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Effects of management objectives and rules on marine conservation outcomes

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Abstract

Understanding the relative effectiveness and enabling conditions of different area-based management tools is essential for supporting efforts that achieve positive biodiversity outcomes as area-based conservation coverage increases to meet newly set international targets. We used data from a coastal social-ecological monitoring program in six Indo-Pacific countries to analyze whether social, ecological, and economic objectives and specific management rules (temporal closures, fishing gear-, species-specific restrictions) were associated with coral reef fish biomass above sustainable yield levels across different types of area-based management tools (i.e., comparing those designated as marine protected areas [MPAs] with other types of area-based management). All categories of objectives, multiple combinations of rules, and all types of area-based management had some sites that were able to sustain high levels of reef fish biomass – a key measure for coral reef functioning– compared with reference sites with no area-based management. Yet the same management types also had sites with low biomass. As governments advance their commitments to the Kunming-Montreal Global Biodiversity Framework and the target to conserve 30% of the planet’s land and oceans by 2030, we found that although different types of management can be effective, most of the managed areas in our study regions did not meet International Union for the Conservation of Nature criteria for effectiveness. These findings underscore the importance of strong management and governance of managed areas and the need to measure the ecological impact of area-based management rather than counting areas because of their designation.

Introduction

As global marine biodiversity continues to decline, efforts to conserve the ocean through area-based management tools are increasing (Gorud-Colvert et al. 2021), yet understanding of biodiversity outcomes associated with diverse tools other than marine protected areas (MPAs) is limited (but see McClanahan et al. [2015]). Over the past decade, global commitments to the Convention on Biological Diversity (CBD) Aichi Biodiversity Targets have guided national conservation efforts (CBD 2010; Bingham et al. 2019). Parties to the CBD have now agreed to new targets under the Kunming-Montreal Global Biodiversity Framework (CBD 2022) that set the global conservation agenda for the next decade, including the commitment to protect and conserve 30% of the planet's land and oceans by 2030 ('30 x 30'). Foundational to the 30x30 target are protected areas, defined as “a geographically defined area, which is designated or regulated and managed to achieve specific conservation objectives” (CBD 2006). In the ocean, marine protected areas (MPAs) are an effective conservation tool for biodiversity conservation in some contexts (Edgar et al. 2014; Zupan et al. 2018b), and there is growing recognition that other forms of area-based management can have positive conservation outcomes without conservation-focused objectives (e.g., Jupiter et al. 2014; Gurney et al. 2021; Reimer et al. 2021).

The potential of area-based management tools other than protected areas to contribute to maintaining biodiversity is now at the forefront of international policy (CBD 2022). Notably, other effective area-based conservation measures (OECMs) are included in the Kunming-Montreal Global Biodiversity Framework, defined as “a geographically defined area other than a

Protected Area, which is governed and managed in ways that achieve positive and sustained long-term outcomes for the in situ conservation of biodiversity, with associated ecosystem functions and services and, where applicable, cultural, spiritual, socioeconomic, and other locally relevant values” (CBD 2018). Area-based management has different objectives and applies a diverse suite of rules to achieve those objectives. Assessing conservation effectiveness of OECMs is a challenge (Claudet et al. 2022), and an improved understanding of the outcomes for species, resources, and ecosystems is needed to know how different area-based management tools can achieve positive biodiversity outcomes. In particular, protected area coverage is often reported as a positive outcome, but coverage alone does not guarantee benefits for biodiversity (McClanahan et al. 2015; Relano & Pauly 2023). Key gaps in understanding as CBD Parties and the conservation community grapple with the relative role of protected areas and OECMs in meeting global area-based targets to conserve biodiversity include the role of the motivations (i.e., objectives) and rules of different area-based management tools and the role of MPAs and OECMs.

Objectives of marine area-based management tools are diverse. Marine protected areas (MPAs) usually have biodiversity conservation as a primary objective, whereas other managed areas, including those that could potentially be recognized as OECMs, often have a range of objectives, not necessarily including biodiversity conservation. These include sustainable use, fisheries management, community well-being, food security, exclusive local use, and maintaining traditional practices (Mcleod et al. 2009; Jupiter et al. 2014). Some studies show that these areas can be successful in meeting ecological and social goals (Cinner et al. 2012; Goetze et al. 2018). They are commonly managed by communities for local objectives, whereas MPAs are often

implemented and thus managed through government agencies or their designates (UNEP-WCMC et al. 2018). A gap remains in understanding whether area-based management tools with biodiversity-focused objectives – be they MPAs or other managed areas – are more effective at achieving key ecosystem functions, such as sustaining high reef fish biomass, than those with socially focused objectives (e.g., OECMs or other community management types). Coral reef fish biomass is often correlated with coral reef fish species diversity and is a good predictor of fishery yields and therefore a good proxy for biodiversity outcomes and ecosystem services independent of area (McClanahan 2015; McClanahan 2022). It is used extensively as a measure of area-based conservation outcomes (e.g., Edgar et al. 2014; Zupan et al. 2018b; Di Lorenzo et al. 2020).

Studies about the effectiveness of conservation in achieving biodiversity gains (hereafter, conservation effectiveness) commonly focus on levels of protection, with no-take areas thought to be most effective (Grorud-Colvert et al. 2021). Formal rules are influential in managing wealthy nation fisheries (Melnychuk et al. 2021), but less is known about relationships between tropical fish biomass and more specific rules-in-use (but see Zupan et al. [2018b]). For area-based management tools focused on fisheries management, rules can include species restrictions (e.g., only some species or sizes can be fished), fishing gear restrictions (e.g., only some gears allowed), and temporal restrictions (e.g., only some times of the year open to fishing) (e.g., Horta e Costa et al. 2016; Campbell et al. 2020). Whether some of these types of rules are less or more effective at maintaining high reef fish biomass than no-take areas is not fully understood (McClanahan 2015).

Despite numerous studies on the conservation effectiveness of marine area-based management tools, especially MPAs, there has been little research that characterizes how different objectives and rules-in-use can provide conservation benefits. We used the metric of high reef fish biomass. We sought to examine how conservation outcomes are influenced by the motivations (i.e., objectives) of different forms of area-based management tools and the restrictions therein (i.e., the rules) and how some area-based management tools could qualify under the new concept of OECMs and the enabling conditions that drive their effectiveness. Specifically, we examined the following questions: are there certain rules-in-use that influence the likelihood of having high reef fish biomass; are certain management objectives associated with a greater likelihood of high reef fish biomass; do MPAs and other managed areas achieve sustainable levels of reef fish biomass; how can the definition of and guidance about OECMs (CBD 2018; IUCN-WCPA 2019) be applied to specific area-based management sites when data are limited? We focused on coral reef systems and used data from a multi-country social-ecological systems monitoring effort (Gurney et al. 2019). We referred to areas that meet the OECM definition but did not yet have consent of governing actors as “potential OECMs.” (See Table 1 for our operationalization of the CBD definition.)

Methods

We used data from a social-ecological systems monitoring program of the Wildlife Conservation Society (WCS) developed through a transdisciplinary process: Marine and Coastal Monitoring (MACMON)(Gurney et al. 2019, wcs.org/coral). The WCS has implemented the program in 6 countries across the Indo-Pacific: Kenya, Madagascar, Mauritius, Indonesia, the Solomon

Islands, and Fiji (Fig. 1). The MACMON framework is the first marine operationalization and implementation of Nobel prize winner Elinor Ostrom's (2009) influential social-ecological systems framework for monitoring conservation practice across multiple countries (Cox et al. 2021). These six countries and the respective sites were included in the monitoring program because they have ongoing spatial management through long-term partnerships with WCS. We used data collected in 126 villages through key informant interviews about the local area-based management rules ($n = 381$), local country expert validation, and underwater visual census of reef fishes (895 transects at 201 reef sites). Detailed data collection protocols and interview guides are documented in Gurney and Darling (2017). Data were collected in the field from 2012 to 2019 by local reef practitioners and national scientists. All social and ecological surveys were compliant with ethics specified by the WCS Institutional Review Board. Fish biomass summaries are available on MERMAID for most sites, dashboard.datamermaid.org. Code and other data are available upon request (see Appendix S1)

Management categories

We considered 3 types of area-based management tools in our research: MPAs, areas designated as such by their country; other area-based management, areas with area-based management but not designated or reported as MPAs by countries (hereafter other managed areas); and reference sites, areas without active area-based management (Table 1).

We further examined the other managed areas to assess whether any meet the definition of other effective area-based managed area (potential OECM). We include *potential* because governance

authorities had not yet consented to their inclusion as OECMs. Guidelines to assist countries in identifying potential OECMs have been developed by the task force established through the International Union for Conservation of Nature (IUCN) (IUCN-WCPA 2019) and are being drafted by Food and Agriculture Organization of the United Nations (FAO) specifically for the fisheries sector (para. 17[e] of the 34th Session of the FAO Committee on Fisheries) (FAO 2021).

Our study was a first attempt to examine more closely how to operationalize the concept of OECMs drawing on data from monitoring programs across multiple countries. We used the CBD definition (CBD 2018) and IUCN guidelines (IUCN-WCPA 2019) to draft a set of scoping questions to ask experts about each managed area, governance and management arrangements, and long-term intentions (Table 2). These responses were collected from 2020 to 2022. To gauge achievement of positive biodiversity conservation outcomes, we classified sites based on their ability to sustain fish populations above biomass thresholds of reef fishes reported in the literature: biomass of ≥ 500 kg/ha for sustaining reef functions and ≥ 1000 kg/ha as akin to unfished areas. We refer to sites that have biomass of ≥ 500 kg/ha as having high reef fish biomass or high biomass (MacNeil et al. 2015; McClanahan 2015; McClanahan et al. 2015). Reef fish biomass is a useful metric for assessing coral reef condition across broad geographies (MacNeil et al. 2015; McClanahan et al. 2021) and is linked to many of the objectives of area-based management (e.g., ecosystem health, short- and long-term yields, improved livelihoods) (Smallhorn-West et al. 2022). This operationalization was a first attempt to investigate differences in and relationships between biomass, rules, and objectives between MPAs and other forms of area-based management in coral reef social-ecological systems.

Data description

Our focal scale was spatially contiguous areas that shared a common set of rules, which we called zones ($n = 95$). Eighty zones had area-based management, and 15 were reference sites, where additional area-based management was limited or absent and only national rules applied. Two countries did not have reference sites (Solomon Islands, Fiji) because all surveyed reefs were managed to some extent within customary fishing ground boundaries.

We summarized information about rules for each zone based on key informant interviews, which specifically asked about rules related to gears, times, and species. We used key informants to identify the rules because not all the zones had written management plans and because we were interested in the rules-in-use (i.e., the rules being followed on the water). In-country experts then reviewed and updated the information based on their local knowledge and experience working at these sites. Each type of rule had four categories: none (no rules), limited, moderate, and all gears, times, or species prohibited (no take) (details in Appendix S2). We developed these categories based on the range of rules provided by key informants. In-country experts shared information about the main management objective or objectives, which we coded into three categories: biodiversity only; social, economic, cultural (SEC); or both. We also coded them into more detailed categories (hereafter detailed objectives) (Appendix S3). In-country experts provided information about the size of the zones and age category (young, <5 years; medium, 5-15 years; old, ≥ 16 years; including those with customary tenure). Biomass data were collected with standard underwater visual census surveys of belt transects. Data were processed in the

open source data application MERMAID (datamermaid.org), which uses standard length-weight conversions for observations of reef fish abundance and size classes. We averaged total reef fish biomass by zone from underwater survey data (mean kilograms per hectare of 22 common coral reef fish species [Appendix S4]). Sixty-eight of the 95 zones had associated biomass data.

Objectives, rules, and reef fish biomass in area-based management tools

We used hierarchical cluster analysis of variables to examine the range of objectives and rules used in area-based management and whether some rules or combinations of rules linked to specific objectives. We clustered only the rules, then rules and objectives categories, and finally added management type. This identified co-occurrence across rules, objectives, and management. We ran stability plots to see whether and how many clusters emerged. We visualized objectives and rules by management type (Table 1) and used Fisher's exact tests to explore the relationships. See Appendices S1-S10 for additional details and references.

We used Bayesian multilevel models to examine the effects of objectives, rules, and types of area-based management tools on fish biomass. To better isolate the effects of management from other factors affecting biomass and avoid overparameterization of our models, we first examined the relationship between biomass and the various site attributes summarized at the scale of our analyses (zones): reef habitat type, depth, size and age of managed area, human gravity (function of population size and reef accessibility [Cinner et al. 2018]), and distance to deep water (proxy for isolated sites, one of the contributors of large biomass [Edgar et al. 2014]) in a random forest

model. Based on the model results of variable importance, we excluded deep water given its limited predictive power (see Appendix S1).

We then ran three separate models for total biomass (log) and rules, objectives, and management, respectively, with normally distributed priors, 10,000 iterations, and four chains. We included the reference sites not locally managed in the models to compare zones with and without area-based management. We treated rules as ordinal factors and tested for linear relationships, hypothesizing that stricter rules would be associated with higher biomass. We coded objectives and management types as categorical variables; each category was compared with a reference category (none for objectives, reference for management). Not all zones had associated biomass data. For analyses that included biomass, we excluded zones with missing data (Table 1). We included standardized covariates (z scores) of depth, size (log), and gravity, fixed factors of management age (ordered factor) and reef habitat (categorical variable), and the random factor country in all models.

Results

In the 80 managed zones from six countries, temporal, gear-, and species-specific rules were applied at varying levels of restrictions (Fig. 2). Gear-use-associated rules were most common. Objectives that encompassed both biodiversity and social, economic, and cultural (hereafter referred to as ‘social’) objectives were most common, followed by those with only social objectives (Fig. 3a). When coding objectives in detailed categories (detailed objectives), many

detailed objectives existed across all area-based management tools analyzed. Sustainable use was the most common, followed by biodiversity conservation (Fig. 3c).

Various combinations of gear, temporal, and species rules occurred in area-based management, such that rules did not cluster in a meaningful way (Appendix S8). Fisher's exact tests indicated no statistical differences between the rules applied to zones with different categories of objectives. The exception was that species rules were different in zones that had biodiversity versus social objectives and in zones that had both biodiversity and social objectives versus social objectives only (Appendix S5).

The MPAs had the highest proportion of biodiversity-only primary objectives (Fig. 3b,d). Primary objectives that were either focused on social only or encompassed both biodiversity and social were present for all area-based management tools (Fig. 3). Other managed areas had more diverse objectives than MPAs, whereas MPAs tended to have biodiversity or sustainable use objectives (Appendix S5). Detailed objectives (Fig. 3c and d) had insufficient sample sizes for statistical analyses. Area-based management tools, including MPAs, comprised a range of sometimes similar or the same rules and objectives (Appendix S5). For example, the same rules were found within MPAs and, for instance, locally managed marine areas.

Biomass varied greatly by rules, objectives, and management (Fig. 4), and the Bayesian multilevel model results showed no clear patterns as to which objectives, rules, and area-based management tools had high biomass when accounting for site attributes (Fig. 5). Objectives were not related to biomass, although areas with social and both objectives had the most variability (including the highest biomass), and those with both had the highest median biomass (Fig. 4d).

Plotting the rules pointed to a potentially greater biomass when temporal and gear rules existed compared with having no rules in place and showed high variability for each category of rules (Fig. 4). Similarly, the raw data depicted a pattern of increasing median biomass from reference, MPAs, and other management (Fig. 4e) and for sites that had objectives compared with no objectives (Fig. 4d). Observed patterns in the raw data were partially due to differences in countries, but country effects were accounted for in Bayesian multilevel models (Fig. 5). These models did not show the differences apparent in the raw data; the posterior estimates for MPAs and other management overlapped substantially.

When applying our operationalization of the OECM criteria to other managed sites and considering the ≥ 500 kg/ha biomass threshold as an indicator of effectiveness, 15 out of 37 (41%) met all criteria (Table 2). Of the five criteria in the definition, achieving positive outcomes for in situ biodiversity, with biomass as an indicator, was most commonly missed. Only five out of 37 zones met all potential OECM criteria at the ≥ 1000 kg/ha biomass threshold. If the potential OECM criteria were also applied to MPAs – which they currently are not – many MPAs in our study region did not meet them. Twelve of 20 zones (60%) in MPAs did not meet the ≥ 500 kg/ha biomass threshold, and 11 of 37 did not meet the “governed and managed” criterion (Table 2). Only two out of 20 MPA zones met all potential OECM criteria at the ≥ 1000 kg/ha biomass threshold. The average biomass in reference sites was 226 kg/ha, compared with 720 kg/ha in other area-based management and 532 kg/ha in MPAs. Breaking down the other area-based management category further, potential OECMs at the ≥ 500 kg/ha biomass threshold had an average biomass of 788 kg/ha; potential OECMs at the ≥ 1000 kg/ha biomass threshold had an average biomass of 1667 kg/ha in pOECM1000; and area-based management that did not meet the OECM criteria had an average biomass of 474 kg/ha. The average biomass for

areas-based management that did not meet the OECM criteria was close to 500 kg/ha, largely due to inclusion of certain sites with high biomass that failed to meet other OECM criteria.

Discussion

Our results illustrate the diversity of rules, objectives, and management tools employed in area-based management and that their multiple configurations can lead to reef fish biomass above the sustainability threshold. At the same time, much of our results indicated there were no clear average relationships among the type of area-based management tool (i.e., MPAs or other area-based management), objectives, rules, and high biomass. Our study makes three important contributions to informing discussions regarding the value of different types of management tools in meeting global conservation goals (Grorud-Colvert et al. 2021; Jonas et al. 2021). We first found that there were many paths to achieving conservation effectiveness: our data included areas characterized by diverse objectives and multiple combinations of temporal, gear, and species rules that could sustain high levels of reef fish biomass. Yet the same categories also had sites with low biomass, and statistical patterns influencing biomass were not discernable. These results highlight the importance of tracking outcomes and supporting a range of locally appropriate area-based management tools in conservation that are achieving conservation outcomes (Reimer et al. 2021).

Our results that not all MPAs had conservation objectives also indicated that there was not a consistent application of the CBD MPA definition in practice, consistent with regional interrogations of the World Database of Protected Areas (Jupiter & Govan 2022). Indeed, while

MPAs are supposed to have biodiversity conservation as the primary objective as required by the CBD definition, our own experience with what countries report to the CBD highlights that actions to meet these objectives and reporting on progress on meeting these objectives were not always in place (Jupiter & Govan 2022). Tools, such as The MPA Guide, may help resolve definitional challenges in the future and shed light on MPA protection levels (Grorud-Colvert et al. 2021).

Our finding that there were no consistent combinations of objectives or rules associated with high reef fish biomass aligns with research indicating that there is no one-size-fits-all solution to fit all contexts and that management must strive to be locally appropriate for effective outcomes (e.g., Ostrom & Cox 2010). Other studies show that, if well designed and managed, no-take areas (sensu Horta e Costa et al. 2016) – be they MPAs or other managed areas – consistently result in higher biomass than areas that allow some use (e.g., Edgar et al. 2014; Sala et al. 2018). However, together with emerging studies (e.g., Campbell et al. 2020; Reimer et al. 2021; Fidler et al. 2022), our findings showed that areas allowing sustainable use can still support biomass above key thresholds. Utilizing multiple area-based management tools – MPAs and other managed areas – can help ensure that management fits its social-ecological context and supports diversity and redundancy in the global conservation system in terms of tools and associated governance arrangements (Gurney et al. 2021). Similarly, a study about fisheries management actions showed that benefits of having multiple actions are cumulative and that a broad suite of management measures is key to sustaining fish populations (Melnychuk et al. 2021). We suggest that recognizing and supporting the many paths to conservation effectiveness is critical to

ensuring a resilient ocean and achieving ambitious targets set out in the Kunming-Montreal Global Biodiversity Framework.

Second, as far as we are aware, we are the first to attempt to show how one could operationalize the OECM concept with real-world social-ecological data (Gurney et al. 2019). With a combination of data from reef transects, key informant interviews, and expert validation, we were able to apply the definition and identify potential OECMs within multiple countries.

Measuring effectiveness of area-based management tools is a key topic in policy discussion because the OECM definition requires it. We used reef fish biomass – a common used indicator for MPA ecological assessments and one that is linked to many objectives – as a feasible and practical metric that can be obtained for coral reef sites (McClanahan et al. 2021; Smallhorn-West et al. 2022). High variability due to environmental factors (e.g., time of day, tides) and methods (e.g., surveyed species, spatial coverage) can make interpretation challenging (McClanahan et al. 2007). Future research is needed to ascertain whether the simple biomass metric and thresholds, or indicators, we used for the other elements of the OECM definition are globally relevant and robust indicators of positive biodiversity outcomes. Biomass is, after all, only one aspect of biodiversity and may not fully capture richness, for instance (but see positive relationships between biomass and biodiversity in McClanahan [2022]).

A danger of not tracking ecosystem-wide outcomes of biodiversity conservation in OECMs is that this could lead to the compartmentalization of conservation (Claudet et al. 2022). Key questions that require answers for improved operationalization of OECMs include the following. How should positive biodiversity outcomes be defined so as to reflect perceptions of effectiveness across multiple knowledge systems? Do outcomes need to include increases in

biodiversity over time or evidence that biodiversity is larger than in a similar area without management or both? How might appropriate metrics or thresholds vary across regions and habitats? Importantly, indicators should be able to be used to assess the status and achievement of the specific objectives of that area-based management tool (Claudet & Guidetti 2010). While there is much more to be learned, providing a tractable and consistent way of operationalizing OECMs across multiple contexts – as we did in our study – will address a key barrier that the CBD Parties have been facing in trying to use this policy tool and will allow others to expand on our methods for different contexts and data availability.

Third, our study highlights the importance of measuring effectiveness for all area-based management tools, not just for potential OECMs (Barnes et al. 2018; Gurney et al. 2021; Jonas et al. 2021). Currently, MPAs only need to be officially designated to be reported and count toward countries' commitments under the CBD. We found that 60% of zones in MPAs could fail to meet the criteria laid out for OECMs in CBD decision 14/8 (see also Zupan et al. 2018a). This suggests that MPAs are not being sufficiently managed to achieve positive conservation outcomes, perhaps because of capacity limitations (Gill et al. 2017) or noncompliance (Iacarella et al. 2021) or because rules are insufficient to protect biodiversity from threats (Zupan et al. 2018a; Zupan et al. 2018b). Monitoring and evaluation can help managers determine whether their rules are effective in their specific social, economic, and cultural contexts. This information can then be used to adaptively manage to achieve the targeted outcomes and objectives.

Following Jonas et al. (2021), we suggest that the criteria laid out in the CBD definition of OECMs should also be applied to MPAs, thereby creating a universal set of outcome-based standards and ensuring that only areas that meet the criteria for effectiveness and equity are

counted against global biodiversity targets. We used reef fish biomass as a conservation-relevant outcome because it is commonly tracked and is applicable for multiple objectives. Other potential outcome indicators include avoided biodiversity loss (i.e., comparing outcomes against expected outcomes without the intervention) (Pressey et al. 2021; Claudet et al. 2022) and social outcomes, such as well-being (Mascia et al. 2017; Ban et al. 2019). Such outcome-based standards would need mechanisms that provide reasonable locally relevant benchmarks and time frames, including support for managers to monitor and assess sites.

Future studies can improve on our first attempt at illustrating how one could operationalize OECMs and compare them to MPAs and other area-based management tools. First, expanding the social-ecological monitoring program to include other countries and social-ecological contexts would result in a more robust analyses. While our study involved a large effort encompassing six countries and hundreds of underwater transects and key informant interviews, when summarizing these data into zones, the sample size was small and its statistical power limited. Including additional countries could provide insight as to whether our illustration of how one can operationalize OECMs is transferable to other contexts.

Second, whilst snapshot approaches to examining the outcomes of conservation and management are common, especially when they involve a large number of sites across multiple countries (e.g., Persha et al. 2011; Oldekop et al. 2015; Ban et al. 2019; Darling et al. 2019; Cinner et al. 2020), longitudinal data from protected and contextually similar unprotected reference sites allow for more confidence in attributing outcomes to management (Ahmadi et al. 2015; McClanahan et al. 2022). Continued implementation of social-ecological monitoring to generate long-term data

sets (including biomass trends) will help managers and researchers establish causal relationships. Nevertheless, individual studies at some of our sites with counterfactual or longitudinal data show that management does result in sustained high fish biomass levels (e.g., for Fiji, Jupiter et al. [2017] and for Indonesia, Campbell et al. [2020]).

Additional factors and outcomes should be explored. In addition to the objectives and rules we investigated, many studies provide insights into other characteristics associated with marine conservation effectiveness. For example, management capacity (Gill et al. 2017) and socioeconomic characteristics that gauge human impact, such as population density (Cinner et al. 2018), among others, are also important. However, data are rarely available on the wide range of potentially influential ecological, social, and institutional factors (Wamukota et al. 2012).

Analyses thus have to contend with data limitations and rely on scattered and incomplete real-world data to provide management and policy advice. Our study was not designed to examine some important factors that could influence conservation outcomes, such as preexisting reef conditions and management, local resource dependency and use patterns, compliance, the politics of management tools designation and implementation, among others (Ostrom 2009; Gurney et al. 2019). Enforcement of the rules and boundaries is also likely to play a key role in achieving outcomes (McClanahan & Abunge 2019; McClanahan & Abunge 2020; Iacarella et al. 2021). Further assessing other social and biological outcomes will be essential to obtaining a more complete understanding of the value of different area-based management tools (Geldmann et al. 2021; Reimer et al. 2021).

Our study drew on data from a global monitoring program across six countries (Gurney et al. 2019, [wcs.org/coral](https://www.wcs.org/coral)), which represents one of the largest and most comprehensive sets of data on coral reef social-ecological systems (Cox et al. 2021). Our findings can inform the dialogue in global conservation policy by providing supportive evidence that achieving biodiversity outcomes requires a diversity of rules and tools, which are fit to local context. No matter what tool is used, policy makers and practitioners should ensure relevant governing actors are provided with sufficient support (e.g., recognition, funding, secure rights, capacity) and that programs are designed and managed to strengthen existing local sustainable governance systems, rather than displace or substantially alter them (CBD 2018; Gurney et al. 2021). Engagement in the process of design or management of these must be based on human rights standards and promote equitable governance arrangements (Jonas et al. 2018). The recognition, inclusion, and funding of area-based management tools will require governments to mobilize significant resources to meet the global goals of the Kunming-Montreal Global Biodiversity Framework. With this, the diverse social and ecological goals needed to advance conservation can be met.

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References

- Ahmadia, G. N., L. Glew, M. Provost, D. Gill, N. I. Hidayat, S. Mangubhai, Purwanto, and H. E. Fox. 2015. Integrating impact evaluation in the design and implementation of monitoring marine protected areas. *Philosophical Transactions of the Royal Society B: Biological Sciences* **370**:20140275.
- Ban, N. C., et al. 2019. Well-being outcomes of marine protected areas. *Nature Sustainability* **2**:524–532.
- Barnes, M. D., L. Glew, C. Wyborn, and I. D. Craigie. 2018. Prevent perverse outcomes from global protected area policy. *Nature Ecology & Evolution* **2**:759-762.
- Bingham, H. C., et al. 2019. Sixty years of tracking conservation progress using the World Database on Protected Areas. *Nature Ecology & Evolution* **3**:737-743.
- Campbell, S. J., E. S. Darling, S. Pardede, G. Ahmadia, S. Mangubhai, Amkieltiela, Estradivari, and E. Maire. 2020. Fishing restrictions and remoteness deliver conservation outcomes for Indonesia's coral reef fisheries. *Conservation Letters* **13**:e12698.
- CBD. 2006. Convention on Biological Diversity, Article 2. Use of Terms. Convention on Biological Diversity, Montreal, Canada.
- CBD. 2010. Aichi Biodiversity Targets. Convention on Biological Diversity, <http://www.cbd.int/sp/targets/>.
- CBD. 2018. Protected areas and other effective area-based conservation measures. Pages 1-19. Subsidiary body on scientific, technical and technological advice, Convention on Biological Diversity, Montreal, Canada.

- CBD. 2022. The final text of the historic Kunming-Montreal Global Biodiversity Framework, agreed at the 15th meeting of the Conference of Parties to the UN Convention on Biological Diversity is now available as document CBD/COP/15/L25. Convention on Biological Diversity, Montreal.
- Cinner, J. E., et al. 2018. Gravity of human impacts mediates coral reef conservation gains. *Proceedings of the National Academy of Sciences* **115**:E6116-E6125.
- Cinner, J. E., et al. 2012. Comanagement of coral reef social-ecological systems. *Proceedings of the National Academy of Sciences* **109**:5219-5222.
- Cinner, J. E., et al. 2020. Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science* **368**:307-311.
- Claudet, J., et al. 2022. Avoiding the misuse of other effective area-based conservation measures in the wake of the blue economy. *One Earth* **5**:969-974.
- Claudet, J., and P. Guidetti. 2010. Improving assessments of marine protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**:239-242.
- Cox, M., et al. 2021. Lessons learned from synthetic research projects based on the Ostrom Workshop frameworks. *Ecology and Society* **26**.
- Darling, E. S., et al. 2019. Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. *Nature Ecology & Evolution* **3**:1341-1350.
- Di Lorenzo, M., P. Guidetti, A. Di Franco, A. Calò, and J. Claudet. 2020. Assessing spillover from marine protected areas and its drivers: A meta-analytical approach. *Fish and Fisheries* **21**:906-915.
- Edgar, G. J., et al. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**:216-220.

- FAO. 2021. Report of the 34th Session of the Committee on Fisheries (1-5 February 2021). Page <http://www.fao.org/3/ne907en/ne907en.pdf>. UN Food and Agriculture Organization, Rome.
- Fidler, R. Y., et al. 2022. Participation, not penalties: Community involvement and equitable governance contribute to more effective multiuse protected areas. *Science Advances* **8**:eabl8929.
- Geldmann, J., et al. 2021. Essential indicators for measuring site-based conservation effectiveness in the post-2020 global biodiversity framework. *Conservation Letters*:e12792.
- Gill, D. A., et al. 2017. Capacity shortfalls hinder the performance of marine protected areas globally. *Nature* **543**:665-669.
- Goetze, J. S., J. Claudet, F. Januchowski-Hartley, T. J. Langlois, S. K. Wilson, C. White, R. Weeks, and S. D. Jupiter. 2018. Demonstrating multiple benefits from periodically harvested fisheries closures. *Journal of Applied Ecology* **55**:1102-1113.
- Grorud-Colvert, K., et al. 2021. The MPA Guide: A framework to achieve global goals for the ocean. *Science* **373**:eabf0861.
- Gurney, G. G., and E. S. Darling. 2017. A global social-ecological systems monitoring framework for coastal fisheries management: A practical monitoring handbook. Page 63 pp. Wildlife Conservation Society, New York.
- Gurney, G. G., et al. 2021. Biodiversity needs every tool in the box: use OECMs. *Nature* **595**:646-649.

- Gurney, G. G., et al. 2019. Implementing a social-ecological systems framework for conservation monitoring: lessons from a multi-country coral reef program. *Biological Conservation* **240**:108298.
- Horta e Costa, B., J. Claudet, G. Franco, K. Erzini, A. Caro, and E. J. Gonçalves. 2016. A regulation-based classification system for Marine Protected Areas (MPAs). *Marine Policy* **72**:192-198.
- Iacarella, J. C., G. Clyde, B. J. Bergseth, and N. C. Ban. 2021. A synthesis of the prevalence and drivers of non-compliance in marine protected areas. *Biological Conservation* **255**:108992.
- IUCN-WCPA. 2019. Recognising and Reporting Other Effective Area-based Conservation Measures. Technical Report. IUCN, Gland, Switzerland.
- Jonas, H. D., et al. 2021. Equitable and effective area-based conservation: Towards the conserved areas paradigm. *PARKS* **28**.
- Jonas, H. D., et al. 2018. Other Effective Area-based Conservation Measures: From Aichi Target 11 to the Post-2020 Biodiversity Framework. *PARKS* **24**.
- Jupiter, S., G. Epstein, N. C. Ban, S. Mangubhai, M. Fox, and M. Cox. 2017. A social-ecological systems approach to assessing conservation and fisheries outcomes in Fijian locally managed marine areas. *Society and Natural Resources* **30**:1096-1111.
- Jupiter, S. D., P. J. Cohen, R. Weeks, A. Tawake, and H. Govan. 2014. Locally-managed marine areas: Multiple objectives and diverse strategies. *Pacific Conservation Biology* **20**:165-179.

- Jupiter, S. D., and H. Govan. 2022. Introduction in P. Nimwegen, F. Leverington, S. Jupiter, and M. Hockings, editors. *Conserving our sea of islands: State of Protected and conserved areas in Oceania*. IUCN, Gland, Switzerland.
- MacNeil, M. A., et al. 2015. Recovery potential of the world's coral reef fishes. *Nature* **520**:341-344.
- Mascia, M. B., et al. 2017. A novel framework for analyzing conservation impacts: evaluation, theory, and marine protected areas. *Annals of the New York Academy of Sciences* **1399**:93-115.
- McClanahan, T. 2015. Biogeography versus resource management: how do they compare when prioritizing the management of coral reef fish in the south-western Indian Ocean? *Journal of Biogeography* **42**:2414-2426.
- McClanahan, T., and C. Abunge. 2020. Perceptions of governance effectiveness and fisheries restriction options in a climate refugia. *Biological Conservation* **246**:108585.
- McClanahan, T. R. 2022. Fisheries yields and species declines in coral reefs. *Environmental Research Letters* **17**:044023.
- McClanahan, T. R., and C. A. Abunge. 2019. Conservation needs exposed by variability in common-pool governance principles. *Conservation Biology* **33**:917-929.
- McClanahan, T. R., A. M. Friedlander, N. A. Graham, P. Chabanet, and J. H. Bruggemann. 2021. Variability in coral reef fish baseline and benchmark biomass in the central and western Indian Ocean provinces. *Aquatic Conservation: Marine and Freshwater Ecosystems* **31**:28-42.

- McClanahan, T. R., A. M. Friedlander, L. Wantiez, N. A. Graham, J. H. Bruggemann, P. Chabanet, and R. M. Oddenyo. 2022. Best-practice fisheries management associated with reduced stocks and changes in life histories. *Fish and Fisheries* **23**:422-444.
- McClanahan, T. R., N. A. J. Graham, M. A. MacNeil, and J. E. Cinner. 2015. Biomass-based targets and the management of multispecies coral reef fisheries. *Conservation Biology* **29**:409-417.
- McClanahan, T. R., N. A. J. Graham, J. Maina, P. Chabanet, J. H. Bruggemann, and Polunin. 2007. Influence of instantaneous variation on estimates of coral reef fish populations and communities. *Marine Ecology Progress Series* **340**:221-234.
- McLeod, E., B. Szuster, and R. Salm. 2009. Sasi and Marine Conservation in Raja Ampat, Indonesia. *Coastal Management* **37**:656-676.
- Melnchuk, M. C., et al. 2021. Identifying management actions that promote sustainable fisheries. *Nature Sustainability* **4**:440-449.
- Oldekop, J. A., G. Holmes, W. E. Harris, and K. L. Evans. 2015. A global assessment of the social and conservation outcomes of protected areas. *Conservation Biology*:n/a-n/a.
- Ostrom, E. 2009. A general framework for analyzing sustainability of social-ecological systems. *Science* **325**:419-422.
- Ostrom, E., and M. Cox. 2010. Moving beyond panaceas: a multi-tiered diagnostic approach for social-ecological analysis. *Environmental Conservation* **37**:451-463.
- Persha, L., A. Agrawal, and A. Chhatre. 2011. Social and Ecological Synergy: Local Rulemaking, Forest Livelihoods, and Biodiversity Conservation. *Science* **331**:1606-1608.

- Pressey, R. L., P. Visconti, M. C. McKinnon, G. G. Gurney, M. D. Barnes, L. Glew, and M. Maron. 2021. The mismeasure of conservation. *Trends in Ecology & Evolution* **36**:808-821.
- Reimer, J. M., R. Devillers, and J. Claudet. 2021. Benefits and gaps in area-based management tools for the ocean Sustainable Development Goal. *Nature Sustainability* **4**:349-357.
- Relano, V., and D. Pauly. 2023. The ‘Paper Park Index’: Evaluating Marine Protected Area effectiveness through a global study of stakeholder perceptions. *Marine Policy* **151**:105571.
- Sala, E., J. Lubchenco, K. Grorud-Colvert, C. Novelli, C. Roberts, and U. R. Sumaila. 2018. Assessing real progress towards effective ocean protection. *Marine Policy* **91**:11-13.
- Smallhorn-West, P., P. J. Cohen, M. Phillips, S. D. Jupiter, H. Govan, and R. L. Pressey. 2022. Linking small-scale fisheries co-management to U.N. Sustainable Development Goals. *Conservation Biology* **36**:e13977.
- UNEP-WCMC, IUCN, and NGS. 2018. Protected Planet Report 2018. United Nations Environment Programme (UNEP) World Conservation Monitoring Centre (UNEP-WCMC), International Union for Conservation of Nature (IUCN), and National Geographic Society (NGS), Cambridge, UK; Gland, Switzerland; and Washington D.C., USA.
- Wamukota, A., J. Cinner, and T. McClanahan. 2012. Co-management of coral reef fisheries: a critical evaluation of the literature. *Marine Policy* **36**:481-488.
- Zupan, M., et al. 2018a. How good is your marine protected area at curbing threats? *Biological Conservation* **221**:237-245.

Zupan, M., E. Fragkopoulou, J. Claudet, K. Erzini, B. Horta e Costa, and E. J. Gonçalves. 2018b.
Marine partially protected areas: drivers of ecological effectiveness. *Frontiers in Ecology
and the Environment* **16**:381-387.

Table 1. Descriptions and sample sizes of the area-based management tools and reference areas included in considered in this study on the effects of management objectives and rules on marine conservation outcomes x

Management category (abbreviation)	Description	Sample size	No. of samples with biomass data
Reference sites (reference)	areas with no area-based management rules beyond those that apply to the whole country's waters (e.g., national laws and policies)	15	11
Area-based management tools (ABMTs)			
marine protected areas (MPAs)	areas designated as a marine protected area by the country in which it is situated; defined as "a geographically defined area, which is designated or regulated and managed to achieve specific conservation objectives" (CBD 2006)	37 zones in 20 MPAs	20 zones in 9 MPAs
other area-based management (other)	areas that have area-based management other than MPAs; includes those that do and do not meet definition of potential Other Effective Area-Based Management (CBD 2018) (Table 2.	43 zones in 34 areas	37 zones in 30 areas

Table 2. Application of the Convention on Biological Diversity's (CBD) definition of "other effective area-based conservation measures" (OECMs) to coral reef marine area-based management.^a

^aZones had to meet all five of the elements of the CBD OECM definition below to be considered "potential OECMs" in our analysis. We refer to them as "potential" OECMs because, while they meet the CBD definition, managers of those areas need to provide their consent and there needs to be a formal assessment process for the areas to be listed as an OECM.

^b Method for operationalizing each element used in this study.

^cThe remaining columns indicate how many areas meet the criteria for MPAs and other managed areas, respectively. Not all areas have biomass data.

Element of CBD OECM definition	Indicator question ^b	Data used for operationalization	No. marine protected areas (MPAs) not meeting criteria ^c	No. other managed areas not meeting criteria ^c
Geographically defined	Is managed area well defined geographically? (yes or no)	expert assessment (in-country experts)	6 out of 37	13 out of 43
Other than a protected area	Is area not designated as a marine protected area (MPA)? (yes or no)	not legally recognized as a MPA	37 out of 37	0 out of 43
Governed and managed	Is area governed and managed? (yes or no)	expert assessment (in-country experts)	11 out of 37	8 out of 43
Sustained	Is management intended to be in place for over ~25 years? (yes or no)	expert assessment (in-country experts)	4 out of 37	11 out of 43
Achieve positive outcomes for the in situ conservation of biodiversity	Does biomass meet or exceed threshold to sustain reef fish productivity and energy flows (≥ 500 kg/ha) or have biomass akin to unfished areas (≥ 1000 kg/ha)?	underwater visual census of reef fishes	12 out of 20 (≥ 500 kg/ha) 18 out of 20 (≥ 1000 kg/ha)	15 out of 37 (≥ 500 kg/ha) 32 out of 37 (≥ 1000 kg/ha)

^aZones had to meet all 5 of the elements of the CBD OECM definition to be considered potential OECMs in our analyses. We refer to them as potential OECMs because, although they meet the CBD definition, managers of those areas need to provide their consent and there needs to be a formal assessment process for the areas to be listed as an OECM.

^b Method for operationalizing each element used in this study.

^c Number of areas that met criteria for MPAs and other managed areas, respectively. Not all areas had biomass data.

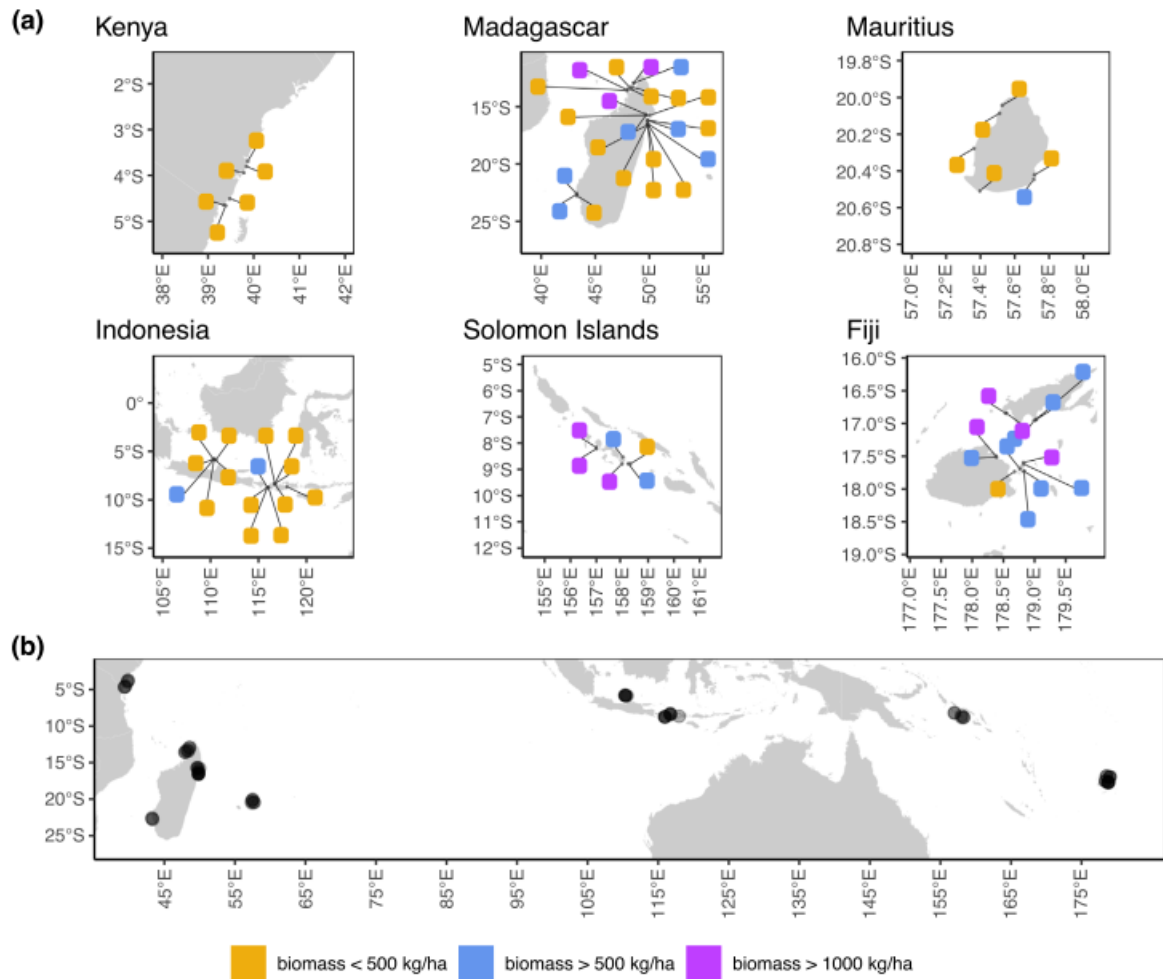


Figure 1. Location of study sites (a) in 6 counties panels and (b) globally (colors, average reef fish biomass; orange, <500 kg/ha; blue, 500-999 kg/ha; purple, ≥ 1000 kg/ha).

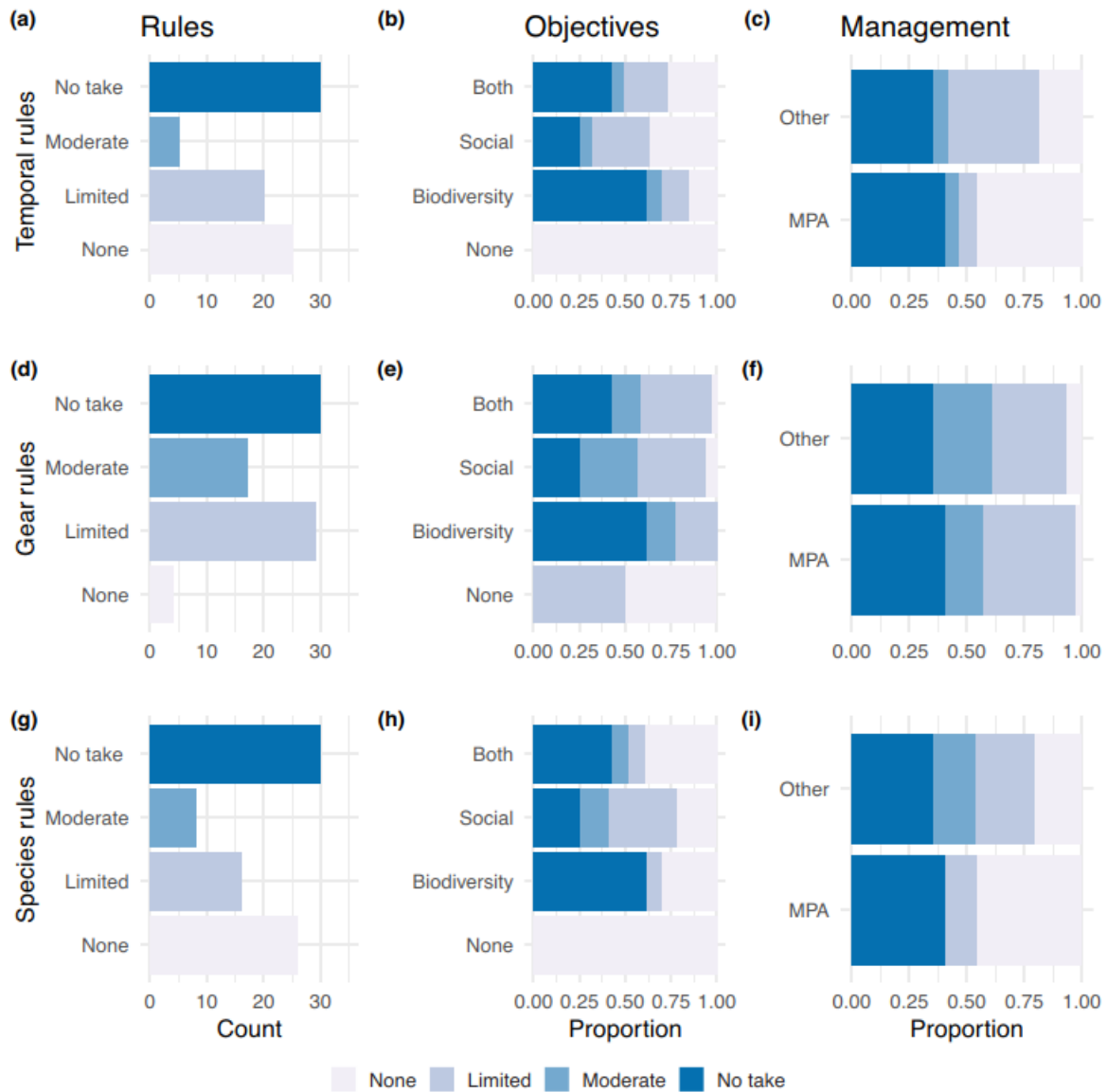


Figure 2. The numbers and proportion of rules, objectives, and management categories in the 80 area-based management sites in 6 Indo-Pacific countries. The first column (a, d, g) shows the number sites in each labelled category of rules. The second column (b, e, h) illustrates the proportion of rules with different objectives. The third column (c, f, i) provides the proportion of rules applied in marine protected areas and other management areas. Rules are explained in Appendix S2, objectives in Appendix S3; and management categories in Table 1.

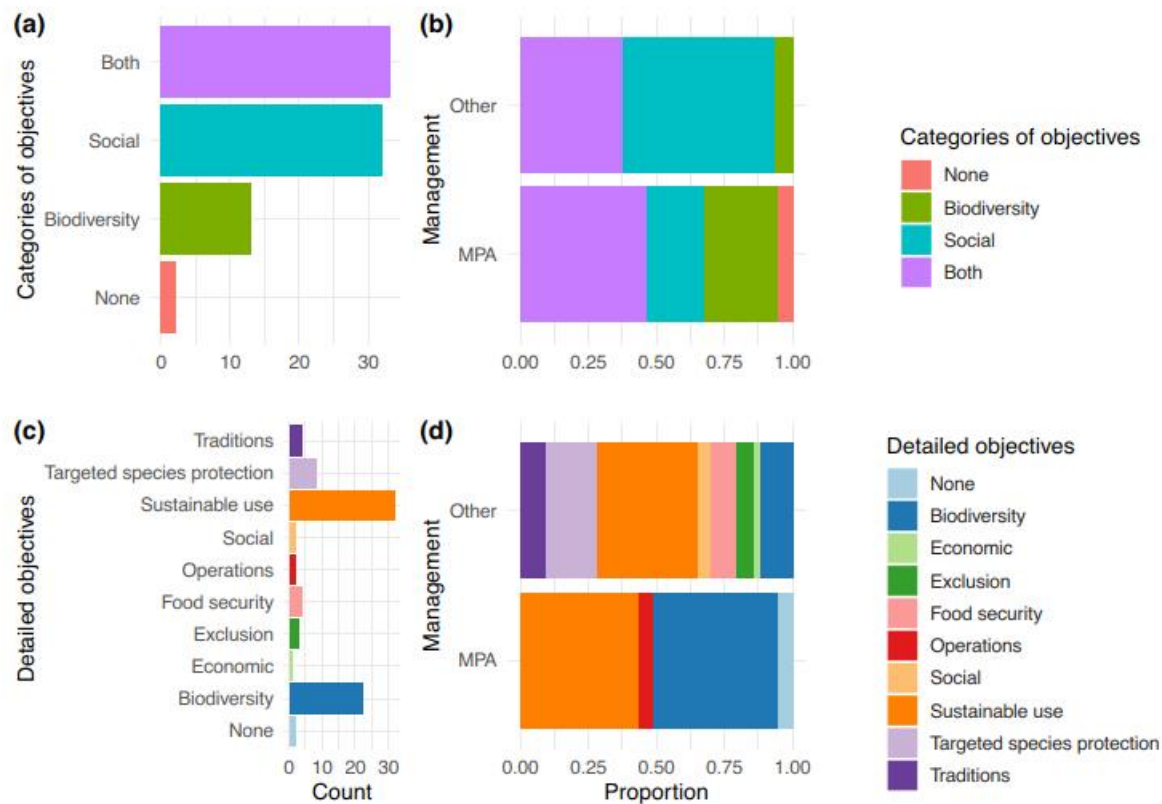


Figure 3. Stated objectives for 80 area-based management sites in 6 Indo-Pacific countries: (a) frequency of categories of objectives, (b) proportion of categories of objectives by area-based management tool, (c) frequency of detailed objectives, and (d) proportion of detailed objectives by area-based management tool (social, social, economic, and cultural objectives; area-based management

categories are MPAs; other, other area-based management). Reference sites do not have local objectives and are not included. Details in Table 1 and Appendix S3.

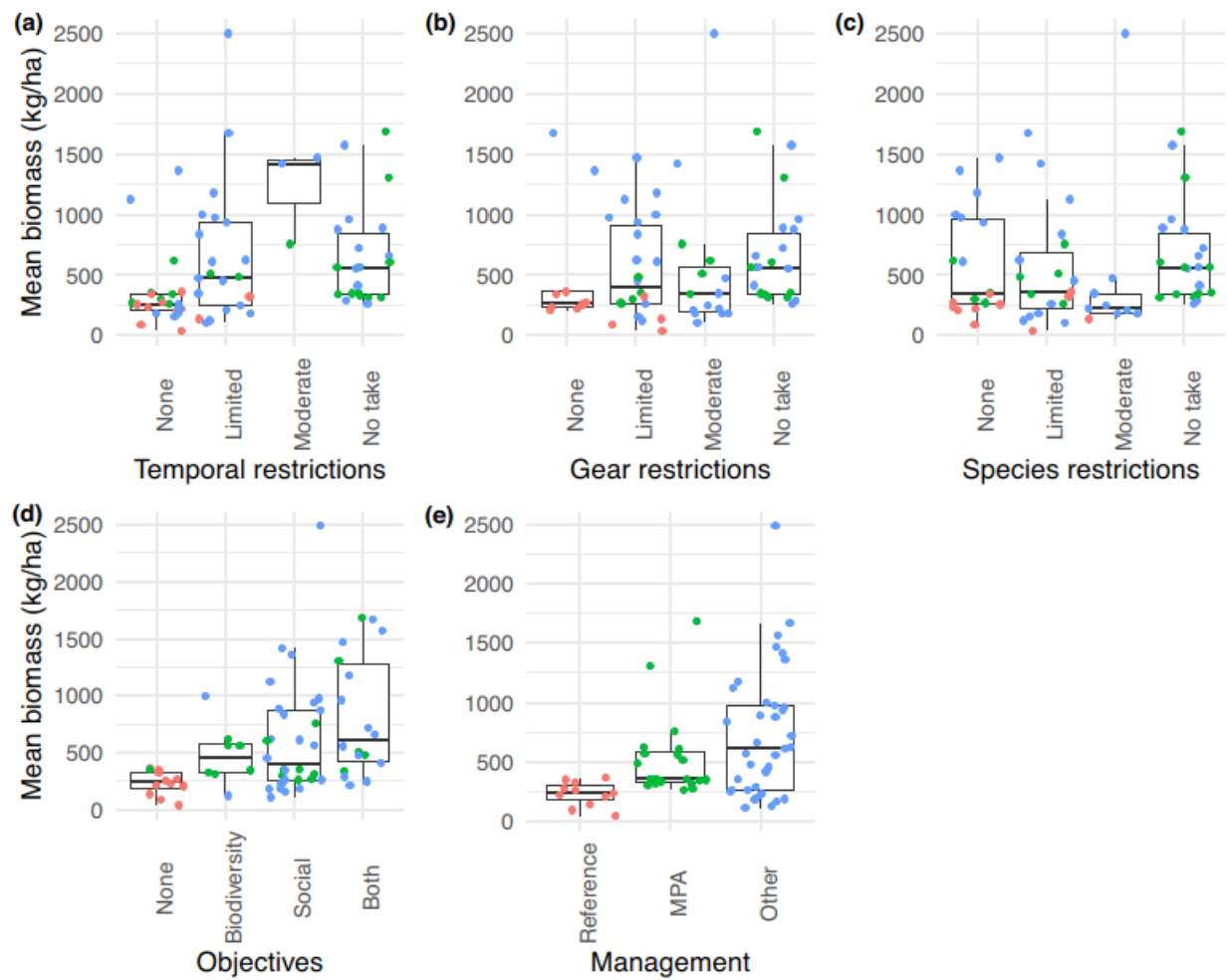


Figure 4. Reef fish biomass under (a) temporal, (b) gear, and (c) species rules and under different (d) management objectives and (e) categories (social, social, economic, and cultural objectives; both, areas with a primary objective that encompassed social, economic,

cultural, and biodiversity objectives; MPA, marine protected areas; other, other area-based management; reference, reference sites; red, reference; green, MPAs; blue, other zones; horizontal lines, median; box ends, the first [25%] and third [75%] quartiles; whiskers, 1.5 times the interquartile range from the bottom and top of the box to the furthest datum within that distance; data beyond that distance are shown individually as points).

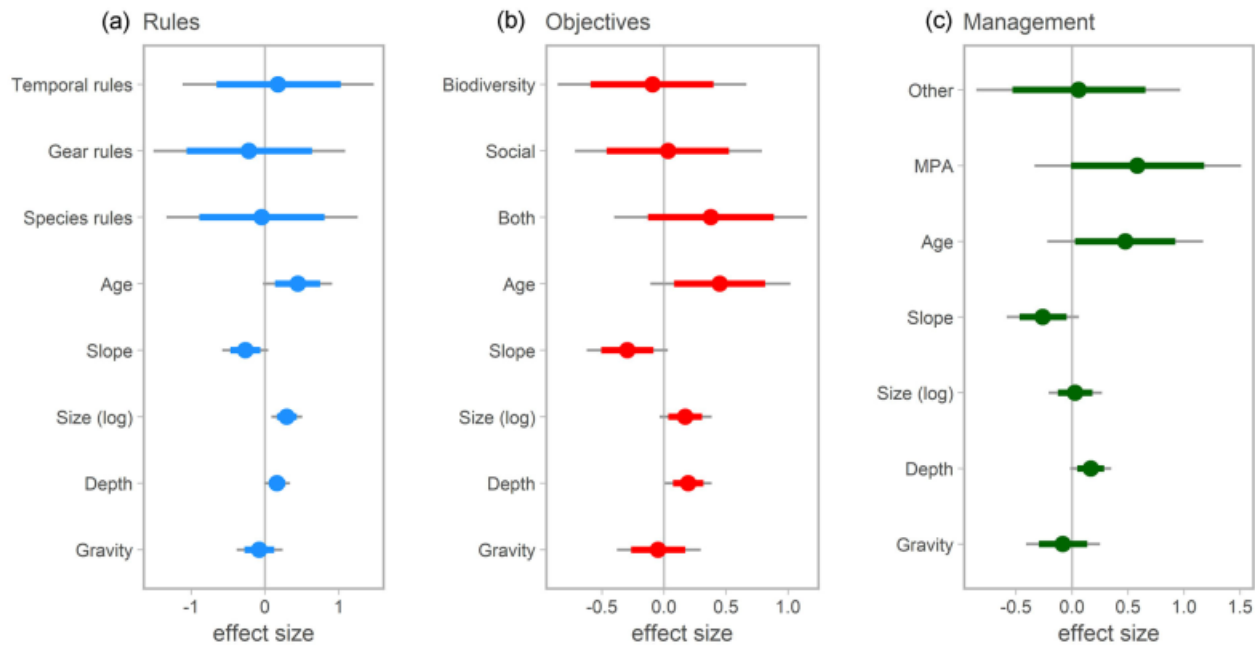


Figure 5. Relationship between (log) reef fish biomass and (a) rules, (b) objectives, and (c) management (points, Bayesian posterior median values [effects sizes standardized]; gray lines, 95% Bayesian credible interval (CI); colored lines, 80% CI; intersection of the horizontal lines with the vertical line, little evidence that the fixed effects were related to fish biomass). Slope reefs were compared with flat reefs. Objectives of biodiversity; social, economic, and cultural (social), and both biodiversity and social were compared with

sites with no objectives. Other management and marine protected areas were compared with reference sites. Data from reference sites were included in all models. Details in Appendix S6.