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Gear restrictions create conservation and fisheries trade-offs for management

Paul G. Carvalho[1] | **Austin Humphries**[1,2]

[1]Department of Fisheries, Animal and Veterinary Sciences, University of Rhode Island, Kingston, USA

[2]Graduate School of Oceanography, University of Rhode Island, Narragansett, USA

Correspondence
Paul G. Carvalho, Department of Fisheries, Animal and Veterinary Sciences, University of Rhode Island, Kingston, RI 02881, USA.
Email: paulcarvalho@uri.edu

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Abstract

Gear-based management for coral reef fisheries is often overlooked in the scientific literature. Empirical studies have demonstrated the conservation benefits of gear-restricted areas (i.e. prohibiting fishing gears), which can support greater biomass than unrestricted areas and protect species that play key functional roles. However, population dynamics of functional feeding groups of reef fishes under specific gear-restriction regimes remains uncertain. Here, we constructed a multi-species, length-based fisheries model to observe relative biomass and catch of reef fishes under various gear-restriction management scenarios. We used fishery-dependent and fishery-independent data to determine the catchability of functional groups and selectivity of size classes for hook-and-line, net and spear fishing, which are widely used gear types on coral reefs globally. Our model revealed trade-offs involved with gear-restriction management such that no single management strategy was able to maximize biomass or catch of all functional groups simultaneously. Also, we found that spear fishing (i.e. prohibiting hook-and-line and net fishing) maintained the highest total biomass summed across functional groups, whilst hook-and-line fishing (i.e. prohibiting net and spear fishing) and a ban on spears maintained the lowest biomass. However, hook-and-line fishing generated the highest catch-per-unit-effort. Our model results were primarily driven by differential growth rates, maximum per capita production of recruits, and catchability of functional groups targeted by each fishing gear. We demonstrate that gear restrictions can be a critical management tool for maintaining biomass and catch of certain functional groups but will likely require additional management to protect all key functional feeding groups of coral reef fishes.

KEYWORDS
coral reefs, ecosystem-based management, fisheries ecology, fisheries management, gear-based management, population dynamics

1 | INTRODUCTION

Coral reefs are under immense pressure to support the livelihoods of millions of people in an increasingly globalized world (Hughes et al., 2017). The lifestyles and identities of many tropical, coastal communities are tightly connected to reef fisheries, and there are often few alternative sources for income and nutrition (Cinner, 2014). Fishing is, however, one of the primary drivers of marine ecosystem structure and function and has had profound negative effects, both direct and indirect, on coral reefs (Pandolfi et al., 2003). For example, fishing can directly impact reefs by reducing fish abundance, biomass and size structure and indirectly through compromising ecosystem functions (Carvalho, Setiawan, et al., 2021; DeMartini & Smith, 2015). The ability of coral reefs to continue providing ecosystem services to coastal communities relies on the development of management strategies that can support fisheries production and preserve biomass of fish that perform vital ecosystem functions.

Fishing gear restrictions have been proposed as adaptive management strategies to help balance the trade-offs of fisheries catch and protecting key functional groups of reef fishes (Cinner, McClanahan, Graham, et al., 2009; McClanahan & Cinner, 2008). The motivation for scientific inquiry into gear restrictions and gear-based management is that fishers on coral reefs use multiple gear types (e.g. hook-and-line, nets and spears) that differentially impact functional feeding groups (hereafter referred to as functional groups) of reef fishes (Mbaru et al., 2020). For example, hook-and-line fishing targets piscivorous fishes with baited hooks (Humphries et al., 2019). Nets generally target a wide diversity of species and, with small mesh sizes, can have high catch rates for small and immature fishes (Cinner, McClanahan, Graham, et al., 2009). Spears target both piscivores and herbivores, but typically catch larger individuals than other gear types (Frisch et al., 2008, 2012). Thus, gear-based management can potentially provide fisheries production and leverage the characteristic catchabilities of fishing gear to protect important functional groups of reef fishes.

Support and compliance from fishers is critical for successful management of dispersed and small-scale coral reef fisheries (Campbell et al., 2012; Gill et al., 2017). Indeed, fishers have expressed more support for gear-based management over other management regulations (McClanahan & Abunge, 2018), and studies have demonstrated that gear restrictions can support higher fish biomass than unrestricted fishing areas and protect key ecological functions (Bozec et al., 2016; Campbell et al., 2018). Whilst empirical studies demonstrate the benefits of gear-restriction management through increased fish biomass, and gear selectivity studies provide a framework for gear-based management through describing fishing gear catchabilities for different functional groups, the population dynamics of fishes under specific gear-restriction regimes remains uncertain.

In this study, we constructed a length-based, multi-species fisheries model and used fishery-dependent and independent data to generate gear-specific catchability and selectivity parameters for functional groups and size classes, respectively. We modelled hook-and-line, net and spear fishing, which are widely used gear types in coral reef fisheries around the world (Johnson et al., 2013). We strategically designed the model to explore emergent properties of community and functional group specific population dynamics in response with fishing effort and various gear-restriction scenarios. In addition, we examine the trade-offs between gear-restriction scenarios for maximizing biomass and catch of each functional group, as well as total biomass and catch summed across functional groups. Our baseline model allowed all fishing gears with equal fishing pressure, and subsequent scenarios included a full factorial design of prohibiting gear types. Modelling combinations of fishing gears allowed us to investigate potential interactions between fishing gears that have distinct catchabilities for different functional groups of coral reef fishes.

2 | METHODS

2.1 | Model summary

We developed a length-based, multi-species population model to simulate gear-restriction scenarios for coral reef fisheries. Our model focussed on representative species from nine functional feeding groups of reef fishes (Table S1): browsers (orangespine unicornfish, *Naso lituratus*, Acanthuridae), detritivores (striated surgeonfish, *Ctenochaetus striatus*, Acanthuridae), excavators/scrapers (dusky parrotfish, *Scarus niger*, Scaridae), grazers (goldspotted spinefoot, *Siganus punctatus*, Siganidae), macro-invertivores (manybar goatfish, *Parupeneus multifasciatus*, Mullidae), micro-invertivores (two-lined monocle bream, *Scolopsis bilineata*, Nemipteridae), pisci-invertivores (peacock hind, *Cephalopholis argus*, Serranidae), piscivores (redmouth grouper, *Aethaloperca rogaa*, Serranidae) and planktivores (yellow and blueback fusilier, *Caesio teres*, Caesionidae). Functional groups were designated based on primary literature (Cinner et al., 2013; Froese & Pauly, 2021; MacNeil et al., 2015). We calculated gear-specific functional group catchability and size selectivity parameters to model hook-and-line, net and spear fishing. These parameters were derived from fishery-dependent and fishery-independent data collected from coral reefs in Wakatobi National Park in Southeast Sulawesi, Indonesia (Appendices S1 and S2; Carvalho, Zhu, et al., 2021). Hook-and-line fishing trips included one to three fishers using small, baited hooks (1–2 cm gape) and monofilament line. Spear fishers used 1-meter long wooden speargunspropelled by a single rubber tube, and spear fishing trips ranged from one to six fishers. Net dimensions were 75 × 3 m gillnets with approximately 6.5 cm mesh size, and sometimes multiple nets were tied together and deployed on shallow reefs. Net fishing trips included as many as 14 people. Fishing gear selectivity for size classes was modelled using lognormal distributions and was dependent on gear specifications (i.e. hook gape size and net mesh size). We also modelled changes to gear specifications by increasing the mean size for lognormal functions of selectivity for hook-and-line (representing an increase in hook size) and net (representing an increase in mesh size) fishing (Appendix S3). Initial population sizes for each functional group were based on fishery-independent surveys, and recruitment was modelled using a Beverton–Holt stock-recruitment relationship. The purpose of this model was to simulate relative biomass and catch in response to gear restrictions. Therefore, we have prioritized generality and realism, rather than providing specific quantitative estimates (i.e. accuracy and precision) for biomass or catch targets in a particular coral reef system (Levins, 1966). This model was strategically designed to understand the basic emergent properties of fish communities in response to gear-restriction management by integrating catchability and selectivity parameters for the most commonly used fishing gear types on coral reefs. All simulations followed the same model sequence: (a) introduce recruits, (b) impose natural and fishing mortality and (c) allow fish to grow.

2.2 | Recruitment

We used the Beverton–Holt equation to model stock-recruitment relationships for all functional groups (Appendix S4.1). Recruitment parameters (α and β; Table S1) were estimated through an optimization function such that equilibrium biomass of each functional group reached a level that resembles fish populations on remote, or pristine, coral reefs in the absence of fishing effort (Campbell et al., 2020; MacNeil et al., 2015). In addition, a sensitivity analysis was conducted to observe changes in biomass and catch with a 10% increase or decrease in recruitment parameter values.

2.3 | Natural (residual) mortality

Studies have found that the natural mortality of marine fishes, including coral reef species, is correlated with fish length and von Bertalanffy growth parameters (Gislason et al., 2010). Thus, natural mortality, excluding predation mortality, of each functional group was a function of the midpoint of each size class, asymptotic length and instantaneous growth rates (Appendix S4.2; Table S1). Natural mortality was highest for small size classes and exponentially decreased as body size increased, which is corroborated by empirical estimates of natural mortality of coral reef fishes in relation to body size (Goatley & Bellwood, 2016).

2.4 | Predation mortality

Predation mortality for each functional group and size class was calculated following the methods of (Hall et al., 2006). Predation mortality was a function of (1) ingestion rates for predator functional groups (i.e. pisci-invertivores and piscivores) in each size class, (2) the suitability of prey functional groups and size classes and (3) the abundance of predators and prey (Appendix S4.3). Ingestions rates captured the allometric relationships between ingestion rate, energy expenditure and production that has been observed for marine fishes (Hall et al., 2006). The suitability of prey functional groups and size classes was the product of size preference and functional group preference by predators (Appendix S4.3). Predators maximized preference for prey that were 3% of their body mass, which is consistent with predator-prey size relationships for coral reef fishes (Dunic & Baum, 2017; St John, 1999). Coral reef pisci-invertivores and piscivores typically feed on a wide-range of prey species, but a majority of their diets are composed of planktivores (Greenwood et al., 2010; Skinner et al., 2019). Thus, pisci-invertivore and piscivore preferences for planktivores were set at 1 and set at 0.5 for all other prey species (Table S2). To account for uncertainty in predator-prey parameters, a sensitivity analysis was conducted such that key parameters were increased or decreased by 10% and model outcomes were compared with the base model.

2.5 | Fishing mortality

Fishing mortality was modelled with the equation:

$$F_{i,j,g} = q_{i,g} s_{j,g} E, \qquad (1)$$

where $F_{i,j,g}$ is the fishing mortality for functional group (i) and size class (j) by gear type (g), q is catchability for each functional group, s is selectivity of size classes and E is fishing effort (fishing effort was equivalent for each gear type included in a management scenario). Selectivity for size classes (s) was modelled with a lognormal distribution for all gear types and parameter values were fitted using fishery-dependent data from Wakatobi (Figure S1). To estimate $q_{i,g}$ parameters, we used an optimization function to minimize the sum of squared error (SSE) for the equation:

$$\mathrm{SSE} = \sum_{g} \sum_{i} \sum_{j} \left(q_{i,g} s_{j,g} - \frac{y_{i,j,g}}{n_{i,j}} \right)^2, \qquad (2)$$

where $y_{i,j,g}$ is the proportion of catch per fishing trip from fishery-dependent surveys and $n_{i,j}$ is the abundance observed from fisheries-independent surveys. In addition, the estimated products of $q_{i,g}$ and $s_{j,g}$ were normalized such that values for all functional group-size class combinations summed to one for each gear type. To quantify uncertainty in the catchability and selectivity parameters, non-parametric bootstrapping was used to resample fisheries-dependent and fisheries-independent data 100 times. Bootstrapped values of qs were used to simulate each management scenario with light ($E = 0.25$), moderate ($E = 0.50$) and heavy ($E = 0.75$) fishing effort. Catch (C) for each functional group and size class was calculated using the Baranov catch equation and converted to values relative to the maximum observed catch (C_{max}) for each functional group across all management scenarios (Appendix S4.4).

2.6 | Growth

Individual fish grew according to a modified von Bertalanffy growth function that accommodated the binned size structure of the model (Appendix S4.5). The number of fish that grew into the next size class was proportional to the time it took for fish to grow from the lower to upper limit of each size class (Appendix S4.5). Thus, if $t_{i,j}$ represents the time it takes for functional group i to grow from the lower to upper limit of size class j, then the proportion of fish that grow to the next size class is $1/t_{i,j}$ (Hilborn & Walters, 1992). Values for each functional group and size class were rescaled such that fish were unable to skip size classes in a single timestep (Appendix S4.5).

2.7 | Gear-restriction scenarios

Our baseline management scenario included all fishing gears (i.e. hook-and-line, net and spear) with total effort equally divided amongst gears. Subsequent management scenarios included a full

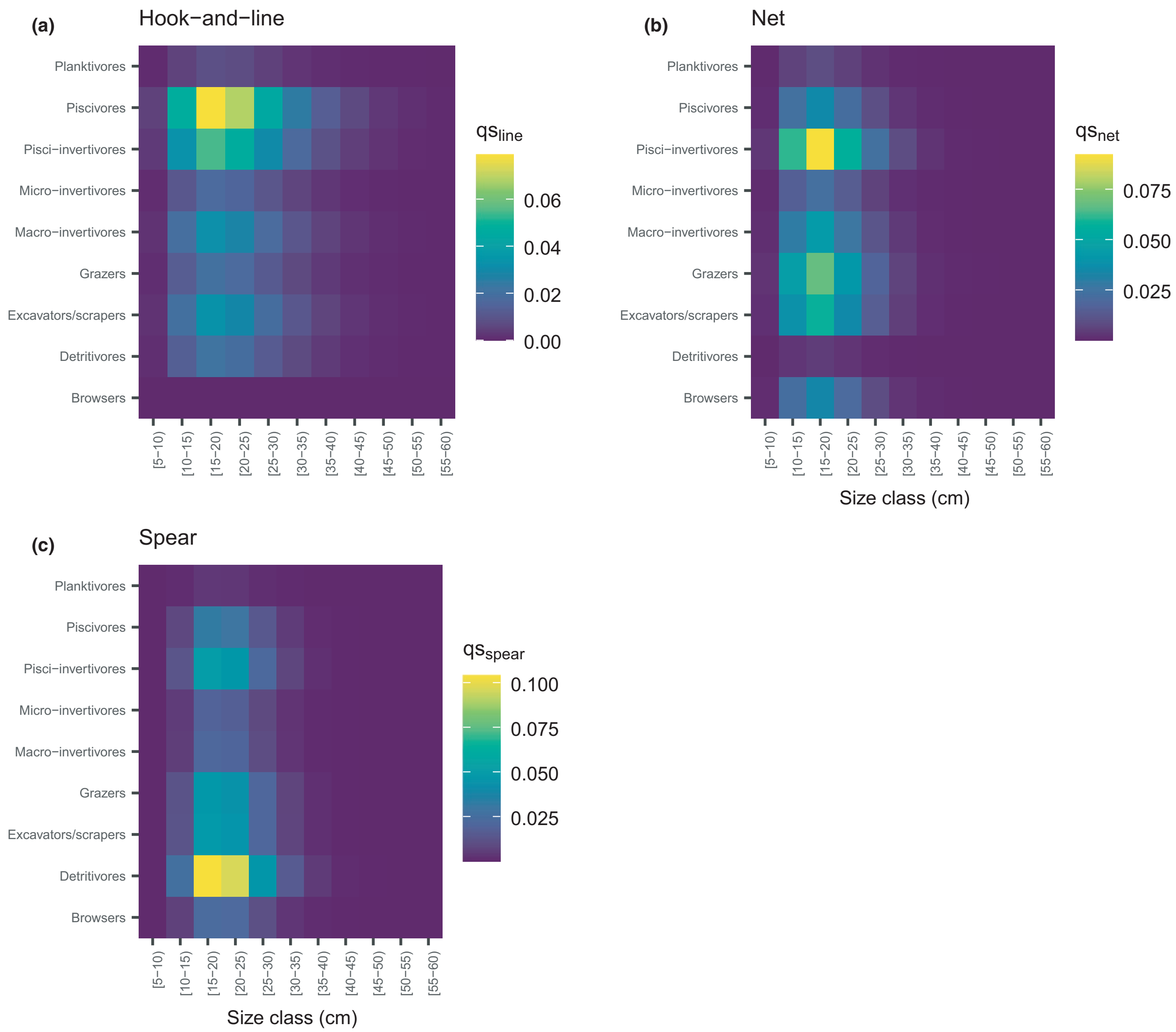
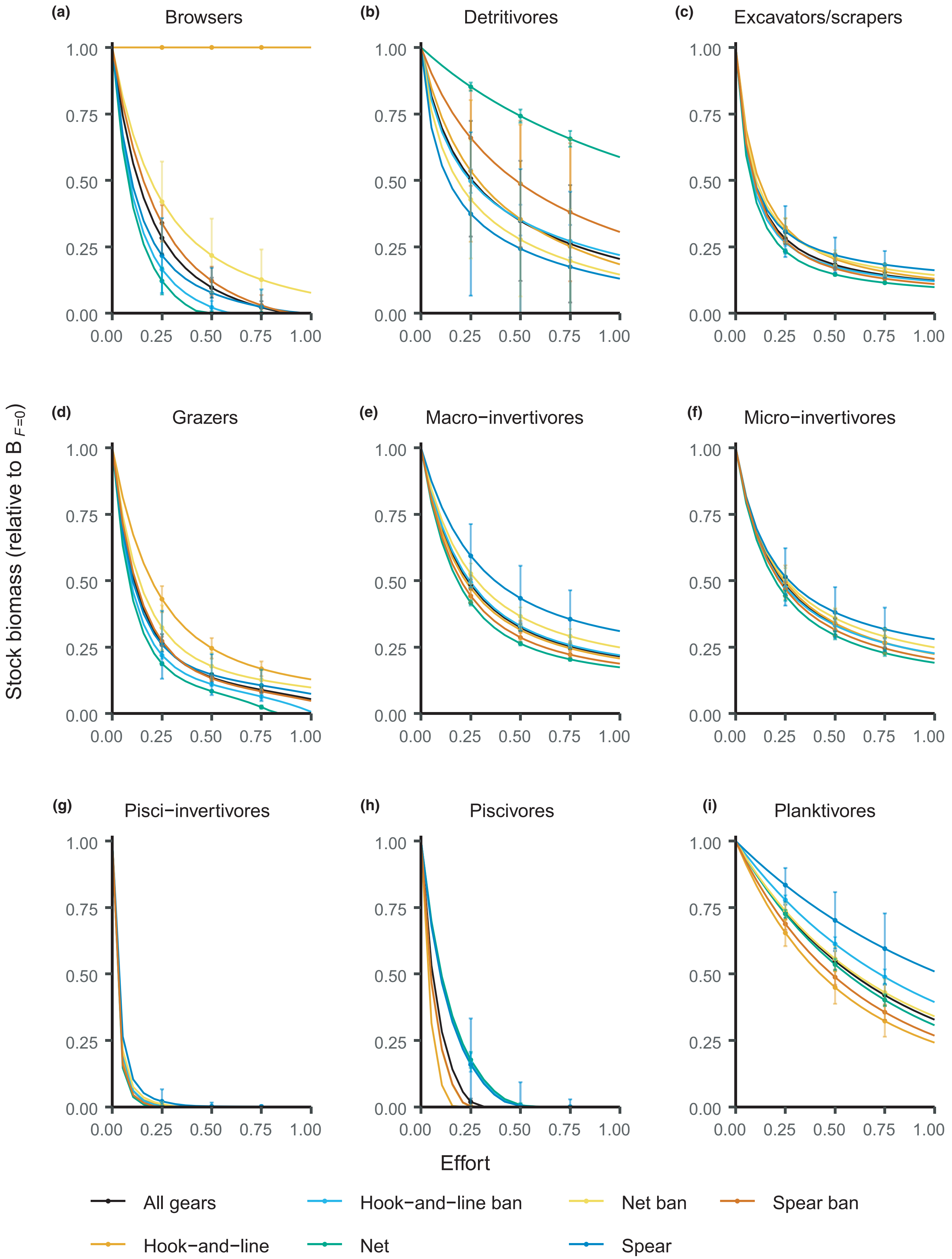


FIGURE 1 Product of catchability (q_i) and selectivity (s_j) for each functional feeding group (i) and size class (j) by fishing gear type. The product qs was calibrated using an optimization function (Equation 2) and scaled such that values for all functional group-size class combination summed to one. Figure appears in colour in the online version only

FIGURE 2 Biomass for each functional feeding group in relation with fishing effort and gear-management scenario. Biomass is relative to the 'pristine' biomass (i.e. when fishing effort is absent) of each functional group. Colours represent different management scenarios and bars represent the interquartile range at light ($E = 0.25$), moderate ($E = 0.50$) and heavy ($E = 0.75$) fishing effort based on non-parametric bootstrap resampling to quantify uncertainty in catchability and selectivity (qs). Figure appears in colour in the online version only


(a) Browsers
(b) Detritivores
(c) Excavators/scrapers
(d) Grazers
(e) Macro−invertivores
(f) Micro−invertivores
(g) Pisci−invertivores
(h) Piscivores
(i) Planktivores
Stock biomass (relative to B F=0)
Effort
0.00
0.25
0.50
0.75
1.00
All gears
Hook−and−line
Hook−and−line ban
Net
Net ban
Spear
Spear ban

factorial design of gear combinations to test interaction effects from fishing gears due to differences in catchabilities and selectivities for functional groups and size classes, respectively. For each management scenario, we tested a range of total fishing effort, which was divided equally amongst each gear type included in a particular scenario. We ran each model simulation to equilibrium and compared stock biomass (summed across all size classes) and catch of each functional group across management scenarios and range of fishing efforts. We also compared the total stock biomass and catch for each management scenario and effort level by summing biomass and catch for all functional groups.

3 | RESULTS

Fishing gear types had distinct catchability and selectivity for functional feeding groups and size classes, respectively (Figure 1). Hook-and-line fishing heavily targeted piscivores, net fishing primarily targeted pisci-invertivores and had relatively high catchability for grazers, and detritivores had the highest catchability by spear fishing (Figure 1). Whilst each gear had high selectivity for fish in the 15–20 cm size class, spear fishing exhibited a slightly higher mean selectivity (21.6 cm) than hook-and-line (20.0 cm) and net (18.9 cm) fishing (Figures 1 and S1).

Biomass and catch in relation to fishing effort for each functional group demonstrated the trade-offs of gear-based management in that no single management scenario was able to maximize stock biomass or catch for all groups simultaneously (Figures 2 and 3). Hook-and-line fishing (i.e. prohibiting net and spear fishing) maintained the highest biomass for browsers and grazers due to low catchabilities for these functional groups compared with other gear types (Figures 1 and 2). Given uncertainty in catchability and selectivity, grazer biomass was still higher under hook-and-line fishing than management scenarios that permitted net fishing (alone or in combination with other gear types) across the full range of fishing effort (Figure 2). However, hook-and-line fishing had the highest catchability for piscivores, which in combination with a slow growth rate (Table S1) caused piscivores to be depleted at lower effort ($E = 0.10$) than alternative management scenarios (Figures 2 and 3). Hook-and-line fishing also had a higher catchability for planktivores than other gear types and achieved higher catch per unit effort (CPUE) than net and spear fishing, but maintained lower levels of biomass (Figures 2 and 3).

Net fishing (i.e. prohibiting hook-and-line and spear fishing) was able to maintain the highest biomass only for detritivores due to their fast growth rate and low catchability by nets (Figure 2 and Table S1). Variability in detritivore biomass and catch from bootstrap resampling was also smaller for net fishing than hook-and-line and spear fishing (Figure 2). Net fishing, however, maintained the lowest biomass of herbivores (browsers, excavators/scrapers, and grazers) and macro- and micro-invertivores (Figure 2). As net fishing targeted smaller individuals than other gear types, it also achieved suboptimal CPUE for herbivores (Figures 3 and S1). Macro- and micro-invertivore catch was similar across management scenarios and remained high at heavy fishing effort because they had fast growth rates and high maximum per capita recruitment ($1/\alpha$; Table S1).

Biomass of planktivores and macro- and micro-invertivores was highest for spear fishing (i.e. hook-and-line and net fishing prohibited) due to lower catchability and higher selectivity for larger fishes than other gear types (Figures 2 and 3). Thus, spear fishing also generated the lowest CPUE for macro-invertivores and planktivores (Figure 3). Bootstrap resampling revealed that spear fishing had the highest variability in biomass and catch for planktivores and macro- and micro-invertivores (Figures 2 and 3). Even with uncertainty in catchability and selectivity parameters, spear fishing maintained higher biomass for macro-invertivores compared with net fishing and higher planktivore biomass compared with hook-and-line and net fishing (Figure 2). Spear fishing resulted in the lowest biomass only for detritivores and was highly variable (Figure 2).

Gear restrictions also had a considerable impact on total fish biomass and catch summed across all functional groups (Figure 4). Spear fishing maintained higher total biomass compared with alternative gear-restriction scenarios across the full gradient of fishing effort (Figure 4). Although total biomass was most variable under spear fishing, the interquartile range was still greater than that of hook-and-line and net fishing (Figure 4). Total fish biomass and catch were heavily influenced by the response of planktivores to management and fishing effort because of their high reproductive output ($1/\beta$; Table S1) and, thus, large contribution to the total biomass and catch (Figure 5). For spear fishing, we found a monotonic increase in the proportional contribution of planktivores to total biomass as fishing effort increased (Figure 5).

Hook-and-line fishing and a ban on spear fishing (i.e. hook-and-line and net fishing permitted) had the lowest total biomass due to a higher catchability for planktivores by hook-and-line compared with other gear types (Figures 2 and 4). Despite having the lowest total biomass, hook-and-line fishing maintained a relatively consistent proportion of functional groups in response to fishing effort and higher CPUE than alternative management scenarios (Figure 5). Generally, management scenarios that permitted hook-and-line fishing produced higher catch than scenarios that prohibited hook-and-line gear (Figure 4).

Outputs from gear-restriction scenarios were dependent on gear specifications from Wakatobi, where fishery-dependent data were collected. Thus, we simulated increased hook gape size and net mesh size (1- and 2-cm increases for both gears) to observe the impact of gear specifications, which might occur in other coral reef fisheries globally. The only management scenario tested for models with increased gear size was permitting all fishing gears, and increasing gear size effectively shifted the selectivity for larger fishes. The output for total biomass was analogous to spear fishing in relation to other fisheries management strategies such that increased gear size maintained higher biomass across the full range of fishing effort (Figure S2).

Model outputs were robust to most of the key parameters. A 10% increase or decrease in maximum per capita production of recruits ($1/\alpha$) resulted in a ±2% and ±1.7% change in total biomass and

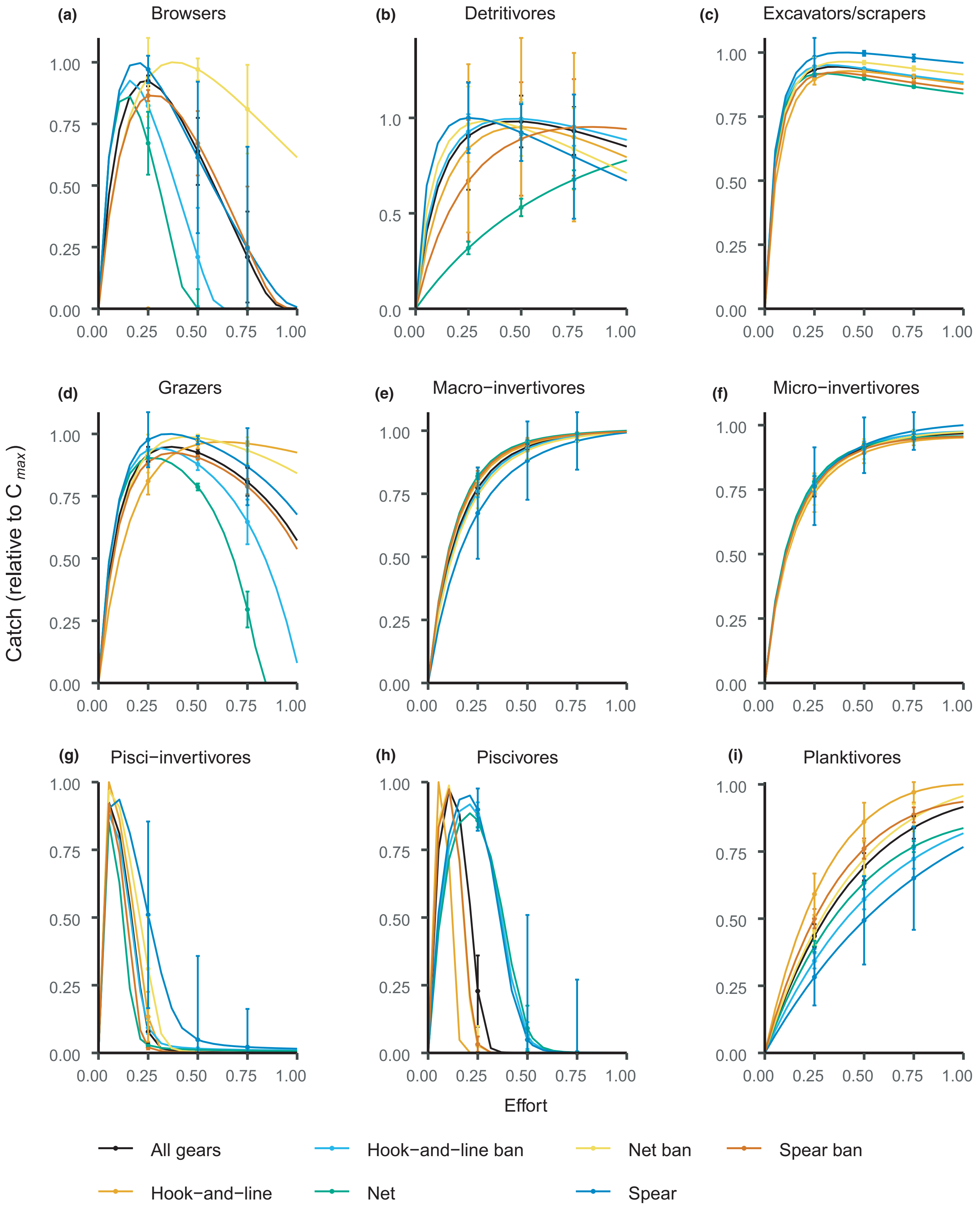


FIGURE 3 Catch (kg) for each functional feeding group in relation to fishing effort and gear-management scenario. Catch is relative to the maximum observed catch (C_{max}) for each functional feeding group across all management scenarios and the full range of fishing effort in the base model. Colours represent different management scenarios and bars represent the interquartile range at light ($E = 0.25$), moderate ($E = 0.50$) and heavy ($E = 0.75$) fishing effort based on non-parametric bootstrap resampling to quantify uncertainty in catchability and selectivity (*qs*). Figure appears in colour in the online version only

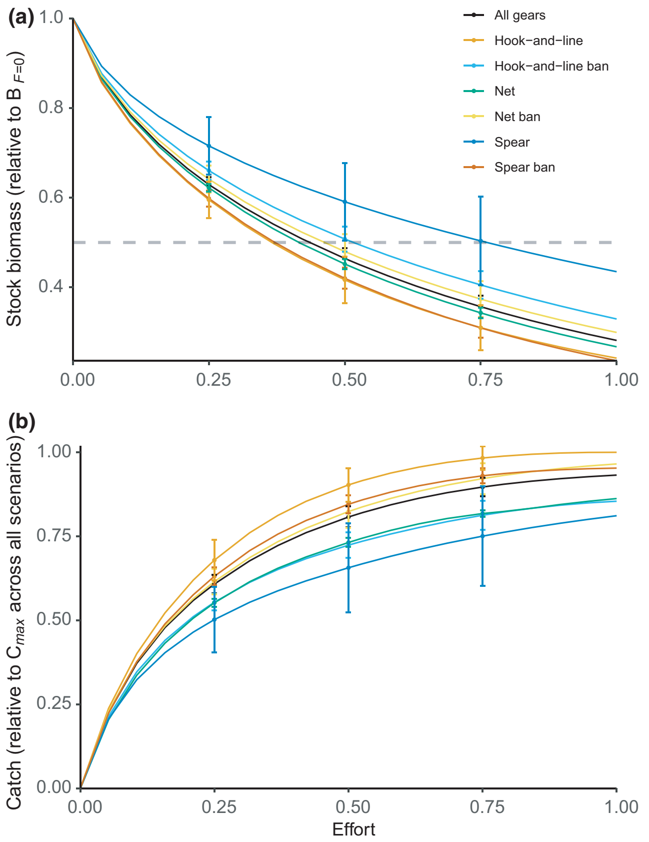


FIGURE 4 Total biomass (a) and catch (b), summed across all functional feeding groups, in relation to fishing effort and gear-management scenario. Biomass is relative to the 'pristine' total biomass (i.e. in the absence of fishing effort) and catch is relative to the maximum observed total catch (C_{max}) across all management scenarios and the full range of fishing effort. Colours represent management scenarios and bars represent the interquartile range at light ($E = 0.25$), moderate ($E = 0.50$) and heavy ($E = 0.75$) fishing effort based on non-parametric bootstrap resampling to quantify uncertainty in catchability and selectivity (qs). Figure appears in colour in the online version only

catch, respectively (Figure S3). Maximum per capita production of recruits decreased as α increased and, thus, generated lower total biomass and catch. In addition, a 10% increase or decrease in the Beverton–Holt parameter β (recruitment approaches $1/\beta$ as spawning stock biomass increases, see Appendix S4.1) produced a − 9% or +11% change in total biomass and catch (Figure S3). As β increased, the asymptotic recruitment level decreased and produced lower biomass and catch. Total biomass and catch had a < 1% change in response to an increase or decrease of other parameters (Figure S3).

4 | DISCUSSION

In this study, we used fishery-dependent and fishery-independent data to develop gear-specific catchability and selectivity parameters for functional feeding group and size class combinations of coral reef fishes. We then integrated these data with a multi-species fisheries model to investigate the impacts of gear restrictions and fishing effort on population dynamics and catch. We show that gear-restriction management presents trade-offs in maximizing biomass, catch and proportional contribution of functional groups (Table 1).

Spear fishing (i.e. prohibiting hook-and-line and net fishing) maintained the highest biomass of planktivores, which play a key role in transporting pelagic nutrients to coral reef ecosystems and driving fish productivity on coral reefs (Morais & Bellwood, 2019). The high productivity of planktivores was reflected in our model by their reproductive output (Table S1) and, thus, planktivores heavily influenced the total biomass and catch summed across groups (Campbell et al., 2020; MacNeil et al., 2015). Planktivores are relatively understudied in the scientific literature, but research on coral reefs in the Philippines demonstrated that no-take marine-protected areas generated a significant increase in planktivores biomass (Russ et al., 2017). Our results demonstrate that gear-based management may also be an effective tool for conserving planktivore biomass and promoting nutrient transport from pelagic to reef ecosystems.

Although spear fishing maintained high biomass of planktivores and total biomass across functional groups, this came at the cost of suboptimal biomass of detritivores, browsers and grazers and low total catch (summed across functional groups) compared with alternative management scenarios. Thus, spear fishing may compromise herbivory and detritivory, which are vital functions for healthy reef ecosystems and reef fish production (Rasher et al., 2013). Importantly, our results also demonstrate that management strategies seeking to maximize total biomass of reef fish, or maintain biomass above a reference level, may fail to protect certain functional groups or jeopardize the livelihoods of small-scale fishers on coral reefs.

We found that hook-and-line fishing maintained one of the lowest levels of total biomass, but generated higher CPUE and more even proportional contribution of functional groups than other gear types. This presented a particularly important trade-off, when considering gear-based management strategies such that maintaining biomass of a diversity of functional groups may lead to lower total fish biomass. However, this trade-off may be in favour of implementing hook-and-line management and prohibiting nets and spears because fishers can continue to generate high yield, whilst maintaining high biomass of key functional groups (e.g. browsers and grazers). There is empirical evidence from reef fisheries in Bonaire where managers permitted only hook-and-line fishing and subsequently increased herbivore biomass (Steneck et al., 2009).

Our results of total biomass and catch are also corroborated by empirical studies that found higher biomass in gear-restricted areas compared with open access fishing areas (Campbell et al., 2018). For example, gear-restricted sites (e.g. net bans) across Indonesia had ~40% higher total biomass than open access sites (Campbell et al., 2020). In addition, a global study on coral reef fishes found that fisheries restrictions (including gear restrictions) were successful at maintaining total biomass above 50% of the pristine biomass ($0.5B_{F=0}$), whilst biomass levels in most open access sites

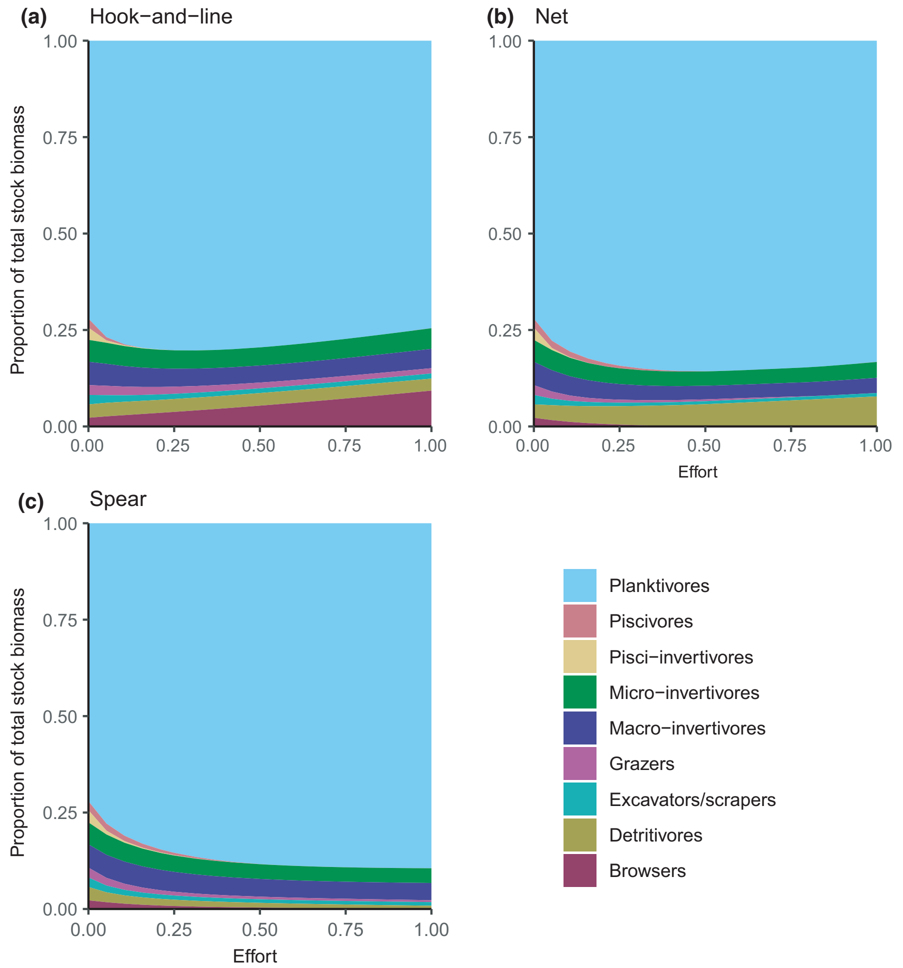


FIGURE 5 Proportional contribution of each functional group to total fish biomass for (a) hook-and-line, (b) net, (c) and spear fishing management scenarios. Colours represent functional feeding groups. Figure appears in colour in the online version only

TABLE 1 Summary of the main benefits and trade-offs of hook-and-line, net and spear fishing

Gear type	Benefits	Trade-offs
Hook-and-line	High herbivores biomass High total catch and CPUE Even distribution of functional groups	Rapidly deplete piscivores Low planktivore biomass Low total biomass
Net	High detritivore biomass	Low herbivore biomass Suboptimal total biomass and catch
Spear	High macro- and micro-invertivore biomass High planktivore biomass High total biomass	Low detritivore biomass Low total catch

were below $0.5B_{F=0}$ (MacNeil et al., 2015). Empirical studies, however, often examine all forms of gear restrictions as a single management option, or grouped with other fisheries restrictions, and have difficulty distinguishing gear from effort effects (Campbell et al., 2020; MacNeil et al., 2015). In this study, we used fisheries models to explicitly compare the conservation and fisheries benefits of specific gear-restriction, and gear-modification, scenarios that otherwise would be infeasible for an empirical study. Thus, our results extend the implications of previous research and identify life-history characteristics and functional group-fishing gear interactions that can drive differences in outcomes for gear-based fisheries management.

Trade-offs between total biomass and ecosystem functions can be mitigated with additional management actions such as gear modifications, size limits, or marine protected areas. We demonstrated that a 1–2 cm increase of hook gape and net mesh size, essentially increasing the mean size of fishes caught, can increase both biomass and catch. This finding is consistent with empirical studies that have suggested increasing net mesh size from 6.3 cm to 8.8–9.2 cm to reduce the catch of fish below sizes that generate optimal yield for a seagrass and coral reef fishery in Kenya (Hicks & McClanahan, 2012). Also, modelling studies on Caribbean coral reefs have shown that banning trap fishing (similar to spear and net fishing in that traps target herbivorous fishes) and implementing a minimum size limit of

30 cm for parrotfishes increased herbivore biomass, annual yields and maintained higher rates of herbivory (Bozec et al., 2016).

Adaptive gear-based management and additional management actions may help balance trade-offs or increase herbivory, but our results show that pisci-invertivores and piscivores are severely depleted at low levels of fishing effort for all management scenarios. Piscivorous fishes are particularly vulnerable to fishing pressure due their life-history characteristics (greater maximum body sizes, slower growth rates and greater lengths at maturity than lower trophic species; Abesamis et al., 2014) and high catchability by all fishing gears. Thus, preserving predation on coral reefs requires more harvest controls on these species or marine protected areas, or both (Campbell et al., 2018). In Indonesia, fisheries restrictions were relatively unsuccessful at protecting high-trophic level fishes, but remoteness of reefs and deep habitat provided biomass gains (Campbell et al., 2020). Thus, gear-restriction management should be viewed as a tool that managers can use within a broader ecosystem-based fisheries management framework, rather than an isolated action to maximize biomass or preserve some ecological functions.

The full range of fishing effort we examined was below the effort level that achieved total maximum sustainable yield (MSY), and high yields were maintained at relatively low biomass due to the high resilience of certain functional groups to fishing pressure (Figure 5). Particularly, excavators/scrapers, macro- and micro-invertivores and planktivores had short generation times and life-history characteristics that have been associated with empirical estimates of reef fish vulnerabilities to fishing (Abesamis et al., 2014). In addition, the relationship we observed in our model between biomass, catch and effort has been observed empirically in coral reef fisheries. For example, high yields were maintained at high levels of fishing effort in Fijian coral reef fisheries (Jennings & Polunin, 1996), and a study on Kenyan coral reef and seagrass fisheries demonstrated that high, but variable, yields can be maintained at low overall biomass due to a few highly productive species (McClanahan et al., 2008). Whilst total yield might remain high with heavy fishing effort, the shifts in community structure, loss of biodiversity and low biomass at high fishing effort compromise ecosystem functioning and resilience (Hughes et al., 2007; McClanahan et al., 2008).

Our model results are based on catchability and selectivity parameters derived from the coral reef fishery in Wakatobi, Indonesia. Although these parameters were developed from a single region, catchability of functional groups was consistent with existing literature on gear-based management for coral reef fisheries in Kenya, Madagascar, Papua New Guinea and other regions of Indonesia (Cinner, McClanahan, Graham, et al., 2009; Davies et al., 2009; Humphries et al., 2019; McClanahan & Cinner, 2008; McClanahan & Mangi, 2004). Thus, we expect functional group and fishing gear interactions modelled in this study to extend beyond Wakatobi. However, future research on catchability of functional groups, and size selectivity, in relation with fishery status (i.e. under-, fully-, and over-exploited) would provide important insight for the implementation of gear-based fisheries management.

Our study demonstrates the conservation and fisheries benefits of gear-based management on coral reefs, along with inherent trade-offs due to catchability and life-history characteristics of different functional groups. Thus, our models suggest that gear-based management would work best with additional management actions, such as gear modifications and/or marine protected areas that are aligned with the local socio-cultural, economic and ecological contexts. An important insight from this study is that aiming to achieve a total biomass target level without consideration of gears used in the fishery can still compromise key ecological functions on coral reefs. Overall, our study suggests that gear restrictions can provide a critical management tool in locations at intermediate socio-economic development for avoiding the valley of reef fish depletion—a social–ecological trap whereby the depletion of key functional roles in coral reef ecosystems is deteriorated to an extent where reefs shift to a less productive, alternative stable state (Cinner, McClanahan, Daw, et al., 2009).

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DATA AVAILABILITY STATEMENT

All models were developed in R version 4.0.3 and openly available, with fisheries-dependent and fisheries-independent data, at https://github.com/paulcarvalho

ORCID

Paul G. Carvalho https://orcid.org/0000-0003-2106-4954

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SUPPORTING INFORMATION

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