

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

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Nature Ecology and Evolution

DOI:

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

Published: 01/11/2023

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*, 7(11), 1844-1855. <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

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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^{1–3}, inherently introducing scale-dependent patterns and
58 heterogeneity in observed local community structure^{4–6}. To understand ecological generality, a large
59 enough lens across a land- or seascape is required to encompass these processes⁷. However, many
60 influential paradigms were developed from single-point studies in the mid-20th century (e.g. ^{6–8}).
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^{7,11}. Second, escalating anthropogenic impacts confound natural drivers of ecological
64 organisation^{12–14} such that humans are now considered the dominant force of planetary change¹⁵.
65 Where theories are founded on a premise that ecological organisation occurs in isolation of
66 anthropogenic forcing^{16,17}, the predictive capacity of historical paradigms can breakdown (e.g. island
67 biogeography theory¹⁸), requiring thorough reassessment of their applicability in this era of rapid
68 change^{16,19}.

69 Ecological zonation—the distribution of organisms across space—represents one of the oldest
70 ecological concepts^{8,9,20}. 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^{10,21–23},
73 and recently shown to be an important predictor of fish diversity²⁴. 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^{21,25–27}. With increasing depth, there are predictable
76 changes in energetic resource supply. Light for primary producers diminishes²⁵ but particulate foods
77 and nutrients derived from deeper water that support higher trophic levels such as planktivorous
78 predators, secondary consumers, and piscivores^{28–30}, increase with depth with increased proximity
79 to sources of upwelling^{26,31,32}. The degree to which upwelling can boost shallow-water (<30 m
80 depth³³) 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^{26,31,32}. Where bathymetry mediates local hydrodynamics around islands, upwelling
83 processes can concentrate in specific areas^{34,35}, creating intra-island variation in pelagic resource
84 supply³⁶. At larger spatial scales, cross-regional gradients in primary production³ 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 baselines³⁷. 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^{19,38}. Traversing numerous biophysical gradients that
93 mediate ecological organisation across scales⁶, 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^{16,19,39}. Reefs are exposed to ocean
96 warming and acidification, and a suite of local human impacts that deplete biological communities
97 and degrade habitats^{16,19}. 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^{40–42}. With human

100 impacts on coral reefs globally widespread³⁸, 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 spectrum³⁷. Using a
105 standardised Pacific-wide set of reef fish surveys⁴³, 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^{3,44}. In doing so, we intentionally
112 exclude other known influential biophysical and anthropogenic covariates on reef fish biomass (e.g.
113 ^{44,45}) to test the predictive capacity of depth at an ocean-basin scale on the biomass of fishes
114 grouped by their major dietary sources⁴⁶ – 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 ecoregions⁴⁷ 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 research⁴⁸. 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)^{10,22,23}, 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^{25,28}. 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)²⁴. 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 baselines⁴⁸, 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 theory¹⁸) that may no longer
204 capture ecological patterns and processes in a human-dominated world¹⁶.

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^{3,29,45}. 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^{33,49}. However, broad energetic pathways are governed
211 by primary productivity, generally with nutrient limitations in the shallows³² but greater productivity
212 with depth, which at broader scales may cause the more consistent zonation pattern of this
213 group^{25,50}. Planktivore and piscivore biomass increased across 0–30 m depth, likely reflecting the
214 increased proximity to pelagic energetic subsidies^{25,26,32} delivered by upwelling that support the
215 growth of planktonic prey for planktivorous fishes^{51,52}. These planktivorous fishes are in turn prey for
216 higher trophic level piscivores²⁸, such that the distribution of piscivores can be indirectly governed
217 by the availability of pelagic energetic subsidies^{29,44,53}. 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 depth²⁵.
222 This can be due to friction caused by the reef topography slowing the propagation of these nutrient-
223 rich waters up the reef slope⁵⁴ and limiting their positive benefits on the concentration of
224 zooplankton to greater depths²⁵. 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 depth²⁵. Across latitudinal gradients, primary consumer biomass is higher in areas of greater
227 irradiance²⁹. 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 hydrodynamics³⁴ and physical hydrodynamic interactions
233 with the benthos⁵⁴ in determining the delivery of nutrient-rich subthermocline water up onto
234 shallow reefs²⁶. 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 waters³¹ and likely set natural limits on the distribution and productivity of reef fishes^{55–58}. 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 productivity⁵², possibly
240 highlighting critical scale-dependency in localised upwelling processes created by physical features
241 like internal waves³⁶. Planktivores and primary consumers are strongly influenced by energetic
242 subsidies to coral reefs^{29,44,59}, and their biomass is naturally higher in areas of higher oceanic primary
243 production^{45,52}. 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 atolls³¹. 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^{35,60,61}. 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^{49,62}. These variable peaks may be indicative of spatial variation in upwelling, potentially linked
258 to—among other oceanographic factors and associated changes in benthic composition³³—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^{16,19}. Human-driven declines
271 in reef fish biomass even at relatively low levels of human exploitation are well documented in the
272 Pacific^{44,63}. Fishing reduces the overall standing biomass of reef fishes across trophic groups⁴⁴, often
273 with marked losses of piscivores and herbivores^{42,64–66}. 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^{33,42,49,67}.
276 It does, though, underscore the vulnerability of herbivorous fishes that are largely restricted to
277 shallow reef zones⁶⁸. We note that human impacts on reef fish assemblages are not limited to the
278 effects of fishing^{16,63}. 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^{16,69}. As a result of these multiple stressors, underlying relationships between reef organisms
281 and their surrounding environmental settings have been blurred across the region^{14,39}. 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^{16,38}, 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 variance⁷⁰. 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^{1,2,50}. 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^{36,71}. For reef fish assemblages, inter-island variability in oceanic productivity
294 and island geomorphology can mediate levels of species richness and functional redundancy⁵.
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^{5,6}. As a result, variation in these biophysical processes through space can create inherent
298 ecological heterogeneity across those spatial scales^{4,70}.

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^{1,72}. 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^{3,14,29,44}.
306 These scale-dependent gradients can influence the biomass of herbivorous, planktivorous, and
307 piscivorous reef fishes observed across the region^{44,45,52}. 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 scale⁶. Nonetheless, the importance of site-scale characteristics, indicated by this
312 intra-island heterogeneity, supports numerous studies that identify habitat availability⁷³, local
313 hydrodynamics⁵, and local disturbances^{16,63,74} as predominant mediators of the biomass of those
314 groups⁶. 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^{33,49}. Conversely, spatial variance in planktivore biomass was greatest at the
317 ecoregion-scale, pointing towards regional disparities in primary production³ and the availability of
318 pelagic subsidies as a primary correlate in the distribution of planktivorous fish biomass^{30,52}. 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 productivity⁶. 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 areas⁷⁵ (assuming a source of larval supply),
328 habitat restoration, or better regulated destructive human activities⁷⁴. Local management of
329 planktivores is no doubt also important³⁰, 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 levels²⁸, more nuanced, region-specific targets for recovery⁷⁶ 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^{10,21–23}—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^{12,14,39}.

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 Pacific⁴³. Specifically, 5,525 distinct surveys from 2,253 forereef sites (≤ 30 m depth)
350 conducted on 35 US and US-affiliated islands and atolls across 42 degrees ($^{\circ}$) of latitude (14° S to
351 28° N), and 62° of longitude (178° W to 145° 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)⁴³. 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) (*sensu*^{14,63}). 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 Islands⁴⁷. 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)⁴³. 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*^{5,43,44,77-79}). 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 visibility⁴³. 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 estimation⁴³. 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*⁴⁸). 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 (from⁸⁰). Fish
386 biomass (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’⁴⁶. 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 estimates⁸¹ (*sensu*^{44,48}; 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^{44,45}. 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^{82,83} and for this upwelling to propagate onto shallow reef
414 habitats at depths $\leq 30 \text{ m}$ ³¹ (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 brms⁸⁴. Fish biomass (biomass density; g m⁻²) 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 α is the trophic group (or total biomass) specific intercept, β 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 μ_j . Group-level coefficients γ 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 steepness³¹. 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 spline³⁰.

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^{85,86}. 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*⁴⁸), we were then able to estimate isolated
445 population level effects (i.e. depth, human population status, bathymetric steepness) (*sensu*⁴⁸).
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 strength⁶.

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*⁴). 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^{25,36,87}. For example, regional-scale oceanographic currents and
455 sea-surface temperatures drive regional differences in primary production and net resource
456 availability^{3,87}. These net gradients in availability can be modified at smaller spatial scales by
457 oceanographic features interacting with local bathymetry³¹ 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 sites²⁵. 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*⁴). 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 overdispersed⁸⁸. 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 fishing⁴⁸. We integrate this prior
479 information by using their published posterior biomass estimate (1,013 kg ha⁻¹) as the mean of the
480 prior for log of total biomass (α ; converted to g m⁻²) (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. [48]. 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 omnivores⁴⁶) differed to those used in MacNeil et al. [48].
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 [48]. MacNeil et al.⁴⁸ 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 squared⁸⁹. An effective sample size of >1,000 was chosen to determine stable parameter
501 estimates⁹⁰. 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)⁸⁹. 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 4.2.1⁹¹. Bayesian hierarchical models were implemented in
510 cmdstanr using *brms* 2.17.0⁹⁰; probability of covariate effect direction was estimated with
511 *bayestestR* 0.10.0⁹²; model information for querying posterior predictions was extracted with
512 *tidybayes* 3.0.2⁹³; cross-spatial model variance was plotted with TernaryPlot in *Ternary* 1.2.3⁹⁴;
513 model fits assessed using *r2_bayes* in *performance* 0.9.2⁹⁵, and independence of model predictors
514 assessed with *ggpairs* in *GGally* 2.1.2⁹⁶. Fish symbols used in figures were created with *fishualize*
515 0.1.0⁹⁷.

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**

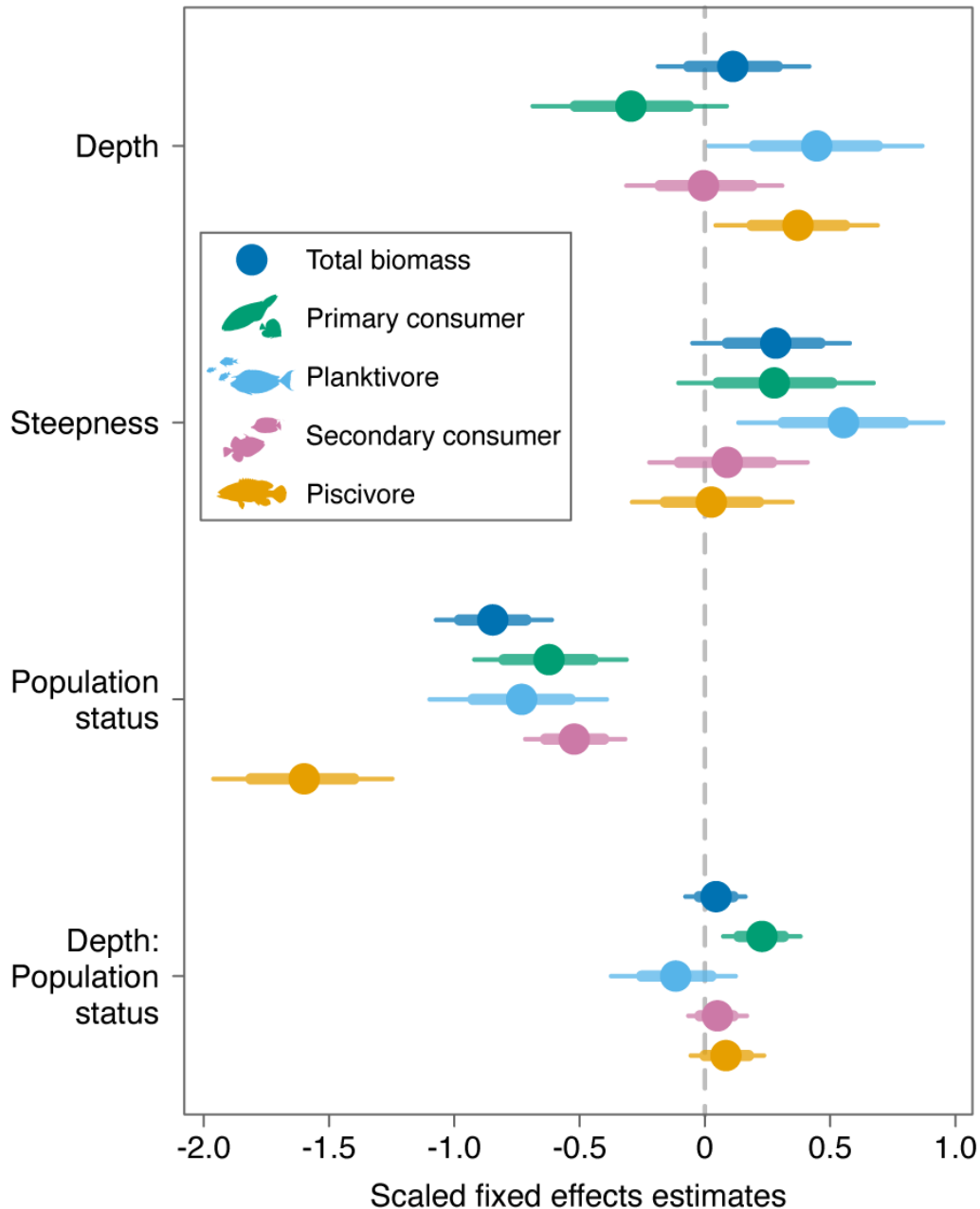
543 **Table 1 Probabilities of an increase in fish biomass across specified depths at unpopulated (U) and populated (P) islands.**
 544 Probability estimates are derived from posterior model distributions comparing biomass at one fixed depth versus a deeper
 545 depth (i.e., at 0 vs 10 m depth), with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

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

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

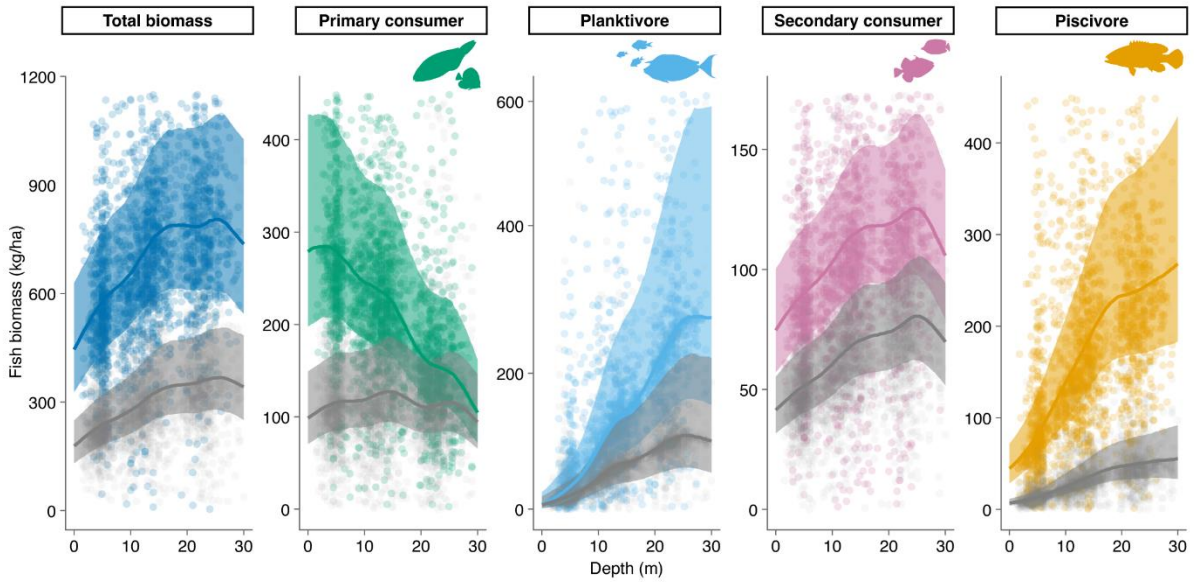
549 **FIGURE LEGENDS/CAPTIONS (FOR MAIN TEXT FIGURES)**



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).

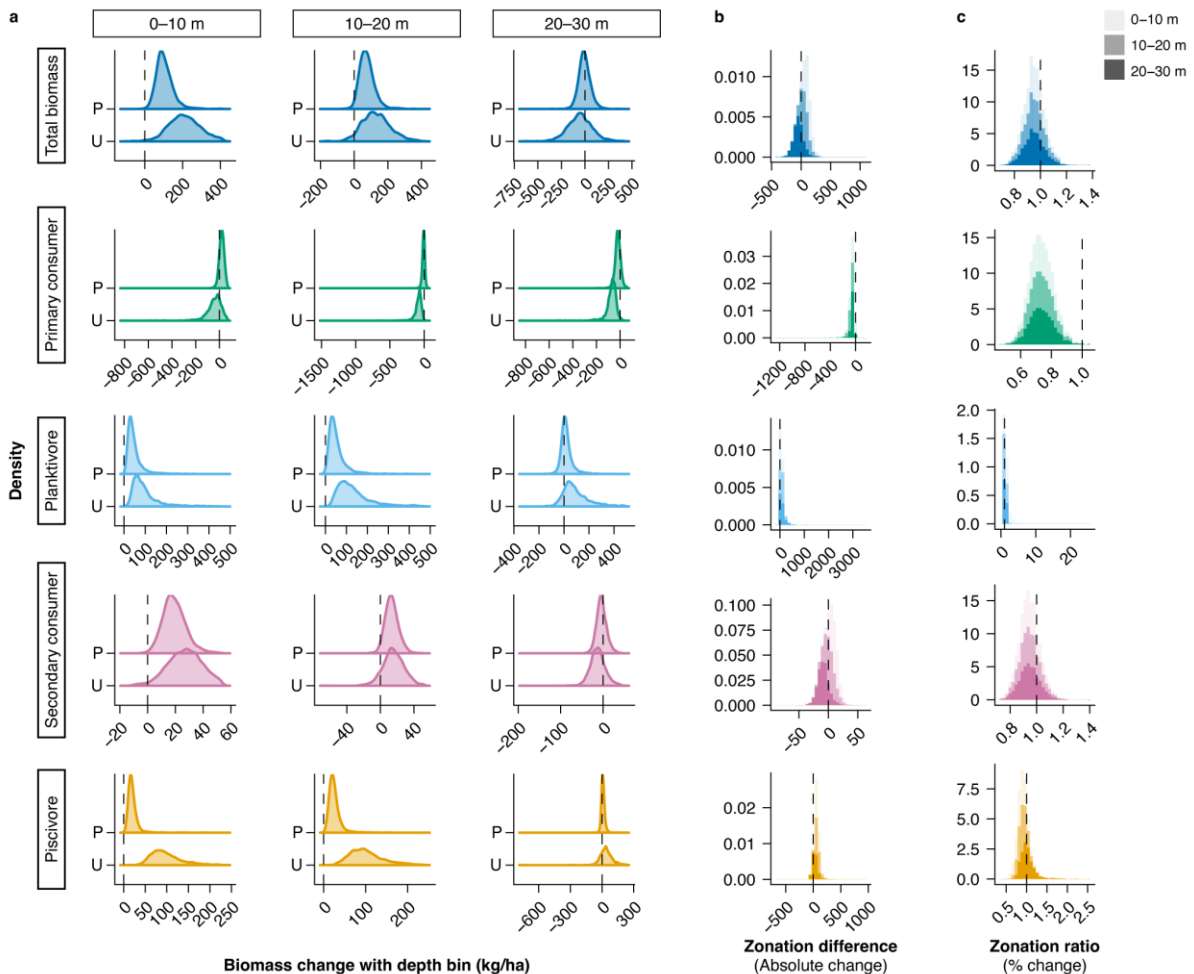
562



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).

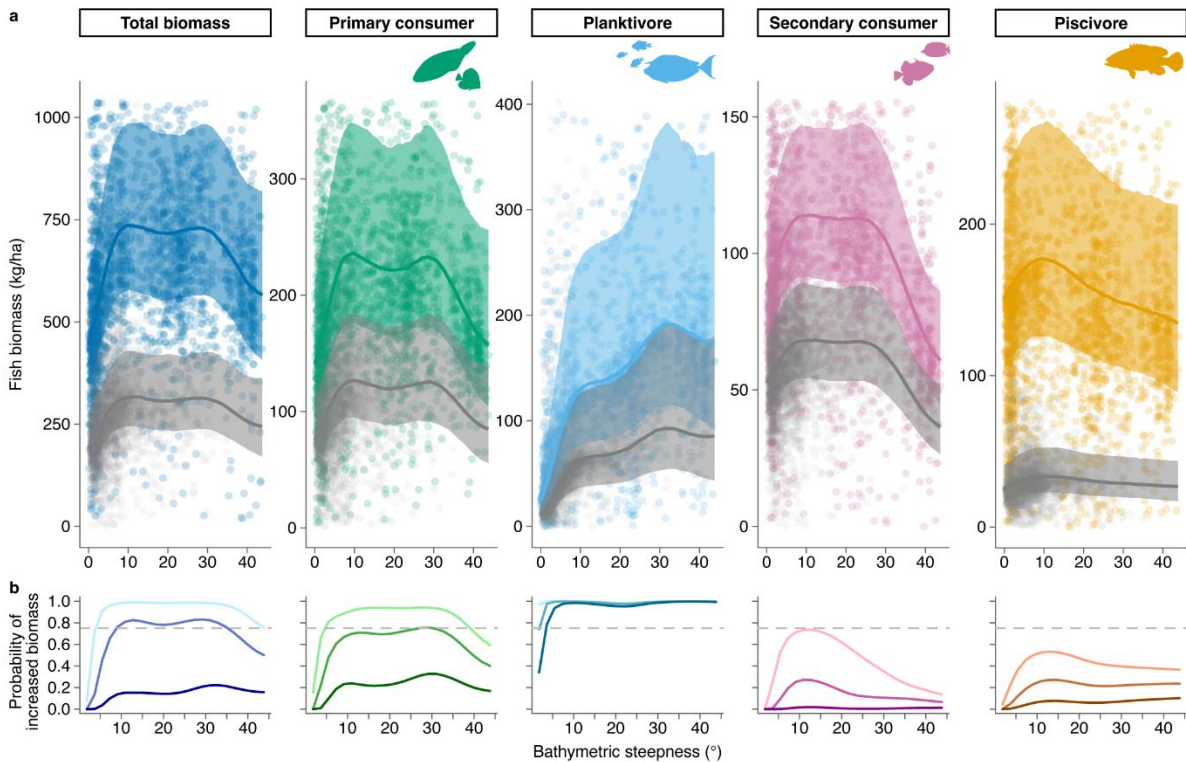
569



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.

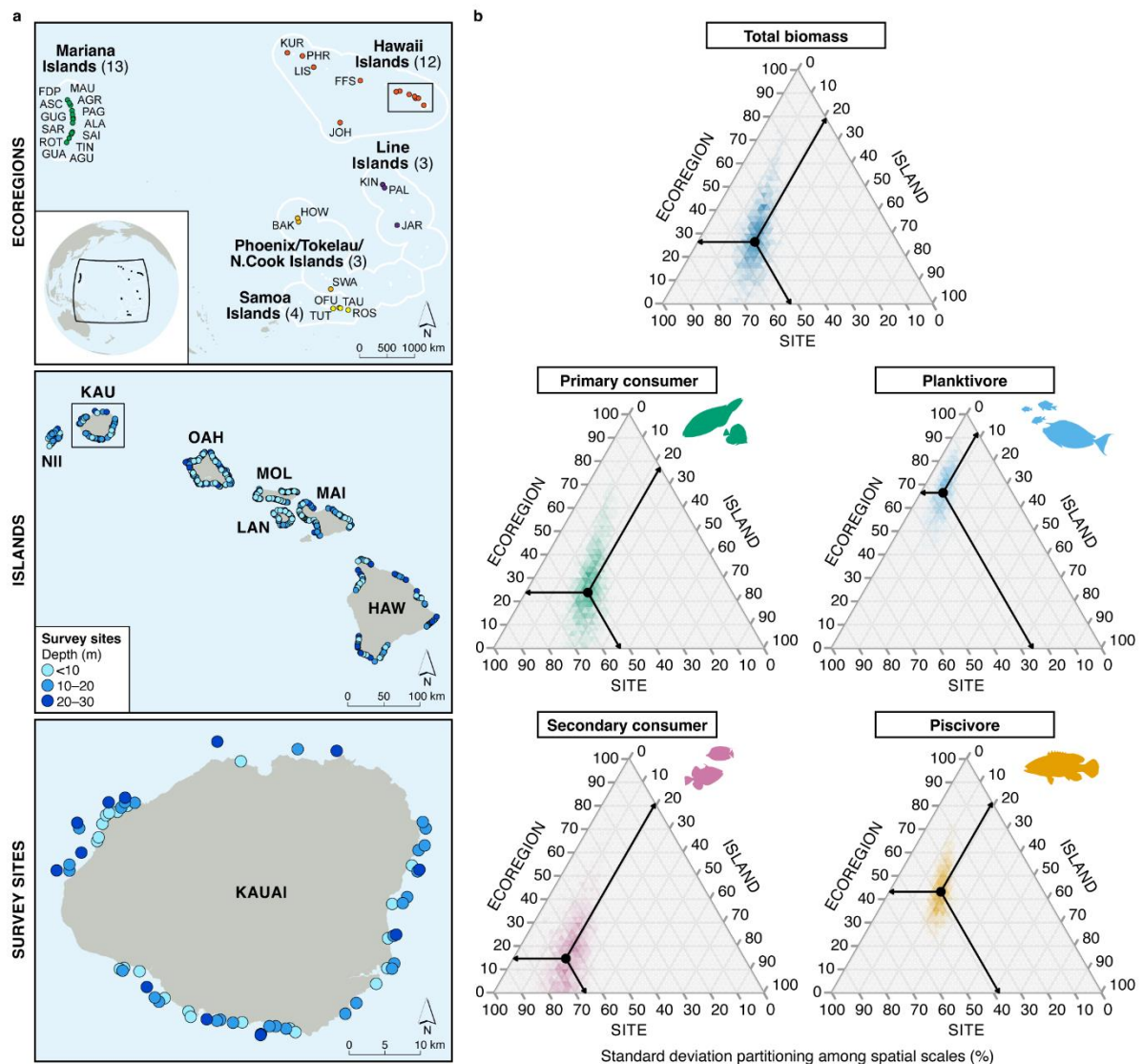
580



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

600 **REFERENCES**

601 1. Levin, S. A. The problem of pattern and scale in ecology: The Robert H. MacArthur Award
 602 lecture. *Ecology* **73**, 1943–1967 (1992).

603 2. Peterson, G. D. Scaling ecological dynamics: Self-organization, hierarchical structure, and
 604 ecological resilience. *Clim. Change* **44**, 291–309 (2000).

605 3. Gove, J. M. *et al.* Quantifying climatological ranges and anomalies for Pacific coral reef
 606 ecosystems. *PLoS One* **8**, e61974 (2013).

607 4. Hughes, T. P. *et al.* Patterns of recruitment and abundance of corals along the Great Barrier
 608 Reef. *Nature* **397**, 59–63 (1999).

- 609 5. Yeager, L. A., Deith, M. C. M., McPherson, J. M., Williams, I. D. & Baum, J. K. Scale
610 dependence of environmental controls on the functional diversity of coral reef fish
611 communities. *Glob. Ecol. Biogeogr.* **26**, 1177–1189 (2017).
- 612 6. MacNeil, M. A. *et al.* Hierarchical drivers of reef-fish metacommunity structure. *Ecology* **90**,
613 252–264 (2009).
- 614 7. Marquet, P. A. Macroecological perspectives on communities and ecosystems. in *The*
615 *Princeton guide to ecology* (ed. Simon A. Levin, Stephen R. Carpenter, H. Charles J. Godfray,
616 Ann P. Kinzig, Michel Loreau, Jonathan B. Losos, B. W. and D. S. W.) 386 (2009).
- 617 8. Lewis, J. R. The littoral zone on rocky shores: A biological or physical entity? *Oikos* **12**, 280–
618 301 (1961).
- 619 9. Whittaker, R. H. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* **26**, 2–80 (1956).
- 620 10. Odum, H. T. & Odum, E. P. Trophic structure and productivity of a windward coral reef
621 community on Eniwetok Atoll. *Ecol. Monogr.* **25**, 291–320 (1955).
- 622 11. Farley, S. S., Dawson, A., Goring, S. J. & Williams, J. W. Situating ecology as a big-data science:
623 Current advances, challenges, and solutions. *Bioscience* **68**, 563–576 (2018).
- 624 12. Ellis, E. C. Ecology in an anthropogenic biosphere. *Ecol. Monogr.* **85**, 287–331 (2015).
- 625 13. Ellis, E. C. *et al.* Used planet: A global history. *Proc. Natl. Acad. Sci.* **110**, 7978–7985 (2013).
- 626 14. Williams, G. J., Gove, J. M., Eynaud, Y., Zgliczynski, B. J. & Sandin, S. A. Local human impacts
627 decouple natural biophysical relationships on Pacific coral reefs. *Ecography (Cop.)*. **38**, 751–
628 761 (2015).
- 629 15. Rockström, J. *et al.* Planetary boundaries. *Ecol. Soc.* **14**, (2009).
- 630 16. Williams, G. J. *et al.* Coral reef ecology in the Anthropocene. *Funct. Ecol.* **33**, 1014–1022
631 (2019).
- 632 17. Golley, F. B. Paradigm shift. *Landsc. Ecol.* **3**, 65–66 (1989).
- 633 18. Helmus, M. R., Mahler, D. L. & Losos, J. B. Island biogeography of the Anthropocene. *Nature*
634 **513**, 543–546 (2014).
- 635 19. Hughes, T. P. *et al.* Coral reefs in the Anthropocene. *Nature* **546**, 82–90 (2017).
- 636 20. von Humboldt, A. & Bonpland, A. *Ideen zu einer Geographie der Pflanzen nebst einem*
637 *Naturgemälde der Tropenländer: auf Beobachtungen und Messungen gegründet, welche vom*
638 *10ten Grade nördlicher bis zum 10ten Grade südlicher Breite, in den Jahren 1799, 1800, 1801,*
639 *1802 und 1803 angestellt w.* vol. 1 (Cotta, 1807).
- 640 21. Huston, M. A. Patterns of species diversity on coral reefs. *Annu. Rev. Ecol. Syst.* **16**, 149–177
641 (1985).
- 642 22. Goreau, T. F. The ecology of Jamaican coral reefs I. Species composition and zonation.
643 *Ecology* **40**, 67–90 (1959).
- 644 23. Wells, J. W. *Recent corals of the Marshall Islands.* (US Government Printing Office, 1954).
- 645 24. Pinheiro, H. T. *et al.* Assembly rules of coral reef fish communities along the depth gradient.
646 *Curr. Biol.* **33**, 1421-1430.e4 (2023).
- 647 25. Williams, G. J. *et al.* Biophysical drivers of coral trophic depth zonation. *Mar. Biol.* **165**, 60
648 (2018).

- 649 26. Leichter, J. J., Shellenbarger, G. & Genovese, S. J. Breaking internal waves on a Florida (USA)
650 coral reef: a plankton pump at work? . *Mar. Ecol. Prog. Ser.* **166**, 83–97 (1998).
- 651 27. Roberts, H., Murray, S. & Suhayda, J. Physical processes in a fringing reef system. *J. Mar. Res.*
652 **33**, 233–260 (1975).
- 653 28. Skinner, C. *et al.* Offshore pelagic subsidies dominate carbon inputs to coral reef predators.
654 *Sci. Adv.* **7**, eabf3792 (2022).
- 655 29. Heenan, A., Williams, G. J. & Williams, I. D. Natural variation in coral reef trophic structure
656 across environmental gradients. *Front. Ecol. Environ.* **18**, 69–75 (2020).
- 657 30. Morais, R. A. & Bellwood, D. R. Pelagic subsidies underpin fish productivity on a degraded
658 coral reef. *Curr. Biol.* **29**, 1521-1527.e6 (2019).
- 659 31. Gove, J. M. *et al.* Near-island biological hotspots in barren ocean basins. *Nat. Commun.* **7**,
660 10581 (2016).
- 661 32. Leichter, J. J., Stewart, H. L. & Miller, S. L. Episodic nutrient transport to Florida coral reefs.
662 *Limnol. Oceanogr.* **48**, 1394–1407 (2003).
- 663 33. Stefanoudis, P. V *et al.* Depth-dependent structuring of reef fish assemblages from the
664 shallows to the rariphotic zone. *Frontiers in Marine Science* vol. 6 307 (2019).
- 665 34. Aucan, J., Merrifield, M. A., Luther, D. S. & Flament, P. Tidal mixing events on the deep flanks
666 of Kaena Ridge, Hawaii. *J. Phys. Oceanogr.* **36**, 1202–1219 (2006).
- 667 35. Masunaga, E., Arthur, R. S. & Fringer, O. B. Internal wave breaking dynamics and associated
668 mixing in the coastal ocean. in (eds. Cochran, J. K., Bokuniewicz, H. J. & Yager, P. L. B. T.-E. of
669 O. S. (Third E.) 548–554 (Academic Press, 2019). doi:<https://doi.org/10.1016/B978-0-12-409548-9.10953-4>.
- 671 36. Aston, E. A. *et al.* Scale-dependent spatial patterns in benthic communities around a tropical
672 island seascape. *Ecography (Cop.)*. **42**, 578–590 (2019).
- 673 37. Knowlton, N. & Jackson, J. B. C. Shifting Baselines, Local Impacts, and Global Change on Coral
674 Reefs. *PLOS Biol.* **6**, e54 (2008).
- 675 38. Obura, D. *et al.* Vulnerability to collapse of coral reef ecosystems in the Western Indian
676 Ocean. *Nat. Sustain.* **5**, 104–113 (2022).
- 677 39. Ford, A. K. *et al.* Local human impacts disrupt relationships between benthic reef
678 assemblages and environmental predictors. *Frontiers in Marine Science* vol. 7 (2020).
- 679 40. Taylor, B. M. Standing out in a big crowd: High cultural and economic value of *Naso unicornis*
680 in the Insular Pacific. *Fishes* vol. 4 (2019).
- 681 41. Houk, P. *et al.* Commercial coral-reef fisheries across Micronesia: A need for improving
682 management. *Coral Reefs* **31**, 13–26 (2012).
- 683 42. Asher, J., Williams, I. D. & Harvey, E. S. An assessment of mobile predator populations along
684 shallow and mesophotic depth gradients in the Hawaiian Archipelago. *Sci. Rep.* **7**, 3905
685 (2017).
- 686 43. Heenan, A. *et al.* Long-term monitoring of coral reef fish assemblages in the Western central
687 pacific. *Sci. Data* **4**, 170176 (2017).
- 688 44. Williams, I. D. *et al.* Human, oceanographic and habitat drivers of Central and Western Pacific
689 coral reef fish assemblages. *PLoS One* **10**, e0120516 (2015).

- 690 45. Heenan, A., Hoey, A. S., Williams, G. J. & Williams, I. D. Natural bounds on herbivorous coral
691 reef fishes. *Proc. R. Soc. B Biol. Sci.* **283**, 20161716 (2016).
- 692 46. Sandin, S. A. & Williams, I. Trophic classifications of reef fishes from the tropical US Pacific
693 (Version 1.0). (2010).
- 694 47. Spalding, M. D. *et al.* Marine ecoregions of the world: A bioregionalization of coastal and shelf
695 areas. *Bioscience* **57**, 573–583 (2007).
- 696 48. MacNeil, M. A. *et al.* Recovery potential of the world’s coral reef fishes. *Nature* **520**, 341–344
697 (2015).
- 698 49. Scott, M. E. *et al.* Variation in abundance, diversity and composition of coral reef fishes with
699 increasing depth at a submerged shoal in the northern Great Barrier Reef. *Rev. Fish Biol. Fish.*
700 (2022) doi:10.1007/s11160-022-09716-9.
- 701 50. Hatcher, B. G. Coral reef primary productivity. A hierarchy of pattern and process. *Trends*
702 *Ecol. Evol.* **5**, 149–155 (1990).
- 703 51. Hamner, W. M., Jones, M. S., Carleton, J. H., Hauri, I. R. & Williams, D. M. Zooplankton,
704 planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia.
705 *Bull. Mar. Sci.* **42**, 459–479 (1988).
- 706 52. Morais, R. A., Siqueira, A. C., Smallhorn-West, P. F. & Bellwood, D. R. Spatial subsidies drive
707 sweet spots of tropical marine biomass production. *PLOS Biol.* **19**, e3001435 (2021).
- 708 53. Nadon, M. O. *et al.* Re-creating missing population baselines for Pacific reef sharks. *Conserv.*
709 *Biol.* **26**, 493–503 (2012).
- 710 54. Monismith, S. G., Rogers, J. S., Koweeck, D. & Dunbar, R. B. Frictional wave dissipation on a
711 remarkably rough reef. *Geophys. Res. Lett.* **42**, 4063–4071 (2015).
- 712 55. Wedding, L. M. & Friedlander, A. M. Determining the influence of seascape structure on coral
713 reef fishes in Hawaii using a geospatial approach. *Mar. Geod.* **31**, 246–266 (2008).
- 714 56. Pittman, S. J., Costa, B. M. & Battista, T. A. Using lidar bathymetry and boosted regression
715 trees to predict the diversity and abundance of fish and corals. *J. Coast. Res.* 27–38 (2009)
716 doi:10.2112/S153-004.1.
- 717 57. Brokovich, E., Baranes, A. & Goren, M. Habitat structure determines coral reef fish
718 assemblages at the northern tip of the Red Sea. *Ecol. Indic.* **6**, 494–507 (2006).
- 719 58. Jankowski, M. W., Gardiner, N. R. & Jones, G. P. Depth and reef profile: effects on the
720 distribution and abundance of coral reef fishes. *Environ. Biol. Fishes* **98**, 1373–1386 (2015).
- 721 59. Siqueira, A. C., Morais, R. A., Bellwood, D. R. & Cowman, P. F. Planktivores as trophic drivers
722 of global coral reef fish diversity patterns. *Proc. Natl. Acad. Sci.* **118**, e2019404118 (2021).
- 723 60. Thorpe, S. A. Fronts Formed by Obliquely Reflecting Internal Waves at a Sloping Boundary. *J.*
724 *Phys. Oceanogr.* **29**, 2462–2467 (1999).
- 725 61. Smyth, W. D. & Moum, J. N. Ocean mixing by Kelvin-Helmholtz instability. *Oceanography* **25**,
726 140–149 (2012).
- 727 62. Thresher, R. E. & Colin, P. L. Trophic structure, diversity and abundance of fishes of the deep
728 reef (30–300m) at Enewetak, Marshall Islands. *Bull. Mar. Sci.* **38**, 253–272 (1986).
- 729 63. Williams, I. D. *et al.* Differences in reef fish assemblages between populated and remote reefs
730 spanning multiple archipelagos across the Central and Western Pacific. *J. Mar. Biol.* **2011**,

- 731 826234 (2011).
- 732 64. Edwards, C. B. *et al.* Global assessment of the status of coral reef herbivorous fishes: evidence
733 for fishing effects. *Proc. R. Soc. B Biol. Sci.* **281**, 20131835 (2014).
- 734 65. Cinner, J. E. *et al.* Gravity of human impacts mediates coral reef conservation gains. *Proc.*
735 *Natl. Acad. Sci.* **115**, E6116–E6125 (2018).
- 736 66. Abel, V., Ellen, C. C. & Francis, B. J. Predatory fish depletion and recovery potential on
737 Caribbean reefs. *Sci. Adv.* **3**, e1601303 (2022).
- 738 67. Lindfield, S. J., Harvey, E. S., Halford, A. R. & Mcllwain, J. L. Mesophotic depths as refuge areas
739 for fishery-targeted species on coral reefs. *Coral Reefs* **35**, 125–137 (2016).
- 740 68. Lindfield, S. J., Mcllwain, J. L. & Harvey, E. S. Depth refuge and the impacts of SCUBA
741 spearfishing on coral reef fishes. *PLoS One* **9**, e92628 (2014).
- 742 69. Rogers, C. S. Responses of coral reefs and reef organisms to sedimentation. *Mar. Ecol. Prog.*
743 *Ser. Oldend.* **62**, 185–202 (1990).
- 744 70. Cumming, G. S. & Dobbs, K. A. Quantifying social-ecological scale mismatches suggests people
745 should be managed at broader scales than ecosystems. *One Earth* **3**, 251–259 (2020).
- 746 71. Ford, H. V. *et al.* Spatial scaling properties of coral reef benthic communities. *Ecography*
747 *(Cop.)*. **44**, 188–198 (2021).
- 748 72. Lawrence, A. *et al.* Spatial and temporal scales of coral reef fish ecological research and
749 management: a systematic map protocol. *Environ. Evid.* **10**, 3 (2021).
- 750 73. Friedlander, A. M. & Parrish, J. D. Habitat characteristics affecting fish assemblages on a
751 Hawaiian coral reef. *J. Exp. Mar. Bio. Ecol.* **224**, 1–30 (1998).
- 752 74. Wedding, L. M. *et al.* Advancing the integration of spatial data to map human and natural
753 drivers on coral reefs. *PLoS One* **13**, e0189792 (2018).
- 754 75. Williams, I. D. *et al.* Responses of herbivorous fishes and benthos to 6 years of protection at
755 the Kahekili Herbivore Fisheries Management Area, Maui. *PLoS One* **11**, e0159100 (2016).
- 756 76. Ingeman, K. E., Samhour, J. F. & Stier, A. C. Ocean recoveries for tomorrow’s Earth: Hitting a
757 moving target. *Science (80-.)*. **363**, eaav1004 (2019).
- 758 77. Towle, E. K. *et al.* A national status report on United States coral reefs based on 2012–2018
759 data from National Oceanic and Atmospheric Administration’s National Coral Reef
760 Monitoring Program. *Frontiers in Marine Science* vol. 8 (2022).
- 761 78. Heenan, A., Williams, G. J. & Williams, I. D. Natural variation in coral reef trophic structure
762 across environmental gradients. *Front. Ecol. Environ.* **18**, 69–75 (2020).
- 763 79. Caldwell, Z. R., Zgliczynski, B. J., Williams, G. J. & Sandin, S. A. Reef Fish Survey Techniques:
764 Assessing the Potential for Standardizing Methodologies. *PLoS One* **11**, e0153066 (2016).
- 765 80. Froese, R. & Pauly, D. FishBase. World Wide Web electronic publication. www.fishbase.org
766 (2021).
- 767 81. Richards, B. L., Williams, I. D., Nadon, M. O. & Zgliczynski, B. J. A towed-diver survey method
768 for mesoscale fishery-independent assessment of large-bodied reef fishes. *Bull. Mar. Sci.* **87**,
769 55–74 (2011).
- 770 82. de Boyer Montégut, C., Madec, G., Fischer, A. S., Lazar, A. & Iudicone, D. Mixed layer depth

- 771 over the global ocean: An examination of profile data and a profile-based climatology. *J.*
772 *Geophys. Res. Ocean.* **109**, (2004).
- 773 83. Guillaume-Castel, R., Williams, G. J., Rogers, J. S., Gove, J. M. & Green, J. A. M. Quantifying
774 upwelling in tropical shallow waters: A novel method using a temperature stratification index.
775 *Limnol. Oceanogr. Methods* **19**, 566–577 (2021).
- 776 84. Bürkner, P.-C. brms: An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Softw.*
777 **80**, 1–28 (2017).
- 778 85. Sale, P. F., Doherty, P. J., Eckert, G. J., Douglas, W. A. & Ferrell, D. J. Large scale spatial and
779 temporal variation in recruitment to fish populations on coral reefs. *Oecologia* **64**, 191–198
780 (1984).
- 781 86. Milicich, M. J. Dynamic coupling of reef fish replenishment and oceanographic processes.
782 *Mar. Ecol. Ser.* **110**, 135 (1994).
- 783 87. Fox, M. D. *et al.* Gradients in primary production predict trophic strategies of mixotrophic
784 corals across spatial scales. *Curr. Biol.* **28**, 3355-3363.e4 (2018).
- 785 88. Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. *Mixed effects models and*
786 *extensions in ecology with R.* (Springer Science & Business Media, 2009).
- 787 89. McElreath, R. *Statistical rethinking: A Bayesian course with examples in R and Stan.* (Chapman
788 and Hall/CRC, 2020).
- 789 90. Bürkner, P.-C. Advanced Bayesian multilevel modeling with the R package brms. *arXiv Prepr.*
790 *arXiv1705.11123* (2017).
- 791 91. R Core Team. R: A language and environment for statistical computing. (2021).
- 792 92. Makowski, D., Ben-Shachar, M. S. & Lüdecke, D. bayestestR: Describing effects and their
793 uncertainty, existence and significance within the Bayesian framework. *J. Open Source Softw.*
794 **4**, 1541 (2019).
- 795 93. Kay, M. tidybayes: Tidy data and geoms for Bayesian models. *R package* (2022)
796 doi:10.5281/zenodo.1308151.
- 797 94. Smith, M. R. Ternary: an R package for creating ternary plots. *Zenodo. French Cons. Eur. pour*
798 *la Rech. Nucléaire (CERN), Geneva, Switzerland. doi* **10**, (2017).
- 799 95. Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P. & Makowski, D. performance: An R
800 package for assessment, comparison and testing of statistical models. *J. Open Source Softw.*
801 **6**, (2021).
- 802 96. Schloerke, B., Crowley, J. & Cook, D. Package ‘GGally’. *Ext. to ‘ggplot2.’ See* **713**, (2018).
- 803 97. Schiettekatte, N. M. D., Brandl, S. J. & Casey, J. M. fishualize: Color palettes based on fish
804 species. *CRAN version 0.2. 0* (2019).
- 805