




Fishing-gear restrictions and biomass gains for coral reef fishes in marine protected areas

Stuart J. Campbell,¹ Graham J. Edgar,² Rick D. Stuart-Smith,² German Soler,² and Amanda E. Bates ^{3*}

¹RARE, Jl, Gunung Gede 1 No. 6, Taman Kencana, Bogor, 16151, Indonesia

²Institute for Marine and Antarctic Studies, University of Tasmania, Hobart 7001, Tasmania, Australia

³National Oceanography Centre, University of Southampton Waterfront Campus, Southampton SO14 3ZH, U.K.

Abstract: *Considerable empirical evidence supports recovery of reef fish populations with fishery closures. In countries where full exclusion of people from fishing may be perceived as inequitable, fishing-gear restrictions on nonselective and destructive gears may offer socially relevant management alternatives to build recovery of fish biomass. Even so, few researchers have statistically compared the responses of tropical reef fisheries to alternative management strategies. We tested for the effects of fishery closures and fishing gear restrictions on tropical reef fish biomass at the community and family level. We conducted 1,396 underwater surveys at 617 unique sites across a spatial hierarchy within 22 global marine ecoregions that represented 5 realms. We compared total biomass across local fish assemblages and among 20 families of reef fishes inside marine protected areas (MPAs) with different fishing restrictions: no-take, hook-and-line fishing only, several fishing gears allowed, and sites open to all fishing gears. We included a further category representing remote sites, where fishing pressure is low. As expected, full fishery closures, (i.e., no-take zones) most benefited community- and family-level fish biomass in comparison with restrictions on fishing gears and openly fished sites. Although biomass responses to fishery closures were highly variable across families, some fishery targets (e.g., *Carcharbinidae* and *Lutjanidae*) responded positively to multiple restrictions on fishing gears (i.e., where gears other than hook and line were not permitted). Remoteness also positively affected the response of community-level fish biomass and many fish families. Our findings provide strong support for the role of fishing restrictions in building recovery of fish biomass and indicate important interactions among fishing-gear types that affect biomass of a diverse set of reef fish families.*

Keywords: adaptive management, conservation planning, fisheries, global ecology

Restricciones en el Equipo de Pesca y las Ganancias de Biomasa para los Peces de Arrecifes de Coral en Áreas Marinas Protegidas

Resumen: *Hay fuertes evidencias empíricas que respaldan la recuperación de las poblaciones de peces de arrecifes con el cierre de las pesquerías. En los países en los que la exclusión total de pescadores puede ser percibida como injusta, las restricciones de equipos de pesca para equipos no selectivos y destructivos pueden ofrecer alternativas de manejo socialmente relevantes para construir la recuperación de la biomasa de los peces. Aún así, pocos investigadores han comparado estadísticamente las respuestas de las pesquerías de peces tropicales de arrecifes a las estrategias de manejo alternativo. Probamos los efectos de los cierres de las pesquerías y las restricciones del equipo de pesca sobre la biomasa de peces tropicales a nivel familia y a nivel comunidad. Realizamos 1,396 censos submarinos en 617 sitios únicos a través de una jerarquía espacial dentro de 22 ecoregiones marinas mundiales que representaron cinco ámbitos. Comparamos la biomasa total entre los grupos de peces locales y entre 20 familias de peces de arrecife dentro de áreas marinas protegidas.*

*email bates.amanda@gmail.com

Article impact statement: No-take MPAs provide biomass gains, but imposing gear restrictions can provide intermediate biomass gains for coral reef fishes.

Paper submitted September 26, 2016; revised manuscript accepted June 14, 2017.

(AMP) con diferentes restricciones para la pesca: pesca prohibida, pesca de anzuelo y sedal únicamente, varios equipos de pesca permitidos, y sitios abiertos a todo tipo de equipos de pesca. Incluimos una categoría más que representó a los sitios remotos, en donde la presión por la pesca es baja. Como se esperaba, el cierre total de las pesquerías (es decir, zonas de pesca prohibida) benefició más a nivel de la comunidad y de la familia la biomasa de los peces en comparación con las restricciones para los equipos de pesca y los sitios con pesca abierta. Aunque las respuestas en la biomasa al cierre de las pesquerías fueron altamente variables entre familias, algunos objetivos de la pesca (p. ej.: *Carcharinidae* y *Lutjanidae*) respondieron positivamente a las restricciones múltiples para los equipos de pesca (es decir, en donde no estaban permitidos otros equipos además del sedal y el anzuelo). La lejanía también afectó positivamente la respuesta de la biomasa de peces a nivel de comunidad y de muchas familias. Nuestros resultados proporcionan un fuerte respaldo para el papel de las restricciones de pesca en la construcción de la recuperación de la biomasa de peces e indican interacciones importantes entre los tipos de equipos de pesca que afectan a la biomasa de un conjunto diverso de familias de peces de arrecife.

Palabras Clave: ecología global, manejo adaptativo, pesquerías, planeación de la conservación

Introduction

Fishery closures clearly promote the recovery of fish biomass following exploitation (Russ et al. 2005; MacNeil et al. 2015). Even so, fishing is an important activity in many tropical countries, and fishers rely on fishing for their income and subsistence. Where management institutions are often weak or missing (Walker et al. 2009), governments and communities may adopt some intermediate form of fisheries protection between no-take protected areas and openly fished sites to improve fish-biomass recovery (McClanahan et al. 2011).

Fishery closures and other restrictions on fishing, including periodic closures (Cohen & Alexander 2013), gear controls (McClanahan et al. 2014), and rights-based approaches that allocate fisheries to individuals or communities (Aswani 2005), are commonly implemented together in marine protected areas (MPAs) or may operate independent of each other. When implemented together, areas with fishing restrictions nested within MPAs may achieve both conservation and fisheries goals. Community, family and functional-level fish biomass (Gillett & Moy 2006; McClanahan et al. 2011, 2014) benefit from the complementary effects of fishery closures and fishing restrictions, and such protection contributes to improved fishing yields relative to openly fished areas (McClanahan & Mangi 2000; McClanahan 2010) and to economic sustainability of fisheries (Mangi et al. 2007; Little et al. 2010).

Fishing-gear restrictions have substantial effects on the composition of functional groups (MacNeil et al. 2015) because gears impose unique and consistent partitioning of the species and families they target. Generally, hook-and-line fisheries target large-bodied fishes and piscivores (Mumby et al. 2014), nets catch a diversity of fishes (Mangi & Roberts 2007), and spearguns and traps target herbivores and piscivores (e.g., Hawkins et al. 2007; Frisch et al. 2012).

Strong evidence exists for the recovery of community-, family-, and functional-level fish biomass in fishery clo-

tures and where restrictions on destructive gears are strong (McClanahan et al. 2007; 2011; 2014). Catches of various fish families have also benefited from restrictions on fishing gears in areas located close to fishery closures (McClanahan & Mangi 2000; McClanahan 2010). However, it is still unclear to what extent such restrictions may provide intermediate benefits to the recovery of fish populations, and the level of response that occurs within and among fish families to various fishing controls is unknown. Such knowledge could provide more informed and broadly applicable management decisions regarding fishing-gear use (Johnson et al. 2013).

We examined the effects of fishing-gear restrictions on biomass of tropical reef fishes. We predicted that total fish biomass would respond positively at sites where 3 types of restrictions on fishing activity (no fishing, line fishing only, multiple fishing gears) occurred in MPAs relative to sites outside MPAs, where there were no restrictions on fishing. We quantified the sensitivity of 20 fish families to gear restrictions according to whether the family was primarily targeted for commercial markets, local markets, or were rarely fished. Our prediction was that more commonly targeted families would be relatively responsive to fishing restrictions.

Methods

Study Region and Survey Methods

From September 2006 to November 2012, 1396 underwater surveys were conducted at depths from 0.5 m to 22 m (50 × 10 m transects) at sites open to fishing ($n = 168$), MPAs with gear restrictions ($n = 173$), and no-take MPAs ($n = 265$) in 5 realms (Fig. 1). Fish species, abundance, and size classes were recorded, using methods and data-quality control processes described in Edgar and Stuart-Smith (2014), by professional scientists and trained volunteer divers. Divers laid a 50-m transect line and surveyed fishes within duplicate 5-m strips on either side of the line (total area surveyed 500 m²). All

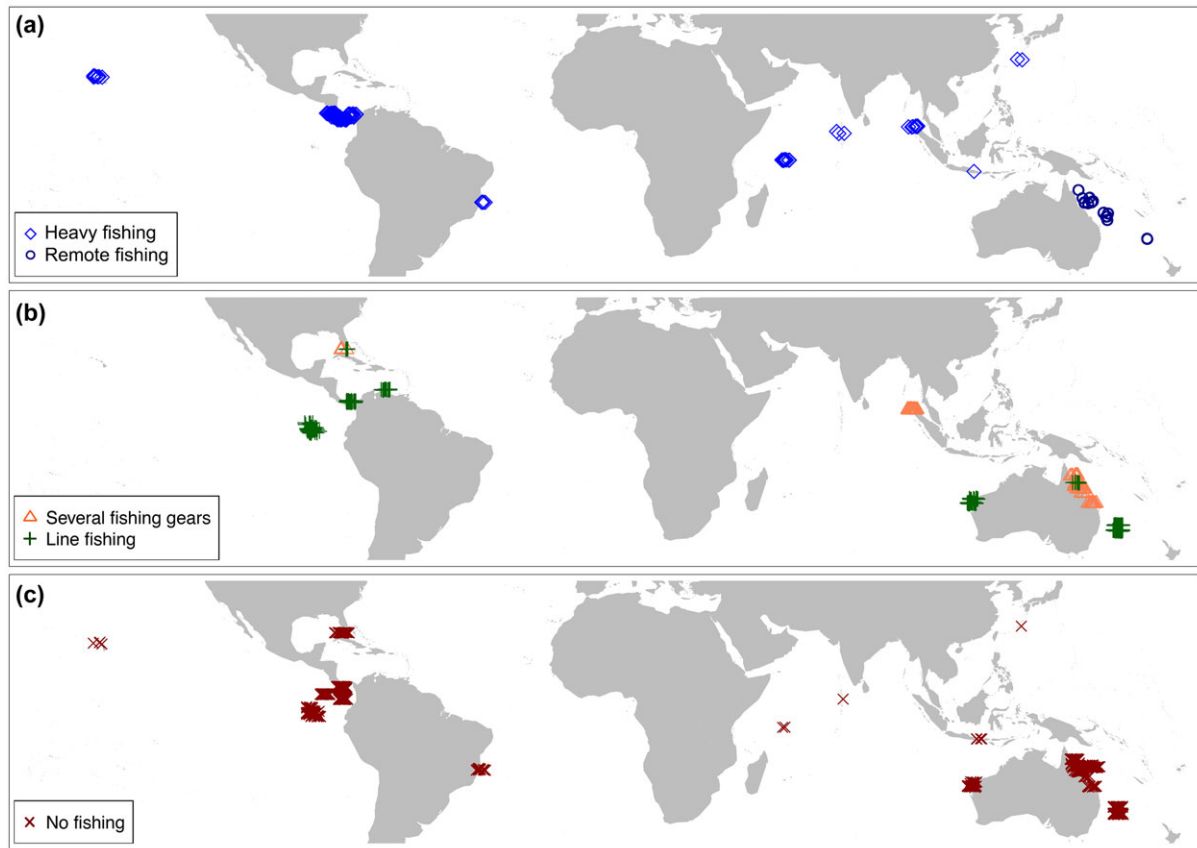


Figure 1. Location of 1,396 surveys at 617 unique sites across 12 countries in tropical waters: (a) 117 surveys with heavy fishing surveyed in 8 countries and 213 surveys in remote sites with fishing outside marine protected areas (MPAs) in 2 countries; (b) 92 surveys with several fishing gears surveyed in 3 countries and 287 surveys with line fishing in MPAs surveyed in 5 countries; (c) 687 surveys with no fishing inside MPAs surveyed in 11 countries. Biomass was contrasted across different gear categories after accounting for the spatial structure in the data.

fish species present in each survey were identified to species, and their abundances and sizes were estimated. Fish lengths were grouped in 2.5-cm bins up to 15 cm, 5-cm bins up to 50 cm, and 12.5-cm bins for fishes >50 cm. Fish biomass (grams per 500 m²) was estimated using the abundance and sizes of fishes observed and species-specific length–weight relationships provided in Fish-Base (<http://www.fishbase.org>). When length–weight relationships were unknown for a species, we used values from a similarly shaped congener.

Fishing-Gear Restriction Parameterization

We examined whether fishing-gear restrictions across 22 MPAs influenced fish biomass in comparison with locations entirely open to fishing. We determined fishing restrictions in place at each survey site by examining MPA management plans and zoning maps and through discussions with local MPA practitioners. To identify the exact location of survey sites in management zoning plans, we used Google Earth to overlay MPA maps with coordinates

of the 438 unique sites inside MPAs. Sites were categorized as 1 of 5 types of fishing: no fishing, only hook-and-line fishing (hereafter line fishing); multiple fishing gears (most commonly various types of nets, spears, and hook and line); low fishing pressure (>200 km from densely populated human settlements) (hereafter remote fishing); and high fishing pressure (nearshore) (hereafter heavily fished). Inshore sites open to fishing tended to have human population densities at least an order of magnitude greater than remote sites (Edgar et al. 2014). Sites with no fishing, hook-and-line fishing, and multiple gears were in MPAs, and the other 2 types were outside MPAs.

Analysis of Summed Biomass

To test for differences in the biomass of local fish communities, we applied a mixed-effects linear modeling approach fitted using maximum likelihood (function `lme` in the package `nlme` [Pinheiro et al. 2015]). We log transformed community-level biomass data for this analysis, which provided a better fit relative to

alternatives for modeling overdispersed data, such as a general linearized model with family equal to quasi-Poisson and link equal to log. Multimodel inference produced model-averaged parameter estimates based on AIC_c (Akaike information criterion corrected for small sample sizes) for all fixed effects (gear restrictions and covariates) included in the global model. The component model set (Table 1) included models within a 95% confidence threshold (summed weight based on AIC_c [Burnham & Anderson 2002]) calculated with the package MuMIn (Bartoń 2009) and the function model.avg (missing coefficients were set to 0).

The fixed effects of survey depth and MPA age were included as covariates—larger bodied fishes are often found in deeper waters (Goetze et al. 2011) and long-term establishment of MPAs can contribute to recovery and enhancement of fish biomass (Edgar et al. 2014). Direct positive influences of low human population densities through low fishing pressure may be dampened over regional scales if driving factors such as market pressure lead to high exploitation (Cinner et al. 2013). We therefore measured the distance from our survey sites to the closest provincial township (distance to market) under the assumption that shorter distances from fishing grounds to townships imply greater market access and greater potential for depletion of fish populations. We also fitted a polynomial term (site latitude^2) to the relationship between biomass and latitude because biomass showed no consistent trend across tropical latitudes but was lower in higher latitudes.

We aimed to account for biogeographic patterns not because of a focus on biogeographic patterns, but to ensure our global estimates of coefficients related to gear restrictions were not confounded by spatial structuring of the data. There were multiple site-specific parameters that differed across the areas surveyed. Some were possible to estimate (e.g., sea surface temperature), whereas others could not be measured directly (e.g., productivity). A discussion and analysis of parameters related to physical (chlorophyll and temperature) and habitat properties (coral cover) across sites is provided in Supporting Information. Including the spatial structure of the data as nested random effects on our model intercept (realm, ecoregion, and site; Spalding et al. 2007) functioned as a blocking factor and controlled for geographic variation in biomass. The nested spatial structure also accounted for nonrandom sampling across space in coefficient estimation (i.e., categories of fishing-gear restrictions were not evenly represented across ecoregions [Fig. 1]). Tables 1 and 2 summarize the model structure and results.

Analysis of Family-Level Summed Biomass

Fishery targets can vary substantially among different countries in the tropics, according to demands from

Table 1. A model-average approach included 3 component models to produce parameter estimates reported in Table 2. Six fixed effects are identified as follows: 1 = Fishing restrictions, 2 = Survey depth, 3 = $\log_{10}(\text{MPA age} + 1)$, 4 = $\log_{10}(\text{Distance to market})$, 5 = Latitude, and 6 = Latitude^2 .

Component model ^a	df	AICc ^b	Delta ^c	Weight ^d
1,2,3,6	16	1458.57	0.00	0.55
1,2,3,4,6	17	1460.17	1.59	0.25
1,2,3,5,6	17	1460.50	1.93	0.21

^aSix fixed effects are identified as follows: 1, fishing restrictions; 2, survey depth; 3, $\log_{10}(\text{MPA age}+1)$; 4, $\log_{10}(\text{Distance to market})$; 5, latitude; 6, latitude^2 .

^bThe small-sample-size corrected version of Akaike information criterion (AIC), a statistic used to measure goodness of fit for a model.

^cChange in AICc.

^dWeight of each model used to calculate the parameter estimates reported in Table 2.

domestic and export markets and localized human dietary preferences. Based on our knowledge of the use of fish in each country surveyed, we tested the responses of families commonly fished for commercial markets (i.e., Carangidae, Carcharhinidae, Lutjanidae, Serranidae) and local markets (i.e. Acanthuridae, Balistidae, Caesionidae, Haemulidae, Holocentridae, Kyphosidae, Lethrinidae, Mullidae, Pomacanthidae, Scarinae, Scorpaenidae, Siganidae) and of families that are rarely fished (i.e., Chaetodontidae, Cirrhitidae, Pomacentridae, Tetraodontidae) to fishing restrictions. For families targeted for export and domestic commercial markets, we expected a positive response to fishing restrictions, whereas for the 12 families fished for local markets we expected a varied response to fishing restrictions because fishing pressure may vary according to local preferences. For those families rarely fished, we did not expect high levels of sensitivity to fishing restrictions.

To test for differences in the summed biomass for each of 20 common coral reef fish families among each of the 5 fishing categories, we used a generalized linear mixed-effects model with a zero-inflation term (fitted as a constant term across all groups where the zero-count outcomes are a mixture of structural and sampling zeros) and a Gaussian distribution with the function glmmadmb in the package glmmADMB (Skaug et al. 2014). We log transformed the biomass response data prior to the analysis because this approach offered the best fit to the data. The nested random effect of (realm or province) was included as a random effect in each model to account for geographic differences in family-level biomass and spatial structuring of the data (as detailed above). The model structure and results are reported in Supporting Information.

Back Transformation of Biomass Data to Percent Differences

In all models, coefficients (95% CI) represented treatment contrasts for each type of fishery-restriction

Table 2. Average coefficient estimates returned using a linear mixed-effects modeling approach fitted with a zero-inflation term and Gaussian data distribution to test for the relationship between fishing-gear restriction categories and community-level fish biomass.*

Fixed effect	Estimate	SE	z	p	2.5% CI	97.5% CI
Intercept	4.444	0.091	48.842	<0.001	4.266	4.622
Fishing restrictions						
remote fishing	0.250	0.089	2.783	0.005	0.074	0.426
several fishing gears	0.026	0.117	0.223	0.824	-0.204	0.257
line fishing	0.137	0.110	1.246	0.213	-0.079	0.354
no fishing	0.211	0.101	2.090	0.037	0.013	0.408
Covariates						
survey depth	0.010	0.003	3.442	<0.001	0.004	0.016
log10(MPA age+1)	0.197	0.084	2.343	0.019	0.032	0.363
log10(Distance to market)	0.023	0.034	0.689	0.491	-0.043	0.090
Latitude	-0.001	0.003	0.356	0.721	-0.007	0.005
Latitude ²	-0.001	0.0001	3.858	<0.001	0.001	-0.0003

* Sites with heavy fishing are the intercept - the reference for the contrast treatments. We accounted for 5 covariates that affect total fish biomass at the community level (Table 1). A model average approach was used, and the component models are reported in Table 1. The standard deviation explained by the random effects was: realm, 0.08; Ecoregion nested in realm, 0.13; site nested in ecoregion nested in realm, 0.27; and residual standard deviation, 0.33.

category relative to the reference, heavy fishing sites. Because our biomass data were log transformed prior to analyses, the coefficients returned from each model (Table 2 and Supporting Information) needed to be back transformed to raw units (grams per 500 m²) and were subsequently converted into a percent difference (i.e., higher or lower) relative to heavy fishing sites (which were scored as 0). This conversion was completed by first back transforming the intercept parameter from the summary table—the estimate for heavy fishing, β_1 . For each gear category, we added the intercept parameter to the appropriate coefficient from the summary table, and back transformed this value (G_i). The percent difference is thus $100 \cdot (\beta_1 + G_i) / \beta_1$. This approach was applied to each gear category and to the upper and lower 95% confidence limits.

Results

Analysis of Summed Biomass Across Communities

Community-level fish biomass at sites inside MPAs with no fishing had significantly higher biomass values relative to sites open to fishing (62.4% higher; CI, 3.0–155.9; $p = 0.037$). At sites inside MPAs with line fishing, the % biomass increase relative to heavy fishing areas was not significant (37.2%; CI, -16.6–125.9; $p > 0.05$). Biomass in MPAs with several gear restrictions did not differ significantly from heavy fishing locations (6.2%; $p > 0.05$) (Fig. 2 and Table 2).

Although remote sites (e.g., Coral Sea) had higher biomass relative to heavy fishing sites (77.7% higher; CI, 18.6–166.7; $p = 0.005$), the distance to the closest market was not a significant covariate affecting community-level fish biomass (Table 2). Survey depth and MPA age significantly and positively affected community-level fish biomass (Table 2).

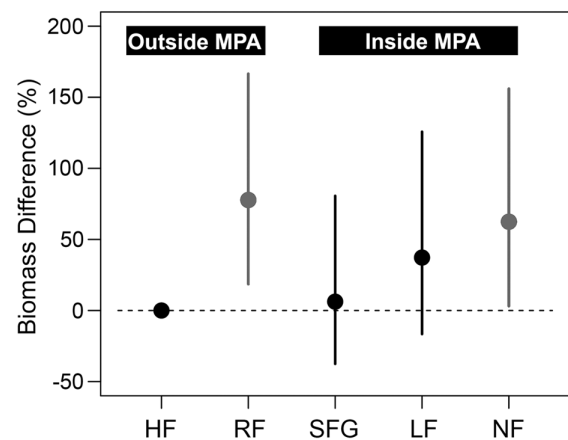


Figure 2. Percent difference in community-level fish biomass (95% CI) between heavily fished sites and sites where 4 different types of fishery management are applied in tropical waters. Values are back-transformed; percent biomass difference is relative to heavy fishing sites. Fishing management categories (HF, heavy fishing; RF, remote fishing; SFG, several fishing gears; LF, line fishing; NF, no fishing) were analyzed with data from 1,066 surveys inside 21 MPAs and 330 surveys outside MPAs. Estimated treatment contrasts account for spatial structuring in the data.

Analysis of Summed Biomass across Different Families

For 9 families, biomass in MPAs with no fishing was significantly higher than in heavy fishing sites. This also was the case for 4 families in MPAs with line fishing and for 5 families at remote fishing sites. However, biomass was not significantly higher in MPAs with several gear restrictions than in heavy fishing sites (Fig. 3).

For MPAs with no fishing, percent biomass difference relative to heavy fishing areas for all 4 commercially

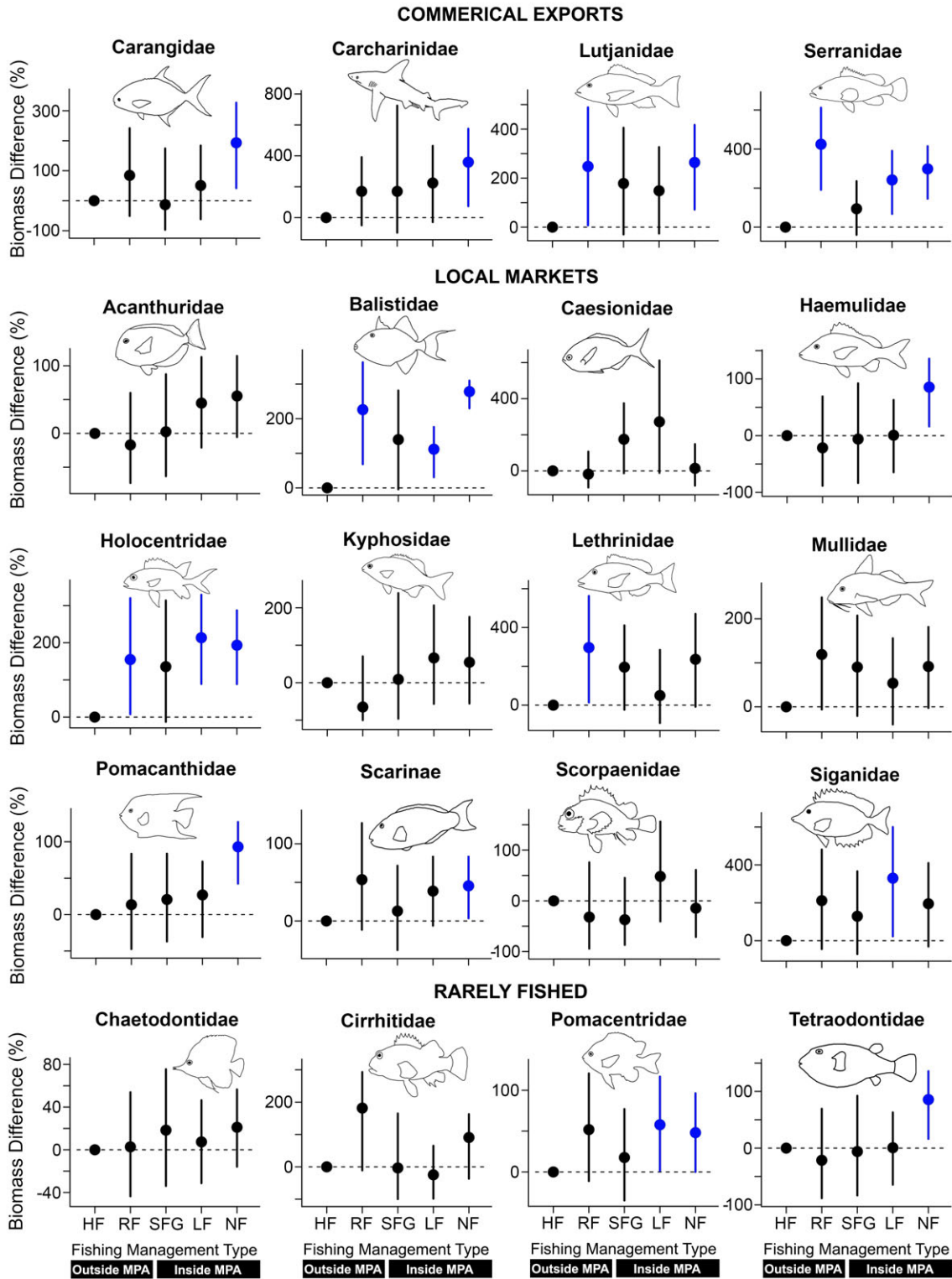


Figure 3. Percent family-level biomass difference (95% CI) between heavily fished sites and sites where 4 different types of fishery management are applied in tropical waters ($n = 1,396$ surveys) (gray, significant difference from heavily fished sites; black, estimates with confidence intervals that cross zero [0% difference from heavy fishing sites]). Heavy fishing and remote fishing sites are outside marine protected areas (MPAs), and sites with several gears, line fishing, and no fishing are inside MPAs (HF, heavy fishing; RF, remote fishing; SFG, several fishing gears; LF, line fishing; NF, no fishing).

marketed families was significantly higher: Carangidae, 193% higher, $p = 0.012$; Carcharhinidae, 359% higher, $p = 0.014$; Lutjanidae, 292% higher, $p = 0.003$; and Serranidae, 298% higher, $p < 0.001$. Biomass of 4 of 12 locally marketed fish families was significantly higher in no-fishing MPAs than in heavy fishing areas: Balistidae, 274% higher, $p < 0.001$; Holocentridae, 193% higher, $p < 0.001$; Scarinae, 46% higher, $p = 0.034$; and Pomacanthidae, 93% higher, $p = 0.002$. Lethrinid biomass was 236% higher in no-fishing MPAs than in heavily fished areas, although this difference was inconsistent across sites (Fig. 3; Supporting Information).

Several families had significantly higher biomass at MPA sites with line fishing than at heavily fished sites: Balistidae, 112% higher, $p = 0.009$; Holocentridae, 214% higher, $p < 0.001$; Serranidae, 242% higher, $p < 0.006$; Siganidae, 330% higher, $p = 0.034$; and Pomacentridae, 48% higher, $p = 0.046$.

The following families displayed significantly higher biomass in remote fishing sites than in heavily fished sites: Balistidae, 226% higher, $p < 0.005$; Holocentridae, 155% higher, $p < 0.038$; Lethrinidae, 297% higher, $p < 0.038$; Lutjanidae, 248% higher, $p < 0.042$; and Serranidae, 425% higher, $p < 0.001$ (Fig. 3; Supporting Information).

Discussion

Community- and family-level fish biomass differed substantially from fishery-closure sites and sites where there were restrictions on multiple fishing gears. This finding implies that strict fishery closures and controls on fishing-gear use could benefit reef fisheries. As expected, complete fishery closures benefited overall fish biomass more than restrictions on fishing gears, but the higher biomass of many reef fish families at line-fishing sites compared with sites fished with multiple gears and at sites where there were no restrictions on fishing (i.e., openly fished sites) suggest potentially important differences in biomass and associated ecological functions in areas subject to multiple gear restrictions (McClanahan et al. 2014). We found a positive response of community-level fish biomass at remote offshore sites open to fishing, which was generally comparable to the effect of fishery closures. Isolation is a key feature of MPAs that exerts a relatively strong influence on community-level fish biomass (Graham & McClanahan 2013; D'agata et al. 2016).

Although full closures provided the greatest benefit to overall fish biomass, responses of reef fish families to fishery closures were highly variable, which likely reflects the unpredictable and slow recovery rates of reef fish families, a characteristic that makes them highly vulnerable to fishing (Russ & Alcala 2004; McClanahan et al. 2007). Eight reef fish families, 4 of which are

targeted for export, benefited most from full protection. Of these 8 families, large piscivores in the families Haemulidae, Lutjanidae, and Serranidae are heavily targeted by line fishers for export, but they are also targeted by traps and spears (Mangi & Roberts 2007). Balistids (triggerfishes) and pomacanthids (angelfishes) are also caught by nets and targeted by spears (Campbell & Pardede 2006), generally for local markets. Similarly, holocentrids (soldierfishes) are targeted by fishers in some Pacific countries, particularly in locations where the prevalence of ciguatera among larger fish species is high. Long-term fishing closures around coral reefs can benefit many fish families vulnerable to multiple gears, although recovery can take more than 10 years for balistids and up to 20 years for slow-growing lethrinids, lutjanids, and serranids (McClanahan et al. 2007).

Parrotfishes (subfamily Scarinae) also benefited from full protection. Species-level data showed many species that benefited were smaller-bodied species that graze macroalgae and sediments on coral reefs. Recovery of small- and medium-sized parrotfishes can take from 5 to 10 years (Stockwell et al. 2009), whereas large-bodied species can take up to 25 years for full recovery (McClanahan et al. 2007). Our finding that the overall biomass of parrotfishes at remote sites showed little overall difference from biomass at heavily fished sites is also consistent with findings that small- and medium-sized parrotfishes are relatively resilient to fishing pressure (Bellwood et al. 2012) and that herbivore biomass can be maintained at intermediate levels of fishing (MacNeil et al. 2015). The vulnerability and subsequent depletion of large-bodied bioeroding parrotfishes, in particular by spear fishing (Bellwood et al. 2012), have elevated the relative effect small- and medium-sized parrotfishes have on fished coral reefs through mitigating processes that lead to reef degradation (Hughes et al. 2010) and their contribution to the livelihoods of artisanal fishers in the tropics (Hicks & McClanahan 2012).

The positive effect of full protection identified for Carangidae (jacks) is also consistent with global findings that jacks are not dependent on isolation and age for recovery but receive considerable protection from fishing mortality within large, well-enforced, no-take MPAs (Edgar et al. 2014). The high biomass of sharks we found inside fishing closures was consistent with global findings that these fishes receive considerable protection from fishing mortality within large, well-enforced, and old no-take MPAs (Edgar et al. 2014; Salinas de León et al. 2016) and was somewhat contrary to concerns that the mobility of large pelagic species impedes recovery in fully protected MPAs (Gruss et al. 2011). Both families are highly targeted for commercial export and domestic markets, and our findings imply that fishing-gear and size restrictions and quotas to limit fishing effort could be key strategies to building sustainable fishing practices.

Community-level fish biomass at remote fishing sites was generally comparable to that at sites closed to fishing, presumably because distance to human population centers reduces fishing pressure at remote sites (Graham & McClanahan 2013). The fishes that contributed to the elevated community-level biomass at remote locations included highly targeted and commercially exported lutjanid, lethrinid, and serranid piscivores, whose small home ranges make them sensitive to human fishing pressure (Mellin et al. 2016). These fishes apparently benefit from low fishing pressure (MacNeil et al. 2015) associated with remoteness, where their vulnerability to fishing is reduced (Estes et al. 2011; D'agata et al. 2016). Consistent with these findings, although the effect was not significant due to high local-scale variability, community-level fish biomass was lowest in proximity to provincial towns, indicating a negative effect of market access on fisheries (Cinner et al. 2013). This result is also consistent with findings that travel time from markets is a strong predictor of fish biomass on coral reefs; protection of coral reef areas near markets is weak compared with protection of reefs more distant from markets or in areas where de facto protection occurs due to isolation (Maire et al. 2016).

The benefits afforded the biomass of 5 reef fish families from exclusive line fishing was most likely due to the removal of fishing gears used to target specific fish families. Prohibitions on nets that commonly select for siganids (rabbitfishes) (Russ & Alcalá 1998) is a likely contributing factor explaining their higher biomass, whereas controls on spear guns would benefit balistids (triggerfishes) and serranids (groupers), which are selectively targeted by spear fishers (Campbell & Pardede 2006). For the highly valued groupers, which are generally targeted by spears but are vulnerable to nonselective fishing with other gears including line fishing, the benefits of exclusive line fishing implies that targeted gear restrictions may provide a more sustainable method of fishing relative to uncontrolled use of spears, nets, and other gears. Such strategies, if suitably targeted, could take advantage (e.g., through spillover processes) of the elevated piscivore biomass in no-take areas globally (this study; Edgar et al. 2014; MacNeil et al. 2015).

The large variation in caesionid (fusiliers) biomass at sites only fished with lines also suggests that prohibitions on gears such as nets, which target planktivores (Russ & Alcalá 1998), may in some places benefit this emergent fishery in the tropics. Our findings support recent evidence that planktivore biomass can rise rapidly when restrictions on fishing are in place (MacNeil et al. 2015). The lower biomass of caesionids in no-take zones in MPAs than in areas where line fishing was permitted may be a consequence of cascading ecological interactions. Members of this family are important prey for reef predators such as carangid jacks and carcharhinid reef sharks, which appeared to be depressed in all sites except MPAs closed to fishing. Partial protection may therefore

benefit prey species that may otherwise also be fished heavily in areas with no fishing restrictions.

We suggest that appropriate fishing restrictions, such as removing all fishing pressure other than line fishing, can support fish biomass at levels higher than in openly fished sites. Although there was marked variability across locations in the response of biomass to gear restrictions that led to a lack of general statistical significance, some families and locations may retain high biomass when fished with lines only. Similarly, bans on fishing nets have protected a range of functional groups and increase fish catches especially when located close to fishery closures (McClanahan 2010), and spearfishing controls improve parrotfish and serranid abundance (Gillett & Moy 2006; Frisch et al. 2012; Yulianto et al. 2015). Modifications to traps can increase catch yields and reduce the catch of immature lethrinid and siganid species (Hicks & McClanahan 2012).

In some of the MPAs we studied, areas with fishing-gear restrictions were near areas closed to fishing, and higher biomass inside areas with multiple fishing restrictions may have occurred because of the so-called spillover effect, in which movement of fish to adjacent areas leads to increased fish biomass (Russ et al. 2005) and fish catches (McClanahan & Mangi 2000). Most tropical reef fisheries are now regarded as overfished, but substantial net catch gains are possible through reduction in fishing effort (Costello et al. 2012). Models suggest that the simultaneous use of fishery closures and fishing controls on total allowable catch, facilitated through individual transferable quotas, may result in higher biomass and net economic returns compared with restrictions on fishing effort and fishery closures (Little et al. 2010). Irrespective of the mechanisms that led to biomass enhancement in areas fished only by lines, our findings imply that across tropical latitudes restrictions on fishing gears can have a positive influence on biomass of targeted reef fishes.

Of the families rarely fished or infrequently fished for local consumption, Pomacentridae and Tetraodontidae had higher biomass in fishery closures, suggesting that they may be affected by netting and illegal fishing with dynamite in some locations. Pomacentrids can benefit globally from large MPAs (Edgar et al. 2014), which, although an unexpected result because they are not directly fished, is consistent with our findings that fishing restrictions afforded protection to their overall biomass. Two families that are rarely fished and 3 families fished for local consumption were not affected by any fishing-restriction categories. Hence, we did not detect any indirect depletion in their biomass from fishery closures due to size and species-specific predatory controls.

The positive effect we found for MPA age on community-level fish biomass parallels findings of biomass buildup in older, well-enforced fishing closures (Graham & McClanahan 2013; Edgar et al. 2014) and in areas with restrictions on fishing gear (McClanahan

et al. 2011). At the same time, the positive effect of depth (included as a covariate) supports the notion that shallow waters are more vulnerable to exploitation from overfishing (Tyler et al. 2009) because gear availability may limit the ability of artisanal fishers to fish depths >15 m (Brokovich et al. 2008; Goetze et al. 2011).

Adopting culturally and socially appropriate fishing-gear regulations in space (e.g., depth) and time may provide gains in biomass and associated ecological functions if opportunity for fishery closures in MPAs are few or enforcement potential is limited or likely to fail. In our study, the weak or nonexistent responses of fish biomass recovery to multiple fishing restrictions for some families could potentially be due to factors driving large variations in compliance with fisheries controls. For young and low-compliance fishery closures, bans on destructive and exploitative gears can potentially increase fish biomass on reefs (McClanahan et al. 2014) and total catch overall (Costello et al. 2012) and provide a first step to demonstrating to fishing communities benefits from gear restrictions before more targeted or nuanced fishing restrictions are achievable (Campbell et al. 2012).

Although areas with strict fishery closures had the highest reef fish biomass at community and family levels, restrictions on fishing gear use may also benefit some targeted reef fish families, including those traded in international and domestic markets. A priority for future research is to assess whether controls on certain fishing gears lead to increased fishing effort with permitted gears and subsequent potential impacts on targeted fisheries. Our findings support recent evidence that wilderness areas support unique ecological values compared with well-managed marine protected areas and may provide the last refuges for vulnerable functional roles of fish populations (D'agata et al. 2016). When interpreted in the context of recent findings on the impacts of human behavior on reef fisheries, we suggest that, although no-fishing zones with high compliance provide the best conservation outcomes, useful policies also include those aimed at limiting and regulating human fishing pressures through socially appropriate and practical fishery closures and fishing restrictions. These could be coupled with combinations of appropriately tailored catch limits and rights-based fisheries approaches that aim to improve economic incentives and fishery outcomes for fishers (Worm et al. 2009; Barner et al. 2015). We suggest that such approaches would assist fisheries managers to overcome some of the complexity inherent in multispecies fisheries management and improve the chances of building food security in densely populated tropical countries.

Acknowledgments

We thank the many Reef Life Survey (RLS) divers and scientific colleagues who participated in data collection,

and University of Tasmania staff, including J. Berkhout, A. Cooper, M. Davey, J. Hulls, E. Oh, and N. Barrett. Development of RLS was supported by the former Commonwealth Environment Research Facilities Program, and analyses were supported by the Australian Research Council (Grant No. LP100200122) and the Marine Biodiversity Hub, a collaborative partnership supported by the Australian Government's National Environmental Science Programme. Additional funding and support for field surveys was provided by grants from the Ian Potter Foundation, CoastWest, National Geographic Society, Wildlife Conservation Society Indonesia, The Winston Churchill Memorial Trust, Australian-American Fulbright Commission, and ASSEMBLE Marine.

Supporting Information

Model results summaries (Appendices S1 & S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

- Aswani S. 2005. Customary sea tenure in Oceania as a case of rights-based fishery management: Does it work? *Reviews in Fish Biology and Fisheries* **15**:285–307.
- Barner AK, Lubchenco J, Costello C, Gaines SD, Leland A, Jenks B, Murawski S, Schwaab E, Spring M. 2015. Solutions for recovering and sustaining the bounty of the ocean: Combining fishery reforms, rights-based fisheries management, and marine reserves. *Oceanography* **28**:252–263.
- Barton K. 2009. MuMIn: multi-model inference. R package. Version 0.12.2. R Foundation for Statistical Computing, Vienna. Available from <http://r-forge.r-project.org/projects/mumin/> (accessed September 2015).
- Bellwood DR, Hoey AS, Hughes TP. 2012. Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B* **279**:1621–1629.
- Brokovich E, Einbinder S, Shashar N, Kiflawi M, Kark S. 2008. Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. *Marine Ecology Progress Series* **371**:253–262.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretical approach*. 2nd edition. Springer, New York.
- Campbell SJ, Cinner JE, Ardiwijaya RL, Pardede ST, Kartawijaya T, Mukmunin A, Herdiana Y, Hoey AS, Pratchett MS, Baird AH. 2012. Avoiding conflicts and protecting coral reefs: customary management benefits marine habitats and fish biomass. *Oryx* **46**:486–494.
- Campbell SJ, Pardede ST. 2006. Reef fish structure and cascading effects in response to artisanal fishing pressure. *Fisheries Research* **79**:75–83.
- Cinner JE, Graham NAJ, Huchery C, MacNeil A. 2013. Global effects of local human population density and distance to markets on the condition of coral reef fisheries. *Conservation Biology* **27**:453–458.
- Cohen PJ, Alexander TJ. 2013. Catch rates, composition and fish size from reefs managed with periodically-harvested closures. *PLOS ONE* **8**:(e73383) <https://doi.org/10.1371/journal.pone.0073383>.

- Costello C, Ovando D, Hilborn R, Gaines SD, Deschenes O, Lester SE. 2012. Status and solutions for the world's unassessed fisheries. *Science* **338**:517–520.
- D'agata S, Mouillot D, Wantiez L, Friedlander AM, Kulbicki M, Vigliola L. 2016. Marine reserves lag behind wilderness in the conservation of key functional roles. *Nature Communications* <https://doi.org/10.1038/ncomms12000>.
- Edgar GJ, et al. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**:216–220.
- Edgar GJ, Stuart-Smith RD. 2014. Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data* **1**:140007:1–8.
- Estes JA, et al. 2011. Trophic downgrading of planet Earth. *Science* **333**:301–306.
- Frisch AJ, Cole AJ, Hobbs J-PA, Rizzari JR, Munkres KP. 2012. Effects of spearfishing on reef fish populations in a multi-use conservation area. *PLoS ONE* **7**:(e51938) <https://doi.org/10.1371/journal.pone.0051938>.
- Gillett R, Moy W. 2006. Spearfishing in the Pacific Islands. Current status and management issues (No. 19). FAO/ FishCode Review, Rome.
- Goetze JS, Langlois TJ, Egli DP, Harvey ES. 2011. Evidence of artisanal fishing impacts and depth refuge in assemblages of Fijian reef fish. *Coral Reefs* **30**:507–517.
- Graham NAJ, McClanahan TR. 2013. The last call for marine wilderness? *BioScience* **63**:397–402.
- Gruss A, Kaplan DM, Guenette S, Roberts CM, Botsford LW. 2011. Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation* **144**:692–702.
- Hawkins JP, Roberts CM, Gell FR, Dytham C. 2007. Effects of trap fishing on reef fish communities. *Aquatic Conservation Marine Freshwater Ecosystems* **17**:111–132.
- Hicks CC, McClanahan TR. 2012. Assessing gear modifications needed to optimize yields in a heavily exploited, multi-species, sea-grass and coral reef fishery. *PLoS ONE* **7**:e36022 <https://doi.org/10.1371/journal.pone.0036022>.
- Hughes TP, Graham NAJ, Jackson, JBC, Mumby PJ, Steneck RS. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution* **25**:633–642.
- Johnson AE, Cinner JE, Hardt MJ, Jacquet J, McClanahan TR, Sanchirico JN. 2013. Trends, current understanding and future research priorities for artisanal coral reef fisheries research. *Fish and Fisheries* **14**:281–292.
- Little LR, Grafton RQ, Kompas T, Smith ADM, Punt AE, Mapstone BD. 2010. Complementarity of no-take marine reserves and individual transferable catch quotas for managing the line fishery of the Great Barrier Reef. *Conservation Biology* **25**:333–340.
- MacNeil MA, et al. 2015. Recovery potential of the world's coral reef fishes. *Nature* **520**:341–344.
- Maire E, et al. 2016. How accessible are coral reefs to people? A global assessment based on travel time. *Ecology Letters* **19**:351–360.
- Mangi SC, Roberts CM. 2007. Factors influencing fish catch levels on Kenya's coral reefs. *Fisheries Management and Ecology* **14**:245–253.
- Mangi SC, Roberts CM, Rodwell LD. 2007. Financial comparisons of fishing gear used in Kenya's coral reef lagoons. *Ambio* **36**:671–676.
- McClanahan TR. 2010. Effects of fisheries closures and gear restrictions on fishing income in a Kenyan coral reef. *Conservation Biology* **24**:1519–1528.
- McClanahan TR, Mangi S. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications* **10**:1792–1805.
- McClanahan TR, et al. 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences of the USA* **108**:17230–17233.
- McClanahan TR, Graham NAJ, MacNeil MA, Cinner JE. 2014. Biomass-based targets and the management of multispecies coral reef fisheries. *Conservation Biology* **29**:409–417.
- McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA. 2007. Towards pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications* **17**:1055–1067.
- Mellin C, et al. 2016. Humans and seasonal climate variability threaten large-bodied coral reef fish with small ranges. *Nature Communications* **7**:10491 <https://doi.org/10.1038/ncomms10491>.
- Mumby P, et al. 2014. Towards reef resilience and sustainable livelihoods. A handbook for Caribbean coral reef managers. University of Exeter, United Kingdom. 172pp.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2015. nlme: linear and nonlinear mixed effects models. R package version 3.1-120. R Foundation for Statistical Computing, Vienna. Available from <http://CRAN.R-project.org/package=nlme> (accessed September 2015).
- Russ GR, Alcala AC. 1998. Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. *Coral Reefs* **17**:399–416.
- Russ GR, Alcala AC. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* **138**:622–627.
- Russ GR, Stockwell B, Alcala AC. 2005. Inferring versus measuring rates of recovery in no-take marine reserves. *Marine Ecology Progress Series* **292**:1–12.
- Salinas de León P, Acuña-Marrero D, Rastoin E, Friedlander AM, Donovan MK, Sala E. 2016. Largest global shark biomass found in the northern Galápagos Islands of Darwin and Wolf. *PeerJP* **4**:e1911 <https://doi.org/10.7717/peerj.1911>.
- Skaug H, Fournier D, Bolker B, Magnusson A, Nielsen A. 2014. Generalized linear mixed models using AD model builder. R package version 0.8.0. R Foundation for Statistical Computing, Vienna.
- Spalding MD, et al. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* **57**:573–583.
- Stockwell B, Jadloc CRL, Abesamis RA, Alcala AC, Russ GR. 2009. Trophic and benthic responses to no-take marine reserve protection in the Philippines. *Marine Ecology Progress Series* **389**:1–15.
- Tyler EHM, Speight MR, Henderson P, Manica A. 2009. Evidence for a depth refuge effect in artisanal coral reef fisheries. *Biological Conservation* **142**:652–667.
- Walker B, et al. 2009. Looming global-scale failures and missing institutions. *Science* **325**:1345–1346.
- Worm B, et al. 2009. Rebuilding global fisheries. *Science* **325**:578–585.
- Yulianto I, Hammer C, Wiryawan B, Palm HW. 2015. Fishing induced groupers stock dynamics in Karimunjawa National Park, Indonesia. *Fisheries Science* **81**:417–432.

