

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

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## **TITLE**

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

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## ABSTRACT

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

## KEYWORDS

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

## 54 MAIN TEXT

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

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

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

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

## RESULTS

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

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

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

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

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

## DISCUSSION

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

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

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

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

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

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



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

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

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

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

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

## METHODS

### Study location

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

### Reef fish survey data

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

#### Bathymetric reef steepness

We derived site-level estimates of bathymetric steepness ( $^{\circ}$ ) from depth mosaics created from multibeam SONAR, bathymetric LiDAR, and imagery derived depths in ArcGIS Pro v2.7 using the ‘Slope’ tool (Spatial Analyst) (Supplementary Table 2). Resulting mosaics ranged in spatial resolution from 5–50 m. Steepness estimates were calculated by averaging steepness values within a 400 m radial buffer around each replicate SPC site, and manually excluding backreef and lagoon areas and land-mass elevation using NOAA PIFSC ESD habitat map information. All analyses were done in the appropriate Universal Transverse Mercator zone for each island. A radial buffer-size of 400 m was selected to encompass depths that would capture the propensity for pulsed delivery of nutrient-rich sub-thermocline water by upwelling<sup>82,83</sup> and for this upwelling to propagate onto shallow reef habitats at depths  $\leq 30 \text{ m}$ <sup>31</sup> (maximum depth range within slope buffers: 596.2 m). Buffer-size extent was also selected to cover a reliable gradient in steepness while avoiding buffers-sizes that would easily extend across small island-masses to include bathymetry on opposite sides of the island. All sites were visually cross-checked for island overlap, and those including  $>5\%$  radial-buffer 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<sup>84</sup>. Fish biomass (biomass density; g m<sup>-2</sup>) was modelled separately for each trophic group and total fish biomass, using the following general model:

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

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

where  $\alpha$  is the trophic group (or total biomass) specific intercept,  $\beta$  is a vector of population-level regression coefficients relating covariates  $X_i$  for observation  $i$  to the log of the expected biomass density  $\mu_j$ . Group-level coefficients  $\gamma$  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<sup>31</sup>. 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<sup>30</sup>.

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<sup>85,86</sup>. 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*<sup>48</sup>), we were then able to estimate isolated population level effects (i.e. depth, human population status, bathymetric steepness) (*sensu*<sup>48</sup>). 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<sup>6</sup>.

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*<sup>4</sup>). 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<sup>25,36,87</sup>. For example, regional-scale oceanographic currents and sea-surface temperatures drive regional differences in primary production and net resource availability<sup>3,87</sup>. These net gradients in availability can be modified at smaller spatial scales by oceanographic features interacting with local bathymetry<sup>31</sup> 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<sup>25</sup>. 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*<sup>4</sup>). We quantified variation by extracting posterior standard

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

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

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

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

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

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

## DATA AND CODE AVAILABILITY

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

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## AUTHOR CONTRIBUTIONS STATEMENT

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 the methodology; A.H. contributed to survey data collection; T.L.K. provided NOAA's fish survey data; J.L., J.M.G. computed satellite derived bathymetric slope steepness estimates; L.E.R. and P.N. conducted the analyses with input from A.J.D.; L.E.R. led manuscript writing with input from A.H., 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 approved the final version for publication.

## COMPETING INTERESTS STATEMENT

The authors declare no competing interests.

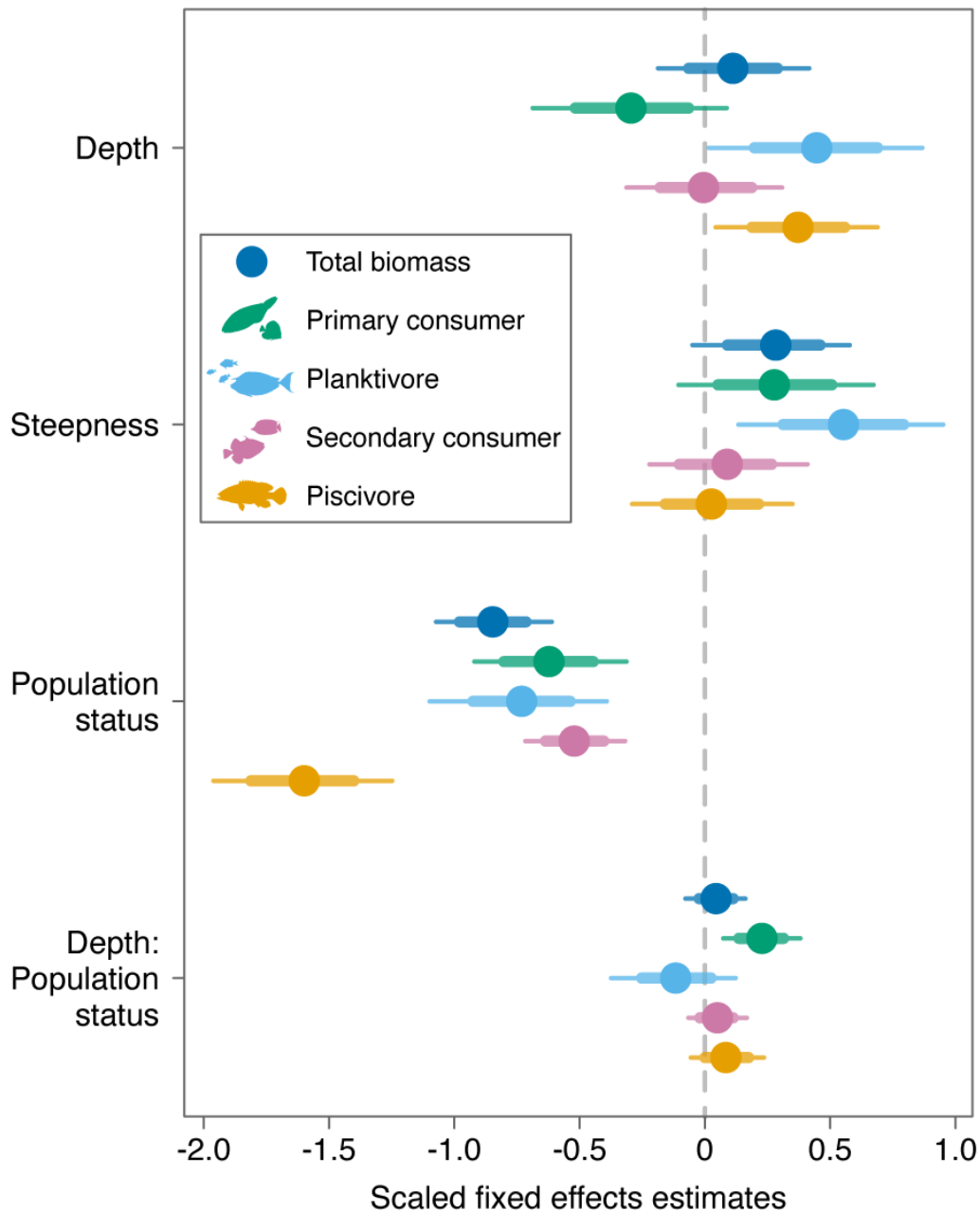
## TABLES

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

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

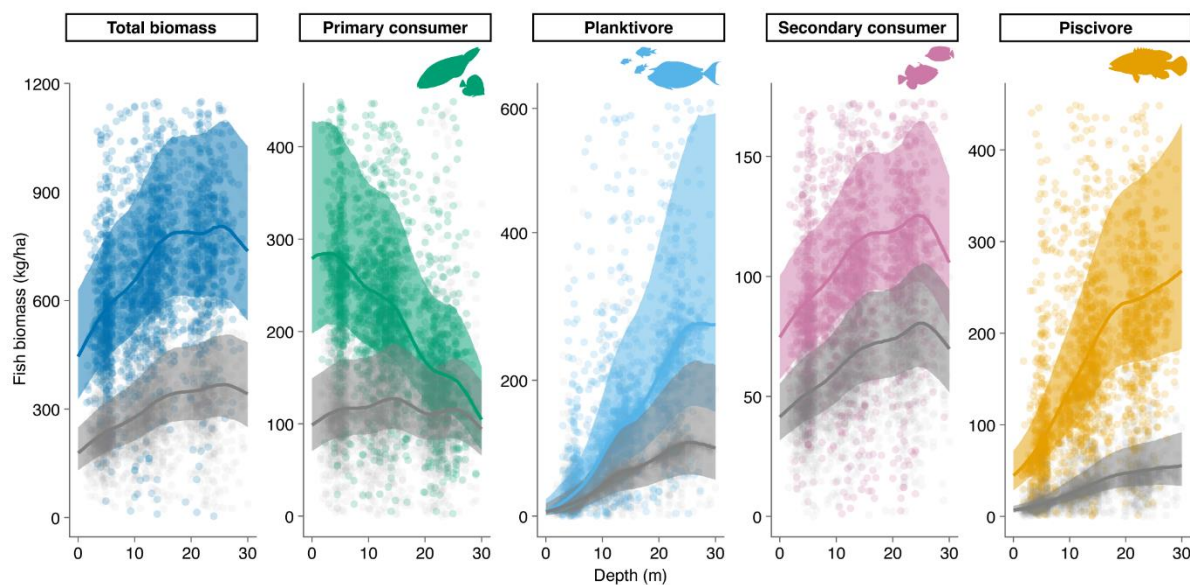
Probabilities  $\geq 75\%$  highlighted in bold. Probabilities  $\geq 75\%$  of the inverse difference (i.e., a high probability of a decrease in biomass with increasing depth) are underlined.

## FIGURE LEGENDS/CAPTIONS (FOR MAIN TEXT FIGURES)

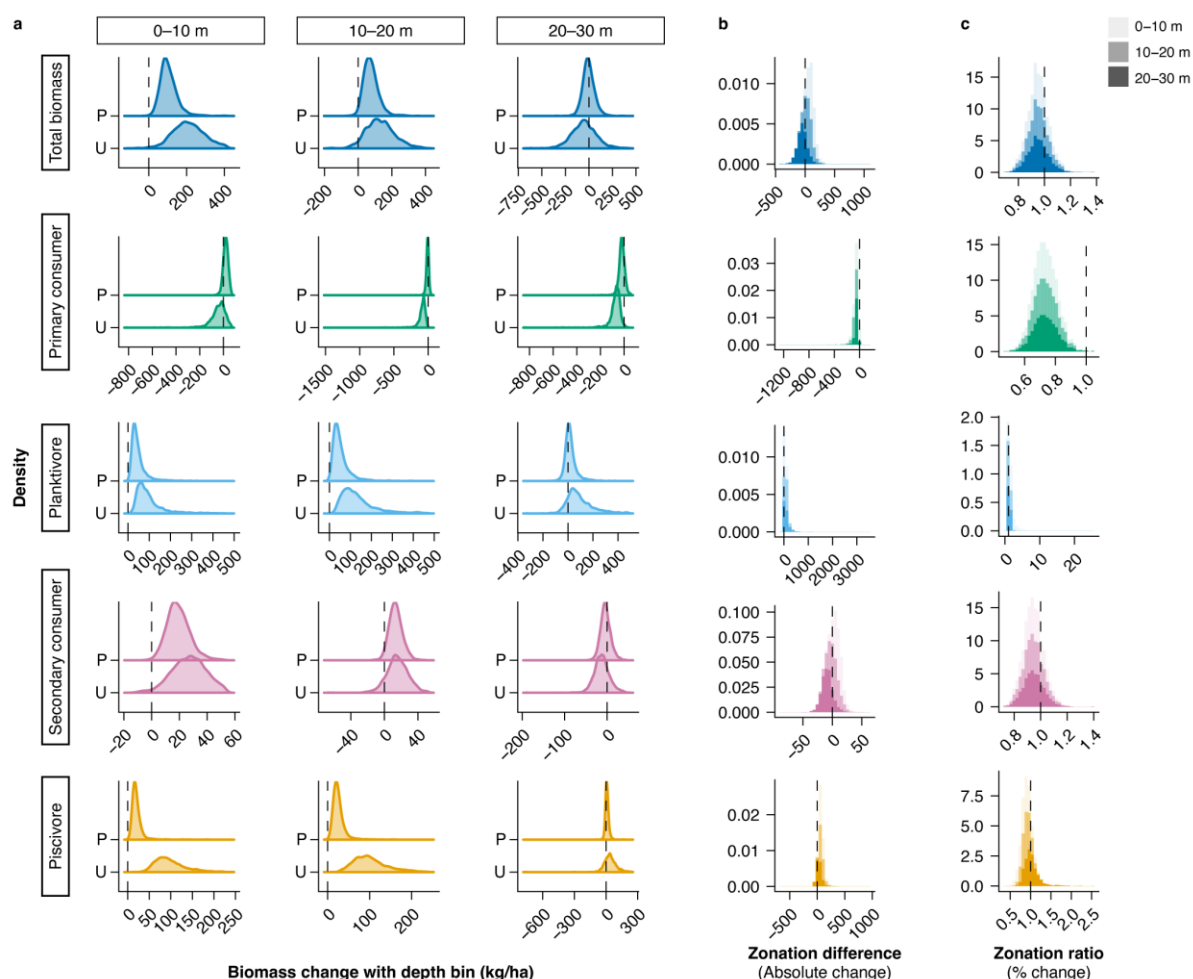


**Figure 1 Relationships between coral reef fish biomass of distinct trophic groups and overall effects of shallow reef depth, bathymetric steepness, and human population status of islands (*Population status* indicates the effect of ‘populated’ by humans versus ‘unpopulated’).** Effect sizes are scaled 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).

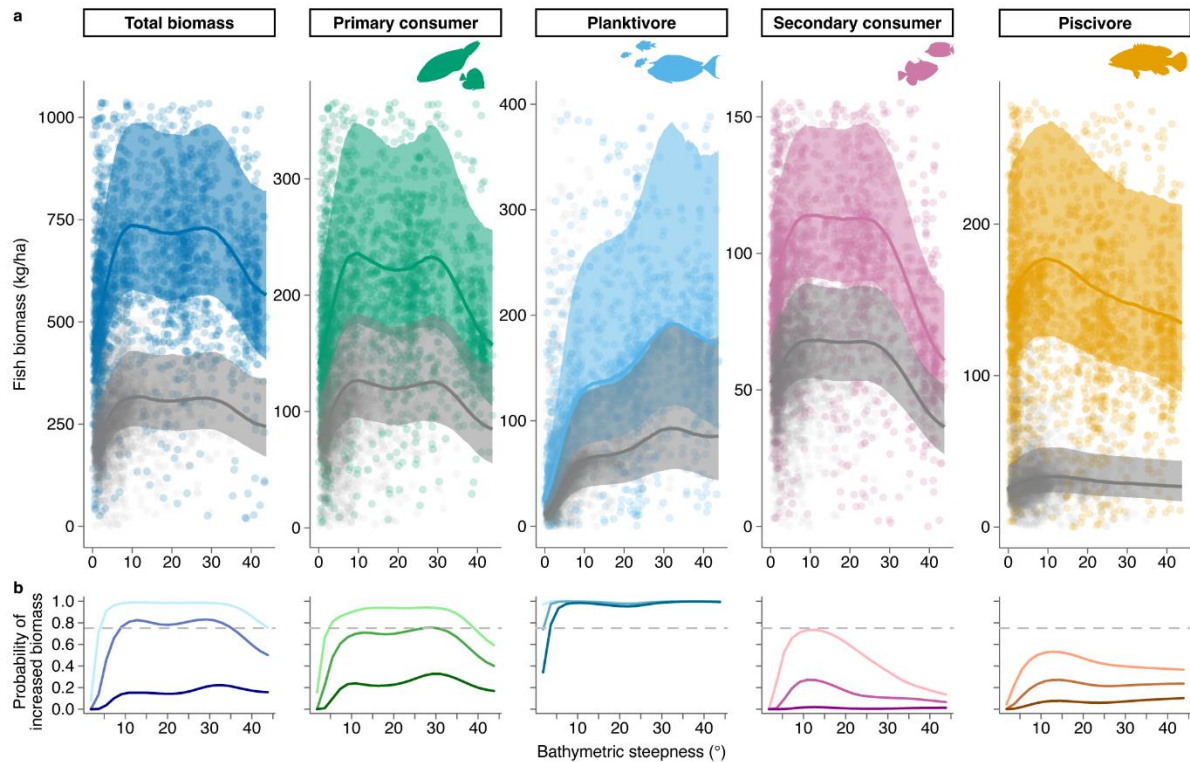




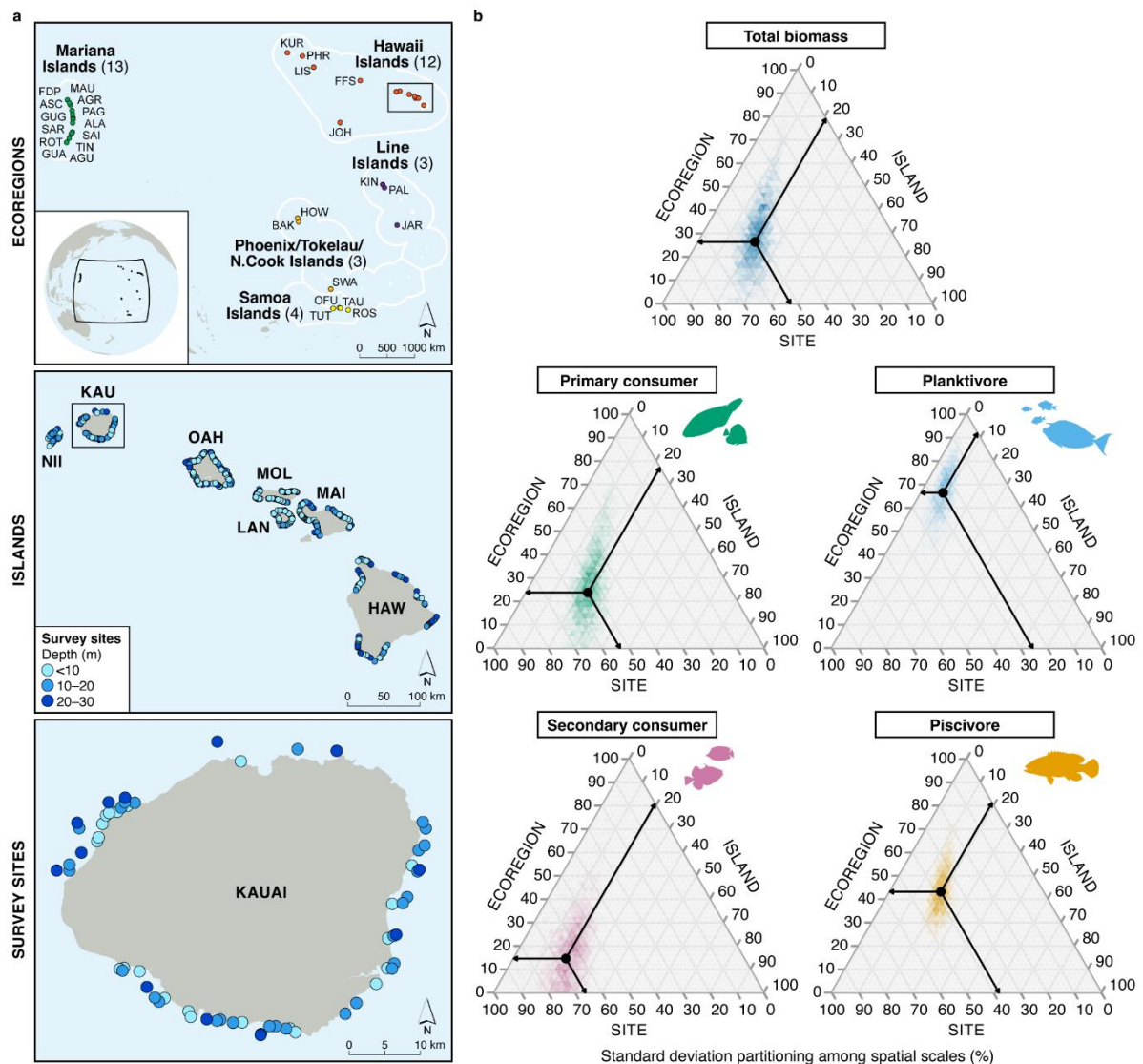
**Figure 2** Coral reef fish biomass across a shallow depth gradient at unpopulated (colour) and populated (grey) islands. Estimates represent conditional posterior medians (lines), 75% percentiles (shaded areas), and partial residuals (points) at the study mean value of bathymetric steepness. The y 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).



**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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