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

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Nature Ecology and Evolution

Cyswllt i'r cyhoeddiad / Link to publication

1   **TITLE**

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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

MAIN TEXT

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

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

100   impacts on coral reefs globally widespread[38], 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[37]. Using a
105   standardised Pacific-wide set of reef fish surveys[43], 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 sources[46] – 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[47] 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[48]. 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.

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 (°) 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° 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° with the
167 sharpest increase between 0 to 5–10°, and plateauing around 30°. Conversely, total biomass and
168 primary consumer biomass plateaued around 10°, then declined from 30° (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 ($P(sdsSITE > \text{sdsISLAND}) \geq 0.99$; 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 ($P(sdsSITE >$
182 sdsECOREGION) ≥ 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 baselines[48], 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[18]) that may no longer
204   capture ecological patterns and processes in a human-dominated world[16].

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 shallows[32] 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 piscivores[28], 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 depth[25].
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[54] and limiting their positive benefits on the concentration of
224   zooplankton to greater depths[25]. 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[25]. Across latitudinal gradients, primary consumer biomass is higher in areas of greater
227   irradiance[29]. 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[34] and physical hydrodynamic interactions
233   with the benthos[54] in determining the delivery of nutrient-rich subthermocline water up onto
234   shallow reefs[26]. 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[31] 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 productivity[52], possibly
240 highlighting critical scale-dependency in localised upwelling processes created by physical features
241 like internal waves[36]. 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 atolls[31]. 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 composition[33]—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 groups[44], 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 zones[68]. 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 variance[70]. 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 redundancy[5].
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 scale[6]. Nonetheless, the importance of site-scale characteristics, indicated by this
312   intra-island heterogeneity, supports numerous studies that identify habitat availability[73], local
313   hydrodynamics[5], and local disturbances[16,63,74] as predominant mediators of the biomass of those
314   groups[6]. 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 production[3] 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 productivity[6]. 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[75] (assuming a source of larval supply),
328   habitat restoration, or better regulated destructive human activities[74]. Local management of
329   planktivores is no doubt also important[30], 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[28], more nuanced, region-specific targets for recovery[76] 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

METHODS

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[43]. 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 (°) 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 Islands[47]. 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
370 e07

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 visibility[43]. 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[43]. 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 (from[80]). 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 estimates[81] (*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 (°) 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 ≤ 30 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.

Statistical analysis

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

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

$$\log(\mu_{ji}) = \alpha + \beta X_i + Z_i \gamma$$

where α is the trophic group (or total biomass) specific intercept, β is a vector of population-level regression coefficients relating covariates X_i for observation *i* to the log of the expected biomass density μ_j. Group-level coefficients γ are estimated for random effects encoded in design matrix Z.

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

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

To understand whether the ecological organisation of coral fish assemblages in relation to these biophysical processes holds true across varying spatial scales, we first accounted for the inherent hierarchical structure in the data by including random intercepts for ecoregions, islands within ecoregions, and sites within islands (*sensu*[4]). We hypothesized that patterns of fish biomass across bathymetric gradients may track scale-dependent biophysical drivers that regulate energetic resource supply to shallow coral reefs[25,36,87]. For example, regional-scale oceanographic currents and sea-surface temperatures drive regional differences in primary production and net resource availability[3,87]. These net gradients in availability can be modified at smaller spatial scales by oceanographic features interacting with local bathymetry[31] such that, depending on the prevailing direction of internal tidal energy, upwelling processes can drive strong intra-island gradients in nutrient and planktonic resource supply among sites[25]. As potential indicators of these scale-dependent processes, we then measured the variation in reef fish biomass at these three hierarchical scales (sites within islands within ecoregions) and compared the proportion of the total 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 overdispersed[88]. 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[48]. 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 omnivores[46]) 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 squared[89]. An effective sample size of >1,000 was chosen to determine stable parameter
501 estimates[90]. 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 4.2.1[91]. Bayesian hierarchical models were implemented in

510   cmdstanr using *brms* 2.17.0[90]; probability of covariate effect direction was estimated with

511   *bayestestR* 0.10.0[92]; model information for querying posterior predictions was extracted with

512   *tidybayes* 3.0.2[93]; cross-spatial model variance was plotted with TernaryPlot in *Ternary* 1.2.3[94];

513   model fits assessed using r2_bayes in *performance* 0.9.2[95], and independence of model predictors

514   assessed with ggpairs in *GGally* 2.1.2[96]. Fish symbols used in figures were created with *fishualize*

515   0.1.0[97].

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).

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 <u>underlined</u>.

548

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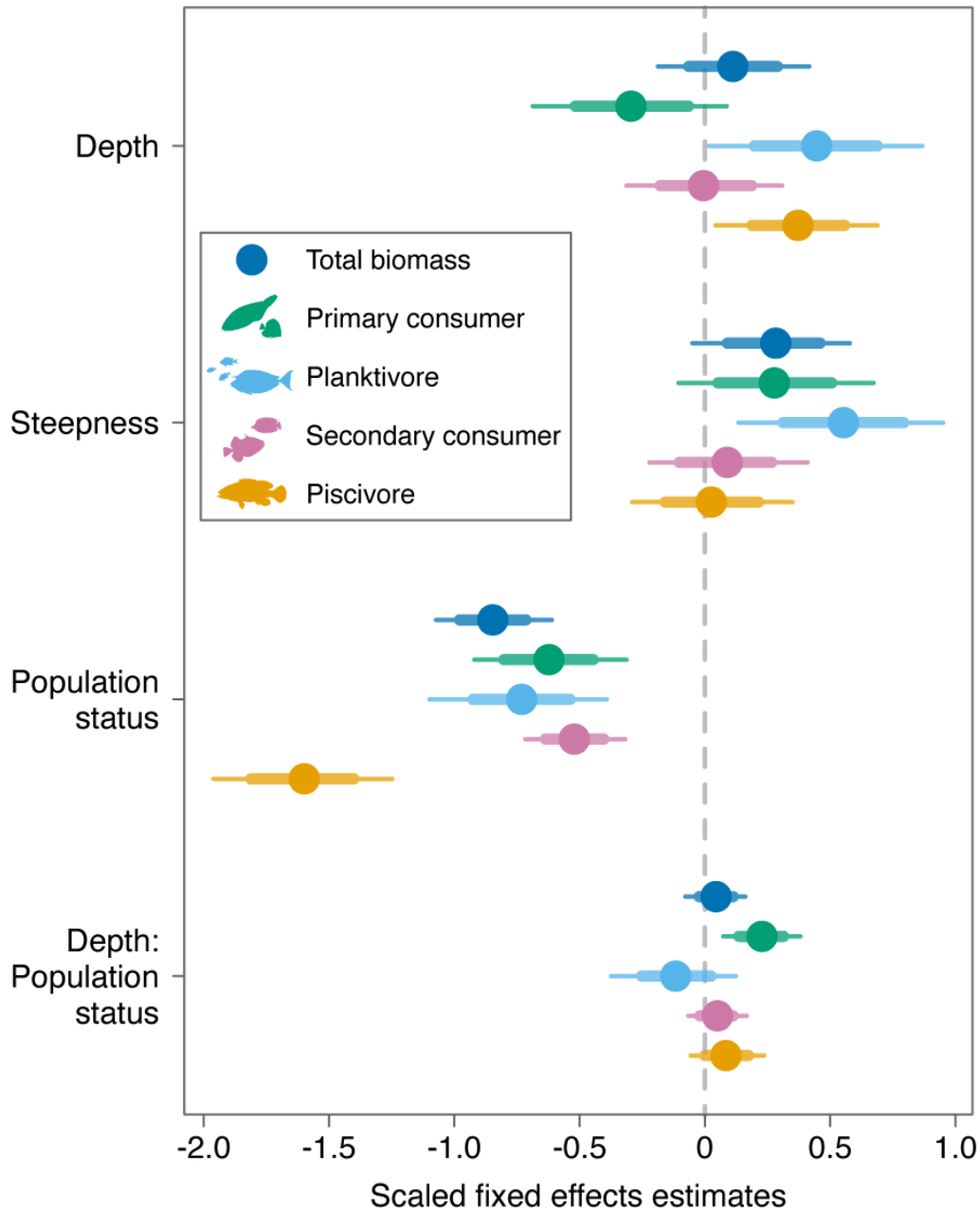
Figure 1 Relationships between coral reef fish biomass of distinct trophic groups and overall effects of shallow reef depth, bathymetric steepness, and human population status of islands (*Population status* indicates the effect of 'populated' by humans versus 'unpopulated'). Effect sizes are scaled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

563
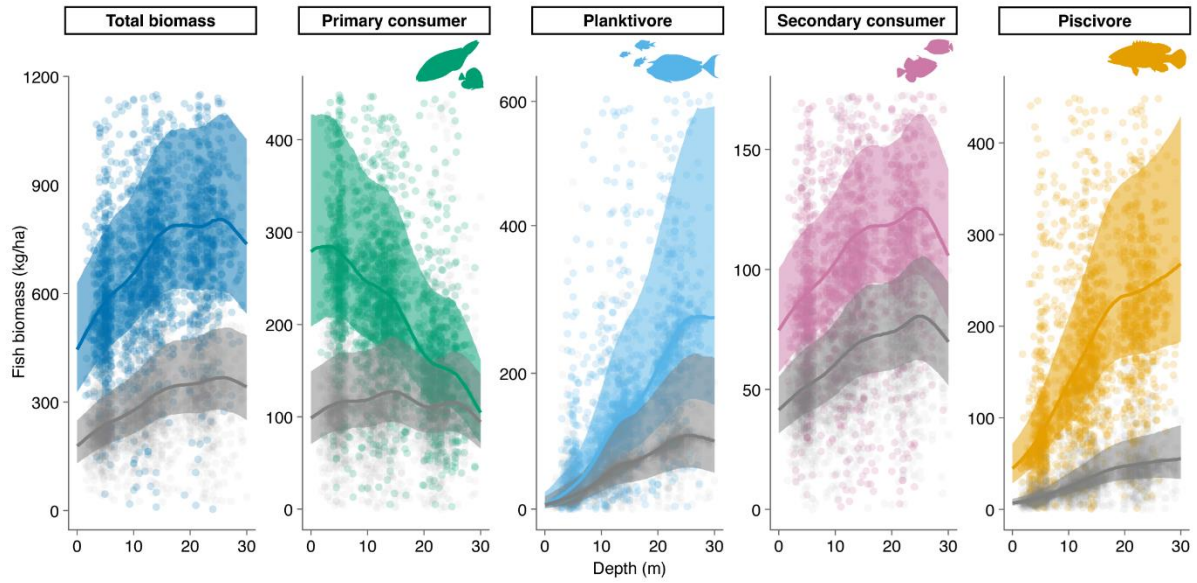
Figure 2 Coral reef fish biomass across a shallow depth gradient at unpopulated (colour) and populated (grey) islands.
Estimates represent conditional posterior medians (lines), 75% percentiles (shaded areas), and partial residuals (points) at the study mean value of bathymetric steepness. The y axis is limited to 1.05x the maximum value of the 75% CI so partial residuals exceeding axis limits are not displayed. *N* = 5,525 stationary point count (SPC) surveys (across 2,253 forereef sites, 35 islands, five ecoregions).
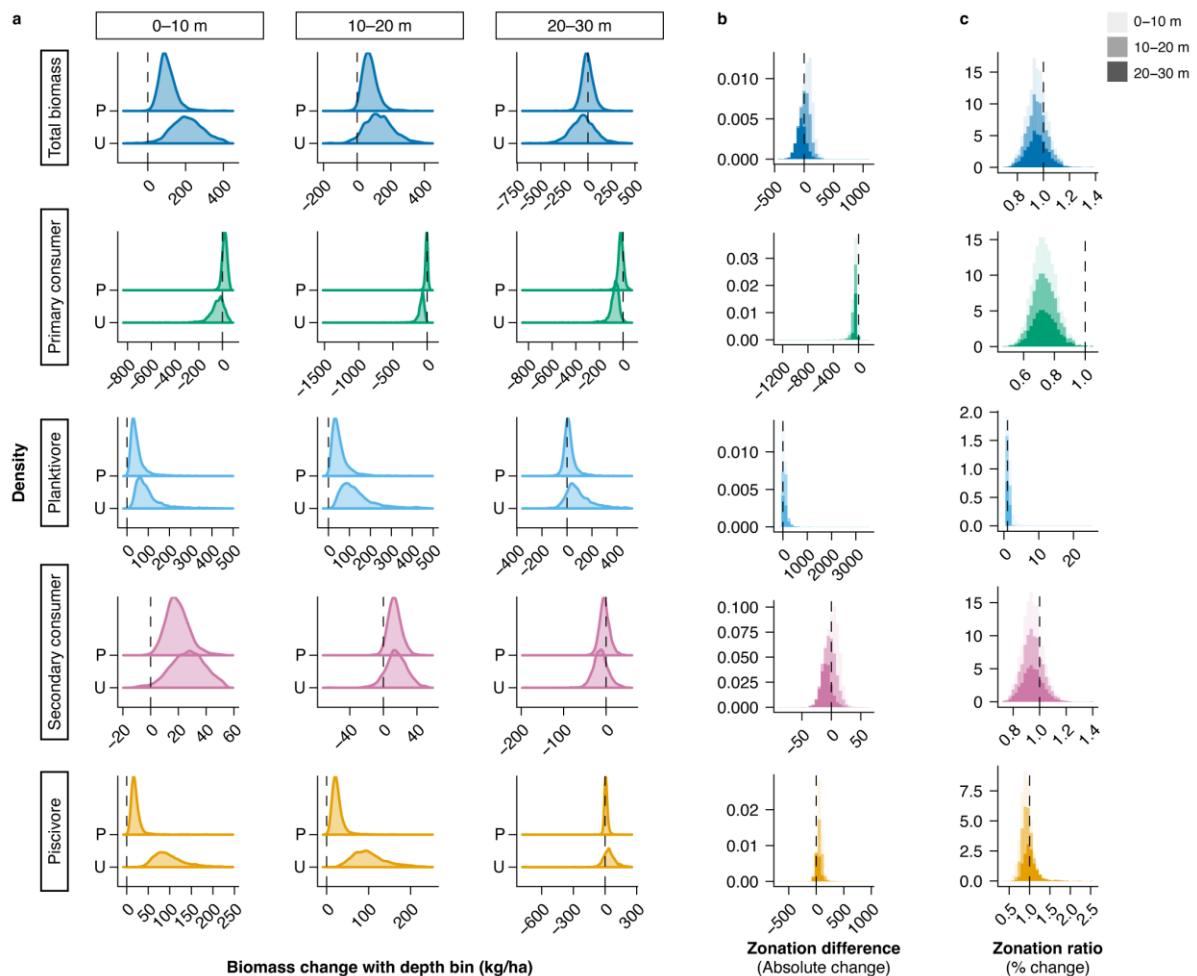
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570

Figure 3 Changes in reef fish biomass across shallow reef depth: A) Conditional posterior distribution of changes in biomass of each trophic group of fish (rows labeled on left) with each 10 m depth bin (columns labeled at top), at populated (P) and unpopulated (U) islands. **B)** Conditional posterior distributions of differences in zonation, measured as differences in absolute increase or decrease in biomass within each depth bin at populated versus unpopulated islands. **C)** Conditional posterior distributions of zonation ratios, measured as the ratio of percentage change in biomass in each depth bin at populated versus unpopulated islands. For example, panel A and B show a greater increase in absolute biomass of piscivores across depth bins at unpopulated islands than at populated islands (further right of the dotted line), but panel C shows that the zonation ratio of percentage change biomass is greater at populated islands in 0–20 m, spanning two bins (left of dotted line). All plots display change in biomass with depth standardized at the study mean value of bathymetric steepness.
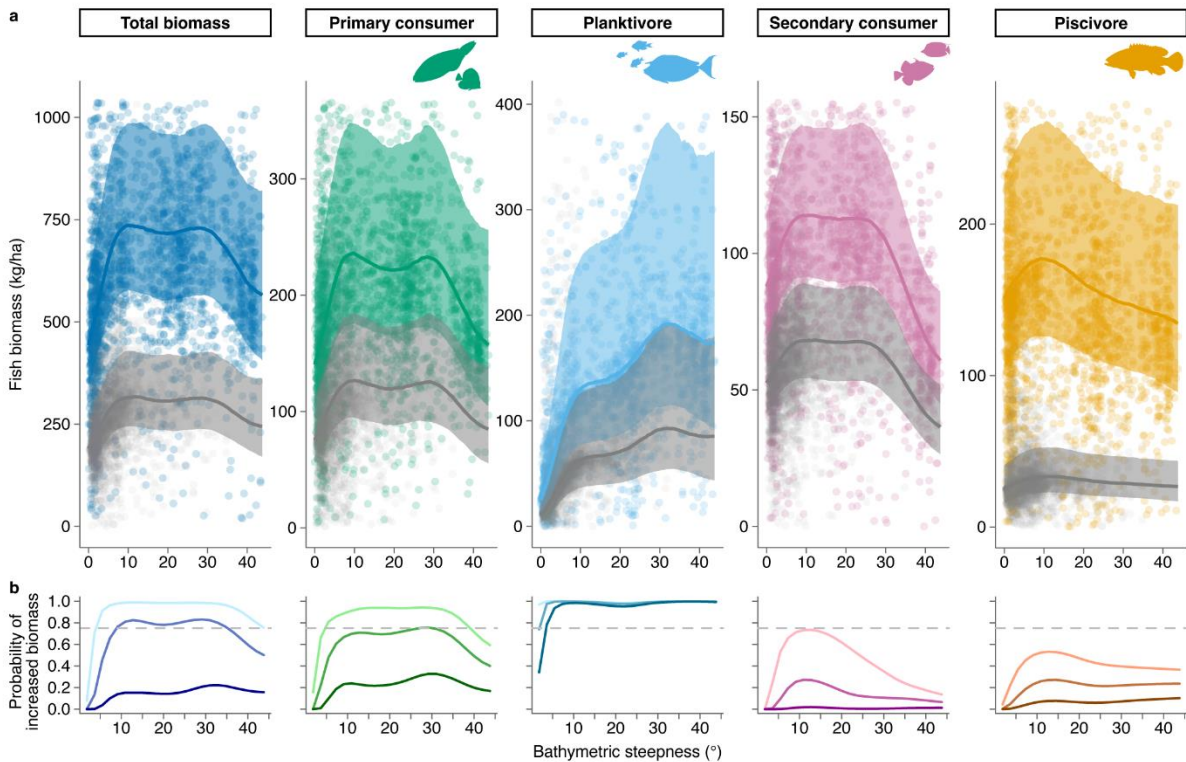
Figure 4 Coral reef fish biomass across a gradient of reef bathymetric steepness at unpopulated (colour) and populated (grey) islands. A) Estimates represent marginal (integrated over depths from 0–30 m) posterior medians (lines), 75% percentiles (shaded areas), and partial residuals (points) at the study-mean value of depth. The y axis is limited to the maximum value of the 75% CI so partial residuals exceeding axis limits are not displayed). *N* = 5,525 SPC surveys (across 2,253 forereef sites, 35 islands, five ecoregions). **B)** Probability of increased fish biomass with increasing bathymetric steepness from 0–44°. Coloured lines show the marginal posterior distribution derived probabilities of proportionate increases in reef fish biomass with increasing bathymetric steepness (°) among trophic groups. Shading of coloured lines represent probabilities of biomass increase by 25% (light), 50% (medium), and 100% (dark). Grey line dotted line highlights probability threshold of 0.75.

Figure 5 The proportion of residual variation in coral reef fish biomass explained by the hierarchical structure of site, 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 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 nested spatial scale (median SD estimates and CIs in Supplementary Table 10).

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