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LETTER

Fishing restrictions and remoteness deliver conservation outcomes for Indonesia's coral reef fisheries

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Abstract
Coral reef fisheries depend on reef fish biomass to support ecosystem functioning and sustainable fisheries. Here, we evaluated coral reefs across 4,000 km of the Indonesian archipelago to reveal a large gradient of biomass, from <100 kg/ha to >17,000 kg/ha. Trophic pyramids characterized by planktivore dominance emerged at high biomass, suggesting the importance of pelagic pathways for reef productivity. Total biomass and the biomass of most trophic groups were higher within gear restricted and no-take management, but the greatest biomass was found on unmanaged remote reefs. Within marine protected areas (MPAs), 41.6% and 43.6% of gear restricted and no-take zones, respectively, met a global biomass target of 500 kg/ha, compared with 71.8% of remote sites. To improve conservation outcomes for Indonesia's biodiverse and economically important coral reef fisheries, our results suggest to: (1) strengthen management within Indonesia's existing MPAs and (2) precautionarily manage remote reefs with high biomass.

KEYWORDS
data-poor fisheries, food webs, gear restrictions, marine protected areas, small-scale fisheries, South East Asia

1 | INTRODUCTION

Increasing human pressure affects the ecological functioning of tropical coral reefs (D'agata et al., 2016). Fishing can impact the flow of energy and productivity of reef food webs (Allgeier, Valdivia, Cox, & Layman, 2016) and the biomass needed to maintain ecological functions through retention of trophic structure (Graham et al., 2017; McCauley et al., 2018). For the management of multispecies and multigear fisheries common to tropical coral reefs, biomass-based targets (McClanahan et al., 2011; McClanahan, Graham, MacNeil, & Cinner, 2015) are proposed as an alternative to yield-based targets (Hilborn & Stokes, 2010).

Regional and global studies estimate average reef fish biomass in the absence of fishing at 740–1,300 kg/ha (Karr et al., 2015; MacNeil et al., 2015; McClanahan et al., 2011; McClanahan et al., 2019), however a majority (83%) of the world's fished reefs contain less half their expected biomass with severe consequences for ecosystem function and productivity (MacNeil et al., 2015). To sustain ecosystem functions and biodiversity, biomass targets of 300–1,000 kg/ha have been proposed for coral reef fisheries management (Graham et al., 2017; MacNeil et al., 2015; McClanahan & Jadot, 2017; McClanahan et al., 2011; see Table S1). While different ecosystem functions (e.g., coral accretion, herbivory, predation) require different biomass values, there is emerging consensus that 500–650 kg/ha is required to sustain reef fish productivity and energy flows among trophic levels (Graham et al., 2017; MacNeil et al., 2015; McClanahan et al., 2015).

Indonesia supports the highest number of reef fishers (Teh, Teh, & Sumaila, 2013) and is the second largest fish producer globally, with 55% sourced from coastal areas (CEA, 2018). Indonesia is committed to achieve 32.5 million hectares of MPAs, or 10% of Indonesia's EEZ, by 2030 (Indonesia Ministry of National Development Planning, 2019). Evaluating management effectiveness can be critical to achieving conservation outcomes from area-based targets (e.g., Campbell et al., 2012; Firmansah et al., 2017; Glew et al., 2015; Yulianto, Hammer, Wiryawan, & Palm, 2015); however, Indonesia's reefs are generally underrepresented in global coral reef assessments (e.g., MacNeil et al., 2015; McClanahan et al., 2019). Here we provide the first national assessment of biomass-based targets from surveys across 4,000 km of the Indonesian archipelago to (1) assess reef fish trophic structure across a large gradient of biomass from heavily fished reefs (<100 kg/ha) to remote reefs (>17,000 kg/ha) and (2) model the impacts of management and remoteness on coral reef fish assemblages.

2 | METHODS

2.1 | Field surveys

We conducted underwater visual surveys of coral reef fish assemblages in Indonesia across 36.9° of longitude and 14.9° of latitude, at 622 coral reef sites in 17 geographic regions (Figure 1). In total, we surveyed 5,208 replicate belt transects between depths of 1 and 13 m (median ± standard deviation, 7.0 ± 2.8 m), and the majority of transects were conducted between 1 and 8 m depth (n = 4,461 out of 5,208, or 85.7%). Surveys were conducted primarily on reef slope (n = 2,978 transects) and reef crest habitats (n = 2,090 transects), with a few transects from lagoons (n = 108 transects) and reef flats (n = 32 transects). Surveys were conducted between 2005 and 2016 and resulted in a database of 1,017 sites by year combinations ("surveys"); repeated surveys occurred at some sites (e.g., Aceh and Karimunjawa; n = 82 out of 622 sites, or 13.8%), which we accounted for in all regression models (see Supplementary Methods).

The size and abundance of reef fish were recorded on replicate 50 m transects, and the majority of surveys comprised 3–6 replicate transects on each survey (928 out of 1,017 surveys, or 91.2%). Small fish <10 cm were recorded using a 2 m transect width (200 m^2 area) and all other fish were recorded within 5 m transect widths (500 m^2 area) (Campbell & Pardede, 2006). On all transects, fishes were recorded to species and their abundance estimated to the nearest 5-cm size bin; the midpoint of each size bin was used to calculate biomass. Fish biomass (kg/ha) was estimated using species-specific length-weight relationships (Froese & Pauly, 2019; datamermaid.org). Nine highly trained and experienced observers conducted the surveys, and the effect of data observer was accounted for as a random effect in our linear regression models. For all analyses, 24 families were used that are diurnally-active, noncryptic, associated with coral reef habitats and contribute to the small-scale fishery in Indonesia (Table S2).

2.2 | Coral reef trophic pyramids

Observed reef fish species were identified to one of five trophic groups defined by FishBase: herbivore-detritivore, omnivore, planktivore, invertivore, and piscivore (Table S2). We used trophic groups to characterize the food web structure of reef fish assemblages, as trophic groups are generally synonymous with species guilds from different trophic levels within a food web and reflect biological roles as conduits for energy flows on reefs (Bellwood, Hughes, Folke, & Nystrom, 2004; Figure S1). On each transect, we calculated the relative biomass within each trophic group and constructed trophic pyramids based on the average of relative biomass of trophic groups within 1.0 log-unit biomass bins across the total gradient of fish biomass.

For trophic groups and trophic levels, we visualized changes in the trophic structure of coral reef food webs following Graham et al. (2017). Across a log-transformed gradient of total reef fish biomass (kg/ha), we fit third-order polynomial relationships with the relative biomass of five trophic groups, and visualized biomass pyramids across all sites, and by the four fisheries management regimes described below. We also evaluated trophic pyramids using trophic levels (as opposed to trophic group), which revealed similar and complementary patterns (Figure S2).

2.3 | Fisheries management and remoteness

Surveys occurred within four categories of management: (i) no-take zones where fishing activities are banned (n = 235 of

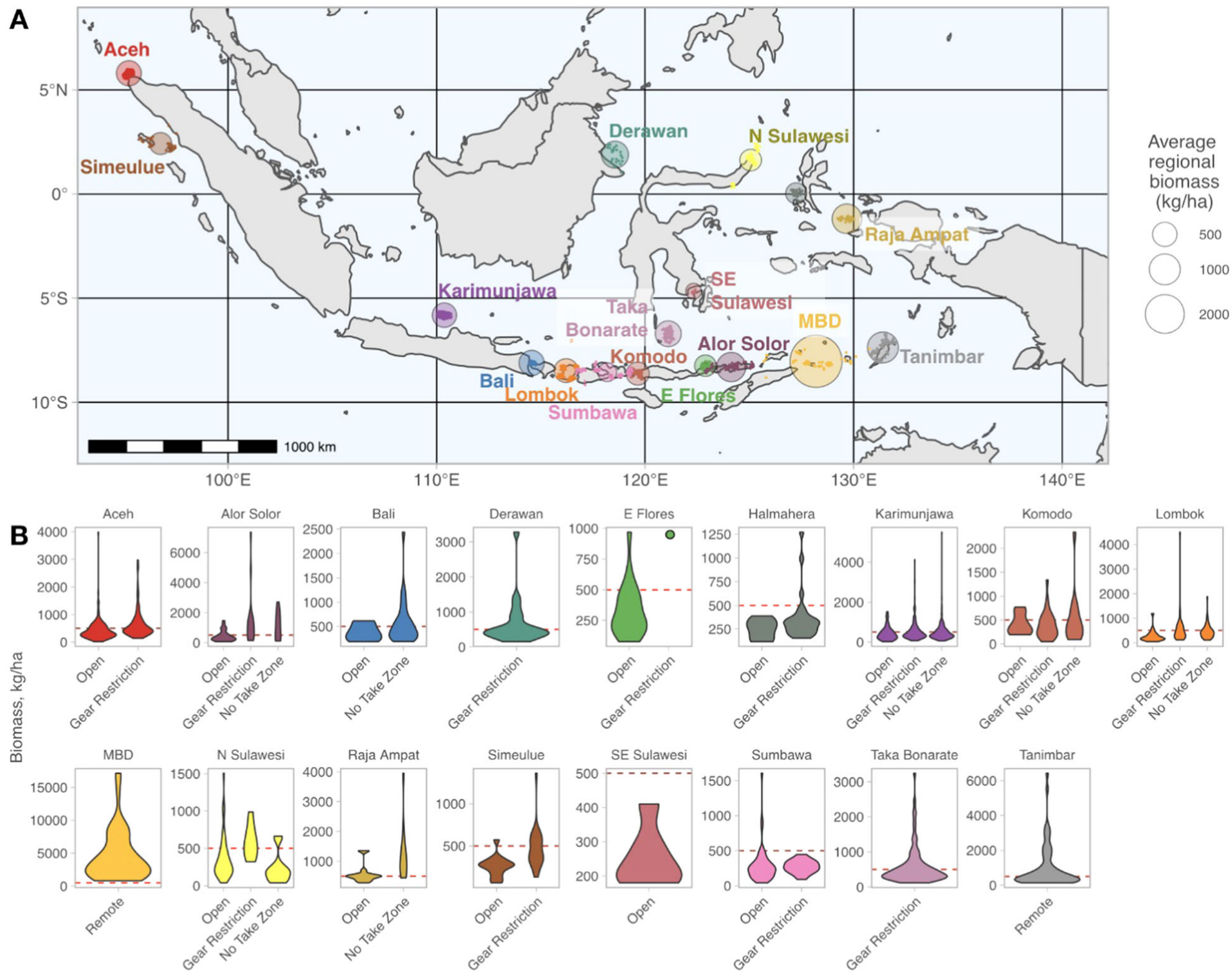

FIGURE 1 (A) Map of 622 coral reef survey sites across 4,000 km of the Indonesian archipelago. Colors and text labels identify the 17 broad geographic regions that surveys occurred in; MBD stands for Maluku Barat Daya. Bubble size identifies the total reef fish biomass averaged across each region; the regions of Maluku Barat Daya, Tanimbar, and Solor Alor have, on average, the highest observed reef fish biomass. (B) Violin plots show the distribution of total biomass across management categories in each region; the red dashed line indicates a previously proposed threshold for ecosystem function and fisheries sustainability at 500 kg/ha

1,017 surveys); (ii) gear-restricted management where fishing is allowed but certain gears are restricted ($n = 386$); (iii) open access sites typically located nearby managed areas, but could also occur inside managed "fishery use" zones ($n = 310$); and (iv) "remote" unmanaged sites that are typically >9 hours from population centers and markets compared to other fished sites (n = 86). Managed sites were located within 25 nationally or locally designated marine protected areas, and we recorded the number of years since legal implementation (using the first legal ordinance) and the size (ha) of each MPA when surveys were conducted (Table S3). Remote locations were determined based on surveyors' knowledge of accessibility by small-scale and commercial fishers to each reef (following Cinner et al., 2018; McClanahan et al., 2019), and corroborated with a global dataset on travel time (Maire et al., 2016) (Figure S3). We identified reefs in Maluku Barat Daya (MBD) and Tanimbar regions as remote (Figure 1), and these reefs were, on average, 8.5 times further away from larger cities (median travel time in hours ± SD: 26.3 ± 9.1 hours) compared to open access reefs (3.1 ± 4.7 hours). For a definition of population centers and market gravity, see Cinner et al. (2018).

2.4 | Data analysis

To explore relationships between the trophic structure of fish communities and the key environmental and socioeconomic variables, we performed a redundancy analysis (RDA) multivariate ordination. This summarizes the main patterns of variation of the relative biomass of the five trophic groups related to linear combinations of environmental and socioeconomic variables.

To evaluate the drivers of total biomass and the biomass of each trophic group, we used linear mixed-effects regression

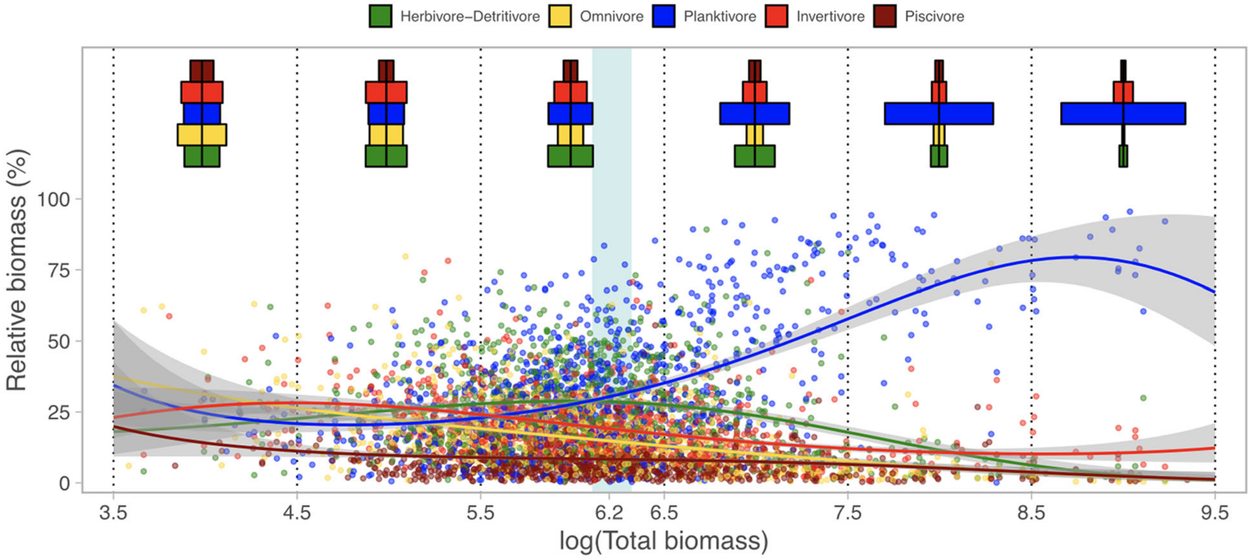

FIGURE 2 Change in reef fish trophic pyramids across a biomass gradient. Relative biomass indicates the relative biomass of each trophic group relative to total biomass estimated on 5,208 transects. Mean trophic pyramid shape is based on the average relative biomass within each 1.0 log-unit interval. Lines show third-order polynomial trends lines with 95% confidence intervals and the blue-shaded region indicates a proposed benchmark of ~500 kg/ha that supports ecosystem function and fisheries sustainability. Trophic groups within pyramids are ordered from lowest to highest mean TL (see Figures S1 and S2)

models to evaluate the influence of depth, habitat, human gravity, coastal and oceanic productivity, management type, and MPA characteristics. Productivity and gravity covariates, data preparation, model structure, and diagnostics are described in the Supplemental Methods.

3 | RESULTS

Our dataset reveals a large gradient of site-level reef fish biomass from 19.7 kg/ha to 17,127.9 kg/ha (mean = 666.0 kg/ha, median ± standard deviation, 386.2 kg/ha ± 1,148.6 kg/ha). Generally, unique trophic structures of reef fish assemblages emerged above 500–650 kg/ha total biomass (Graham et al., 2017; MacNeil et al., 2015) (Table S1). Caesionid planktivores dominated trophic pyramids at high biomass (>1,800 kg/ha or log 7.5, Figures 2 and 3); Figure S4 describes species composition at high-biomass sites. At high biomass (>1,800 kg/ha or log 7.5), herbivore-detritivores and omnivores were higher in no-take zones and gear restricted sites, and invertivores were higher in remote sites, relative to openly fished sites (Figure 3). Absolute biomass of invertivores and herbivores-detritivores was maintained or increased above 1,800 kg/ha (log7.5) (Figures S5 and S6).

Multivariate ordination by RDA found that planktivores tended to be associated with deeper and remote reefs (Figure S7). However, linear relationships provided by RDA have a weak explanatory power as only 15.4% of the variation in the trophic structure of fish communities. Thus, other variables are required to better explain the trophic structure of fish communities, including the hierarchical structure of the data that we account for in linear mixed-effect models.

Linear mixed-effects models describe the results of management and remoteness, human gravity, habitat and primary productivity for total biomass (Table 1) and for biomass of trophic groups (Tables S5–S9). For management and remoteness, gear restrictions were associated with significantly higher biomass of all reef fish, herbivore-detritivores, omnivores, and planktivores (relative to open access sites); no-take reserves were associated with a higher biomass of all reef fish, herbivores-detritivores, and planktivores; and remote sites were associated with a higher biomass of all reef fish, planktivores, and invertivores. All groups were positively associated with MPA age. Market gravity was associated with significantly less total biomass, and the biomass of all trophic groups with the exception of planktivores. The gravity of human settlements—a broader indicator of any accessible human population, not just markets—was negatively associated with only herbivores. Depth, habitat, and productivity also showed significant relationships with various trophic groups. Transects at deeper depths had significantly higher biomass of planktivores, invertivores, and piscivores, while reef slopes supported higher planktivore biomass. Reef crests were associated with a higher biomass of omnivores and invertivores, compared to reef slopes. And sites with higher coastal productivity were negatively associated with herbivores-detritivores and omnivores; oceanic productivity was positively associated with herbivores-detritivores.

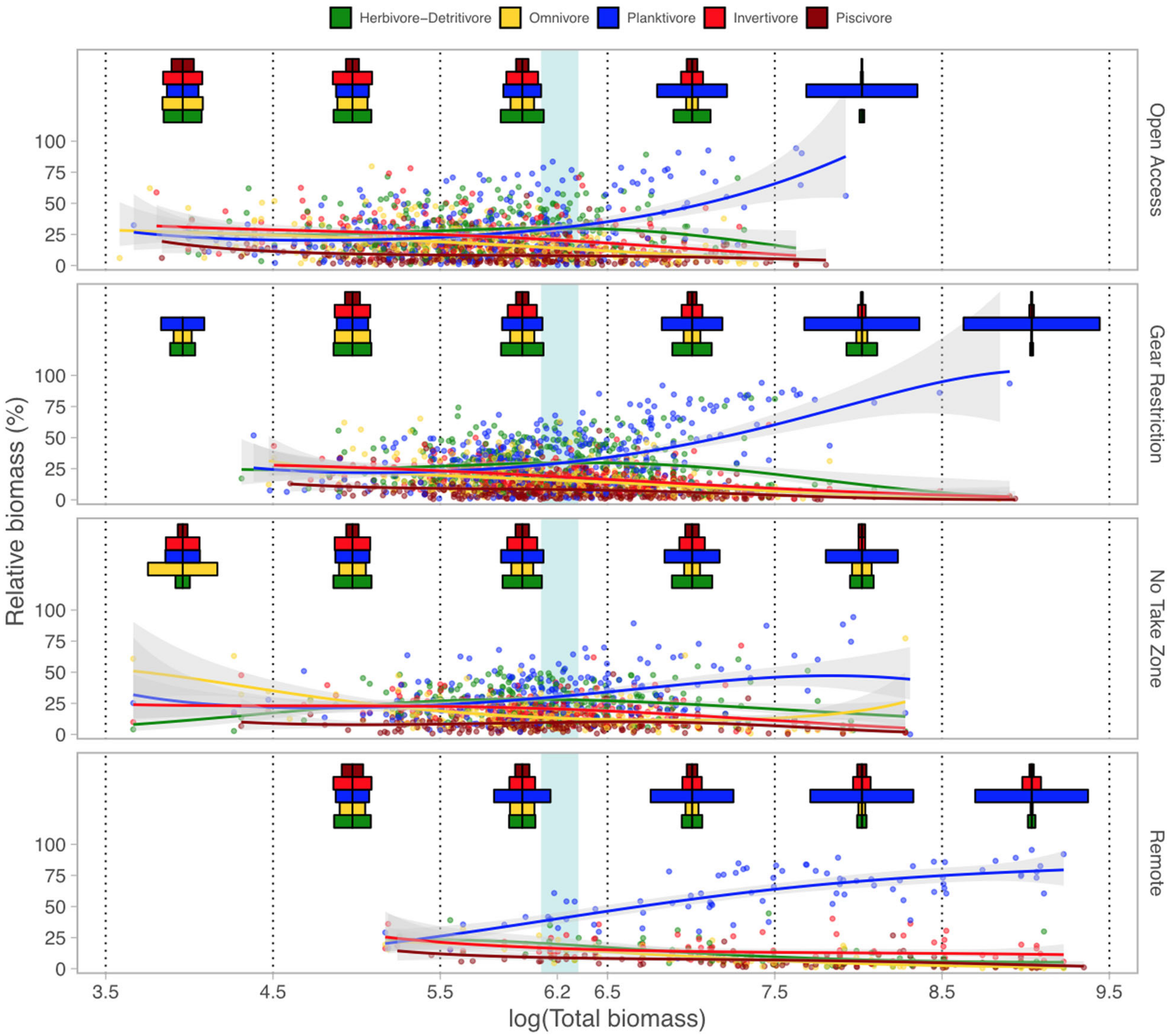

FIGURE 3 Change in relative food web structure across a biomass gradient of total reef fish biomass (kg/ha) within four fisheries management types. Lines show third-order polynomial trends lines with 95% confidence intervals and the blue-shaded region indicates a proposed benchmark of 500 kg/ha ecosystem function and fisheries sustainability

Total reef fish biomass at remote sites was, on average, 4.6 times higher than open access sites (remote: 1432.1 ± 3258.8 kg/ha SD; open access: 309.8 ± 346.8 kg/ha SD). Total biomass in no-take reserves (445.4 ± 553.5 kg/ha) and gear restricted sites (427.1 ± 634.9 kg/ha) was ~1.4 times higher than open access sites (Figure 4; Table S4). Comparing site-level biomass to a global biomass target of 500 kg/ha (Table S1), we found that 71.8% of remote sites exceeded this target, compared to 25.3%. 41.6%, and 43.6% of open access, gear restricted and no-take sites, respectively (Figure 4; Table S4). Considering a "conservation" biomass target of 1,150 kg/ha (McClanahan et al., 2015), 53.0% of the remote sites exceeded this target, compared to 3.6%, 10.9%, and 8.0% of open access, gear restricted and no-take sites, respectively (Figure 4; Table S4).

4 | DISCUSSION

Indonesia's reefs support one of the largest reported gradients of coral reef fish biomass in the world, from <100 kg/ha to >17,000 kg/ha, comparable to other global (MacNeil et al., 2015; McClanahan et al., 2019) and regional studies (Graham et al., 2017; Karr et al., 2015). Across this gradient, unique trophic structures typically emerged above 500 kg/ha, a finding consistent with global benchmarks of fisheries sustainability and ecosystem function (Graham et al., 2017; MacNeil et al., 2015; McClanahan et al., 2011). At high levels of biomass, trophic pyramids became dominated by planktivores, a finding consistent across unmanaged, managed and remote reefs and comparable with Pacific reefs where biomass is greatest at intermediate consumer levels

TABLE 1 Mixed-effect model results of total biomass (kg/ha) evaluated for the effects of depth (m), habitat, human gravity, productivity, fisheries management and remoteness. Management type and habitat are categorical variables; categorical coefficients are relative to the intercept of slope (habitat) and open access fished sites. Tables S5–S9 present results for each of the five trophic groups. Bold text indicates significance levels below $p < 0.05$. Model random structure accounted for observer and the hierarchical design of surveys (see Supplement)

	Total reef fish biomass		
Predictors	**Estimates**	**95% CI**	***p*-value**
Intercept	5.67	5.17 to 6.18	**<0.001**
Depth	0.56	0.40 to 0.72	**<0.001**
Habitat, crest	0.15	–0.00 to 0.29	0.052
Market gravity	–0.31	–0.45 to –0.17	**<0.001**
Gravity of nearest settlement	–0.05	–0.15 to 0.06	0.377
Net primary productivity	–0.09	–0.19 to 0.02	0.112
Oceanic productivity	0.07	–0.17 to 0.30	0.586
Management, gear restriction	0.39	0.25 to 0.53	**<0.001**
Management, no-take	0.27	0.12 to 0.43	**0.001**
Management, remote	1.60	0.54 to 2.66	**0.003**
MPA age	0.84	0.61 to 1.07	**<0.001**

Marginal R^2/conditional R^2 0.285/0.758

(Heenan, Williams, & Williams, 2019). In addition to the dominance of planktivores, sites with very high biomass (i.e., >1,800 kg/ha or log 7.5) also showed increases in herbivore-detritivores including parrotfish at managed sites, and increases in invertivores including jacks, sweetlips, snappers and groupers at remote sites. In general, these patterns of unique trophic structure emerging at high biomass are consistent with global benchmarks of remote coral reef wilderness (1,101.6–1,926.5 kg/ha, McClanahan et al., 2019).

The dominance of planktivores at high biomass suggests very high levels of productivity may be subsidized by pelagic processes and access to plankton-rich oceanic waters (Morais & Bellwood, 2019). Indonesian reefs therefore could be described as "middle-driven or convex" systems where trophic structure is predicted by energy into the middle of the food web (Heenan et al., 2019). They contrast with bottom-driven, high-biomass Western Indian Ocean (WIO) reefs characterized by greater herbivore biomass (Graham et al., 2017), perhaps because the fringing and platform reefs typical of the WIO are associated with reef-based productivity of turf algae and herbivores. Indonesia's reef slopes likely have greater access to pelagic subsidies from oceanographic transport through currents, tidal waves, or deep-water upwelling, which may subsidize reef productivity when planktivores move off the reef to access and bring back oceanic primary productivity into reef food webs (Morais & Bellwood, 2019). Surprisingly, we found no relationship between planktivore biomass with modeled estimates of primary productivity, suggesting that remotely sensed global models may not be detecting effects of local currents or other biophysical processes that we believe are driving plankton enrichment at the surveyed sites. Although planktivores are commonly removed from reef studies as their schooling behavior can bias biomass estimates, planktivores contribute to fisheries and food supply

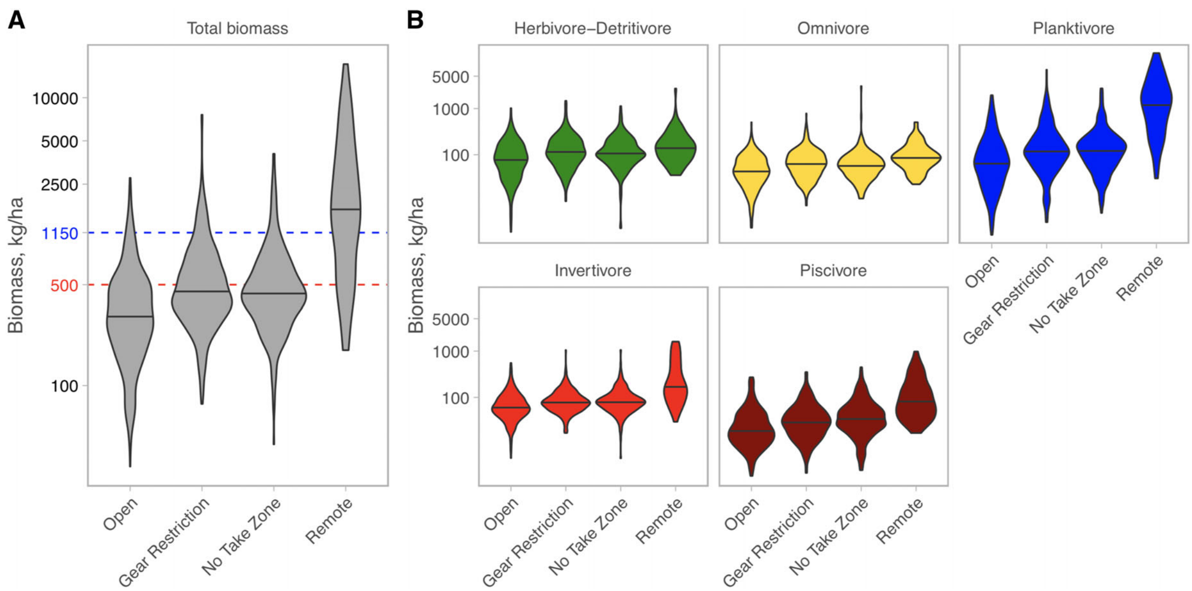

FIGURE 4 Comparison of (A) total reef fish biomass and (B) the biomass of five trophic groups across four management types in Indonesia. Violin plots show density distribution of points within 95% credible intervals; solid black lines are median values. The red dashed line shows a global biomass reference point of 500 kg/ha for total reef fish (MacNeil et al., 2015), and the blue dashed line indicates a conservation biomass target of 1,150 kg/ha (McClanahan et al., 2016)

(McDonald et al., 2018; Russ, Aller-Rojas, Rizzari, & Alcala, 2017; Yusrizal, Simbolon, & Solihin, 2018). Removing planktivores from survey analyses risks losing important information on pelagic energy transfer to reef systems and the ecological function on planktivores on reefs (Russ et al., 2017).

Comparing management approaches across Indonesia, our findings suggest similar biomass levels within no-take reserves and sites with fishing restrictions. One on hand, the biomass of total reef fish, herbivore-detritivores, omnivores, and planktivores increased at managed sites to suggest positive ecological outcomes can result from fishing gear restrictions (e.g., net bans) (Campbell, Edgar, Stuart-Smith, Soler, & Bates, 2018; MacNeil et al., 2015). However, for higher trophic-level invertivores like groupers, snappers, jacks, emperors and sweetlips, our findings suggest only deep habitats, low market gravity and remoteness protect their biomass in Indonesia. For these fish, even when nonselective gears (e.g., nets, traps) are banned, more targeted controls on selective gears (e.g., spearguns) are also required especially in areas that are moderate to highly populated by people (Campbell et al., 2018; Cinner et al., 2009). For Indonesia, this finding implies that if MPAs are to elevate total biomass and ecosystem functioning above the levels of gear-based management (McClanahan, Maina, Graham, & Jones, 2016), permanent closures require: (1) strengthening of customary or local co-management institutions (Cinner et al., 2012), (2) stronger community compliance than has been shown to date (Bejarano, Pardede, Campbell, Hoey, & Ferse, 2019), (3) a demonstration that they confer equitable benefits to strengthen legitimacy and compliance (Glaser, Breckwoldt, Deswandi, Radjawali, & Ferse, 2015), and (4) be of sufficient size to protect home ranges of roaming fishery targets like piscivores (Green et al., 2014).

The exceptionally high biomass in remote areas suggests the importance of precautionary management for Indonesia's remote reefs. Median biomass of remote reefs was above the 1,150 kg/ha proposed as a conservation target (McClanahan et al., 2015), and was also substantially higher than biomass observed within managed and unmanaged areas. Biophysical modelling of larval dispersal from these reefs further suggests that they may act as larval sources aiding recovery of nearby and more distant reefs (Treml & Halpin, 2012). Biomass gains associated with remote reefs are likely associated with low market gravity (Cinner et al., 2018) as, on average, remote reefs were 26 hours from major population centers or markets, or 8.5 times further away than open access reefs. The prevalence of customary management on these reefs might also limit unsustainable fishing through access rights, gear restrictions and periodic closures (Harkes & Novaczek, 2002).

While older MPAs benefited all trophic groups, most MPAs at the time of surveys were young (<10 years), which may explain the lack of effect by gear management and no-take reserves on higher-trophic reef fish like invertivores and piscivores, which can require 30–40 years of recovery time (MacNeil et al., 2015). Within gear restricted and open access sites, 41.6% and 43.6% of sites, respectively, exceeded a biomass benchmark of 500 kg/ha, compared to 25.6% of fished reefs. On remote reefs, 71.8% of our surveyed sites exceeded 500 kg/ha, suggesting the need for continued biomass gains through improved long-term management and compliance.

4.1 | Conclusions

In one of the first national assessments of Indonesia's coral reefs, we found that total reef fish biomass and trophic structure was responsive to both management and remoteness. This implies that MPAs and remote areas both contribute to critical ecosystem functions on Indonesia's coral reefs. Multiple-use MPAs that include fishing gear restrictions and permanent fishing closures support higher reef fish biomass than open-access reefs in Indonesia, but no-take management did not provide additional conservation outcomes from gear restrictions. This finding may be associated with weak compliance of no-take management or the slow recovery of species in response to permanent closures. To increase compliance and effective conservation outcomes, management should adopt holistic approaches including formal comanagement where local fishers are granted managed access of marine resources for long-term sustainability (Glaser et al., 2015; Gómez & van Vliet, 2018). We also find that remote sites can protect globally high levels of fish biomass, and suggest these sites require precautionary management to avoid overexploitation by commercial and small-scale fisheries. In general, applying a 500 kg/ha management guideline to Indonesia's coral reef fisheries can provide managers with tangible targets when evaluating conservation and management outcomes. These measures may help achieve the ambitious objectives to increase Indonesia's MPA coverage to 32.5 million hectares by 2030, and support national commitments to biodiversity, food security and livelihoods through the Convention on Biological Diversity and the Sustainable Development Goals (Indonesia Ministry of National Development Planning, 2019).

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ETHICS STATEMENT

Work was permitted under memoranda of understanding with the Indonesian Ministry of Environment and Forestry (WCS, TNC) and the Ministry of Marine Affairs and Fisheries (WWF). No fauna or flora were collected or manipulated.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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