size of 400 m was  
412 selected to encompass depths that would capture the propensity for pulsed delivery of nutrient-rich  
413 sub-thermocline water by upwelling<sup>82,83</sup> and for this upwelling to propagate onto shallow reef  
414 habitats at depths  $\leq 30 \text{ m}$ <sup>31</sup> (maximum depth range within slope buffers: 596.2 m). Buffer-size extent  
415 was also selected to cover a reliable gradient in steepness while avoiding buffers-sizes that would  
416 easily extend across small island-masses to include bathymetry on opposite sides of the island. All  
417 sites were visually cross-checked for island overlap, and those including  $>5\%$  radial-buffer  
418 bathymetry on the opposite site of a landmass were excluded from all analyses.

## 419 Statistical analysis

420 To determine cross-spatial-scale depth zonation patterns in reef fish biomass, we fitted multi-level  
421 Bayesian regression models with brms<sup>84</sup>. Fish biomass (biomass density; g m<sup>-2</sup>) was modelled  
422 separately for each trophic group and total fish biomass, using the following general model:

$$423 y_i \sim \text{Gamma}(\mu_j, \zeta)$$

$$424 \log(\mu_j) = \alpha + \beta X_i + Z_i \gamma$$

425 where  $\alpha$  is the trophic group (or total biomass) specific intercept,  $\beta$  is a vector of population-level  
426 regression coefficients relating covariates  $X_i$  for observation  $i$  to the log of the expected biomass  
427 density  $\mu_j$ . Group-level coefficients  $\gamma$  are estimated for random effects encoded in design matrix  $Z$ .

428 We used depth and bathymetric steepness here as proxies for biophysical processes which influence  
429 coral reef fish assemblage structure. Population-level effects therefore included forereef depth (1.3–  
430 30.0 m), bathymetric steepness (0.01–43.78 °; mean 10.53 °), and the interactions of depth with  
431 each of bathymetric steepness and human population status. Near-island primary production can  
432 decrease exponentially with increasing island bathymetric steepness<sup>31</sup>. Therefore, potential non-  
433 linear effects of bathymetric predictors on fish biomass was included in the interaction of steepness  
434 with depth by fitting it as a random effect with a cubic-basis spline<sup>30</sup>.

435 To account for confounding effects of local human impacts on biomass density, we also included a  
436 population level effect for human population status (‘populated’ or ‘unpopulated’). Temporal  
437 variability in reef fish survey estimates can be introduced by observers and can also reflect dynamic  
438 processes such as those determining inter-annual variation in larval recruitment or nutrient  
439 availability across the region<sup>85,86</sup>. We therefore included group level effects for observation year (5  
440 years; 2010–2014), and year nested within both ecoregion and island in our models to account for  
441 this potential variation and avoid potential sampling bias. A group-level random intercept for ‘diver  
442 identity’ was included to account for the potential effect of individual observer bias. By assuming an  
443 inherent non-independence within divers and their observations that might affect the estimated  
444 means and associated errors of fish biomass (*sensu*<sup>48</sup>), we were then able to estimate isolated  
445 population level effects (i.e. depth, human population status, bathymetric steepness) (*sensu*<sup>48</sup>).  
446 More broadly, by controlling these potential sources of variability, we can more accurately test *a-*  
447 *priori* hypotheses about ecological zonation occurring across spatial scales and with greater  
448 inferential strength<sup>6</sup>.

449 To understand whether the ecological organisation of coral fish assemblages in relation to these  
450 biophysical processes holds true across varying spatial scales, we first accounted for the inherent  
451 hierarchical structure in the data by including random intercepts for ecoregions, islands within  
452 ecoregions, and sites within islands (*sensu*<sup>4</sup>). We hypothesized that patterns of fish biomass across  
453 bathymetric gradients may track scale-dependent biophysical drivers that regulate energetic  
454 resource supply to shallow coral reefs<sup>25,36,87</sup>. For example, regional-scale oceanographic currents and  
455 sea-surface temperatures drive regional differences in primary production and net resource  
456 availability<sup>3,87</sup>. These net gradients in availability can be modified at smaller spatial scales by  
457 oceanographic features interacting with local bathymetry<sup>31</sup> such that, depending on the prevailing  
458 direction of internal tidal energy, upwelling processes can drive strong intra-island gradients in  
459 nutrient and planktonic resource supply among sites<sup>25</sup>. As potential indicators of these scale-  
460 dependent processes, we then measured the variation in reef fish biomass at these three  
461 hierarchical scales (sites within islands within ecoregions) and compared the proportion of the total  
462 variation explained by those scales (*sensu*<sup>4</sup>). We quantified variation by extracting posterior standard

463 deviations of random effects at these distinct geographical scales in the fish biomass models and  
464 compared them across trophic groups. We further included a random slope term for depth-within-  
465 island to account for potentially variable depth zonation of biomass across islands.

466 All models were fitted with a Gamma response distribution, using a log-link function as biomass was  
467 positive, continuous, and overdispersed<sup>88</sup>. Fish of each trophic group were not observed in every SPC  
468 survey. To account for these zero-count observations, hurdle models were used, first fitting the  
469 presence-absence of fish biomass as a function of the predictors described above, with a binomial  
470 distribution and logit function, and then fitting the non-zero biomass data with the Gamma multi-  
471 level model outlined above. Where the proportion of zeros was too low to effectively estimate effect  
472 sizes in the presence-absence component (i.e. an insufficient contrast between the number of zeros  
473 and ones), the use of a hurdle structure affected model convergence and only added noise. This  
474 occurred for primary consumers (1.09% zeros) and secondary consumers (0.05% zeros), so for these  
475 groups the zero biomass replicates were removed from the analysis and the Gamma model detailed  
476 above was fitted.

477 This study builds on existing knowledge established in previous research that estimated a global  
478 baseline of total resident reef fish biomass in the absence of fishing<sup>48</sup>. We integrate this prior  
479 information by using their published posterior biomass estimate (1,013 kg ha<sup>-1</sup>) as the mean of the  
480 prior for log of total biomass ( $\alpha$ ; converted to g m<sup>-2</sup>) (with standard deviation set at 1):

481 
$$\alpha \sim N(\log(101.3), 1)$$

482 The intercept prior for each trophic group was estimated as a proportion of this total unfished global  
483 biomass estimate as approximated in MacNeil et al. [<sup>48</sup>]. The grouping of secondary consumers as  
484 defined in this study (a coarse group based on diverse diet items typically targeted by species  
485 including invertivores, corallivores, and omnivores<sup>46</sup>) differed to those used in MacNeil et al. [<sup>48</sup>].  
486 Therefore, the intercept prior for this group was determined by the proportion of secondary  
487 consumers in the total biomass from the present study data, applied to the unfished biomass  
488 estimate in [<sup>48</sup>]. MacNeil et al.<sup>48</sup> and our study employ comparable data (i.e. *in situ* counts of  
489 diurnally active, non-cryptic reef fish on forereef slopes, excluding sharks and semi-pelagics such as  
490 jacks). However, to account for potential differentiating factors between the studies, such as species  
491 filtering approaches, census method, or geographical representativeness, we inflated the prior  
492 standard deviation in the intercepts for our models by an order of magnitude. Model priors are  
493 detailed in Supplementary Table 3 and plotted with unpopulated posterior intercept estimations in  
494 Extended Data Fig. 5. Marginal posterior distributions for model parameters were estimated by  
495 Hamiltonian Monte Carlo (HMC) sampling, using 10,000 iterations across four chains, with a warm-  
496 up of 2,000 iterations, and a thinning factor of four. To ensure unbiased parameter estimates (i.e.,  
497 absence of divergent transitions), we set adapt delta to 0.995 and a maximum tree-depth of 12.  
498 Model fits and convergence were assessed with graphical posterior predictive checks and via trace  
499 and effective sample size plots, the Gelman-Rubin R-hat diagnostic and Bayesian adaptation of R-  
500 squared<sup>89</sup>. An effective sample size of >1,000 was chosen to determine stable parameter  
501 estimates<sup>90</sup>. Medians of posterior distributions were calculated to obtain a single point estimate and  
502 75% and 95% credible intervals (CIs) were calculated from the respective quantiles of the posterior  
503 distributions of all metrics presented. Non-independence of population-level predictors was  
504 assessed by plotting bivariate correlations between the posterior samples (MCMC draws) of  
505 predictor coefficients and quantifying Pearson correlation coefficients between paired samples  
506 (Supplementary Figure 1)<sup>89</sup>. Correlation coefficients were all <5%, bar one: a single pairwise  
507 correlation coefficient for hurdle components depth and steepness in the planktivore model which  
508 was still relatively low at 28%.

509 All analyses were conducted in R 4.2.1<sup>91</sup>. Bayesian hierarchical models were implemented in  
510 cmdstanr using *brms* 2.17.0<sup>90</sup>; probability of covariate effect direction was estimated with  
511 *bayestestR* 0.10.0<sup>92</sup>; model information for querying posterior predictions was extracted with  
512 *tidybayes* 3.0.2<sup>93</sup>; cross-spatial model variance was plotted with TernaryPlot in *Ternary* 1.2.3<sup>94</sup>;  
513 model fits assessed using *r2\_bayes* in *performance* 0.9.2<sup>95</sup>, and independence of model predictors  
514 assessed with *ggpairs* in *GGally* 2.1.2<sup>96</sup>. Fish symbols used in figures were created with *fishualize*  
515 0.1.0<sup>97</sup>.

516

#### 517 **DATA AND CODE AVAILABILITY**

518 All data and R code used in this study are available at an open-source repository  
519 (<https://github.com/LauraERichardson/Depth-Fish>).

520 **ACKNOWLEDGEMENTS**

521 We thank Ivor Williams and the staff at the Pacific Island Fisheries Science Center (NOAA) for  
 522 extensive survey data collection. NOAA’s Coral Reef Conservation Program (CRCP) supported and  
 523 funded the National Coral Reef Monitoring Program (NCRMP); CRCP project #743. This research was  
 524 funded by the European Commission supported by a Marie Skłodowska-Curie Sêr Cymru II COFUND  
 525 Fellowship (ref: BU191) and a Marie Skłodowska-Curie European Fellowship (ref: 844213 –  
 526 FISHSCALE) awarded to LER. We thank Sarah Bond and Alice Lawrence for useful discussions, Alastair  
 527 Feather and Sivajyodee Sannassy Pilly for technical code assistance, Amanda Merritt for contributing  
 528 to figure preparation, Jan Hiddink and an anonymous internal NOAA reviewer for critical feedback  
 529 that contributed to preparation of the manuscript.

530

531 **AUTHOR CONTRIBUTIONS STATEMENT**

532 L.E.R., A.H., and G.J.W. conceived this study; L.E.R., A.H., G.J.W., J.M.G., J.L., and J.A.M.G. designed  
 533 the methodology; A.H. contributed to survey data collection; T.L.K. provided NOAA’s fish survey  
 534 data; J.L., J.M.G. computed satellite derived bathymetric slope steepness estimates; L.E.R. and P.N.  
 535 conducted the analyses with input from A.J.D.; L.E.R. led manuscript writing with input from A.H.,  
 536 G.J.W., J.L., P.N., A.J.D., T.L.K., and K.E.I. All authors contributed significantly to the drafts and  
 537 approved the final version for publication.

538

539 **COMPETING INTERESTS STATEMENT**

540 The authors declare no competing interests.

541

542 **TABLES**

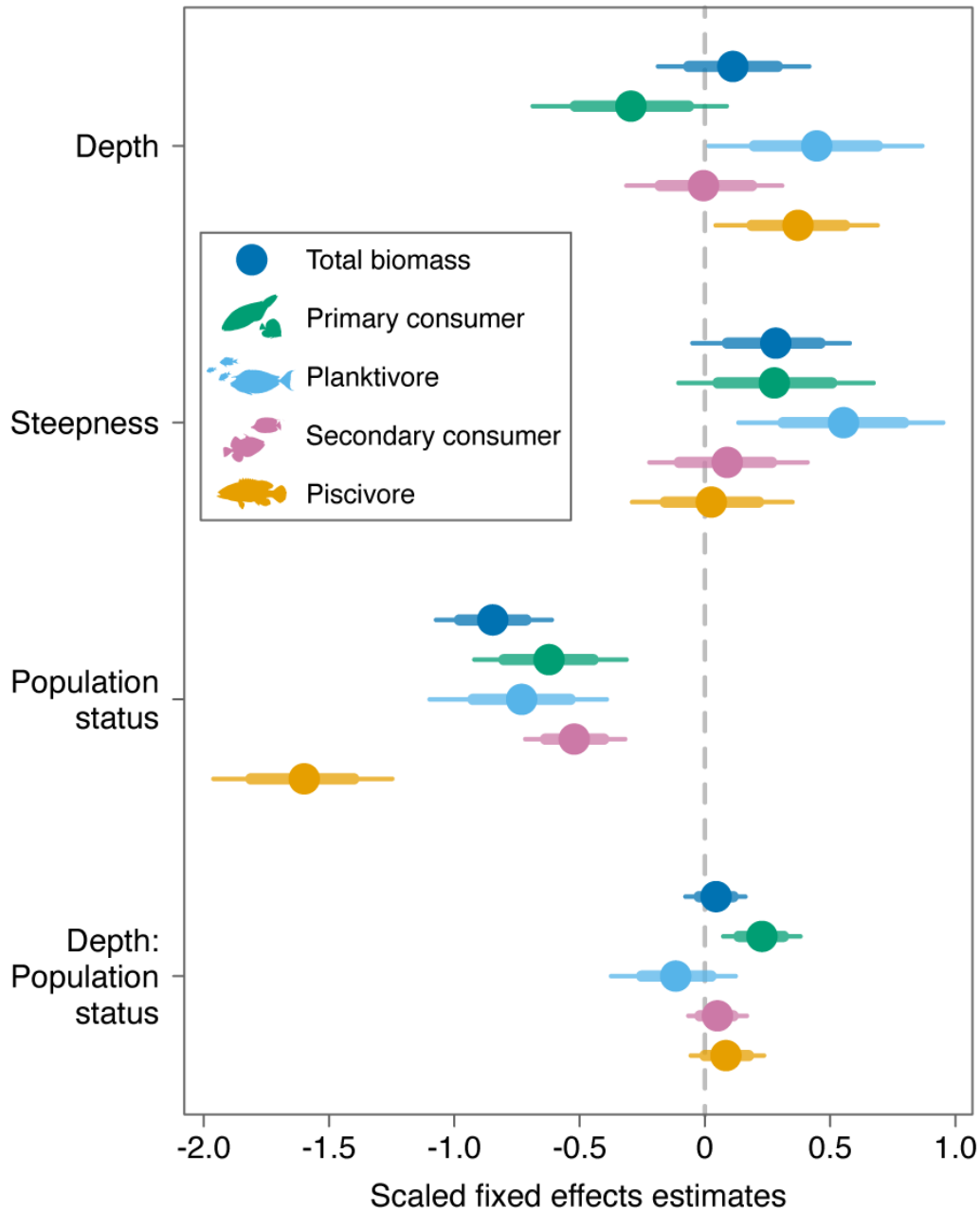
543 **Table 1 Probabilities of an increase in fish biomass across specified depths at unpopulated (U) and populated (P) islands.**  
 544 Probability estimates are derived from posterior model distributions comparing biomass at one fixed depth versus a deeper  
 545 depth (i.e., at 0 vs 10 m depth), with steepness held at the study mean value.

Depth (m)	Population status	Total biomass	Primary consumer	Planktivore	Secondary consumer	Piscivore
0 vs 10	U	<b>0.95</b>	<u><b>0.81</b></u>	<b>1.00</b>	<b>0.87</b>	<b>1.00</b>
	P	<b>0.96</b>	0.65	<b>1.00</b>	<b>0.90</b>	<b>1.00</b>
10 vs 20	U	<b>0.95</b>	<u><b>0.92</b></u>	<b>1.00</b>	0.63	<b>1.00</b>
	P	<b>0.98</b>	0.58	<b>0.98</b>	0.73	<b>1.00</b>
20 vs 30	U	0.41	<u><b>0.95</b></u>	<b>0.86</b>	<u><b>0.81</b></u>	<b>0.84</b>
	P	0.50	0.29	0.71	0.29	<b>0.78</b>

546 Probabilities ≥75% highlighted in bold. Probabilities ≥75% of the inverse difference (i.e., a high probability of a decrease in  
 547 biomass with increasing depth) are underlined.

548

549 **FIGURE LEGENDS/CAPTIONS (FOR MAIN TEXT FIGURES)**

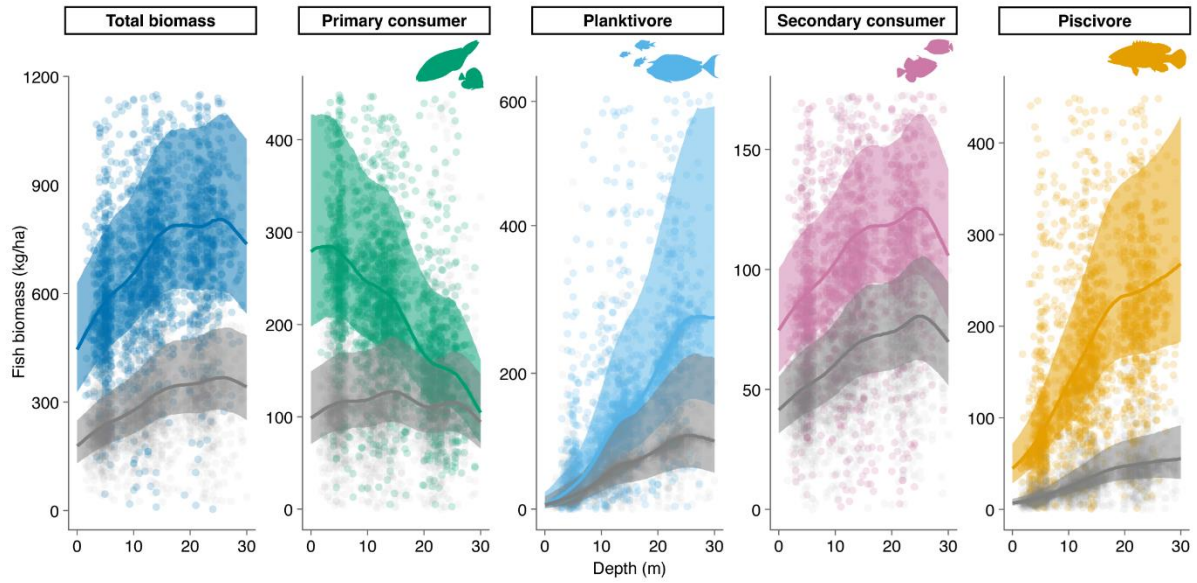


550

551 **Figure 1 Relationships between coral reef fish biomass of distinct trophic groups and overall effects of shallow reef depth,**  
 552 **bathymetric steepness, and human population status of islands (*Population status* indicates the effect of ‘populated’ by**  
 553 **humans versus ‘unpopulated’).** Effect sizes are scaled and includes the interaction of depth with population status  
 554 (*Depth:Population status*). Points represent posterior median estimates from Bayesian hierarchical models testing for an  
 555 effect of each explanatory variable on reef fish biomass, with 75% (thick lines) and 95% (thin lines) percentiles. Explanatory  
 556 variables were mean-centred and scaled by one standard deviation to facilitate comparisons of effect sizes among them. For  
 557 estimates of hurdle components (piscivore and planktivore models), see Extended Data Fig. 1 and Supplementary Table 4.  
 558 Unadjusted Bayesian conditional  $R^2$  values and 95% CI: total fish biomass, 0.55 (0.44–0.67); primary consumers, 0.54 (0.51–  
 559 0.57); planktivores, 0.48 (0.24–0.67); secondary consumers, 0.37 (0.31–0.47); piscivores, 0.52 (0.38–0.62) (Supplementary  
 560 Table 6 for marginal unadjusted  $R^2$  estimates).  $N = 5,525$  stationary point count (SPC) surveys (across 2,253 forereef sites, 35  
 561 islands, five ecoregions).

562

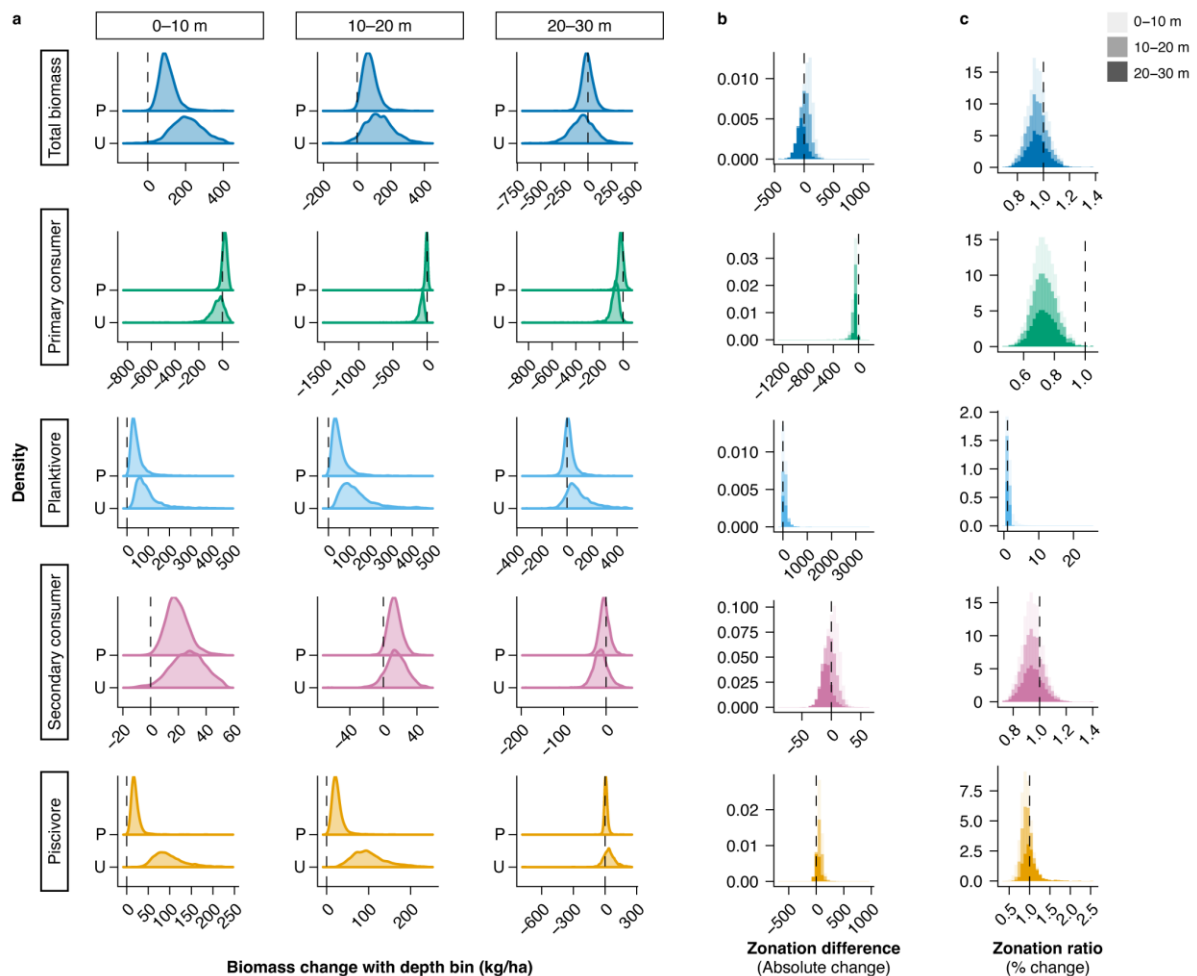




563

564 **Figure 2 Coral reef fish biomass across a shallow depth gradient at unpopulated (colour) and populated (grey) islands.**  
 565 Estimates represent conditional posterior medians (lines), 75% percentiles (shaded areas), and partial residuals (points) at  
 566 the study mean value of bathymetric steepness. The y axis is limited to 1.05x the maximum value of the 75% CI so partial  
 567 residuals exceeding axis limits are not displayed.  $N = 5,525$  stationary point count (SPC) surveys (across 2,253 forereef sites,  
 568 35 islands, five ecoregions).

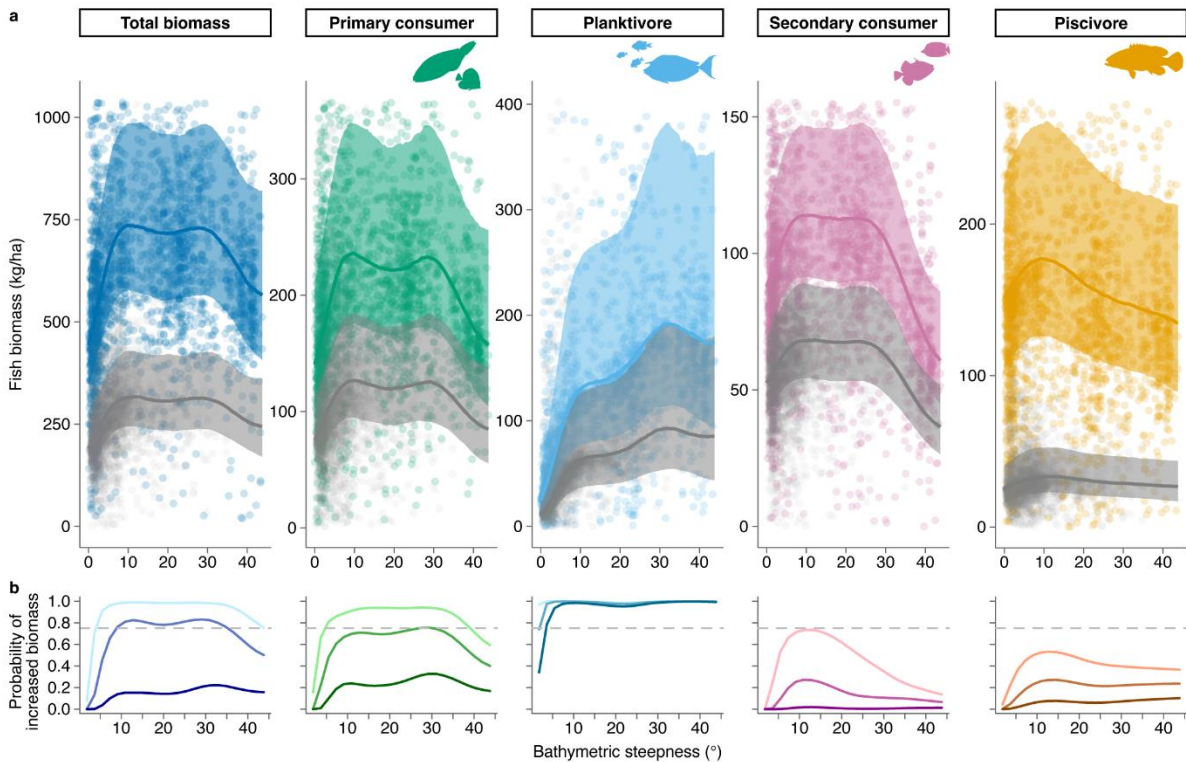
569



570

571 **Figure 3 Changes in reef fish biomass across shallow reef depth:** **A)** Conditional posterior distribution of changes in biomass  
 572 of each trophic group of fish (rows labeled on left) with each 10 m depth bin (columns labeled at top), at populated (P) and  
 573 unpopulated (U) islands. **B)** Conditional posterior distributions of differences in zonation, measured as differences in absolute  
 574 increase or decrease in biomass within each depth bin at populated versus unpopulated islands. **C)** Conditional posterior  
 575 distributions of zonation ratios, measured as the ratio of percentage change in biomass in each depth bin at populated versus  
 576 unpopulated islands. For example, panel A and B show a greater increase in absolute biomass of piscivores across depth bins  
 577 at unpopulated islands than at populated islands (further right of the dotted line), but panel C shows that the zonation ratio  
 578 of percentage change biomass is greater at populated islands in 0–20 m, spanning two bins (left of dotted line). All plots  
 579 display change in biomass with depth standardized at the study mean value of bathymetric steepness.

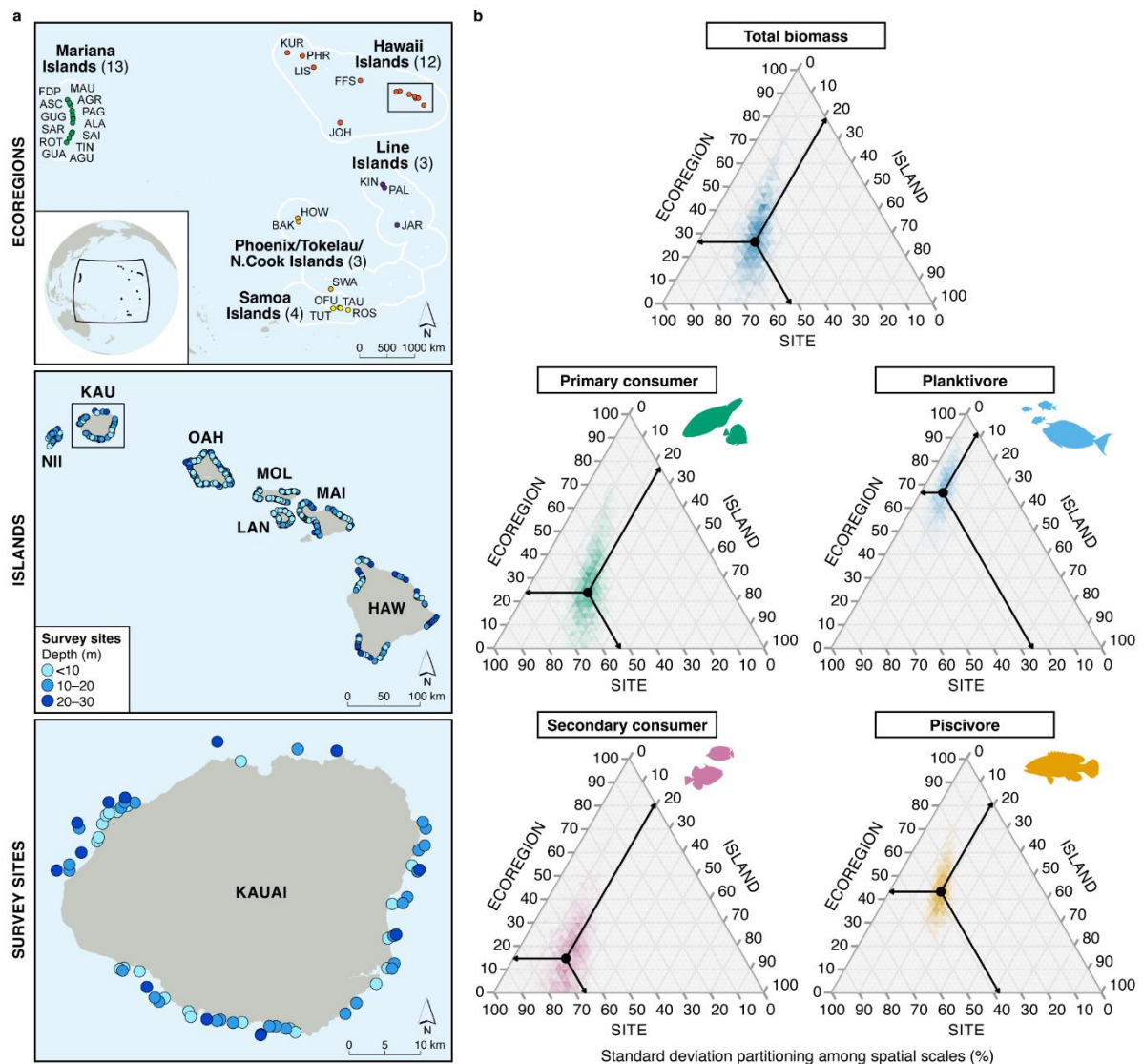
580



581

582 **Figure 4 Coral reef fish biomass across a gradient of reef bathymetric steepness at unpopulated (colour) and populated**  
 583 **(grey) islands.** **A)** Estimates represent marginal (integrated over depths from 0–30 m) posterior medians (lines), 75%  
 584 percentiles (shaded areas), and partial residuals (points) at the study-mean value of depth. The y axis is limited to the  
 585 maximum value of the 75% CI so partial residuals exceeding axis limits are not displayed).  $N = 5,525$  SPC surveys (across 2,253  
 586 forereef sites, 35 islands, five ecoregions). **B)** Probability of increased fish biomass with increasing bathymetric steepness  
 587 from 0–44°. Coloured lines show the marginal posterior distribution derived probabilities of proportionate increases in reef  
 588 fish biomass with increasing bathymetric steepness (°) among trophic groups. Shading of coloured lines represent  
 589 probabilities of biomass increase by 25% (light), 50% (medium), and 100% (dark). Grey line dotted line highlights probability  
 590 threshold of 0.75.

591



592

593 **Figure 5 The proportion of residual variation in coral reef fish biomass explained by the hierarchical structure of site,**  
 594 **island, and ecoregion spatial scales across the central and western Pacific.** A) Maps illustrate the spatial scales (from top to bottom): Ecoregions, example of islands within ecoregions (main Hawaiian Islands shown), and example of sites within  
 595 islands (Kauai shown), B) Ternary plots of the relative posterior standard deviations explained by the spatial scales for total biomass and each trophic group. Black arrows indicate geometric mean percentage of standard deviations (SD) at each  
 596 nested spatial scale (median SD estimates and CIs in Supplementary Table 10).  
 597  
 598

599

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